The influence of soil tillage intensity on extended phenotypes and predator dynamics of *Tenuiphantes tenuis* and Linyphiidae spp.

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Abstract

Tenuiphantes tenuis (Linyphiidae) is a common arachnid found in British agricultural habitats*.* *T. tenuis* is a pioneer species, recolonises disturbed habitats rapidly and is a key predator of cereal pests. It has been estimated that Linyphiidae can reduce peak Aphididae populations by 49% in a wheat crop, a major gain when Aphididae cause loss of yields through direct feeding and as viral vectors. Soil tillage is normal practice to ensure the correct seedbed is constructed to allow successful germination. Conventional inversion tillage (use of a plough) causes comparatively more disturbance to *T. tenuis* than that of non-inversion tillage. One approach to the latter, direct drilling, is a method of inserting seeds directly into the soil with little prior disturbance. This research assessed how different intensities of soil tillage affected *T. tenuis'* capacity to control pests through examination of its extended phenotype, the web. Field trials were conducted on a NIAB experimental farm investigating different tillage systems; Conventional non-inversion tillage of sub-soiling and two forms of direct drilling; Direct Drill and Direct Drill Managed - a shallower form of tillage. Glasshouse trials, incorporating small aspects of the fieldwork, were undertaken to analyse *T. tenuis* behaviour in a controlled environment.

Clear differences of *T. tenuis* behaviour were identified between the different soil tillage intensities at times of primary and secondary cultivation. The zero-till area of Direct Drill allowed extensive short-ranged dispersal to commence and small webs to be woven into the structures left above ground. Large webs were spun between soil aggregates and remaining crop residue of the Conventional tillage due to the sub-soil technique. Low activity was observed in Direct Drill Managed, where the shallow tillage led to an increase in landscape homogeneity. Similar findings were found in glasshouse trials mimicking the cultivation processes.

In later growth stages of *Hordeum vulgare* (barley) the density and height of the plant within each soil tillage intensity was important. Increased landscape heterogeneity permitted greater web abundance by providing a plethora of anchor materials. In the field and glasshouse trials, the zero-till and shallower cultivated areas aided prey abundance due to the increased straw mass remaining on the surface. *T. tenuis* responded by entrapping a higher prey density. Research further indicated anchor point height of a web can over-ride web area for prey suppression, if attached at a beneficial stratum.

T. tenuis biological control potential was exhibited by webs spun of a greater area and height in an area of Barley Yellow Dwarf Virus-infected *H. vulgare* in the Conventional area. DNA bar-coding identified *S. avenae* in the gut of *T. tenuis* from the Conventional and Direct Drill Managed tilled areas. This was hypothesised to be due to these areas of less migration distance to the shelterbelt.

Combined aspects of this research have gained insights into how *T. tenuis* behaviour, thus potential for biological control, could assist in achieving agricultural sustainability. Conventional delivering greater yields and enabled prey capture from *T. tenuis* showed the benefit to non-inversion sub-soiling. A recommendation to an Integrated Pest Management Plan is to increase *T. tenuis* biological control capacity of this till method by influencing greater migration from the shelterbelt.

Keywords: Aphididae, Biological Control, BYDV, Cultivation, Extended Phenotype, Linyphiidae, *Sitodiplosis mosellana, Tenuiphantes tenuis,* Tillage, Zero-till

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Glossary and Acronym List

Amplicon *Chapter Twelve*	An amplification of an intron.
Ballooning *Chapter Five (Sub-Chapter Five One, Sub-Chapter Five Two and Sub-Chapter Five Three)*	The long-range migration of an arachnid using a length of silk thread to swing into a new location.
Bet - Hedging *Chapter Five (Sub-Chapter Five Three)*	Concerning the placement of arachnid egg sacs in several locations to aid success of hatching and a subsequent generation.
Biological Control *All Chapters*	Method of using a natural enemy species of crop pests to reduce a pest's population as an alternative to chemical control.
bp *Chapter Twelve*	Base Pairs of DNA. These are the pairing of the nucleotide amino acids: - adenine-thymine and guanine-cytosine. The number of these pairings within a specific gene are used as an identification in DNA Bar-coding.
Bridging *All Chapters*	The short-ranged migration of arachnids.
BYDV *Chapter Six*	Barley Yellow Dwarf Virus. A virus spread through the vector of cereal Aphididae and causes damage to cereal crops.
Chemical Control *Chapter Two and Chapter Thirteen*	The use of chemicals (for example pesticides and insecticides) to reduce a crop pest population.
Cultivation *All Chapters*	Method by which tillage is formed.
DNA Bar-coding *Chapter Twelve*	A method at which DNA is amplified and read.
ELISA *Chapter Six*	Enzyme-linked immunosorbent assay. A method of identifying a virus within a specimen by locating the presence of a specific antigen relating to the virus.
Extended Phenotype *All Chapters*	An extension of an organism without attachment to the organism.
Gel Electrophoresis *Chapter Twelve*	The method of moving an electric current from a negative charge to a positive charge, aiding the movement of substances within a gel. Commonly used in DNA Bar-coding.

Gravity Hypothesis *Chapter Five (Sub-Chapter Five One and Sub-Chapter Five Two)*	Is used to explain SSD. Body mass of male spiders is inversely proportional to climbing speed. Climbing speed is an attractive trait to females and males tend to spin a web at a high aspect. Males of low mass ascend to a higher female web. Male off-spring will have the genotype for small body mass. Females with a larger abdomen due to SSD impacts bridging potential, increased weight impacting strain placed onto silk.
Green-Bridge *Chapter Five (Sub-Chapter Five One, Sub-Chapter Five Two, Sub-Chapter Five Three), Chapter Six and Chapter Thirteen*	Foliage (for example weeds) that provide vegetation in times of a field out of crop.
GS *Chapter Four, Chapter Five (Sub-Chapter Five One, Sub-Chapter Five Two, Sub-Chapter Five Three), Chapter Six, Chapter Eight and Chapter Ten*	Growth Stage. A definite stage in the development of a cereal crop.
Hyperladder *Chapter Twelve*	A measurement tool in DNA Bar-coding. It allows a DNA sample to be read at a specific base pair by incorporating base pairs of a definite length.
Intron *Chapter Twelve*	A gene expression. The nucleotide sequence of a gene.
kdr *Chapter Two and Chapter Thirteen*	Knockdown resistance. Where sensitivity to chemical control (e.g. pesticides) has been subdued due to genetic mutation.
Landscape Heterogeneity *All Chapters*	A landscape of complex vegetation structure in height and density.
Landscape Homogeneity *All Chapters*	A landscape lacking complex vegetation structure.
Mass Action *Chapter Five (Sub-Chapter Five One, Sub-Chapter Five Two, Sub-Chapter Five Three) and Chapter Eleven*	In ecology the movement of a small density of natural enemies triggering a larger density to follow.
Parthenogenesis *All Chapters*	Reproduction without fertilisation of an ovum.
PCR *Chapter Twelve*	Polymerase Chain Reaction. A method used in DNA Bar-coding. A specific intron is amplified to a large enough quantity it can be read in DNA Bar-coding.
Pendulum Motion *Chapter Five (Sub Chapter Five Two and Sub-Chapter Five Three)*	Use of gravity to assist in arachnid locomotion when spinning a long thread upside down.

Phenotypic Plasticity *Chapter Five (Sub-Chapter Five Two, Sub-Chapter Five Three) and Chapter Eleven*	Level of adaptability within a phenotype that an organism physically alters in response to external stimuli. For example, altering strain placed on silk in web-building due to orientation of attachment materials.
PNPP *Chapter Six*	p-Nitrophenyl Phosphate, Disodium Salt. A substrate used in ELISA to help in detection of a particular antigen by allowing a reaction to occur where colour is the product.
Polymorphism *Chapter Five (Sub-Chapter Five Three), Chapter Six and Chapter Eight*	Differences in phenotype in a species which are produced from an identical genotype. For example, apterous or alate morphs in Aphididae.
Polyphenism *Chapter Five (Sub-Chapter Five Three), Chapter Six and Chapter Eight*	A production of an alate morph within Aphididae.
Primer *Chapter Twelve*	Short strand of single DNA. Used in DNA Bar-coding to allow amplification of an intron.
Rappelling *All Chapters*	Another word for bridging.
SSD *Chapter Five (Sub-Chapter Five One, Sub-Chapter Five Two, Sub-Chapter Five Three) and Chapter Eleven*	Sexual Sized Dimorphism. Phenotypical traits that differ in a male and female, outside of the sexual organs.
Tillage *All Chapters*	The action of preparing the soil for the seeding of a crop.
Volunteer Crop *Chapter Five (Sub-Chapter Five One)*	Harvested grain which re-seeds after discarded in the field at a random location.

Chapter One

1.0. Introduction

1.1 Background

Tenuiphantes tenuis (Araneae: Linyphiidae) (Blackwall, 1852) is a common ground-dwelling spider found within British agricultural systems (Barriga *et al.,* 2010; Öberg & Ekbom, 2006). This Linyphiidae is a generalist predator, identified as a dominant natural enemy, due to evolved coping mechanisms for starvation and gorging (Bell *et al.,* 2002). *T. tenuis* is carnivorous, thus does not harm crops (Diel *et al.,* 2013; Rajeswaran *et al.,* 2005). Furthermore, *T. tenuis* is a key, non-chemical control agent in removing Aphididae (true aphids), that are known to cause crop damage via direct feeding through the phloem and as vectors of diseases (e.g. Barley Yellow Dwarf Virus). Barley Yellow Dwarf Virus (BYDV) transmission from *Sitobion avenae* (English Grain Aphid) was of greater cost in grain yield reduction to a *Hordeum vulgare* (Spring Barley) crop in the UK than direct feeding (Choudhury *et al.,* 2019). In 2018, an average 30% yield loss of *H. vulgare* (UK wide) was caused by BYDV on untreated (pesticide-free) ground, at a potential cost of £2 million to British agriculture (AHDB, 2019). Moreover, *Sitodiplosis mosellana* (Orange Blossom Wheat Midge), which causes yield reduction through damage to the pericarp of grain in cereal crops, are removed from a crop system by entrapment in *T. tenuis* sheet webs (Price *et al.,* 2011).

Aphididae may contribute 55% of pests identified in a crop field habitat and 37% of prey consumed by Linyphiidae within one generation (Halley *et al.,* 1996). *T. tenuis,* as a biological control agent, may reduce the need for insecticide use (Aradottir *et al.,* 2017; Holland & Oakley, 2007; Jonsson *et al.,* 2014; Lüscher *et al.,* 2014). Insecticidal chemicals are known to harm the environment by being leached into waterways and target organisms have been shown to gain resistance negating their intended use and force synthesis of new products. Bass *et al.* (2014) and Silva *et al.* (2012) comment that *Myzus persicae* (Peach-Potato Aphid) exposure to insecticides has led to the engineering of seven independent genetic pathways. Due to the polyphagous nature of *M. persicae*, this resistance has led to substantial economic losses in British arable agriculture. Direct feeding of *M. persicae* primarily led to a 45% reduction in sugar beet yield in Europe, which in 2016 had an approximate market value of £23 million (Hogenhout, 2016). The loss of income from yield reduction has a social impact to agricultural industry, with arable farms not able to sustain a crop failure (Brewer, 2019; Zhang *et al.,* 2016). Halley *et al.* (1996) examined average annual pesticide use and identified a 50 - 90% decrease in field populations of Linyphiidae, which persisted for several generations. Despite this, pesticide use is still common, as 70% of pest-related crop damage can occur without their application, resulting in a loss of capital and food (Al Hassen *et al.,* 2012).

1.2. Research Aims

The aims of this research project were to: -

1. Identify the potential biological control by *T. tenuis* of Aphididae and *S. mosellana* within different intensities of tillage in an arable crop.
2. Identify any differences in extended phenotypes of *T. tenuis* within tillage practices, e.g. web dimensions and bridge thread length.
3. Understand whether *T. tenuis* behaviour is stimulated by the presence of Aphididae and *S. mosellana*.
4. Comprehend if a certain level of landscape heterogeneity affects *T. tenuis* ability to predate on Aphididae and *S. mosellana*.
5. Quantify *T. tenuis* biological control by comparing Aphididae and *S. mosellana* DNA presence in *T. tenuis* gut and Linyphiidae webs with Aphididae and *S. mosellana* populations within different intensities of tillage.

The incorporation of *S. mosellana* within the Research Aim 1, 3, 4 and 5 relate to Chapter 5 (Sub-Chapter 5.1. & Sub-Chapter 5.3.) and Chapter 12.0. Aphididae within the same Research Aims are represented in every experimental chapter.

To address these aims, a number of approaches were undertaken. These involved both field and laboratory-based investigations (*Chapters 3.0. to 12.0.*). Specific objectives are provided within each of the experimental chapters.

1.3. Overview of Thesis

- **Chapter Two - Literature Review**

  This chapter reviews the relevant literature and places the current research into context. The review begins by exploring the Linyphiidae family and more specifically the biology and behaviour of *T. tenuis*. Literature surrounding British arable agriculture production is explored with interest in tillage techniques. Crop pests are introduced with reference to how *T. tenuis* may interact with these pests and offer elements of biological control.

- **Chapter Three - Fieldwork Site Introduction**

  This chapter explores in-depth a National Institute of Agricultural Botany (NIAB) trial, the field site for this research. It identifies how the levels of soil tillage intensity are established and measured by NIAB. Lastly, the contributions to the scientific community that this research could bring is highlighted.

- **Chapter Four - Method Development for Fieldwork**

  How the final fieldwork methodology was developed is the focus of this chapter. It includes learning and experience gained from preliminary investigations.

- **Chapter Five - Fieldwork - 2016 / 2017 Season and 2017 / 2018 Season**

  This chapter is divided into three sub-chapters. Sub-Chapter 5.1 seeks to understand how *T. tenuis* behaves in a field where it is split into areas of differing soil tillage intensity. Sub-Chapter 5.2 reports an in-field experiment, where the abundance of upright stubble, identified from the scientific literature as a key component within the landscape, was manipulated. Sub-Chapter 5.3 examines *T. tenuis* behaviour within hedgerows that surround the cultivated area.

- **Chapter Six - Interactions of *T. tenuis* and Linyphiidae with Aphididae Causing Barley Yellow Dwarf Virus (BYDV) in *H. vulgare***

  T. tenuis and pest interaction in *H. vulgare* infected with BYDV-PAV is analysed from testing for BYDV-PAV to understanding if there was increased Aphididae abundance and if this heightened associated *T. tenuis* behaviour.

- **Chapter Seven - Method Development for Glasshouse Experiments**

  This chapter narrates the development of glasshouse experiments used in this research. It informs how designs were built and learnt from, allowing experience to be incorporated into final investigations. The chapter highlights how methodologies were refined into final methods.

- **Chapter Eight - Effects of Soil Tillage Intensity on Prey Capture by *T. tenuis* in Mesocosms of *H. vulgare***

  This experiment was designed to simulate the conditions observed in the field created by the differing levels of soil tillage intensity under controlled conditions.

- **Chapter Nine - Effects of Primary and Secondary Cultivation on *T. tenuis* Behaviour Under Controlled Experimental Conditions: A Mesocosm Experiment**

  This chapter communicates a further glasshouse experiment. These mesocosms were specifically set-up to closely observe *T. tenuis* interaction with the habitat created after primary and secondary cultivation of the different intensities of soil tillage.

- **Chapter Ten - *T. tenuis* Behaviour with Different Soil Tillage Intensities and Different Abundances of Cereal Aphididae: A Microcosm Experiment**

  The focus on this experiment was to further investigate *T. tenuis* behaviour when placed in controlled conditions with different levels of Aphididae. It set out to determine whether a greater Aphididae density influenced *T. tenuis* activities. The experiment was set in small habitats (microcosms), a small area allowing *T. tenuis* and Aphididae interactions to be clearly determined.

- **Chapter Eleven - Choice Chambers for Selection of Upright Stubble and Furrow With or Without the Presence of Aphididae**

  The element of choice was central to this experiment, where a *T. tenuis* was offered simulated habitats containing different levels of landscape heterogeneity (formed from the different intensities of soil tillage). The experiment was extended by inclusion or exclusion of Aphididae.

- **Chapter Twelve - DNA Bar-Coding of *T. tenuis* Gut and Linyphiidae Web**

  The technique of DNA Bar-coding was applied to analyse whether prey DNA exists in *T. tenuis* gut or Linyphiidae web from specimens collected from different soil tillage areas. The premise was that the results would allow a greater understanding of the prey capture behaviour of *T. tenuis*.

- **Chapter Thirteen - Final Discussion**

  This chapter concludes the research. It is divided into three sections. The final discussion where *T. tenuis* activity towards crop pests within different tillage intensities is concluded. Recommendations for future work are offered as a platform for other works. Finally, an Integrated Pest Management Plan is drawn up, with an aim to be accessible to those within the arable agriculture industry. Here contributions to the scientific community are re-visited.

1.4. Summary of Results Section

At the beginning of each results section of the experimental chapters, there is a summary of the results, the section and page number of which are noted below. The reasoning behind this is to give an overview of the key results from each experimental chapter before the detailed analysis is explained.

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Chapter Two

2.0. Literature Review

2.1. The Linyphiidae Family and *Tenuiphantes tenuis*

The Linyphiidae (Blackwell 1857) are sheet-weavers and a family of small spiders, all species being less than 5 mm in body length from the cephalothorax (head) to the abdomen (main body). Globally, the family has 430 species in 601 genera. Linyphiidae are the largest family found in the British Isles, with 270 species comprising 40% of the total spider population (Coddington, 2005).

Tenuiphantes tenuis is found in a variety of habitats across temperate Europe and Northern America and has been sampled in various lowland habitats throughout the UK. *T. tenuis* is distributed equally within England, Wales and Northern Ireland and less common in the North of Scotland, with decreasing temperatures (Harvey *et al.,* 2002). The lowland habitats include grasslands, woodlands, moorlands, and wetlands, all of which incorporate a variety of flora. It is uncommon in areas with sparse vegetation strata, for example the uplands (Harvey *et al.,* 2002). The ubiquitous nature of *T. tenuis* identifies its biological control potential, able to sustain in a multitude of habitats and exert predatory behaviour.

2.1.1. The Biology of *T. tenuis*

Adult *T. tenuis* are generally between 2 and 3 mm in body length meaning they are of the smaller size within the Linyphiidae. *T. tenuis* has a distinctive set of markings on the abdomen (*Figure 2.1*). The female has two linear sets of brownish spots, graduating in size, which are on a background of beige and brown areas on the abdomen (Bradley, 2013; Roberts, 1993) (*Figure 2.1.*). Males have a darker brown abdomen, where the markings are less identifiable, though two anterior white spots on the abdomen are unique to male *T. tenuis* and allow field identification (Bradley, 2013; Roberts, 1993) (*Figure 2.1.*). *T. tenuis* can be separated by sex by a unique epigene, an external female sexual organ, and a palp, a swollen appendage in males whose primarily aim is to transfer sperm in copulation, both epigene and palp require microscopic observation to identify unique markings (Roberts, 1993) (*Figure 2.1*).

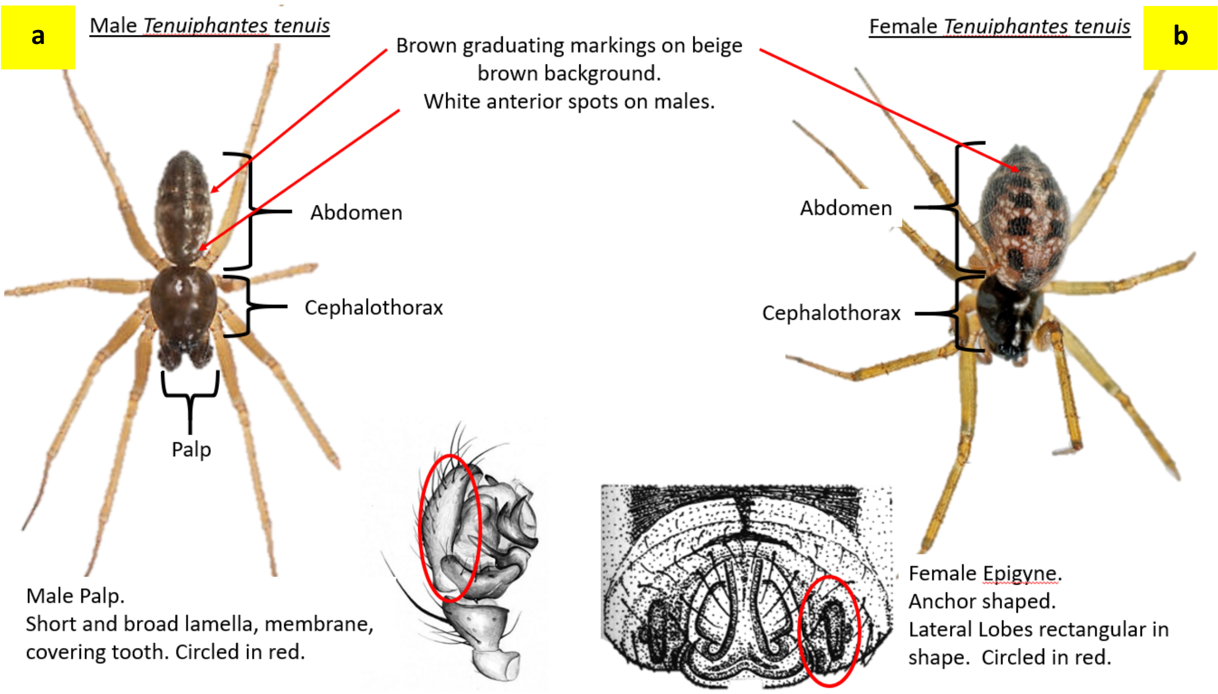


Figure 2.1: a = Male and b = Female T. tenuis*, dorsal view (InfluentialPoints, 2019). Pencil drawing of male palp and female epigyne (Roberts, 1993).*

T. tenuis have four pairs of small eyes which only allow near-sighted vision, meaning they are incapable of rendering a complete picture of their surroundings. The long thin legs of *T. tenuis* have many macrosetae, sensitive fine hairs, which collect sensory information to allow *T. tenuis* to respond to its surroundings (Bradley, 2013; Roberts, 1993) (*Figure 2.2*). *T. tenuis* thus hunt within a small spatial scale. *T. tenuis* are highly flexible animals, easily able to ascend structures (Bradley 2013, Řezáč & Řezáčová, 2019; Woolley *et al.,* 2016). Lichtenstein *et al.* (2019) discussed climbing allows *T. tenuis* to exploit prey that may be within the upper strata of a habitat. Within an agricultural setting *T. tenuis* as effective climbers can respond to aerial prey more than carabidae (ground beetles) which are confined to the basal stratum (Cowles, 2018; Davey *et al.,* 2013).

Figure 2.2: Female T. tenuis*, lateral view, under KERN™ compound microscope OBS-1 binocular achromat resolution 4x, showing long legs with macrosetae.*

2.1.1.1. Reproduction and Life Cycle of *T. tenuis*

T. tenuis reproduces rapidly and often produces two generations within a cropping season, commonly September to February and February to April. At peak reproductive rates, *T. tenuis* can reach a population density of up to 1,000 m^{-2} in an arable cropped field (Bell *et al.,* 2002; Schellhorn *et al.,* 2014). It is identified as a pioneer species, by rapidly recolonising areas subjected to a recent disturbance, in this instance a cultivated arable field, and is therefore a viable candidate of biological control (Thomas & Jepson, 1999).

After mating, female *T. tenuis* search for a refugia (safe place), camouflaged and secure from the elements, and begin to spin an egg sac where a clutch can be laid. Eggs are light cream/beige in colour and darken through the incubation period which lasts for 10 to 15 days (Thorbek *et al.,* 2003). Clutch size is on average 20 to 30 eggs. Spagna & Gillespie (2008) showed *T. tenuis* females abandon their egg sacs negating parental care, though care is taken in choosing suitable oviposition sites (Bradley, 2013). The number of hatchlings varies with temperature, higher temperatures increasing hatching rate (Simpson, 1995; Thorbek *et al.,* 2003). Spiderlings (infant spiders) all hatch from the eggs at the same time, as ‘sexless’ miniature forms of the adult with abdominal markings established. They are able to spin silk upon hatching and often balloon (disperse) directly away from the egg sac immediately to avoid intra-specific predation, weaker spiderlings in size and fitness, can become a protein meal for stronger siblings (Thorbek *et al.,* 2004).

The spiderlings go through three ecdyses, shedding of exoskeleton, before acquiring a distinguishable sex and becoming adult. The period between ecdysis are known as instars and *T. tenuis* juveniles are classed into three instars (Peng *et al.,* 2013; Preston-Mafham & Preston-Mafham, 1996). Ecdysis allows growth, having an inflexible exoskeleton *T. tenuis* are required to grow in definite stages. Ecdysis leaves an instar vulnerable to predation, as prior to ecdysis the juvenile ceases to feed and hangs from a strand of strong dragline silk, from the ampullate gland, for two to four days until the old exoskeleton is shed (Higgins, 1993; Preston-Mafham & Preston-Mafham, 1996). Male *T. tenuis* reach the third instar before females, due to males generally being smaller in body mass, and are therefore sexually mature before females (Akita, 1992; Preston-Mafham & Preston-Mafham, 1996). A successful next generation of adult *T. tenuis*, with spiderlings able to successfully reach each instar, is of importance to the biological control *T. tenuis* can apply within a crop. Adult *T. tenuis* weave webs of greater area within higher strata, establishing a greater potential to intercept aerial prey (Brunetta & Craig, 2010; Craig, 1987). *T. tenuis* reproductive capacity in multiple generations allows an adult population to be apparent when an arable crop has germinated and within early growth stages (GS), thus susceptible to action of pests (He *et al.,* 2020; Schellhorn *et al.,* 2014; Welch *et al.,* 2013). The greater mobility and dexterity of adult *T. tenuis* can effectively weave webs in a multitude of locations to ensnare prey (Kraftt & Cookson, 2012).

2.1.2. Extended Phenotypes of *T. tenuis* and Linyphiidae

An extended phenotype is expressed as an extension of an organism without being attached to the organism. For example, an extended phenotype of a bird (Aves) would be a nest, or a burrow for an earthworm (*Lumbricus*). The extended phenotype of *T. tenuis* is its ability to construct a web (Blackledge *et al.,* 2002; Blamires *et al.,* 2013). This extended phenotype differs in form and construction between web-building spiders. The extended phenotype of Linyphiidae is a horizontal sheet web, spun of fine silk.

2.1.2.1. Web-building Behaviour in Silk and Design of *T. tenuis* and Linyphiidae

T. tenuis web size can vary from 5 cm^2 to 550 cm^2 depending on the landscape (Gómez *et al.,* 2016). They create sheet webs which are a horizontal close woven web where the internal structure does not form a symmetrical pattern rather a random crisscross. Spider silks are highly complicated at a molecular level, however, silks are constructed of repetitive patterns of amino acids that are intercepted with crystalline structures or spacers (gene expression breaking up dominant repeats) (Blackledge & Elaison, 2007; Chen *et al.,* 2012; Colgin & Lewis, 1998). The sequence of amino acids and associate structure or spacer allows differences between silk to occur, each silk having a molecular structure relating to its intended purpose (Basu, 2015; Brunetta & Craig, 2010).

Support threads are created from the major and minor ampullate glands which emit a non-sticky dragline silk (Craig, 2003). Major ampullate silk is fibrins (fibrous protein) attached with hydrogen bonds that are strengthened with hydroponic crystals (named β-sheets due to its secondary structure) giving this silk its high tensile strength and tough characteristic (Craig, 2003; Hardy *et al.,* 2008; Heidebrecht & Scheibel, 2013) (*Figure 2.3a*). Support threads are usually two fibres thick due to Linyphiidae having only one pair of spinnerets, allowing the maximum of two fibres to be woven at one time. Silk from the minor ampullate gland is only half as strong as that from the major ampullate gland due to the absence of hydroponic crystals. Spacers, rich in serine, are not uniformly repeated and are unique to this silk (Basu 2015; Rising *et al.,* 2005) (*Figure 2.3b*). The function of this spacer is thought to be in protein synthesis to aid fibrin formation (Tokareva *et al.,* 2014). This silk is used by Linyphiidae as a temporary bridging thread, which *T. tenuis* may use to assess a web structure before the costly, in energy, major ampullate silk is laid. Bridging relates to the action of lying a thread to allow small scale migration between structures. It is not incorporated into a web and its lying is predominately an exploratory or dispersal tool (Bonte & Saastamoinen, 2013; Řezáč & Řezáčová, 2019).

Anchorage of support threads at different orientations is made possible by the piriform gland. The piriform silk forms discs that allow support threads to protrude from the main sheet web and access otherwise difficult substrate (Craig, 2003). These discs enable the support webs to turn through the creation of junctions and allow *T. tenuis* to manipulate a web to sit within an arable crop. Piriform silk, through large repeats of amino acid rich in alternative glutomaine and proline sequences, is able to produce thick layers (creating the discs) with silk being deposited in a zig-zag motion over a small area (Craig, 2003; Perry *et al.,* 2010) (*Figure 2.3d*). Only termini break the amino acid repeats instead of spacers, due to its assistant role in guiding support threads to an appropriate orientation (Perry *et al.,* 2010).

Sheet webs comprise of anchor threads that arise from the support threads and attach to the substrate to give reinforcements to the web, this allows loading stress of the web to be increased. Flagelliform silk forms the sheet threads that make up the internal body of the sheet web and is highly extensible, with a disorderly molecular structure with weak bonds. It contains glycine and proline bonded by strong hydrogen bonds that are structured to form a β-helix which gives the silk its strength and elasticity (Ayoub *et al.,* 2007; Hayashi & Lewis, 1998; Hayashi & Lewis, 2001) (*Figure 2.3c*). It makes an excellent material for the internal structure as it can be laid rapidly with little energetic output due to less force required for its extension, pulling of the thread, compared to the earlier mentioned dragline silk (Pasquet, 2014; Rojas, 2011; Toft 1987). Key to highly mobile *T. tenuis* to promptly lay a web in advantageous locations, responding to an agricultural disturbance for example (Pedley & Dolman, 2014).

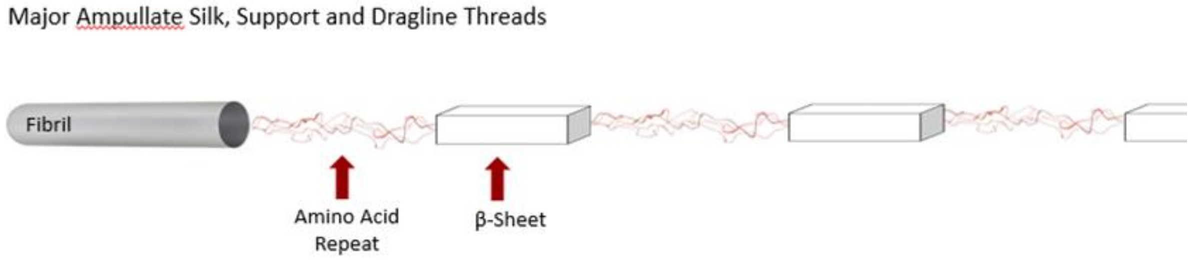


Figure 2.3a: Schematic diagram of secondary molecular structure of the major ampullate silk fibril (Adapted from writings of Craig (2003), Hardy et al. (2008) and Heidebrecht & Scheibel (2013)).

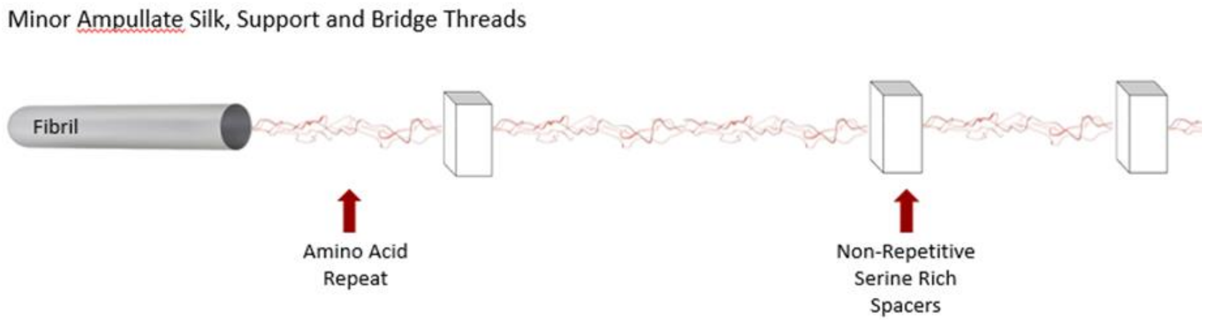


Figure 2.3b: Schematic diagram of secondary molecular structure of the minor ampullate silk fibril (Adapted from writings of Basu (2015), Craig (2003), Rising et al. (2005) and Tokareva et al. (2014)).

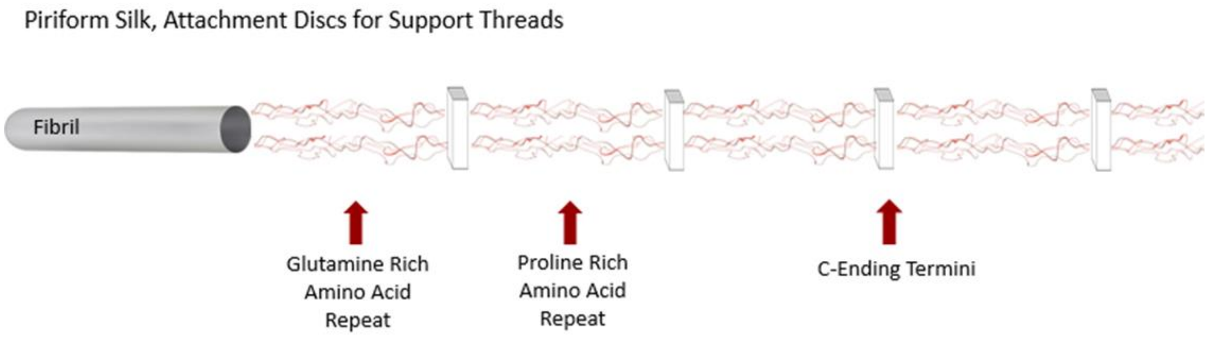


Figure 2.3c: Schematic diagram of secondary molecular structure of the piriform silk fibril (Adapted from writings of Craig (2003) and Perry et al. (2010)).

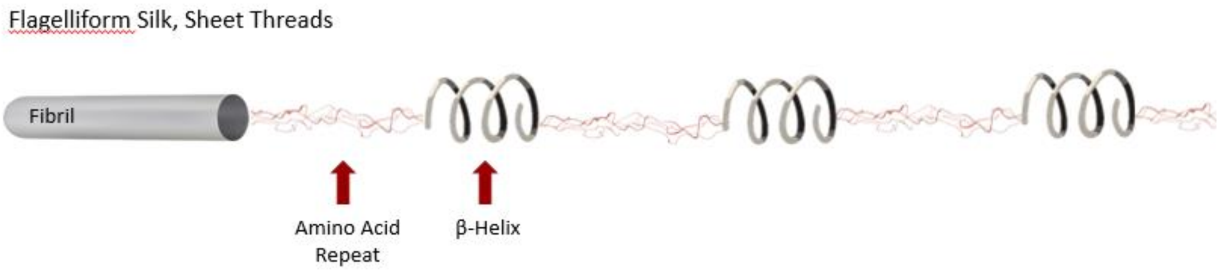


Figure 2.3d: Schematic diagram of secondary molecular structure of the flagelliform silk fibril (Adapted from writings of Ayoub et al. (2007), Craig (2003) and Hayashi & Lewis (2001)).

The yield of silk can have a limiting factor on the way a silk performs when a web is constructed. Yield is measured in strain and is described as the moment when silk is pulled far enough away from the spinnerets that the proteins are able to deform and exhibit their intended characteristics (Craig, 2003; Römer & Scheibel, 2008). For example, the yield required for major ampullate silk to strengthen and set is 2 - 3% strain required by the Linyphiidae (Hardy *et al.,* 2008). If the correct yield is not met the constructed web may perform differently in environmental stresses, like wind, or its intended stress loading capability may not be met, meaning its prey-capturing potential may be lowered (Blackledge *et al.,* 2011; Tokareva *et al.,* 2014).

All elements of a web, silk threads of supports and sheets, differ marginally in thickness, expressing a difference in energy output for their creation (Beals, 1999; Benjamin *et al.,* 2002). Benjamin *et al.* (2002) found increased levels of silk globules in support threads of *Linyphia triangularis,* Linyphiidae, which suggested a higher demand for silk production (Beals, 1999; Pasquet, 2014; Rojas, 2011; Toft, 1987). The area of a web can be identified as a measurement of an individual *T. tenuis* prey-capture capacity as this the extended phenotype that ensnares the prey (Blackledge *et al.,* 2002; Harmer *et al.,* 2011; Toft, 1987). DiRienzo & Aonuma (2018) discussed web orientation alongside dimensions can affect the webs capacity to capture prey.

Understanding the molecular composition of each silk fibril woven by Linyphiidae in relation to the silks intended purpose is of importance when analysing the prey-capturing ability of their extended phenotype (Römer & Scheibel, 2008). Benjamin & Zschokke (2004) and Xu *et al.* (2015) discuss the increase laying of flagelliform silk in a webs internal structure, although of extra energy output, aids the webs structural integrity and allows greater persistence in times of disturbance. A greater yield of piriform silk obtained allows attachment discs to be spun of enhanced thickness, providing a web anchored with increased security onto a substrate (Japyassú & Laland, 2017; Stenchly *et al.,* 2011; Tokareva *et al.,* 2014). The decisions in the manufacturing processes of a web clearly affects its ability to endure in an agricultural setting and therefore alters the biological control potential the web can exhibit (Blackledge *et al.,* 2005; Blackledge *et al.,* 2009; Vollrath, 1986).

2.1.2.2. Location of Web-building Behaviour of *T. tenuis* and Linyphiidae

In web construction, it is suggested that *T. tenuis* makes a conscious decision whether the output of kinetic energy required to lay threads and energy used to produce proteins for silk will be profitable, in terms of energy income through prey capture (Benjamin & Zschokke*,* 2003; Campbell *et al.,* 2020; Henschel & Lubin*,* 2018). The anchor point is a key factor in prey capture, as it is the starting point for creation of a web. Identifying a *T. tenuis* choice of anchor point within a complex environment allows exploration of decision-making on web location (Dennis *et al.,* 2015; Pasquet, 2014).

Hardwood *et al.* (2003) noted that there are similarities between the surrounding plant communities and *T. tenuis* web location observed. It has been suggested that web location may be a compromise between the micro-habitat in plant density, climate, prey availability and predator avoidance (Hardwood *et al.,* 2003). *T. tenuis* are highly adaptive in web construction and can adapt into a small niche unsupported by another Linyphiidae, allowing prey to be utilised with limited predation. Birkhofer *et al.* (2008) highlighted, where artificial plants were incorporated into a *Triticum* (wheat) field to increase vegetation complexity, *T. tenuis* abundance was significantly correlated with vegetation complexity. This was attributed to the increased number of potential web-sites that could be utilised by *T. tenuis* (Birkhofer *et al.,* 2008). *T. tenuis* were identified as having a significant preference to perennial habitats over mono-cropped fields of *Beta vulgaris* (Sugar Beet), *Triticum aestivum* (Winter Wheat) and *Brassica napus* (Oilseed Rape). In this same study, *T. tenuis* were at significantly high density in the annual cropped fields than other spider populations, which identifies that *T. tenuis* may not have a definite habitat criteria but monopolise areas where other spider populations are low. The fact that spider webs have been shown as prevalent when land was fallow suggests a low level of vegetation complexity maybe required for thread attachment. This agrees with work by Groeneveld *et al.* (2015) and Schmidt & Tscharntke (2005) who analysed Linyphiidae abundances in fallow and field in crop. This idea of monopolising cereal fields and requiring basic plant physiognomy is supported by Mader *et al.* (2017), when the arachnid of highest abundance in an organically managed cereal crop was *T. tenuis.* This occurred when arthropod sampling was compared between a flowering field in the Agriculture Environment Scheme and an organic *T. aestivum*.

Buri *et al.* (2016) introduce the 'carry over' hypothesis, where allowing all year vegetation availability means a Linyphiidae generation can be carried over in the same habitat vicinity. It was identified that a *T. tenuis* population remained abundant with delayed mowing of a perennial grassland. This was accredited to annual availability of vegetation allowing web construction to continue and support the life cycle of the web-building behaviour of *T. tenuis* (Buri *et al.,* 2016).

Changes in vegetation architecture, in its height, density and foliage present, has been shown by Gómez *et al.* (2016) to contribute to web location and construction. In Northern Kansas, vegetation architecture of a prairie was analysed with the use of three grassland field sites with differing populations of woody shrubs and forbes (flowering herbicious plants). Gómez *et al.* (2016) identified a significant positive correlation between Linyphiidae web abundance and vegetation height and number of vegetation layers. It is theorised that web-anchoring is driven by the implementation of differences in vegetation architecture in layers and increasing foliage density. Increased vegetation is noted to benefit Linyphiidae by providing webs with a background cover. Insects may not identify a web in this situation and may not be able to avoid entrapment (Fasola & Mogavero 1995).

With cereal crops, *T. tenuis* and Linyphiidae in general have been shown to utilise straw and previous crop stubble for web construction. In a study in Argentina, abundance of Linphiidae increased by 12.30% in an area of *T. aestivum* which incorporated stubble against an area without stubble (Armendano & González, 2011). Armendano & González (2011) suggested that Linyphiidae were capable of occupying a niche habitat and utilising available material for webs. This supported work by Thomson & Hoffmann (2007) where a higher abundance of *T. tenuis* was identified in areas where straw mulches had been applied providing small scale habitat materials for web construction.

With arable fields, the distance from the field margin has been communicated as a factor that drives the location of spider web creation. Pfister *et al.* (2015) discussed that the abundance of web-building spiders increasing towards a hedgerow (measured in scale of log transformations) may be due to their lifecycles, where the availability of a micro-habitat differing in vegetation complexity in close proximity, may benefit shelter, egg-laying and a different prey availability. Movement towards the centre of a cropped field may cause increased predation and limited complexity of plant physiognomy for anchor points for webs. Garratt *et al.* (2017) found a significant decline in Linyphiidae abundance in a *T. aestivum* crop in Southern England with increased distance from the hedgerow. Abundance of *T. tenuis* in the *T. aestivum* was shown to relate to the maturity of the vegetation within the hedgerow, with increased abundance occurring when the hedgerow had a high vegetation density being well established with little gaps. This suggests the requirement for an area of complex vegetation to provide a background to allow *T. tenuis* to utilise an area of mono-cropping. The idea of edge effect is also considered here where at the boundary of two habitats a unique micro-ecosystem can sustain. The difference in landscape heterogeneity often observed between the two habitats, for example a cropped field and managed margin, can allow communities to interact that are normally confined to a particular habitat (Blake *et al.,* 2013; Buchholz, 2010; Horváth *et al.,* 2015; Opatovsky & Lubin, 2012). The strength of the edge effect is noted by De Smedt *et al.* (2019) where it was understood a higher density of spider assemblages' activity was identified at the edge of Western European forest due to different orientation of plant physiognomy established.

It has been identified that webs of Linyphiidae are constructed in areas of high prey density (Harwood & Obrycki, 2005). A higher density of Aphididae and Thysanoptera (Thrips), prey capable of flight, were found nearer to above ground *T. tenuis* webs than to ground dwelling spiders (Harwood *et al.,* 2003). This suggests learnt behaviour that webs above the ground within vegetation will be able to access elevated dwelling and aerial prey. Significant higher abundance of Linyphiidae identified within a row *T. aestivum* rather than the space in between the crop, caught by sticky traps within a *T. aestivum* field in Warwickshire, may be attributed to a higher density of prey habituating on the height of the crop (Harwood *et al.,* 2003).

2.1.2.3. Web Renewal *of T. tenuis* and Linyphiidae

Web renewal in this context is the frequency that a web is repaired and put back into a working condition after damage which renders the web functionless (Blackledge *et al.,* 2002; Blackledge *et al.,* 2009).

Linyphiidae are part a Retrolateral Tibial Apophysis (RTA) Clade spider, spiders where the male retains an RTA, a backward projection extending from the male palps, that through evolution has equated to the loss of the cribellate gland. These RTA Clade spiders are of the family class araoeidea apart from the venomous araoemorph class that still use the cribellate gland (Craig, 2003; Millidge, 1988). Cribellate silk from the cribellate gland requires a large amount of energy expenditure to lay with the adhesive silk required to be combed out (Blackledge *et al.,* 2009). It can take an araeomorph up to three hours to create a simple one layered web, whereas a similar web can take 30 minutes for an araoeidae.

Linyphiidae, using silk from the ampulate gland can be laid down rapidly with less energy expenditure than would be required for cribellate silk which may suggest web renewal may be beneficial (Blackledge *et al.,* 2009). However, *T. tenuis* does not tend to renew a web and if one is built at a less favourable site, it may lead to implications of hunger, inability to attract a mate or offer unsuitable protection (Benjamin & Zschokke, 2003; Segoli *et al.,* 2004; Tanaka, 1989). Webs of Linyphiidae tend to have longevity, laid in flat sheets amongst vegetation. These webs can withstand basic disturbance, meaning if damage has occurred, rendering the web functionless, it is likely to be extensive which discourages web renewal (Römer & Scheibel, 2008; Segoli *et al.,* 2004). Agricultural landscapes are areas of high disturbance predominately through the action of machinery, this behaviour of negating web renewal suits this dynamic environment. Harmer *et al.* (2011) and Zhang *et al.* (2016) discussed the energy output to spin silk to repair a web is an inefficient use of *T. tenuis* resources in habitats where disturbance is a common practice. A *T. tenuis* is likely to remain under its web for several days until prey has been captured. The web is then abandoned and left to degenerate in the breakdown of silk proteins (Schmidt & Tscharntke 2005). *T. tenuis* has the ability to lay new silk to a web, if the web area is required to be enlarged to increase its functionality in prey capture or marking territory, which is seen as a conservation of the energy output needed to create a new web (Segoli *et al.,* 2004).

2.1.2.4. Egg Sac Development of *T. tenuis and* Linyphiidae

Egg sac formations are unique to a spider family. Female *T. tenuis* lay small spherical eggs onto a pad of silk and then wrap two layers of silk around the eggs, enclosing at the top until a pear shape egg sac is created (Dondale, 2010). The eggs are held together by a liquid that quickly evaporates (Nentwig and Heimer, 1987). The internal surface is smooth (Humphreys, 1983). It has been shown that diet can affect the fecundity rate in number of eggs laid per sac of *T. tenuis* where continual exposure to Aphididae resulted in lowered fecundity (Bilde & Toft, 2008; Toft, 1995). This is due to low-nutritional value of Aphididae relating to a smaller bodied female after repeated consumption, which leads to low energy availability to lay a large clutch (Alland & Yeargan, 2005; Madsen *et al.,* 2004; Toft, 1995) (*Section 2.1.1.1*.).

Egg sacs are spun by silk formed in the cylindrical gland (Rajkhowa *et al.,* 2015). Cylindrical or tubuliform gland silk (‘wrapping silk’) has a composition higher in alanine and glycine which are amino acids accredited to providing toughness (Craig, 2003; Heidebrecht & Scheibel, 2013) (*Figure 2.3e*). Beta sheets are repetitions in the silk, which have a ‘grooved’ surface (Jiang *et al.,* 2011; Lin *et al.,* 2009). The grooves are hydroponic and allow a textured, highly water-proof sac to be spun (Zhao *et al.,* 2006; Zheng & Ling, 2018). Prior to egg laying, the cylindrical glands become extended ready to manufacture a large amount of this silk in a short space of time which results in an energy output equivalent to 70% of the female’s body weight (Peters & Koovor, 1991). A female of a greater prey consumption (exhibiting increased biological capacity) is likely to spin an egg sac of enhanced design, to aid protection of eggs laid within (Blackledge *et al.,* 2009; Craig, 1986; Peters & Koovor, 1991).

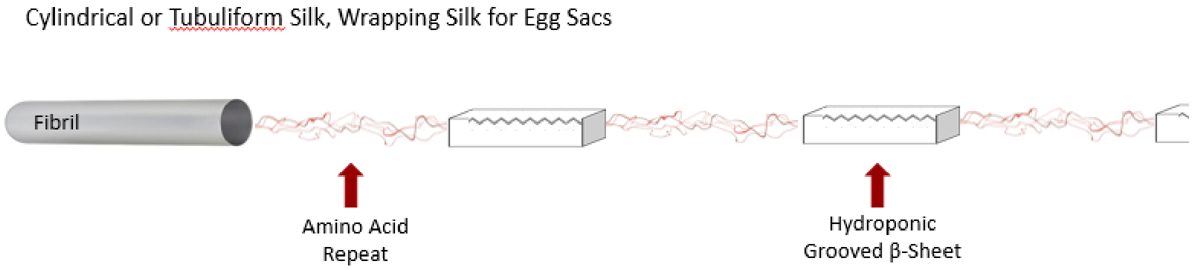


Figure 2.3e: Schematic diagram of secondary molecular structure of the cylindrical / tubuliform silk fibril (Adapted from writings of (Craig, (2003), Heidebrecht & Scheibel (2013) and Jiang et al. (2011)).

2.1.2.5. Oviposition of *T. tenuis* and Linyphiidae

The oviposition of an egg sac is a key decision with the criteria of providing safety from predation and external elements and also allowing the correct light and humidity to be met for the eggs to hatch (Blackledge *et al.,* 2011; Suter *et al.,* 1987). The selection of egg sites are very different from where *T. tenuis* webs are sited for construction, where the webs main function is to capture prey the egg sacs are to be primarily protected against predators. *T. tenuis* exhibit off-web oviposition where they vacate the egg sac once creation is complete. Camouflage is a key factor in oviposition and *T. tenuis* egg sacs have been found low to the ground in field margins woven into the vegetation (Finch 2005).

Gravity, moisture content from the air or substrate and the micro-habitat can affect egg incubation. Egg sacs of *T. tenuis* require high humidity and low light. Gravity aids the development of the ovum and the base of the sac is orientated with gravity. Egg sacs are spun at night to avoid predation and allow camouflage to be in place before daylight returns. The outer layer of the egg sac is waterproof to prevent additional moisture from entering the ovum, not to interfere with the unique level of variants required for successful incubation. This is key as egg sacs are often in heavily vegetated area that collect moisture. Propensity to oviposition is temperature dependant, low temperature may impede the development rate of the eggs (De Keer & Maelfait, 1988; Finch, 2005; Thorbek *et al.,* 2003) (*Section 2.1.1.1*.).

2.1.3. Social Phenotypes of *T. tenuis*

2.1.3.1. Predation Behaviour of *T. tenuis*

T. tenuis is a ‘sit and wait predator’ within the web. *T. tenuis* do not actively forage, rather waiting for food to come and enter the web (Benjamin *et al.,* 2002). Predation effort can be determined by the *T. tenuis* commitment to web-building which can be measured by web size (Janetos, 1984; Segoli *et al.,* 2004; Toft & Lövei, 2002). It is viewed that the greater the web size, occupying more space in a habitat, can result in a greater number of prey being caught and an increased predation success. The size of *T. tenuis* abdomen was identified to be related to higher prey attainment, as shown by Segoli *et al.* (2004), where body condition (measured from residuals of abdomen depth against leg length) was significantly positively regressed with web area. It was shown that a *T. tenuis* of greater body condition can exert higher energetic output that *T. tenuis* can give to web construction.

T. tenuis is a solitary species, only coming together to briefly mate (McCanny *et al.,* 1996; Suter & Keiley, 1984). Searching for potential web-sites and web construction is carried out alone. Attractive web-sites, of higher aspect or near to a potential prey source, are in high demand. With the high abundance of *T. tenuis* and Linyphiidae that may reside in agricultural settings competition exists to acquire the most lucrative site in low arachnid predation and high prey nutritional content to construct a web (Benjamin *et al.,* 2002).

T. tenuis foraging activity has been shown to take place during the day and night though *T. tenuis* are most active during the early hours of the morning. Krol *et al.* (2018) suggested this was due to the larger families of spiders common in agriculture, Lycosidae (wolf spider) and the Philodromidae (crab spider) showing increased activity in the afternoon. Krol *et al.* (2018) proposed that the morning activity of *T. tenuis* enabled foraging and web-building to occur without the increased prey competition. Lycosidae and Philodromidae are a predatory risk to the Linyphiidae due to the smaller body size of the latter.

2.1.3.2. Competition of *T. tenuis*

T. tenuis are territorial of their web and its defence is a key strategy. *T. tenuis* hang centrally under their web obscuring themselves from view from potential prey above. *T. tenuis* and Linyphiidae exhibit both intra-specific and inter-specific competition. Intra-specific competition is a real threat, with cannibalism occurring for the retrieval of an attractive web-site (Wise 2006). Juvenile cannibalism is prevalent in *T. tenuis* and usually occurs after the hatching of eggs. Vanacker *et al.* (2004) identified that larger spiderlings will predate on smaller spiderlings for a protein source and to express dominance. Smaller, similar sized spiderlings in the 1st instar were shown to prey-share out of necessity, which suppresses cannibalistic tendencies. Heuts & Brunt (2002) found, through placing female and male *T. tenuis* in arenas 11 cm in depth, no adult cannibalism occurred between the same sex and different sex if web-sites could be constructed by both parties and no copulation was undertaken. This suggests that *T. tenuis* as adults were not inclined to non-sexual cannibalise if they were able to establish a territory.

Thorbek *at el.* (2004) recognised that fecundity rates of *T. tenuis* can aid its survival by outcompeting other Linyphiidae for space. *T. tenuis* is noted to have a large clutch size but relatively low egg sac production rate. This is counteractive as it allows *T. tenuis* to ensure long reproductive periods. A long reproductive period means eggs are likely to hatch at a different time to other Linyphiidae clutches, so competition for prime web-sites may be low at the time of a clutch hatching (Thorbek *at al.,* 2004).

Harwood & Obrycki (2005) conducted an experiment to identify competition between several species of Linyphiidae and identified that *Erigone autumnali* and *Meioneta unimaculata* were able to cohabit due the micro-niches of each species being different. *M. unimaculata* construct webs higher within the vegetation and *E. autumnali* is confined to foraging activities in lower areas of the habitat due to its dwarf size. Harwood & Obrycki (2005) show Linyphiidae may reside in the same habitat if there appears no direct threat to potential web-sites.

Energy flow within an ecosystem food web can aid in the identification of competition by establishing which species have increased organic stable isotopes within their mass (Zimmo *et al.,* 2012). Stable isotope analysis has been used to understand the energy flow between *T. tenuis* and Collembola (springtails), in a limestone grassland in Germany. This method measures the organic isotopes within the body mass of a sample with a mass spectrometry measured on the delta scale, δ (Sanders & Platner, 2007; Zimmo *et al.,* 2012). The stable isotope $\delta^{15}N$, Nitogen 15, was identified in higher quantities in *T. tenuis* than Collembola measured. This suggests *T. tenuis* has acquired more energy and the predation rate was higher than that of Collembola (Sanders & Platner, 2007). Linyphiidae can be identified as providers of ecosystem services; where natural processes conserve and regulate the environment to the benefit of wildlife and humans (Honek *et al.,* 2018; Lutman *et al.,* 2013; Roberson *et al.,* 2016). Birkhofer *et al.* (2018) discusses ecological intensification as an ecosystem service where Linyphiidae abundance is encouraged to intensify in an arable landscape to aid removal of crop-damaging pests, thus forfeiting the need for pesticide use.

2.1.3.3. Migratory Behaviour of *T. tenuis*

T. tenuis migrate over a landscape in two distinctly different methods, ballooning and rappelling. In both ballooning and rappelling *T. tenuis* produces a long silk thread by stretching of the legs and raising of the abdomen. The difference in movement being rappelling anchors silk to a substrate and then exhibits forward movement until another substrate is reached where the thread is once again anchored. Ballooning does not require attachment of silk onto the substrate and instead swings on the spun thread. Bridge threads spun in rappelling are generally smaller in length than dragline threads for ballooning and due to attachment have low deterioration rate and can be identified after short dispersal has taken place (Blandenier 2014; Bonte, 2013; Thomas *et al.,* 2003; Thorbek, 2003).

Linyphiidae move locally via rappelling, the laying of a bridge thread which enables movement between adjacent materials. It allows rapid movements, for example between neighbouring crops without the need to move up and down the stem. Rappelling is observed as local movement to identify a nearby suitable web construction site. Bridge threads are similar in silk complex and production as support threads, though are separate from a web structure (*Section 2.1.2.1*.). Bridge threads for *T. tenuis* differ greatly in length depending on the local landscape heterogeneity and availability of web-sites, lengths generally range from 10 mm to 200 mm. Bridging propensity is a term referring to a tendency of a *T. tenuis* to spin a bridge thread and rappel (Bonte & Saastamoinen, 2013; Woolley et al., 2016). Rappelling behaviour of female *Erigone atra*, Linyphiidae, was affected by increased species abundance during their developmental stages. This highlights density information, collected by juveniles during development leads to increased short-distance dispersal (De Meester & Bonte, 2010). Bonte *et al.* (2008) identified the tendency to rappel in juvenile *E. atra* increased in warm humid temperatures, 20 ^{o}C to 25 ^{o}C and propensity in rappelling was lowest at 15 ^{o}C.

T. tenuis ability to 'balloon' or aerial-disperse is another factor promoting its dominance in predation (Thomas *et al.,* 2003; Welch *et al.,* 2011). Ballooning is the action of a *T. tenuis* "throwing" a strong but flexible dragline support thread into the air and then swinging on this thread to a new location, so being able to travel further distances than cursorial, running, spiders (Bonte *et al.,* 2002). Ballooning enables rapid re-colonisation of a habitat, which may be triggered by food shortages or habitat disturbance (Thompson *et al.,* 1999). Ballooning has limitations in having a narrow meteorological window with wind speed required to be less than 3 ms^{-1} and air temperature above 19 ^{o}C (Bonte *et al.,* 2002; Pekár, 2014; Simonneau *et al.,* 2016).

After sampling the dispersal activities of spiders found in the farmland of Southern England, Woolley *et al.* (2016) identified spring dispersal was low for *T. tenuis* and peaked in autumn mainly indicated to be due to habitat disturbance. Low dispersal in spring communicated *T. tenuis* may identify adequate web-building locations in accelerated crop growth. Woolley *et al.* (2016) found that there was significant positive correlation between ground population and dispersal population of *T. tenuis* suggesting that ballooning is a function resulting from high population densities perhaps more problematic in times of disturbance (Bell *et al.,* 2002).

2.1.3.4. Courtship Behaviour of *T. tenuis*

T. tenuis exhibit Sexual Size Dimorphism (SSD) which describes differences between male and female other than the genital organs (Bowden *et al.,* 2013; Kuntner & Coddington, 2020). Linyphiidae and *T. tenuis* demonstrate extreme SSD in abdomens being larger in females (*Figure 2.1.*). It is thought that SSD in *T. tenuis* has been driven by selection pressure with males' preference of larger females due to increased fecundity, in clutch size, of a large abdomen (Shine, 1988). Recently, extreme SSD has been attributed to the 'Gravity Hypothesis' where small males select larger females due to a small male finding it easier to climb onto a larger female frame during copulation (Corcobado *et al.,* 2010). In bridging propensity, a small body frame is favoured to facilitate the quick rapid movement rappelling requires. This may have driven the selection of a female to a small abdomen phenotype in males, where males are required to disperse more frequently than females to find a suitable mate (Corcobado *et al.,* 2010).

Male *T. tenuis* generally do not weave webs, their main goal being to locate a suitable female for mating. Males observed under webs without a female is often spinning a sperm web. When a male is ready to mate it will weave a web where sperm can be deposited onto the sheet threads in the centre of the web which is then collected by the front palps of the male. It is at this stage the male will abandon the web and search for a potential mate (Dondale 2000; Preston-Mafham & Preston-Mafham, 1996). Female *T. tenuis* exert the greater biological control within agricultural landscape due to females spinning most sheet webs (Bowden *et al.,* 2013). This can identify that female *T. tenuis* have a greater ability to predate, as male's choice of web-site location may be due to the function of courtship more than inception of a stimuli of prey. De Meester & Bonte (2010) and Huang *et al.* (2018) explain females hunt for prey with increased activity than males, thus are a more attractive predator to crop pests.

The male can receive an airborne sex pheromone (R)-3-hydroxybutyric acid (HBA) that is emitted by a female *T. tenuis* when ready to copulate (Gaskett, 2007; Maklakov *et al.,* 2003). *T. tenuis* males select virgin over fecund females, as the virgin provides the male the opportunity to dominate the transferral of genetic material. If such a virgin is unavailable, another mate is required or the male risks losing the genetic transferral of active sperm (Preston-Mafham & Preston-Mafham, 1996; Volltrath, 1986).

As most female *T. tenuis* spend most of their adult life occupying a web the male uses several tactics to receive the female's attention using the web (Preston-Mafham & Preston-Mafham, 1996; Rundus *et al.,* 2011). The male performance on web arrival may result in pre-copulation cannibalism by the female. The threat of pre-copulation cannibalism to the male can be seen as a form of natural selection where a male's genetic material may not be transferred to a specific female due to the threat being too great (Vanacker et *al.,* 2004). Females select males on several traits, which can be demonstrated with web arrival of the male. Heritable fitness benefits in longevity and fecundity are attractive to the female and can be shown by manipulating the female's web. Male's exhibit longevity in vibrating the web at high rates, this action being costly in energy identifies a high level of fitness in the male (Preston-Mafham & Preston-Mafham, 1996; Thorbek *et al.,* 2004). Pekár (2014) and Rundus *et al.* (2011) discussed male *T. tenuis* may exhibit superior traits by ascending structures to display flexibility and cognition. This behaviour can alter male *T. tenuis* location and thus web-spinning to the vicinity of potential prey within an agricultural setting (Boisseau *et al.*, 2017; Gómez *et al.,* 2016; Řezáč & Řezáčová, 2019).

Threat of competition in *T. tenuis* is the main contributor to the courting times. Courting in larger males can be as long as 200 minutes with a slow and laborious approach guarding the chosen female. Smaller males are quicker to copulate with courtship lasting 50 - 80 minutes and produce a scramble approach to copulate before a large, more attractive male may approach. Due to selective pressure in pre-copulation cannibalism more female *T. tenuis* are often within a habitat than males (Dondale, 2000; Mafham & Preston-Mafham, 1996, Vanacker *et al.,* 2004). This can be of benefit to increased predatory behaviour as females generally require a greater protein in-take due to their enhanced propensity to web-build (Bonte *et al.,* 2008; De Meester & Bonte, 2010). Copulation timing is an important consideration to predation pressure *T. tenuis* can exert, due to time taken away from responding to stimuli of potential crop pests. Prey falling into a web may not be discovered by *T. tenuis* copulating, vibrations in the web from prey insertion may be distorted (Eberhard, 2019; Rodríguez & Gloudeman, 2011; Vibert, 2016). Moreover, copulation leaves *T. tenuis* vulnerable to predation, thus, rapidity can assist pest suppression in a highly changeable environment such as a working arable field (Herberstein *et al.,* 2014; Keil & Watson, 2010).

2.1.3.5. Sensitivity of *T. tenuis* to Disturbance

T. tenuis can adapt quickly to disturbance and therefore monopolises the creation of webs at beneficial web-sites before another arachnid. *T. tenuis* pioneers a recently disturbed landscape due to its life strategy. *T. tenuis* may have two annual generations where reproduction occurs in staggered periods (Downie *et al,* 2000; Topping & Lövei, 1997). The aeronaut ability of *T. tenuis* is often cited as one of the reasons for rapid dispersal as ballooning allows 2 km distance in travel (Downie *et al,* 2000). The wide array of habitats that *T. tenuis* can colonise may ensure a population can survive in a neighbouring habitat while their previous occupied landscape is being disturbed.

Simonneau *et al.* (2016) and Thorbek *et al.* (2004) described female *T. tenuis* behaviour of 'bet hedging' of egg sac location being induced from threat of disturbance. This is where egg sac placement is dispersed through large areas of space to limit damage from localised disturbance and improve survival chances of the clutch. *T. tenuis* large clutch size in Linyphiidae is seen as a strategy to ensure a future generation even if the egg sac is disturbed or predated upon. This future generation if successful, offers a continuation of possible prey capture, thus implement biological control.

In an experiment where Linyphiidae abundance and small-scale spatial arrangements of webs was analysed before and after the cutting of alfalfa, it was noted that overall density decreased after cutting, though the spatial distribution of webs remained the same (Birkhofer *et al.,* 2007). Linyphiidae webs were noted to be in closer approximation, less than 20 cm, immediately before and after cutting. This highlighted that Linyphiddae were most active within this period, suggesting a race to acquire small beneficial habitats of debris created after cutting (Birkhofer *et al.,* 2007).

From a study analysing the abundance of spider species in a sheep pasture in Canterbury, New Zealand, and its surrounding margin, it was observed that *T. tenuis* adults and juveniles were found in the highest abundance 50 m away from the field margin into the sheep pasture (Mclachlan & Wratten, 2003). This shows the pioneer approach of *T. tenuis* and suggested the ballooning nature of *T. tenuis* reduces the field size effect allowing further migration from a margin into a disturbed field (Mclachlan & Wratten, 2003). Clark *et al.* (2004), commenting on spider abundance in four monthly intervals after a pasture was cultivated, indicated that even though *T. tenuis* was present in each sampling period after cultivation its abundance was significantly lower in months one, two and three only reaching abundance equal to before cultivation in month four. This was discussed to contribute to the cyclic grazing by cattle that is carried out in the pasture, preventing *T. tenuis* from taking the stronghold (Mclachlan & Wratten, 2003). Furthermore, *T. tenuis* abundance was surprisingly not correlated to weed percentage. Unwanted plants (weeds) are small-scale micro-habitats that aid web construction. It can be identified from this experiment that *T. tenuis* does have limits in colonising disturbed habitats, viewed in both papers as a high aeronaut spider density overall having diluted *T. tenuis* pioneering capability (Clark *et al.,* 2004; Mclachlan & Wratten, 2003).

2.2. British Arable Agricultural Systems

2.2.1. British Grown Cereal Crops

Cereal crops have been grown in British soils since prehistory to provide food. Today the cereals grown are the same with only the varieties differing due to increased technology, allowing varieties to be resistant to disease and favouring certain phenotypes like crop height for increased yields (Townsend *et al.,* 2016). *Triticum* (wheat) and *Hordeum* (barley) are the main cereals that are grown in the UK, followed by *Avena* (oats). *Triticum* varieties are grown for differing reasons, to be milled into bread flour or dried for animal feed. Similarly, depending if the *Hordeum* harvested is to be malted for beer production or be milled into flour, different varieties of *Hordeum* are grown (NABIM, 2018). The growth stages (GS) of the plant are definite periods where the physiology of the plant changes, for example, GS 11 is where the first leaf unfolds on the *H. vulgare* plant, to five leaves unfolding in GS 15. GS 83 relates to the dough development, which is the ripening of the kernel and GS 87 identifies the hard dough stage, fully ripened (AHDB, 2015; McFarland, 2014).

There are two sowing periods within a year, spring and winter. The spring and winter varieties differ in the germination requirements and tolerance to temperatures. As of 2016, spring and winter crops are defined by their drilling date (FarmPlan, 2016). A crop drilled before 1st February is a winter crop whereas a variety drilled on or after 1st February it is a spring crop. Seed varieties grown in the UK must be on a National List where the grain has been certified to be implemented into the UK market (NABIM, 2018). The most important factor in winter cropping is seen as the sowing date. Early sowing of *Triticum aestivum* (Winter Wheat) can increase yields, however, increase risk of slug damage (DEFRA, 2011). In spring cropping, it is the condition of the seedbed, generally this is required to be firm and dry (DEFRA, 2011).

There are advantages and disadvantages to both crop varieties. *Hordeum vulgare* (Spring Barley) has lower yields than winter *Hordeum*, however, is fast growing and input requirements are less (Reuss, 2003). The main cultivation difference between spring and winter crops is weed management. *Alopecurus myosuroides* (Black-grass) is primarily a concern in *T. aestivum* and within *H. vulgare* broad leaved weeds, i.e. *Stelleria media* (Chickweed) and *Ranunculus repens* (Creeping Buttercup) may appear. Spring crops allow persistent herbicide-resistant weeds, for example *A. myosuroides,* to be tackled by allowing the first flush to emerge and dealt with without harming the later drilled spring crop. Spring crops are beneficial as their fast turn-over reduces workload and labour costs on the farm.

Fallow fields over winter are considered bio-conservative providing a food source and a refuge area for wildlife (ADAS, 2007; DEFRA, 2011). Řezáč & Řezáčová (2019), Welch *et al.* (2013) and Wiśniewski *et al.* (2018) explained spring cropping, drilled later than winter, fits the *T. tenuis* predator response due to a generation stage of *T. tenuis* as mature adults when the crop is drilled. Thus, adults having the ability to reach a multitude of web-site locations through greater propensity to balloon and weave webs of beneficial orientation (Bonte *et al.,* 2008; Dinter, 2004; Řezáč & Řezáčová *et al.,* 2019).

Winter crops may prevent soil erosion and nutrient leaching with the large elongated root system anchoring into the soil. Bare soil can be vulnerable to the extreme weather conditions of winter where erosion and run-off can cause considerable damage to the higher profiles of the soil (Western Winter Wheat Initiative, 2013). Winter cropping can manage annual pests that dwell in the soil as larval form, for example *Sitodiplosis mosellana* (Orange Blossom Wheat Midge), with tillage disrupting their hibernation cycle (AHDB, 2018). Winter and spring crops differ in response to the vernalisation process, where seeds are introduced to a period of low temperatures ranging from 0 °C - 12 °C during the germination phase, which promotes earlier anthesis, (flowering) (AHDB, 2018; DEFRA, 2011). Winter varieties respond strongly to this process whilst spring crops show little response. Vernalisation is a costly process and gains in yield are required to support the use of this technique (AHDB, 2018).

Winter crops are now the most favourable cereal crop due to the economic return that winter yields can gain. Spring crop prices fluctuate on the global market due to their short growth season causing uncertainty in final yield, and therefore are less attractive from a business perspective (AHDB, 2018; Davies & Finney, 2002). Spring crops are generally harvested later than winter crops which may be an economic burden as expensive cultivation equipment, if hired, may be utilised at different times (AHDB, 2018; Godwin, 2014).

The cropping of both winter and spring cereals on a UK arable farm in a structured rotation allows the advantages of both to be utilised, a *T. aestivum* crop in one field may ensure economic stability for the farm while another field left fallow ready for a spring crop may reduce the weed density once the crop is drilled (AHDB, 2018; ADAS, 2007).

2.2.2. Soil Properties in British Arable Agriculture

Soil is the most important factor in arable agriculture providing the growth medium for the cereals planted. The health of the soil is required to be continually monitored to ensure it is optimal to provide the best yields. Soil health is defined as its capacity to function as a living system (Bommarco *et al.,* 2013; Sagoo, 2018). This can be measured in many differing aspects from enhancing water quality, sustaining plant productivity while supporting a varied community of soil organisms. Growing cereals seems to be a small part of the role of soil, however, it is essential in allowing economic sustainability and food availability (Ashmin & Puri, 2002; DEFRA, 2018; Sagoo, 2018).

Many soil types are found throughout the British Isles, each having a unique set of physico-chemical properties that contribute as a growth medium. Most cereals are grown in East Anglia, South East and the East Midlands in the UK (DEFRA, 2010; 2017; NABIM, 2018). Generally, the summers are warm in these regions with low lying land and a highly fertile soil combine to produce cereals of viable yields. The main soil types of these regions, Hanslop, Salop and Evermore, are a loamy clay where the highest mineral content of the soil is clay (Cranfield University, 2017). They are described as generally being seasonally wet with slow permeability due to the silicate sheets of clay particles having a high surface area adhering to water particles (Ashman & Puri, 2002). Clay rich soils reduce nutrients from being leached as the micelles (negatively charged silicate crystals), act as a large anion and attract cations, Ammonium (NH_4^+), Potassium (K^+) and Calcium (Ca^+) (Paul, 2015). The high Cation Exchange Capacity (CEC) of clay soils, the rate of binding cations, reduces soil pH (Ashman & Puri, 2002). Acidic soil disrupts a crops ability to uptake certain nutrients causing tissue necrosis and delayed growth (Knight *et al.,* 2012). Through these factors a soil containing a high percentage of clay is seen as being fertile (Ashman & Puri, 2002; Paul, 2015). Difference in soil physico-chemical make-up of a soil can affect plant diversity and population, for example high field capacity of clay soil allows some moisture availability in times of drought (Badalı´kova, 2010). Vegetation complexity and plant physiognomy can affect a *T. tenuis* ability to weave, thus noting parameters of soil health can aid inclusion of a *T. tenuis* population (Campbell *et al.,* 2020; Lyons *et al.,* 2018; Paul, 2015).

2.2.3. Soil Tillage Methods in British Arable Agriculture

Tillage is an agricultural term and describes action that is given to a soil. Tillage is standard practice to ensure a seedbed is optimised for the growth of a crop by controlling weeds and turning of the soil, allowing buried nutrients to be transferred to higher profiles and more accessible by roots (Morris *et al.,* 2007; Sharley *et al.,* 2008).

Conventional tillage (inversion tillage) is a term that refers to the traditional methods of preparing soil. It involves primary and secondary cultivations that commences before the seed is drilled. The primary cultivation involves the use of a mould board plough which has been used since the 18th century and greatly reduced the time it takes to prepare a seedbed. The plough consists of a coulter (sieth) which cuts vertically usually 300 mm deep into the topsoil, and a shear that cuts horizontal (Jones, 2008). The clods, soil aggregates, are then inverted with a curved elongated disc, the mould board. The resulting gap that follows the plough is called the furrow and this is where the seed is inserted. There is a period of on average a month for winter crops before seed is drilled to allow soil to ‘rest’, increase in nutrient availability. One of the principals behind this technique is to quickly release nutrients that may be locked in the soil and bring them to the surface where they can be utilised by the seed once germination begins (Morris *et al.,* 2007).

Secondary cultivation completes the creation of the seedbed by breaking up the clods that have been formed from the previous plough, creating a finer soil structure that will allow increased aeration, germinating plants roots are able to spread and access nutrients more easily. In a conventional approach, secondary cultivation is usually carried out by finishing discs. In the UK, the majority of seedbeds are moulded using a disc harrow. The finishing disc diameter here usually ranges from 590 mm - 610 mm depending the heavy duty of the machinery (Bullock Tillage, 2014; Morris *et al.,* 2007; SARE, 2012). After which remains a homogenous landscape, with little landscape material to uphold a population of ground dwelling arthropods, such as Linyphiidae.

The seed is sown after the cultivations with a seed drill, whose purpose is to insert the seed directly into the soil, each being sown at a depth of approximately 350 mm at a specified distance apart for cereal crops. The seed drills are often pneumatic and the lightest piece of machinery in the cultivations (Kverneland, 2018). The seed comes from a hopper where the seed is easily transferred to shoots to be inserted. The soil over the seed is reconsolidated after seed insertion by a roller, that is the last pass, this ensures the seed has adequate soil coverage for successful germination (Väderstad, 2017).

Conservation non-inversional tillage systems, where soil disturbance is reduced by not being inverted, are now increasingly applied to farming systems in the UK (CTIC, 2002; Godwin 2014, Lafage *et al.,* 2015; Morris *et al.,* 2007; Morris *et al.,* 2010). Direct drilling is one method of non-inversional tillage and involves seed insertion directly into the soil with limited soil disturbance (CTIC, 2002; Morris *et al.,* 2007). Different levels of non-inversion tillage, deep to zero are implemented now in UK arable farming systems (Kertész & Madarász, 2014; Townsend *et al.,* 2016) (*Figure 2.4a & b*).

In modern agriculture, soil tillage can be measured by the percentage of crop residue that is left on the surface (SARE, 2012). With research into sustainable agriculture, agriculture than conserves resources to allow continued food production, there are different soil tillage methods coming into effect which sit between conventional and conservation in the level of residue that remains on the surface. The use of a sub-soiler for primary cultivation instead of the mould board plough is beneficial for soil health as being of lighter weight and uses points, legs and tines (sharp point attached to the legs), instead of the sieth and mould board meaning soil is not inverted (*Figure 2.4a*). The point carries out most of the loosening and passes through first and can be winged to maximise the tillage. The legs can be different widths and curved or straight depending on the level of cultivation required, curved legs loosening soil further than straight, lifting the structure slightly. Discs can be applied to the tines and have a diameter of approximately 510 mm. The sub-soiler is ideal to aide soils that are prone to compaction due to reduced clods being formed because of the machines lighter frame (Bullock Training, 2014; He-Va, 2018; Weill, 2015).

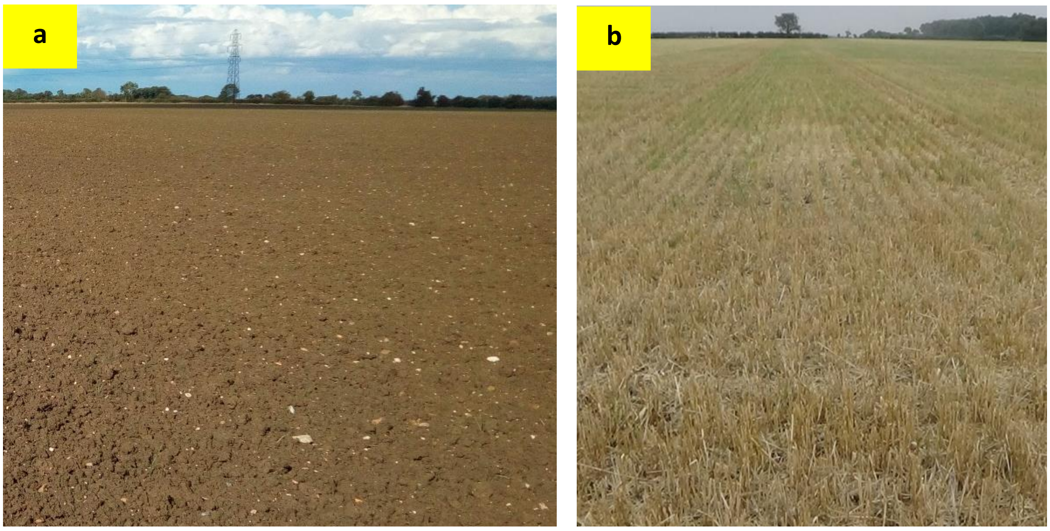


Figure 2.4a & b: After secondary cultivation on two fields on the same arable farm in Cambridgeshire. a = Conventional tillage with a sub-soiler and disc harrow. b = Conservational zero-tillage.

2.2.4. Advantages and Disadvantage of Different Soil Tillage Methods

A key advantage to the use of a conventional tillage system over conservation is the crop yields that are reported to be greater in the former with an economical benefit to the farmer and British agriculture. In a report by the Farming Association the yield of winter *Hordeum* was 0.65 tha^{-1} (+9.6%) higher in cultivation of always plough compared to non-plough. Similarly, winter oilseed rape's yield was increased by 0.15 tha^{-1} (+3.9%) with plough (Townsend *et al.,* 2016). Between the years of 2009 and 2011, Brennan *et al.* (2014), reported a significantly higher yield in *T. aestivum* in conventional tillage than reduced tillage in Central Ireland. Vakali *et al.* (2011) found the use of the plough gave significant higher yields, 73%, in organic *Hordeum* grown in a clay loam in the years five to seven of a long term experiment in South-West Germany which was partly attributed to the higher rate of nitrogen fertiliser uptake (Brennan *et al.,* 2014). However, higher yields my not directly relate to increased profitability due to the outlay cost it may take to ensure the growing medium of the land is fit for purpose (in nutritional availability and soil structure) (Arvidsson *et al.,* 2014; Edgerton, 2009; Forristal & Murphy, 2010).

Inversion tillage has been shown to remove pests to a higher degree than other tillage systems by destroying their habitat and exposing pests to predation. Voles are common herbivores in temperate regions, causing damage to cereals due to extensive feeding (Brown *et al.,* 2007). In the Czech

Republic, significantly greater vole activity in burrowing was identified in spring of cereal crops in areas under zero-tillage management (Heroldová *et al.,* 2017). The inversion action of the plough has been identified to bury cocoons of midges that cause crop damage further into the soil disrupting their life cycle (*Section 2.2.1*.). Chen & Shelton (2009) found that common European arable pest *Contarinia nasturtii* (Swede Midge) was unable to pupate at soil depths greater than 5 cm. In a trial on oilseed rape in Germany, *Dasineura brassicae* (Brassica Pod Midge) reproduction and infestation rates increased in plots where less intense soil tillage of harrowing and addition of mulch occurred compared to the ploughed plots. Decreased aeration and the addition of organic material allowed the soil to remain at an optimal temperature for hatching (Buechs & Katzur, 2004).

Weeds have been reported as less prevalent under conventional than conservational tillage. Lutman *et al.* (2013) investigated soil tillage methods on the control of *A. myosuroides* in twenty-five experiments across the UK. Meta-analysis of the experiments showed a 67% reduction in *A. myosuroides* density m^{-2} in Conventional compared to non-inversion tillage. Removal of weeds is also beneficial in controlling Aphididae, as weeds and volunteer crops, crops that germinate from seeds dropped in harvest, can produce ‘green bridges’ to allow a colony to prevail until cereal crop is established (Ball & Bingham, 2003; Milner, 2002).

The disadvantages to conventional tillage are well documented and include factors such as the deterioration of soil health in nutritional content and aeration and the decrease in density of beneficial predators. Aeration is reduced in soil with the bulk density often being increased initiating compaction, this is more from the heavy machinery passing over the soil rather than the inversion of the soil (Badalı´kova, 2010; Lui *et al.,* 2013a). This is a ‘plough pan’ and is generally of 2 - 3 cm in thickness, identified at a depth of >20 - <35 cm in the soil (Knight *et al.,* 2012 Peigné *et al.,* 2007). A soil with increased bulk density will likely impede root growth in its structure of limited air pores. Vakali *et al*. (2011) identified that root penetration (mPa) for *Hordeum* was significantly higher, 30% higher, at the soil depth of 25 - 50 cm with reduced tillage than for mould board plough.

Soil nutrients are seen to be poor in continually inverted soils due to the evaporation of the key nitrogen into the atmosphere due to exposure of the B profile of the soil as it comes into contact with rain water (Morris *et al.,* 2007). Conventional inversion tillage causes much disturbance to the habitat; by reduction of ground litter, development of a poor soil structure which decreases water draining capabilities and affects soil inhabitants through the direct action of the plough (Holland & Reynolds, 2003; Morris *et al.,* 2007).

Conservational tillage, leaving a higher percentage of crop residue on the surface and less intensive management, leads to a higher percentage of organic matter being present after cultivation. Essential nutrients are prevented from leaching by being locked in. Reduced tillage significantly increased the essential plants nutrients P, K and Ca content within a silt loam from an arable farm in west Tennessee (Mbuthia *et al.,* 2015). Shrestha *et al.* (2015) used Nuclear Magnetic Resonance (NMR) Spectroscopy to identify the levels of Soil Organic Carbon (SOC) and Soil Organic Nitrogen (SON) within different tilled soils, conventional and non-till. Soil samples were a clay loam acquired from a 6-year cereal crop rotation experiment in Norway. A significant difference was identified between the content of SOC and SON of each soil at a depth of 0 cm to 10 cm. Both compounds were found in higher quantities in the non-till soil (Shrestha *et al.,* 2015). At the further depth interval of 10 - 30 cm no significance between kg of SOC and SON were identified, supporting tillage only effecting the top A - profile of soil.

Disadvantages with conservation tillage are that improved soil health and increased microbial activity takes several seasons to be of significance to crop health and subsequent yields, time and patience is required which is not an option if revenue is required annually. In arable farms, around 40% of upfront costs goes to machinery (Morris *et al.,* 2010). A direct drill is considerably more expensive to purchase than a plough and sub-soiler. It is apparent that because of the above factors conservational till tends to be in operation on larger farms in England. Out of 3% of farms participating in the Farm Business Survey 2010, 69% of large farms within the study incorporated some form of reduced tillage within their cultivations, whereas only 22% of small farms used reduced till (Townsend *et al.,* 2016).

Increased herbicide use is a problem that has been identified with non-inversion tillage, without the action of a plough weeds are left in the soil to flourish. In a review of thirty *T. aestivum* and *Helianthus* (sunflower) farms in Southern Spain, 34% of the cereal farms reported issues with weeds, the most significant issue that was presented. Subsequent problems arising from poor weed management was resistance from herbicides, because of increased use and the cost of the herbicide required (Carmona *et al.,* 2015).

The increased moisture within conservation soils, due to the aeration and improved capillary action of the soil, can lead to higher instances of fungal disease being prevalent. Váňová *et al.* (2011) discussed the significantly higher level of mycotoxin deoxynivalenol (DON), toxin produced from *Fusarium* affecting the ears of *Triticum*, was identified in the *T. aestivum* of conservational tillage than conventional tillage annually (2005 - 2008) in Prague, Czech Republic.

Conservation tillage is not suitable for every soil type. Soils with a high sand and silt content have a weaker structure due to small particles equalling soil with larger pores (Alhammadi & Al-Shrouf, 2013). The texture is usually a crumb with little adhesion without the moisture-attracting ability of clay

(Ashman & Puri, 2002; USDA, 1988). A small proportion of clay in soil allows expansion and shrinkage through times of heavy rain and drought which can disturb a structure like a seedbed. Direct drill requires a well-formed seedbed to allow a seed to have the correct conditions for germination, without the use of additional tillage methods (Morris *et al.,* 2010; Peigné *et al.,* 2007).

Differing tillage intensities have shown throughout recent research to manipulate Linyphiidae abundance and activity. Methods of tillage can be seen to affect the biological control potential of Linyphiidae. To enhance *T. tenuis* capacity for biological control, surrounding ecosystem elements are required, for example plant litter, which may increase prey conversion efficiency and fecundity (Alignier *et al.,* 2014; Horváth *et al.,* 2015; Thorbek *et al.,* 2004). Reducing ground litter can affect Linyphiidae presence. Wagner *et al.* (2003) recognised a higher number of Linyphiidae within deeper litter levels in a forest. Increased litter levels and enclosed structure are identified in non-inversion tillage, where previous crop stubble is not incorporated into the soil and offers an area to over-winter which is beneficial for the protection of egg sacs to secure a large population in the next generation (Holland & Oakley, 2007; Morris *et al.,* 2010; Öberg *et al,* 2008).

When analysing spider abundance on a *T. aestivum* crop and on stubble of the previous crop of a drilled field in Argentina, Armendano & González (2011) identified that 21.35% of spiders in the stubble were Linyphiidae. This was against 9.05% of spiders being Linyphiidae in the *T. aestivum* crop. The difference of 12.3% Linyphiidae population demonstrates that Linyphiidae are inclined to inhabit the stubble when both stubble and crop are available. A study in the Loire Valley, examining landscape factors that cause variations of species richness of Linyphiidae, found species richness decreased with increased moisture due to intensive soil management (Lafage *et al.,* 2015).

In an experiment that investigated the occurrence of the Barley Yellow Dwarf Virus (BYDV) in *Hordeum*, with the implementation of minimal tillage and conventional tillage, it was found that within minimum tillage 48% fewer Aphididae were identified within the sample crop and this related to 78% less BYDV instances observed than with the conventional plough. This had the economic benefit of the yield harvested from the minimum till area being 1.24 th^{-1} greater than conventional till. The addition of straw to separate minimal till and conventional plots was compared to the original plots of no straw. There was a significant difference in Aphididae and BYDV occurrence between the conventional no straw and straw, no straw held the greater occurrence. Within minimal tillage, the addition of the straw observed a further 68% less Aphididae than the minimal tillage alone (Kennedy & Connery 2005; Kennedy *et al.,* 2010). Discussed is the potential of straw to support an increased number of natural enemies. Scattered *T. aestivum* straw mulches have been identified to reduce instances of aphid-borne virus in a zucchini squash plant in California (Summers *et al.,* 2004). The *T.*

asetivum straw is shown to deter alate, winged, Aphididae morphs from colonising a crop by disturbing their landing potential with key sites partially covered with the mulch (Summers *et al.,* 2004).

2.2.5. Popularity of Soil Tillage Methods in British Arable Agriculture

In recent years, development has moved towards agro-ecology through adapting non-inversion tillage in agriculture (Ball & Bingham, 2003). In 2010, 6,000 ha of UK arable land used direct drill as its tillage system (Goodwin, 2014). This equates to 32% of arable land established with conservation tillage, with 46% of farms using methods other than the mould board plough (Townsend *et al.,* 2016).

Communications with Mr. Martin Jenkins of Martin Jenkins Farming Ltd in Childerley, Cambridgeshire, commented that by using a sub-soiler rather than a plough, more organic material is left on the surface which has benefited soil health in the increased content of micro-nutrients. Ingram (2010) studied farmers who had adopted reduced tillage practices and recognised that the reasons were to improve soil for improved future yields and to allow large areas to be cultivated rapidly. An increased number of invertebrates, e.g. Arachnids and Coleoptera; Carabidae, were identified on soil with reduced till than conventional till by Soane *et al.* (2012) who reviewed UK involvement in reduced till farming.

Further case studies undertaken by Goodwin (2014) on a variety and size of farms across the UK, where the owners have adapted the direct drill till approach, provide an insight into how conservational tillage is working in practicing farms. A 440 ha farm in Yorkshire adapted to non-till for financial reasons and to improve the soil health of the farm. In two years of application, the farm's labour and fuel costs reduced, and earthworm activity increased. Disadvantages were expressed as an increase in slug damage especially in *Brassica napus* (Oil Seed Rape) and compaction of the heavy clay soil without the inversion action of the plough. In Oxfordshire, a 404 ha farm with silt / clay loam has been practicing direct drill tillage for six years. The major advantages were shown to be matched to the case study in Yorkshire in cost saving benefits and improved soil structure which enables the soil to recover quicker after extreme weather events. The farm has experienced 20% less seed emergence in the direct drill approach with lower yields. Another disadvantage was expressed as direct drill manufacturers becoming complacent in the machinery as equipment is slow to adapt and improve to better suit a farm's needs (Goodwin, 2014).

2.2.6. Crop Pests in British Arable Agriculture - Aphididae and *Sitodiplosis mosellana*

2.2.6.1. Biology and Ecology of Cereal Aphididae

Rhopalosiphum padi (Bird Cherry Oat Aphid) (Linnaeus, 1758), *Sitobion avenae* (English Grain Aphid) (Fabricius, 1775) and *Metopolophium dirhodum* (Rose Grain Aphid) (Walker, 1849) are classed as cereal Aphididae, true aphids, and reside on cereal crops within spring and summer months (Buriro *et al.,* 2006). *S. avenae*, *R. padi* and *M. dirhodum* are polyphagous species, feeding on different plant materials through a generation (Gullan & Cranston, 2010). During summer months each Aphididae colonises cereal crops (*Triticum, Hordeum, Avena*) taking advantage of the high monosaccharide content of the phloem in the upper parts of the tiller and subsequent leaves (Price *et al.,* 2011).

Temperature is the key variable that regulates the numbers of Aphididae with fecundity increasing with temperature, though each Aphididae will have an optimum temperature where fecundity decreases once overcome. *R. padi, S. avenae and M. dirhodum* reproduce in two ways in temperate regions (Lombaert *et al.,* 2006). Parthenogenesis (asexually), which occurs usually in warmer temperatures where the high availability of food in cereal crops allows a large colony to be supported. Young (nymphs) are born live being sexless and capable of producing offspring once maturity is reached usually within seven days (Mehrparvar *et al.,* 2013; Price *et al,* 2011). As temperatures and food availability drops to a limiting resource, *R. padi, S. avenae* and *M. dirhodum* are able to reproduce a female which is capable of laying eggs usually at the base of the over-wintering host plant, *Rosea* (rose) for *R. padi* and *M. dirhodum* and Poaceae (grass) for *S. avenae.* Eggs, able to survive through winter, are small and difficult to identify (Goggin, 2007; Lombaert *et al.,* 2006).

As with Linyphiidae, Aphididae undergo ecdysis to develop. *R. padi, S. avenae* and *M. dirhodum* have four instars equalling four ecdysis stages to reach adult maturity. *R. padi, S. avenae* and *M. dirhodum* nymphs being polyphagous may produce alate morphs, offspring capability of producing wings, to allow for extended migration (Goggin, 2007; Jeffs & Leather, 2014). Alate morphs are produced instead of apterous (wingless) morphs, in a response to a set of stimuli. The key stimulus being over-crowding where food availability is identified as a limiting factor, other factors include temperature and daylight hours, though each above Aphididae has a different threshold to environmental conditions controlling the reproduction of alate morphs (Mehrparvar *et al.,* 2013; Price *et al.,* 2011). Some species of Aphididae alternate between polyphonic (environmental) and polymorphic (genetic) control of wing morph which enables numerous factors to promote wing growth (Goggin, 2007).

Alate morphs are physiologically different to apterous morphs, due to their main role being to colonise a new host plant, instead of reproduction. Alate morphs have longer antenna, longer legs and well-developed sensory organs to allow the correct host to be found in nutritious availability and longevity. For example, in *S. avenae,* the colour of the host plant is thought to be key, where green identifies a high nutritional content and where yellow leaves often mean new shoots or senescing leaves (Jeffs & Leather, 2014; Mehrparvar *et al.,* 2013; Parker & Brisson, 2019).

Yu (2019) notes, apterous morphs have low energy availability to translocate large distance, the tendency to ascend and descend adjacent plants in a community. Reynold & Reynolds (2009) discuss within an early growth stage of a cereal, wing polyphenism (a different phenotype; alate morph, produced from the identical genotype) may have occurred due to stimuli of plant growth accelerating parthenogenesis rate, however, Parry (2013) explains winged dispersal of cereal Aphididae is regularly short (20 m) and sporadic, the priority to locate plants of low Aphididae density.

Cereal Aphididae ensure survival by living in large colonises as clones, produced from parthenogenesis, often observed only implementing localised migration to nearby plants. One advantage of this is an Aphididae may produce a warning pheromone if threatened that alerts the rest of the clones of the threat, promoting Aphididae to stop feeding and drop from the plant (Goggin, 2007; Lombaert *et al.,* 2006; Price *et al.,* 2011). Another advantage to communal living is metabolic sinks that are created within the host plant by excessive direct feeding by many Aphididae. A positive feedback loop is created where Aphididae feeding promotes the assimilation of monosaccharides to the feeding site of the phloem (Price *et al.,* 2011).

R. padi, adults are 2 - 3 mm in body length, oval with a short caunda (tail) which is red at the base (*Figure 2.5*.). The colour of dark green to a burnt red, with darker red patches to the rear segments (seventh to eighth) of the abdomen makes *R. padi* easily identifiable on a cereal leaf (*Figure 2.5*). Siphunculi, dorsal tubes which emit pheromones, are short on *R. padi*. Alate morphs abdomens are principally dark green in colour and have black wings (Bayer 2013; Campos & García-Marí, 2014; Price *et al.,* 2011) (*Figure 2.5*).

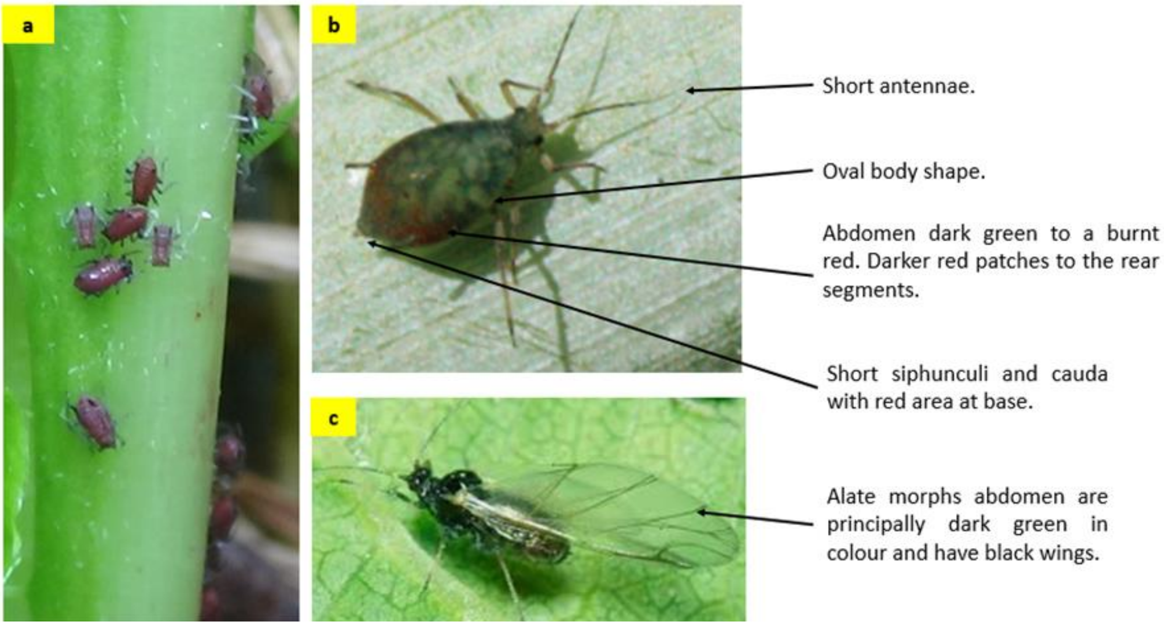


Figure 2.5a -c: a = R. padi *nymphs in NIAB field trial. b =* R. padi *adult apterous morph (InfluentionalPoints, 2018). c =* R. padi *adult alate morph (InfluentionalPoints, 2018).*

M. dirhodum are less easily identified on a crop due to their colour being a light green, even translucent, shade (*Figure 2.6*.). Cauda are the same translucent green and longer than *R. padi*. They are positively identified by a dark green strip on the dorsal aspect down all segments of the abdomen (*Figure 2.6*). Siphunculi are long and dark. Alate morphs are the same light green but the dark green strip is absent, wings are a light grey colour (Bayer 2013; Campos & García-Marí, 2014; Price *et al.,* 2011) (*Figure 2.6*).

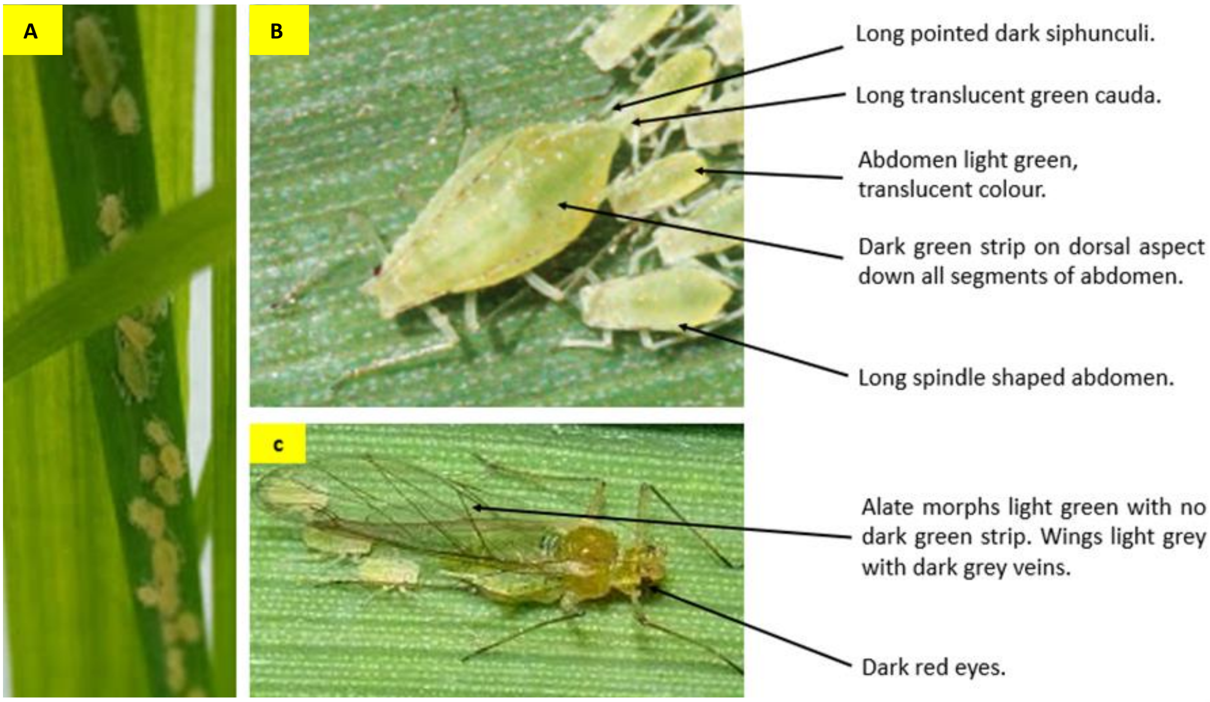


Figure 2.6a -c: a = M. dirohodm *adults & nymphs in glasshouse trials. b =* M. dirohodum *adult & nymph apterous morph (InfluentionalPoints, 2018). c =* M. dirhodum *adult alate morph & nymphs apterous morph (InfluentionalPoints, 2018).*

S. avenae in western and central Europe exhibits the trait of colour polymorphism*. S. avenae* abdomen ranges from pale green to reddish orange to a dark brown in colour (*Figure 2.7*). Colour morphs are a response to changes in environmental factors for example light intensity and temperatures, colour may be further induced by a genetic predisposition (Alkhedir, *et al.,* 2010). Colour morphs arise due to the different levels of carotenoid pigments that are present within the cells (Alkhedir *et al.,* 2010; Price *et al.,* 2011). Cauda is the same shade as abdomen and siphunculi, as in *M. dirhodum,* are long and black (Bayer 2013; Campos & García-Marí, 2014; Price *et al.,* 2011) (*Figure 2.7.*).

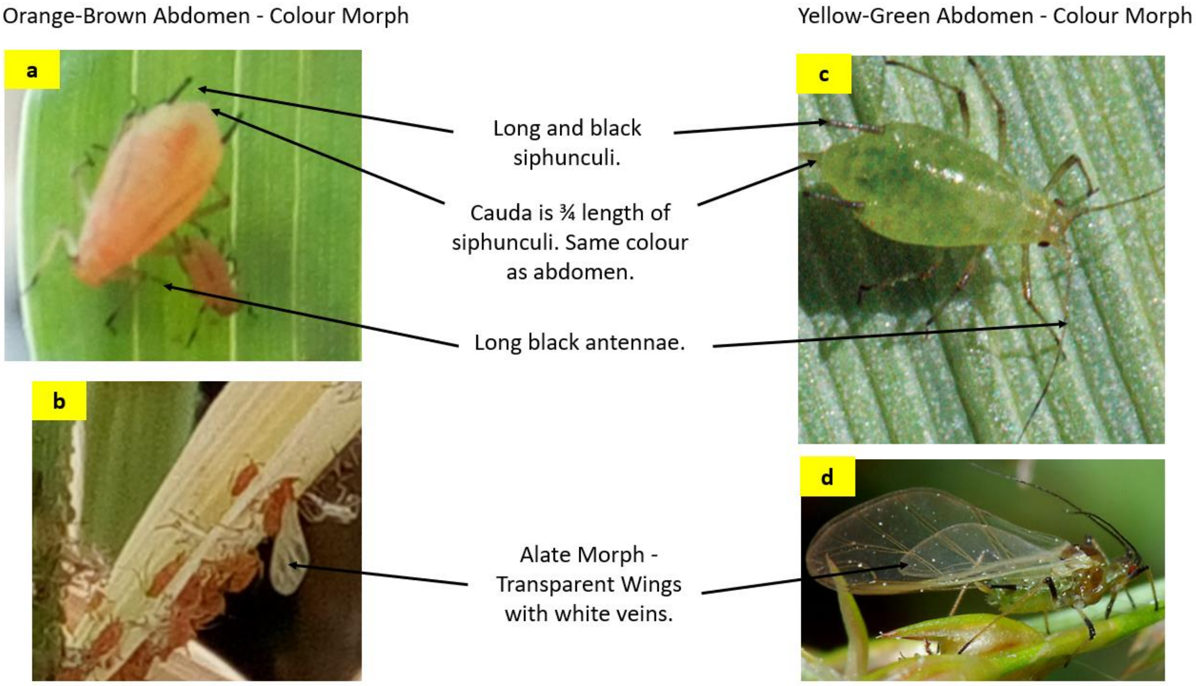


Figure 2.7a -d: a = S. avenae *adult in glasshouse trials. b =* S. avenae *adult alate morph & nymph apterous morph. c =* S. avenae *adult apterous morph (InfluentionalPoints, 2018). d =* S. avenae *adult alate morph (InfluentionalPoints, 2018).*

2.2.6.2. Cereal Aphididae as a Crop Pest

R. padi, S. avenae and *M. dirhodum* insert their stylets, mouthpieces, into the cells and penetrate the cell wall of plants by the assistance of a secreted saliva, the pectinase in the saliva breaks down the tough cell wall (Dixon, 1987, Gullan & Cranston, 2010). Turgor pressure of the plant aids the phloem sap to be obtained. Aphididae spend a large proportion of the day feeding due to the large amount of phloem sap required, as the amino acid content is low in the sap. Therefore, excess sugars are stored in the rectum whilst enough amino acids are absorbed by the Aphididae for essential proteins to be assembled.

In time of heavy infestations on a leaf and persistent feeding, the monosaccharide content of the leaves will be depleted to such an extent that the growth rate will decrease and development of new leaves from tillers will be compromised. If feeding pressure exhausts a plant of its nutritional content anthesis may be aborted. Muhammod *et al.* (2012) identified a 4.57% loss in the yield of the *T. aestivum* cultivar BK-2002 was directly related to the phloem feeding pressures of *S. avenae*. *Rhopalosiphum maidi* (Corn Leaf Aphid) was found to be the most damaging through direct assimilation of *Hordeum in* terms of yield reduction (25.5% loss) in cereal crops grown in Australia. This was estimated as an economic loss of \$12.1 ha^{-1} (Valenzuela & Hoffmann, 2014).

A secondary method where *R. padi, S. avenae* and *M. dirhodum* affect crop growth and subsequent yields is the production of a honeydew, a liquid with high sugar content (Prado *et al.,* 2015). Honeydew is secreted as a waste product from the anus when the stylets penetrate the phloem cell wall. The amount of honeydew produced by cereal Aphididae is less than other Aphididae for example *Acrthosiphon pisum* (Pea Aphid), feeding on fruit plants and legumes with high monosaccharide content, however the minimal presence of honeydew may initiate a fungal growth on *Triticum* and *Hordeum* (Prado *et al.,* 2015; Watanabe *et al.,* 2018). Fungi present in the atmosphere may be attracted to the honeydew, where the subsequent growth forms into powdery mildew or sooty mould which causes white or black pustules and darkening of the ears before harvest. Fungal diseases do not affect the cereal directly, though the presence of the markings may decrease the photosynthetic ability of the leaves and therefore affect the vigour of the crop. This may reduce the marketability of the cereal (AHDB, 2018; Bayer, 2018; Williams *et al.,* 2017).

The most damaging aspect to a crop via *S. avenae* and *R. padi* is viral transmission where the Aphididae becomes a vector and transmits a virus directly into the phloem of a plant whilst it feeds. The most common and harmful virus seen in the UK cereal crops is the luteovirus BYDV. BYDV requires a vector, namely an Aphididae, to ingest BYDV particles from an infected plant and introduce the particles into a new host plant via saliva when the Aphididae penetrates the phloem cell wall (Dorokhov *et al.,* 2014; Reddy *et al.,* 2009). The virus, once embedded, causes a volatile odour to be released from the host plant that entices another vector to feed, ensuring continued survival. Carrier Aphididae must feed for a considerable time to transfer BYDV or in large vector numbers for the virus to attack the plants natural resistance. BYDV only effects the phloem and causes the specialized sieve cells, which conduct materials throughout the phloem, to collapse which ultimately leads to plant tissue necrosis (Dancewicz *et al,* 2018; Paulmann *et al.,* 2018). The BYDV causes considerable growth impairments and senescence (yellowing) of leaves. It has been recently estimated that BYDV caused an estimated average annual yield loss of 30% in *Hordeum* and 50% of crop affected in *Triticum,* on land not treated with pesticides within the UK (AHDB, 2019). This is of significant financial loss to the arable market. *S. avenae* contributes as the main vector of BYDV in most regions of the UK apart from the South-West of England where *R. padi* is the principal vector of BYDV cases (AHDB, 2018). BYDV is placed into two subgroups depending on the Aphididae of vector, BYDV-PAV is the virus induced by *S. avenae* and BYDV-MAV is the subclass carried by *R. padi* (Reddy *et al.,* 2009).

BYDV particles can persist over-wintering in hedgerow vegetation and thus can be ingested by nymphs, hatching from eggs or produced by parthenogenesis, at the start of spring. Carrier Aphididae could then inoculate cereals in early growth stages (Choudhury *et al.,* 2019). Dorokhov *et al.* (2014) and Reddy *et al.* (2009) note that it takes excessive feeding by carrier Aphididae before a host plant is receptive and symptoms of the virus arise. Therefore, Aphididae may be in abundance before BYDV symptomatic cereals are apparent.

McKirdy *et al.* (2002) reported that incidences of BYDV showed a significant direct relationship to gaps in *T. aestivum* yield. A significant positive correlation was found between the occurrence of BYDV and *T. aestivum* seed weight, weight in g of 1000 seeds. A seed weight of 500 g was most likely to be infected with BYDV compared to lower seed weights (AHDB, 2015; McKirdy *et al.,* 2002). BYDV cereal crop yield loss can vary depending on when in the growth cycle the virus transmission was induced. *Triticum* and *Hordeum* are vulnerable to infection during early GS of shoot emergence (Turanli *et al.,* 2012). Trębicki *et al.* (2016) found that infection before tillering can reduce *T. aestivum* yield up to 79%. Later infection of stem elongation and tillering can reduce the yield loss by 6 - 9% showing that as new growth occurs the crop can tolerate some tissue necrosis directing essential substances through the phloem elsewhere.

It is important in understanding the positive potential of *T. tenuis* in predator dynamics where its activity is in relation to possible symptomatic BYDV crops, however, certainty is required if a crop is infected with BYDV-PAV or MAV. From here, *T. tenuis* biological control impact of the reduction of disease-carrying Aphididae can be assessed. The test for BYDV in a crop is commonly carried out by an Enzyme-linked Immunosorbent Assay (ELISA) (Bar-Joseph & Garnsey, 1981). The principal behind ELISA is to detect the presence of an antigen that is specific to the virus being tested. The antigen is produced by the viral genome which induces the response in the host (Lequin, 2005). The ELISA test in this instance is generally a 'Elisa Sandwich Test' where the sample is placed in between two target antibodies whose job is to draw out and collect any protein cytokines secreted due to the BYDV-MAV or PAV antigen (Horlock, 2018; Lequin, 2005). The presence of the antigen is determined via chromatography using a substrate**,** p-Nitrophenyl Phosphate Disodium Salt (PNPP) is commonly used**.** PNPP converts the specific antigen into a water-soluble yellow hue if present, that can be visually identified, and intensity read with a colour spectrometer at a wavelength of 405 nm (Horlock, 2018; Lequin, 2005; ThermoFisher Scientific, 2018).

Chabert & Sarthou (2017) and Gronle *et al.* (2014) identified that tillage levels have been shown to affect the availability of Aphididae within an arable crop. Aphididae require a high level of vegetative material to access phloem to sustain a developing colony. Conventional tillage, establishing a greater yield of crop, may allow accelerated parthenogenesis due to high phloem availability. Tamburini *et al.* (2015) and Wenninger *et al.* (2020) explained conservation tillage may impede Aphididae ability to predate due to greater accumulation of organic material obscuring Aphididae feeding sites. Specifically, within early growth stages of a crop, the prime time for Aphididae to develop a colony. Conservation tillage may support a greater degree of persistent unwanted weeds where seeds may not have been chitted (pre-germinated) with the low intensity cultivation of this area. It was discussed by Balfour & Rypstra (1998) and Dahlin & Ninkovic (2013) that weeds may support an Aphididae population differently than a mono-crop. This is agreed by Milner (2002), who suggested *A. myosuroides* provide shelters away from predation, and Weibull (1993) found *R. padi* population growth accelerated in the vicinity of perennial *A. myosuroides*.

2.2.6.3. Biology and Ecology of *S. mosellana*

Sitodiplosis mosellana (Orange Blossom Wheat Midge) (Gehin, 1857) adults have a bright orange abdomen and thorax with iridescent wings and are 2 to 3 mm in body length (*Figure 2.8*). Larvae are a bright orange colour making them easily identifiable. *S. mosellana* are classed as weak fliers compared with other Diptera (true flies), not having the wing strength to fly large distances. Short localised flights are from crop to crop with a sharp take off. Female *S. mosellana* fly between fields to disperse and oviposition, where males locate in a small area due to the need to find an adequate number of mates (AHDB, 2016; Bayer, 2018; Price *et al.,* 2011).

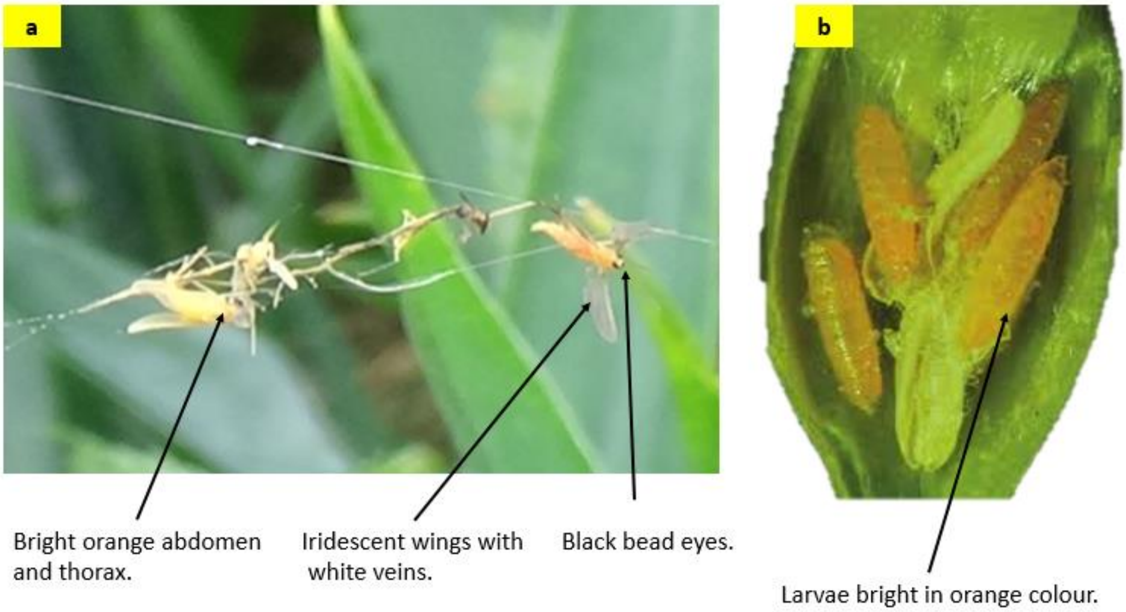


Figure 2.8a & b: a = S. mosellana *adults caught in web in NIAB field. b =* S. mosellana *lavae in* T. aestivum *ear (AHDB, 2016).*

S. mosellana live in the soil as larvae in cocoons and only pupate onto the soil surface when soil temperature begins to increase (13 - 15 ^{o}C) and has an acceptable moisture level. The *S. mosellana* adults fly as soon as air temperature reaches around 15 ^{o}C. After mating, eggs are laid in the inside florets of emerging *Triticum* ears. Larvae hatch within four to ten days and crawl into the developing grain, GS 53 of ear formation to GS 59 for anthesis (AHDB, 2016; 2018; Bayer, 2018).

2.2.6.4. *S. mosellana* as a Cereal Crop Pest

S. mosellana feed by exuding enzymes that break down the cell walls and then convert this stored starch back into sugar which is ingested. This causes poor grain quality, which is shrivelled and reduces germination capability. Damage to the pericarp (outer layer) of the seed causes water to enter which may mean spontaneous early germination or favourable conditions for the emittance of fungi causing Fusarium head blight and *Septoria tritici* leaf spot (AHDB, 2016; Price *et al.,* 2011). Once *Triticum* has reached GS 61 of grain filling, larvae are no longer able to break the cell wall down in the hardened pericarp, ensuring the crop is defended against *S. mosellana* damage (AHDB, 2016; 2018; Bayer, 2018). Larvae, after feeding, drop from the crop into the soil to be cocooned until soil temperature and moisture reaches the acceptable parameters for pupation (AHDB, 2016; Price *et al.,* 2011). *S. mosellana* can persist as larvae in cocoons for ten to fifteen years if soil condition is not favourable to hatching. The major threat of crop damage from the pupae of the cocoon is four years, after which pupae fecundity levels are seen to decrease (AHDB, 2016; Price *et al.,* 2011).

Echegaray *et al.* (2018) described that ear emergence had a significant positive relationship with *S. mosellana* density, later maturity of the *T. aestivum* having occurred at higher densities of *S. mosellana.* This had a negative economic effect due to later maturity equalling poor grain establishment and reduced yields. The pivotal density of midge for late ear emergence was placed at twelve larvae per spike (Echegaray *et al.,* 2018; Elliot *et al.,* 2011). Trials analysing *S. mosellana* infestation on *T. aestivum* cultivars in Montana, USA, reported that the protein content of the grain had a significant positive relationship with *S. mosellana* density with higher protein density leading to increased *S. mosellana* abundance on the *T. aestivum* florets (Echegaray *et al.,* 2018). Lamb *et al.* (2000) investigated the trophic relationship between *T. aestivum* and *S. mosellana* by analysing the biomass loss of *T. aestivum* and biomass gain to *S. mosellana*. Grain within the ear held different biomass potential for *S. mosellana* feeding, impact varied from 4.1 mg to 8.5 mg of seed biomass lost for each milligram of biomass gained by a larva, suggesting poor conversion from *S. mosellana* leads to intense periods of feeding on several grains. Tolerance of *T. aestivum* grain was identified as 6% biomass loss of the seed before its germination rate was impaired (Elliot *et al.,* 2011; Lamb *et al.,* 2000).

2.2.6.5. Chemical Control of Cereal Aphididae and *S. mosellana*

Pyrethroid chemicals, used to control cereal Aphididae, disturb the nervous system leading to fatality (Bass *et al.,* 2014; Kennedy & Connery, 2005). This insecticide became popular when neonicotinoids were banned in 2014, due to environmental concerns (Dewar *et al.,* 2014). Pyrethroids, though identified as a 'cleaner' insecticide breaking down in sunlight, its mode of action is less effective than previous banned insecticides (Ikonov *et al.,* 2019; Kumar *et al.,* 2018). There is a concern where its use may incur further genetic resistance without the assurance it will have the desired effect on an Aphididae population. *S. avenae* is noted to be becoming increasingly resistant to this compound in the UK, continually creating morphs with genetically reheard resistance mechanisms (Bass *et al.,* 2014). Dewar *et al*. (2014) identified that in 2013, 35 - 50% of *S. avenae* within the UK arable agriculture contained genes that produced knockdown resistance (kdr), a subdued sensitivity to the neurone inhibitor action of the pyrethroid compound (Bass *et al.,* 2014). From recent literature it is explained the increase in kdr occurrence rate appears to have slowed for *S. avneae,* and *M. dirhodum* and *R. padi* kdr capabilities are noted to be of a lesser degree (De La Pasture, 2018). However, the genetic mutations behind kdr still exits.

Outbreak of *S. mosellana* previously was effectively controlled by the insecticide Chlorpyrifos, causing death by inhibiting neural pathways (Bruce *et al.,* 2007; Christensen *et al.,* 2009; Edwards & Dodgson, 2009). Since March 2016, this insecticide had been banned by the UK government, undertaken by the Health and Safety Executive due to concerns of its persistence within the environment (HSE, 2016). Isolation of a *S. mosellana* resistant gene (Sm1) has allowed *T. aestivum* cultivars to be engineered with inbred *S. mosellana* resistance. The Sm1 gene alters the structure of the grain, creating an antibiosis (antagonistic) effect to *S. mosellana* by lowering oviposition availability (Blake *et al.,* 2014; Ellis *et al.,* 2009; Kassa *et al.* 2016). However, this is at a cost and signs of tolerance from *S. mosellana* have been identified in Canadian agriculture where the resistant cultivars have been extensively used (Bruce *et al.,* 2007).

From this evidence, pests gaining tolerance to chemical control and resistant cultivars, biological control can seem favourable where resistance does not exist in the consumption of prey by a natural enemy. Furthermore, Mazzia *et al.* (2015), analysing fecundity rates of epigeal (dwelling close to the ground) spiders (including Linyphiidae) in vineyards with pesticide application against organic, identified lower fecundity rate (in egg sac development) in areas of pesticide use. This was theorised to be because of a reduced abundance of natural enemies in areas where chemical control was applied. This subsequently lowered female body mass, lessening the female's egg production capacity (Beck & Toft, 2000; Mazzia *et al.,* 2015; Peters & Koover, 1991; Romero & Harwood, 2010).

Dewar *et al.* (2014) explains that spraying of insecticides does not harm *T. tenuis* directly, though alters the food web of the ecosystem and further alters the vegetation orientation of the landscape. Haughton *et al.* (1999) and Řezáč & Řezáčová (2019) concurred, investigating effect of glyphosate drift to a field margin, found in times of increased glyphosate application the drift reduced landscape heterogeneity. This was shown to have a greater negative impact to *T. tenuis* density than the glyphosate application. This is further agreed by Isaia *et al.* (2007) and Ysnel & Canard (2000) who viewed an increased vegetation complexity as a propensity to web-build. Ikonov *et al.* (2019) discussed that persistent interaction with a pyrethroid insecticide altered female *Oedothorax apicatus* (Linyphiidae) morphology, the chemical composition stimulating homeotic pathways increasing the size of the abdomen. This may lead to extreme SSD and gravity hypothesis, where large females are unable to sustain lying a dragline thread, the extra weight of the *T. tenuis* disrupting the strain needed to yield the silk (*Section 2.1.2.1. & Section 2.1.3.4*.). Moreover, Peng *et al.* (2010) showed clutch sizes decreased in Linyphiidae when in contact with pyrethroids, the pathway for the enzyme carboxylesterase key in ovulation, disrupted by the insecticide. Leccia *et al.* (2015) concurred, suggesting pyrethroids may further affect the chemical composition of the sex pheromone omitted when a female is fecund, both actions impeding Linyphiidae ability to succeed in another generation and exert pest suppression within a crop (*Section 2.1.3.4*.).

2.3. Biological Control

2.3.1. The Premise Behind Biological Control in British Arable Agriculture

The concept of biological control is the method of using natural enemies to control and limit the number of crop pests within an agricultural environment and is classed as an ecosystem service. The natural enemies themselves are identified as non-phytophagous and therefore will not directly harm the crop. Most pests have naturally occurring enemies that may be generalist predators eating a wide variety of insects, or specific predators that require a narrow niche of prey (Ramsden *et al.,* 2016). Biological control seeks to harness this ideal and create opportunities where natural enemies can thrive and naturally convene on a pest population (Nyffeler & Sutherland, 2003). Biological control is a method to pest suppression that may reduce the need of chemical control (Ramsden *et al.,* 2016; Rusch *et al.,* 2016).

In British arable agriculture at present, much has been published regarding the need to produce food in a sustainable manner. Sustainable here meaning to ensure the availability of raw materials, for example soil nutrients, and condition of these raw materials, as in soil health, is such that food in enough supply can be produced in future years. Increasing the practice of biological control can reduce the amount of pesticides that are needed for crop application (Ramsden *et al.,* 2016; Rusch *et al.,* 2016). This may contribute to becoming sustainable, as soil health is shown to be degraded due to pesticides being toxic to essential microorganisms, that are important to soil aeration and decomposition of detritus (Shayler, 2005). There is, at present, political demand to lower the application of pesticides and government papers, e.g. Food Safety Authority and Ectophyto Plan, dictate targets of decreased use (Diehl *et al.,* 2013, Macfadyen *et al.,* 2014). Biological control would appear to be the key answer to crop pest reduction, therefore, it is of concern why biological control is not used more widely. Biological control is not an exact science, there are many complex pathways that may impede or promote biological control. Hajek & Eilenberg (2018) and Lichtenstein *et al.* (2016) discussed failures to biological control may be due to fecundity rates of a natural enemy reduced, thus reducing the mass action effect that a colony can exert, and fitness of a predator including boldness where a natural enemy is dominant in search for prey. Further discussed is devoid of a precise system where beneficial predators are present at the exact place at the correct time to capture prey (Hajek & Eilenberg, 2018; Jonsson *et al.,* 2014; Lichtenstein *et al.*, 2016). A stimuli of a crop pest presence is required to be received by a predator, such as Linyphiidae, to encourage relocation to prey and suppress pests effectively (McHugh *et al.,* 2020; Rodríguez & Gloudeman, 2011). Japyassú & Laland (2017), Kraftt & Cookson (2012) and McHugh *et al.* (2020) discussed a stimuli to Linyphiidae may be obscured by climatic factors or impeded by the orientation of landscape features, often observed within the open aired environment of an agricultural setting.

2.3.2. *T. tenuis* Potential in Biological Control

As identified in Section 1.1 and Section 2.1.3.1., *T. tenuis* is a generalist predator and a carnivore, meaning it causes no threat to a crop. *T. tenuis* is stenophagous (narrow ranged) in prey capture and only captures prey within a web and therefore web construction is an important factor within a *T. tenuis* life cycle (Pekár, 2014). The silk is not sticky, rather fine hairs of the Aphididae become entangled into the web and so Aphididae have a low frequency of escape (Harwood *et al.,* 2003) (*Figure 2.9*). In this instance, it can be identified that even if prey fallen into a web is not consumed, the low escape instances renders this prey unable to carry out its intended function, e.g. to direct feed in the case of Aphididae (*Section 2.2.6.2.*). Harwood *et al.* (2003) identified that significantly more Aphididae (mean 0.81), were collected from webs constructed by *T. tenuis* at sample sites, 78.5 cm^2, compared with 0.56 being identified outside of webs. This coincides with a tendency to construct webs high in a crop to capture Aphididae effectively and handle them promptly.

Figure 2.9: Female T. tenuis *in NIAB field from fieldwork. Wrapped prey is Aphididae, exact species unknown.*

Aphididae are of low nutritional value to *T. tenuis* and other Linyphiidae. Toft (1995) showed that the duration of the 1st instar was increased, when a *T. tenuis* juvenile was fed on a sole Aphididae diet, increasing the time when maturity could be reached. Toft (1987) noted that *T. tenuis* went through a cycle of rejecting cereal Aphididae after repeated exposure to a lone Aphididade diet for a day. *T. tenuis* showed a rapid aversion to *R. padi* than to the more palatable *M. dirhodum* and *S. avenae*, and after an hour to a day, Aphididae were again accepted. This suggests that *T. tenuis* are likely to choose another prey, a possibility is another natural enemy, to consume in between Aphididae and this may be a negative to its potential as a biological control agent (Nyffeler & Sutherland, 2003; Toft, 1989).

2.3.3. Measuring Biological Control with DNA Bar-Coding and PCR

Predator and prey relationships can often be difficult to quantify, due to the complex environments in which they exist. Prey consumed by *T. tenuis* is ideal evidence to express such an interaction, however it is difficult to establish through simple observation, as prey are often wholly consumed and soft bodies of prey are easily digested and ephemeral within a system (Birhofer *et al.,* 2017; Eitzinger *et al.,* 2013; Furlong, 2015). Polymerase Chain-Reaction (PCR) is an advanced method of gaining verification in *T. tenuis* prey interactions. It involves the ability to identify specific prey DNA e.g. of Aphididae, from DNA extracted from *T. tenuis* (Davey *et al.,* 2013; King *et al.,* 2011; Powell *et al.,* 2004). DNA bar-coding incorporates several steps from extraction of DNA to the reading of the product of a Polymerase Chain Reaction (PCR) cycle.

The DNA for bar-coding is required to be extracted from the sample. There are several steps to extract and clean the desired DNA: cell and tissue lysis, precipitation of the final DNA and purification of the DNA through washing. Amplification is required due to the difficulty in reading a small intron (gene expression) of the species that may have been ingested. Amplification involves a primer of a specific DNA sequence (of species potentially consumed) which is able to insert into the corresponding intron and replicate the intron under a cycle of differing temperatures to allow catalysis synthesis (Davey *et al.,* 2013; Furlong *et al.,* 2015; King *et al.,* 2011; Powell *et al.,* 2004). Nuclear (nDNA) or Mitochondrial DNA (mtDNA) may be targeted for primer insertion, however, mtDNA is beneficial to locate and amplify as several intron sites for the desired gene are found within mitochondrial cells (Chen *et al.,* 2000; Powell *et al.,* 2004; Rice, 2015). Two primers are required in each PCR analysis to insert into the intron of each strand of the DNA double helix. Forward primer represents forward sequence of the gene expression and reverse primer the reverse sequence (Harper *et al.,* 2005; Macías-Hernández *et al.,* 2018; Ye *et al.,* 2017).

Several reagents alongside the primers enable PCR to occur. The buffer Tris(hydroxymethyl) aminomethane hydrochloride (Tris-HCl) at pH 9.0 creates an environment of constant pH for protein synthesis. Magnesium Chloride ($MgCl_2$) and Potassium Chloride (KCl) aid the binding of the primer to the correct intron, nucleoside triphosphate containing deoxyribose (dNTP) provides cytosine, guanine, adenine and thymine for replicates to be synthesised, and Taq DNA polymerase is an enzyme that acts as a catalyst to DNA synthesis (Chen *et al.,* 2000; University of Utah, 2016). A negative and positive template ensure validity in a result. Slight contamination can occur with many procedures and interference with the amplification of the specified DNA. A negative template incorporates all reagents, using a substitute to the DNA (PCR grade sterile water) and positive involves the use of a known DNA sample of the species.

Genomic DNA sequences or amplicons (amplified introns) obtained from PCR are read in an agarose gel (seaweed extract of neutral charge) after gel-electrophoresis for clarification under UV light box (Ayoub *et al.,* 2007; Chapman *et al.,* 2013). A loading dye is added to the amplicon before gel-electrophoresis begins for tracking of the amplicons as they run through the gel. Gel-electrophoresis works on the principal that DNA has an overall negative charge due to the phosphate backbone of the strand (Brownie *et al.,* 1997; King *et al.,* 2012). Any DNA present, amplified through the PCR process, will be pulled towards a positive charge. Nucleotide base pairs (for example a bond between cytosine and guanine) are read to the nearest kilo base-pair (kbp) (Eitzinger *et al.,* 2013) (*Figure 2.10*). A hyperladder, a solution containing base-pairs (bp) of definite size, is used to read bp of a sample (Ayoub *et al.,* 2007; Chen *et al.,* 2000; Cold Spring Harbour Laboratory, 2015; Powell *et al.,* 2004). Small bp will be pulled to the positive charge at a faster rate, thus the marker of 200 bp of the hyperladder will be closest to positive electrode, whereas (with a hyperladder containing a 1 kbp marker) the band nearest to the negative electrode will be the largest bp of 10,000 bp (*Figure 2.10*). Over-running of gel-electrophoresis may mean an amplicon bleeds out of the gel into solution (Brownie *et al.,* 1997; Chen *et al.,* 2000).

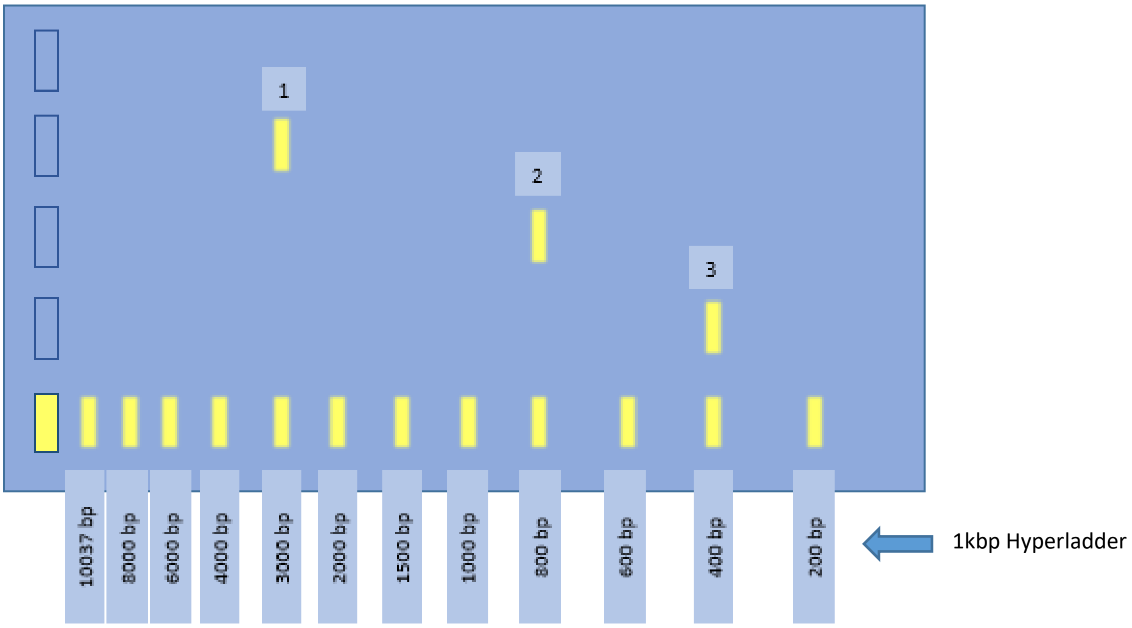


Figure 2.10: Schematic diagram of agarose gel after electrolysis with 1kbp Hyperladder used. The bp for the following bars are read as 1 = 3000 bp. 2 = 800 bp. 3 = 400 bp.

Recent research has analysed the prey content of web-building spiders to further examine the biological control potential of arachnids (Xu *et al.,* 2015). The principal to the research is exploring the potential life span of prey DNA within the extended phenotype of a web, and if the longevity is greater than prey DNA within a gut. With prey known to fall into a web, without needed to be consumed, measuring predator potential solely on gut content may under value the biological control web-building spiders can offer.

Chapter Three

3.0. Introduction to Fieldwork

Fieldwork is a key element to this research and allows *T. tenuis* behaviour to be explored in a natural habitat. It provides primary data on how *T. tenuis* reacts within areas of different tillage intensities on a working arable farm.

This Chapter introduces the arable farm where fieldwork was undertaken, exploring its climate, topography and agricultural practices implemented on the land. It concludes with a short discussion of how the research fits into the present scientific community and its benefit to the arable agriculture industry.

3.1. Fieldwork Site

3.1.1. Location

Permission was granted to access a site at an arable farm in Childerley, Cambridgeshire (National Grid Reference: TL 35643 61654), where a Direct Drilling Project, funded by the National Institute of Agricultural Botany (NIAB) in partnership with The Arable Group Ltd. (TAG), was (and is currently) examining tillage systems to develop methods of sustainable arable production (NIAB TAG, 2016). The farmland at Childerley, housing the NIAB trials, covers 1,294 hectares and is of a low gradient, maximum incline of 2%, and is around 7 m above sea level. The farm is operated by Martin Jenkins Farming™ and grows cereals in the majority with brassica fields used in crop rotations. A smallholding of Cheviot sheep (around a hundred and forty) is used for sporadic grazing, utilised primarily to control *Alopecurus myosuroides* (Black-grass). The sheep graze as part of a crop rotation system, inhabiting a field which is within a fallow period. Details of location are shown in Figure 3.1. - Figure 3.3.

Figure 3.1: Map showing location of Martin Jenkins Farming™ (red dot), within the UK, created from Google Earth© and QGis© 3.4 Madeira™.

Figure 3.2: Scale map showing location of Martin Jenkins Farming™ (red dot) created from Google Earth© and QGis© 3.4 Madeira™.

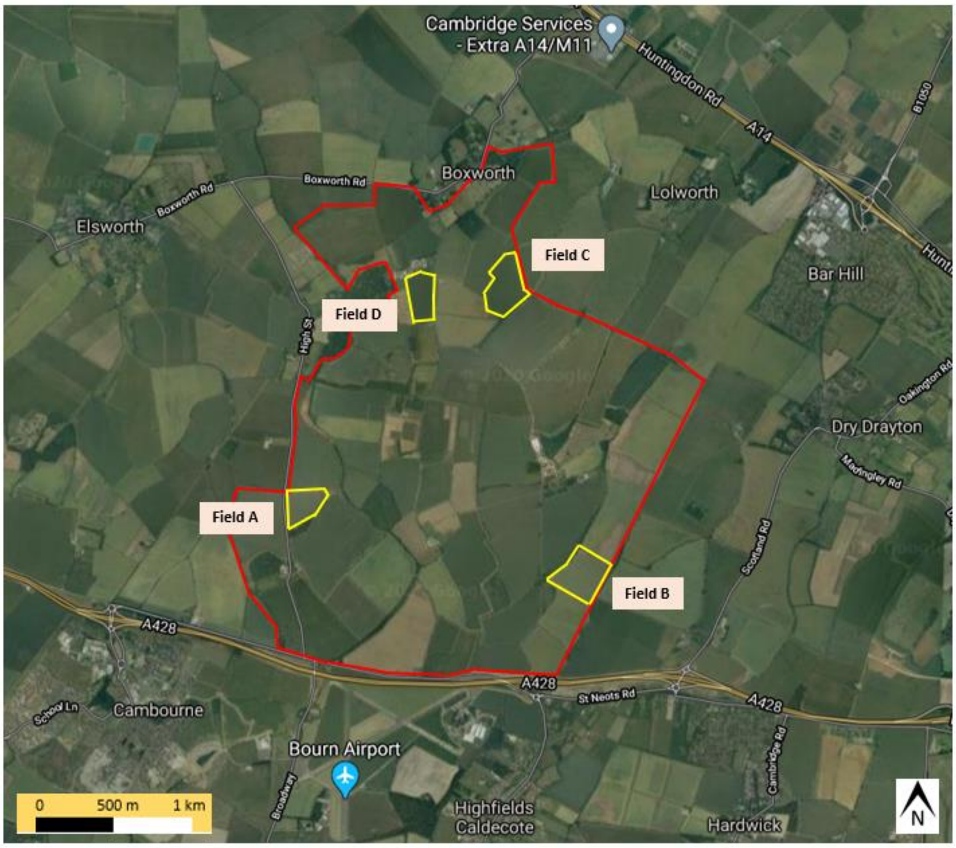


Figure 3.3: Scale Map showing location of Martin Jenkins Farming™ created from Google Earth© and QGis© 3.4 Madeira™. Red line showing borders of farm. Yellow line showing borders of fields within the NIAB trials.

3.1.2. Climate

The climate for the rural outskirts of Cambridge (Childerley) is warm and temperate with low rainfall compared to UK average and moderate to average wind speeds especially seen over low-lying land. The average climate for this area for 2017 (year of sampling) was an average daytime temperature of 14.5 °C, maximum observed in July with 27.1 °C and lowest 3.1 °C in January 2017. The total rainfall measured 576.5 mm over 164 days. The average maximum wind speed was calculated at 39.9 kmh^{-1} (24.8 mph), the lowest monthly maximum of 32.2 kmh^{-1} (20 mph) was identified in August and 48.6 kmh^{-1} (30.2 mph) was the highest wind speed reached, measured in December. For 2018, again a year field sampling occurred, 15.1 °C was the average daytime temperature with a maximum of 36.4 °C recorded in July and 2 °C measured in February. There were 107.5 rainfall days in 2018 with a total rainfall of 533 mm. The average maximum wind speed recorded for 2018 was 40.4 kmh^{-1} (25.1 mph), the lowest monthly maximum wind speed was 29.1 kmh^{-1} (18.1 mph) identified in June and the highest was 51.2 kmh^{-1} (31.8 mph) measured in January (Met Office, 2017; Met Office, 2018; World Weather Online, 2020).

3.1.3. Set - Up of NIAB Trial

3.1.3.1. Aim of NIAB Trail

The NIAB trial is long-term, which began in 2012, and is on-going. It is based on a four-year rotation on spring and winter cereals (*Table 3.1.*). The trial aims to analyse the impact that differences in tillage techniques may have on cereal crop performance and soil composition. The key findings are to demonstrate to farmers, that Direct Drill tillage could be a possible alternative to Conventional tillage, on heavy clay soil (NIABTAG, 2017).

3.1.3.2. Soil

The site comprises four fields in the NIAB trial of Hanslope Soil Series, non-alluvial clayey loam (Cranfield University, 2017) (*Figure 3.4.*).

A Profile – Dark brown. Slight stoney clay / clay loam. Fine texture. Calcareous.

B Profile – Lighter brown. Slight stoney clay. Slight sub-angular block structure formed . Calcareous

Lighter, slightly yellow brown. Moderate stoney clay. Medium sub-angular block structure formed. Calcareous.

Limestone bedrock. Calcareous.

Figure 3.4: Schematic diagram showing soil profile of Hanslope soil series 4.1 (Adapted from Cranfield University 2017).

As Figure 3.4 identifies, the A - profile of Hanslope soil is an alkaline clay loam, usually dark brown in colour. It has a high field capacity and ability to incorporate organic matter into humic material. Its texture is fine and is defined as having a 'sticky' consistency. These properties are due to positively charged clay micelle complexes that allow aggregation of negatively charged ions. Water particles, negative charge from the oxygen atom, are bound to the micelle ensuring a 'sticky' consistency and high field capacity. Hummus is incorporated as negative organic fractions, which are further bound to the micelle, allowing a clay loam to be fertile soil. Further down the Hanslope profile, the soil forms blocky sub-angular stoney aggregates, calcareous in nature, where eroded bedrock is incorporated into the clay fractions. This meaning, deep cultivations of Hanslope can be laboursome (Ashman & Puri, 2002; Cranfield University, 2017; Paul, 2015; Williams, 1979) (*Section 2.2.2.*).

3.1.3.3. Fields

The four fields are named: “Bendy” Field A, “Carrot Ground” Field B, “Stargoose” Field C and “Weatherfield” Field D, as shown with crop rotations (*Table 3.1, Figure 3.3. & Figure 3.5a - d*).

Table 3.1: The four fields of the NIAB field trial and the crop rotations (NIAB TAG, 2018).

NIAB Field Name	Project Field Name	Crop Rotation 2012/13	Crop Rotation 2013/14	Crop Rotation 2014/15	Crop Rotation 2015/16	Crop Rotation 2016/17	Crop Rotation 2017/18	Crop Rotation 2018/19
Bendy	A	Oil Seed Rape	Winter Wheat	Winter Wheat	Spring Barley	Spring Barley	Winter Wheat	Spring Barley
Carrot Ground	B	Spring Barley	Spring Barley	Oil Seed Rape	Winter Wheat	Spring Barley	Spring Barley	Spring Barley
Stargoose	C	Spring Wheat	Winter Wheat	Spring Barley	Winter Oats	Winter Wheat	Spring Barley	Spring Barley
Weatherfield	D	Spring Barley	Oil Seed Rape	Winter Wheat	Winter Wheat	Spring Barley	Spring Barley	Winter Wheat

3.1.3.4. Soil Tillage Methods

Each field is divided into three plots, each with a different soil tillage technique, which are:

1. ‘Conventional’ approach. The primary cultivation involves management from a winged sub-soiler with discs 60 cm apart. The soil is worked and broken up to a 24.5 cm depth. It is disc harrowed, the chain disc giving 1.27 cm penetration, for secondary cultivation. This is carried out two or three times per week until the soil is level to the ridges from the sub-soiler.
2. ‘Direct Drilled Managed’ approach. The primary cultivation is shallower, with a 20 cm depth. The managed approach includes the additional management techniques of straw raking (NIAB TAG, 2016).
3. ‘Direct Drilled’ approach. This uses a John Deere 750A Direct Drill only to sow.

Conventional and Direct Drill Managed are sown with John Deere 750A Direct Drill after cultivation.

The four fields are divided into the three soil tillage intensities. Direct Drill was assigned to the middle area of the field with Conventional and Direct Drill Managed soil tillage either side (*Figure 3.5a - d*).

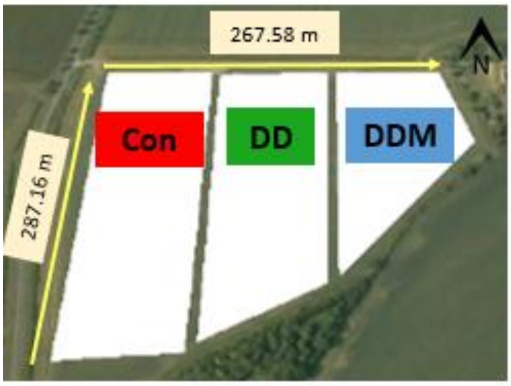


Figure 3.5a: Field A, shown from Google Earth© - 52°13’56.64” N, 0°02’48.48” W

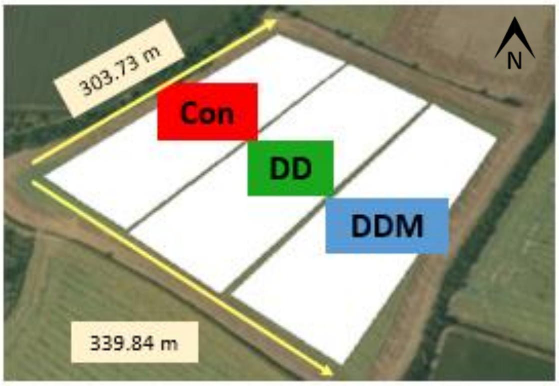


Figure 3.5b: Field B, shown from Google Earth© - 52°13’30.72” N, 0°00’38.88” W

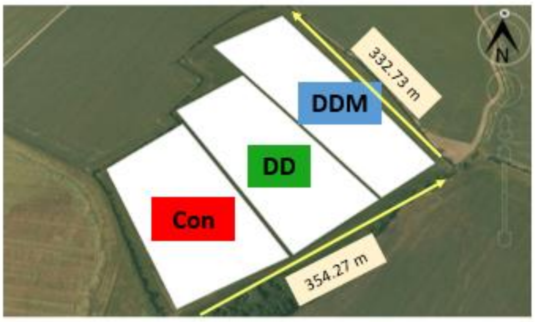


Figure 3.5c: Field C, shown from Google Earth© - 52°14’58.26” N, 0°01’08.36” W

Figure 3.5d: Field D, shown from Google Earth© - 52°15’14.4” N, 0°01’56.64” W

(*Figure 3.5a - d: Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green*)

3.2. Contributions to the Scientific Community

The fieldwork in Cambridgeshire forms part of a long-term trial that enables data to be collected over several seasons. The unique nature of the NIAB trial with four fields incorporating different crop rotations allows data to be collated from a wide set of circumstances, for example, fallow or *H. vulgare* (Spring Barley) following *T. aestivum* (Winter Wheat) within an arable habitat. Different time periods are important, capturing elements of *T. tenuis* biology; stenochronous, short-lived and rapid growth, and eurychronous, over-wintering in different stages. Research from Halley *et al.* (1996) and Welch *et al.* (2011) has gained an understanding that *T. tenuis* has adapted its life cycle to a crop system in fecundity rate heightened at a time of post-cultivation, where prey abundance and disturbance is low. This transfers to a generation existing in later Growth Stages (GS) of a crop, and viable for pest predation (Thorbek *et al.,* 1994) (*Section 2.2.1*.). Therefore, the benefit of having fields within the NIAB site differing in crop rotations, allows insight into how the life cycle of *T. tenuis* may change.

The long-running of the trial and the position of tillage intensity not altering within the fields, is of scientific interest (*Table 3.1. & Figure 3.5a - d*). Soil fertility, with inoraganic matter build-up, may have increased in the Direct Drill area, encouraging robust plant growth and high yields, which in turns favours Linyphiidae abundance (Mbuthia *et al.,* 2015; Shrestha *et al.,* 2015). *A. myosuroides* abundance, a weed prevalent within south-east Britain, may have excelled within a long-term Direct Drill zero-till environment, potentially supporting greater Aphididae abundance (Lutman *et al.,* 2013; Milner 2002). This may impact *T. tenuis* ability to impact biological control and suppress greater Aphididae numbers (*Section 2.2.4*.).

In addition to the tillage, there are other management techniques employed in the fields; glyphosate application, where a long trial is beneficial. Herbicide that had been applied 360 a.i.ha^{-1} (active ingredients per hectare) to a margin of a *T. aestivum* field, has been shown to cause drift which reduced *T. aestivum* height and hence decreased crop residue, changing the habitat which may impact *T. tenuis* behaviour (Haughton *et al.,* 1999) (*Section 2.2.6.5*.).

There is a need for a more detailed analysis of how Linyphiidae behave, regarding predator dynamics, within a zero-tilled habitat, such as a method of Direct Drill, where seed is drilled without prior cultivation. Much work only analysing the ecology of Linyphiidae under ploughing / a simplified landscape against landscape heterogeneity. Data collected from a Direct Drill Managed approach will have a key place in agroecology, as this tillage technique is innovative and its biological control regarding *T. tenuis* has not been explored. The diversity of *T. tenuis* web structures, for pest suppression, that may be created in this management technique is barely known. Of particular interest, is how the lower levels of cultivation applied within Direct Drill Managed, at primary cultivation, alters *T. tenuis* web-spinning behaviour. Measurements have previously been gained from webs spun in grasslands and agricultural margins from research by Clark *et al.* (2004), Horváth *et al.* (2015) and Thorbek & Bilde (2004), however, differences / similarities of the structures of a web and prey capture rate within different tilled areas have not been extensively explored or quantified.

Chapter Four

4.0. Fieldwork Method Development

4.1. Introduction

This Chapter discusses how the final methods for data collection in the field were established. Experimental work (notably in the summer of 2016) explored data collection practicality and repeatability and whether the intended procedural aim was met in a non-biased way. The Chapter is split into three sections, the main fieldwork (*Section 4.2. & Section 4.3.*), an in-field experiment analysing a key theme from fieldwork (*Section 4.4.*) and sampling of hedgerows bordering the main field (*Section 4.5.*).

4.2. Field Sampling

The field sampling period of summer 2016 allowed investigation across the dimensions and orientation of the tilled areas within each field in the NIAB investigation, where a variety of cereals were grown (*H. vulgare, T. aestivum* and *A. sativa*) (*Table 3.1.*, *Section 3.1.3.3., Page 50*). The length (m) and width (m) measured from Google Earth images of all four fields was rounded to the nearest 1.0 m (*Figure 3.5.a - d, Section 3.1.3.4., Page 51*). It was essential to consider edge effects when planning areas to sample. The edge effect here refers to the boundary of the field edge, the division between the main field and a 1 m margin before the hedgerow begins (*Figure 4.1.*). The field edge is important to consider due to the difference of habitat in vegetation density and species which then relates to a difference in animal species populations (*Section 2.1.4.5.*). Sampling within this area would disrupt the results collected from the main field habitat. To remove the edge effect, no samples were collected from within 1 m of the field edge (*Figure 4.1*). An edge effect further existed between each soil tillage intensity where field vegetation was not a true representation of the soil tillage (*Figure 4.2a & b*).

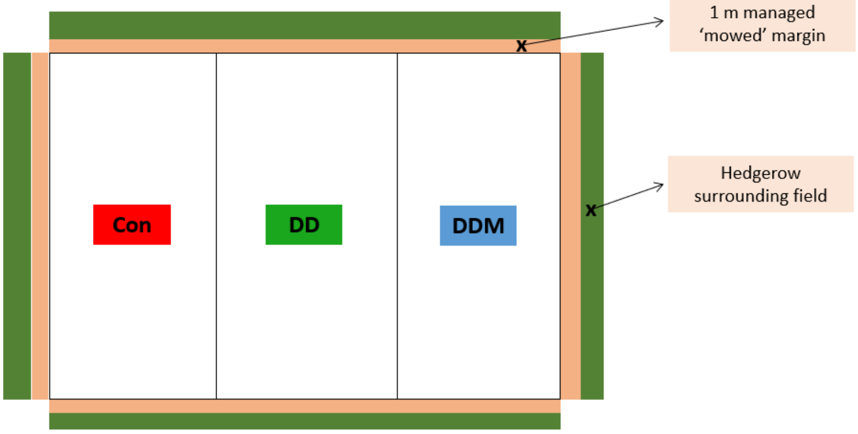


Figure 4.1: Schematic diagram of layout of NIAB field (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green).

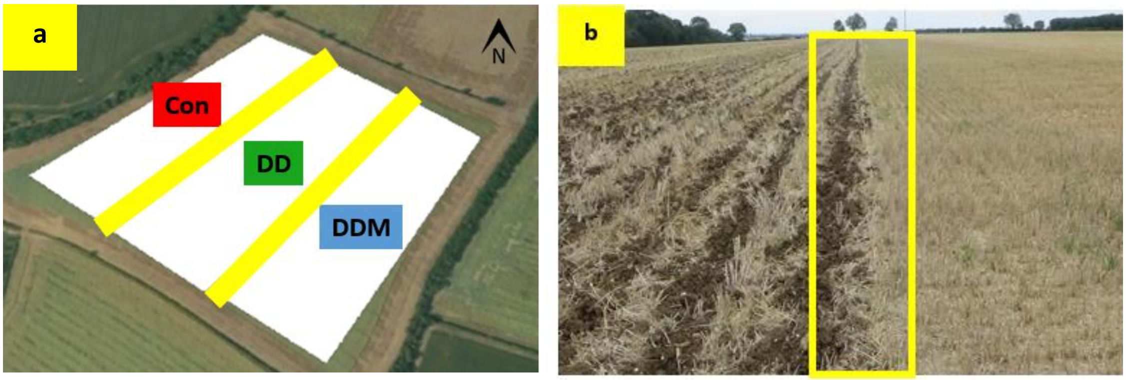


Figure 4.2a & b: a = Yellow rectangles identifying margin of soil tillage intensity (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). b = Margin of soil tillage intensity, Field B between Direct Drill (left) and Direct Drill Managed (right) September 2018.

The 1 m^2 quadrat sample areas were assigned from two random numbers which related to length and width of the tilled area, minus 1 m from the edge into the field (Random.org 2018). From this co-ordinate, a 1 m^2 sample area was taken north easterly from this point (*Figure 4.3.*). The co-ordinate position was found with a distance measuring wheel (Amtech® P1910 Measuring Wheel) with a measuring capacity of 1000 m.

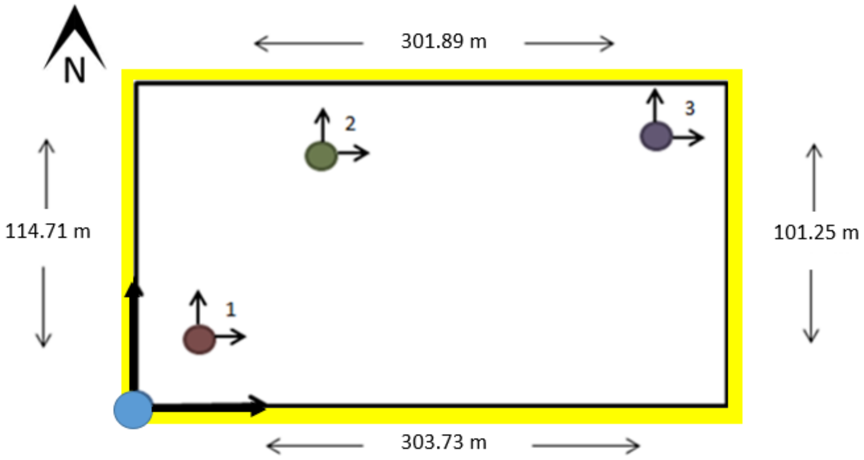


Figure 4.3: Example of how random sampling was generated in Field B Conventional tillage of preliminary fieldwork. Yellow area represents 1 m margin removed to negate edge effect.

Each field was required to be sampled within the same day to reduce the effect of external factors, e.g. bias from wind and rain. After experimenting with numbers of 1 m^2 samples where all measurements could be attained in the shortest daylight hours of winter, 8 hours, it was concluded realistically three replicated samples (equalling nine) could be measured in each tillage in this time period. It was identified, after the preliminary fieldwork, that samples were required to be taken in the order of one from Conventional, one from Direct Drill and then one from Direct Drill Managed instead of all three samples taken from one tillage sequentially. This was deemed important as with one sample area taking on average forty minutes to complete, the weather may have altered from the first sample to the last which could have obscured results. For example, differences in wind speeds across the day may affect the integrity of webs that had been constructed during the night.

4.3. Data Collection

As the field sampling progressed from the preliminary investigations into the first few months of sampling within the 2017 season, adjustments were made to methodology in the field site. This allowed the development of a robust field data collection method.

4.3.1. Straw / Plant Residue

A system of collecting straw / loose crop residue, was established in the explorative fieldwork of summer 2016. Straw residue was collected from two lengths of 1 m x 0.15 m (allowing for overlap) and from this, the mass for a 1 m^2 sample area was calculated (*Figure 4.4a & b*). This method saved time out of a tight sampling schedule rather than collecting from a full m^2.

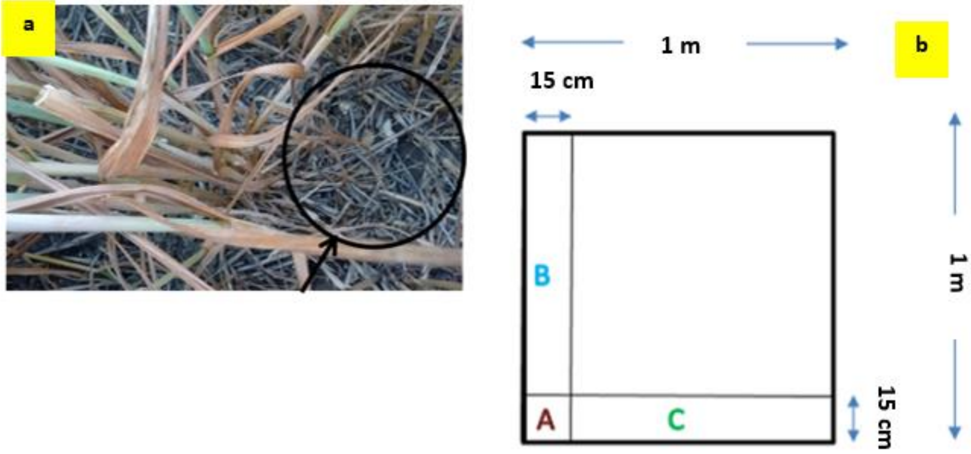


Figure 4.4a & b: a = Straw mass collected measured to nearest 0.1 g. Elevated view. b = Schematic diagram of sample plot. Areas A, B and C are from where straw was collected, preliminary fieldwork. Summer 2016.

It was identified that the method used for preliminary fieldwork would not accurately represent the straw mass of the tillage intensity, this variable shown to be key to Linyphiidae behaviour in previous research and preliminary work identified straw as a key material for web construction (Diehl *et al.,* 2013; Thomson & Hoffmann, 2007). All loose straw mass was therefore collected from in between each plant row of the sample area. As the seeding rows were the same distance apart, six lines of potential straw mass was collected. The straw mass was then weighed to 0.01 g at Myerscough College, using a balance.

4.3.2. Upright Stubble Height and Plant Height

Upright stubble corresponds to stubble that is of an angle between 45^{o} - 90^{o} from the ground (*Figure 4.5.*). Ten randomly chosen upright stubble were measured within each sample area and the mean established. Upright stubble density and straw mass were not analysed after *H. vulgare* growth stage (GS) reached on average 25 cm (GS 37 - GS 39) as the importance of stubble for Linyphiidae anchor points appeared to be reduced and the total amount of stubble in each cultivated area generally remained the same after the last soil activity of drilling (AHDB, 2018) (*Section 2.2.1.*).

Plant height data was collected from each sample area. Average plant height in the first instance was gathered by measuring the height of each plant within the 1 m^2 sample area. This took a large amount of time and it was noticed that little difference existed between most plants within the sample area. Thereafter, average plant height was gained by measuring the heights of ten randomly chosen plants within the 1 m^2 measured to the nearest 0.1 cm by a metre rule. A question arose, as to where the height of *H. vulgare* should be taken, as the plant went through certain GS. It was noted that the height had to be taken from the identical place on each plant at every field site visit for height to be used as an independent variable within this research. Observing the difference in plant physiology, the preliminary fieldwork identified a comprehensive system was required to note where plant height measurements were taken from at each growth stage. Before ear emergence, the tallest aspect of the plant was not the same feature, leaf or stem for example. In a survey of 50 randomly selected plants across the whole field within the preliminary fieldwork, the apex of the stem was the tallest aspect for many plants. From this, a system of measuring height was conducted as follows; before the growth of the flag leaf, GS 37 which represents the growth of the final leaf later sheathing ear emergence, the apex of the stem was measured as the highest point of each plant. After flag leaf emergence it was found this leaf, in the majority of cases was the highest point of the stem, growing out from the apex, therefore measurements of height to the top of the flag leaf was used until ear emergence (usually identified in GS 51). Thereafter, height was gained from the top of the ear (*Figure 4.6.*).

Figure 4.5: Upright stubble (circled in black). Height measurement to nearest 0.1 cm Field B, March 2017.

Figure 4.6: T. aestivum *height measured to ear, nearest 0.1 cm, Field C, July 2016.*

4.3.3. Upright Stubble Density and Plant Density

The number of plants and upright stubble were counted within each sample area to determine density of *H. vulgare*, as *T. tenuis* has been shown to be sensitive to plant physiognomy, vegetation arrangement in space (Bell *et al.,* 2002). This method was kept the same throughout sampling, as it was important to acquire an exact figure for the sample area to understand whether vegetation density in the field impacted Linyphiidae and *T. tenuis* abundance in any way.

4.3.4. Linyphiidae Sheet Web Identification and Area Calculation

Sheet webs created by *T. tenuis* and Linyphiidae are the key elements which describe *T. tenuis* biological control capability. The design of a web impacts the way a pest is captured, with Toft (1987) explaining that webs with more radial sheet threads exhibiting a finer mesh for greater prey entrapment, were constructed by *T. tenuis* in areas of high prey abundance. Linyphiidae sheet webs were identified by certain characteristics, with anchor points above the webs main body, possible two sheet layers and sheet threads being woven into a hexagon structure (Herberstein, 2011; Krink & Vollrath, 1997; Roberts, 1993) (*Figure 4.7a & b*). Sheet webs were viewed as a product of Linyphiidae activity unless a *T. tenuis* was observed under the web. This was due to similarities in the nature of the sheet web spun by many Linyphiidae. A web that contained a Linyphiidae that was not a *T. tenuis* was discounted from the research. Further, it was important to consider *T. tenuis* tendency to create webs at a certain height within a landscape. For example, webs woven high within the branches of a hedgerow were discounted, a stratum not often utilised by *T. tenuis* web-building (Bell *et al.,* 2002).

Figure 4.7a & b: Photographs of Linyphiidae sheet webs at NIAB field site showing sheet threads woven into a hexagon structure. Elevated view.

Webs located were the focus of every field sampling session after the preliminary fieldwork. From the experimental work in summer 2016, it was identified that Linyphiidae webs are complex structures in dimensions and location. A robust system was required to acquire the measurements of a web found in the field. Small differences needed to be identified between the webs to assess subtle differences in potential biological control of Linyphiidae between different sample areas within the three tillage intensities. Each support thread, providing the external framework of the web, was measured to the nearest 0.1 mm. Measurements were taken with a Zukvye© Electronic Vernier Callipers 150 mm Carbon Fibre Body Measuring Tool, use of which is shown in Figure 4.8b. To assist in observation and measurement webs were illuminated with an OneNight™ 700 Trekking Head Torch with capacity of 250 lumens (*Figure 4.8a &b*).

Figure 4.8a & b: Sheet web dimensions measured Field B, March 2017. (Yellow circles identify anchor point of web). a = Sheet web illuminated. Lateral view. b = Web measured with Zukvye© electronic vernier callipers. Lateral view. (Red arrow = 31.6 mm).

Different methods of calculating web area were processed for accuracy and practicability within the field. Heron's formula was found to be the most reliable and precise method as the web's area was split into triangles ensuring no part of the web was missed. Area of triangle by Heron's formula uses sum of all sides (abc = $\surd s(s-a)(s-b)(s-c)$ where $s=(a+b+c)^2$) where S is the perimeter (Casio, 2017). As the formula used to calculate the area of a triangle required all three side lengths, internal distances of the web were needed. Distance from anchor point to anchor point was measured using the same method as support threads. This took the largest amount of time and accuracy in sampling, the web the essential element when analysing predator behaviour within the different tilled areas. Several, methods were applied to support the understanding of web construction and learn how to accurately record the dimensions of a web. The use of 3D computer-aided web design allowed measurements taken in the field to be verified (Krink & Vollrath, 1997; Qin *et al.,* 2015). Data Collected from fieldwork was transferred to SolidWorks© (2017) to create 3D computer-aided designs (*Figure 4.9.*). The use of SolidWorks© was used to identify any errors in calculations. In early field sampling, a few measurements did not fit into the expected design when transferred to SolidWorks© and therefore in following sampling periods, a Viking Optical™ 10 x Folding Magnifier Glass (1.9 mm diameter) was used to determine the exact attachment point of a support thread to be able to measure from this point.

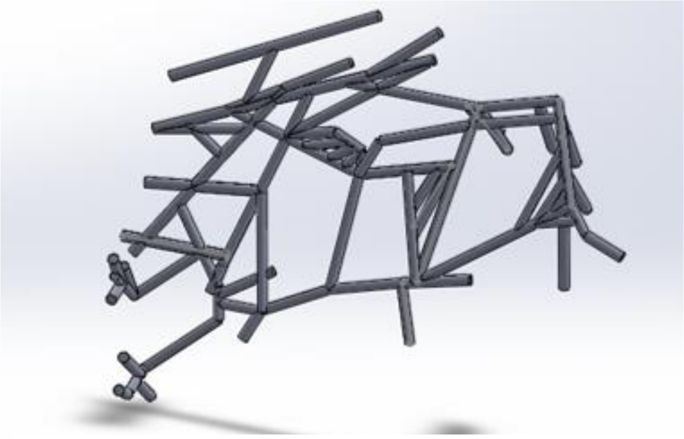


Figure 4.9: Measurements taken from field sampling and inputted into Solidworks© 2017

4.3.5. Web Anchor Point Height

The location of the webs was essential to record, as different heights of webs may intercept prey of different species and in different numbers. Each anchor point height of the support threads within the web was measured to the nearest 0.1 cm. The material (vegetation) that the sheet thread was anchored to was recorded. Even though measuring the height of each anchor point took time, it was viewed as key data to collect. Sheet webs are usually woven within a horizontal plane, however there were times within preliminary investigation that a web was woven at an angle to facilitate the web around available vegetation. Such angled webs may have affected prey capture and therefore reference to this was collected in anchor point height of the support thread (Batáry *et al.,* 2008; Dennis *et al.,* 2015).

4.3.6. Migratory Behaviour

It is important to recognise migratory behaviour in aerial dispersal of *T. tenuis*, as locomotion allows this species to move to a superior web construction site, which may be in an area with potential Aphididae (Bonte *et al.,* 2002; Pekár, 2014; Simonneau *et al.,* 2016) (*Section 2.2.1.4*.). Locomotion can identify vacating a disturbed area or abandonment of a web not meeting its intended function. Prior to any sampling, quadrats were observed to identify any 'throwing' of a dragline thread. The time for observation required prior consideration. It was noted that the small physical disturbance of locating and lying the quadrat may have created a low level of unease with Linyphiidae that are highly sensitive to fine movements (Simmouea *et al.,* 2016). It was felt a period of complete calm should be applied to allow the normal habitat of the quadrat to resume. First, ten minutes was given to observing any movements of migration though it was noted if any activity occurred, it was within the first five minutes of observation. Five minutes was applied to assess whether any throwing was used to rappel (short migration) or balloon for longer migration (*Figure 4.10.*). This was important to assess, as different locomotive methods may be used in different situations. Ballooning can be a product of disturbance where rappelling may be used to identify a prime web-site in a small micro-habitat. The length of the dragline silk was a clue to the choice of locomotion, a longer dragline is required to propel *T. tenuis* over a longer distance and balloon. Preparation for ballooning generally takes more time than bridge threads being laid for rappelling (Thorbek 2003). Anchor point height of bridge and ballooning threads were measured as with support threads (*Section 4.3.5*.).

Figure 4.10: Bridge threads spun by a rappelling T. tenuis. *(*T. tenuis *circled in yellow).*

4.3.7. Abundance and Phenology of *T. tenuis*

Numbers, sex and body length measurements of *T. tenuis* in each sample was important data to acquire, to establish whether tillage affects the numbers and phenology of *T. tenuis* and understand if this may affect the biological control potential of each sample plot. Much can be gained from measuring *T. tenuis* as it has been shown that individuals with a longer abdomen are more likely to invade a web (Dennis *et al.,* 2015). Male size is directly proportional to climbing speed, which may mean webs are constructed higher in a crop (Prenter *et al.,* 2010). Identifying gender of *T. tenuis* within the sample is key, as females have been cited to eat more prey (Harwood *et al.,* 2004). Number of spiderlings in each sample was also counted to reference reproduction rate (Toft, 1987). *T. tenuis* density was sampled with the use of a modified g-vac (Stihl® BG - 55 - 65) with nozzle air velocity of around 40 ms^{-1}. Equipment guidance and practice of the use of the g-vac was attained at Myerscough College fields before commencing sampling work in the NIAB fields in Cambridge. It was essential that use of the equipment was comfortable with health and safety requirements carried out efficiently and effectively, due to lone working in Cambridge. G-vac sampling was the last activity carried out on a sampling plot so as not to disturb other data gathered, such as web dimensions and anchor height. Sampling was continuous with a slow and steady motion, the g-vac being implemented over each plant row and space in between the plant row once (*Figure 4.11. & Figure 4.12.*). The contents were dispensed into a white plastic trug, a clear sample tray used to analyse small quantities of the sample at one time (Wheater *et al.*, 2011).

Figure 4.11: G-vac in use for T. tenuis *sampling, Field D summer 2016.*

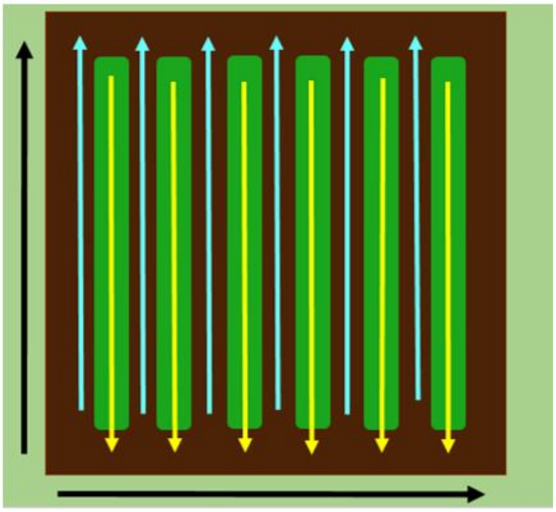


Figure 4.12: Method of T. tenuis *sampling in quadrat. Green boxes represent plant rows. Light blue arrows represent forward movement in between plant rows and yellow arrows represents reverse movement through plant rows.*

In wet conditions, the collection bag became moist from sampling wet vegetation and therefore not able to collect a realistic sample. In these circumstances, *T. tenuis* were collected by hand searching, gently moving crop, loose soil and substrate to locate possible *T. tenuis*. Phenology of *T. tenuis* was recorded by the same method as collection via g-vac. Spiderlings were not sampled via hand searching, as their small size meant they were difficult to locate without causing considerable disturbance to the vegetation of the sample area and therefore any sample would be unrepresentative. Measurement of *T. tenuis* required precise equipment due to the small size of the animal. The first problem was identified as 'stilling' a *T. tenuis* upon capture to be able to measure body dimensions accurately. It was observed that removing the *T. tenuis* to a smaller environment devoid of any other species, away from the plastic trug holding the contents of the g-vac, helped create a stable stilling habitat. *T. tenuis* was thus placed in a Petri dish to be measured and sexed. A hand-held magnifying glass, Viking Optical™10 x Folding Magnifier Glass (1.9 mm diameter) was used to ensure *T. tenuis* identity through analyse of abdominal markings (*Figure 4.13a - c*). This is important with spiderling identification, where the markings on the abdomen are present after hatching from the egg sac (*Section 2.1.1.2*.). Adult *T. tenuis* were determined if they had a combined cephalothorax and abdomen length over 2 mm. Time was given to allow an active *T. tenuis* to settle in the Petri dish, after which body length (incorporating cephalothorax and abdomen lengths) were recorded to 0.1 mm with the Zukvye© Electronic Vernier Callipers (*Figure 4.14a - c*). Spiderling dimensions were not taken, due to in-field measurement tools unable to accurately record any differences in spiderling body lengths.

4.13a - c: Species and gender identification of T. tenuis *in fieldwork, Field A, November 2017.*

4.14a - c: T. tenuis *left to still in Petri dish. Body length measured by Zukvye© electronic vernier callipers.*
c = Sample reads 2.2 mm for T. tenuis *abdomen length.*

4.3.8. Web Occupation

From initial fieldwork, *T. tenuis* occupying a web was recorded to add to data analysing predator behaviour within the field (*Figure 4.15a - c*). An occupied web suggests recent construction of the web, and the prey capture potential of the web is yet to be attained. Web occupation may give information of courtship behaviours where a female in a web may be fecund and a male occupying a web alone may suggest it is a sperm web, allowing the transfer of sperm to the palps (*Section 2.1.3.4.*). Webs with no *T. tenuis* occupation may have been abandoned due to poor prey capture, suggesting a negative energy flow where energy output for web creation was not regained through prey consumption (Benjamin & Zschokke, 2003; Segoli *et al.,* 2004). *T. tenuis* and prey within the same web were recorded and identified as a successful web construction in site and location, implying *T. tenuis* will be able to predate on the prey in the web.

Figure 4.15a - c: Female T. tenuis *hanging underneath sheet webs from field sampling. Lateral view.*

4.3.9. Prey Abundance in Webs

In the preliminary experiment of summer 2016, all Aphididae found within the Linyphiidae webs were recorded. Concentrating on cereal Aphididae that cause direct damage to cereal crops was identified to benefit the research. Continual identification of migratory Aphididae in field examination, or retrieval for further observation, compromised the recording of the Aphididae that cause the most damage and are required to be controlled biologically by *T. tenuis*. The cereal Aphididae found in the preliminary experiment, *S. avenae*, *R. padi* and *M. dirhodum* are identified to cause significant *H. vulgare* damage and were the Aphididae recorded in 2016 / 2017 and 2017 / 2018 field sampling (*Section 2.2.6.2.*). *S. mosellana* was also considered due to appearance in preliminary fieldwork sampling. After positive identification it was noted that *S. mosellana* appearance in *H. vulgare* was possibly from the adjacent *T. aestivum* field. Due to *S. mosellana* causing damage to *H. vulgare* via grain degradation through feeding, it would be beneficial to understand whether *S. mosellana* abundance affected *T. tenuis* density or activity (*Section 2.2.6.4.*).

During April sampling of the 2017 season, small white fragile debris was viewed within a Linyphiidae web. Laboratory analysis confirmed this was Aphididae exuviae, the soft shell removed from an Aphididae as it transitions through the instars (*Section 2.2.6.1.*). This was an important element to measure as it shows evidence of nearby or caught Aphididae activity, for example presence of exuviae could indicate an Aphididae of the first instar becoming entangled in a web, however, able to escape through shedding of an exuviae into the next instar. Exuviae may be incorporated into the web through wind dispersal and therefore can be a measure of nearby Aphididae activity, and this may be a reason why a Linyphiidae web was woven in the vicinity.

Spring to summer season field sampling included measuring *R. padi*, *S. avenae* and *M. dirhodum*, and *S. mosellana* abundance within the 1 m^2 sample area, to analyse further whether prey availability affects *T. tenuis* activity in the different tilled areas (*Figure 4.16. & 4.17.*). Prey (cereal Aphididae and *S. mosellana*) was recorded in the g-vac sampling that was implemented for *T. tenuis* abundance (*Section 4.2.7.*).

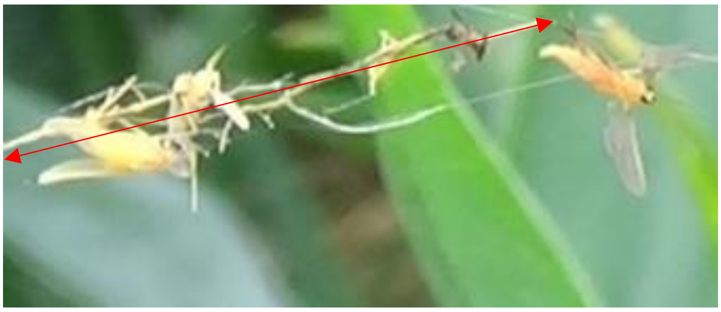


Figure 4.16: S. mosellana *in rappel threads* T. aestivum *May 2018. (Circled in yellow). Lateral view (Red arrow = 49.7 mm).*

Figure 4.17: Colony of R. padi *identified on* Rubus fruticosus *(Bramble).*

4.3.10. *Alopecurus myosuroides* Density

Alopecurus myosuroides (Black-grass) is a common invasive weed prevalent on many arable farms, especially in the Southern regions of the UK, with warmer and drier climates (Melander *et al.,* 2013). *A. myosuroides* density was recorded for each sample plot (*Figure 4.18a & b*). The incorporation of *A. myosuroides* within the sample area may have had a small effect on *T. tenuis* activity due to slight increase to landscape heterogeneity (Dennis *et al.,* 2001; Gómez *et al.,* 2016) (*Section 2.1.3.3.*). *A. myosuroides* grows at a faster pace than *H. vulgare* and is different in phenology, in increased height and with an increased abundance of tillers (Milner, 2002). This could aid web construction, providing another platform for support thread anchorage. This may be a piece of evidence to negate the idea that webs are largely constructed near sites of increased prey abundance, instead finding areas with increased anchorage potential.

Figure 4.18a & b: A. myosuroides *identified in the field sites. a = Field B August 2017. b = Field C September 2017. (*A. myosuroides *circled in black).*

4.3.11. Physical Features of Soil

4.3.11.1. Soil Furrows / Seedbeds

At time of field sampling after drilling of seed (*Section 3.1.3.4.*), differences were observed in the soil physical features, after it was noted that deeper, narrower and more defined furrows created the seedbed in the Conventional tilled area (*Figure 4.19a*) against the Direct Drill Managed (*Figure 4.19b*) and Direct Drill (*Figure 4.19c*) tilled areas. This may correspond to difference in soil moisture due to the tillage technique. Differences in soil landscape has been shown to promote changes in Linyphiidae activity (Alderweireldt, 1994; Samu *et al.,* 1996). Each furrow (seedbed) was measured to the nearest 0.1 cm in width and depth. These measurements were gained for both crops (*T. aestivum* and *H. vulgare*) until harvest and primary cultivation.

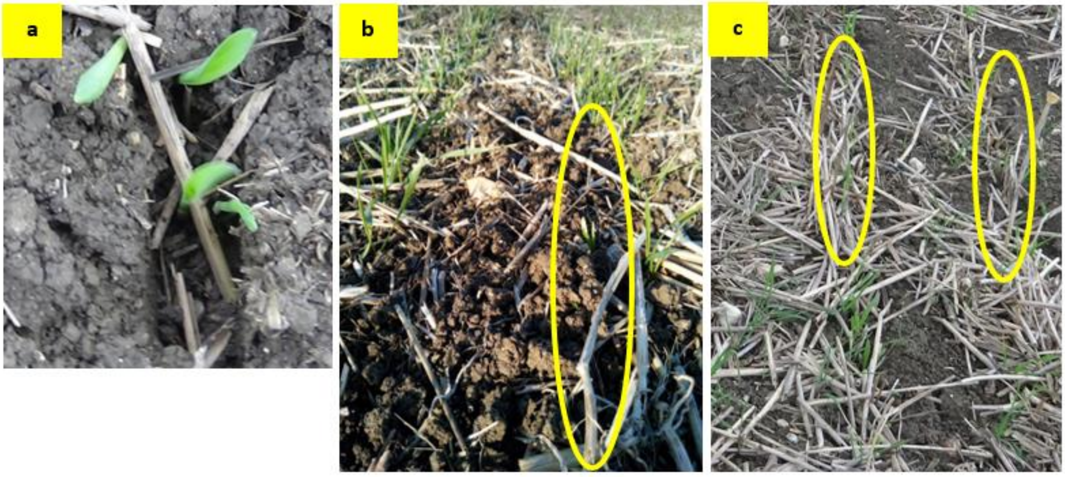


Figure 4.19: a - c: Furrows created after seed drill. (Yellow circles show furrows). Field B, a = Conventional, May 2017. b = Direct Drill Managed, November 2017. c = Direct Drill, April 2018.

4.3.11.2. Soil Clods

After primary and secondary cultivation (*Section 2.2.4. & Section 3.1.3.4.*), clod height and abundance in sample plots were measured to discover if this element of the micro-habitat influenced *T. tenuis* activity (*Figure 4.20a & b; Figure 4.21a & b*). Clods were identified as man-made aggregates over 1 cm in dimensions of height, length and width (Ashman & Puri 2002). Following the pattern of plant height and upright stubble, ten clods were chosen in each sample area and their height measured from the ground surface to the top of the highest point of the clod.

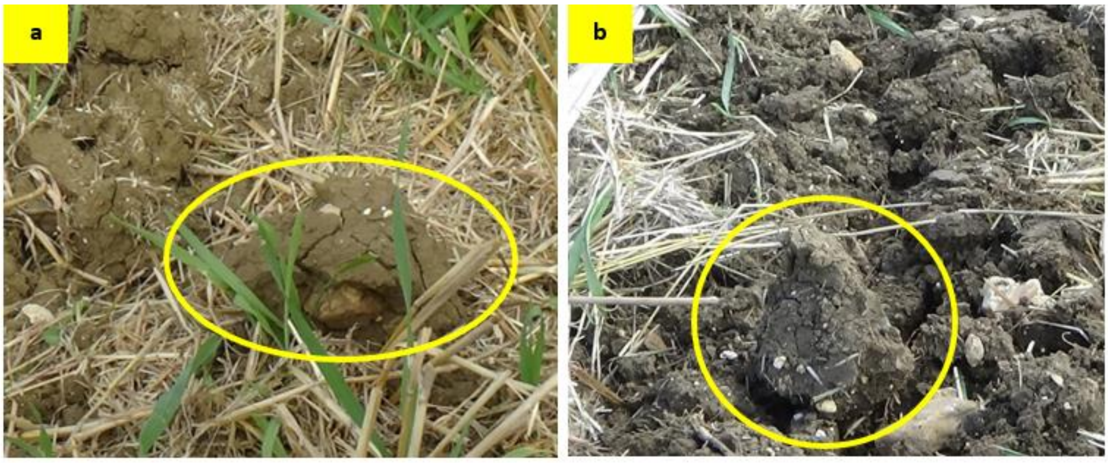


Figure 4.20a & b: Soil clods formed after primary cultivation in Field B 2018. a = Conventional. b = Direct Drill Managed.

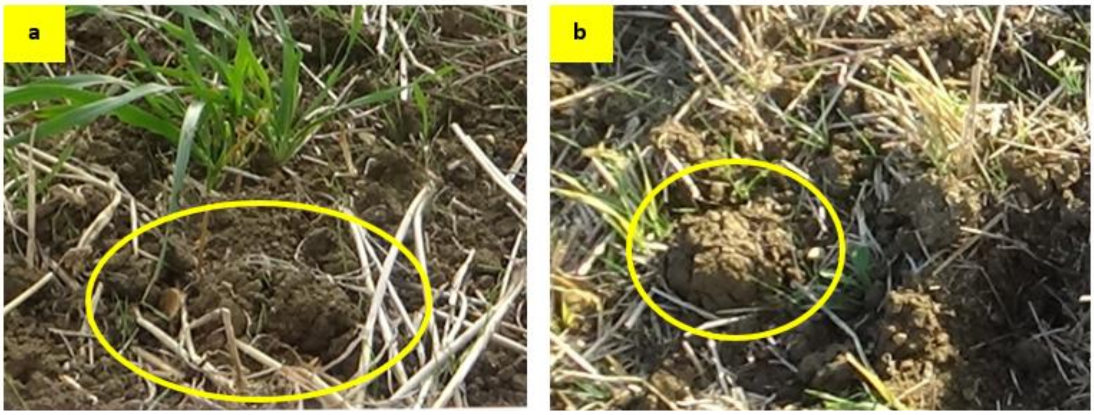


Figure 4.21a & b: Soil clods formed after secondary cultivation in Field B 2018. a = Conventional. b = Direct Drill Managed.

4.3.12. Overall

Data collection developed as fieldwork progressed and was necessarily changed as each crop went through progressive growth stages and cultivation activity occurred. For example, in periods where fields were fallow, cultivated or crop was in early GS, straw mass was measured in addition to total amount of upright stubble present. In times of crop, plant height, density and *A. myosuroides* density was measured. Further information gained at the time of cultivations and seeding, included measuring physical structures of soil (furrows and clods).

4.3.12.1. In-Between Sampling Periods

It was necessary to sanitise all equipment used in between sampling period to remove soil and debris. Kilco© Virex™ Disinfectant (dilution rate 1:300), applied via a spraying system was used at Myerscough College to wash all equipment. Attention was given to the bag (made of woven nylon) that collected the material sampled by the g-vac. This was to ensure removal of all fauna and flora remains and debris that may have impeded air flow.

4.3.12.2. Data Collection and Analysis in *H. vulgare* and *T. aestivum*

It was viewed important to collect data from both crops as they are both grown widely in the UK, both having a place in global markets. *T. aestivum* growth is slower than the fast development of *H. vulgare* (*Section 2.2.1*.). Therefore, each crop involves different times of harvest, cultivation and drilling. It was thought that these differences in growth and timing of farm activities could alter the predator behaviour of Linyphiidae and *T. tenuis* and affect capacity to biological control pests (*Section 3.2*.). After preliminary data analysis, it became clear that there were more similarities than differences of *T. tenuis* predator dynamics within *T. aestivum* and *H. vulgare*. It was considered that it would be beneficial to this research to concentrate on one cereal and be able to explore in depth *T. tenuis* behaviour within the life cycle of the one crop.

After analysing NIAB's crop rotation in the fields there was one field that since 2016, when preliminary work began, had grown the same crop of *H. vulgare*, Field B. When the images of the NIAB fields were viewed from Google Earth© it became clear that Field B housed the most similar dimensions for areas of differing tillage intensity (*Figure 3.5b*). The other fields in the investigation held differences in areas for each tillage intensity which could likely skew results. Field A clearly shows Conventional of a greater area than the Direct Drill Managed area, for example (*Figure 3.5a*). This may allow any differences in *T. tenuis* abundance and activity measured to be linked with area of the soil tillage intensity instead of the intensity of tillage itself. From the above information it was determined that data represented in this thesis would be presented from Field B, cropped with *H. vulgare* in each season sampled (March 2017 to November 2018).

4.4. In-field Experiment: Addition of Upright Stubble to Conventional Tillage Trials

4.4.1. Introduction

Upright stubble left intact thorough minimal or direct drill tillage can increase the abundance of *T. tenuis*, its activity in web-spinning and short-range dispersal in rappelling (Bianchi *et al.,* 2017; Holland & Reynolds, 2003; Witmer *et al.,* 2003). From this, a useful approach, was to investigate whether the soil under the different tillage practices had a direct effect on *T. tenuis* activity and abundance, or if these variables were affected by the above ground habitat created as a result of each tillage practice. From here an in-field experiment was designed where upright stubble, of a certain height and density, was placed into an area of Conventional tillage, which had undergone secondary cultivation. This experiment underwent two prototype trials to assess the methodology and develop a well-rounded design.

4.4.2. Prototype One: Ploughed Field - Myerscough College - September 2017

A first experiment was set up in a *T. aestivum* field at Myerscough College in September 2017. The field had been harvested and ploughed just prior to the experiment. Three sample quadrats of 2500 cm^2 were set up for each tillage type. A 50 cm border was established between each quadrat and sample areas not enclosed, to simulate the field trials of NIAB (*Figure 4.22.*). It was considered a sample size of 1 m^2, as sampled in the field, would take much time to construct with little added value. There was no enclosure, as the aim of this experiment was to simulate the field where *T. tenuis* have the freedom to choose to be within a habitat or not.

At this stage, upright stubble that had been collected from the field had been degrading and its integrity was lost. It had been collected on dates where there had been heavy rainfall. The need to cut the stubble to a corresponding height to that of the NIAB field and for the stubble to be upright when inserted into the experimental field, led to substituting bamboo canes (6 mm in diameter) (*Figure 4.24a - c*). Canes used, corresponded to upright stubble density collected in March 2017 in Field B where all cultivations had taken place and was yet to be seeded with the *H. vulgare* (*Figure 4.24a - c*). The bamboo was cut to the mean height found in the different tilled areas, plus 1 cm to allow insertion into the soil. There was some thought applied to how the canes should be arranged, noting the canes in each tillage intensity, Conventional for example, was required to be arranged the same. From field observations the cluster size of upright stubble varied immensely depending on how the angle of the harvester had struck the cereal heads, however it was clearly shown that cluster size was on average less than that of Direct Drill Managed and Direct Drill, the latter two intensities having similar cluster sizes (Morris *et al.,* 2010). From this, the bamboo was set to represent the stubble as it was in the field with the bamboo being incorporated into clusters of two to four for Conventional and two to six for Direct Drill Managed and Direct Drill (*Figure 4.23.*). Bamboo number in the cluster was randomly generated (Random.Org, 2018). The clusters were set 2 cm apart horizontally within the plant rows and 15 cm was set vertically between each row of bamboo clusters (*Figure 4.22 & 4.24c*). Dimensions of three female *T. tenuis* were recorded (same method as dictated in Section 4.3.7.) and these animals were introduced to the centre of each sample plot, to determine whether body length and mass influenced web construction to a higher degree than upright stubble availability and whether a decrease in upright stubble promoted *T. tenuis* dispersal. This density (three per plot), corresponded to that of *T. tenuis* identified from the field after secondary cultivation. It was theorised that placing measured *T. tenuis* into the experiment would potentially allow results, web area for example, to be related to the dimensions of the *T. tenuis* assigned.

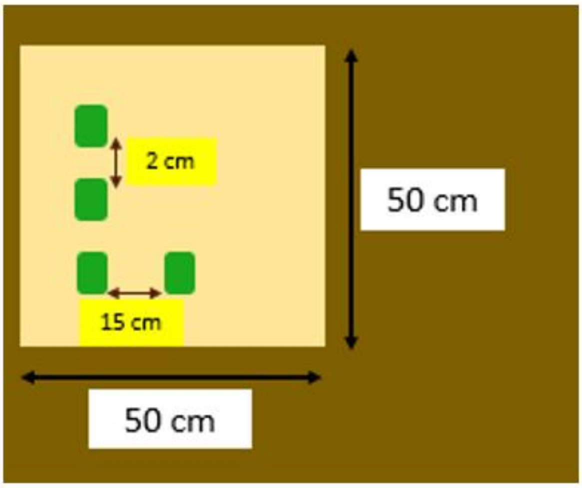


Figure 4.22: Schematic diagram of set-up of prototype one - ploughed field at Myerscough College, September 2017, of addition of upright stubble to Conventional tillage trials. (Green boxes are upright stubble clusters).

Figure 4.23: Upright stubble was counted in field sampling and cluster design noted for prototype one - ploughed field at Myerscough College, September 2017, of addition of upright stubble to Conventional tillage trials. (Clusters circled in yellow).

Figure 4.24a - c: Addition of upright stubble to prototype one - ploughed field at Myerscough College, September 2017, of addition of upright stubble to Conventional tillage trials. (Cluster for Conventional in black circles). a = Conventional, b = Direct Drill Managed, c = Direct Drill.

4.4.3. Prototype Two: NIAB Field B - After Secondary Cultivation - November 2017

After the set-up was established at Myerscough College, the experiment was trialled at the NIAB fields (*Section 4.3.2.*). The conventional area of Field B housed the experiment in November 2017 (*Figure 4.25a* - *c*). The primary and secondary cultivations had taken place at this stage plus the glyphosate spraying (360 g L^{-1} Rodeo® at application rate 3.1 L ha^{-1}) (NIAB TAG, 2017). Unlike the Protype One, *T. tenuis* were not added into the sample plots. It was seen that this experiment should use the *T. tenuis* resources in the field only, as these are the resources that are available to provide biological control. It was also identified that there were no significant correlations between the measurements gained of the *T. tenuis* in Prototype One with dimensions of sheet webs calculated. Further, it was impossible without highlighting the *T. tenuis* first, if any *T. tenuis* identified at the end of the experiment was indeed from the original stock. The sample plots were in a random area, generated via the same method discussed for field sampling in Section 4.2.

Figure 4.25a - c: Set-up of prototype two, NIAB Field B, Cambridge, November 2017, of addition of upright stubble to Conventional tillage trials. a = Conventional, b = Direct Drill Managed, c = Direct Drill.

There appeared to be significant use of the bamboo canes at the outer reaches of the sample area within Direct Drill in Prototype One (*Section 4.4.2.*). To identify if there was any edge effect to Linyphiidae activity, the clusters of bamboo in Direct Drill were labelled from 1 to 16 starting from the south-west aspect of the sample plot (*Figure 4.26.*).

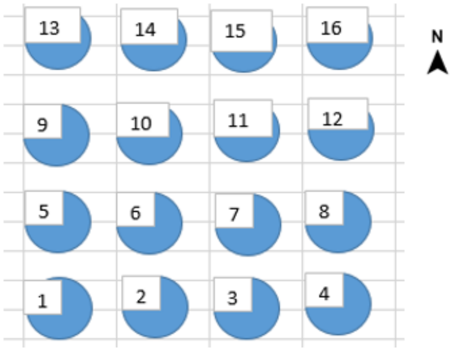


Figure 4.26: Schematic diagram showing the numbering system for each group of upright stubble for Direct Drill. Prototype two, NIAB Field B, Cambridge, November 2017, of addition of upright stubble to Conventional tillage trials.

It was noted that the bamboo canes needed to be disposed of and actual upright stubble from the field used. This required collection well in advance, to ensure upright stubble had a chance to dry and its integrity remain intact. Bamboo canes were too thick and uniform to act as upright stubble for Linyphiidae activity to simulate that of the field. The impact of the numbering system of the groups of stubble to identify any edge effect to the results was void. There was no clear indication if the outside cluster of stubble was favoured as a web-building material than the inside clusters. This was negated from the final experiment; however, observations were still made if there were notable differences in the clusters used. Prototype Two, where *T. tenuis* were not implemented from the start, was successful. *T. tenuis* identified at the end of experiment were measured as in Section 4.3.7. This supported the idea that there was free movement within the experiment, and it could be identified whether the addition of upright stubble encouraged the settlement of *T. tenuis* not previously present in the sample area.

4.5. Hedgerows Opposite Soil Tillage Intensities

4.5.1. Introduction

Field margins act as a refugia, as *T. tenuis* do not complete their life cycles in cultivated fields, finding shelter for refuge and development of egg sacs (Welch *et al.,* 2011). *T. tenuis* migrate to field edges and shelterbelts when the field is uncultivated as increased vegetation offers habitat to potential prey. Therefore, it was important to sample the field margins of the NIAB fields to fully understand predator and prey dynamics of *T. tenuis* within the NIAB fields, cultivated to different levels of intensity. Each field is surrounded by a 1 m grass strip that is mowed twice annually. A hedgerow forms the surrounding boundary to each side of the NIAB fields (*Figure 4.1*.). The vegetation of the grassland strip was, at most times of sampling, noted to be too short and sporadic to support high Linyphiidae activity (Hof & Bright, 2010) (*Figure 4.27a & b*). The grass strip was not seen to be a refuge habitat. From this information, the hedgerow was viewed as the focus when sampling the field margins.

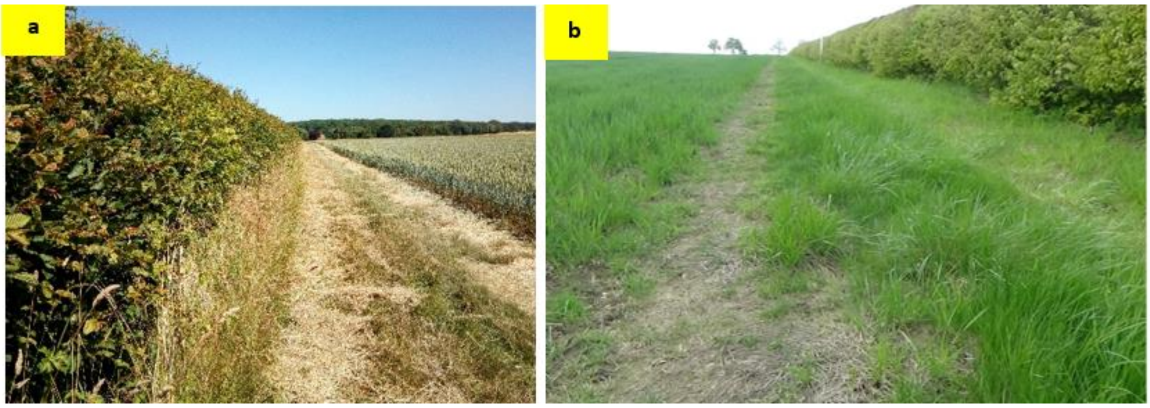


Figure 4.27a & b: Field margins identifying mowed with sporadic vegetation growth. a = Field A June 2017. b = Field B April 2018.

A vegetation survey was carried out on the hedgerows that were sampled (Wheater *et al.,* 2011). Each hedgerow incorporated these floral species: *Alnus glutinosa* (Alder), *Anthriscus sylvestris* (Cow Parsley), *Crataegus monogyna* (Hawthorn), *Dactylis glomerata* (Cocksfoot), *Lolium multiflorum Lam* (Italian Ryegrass), *Poa trivialis* (Rough Meadow Grass), *Rosa canina* (Dog Rose), *Rubus fruticosus* (Brambles), *Sambucus nigra* (Elder) and *Urtica dioica* (Common Nettle) (DEFRA, 2011; Rose, 1991).

4.5.2. Method Development

4.5.2.1. Choice of Hedgerow

Only one hedgerow was sampled in each field, the hedgerows that bordered each tillage (*Figure 4.28.*). Two hedgerows bordered only one tillage treatment, Conventional and Direct Drill Managed which would not identify any differences in *T. tenuis* activity within each tilled area (*Figure 4.28.*). It was determined that sampling only one of these two available hedgerows kept data consistent and relevant. As with the field areas, the hedgerows sampled could be known in depth, from species it supports to areas of varying vegetation density.

Figure 4.28: Rectangles identifying hedgerows of Field B bordering all soil tillage intensities. (Yellow rectangle = hedgerow chosen for sampling).

4.5.2.2. Data Collection

The sampling area began 1 m away from the field edge (*Figure 4.1.*). The length of the hedgerow in each tillage was recorded via the Amtech® P1910 Measuring Wheel and a sample point was randomly selected and located from west to east. The sample size was 1 m^2 following the field sample quadrats (*Figure 4.29a - c & Section 4.2.*). If a ditch prohibited sampling from extending 1 m into the hedgerow, a new location was randomly selected.

Figure 4.29a & b: Sample areas in hedgerows opposite soil tillage intensities, Field B. a = November 2017. b = August 2017.

Sampling consisted of collecting similar data as within the field, with respect to web dimensions, web occupation and g-vac sampling (*Section 4.3.*). The distance from the field edge was an important feature to survey, it may have shown the migration distance of a Linyphiidae into the hedgerow and its relation to prey availability. Only one anchor point of each web was required to identify migration distance, that closest to the field edge was recorded for each web (*Figure 4.30a*). Numerous methods were tested to establish this, first with a laser tape measure being shone from the anchor point onto a white sheet at a given distance away from the field edge. This was deemed too inaccurate, as it was difficult to place the measure exactly at the anchor point. A simpler approach was adopted where another 1 m rule was placed just in front of the anchor point. This ruler intercepted the metre rule of the sample that ran vertically into the hedgerow, distance of anchor point was read on the vertical ruler to 0.1 cm (*Figure 4.30b*). From all measurements, 1 m was added to incorporate the distance from the field edge to the start of the sample area (*Figure 4.1.*).

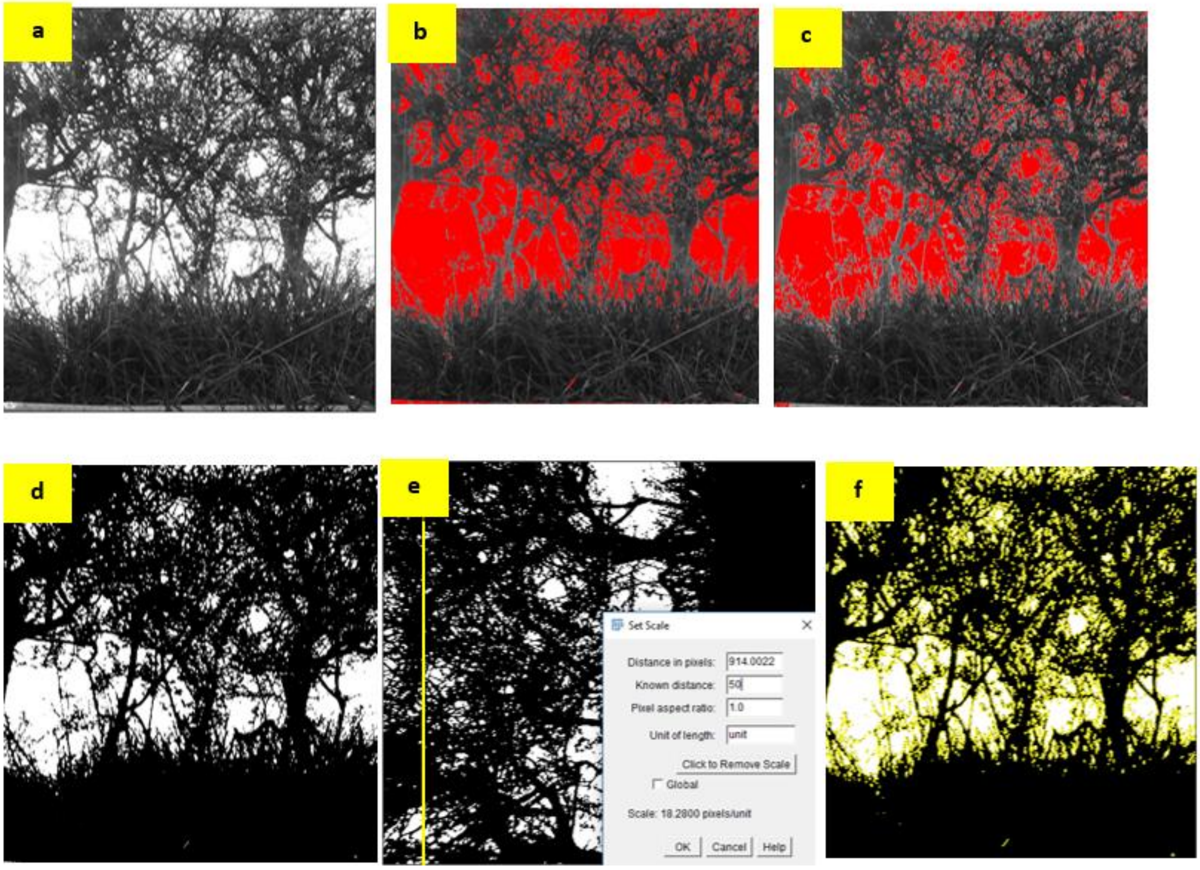
Figure 4.30a & b a = Anchor point closest to field edge identified and marked with meter rule. (Anchor point circled in yellow). b = Distance measured on metre rule of quadrat laid into hedgerow.

4.5.2.3. Hedgerow Vegetation Density

Through literature and initial fieldwork of summer 2016 and early 2017, it was identified that the vegetation density of the hedgerows of the NIAB fields may have an interaction with Linyphiidae and *T. tenuis* activity (Garratt *et al.,* 2017; Pfister *et al.,* 2015; Rosas-Ramos *et al.,* 2018). To be able to assess this, the vegetation density of sample areas within the hedgerows was measured at the time of sampling. Density was measured using the computer software ImageJ©. A photograph was taken at 1 m away. Zoom was not used, to ensure the same focal length in every photograph. To enable no disturbance of additional vegetation from the field beyond, the photograph was taken lying on the ground, with the camera on average 30 cm from the ground. A tripod was not used for this height. Several photographs were taken at each sample plot, reviewing each to ensure the one used was taken with a steady and level camera. It was observed that not all the hedgerow width could be incorporated into one photograph in this position. Two photographs were obtained for each plot with the use of a 1 m rule identifying the sample plot. The centre of the ruler was marked to establish a 50 cm width section of the hedgerow (*Figure 4.31a*). Any excess vegetation not within the 50 cm marked was then cropped from the photograph before being processed by ImageJ© (*Figure 4.31b*).

Figure 4.31a & b: Hedgerow sample Field B a = 50 cm marker (circled in yellow) identifying where the photograph should be cropped for ImageJ©. b = Cropped photograph to be used with ImageJ©.

The photograph was cropped using Paint3D® and saved as a JPEG. The photograph was turned into an 8-bit binary image via ImageJ© (*Figure 4.32a*). A tone threshold was then identified and adjusted to ensure all vegetation in the photo was recognised (*Figure 4.32b & c*). The picture was then turned into a binary image (*Figure 4.32d*). A known measurement, the 50 cm, was placed into the programme to set a scale to allow the pixels in the photograph to relate to a measurement (*Figure 4.32e*). A selection was then created, and area measured (*Figure 4.32f*). It was key to understand which selection was being measured, dark for vegetation or light for sky. To switch between both the selected area was inverted.



Distance in pixels: 914.0022
Known distance: 50
Pixel aspect ratio: 1.0
Unit of length: unit
☐ Global
Scale: 18.2800 pixels/unit

Figure 4.32a - f: Process of measuring hedgerow density sample Field B with ImageJ©. a = Converting image to 8-bit grey scale. b = Adjusting tone threshold. c = Image after threshold manually corrected. d = Image converted into binary after threshold established. e = Setting the scale with the known length of 50 cm. Scale line highlighted in yellow. f = Selection created from which area of black (vegetation) can be measured in cm^2.

As sampling of the hedgerows continued, it became clear that *T. tenuis* and Linyphiidae activity was focused in the foreground vegetation of the grasses rather than in the branches of the shrubs. Within the photographs of the entire hedgerow profile, the foreground vegetation density could not be measured (*Figure 4.33a & Figure 4.35a*). To solve this, a white background was created from a clothes horse measuring 144 cm in height and 60 cm in width (*Figure 4.33b & c, Figure 4.34a & b & Figure 4.35b*). A white sheet was draped over and secured by plastic tags to make tight and remove creases. This made an easily moveable white background that was high enough to remove any background disturbance. The width of the clothes horse at 60 cm was 40 cm less than the sample plot of 1 m. Two photographs were taken of every hedgerow sample because of this. The metre rules and measured markers on the sheet were used to allow 10 cm to be cropped from either side of the white sheet as described in Figure 4.33b & c. The result is shown in Figure 4.34a & b.

Figure 4.33a - c: Process of establishing a white background for 1 m hedgerow samples. a = Sample without white background. b & c = Using the meter rule and marker to remove 10 cm of white background from right and left side. Red arrows portray 10 cm on white sheet. Yellow arrows portray 10 cm on meter rule.

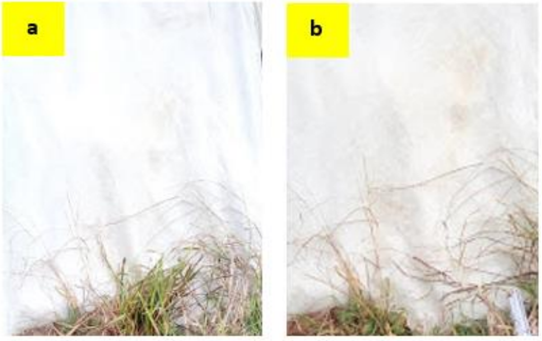


Figure 4.34a & b: Cropped photographs of hedgerow sample from Figure 4.33a & c used to measure vegetation density with ImageJ©.

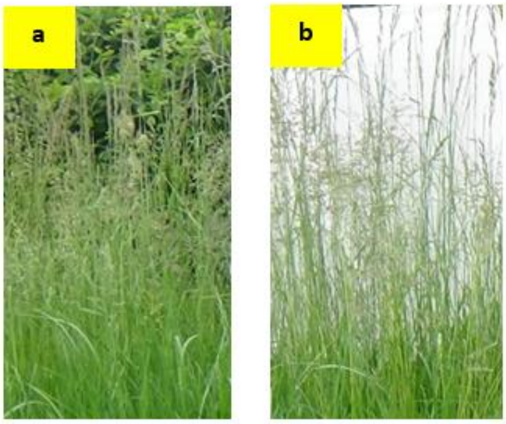
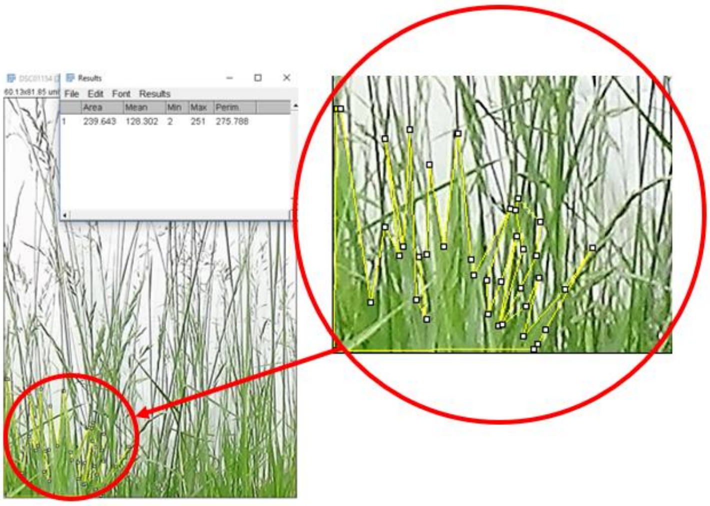


Figure 4.35a & b: a = Before white background was added. b = After white background was added.

To validate ImageJ© calculation of the area, using the tone threshold scale to achieve the binary image, the first data set from the hedgerows of Field B May 2018 was calculated by manually drawing around each aspect of vegetation (*Figure 4.36*.). This created a selection where, with the known length, an area could be identified. There was an average ±5% difference in hand-drawn selection and tone threshold scale. From this, the tone threshold scale was used thereafter.



	Area	Mean	Min	Max	Perim.
1	239.643	128.302	2	251	275.788

Figure 4.36: Vegetation manually selected in ImageJ© to verify the use of the threshold scale in ImageJ©.

4.5.2.4. *T. tenuis* and Linyphiidae Egg Sacs

From October to February, in the *H. vulgare* fields, the two hedgerows bordering all soil tillage intensities were sampled for the presence of *T. tenuis* and Linyphiidae egg sacs (*Figure 4.2. & Figure 4.37a - d*). The presence of egg sacs is a measure of fecundity and reproductive potential. High egg sac density equates to increased hatchlings which may increase the biological control capability of the next generation (Thorbek, 2003). This was an important factor to measure against the different soil tilled areas. The type of soil tillage intensity that the egg sac was located opposite, was noted.

The height of the attachment point of the egg sac was measured to 0.1 cm. This was to aid understanding in whether Linyphiidae establish egg sac position in relation to threat of predation, an egg sac higher within the hedgerow is seen as having more protection, as the trade-off is that it takes more energy for egg sacs creation (Lowe *et al.,* 2014; Segoli *et al.,* 2004; Vollrath, 1986). Dimensions of unhatched egg sac, height and width, were recorded to the nearest 0.1 cm to quantify reproductive output potential for each tilled area. Hatched egg sacs are often elongated where the protective silk has been torn by spiderlings hatching (Dondale, 2000) (*Figure 4.37d*).

The entire length of the hedgerow was surveyed for egg sacs observed via a slow-paced walk positioned in the grassland area between the field edge and hedgerow (*Figure 4.1.*). *T. tenuis* could not be assigned to an egg sac, as neither egg sacs were observed during construction by *T. tenuis* nor hatching *T. tenuis* spiderlings. Several Linyphiidae create similar egg sac formations to *T. tenuis* (Dondale, 2000). Egg sac abundance in this research is a feature of Linyphiidae fecundity in general. Each egg sac identified was investigated to identify if spiderlings had hatched or eggs were still present, via gentle examination of the egg sac. Care was taken not to disturb the integrity of the egg sac and the eggs inside (*Figure 4.37a*).

Figure 4.37a - d: Linyphiidae egg sacs identified in sample hedgerows Field B after secondary cultivation 2018. a = Open egg sacs showing unhatched eggs. b & c = Intact egg sacs with eggs inside. d = Broken egg sac where eggs have hatched.

4.6. Meteorological Information

4.6.1. Main Field and In-Field Experiment: Addition of Upright Stubble to Conventional Tillage Trials

Meteorological information (temperature and wind speed and direction), appropriate to location, was obtained from the Met Office© weather app for Android at the start of each field sampling period (*Section 4.2*.), and for the Addition of Upright Stubble to Conventional Tillage Trials (*Section 4.4.*). It became clear that advanced meteorological data was required to assess wind speed at the sample site as this may affect the ability of a *T. tenuis* to balloon and reduce dispersal rate (Thomas & Jepson 1999; Thomas *et al.,* 2003), which may have implications to *T. tenuis* ability to predate on Aphididae. Wind speed was measured to the nearest 0.1 mph (converted to kmh^{-1}) with the anemometer, Cateye Velo®. Wind speed was measured in each sample plot prior to sampling and after analysis of migratory *T. tenuis* (*Section 4.3.6*.). In fallow fields and for the in-field experiment, the anemometer was placed vertically 15.5 cm, the height of the anemometer, above the ground. When in crop, the anemometer was held vertically above the tallest plant in the sample area. Care was taken when using the anemometer to not disturb the same area.

4.6.2. Hedgerow Opposite Main Field

The hedgerow density varied within each sample area, which could alter the level of wind speed that passes through the hedgerow. To capture this, three wind speed measurements were taken within each sample area (*Figure 4.38*.). To measure the level of wind speed traversing through the hedgerow, a measurement was taken at the field edge and 0.5 m away from the field edge into the field margin. Level of air flow inside the hedgerow was taken at ground level. All measurements with the anemometer were taken after other sampling was complete.

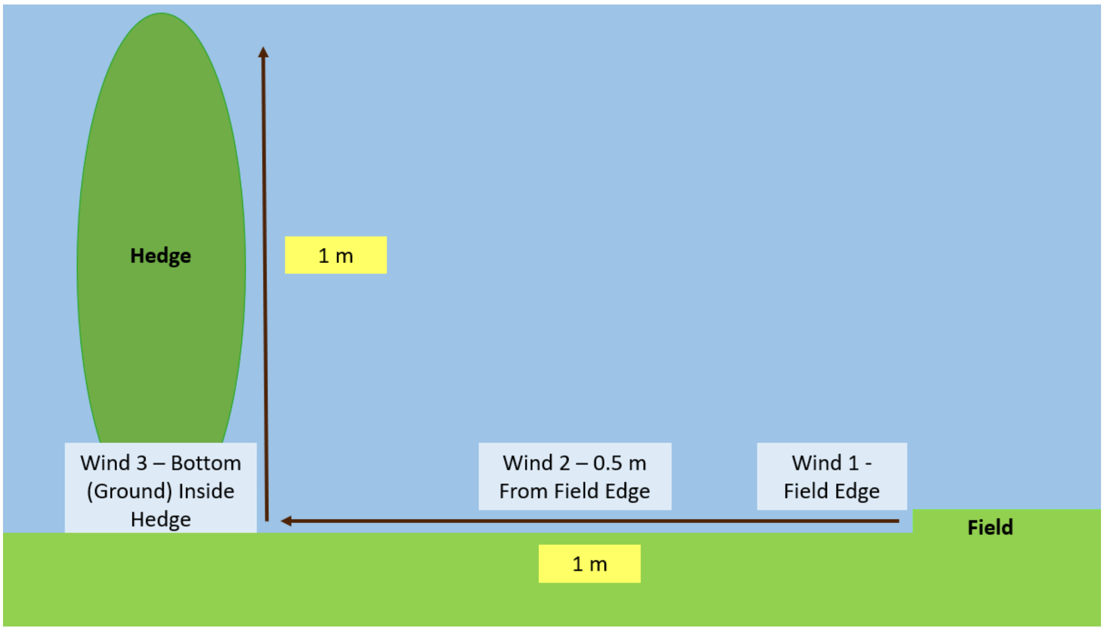


Figure 4.38: Schematic diagram of three points where wind speed was measured when sampling the hedgerow opposite main field.

4.7. Collection of Photographic Evidence

Images were identified as an essential element of data collection. Within early fieldwork, photographs were obtained by an android phone, however, to be able to use photographs as evidence it became apparent that photographs of a high quality were required. After preliminary fieldwork, all photographs in the field, and presented within this thesis, were taken with a Sony® HDR CX240 Full HD Camcorder with 27 x optical zoom and 320 x digital zoom. A period of training was undertaken to obtain precise photographs.

Chapter Five

5.0. Fieldwork - 2016 / 2017 Season and 2017 / 2018 Season

This Chapter is divided into three Sub-Chapters as referenced in Section 1.2., Page 2. The first (5.1.) reports the findings of measurements taken from the NIAB field at the fieldwork site in Childerley, housing the areas of differing soil tillage intensity (*Section 3.0.*). The second (5.2.) discusses data collected from an in-field experiment, where upright stubble was applied to land which had undergone Conventional primary and secondary cultivation (*Section 3.1.3.4.*). The final Sub-Chapter (5.3.) addresses *T. tenuis* interactions within the hedgerows that are opposite the NIAB field referenced in Figure 4.28., Section 4.5.2.1., Page 72.

Sub-Chapter Five One

5.1. Main Field

5.1.1. Introduction

T. tenuis activity recorded during both years of sampling followed the growth of the commercial cereal crop *H. vulgare* from seed to harvest over 2016 / 2017 and 2017 / 2018. Field sampling was carried out after primary and secondary soil cultivation, glyphosate application and drilling of seed for the following crop (*Table 3.1., Section 3.1.3.3., page 50*). Seeding took place in April and harvest was in mid-July.

5.1.2. Aims and Specific Objectives

5.1.2.1. Aims

Sampling within the main field occurred to address Research Aims 1 - 4 presented in Section 1.2., Page 2.

1. Identify the potential biological control by *T. tenuis* of Aphididae and *S. mosellana* within different intensities of tillage in an arable crop.
2. Identify any differences in extended phenotypes of *T. tenuis* within tillage practices, e.g. web dimensions and bridge thread length.
3. Understand whether *T. tenuis* behaviour is stimulated by the presence of Aphididae and *S. mosellana*.
4. Comprehend if a certain level of landscape heterogeneity affects *T. tenuis* ability to predate on Aphididae or *S. mosellana*.

5.1.2.2. Specific Objectives

Specific objectives were to:

- Measure behavioural changes under different tillage practices, e.g. measure migratory patterns, and consider how they affect *T. tenuis* ability to capture Aphididae.
- Assess potential differences in extended phenotypes of *T. tenuis* within tillage practices, e.g. measure web dimensions and architecture.
- Measure Linyphiidae web location in anchor height and anchor materials, within the different tilled areas, including *T. tenuis* web occupation, and relate to possible *T. tenuis* prey capture interactions.
- Identify and quantify crop pest abundance amongst crop and prey capture rate in Linyphiidae webs in areas of differing soil tillage intensity.
- Quantify variables associated with the landscape of the different tilled areas, e.g. upright stubble density, and use this to address how landscape homogeneity / heterogeneity may affect *T. tenuis* ability to predate on crop pests.

5.1.3. Methodology

5.1.3.1. Field Sampling

The methods used were exactly as discussed previously for method development of field sampling (*Section 4.2.*). Each of the nine sample sites (each visit) were located with an Amtech® P1910 Measuring Wheel.

Table 5.1.1. describes sampling visits carried out on the NIAB Field B and the relevant hedgerow between 2016 / 2017 and 2017 / 2018 seasons. Data collected from these visits is the basis of the results in this thesis but does not include any preliminary fieldwork of Summer 2016 where initial data was collected.

The 'Cultivation Stage / Farm Activity' (*Table 5.1.1.*) describes any activity that significantly changed the landscape heterogeneity of the field (cultivations for example) or activity which occurred within one week before the sampling visits (herbicide sprays) that may have affected Linyphiidae activity when data was collected. It has been identified by Bell *et al.* (2002) and Woolley *et al.* (2016) that *T. tenuis,* though sensitive to disturbance, can recolonise and re-inhabit an area within a few days of disturbance (*Section 2.1.3.3.*).

Growth Stage (GS) represents the cereal growth that had occurred prior to sampling (*Section 2.2.1.*).

Table 5.1.1: Sampling visits of NIAB Field B and relevant hedgerows, incorporating farm activity one week prior to visit.

Visit	**Year**	**Month**	**Season**	**Growth Stage (GS) of Plant**	**Cultivation Stage / Farm Activity**
1	2017	March	Spring	Fallow	-
2	2017	April	Spring	GS 11 - GS 15	Propino™ *H. vulgare* drilled.
3	2017	May	Spring	GS 33 - GS 37	-
4	2017	June	Summer	GS 55 - GS 61	-
5	2017	July	Summer	GS 83 - GS 87	-
6	2017	August	Summer	Fallow	After primary cultivation, six days after action of sub-soiler.
7	2017	September	Autumn	Fallow	After secondary cultivation, two days after last action of disc harrow.
8	2017	October	Autumn	Fallow	One day after Glyphosate 360 Rodeo® spray.
9	2017	November	Autumn	Fallow	-
10	2017	December	Winter	Fallow	-
11	2018	January	Winter	Fallow	-
12	2018	February	Winter	Fallow	-
13	2018	March	Spring	Fallow	-
14	2018	April	Spring	GS 11 - GS 15	Propino™ *H. vulgare* drilled, five days after Glyphosate 360 Rodeo® spray.
15	2018	May	Spring	GS 33 - GS 37	Six days after Compitox Plus (broad leaved herbicide) spray.
16	2018	June	Summer	GS 61 - GS 65	-
17	2018	July	Summer	GS 83 - GS 87	-
18	2018	August	Summer	Fallow	Immediately after primary cultivation. Field sampled as soon as sub-soiler left field.
19	2018	August	Summer	Fallow	After primary cultivation. Twenty-four hours after action of sub-soiler.
20	2018	September	Autumn	Fallow	After secondary cultivation, five days after last action of disc harrow.
21	2018	October	Autumn	Fallow	-
22	2018	November	Autumn	Fallow	One week after Glyphosate 360 Rodeo® spray.

5.1.3.2. Data Collection

Data collection commenced within each 1 m^2 field sample area (n = 9, 3 from each soil tillage area) at every field visit. Measurements were taken in the order specified in Table 5.1.2 and relate to method development work in Section 4.3. Webs counted were viewed as a product of Linyphiidae activity as species identification relating to web design was uncertain unless a web was occupied by a *T. tenuis* (*Section 4.3.4.*). Each measurement recorded was assigned the tillage intensity (Conventional, Direct Drill Managed, Direct Drill) where the sampling took place.

Table 5.1.2: Measurements taken on each fieldwork sampling period for main field from Table 5.1.1. and its relation to T. tenuis *activity.*

	Measurement Taken	**Months Measured**	**Relation to *T. tenuis* Activity**
1	Number of *T. tenuis* rappelling or ballooning	All	*T. tenuis* migration in / out of habitat.
2	Wind speed (km^{-h})	All	How wind velocity relates to *T. tenuis* abundance / activity.
3	Number of bridge threads	All	Frequency of *T. tenuis* locomotion / migration.
4	Anchor point height of bridge threads (cm)	All	Height locomotion / where migration is occurring.
5	Attachment material for bridge threads	All	Material facilitating locomotion / migration.
6	Number of webs	All	Frequency of web-building.
7	Support thread length (cm)	All	Quantify web area.
8	Anchor point height of support threads (cm)	All	Height web-building is occurring.
9	Attachment material for support threads	All	Material facilitating web-building.
10	Number of *T. tenuis* within web	All	How web occupation relates to habitat and prey abundance.
11	Number of prey within web	All	Prey capture rate via web.
12	Plant height (cm)	April - July	How height affects *T. tenuis* abundance / activity.
13	Plant density (N^{o}m^{-2})	April - July	How density affects *T. tenuis* abundance / activity.
14	Volunteer plant density (N^{o}m^{-2})	Aug - Feb	How density affects *T. tenuis* abundance / activity.
15	Upright stubble density (N^{o}m^{-2})	Aug - April	How density affects *T. tenuis* abundance / activity
16	*A. myosuroides* density (N^{o}m^{-2})	May - July	How density affects *T. tenuis* abundance / activity
17	Soil clod height (cm)	Aug - Nov	How height effects *T. tenuis* abundance / activity
18	Furrow width /depth (cm)	All	How dimensions affect *T. tenuis* abundance / activity
19	*T. tenuis* abundance quantified	All	How abundance relates to habitat and prey availability.
20	*T. tenuis* body dimensions (abdomen & cephalothorax length (mm))	All	How dimensions relate to habitat and prey availability.
21	Prey identification and abundance quantified	All	How prey quantity relates to habitat and *T. tenuis* abundance / activity.

The final methodology incorporating all measurements mentioned above followed the steps below.

1. Five minutes observation of the undisturbed 1 m^2 sample area for rappelling or ballooning *T. tenuis.*
2. Wind speed was measured to the nearest 0.1 mph (converted to kmh^{-1}) with the anemometer, Cateye Velo®. In fallow periods the anemometer was placed vertically 15.5 cm, the height of the anemometer, above the ground. When in crop, the anemometer was held vertically above the tallest plant in the sample area.
3. Any bridge threads were counted, and length measured to the nearest 0.1 mm with Zukvye© Electronic Vernier Callipers 150 mm Carbon Fibre Body Measuring Tool.
4. Material: plant or straw for example, used for bridge thread attachment was recorded.
5. Linyphiidae sheet webs were recognised due to the horizontal plane and hexagonal mesh incorporating the internal structure and quantity established.
6. Length of the support threads of the external web structure was measured to the nearest 0.1 mm with Zukvye© Electronic Vernier Callipers 150 mm Carbon Fibre Body Measuring Tool.
7. Material: plant or straw for example, used for support thread attachment was recorded.
8. Contents of webs inspected. Quantity of *T. tenuis* within webs were recorded along with gender. Prey quantity within webs recorded included the cereal Aphididae *M. dirhodum*, *R. padi* and *S. avenae*, and *S. mosellana*. Aphididae exuviae were recorded once identified using the handheld magnifying glass, Viking Optical™ 10 x Folding Magnifier Glass with 1.9 mm diameter.
9. Between April and July when *H. vulgare* was in crop, plant density was affirmed via counting all individual stems within the sample area. Between September and February, volunteer crop density was calculated in the same way.
10. Ten randomly chosen *H. vulgare* plant heights were measured from base of stem to top of shoot within GS 11 - GS 15 in April. Height was then measured from base of stem to top of flag leaf within GS 31 - GS 37 in May, then from June onwards after ear emergence of GS 51, plant height was measured from base of stem to the top of emerging ear. Height was measured to 0.1 cm with the use of a metre rule.
11. Upright stubble, lying above the horizontal axis and fixed to the soil, density was calculated by individually counting each stubble within the 1 m^2 sample area.
12. Straw / loose plant residue was collected in its entirety from between each crop row and placed into pre-labelled plastic freezer bags. Material was then measured on a balance to 0.01 g within 48 hours before material began to degrade.
13. *A. myosuroides* density, if present, was attained by counting each plant within the 1 m^2 sample area.

14. After soil cultivations had taken place, the height of 10 randomly chosen soil clods, soil aggregates over 1 cm^3, was confirmed to 0.1 cm with the use of a metre rule.
15. After cultivation and action of direct drill each furrow, trench incised for seeding, width and depth were measured in the 1 m^2 sample area and a mean ascertained. A metre rule was used for the measurements collected to 0.1 cm.
16. A Stihl® BG – 55 – 65 g-vac was applied to each sample area to determine *T. tenuis* and prey density. The g-vac was moved steadily up and down crop rows and areas in between, passing each area only once. Contents were then dispensed into a white plastic trug.
17. *T. tenuis* were removed and placed into Petri dishes and left still on the ground for 5 minutes. When *T. tenuis* were still, correct identification and gender were assigned with the use of the Viking Optical™ 10 x Folding Magnifier Glass with 1.9 mm diameter. Body dimensions (cephalothorax and abdomen length) were recorded to 0.1 mm with the Zukvye© Electronic Vernier Callipers 150 mm Carbon Fibre Body Measuring Tool.
18. *T. tenuis*, after correct identification, if body length < 2 mm were classed as spiderlings and abundance recorded.
19. Cereal Aphididae (*M. dirhodum*, *R. padi* and *S. avenae*) and *S. mosellana,* after correct identification with the Viking Optical™ 10 x Folding Magnifier Glass with 1.9 mm diameter if needed, were counted from the white plastic trug and placed into a separate container to negate a specimen being counted twice.

5.1.4. Statistical Analysis

5.1.4.1. Normality Testing

Several steps were taken to understanding whether a dataset held normal or non-normal distribution. A histogram set with normal fit was used firstly to understand the overall shape of the distribution of data. Level of skew (level of asymmetry within the distribution) and kurtosis (distribution of outliers in the dataset altering the height of the bell curve) were analysed. If a standard bell-shaped curve was established the data was thought to have normal distribution (Field, 2009; Hawkins, 2014; Wheater *et al.,* 2011).

Secondly the use of a probability plot (quartile to quartile plot) was used to plot the percentage value of each data point. Percentage value position about the trend line was observed. Non-normal distribution was assumed if a high percentage of points fell above or below the trend line. Further percentile lines, dividing the quartiles, were viewed to understand discrepancy of the distribution from the trend line (Ghasemi & Zahediasl, 2012; Field, 2009; Khan, 2013).

A normality test was then utilised. Anderson-Darling test was used due to its dealing with critical values in the distribution and placing weight to the tails (the ends of the bell curve in the histogram where frequency becomes smaller). P-value α was set at 0.05. If <0.05, the distribution was found to be significantly different from normal distribution. Further, the null hypothesis of normal data was rejected (Khan., 2013; Jäntschi & Bolboacă, 2018). Where datasets were large it was considered that the Anderson-Darling test may become too sensitive and show significance in favour of non-normal distribution when only slight deviations from the trend line may exist (Field, 2009; Jäntschi & Bolboacă, 2018).

If significance was assumed with the Anderson-Darling test, however doubts rose on the distribution presented on the histogram and probability plot, especially in larger datasets, the Ryan-Joiner test (similar to Shapiro-Wilk test) was utilised to compare results. This is a useful test due to calculating the correlation between the actual data points and the score the data would hold in normal distribution (Ghasemi & Zahediasl, 2012; Jäntschi & Bolboacă, 2018; Yap & Sim, 2011). Here the test statistic is a correlation coefficient (0 - 1), a value close to one assumes normal distribution in the data. Further the P-Value α is set at 0.10, higher than Anderson-Darling test, if the P-Value is <0.10 the null hypothesis is rejected and distribution within the dataset was assumed significantly different from the normal distribution (Ghasemi & Zahediasl, 2012; Khan 2013).

These steps gained confidence in acknowledging whether a dataset was classed as non-normal and non-parametric tests were therefore run.

5.1.4.2. General Statistics

Through normality testing, all data was found to be non-normal in this Chapter (*Section 5.1.4.1.*).

Kruskal-Wallis Test was run as a one-way test due to no extreme outliers found (Hawkins, 2014). Software used was Minitab18©. Dunn's multiple comparison test was performed on Minitab18© with the incorporation of a macro (KrusMC.mac) downloaded from Mintab18© libray (Orlich, 2000).

Spearman's Rank (Rho) examined whether a significant relationship existed between variables, e.g abdomen length and anchor height. Spearman's Rank (Rho) was used for the non-normal data, able to incorporate outliers due to ranking the data (Bass, 2017; Hawkins, 2014).

Two-way rank ANOVAs assessed variance in a mean of a response (e.g. anchor point height) and two categorical factors, due to non-normality (Hawkins, 2014; Wheater *et al.,* 2011). One factor was soil tillage intensity (referring to Conventional, Direct Drill Managed and Direct Drill), a factor used in every model due to tillage intensity central to the fieldwork. The other factor was an element of *T. tenuis* behaviour, for example, whether an anchor point height belonged to a thread inside or outside a web. When the field was cropped with *H. vulgare*, a factor was whether crop pests where found in the web. Crop pests here refers to Aphididae (*S. avenae, M. dirhodum and R. padi*) and *S. mossellana*. These pests are viewed as potential prey to *T. tenuis.* The rank was generated through Mintab18© and descriptive statistics placed into FCSTats V2_1a© (Wheater & Cook, 2000). From here, significance was gained and multiple comparison performed via the Dunn's test. Letters to identify significance were checked through use of the Bonferroni post-hoc test on the rank data in Mintab18© (Field, 2009). Bonferroni was used due to comparisons greater than the degress of freedom, no independence is assumed and Type I errors are lowered by reducing the α-level (Field, 2009).

Multiple regression models were built using the stepwise backwards elimination method via Minitab18©. The use of the model enabled the analysis of variables that were viewed as independent, for example number of *T. tenuis* in the web and mean abdomen length of *T. tenuis* identified. In each case, the response was placed against certain explanatory independent variables, upright stubble and plant density for example. No categorical predictor, soil tillage intensity, was assigned due to wanting to understand if certain variables swayed the response outside the soil tillage intensity. The idea to understand if variables, such as number of crop pests, affected numbers of *T. tenuis* in the web outside the effects given by soil tillage intensity. All variables were entered as factors into the model against the response, backwards elimination removing insignificant variables to provide the strongest model at $\alpha < 0.05$. Steps were analysed to assess when independent variables were removed (Hawkins, 2014; Wheater *et al.,* 2011). Associated statistics were analysed to further confirm normality. Variance Inflation Factor (VIF) was required to be <5 to remove the possibility of multicollinearity, where two variables are closely associated outside of the response factor (Bass, 2007). Standard error of coefficients was viewed acceptable if <2, identifying low variation in the figures the coefficients of the model predicts. A high F - value explains the result is less likely to be due to chance alone and supports the response variables relationship with independent variables (Bass, 2007; Hawkins, 2014).

Plant heights were explanatory x variables that were entered as means. All other explanatory variables were entered as the actual result measured. Normality was checked for each stepwise regression model via a residual vs fitted values plot. Trends to identify multicollinearity were analysed, ideally wanting random distribution of residuals around the fit line. Large residuals observed were checked and taken into consideration. If large residuals occurred, the datasets were considered normal due to the large numbers of data placed into each model (Khan, 2013).

5.1.4.3. Shannon-Weiner Diversity Index

A species richness index, Shannon-Weiner Diversity Index (H'), for prey / crop pests central to this investigation (cereal Aphididae of *R. padi, M. dirhodum* and *S. avenae,* and *S. mosellana*) in the different tilled areas was established from data collated in fieldwork, at times field was in crop (Öberg *et al.,* 2008). H' was established from the natural log (LogN). The values used for the diversity index came from g-vac sampling only. The use of a diversity index allowed the investigation into the relationship between *T. tenuis* and prey abundance alongside soil tillage intensity and how this corresponds to Linyphiidae activity. Species evenness (J') was calculated from the figures of prey recorded in each tilled area, this figure analysed the variance in numbers of the prey identified, allowing differences in prey distribution within the soil tillage intensities to be understood. A maximum Shannon-Weiner Diversity Index (H') Max was calculated for the entire field to understand the maximum potential diversity that the prey recorded from the field could have. The values for the index were input manually into Excel for Microsoft Windows10$^{©}$ and formulae applied (Beauchamp, 2016; Wheater *et al.,* 2011). This data was found to be normal, thus a one-way ANOVA was applied for analysis of significance of means with Minitab18$^{©}$. Tukey was utilised as a multiple comparison method.

5.1.5. Results

The results follow the events that were taking place within the main field. Firstly, all the data collected at the time when the field was out of crop (fallow and after primary and secondary cultivation) and secondly from the sampling that had taken place when the field was in crop (seeded with *H. vulgare*) (*Table 5.1.1.*). This period was split into two distinct stages for the analysis, the Early Stage (this incorporated GS from 11 – 15 and GS 33 – 37) and the Late Stage (GS 55 – GS 65 and GS 83 – GS 93) (*Table 5.1.1.*). Data from the two seasons sampled (2016 / 2017 and 2017 / 2018) were placed together.

Within each stage of the field (in and out of crop), differences in landscape features of the field that were measured in each soil tillage intensity were examined for significance. The occurrence of three main dependant variables were then investigated: anchor point height, thread length and web area. Anchor point height and thread length were split into whether they belonged to threads inside webs (support treads) and threads outside webs (bridge threads), due to the different function for *T. tenuis* of these two threads (*Section 2.1.2.* and *Section 2.1.3.3.*). Other variables measured were then analysed with correlations. When the field was out of crop, results are reported of the data collected immediately after the field had been cultivated (primary) by the disc harrow (*Section 3.1.3.4.*).

5.1.5.1. Out of Crop - Fallow and After Primary and Secondary Cultivation

5.1.5.1.1. Summary of Results

- Significantly greater medians of upright stubble density, straw mass and volunteer plant density were found in Direct Drill (*Figure 5.1.1. Figure 5.1.2. & Figure 5.1.4.*).

Fallow

- Mean rank anchor point height outside webs was significantly higher (*Figure 5.1.5.*).
- Straw mass was significantly positively correlated to support thread length (*Table 5.1.12*).
- Anchor point height of bridge threads was significantly positively correlated to upright stubble density (*Table 5.1.4.*).
- Significantly higher mean rank anchor point height was found attached to upright stubble in all soil tillage intensities (*Figure 5.1.6*.). Anchor point of support threads and upright stubble density were significantly positively correlated (*Table 5.1.3*.).
- Volunteer plant density was significantly positively correlated to anchor point height of support threads (*Table 5.1.3*.). Volunteer plant and upright stubble density were significantly negatively correlated to support thread length (*Table 5.1.12*).
- Bridge thread length was significantly positively correlated to number of *T. tenuis* rappelling (*Table 5.1.13*.).

Primary Cultivation

- Mean rank anchor point height outside of webs was significantly higher than inside webs in Conventional (*Figure 5.1.7*.). Mean rank anchor point height of support threads was significantly lower attached to straw and soil than upright stubble in Conventional (*Figure 5.1.8a*.).
- Straw mass was significantly negatively correlated to bridge thread length (*Table 5.1.13*.).
- Mean rank anchor point height of bridge threads was significantly higher attached to upright stubble for Direct Drill than attached to straw in Conventional and Direct Drill Managed (*Figure 5.1.8b*.).
- Mean soil clod height and support thread length were significantly positively correlated (*Table 5.1.12*.).
- Anchor point height and length of bridge threads were significantly positively correlated to number of *T. tenuis* rappelling (*Table 5.1.4. & Table 5.1.13*.).
- Mean abdomen length, upright stubble density and straw mass were significantly positively correlated to anchor point height of support threads (*Table 5.1.3*.).
- Wind speed and anchor point height of bridge threads were significantly positively correlated (*Table 5.1.5*.).

Secondary Cultivation

- Significant difference in mean rank anchor point height out of webs was found between Conventional and Direct Drill Managed (*Figure 5.1.9.*).
- Mean rank anchor point height of bridge threads attached to upright stubble and straw were significantly different in Direct Drill Managed (*Figure 5.1.10b.*). For support threads homogeneity was found for Direct Drill and Direct Drill Managed in mean rank anchor point height attached to upright stubble and straw (*Figure 5.1.10a.*).
- Anchor point height of support threads was significantly positively correlated to upright stubble density and straw mass (*Table 5.1.3.*).
- Mean soil clod height was significantly negatively correlated to anchor point height in webs (*Table 5.1.3.*), and significantly positively correlated to support thread length (*Table 5.1.12.*).
- Straw mass was significantly negatively correlated to support thread length (*Table 5.1.12.*).
- Number of female *T. tenuis* was significantly positively correlated to length of support threads (*Table 5.1.3. & Table 5.1.12.*).
- Mean abdomen length was significantly negatively correlated to anchor point height of support threads (*Table 5.1.3.*).

Immediately After Primary Cultivation

- Thread length out of webs for Direct Drill was significantly longer (*Figure 5.1.12.*).
- The attachment material of upright stubble identified the significantly higher mean rank anchor point height inside and outside of webs for Direct Drill (*Figure 5.1.11*).

5.1.5.1.2. Field Landscape Features

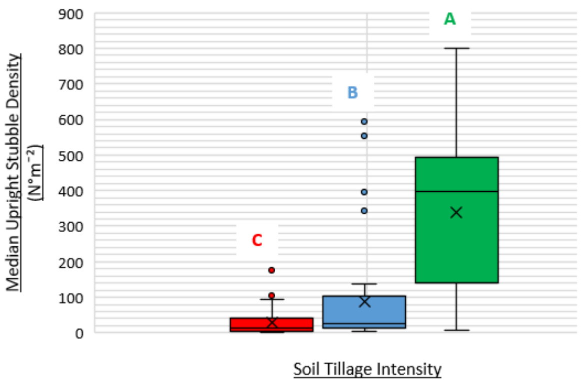


Figure 5.1.1: Median upright stubble density (N°m^{-2}) in the differing soil tillage intensity, for field when fallow and after primary and secondary cultivation. (df = 2, Adjusted for ties H - 44.29, P - 0.001, n = 114). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional (n = 38), Direct Drill Managed (n = 38), Direct Drill (n = 38)).

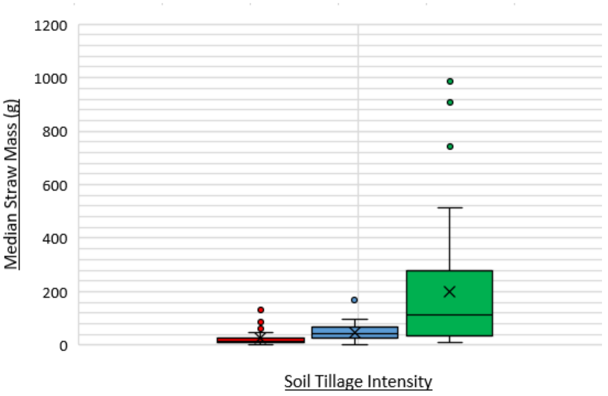


Figure 5.1.2: Median straw mass (g) in the differing soil tillage intensity, for field when fallow and after primary and secondary cultivation. (df = 2, Adjusted for ties H - 41.21, P - 0.001, n = 132). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional (n = 44), Direct Drill Managed (n = 44), Direct Drill (n = 44)).

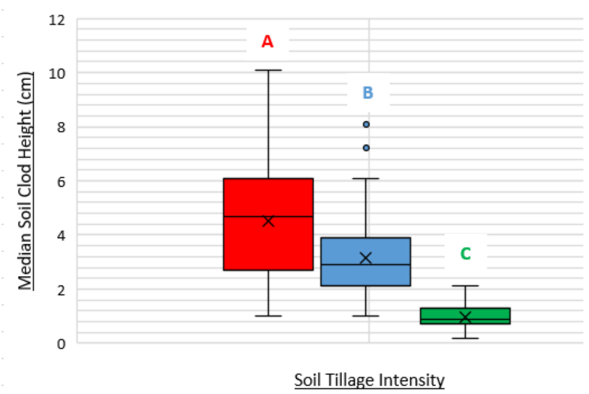


Figure 5.1.3: Median soil clod height (cm) in the differing soil tillage intensity, for field when fallow and after primary and secondary cultivation. (df = 2, Adjusted for ties H - 136.58, P - 0.001, n = 225). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional (n = 75), Direct Drill Managed (n = 75), Direct Drill (n = 75)).

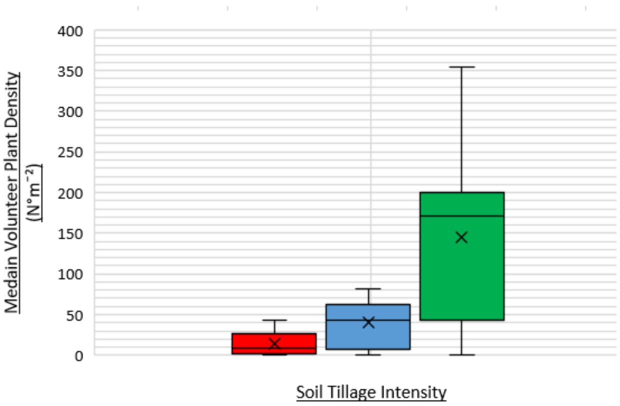


Figure 5.1.4: Median volunteer plant density (N°m^{-2}) in the differing soil tillage intensity, for field when fallow and after primary and secondary cultivation. (df = 2, Adjusted for ties H - 12.05, P - 0.002, n = 36). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional (n = 12), Direct Drill Managed (n = 12), Direct Drill (n = 12)).

The significantly greater median density for upright stubble was recorded in the Direct Drill (*Figure 5.1.1.).* The greatest variability within the dataset was established in the Direct Drill tillage, much of this variability found in the top 25% of data. The greater dispersion of values was established between the lower quartile and median within the inter-quartile range.

Straw mass gained from the Direct Drill soil tillage was skewed in a positive upwards trend where most dispersion recorded was identified in the third, upper quartile (*Figure 5.1.2*.). The significantly greater median straw mass found with Direct Drill.

A significantly greater median was identified within the Conventional soil tillage for mean soil clod height measured, the significantly lower median was measured within the Direct Drill soil intensity (*Figure 5.1.3*.).

The significantly greater median of volunteer plant density was measured within the Direct Drill intensity and Conventional held the significantly lower median volunteer plant density (*Figure 5.1.4*.). Similar in trend to Figure 5.1.1., the greater variability was found within the top 25% of data for Direct Drill.

5.1.5.1.3. Anchor Point Height

Table 5.1.3: Correlations of independent variables measured in the field with the dependant variable of anchor point height (cm) inside webs (of support threads) for field when fallow and after primary and secondary cultivation. (relates to significant with α <0.05).*

	Fallow			**Primary Cultivation**			**Secondary Cultivation**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**	**(Rho)**	***P***	**n**
Mean Abdomen Length (mm)	0.116	0.169	142	0.716	0.001*	136	-0.385	0.001*	108
Mean Soil Clod Height (cm)	0.005	0.944	205	-0.103	0.071	33	-0.207	0.022*	124
Mean Upright Stubble Height (cm)	-0.014	0.870	133	0.593	0.001*	147	0.602	0.001*	32
Number of Female *T. tenuis*	0.243	0.001*	280	0.068	0.367	179	-0.212	0.008*	155
Number of Male *T. tenuis*	0.087	0.147	280	0.073	0.295	179	-0.094	0.065	155
Number of *T. tenuis* Rappelling	0.134	0.025*	280	0.323	0.001*	180	0.099	0.053	155
Straw Mass (g)	-0.038	0.673	142	0.777	0.001*	180	0.337	0.001*	155
Upright Stubble Density (N^{o}m^{-2})	0.395	0.001*	413	0.734	0.001*	180	0.363	0.001*	155
Volunteer Plant Density (N^{o}m^{-2})	0.169	0.019*	192	0.121	0.053	33	0.339	0.001*	124

After cultivations and when the field was fallow, upright stubble density was significantly positively correlated to anchor point heights measured in webs (*Table 5.1.3.*). Straw mass and mean upright stubble height were further significantly positively correlated to anchor point height of support threads when the field had recently undergone primary and secondary cultivations. After secondary cultivation and when the field was fallow, anchor point height within webs was significantly positively correlated to volunteer plant density. Mean soil clod height was found to be significantly negatively correlated to the anchor point height of webs when the field had undergone secondary cultivation. Number of female *T. tenuis* recorded was significantly positively correlated, when the field was fallow, and was significantly negatively correlated after secondary cultivation. Significant positive correlation existed between the mean abdomen length of *T. tenuis* and the anchor point height inside webs at times the field had undergone primary cultivation and significant negative correlation after secondary cultivation. Significant positive correlation existed with anchor points of support threads and the number of *T. tenuis* observed rappelling after primary cultivation and at times of fallow.

Table 5.1.4: Correlations of independent variables measured in the field with the dependant variable of anchor point height (cm) outside of webs (of bridge threads) for field when fallow and after primary and secondary cultivation. (relates to significant with α <0.05).*

	Fallow			**Primary Cultivation**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**
Mean Upright Stubble Height (cm)	0.089	0.068	933	0.617	0.001*	1587
Number of Female *T. tenuis*	0.733	0.001*	99	-0.509	0.001*	1211
Number of Male *T. tenuis*	0.731	0.001*	99	-0.241	0.001*	1211
Number of *T. tenuis* Rappelling	0.056	0.079	99	0.597	0.001*	1211
Upright Stubble Density (N°m^{-2})	0.733	0.001*	933	0.248	0.001*	1955

Number of female *T. tenuis* and male *T. tenuis* was significantly positively correlated to anchor point height of bridge threads when the field was fallow and significantly negatively correlated when the field had undergone primary cultivation (*Table 5.1.4*.). Upright stubble density recorded was significantly positively correlated in times of fallow and after primary cultivation. Mean upright stubble height and number of *T. tenuis* observed to be rappelling were significantly positively correlated when the field had undergone primary cultivation only.

There was no significant correlation recorded at times the field had undergone secondary cultivation between anchor point height out of webs and any independent variable measured.

Table 5.1.5: Correlations of wind speed (kmh^{-1}) with the dependant variable of anchor point height (cm) outside of webs (of bridge threads) and inside webs (of support threads) for field when fallow and after the field had undergone primary and secondary cultivation. (relates to significant with α <0.05).*

	Out of Web			**In Web**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**
Wind Speed (kmh^{-1})	0.280	0.001*	289	-0.038	0.453	385

At times of fallow and after cultivations (primary and secondary) collectively, wind speed was only significantly positively correlated to anchor point height of bridge threads (*Table 5.1.5*).

Data for wind speed collected in times of fallow and after primary and secondary cultivation was analysed against anchor point height (of both support and bridge threads) together due to no significance identified when variables were analysed in their respective sampling times.

Table 5.1.6: Response of rank anchor point height and factors of soil tillage intensity and inside or outside of webs, for field when fallow (n = 1345). (relates to significant with α <0.05).*

Categorical Predictor	**Df**	***H***	***P***
Soil Tillage Intensity	2	19.654	0.001*
In / Out of Web	1	513.633	0.001*
Interaction: Soil Tillage Intensity * In / Out of Web	2	22.172	0.001*

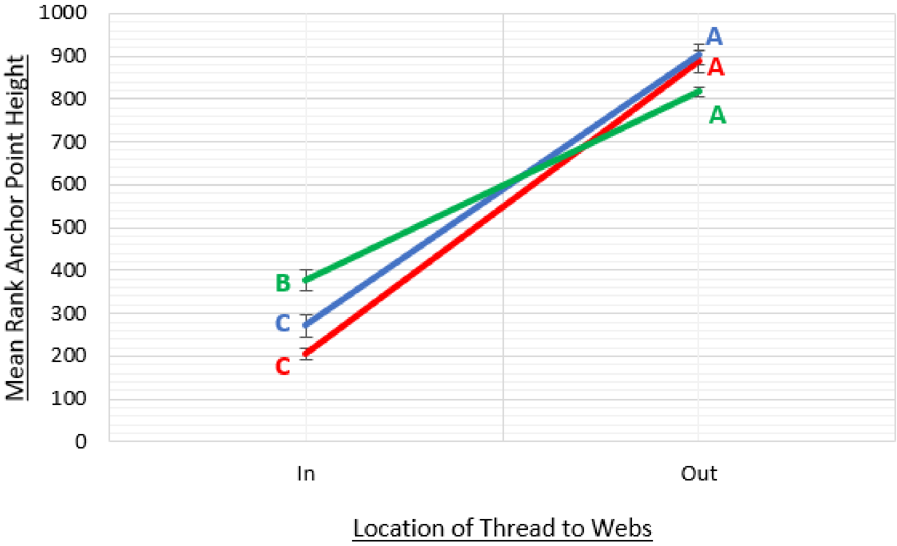


Figure 5.1.5: Interaction of mean rank anchor point height, soil tillage intensity and inside or outside of webs, for field when fallow (n = 1345). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional In ±s.e.13.616 (n = 112), Conventional Out ±s.e.25.659 (n = 132), Direct Drill Managed In ±s.e.24.552 (n = 110), Direct Drill Managed Out ±s.e.24.370 (n = 114), Direct Drill In ±s.e.25.614 (n = 191), Direct Drill Out ±s.e.11.771 (n = 686)). (Points that do not share the same letter are significantly different at the p<0.05 level).

Heterogeneity was identified in the interaction of mean rank of anchor point height with soil tillage intensity and whether threads were inside or outside of the web (*Figure 5.1.5*. & *Table 5.1.6*.). The mean rank anchor point for all soil tillage intensities was significantly higher in threads that were outside of webs used for rappelling. Direct Drill mean rank anchor point height of support threads was further significantly higher than that of Direct Drill Managed and Conventional.

Table 5.1.7: Response of rank anchor point height inside webs (of support threads), and factors of soil tillage intensity and anchor point attachment material, for field when fallow (n = 372). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	9.673	0.038*
Anchor Point Attachment Material	2	74.235	0.001*
Interaction: Soil Tillage Intensity * Anchor Point Attachment Material	4	12.454	0.014*

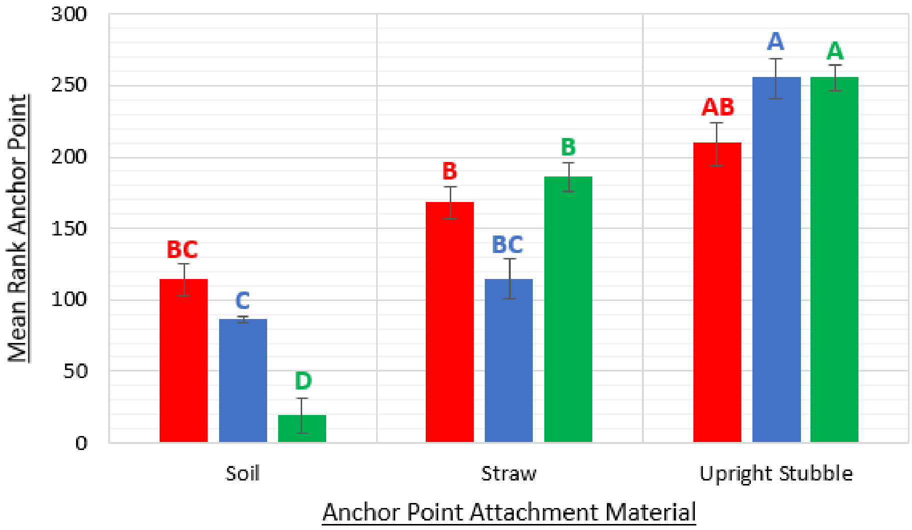


Figure 5.1.6: Interaction of mean rank anchor point height inside webs (of support threads), soil tillage intensity and anchor point attachment material, for field when fallow (n = 372). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Soil ±s.e.11.321 (n = 39), Conventional Straw ±s.e.11.197 (n = 23), Conventional Upright Stubble ±s.e.15.070 (n = 38), Direct Drill Managed Soil ±s.e.2.098 (n = 31), Direct Drill Managed Straw ±s.e.13.780 (n = 25), Direct Drill Managed Upright Stubble ±s.e.14.006 (n = 40), Direct Drill Soil ±s.e.12.174 (n = 22), Direct Drill Straw ±s.e.10.016 (n = 34), Direct Drill Upright Stubble ±s.e.9.202 (n = 120)). (Points that do not share the same letter are significantly different at the p<0.05 level).

There was significance noted within the mean rank anchor point height for support threads and the interaction between soil tillage intensity and the attachment material (*Figure 5.1.6.* & *Table 5.1.7.*). Mean rank anchor point height attached to upright stubble was significantly higher for Direct Drill Managed and Direct Drill than that found attached to straw and upright stubble within all three soil tillage intensities.

No model was established for mean anchor point height of bridge threads as no bridge thread was found attached to straw within Direct Drill Managed and no bridge thread recorded attached to soil in the Direct Drill soil tillage.

Table 5.1.8: Response of rank anchor point height and factors of soil tillage intensity and inside or outside of webs, for field after primary cultivation (n = 1096). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	141.818	0.001*
In / Out of Web	1	24.959	0.001*
Interaction: Soil Tillage Intensity * In / Out of Web	2	5.265	0.070

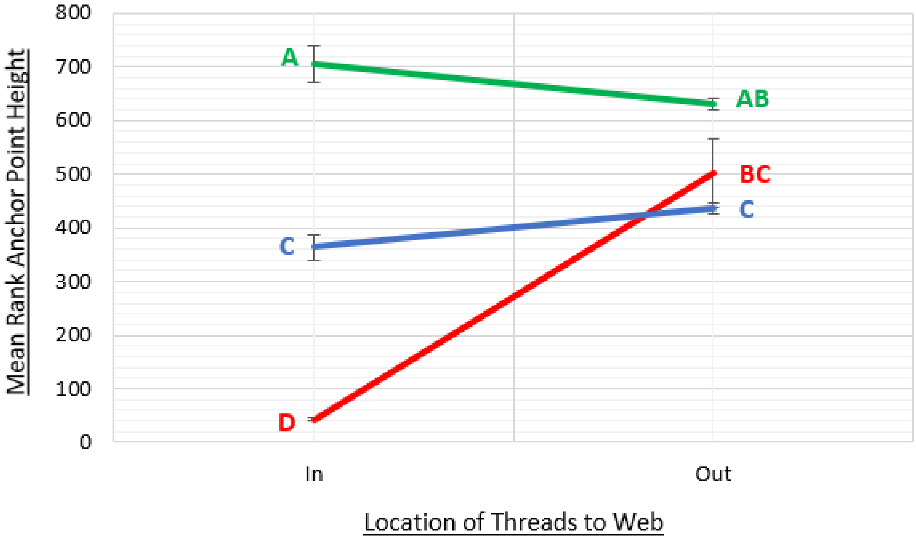


Figure 5.1.7: Interaction of mean rank anchor point height, soil tillage intensity and inside or outside of webs, for field after primary cultivation (n = 1096). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional In ±s.e.3.001 (n = 80), Conventional Out ±s.e.63.910 (n = 30), Direct Drill Managed In ±s.e.24.611 (n = 35), Direct Drill Managed Out ±s.e.11.064 (n = 177), Direct Drill In ±s.e.34.663 (n = 64), Direct Drill Out ±s.e.11.484 (n = 710)). (Points that do not share the same letter are significantly different at the p<0.05 level).

No Significance existed in the interaction of this model (*Figure 5.1.7. & Table 5.1.8.*). When the mean rank anchor point height was found inside webs, the significantly lower mean rank was found in the soil tillage intensity of Conventional, whereas the significantly higher mean rank anchor point height was identified in the Direct Drill tillage. Regarding mean rank anchor point heights outside of webs, the significantly higher mean rank was found in Direct Drill compared to that of Direct Drill Managed. Significance was identified only within the Conventional soil tillage intensity between the mean rank anchor point heights inside or outside of webs. The mean rank for this tillage was significantly lower for anchor points recorded inside webs than outside of webs.

Table 5.1.9a: Response of rank anchor point height inside webs (of support threads) and factors of soil tillage intensity and anchor point attachment material, for field after primary cultivation (n = 178). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	14.523	0.001*
Anchor Point Attachment Material	2	23.030	0.001*
Interaction: Soil Tillage Intensity * Anchor Point Attachment Material	4	5.528	0.043*

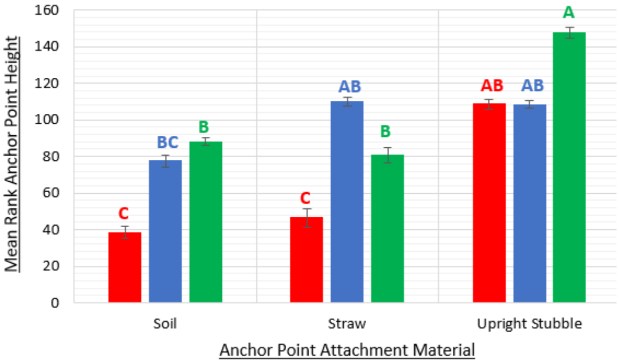


Figure 5.1.8a: Interaction of mean rank anchor point height inside webs (of support threads), soil tillage intensity and anchor point attachment material, for field after primary cultivation. (n = 178). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Soil ±s.e.3.207 (n = 48), Conventional Straw ±s.e.5.040 (n = 32), Conventional Upright Stubble ±s.e.2.501 (n = 2), Direct Drill Managed Soil ±s.e.3.279 (n = 3), Direct Drill Managed Straw ±s.e.2.500 (n = 3), Direct Drill Managed Upright Stubble ±s.e.2.078 (n = 24), Direct Drill Soil ±s.e.2.001 (n = 2), Direct Drill Straw ±s.e.3.931 (n = 6), Direct Drill Upright Stubble ±s.e.2.831 (n = 58)). (Points that do not share the same letter are significantly different at the p<0.05 level).

Table 5.1.9b: Response of rank anchor point height outside of webs (of bridge threads) and factors of soil tillage intensity and anchor point attachment material, for field after primary cultivation (n = 889). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	52.120	0.001*
Anchor Point Attachment Material	1	21.484	0.001*
Interaction: Soil Tillage Intensity * Anchor Point Attachment Material	2	8.867	0.012*

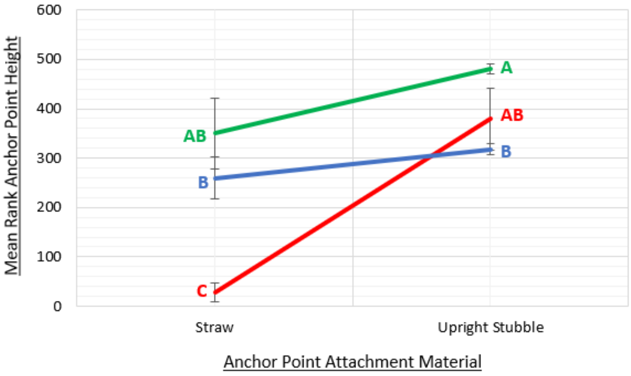


Figure 5.1.8b: Interaction of mean rank anchor point height outside of webs (of bridge threads), soil tillage intensity and anchor point attachment material, for field after primary cultivation. (n = 889). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Straw ±s.e.18.648 (n = 3), Conventional Upright Stubble ±s.e.62.300 (n =25), Direct Drill Managed Straw ±s.e.41.934 (n = 17), Direct Drill Managed Upright Stubble ±s.e.10.150 (n = 149), Direct Drill Straw ±s.e.71.478 (n = 18), Direct Drill Upright Stubble ±s.e.10.150 (n = 677)). (Points that do not share the same letter are significantly different at the p<0.05 level).

Significant difference between mean rank anchor point height inside webs existed between the soil tillage intensity and the attachment material of the anchor point height (*Figure 5.1.8a*. & *Table 5.1.9a*.). The significantly higher mean rank anchor point height was attached to the material upright stubble in the Direct Drill soil tillage compared to that attached to straw and soil in the soil tillage intensities of Conventional and Direct Drill and significantly higher than attached to the material of soil within Direct Drill Managed.

For mean rank anchor point height for bridge threads significance was also found in the interaction of attachment material and soil tillage intensity (*Figure 5.1.8b*. & *Table 5.1.9b*.). The mean rank anchor point height for Conventional attached to straw and Direct Drill Managed attached to straw and upright stubble were significantly lower than the mean rank anchor point height attached to upright stubble for Direct Drill. The attachment material of soil was removed as no bridge threads were recorded attached to this material within Direct Drill Managed.

Table 5.1.10: Response of rank anchor point height and factors of soil tillage intensity and inside or outside of webs, for field after secondary cultivation (n = 259). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	6.801	0.033*
In / Out of Web	1	74.040	0.001*
Interaction: Soil Tillage Intensity * In / Out of Web	2	7.377	0.025*

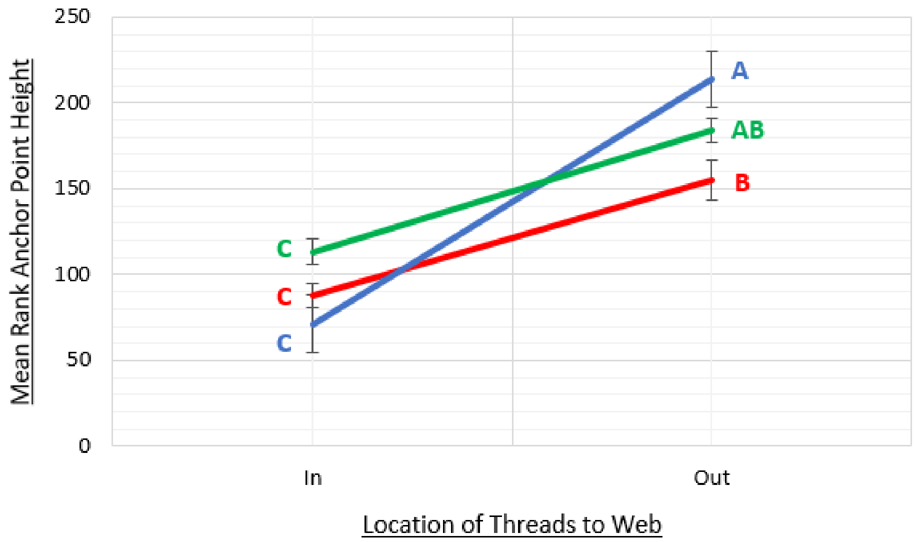


Figure 5.1.9: Interaction of mean rank anchor point height, soil tillage intensity and inside or outside of webs, for field after secondary cultivation. (n = 259). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional In ±s.e.6.979 (n = 76), Conventional Out ±s.e.11.685 (n = 30), Direct Drill Managed In ±s.e.16.587 (n = 19), Direct Drill Managed Out ±s.e.16.450 (n = 16), Direct Drill In ±s.e.7.617 (n = 59), Direct Drill Out ±s.e.7.095 (n = 59)). (Points that do not share the same letter are significantly different at the p<0.05 level).

In all three soil tillage intensities examined, the significantly lower mean rank anchor point height belonged to threads found inside of webs, following the trend found when the field was fallow (*Figure 5.1.9., Table 5.1.10. & Figure 5.1.5.*). The greater significant mean rank anchor point height outside of webs, belonged to the soil tillage intensity of Direct Drill Managed, and the lower found within Conventional.

Table 5.1.11a: Response of rank anchor point height inside webs (of support threads) and factors of soil tillage intensity and anchor point attachment material, for field after secondary cultivation (n = 239). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	0.462	0.794
Anchor Point Attachment Material	2	34.515	0.001*
Interaction: Soil Tillage Intensity * Anchor Point Attachment Material	4	11.773	0.019*

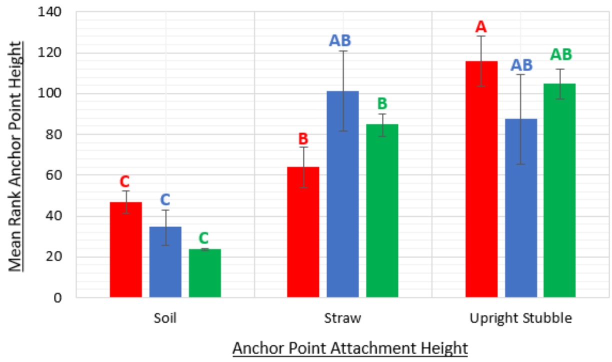


Figure 5.1.10a: Interaction of mean rank anchor point height inside webs (of support threads), soil tillage intensity and anchor point attachment material, for field after secondary cultivation (n = 156). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Soil ±s.e.5.514 (n = 41), Conventional Straw ±s.e.9.880 (n = 7), Conventional Upright Stubble ±s.e.12.320 (n = 28), Direct Drill Managed Soil ±s.e.8.820 (n = 13), Direct Drill Managed Straw ±s.e.19.718 (n = 6), Direct Drill Managed Upright Stubble ±s.e.21.779 (n = 2), Direct Drill Soil ±s.e.0.500 (n = 2), Direct Drill Straw ±s.e.5.673 (n = 29), Direct Drill Upright Stubble ±s.e.7.508 (n = 28)). (Points that do not share the same letter are significantly different at the p<0.05 level).

Table 5.1.11b: Response of rank anchor point height outside of webs (of bridge threads) and factors of soil tillage intensity and anchor point attachment material, for field after secondary cultivation (n = 82). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	0.146	0.930
Anchor Point Attachment Material	1	10.647	0.001*
Interaction: Soil Tillage Intensity * Anchor Point Attachment Material	2	3.164	0.206

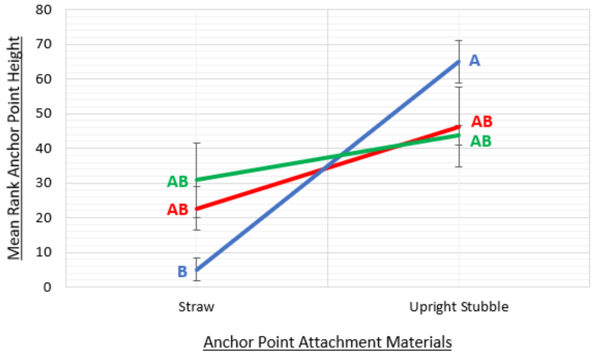


Figure 5.1.10b: Interaction of mean rank anchor point height outside of webs (of bridge threads), soil tillage intensity and anchor point attachment material, for field after secondary cultivation (n = 82). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Straw ±s.e.6.185 (n = 10), Conventional Upright Stubble ±s.e.11.431 (n = 6), Direct Drill Managed Straw ±s.e.3.250 (n = 6), Direct Drill Managed Upright Stubble ±s.e.6.137 (n = 3), Direct Drill Straw ±s.e.10.748 (n = 8), Direct Drill Upright Stubble ±s.e.2.913 (n = 49)). (Points that do not share the same letter are significantly different at the p<0.05 level).

Interaction between mean rank anchor point height for support threads, anchor point height attachment material and soil tillage intensity was found to be significant (*Figure 5.1.10a. & Table 5.1.11a*.). The significant higher mean rank anchor point height was identified attached to upright stubble compared to the mean rank anchor point height calculated when attached to soil between all soil tillage intensities. Further the mean rank anchor point height for Conventional attached to the material of upright stubble was significantly higher than that found attached to straw within Conventional and Direct Drill.

Significance only existed between the term of anchor point attachment materials (*Figure 5.1.10b. & Table 5.1.11b.*). Significant difference was found between the mean rank anchor point height for bridge threads attached to the materials straw and upright stubble within the soil tillage Direct Drill Managed, the significantly higher found attached to upright stubble. Soil was removed from the model due to no bridge threads recorded attached to soil within the Direct Drill tillage.

5.1.5.1.4. Thread Length

Table 5.1.12: Correlations of independent variables measured in the field with the dependant variable thread length (mm) inside webs (of support threads) for field when fallow and after primary and secondary cultivation. (relates to significant with α <0.05).*

	Fallow			**Primary Cultivation**			**Secondary Cultivation**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**	**(Rho)**	***P***	**n**
Mean Abdomen Length (mm)	0.008	0.922	144	-0.270	0.002*	136	0.028	0.787	97
Mean Soil Clod Height (cm)	0.107	0.165	132	0.372	0.014*	44	0.270	0.001*	198
Number of Female *T. tenuis*	0.289	0.001*	286	0.157	0.042*	169	0.163	0.041*	159
Number of Male *T. tenuis*	0.203	0.001*	286	0.184	0.018*	169	0.127	0.111	-159
Number of *T. tenuis* Rappelling	0.054	0.363	285	0.283	0.001*	169	0.101	0.204	159
Straw Mass (g)	0.321	0.001*	286	0.103	0.185	169	-0.193	0.015*	159
Upright Stubble Density (N°m^{-2})	-0.262	0.001*	430	-0.093	0.233	169	-0.194	0.014*	159
Volunteer Plant Density (N°m^{-2})	-0.313	0.001*	198	-0.305	0.046*	44	0.113	0.202	128

Length from support threads was significantly negatively correlated to the upright stubble density recorded when the field was in fallow and after secondary cultivation (*Table 5.1.12.*). Straw mass was further significantly negatively correlated with thread length inside webs when the field had undergone secondary cultivation, however significantly positively correlated when the field was fallow. Volunteer plant density showed significant negative correlation to thread length inside webs when the field had been primary cultivated and when the field was fallow. Mean soil clod height was significantly positively correlated to support thread lengths after primary and secondary cultivation. The number of female and male *T. tenuis* recorded were significantly positively correlated to support threads inside webs after primary cultivation and in times of fallow. Whereas, after secondary cultivation the number of female *T. tenuis* only was significantly positively correlated to length of support threads. The number of *T. tenuis* observed rappelling was significantly positively correlated, and mean abdomen length was significantly negatively correlated, to thread length inside of webs when the field was primary cultivated.

Table 5.1.13: Correlations of independent variables measured in the field with the dependant variable thread length (mm) outside of webs (of bridge threads) for field when fallow and after primary and secondary cultivation. (relates to non-significant with α <0.05).*

	Fallow			**Primary Cultivation**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**
Mean Abdomen Length (mm)	0.028	0.845	28	-0.098	0.036*	467
Number of *T. tenuis* Rappelling	0.412	0.004*	48	0.124	0.003*	576
Straw Mass (g)	0.046	0.271	576	-0.105	0.012*	576
Volunteer Plant Density (N°m^{-2})	-0.117	0.140	156	-0.176	0.042*	134

Bridge thread length was significantly negatively correlated to straw mass, volunteer plant density and mean *T. tenuis* abdomen length after primary cultivation (*Table 5.1.13*.). Number of *T. tenuis* recorded rappelling was found to be significantly positively correlated to length of bridge threads in times of fallow and after primary cultivation.

No analysis is represented for secondary cultivation, as with the variable anchor point height no significance was identified (*Table 5.1.4*.).

5.1.5.1.5. Immediately After Primary Cultivation

Table 5.1.14: Response of mean rank anchor point height and factors of inside and outside of webs for Direct Drill and anchor point attachment material, for field immediately after primary cultivation (n = 223). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
In / Out of Web for Direct Drill	2	1.795	0.180
Anchor Point Attachment Material	1	11.497	0.003*
Interaction: In / Out of Web for Direct Drill * Anchor Point Attachment Material	2	1.580	0.454

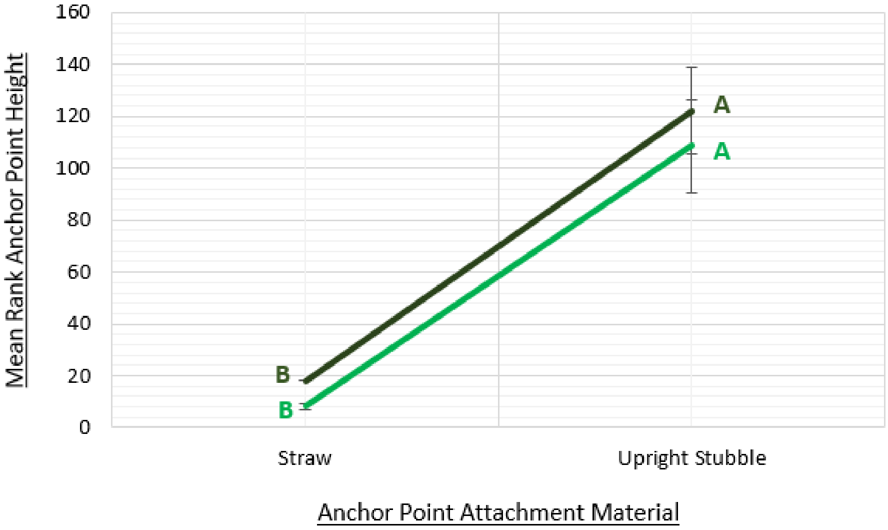


Figure 5.1.11: Interaction of mean rank anchor point height, inside and outside of webs for Direct Drill and anchor point attachment material, immediately after primary cultivation (n = 223). (Direct Drill In = Green, Direct Drill Out = Dark Green). (Direct Drill In Straw ±s.e.1.437 (n = 13), Direct Drill In Upright Stubble ±s.e.17.834 (n = 19), Drill Out Straw ±s.e.0 (n = 1), Direct Drill Out Upright Stubble ±s.e.16.746 (n = 190)). (Points that do not share the same letter are significantly different at the p<0.05 level).

The mean rank anchor point height inside and outside of webs was significantly higher attached to upright stubble than the mean rank anchor point of support threads attached to straw (*Figure 5.1.11. & Table 5.1.14.*). No significance existed within the interaction.

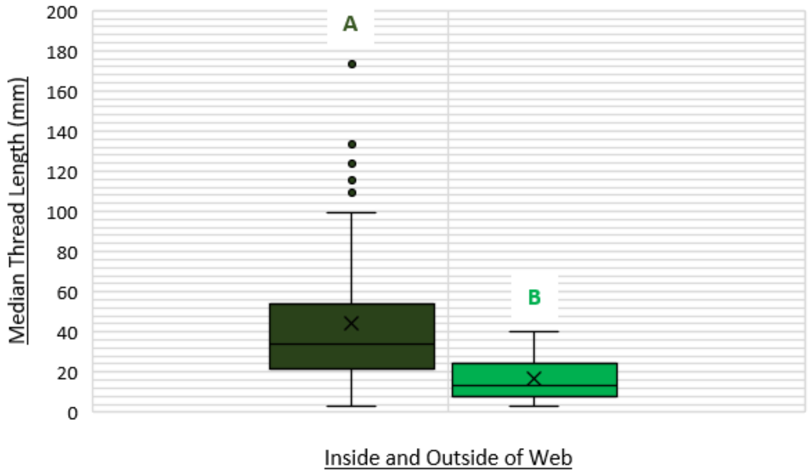


Figure 5.1.12: Median thread length (mm), inside and outside of webs for Direct Drill, immediately after primary cultivation (df = 2, Adjusted for ties H - 32.21, P - 0.001, n = 137). (Direct Drill Out = Dark Green, Direct Drill In = Green). (Out (n = 105), In (n = 34)).

There was a significant difference between the medians of the lengths of support and bridge threads identified in the Direct Drill tillage immediately after primary cultivation, threads were significantly longer for bridge threads (*Figure 5.1.12.*). Both median thread lengths inside or outside of webs have data positively skewed and identify the greater range of the data existed in the third quartile.

5.1.5.2. In Crop (Early and Late Growth Stages)

5.1.5.2.1. Summary of Results

Early Growth Stages

- Upright stubble held bridge threads that had a significantly higher mean rank anchor point height than plant within Direct Drill Managed (*Figure 5.1.14.*).
- Upright stubble density was significantly positively correlated to anchor point height of support threads (*Table 5.1.15*).
- Mean rank anchor point height of bridge threads was significantly higher with each soil tillage intensity (*Figure 5.1.13.*).
- Significantly greater Shannon-Weiner Diversity Index and species evenness were identified in Conventional tillage (*Figure 5.1.18. & Figure 5.1.19.*).

- Plant density and anchor point height of bridge threads were significantly positively correlated (*Table 5.1.16.*). This variable was significantly positively correlated to length and anchor point height of support threads (*Table 5.1.15. & Table 5.1.19.*).
- Mean rank support anchor point height was significantly higher in Conventional (*Figure 5.1.13.*).
- Number of crop pests within webs held significant positive regression to the number of *T. tenuis* found under a web (*Table 5.1.20.*).
- Number of *S. mossellana* in webs were significantly negatively correlated to anchor point height and length of support threads (*Table 5.1.15. & Table 5.1.19.*). Number of *T. tenuis* in webs held significant positive correlation to anchor point height of support threads (*Table 5.1.15.*).
- Mean abdomen length was significantly positively correlated to anchor point height and length of support threads (*Table 5.1.15. & Table 5.1.19*).
- Number of *S. mosellana* and exuviae in webs and number of *S. avenae* were significantly negatively correlated to anchor point height of bridge threads (*Table 5.1.16.*). Mean abdomen length was significantly positively correlated to anchor point height of bridge threads (*Table 5.1.16.*).

Late growth stages

- Mean plant height was significantly positively correlated to anchor point height and length of support threads (*Table 5.1.15. & Table 5.1.19.*).
- Median plant height was significantly higher within Conventional (*Figure 5.1.15.*).
- Number of *S. mosellana* in webs and vegetation were significantly positively correlated to anchor point height of support threads (*Table 5.1.15.*). Number of *S. avenae* and Aphididae exuviae in webs were significantly positively correlated to support thread length (*Table 5.1.19.*).
- Number of *T. tenuis* (female and male) were significantly negatively correlated to anchor point height and length of support threads, furrow dimensions only significantly negatively correlated to length of support threads (*Table 5.1.15. & Table 5.1.19.*).
- Mean abdomen length was significant positively correlated to anchor point height of support threads (*Table 5.1.15.*).
- Number of spiderlings was significantly negatively correlated to support thread length (*Table 5.1.19.*).

Overall - When in Crop (Early and Late Growth Stages)

- Number of *T. tenuis* in web and mean plant height were significant predictors to mean abdomen length (*Table 5.1.21.*). Plant and *A. myosuroides* density were significant predictors to number of *T. tenuis* occupying webs (*Table 5.1.20.*).
- Conventional held the significantly mean rank higher anchor point height and significantly mean rank lower web area when webs contained crop pests (*Figure 5.1.16. & Figure 5.1.17.*).

5.1.5.2.2. Anchor Point Height

Table 5.1.15: Correlations of independent variables measured in the field with the dependant variable of anchor point height (cm) inside webs (of support threads) for field when in crop (early and late growth stages). (relates to significant with α <0.05).*

	Early			**Late**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**
A. myosuroides Density (N°m^{-2})	-0.085	0.346	126	-0.121	0.005*	550
Furrow Depth (cm)	-0.539	0.021*	19	-0.068	0.384	166
Mean Abdomen Length (mm)	0.434	0.001*	452	0.109	0.006*	786
Mean Plant Height (cm)	-0.087	0.102	512	0.244	0.001*	989
Number of Female *T. tenuis*	-0.009	0.804	506	-0.161	0.001*	989
Number of Male *T. tenuis*	-0.041	0.306	506	-0.196	0.001*	989
Number of *S. avenae*	0.210	0.001*	469	-0.014	0.374	635
Number of *S. mosellana*	-0.055	0.227	469	0.169	0.001*	635
Number of *S. mosellana* in Web	-0.116	0.012*	469	0.108	0.007*	635
Number of *T. tenuis* in Web	0.153	0.001*	487	0.007	0.829	989
Plant Density (N°m^{-2})	0.112	0.013*	487	-0.041	0.199	989
Upright Stubble Density (N°m^{-2})	0.591	0.001*	52	No Data Collected		

Within early stages of growth; upright stubble density, plant density, numbers of *T. tenuis* observed within the web, mean abdomen length of *T. tenuis* and numbers of *S. avenae* found after g-vac sampling held significant positive correlation with anchor point heights of support threads (*Table 5.1.15.*). For early growth stages, significant negative correlation was identified with numbers of *S. mosellana* found in the web and furrow depth. Number of *T. tenuis* (male and female) were significantly negatively correlated to anchor point height inside webs at late growth stages, alongside *A. myosuroides* density. In later growth stages, mean *T. tenuis* abdomen length, mean plant height, numbers of *S. mosellana* found in the web and collected after g-vac sampling was positively significantly correlated to anchor point inside of webs.

Table 5.1.16: Correlations of independent variables measured in the field with the dependant variable of anchor point height (cm) outside of webs (of bridge threads) for field when in crop (early growth stages). (relates to significant with α <0.05).*

	Early		
	(Rho)	***P***	**n**
Mean Abdomen Length (mm)	0.447	0.001*	464
Mean Plant Height (cm)	-0.405	0.001*	756
Number of Aphididae Exuviae in Web	-0.232	0.001*	481
Number of *S. avenae*	-0.168	0.001*	481
Number of *S. mosellana* in Web	-0.139	0.002*	481
Number of Spiderlings	-0.106	0.017*	507
Number of *T. tenuis* in Web	0.141	0.001*	507
Plant Density (N°m^{-2})	0.108	0.015*	507

Plant density, numbers of *T. tenuis* within the web and mean *T. tenuis* abdomen length were significantly positively correlated to the anchor point height of bridge threads (*Table 5.1.16.*). Significant negative correlation was identified between anchor point height outside of webs and mean plant height, number of *T. tenuis* spiderlings recorded, number of Aphididae exuviae and *S. mosellana* observed within sheet webs and number of *S. avenae* found within the sample area.

Only fourteen pieces of data (anchor point heights out of the web) were recorded for the late growth stages of *H. vulgare*. These were not reported as no viable significant correlation existed with independent variables recorded.

Table 5.1.17: Response of rank anchor point height and factors of soil tillage intensity and inside or outside of web, for field when in crop, early growth stages (n = 755). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	37.057	0.001*
In / Out of Web	1	184.651	0.001*
Interaction: Soil Tillage Intensity * In / Out of Web	2	16.400	0.001*

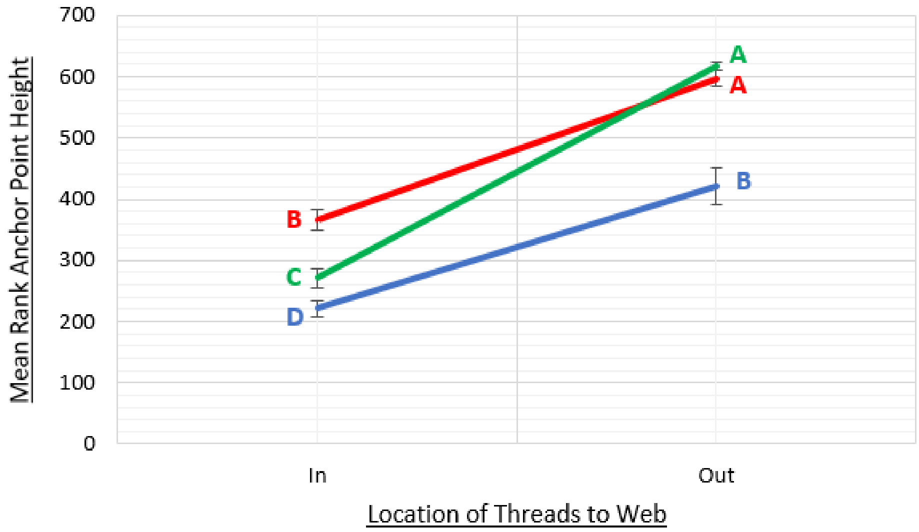


Figure 5.1.13: Interaction of rank mean anchor point height and inside or outside of webs, for field when in crop, early growth stages (n = 755). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional In ±s.e.17.227 (n = 111), Conventional Out ±s.e.13.127 (n = 44), Direct Drill Managed In ±s.e.14.142 (n = 149), Direct Drill Managed Out ±s.e.29.595 (n = 20), Direct Drill In ±s.e.15.319 (n = 257), Direct Drill Out ±s.e.6.830 (n = 174)). (Points that do not share the same letter are significantly different at P <0.05).

Conventional and Direct Drill mean rank anchor point height of bridge threads were significantly higher than the mean rank anchor point height of support threads of all three soil tillage intensities (*Figure 5.1.13 & Table 5.1.17*.). Direct Drill Managed held a significant higher mean rank anchor point height outside of webs than that found inside webs of Direct Drill Managed and Direct Drill only.

Table 5.1.18: Response of rank anchor point height outside of webs (of bridge threads) and factors of soil tillage intensity and anchor point attachment material, for field when in crop, early growth stages (n = 288). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	4.566	0.102
Anchor Point Attachment Material	1	14.969	0.001*
Interaction: Soil Tillage Intensity * Anchor Point Attachment Material	2	11.232	0.001*

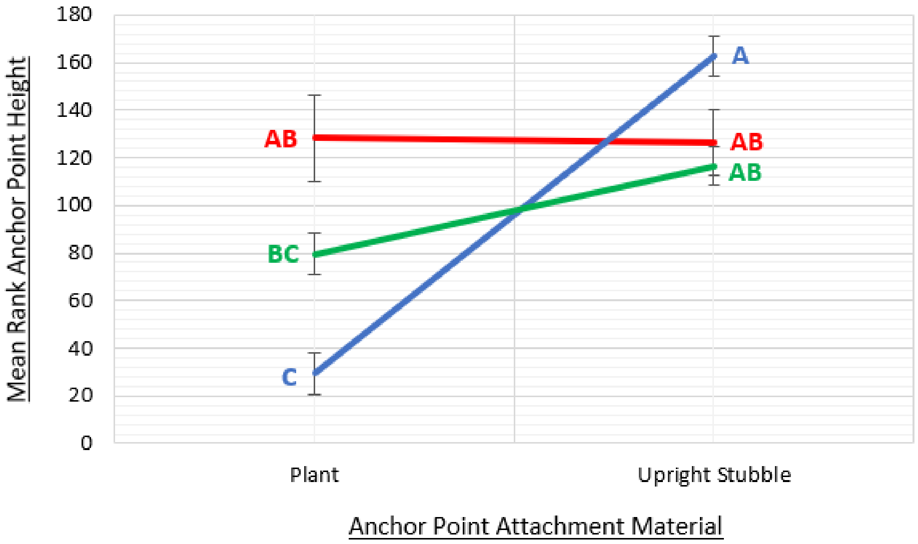


Figure 5.1.14: Interaction of mean rank anchor point height outside of webs (of bridge threads) and anchor point attachment material, for field when in crop, early growth stages (n = 228). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green) (Conventional Plant ±s.e.18.060 (n = 25), Conventional Upright Stubble ±s.e.13.820 (n = 12), Direct Drill Managed Plant ±s.e.8.920 (n = 7), Direct Drill Managed Upright Stubble ±s.e.8.240 (n = 10), Direct Drill Plant ±s.e.8.838 (n = 20), Direct Drill Upright Stubble ±s.e.8.240 (n = 154)). (Points that do not share the same letter are significantly different at P <0.05).

There was significance in interaction between mean rank anchor point height of bridge threads and the materials of plant and upright stubble within Direct Drill Managed and Direct Drill (*Figure 5.1.14. & Table 5.1.18.*). The mean rank significantly higher attached to upright stubble for Direct Drill Managed.

With only thirteen data points recorded for anchor points of bridge threads for the late growth stages of *H. vulgare,* only anchor points outside of webs at early growth stages are incorporated into an interaction plot against its retrospective attachment material.

Straw and soil were removed due to no recordings of anchor point heights inside webs attached to straw and soil within the Conventional tillage. Leaving plant and upright stubble within this model, as terms within the attachment material categorical factor, left a model with VIF >20.

5.1.5.2.3. Thread Length

*Table 5.1.19: Correlations of independent variables measured in the field with the dependant variable of thread length (mm) inside webs (of support threads) for field when in crop (early and late growth stages). (*relates to significant with α <0.05).*

	Early			**Late**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**
A. myosuroides Density (N°m^{-2})	-0.235	0.007*	134	-0.050	0.243	523
Furrow Depth (cm)	0.162	0.133	17	-0.398	0.001*	192
Furrow Width (cm)	-0.185	0.130	17	-0.383	0.001*	192
Mean Abdomen Length (mm)	0.228	0.001*	452	0.352	0.001*	923
Mean Plant Height (cm)	0.242	0.001*	516	0.599	0.001*	923
Number of Aphididae Exuviae in Web	-0.089	0.054	469	0.245	0.001*	923
Number of Female *T. tenuis*	-0.090	0.049*	485	-0.371	0.001*	923
Number of *M. dirhodum* in Web	-0.124	0.007*	469	-0.098	0.084	923
Number of Male *T. tenuis*	-0.114	0.033*	485	-0.492	0.001*	923
Number of *S. avenae*	0.227	0.001*	469	0.156	0.013*	923
Number of *S. avenae* in Web	0.018	0.701	469	0.119	0.021*	923
Number of *S. mosellana*	-0.082	0.077	469	0.336	0.001*	923
Number of *S. mosellana* in Web	-0.137	0.003*	469	-0.087	0.104	923
Number of Spiderlings	-0.038	0.400	485	-0.510	0.001*	923
Plant Density (N°m^{-2})	0.294	0.001*	485	-0.223	0.001*	923

In both growth stages (early and late), the number of female and male *T. tenuis* recorded were significantly negatively correlated to length of support threads (*Table 5.1.19*.). Plant density was significantly positively correlated to thread length inside webs at times the *H. vulgare* was in early growth stages, though significantly negatively correlated in later growth stages. Numbers of *S. mosellana* and *M. dirhodum* found in webs and *A. myosuroides* density were significantly negatively correlated to support thread length in early growth stages. Regarding later growth stages, numbers of Aphididae exuviae and *S. avenae* observed within the web, were significantly positively correlated to length of support threads. Significant negative correlation existed between number of spiderlings found in the g-vac, furrow width and depth and thread lengths of webs at the later growth stages. Significant positive correlation was identified between mean plant height, mean abdomen length of *T. tenuis* and number of *S. avenae* recorded and length of support threads at times of *H. vulgare* in early and late growth stages.

5.1.5.2.4. Overall - When in Crop (Early and Late Growth Stages)

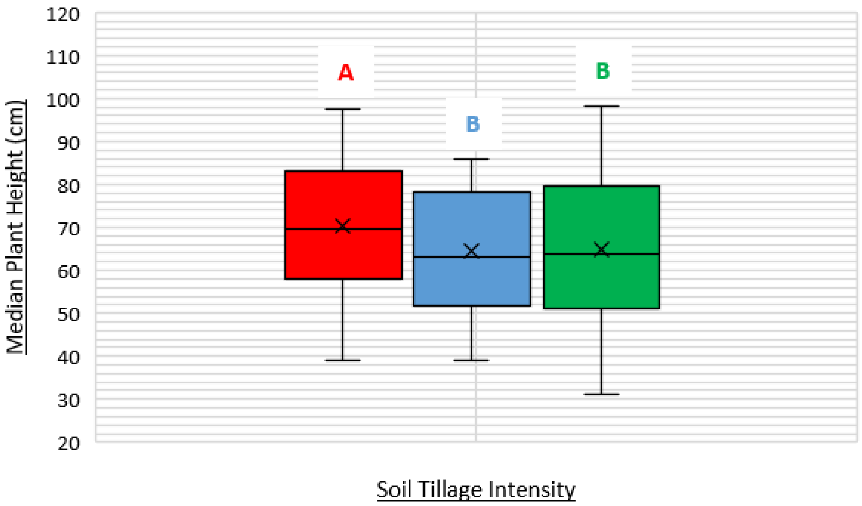


Figure 5.1.15: Median plant height (cm) in the differing soil tillage intensity, for field when the field was in crop, late growth stages (df = 2, Adjusted for ties H - 10.12, P - 0.006, n = 360). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional (n = 120), Direct Drill Managed (n = 120), Direct Drill (n = 120)).

Significantly higher median plant height was found in the Conventional area with a median of 69.9 cm (*Figure 5.1.15*.). This was 5.9 cm higher than the median of Direct Drill Managed and 6.8 cm higher than that measured in Direct Drill. For all soil tillage intensities, the greater dispersion of heights was measured in the upper quartile. Greater range in data was found in Direct Drill.

Table 5.1.20: Significant predictors to the response number of T. tenuis *in webs for field when in crop (early and late growth stages). (n = 82, R-sq - 68.11%). (*relates to significant with α <0.05).*

Continuous Predictor	**Coefficients**	**Standard Error Coefficients (SE Coeff)**	***T***	***P***	**VIF**
A. myosuroides density (N°m^{-2})	0.03134	0.00890	3.52	0.001*	1.96
Number of Crop Pests in Web	1.3111	0.0973	13.48	0.001*	4.58
Number of *T. tenuis*	0.2123	0.0386	5.50	0.001*	4.13
Plant Density (N°m^{-2})	0.03371	0.00642	5.25	0.001*	2.67

When the data from early and late growth stages of *H. vulgare* were analysed collectively it was identified that four variables were significant predictors to the response of number of *T. tenuis* in webs recorded in the field. The variables were plant density, number of *T. tenuis* (male and female combined), number of crop pests (Aphididae and *S. mosellana*) found in the web and *A. myosuroides* density. The four variables were found to have significant positive regression to number of *T. tenuis* in the web.

*Table 5.1.21: Significant predictors to the response mean abdomen length (mm) for field when in crop (early and late growth stages). (n = 79, R-sq - 58.56%). (*relates to significant with α <0.05).*

Continuous Predictor	**Coefficients**	**Standard Error Coefficients (SE Coeff)**	***T***	***P***	**VIF**
Mean Plant Height (cm)	0.006223	0.000609	10.22	0.001*	4.81
Number of Aphididae Exuviae in Web	0.003560	0.000831	20.18	0.001*	2.91
Number of Sheet Webs	0.01458	0.00170	8.59	0.001*	3.80
Number of *T. tenuis*	0.01477	0.00208	7.11	0.001*	4.06
Number of *T. tenuis* in Web	0.00845	0.00252	3.36	0.001*	3.06

The variables of number of *T. tenuis* (male and female combined), mean height of *H. vulgare*, number of sheet webs recorded, number of *T. tenuis* in the web and number of Aphididae exuviae found in the web held significant positive regression to the response of mean abdomen length of *T. tenuis* recorded in the sampled area (*Figure 5.1.21*.).

*Table 5.1.22: Response of rank anchor point height inside webs (of support threads) and factors of soil tillage intensity and presence of crop pests in web, for field when in crop (early and late growth stages) (n = 1102). (*relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	39.393	0.001*
Presence of Crop Pests in Web	1	17.905	0.001*
Interaction: Soil Tillage Intensity * Presence of Crop Pests in Web	2	9.746	0.007*

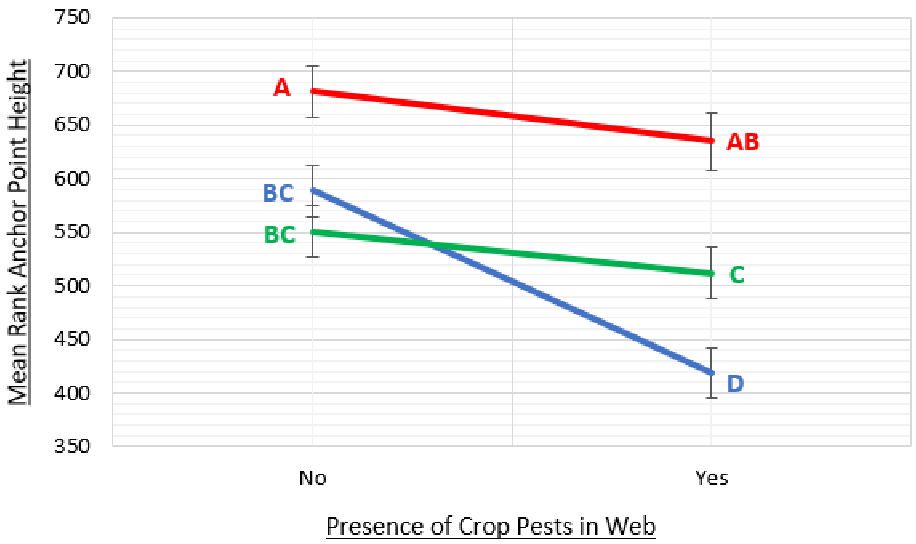


Figure 5.1.16: Interaction of mean rank anchor point height inside webs (of support threads), soil tillage intensity and presence of crop pests in web, for field when in crop (early and late growth stages) (n = 1102). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Yes ±s.e.24.002 (n = 109), Conventional No ±s.e.26.729 (n = 162), Direct Drill Managed Yes ±s.e.23.775 (n = 184), Direct Drill Managed No ±s.e.22.973 (n = 185), Direct Drill Yes ±s.e.23.877 (n = 313), Direct Drill No ±s.e.24.505 (n = 149)). (Points that do not share the same letter are significantly different at P <0.05).

There was a significant difference between the mean rank anchor point height of support threads where webs did or did not contain crop pests of the differing intensities of soil tillage, recorded in the early and late growth stages of *H. vulgare* (*Figure 5.1.16. & Table 5.1.22.*).

Conventional held a mean rank anchor point inside webs, where crop pests were not recorded, that was significantly higher than that of Direct Drill Managed and Direct Drill where crop pests were found and were not found within sheet webs.

*Table 5.1.23: Response of rank web area and factors of soil tillage intensity and presence of crop pests in web, for field when in crop (early and late growth stages). (n = 294). (*relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	44.765	0.001*
Presence of Crop Pests in Web	1	60.585	0.001*
Interaction: Soil Tillage Intensity * Presence of Crop Pests in Web	2	146.135	0.001*

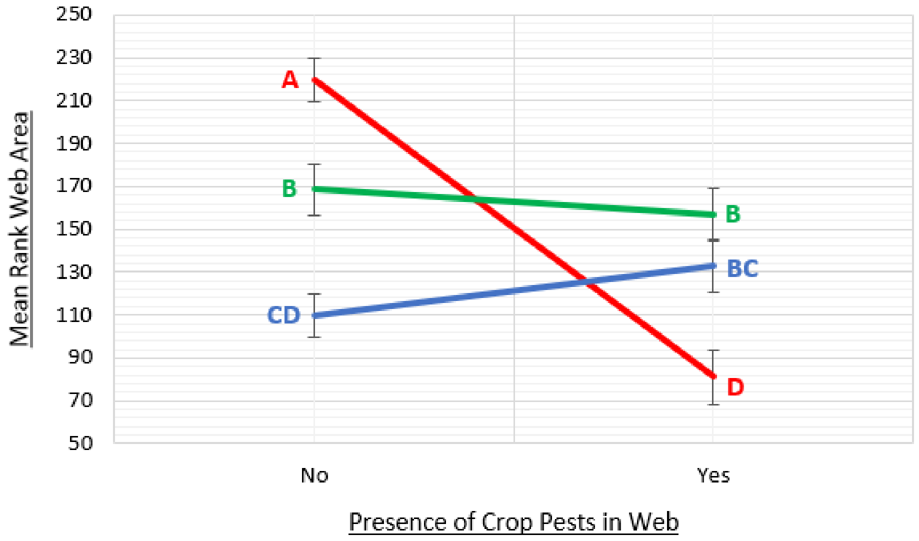
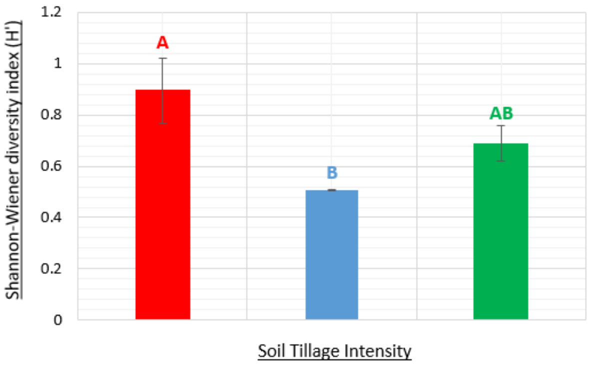


Figure 5.1.17: Interaction of mean rank web area, soil tillage intensity and presence of crop pests in web, for field when in crop (early and late growth stages) (n = 295). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional No ±s.e.10.030 (n = 42), Conventional Yes ±s.e.12.745 (n = 32), Direct Drill Managed No ±s.e.10.120 (n = 37), Direct Drill Managed Yes ±s.e.12.310 (n = 67), Direct Drill No ±s.e.12.267 (n = 43), Direct Drill Yes ±s.e.12.258 (n = 74)). (Points that do not share the same letter are significantly different at P <0.05).

Significance was identified in all terms in this model (*Figure 5.1.17. & Table 5.1.23.*). The mean rank web area, when crop pests were not observed within the web, was significantly higher in Conventional tillage than the other two tillage intensities where crop pests were not recorded, and significantly higher than the mean rank web area of the three tillage intensities when crop pests were recorded within the web. The opposite trend is true for Conventional when pests were found within the web.

5.1.5.2.5. Shannon-Wiener Diversity Index



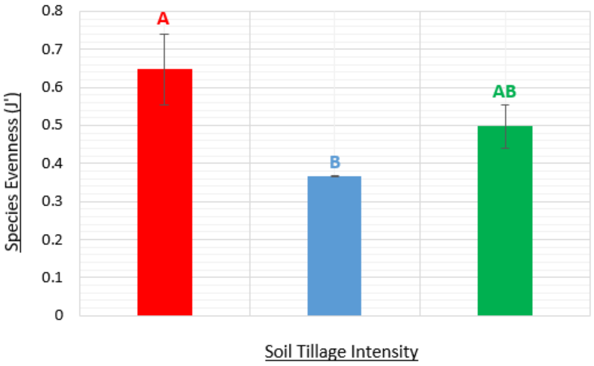


Figure 5.1.18: Mean Shannon – Wiener Diversity Index (H') in differing soil tillage intensities for field when in crop (early and late growth stages). (n = 30, df - 2, P - 0.001) (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green) (Conventional ±s.e.0.128 (n = 12), Direct Drill Managed ±s.e.0.003 (n = 9), Direct Drill ±s.e.0.068 (n = 9)). (Bars that do not share the same letter are significantly different at P <0.05).

Figure 5.1.19: Mean Species Evenness (J') in differing soil tillage intensities for field when in crop (early and late growth stages). (n = 30, df – 2. P - 0.001) (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green) Conventional ±s.e.0.092 (n = 12), Direct Drill Managed ±s.e.0.002 (n = 9), Direct Drill ±s.e.0.056 (n = 9)). (Bars that do not share the same letter are significantly different at P <0.05).

Shannon-Wiener Diversity Index (H') Max	1.38629436

The significant greater mean Shannon-Wiener Diversity Index (H') of 0.895 H' (*Figure 5.1.18*.) and the significant greater mean species evenness (J') (0.646 J') (*Figure 5.1.19*.) was found to be contained within the Conventional soil tillage sampled. With a mean Shannon-Wiener Diversity Index 0.205 lower than Conventional, Direct Drill Managed tillage held the significantly lower mean Shannon-Wiener Diversity Index. Direct Drill Managed further displayed the significantly lower mean species evenness, 0.280 J' lower than the mean for Conventional. The mean for Direct Drill tillage for Shannon-Wiener Diversity Index and species evenness was found not to hold any significant difference. The possible Shannon-Wiener diversity index (H') Max for the field was calculated to be 1.386 (3dp).

5.1.6. Discussion

5.1.6.1. Out of Crop - Fallow and After Primary and Secondary Cultivation

5.1.6.1.1. Fallow

Straw appeared to promote construction of webs at a higher point, in Direct Drill tillage, where the mass was the greatest (*Figure 5.1.2. & Figure 5.1.5.*). In fallow, little prey was active which questions whether web-building was due to capture of prey or survival. Norma-Rashid *et al.* (2014) and Nyffeler & Sunderland (2003) explained straw was used as a place to create small Linyphiidae webs throughout the growth of a crop. These were identified as refugia, mainly from predation, more than for biological control. Webs were found partially hidden by straw, agreeing with the above statement. Straw mass was significantly positively correlated to support thread length within the fallow period, however this due to threads yielding between clumps spread along the surface (*Table 5.1.12*).

It seems that upright stubble was used to support bridge threads and much rappelling was identified in the Direct Drill habitat because of this material (*Figure 5.1.1. & Table 5.1.4.*). Rappelling activity is required to begin at a high take-off point to allow eventual descent into a habitat (Hogg & Daane, 2018). Lubin & Suter (2013) and Bonte *et al.* (2008) commented that the tiptoe behaviour of a dispersing Linyphiidae is often carried out on a substrate that offers high anchorage points and stability. This identifies the benefits of using upright stubble to aid dispersal.

Upright stubble further allowed webs of greater height to be constructed, a tendency for non-dwarf Linyphiidae to display dominance and increase prey capture (Armendano & González, 2011; Sunderland & Samu, 2000) (*Figure 5.1.6. & Table 5.1.3.*). The nature of the higher stratum that upright stubble offers, is a sturdy base for silk to be laid rapidly upon where the highly mobile *T. tenuis* is inclined to construct webs at a rapid pace, hence the attractiveness of stubble allowing a strong foundation (Toft, 1989; Mclachlan & Wratten 2003).

With fallow only, volunteer plant density was significantly positively correlated to anchor point height of support webs, exhibiting this material as an asset to web-spinning when the field was out of crop (*Table 5.1.3.*). There was increased growth of volunteer crop in the Direct Drill area leading to the significantly higher mean anchor point height of support threads (*Figure 5.1.4.*). The increased growth is because of the zero cultivation, allowing seeds abandoned by the harvester to persist, their presence can simulate a crop canopy when void of *H. vulgare* (Morris *et al.,* 2010; Welch *et al.,* 2016). This accords with Birkhofer *et al.* (2008) & Buri *et al.* (2016), who suggest that random orientation of features, here performed by volunteer plant dispersal, can change the micro-habitat of a small area and thus web-building potential. Interestingly, thread length within webs was negatively significantly correlated to landscape feature of upright stubble density and volunteer plant density (*Table 5.1.12*.). The increased availability and orientation of anchor materials in proximity within the Direct Drill tillage allowed a site to hold a wide range of web design opportunity of smaller areas (Kovac & Mackay, 2009; Stenchly *et al.,* 2011; Welch *et al.,* 2011) (*Figure 5.1.1., Figure 5.1.2. & Figure 5.1.4*.).

Thread length out of web was significantly positively correlated to number of *T. tenuis* observed rappelling, explaining active movement in short-ranged dispersal was occurring (*Table 5.1.13*.). The greatest number of rappelling *T. tenuis* was observed in the Direct Drill area, utilising upright stubble for lift. Bonte *et al.* (2008) described, the linear movement of laying a bridge thread across upright stubble as less costly than descending and ascending structures within a habitat, when in web site exploration. The greatest number of anchor points found for rappel threads in Direct Drill areas were indeed attached to upright stubble (*Figure 5.1.5*.). In accord, Bonte (2013) discussed the cost of producing long dragline silk for a dispersal is far more costly than successive short threads that were identified in Direct Drill. This may identify why more bridge threads were found in Direct Drill, the low-cost exploration leading to successful web creation (Bonte, 2013; Knight & Vollrath, 2002). A fallow field, devoid of complex landscape architecture, could promote migration in the area noted for highest landscape heterogeneity (Birkhofer *et al.,* 2014; Sunderland & Samu, 2000; Thomson & Hoffman, 2007).

It was difficult to assess whether the field-wide glycosphate application had affected Linyphiidae activity when the field was sampled the following day in October 2017, as no comparative sampling commenced before the glycosphate had been applied (*Table 5.1.1*.). However, evidence of the disturbance effect could be seen with high rappel threads noticed attached to the upright stubble of all tillage, the application occurring field wide. De Keer & Maelfait (1988), Holland & Oakley (2007) and Thorbek & Topping (2005) suggest that rappelling is often intensified in times of disturbance, a survival strategy to avoid the threat and pioneer a new web-site.

5.1.6.1.2. Primary Cultivation

After primary cultivation, there was heterogeneity between mean rank anchor point height inside and outside of the web for Conventional only (*Figure 5.1.7*.). This was a different result than found within fallow (*Figure 5.1.5*.). Motobayashi & Tojo (2020) described stubble is useful for a temporary habitat while a crop is not in growth, Conventional holding the lower upright stubble density (*Figure 5.1.1*.). Macfadyen *et al.* (2019) & Zou *et al.* (2020) agree, discussing that upright stubble helps to sustain the life cycle of Linyphiidae by providing a habitat of landscape complexity outside of the shelterbelts. A *T. tenuis* is inclined to rappel from the top of material to allow flexion in the legs (Bonte *et al.,* 2008;

De Meester & Bonte, 2010). *T. tenuis,* being poor sighted, also requires a platform with fewer obstructions in its path to be able to repel (Bradley, 2013; Roberts, 1993). Both behaviours of *T. tenuis* are of value to biological control. Rappelling offers the potential for a *T. tenuis* to locate a superior web-site, either in low intra-specific competition or prey availability conditions (Diehl *et al.,* 2013 Harwood *et al.,* 2003; Thomas *et al.,* 2003). The use of upright stubble may have prompted web-building due to its enhancement to landscape heterogeneity, without any prey information received (Japyassú & Laland, 2017).

At lower height within Conventional, larger webs were spun close to the soil surface, which was identified as beneficial by Alderweireldt (1994), Rodríguez & Gloudeman (2011) and Zschokke *et al.* (2006), who commented that increased surface area allowed greater prey capture potential (*Figure 5.1.7.*). With the landscape open in the cultivated areas, compared to Direct Drill, there was a greater potential of aerial prey contact (Hogg & Daane, 2018; Miyashita *et al.,* 2012). The openness of the Conventional landscape can be seen with a mean negative anchor point height within webs measured due to the depressions created in the ground by the sub-soiler (*Figure 5.1.7., Figure 5.1.8a. & Section 3.1.3.4.*). The trade-off with web-spinning in this manner is shown by Obrycki & Harwood (2005), Toft (1987) and Wagner *et al*. (2003) expressing, webs with low protection from surrounding vegetation may fall to predation or web-take over if intra or inter-specific competition is prevalent. However, low prey was found at this time due to low temperatures and reduced green index in the field. Soil-dwelling prey though will be present, a web spun traversing the ground may intercept this prey (Agusti *et al.,* 2003; Rodríguez & Gamboa, 2000; Vink & Kean, 2013).

It appeared that straw mass had an indirect function to the promotion of web construction in Direct Drill Managed and Direct Drill, by increasing the anchor point height of support and bridge threads and web area along the vertical length of the upright structures of upright stubble (*Table 5.1.3*., *Figure 5.1.8a., Figure 5.1.8b., Figure 5.1.20. & Figure 5.1.21.*). It can be concluded that limited *T. tenuis* activity used the straw as refuges at this time due to low webs anchored in straw in any soil tillage. *T. tenuis* are 'sit and wait' predators and thus their main goal is to occupy a web (Diehl *et al.,* 2013; Samu *et al.,* 1996; Sunderland *et al.,* 1986). At times of cultivation, straw offered the complexity in a micro-landscape required by *T. tenuis* for a beneficial web. It may be that straw contained a higher degree of prey residing within, where a large bio-community was supported due to the increased straw mass (Davey *et al.,* 2013). Costello & Danne (1998) concur, by concluding the use by Linyphiidae of straw within a vineyard was due to the increased presence of prey foremost, and not as an additional habitat material. Straw may reduce evaporation and affect the micro-climate at the surface of the soil, and therefore allow a breeding site for several arthropods that can be of potential Linyphiidae prey (Thompson & Hoffman, 2007). Buchholz & Hartmann (2008), when analysing spider appendages in a semi grassland habitat, identified that *T. tenuis* built their webs within the higher herbaceous layer. This agrees with the webs in Direct Drill attached at an increased height to stubble to occupy the landscape strata favoured by these Linyphiidae.

Figure 5.1.20: Web within upright stubble. Direct Drill of H. vulgare, *primary cultivation, 2016 / 2017 Season. Elevated view. (Yellow arrow = 34.5 mm).*

Figure 5.1.21: Straw alongside upright stubble. Direct Drill of H. vulgare, *primary cultivation, 2016 / 2017 Season. Lateral*

Straw may have had an effect, enticing rappelling into the habitat by offering areas of complex structural diversity, favoured for web-spinning (Lubin *et al.,* 2011; Öberg 2007; Prieto-Benítez & Méndez, 2011; Rusch *et al.,* 2016). The spatial arrangement of material with greater densities (in straw mass and volunteer plant) permit shorter steps in dispersal (*Table 5.1.13*.). Many variations of bridge threads were identified for upright stubble where larger bridge threads were woven diagonally across upright stubble clusters of Direct Drill attached to the apex of the stubble (*Figure 5.1.8b*.). The fundamental reason behind rappelling is to find a suitable web location within a micro-habitat. It may be that the presence of straw allowed these webs to be created and extensive prior exploration of the area was not required (Bonte, 2013; De Meester & Bonte, 2010).

The act of cultivation introduces the landscape feature of soil clod height as a key attachment material in the Direct Drill Managed and Conventional areas. The structure of soil clods was influencing *T. tenuis* activity, the greater number of anchor points for support threads were found in the Conventional area, where the significant higher median soil clod height was measured (*Figure 5.1.3*. & *Figure 5.1.8a*.). It has been recognised that *T. tenuis* preference is not to anchor at ground level, preferring to anchor to the higher point within a micro-habitat (Davey *et al.,* 2013; Platen *et al.,* 2017). It may be that these webs were created by Erigoninae that prefer to build webs near the ground surface (De Keer & Maelfait, 1988; Downie *et al.,* 2000: Pommeresche *et al.,* 2013). However, *T. tenuis* were identified under some webs woven across the soil clods within Conventional (*Figure 5.1.22a & b*). The pioneering ability of *T. tenuis* may be expressed here, a larger sheet web woven within soil clods that had been developed from the sub-soiler (Armendano & González, 2011; Bell *et al.,* 2002; Chapman *et al.,* 2013; Sunderland & Samu, 2000) (*Table 5.1.12*.). Linyphiidae activity was prepared to spin silk from soil, however, it appears that Linyphiidae and *T. tenuis* favoured the greater height difference of soil clods in Conventional to weave in-between and express the 'sit and wait' strategy under a web (*Figure 5.1.3. & Figure 5.1.8a*.).

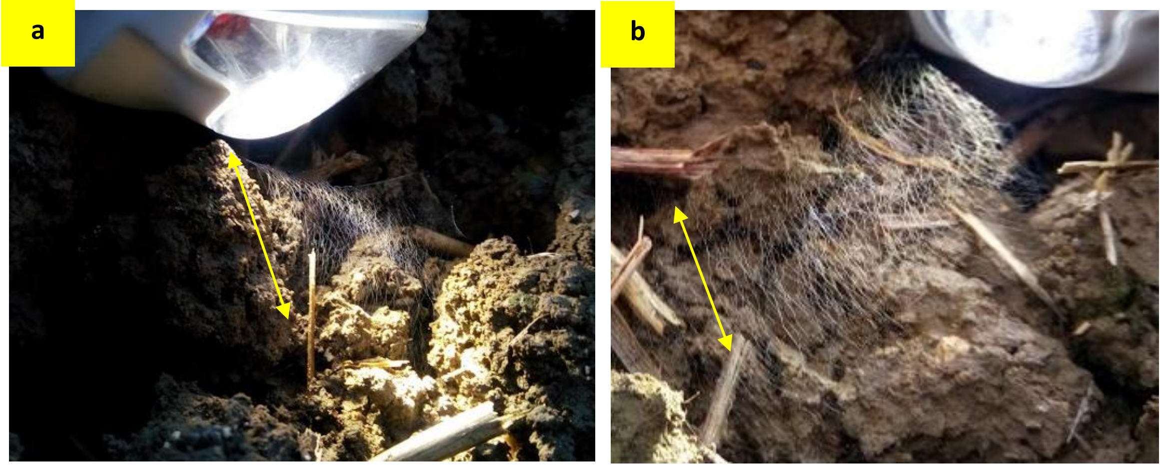


Figure 5.1.22a & b: Sheet webs attached to soil clods. Conventional. H. vulgare*, primary cultivation, 2017 / 2018 season. Elevated view. (a: Yellow arrow = 33.6 mm). (b: Yellow arrow = 37.3 mm).*

The length and anchor point height of bridge threads were positively significantly correlated with the number of *T. tenuis* noted to be rappelling (*Table 5.1.4. & Table 5.1.13*.). Bonte (2013) and Mestre *et al.* (2018) discussed the need for a strong platform to assist in support of the flex in the abdomen to initiate take-off when rappelling. Upright stubble is ideal for this platform and allows greater height and length of silk to be obtained. It can be discussed that a greater abundance of *T. tenuis* was dispersing locally by rappelling than web-building in the Direct Drill areas (*Figure 5.1.7. & Figure 5.1.8b*.). After twenty-four hours, it is expected that a web-site will be located and web-spinning commences, rapid dispersal after a disturbance (cultivation) shown by Harwood & Obrycki (2005) and Opatovsky & Lubin (2012) to lead to subsequent web creation. Blackledge *et al.* (2009) and Segoli *et al.* (2004) showed a sheet web can take less than thirty minutes to weave. However, it appears that migration is still occurring. It can be identified that there may still be an influx of *T. tenuis* ballooning into the Direct Drill habitat with its high landscape density (*Figure 5.1.1., Figure 5.1.2. & Figure 5.1.4*.). Gómez *et al.* (2016) and Horváth *et al.* (2009) showed materials of a higher aspect were of preference to a habitat lowered in vegetation complexity and where bare soil is evident.

More female *T. tenuis* were recorded than male *T. tenuis* in all areas, where females tend to have larger abdomens, and greater numbers were identified in the Direct Drill area. Craig (1987), Houser *et al.* (2016) and Segoli *et al.* (2004) comment that larger-bodied *T. tenuis* may create webs at a higher aspect to enforce dominance and enhance prey capture capability (*Table 5.1.3.*). The greater densities of attachment materials in Direct Drill allowed webs to be spun at higher heights (*Table 5.1.3.*). Female *T. tenuis* with large abdomen lengths were found in this area, the larger-bodied *T. tenuis* exerting territory with the prime web-site amongst upright stubble. The wind speed within a Direct Drill plot was 15.6 kmh^{-1}, which may have deterred silk-spinning high within the upright stubble (*Table 5.1.5.*). For rappelling, some moderate wind speed is essential to allow a 'lift' of the dragline as its being thrown (Hogg & Daane, 2018; Saravanan, 2006; Simoneau *et al.,* 2016; Tew & Hesselberg 2017). Increased wind influenced rappelling on stubble of a greater height, it appeared the greater wind speed of 15.6 kmh^{-1} was adequate to aiding laying of dragline silk in a conscious direction (Blackledge *et al.,* 2011; Craig, 2003; Tew & Hesselberg 2017) (*Table 5.1.5.*).

5.1.6.1.3. Secondary Cultivation

Within the main field, only twenty-eight bridge threads were found in the Direct Drill area spun across upright stubble. This is a stark difference to the primary cultivation when bridge threads were measured in abundance (*Figure 5.1.7. & Figure 5.1.9.*). Short ranged dispersal from Linyphiidae and *T. tenuis* was not taking place. There were no correlations between above-ground vegetation and Linyphiidae activity in spinning bridge threads within the secondary cultivation, a quite different result from primary cultivation where total upright stubble, straw and soil clod height affected propensity to bridge (*Table 5.1.4. & Table 5.1.13.*). Low propensity to migrate was identified by Halley *et al.* (1996), Hogg & Daane (2018) and Thorbek (2003) in low temperatures. The temperature ranged from 8 - 12 °C in the main field within this sampling period. The minimum temperatures recorded for this area are not considered extreme to prevent silk production from glands, the fibrils still holding their integrity allowing yielding to be bestowed on the silk (*Section 2.1.2.1.*). This permits thread spinning for web creation (Craig, 2003; Harmer *et al.,* 2011; Vollrath, 1986). Indeed, this temperature range has been shown to facilitate some Linyphiidae activity and persistence of a generation in the field (Halley *et al.*, 1996; Welch *et al.*, 2011).

Heterogeneity was identified between the mean anchor point height of bridge threads between Direct Drill Managed and Conventional soil tillage intensities (*Figure 5.1.9.*). Elements of the field landscape have altered after secondary cultivation; action of the prongs of the disc harrow and additional raking in the Direct Drill Managed, thinning straw abundance which previously formed large clumps (*Figure 5.1.10b.* & *Section 3.1.3.4.*). The upright stubble density was additionally reduced in Direct Drill, with no cultivation the delicate balance of stubble falling over possibly due to wind speed, large mammal or bird disturbance (Heroldová *et al.,* 2017; Morris *et al.,* 2010; Öberg *et al,* 2008). Bonte *et al.* (2008) and Hogg & Daane (2018) explain frequent attachment material is essential in driving rappelling, thus the fallen upright stubble not providing the frequency required in bridging. Due to differences in abundance in attachment material apparent, anchor point height within webs was significantly positively correlated with straw mass and upright stubble density. Bowden & Buddle (2010), Herrmann *et al.* (2010) and Obrycki & Harwood (2005), observed small differences in micro-landscape significantly altered *T. tenuis* and Linyphiidae web-spinning activity (*Figure 5.1.10a. & Table 5.1.3*.).

Soil clod height was negatively correlated to anchor point height after secondary cultivation but was not found to be significant after primary cultivation (*Table 5.1.3*.). This is despite the secondary role of the disc harrow to break up clods, and thus the difference in soil clods height between the cultivation areas is less defined than that of primary soil cultivation (Davies & Finney, 2002; Peigné *et al.,* 2007) (*Section 3.1.3.4*.). Greater areas of bare soil were evident with the disturbance of surface materials, attachment was still occurring, and longer webs were spun from soil clods of a greater height (*Figure 5.1.23., Figure 5.1.24. & Table 5.1.12*.).


Figure 5.1.23: Soil clods after primary cultivation. Conventional. H. vulgare*, primary cultivation, 2016 / 2017 season.*


Figure 5.1.24: Soil clods after secondary cultivation. Conventional. H. vulgare, *secondary cultivation, 2017 / 2018 season.*

Webs with large areas were spun across soil and straw within the Direct Drill Managed area (lower straw mass and stubble density found within this tillage intensity) (*Figure 5.1.1., Figure 5.1.2. & Table 5.1.12*.). However, this did not lead to a significantly mean greater web area found in Direct Drill Managed. Fewer (ten less) webs were observed in Direct Drill Managed than Conventional and Direct Drill which suggests the habitat of Direct Drill Managed was still not identified as a prime location for web-building. The disc harrow reducing clod height further and may have increased landscape homogeneity to a greater degree in Direct Drill Managed, therefore as shown by Borges & Brown

(2001) and Poggio *et al.* (2013) to offer a low abundance of attachment sites for threads (*Section 3.1.3.4.*).

Moreover, with the habitat unchanged by machinery in the Direct Drill area, thus material still arranged in proximity, it can be asked why thread length was significantly negatively correlated to upright stubble density and straw mass (*Table 5.1.12.*). It was observed that large webs were due to threads of a larger length being spun to non-adjacent upright stubble, at a greater height than the webs of primary cultivations (*Figure 5.1.25.*). The difference here may be due to wind speed. In the primary cultivation, the mean wind speed for field sampling was 13.8 kmh^{-1}, in secondary cultivation, it was 0.6 kmh^{-1}. Minor damage to webs had been identified throughout the datasets, and it has been previously discussed by Barriga *et al*. (2010), Gan *et al.* (2015) and Tew & Hesselberg (2017) that at higher wind speeds, webs of a higher anchorage would incur damage. Schmidt & Tscharntke (2005) & Segoli *et al.* (2004) discuss vegetation can impede wind flow, protecting force exerted onto a web. However, at secondary cultivation there was no vegetation growth apart from germinating volunteer crops, therefore no protection from wind was provided. Baldissera *et al*. (2004) and Tew and Hesselberg (2017) discussed that a reduction in vegetation complexity increased the level of impact wind speed disturbance could have on Linyphiidae web-spinning. It may be that after primary cultivation, a persistent wind disturbance may have deterred *T. tenuis* and Linyphiidae from weaving webs amongst the upright stubble, the seemingly favoured strata for *T. tenuis* to exhibit dominance and an ability to capture a greater array of moving prey, throughout fieldwork.

Figure 5.1.25: Small sheet web woven at top of upright stubble. (Female T. tenuis *circled in light blue). Direct Drill,* H. vulgare *secondary cultivation, 2017 / 2018 season. Elevated View. (Yellow arrow = 14.9 mm).*

Larger webs were found in areas with greater numbers of female *T. tenuis* recorded, this may be an element of intra-specific competition (*Table 5.1.12.*). The greater number of *T. tenuis* recorded was four in the Direct Drill tillage. Four Linyphiidae within an area of 1 m^2 gives adequate web building space to each *T. tenuis* without necessary relating to intra-specific dynamics (Benjamin & Zschokke, 2003; Harwood *et al.,* 2003; Pasquet *et al.,* 2014; Shaw *et al.,* 2005). Bianchi *et al.* (2017) and Krafft & Cookson (2012) discuss the hypothesis of mass action, where the spinning of silk through delicate vibrations can act as a stimulus and induce further web-spinning in close vicinity. However, five sheet webs attached to stubble were found in this area and cannot be identified as a significant stimulus. Again, the dominance of the anchor material of upright stubble can be defined, offering a robust structure for web-weaving of several dimensions (Birkhofer *et al.,* 2008; Buri *et al.,* 2016).

The larger *T. tenuis* had abdomen lengths 1.8 mm to 2.1 mm and were found within Conventional. This could suggest intra-specific competition, where *T. tenuis* of larger abdomens were seen to dominate within a habitat, driving away small *T. tenuis*. Štokmane & Spuņģis (2016) and Gómez *et al.* (2016) discussed, a habitat similar in landscape heterogeneity to Conventional, is not ideal for web-spinning with less complexity in the plant physiognomy. However, it did not provide the opportunity for significantly larger webs to be spun, across the bare soil when predation was low (*Figure 5.1.3*. & *Table 5.1.12*.). Web take-over in Linyphiidae by species of a larger size has been described in work by Eichenberger *et al.* (2009) and Harwood *et al.* (2003), where *T. tenuis* compete strongly for web territories and building a larger web is seen as a greater display of territory. However perhaps in Conventional small webs, to conserve energy, were adequate if other small *T. tenuis* had been driven away (Beck & Toft, 2000; Segoli *et al.,* 2004).

5.1.6.1.4. Immediately After Primary Cultivation

Much Linyphiidae and *T. tenuis* activity were recorded in the Direct Drill areas sampled. These areas were untouched by the sub-soiler due to zero-tillage (*Section 3.1.3.4.*). Schmidt & Tscharntke (2005), Schmidt *et al.* (2008a) and Topping & Lövei (1997) showed similar findings where zero-tillage increased the observed *T. tenuis* and Linyphiidae abundance and activity compared to cultivated areas. Longer bridge threads were mostly identified at the top of the upright stubble (*Figure 5.1.11., Figure 5.1.12., Figure 5.1.26a & b*). Rappelling anchors silk to a substrate and then exhibits forward movement until another substrate is reached. A solid inflexible structure is shown to aid this movement and allow *T. tenuis* to rappel with relative ease (Bonte, 2013; Craig, 2003).

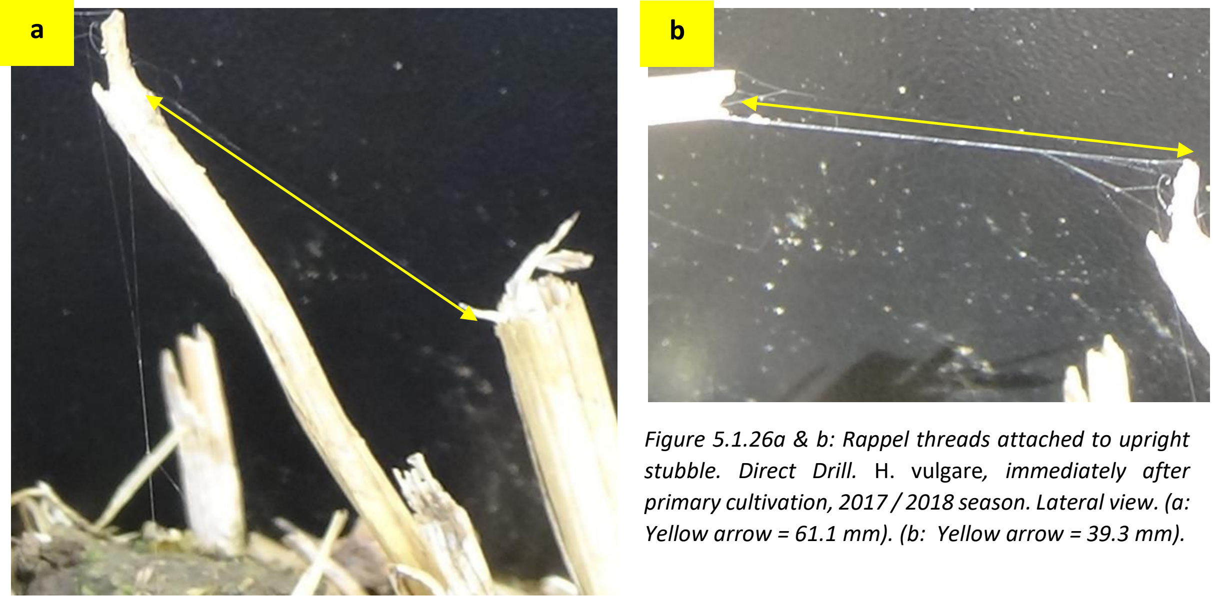


Figure 5.1.26a & b: Rappel threads attached to upright stubble. Direct Drill. H. vulgare*, immediately after primary cultivation, 2017 / 2018 season. Lateral view. (a: Yellow arrow = 61.1 mm). (b: Yellow arrow = 39.3 mm).*

It appears that migration activity occurred at a greater rate than web-building. This is an unusual result, as Alderweireldt (1994), Opatovsky *et al.* (2016) and Wagner *et al.* (2003) found short distance dispersal should result in web creation. It may be after the cultivation had occurred in the adjacent soil cultivations (Direct Drill centred in the middle of the field) *T. tenuis* had identified an area of low Linyphiidae abundance to pioneer and were therefore dispersing (*Figure 3.5b, Section 3.1.3.3., Page 51*). Perhaps due to the pass of the cultivators, *T. tenuis* were dispersing into an area of high landscape heterogeneity offering shelter. Buchholz & Hartmann (2008) and Pommeresche (2002) communicated the pioneering capability of *T. tenuis.* Bianchi *et al.* (2017) and Halley *et al.* (1996) discussed *T. tenuis* dispersal strategies from a disturbance. It appears two-way migration may have been occurring.

The greater number of anchor points measured were anchored to upright stubble and straw, material clearly favoured for web-spinning (*Figure 5.1.11.*). This is a similar finding to that from primary cultivation, where it was noted that the addition of straw and upright stubble in the same area is of advantage to web-building, upright stubble offering a platform of greater height (*Figure 5.1.11. & Section 5.1.5.1.3.*). Straw, combined with the upright stubble, increased landscape heterogeneity, shown to be influencing web-building by Blake *et al*. (2013) and Borges & Brown (2001) by offering many orientations in which a web can be spun (*Figure 5.1.11.*). Volunteer plants, used sparingly for an attachment material, shows the beneficial level of landscape heterogeneity was reached with straw and upright stubble alone (Lenoir & Lennartsson, 2010; Pathan, 2002).

No sign of *T. tenuis* or Linyphiidae was observed in the Conventional plots immediately after primary cultivation. Four female *T. tenuis* were observed within one sample from the Direct Drill Managed cultivations. It may be that the shallower cultivation of Direct Drill Managed had allowed pockets of *T. tenuis* to remain (Henschel & Lubin, 2018; Schirmel *et al.,* 2016; Tamburini *et al.,* 2015) (*Section 3.1.3.4.*). No web-building activity was identified within this area, and it may be that the *T. tenuis* dispersed away from the sub-soiler to an area of the field where tyres of the machinery did not tread and the tines did not strike (*Section 3.1.3.4.*).

The destruction of any web-building activity, identified after primary cultivation, damaged the Linyphiidae community. The above-ground vegetation disturbed, material where web attachment may have occurred. This agrees with evidence from Holland & Reynolds (2003) and Thorbek & Bilde (2004) who both demonstrated the action of loosening the soil, regardless of whether inversion was implemented, decreased *T. tenuis* abundance dramatically. This is a cost to energy output of the Linyphiidae where any web constructions may not have fulfilled their intended purpose (Benjamin *et al.,* 2002; Harmer *et al.,* 2011). Barriga *et al.* (2010), Bell *et al.* (2002) and Clark *et al.* (2004) communicated that after soil disturbance, the presence of *T. tenuis* may still be identified due to its rapid dispersal to pioneer a disturbed habitat. However, this is viewed after a certain time frame where the field in this dataset was analysed immediately after cultivation.

5.1.6.2. In Crop - Early and Late Growth Stages

5.1.6.2.1. Early Growth Stages

The upright stubble was dominant in times of cultivation and again when the field was in crop, upright stubble appeared to be prevalent as a bridging attachment material (*Figure 5.1.14. & Section 5.1.5.1.*). Further, Armendano & González (2011) and Bianchi *et al.* (2017) found the use of stubble influenced Linyphiidae web height (*Table 5.1.15.*). The upright stubble was still utilised even though the density was reduced (*Figure 5.1.14.*). The reason for this decline in upright stubble can be due to the direct drilling process (*Section 3.1.3.4.*). Following evidence of the direct drill machinery in the field, it appeared that upright stubble had fallen and became straw on the ground (*Figure 5.1.26. & Figure 5.1.27.*). This additional straw, created by the fallen upright stubble, on the surface of Direct Drill did not appear to increase *T. tenuis* activity in web construction. This disagrees with the fallow period where straw gave Linyphiidae an area of refugia (*Section 5.1.5.1.3.*). Armendano & González (2011), analysing Linyphiidae in a *T. aestivum* crop in Argentina, and Tahir & Butt (2009), studying Linyphiidae in a rice system, both discussed the need for both straw and stubble abundance to promote web-building and refugia. This is due to Linyphiidae requirements focused on the need for a habitat of complex landscape feature.

Rappel threads within all tillage intensities still had significantly higher mean anchor point height compared to support threads (*Figure 5.1.13*.). Most bridging occurred upon the upright stubble when the field was out of crop, however, there was no significance between these two variables at this early growth stage (*Section 5.1.5.1*.). This exhibits, lower short-ranged migration was occurring, compared to in periods of fallow (*Section 5.1.6.1.1*.). Woolley *et al*. (2016), identified a significant decrease in adult Linyphiidae population after removal of maize stubble in an agricultural setting. Wenninger *et al.* (2020) concur, signalling in zones of strip tillage of sugar beet, reduction in prominent ground cover reduced Linyphiidae abundance. The reason for this decline in short dispersal may be due to the decrease in mean upright stubble within the Direct Drill area, where a mean decrease of 267, was identified between the fallow stage and GS 11 - GS 15 (*Figure 5.1.27. & Figure 5.1.28*.). This occurred due to the action of sowing the crop with a direct drill (*Table 5.1.1*.). It appeared that the low population of *T. tenuis* in the crop and low propensity to disperse at this stage could influence the biological control capacity that Linyphiidae exerted as the crop began to grow. Mestre *et al.* (2018) and Zou *et al*. (2020) both discussed that the promotion of settlement by natural enemies (Linyphiidae) within a crop at early growth stages is an essential tool in increasing biological control when pests begin colonising a crop. Boreau de Roincé *et al.* (2013) & Schellhorn *et al.* (2014), showed colonisation prospects have been lowered in Aphididae if early pest suppression is applied in a crop. Holland *et al.* (2012) however, showed increased biological control rate when Aphididae were allowed to build up a colony to provide adequate stimuli for Linyphiidae.

Figure 5.1.27: Direct Drill prior to direct drilling of H. vulgare *in* H. vulgare*, fallow, 2016 / 2017 Season.*

Figure 5.1.28: Direct Drill after direct drilling of H. vulgare *in* H. vulgare*, GS 11 - GS 15, 2016 / 2017 Season.*

T. tenuis in Conventional appeared to be utilising greater plant growth for rappel threads (*Figure 5.1.14. & Table 5.1.16*.). Blandenier (2014) referenced rappelling as ‘ridging’, stating that bridge threads are like climbing structures allowing ascension to an increased height for further exploration of a possible web-site location. Conventional held less diversity in attachment material, even after drilling, with lower landscape features in straw and stubble present after cultivations (*Section 5.1.5.1*.).

Conventional incorporated *H. vulgare* with increased numbers of tillers and subsequent leaf growth, increasing the overall plant physiognomy of the sample. The available growth of *H. vulgare* plant providing new stem elongation of somewhat rigidity and perhaps offered a substrate robust enough to exhibit forward movement until another substrate is reached (Bonte *et al.,* 2016; Craig, 2003). The greater *S. mosellana* found within the Conventional tillage was identified in the sampling where rappelling occurred, which feeds into the higher Shannon-Weiner Diversity Index found in this area (*Figure 5.1.18. & Table 5.1.16.*). The higher air temperature would have allowed pupation from cocoons in the soil of *S. mosellana* nymphs (AHDB, 2016; 2018; Bayer, 2018). *T. tenuis* with the poor vision of distant objects, removal of obstructing features may have allowed the vibrant orange of *S. mosellana* to have been received by the eyesight of *T. tenuis* (Herberstein, 2011; Lichtenstein *et al.,* 2019; Young & Wanless, 2009). Preston-Mafham & Preston-Mafham (1996) and Young & Wanless (2009) showed contrast in colour aids reception of the Linyphiidae optic system and thus inclined bridging.

The greater plant density measured was in Conventional, which contributed to webs of a greater height and area (*Table 5.1.15. & Table 5.1.19.*). At this GS of *H. vulgare,* stem elongation was in early development and therefore the tillers had a high spatial orientation and allowed small changes in micro-habitat for web-spinning at an increased height (AHDB, 2015) (*Figure 5.1.13. Figure 5.1.29. & Figure 5.1.30.*). Gómez *et al.* (2016) and Mader *et al*. (2017) state that difference in plant physiognomy, provided through greater vegetation density, can push an anchor point height further up the crop.

The largest web of the dataset was in Conventional, spun traversing crop rows and may suggest why thread length increased along with the height and density of *H. vulgare* (*Table 5.1.19. & Figure 5.1.29.*). Holland & Oakley (2007), manipulating row spacing between crops, found this area to be a web-site potential for Linyphiidae. This agrees with Harwood *et al.* (2003) who commented that spaces between a *T. aestivum* crop may become a potential web-site if adjacent stem orientation was such to allow the creation of a sheet web (Harwood *et al.,* 2001). This is advantageous to an arable field, where crops are set in definite rows. The availability of an anchor material, plant, is therefore in proximity and allows the weaving of a uniform sheet web. The webs between crops were spun at an aspect of <10 cm, not utilising the increased mean height of *H. vulgare* in the Conventional area. Benjamin & Zschokke (2004) and Scheidler (1990) discuss the necessity for anchor vegetation to be structurally robust to adequately support a sheet web. This requirement increases with larger webs (Greenstone, 1984; Toft, 1987). It was theorised that the webs in between crop rows were attached lower to *H. vulgare* stem to allow for sheet web to be spun within a sturdy platform. This agrees with Benjamin & Zschokke (2004) and Rybak (2007) where Linyphiidae were found to spin a thread across a large open space, if the resultant web construction would be viable in its intended purpose.

Figure 5.1.29. Greater H. vulgare *growth. Conventional of* H. vulgare, *GS 33 - GS 37, 2016 / 2017 Season.*

Figure 5.1.30: Lesser H. vulgare *growth. Direct Drill Managed of* H. vulgare, *GS 33 - GS 37, 2016 / 2017 Season.*

Crop pests (*S. avenae, M. dirhodum* and *S. mosellana*) at the early growth stages, were found to be active within *H. vulgare,* with an increased green canopy index (Kennedy & Connery, 2005; Price *et al.,* 2011). *T. tenuis* seemed to be exerting their biological control potential, with number of crop pests within the web a positive significant predictor to the number of *T. tenuis* within the web (Prieto-Benítez & Méndez, 2011; Sunderland & Samu, 2000) (*Table 5.1.20.*). Fourteen *S. mosellana* and twelve *M. dirhodum*, the greatest captured, were caught in five small webs of Direct Drill, spun within the lower aspect of *H. vulgare*, four *T. tenuis* shared webs with *S. mosellana* nymphs (*Table 5.1.15. & Table 5.1.19.*). This disagrees with work by Davey *et al.* (2013) and Samu *et al.* (1996) who express larger webs spun at a greater height are often spun in a response to prey stimuli. The evidence suggested that *T. tenuis* here, spun webs within the correct location to capture prey. The capture of fourteen *S. mossellana* was within the early growth stages in 2017 season. The temperature at the time of sampling (highs of 13 ^{o}C - 16 ^{o}C) was adequate to allow the pupation of *S. mosellana* within the soil, however, low enough to discourage flight at a high level (Echegaray *et al.,* 2018; Elliot *et al.,* 2011; Lamb *et al.,* 2000). Thus, stimuli of *S. mosellana* presence may have been intercepted by Linyphiidae, towards ground level (Japyassú & Laland, 2017).

Seven *S. avenae* were found in webs at a lower stratum in Direct Drill Managed, with three *T. tenuis* underneath webs which contained the Aphididae. This is a success of predator dynamics and biological control (*Table 5.1.20.*). Webs of a larger orientation were anchored higher amongst the *H. vulgare* in a Conventional area, five *S. avenae* were noted from g-vac sampling in this area, however none within the web (*Figure 5.1.13.*). Five *T. tenuis* were under these webs, shown in significant positive correlation to anchor point height of support threads (*Table 5.1.15.*). The large webs of Conventional area in between crop rows do not appear to have exerted much predator dynamics. It may be that these webs were created to allow a greater surface area to snare prey, unable to pinpoint exact location of potential aerial prey (Agusti *et al.,* 2003; Rodríguez & Gamboa, 2000; Vink & Kean, 2013) (*Figure 5.1.13*.).

Within this dataset, it was identified that the number of webs is a useful measure for biological control, with webs less numerous in Conventional. Schmidt *et al.* (2004) and Wyss *et al.* (1995) concur, discussing that the construction of smaller webs in numerous areas enable predator dynamics of Linyphiidae to extend over a larger area (*Figure 5.1.31.*). Moreover, the greatest number of *T. tenuis* were found within a Direct Drill area, with similar comparative small abdomen lengths, where smaller lower webs were found (*Table 5.1.15. & Table 5.1.19.*). Low intra-specific competition is found with *T. tenuis* of similar bodied size, comparable strengths indicating low signs of dominance, for example, web take-over (Gan *et al.,* 2015). With this, co-existence can occur, and each *T. tenuis* may assign web territory with relative ease (Rojas, 2011; Segoli *et al.,* 2004). The smaller webs within the early growth of *H. vulgare* in this area have been successful in biological control. Barro (1992), Oliver (2007) and Zhang *et al.* (2016) discussed Aphididae in early growth stages of a crop, are likely to be in greater numbers as apterous morphs. At early growth stages, high densities of Aphididae or high temperatures not likely to have been present, both precursors of the parthenogenesis of alate morphs (Alkhedir *et al.,* 2010; Barro, 1992, Mehrparvar *et al.,* 2013). Apterous morphs seldom migrate over a large distance, their movement laboured and an energy-draining process, thus are likely to be feeding on the basal level of *H. vulgare* (Zhang *et al.,* 2016).

Figure 5.1.31: Small web woven in an area of dense H. vulgare*. (Web circled in light blue). Direct Drill Managed.* H. vulgare, *GS 33 - GS 37, 2017 / 2018 season. Elevated view. (Yellow arrow = 25.9 mm).*

Rappelling offers the potential for a *T. tenuis* to locate a superior web-site, either in low intra-specific competition or prey availability conditions (Diehl *et al.,* 2013 Harwood *et al.,* 2003; Thomas *et al.,* 2003). Bonte *et al*. (2008) and Bonte *et al.* (2011) discussed the high energy cost, with a little return in terms of the outcome being web-site selection, associated with creating bridge threads. With anchor point for bridge threads, *S. mosellana* and numbers of exuviae in the webs along with *S. avenae* in the vegetation were all significantly negatively correlated (*Table 5.1.16.*). This accords with evidence that explains yielding a length of bridging thread with such extension is energy demanding, due to sustaining adequate tension (Blandenier *et al.,* 2013; Bonte 2013). Its necessity only implemented when it is apparent that low prey density is in the vicinity and search for a new web-site is promoted. The mean larger abdomen lengths were identified within the Conventional areas where the higher bridge threads were spun (*Table 5.1.16.*). The stimuli of *S. mosellana* nymphs, several collected by the g-vac within these areas as previously highlighted, maybe enough of a stimulus for a response by *T. tenuis* and drive bridging propensity (Rodríguez & Gloudeman, 2011; Zschokke, *et al.,* 2006). Rappelling at a greater height is of an advantage, *T. tenuis* can migrate rapidly with less obstruction. Gan *et al.* (2015) and Rusch *et al.* (2015) showed, that larger-bodied Linyphiidae can expel greater energy to ascend higher. This discords with Corcobado *et al.* (2010) who comment, that a larger-bodied female Linyphiidae, with a greater mass (due to extreme SSD), may not have sustained the lying of a horizontal bridge thread, the dragline silk unable to hold the weight. However, it cannot be identified whether the bridge threads in question were spun by a male or female. The time of this sampling was outside of courtship and reproduction of the life cycle leading to lower intra-specific competition between each sex (Beck & Toft., 2000; Thorbek & Bilde, 2004).

5.1.6.2.2. Late Growth Stages

Unlike at early growth stages, plant height influenced the size of webs that Linyphiidae wove and their placement (*Table 5.1.16 & Table 5.1.19.*). It has been shown by Borges & Brown (2001) and Mclachlan & Wratten (2003) that manipulation of vegetation height alone did not alter *T. tenuis* abundance or promote web-spinning, density and vegetation richness combined with height influenced Linyphiidae behaviour. This significant difference in median plant height recorded is likely to have changed the vegetation architecture of the sample area, increasing its complexity (*Figure 5.1.15*.). Providing a habitat of vegetation enhanced heterogeneity was shown, by Platen *et al.* (2017) and Schmidt & Tscharntke (2005), to increase *T. tenuis* productivity providing an enhanced matrix of anchor points.

Six *S. mosellana* were recorded in vegetation and collectively fourteen *S. mosellana* were found in two webs attached near the *H. vulgare* ears with thread lengths >90 mm in a Direct Drill sample (*Table 5.1.15.*). Web construction was identified to be following areas of increased prey abundance within the Direct Drill tillage. This showed high *T. tenuis* biological control potential as the extended phenotype of the web ensnares the prey. Thus, the increase in web area increased the biological control capacity of this sampled plot (Chapman *et al.,* 2013; Nyffeler & Sunderland 2003; Pekár 2000; Toft 1987). It is of interest, why the more prominent webs in the Conventional tillage did not intercept

S. mosellana when the higher webs of the Direct Drill tillage succeeded in snaring prey. *S. mosellana* was present within the Conventional area in vegetation in similar numbers to Direct Drill. Alderweireldt (1994) and Rodríguez & Gamboa (2000) discussed, these numbers of *S. mosellana* (n = <10) too difficult for *T. tenuis* and Linyphiidae to register. Extreme temperatures were observed in 2018 and were thought to be the reason for a reduction in pupation and growth rate that occurred in the *S. mosellana* population (Blake *et al.,* 2013). Cheng *et al.* (2017) identified that in times of higher than optimal temperatures, *S. mosellana* are induced into early diapause (dormancy). Female fliers have been known to migrate into a shelterbelt during dispersal (Cheng *et al.,* 2017; Elliot *et al.,* 2011).

The greater number of *S. avenae* within the web was found in the area where the greater number of Aphididae exuviae was identified in the Direct Drill area (*Table 5.1.19.*). This agrees with Muratori *et al.* (2008), who present evidence that exuviae are commonly near an Aphididae population, reproduction being carried out in definite areas. Muratori *et al.* (2008) commented, that exuviae may be dealt with by predators in the same manner as Aphididae, allowing time for said pest to vacate. However, the benefit of Linyphiidae adapting passive foraging through the web, allows the same potential for both Aphididae and exuviae to be ensnared in the web (Diehl *et al.,* 2013; Feber *et al.,* 2015; Haughton *et al.,* 1999).

Very few *T. tenuis* were noted occupying webs in all tillage intensities. It appeared web abandonment had frequently occurred, much of this action in the Conventional area. Sunderland & Samu (2000) and Vink & Kean (2013) commented that the main drivers of web abandonment are low prey retrieval, physical disturbance, or threat of predation. Wind speed (14 kmh^{-1}) was considered high at times in terms of levels a sheet web can potentially withstand without fracturing hydrogen bonds, however, there were periods of calm within sampling in later stages (Blackledge *et al.,* 2009; Tew & Hesselberg, 2017) (*Section 2.1.2.2.*). It seems biological control was being implemented, though low amounts of cereal Aphididae activity was found within this dataset (*Table 5.1.20.*). Maximum daily temperatures for the Summer of 2018 sampling ranged from 25 - 31 ^{o}C (Met Office, 2018). This period of extreme heat seemed to have affected *S. avenae* fecundity rate and dispersal of other cereal Aphididae into the field. Asin & Pons (2001) identified that temperatures over 28.5 ^{o}C become a limiting factor in an *S. avenae* life cycle. Mortality rate was found to increase for nymph and adult, and reproduction rate decreased due to inability to thermo-regulate internal temperatures (Brabec *et al.,* 2014; Newman, 2005). *M. dirhodum* was found to be sensitive to a lower threshold temperature of 26.5 ^{o}C. This may be a reason why low numbers of *M. dirhodum* were identified (Aspin & Pons, 2001). This supports the low Shannon-Weiner Diversity Index found (compared to the Max H') across all soil tillage intensities, the high temperatures acting as a pest suppressant, perhaps as a consequence of *T. tenuis'* ability to persist with a biological control potential offering food through capture (Ramsden, 2016; Rusch *et al.,* 2016) (*Section 5.1.5.2.5*.).

It was identified that the greater *A. myosuroides* density was found in the Direct Drill Managed areas, yet few anchor points of webs were anchored to their stems. It appears that the addition of another plant species, if only in small quantities, increased *T. tenuis* activity in creating webs of a larger area and increased number of webs (*Table 5.1.15.*). Barriga *et al.* (2010) and Glime & Lissnier (2017) both describe changes in vegetation structure at a small spatial scale that induced an increase in Linyphiidae web-building and web occupancy (*Table 5.1.20*.). It appears that the structural difference in dimensions of *A. myosuroides,* elongated stem and low canopy growth, created the change in vegetation complexity required (AHDB, 2015; Borges & Brown, 2001; Marshall 2004; Schmidt & Tscharntke, 2005; Thomson & Hoffman, 2007).

Number of *T. tenuis* (female and male) were significantly negatively correlated to anchor point height and thread length within the webs (*Table 5.1.15. & Table 5.1.19.*). This disagrees with research from Harwood & Obrycki (2005) and Opatovsky *et al.* (2016) who identified that a greater number of *T. tenuis* increased general anchor point height, dominant *T. tenuis* driving webs higher at times of increased competition. The result is driven by a sample plot, where the greater *T. tenuis* abundance was identified, in an area where 75% of the webs created were in Conventional furrows with extensive shrinkage of the soil, due to the abnormally high temperatures (*Table 5.1.15. & Figure 5.1.19*.). The soil moisture was noted to be 19.3% in this area, below field capacity for Hanslop clay soil (Ashman & Puri, 2002) (*Figure 5.1.32. & Figure 5.1.33.*) (*Section 2.2.2*.). These webs had little contact with the above canopy. It is possible that this web would not have been constructed here, but for the low soil moisture inducing the extensive cracking. The canopy had shrunk due to moisture loss in the plant, thus it can be deduced that the web was in the furrow because of high spatial availability in higher aspects of *H. vulgare* (AHDB, 2018; Gómez, *et al.,* 2016; Roberson *et al.,* 2016). The creation of this web-site location in the habitat is not shown as beneficial to pest suppression. It appears that environmental conditions had altered the landscape offered by Conventional, allowing *T. tenuis* and Linyphiidae to exploit the potential web-sites (Ball & Bingham, 2003; Knight *et al.,* 2012; Peigné *et al.,* 2007; Zheng *et al.,* 2014). However, Betz & Tscharntke (2017), Campbell *et al.* (2020) and Romero & Harwood (2010), explored a web spun away from possible habitats of crop pests (upper crop canopy), would not have a high interception rate to entrap prey.

Figure 5.1.32: Furrow. Conventional. H. vulgare, *GS 87 - GS 91, 2017 / 2018 season.*

Figure 5.1.33: Furrow. Direct Drill. H. vulgare, *GS 87 - GS 91, 2017 / 2018 season.*

In the Direct Drill Managed area, the greater abdomen length of all female *T. tenuis* was found in the area that held webs spun at the apex of the plant (*Table 5.1.15*.). Males abdomens measured on average >0.2 mm smaller in length. Increased anchor height may be linked to males exhibiting enhanced fitness traits to dominant females with extreme SSD, expressed in a large female abdomen (Corcobado *et al.,* 2010; De Mas *et al.,* 2009; Prenter *et al.*, 2010) (*Section 2.1.2.3*.). Higher webs spun by large-bodied females equates to males required to present climbing efficiently and articulation to enter the web. This data was taken at the end of July. It may be argued that this is too early in *T. tenuis* life history for copulation to commence (Vanacker *et al.,* 2004; Watson, 1993). Prenter *et al.* (2010) and Toft (1989) discuss that male *T. tenuis* with a larger abdomen have a greater degree of success in courtship, being able to promote heritable benefits and exert dominance over the female. Maklakov *et al.* (2003) and Rundus *et al.* (2011) identify that males with smaller abdomens require a greater time to search for a female.

A greater number of spiderlings were identified at GS 47 - GS 61 and generally identified to be in third instar, a stage prior to last ecdysis and maturity into an adult, life generations occurring in waves (Peng *et al.,* 2013; Preston-Mafham & Preston-Mafham, 1996) (*Table 5.1.1. & Section 2.1.1.2*.). Spiderlings tend to create small webs closer to the ground, with Vanacker *et al.* (2004) explaining that this is a protective strategy, and Thorbeck (2003) discussing that spiderlings are competent web spinners, though have low fitness to be able to outlay large expanse of silk (*Table 5.1.19.*).

5.1.6.2.3. Overall - When in Crop (Early and Late Growth Stages)

Intra-specific relationships have been exhibited and show *T. tenuis,* of greater abdomen length, exercise dominance to locate an ideal web-site often with increased vegetation abundance. Gan *et al*. (2015) showed dominance, to be an act of claiming prime territory. This concurs with number of *T.*

tenuis found in the web and mean *H. vulgare* height as significant predictors to *T. tenuis* mean abdomen length (*Table 5.1.21*.). Greater body size allows a *T. tenuis* to exert priority if competition in web-sites may be identified, leading to cannibalism in a show of this authority (Gregori *et al.,* 2015; Lowe *et al.,* 2014; Wise, 2006). Gómez *et al.* (2016) and Štokmane & Spuņģis (2016) note web-spinning propensity increases with increased complexity in the plant physiognomy. Campbell *et al.* (2020) agreed, discussing an ideal web-site is an area of greater landscape heterogeneity, a location a larger-bodied *T. tenuis* may compete for.

Activity of *T. tenuis* in web-spinning was identified to be sensitive to the level of landscape heterogeneity with number of *T. tenuis* occupying webs significantly associated with the density of *H. vulgare* and *A. myosuroides* (*Table 5.1.20.*). This agrees with Holland *et al.* (2003), Lafage *et al.* (2015) and Schmidt & Tscharntke (2005) who suggested that complex vegetation structure promote *T. tenuis* occupation, due to the increased anchorage possibilities creating webs of greater size and strength. A web gains strength with the greater number of attachment points it contains, the piriform discs providing attachment (*Figure 2.3c., Section 2.1.2.1. Page 11*).

The greater number of *T. tenuis* were found in summer of 2017 within Conventional when *H. vulgare* was within the later growth stages, when no prey was recorded in web or crop. This growth stage defines dough development to when the kernel is identified to be at the hard dough stage, i.e. fully ripened. As further senescence had occurred and moisture loss increased, the head endures bending (AHDB, 2015; Holopainen-Mantila, 2015; McFarland *et al.,* 2014). The reduced rigidity of the stem lowers the height of the plant. In this area, all *T. tenuis* were of low abdomen length perhaps from a new generation (Opatovsky *et al.,* 2016; Welch *et al.,* 2013) (*Table 5.1.21*.). The condition of the crop appeared to be detrimental to *T. tenuis* ability to weave substantial webs. Additionally, low dispersal activity was recorded at the late growth stage. De Meester & Bonte (2010) explained that migration effort spun with multiple shorter threads is of lower energy consumption than extended dragline silk. Gan *et al.* (2015) and Segoli *et al.* (2014) suggest that an increase in body size can relate to higher energy outlay, therefore, the *T. tenuis* of low abdomen length were unable to expel greater energy to migrate to the shelterbelt or a prime web-site location.

Webs in all soil tillage intensities were successful at prey capture at a variety of anchor point heights, which shows the *T. tenuis* ability to spin webs in many locations (*Figure 5.1.16*.). It appears that no height was beneficial to capture prey, which disagrees with Davey *et al.* (2013) and Samu *et al.* (1996) who highlighted that a web of a high aerial aspect may presume it would be beneficial to capture aerial prey. The *T. tenuis* behaviour appeared to be similar in Direct Drill Managed and Direct Drill, suggesting that *T. tenuis* and Linyphiidae were responding to either prey abundance or difference in habitat requirements, plant height and density shown to affecting *T. tenuis* behaviour. It appears that both stimuli may be inseparable with Harwood *et al*. (2001), Kraftt & Cookson (2012) and Sunderland & Samu (2000) establishing that *T. tenuis* respond to the same cues in micro-habitats as prey, an increase in vegetation complexity and nutritional status.

Within a different sampling period, webs attached >60 cm to the *H. vulgare* stem did entrap three adult *S. mosellana* within Conventional (*Figure 5.1.16*.). The greater Shannon-Weiner Diversity Index was established in the Conventional plot, due to *S. mosellana*, *M. dirhodum* and *S. avenae* identified collectively, in ten out of the twelve sampling periods of Conventional, when *H. vulgare* was in crop (*Table 5.1.1., Figure 5.1.16. & Figure 5.1.18*.). Additionally, *S. mosellana* was identified at greater abundance as adults in Conventional. The greater number of *S. mosellana* was found on the crops due to perhaps the greater plant height (*Figure 5.1.15. & Figure 5.1.16.*). This is as expected due to *H. vulgare* of increased height having a higher yield of grain (AHDB, 2018). *S. mosellana* may seek this increased grain for potential areas where access through the pericarp is attainable (AHDB, 2018; Price *et al.,* 2011). *S. mosellana* are weak fliers with poor optic ability, their strategy of chaotic rapid flight covers short distances (Bayer, 2018; Blake *et al.,* 2013). Blackledge & Eliason (2007) and Gómez *et al*. (2016) discussed aerial pests may have promoted webs spun at a greater height. It may be that *T. tenuis* in the Conventional area were unable to sense *S. mosellana*, their cognitive receptors not able to pinpoint the location of the stimuli, to be able to entrap further *S. mosellana* (Rodríguez & Gamboa, 2000; Rodríguez & Gloudeman, 2011).

Small webs were found in areas where high wind speeds were measured. Smaller webs were shown by Blackledge *et al.* (2009) and Segoli *et al.* (2004) to offer a higher degree of structural support in times of increased physical disturbances. Webs of a lesser area may have been woven tightly within vegetation at a previous exposure to high wind speeds, agreeing with smaller webs successful in prey captured (Harwood *et al.,* 2003; Toft 1989) (*Figure 5.1.17*.). Seven alate morphs were observed at a wind speed of 16.6 kmh^{-1}. The alate were not in flight and recorded due to g-vac sampling. The wind speed at this level is considered too great to allow lift for *S. avenae* according to Parry (2013) and Reynolds & Reynolds (2009). Three alate *S. avenae* were captured with two webs. The alate were recorded in Direct Drill Managed where the greater density of *S. avenae* were found. It may be that alate morphs were asexually reproduced as a product of increasing *S. avenae* abundance in the Direct Drill Managed area, high density being a driver for parthenogenesis of alate morphs here, more than dispersal along wind speed currents (Parry *et al.,* 2006; Parry 2013; Price *et al.,* 2011; Summers *et al.,* 2004). *T. tenuis* can sense alate morph movement by subtle cues in movement in vegetation (Rodríguez & Gamboa, 2000; Rodríguez & Gloudeman, 2011). It could be said if the wind speed was lower, *S. avenae* may have taken flight and webs woven at a higher stratum would have ensnared prey.

S. mosellana, as cocoons from a previous season, may have been abundant in soil of each cultivation allowing the occurrence of pupation to be similar, however, its greater presence in Conventional suggests dispersal from a shelterbelt, with Conventional field length bordering a hedgerow (*Figure 3.5b*). This would explain *S. mosellana* presence within *H. vulgare,* when it is mostly associated with *T. aestivum* (Goggin, 2007; Lombaert *et al.,* 2006). *S. mosellana* as adults are winged, even though they are poor fliers, the short rapid aerial dispersal allows movement between crop ears (AHDB, 2016; Bayer, 2018; Price *et al.,* 2011). Aphididae depend on stimuli from environmental conditions to produce an alate morph to allow dispersal thus are restricted to when a stimulus may be presented (Mehrparvar, 2013; Price *et al.,* 2011). From the different reproduction and dispersal methods of the two pests above within the field, may explain why two webs of different strata and size capture different prey (*Figure 5.1.16. & Figure 5.1.17*.).

Greater web dimensions do not necessary ensnare prey (*Figure 5.1.17*.). This disagrees with Chapman *et al.* (2013) and Pekár (2000) who discuss the extended phenotype of the web exhibits pest suppression with an increase in web area supporting escalated biological control capacity. It appears that the location of the web is more important than the dimensions, small prey becoming attached to flagelliform silk of webs of any dimensions (Diehl *et al.,* 2013; Harwood *et al.,* 2003; Nyffeler & Sunderland., 2003) (*Section 2.1.2.1*.). The greater webs woven where no prey was identified was costly in energy. Linyphiidae are highly sensitive to the energy depletion of silk production (Benjamin *et al.,* 2002; Segoli *et al.,* 2004). The large webs of Conventional might have been beneficial if prey was evident, though it seems that the drive to assemble webs of a high aspect here had occurred as an act of dominance, from females of a larger abdomen, than the desire to construct their extended phenotype of the web to capture prey (Birkhofer *et al.,* 2017; Eichenberger *et al.,* 2009; Stenchly *et al.,* 2011).

Overall, there was no statistical difference between the abundance of prey found in the web and within the vegetation between the three soil tillage intensities, confirming the similar biological control opportunity existed in each. Perhaps if temperatures were favourable and greater prey was able to persist, the Shannon-Weiner Diversity Index and evenness would have been enhanced and significant differences of prey type and abundance may have been identified in the soil tillage intensities (*Figure 5.1.18. & Figure 5.1.19*.). This diversity index does not calculate the abundance of a species, it is a measurement only to describe biodiversity within a sample. The index was low with Shannon-Weiner Diversity Index falling between 1.5 and 3 for many ecological systems (Beauchamp, 2016). However, the habitat sampled was a mono-cropped area with little diversity of floral species. The growth pattern of *H. vulgare* extending over the field provided little landscape heterogeneity compared e.g. to a wildflower meadow. This agreed with findings of Sithole *et al.* (2018), a Shannon-Weiner Diversity Index was similar in a field mono-cropped with maize where a straw mulch was / was not applied, the straw having little impact on an increase in biodiversity. Meena *et al.* (2019) concur with a greater Shannon-Weiner Diversity Index (1.447 H') when wildflower strips were intercropped into okra plantations, compared to 1.392 H' without the strip intervention. This diversity without the wildflower strips was greater than measured from the *H. vulgare* field, the high fructose content of such a vegetable attracting an array of prey and predators (Meena *et al.,* 2019). This value of 1.392 H' was similar to the 1.386 H' maximum calculated for the research field. This was 0.521 away for the H' of Conventional, the discrepancy due to weak *M. dirhodum* presence.

5.1.7. Final Discussion - Fieldwork - 2016 / 2017 Season and 2017 / 2018 Season

Through the complexities of an open environment of the field with extensive interactions occurring from independent variables of weather, climate, predators and the landscape set from the soil tillage intensity, an element of the biological control potential of *T. tenuis* has been observed in each soil tillage. This is identified from prey of Aphididae and *S. mosellana* observed in webs in each soil tillage intensity. Signs of *T. tenuis* responding to stimuli exhibited by prey was measured with *T. tenuis* web-spinning in numerous orientations in areas where alate morphs and exuviae related nearby presence. This, therefore, addresses the third aim of this fieldwork Chapter (*Section 5.1.2.1.*).

One of the key themes running through this research is the need for a certain level of landscape heterogeneity to provide a *T. tenuis* and Linyphiidae with a multitude of materials suitable to allow attachment of threads, relating to the fourth aim (*Section 5.1.2.1.*). The orientation of said materials is worth considering, as a greater distance that a thread is spun has shown to increase the energy output required. The differences in plant height and density between the soil tillage intensities as the GS stages of *H. vulgare* progressed became the key parameter in understanding whether an adequate level of landscape heterogeneity had been reached to allow the commencement of a web, this the extended phenotype in which *T. tenuis* exerts biological control. Different sheet webs were observed woven into different structures created by differing plant physiognomy, where an energetic output had not necessarily met the intended return. This a loss in terms of predator dynamics of *T. tenuis* and Linyphiidae.

An important difference identified in the soil tillage intensities was at times of cultivation and the period until GS of crop provided adequate above-ground vegetation for web-spinning (GS 30 - GS 40). The zero-till of Direct Drill supported *T. tenuis* activity, where immediately after primary cultivation the predator capture ability of *T. tenuis* had been removed in Conventional and Direct Drill Managed. The pioneering ability of *T. tenuis* was observed when webs were woven into the cultivated land after twenty-four hours, allowing predator dynamics of *T. tenuis* and other Linyphiidae to prevail in the cultivated areas. It was shown that Direct Drill Managed held less biological control potential of *T. tenuis* with low web-spinning and rappel threads, found to be due to the low depth of the cultivation creating a micro-habitat of less complex structural architecture. With the action of the disc harrow breaking up clods, both cultivated areas supported less landscape heterogeneity in secondary cultivation and subsequently a habitat less likely to support *T. tenuis* web-construction. Direct Drill with zero-till had a key role in secondary cultivation to provide an area continually suitable for web-site location and therefore an ability to capture prey. These differences exhibiting understanding for the second aim for this Chapter (*Section 5.1.2.1*.).

From this, aside of the mechanical action of the primary and secondary cultivations, the differences in *T. tenuis* predator dynamics due to elements relating to the intensity of soil tillage was less clear. Secondary consequences of cultivation appeared to drive a propensity to web-spin. For example, an increase in *A. myosuroides* in Direct Drill was found due to zero-till, allowing persistence. The widening of furrows in Conventional, induced by the cultivation method, increasing moisture stress. Both circumstances enhanced landscape heterogeneity and could promote web-site selection. These features relevant to specific tillage intensities altered biological control potential of *T. tenuis* and addressed the first aim (*Section 5.1.2.1*.).

Sub-Chapter Five Two

5.2. Addition of Upright Stubble to Conventional Tillage Trials

5.2.1. Introduction

Fieldwork of *H. vulgare,* within times of primary and secondary cultivation, highlighted that the presence of upright stubble increased the abundance of *T. tenuis,* its activity in web-spinning and short-range dispersal in rappelling (*Section 5.1.5.1.*). From this, a useful approach, was to investigate whether the soil under the different tillage practices had a direct effect on *T. tenuis* activity and abundance, or if these variables were affected by the above ground habitat created as a result of each tillage practice. From here several trials were run placing upright stubble, of a certain height and density, into an area of Conventional tillage, which had undergone secondary cultivation (*Section 4.4.2. & Section 4.4.3*.).

In August 2018, the trial took place on an additional field on Martin Jenkins™ farm (*Figure 5.2.1*.). A field that only had conventional tillage methods was an ideal location to explore the benefits of upright stubble further. The NIAB fields have been hypothesised as able to support increased *T. tenuis* activity due to the Direct Drill Managed and Direct Drill sections. A field outside of the experiment, which had undergone one tillage treatment was observed to have similar *T. tenuis* activity to the Conventional area of the NIAB fields. This field had been fallow for a year. The field under-went primary cultivation in July 2018 of sub-soil cultivation with Kelly® Big Diamond with chain bites 1 cm in the soil, and secondary cultivation in August 2018 consisting of an Optimer® Cultivator where the discs were inserted 5 to 7 cm into the soil.

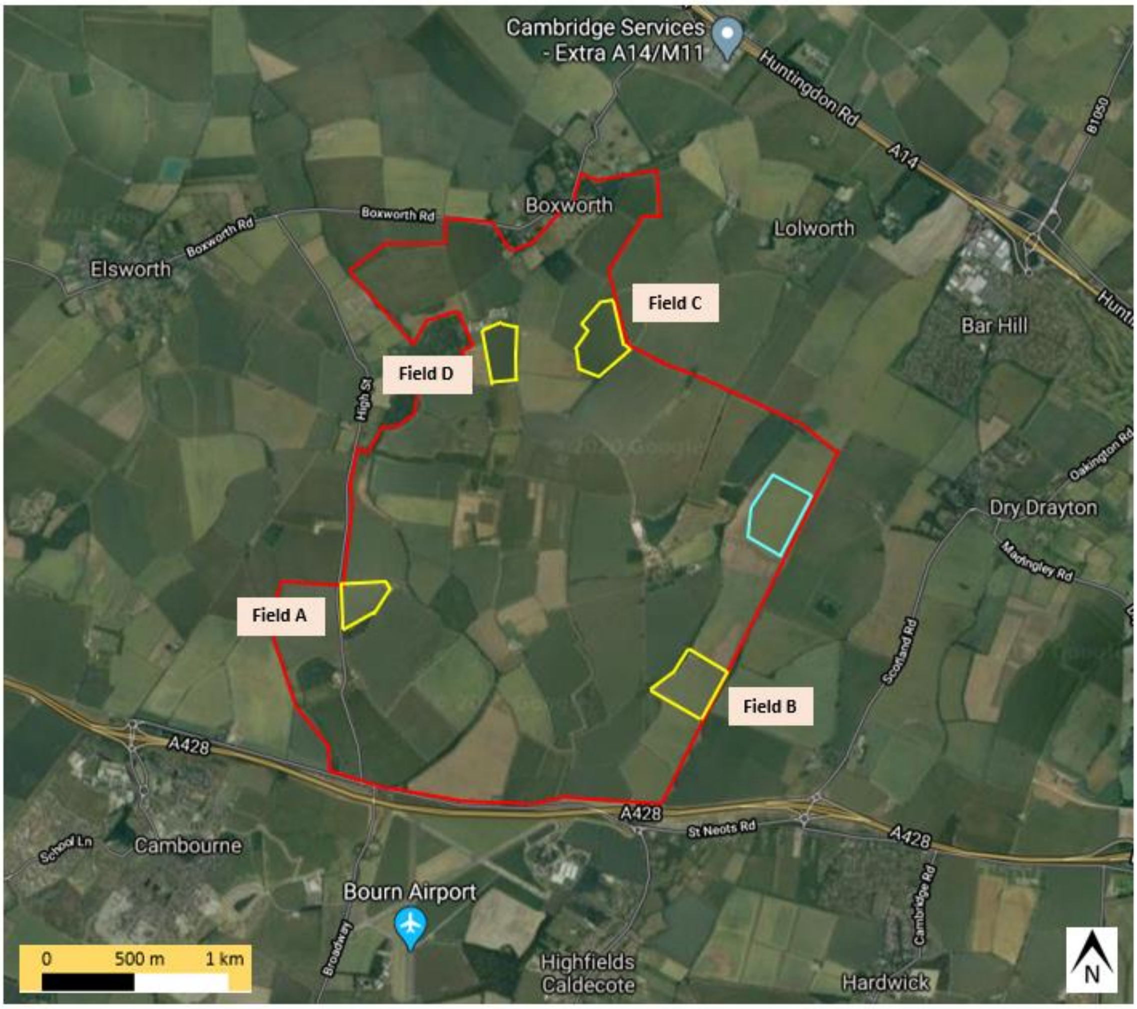


Figure 5.2.1: Scale map showing location of Martin Jenkins Farming™ created from Google Earth© and QGis© 3.4 Madeira™. Red line showing borders of farm. Yellow line showing borders of fields within the NIAB trials. Light blue line showing borders of field used for addition of upright stubble to Conventional tillage trials.

5.2.2. Aims and Specific Objectives

5.2.2.1. Aims

Research aims for this Sub-Chapter are 2 and 4 noted in Section 1.2., Page 2.

2. Identify any differences in extended phenotypes of *T. tenuis* within tillage practices, e.g. web dimensions and bridge thread length.
4. Comprehend if a certain level of landscape heterogeneity affects *T. tenuis* ability to predate on Aphididae.

5.2.2.2. Specific Objectives

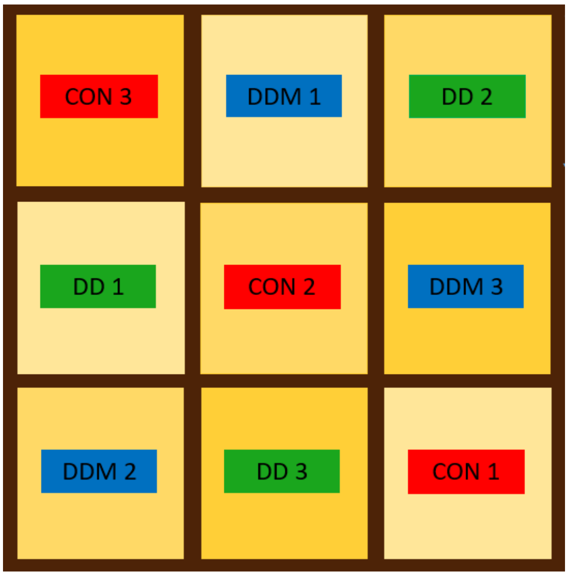
The specific objectives to fit the aims for this Sub-Chapter were as follows:

- Calculate *T. tenuis* energy output by measuring web area and address biological control potential of *T. tenuis* in the different densities of upright stubble.
- Assess *T. tenuis* migration through evidence of bridge threads for rappelling and ballooning in areas replicating soil tillage method with upright stubble abundance.
- Record *T. tenuis* abundance, calculate body dimensions, and consider the impact of this to possible prey capture in the upright stubble representing different levels of soil tillage intensity.

5.2.3. Methodology

The trial was placed at a substantial distance away from all field margins and hedgerows, to negate edge effect and allow migration for *T. tenuis* that may have been residing in the hedgerows. The first 2500 cm^2 quadrat (50 cm x 50 cm) was placed at 153 m from the east field edge and 15 m from the south field edge (*Figure 4.4.2., Page 68 & Figure 5.2.1.*).

Upright stubble from the NIAB fields had been collected throughout the year, dried and stored in plastic containers. This allowed cereal stubble to be used in this experiment, as the stubble had remained rigid and was able to be cut to size and inserted back into the soil without damaging its integrity. Cut sizes corresponded to mean height measured in the field plus the 1 cm insertion length. Three sample plots were employed for Conventional, Direct Drill Managed and Direct Drill (*Figure 5.2.2., 5.2.3a & b. & Section 4.4.2.*). Data of upright stubble quantity and height were taken from September 2017 when primary and secondary cultivations were complete, and no drilling had taken place. The set-up followed that of development work (*Section 4.4.2*). The stubble was placed in clusters of two to four for Conventional and two to six for Direct Drill Managed and Direct Drill, set vertically 2 cm apart in rows 15 cm apart (*Figure 5.2.4a - c*). The sample plots for upright stubble for each crop were arranged in a Latin Square design, each separated vertically and horizontally by 50 cm apart (*Figure 5.2.2.*).



CON 3	DDM 1	DD 2
DD 1	CON 2	DDM 3
DDM 2	DD 3	CON 1

Figure 5.2.2: Schematic diagram of Latin Square design of sampling plots for addition of upright stubble to Conventional tillage trials. (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green).

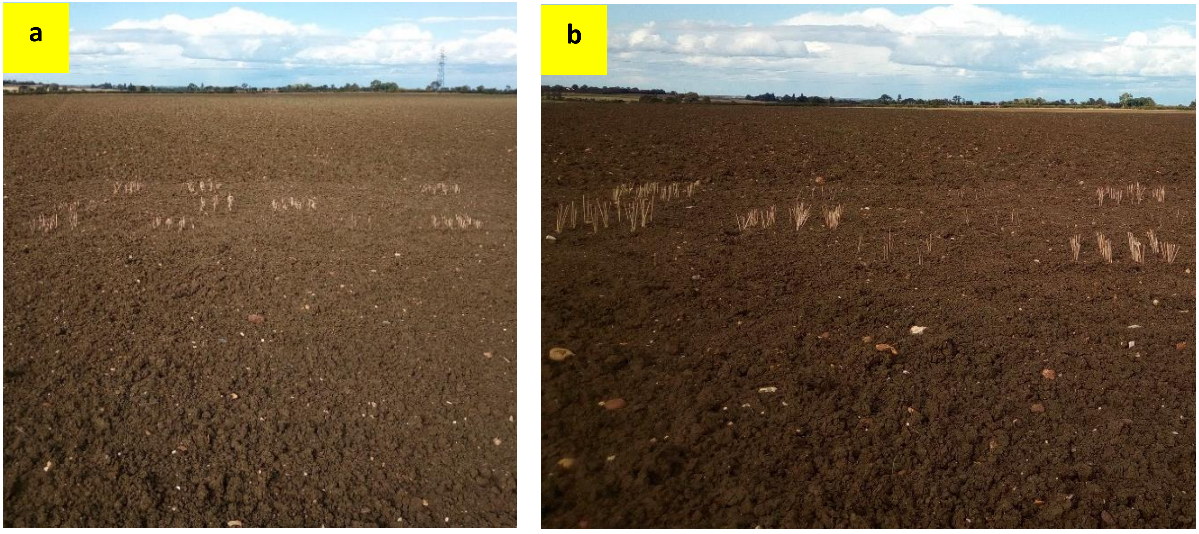


Figure 5.2.3a & b: Addition of upright stubble to Conventional tillage trials photographed at different focal lengths from field margin.

Figure 5.2.4a - c: Close-up view of addition of upright stubble to Conventional tillage trials. a = Conventional. b = Direct Drill Managed. c = Direct Drill.

5.2.4. Data Collection

The experiment ran for twenty-four hours. Linyphiidae activity was assessed by measuring support and bridge thread length (mm), web area (mm^2), anchor point height (cm) and anchor material. Body length, abdomen to cephalothorax length (mm), and gender was recorded for any *T. tenuis* observed. Methods were identical to fieldwork described in Section 5.1.3.

5.2.5. Statistical Analysis

Staistical analysis was carried out with Minitab18$^{©}$. A Principal Component Analysis (PCA) was utilised to observe if any associations were formed between the mean of the variables measured and which associations formed the principal component, having the most influence over the other variables quantified (Bass, 2007; Khan, 2013).

Two-way rank ANOVA was utilised due to non-normal data found via Anderson-Darling test, analysing skew and kurtosis of histograms and distribution represented on a probability plot (*Section 5.1.4.1.*). This analysis was used to test if there were any significant differences between certain two dependent variables (factors) measured; i.e. anchor point height out of webs (bridge threads) and anchor point height in webs (support threads), within the differing abundance of upright stubble representing each soil tillage intensity (independant variable). The method for two-way rank ANOVA followed the method described in previous Fieldwork Sub-Chapter (*Section 5.1.4.2.*). The programmes used were FCSTats V2_1a© and Mintab18© (Wheater & Cook, 2000). Dunn's test was used to show where the significance lay.

Correlations were used to indentify any significant trends between two continuous random variables (independent / dependant) for example web area (dependent) against amount of upright stubble added (independant). Normality was checked through the method mentioned above. Pearsons (r) was implemented if the null hypthesis was not rejected, found in data relating to length of bridge threads. Spearman Rank (Rho) was used to analyse non-normal data, where anomalies were included due to the ranking of data (Hawkins, 2014; Khan, 2013).

5.2.6. Results

5.2.6.1. Summary of Results

- Mean rank anchor point height was significantly higher inside of webs in Conventional plots (*Figure 5.2.6.*).
- Within the Conventional and Direct Drill tillage replicated areas, there was homogeneity between the mean rank anchor point height of support threads measured on the attachment material of upright stubble and soil (*Figure 5.2.7.*).
- Anchor point height of threads outside of webs and thread length inside of webs were significantly positively correlated to features of soil tillage intensity (upright stubble density and upright stubble height). These features were significantly negatively correlated to anchor point height of threads inside the web (*Table 5.2.5.*).
- Mean rank thread length was significantly longer in Direct Drill Managed inside of the web and mean rank thread length outside of webs was significantly longer in Conventional and Direct Drill Managed (*Figure 5.2.8.*).
- Mean total thread length outside of webs was significantly positively correlated to number of Linyphiidae webs (*Table 5.2.6.*).
- Products of *T. tenuis* activity (thread length and anchor point height) held the greatest overall influence over the data recorded (*Figure 5.2.5.*).

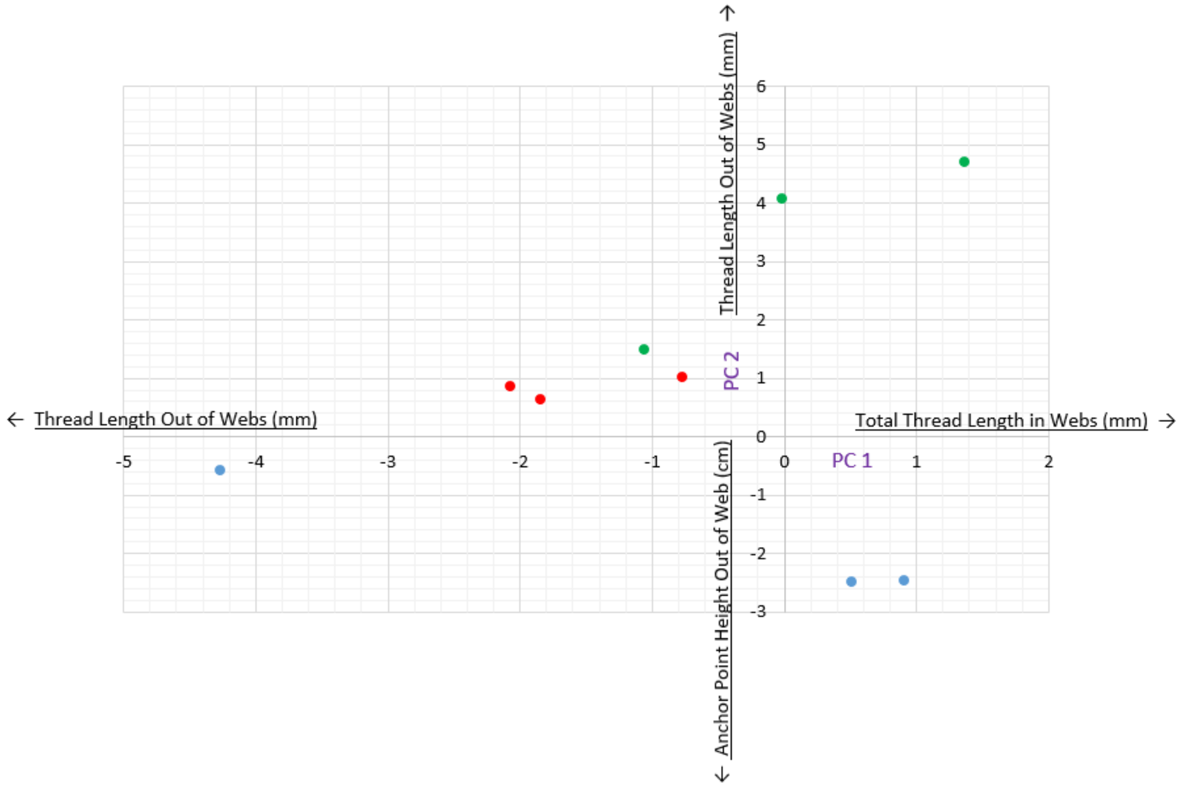


Figure 5.2.5: PCA of variables measured in addition of upright stubble to Conventional tillage trials along the first two principal components and variables correlating to each component. (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green).

Table 5.2.1: The variance in data explained by principal component 1 and principal component 2 and associated eigenvalues for the variables which held the most influence within the data in each component, addition of upright stubble to Conventional tillage trials.

	Principal 1	**Principal 2**
Variance	48.2%	19.1%
Variables	**Eigenvalue**	**Eigenvalue**
Total Thread Length in Webs (of support threads) (mm)	0.357	
Thread Length out of Webs (of bridge threads) (mm)	-0.261	
Thread Length out of Webs (of bridge threads) (mm)		0.281
Anchor Point Height out of Webs (of bridge threads) (cm)		-0.436

The first principal component was associated with the variables total thread length inside webs and thread length outside of webs (*Figure 5.2.5. & Table 5.2.1.*). Thread length and anchor point height outside of webs lay in the second principal component. The variables that had the greater influence on the data were those that measured the product of *T. tenuis* activity, more than the variables associated to the field conditions, i.e. upright stubble density and height. The data for Direct Drill and Conventional were influenced the most by thread length out of webs and total thread length inside of webs, anchor point height outside of web had the main effect within Direct Drill Managed.

Table 5.2.2: Response of rank anchor point height and factors of soil tillage intensity, inside or outside of webs. Addition of upright stubble to Conventional tillage trials (n = 233). (relates to significant with α <0.05).*

Categorical Predictor	**Df**	***H***	***P***
Soil Tillage Intensity	2	35.564	0.001*
In / Out of Web	1	130.62	0.001*
Interaction: Soil Tillage Intensity * In / Out of Web	2	62.6694	0.001*

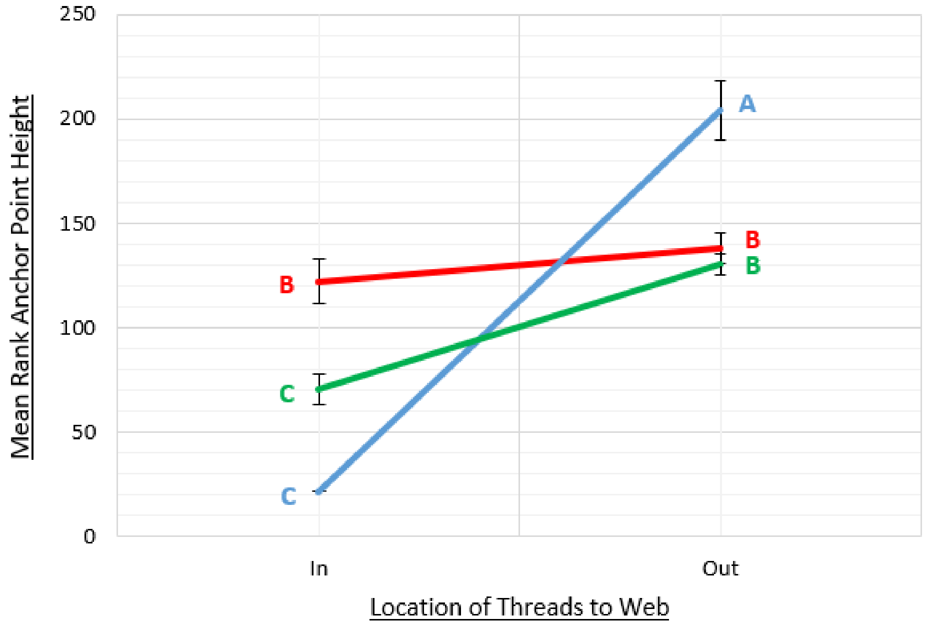


Figure 5.2.6: Interaction of mean rank anchor point height, soil tillage intensity and inside or outside of webs, addition of upright stubble to Conventional tillage trials (n=233). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional In ±s.e.10.816 (n = 27), Conventional Out ±s.e.7.603 (n = 39), Direct Drill Managed In ±s.e.0.089 (n = 3), Direct Drill Managed Out ±s.e.14.020 (n = 20), Direct Drill In ±s.e.7.616 (n = 73), Direct Drill Out ±s.e.5.227 (n = 71)). (Points that do not share the same letter are significantly different at the p<0.05 level).

There was a significant difference identified between the interaction of the soil tillage intensity and whether the mean rank anchor point heights were inside or outside of the web (*Table 5.2.2. & Figure 5.2.6.*). Mean rank anchor point height for support threads in Direct Drill and Direct Drill Managed were significantly lower than the mean rank anchor point height of bridge threads in all soil tillage intensities. The mean rank anchor point height outside of webs (bridge threads) for Direct Drill Managed was further significantly higher than the mean rank anchor point height inside webs (support threads) found within Conventional.

Table 5.2.3: Response of rank anchor point height inside webs (of support threads) and factors of soil tillage intensity and anchor point attachment material, addition of upright stubble to Conventional tillage trials (n = 100). (relates to significant with α <0.05).*

Categorical Predictor	**Df**	***H***	***P***
Soil Tillage Intensity	1	0.00962	0.922
Anchor Point Attachment Material	1	53.2587	0.001*
Interaction: Soil Tillage Intensity * Anchor Point Attachment Material	1	0.18619	0.666

Figure 5.2.7: Interaction of mean rank anchor point height inside webs (of support threads), soil tillage intensity and anchor point attachment material, addition of upright stubble to Conventional tillage trials (n = 100). (Conventional = Red, Direct Drill = Green). (Conventional Soil ±s.e.0.054 (n = 3), Conventional Upright Stubble ±s.e.2.725 (n = 24), Direct Drill Soil ±s.e.2.054 (n = 41), Direct Drill Upright Stubble ±s.e.3.221 (n = 32)). (Points that do not share the same letter are significantly different at the p<0.05 level).

Significance was only identified within the term anchor point attachment material (*Figure 5.2.7. & Table 5.2.3.*). The mean rank anchor point height of support threads attached to the material of upright stubble was significantly higher within the area representing Conventional and Direct Drill tillage than the mean rank anchor point height measured attached to soil.

Direct Drill Managed was taken out of the model as only one anchor point was measured attached to soil and altered the validity of the model.

Table 5.2.4: Response of rank thread length and factors of soil tillage intensity and inside or outside of webs, addition of upright stubble to Conventional tillage trials (n = 262). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	10.2791	0.006*
In / Out of Web	1	16.6134	0.001*
Interaction: Soil Tillage Intensity * In / Out of Web	2	21.675	0.001*

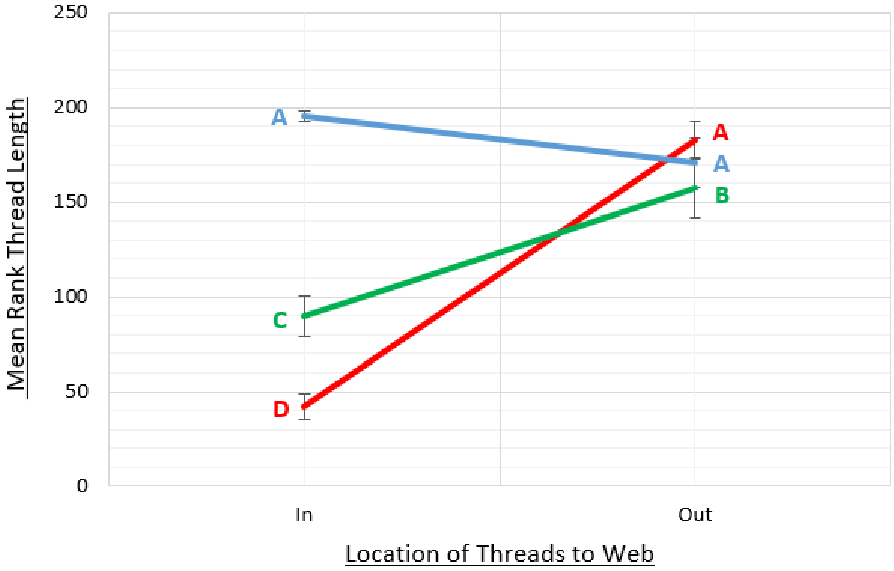


Figure 5.2.8: Interaction of mean rank thread length, soil tillage intensity and inside or outside of webs, addition of upright stubble to Conventional tillage trials (n = 262) (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional In ±s.e.6.785 (n = 29), Conventional Out ±s.e.9.908 (n = 38), Direct Drill Managed In ±s.e.2.962 (n = 3), Direct Drill Managed Out ±s.e.13.014 (n = 20), Direct Drill In ±s.e.10.631 (n = 71), Direct Drill Out ±s.e.15.688 (n = 101)). (Points that do not share the same letter are significantly different at the p<0.05 level).

A significant difference was found when soil tillage intensity (Conventional, Direct Drill Managed, Direct Drill) interacted with location of thread length (inside or outside of a web) for mean rank thread length (*Table 5.2.4. & Figure 5.2.8.*). Significant heterogeneity existed with the mean rank thread length inside webs for Conventional and Direct Drill and the mean rank thread length outside of webs for Direct Drill. The mean rank thread length inside webs for Conventional was significantly lower than any other mean rank thread length of the model.

Table 5.2.5: Correlations (Spearman's Rank) between independent variables and dependant variables measured, addition of upright stubble to Conventional tillage trials. (relates to significant with α <0.05).*

Independent Variable		**Dependant Variable**	**(Rho)**	***P***	**n**
Anchor Point Height in Web (cm)	x	Mean Upright Stubble Height (cm)	-0.399	0.001*	103
Anchor Point Height in Web (cm)	x	Upright Stubble Density (Nº0.25m^{-2})	-0.264	0.007*	103
Anchor Point Height Out of Web (cm)	x	Mean Upright Stubble Height (cm)	0.304	0.001*	130
Anchor Point Height Out of Web (cm)	x	Upright Stubble Density (Nº0.25m^{-2})	0.393	0.001*	130
Number of *T. tenuis*	x	Upright Stubble Density (Nº0.25m^{-2})	0.461	0.001*	9
Thread Length in Web (mm)	x	Mean Upright Stubble Height (cm)	0.302	0.002*	103
Thread Length in Web (mm)	x	Upright Stubble Density (Nº0.25m^{-2})	0.500	0.001*	103

Table 5.2.6: Correlations (Pearsons) between independent variables and dependant variables measured, addition of upright stubble to Conventional tillage trials. (relates to significant with α <0.05).*

Independent Variable		Dependant Variable	(r)	*P*	df
Thread Length Out of Web (mm)	x	Upright Stubble Density (N^{o}0.25m^{-2})	-0.173	0.029*	157
Total Thread Length Out of Web (mm)	x	Number of Webs	0.685	0.001*	7

Anchor point height for threads outside of the web and thread length inside of webs were significantly positively correlated to upright stubble height and upright stubble density (*Table 5.2.5*.). Whereas anchor point for threads inside of webs was significantly negatively correlated to the same two dependant variables (upright stubble height and density). Number of *T. tenuis* recorded in the sample plots was significantly positively correlated to upright stubble density.

Independent variables in Table 5.2.6. were found to be normal. Thread length out of webs was significantly negatively correlated to upright stubble density. Whereas, total thread length outside of the web was significantly positively correlated to number of Linyphiidae webs recorded (*Table 5.2.6*.).

5.2.7. Discussion

Mean anchor point height was found to be significantly higher within Conventional in the web and Direct Drill Managed out of the web (*Figure 5.2.6.*) This is an unexpected result, with the mean higher anchor points found to be higher from bridging threads in times of cultivation in fieldwork, *T. tenuis* accessing apex of materials for rapid dispersal (Bonte *et al.*, 2003; Hogg and Danne, 2018) (*Section 5.1.6.1.*). This is seen to be due to the difference in heights of upright stubble between the tillage areas, a product of harvest where grain is cut from the dried stem creating the stubble (AHDB, 2015; Davies & Finney, 2002; Morris *et al.,* 2010) (*Section 3.1.3.4.*). Its resultant height is due to its orientation when cut, and slight depressions in land causing elevation or suppression of the rotating wheels of the harvester (AHDB 2015; 2018; Kennedy & Connery, 2005). Eight out of the nine webs for Conventional were woven at the top of the upright stubble. The field of this trial, having undergone Conventional secondary tillage, was void of other landscape features (soil clods and volunteer plants for example), which could have provided additionally anchor points for webs, other than upright stubble (Jarvis & Woolford, 2017; Morris *et al.,* 2010; Peigné *et al.,* 2007) (*Figure 5.2.3a* & *b* & *Section 5.2.3*.).

Little *T. tenuis* and Linyphiidae activity occurred within Direct Drill Managed habitat, where only one web was woven at ground level. This web was abandoned; however, it may have been woven by a Linyphiidae with a prey preference of ground dwelling arthropods, which favour this web-site (García *et al.,* 2013; McCanny *et al.,* 1996; Oxbrough *et al.,* 2006). The disparity appears to be due to upright stubble density. Rappel threads were measured at the pinnacle of stubble in Direct Drill Managed (*Figure 5.2.6.*). Dispersal had perhaps occurred, possibly to the adjacent Direct Drill habitat treatment where the greater web area was identified, this expressing a higher presence of *T. tenuis* and Linyphiidae (*Figure 5.2.4a & b*).

In all soil tillage intensities, upright stubble in height and abundance affected web-building, a re-occurring theme throughout fieldwork when out of crop (*Section 5.1.6.1.*). A higher number of webs built between adjacent stubble in the same cluster were observed with Direct Drill (*Table 5.2.5.*). This supports work of Aaserud (2005), Alderweireldt (1994) and Miller (2007), where web-building spiders were shown to require above ground materials for attachment points of silk. The nature of the horizontal aerial web is a requirement to have multiple structures in the vicinity for threads to be woven between (Blackledge *et al.,* 2005; Harwood *et al.,* 2003; Marc & Canard, 1997 Zschokke & Herberstein, 2005). If such material is not available, the site may not allow a web to be spun, and thus, the area is void of the biological control potential that a web may bring (Betz & Tscharntke, 2017; Krink & Vollrath, 1997).

Webs in Direct Drill were either measured attached to apex of the habitat, amongst upright stubble, or anchored to the lower aspects of the stubble and a soil aggregate (*Table 5.2.5.*). This could point to utilisation of the treatment by different Linyphiidae. A female *T. tenuis* was found underneath a web at the top of the stubble and under a web spun within the base in Direct Drill. This showed the pioneering ability of *T. tenuis* and agrees with Isaia *et al.* (2007) and Samu *et al.* (1996), where *T. tenuis* is seen to exploit a varied position created by a disturbed landscape. Although, Alderweireldt (1994) Samu *et al.* (1996), and Štokmane & Spuņģis (2016) discuss the key with *T. tenuis* is a requirement to have space underneath a web for 'sit and wait' predation and allow mobility when prey is ensnared.

The stark difference in web-site locations, shows that different Linyphiidae species may be involved in weaving sheet webs within this experiment. Schirmel *et al.* (2016) and Schütt (1997) explain the choice of a vegetation layer differs within Linyphiidae, allowing co-habitation. A *T. tenuis* was found under a large web at the lower strata of the habitat in Direct Drill Managed, which differs from recordings by Beck & Toft (2000) and Davey *et al.* (2013) who noted that *T. tenuis* spin webs above the ground layer in an agricultural setting (*Figure 5.2.8.*). Bell *et al.* (2002), Harwood *et al.* (2001) and Sunderland & Samu (2000) comment that weaving a web higher within vegetation, a greater advantage point, is achieved to capture prey residing in upper canopies of crop vegetation and aerial prey. However, the field of this trial was out of crop and the cultivation applied field wide, which rendered the field to be of an open nature, thus, prey dispersal could have occurred with little obstruction (*Figure 5.2.3a & b* & *Section 5.2.3.*). Blackledge *et al.* (2009) and Diehl *et al.* (2013) discussed that reduced level of landscape heterogeneity could enable webs spun near the soil surface to access aerial prey (Romero & Harwood, 2010; Sanders *et al.,* 2015).

The creation of the two different strata used in Conventional and Direct Drill habitat allowed different sheet webs to be woven (*Figure 5.2.7.*). This explores similar findings to the main field sampling after secondary cultivation (*Section 5.1.5.1.3.*). A sheet web of a small area, woven into the tops of the stubble in Conventional was seen to be protected from disturbance, as noted by Diehl *et al.* (2013) and Harwood *et al.* (2003) to be environmental in nature, and be closer to a potential aerial prey source (Harwood *et al.,* 2004) (*Figure 5.2.7., Figure 5.2.8. & Figure 5.2.10.*). However, Obryck & Harwood (2005) and Toft (1987) identified possible limitation in prey capture due to small surface area of the web and obstruction to entrapment that surrounding stubble may cause (Dennis *et al.,* 2001; Roberson *et al.,* 2016). The webs spun into soil of lower level, have a greater prey interception potential with a large open web area, though very little protection is provided from surrounding simplified landscape of the fallow field (Beck & Toft, 2000; Rybac, 2007; Welch *et al.,* 2013) (*Figure 5.2.7., Figure 5.2.8. & Figure 5.2.9.*). It can be identified that both treatments have enabled webs with differing trade-offs to be established. Robertson & Avilés (2018) and Segoli *et al.* (2004) explained web-building behaviour to be a form of compromise, with not every desired specification met. With no prey identified in both, it is difficult to assess which may have been successful in predator dynamics (Barriga, 2010; Buri *et al.,* 2016; Sanders *et al.,* 2015).

Figure 5.2.9: Sheet web within base of upright stubble and soil. Direct Drill tillage. Addition of upright stubble to Conventional tillage trials. Elevated view. (Red arrow = 12.4 mm).

Figure 5.2.10: Sheet web within upright stubble. Direct Drill tillage. Addition of upright stubble to Conventional tillage trials. Lateral view. (Red arrow = 21.3 mm).

Mean thread length was significantly longer in Conventional and Direct Drill Managed, out of webs, than that seen in Direct Drill (*Figure 5.2.8.*), however, greater rappelling action occurred within Direct Drill (*Figure 5.2.11.*). Due to the lack of stubble density in Conventional and Direct Drill Managed, longer bridge threads were identified, spun between upright stubble across rows instead of stubble in the same cluster (*Figure 5.2.4a-c*). Alderweireldt (1994), Bonte *et al.* (2011) and Peters & Koover (1991) explain features of the landscape used in rappelling are favoured to be of a similar height and dimensions to facilitate fast dispersal. This long dragline silk is likely to have consumed much energy and could explain why little rappelling was identified (Bonte 2013; Hesselberg & Vollrath 2012) (*Figure 5.2.11.*). Rappelling was likely a trade-off, with Moya-Laraño *et al.* (2008) and Szymkowiak *et al.* (2007) discussing the energy consumption used in the climbing of a structure to begin dispersal. This energy loss may not be counteracted, if a potential web-site is not found (Blackledge *et al.,* 2011; De Meester & Bonte, 2010). Low abundance in rappelling material in Conventional plot may have led to ballooning into a neighbouring treatment or towards a shelterbelt. Moya-Laraño *et al.* (2008) and Simonneau *et al.* (2016) discuss how ballooning uses less energy than rappelling, after the initial ascent, due to pendulum motion created by gravity, swinging the dragline thread into a new location. This allows long-ranged dispersal to be advantageous if there are low beneficial web-site opportunities within the vicinity.

Figure 5.2.11: Female T. tenuis *rappelling across upright stubble (circled in yellow). Direct Drill tillage. Addition of upright stubble to Conventional tillage trials. Elevated view. (Red arrow = 18.7 mm).*

Within this trial, unlike fieldwork of *H. vulgare* at primary cultivation, number of webs and total thread length out of web, were significantly positively correlated (*Table 5.2.6. & Section 5.1.5.1.4.*). The energy output for bridging can be observed to have been positively rewarded, by a key web-site exploited in the Direct Drill area (Ford, 1977; Robertson & Avilés, 2018; Schütt, 1997; Simonneau *et al.,* 2016). The increased upright stubble may be beneficial to the future potential of prey capture, the web (the extended phenotype) to remove active prey from an ecosystem (Kovac & Mackay, 2009; Lichtenstein *et al.,* 2016; Pathan 2002). If *T. tenuis* remains in the web any future prey caught in the silk fibres will become a source of food for the *T. tenuis*. (Štokmane & Spuņģis, 2016; Welch *et al.,* 2013). Marc & Canard (1997), Millidge (1988) and Saravanan (2006) comment that if a web is vacated, the prey potential remains, as it is still able to by-catch prey into the web and become entangled in its sheet web construction.

The number of *T. tenuis* was positively correlated to upright stubble density, due to three females and one male *T. tenuis* identified in the Direct Drill treatment, with two females occupying webs (*Table 5.2.5*.). It can be observed that upright stubble facilitated the movement of female *T. tenuis* more than males, through bridging and possible balloon dispersal between treatments. The combination of the height of the stubble, its orientation allowing access to a large open area, may have promoted this area as a key web-site, pioneered by a large bodied female (Chapman *et al.,* 2013; Eichenberger *et al.,* 2009; Stenchly *et al.,* 2011). Indeed, Bonte *et al.* (2011), Gan *at al.* (2015) and Samu *et al.* (1996) explain web take-over could have occurred, where *T. tenuis* of a larger frame are likely to exert dominance. This web of the ground strata may have been spun previously by a ground dwelling dwarf Linyphiidae (Dondale, 2000; Downie *et al.,* 2000).

Bonte *et al.* (2008), identified that females had a greater propensity to rappel and balloon, and Lombaert *et al.* (2006), explained rappelling closely correlates to body fitness. This experiment was carried out at the beginning of September 2018. Samu *et al.* (1996) and Welch *et al.* (2013) discussed that life cycles of *T. tenuis* have evolved to be in line with the cropping system, and fecund females have differing dispersal strategies (Mazzia *et al.,* 2015; Thorbek *et al.,* 2004). Zschokke & Herberstein (2005) explained that females are energy maximisers at times of peak fecundity, dispersing emphatically in between web-building. A greater number of web-sites were seen to lead to increased number of male suitors and sperm selection (Gaskett, 2007). Thomas & Jepson (1999) suggest males have a higher preference to balloon due to fewer requirements than fecund females, however Thomas & Jepson (1999) discuss dispersal from a grassland to a cereal crop. This trial carried out upon a disturbed fallow field, a female *T. tenuis* may be rappelling at a greater propensity to find a web-site within the upright stubble, sensing little potential within the simplified landscape of the field. Corcobado *et al.* (2010), De Mas *et al.* (2009) and Kuntner & Coddington (2020) explore that female *T. tenuis* with a larger abdomen, to increase attraction from male suitors, may be unable to bridge and thus is a function of extreme SSD (Sexual Size Dimorphism) (*Section 2.1.3.4*.). Dragline silk is required to be spun at a fast pace due to exertion required with gravity (Moya-Laraño *et al.,* 2008; Prenter *et al.,* 2010; Rodríguez & Gloudeman, 2011). A larger bodied *T. tenuis* may not be able to bridge at this pace creating a negative feedback loop where the initial output of energy for ascent is lost (Entling *et* *al.,* 2011; Simonneau *et al.,* 2016). Only one large bodied female *T. tenuis* (abdomen 2 mm) was noted under a web of the bottom strata of Direct Drill treatment. This may identify a lack of rappelling ability. One female *T. tenuis* (abdomen 1.3 mm) was observed at the pinnacles of the stubble retreating downwards upon disturbance. Upright stubble in the Direct Drill treatment may have aided fecund females for web creating for copulation.

Interestingly, four variables that relate to *T. tenuis* activity explained the greatest variance found within the data (*Figure 5.2.5.*). This identified that action of *T. tenuis* appeared to be a response to previous activity. The mass action hypothesis can be applied here where the upright stubble is identified as a 'functional landscape unit' altering the response of *T. tenuis* activity as a population (Bianchi *et al.,* 2017; Fahrig *et al.,* 2011). The landscape features, upright stubble density, has been shown to alter *T. tenuis* behaviour in web-building and rappelling, though it is the action of the *T. tenuis* themselves which is acting as a positive feedback response. *T. tenuis* are noted to be solitary species, however, Kraft & Cookson (2012) introduced the idea that the response of one Linyphiidae to lay silk alters a landscape and leaves a vibration pattern that can be sensed by other near *T. tenuis* of activity, thus producing a group predation effect.

5.2.8. Final Discussion - Addition of Upright Stubble to Conventional Tillage Trials

The above trial identified that upright stubble, in abundance, height and orientation to one another, appeared to have been influential in driving *T. tenuis* and Linyphiidae activity in a disturbed landscape and relates to the second and fourth aim of Section 5.2.2.1. Small differences in upright stubble, in terms of the factors discussed, were shown to increase rappelling and web-spinning. Different webs in dimension and location, were identified within the treatments, suggesting creation by different Linyphiidae. Small webs woven within the stubble or large webs woven from soil clods, identified differing trade-offs further addressing the second aim (*Section 5.2.2.1.*). On the surface, Direct Drill treatments, with increased upright stubble, were shown to encourage predator dynamics of *T. tenuis* and Linyphiidae with greater web abundance, and *T. tenuis* present underneath webs, linking to the fourth aim of this Sub-Chapter (*Section 5.2.2.1.*).

It would have been useful to observe a higher degree of prey capture in webs to quantify this and bring clarity to the presented fourth aim of understanding *T. tenuis* ability to predate on Aphididae in the different array of upright stubble offered. However, it is noted, that the trial would be required to run over a longer time frame to fully understand how upright stubble could have altered the pest suppression ability of *T. tenuis*.

Sub-Chapter Five Three

5.3. Hedgerows Opposite Soil Cultivations of Different Tillage Intensity

5.3.1. Introduction

Hedgerows are an important aspect of a field for consideration when aiming to understand *T. tenuis* relationship with prey in an arable agricultural system. Garratt *et al.* (2017) and Pfister *et al.* (2015) both discussed the impact of a hedgerow surrounding a cropped field, noting *T. tenuis* preference for the hedgerow in times when the field was fallow (*Section 2.1.2.2.*). It was commented that the distance from the hedgerow into the main field was a key function of *T. tenuis* behaviour with Linyphiidae numbers decreasing as distance from hedgerow increased.

For this research to fully comprehend *T. tenuis* ability for predation, it was important to sample hedgerows in addition to the main field. Due to the project seeking to understand if soil tillage intensity influenced *T. tenuis* behaviour, the hedgerow needed to be divided into areas of tillage that it was adjacent to, as described in Figure 4.28., Section 4.5.2.1., Page 72.

5.3.2. Aims and Specific Objectives

5.3.2.1. Aims

This element of fieldwork relates to Research Aims 1 - 4 (*Section 1.2.*, *Page 2*).

1. Identify the potential biological control by *T. tenuis* of Aphididae and *S. mosellana* within different intensities of tillage in an arable crop.
2. Identify any differences in extended phenotypes of *T. tenuis* within tillage practices, e.g. web dimensions and bridge thread length.
3. Understand whether *T. tenuis* behaviour is stimulated by the presence of Aphididae and *S. mosellana*.
4. Comprehend if a certain level of landscape heterogeneity affects *T. tenuis* ability to predate on Aphididae and *S. mosellana*.

5.3.2.2. Specific Objectives

Objectives below are specifically placed to meet the aims of this Sub-Chapter.

- Measure Linyphiidae web location in anchor point height and anchor materials, within a hedgerow adjacent to the different tilled areas of the field.
- Observe *T. tenuis* web occupation and prey (Aphididae and *S. mosellana*) density in web and relate to potential *T. tenuis* prey capture interactions.
- Identify and quantify crop pest / prey and *T. tenuis* abundance (from g-vac sampling) in the hedgerow and compare relative density relationships.
- Quantify migratory distance of *T. tenuis* by measuring the distance of a web and bridge thread from the field edge.
- Assess potential differences in extended phenotypes of *T. tenuis* within a hedgerow adjacent to the differing intensity of soil tillage, e.g. measure web dimensions and architecture.

5.3.3. Methodology

5.3.3.1. Field Sampling

Sampling commenced at the identical periods described in Table 5.1.1. of Section 5.1.3. (*Page 82*). This spanned the period of March 2017 to November 2018.

5.3.3.2. Data Collection

Table 5.3.1: Measurements taken on each fieldwork sampling period for the hedgerows opposite soil cultivations of different tillage intensities and its relation to T. tenuis *activity.*

	Measurement Taken	**Months Measured**	**Relation to *T. tenuis* Activity**
1	Number of *T. tenuis* rappelling or ballooning	All	*T. tenuis* migration in / out of habitat.
2	Number of bridge threads	All	Frequency of *T. tenuis* locomotion / migration.
3	Anchor point height of bridge threads (cm)	All	Height locomotion / migration is occurring.
4	Attachment material for bridge threads	All	Material facilitating locomotion / migration.
5	Distance of nearest anchor point from field edge (cm)	All	Migration distance into hedge.
6	Number of webs	All	Frequency of web-building.
7	Support thread length (mm)	All	Quantify web area.
8	Anchor point height of support threads (cm)	All	Height web-building is occurring.
9	Attachment material for support threads	All	Material facilitating web-building.
10	Distance of nearest anchor point from field edge (cm)	All	Migration distance into hedge.
11	Number of *T. tenuis* within web	All	How web occupation relates to habitat and prey abundance.
12	Number of prey within web	All	Prey capture rate via web.
13	Egg sac abundance	Sept - Feb	Quantify Linyphiidae potential reproductive output.
14	Egg sac attachment material and anchor point height (cm)	Sept - Feb	Understand oviposition location.
15	Egg sac dimensions (width & length (mm))	Sept - Feb	Reproductive output for next generation.
16	Egg sacs examined for eggs within	Sept - Feb	Reproductive stage for next generation.
17	Wind speed (kmh^{-1})	All	How wind speed relates to *T. tenuis* abundance / activity.
18	*T. tenuis* abundance quantified	All	How abundance relates to habitat and prey availability.
19	*T. tenuis* body dimensions (abdomen & cephalothorax length (mm))	All	How dimensions relate to habitat and prey availability.
20	Prey identification and abundance quantified	All	How prey quantity relates to habitat and *T. tenuis* abundance / activity.

Measurements collected in the hedgerows centred on the suitability of the habitat to be a reservoir for *T. tenuis* activity outside of the field (*Table 5.3.1*.). As in the main field, measurements acquired were assigned to the tillage intensity that the hedgerow was opposite.

1. Bridge threads and web in anchor height, quantity and dimensions were measured following the methodology used in the field (*Section 5.1.3.2*.). Balloon threads were noted by long length anchored singularly to the apex of an outmost structure for downwards projection.
2. Contents of the web were examined, species identified, and prey quantified.
3. The nearest anchor point of a bridge thread and web to the external of the hedgerow, thus nearest to the field edge, was identified. A 1 m rule was placed just in front of the anchor point. This ruler intercepted the metre rule of the sample that ran vertically into the hedgerow. The measurement of the distance of anchor point to start of the sample area, field margin, was read on the vertical ruler to 0.1 cm (*Figure 4.30a & b, Section 4.5.2.2, Page 73*). From all measurements, 100 cm was added to incorporate the distance from the field edge to the start of the sample area.
4. Wind speed was measured in the four areas noted in Figure 4.38. (*Section 4.6.2., Page 79*). to 0.1 mph (converted to kmh^{-1}) with the anemometer, Cateye Velo®.
5. Abundance of *T. tenuis* and prey were attained with the g-vac as in the fieldwork (*Section 5.1.3.2*.). Dimensions of *T. tenuis* abdomen and cephalothorax were quantified via the same methodology as fieldwork with a period of rest in Petri dishes before measurement to 0.1 mm with a Zukvye© Digital Calliper (*Section 4.3.7*.).
6. Hedgerow vegetation density was acquired by photography at 1 m away from the hedgerow and 30 cm from the ground with the Sony® HDR CX240 Full HD Camcorder with 27 x optical zoom and 320 x digital zoom (*Section 4.5.2.3*.).
7. For the fore-ground hedgerow vegetation density, a pre-tied white sheet onto a support frame, clothes horse, was placed behind the foreground vegetation of the hedge. A photograph was taken at the exact specifications as quoted above with the same camera (*Section 4.5.2.3*.).
8. Photographs were then formatted with Paint 3D into a JPEG and imported into ImageJ. Methodology then adhered to specifications noted in Section 4.5.2.3. (*Page 74 - 77*) and area of vegetation for hedgerow vegetation density quantified.
9. The length of hedgerow was examined for egg sac abundance. Once located, dimensions were measured to 0.1 mm with the Zukvye© Electronic Vernier Callipers 150 mm Carbon Fibre Body Measuring Tool. Further, the attachment material was recorded, and the anchor point height was measured to the nearest 0.1 cm. Egg sacs were carefully examined for the presence of eggs within (*Figure 4.37a-d, Section 4.5.2.4. Page 78*).

5.3.4. Statistical Analysis

Normlity was assessed following the proceedure explained in Section 5.1.4.1. of the main field sampling. The Anderson-Darling and Ryan-Joiner test was utilised alongside histograms and probability plots to understand distribution of the datasets.

Statistical Analysis was similar to that used for the fieldwork due to non-normal data established (*Section 5.1.4.2.*), utilising the statistical analysis of correlations (Spearman's Rank) and two-way rank ANOVAs identifying the relationship between categorical factors and a numerical response (Hawkins, 2014). Mean ranks and associated statistics, degrees of freedom (df) and sum of squares (SS), were generated (Mintab18©) and placed into FCSTats V2_1a© (Wheater & Cook, 2000). From here significance for any interaction was gained. The Dunn's test was performed on FCSTats V2_1a© to understand where significance lay (Wheater & Cook, 2000). Significance was checked through use of the Bonferroni post-hoc test (Mintab18©) to establish letters for graphical representationon. Kruskal-Wallis Test was run through Minitab18©. Dunn's multiple comparison test was performed on Minitab18© with the incorporation of a macro (KrusMC.mac) downloaded from Mintab18© libray (Hawkins, 2014; Orlich, 2000).

One result met the null hypothesis for normaility (via Anderson-Darling and Ryan-Joiner test), mean number of sheet webs within the field and hedgerows at times out of crop (*Section 5.1.4.1.*). A two-way ANOVA was run with the post-hoc test of Tukey (Bass, 2007). Associated statistics where analysed to assess validity.

5.3.5. Results

The layout of the results presented below followed the format offered to display the results from the fieldwork section (*Section 5.1.5.*), where the data is split into whether it belonged to hedgerows opposite the field in times out of crop (after primary and secondary cultivation and fallow) and when the field was cropped with *H. vulgare* (early and late growth stages). The information was further split into the main dependant variables measured that related to *T. tenuis* activity; anchor point height, distance of anchor points from the field edge (which was a representation of migration distance into the hedgerow) and thread length. All three variables were divided into whether the information recorded was from inside the web (from a support thread) or outside the web (from a bridge thread).

Anchor point height and web area were investigated with presence of crop pests found in the vegetation and web. Crop pests relate to potential *T. tenuis* prey (*S. avenae, M. dirhodum, R. padi* and *S. mosellana*). Mean variables recorded in the field were analysed against those measured in the hedgerow opposite. Finally, an analysis of data surrounding the presence of egg sacs was interpreted.

5.3.5.1. Summary of Results

Out of Crop - Fallow and After Primary and Secondary Cultivation

- Significantly lower mean rank anchor point height for bridge threads was found in Conventional hedgerows (*Figure 5.3.1.*). Number of female *T. tenuis* and *T. tenuis* in webs was significantly negatively correlated to anchor point height out of webs (*Table 5.3.4.*).
- Number of *T. tenuis* in webs were significantly positively correlated to anchor point height of support threads after primary cultivation and significantly negatively correlated after secondary cultivation (*Table 5.3.2.*).
- Numbers of male *T. tenuis* was significantly positively correlated to anchor point height of support threads at secondary cultivation, mean abdomen length was significantly positively correlated to this variable after primary and secondary cultivations (*Table 5.3.2.*).
- Hedgerow vegetation density was negatively correlated to anchor point height of support threads after primary and secondary cultivations (*Table 5.3.2.*).
- Wind speed (field edge) was significantly negatively correlated to anchor point height in webs (*Table 5.3.3.*) and distance of anchor point of support threads from field edge (*Table 5.3.6.*).
- Mean rank distance of anchor point from the field edge of bridge threads was significantly nearer to the field edge (*Figure 5.3.2.*).
- Number of female *T. tenuis*, *T. tenuis* in webs and number of webs were significantly negatively correlated to distance of anchor point of bridge threads from field edge (*Table 5.3.7.*).
- Median support thread length was significantly longer in Direct Drill hedgerows (*Figure 5.3.3.*) Number of female *T. tenuis* was significantly positively correlated to support thread length when fallow and after secondary cultivation (*Table 5.3.9.*).
- After primary cultivation, hedgerow vegetation density was significantly positively correlated to support thread length, when fallow, both variables were significantly negatively correlated (*Table 5.3.9.*).
- Mean abdomen length was significantly negatively correlated to bridge thread length, whereas number of female and male *T. tenuis* were significantly positively correlated (*Table 5.3.10.*).

In Crop - Early and Late Growth Stages of *H. vulgare*

- Number of *T. tenuis* in webs, *T. tenuis* rappelling, *S. avenae* in webs and wind speed (bottom of hedgerow) were significantly positively correlated to anchor point height of support threads (*Table 5.3.11. & Table 5.3.12.*). Number of *T. tenuis* in webs was significantly positively correlated to support thread length in early growth stages (*Table 5.3.16.*).

- Number of female and male *T. tenuis* were significantly negatively correlated in early growth stages to anchor point height and length of support threads and significantly positively correlated in later growth stages to anchor point height of webs only (*Table 5.3.11. & Table 5.3.16.*).
- Significantly higher mean rank anchor point height of support threads was found in Direct Drill hedgerow when no crop pests were found in the vegetation (*Figure 5.3.4.*).
- Direct Drill Managed and Direct Drill hedgerows exhibited significantly lower mean rank anchor point height of support threads when crop pests were in webs (*Figure 5.3.5.*).
- Hedgerow vegetation density was significantly positively correlated to distance of anchor point of support threads to field edge, whereas number of *S. avenae* and *T. tenuis* in web were significantly negatively correlated (*Table 5.3.15.*).

Variables Measured Within the Field and Hedgerow

- Mean rank number of *T. tenuis* and mean number of sheet webs were significantly greater in hedgerows after cultivations and fallow (*Figure 5.3.6. & Figure 5.3.7.*). Mean rank number of *T. tenuis*, in all growth stages, was significantly greater in hedgerows than field (*Figure 5.3.8.*).
- Significantly greater number of bridge threads in hedgerows were found when field was out of crop for Conventional and Direct Drill Managed (*Figure 5.3.9.*).

Variables Concerning the Presence of Egg Sacs in Hedgerows

- Number of egg sacs was significantly positively correlated to the hedgerow vegetation density. Egg sac width was significantly positively correlated to distance from field edge (*Table 5.3.21.*).

5.3.5.2. Out of Crop - Fallow and After Primary and Secondary Cultivation

5.3.5.2.1. Anchor Point Height

Table 5.3.2: Correlations of independent variables measured in the hedgerow with the dependant variable anchor point height (cm) inside webs (of support threads) for hedgerows when the field was fallow and after the field had undergone primary and secondary cultivation. (relates to significant with α <0.05).*

	Fallow			**Primary Cultivation**			**Secondary Cultivation**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**	**(Rho)**	***P***	**n**
Hedgerow Vegetation Density (cm^2)	0.224	0.064	69	-0.394	0.001*	495	-0.125	0.003*	556
Mean Abdomen Length (mm)	0.044	0.516	216	0.278	0.001*	704	0.125	0.001*	794
Number of Female *T. tenuis*	-0.280	0.001*	372	0.151	0.003*	704	0.040	0.258	794
Number of Male *T. tenuis*	-0.072	0.266	372	-0.091	0.072	704	0.108	0.006*	794
Number of *T. tenuis* in Web	-0.426	0.001*	372	0.161	0.001*	704	-0.110	0.002*	794
Number of Web	0.063	0.322	243	0.191	0.001*	704	0.285	0.001*	794

Table 5.3.3: Correlations of wind speed (kmh^{-1}) measured in the hedgerow with the dependant variable anchor point height (cm) inside webs (of support threads) for hedgerows when the field was fallow and after the field had undergone primary and secondary cultivation. (relates to significant with α <0.05).*

	(Rho)	***P***	**n**
Wind Speed - Field Edge (kmh^{-1})	-0.159	0.001*	1294

When the field had undergone primary and secondary cultivation, the number of webs was significantly positively correlated to anchor point height of threads inside webs (*Table 5.3.2*.). Number of female *T. tenuis* was significantly positively correlated against anchor point height for threads in webs after primary cultivation. After secondary cultivation, the number of male *T. tenuis* was shown to have a significant positive correlation to anchor point height measured inside webs and when fallow number of female *T. tenuis* was significant negatively correlated to anchor point height of support threads. The mean abdomen length of *T. tenuis* had significant positive correlation with anchor point height of support threads after primary and secondary cultivation. Hedgerow vegetation density was significantly negatively correlated to anchor point height of webs after both cultivations. The number of *T. tenuis* observed in webs was significantly positively correlated in times of primary cultivation, and significantly negatively correlated in secondary cultivation and fallow.

When the field was out of crop, wind speed at the field edge was significantly negatively correlated to anchor point height of support threads (*Table 5.3.3*.). Wind speed only identified significance when data from fallow and after cultivations were analysed together.

Table 5.3.4: Correlations of independent variables measured in the hedgerow with the dependant variable anchor point height (cm) outside of webs (of bridge threads) for hedgerows when the field was fallow and after the field had undergone primary and secondary cultivation. (relates to significant with α <0.05).*

	(Rho)	***P***	**n**
Distance of Anchor Point from Field Edge (cm)	0.186	0.004*	241
Number of Female *T. tenuis*	-0.749	0.001*	351
Number of Male *T. tenuis*	-0.542	0.001*	351
Number of *T. tenuis* in Web	-0.734	0.001*	351
Number of *T. tenuis* Rappelling	-0.291	0.001*	351

The distance of the anchor point outside of webs from the field edge was significantly positively correlated to the anchor point height outside of webs (*Table 5.3.4.*). Number of *T. tenuis* (male and female) were significantly negatively correlated to anchor point heights out of webs recorded. The number of *T. tenuis* observed inside sheet webs and were recorded rappelling were both significantly negatively correlated to anchor point height of bridge threads.

Table 5.3.5: Response of rank anchor point height, soil tillage intensity and inside and outside of web, for hedgerows when the field was fallow and after the field had undergone primary and secondary cultivation (n = 2323). (relates to significant with $\alpha < 0.05$).*

	df	***H***	***P***
Soil Tillage Intensity	2	41.181	0.001*
In / Out of Web	1	539.799	0.001*
Interaction: Soil Tillage Intensity * In / Out of Web	2	18.928	0.001*

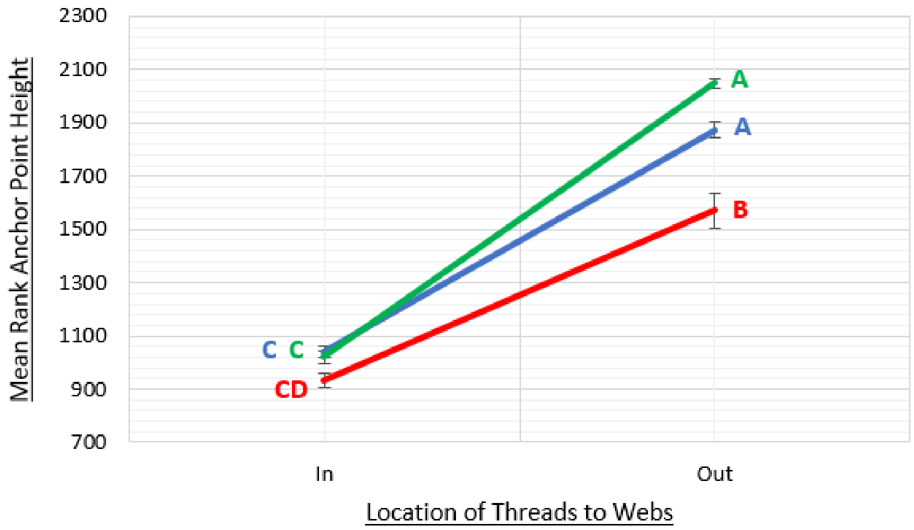


Figure 5.3.1: Interaction of mean rank anchor point height, soil tillage intensities and inside or outside of web for hedgerows when the field was fallow and after the field had undergone primary and secondary cultivation (n = 2323). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional In ±s.e.26.170 (n = 526), Conventional Out ±s.e.67.286 (n = 122), Direct Drill Managed In ±s.e.21.230 (n = 647), Direct Drill Managed Out ±s.e.29.803 (n = 163), Direct Drill In ±s.e.24.101 (n = 714), Direct Drill Out ±s.e.18.978 (n = 151)). (Points that do not share the same letter are significantly different at the p<0.05 level).

The interaction was significant between the soil tillage intensity and whether the mean rank anchor point belonged to a thread which was a support thread or a bridge thread (*Figure 5.3.1. & Table 5.3.5*). The higher mean rank anchor point height was established in the Direct Drill and Direct Drill Managed hedgerows of bridge threads and the lower mean rank anchor point height was found in hedgerows opposite all soil tillage intensities for support threads.

5.3.5.2.2. Distance of Anchor Point from Field Edge

Table 5.3.6: Correlations of wind speed (kmh^{-1}) measured in the hedgerow with the dependant variable distance of anchor point from field edge (cm) inside webs (of support threads) for hedgerows when the field was fallow and after the field had undergone primary and secondary cultivation. (relates to significant with $\alpha < 0.05$).*

	(Rho)	***P***	**n**
Wind Speed – Bottom of Hedgerow (kmh^{-1})	-0.192	0.001*	336
Wind Speed - 0.5 m from Field Edge (kmh^{-1})	-0.131	0.016*	336

The wind speed measured at the bottom of the hedgerow and 0.5 m away from the field edge was significantly negatively correlated to the distance a web was spun within a hedgerow opposite (*Table 5.3.6.*). No significance was found with any other independent variable measured.

Table 5.3.7: Correlations of independent variables measured in the hedgerows with the dependant variable distance of anchor point from field edge (cm) outside webs (of bridge threads) for hedgerows when the field was fallow and after the field had undergone primary and secondary cultivation. (relates to significant with α <0.05).*

	(Rho)	***P***	**n**
Number of Female *T. tenuis*	-0.198	0.048*	241
Number of Male *T. tenuis*	-0.231	0.026*	241
Number of *T. tenuis* in Web	-0.389	0.001*	241
Number of Webs	-0.308	0.003*	241

After cultivations and fallow, the distance away from the field edge a bridge thread was anchored, was significantly negatively correlated to four measured variables (*Table 5.3.7.*). These were number of sheet webs recorded, number of *T. tenuis* observed within a sheet web and number of female and male *T. tenuis*. Significance only occurred when all data out of crop was incorporated together.

Table 5.3.8: Response of rank distance of anchor point height from field edge, soil tillage intensity and inside and outside of web, for hedgerows when the field was fallow and after the field had undergone primary and secondary cultivation (n = 760). (relates to significant with α <0.05).*

	df	***H***	***P***
Soil Tillage Intensity	2	8.686	0.012*
In / Out of Web	1	51.306	0.001*
Interaction: Soil Tillage Intensity * In / Out of Web	2	4.062	0.131

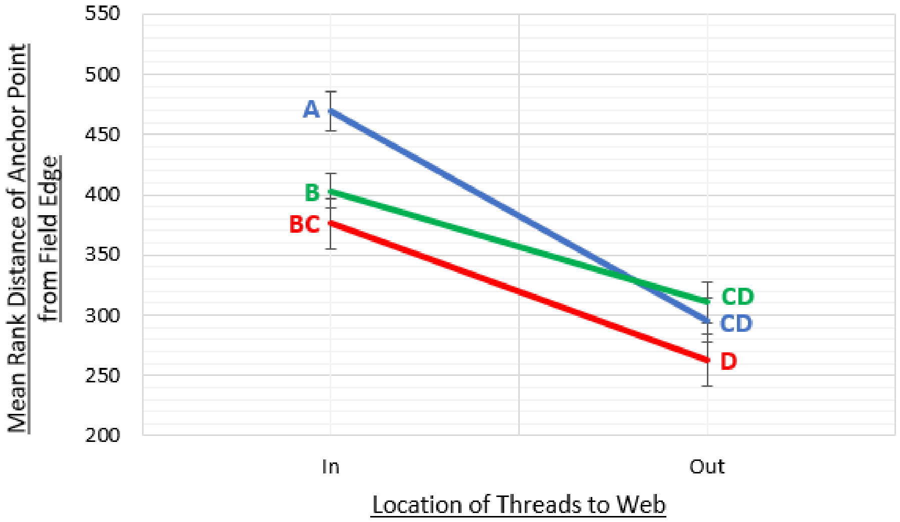


Figure 5.3.2: Interaction of mean rank distance of anchor point from field edge, soil tillage intensity and inside or outside of web for hedgerows when the field was fallow and after the field had undergone primary and secondary cultivation (n = 760). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional In ±s.e.20.649 (n = 148), Conventional Out ±s.e.21.658 (n = 70), Direct Drill Managed In ±s.e.16.724 (n = 177), Direct Drill Managed Out ±s.e.17.940 (n = 85), Direct Drill In ±s.e.14.322 (n = 215), Direct Drill Out ±s.e.16.894 (n = 65)). (Points that do not share the same letter are significantly different at the p<0.05).

No significance was found in the interaction. The significantly greater mean rank distance of anchor point from the field edge, within hedgerows opposite each tillage intensity, was of support threads (inside webs) (*Figure 5.3.2. & Table 5.3.8.*). The mean rank distance of anchor point of support threads from the field edge was significantly greater in the hedgerow of Direct Drill Managed.

5.3.5.2.3. Thread Length

Table 5.3.9: Correlations of independent variables measured in the hedgerow with the dependant variable thread length (mm) inside webs (of support threads) for hedgerows when the field was fallow and after the field had undergone primary and secondary cultivation. (relates to significant with α <0.05).*

	Fallow			**Primary Cultivation**			**Secondary Cultivation**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**	**(Rho)**	***P***	**n**
Hedgerow Vegetation Density (cm^2)	-0.216	0.001*	480	0.285	0.001*	572	-0.121	0.254	580
Mean Abdomen Length (mm)	0.175	0.001*	504	0.286	0.001*	823	0.269	0.001*	803
Number Female *T. tenuis*	0.364	0.001*	504	-0.025	0.471	823	0.325	0.001*	803
Number Male *T. tenuis*	-0.149	0.001*	504	-0.019	0.503	823	-0.098	0.158	803

The number of female *T. tenuis* was significantly positively correlated to support thread length in times of fallow and after secondary cultivation, while number of male *T. tenuis* showed significant negative correlation to support thread lengths in times of fallow only. When the field was out of crop, the mean length of *T. tenuis* abdomen was significantly positively correlated to support thread length. Lengths of support threads, when the field was fallow, was identified to be significantly negatively correlated to hedgerow vegetation density. This independent variable was further significantly positively correlated to support thread lengths after primary cultivation had taken place.

Table 5.3.10: Correlations of independent variables measured in the hedgerow with the dependant variable thread length (mm) outside of webs (of bridge threads) for hedgerows when the field was fallow and after the field had undergone primary and secondary cultivation. (relates to significant with α <0.05).*

	(Rho)	***P***	**n**
Mean Abdomen Length (mm)	-0.218	0.033*	97
Number of Female *T. tenuis*	0.290	0.003*	107
Number of Male *T. tenuis*	0.284	0.003*	107
Number of *T. tenuis* in Web	0.292	0.001*	107
Number of *T. tenuis* Rappelling	0.247	0.013*	107
Numbers of Web	0.243	0.016*	107

The numbers of *T. tenuis* (female and male) were significantly positively correlated to the length of threads outside of the web. The number of *T. tenuis* observed rappelling, the number of *T. tenuis* identified in the web and the number of sheet webs recorded were all significantly positively correlated to the lengths of bridge threads. The mean *T. tenuis* abdomen length recorded was significantly negatively correlated to the bridge thread length.

The thread length of bridge threads at times of cultivations and fallow were analysed together due to low numbers of data identified in each cultivation and fallow period (*Table 5.3.10*).

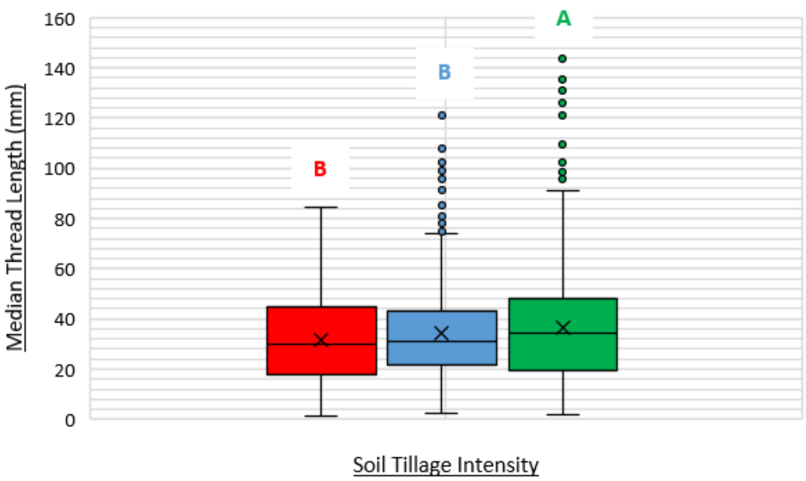


Figure 5.3.3: Median thread length (mm) inside webs (of support threads) in the differing soil tillage intensity, for hedgerows when the field was fallow and after the field had undergone primary and secondary cultivation. (df = 2, Adjusted for ties H - Value 9.94, P - 0.007, n = 2031). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional (n = 584), Direct Drill Managed (n = 697), Direct Drill (n = 750)).

The significantly longer median support thread length was 46.4 mm and was recorded in the Direct Drill hedgerow (*Figure 5.3.3.*). This was 4.7 mm and 4.9 mm longer than the significantly shorter median thread lengths recorded in the hedgerow opposite Conventional and Direct Drill Managed respectively. Positive upwards skew was identified for all soil tillage intensities.

5.3.5.3. In Crop - Early and Late Growth Stages of *H. vulgare*

5.3.5.3.1. Anchor Point Height

Table 5.3.11: Correlations of independent variables measured in the hedgerow with the dependant variable of anchor point height (cm) inside webs (of support threads) for hedgerows when the field was in crop (early and late growth stages). (relates to significant with α <0.05).*

	Early			**Late**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**
Hedgerow Vegetation Density (cm^2)	0.405	0.001*	229	0.072	0.051	708
Number of Female *T. tenuis*	-0.446	0.001*	330	0.087	0.021*	708
Number of Male *T. tenuis*	-0.530	0.001*	330	0.124	0.001*	708
Number of *T. tenuis* in Web	0.333	0.001*	330	0.235	0.001*	708
Number of *T. tenuis* Rappelling	0.478	0.001*	330	0.112	0.003*	708

Table 5.3.12: Correlations of independent variables measured in the hedgerows with the dependant variable of anchor point height (cm) inside webs (of support threads) for hedgerows when the field was in crop (early and late growth stages). (relates to significant with α <0.05).*

	(Rho)	***P***	**N**
Number of *S. avenae*	0.316	0.001*	520
Number of *S. avenae* in Web	0.415	0.001*	520
Wind Speed - Bottom of Hedgerow (kmh^{-1})	0.220	0.001*	1037

Numbers of *T. tenuis* (male and female) recorded at the early growth stages of the crop were significantly negatively correlated to anchor point height noted inside webs (*Table 5.3.11*.). When the field was at the late growth stages of crop, the number of *T. tenuis* (male and female) was significantly positively correlated to anchor point heights of webs measured. Hedgerow vegetation density was significantly positively correlated in the early stages of *H. vulgare* growth. The numbers of *T. tenuis* rappelling and *T. tenuis* observed to be in a web, were significantly positively correlated to anchor point height inside webs in all growth stages (early and late) of the crop.

Wind speed observed at the bottom of the hedgerow was significantly positively correlated to anchor point height of support threads (*Table 5.3.12*). When anchor point heights inside webs were recorded from the early and late periods of *H. vulgare* growth, there was noted to be significant positive correlation to number of *S. avenae* observed in sheet webs and found in the vegetation. Significance only occurred within these independent variables and anchor point height of support threads when data recorded from early and late growth stages were analysed together.

Table 5.3.13: Response of rank anchor point height inside webs (of support threads), soil tillage intensity and presence of crop pests found within the hedgerow vegetation, for hedgerows when the field was in crop (early and late growth stages) (n = 1070). (relates to significant with α <0.05).*

	df	***H***	***P***
Soil Tillage Intensity	2	28.546	0.001*
Presence of Crop Pests in Hedgerow Vegetation	1	0.384	0.535
Interaction: Soil Tillage Intensity * Presence of Crop Pests in Hedgerow Vegetation	2	41.744	0.001*

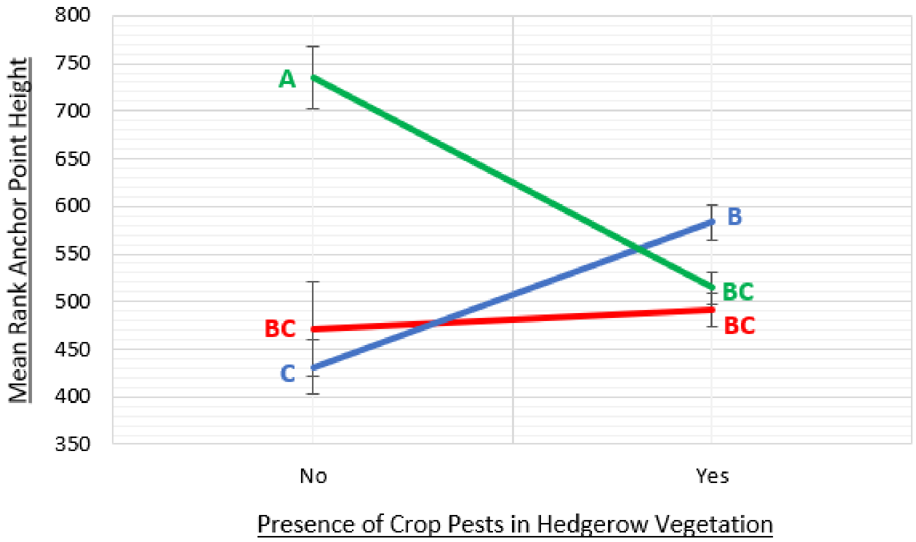


Figure 5.3.4: Interaction of mean rank anchor point height inside webs (of support threads), soil tillage intensity and presence of crop pests found within the hedgerow vegetation, for hedgerows when the field was in crop (early and late growth stages) (n = 1070). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional No ±s.e.49.192 (n = 51), Conventional Yes ±s.e.17.830 (n = 330), Direct Drill Managed No ±s.e.28.412 (n = 50), Direct Drill Managed Yes ±s.e.18.546 (n = 226), Direct Drill No ±s.e.32.762 (n = 96), Direct Drill Yes ±s.e.16.193 (n = 317)). (Points that do not share the same letter are significantly different at the p<0.05).

The mean rank anchor point height for support threads was significantly different between the soil tillage intensities and whether there were crop pests recorded in the hedgerow vegetation (*Figure 5.3.4. & Table 5.3.13*.). Significantly higher mean rank anchor point height occurred when crop pests were not found in the vegetation for Direct Drill than that found in Conventional and Direct Drill Managed hedgerows. This mean rank anchor point height was further significantly higher than the mean rank found when crop pests were located within the vegetation of hedgerows opposite all soil tillage intensities.

Table 5.3.14: Response of rank anchor point height inside webs (of support threads), soil tillage intensity and presence of crop pests found within the webs of hedgerows, for hedgerows when the field was in crop (early and late growth stages) (n = 1070). (relates to significant with α <0.05).*

	df	***H***	***P***
Soil Tillage Intensity	2	3.651	0.161
Presence of Crop Pests in Webs of Hedgerows	1	15.186	0.001*
Interaction: Soil Tillage Intensity * Presence of Crop Pests in Webs of Hedgerows	2	27.395	0.001*

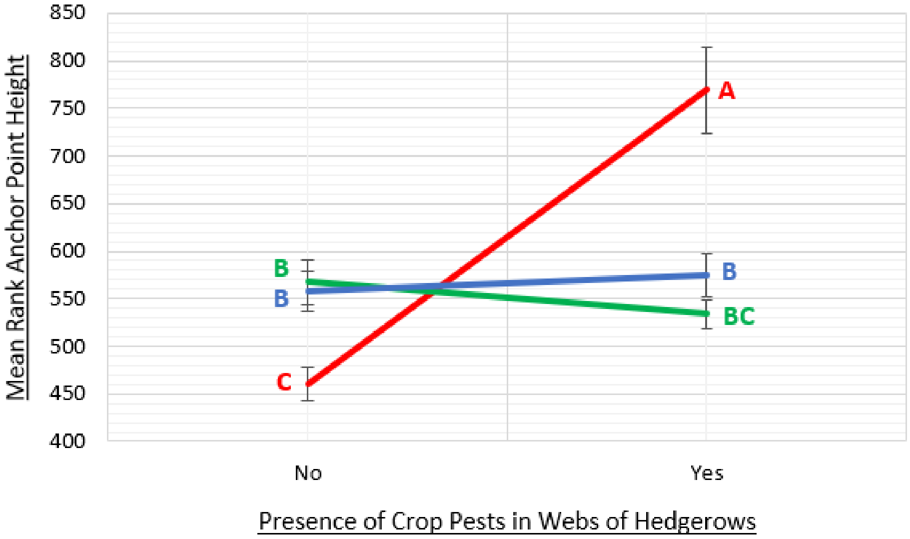


Figure 5.3.5: Interaction of mean rank anchor point height inside webs (of support threads), soil tillage intensity and presence of crop pests found within the webs of hedgerows, for hedgerows when the field was in crop (early and late growth stages) (n = 1070). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional No ±s.e.17.184 (n = 347), Conventional Yes ±s.e.45.344 (n = 34), Direct Drill Managed No ±s.e.23.741 (n = 181), Direct Drill Managed Yes ±s.e.14.877 (n = 95), Direct Drill No ±s.e.21.004 (n = 240), Direct Drill Yes ±s.e.21.927 (n = 173)). (Points that do not share the same letter are significantly different at the p<0.05).

The mean rank anchor point height for webs that contained and did not contain pests in Conventional hedgerows was significant in the interaction. The mean rank anchor point height significantly higher when crop pests were found in webs, within this hedgerow, than any other mean rank anchor point height measured within this model (*Figure 5.3.5. & Table 5.3.14*.).

5.3.5.3.2. Distance of Anchor Point from Field Edge

Table 5.3.15: Correlations of independent variables measured in the hedgerows with the dependant variable of distance of anchor point from field edge (cm) inside webs (of support threads) for hedgerows when the field was in crop (early and late growth stages). (relates to significant with α <0.05).*

	(Rho)	***P***	**n**
Hedgerow Vegetation Density (cm^2)	0.263	0.001*	232
Number of Female *T. tenuis*	-0.345	0.001*	258
Number of Male *T. tenuis*	-0.321	0.001*	258
Number of *S. avenae*	-0.286	0.002*	119
Number of *T. tenuis* in Web	-0.248	0.001*	258
Wind Speed - 0.5 m from Field Edge (kmh^{-1})	0.184	0.003*	258
Wind Speed - Field Edge (kmh^{-1})	0.228	0.001*	258

When the field was cropped with *H. vulgare* (early and late growth stages), the distance that an anchor point of a thread inside webs was to the field edge was significantly negatively correlated to the number of *T. tenuis* (male and female) that were recorded in the hedgerows (*Table 5.3.15*.). The distance was further significantly negatively correlated to the number of *T. tenuis* that were observed within sheet webs and the number of *S. avenae* that was found within the hedgerow vegetation. Hedgerow vegetation density, wind speed, measured at the field edge and 0.5 m to the field edge, were significantly positively correlated to the distance the anchor point was to the field edge.

5.3.5.3.3. Thread Length

Table 5.3.16: Correlations of independent variables measured in the hedgerow with the dependant variable of thread length (mm) inside webs (of support threads) for hedgerows when the field was in crop (early and late growth stages). (relates to significant with α <0.05).*

	Early			**Late**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**
Hedgerow Vegetation Density (cm^2)	-0.120	0.052	252	0.225	0.001*	714
Number of Female *T. tenuis*	-0.135	0.011*	359	-0.158	0.001*	714
Number of Male *T. tenuis*	-0.154	0.003*	359	-0.180	0.001*	714
Number of *S. avenae*	-0.127	0.044*	252	0.031	0.603	286
Number of *S. avenae* in Web	-0.253	0.001*	252	-0.117	0.051	286
Number of *T. tenuis* in Web	0.243	0.001*	359	-0.067	0.075	714

Numbers of *T. tenuis* (male and female) were identified to be significantly negatively correlated to length of support threads when the field was in the early and late growth stages of *H. vulgare* (*Table 5.3.16*.). Number of *T. tenuis* found in the web was significantly positively correlated to thread length inside webs only at times of early growth stages. Hedgerow vegetation density identified significant positive correlation with length of support threads during the late growth stages. There was a significant negative correlation for both variables, number of *S. avenae* recorded in the sample and number of *S. avenae* found in the web, with support thread length, found in the early growth stages.

5.3.5.4. Variables Measured Within the Field and Hedgerow

Table 5.3.17: Response of number of sheet webs, soil tillage intensity and location (field or hedgerows). When the field was fallow and after primary and secondary cultivation (n = 174, R-sq - 11.06%). (relates to significant with α <0.05).*

	df	*F*	*P*
Soil Tillage Intensity	2	0.45	0.641
Location (Field or Hedgerow)	1	23.71	0.001*
Interaction: Soil Tillage Intensity * Location (Field or Hedgerow)	2	0.38	0.684

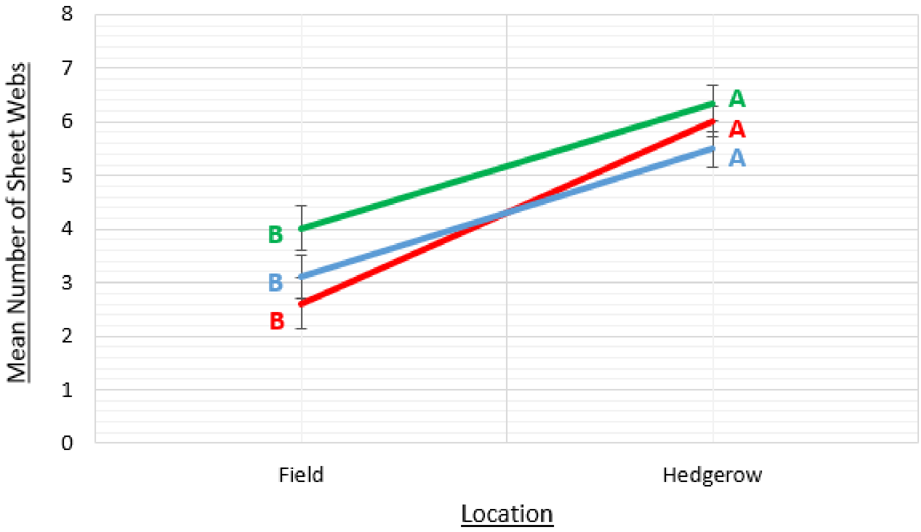


Figure 5.3.6: Interaction of mean number of sheet webs, soil tillage intensity and location (field or hedgerows). When the field was fallow and after primary and secondary cultivation (n = 174, R-sq - 11.06%). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Field ±s.e.0.285 (n = 29), Conventional Hedgerow ±s.e.0.486 (n = 29), Direct Drill Managed Field ±s.e.0.324 (n = 29), Direct Drill Managed Hedgerow ±s.e.0.408 (n = 29), Direct Drill Field ±s.e.0.333 (n = 29). Direct Drill Hedgerow ±s.e.0.407 (n = 29)) (Points that do not share the same letter are significantly different at the p<0.05).

A significant difference existed only between location; whether the sheet web was found within the main field or hedgerow opposite at times when the field was out of crop (primary cultivation, secondary cultivation, and fallow) (*Figure 5.3.6. & Table 5.3.17.*). For all three soil tillage intensities (Conventional, Direct Drill Managed and Direct Drill), the mean number of sheet webs found within the hedgerows was significantly higher than the mean number found within the field.

Table 5.3.18: Response of rank number of T. tenuis*, soil tillage intensity and location (field or hedgerows). When the field was fallow and after primary and secondary cultivation (n = 174). (* relates to significant with α <0.05).*

	df	***H***	***P***
Soil Tillage Intensity	2	0.960	0.619
Location (Field or Hedgerow)	1	24.741	0.001*
Interaction: Soil Tillage Intensity * Location (Field or Hedgerow)	2	0.127	0.938

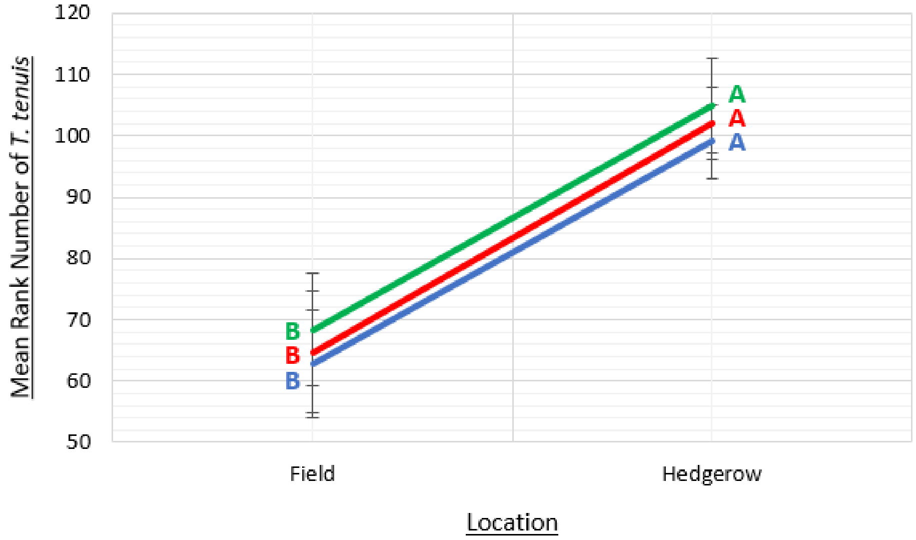


Figure 5.3.7: Interaction of mean rank number of T. tenuis*, soil tillage intensity and location (field or hedgerows). When the field was fallow and after primary and secondary cultivation (n = 174). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Field ±s.e.9.908 (n = 29), Conventional Hedgerow ±s.e.5.811 (n = 29), Direct Drill Managed Field ±s.e.8.842 (n = 29), Direct Drill Managed Hedgerow ±s.e.6.089 (n = 29), Direct Drill Field ±s.e.9.162 (n = 29), Direct Drill Hedgerow ±s.e.7.648 (n = 29)). (Points that do not share the same letter are significantly different at the p<0.05).*

Homogeneity was identified within the soil tillage intensities between the mean rank number of *T. tenuis* identified within the hedgerow and field, within Conventional, Direct Drill Managed and Direct Drill, when the field was out of crop (primary cultivation, secondary cultivation and fallow) (*Figure 5.3.7. & Table 5.3.18.*). The significant categorical factor was whether the mean rank number of *T. tenuis* was identified in the field or hedgerow with a significantly greater mean established in the hedgerow location within all soil tillage intensities.

Table 5.3.19: Response of rank number of T. tenuis*, soil tillage intensity and location (field or hedgerows) at times field in crop (early and late growth stages) (n = 72). (* relates to significant with α <0.05).*

	df	***H***	***P***
Soil Tillage Intensity	2	0.687	0.709
Location (Field or Hedgerow)	1	12.382	0.001*
Soil Tillage Intensity*Location (Field or Hedgerow)	2	0.852	0.653

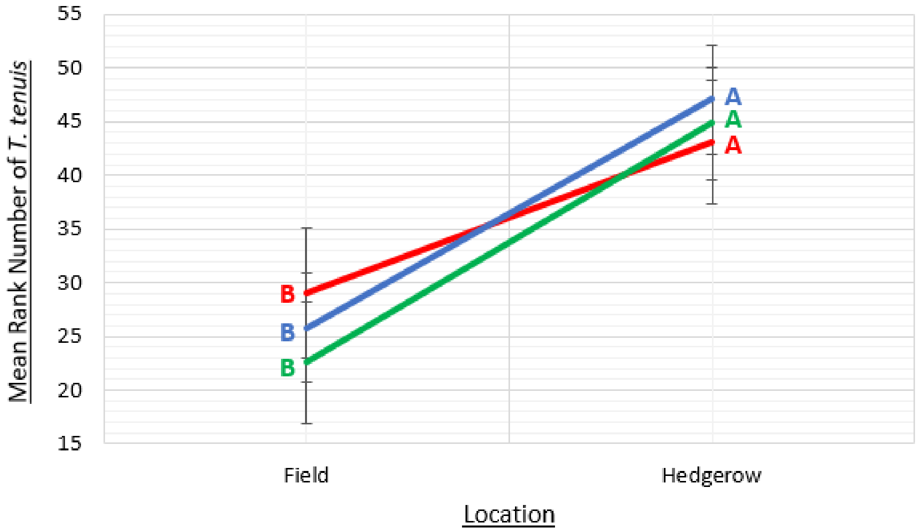


Figure 5.3.8: Interaction of mean rank number of T. tenuis*, soil tillage intensity and location (field or hedgerows) at times field in crop (early and late growth stages) (n = 72). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Field ±s.e.6.045 (n = 12), Conventional Hedgerow ±s.e.5.782 (n = 12), Direct Drill Managed Field ±s.e.5.121 (n = 12), Direct Drill Managed Hedgerow ±s.e.5.115 (n = 12), Direct Drill Field ±s.e.5.684 (n = 12), Direct Drill Hedgerow ±s.e.5.251 (n = 12)). Points that do not share the same letter are significantly different at the p<0.05).*

When the field was cropped, homogeneity was established between mean rank numbers of *T. tenuis* found within the hedgerows and main field opposite for all soil cultivation intensities (*Figure 5.3.8. & Table 5.3.19*.). There was a significant difference in the mean rank number of *T. tenuis* within the two different locations; significantly more *T. tenuis* were found within the hedgerows than the field at times when *H. vulgare* was in crop. This followed the trend of when the field was out of crop (*Figure 5.3.7.*).

Table 5.3.20: Response of rank number of bridge threads, soil tillage intensity and status of field opposite hedgerow (in crop or not in crop) (n = 123). (relates to significant with α <0.05).*

	df	*H*	*P*
Soil Tillage Intensity	2	0.941	0.625
Status of Field Opposite Hedgerow (In Crop or Not in Crop)	1	23.097	0.001*
Interaction: Soil Tillage Intensity * Status of Field Opposite Hedgerow (In Crop or Not in Crop)	2	1.681	0.432

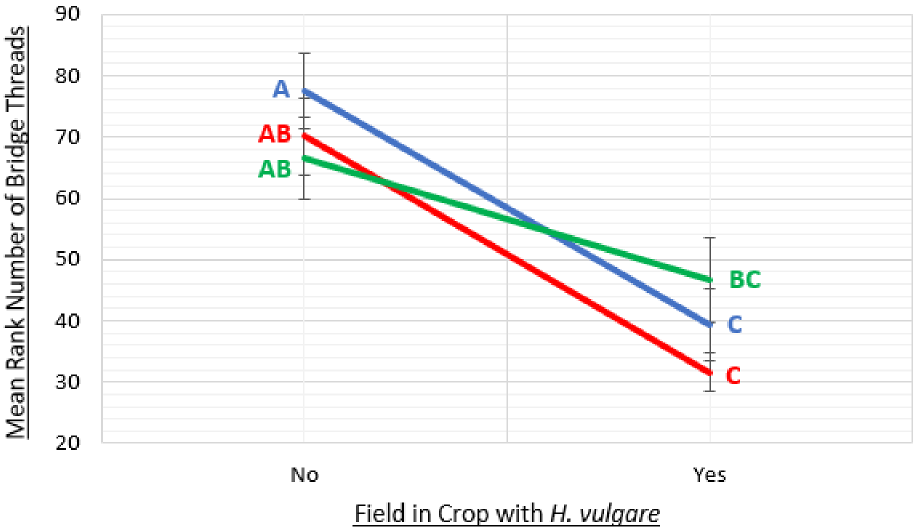


Figure 5.3.9: Interaction of mean rank number of bridge threads, soil tillage intensity and status of field opposite hedgerow (in crop or not in crop) (n = 123). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional No ±s.e.6.260 (n = 29), Conventional Yes ±s.e.3.126 (n = 12), Direct Drill Managed No ±s.e.6.072 (n = 29), Direct Drill Managed Yes ±s.e.5.851 (n = 12), Direct Drill No ±s.e.6.650 (n = 29), Direct Drill Yes ±s.e.6.931 (n = 12)). (Points that do not share the same letter are significantly different at the p<0.05).

The factor which held significance was whether the mean rank number of bridge threads was identified in the hedgerows when the field was either cropped or not cropped (*Figure 5.3.9. & Table 5.3.20.*). When the field was out of crop (after primary and secondary cultivation and fallow) a significantly greater mean rank number of bridge threads was recorded than when the field was cropped with *H. vulgare* at all growth stages for Conventional and Direct Drill Managed.

5.3.5.5. Variables Concerning the Presence of Egg Sacs in Hedgerows

Table 5.3.21: Correlations of independent variables measured concerning egg sacs when the field was fallow and after the field had undergone primary and secondary cultivation. (relates to significant with α <0.05).*

			(Rho)	*P*	n
Egg Sac Width (mm)	x	Distance from Field Edge (cm)	0.294	0.049*	35
Number of Egg Sacs	x	Hedgerow Density Vegetation (cm^2)	0.625	0.001*	28

A significant positive correlation was identified between the variables of egg sac width and the distance the egg sac was from the field margin and further between the number of egg sacs recorded and the hedgerow vegetation density calculated (*Table 5.3.21.*).

5.3.6. Discussion

5.3.6.1. Out of Crop - Fallow and After Primary and Secondary Cultivation

Heterogeneity was found in the anchor point height of bridge threads spun for rappelling, with Conventional hedgerows exhibiting the significant lower mean (*Figure 5.3.1.*). Conventional held the greater number of *T. tenuis* (mainly female) which was shown to be significantly negatively correlated to anchor point height out of webs (*Table 5.3.4.*). It may be that intra-specific competition had occurred, with a greater number rappelling inside and outside of the hedgerow at the basal stratum due to greater *T. tenuis* abundance. Harwood & Obrycki (2005) identified that a propensity to bridge increased at times of over-crowing in Linyphiidae, and rappelling occurred at a lower aspect, a low energy form of dispersal (Bonte *et al.,* 2016). This was further discussed by Pompozzi *et al.* (2019) as 'overspill', where the movement of Linyphiidae spans outwards from high abundance. 'Overspill', in the direction of the field, is of benefit to an agricultural setting to exert early biological control. This 'overspill' occurred due to an area of high *T. tenuis* abundance, identifying the hedgerows to have been a beneficial habitat. In this instance the attractive nature of the hedgerow to web-weaving may have aided the biological control potential in the field (Toft & Lövei, 2002; Vialatte *et al.,* 2007).

However, a lower number of rappel threads was noted within the Conventional hedgerow. Indeed, eleven *T. tenuis* were noted under the webs at time of primary cultivation in this hedgerow, the greater result (*Table 5.3.4.*). These points raise the question of why dispersal was less where the density of *T. tenuis* was high within hedgerows opposite Conventional, the greater level of rappelling occurring within Direct Drill Managed. It would be expected to measure low bridging movement within the Direct Drill hedgerows, due to the zero cultivation occurring in the field opposite at this time due to the greater level of activity occurring in the Direct Drill tillage of the main field (*Section 5.1.5.1.2. & Section 5.1.5.1.3.*). Řezáč & Rezáčová (2019) explain that in agro-ecosystems Linyphiidae activity is diminished after mechanical disturbance in cultivations. The cultivated area of Conventional with reduced landscape heterogeneity may have promoted *T. tenuis* to reside within the hedgerow opposite, perhaps because of greater prey availability (Lang & Barthel, 2011; Schwab *et al.,* 2002; Witmer *et al.,* 2003).

Most support threads were observed to be attached to grass at the forefront of the hedgerow and leaf litter within the hedge. The basal stratum of the hedgerow was identified as a key web-site, where at times of low growth of hedgerow species, webs were woven into the area which might offer protection and a source of nutrition from the capture of ground-dwelling prey (*Figure 5.3.1.*). Badenhausser *et al.* (2020) comment that hedgerows increase predatory opportunities for Linyphiidae and Garrett *et al.* (2017) and Pfister *et al*. (2015) comment that Linyphiidae may be exhibiting scramble competition to colonise areas in close vicinity to capitalise on any prey developments noted in the field.

Six *T. tenuis* under webs of two samples in hedgerows opposite Direct Drill area held the greater height at primary cultivation (*Table 5.3.2. & Figure 5.3.10.*). In these two areas, nine and sixteen webs were measured within distinct strata of the hedgerow with the number of female *T. tenuis* recorded as seventeen and twenty-two, respectively (*Table 5.3.2*.). Gan *et al.* (2015) state that higher webs can be an act of dominance. It appears that webs have been constructed at differing strata within the hedgerow due to increased web-building activity by Linyphiidae and *T. tenuis*. The greater abundance of *T. tenuis* was identified in these Direct Drill sample areas. Birkhofer *et al*. (2017) and Sanders *et al.* (2015) concurred, explaining that in margins, at times of high intra-specific and inter-specific abundance, different vertical levels were occupied by Linyphiidae. Romero & Harwood (2010) suggested that the occupation of different strata was a representation of different prey being predated. This is further supported with high levels of vegetation density noted in this area, able to support a multitude of prey (Campbell *et al.,* 2020).

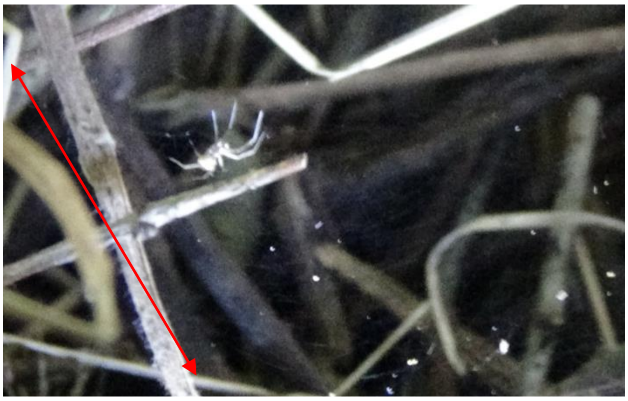


Figure 5.3.10: Female T. tenuis *occupying web anchored to low-lying branches at rear of hedgerow. Direct Drill. In times out of crop, 2016 / 2017 Season. Elevated view. (Red arrow = 33.4 mm).*

It can be deduced that the greater number of webs at a higher level equated to web abandonment at the time of secondary cultivation (*Table 5.3.2*.). Toft (1987) explained that non-productive webs are quickly abandoned, within a couple of days. Sunderland & Samu (2000) and Vink & Kean (2013) commented that the main drivers for web abandonment are low prey retrieval, physical disturbance, or threat of predation. In contrast, Harwood *et al*. (2003) and Harwood & Obrycki (2007) explained that abandonment of webs may happen randomly and not be due to any specific factor and therefore not be a sign of a poor web-site. Intra-specific competition may be a factor with several webs woven in close proximity, no web take-over was observed but the threat of such could cause abandonment, especially in areas of high potential prey capture when the field was low in such opportunities (Jarvis & Woolford, 2017).

Numbers of males was significantly positively correlated to the anchor point height of the webs at secondary cultivation (*Table 5.3.2.*). This was due to timing of courtship (for potential copulation) to seek a mate, the next generation beginning in parallel with the cropping pattern (Thorbek & Bilde, 2004; Welch *et al.,* 2011; Zschokke & Herberstein, 2005). Abdomen length was further significantly positively correlated to anchor point height of webs, where males in this dataset had abdomens >1.5 mm (*Table 5.3.2.*). This suggests copulation was undertaken in the extended phenotype of the web. Males of *T. tenuis* are described as acquiring smaller abdomens due to SSD (Sexual Sized Dimorphism) evolution as shown in fieldwork findings (Corcobado *et al.,* 2010; De Mas *et al.,* 2009) (*Section 2.1.3.4*. & *Section 5.1.6.2.1*.). The significant positive correlation between anchor point height and abdomen length in primary cultivation was driven by nine large-bodied females found in an area with one male (*Figure 5.3.11a & b*). At this time, it appeared that courtship leading to copulation may have begun, thus a higher degree of female occupying webs was expected, expelling a pheromone to communicate readiness to mate (Bonte *et al.,* 2000; Maklakov *et al.,* 2003; Toft, 1989; Watson, 1993) (*Section 2.1.3.4*.). Thorbek & Bilde (2004) & Welch *et al.* (2011) note hedgerows allow generations to persist by offering web-weaving opportunities for courtship / copulation rituals to commence.

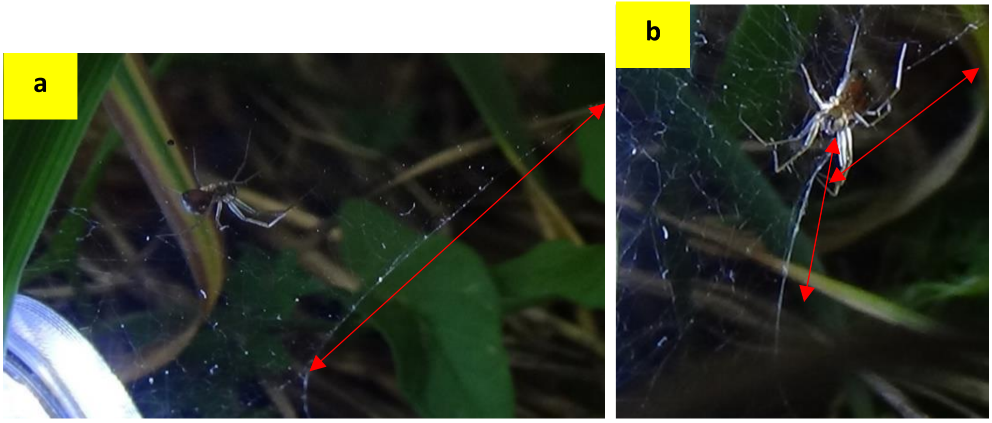


Figure 5.3.11a & b: Female T. tenuis *of large abdomen occupying web. Direct Drill Managed hedgerows, in times out of crop, 2016 / 2017 season. (a: Red arrow = 39.1. mm. b: Combined red arrow = 35.6 mm).*

That the vegetation within this habitat may be too dense, after cultivations (primary and secondary), could be a consideration, as Linyphiidae require a certain level of space to lay a horizontal web (Benjamin *et al.,* 2002) (*Table 5.3.2*.). They are unique in laying sheets in many horizontal arrangements, adapting the sheet to the material on offer for anchorage, though a central space is needed for a web (Barriga *et al.,* 2010; Benjamin *et al.,* 2002; Gagnon *et al.,* 2011).

Wind speed at the field edge affected *T. tenuis* decision for web placement within the hedgerow. The greater wind speed was identified as 10.1 kmh^{-1} with webs spun in the basal layer within the hedgerow opposite Direct Drill tillage and 12.7 kmh^{-1} in Direct Drill Managed both in fallow, where higher webs were identified (*Table 5.3.3.*). Spinning lower webs may be a protection strategy in times of wind speed disturbance. Damage to a web, however slight, can render the web functionless and thus energy outlay not compensated with potential prey capture (Qin *et al.,* 2015; Tew & Hesselberg, 2017).

Furthermore, at times of higher wind speed the distance a web was anchored into the hedgerow was decreased (*Table 5.3.6.*). This is an unusual result, with Schmidt & Tscharntke (2005) and Segoli *et al.* (2004) noting that Linyphiidae are sensitive to environmental disturbance, for example, wind flow, in choosing to construct webs. Webs were spun low, closer to the front of the shelterbelt when wind speed was measured the highest (*Table 5.3.3.*). It may be that the webs were spun at a time when wind speed was lower. Vanacker *et al.* (2004) described that once a web is constructed, it is shown to have longevity and can withstand moderate wind speed disturbance. Linyphiidae evolution has adapted to deal with environmental disturbance by the creation the major ampullate silk, where the beta-sheets are toughened by acquiring strong association between hydrogen bonds (Blackledge *et al.,* 2011; Craig, 2003 Tew & Hesselberg, 2017) (*Figure 2.3a, Section 2.1.2.1.*, *Page 10*). This insistence to spin at the forefront of a hedgerow has been identified as an area of dynamic movement by Isaia *et al.* (2007), Marshall (2004) and Mclachlan & Wratten (2003). A web position near an edge of a shelterbelt is seen to be a result or precursor to migration into a field habitat.

Bridge threads were anchored significantly nearer to the field edge (*Figure 5.3.2.*). Simmoneau *et al.* (2016) and Woolley *et al.* (2016) signal rappelling is a precursor to web-spinning and it is expected that rappelling would occur at the front fringes of the hedgerow once migration has occurred. Blandenier (2014) and Thorbek (2003) suggest that aerial dispersal into a margin is relatively passive, the direction being influenced due to meteorological conditions. Thorbek (2003) suggests that short rapid movements of dragline silk can aid control of dispersal direction. This is supported by Bonte *et al.* (2008), who report high short ballooning helps to find a linear wind current. However, no significant correlation for distance of bridge threads from the field edge with wind speed was found. The greater number of large threads identified for ballooning occurred in the fallow periods, Hein *et al.* (2019) noted that this is due to low vegetation heterogeneity within the field at this time. The greater wind speed from the field edge was 10.1 kmh^{-1} (converted to 2.8 ms^{-1}), this being the upper level acceptable for ballooning (Blandenier, 2014; Simonneau *et al.,* 2016; Thorbeck, 2003). Ballooning begins at a high take-off position and then in a sharp downward projector into vegetation thus some wind flow is required to provide lift (Pekár, 2014). This wind speed was not identified as high enough to disrupt the hydrogen bonds of the major ampullate gland for dragline silk, thus losing its integrity (Craig, 2003) (*Section 2.1.2.1*).

The lower anchor points of the hedgerow opposite Conventional, where the greater female *T. tenuis*, number of webs and numbers of *T. tenuis* under webs were found predominantly within the forefront of the hedgerow habitat (*Table 5.3.7.*). Harwood & Obrycki (2005) and Hein *et al.* (2019), discuss that Linyphiidae are highly competitive for resources, and when identified in high densities, intra-specific competition can drive smaller webs to be spun in the superior web-site. This was concurred by Stenchly *et al.* (2011), who identified this to be due to Linyphiidae known to occupy individual stratum within a habitat, *T. tenuis* preferring a high aspect. It appears that if high densities of one species exist, space for web construction in that stratum would be a limiting factor (Janetos, 1984; Miyashita *et al.,* 2012). This result may describe mass action, where the greater density of migration, perhaps recently ballooned from Conventional with times of secondary cultivation, is driven due to following subtle vibrations produced from a-lying of dragline silk (Bianchi *et al.,* 2017; Kraftt & Cookson, 2012; Řezáč & Řezáčová, 2019).

Several webs were found right at the back of the hedgerow, > 15 cm in height, which were abandoned (*Table 5.3.2.*). Abandonment perhaps having occurred because ensnared prey had been consumed or the web provided no return for the energy cost in its construction (Jurczyk *et al.,* 2012; Opatovsky *et al.,* 2016; Schütt, 1997). It may be, with low densities of prey observed in the field, that *T. tenuis* and Linyphiidae had increased exploratory potential into the hedgerow and relocated to the rear habitat for a considerable period, shown in the large webs created with a considerable energy outlay (Benjamin *et al.,* 2002; Hardy *et al.,* 2008; Saravanan, 2006). Feber *et al*. (2015), Griffiths *et al.* (2018) and Ysnel & Canard (2000) explained that greater bio-diversity and potential prey were identified in the central hub of hedgerows, though not all prey noted were crop pests (Aphididae for example).

Larger females were seen in Direct Drill with twenty females present where six large webs were measured at >3000 mm^2 (*Table 5.3.9.*). Bowden & Buddle (2010), Harwood *et al.* (2004) and Lichtenstein *et al.* (2016) discussed that females with large abdomens express dominance by acquiring prime web-sites, spinning large webs or exert web take-over (*Figure 5.3.3.*). There were no parameters where the hedgerow of the Direct Drill was a prime web-site compared to the hedgerows opposite Conventional tillage. Gan *et al.* (2015), Harwood & Obrycki (2005), Segoli *et al.* (2004) and Toft (1987) detail that body size in Linyphiidae can influence web area that is spun. This observation seems to fit the high web areas recorded, the high vegetation complexity of the hedgerow offering a plethora of opportunities for large webs to be spun (Badenhausser *et al.,* 2020).

In times after primary cultivation, hedgerow vegetation density was significantly positively correlated to thread length, whereas in times the field was fallow, the correlation was negative (*Table 5.3.9.*). The negative correlation is an unusual result with Baxter *et al.* (2005) and Garrett *et al.* (2017), explaining that in times of high vegetation density *T. tenuis* weave in small pockets that may allow extension of silk to reach the adequate loading strain (Craig, 2003; Harmer *et al.,* 2011; Vollrath, 1986). Direct Drill measured a vegetation density of 4715.24 cm^2 at the time of primary cultivation. As noted earlier, low anchor points were found in times of increased vegetation density. Linyphiidae web weaving ability appears forced to the base of the hedge, larger webs woven into the grass swards, where naturally there was greater space achieved by the fanning of the grass pinnacles (Blake *et al.,* 2013) (*Table 5.3.2.*). In times of fallow, hedgerow vegetation density was <4000 cm^2, this due to the autumn and winter seasons, where deciduous species go into dormancy. Barriga *et al.* (2010) and Glime & Lissnier (2017), both describe greater spatial scale induces webs of large threads to be woven, with *T. tenuis* monopolising greater space.

A *T. tenuis* with a small abdomen was identified ballooning out of a Direct Drill hedgerow where three bridge threads >110 mm were measured driving out of the hedgerow (*Table 5.3.10.*). It can be questioned why dispersal out of the hedgerow was occurring within a fallow period where fieldwork identified low landscape heterogeneity, which Lichtenstein *et al*. (2019) noted impeded web-weaving across all tillage intensities (*Section 5.1.5.1.3. & Section 5.1.5.1.4.*). Further, Bonte *et al.* (2008) described ballooning as a cost draining activity, with production of the strong durable major ampullate fibres woven together to provide a dragline thread (Craig 2003, Blackledge *et al.,* 2009) (*Section 2.1.2.1.*). Ballooning causing a greater depletion of energy in small-bodied *T. tenuis*. Blandenier (2014) and Bonte *et al.* (2008) discussed, the ballooning may have occurred due to the pioneering capacity of *T. tenuis*, exploiting recently disturbed territory (Holland *et al.,* 2003; Lafage *et al.,* 2015; Schmidt & Tscharntke, 2005).

Greater number of female and male *T. tenuis* were recorded where two large dragline silks were woven within the Direct Drill Managed hedgerow after primary cultivation (*Table 5.3.10.*). Additionally, greater number of *T. tenuis* observed rappelling was found in a Conventional hedgerow. This sample was measured a day after primary cultivation occurred in the main field, with disturbance applied to the Conventional and Direct Drill Managed areas. It is unexpected that *T. tenuis* would be dispersing out into the field, as Barriga *et al.* (2010) and Bell *et al.* (2002) discuss that an altered landscape, devoid of complexity, will deter Linyphiidae settlement. The hedgerows vegetation density was analysed as moderate and acceptable to facilitate adequate web-spinning. Chapman *et al.* (2013) and Thorbek & Topping (2005) suggested a precursor to ballooning can be starvation or threat of intra-specific competition, Linyphiidae, at times of high density, are fiercely protective of beneficial web-weaving territory (Bell *et al.,* 2002; Harwood *et al.,* 2004). It appears that *T. tenuis* were dispersing to locate a site where web-spinning can commence with low predation and hopeful prey capture.

5.3.6.2. In Crop - Early and Late Growth Stages of *H. vulgare*

The greater number of *T. tenuis* found underneath webs were identified in a Direct Drill hedgerow, where nine out of the ten webs were anchored 10 cm - 12 cm to the apex of grass tillers (*Table 5.3.11.*). This appeared to be a notable stratum for larger web weaving, branches altering the vegetation density at a clear higher level provides a pocket of open space facing the surface of the web (*Table 5.3.16.*). This was seen by Gómez *et al.* (2016) and Schütt (1997) as intercepting a higher degree of prey. Additionally, where four *T. tenuis* occupied webs of a Direct Drill hedgerow, the webs were spun at >30 cm in height. The wind speed at 0.5 m from the field edge was the highest within both hedgerows of Direct Drill (12.9 kmh^{-1} and 14.8 kmh^{-1} respectively) (*Table 5.3.12.*). It is unusual for webs of a higher aspect here, when Tew & Hesselberg (2017) explain that high wind speeds have the potential to lower web placement due to threat that laid silk may be impaired via beta-sheet dislocation (Craig, 2003) (*Section 2.1.2.1.*). With high occupancy, the webs were expected to be woven recently. Bell *et al.* (2002) and Sunderland & Samu (2000) discuss that a web is regularly only occupied for a few days at maximum. Perhaps the webs were woven earlier in the day when wind speed was lower. As Król *et al.* (2018) explain, Linyphiidae spin webs at such times to distinguish territory in periods of reduced predation. Additionally, high vegetation density was identified (>5500 cm^2) in these Direct Drill hedgerows, which could have protected webs from high wind speeds. Batáry *et al.* (2008) and Sharley *et al.* (2008) noted increased vegetation impairs the wind flow into the shelterbelt. Wind speed was noted to be too high to facilitate dispersal, thus the *T. tenuis* recorded occupying a web, remaining in the spun retreat, would be of beneficial to energy preservation (Craig, 2003; Harmer *et al.,* 2011; Segoli *et al.,* 2004).

With the shielding of vegetation, it appears that small scale migration commenced with little intra-specific threat (*Table 5.3.11.*). The act of rappelling, as an explorative behaviour, may allow refining of *T. tenuis* senses to better locate prey (Bonte *et al.,* 2002; Rodríguez & Gloudeman, 2011; Zschokke *et al.,* 2006). Alate *S. avenae* were found entrapped in small webs within low-lying branches (*Table 5.3.12. & Table 5.3.16.*). The hedgerow vegetation was at its greatest when *H. vulgare* was in early growth stages, hedgerow flora having photosynthesised to lay new growth. A small difference of hedgerow vegetation density was observed amongst the samples (5037.8 - 6277.7 cm^2). The lower density was identified in hedgerow opposite Direct Drill Managed, where many of the webs were anchored at <5 cm into grassy tussocks (*Table 5.3.11.*). Bianchi *et al.* (2017) discuss that a small increase in complexity of vegetation can solely promote web anchorage at higher strata and allow capture of alate prey (Birkhofer *et al.,* 2008; Dennis *et al.,* 2001; Kovak & Mckay, 2009).

At later growth stages, hedgerow vegetation density was not of significance, even when the greater difference was examined (higher of 6092.3 cm^2 and lower 2559.5 cm^2). Both areas recorded webs primarily anchored within the lower aspects of the hedgerow. Interestingly, following the pattern of the main field, alate morphs were identified in greater abundance in early growth stages, thus removal of aerial cues pulling web placement lower (*Section 5.1.6.2.1.*). Alignier *et al.* (2014) and Parry (2013) noted that as *H. vulgare* reaches later growth stages of milk and dough development, greater resistance is met in phloem extraction, thus the shelterbelt provides lush vegetation for continual feeding and colony survival (AHDB, 2015; Holopainen-Mantila, 2015; Macfadyen *et al.,* 2014; Vialatte *et al.,* 2007). Apterous morphs feeding upon grass tillers are likely to be ensnared into webs of a lower aspect (Martin *et al.,* 2015; Price *et al*., 2011).

The greater number of *T. tenuis* were noted in a Conventional hedgerow at early growth stages where eleven small webs were noted at <4 cm, woven in the grass of the basal layer of the hedgerow (*Table 5.3.11. & Table 5.3.16.*). Fourteen of the *T. tenuis* held abdomen lengths <1.4 mm. Opatovsky *et al.* (2016) and Romero & Harwood (2010) discuss that much competition exists between *T. tenuis* and Linyphiidae for optimal web-sites, and when identified at high densities, intra-specific competition can drive web placement. However, low abdomen size suggested no dominating *T. tenuis* inflicted excessive competition (Corcobado *et al.,* 2010; De Mas *et al.,* 2009). Stenchly *et al.* (2011) identified that *T. tenuis* are known to occupy a beneficial individual stratum, weaving smaller webs, in a habitat with resource availability and shielding from climatic and predatory factors (Janetos, 1984; Miyashita *et al.,* 2012; Saravanan, 2006). Garrett *et al*. (2017) and Pfister *et al.* (2015), explained that greater abundances of prey resources were present in lower aspects of the hedgerows. At later growth stages, the greater height (>20 cm) for four webs were identified when thirty-five *T. tenuis* were noted (*Table 5.3.11*.). This is double the amount of *T. tenuis* that were noted at early growth stages. Thus, for cohabitation different strata were required for web anchorage within this 1 m^2 sample, the density of *T. tenuis* was too great, as shown by Janetos (1982) and Landsman & Bowman (2017) to comfortably occupy a single optimum layer. Robertson & Avilés (2018) discuss that high *T. tenuis* abundance pushes Linyphiidae into the upper canopy to inhabit an unoccupied vegetation stratum. Little disturbance of increased wind speed facilitated ascension into the branches of the hedgerow with a low energy outlay (Benjamin *et al.,* 2002; Segoli *et al.,* 2004). The greater *T. tenuis* density in the hedgerow was theorised to be driven by the high temperatures recorded in later growth stages in 2018. The heat decreased prey reproductive potential and excessive moisture loss of the mono-cropped field decreasing field architecture complexity (Alderweireldt, 1994; Harwood *et al*., 2004; Winder *et al.,* 2014) (*Section 5.1.6.2.2.*).

Few larger-bodied *T. tenuis* were noted in hedgerows opposite each tillage intensity, though were recorded in the field when *H. vulgare* was in crop. Perhaps *T. tenuis* of greater fitness did exist in the population, as Gan *et al.* (2015) and Rodríguez & Gloudeman (2011) explain there are many factors to describing the level of fitness that a *T. tenuis* exhibits, body size not always relating to greater fitness. Maybe certain *T. tenuis* did exert predatory pressure, finding the optimum web-site in the shelterbelt to entrap the aerial morphs and *S. mosellana* that were identified (Rodríguez & Gamboa*,* 2000; Rodríguez & Gloudeman, 2011). Kraftt & Cookson (2012) note that a *T. tenuis* response of silk-laying is due to a collection of stimuli which requires high levels of perception.

T. tenuis adapted their web-building site as a response to numbers of *S. avenae* found within the web and the vegetation (*Table 5.3.12*.). *T. tenuis* in hedgerows opposite all soil tillage intensities spun webs in similar locations, mainly in the higher aspect of the grass layer formed at the basal stratum of the hedgerow. This placement providing material for adequate anchorage, the apex of tillers increasing surface area of the web for prey capture. Kraftt & Cookson (2012) describe vegetation architecture is often of greater complexity underneath a sheet web, maximising area flagelliform silk can ensnare hairs of prey (*Section 2.1.2.1*.). Webs spun in tight compartments of inter-twinned leaves and branches of the hedgerow species is void of the space to facilitate prey capture.

The fact that Aphididae were caught in webs of all hedgerows opposite each soil tillage, describes that Aphididae colonies were present in all areas of the hedgerow, regardless of tillage intensity (*Figure 5.3.4. & Figure 5.3.5*.). Moreover, alate morphs were recorded in hedgerows bordering all soil tillage intensities. This expressed movement in and out of the shelterbelt from all tilled areas of the field, with Aphididae tendency for migration within a close vicinity (Parry, 2013; Reynolds & Reynolds, 2009). However, Direct Drill Managed hedgerow did not relay a significant prey abundance of *S. avenae*, when in the field *S. avenae* was found at notable density in Direct Drill Managed with polymorphism occurring (*Section 5.1.6.2.3*). Parry (2013) discussed that Aphididae dispersal takes place within a small window, when conditions are optimal for these opportunists to reproduce and disperse rapidly. Newman (2004) accords that Aphididae will not disperse unless certain environmental conditions are met. Wind speed according to Reynolds and Reynolds (2009) is the main variable that dictates the initiation and direction of Aphididae flight, thus linear dispersal is unlikely to occur from the field into the shelterbelt.

It appears that where no prey was located, webs were found at different heights of the hedgerows opposite Direct Drill than the remaining two soil tillage intensities (*Figure 5.3.4*.). This shows that *T. tenuis* were exploring the hedgerow habitat in different ways for prey. For a hedgerow opposite Direct Drill, eight webs were woven >20 cm above the ground and for a hedgerow of Direct Drill Managed, four webs <3 cm were found, both in July 2018, where no crop pests were identified in the g-vac sampling. As discussed within the Fieldwork Sub-Chapter, this absence of pests is hypothesised to be due to abnormally high temperatures, which caused low fecundity in Aphididae and an inability to pathogenesis an abundance of alate morphs, to provide new colonies (Reynolds & Reynolds, 2009; Winder *et al.,* 2014). (*Section 5.6.2.2.*). However, in both areas, webs did contain exuviae which may have been Aphididae prey where contents were consumed through *T. tenuis* expelling enzymes to liquify body tissue and feed (Davey *et al.,* 2013; Macías-Hernández *et al.,* 2018). Aphididae exuviae were evidence of their presence, though its web capture cannot be classed as direct biological control (Goggin, 2007; Lombaert *et al.,* 2006) (*Section 2.3.2.*). It may be that Aphididae had migrated into the shelterbelt where phloem content of vegetation may have been of easier extraction than the drought-stressed *H. vulgare* and webs, at different heights, were a product of this stimulus (Price *et al.,* 2011).

All webs had been abandoned in the areas where no prey was located. Jurczyk *et al.* (2012) and Opatovsky *et al.* (2016) suggesting that *T. tenuis* though a 'sit and wait' predator, are keen to relocate if no cues for prey in the vicinity are processed, Wenninger *et al.* (2020) concur, suggesting a web may snare prey even when abandoned due to premature vacation. The difference in anchor point heights, mentioned above, may be explained predominantly by hedgerow vegetation density recorded at the later growth stages of *H. vulgare*. Direct Drill hedgerow held a density of 2885.9 cm^2, gaps may be attractive to exploit in times of low prey consumed or perhaps webs spun to relate to aerial vibrations of alate prey and aerial *S. mosellana* found in early growth stages (Hogg & Daane, 2018; Miyashita *et al.* 2012) (*Section 5.1.6.2.1.*). Disintegration of webs is timely, resilience of silk creating fibrils of high strength and toughness (Chen *et al.* 2012; Craig, 1987) (*Section 2.1.2.3.*). For Direct Drill Managed, the vegetation density was 5776.6 cm^2, again seen to pull anchorage of webs downwards to lesser heights.

It appeared that webs of lower height in Direct Drill Managed and Direct Drill hedgerows were more successful in ensnaring prey (*Figure 5.3.5.*). Most prey were found in webs within the early growth stages of *H. vulgare,* when temperatures were favourable and growth on hedgerows provided increased availability of feeding sites (Price *et al.,* 2011; Tulli *et al.,* 2013). The lower webs had been successful in prey capture with low levels of energy output. This agrees with Bell *et al.* (2002) and Bowden & Bundle (2010) who identified that Linyphiidae will respond to their habitat in web creation and create a web that allows the least energy cost to construct. Interestingly, more prey entered the webs when no wind was present, this discords with Agabiti *et al.* (2016) and Losey & Denno (1998), who discussed 'dropping action' of Aphididae is influenced by physical disturbances such as wind, disrupting the anchorage of feeding phloem. Kumar *et al.* (2019) discussed a field cropped with *H. vulgare* that was identified to have 22.1% infestation rate in peak growth stage. Thus here, the capture rate was not described as high, with six *S. avenae* the greater prey entrapped. Therefore, in this study, three *S. avenae,* the greater value collected by g-vac sampling, did not present a strong precursor for biological control. Perhaps wind speed measured was irrelevant, low *S. avenae* abundance due to weak fitness traits, transferred within a potential colony (Asin & Pons, 2001; Lombaert *et al.,* 2006). Moreover, when a higher wind of 6.6 kmh^{-1} was measured at the basal stratum of the hedgerow, webs were spun higher attaching to low-lying leaves (*Table 5.3.12*.). Gaps were observed in the swards, revealing bare ground of limited attachment potential. Additionally, no prey was collected via g-vac sampling, revealing the favoured stratum in this hedgerow was lacking the benefits described earlier. *T. tenuis* as an opportunistic predator ascended higher, perhaps able to entrap aerial prey such as dipteria (Ball & Bingham, 2003; Knight *et al.,* 2012; Peigné, *et al.,* 2007; Zheng *et al.,* 2014) (*Figure 5.3.4*.).

Blake *et al.* (2013) and Gómez *et al.* (2016) discuss that *T. tenuis* migrate through a positive vegetation complexity gradient. It appears that the forefront of the hedgerow was yet again the prime location for web-site construction when hedgerow vegetation was lower (*Table 5.3.15*.). Additionally, with respect to a significant negative correlation between number of *S. avenae* found within the vegetation and distance of anchor point height, Feber *et al.* (2015), Griffiths *et al.* (2018) and Ysnel & Canard (2000) discuss Aphididae migration into the hedgerow by primarily alighting onto the outer-most layer of vegetation (*Table 5.3.15*.). The prey consumed, can be thought of as a product of migrating from the relevant field areas. It appears that the webs spun in the front most section responded to cues of *S. avenae* (Hatano *et al.,* 2008; Kraftt & Cookson, 2012; Mansour & Heimbach, 1993).

Eight out of eleven webs at the forefront of the hedgerow, held three *T. tenuis* under the webs in Direct Drill hedgerow of later growth stages (*Table 5.3.15*.). This result explains potential biological control is actively occurring. No prey was captured within these webs or evidence of feeding through exuviae presence, though prey was present in the vegetation. Perhaps the webs were recently spun, and the hope was to entrap prey for consumption. From a biological control perspective, it is encouraging to observe potential prey suppression from Linyphiidae persistence of the web. This extended phenotype can entrap prey through mechanism of the silk, however, Chapman *et al.* (2013) and Pekár (2000) explain Linyphiidae presence is favoured in success of biological control, as *T. tenuis* occupying a web will ensure a prey item is dealt with.

5.3.6.3. Variables Measured Within the Field and Hedgerow

Significantly more *T. tenuis* and sheet webs were noted to be in the hedgerows than the main field, which fits the evidence found by Tamburini *et al.* (2015) and Vollrath (1986), that in times of cultivation and low prey abundance within a main field area, shelterbelts become a reservoir for Linyphiidae activity (*Figure 5.3.6. & Figure 5.3.7.*). Pfingstmann *et al*. (2019) and Rosas-Ramos *et al.* (2018) agree, explaining that hedgerows act to continue flow of ecosystem services in times of field disturbance, ensuring predator and prey interactions persist. Surprisingly in the hedgerow opposite Direct Drill, where zero disturbance was identified, the same trend existed (*Figure 5.3.6. & Figure 5.3.7*). It is of interest that more *T. tenuis* were present alongside numbers of sheet webs in the hedgerow when the field opposite had not been disturbed and *T. tenuis* were active in the field (*Section 5.1.6.1.*). Blandenier (2014) and Thorbek (2003) suggest that aerial dispersal into a margin is relatively passive, the direction being influenced by meteorological conditions. This is concurred by Bonte *et al.* (2008), who report high, short ballooning helps to find a linear wind current. Alignier *et al.* (2014) and Van Alebeek *et al.* (2008) relate that a hedgerow is a separate habitat. Once *T. tenuis* have migrated from the field, their predator - prey connections are predominately from within the hedgerow. Thus, any short-ranged locomotion by *T. tenuis* in the shelterbelt is due to cue / stimuli from within (Pfingstmann *et al*., 2019).

At times of early and late growth stages of *H. vulgare,* there was heterogeneity in the mean number of *T. tenuis* between the locations of the hedgerows and the main field (*Figure 5.3.8.*). This has an implication to the biological control capacity of *T. tenuis* in the field when it is of necessity to suppress prey abundance from congregating on *H. vulgare* (Toft, 1987; Vichitbandha & Wise, 2002; Welch *et al.,* 2016). Isaia *et al.* (2007), Mclachlan & Wratten (2003) and Pfister *et al.* (2015) discuss a deterrent of outward migration from a hedgerow or incentive to inward dispersal may be low densities of prey observed in the field, *T. tenuis* and Linyphiidae thus relocate to the hedgerow for a considerable period of time to continue their life cycle. Passive foraging through the web strategy for predation incurs a need for high prey density (Diehl *et al.,* 2013; Feber *et al.,* 2015; Haughton *et al.,* 1999). Yu (2019), when understanding temperature effects on plasticity (adaptability an organism must physically alter in response to external stimuli) on *Rhopalosiphum maidis* (corn leaf aphid), identified that Aphididae endure a limiting temperature which prohibits wing polyphenism (production of alate morph). Asin and Pons (2001) discussed that *M. dirhodum* and *S. avenae* plasticity to polymorphism altered at temperatures of 27 - 30 ^{o}C and explained low migration into the main field thus, not providing the necessary cues for *T. tenuis* to follow (Brabec *et al.,* 2014; Newman, 2005). Similar numbers of *T. tenuis* were noted in the hedgerow and field in the summer of 2017, when temperatures on sampling days ranged from 22 - 27 ^{o}C, greater abundance of Aphididae were recorded in the field, the environmental factors at an optimal to trigger asexual reproduction in Aphididae and induce plasticity to wing polymorph and disperse (Parry *et al.,* 2006; Parry 2013; Price *et al.,* 2011; Summers *et al.,* 2004). It appears that the field was still not exhibiting potential to be a productive web-site for some

Linyphiidae and *T. tenuis*. Bredeson (2019) notes that mono-cropping disrupts the balance that a stable arthropod community can promote, by reducing vegetation diversity.

Haughton *et al.* (1999), investigating effects of glyphosate drift to a field margin, found in times of increased glyphosate application that the drift reduced landscape heterogeneity. This was shown to have a greater negative impact to *T. tenuis* density than the glyphosate application. However, the glyphosate application appeared not to affect *T. tenuis* abundance in the shelterbelt (*Table 5.1.1.*). A reduction in hedgerow vegetation density seems not to have occurred, low wind may have aided low drift dispersal. Vegetation complexity, agreed by Isaia *et al.* (2007) and Ysnel & Canard (2000), facilitates web-spinning.

The greater number of bridge threads within the hedgerow itself were identified to take place within the times when the field was out of crop (*Figure 5.3.9.*). This shows web site exploration was greater in this period and concurs with Batáry *et al.* (2008), Buri *et al.* (2016) and Horváth *et al.* (2015), who relate Linyphiidae preference to migrate to areas (hedgerows), supporting a degree of vegetation complexity. Here, rappelling commences to acquire knowledge of spatial orientation and prey movements (Ford, 1977; Romero & Hardwood, 2010). This confirmed less movement between hedgerow and field when *H. vulgare* was growing in the latter. This may affect pest suppression rate that Linyphiidae can exert. Marc & Canard (1997) and Rusch *et al.* (2016) suggest, promoted early movement out of a shelter habitat is key to effective biological control, to establish a high density at time of increased prey abundance. De Meester & Bonte (2010) advise that migration rate into a shelterbelt can be difficult to quantify, the upper strata of *H. vulgare* facilitating lower (in height) dragline threads, which are hard to identify and are easily susceptible to external factor disturbances. Perhaps not all evidence of dispersal was measured, though, as it appeared that the hedgerow was a favoured dwelling.

Ballooning was found to occur in greater quantity at times of field disturbance, which concurs with *T. tenuis* pioneer ability to settle in disturbed habitats, shown by Bianchi *et al.* (2017) and Halley *et al.* (1996). Ballooning, when observed, was spun by female *T. tenuis*. Simmoneau *et al.* (2016) and Woolley *et al.* (2016) found no difference in the propensity to balloon for male and female Linyphiidae. Bonte (2013) discussed that female *T. tenuis* propensity to disperse is density dependant on female *T. tenuis* not males, noted to be due to selection pressure of locating a suitable mate (Rundus *et al.,* 2011). The data accords with this observation with female *T. tenuis* most abundant in all main field samples and hedgerows opposite all soil tillage intensities (*Section 5.1.5.*).

5.3.6.4. Variables Concerning Presence of Egg Sacs in Hedgerows

Humpreys (1983) and Vanacker *et al*. (2004) discuss the size of an egg sac, generally presents a potential greater clutch, and Blackledge *et al.* (2011) showed that an egg sac sheltered with a higher degree of vegetation density was less likely to become a product of predation (*Table 5.3.21*.). It appears that egg sacs of a greater clutch were woven at a greater distance into the hedgerow for additional protection to help assure the success of hatching of a new generation.

Hedgerow vegetation density was of significance to egg sac placement (*Table 5.3.21*.). This agrees with findings by Finch (2005) who observed that Linyphiidae females had woven their egg sacs into vegetation to provide camouflage and required low levels of light to incubate which can be achieved within increased vegetation. This also accords with Holland & Oakley (2007) and Öberg *et al.* (2008), where it was shown that egg sacs are required to be woven into dense vegetation for protection. Sanders *et al.* (2015) and Vanacker *et al.* (2004) identified intra-specific and inter-specific predation where egg sacs contain a meal of high nutritional value (Blackledge *et al.,* 2011; Suter *et al.,* 1987) (*Section 2.1.2.5*.). It may be that weaving the egg sac further from the forefront of the shelterbelt may avoid predation with the tendency for *T. tenuis* to construct webs at the forefront of the hedgerow (Blackledge *et al.,* 2011; Opatovsky *et al.,* 2016; Suter *et al.,* 1987; Topping & Lövei, 1997).

Egg sacs (either containing or not containing eggs) were identified opposite each area of soil tillage intensity, presenting the commencement of a different generations. This supports the findings of Bell *et al.* (2002), Opatovsky *et al.* (2016) and Welch *et al.* (2013) who discussed. *T. tenuis* and Linyphiidae have evolved their life strategies around a crop rotation. The conclusion of a generation, therefore, occurs when resources are low. The intensity of soil tillage applied to the main field had little impact on *T. tenuis* and Linyphiidae oviposition behaviour. It could be identified that cultivating at this period in the life cycle of a Linyphiidae is beneficial in having a low consequence to biological control potential of *T. tenuis* and Linyphiidae. Egg sacs were generally found more than a metre apart, spread out across the entire length of the hedgerow. Maklakov *et al.* (2003), Simonneau *et al*. (2016) and Thorbek *et al.* (2004) described an idea of 'bet-hedging' where Linyphiidae weave egg sacs across a large space to improve survival chances of the next generation (*Section 2.1.2.5*.).

5.3.7. Final Discussion - Hedgerows Opposite Soil Cultivations of Different Tillage Intensity

Number of *T. tenuis* webs identified was on most occasions greater in the hedgerows, regardless of soil tillage intensity. The hedgerow throughout fieldwork has been shown to be a reservoir of prey and *T. tenuis* abundance. Migration into and out of shelterbelts is fundamental to prey suppression and health of the crop. Beneficial shelterbelts allow the population of both prey and *T. tenuis* to persist, and subsequently allow the continuation of biological control potential of *T. tenuis*, in times where the field may not be a favourable habitat (i.e. times of extreme climatic conditions). The necessity is dispersal back into the field to exert predator dynamics within. This identifies the importance of aim one, three and four noted in Section 5.3.2.1.

Hedgerow vegetation density appeared to be a predominant factor in altering *T. tenuis* propensity to web build and choice of web-site, more so than the soil tillage the hedgerow was adjacent to, thus communicating the second and fourth aim reported in this Sub-Chapter (*Section 5.3.2.1*.). Additionally, addressing the aim, migration was not occurring linearly due to dispersal patterns and influence of external factors such as wind speed. Soil tillage appeared to alter bridging inclination at a noteworthy abundance when the areas of Conventional and Direct Drill Managed underwent primary cultivation.

Prey was confined in webs in all hedgerows addressing the third aim assigned to this Sub-Chapter (*Section 5.3.2.1*.). Plasticity of the spun web altered with the stimuli of prey, whether aerial prey or apterous morphs. This prey did not appear to link to the density of prey viewed in the main field. Prey capture was not considered high to substantially offer a dominant biological control element. Prey, though, were of low abundance in the vegetation due to high temperatures, limited cues thus not interpreted by *T. tenuis* relying on vibratory stimuli.

The hedgerow provides an area for oviposition and egg sac incubation, to facilitate a subsequent generation. The hedgerow is observed to aid *T. tenuis* activity of revolving around the life cycle of the crop and be in the vicinity to exert predator control on a following crop.

Chapter Six

6.0. Interactions of *T. tenuis* and Linyphiidae with Aphididae Causing Barley Yellow Dwarf Virus (BYDV) in *H. vulgare*

6.1. Introduction

Barley Yellow Dwarf Virus (BYDV) is a common viral disease that causes considerable damage to yield and is transmitted mainly through *S. avenae* and *R. padi* (*Section 2.2.6.2.*). From this, crops showing possible symptoms of BYDV must be laboratory-tested to confirm whether the virus is present and then the relevant action, in controlling *S. avenae* and *R. padi* numbers, can be applied (S*ection 2.2.6.2.*).

In the *H. vulgare* cropping season 2017 / 2018 at GS 61 - GS 65 and GS 87 - GS 91, symptomatic BYDV leaves were identified from afar in the field (*Table 5.1.1.*, *Section 5.1.3.1., Page 82*). On closer inspection, leaves were orange / burnt yellow from the tip to half-way down and each *H. vulgare* had failed to anthesis. Falks & Duffus (1981) discussed that a plant may abort if depletion of a plants nutrition's become too great with weakening phloem tissue caused by BYDV. These observations are shown from research by D'Arcy & Domier (2000), Dorokhov *et al.* (2014), Falks & Duffus (1981) and Reddy *et al.* (2009) to be clear indications of possible BYDV (*Figure 6.1a & b and Figure 6.2a & b*). After field inspection, most areas of symptomatic BYDV were identified within the Conventional tillage. Only one other area was observed in the Direct Drill side of the margin between the Conventional tillage and Direct Drill tillage (*Section 4.2., Figure 4.2a & b, Page 54*).

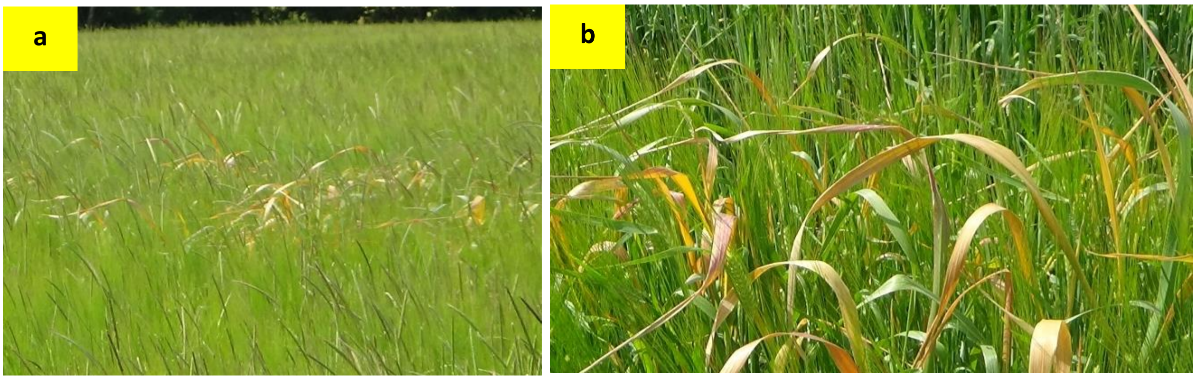


Figure 6.1a & b: Symptomatic BYDV H. vulgare*. Conventional. Field B. GS 61 - GS 65, 2017 / 2018 season.*

Figure 6.2a & b: Symptomatic BYDV H. vulgare*. (Circled in yellow). Conventional. Field B. GS 87 - GS 91. 2017 / 2018 Season.*

Understanding *T. tenuis* activity alongside that of the BYDV-causing Aphididae (*S. avenae & R. padi*) within areas observed with symptomatic BYDV would be useful for this research project. Firstly, acknowledging where, within the areas of differing soil tillage, the symptomatic BYDV occurred and how this knowledge could relate to future soil tillage applications. Secondly, analysing *T. tenuis* interactions in BYDV symptomatic *H. vulgare* may allow further analysis of *T. tenuis* prey capturing abilities and whether its web-site location and web-building are a response to Aphididae incidence. Aphididae incurrence are theorised to be of greater abundance in areas of symptomatic BYDV due to the volatile odours released on virus transference, attracting further Aphididae to feed (Dancewicz *et al.,* 2018; Paulmann *et al.,* 2018) (*Section 2.2.6.2.*).

6.2. Aims and Specific Objectives

6.2.1. Aims

The aims behind measuring *T. tenuis* and prey interactions on *H. vulgare* infected with BYDV follows Research Aims 1 and 3 (*Section 1.2., Page 2*).

1. Identify the potential biological control by *T. tenuis* of Aphididae within different intensities of tillage in an arable crop.
3. Understand whether *T. tenuis* behaviour is stimulated by the presence of Aphididae.

6.2.2. Specific Objectives

Specific objectives were chosen to address the aims of this Chapter.

- Confirm symptomatic BYDV as BYDV-PAV positive.
- Measure abundance and extended phenotypes of *T. tenuis*, i.e. web construction, to calculate *T. tenuis* activity and output in areas of *H. vulgare* and BYDV symptomatic *H. vulgare.*
- Quantify Aphididae activity by abundance in areas of *H. vulgare* and BYDV symptomatic *H. vulgare.*
- Observe Aphididae web capture in areas of *H. vulgare* and BYDV symptomatic *H. vulgare.*

6.3. Methodology

6.3.1. Field Sampling

Three 1 m^2 areas, containing BYDV symptomatic *H. vulgare,* were randomly selected in the Conventional area of Field B, 61 - GS 65 2017 / 2018 season, via the same method of the main field samples (*Section 4.2.*). The same areas were then sampled in GS 87 - GS 91, 2017 / 2018 season. An area of BYDV symptomatic leaves at the margin of soil tillage transition zone was not used, as this was the only observation within this area. The sample plots were measured for *T. tenuis* and Linyphiidae activity by recording sheet web area and its anchor height. Webs were observed for Aphididae and exuviae. G-vac sampling was used to record *T. tenuis* and Aphididae numbers. Vegetation structure was recorded, *H. vulgare* density, height and *A. myosuroides* density.

No symptomatic BYDV was observed in earlier GS of *H. vulgare* in the field. The distance between the sample areas in Conventional of GS 33 - 37 (May) 2017 / 2018 and the three 1 m^2 randomly selected area containing BYDV *H. vulgare* in later growth stages, was calculated to understand if any *S. avenae* activity in May was potentially a precursor to BYDV manifesting in *H. vulgare* (*Section 2.2.6.2. & Table 5.1.1.*).

The summer of 2018 had higher than mean temperatures which resulted in South-Eastern regions experiencing drought conditions (Met Office 2018). The Delta™ Soil Moisture penetrometer was used to measure soil moisture content in the areas of suspected BYDV and other areas within the field, to determine whether the senescing of the leaves was due to poor moisture availability or BYDV (Davis *et al.,* 2015; Knight *et al.,* 2012; MacFarland *et al.,* 2014).

6.3.2. Laboratory Testing

To confirm if BYDV was present, laboratory testing was necessary (Davis *et al.,* 2015; FERA, 2018; Valenzuela & Hoffmann., 2014). Samples were collected from three areas from GS 87 - GS 91 *H. vulgare* season. Following advice from FERA (2018), samples were air-dried, wrapped in clean absorbent paper and refrigerated at 4 °C prior to sampling.

Barley Yellow Dwarf Luteovirus PAV was chosen over MAV, as the PAV strain of the virus is most likely to be transferred to a crop via *S. avenae,* whereas the MAV strain is most commonly associated with *R. padi* (*Section 2.2.6.2.*). From fieldwork, greater *S. avenae* abundance was identified in Field B than *R. padi* (*Section 5.1.6.2.1.).* The samples were tested for BYDV using Loewe® Barley Yellow Dwarf Luteovirus PAV - 2 % Blocking in Conjugate Buffer DAS ELISA (Enzyme-linked Immunosorbent Assay) using polyclonal antiserum from rabbit (*Section 2.2.6.2.*).

Both positive and negative controls were used in the ELISA test. Positive control contained a purified protein which synthesises the BYDV-PAV antigen. The negative control used was a sample that did not contain a protein that produces the BYDV-PAV antigen. A negative control validated the results by removing the possibility of non-specific antigens synthesised being bound to the substrate (Lequin, 2005) (*Figure 6.3b & Section 2.2.6.2*.).

The sap from the phloem is the material used for detection of ELISA. The crops collected from the three areas from GS 87 - GS 91, were ground to extract sap with a pestle and mortar (*Figure 6.3a & b*). The protocol followed required washing the plates between each stage thoroughly with washing buffer. The buffers were used within one week, as this was the optimal period. The ELISA test was conducted over two days, requiring overnight incubation (*Figure 6.3c & d*). The plate was visually inspected for yellow after the procedure, BYDV antigen positively binding to PNPP (p-nitrophenyl phosphate) substrate (*Section 2.2.6.2.*). Positive and negative wells needed to be a yellow hue and blank, respectively. A colour spectrometer was not used as the presence of BYDV-PAV was all that was required and not intensity.

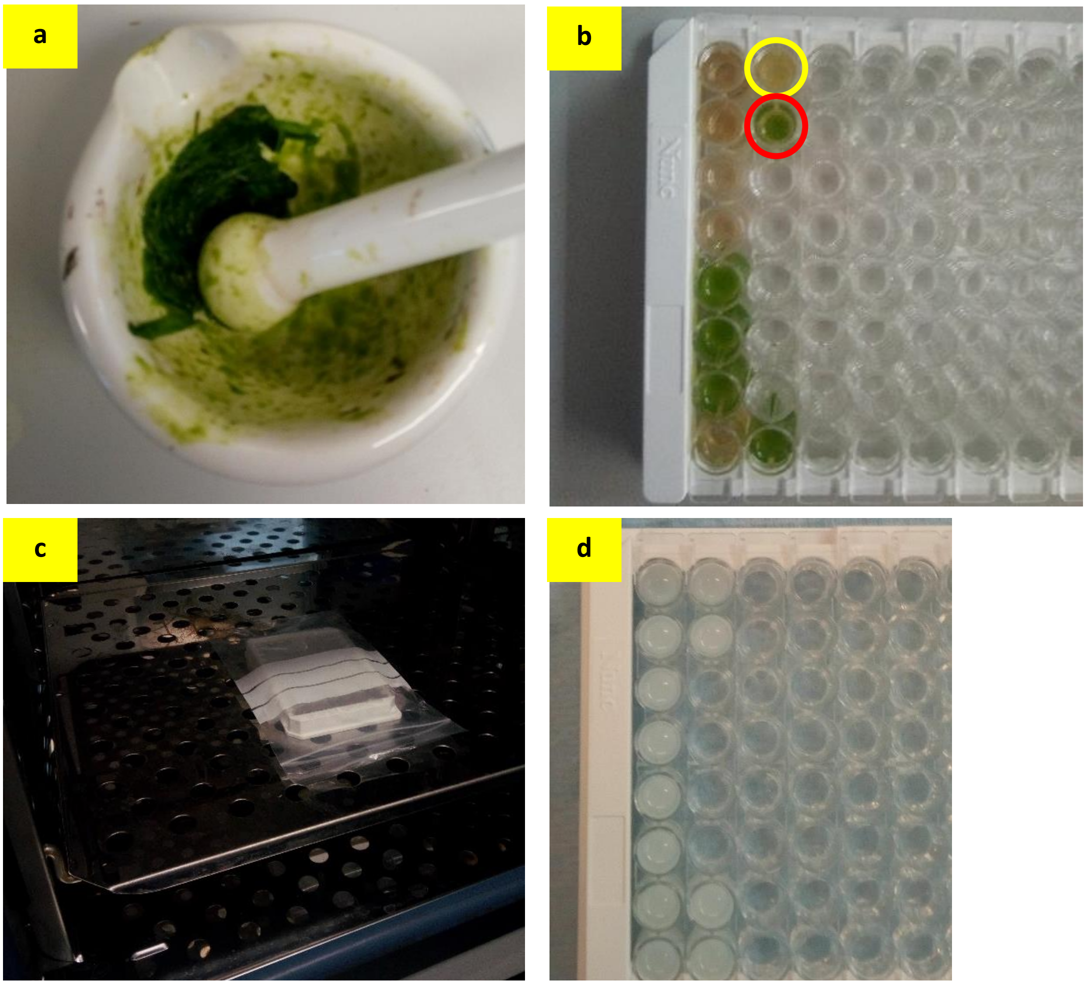


Figure 6.3a - d: Procedures from the Lowe® DAS ELISA Kit.
a = Grinding H. vulgare *leaf to extract sap. b = Sap being placed into wells after first antigen applied. Green samples are sap from later mesocosm experimental trials. Brown samples are sap from NIAB Field B. (Yellow circle is positive. Red circle is negative sample). c = Sealed plate incubated overnight at 37 °C. d = Conjugate antigen added to samples as top of sandwich-second antigen (Section 2.2.6.2.).*

6.4. Statistical Analysis

S. avenae presence was re-analysed in the field sampling of GS 33 – GS 37 (May sampling), to understand if there was an earlier indication of the onset of symptomatic BYDV. Two samples measured in the Conventional soil intensity in May 2018 were < 50 m away from random sample areas with BYDV infected *H. vulgare* in GS 61 - 65 (June) and determined as close enough to compare *T. tenuis* activity to *S. avenae*, as potential vectors of BYDV (*Table 5.1.1. & Section 2.2.6.1.*).

The measurements taken within the six areas of BYDV symptomatic *H. vulgare* from the Conventional tillage (three from GS 61 - GS 65 and three from GS 87 - GS 91), were analysed against the measurements recorded in the six sample areas in the Conventional plots used in the main field sampling (three from GS 61 - GS 65 and three from GS 87 - GS 91), where no BYDV symptomatic leaves were identified (*Section 4.2., Table 5.1.1. & Section 5.1.5.2.*).

Statistics were run for data collected in sample periods of GS 61 - GS 65 and GS 87 - GS 91 together with Minitab18©. A PCA was run, where scores for two principal components were analysed to understand which variables measured held the greater influence (Bass, 2007). Normality testing and visualising distribution on histograms and probability plots, concluded data collected from all samples were non-normal (Khan, 2013) (*Section 5.1.4.1.*).

Kruskal-Wallis was utilised to identify if significant differences existed between the medians for variables measured within Conventional samples without symptomatic BYDV and Conventional with symptomatic BYDV. The macro (KrusMC.mac) was not utilised to apply Dunn's multiple comparison test due to only two sets of data inputted into the model, for example, anchor point height from Conventional symptomatic BYDV and Conventional no symptomatic BYDV (*Section 5.1.4.2.*). Correlations, using Spearman's Rank (Rho), identified any significant relationships between variables recorded (Hawkins, 2014; Khan, 2013; Weather *et al.,* 2011).

Multiple regression models were built, the stepwise backwards elimination method, through the software Minitab18©. The model was created for the responses of anchor point height of support threads and web area measured in the symptomatic BYDV Conventional area and asymptomatic BYDV Conventional samples. As within fieldwork, the response was placed against certain explanatory independent variables (*Section 5.1.4.2.*). Backwards elimination removed insignificant variables at $\alpha < 0.05$ (Hawkins, 2014; Wheater *et al.,* 2011). *T. tenuis* mass, cephalothorax length, abdomen length and plant height were again entered as means as explained in fieldwork (*Section 5.1.4.2.*).

The quadratic equation was $y = ax^2 + bx + c$, where b may have many terms. The outcome of this model, presented by a quadratic curve (parabola), allowed multiple interactions of independent variables with the response variables to be analysed. Normality was further checked via a residual vs fitted values plot, random distribution of residuals around the fit line confirming normality. If large residuals were observed their origin was located and were removed if datasets were not considered normal due to the large numbers of data placed into the model (Khan, 2013) (*Section 5.1.4.2.*).

No bridge threads were identified in the sample areas. All anchor points and thread lengths noted relate to webs woven.

6.5. Results

6.5.1. Laboratory Testing

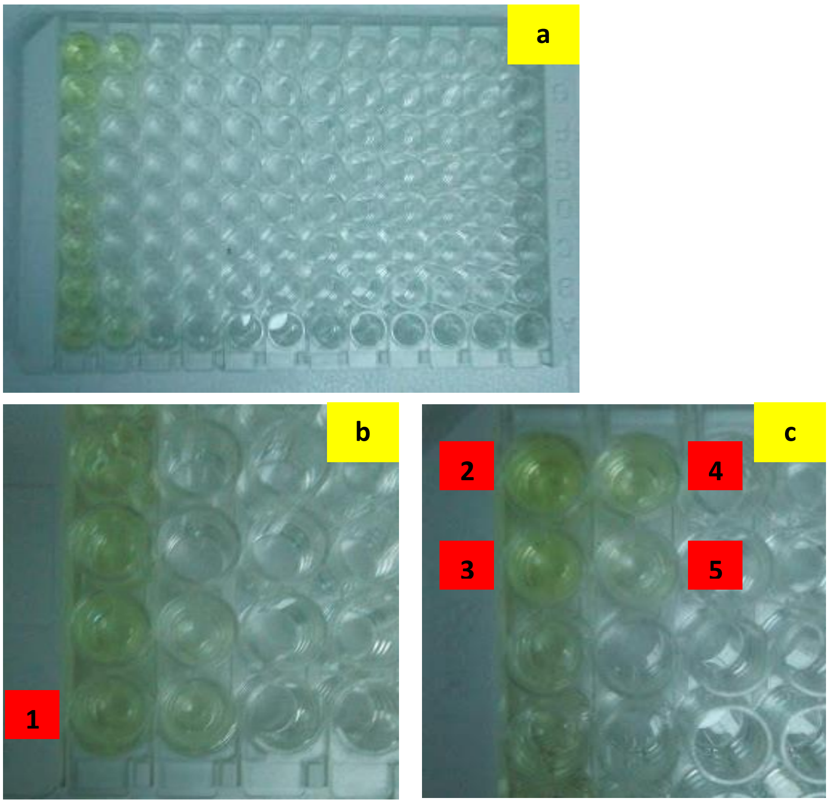


Figure 6.4a - c: Results of ELISA test. a - c = Overview of plate. 1. - 3. = Field samples from GS 87 - GS 91. 4. = Positive sample. 5. = Negative sample.

The presence of the BYDV antigen was identified by the yellow colour of PNPP in each field sample from GS 87 - GS 91 (*Figure 6.4a - c*) (*Section 2.2.6.2.*). The positive result showed the antigen and negative was blank.

6.5.2. Sampling in GS 33 - GS 37 Concerning Later BYDV Infected *H. vulgare*

A 1 m^2 sample from GS 33 - GS 37 was 23.6 m south-east of one BYDV *H. vulgare* 1 m^2 sample area, where five *S. avenae* nymphs were captured by g-vac and none identified in Linyphiidae webs. Another 1 m^2 sample from GS 33 - GS 37 was 33.2 m south-west from a BYDV *H. vulgare* 1 m^2 sample, where two *S. avenae* nymphs were collected by the g-vac and one *S. avenae* captured in a Linyphiidae web.

6.5.3. *T. tenuis* Interactions with Asymptomatic and Symptomatic BYDV in Later Growth Stages of *H. vulgare*

6.5.3.1. Summary of Results

- Significantly higher median anchor point height was identified for Conventional area containing BYDV symptomatic *H. vulgare* (*Figure 6.6*.). Significantly higher median anchor point height was found for webs that contained *S. avenae*, in the same Conventional areas (*Figure 6.7*.).
- Median thread length where *S. avenae* were captured was significantly longer in Conventional area containing BYDV symptomatic *H. vulgare* (*Figure 6.9*).
- Conventional area with symptomatic BYDV was affected by *S. avenae* within the web and thread length shown by a PCA. Conventional area with asymptomatic BYDV identified mean plant height influenced variation in the data measured (*Figure 6.5*.).
- Number of *S. avenae* and plant density exhibited a significant relationship with the dependant variable anchor point height, and both showed significant positive correlation to anchor point height and plant density was positively significantly correlated to thread length (*Figure 6.8. & Table 6.3. Table 6.5*.).
- Number of *T. tenuis* was significantly negatively correlated to thread length and showed quadratic regression with anchor point height and thread length (*Figure 6.8. & Figure 6.10. & Table 6.5*.).
- Number of Aphididae exuviae in the web showed significant regression with anchor point height and thread lengths recorded and was significantly positively correlated to each dependant variable measured (*Figure 6.8. & Figure 6.10., Table 6.3., Table 6.5. & Table 6.6.*).
- Wind speed significantly affected anchor point height and thread length (*Figure 6.8. & Figure 6.10*.) and held significant negative correlation to thread length and web area (*Table 6.3., Table 6.5. & Table 6.6*).

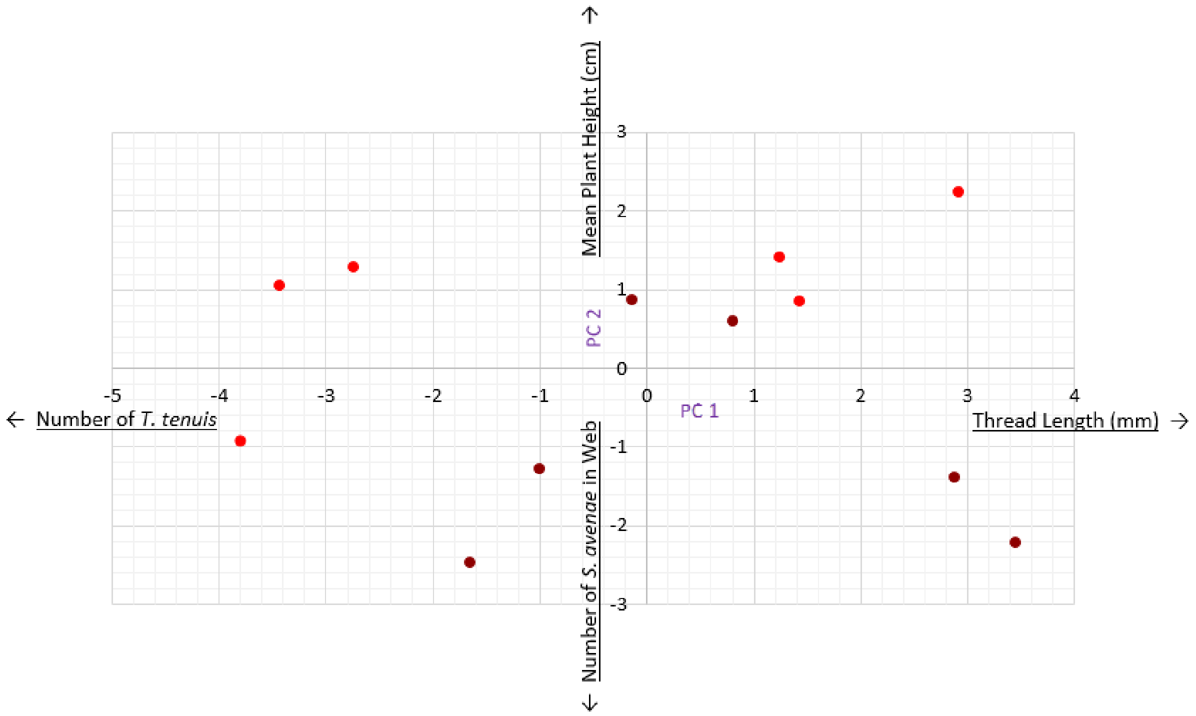


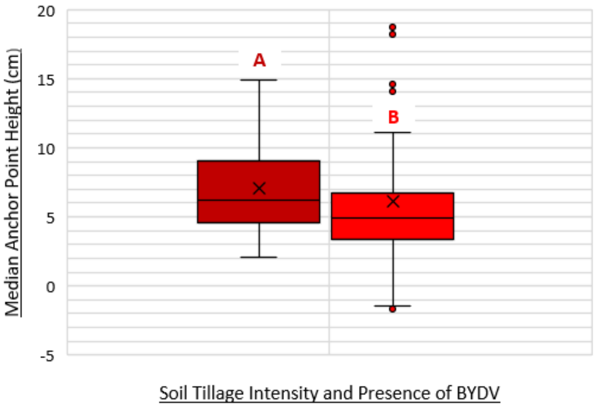
Figure 6.5: PCA of variables measured, along the first two principal components and variables correlating to each component. Interactions of T. tenuis *and Linyphiidae with Aphididae causing Barley Yellow Dwarf Virus (BYDV) in* H. vulgare*. (Conventional with No Symptomatic BYDV* H. vulgare *= Red, Conventional with Symptomatic BYDV* H. vulgare *= Dark Red).*

Table 6.1: The variance in data explained by principal component 1 and principal component 2 and associated eigenvalues for the variables which held the most influence within the data in each component. Interactions of T. tenuis *and Linyphiidae with Aphididae causing Barley Yellow Dwarf Virus (BYDV) in* H. vulgare.

	Principal 1	**Principal 2**
Variance	41.1%	16.9%
Variables	**Eigenvalue**	**Eigenvalue**
Thread Length (mm)	0.343	
Number of *T. tenuis* (male and female combined)	-0.282	
Mean Plant Height (cm)		0.116
Number of *S. avenae* in the Web		-0.551

No clustering was identified, and no close associations existed within the PCA. Overall, it can be identified that the data recorded within the areas of symptomatic BYDV *H. vulgare* was influenced the most by *S. avenae* within the web whereas, for Conventional, where asymptomatic BYDV was identified in the *H. vulgare,* number of *T. tenuis* recorded and mean plant height affected the data the greatest.

6.5.3.2. Anchor Point Height



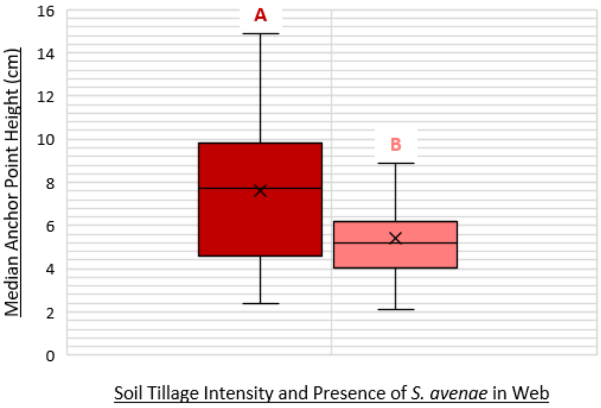


Figure 6.6: Median anchor point height (cm), soil tillage intensity and presence of BYDV. Interactions of T. tenuis *and Linyphiidae with Aphididae causing Barley Yellow Dwarf Virus (BYDV) in* H. vulgare*. (df = 1, Adjusted for ties H - 11.09, P - 0.001, n = 289). (Conventional with Symptomatic BYDV* H. vulgare *= Dark Red, Conventional with No Symptomatic BYDV* H. vulgare *= Red). (Conventional with Symptomatic BYDV* H. vulgare *(n = 158), Conventional with No Symptomatic BYDV* H. vulgare *(n = 131)).*

Figure 6.7: Median anchor point height (cm) for Conventional with Symptomatic BYDV H. vulgare *and presence of* S. avenae *inside webs. Interactions of* T. tenuis *and Linyphiidae with Aphididae causing Barley Yellow Dwarf Virus (BYDV) in* H. vulgare*. (df = 1, Adjusted for ties H - 10.77, P - 0.001, n = 158). (Yes* S. avenae *in web = Red, No* S. avenae *in web = Pink). (Yes* S. avenae *in web (n = 121), No* S. avenae *in web (n = 37)).*

A significantly higher median of anchor point height was identified in the Conventional tillage that held symptomatic BYDV *H. vulgare*, which was 1.3 cm higher than the significant lower median for the anchor point heights measured in the Conventional tillage with no symptomatic BYDV (*Figure 6.6.*). The greater dispersion was identified between the median and upper quartile for Conventional with symptomatic BYDV *H. vulgare*.

The significant higher median was established for anchor point heights of webs containing *S. avenae* in Conventional areas with symptomatic BYDV (*Figure 6.7.*). The greater variability in anchor point heights where there was *S. avenae* present in the webs was found in the top 25%. No *S. avenae* were identified in sheet webs of the Conventional areas where no symptomatic BYDV was identified.

Table 6.2: Significant predictors to the response anchor point height (cm). Interactions of T. tenuis *and Linyphiidae with Aphididae causing Barley Yellow Dwarf Virus (BYDV) in* H. vulgare. *(n = 289, R-sq - 42.51%). (* relates to significant with α <0.05).*

Continuous Predictor	**Coefficients**	**Standard Error Coefficients (SE Coeff)**	***T***	***P***	**VIF**
Number of Aphididae Exuviae in Web	0.1531	0.0224	7.56	0.001*	2.36
Number of *S. avenae* in Web	0.771	0.288	1.80	0.039*	2.56
Number of *T. tenuis*	-0.2230	0.0904	-1.98	0.021*	1.88
Plant Density (N°m^{-2})	0.1754	0.0595	2.85	0.004*	2.46
Wind Speed (kmh^{-1})	0.332	0.0989	3.04	0.001*	2.74

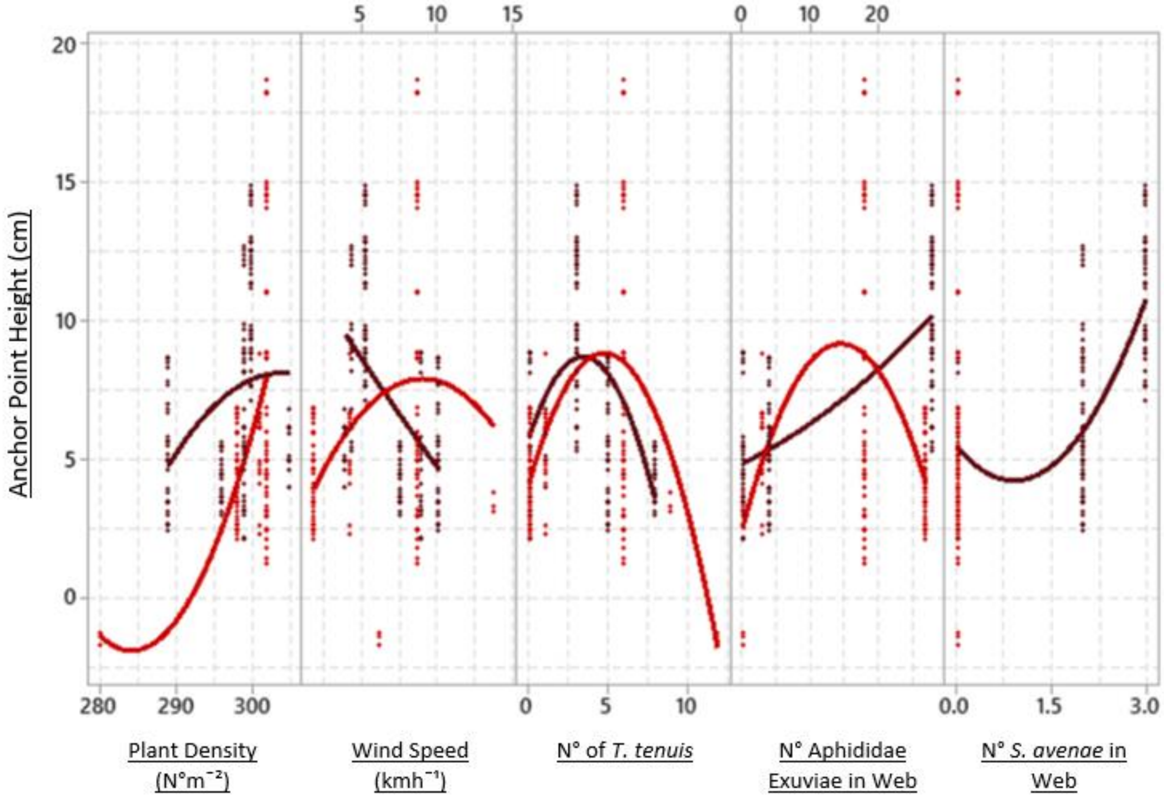


Figure 6.8: Matrix plot with quadratic regression and intercept fitted for anchor point height (cm) with plant density (N°m^{-2}), wind speed (kmh^{-1}), number of T. tenuis*, number of Aphididae exuviae in web and number of* S. avenae *in web. Interactions of* T. tenuis *and Linyphiidae with Aphididae causing Barley Yellow Dwarf Virus (BYDV) in* H. vulgare. *(n = 289, R-sq - 42.51%). (Conventional with Symptomatic BYDV* H. vulgare *= Dark Red, Conventional with No Symptomatic BYDV* H. vulgare *= Red).*

An open, upward parabola was found for the interaction between plant density and anchor point height within the Conventional plot where no BYDV *H. vulgare* was recorded (*Figure 6.8.*), showing anchor point height tended to become higher as *H. vulgare* density increased. The same held for the areas were BYDV *H. vulgare* existed, however, a maximum vertex was reached as the plant density reached three hundred. Little quadratic regression existed for Conventional BYDV when wind speed was investigated against anchor point height, the trend shown to be negatively linear. A maximum vertex was reached for Conventional where asymptomatic BYDV was identified, where anchor point peaked at 7.9 cm when wind speed was 8.9 kmh^{-1}.

For the numbers of *T. tenuis* recorded, both Conventional samples (containing and not containing BYDV affected *H. vulgare*), open downward parabolas existed where the smaller and greater number of *T. tenuis* gave the lower anchor point heights. A maximum vertex was identified when anchor point height in Conventional asymptomatic BYDV was investigated against the number of Aphididae exuviae in the web. Weak regression was exhibited for the same dependent variable when BYDV was identified within Conventional. Due to no *S. avenae* recorded in webs of Conventional asymptomatic BYDV *H. vulgare*, no regression existed for these terms. A steep open upward parabola shows that the anchor point height increased, as greater numbers of *S. avenae* were observed in the web, in areas of BYDV.

Table 6.3: Correlations of independent variables measured in the field with the dependant variable anchor point height (cm). Interactions of T. tenuis *and Linyphiidae with Aphididae Causing Barley Yellow Dwarf Virus (BYDV) in* H. vulgare. *(* relates to significant with α <0.05).*

	(Rho)	***P***	**n**
BYDV Symptomatic *H. vulgare* Density (N°m^{-2})	0.367	0.001*	289
Mean Plant Height (cm)	0.177	0.003*	289
Number of Aphididae Exuviae in Web	0.437	0.001*	289
Number of *S. avenae* in Web	0.346	0.001*	289
Plant Density (N°m^{-2})	0.339	0.001*	289

BYDV symptomatic *H. vulgare* density, mean plant height, number of *S. avenae* and Aphididae exuviae in web and *H. vulgare* plant density were significantly positively correlated to anchor point height measured in Conventional areas of symptomatic and asymptomatic BYDV *H. vulgare* (*Table 6.3.*).

6.5.3.3. Thread Length

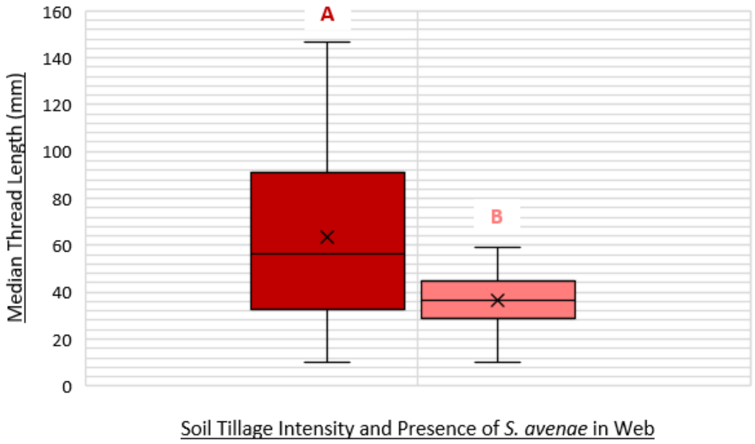


Figure 6.9: Median thread length (mm) for Conventional with Symptomatic BYDV H. vulgare *and presence of* S. avenae *inside webs. Interactions of* T. tenuis *and Linyphiidae with Aphididae causing Barley Yellow Dwarf Virus (BYDV) in* H. vulgare. *(df = 1, Adjusted for ties H - 16.74, P - 0.001, n = 158). (Yes* S. avenae *in web = red, No* S. avenae *in web = Pink). (Yes* S. avenae *in web (n = 121), No* S. avenae *in web (n = 37)).*

The significantly longer median (56.3 cm) was identified for threads spun for webs that had captured *S. avenae* (*Figure 6.9.*), the data skewed in a positive upward trend.

Table 6.4: Significant predictors to the response thread length (mm). Interactions of T. tenuis *and Linyphiidae with Aphididae causing Barley Yellow Dwarf Virus (BYDV) in* H. vulgare. *(n = 289, R-sq - 43.42%). (* relates to significant with α <0.05).*

Continuous Predictor	**Coefficients**	**Standard Error Coefficients (SE Coeff)**	***T***	***P***	**VIF**
Number of Aphididae Exuviae in Web	1.489	0.162	9.09	0.001*	1.47
Number of *T. tenuis*	-1.599	0.854	-1.87	0.049*	2.55
Wind Speed (kmh^{-1})	-2.477	0.881	-3.58	0.007*	1.90

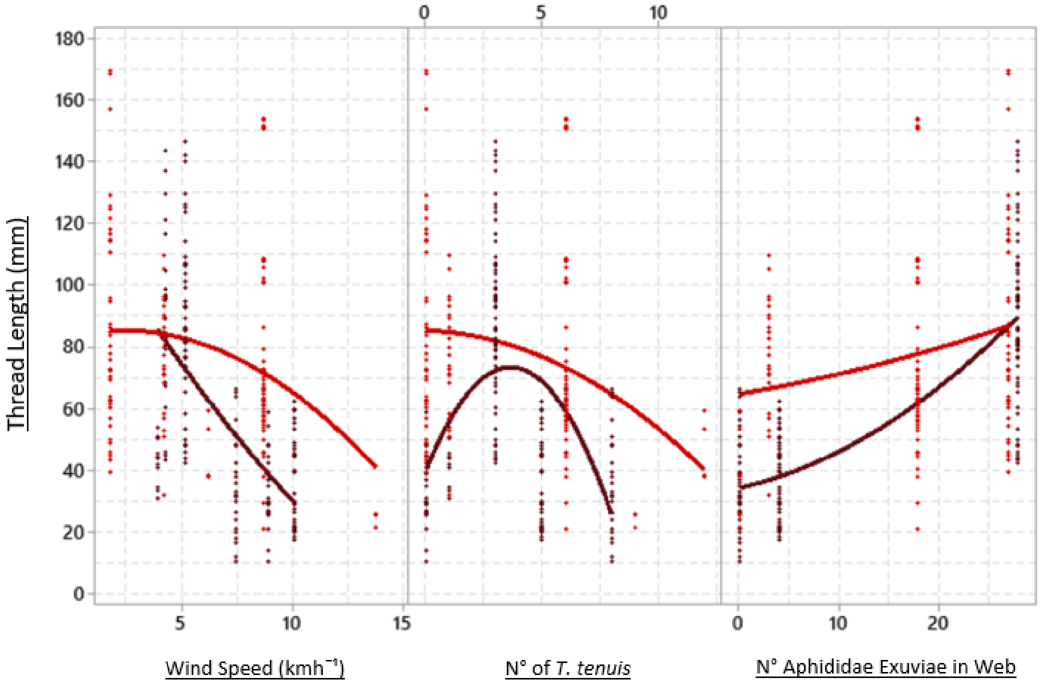


Figure 6.10: Matrix plot with quadratic regression and intercept fitted for thread length (mm) with wind speed (kmh^{-1}), number of T. tenuis *and number of Aphididae exuviae in web. Interactions of* T. tenuis *and Linyphiidae with Aphididae causing Barley Yellow Dwarf Virus (BYDV) in* H. vulgare. *(n = 289, R-sq - 43.42%). (Conventional with Symptomatic BYDV* H. vulgare *= Dark Red, Conventional with No Symptomatic BYDV* H. vulgare *= Red).*

When thread length was analysed with wind speed and number of *T. tenuis* recorded, within the areas of Conventional that did not contain symptomatic BYDV *H. vulgare*, a similar trend of weak quadratic regression was identified (*Figure 6.10.*). A wide-open parabola here showed the maximum thread length was found when wind speed and number of *T. tenuis* measured were at their lower value. Only negative linear regression was observed for wind speed against thread length for areas that contained BYDV. A step downwards open parabola exhibited a maximum vertex where a maximum thread length was reached when three *T. tenuis* were recorded in areas of BYDV *H. vulgare*. Weak regression was seen when numbers of Aphididae exuviae were observed within the web in the Conventional areas free of symptomatic BYDV and containing symptomatic BYDV. Minimum vertex suggested thread length increased as numbers of Aphididae exuviae increased in the web.

Table 6.5: Correlations of independent variables measured in the field with the dependant variable thread length (mm). Interactions of T. tenuis *and Linyphiidae with Aphididae causing Barley Yellow Dwarf Virus (BYDV) in* H. vulgare*. (* relates to significant with α <0.05).*

	(Rho)	***P***	**n**
Mean Plant Height (cm)	0.539	0.001*	289
Mean *T. tenuis* Abdomen Length (mm)	0.300	0.001*	289
Number of Aphididae Exuviae in Web	0.600	0.001*	289
Number of *T. tenuis*	-0.136	0.017*	289
Plant Density (N°m^{-2})	0.293	0.001*	289
Wind Speed (kmh^{-1})	-0.477	0.001*	289

The variables of number of *T. tenuis* recorded and wind speed were significantly negatively correlated to thread lengths measured (*Table 6.5.*). Thread length within the sample areas of both Conventional that incorporated symptomatic and asymptomatic BYDV *H. vulgare* was significantly positively correlated to mean plant height, mean *T. tenuis* abdomen length, number of Aphididae exuviae within the web and plant density.

6.5.3.4. Web Area

Table 6.6: Correlations of independent variables measured in the field with the dependant variable web area (mm^2). Interactions of T. tenuis *and Linyphiidae with Aphididae causing Barley Yellow Dwarf Virus (BYDV) in* H. vulgare*. (* relates to significant with α <0.05).*

	(Rho)	***P***	**n**
Mean Plant Height (cm)	0.570	0.001*	78
Mean *T. tenuis* Abdomen Length (mm)	0.298	0.008*	78
Number of Aphididae Exuviae in Web	0.669	0.001*	78
Wind Speed (kmh^{-1})	-0.477	0.001*	78

Four dependant variables measured were significantly correlated to web area measured in both the symptomatic and asymptomatic BYDV *H. vulgare* areas (*Table 6.6.*). Mean plant height, mean *T. tenuis* abdomen length and number of Aphididae exuviae within the web were significantly positively correlated to web area, while wind speed was significantly negatively correlated.

6.6. Discussion

6.6.1. General Discussion

Barley yellow dwarf virus (strain PAV-A), was identified in all three samples, tested from each sample plot. It can, therefore, be concluded the *H. vulgare* was infected by the virus by vectors in the form of direct feeding *S. avenae* that had been found throughout the *H. vulgare* fieldwork in GS 61 - GS 65 and GS 87 - GS 91 in late growth stages of *H. vulgare* (*Table 5.1.1. & Section 5.1.6.2.2.*).

Mean anchor point height was significantly higher in Conventional areas with BYDV symptomatic *H. vulgare* (*Figure 6.6.*). Romero & Harwood (2010), through analysing Linyphiidae seasonal activity and Opatovsky *et al.* (2016), investigating web height differentials in *T. eastivum* in Israel, recognised that an increased web height is more likely to capture a specific array of prey which includes Aphididae. This is because the Aphididae can aerial disperse by the reproduction of alate morphs and cereal Aphididae dwelling in high canopies of *H. vulgare* at later growth stages, to benefit from leaves in high monosaccharide content (Goggin, 2007; Westwood & Stevens, 2010). The highest web found in the Conventional area was at >14 cm. Bell *et al.* (2002) and Davey *et al.* (2013) suggest that a sheet web found at this height may not be spun by *T. tenuis*, instead perhaps by a larger Linyphiidae such as *Frontinella communis*, a species that was noted in the g-vac sampling of the main field. The variation identified with the mean anchor point heights for both Conventional and Conventional BYDV, signifies the choice of distinctly different strata at each location (Romero & Harwood, 2010; Sanders & Platner, 2007). One *T. tenuis* occupied a web in the Conventional area and four within Conventional BYDV, all within webs spun at a height of 3 - 6 cm, showing as previously discussed in fieldwork, *T. tenuis* preference for an above-ground habitat (Bell *et al.,* 2002; Obrycki & Harwood, 2005; Sunderland & Samu 2000) (*Section 5.1.6.1.2.*). Webs of one Conventional area of no BYDV, were identified in the furrows of the soil (*Figure 6.6*.). Due to the above, mean temperatures experienced in the summer months, the furrow width had increased due to shrinkage in the soil from moisture loss (*Section 5.1.6.2.2.*). Such webs as shown by Diehl *et al.* (2013) and Rybac (2007) are unlikely to capture cereal Aphididae, being a greater distance from the crop canopy, suggesting the web was not spun as a result of cues from this prey species (Gan *et al.* 2015; Welch *et al.,* 2013; Winder *et al.,* 2013).

Rodríguez & Gamboa (2000), Rodríguez & Gloudeman (2011) and Welch *et al.* (2013) discuss the possibility that a stimulus of a higher degree of *S. avenae*, due to cues of movement of high *S. avenae* density or from alate morphs, suggest Linyphiidae may have responded by constructing webs at a higher aspect (*Figure 6.7. & Table 6.3.*). The success of these webs of a greater height can be communicated by number of *S. avenae* observed in the upwards open parabola (*Figure 6.8.*). The *S. avenae* were found in webs >9 cm. With no alate *S. avenae* observed, it appears these *S. avenae* were knocked from higher vegetation. Winder *et al*. (2013) discuss that *S. avenae* 'fall off' from a cereal crop is associated with high densities, especially later in a cropping season. Agabiti *et al.* (2016) agree, explaining a dropping from a host plant may be deliberate, initiated by high densities or could be accidental through physical disturbance. The maximum wind speed had reached 14 kmh^{-1} in a Conventional BYDV sample, however, Gish *et al*. (2012), explained that wind speed of this level is unlikely to dislodge *S. avenae* from direct feeding. Heavy rain, discussed by Parry (2013), can initiate dropping of *S. avenae*, though, at sampling here, no recent rain had been recorded (Met Office 2018). Agabiti *et al.* (2016) and Winder *et al.* (2013) noticed high densities drove dropping behaviour of Aphididae through g- vac sampling. However, it appears Aphididae density (with higher mean of five *S. avenae* in the 1m^2 sample) did not seem to reach values that could be considered high, with Winder *et al.* (2014) finding a mean of 3.2 *S. avenae* per tiller within a *T. aestivum* crop of the equivalent sample time. Higher than mean temperatures were present at this GS, as discussed earlier in 2017 / 2018 fieldwork sampling (*Section 5.1.6.2.2.*). Brabec *et al.* (2014) and Ma & Ma (2012) explain that cereal Aphididae drop due to high temperatures, which allows thermo-regulation of their body systems.

No significant difference was identified for length of support threads between the two areas. Yet, thirty-five webs for Conventional and forty-three for Conventional BYDV were counted. It appears that a far greater abundance of webs was created in areas with BYDV symptomatic *H. vulgare*. The greatest activity of Linyphiidae and *T. tenuis* was in the Conventional BYDV areas and support thread length spun can be used as a measurement for this activity (Borges & Brown, 2001; Harwood *et al.,* 2003; Toft, 1987). This clearly shows a greater degree of web-spinning was undertaken, due to a stimulus indicating *S. avenae* presence (Blackledge *et al*., 2002; Mortimer *et al,* 2016; Welch *et al.,* 2013) (*Figure 6.5*.). This can be confirmed again with the greater thread length alluding to the greater web area found where *S. avenae* was present in the web (*Figure 6.9*.). The stark difference in the number of webs from each GS, may be an indication of a continual presence of *S. avenae* in the areas where BYDV symptomatic *H. vulgare* was identified. Mehrparvar *et al*. (2013) comment that dispersal is important in the creation of meta-populations, key to their survival due to death of previous local sub-populations, suggesting the likelihood that an Aphididae presence would not persist within the later growth stages in the same location. Ma & Ma (2012) comment that the propensity to disperse, is increased with Aphididae who have the potential to greatly damage the host in a limited time, with cereal Aphididae noted within this category. However, *S. avenae* were found in webs at both sampling periods (GS 61 - GS 65 and GS 87 - GS 91). It appears that a population had remained at these sites, wing polyphenism not occurring, which may be due to weakened fecundity and fitness shown to be affected by high temperatures.

It may be that *S. avenae* occurrence was sporadic in the Conventional area, with little dispersal activity. This may be a reason why patches of BYDV symptomatic *H. vulgare* were noted as confined to distinct areas. D'Arcy & Domier (2000) and Moore *et al.* (2011) discussed that isolated cases of alate vector can cause sporadic BYDV. It was noted that it is difficult for *T. tenuis* to respond to a stimulus of increased prey abundance, without movement of alate prey. It may be that *T. tenuis* and Linyphiidae were within the area and increased web height occurred due to local cues of *S. avenae* presence, vegetation disturbance, for example, or colour differentiation of *S. avenae* and *H. vulgare* (Glover, 2013; Japyassú & Laland, 2017) (*Figure 6.7.*). Harwood *et al.* (2004) hypothesise that *T. tenuis* responds to the similar micro-habitat cues as cereal Aphididae and *T. tenuis* were simply in the 'right place at the right time'. This accords with plant height and plant density significantly positively correlated to anchor point height, thread length and web area (*Table 6.3., Table 6.5. & Table 6.6.*) It can be viewed from the evidence that *S. avenae* presence causing BYDV in *H. vulgare*, can be identified as being the main driver in increased Linyphiidae activity (*Table 6.3.*).

Plant physiognomy played an important role in web construction (Dennis *et al.,* 2001; Gómez *et al.,* 2016; Stenchly *et al.,* 2011) (*Table 6.3*. & *Figure 6.6*.). The greater plant density was found within the Conventional BYDV, it may be a healthy *S. avenae* centred within this area for a continual phloem supply to allow feeding sinks to be formed and accelerate growth rate (Goggin, 2007; Lombaert *et al.,* 2006) (*Section 2.2.6.1*.). It may seem that plant height and density was driving *S. avenae* reproduction. Much plant material is required to allow *S. avenae* to amass the amino acids required for protein molecules to be assembled, for growth and subsequent reproduction (Dixon, 1987, Gullan & Cranston, 2010) (*Section 2.2.6.1*.). Plant height influenced the data in the opposite direction of number of *S. avenae* found within the web for BYDV Conventional (*Figure 6.5. & Figure 6.8*.). Greater plant height was found in Conventional with no BYDV occurrence (*Figure 6.5*.). BYDV was shown by Paulmann *et al*. (2018) to interrupt the function of the sieve cells, usually regulating pulses of electro-potential waves which transfer nutrients to outer organs of the plant (leaves) and leads to necrosis and stunted growth. Additionally, a protein accumulation forms a 'wound gum' which aims to repair the role of the sieve cells, requiring further energy to amass (Labandeira & Prevec, 2014; Paulmann *et al.,* 2018).

Number of Aphididae exuviae in web was significantly positively correlated to anchor point height, thread length and web area (*Table 6.3., Table 6.5. & Table 6.6*.). Sixteen more exuviae were noted inside webs of the Conventional BYDV area than Conventional. Alderweireldt (1994) and Muratori *et al.* (2008) explain that Aphididae exuviae within a web does not correlate to Aphididae density at the exact moment the exuviae fall into the web. In times of a predation threat, leaving exuviae can act as a ruse while Aphididae vacate (Muratori *et al.* 2008). This may explain why exuviae were found in webs with no presence of *S. avenae* in Conventional non-BYDV areas. Dispersal of apterous morphs, (walking) is considered by Oliver *et al*. (2007) and Zhang *et al.* (2016) to be slow and laboured, therefore may be close to exuviae formed from instar development. Eberhard *et al.* (2006), Oelbermann & Scheu (2002) and Pekár (2000) explain that exuviae may remain after *T. tenuis* has sucked out the main body of Aphididae. It may seem that exuviae can show direct predation, in this case at a higher rate in Conventional BYDV than Conventional (*Figure 6.8*.). Number of exuviae within the web exhibited a greater response of Linyphiidae in Conventional BYDV by increasing thread length at a greater rate, perhaps signifying a definite response from *T. tenuis* to spin larger webs, the decision to do so commits energy to lay the silk threads over an extended area (Obrycki, 2007; Simonneau *et al.,* 2016; Thorbek & Bilde, 2004). (*Figure 6.10*.). It may be expected that a higher degree of debris, non-soft body appendages, would be left behind after consumption, or as Blackledge *et al*. (2011) and Rodríguez & Gloudeman (2011) discuss, the prey is wrapped in flexible flagelliform silk before consumption, evidence that exuviae have been wrapped in silk may be apparent if contents of *S. avenae* had been removed (Harwood *et al.,* 2004). Further microscopic analyses would be able to verify this (Dondale, 2000; Eberhard *et al.,* 2006; Harwood *et al.,* 2004).

The increase in thread length with *S. avenae* within the web was identified as a potential predator response to a high density of *S. avenae* (*Figure 6.9*.). Bonte *et al.* (2011), Harwood *et al.* (2003), Mclachan & Wratten (2003) and Samu *et al*. (1996) show that *T. tenuis* remain within one web-site, spinning new larger webs in the same vicinity if its purpose in prey capture has been successful. Halley *et al.* (1996) and Welch *et al.* (2013) explain a limiting factor in Linyphiidae survival is web-site security in beneficial areas. The increase in thread length, forming larger webs, in later growth stages, with cereal entering the later ‘dough’ growth stage, food scarcity is a concern, which may indicate that Conventional BYDV areas were prime web-sites with accessibility to a prey source.

The greater number of *T. tenuis* were identified within the Conventional asymptomatic BYDV area where the greater number of smaller webs were recorded at a lower aspect, with low web occupation (*Table 6.5*. & *Figure 6.6.*). The increased *T. tenuis* presence may be due to dispersing Linyphiidae, frequently vacating and web-spinning small webs of low energy outlay to locate the idealistic web-site to benefit survival. Opatovsky *et al.* (2016) and Samu *et al.* (1996) describe the spinning of smaller webs alongside a high rate of web-abandonment may have been due to a lack of prey stimuli. The poor web-site location of these areas, lowers the threat of intra-specific predation, promoting *T. tenuis* tolerance in neighbouring web-weaving (Harwood & Obrycki, 2005; Houser *et al.,* 2016; Opatovsky *et al.,* 2016; Samu *et al.*, 1996).

Optimum anchor point height was reached when the number of *T. tenuis* was found to be five for Conventional and three for Conventional BYDV (*Figure 6.5. & Figure 6.8.*). The greatest thread length was additionally found when *T. tenuis* numbers were lower in Conventional than Conventional BYDV (*Figure 6.10.*). This suggests some intra-specific behaviour altering *T. tenuis* web construction. This concurs with findings of Craig (1987), Houser *et al.* (2016), Nentwig & Heimer (1987), Segoli *et al*. (2004), and Toft (1987) who comment that larger-bodied *T. tenuis* may create larger webs to enforce dominance and enhance prey capture capability (*Table 6.5. & Table 6.6.*). There was a higher degree of web occupation by *T. tenuis* in webs of increased height. This accords with Gan *et al.* (2015) who identified a higher degree of web invasion of sheet webs at a greater height, due to the possibility that a higher abundance of prey can be seized.

Even though wind speed may have not dislodged *S. avenae*, it affected *T. tenuis* activity in sites chosen for web-weaving and the quantity of silk spun (*Figure 6.8., Figure 6.10., Table 6.3., Table 6.5. & Table 6.6.*). Within Conventional with no BYDV, anchor point height appeared to increase alongside wind speed, then declined once wind speed reached 8 - 9 kmh^{-1} (*Figure 6.8*). Wind speed is discussed to be the main variable that dictates the initiation of Aphididae flight to allow fast dispersal and within 0.3 to 2 ms^{-1} (4 - 7.6 kmh^{-1}), wind speed is low enough not to cause damage to a web, of a high aspect, rendering it functionless (Brunetta & Craig, 2010; Craig, 2003; Reynolds & Reynolds, 2009). It can be shown that within Conventional, when the wind speed was lower, webs were spun at a higher aspect to intercept aerial *S. avenae*, though no alate morphs were recorded. As discussed in fieldwork, Linyphiidae evolution has adapted to deal with environmental disturbance by the creation of the beta-sheets in major ampullate silk (Blackledge *et al.,* 2011; Craig, 2003) (*Figure 2.3a, Section 2.1.2.1.*, *Page 10 & Section 5.1.6.1.2.*). Linyphiidae can create a greater abundance of beta-sheets in a fibril by increasing the tension of the silk as it is spun (Blackledge *et al.,* 2011). This is a costly process, and building webs at a lower aspect in the field may allow protection from the wind speed, without incurring the energy cost of creating a web to withstand high wind speeds (Benjamin *et al.,* 2002; Segoli *et al.,* 2004). However, may not have the same potential to ensnare prey as webs spun at a higher level.

It is noted that the low soil moisture percentage (17 - 21%) was below field capacity of 40 - 45% for the high clay percentage, Hanslope soil, for Conventional and BYDV Conventional areas (Ashman & Puri, 2002; Cranfield University, 2017) (*Section 2.2.2. & Section 3.1.3.2.*). There were no significant differences in mean soil moisture percentage for both areas tested. It can be viewed that the drought-stressed *H. vulgare* weakened a defence system, caused the rapid collapse of the sieve cells induced by the virus (Dorokhov *et al.,* 2014; Paulmann *et al.,* 2018; Reddy *et al.,* 2009) (*Section 2.2.6.2.*). Davis *et al.* (2015) and Mornhinweg (2011) state that moisture stress weakens phloem tissue, allowing less turgor pressure to restrict Aphididae direct feeding, thus creating a negative feedback loop. Low soil moisture may have increased BYDV infection rate; however, it is shown not to directly relate to *T. tenuis* predator dynamics with *S. avenae* (Nachappa *et al.,* 2016) (*Section 2.2.6.2*).

Aphididae capture rate was considered low, with Harwood *et al.* (2003) showing the potential of Linyphiidae webs to capture 0.5 *A. pisum* per cm^2. Harwood *et al.* (2003) identified that significantly more Aphididae (mean 0.81), were collected from webs constructed by *T. tenuis* at sample sites (78.5 cm^2) compared with 0.56 being identified outside of webs. Brabec *et al*. (2014) and Valenzuela & Hoffmann (2014) identified peak *S. avenae* abundance in *H. vulgare* is at heading stage and ear emergence (GS 51 - GS 59) (*Table 5.1.1.*). The low green index of *H. vulgare* at the later growth stages, time of sampling, may explain Aphididae decline, as direct feeding is difficult due to thickened cellular walls and biochemical change in phloem, altering its nutritional availability (AHDB 2018; Ma & Bechinsk, 2008; Valenzuela & Hoffmann, 2014) (*Section 2.2.6.2.*). However, *S. avenae* were present, with one alate morph identified in a web, its morphogenesis a product of low food availability (Perry, 2013; Price *et al.,* 2011). The *S. avenae* identified may be a small remnant of a previous population, Watanabe *et al.* (2018), discuss the fitness of survival of small Aphididae population able to withstand low food availability.

6.6.2. *H. vulgare* 2017 / 2018 Season - BYDV Confined to Conventional Tillage

BYDV symptomatic *H. vulgare* were only found in the Conventional area and one small cluster in the margin between the tillage intensities of Direct Drill and Conventional (*Section 4.2.*). It may be due to the higher degree of straw that is incorporated into the soil with the deepened cultivation of Conventional (*Section 3.1.3.4.*). This finding agrees with Kennedy *et al.* (2010), who found that within minimum tillage, 48% fewer Aphididae were identified, relating to 78% fewer BYDV instances observed than with conventional plough. It was identified that straw may support a reservoir of natural enemies. Diehl *et al.* (2013) and Summers *et al*. (2004) showed that straw deters alate Aphididae morphs from colonising a crop by disturbing their landing potential, with key sites partially covered with the mulch. This may explain why low alate morph vectors were not dispersing into the Direct Drill area, a change in straw abundance was identified (*Section 5.1.6.2.1.*). There was no clear observation of BYDV incidences spreading into Direct Drill area in later growth stages.

BYDV sustains in winter on marginal vegetation (grasses) of an agricultural field, transferred by over-wintering *S. avenae* by direct feeding (Falks & Duffus 1981; Marshall & Rashed, 2014) (*Section 2.2.6.2.*). It may be possible to determine if the *S. avenae* vector over-wintered in a Conventional hedgerow after 2017 harvest to create morphs which subsequently dispersed BYDV into the Conventional area of the field as *H. vulgare* developed through the growth stages of 2018. Ben-Issa *et al.* (2017) and Perry

(2013) describe Aphididae dispersal as somewhat passive, whereas Reynolds & Reynolds (2009) suggest there may be some control using lift and drag to cues in wing movement. However, Crossley *et al.* (2017) explained the difficulty in forming a link between 'sink', over-wintering site, and 'source' of BYDV infected crop, due to short life spans providing little genetic traceability and non-linear flight patterns. It can be concluded that it is almost impossible to establish whether an over-wintering *S. avenae* alate vector came from a soil tillage intensity in the previous cropping season or from the field studied at all.

BYDV was not observed in any soil tillage in the previous sampling season in a field-wide inspection, however, small pockets may have existed, symptomatic *H. vulgare* occurring sporadically and less easily observed (Chapman *et al.,* 2013; Eberhand *et al.,* 2006) (*Table 5.1.1.*). *S. avenae* abundance was greater in the 2016 / 2017 cropping season than 2017 / 2018, hypothesised to be due to high temperatures (*Section 5.1.6.2.2.*). Furthermore, within May sampling of 2017 / 2018 no greater abundance of *S. avenae* within the web or found by g-vac sampling was noted in sample areas <50 m from BYDV sampled areas. The high temperatures of the 2018 season causing drought stress to the *H. vulgare* rather than *S. avenae* abundance may be the over-riding factor to succumb to BYDV, unable to prevent the embedment of the virus thus enduring sieve cell function failure (Dorokhov *et al.,* 2014; Reddy *et al.,* 2009) (*Section 2.2.6.2.*).

Within the later growth stages of cropping season 2017 / 2018, the greater *S. avenae* number was identified in the Direct Drill Managed areas with little dispersal activity occurring across the main field (*Section 5.1.6.2.2.*). *A. myosuroides*, greater abundance in Direct Drill Managed, are shown by Lutemen *et al.* (2013) and Milner (2002) to produce 'green bridges', to allow a colony of Aphididae to persist within early growth stages (Ball & Bingham, 2003). The lower intensity of soil tillage of Direct Drill Managed enabling such weeds to prevail as reduced destruction of the seed from cultivators (Berry *et al.,* 2014; Melander *et al.,* 2013; Peigné *et al.*, 2014). (*Section 2.2.4. & Section 5.1.6.2.2.*)

With no BYDV cases within Direct Drill Managed, it can be seen that the alate vectors remained concentrated in the Conventional area and were unable or not inclined, to move across the Direct Drill tillage area in the centre of the field (*Figure 3.5b*, *Section 3.1.3.3., Page 51*). Lombaert *et al.* (2006) identified fitness as a driver to disperse and Mehrparvar *et al.* (2013) agreed, stating alate morphs have a reduced fecundity baseline due to accruing wings. Perhaps the *S. avenae* population in Conventional had weak heritable fitness. Higher dispersal rates into the Direct Drill area may have occurred if temperatures for this season were at normal mean and optimal for Aphididae fecundity (Asin & Pons 2001; Brabec *et al.,* 2014; Zhang *et al.,* 2016). However, without drought stress, *H. vulgare* may have been able to resist continued direct feeding. The latent period is twelve to twenty-four hours of continuous direct feeding to transfer the BYDV particulates in a high enough quantity for infection (Dorokhov *et al.,* 2014; Paulmann *et al.,* 2018; Reddy *et al.,* 2009) (*Section 2.2.6.2*.).

6.7. Final Discussion - Interactions of *T. tenuis* and Linyphiidae with Aphididae Causing Barley Yellow Dwarf Virus (BYDV) in *H. vulgare*

That Linyphiidae and *T. tenuis* increased in web-spinning and choose prime web-sites, can be observed as a predatory response to the presence of *S. avenae* within the later growth stages, and not directly correlated with conditions of habitat (landscape heterogeneity). This addressed the first and third aims linking to biological control (*Section 6.2.1*.). Predatory capture through the extended phenotype of the web had ensnared *S. avenae*. *T. tenuis* is noted to be a positive biological control agent aiding reduction of potential vectors of BYDV. BYDV took hold in the Conventional area and was unable to spread across to the neighbouring soil tillage intensity of Direct Drill. It could be a function of the cultivation methods of inverting straw or it may relate to the climatic factors of the 2017 / 2018 season.

Chapter Seven

7.0. Method Development of Glasshouse Experiments

7.1. Introduction

To trial aspects of the whole field within a controlled environment is a useful way to clearly identify *T. tenuis* interactions with all features of a habitat. Enclosing a smaller version of the field enables external variables, e.g. weather and sheltered areas, to be removed and variables that are of key interest, e.g. plant height, to be clearly defined.

Four laboratory experiments were designed to investigate the relationship between *T. tenuis* and prey interactions in differing levels of soil tillage. Prototyping and learning were involved in the design of each experiment until a final method was robust and the design accepted to adequately house the experiment. The final experiments form the focus of the following Chapters:

- **Chapter Eight - Effects of Soil Tillage Intensity on Prey Capture by *T. tenuis* in Mesocosms of *H. vulgare***

This examines *T. tenuis* predatory behaviour throughout the growth of *H. vulgare* in a simulation of the three tillage intensities with the addition of Aphididae nymphs at germination of *H. vulgare*.

- **Chapter Nine - Effects of Primary and Secondary Cultivation on *T. tenuis* Behaviour Under Controlled Experimental Conditions: A Mesocosm Experiment**

T. tenuis behaviour was assessed in simulations of primary and secondary cultivations of the three tillage intensities of the NIAB field, in controlled conditions without the addition of prey.

- **Chapter Ten - *T. tenuis* Behaviour with Different Soil Tillage Intensities and Different Abundances of Cereal Aphididae: A Microcosm Experiment**

Microcosms were established with *T. aestivum* under simulations of the three soil tillage intensities of the NIAB fields. A range of cereal Aphididae abundances were used and *T. tenuis* predatory behaviour recorded.

- **Chapter Eleven - Choice Chambers for Selection of Upright Stubble and Furrow With or Without the Presence of Aphididae**

Observations were recorded of *T. tenuis* utilisation of upright stubble or a furrow, with dimensions corresponding to the three tillage intensities of the NIAB field, with and without the addition of cereal Aphididae.

7.2. Husbandry and Measuring *T. tenuis* and Prey

7.2.1. Collection of *T. tenuis*

It was planned to establish a *T. tenuis* colony for laboratory experiments, to provide eggs through instars to adulthood, thus offering enough adult *T. tenuis* for all glasshouse experiments. Vegetation material including soil, grass and straw formed the base of an artificial habitat (terrarium) created in a plastic container (81 (l) x 40 (w) x 51 (h) cm) to support *T. tenuis* activity. One hundred holes, 1 mm in diameter, were drilled into the plastic top to provide ventilation. Thereafter, a collection of *T. tenuis,* via g-vac from hedgerows of a *T. aestivum* field at Myerscough College (SD 49867 39959), was put into the plastic container. Females, males and spiderlings were incorporated to replicate the field and allow courtship and reproduction to occur. The box was maintained on a window ledge in the laboratories at Myerscough College to provide adequate daylight. Temperature was monitored.

However, it became clear, due to incidences of cannibalism and evidence of escape that a larger more sophisticated terrarium was required to allow *T. tenuis* the space to acquire sufficient territory. This entailed further materials and time which was ultimately deemed unnecessary, when after several g-vac visits to the hedgerows surrounding Myerscough College farmland, it became clear that there was an adequate supply of *T. tenuis* for glasshouse experiments available throughout the year. The terrarium was cleared of *T. tenuis*. Vegetation was replaced, for the terrarium to become a stabilising habitat to acclimatise g-vac captured *T. tenuis,* for twenty-four hours before being measured and placed into the glasshouse experiments. This was essential as the heightened sensory system of *T. tenuis* responds to any level of disturbance via a tendency to disperse or hide within vegetation (Diehl *et al.,* 2013; Holland & Oakley, 2007; Mader *et al.,* 2017). *T. tenuis* (up to n = 45) were starved to ensure parity in levels of satiation. Moisture was applied to the soil, if dry, as a source of liquid for the *T. tenuis*.

After consideration, only adult female *T. tenuis* were used in glasshouse experiments (apart from choice chamber trials), due to reported behavioural differences in web construction between the genders, females expelling a greater energy expenditure to web-build (Peng 2013, Rojas, 2011; Segoli *et al.,* 2004). Further, interactions between male and female (courtship) was felt to distract from the principal of the trials, for example for Chapter Ten the aim was to understand if soil intensity affected web-spinning at different abundances of Aphididae (*Section 2.1.3.4.*).

7.2.2. Measuring *T. tenuis* within Glasshouse Experiments

It was determined that measuring *T. tenuis* dimensions required increased accuracy beyond the methodology used in the fieldwork trials. This was to explore more detailed relationships between body dimensions and web-building behaviour in the micro/mesocosms, but was a difficult task to achieve due to the small nature of the *T. tenuis* and its tendency to flee as a result of disturbance (Kovac & Mackay, 2009; Pommeresche, 2002).

T. tenuis were left in a Petri dish until becoming motionless in a web (*Figure 7.1a*). This allowed cephalothorax and abdomen length to be measured to 0.01 mm with a KERNTM© Compound Microscope OBS-1 Binocular Achromat at resolution x4 and Measuring Magnifier Achromatic lens 10x multi-scale, graticule optical glass 8LED Scale TT10X50-1, instead of only to 0.1 mm within the field (*Figure 7.1b - c*). A calibration guide of graticule to mm was obtained by Microtec Microscopes© 2018 TEC LTD (Kasumovic & Jorden, 2013; Miller, 2007: Prenter *et al.,* 2010; Rodríguez & Gloudeman, 2011; Tanasevitch, 2014).

Figure 7.1a - c: Measuring a female T. tenuis *for glasshouse experiments. a = Female* T. tenuis *in Petri dish for measurement. b & c = Female* T. tenuis *abdomen and cephalothorax length measured in Petri dish with KERNTM© microscope and graticule.*

T. tenuis mass was measured in a pre-measured test pot to 0.0001 g with the use of a Kern® ABS Analytical Balance. *T. tenuis* were randomly assigned to habitat of experiment (mesocosm, microcosm or choice chamber) after abdomen and cephalothorax length and mass had been determined.

7.2.3. Culture of *S. avenae* and *M. dirhodum*

S. avenae and *M. dirhodum* were required for several laboratory experiments to be able to analyse predatory behaviour of *T. tenuis* in controlled conditions. *S. avenae* nymphs were incorporated into the mesocosms for Chapter Eight, *M. dirhodum* nymphs were required for the microcosm experiment of Chapter Ten. Whereas, *M. dirhodum* adults were used as prey in the choice chamber trial (*Chapter 11.0.).*

An Aphididae culture of one hundred *S. avenae* and *M. dirhodum* were acquired from the Insectary of the Rothamsted Institute. It was agreed that the culture would contain a mixture of adults and nymphs of both species capable of parthenogenesis alate morphs, to aid representation of the field. *S. avenae* were orange coloured morphs (*Section 2.2.6.1.*). Once arrived, *S. avenae* and *M. dirhodum* were placed within pre-grown Synteger® Propino™ *H. vulgare* in a glasshouse to allow development of numerous colonies in plastic containers (81 (l) x 40 (w) x 51 (h) cm) (*Figure 7.2a - c*). The crop health was continually monitored to ensure enough food material was provided.

Figure 7.2a - c: a= H. vulgare *growing in a glasshouse to support a colony of cereal Aphididae. b=* S. avenae. *c =* M. dirhodum. *(Aphididae circled in yellow).*

7.2.4. Measuring *S. avenae* and *M. dirhodum*

Identifying the mass of the Aphididae introduced into glasshouse experiments was an important variable to measure. First, this was to help identify the stage of Aphididae development, i.e. the greater the mass the likelihood the Aphididae would be in its final instar, thus able to reach the parthenogenesis stage more rapidly and contribute to Aphididae abundance. Second it has been shown that the greater the mass of Aphididae, the increased presence allowed *T. tenuis* a greater chance of its detection (Japyassú & Laland, 2017; Rodríguez & Gamboa, 2000) (*Section 2.2.6.1.*).

Nymphs, used in experiments of Chapters Eight and Ten, were collected from the colony formed on the *H. vulgare* leaves. It proved difficult to manoeuvre the nymph from leaf to the sample pot (for measurement) without causing harm, as a nymph stylus is anchored to vegetation to allow continuous feeding (Parry *et al.,* 2006; Parry, 2013) (*Section 2.2.6.1.*). To weigh each nymph on a cut section of *H. vulgare* took much time with inaccuracies occurring in the small mass obtained from each nymph. It was viewed that weighing the number of nymphs destined for each replicate in the experiment would suffice and give an indication whether greater mass of the nymphs collectively triggered increased *T. tenuis* activity and accelerated parthenogenesis rate. Therefore a section of leaf was found with the correct number of nymphs for each experiment and masses determined to 0.0001 g with the used of the Kern® ABS Analytical Balance on small pieces of pre-weighed *H. vulgare* entered into a pre-weighed sample pot (*Figure 7.3.*).

Figure 7.3: Mass determination of six M. dirhodum *nymphs (circled in yellow) weighed on a* H. vulgare *leaf for microcosms of soil tillage and cereal Aphididae abundance,* H. vulgare*.*

Agabiti *et al.* (2016) and Gish *et al.* (2012) showed that, adult Aphididae have a decreased penetration depth than nymphs, due to an increased tendency to rapidly detract from direct feeding of phloem and respond rapidly to predator threat (*Section 2.2.6.1.*). For experiments in Chapter Eleven, adult *M. dirhodum*, over 2 mm in body length, were used and collected from the colony and transferred to a pre-weighed sample pot. From here each adult had mass determined prior to addition into the habitat without the need of a *H. vulgare* leaf, as adults were easier to transfer between materials.

7.3. Preparations for Chapter Eight - Effects of Soil Tillage Intensity on Prey Capture by *T. tenuis* in Mesocosms of *H. vulgare*

7.3.1. Introduction

A natural continuation from fieldwork was to simulate the conditions represented in the field within controlled conditions. This allowed the control of independent variables, for example temperature, and excluded large scale variables like the effects of wind. The data collected from such an experiment contributed to the results of the fieldwork, allowing greater understanding of *T. tenuis* interactions within tillage practices. From this, mesocosms with differing intensities of soil tillage, replicating the field were therefore designed and a robust method for running of the experiment developed.

7.3.2. Method Development

7.3.2.1. Lubricant

Two lubricants, petroleum jelly and olive oil, were thinly applied to the inside of a prototype container. The lubricant was theorised to prevent attachment discs, of support threads, from the piriform gland from being able to adhere to the plastic container as the container was an artefact outside of the NIAB field (Benjamin & Zschokke, 2004; Harwood *et al.,* 2003; Shaw *et al,* 2005) (*Figure 2.3c., Section 2.1.2.1., Page 11*). This did not work as intended and attachment did occur. It was felt that this, and the fact that lubricant could not be applied uniformly, could cause bias. *T. tenuis* are shown to be incredibly sensitive to touch and may utilise points of less lubricant (Bradley, 2013; Roberts, 1993) (*Section 2.1.1.*). Therefore, lubricant was not used further in the method development.

7.3.2.2. Soil Choice

To test conditions as closely as possible, soil of the Hanslope series was collected from relevant tillage plots at the Cambridge field site. Using Hanslope series soil took into consideration the soil micro- and macro-biology and chemistry of the field site (Cranfield University, 2017; Paul, 2015) (*Section 2.2.2. & Section 3.1.3.2.*).

7.3.2.3. *T. tenuis* Population Density Determination

To determine the population density of *T. tenuis* for use in the mesocosm trials, fieldwork results were used. The highest number of *T. tenuis* recorded in GS 33 - GS 37 from the *H. vulgare* crop (2016 / 2017 season) was 32 m^{-2}, which gave 312 cm^2 space for each *T. tenuis* (*Table 5.1.1., Section 5.1.3.1., Page 82*). This is similar to the area provided for one Linyphiidae in the web-building trials of Benjamin & Zschokke (2003) which was 328 cm^2. As the area of the proposed mesocosm was 1521 cm^2, five *T. tenuis* were placed into each and therefore had 304 cm^2 of individual space (Benjamin & Zschokke, 2003; Harwood *et al.,* 2003; Pasquet, 1999; Shaw *et al.,* 2005). In this first mesocosm trial, adult females were used, as female *T. tenuis* propensity to web-spinning is greater than males (Rojas, 2011; Rundus *et al.,* 2011; Segoli *et al.,* 2004) (*Section 2.1.3.2.*).

7.3.2.4. Prey Choice

The first mesocosm were set up with *Drosphila melanogaster* (Common Fruitfly) as prey due to its ease of cultivation. *D. melanogaster* is viewed to be a food source of *T. tenuis*, its aerial movement allowing its capture within a web. De Keer & Maelfait (1988), Harwood & Obrycki (2005) and Oelbermann & Scheu (2002), used *D. melanogaster* as prey for Linyphiidae in laboratory trials, due to their rapid production rate under limited resources (Nouhaud *et al.,* 2018). Bonte *et al.* (2008), Turney & Buddle (2019) and Zschokke & Herberstein (2005) discuss the benefits of using live prey in trials when monitoring Linyphiidae behaviour. It enables the field to be closely replicated and Linyphiidae web-spinning to be attributed to possible cues that moving prey can exhibit.

Winged ebony body *D. melanogaster* were cultured in an incubator at 21 ^{o}C on a protein-based medium with added yeast (both acquired from Blades Biological^{LTD}) (Blades Biological 2017). The larvae hatched were the food source for the prototype mesocosm. Five *D. melanogaster* larvae from the cultures were placed into each mesocosm at GS 21, germination and emergence of tillers, to produce a colony in line with the growth of the cereal seeded. This provided *T. tenuis* with live prey which further recreated the field environment.

In two trials, the population growth of *D. melanogaster* was weak, low fecundity (inbred from colony) observed as the main factor (Klick *et al.,* 2016; Lachaise *et al.,* 1988; Novoseltsev *et al.,* 2005; Telonis-Scot *et al.,* 2006). Furthermore, with the rapid and chaotic flight of *D. melanogaster*, it was difficult to pinpoint where cues of their existence were intercepted by *T. tenuis* (Barnes *et al.,* 2008; Bartholomew *et al.,* 2015). Consequently, low numbers of *D. melanogaster* were observed in webs and after analysis there was little correlation between prey presence and *T. tenuis* movement. The aim of this research was to identify how differing soil tillage intensity may affect *T. tenuis* behaviour toward cereal pests, of which *D. melanogaster* is not one. Therefore, it seemed sensible to learn from the trials with *D. melanogaster* as prey and create further glasshouse experiments which used Aphididae as prey. This change represented prioritisation of prey that would most likely be sourced by *T. tenuis* in the NIAB fields. *S. avenae* is a crop pest which can damage crops and is the main vector for BYDV-PAV (*Section 2.2.6.2. & Chapter 6.0.*). It was important to understand the relationship of *T. tenuis* and *S. avenae* under controlled conditions.

7.3.2.5. Soil Tillage Intensity

It was essential to replicate soil tillage intensity in the mesocosm accurately as this was the fundamental difference in the field trials in Cambridge. There were three distinct tillage stages that were required to be replicated: the sub-soiler for primary cultivation, the disc harrow for secondary cultivation and the creation of the seedbed. Several tools from the Myerscough workshop were applied until it was noted which tools to what extent would bring the desired effect. Straw and upright stubble was required to be included in the mesocosms to further simulate the field. The most reliable way to carry this through was to collect straw and upright stubble, dry to regain integrity and then correspond the field values of these variables to the dimensions of the mesocosms, to precisely replicate the conditions presented by the differing soil tillage intensities in the field.

Furrows were identified to support *T. tenuis* activity, in the NIAB fields in Cambridge, by allowing a definite break in the soil to create anchor points (*Section 4.3.11.1. & Section 5.1.5.2.*). This was an important addition to the mesocosms to allow the glasshouse trials to mirror field trials. Again, furrows dimensions were to replicate the field and be formed from accessible tools as accurately as possible to the creation of the furrows in the field by the disc harrow.

7.4. Preparations for Chapter Nine - Effects of Primary and Secondary Cultivation on *T. tenuis* Behaviour Under Controlled Experimental Conditions: A Mesocosm Experiment

7.4.1. Introduction

In Direct Drill the abundance of upright stubble and straw (which remained on the surface due to zero-till) allowed numerous small webs to be woven within the straw or near / on the apex of the stubble (*Figure 7.4b & Section 5.1.5.1*.). Volunteer crop, abundant in this soil tillage, was also acquired as an attachment material for threads (*Section 5.1.5.1.3*.). Within Conventional and Direct Drill Managed primary cultivation, the effects of the sub-soiler removed much upright stubble and straw from the surface and decreased the potential for this material to be used in web construction (*Section 3.1.3.4*.).

The effects of the tillage practices (primary and secondary cultivation) however, created soil clods in the landscape (*Section 4.3.11.2*.). These were employed as additional anchor materials for support threads in web-building, in fieldwork, alongside patches of crop residues left on the surface (*Figure 5.1.3, Section 5.1.5.1.2., Page 91*). The degree in height of soil clods differed between Conventional and Direct Drill Managed, because of different depths of soil attained by the cultivators (*Figure 7.4a & Section 5.1.5.1.2.*)

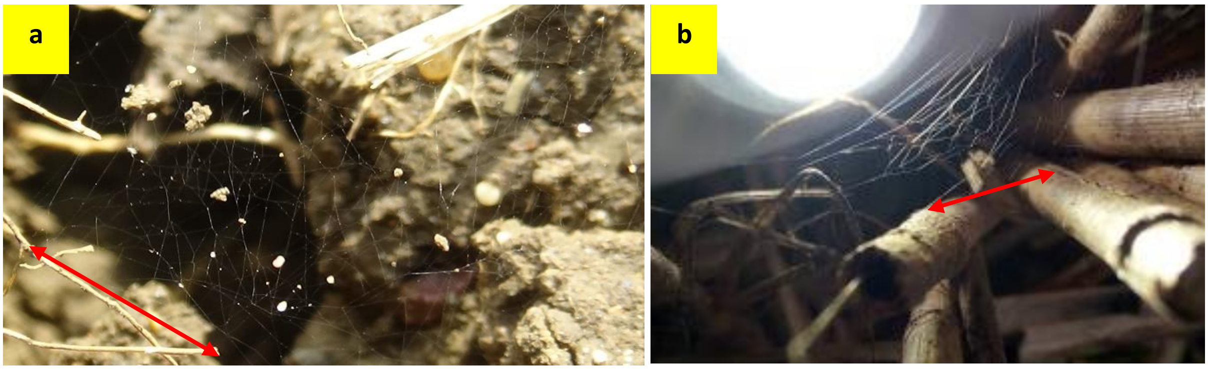


Figure 7.4a & b: Sheet webs after primary cultivation. H. vulgare *2017 / 2018 season. a = Conventional. Web anchored to soil clods. Elevated view. (Red arrow = 21.2 mm). b = Direct Drill. Web anchored to upright stubble. Elevated view. (Red arrow = 15.6 mm).*

To examine *T. tenuis* web-building behaviour more closely within these cultivations, further glasshouse trials were conducted post primary and secondary cultivation. Specific objectives were to measure web formations after a few days and compare the effects of soil tillage intensity.

7.4.2. Method Development

7.4.2.1. Experiment Set-Up

These trials used the same soil in plastic containers as the previous trial, where mesocosms investigated the effect of soil tillage intensity on *T. tenuis* activity with *S. avenae* as prey (*Section 7.3.*). This required thought into how the mesocosms were going to be cleared and thus able to support a different glasshouse experiment.

Within each mesocosm all contents apart from the soil were removed, it was felt too costly in time and resources to re-collect soil from the NIAB sites. Plus, cultivations in the field are carried out in the same soils as the harvested crops. Contents removed included the *H. vulgare* crop, *T. tenuis*, prey of *S. avenae* and any *T. tenuis* activity in bridging threads and webs. Further upright stubble and straw used to replicate the soil intensities in the previous mesocosm were also removed, leaving the soil bare in the containers. Hand searching for additional prey occurred as an extra precaution to ensure no prey remained within the mesocosms (for example, *S. avenae* having fallen off the *H. vulgare* leaves as they were taken out of the mesocosm). The mesocosms were covered with muslin squares and left for one day. This was to allow any *S. avenae* remaining to be found and removed. When *S. avenae* were found trapped in the muslin twenty-fours later, it showed that hand searching alone was not an adequate tool to remove all Aphididae prey. It was key that no prey remained which could alter *T. tenuis* web-building activity, having identified in fieldwork that a prey source is likely to alter *T. tenuis* decision of where to locate a web and its formation (*Section 5.1.5.2.*).

No vertical structures, e.g. in upright stubble or other crop simulations of any significant height were present in the mesocosms, so it was unnecessary to construct a surround here which if not structured correctly would weaken the integrity of the habitat. The surface of the mesocosms therefore consisted of the same plastic used to cover the sides of the earlier mesocosms of Chapter Eight. The plastic was stretched over the plastic containers providing a taut surface free of any creases. This took time to perfect but was identified as a necessity as creases could become a possible artefact for anchor point location. The plastic was pin-pricked fifty times with a needle in a ‘zig-zag’ pattern. The prototype suffered from condensation, therefore the number of needle holes made in the plastic was increased to one hundred establishing circulation throughout the area of the mesocosm.

7.4.2.2. Soil Clods

Soil clods were an important aspect to incorporate, due to this formation shown as seemingly vital for attachment of threads in the Conventional and Direct Drill Managed areas. Twenty-nine soil clods were incorporated into Conventional, and twenty-six for Direct Drill Managed. These numbers represented field-related mean number and clod height identified in primary cultivation of *H. vulgare* (2017 / 2018 season). This feature allowed greater attachment of threads due to the increase in complexity of the landscape architecture, an element that was required to be conserved within these trials (*Section 5.1.5.1.3.*). It was important that variation in clod height representing the cultivations within the field was incorporated, as it was seen the use of the clods as anchor sites was due to the different levels that they bring to the environment (Bell *et al.,* 2002). Therefore, soil clods were formed matching heights collected from the relevant cultivated areas of the field to the nearest 0.1 cm (*Figure 7.5a & b*).

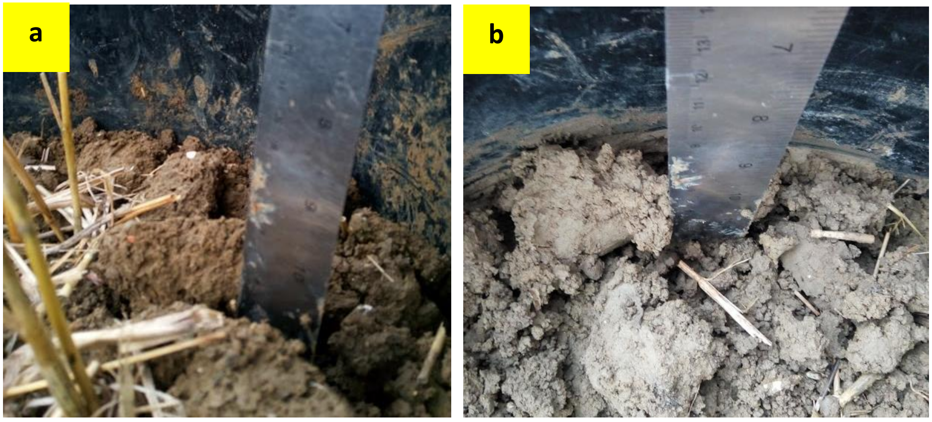


Figure 7.5a & b Clod height measured to ensure correct height is reached for an investigation of primary and secondary cultivation mesocosms. a = Conventional. b = Direct Drill Managed.

For secondary cultivation clod heights, as with primary cultivation, varied and represented a height that was measured after secondary cultivation in the respective soil tillage area of the *H. vulgare* (2017 / 2018 season). Correlating to abundance recorded from the same season, twenty-nine clods were incorporated for Conventional and twenty-four for Direct Drill Managed.

7.4.2.3. Volunteer Crops

Volunteer crops, germination of seeds deposited by the harvester, were present in small numbers in areas sampled in the field (*Figure 5.1.4., Section 5.1.5.1.2., Page 91*). These were not incorporated into the mesocosms as they were not seen as a key material left on the soil surface after cultivation. Volunteer crops would be difficult to replicate in the mesocosms as they are due to grain randomly deposited by heavy machinery, adding unaccountable variation also (Ball & Bingham, 2003; Morris *et al.,* 2010).

7.5. Preparations for Chapter Ten - *T. tenuis* Behaviour with Different Soil Tillage Intensities and Different Abundances of Cereal Aphididae: A Microcosm Experiment

7.5.1. Introduction

In fieldwork, it was shown that *T. tenuis* abundance and web building increased in areas of high Aphididae density (*Section 5.1.6.2.1.*). From this an idea for a controlled glasshouse experiment was identified where different Aphididae densities could be introduced in each soil tillage intensity (Conventional, Direct Drill Managed and Direct Drill) to analyse *T. tenuis* predator dynamics and gain further evidence (from a controlled environment) on Aphididae abundance and *T. tenuis* behaviour.

7.5.2. Method Development

7.5.2.1. Choice of Cereal Crop

It was first proposed that the cereal of choice should be *H. vulgare* due to the fieldwork analysis centred on this cereal due to its continuity of field site in the NIAB trials (*Section 5.1.5.*). *H. vulgare* had also proved to be a successful cereal to early glasshouse trials. Fast growth had enabled weekly *T. tenuis* and *S. avenae* behavioural analysis following the growth of the crop (*Chapter 8.0.*). However, within the prototype and early glasshouse trials *H. vulgare* showed poor growth compared to the prototype trials of *T. aestivum,* theorised due to the higher glasshouse temperatures (range 29.3 ^{o}C - 35.6 ^{o}C midday). The heat appeared to affect the habitat within smaller microcosms more than larger mesocosms with the clay loam of Hanslope soil, clay micelles locking in water molecules, thus unavailable to root penetration (Ashman & Puri, 2002; Paul, 2015) (*Section 2.2.2.*). *H. vulgare* is particularly sensitive to extremities of heat and water availability due to inbred seed adaptions in accelerating germination, lowering tolerance to water stress (McFarland *et al.,* 2014). *T. aestivum* has a slower growth cycle which allows time to tolerate and excel through conditions of stress (*Section 2.2.1.*).

Due to little differences observed of *T. tenuis* activity between *H. vulgare* and *T. aestivum* measured in the NIAB fields, it was beneficial to run an experiment with *T. aestivum* as the cereal of choice (*Section 4.4.*). The important factor of the experiment was to gain a high percentage of plant growth within the microcosms to simulate the field and allow an adequate level of landscape heterogeneity to facilitate potential Aphididae growth and *T. tenuis* predatory behaviour.

7.5.2.2. Choice of Aphididae and Density

S. avenae was considered due to its role as a crop pest previously incorporated into early mesocosms of *H. vulgare*. However, *M. dirhodum* was chosen as the growing colony of *S. avenae* was kept for the larger mesocosms to investigate possible BYDV - PAV incidences. *M. dirhodum* had colonised in the glasshouse habitats grown from the original Rothamsted colony and was viewed as having similar nutritional value as *S. avenae* for *T. tenuis* and similar potential reproductive fitness (Bilde & Toft, 2008; Parry, 2013; Price *et al.,* 2011; Toft, 1987). Further, *M. dirhodum* was present in the g-vac samples and observed in *T. tenuis* webs in the fieldwork (*Section 5.1.5.2.4*.).

As the aim of this experiment was to focus on whether Aphididae density had a higher degree of influence on *T. tenuis* rather than soil tillage alone, it was considered paramount that different numbers of *M. dirhodum* were added to the microcosms. *M. dirhodum* were added as nymphs, as in the mesocosm experiment cultivating *H. vulgare*, as this experiment continued throughout the growth stages (GS) of *T. aestivum* and represented the field as closely as possible (*Chapter 8.0*.). Within the field at time of crop emergence, Aphididae activity was mainly in nymph form until vegetation density increased to enable accelerated parthenogenesis (*Section 5.1.6.2.1*.). The number of *M. dirhodum* nymphs added to the microcosm was considered and it was sensible to have a control microcosm that contained no *M. dirhodum* nymphs (Agabiti *et al.,* 2016; Beck & Toft, 2000). The number of Aphididae to place into a further microcosm treatment was carefully considered, to choose a density of *M. dirhodum* greater than the field average, but also realistic. Many experiments reported within the literature describe incorporating Aphididae at abundances relevant to data gathered from fieldwork, this corresponded to a value of two for the microcosms (Beck & Toft, 2000; Madsen *et al.,* 2004). Nine *M. dirhodum* nymphs were first trialled for the greater value; however, it became clear that the growth potential due to parthenogenesis was too great and unrealistic to mirror a field simulation. Therefore three times mean field value (six *M. dirhodum*) was chosen as this was observed as an extreme field value in a small area of the habitat, and from the literature was viewed as not an unrealistic scenario (Agabiti *et al.,* 2016; Madsen *et al.,* 2004).

7.6. Preparations for Chapter Eleven - Choice Chambers for Selection of Upright Stubble and Furrow With or Without the Presence of Aphididae

7.6.1. Introduction

These experiments were designed to give *T. tenuis* a choice between habitat features measured from fieldwork and in a second set of experiments, prey availability became an element of choice. This glasshouse experiment took much consideration and many prototypes trialling several ideas were implemented before commencement of the final experiments.

7.6.1.1. Choice Chambers for Selection of Upright Stubble

Fieldwork was carried out in *H. vulgare* after primary and secondary cultivation and before glyphosate application and drilling of seeds for 2016 / 2017 season and 2017 / 2018 season (*Figure 7.6a - c & Table 5.1.1.*). Differences in straw and upright stubble were identified in each field sampling period (*Figure 5.1.1. & Figure 5.1.2., Section 5.1.5.1.2., Page 90*).

Figure 7.6a-c: After secondary cultivation, H. vulgare *2017 / 2018 season. a = Conventional, b = Direct Drill Managed, c = Direct Drill.*

As a significant difference was seen in mean straw mass and upright stubble density from the field sampling, it was desirable to remove other variables and analyse how *T. tenuis* interacted with the straw and upright stubble more closely (*Section 5.1.5.1.3. & Section 5.1.5.1.4.*).

7.6.1.2. Choice Chambers for Selection of Furrow

Fieldwork after cultivations (primary and secondary) and use of direct drill of *H. vulgare* cropping in season 2016 / 2017 and 2017 / 2018 season, identified limited upright stubble and straw in the Conventional and Direct Drill Managed plots (*Figure 5.1.1. & Figure 5.1.2. & Section 3.1.3.4.*). However, spider web activity was observed within the furrows in the soil left behind by the seed drill and before germination of crop (*Figure 7.7a & b & Section 5.1.5.2.2.*).

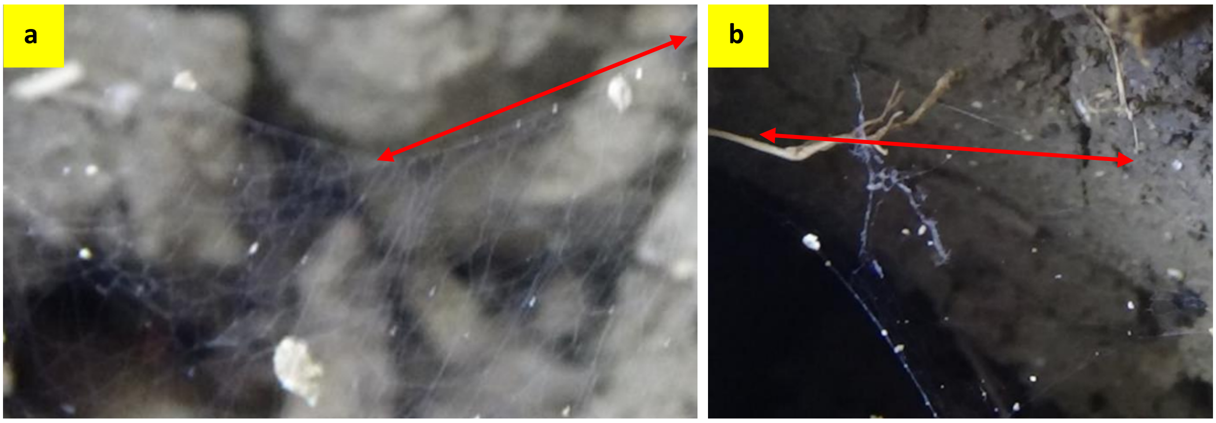


Figure 7.7a & b: Sheet web within a furrow in the Conventional area after drilling. H. vulgare*, 2017 / 2018 season. a = Elevated view. (Red arrow = 22.3 mm). b = Elevated view (Red arrow = 35.9 mm).*

Glasshouse analysis to explore whether sub-soiling impedes or promotes web-building and potential prey capture was thought useful (*Section 3.1.3.4.*). Understanding whether upright stubble or furrows in the soil provide an enhanced environment for web construction would help to identify whether the intensity of soil tillage affects the prey potential of *T. tenuis*.

7.6.1.3. Addition of *M. dirhodum* to Choice Chambers

To examine the relationship between soil tillage and predatory behaviour of *T. tenuis,* key to understanding *T. tenuis* capacity for biological control, choice chambers needed to be set up with a selection of upright stubble / furrow and including the addition of the choice element of prey (Aphididae).

7.6.2. Methodology

7.6.2.1. Choice Chambers for Selection of Upright Stubble

7.6.2.1.1. Set-Up Design

Stability was required for upright stubble, so a material was needed to mimic the action of the soil in the field, anchoring the material and providing rigidity. Blue Tac® was the initial thought, fixing the base of the upright stubble to the plastic container. However, doubts arose whether *T. tenuis* would be inclined to anchor to this point, a feature not present in the field. A prototype was set-up with upright stubble attached with Blue Tac® to one side of the choice chamber and run for twenty-four hours with one male *T. tenuis* being incorporated. No attachment occurred to the Blue Tac® and was incorporated into the main choice chambers trial. Lubricant to prevent *T. tenuis* attachment to plastic was once again trialled, thoughts were that the hard plastic of the containers would potentially support a thicker, more uniform layer of lubricant, however attachment still occurred. Any web that was only attached to the plastic was removed from the results as the use of the internal materials, stubble and straw, was the key factor. Further, Aphididae were applied in later trials to permit comparison and were allowed to move around the container freely as potential prey. However, they could be entangled in any lubricant used.

7.6.2.1.2. Location of Choice Chambers

The trial was carried out in a workshop area where natural daylight is received through large windows. A prototype trial was set-up in the glasshouse which created condensation in the plastic boxes, which an increased number of drilled holes (1.5 mm diameter) did not alleviate. Excessive moisture within the habitats did not align with representation of an open-air field site and moisture lying on materials may have reduced *T. tenuis* ability to lay silk for anchor points. The constant temperature of the workshop ensured no condensation was produced.

7.6.2.2. Choice Chambers for Section of Furrow

The principle was identical to the previous choice chambers with selection of upright stubble, the only change was the choice element of the furrow, with this only established on one half of the habitat. It was noted that Direct Drill tilled area had a furrow, even if not as defined as the other tilled areas, due to the previous crop seedbed being undisturbed from the lack of tillage. Soil used in this trial was Hanslope Series soil taken from the corresponding tilled areas from NIAB Field B (*Figure 3.5b., Section 3.1.3.4., Page 51*). The dimensions of the furrows were related to data gathered after secondary cultivation and seed drilling of *H. vulgare* cropping season 2017 / 2018.

7.6.2.3. Abundance and Gender of *T. tenuis*

This glasshouse experiment presented a great opportunity, due to its quick turnaround and small nature of the habitat, to manipulate abundance of *T. tenuis* and incorporate different genders. This was to allow further investigation into how *T. tenuis* behaviour may alter in the presence of another *T. tenuis* of the same or different gender. This was to relate more information to the field results where elements of intra-specific competition were observed (*Section 2.2.2.1. & Section 5.1.5.*).

First, one female *T. tenuis* was placed into each soil tillage habitat. Then the trial was re-run with a single male adult *T. tenuis*, then with two adult female *T. tenuis*, followed by the addition of two adult male *T. tenuis* and finally a male and female adult *T. tenuis*. All five combinations of *T. tenuis* in gender and numbers mentioned above were replicated three times in each soil tillage. Intra-specific competition has been observed to alter *T. tenuis* behaviour which can translate to adjusting predatory behaviour (Prenter *et al.,* 2010; Samu *et al.,* 1996). For example, incorporation of two male or two female *T. tenuis* may promote competition for web-sites within the habitat. The addition of a male and a female may induce courtship behaviour as the principal goal rather than web construction (*Section 2.1.3.4*.). Examples of this were found in field sampling in areas where prey of *S. mosellana* and *S. avenae* were abundant (*Section 5.1.6.2.1.*). As only female *T. tenuis* had been used in the previous glasshouse trials, it was felt important to incorporate male *T. tenuis* into laboratory work to allow data collected under controlled circumstances to be analysed against equivalent data from the field (*Section 5.1.5.*).

7.6.2.4. *T. tenuis* Nutritional Requirements

For choice chambers that incorporated upright stubble as the variable of selection, a small piece of damp cotton wool was placed in the centre of the container to provide a source of moisture as *T. tenuis* are reported to obtain moisture from a material (e.g. soil or prey) (Zschokke & Herberstein, 2005).

For the experiment where furrow was the element being trialled, moist cotton wool was not incorporated, as *T. tenuis* are shown to use surface moisture from vegetation and the ground (Glime & Lissner, 2017). Soil kept at a given moisture content (30 - 35%), was adequate for *T. tenuis* needs in the twenty-four hour period of the trial and was comparable to the available water found in Hanslope soil (Paul 2015) (*Section 2.2.2*.). The percentage of soil moisture was difficult to keep consistent with the soil contained within a small environment, with no roots providing stability and no lower profiles to drain moisture away. A small pipette was used to drip water into several locations in the soil to allow soil moisture percentage to be relatively homogenous.

Within the choice chambers incorporating prey, *T. tenuis* destined for the experiment needed to be at a similar level of hunger to allow the potential influence of *M. dirhodum* to be equal. Sutherland & Samu (2000) showed enhanced hunger can increase *T. tenuis* receptors to the potential stimuli provided by prey. *T. tenuis* incorporated were therefore taken out of the artificial habitat which served as a place of transition between field and trial and were starved for twenty-four hours in individual Petri dishes with the same basic materials, three sticks, placed in each to provide web-building materials and a small piece of moist cotton wool (*Section 7.2.1.*). It was important not to induce additional stress on the *T. tenuis*.

7.6.2.5. *M. dirhodum* Abundance and Instar

Identifying *M. dirhodum* abundance and at what development stage to place them into the experiment took some deliberation. Since prey was acting here to potentially influence *T. tenuis* behaviour, any change in these two variables concerning *M. dirhodum* could significantly alter the results obtained.

Adults were added as they receive a larger predatory response from *T. tenuis* than nymphs, due to easier identification and increased nutritional content sensed by *T. tenuis* (Agabiti *et al.,* 2016; Madsen *et al.,* 2004). Any *M. dirhodum* identified over 2 mm in body length was classed as an adult, having reached final instar. Alate morphs were not incorporated, as significantly less alate morphs were identified in *T. tenuis* webs and on *H. vulgare* in all field sampling where Aphididae were present (*Section 5.1.6.1.2.*). As shown in fieldwork, the environment of soil tillage was most beneficial when no crop was present or was within an early GS (*Section 5.1.5.1. & Section 5.1.5.2.*). At this period, early Aphididae emergence was likely to be from apterous morphs. It was also felt that alate *M. dirhodum* would render the trial void as rapid dispersal could allow *M. dirhodum* to be in both sides and the trial would not represent a choice between conditions of soil tillage and prey.

It was desired that two adult apterous morph *M. dirhodum* would be incorporated into each habitat corresponding to data collected from GS 31 - GS 33 *H. vulgare* 2016 / 2017 season (*Table 5.1.1. & Section 5.1.5.2.*). This followed the set-up of other independent variables of the glasshouse experiments above, where the number relates to data in the field. Incorporation of only one *M. dirhodum* would have benefited the experiment, as there would then be a clear result that *T. tenuis* would end in the same side as the *M. dirhodum,* potentially allowing conclusions of Aphididae influence being drawn from this result. However, since other elements in the experiment corresponded to NIAB field data, two *M. dirhodum* were incorporated into each experiment, to allow *T. tenuis* the same opportunity to respond to a given Aphididae stimuli as in the field. To negate the fact that adding two Aphididae might upset the interpretation of the results, where it could be questioned whether *T. tenuis* was influenced by prey or landscape feature, *M. dirhodum* were applied to the habitat immediately after *T. tenuis* into the centre of the choice chamber. Where *M. dirhodum* were found in separate sides results were void.

7.7. Culmination

Considerable learning took place within the planning and set-up of each glasshouse experiment. Each thought process and experimental design error allowed robust experiments to be constructed where results collected were valid, fair and met the desired objectives. The following Chapters (*Chapter 8.0.* - *Chapter 11.0*.) outline the developed experiments.

Chapter Eight

8.0. Effects of Soil Tillage Intensity on Prey Capture by *T. tenuis* in Mesocosms of *H. vulgare*

8.1. Introduction

Following fieldwork, mesocosms were set up to observe the effects of landscape heterogeneity shown by soil tillage intensity. This was to investigate whether the increase in upright stubble or straw mass on a larger platform would directly promote *T. tenuis* activity, as in the early growth stages (GS) of fieldwork (*Section 5.1.6.2.1.*). Number of plants and height were measured to determine if levels of soil tillage affected plant development and if this impacted *T. tenuis* decision in web-weaving. This followed from later growth stages of *H. vulgare* in the field where greater plant height in Conventional affected placement of webs (*Section 5.1.6.2.2.*).

8.2. Aims and Specific Objectives

8.2.1. Aims

This experiment sought to address Research Aims 1 and 4 (*Section 1.2., Page 2*).

1. Identify the potential biological control by *T. tenuis* of Aphididae within different intensities of tillage in an arable crop.
4. Comprehend if a certain level of landscape heterogeneity affects *T. tenuis* ability to predate on Aphididae.

8.2.2. Specific Objectives

The following specific objectives set out to meet the aims for this Chapter:

- Measure *T. tenuis* behaviour in quantifying web size, height and instances of rappelling.
- Calculate Aphididae (*S. avenae*) abundance under differing intensities of soil tillage.
- Analyse whether different densities of Aphididae (*S. avenae*) affect *T. tenuis* actions.

8.3. Methodology

Mesocosms were set up as in Figure 8.1 and Figure 8.2a & b. The points below follow the sequence of events applied to create the experiment, which was trialled twice using the same method.

The cultivation machinery in the NIAB trials only affected the A-profile of the soil (0 - 25 cm). Therefore, soil samples (30 cm depth) were collected in 9000 cm^3 blocks. These, pre-tillage, were dug out at random sample points and placed into plastic trugs (40 L Volume) maintaining the original orientation of the soil profile. Expanding clay pellets (hydroponic balls) were used for the lower B-profile due to similarities with the sub-soil properties of Hanslope series. The use of hydroponics ensured no other soil properties disrupted the top layer of soil (Mascher *et al.,* 2003; Paul, 2015).

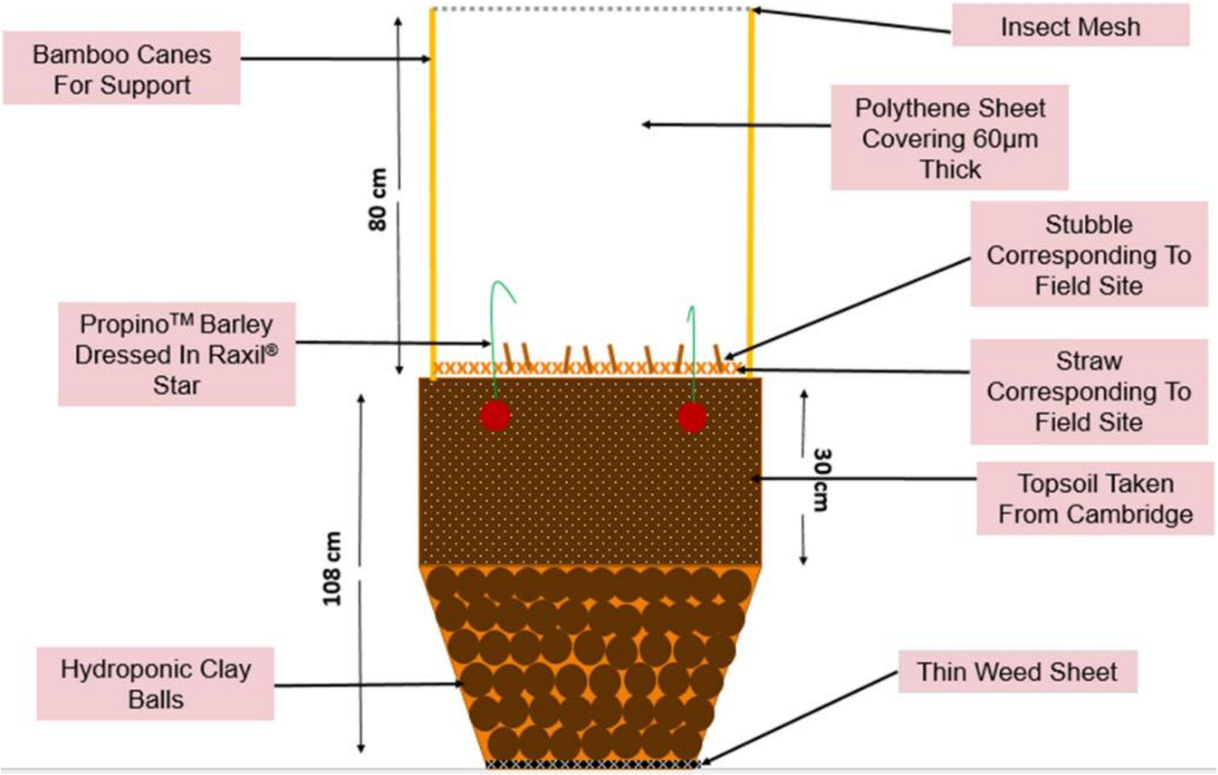


Figure 8.1: Schematic diagram for the elements that created the mesocosms for effects of soil tillage intensity on prey capture by T. tenuis *in mesocosms of* H. vulgare*.*

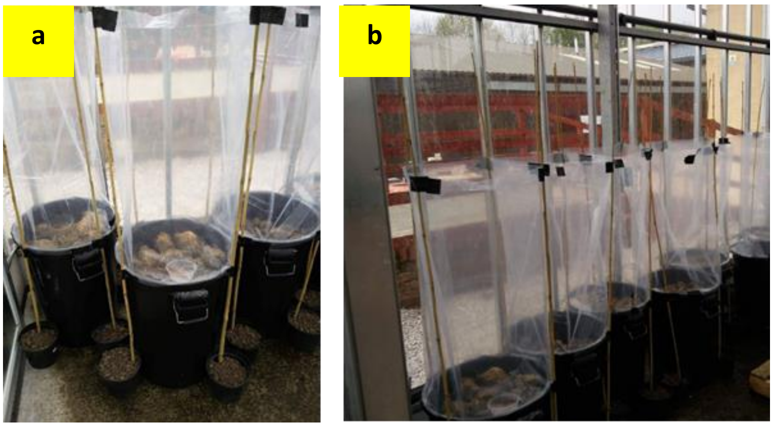


Figure 8.2a & b: Set-Up of mesocosm for effects of soil tillage intensity on prey capture by T. tenuis *in mesocosms of* H. vulgare*.*

Nine plastic containers were used (108 cm height x 44 cm diameter) for three replicates of each soil tillage. The containers were labelled 1 to 9 (1 - 3 represented Conventional tillage, 4 - 6 represented Direct Drill Managed and 7 - 9 represented Direct Drill). The mesocosms were arranged in a random generated number sequence to remove bias as it had been observed that areas of the glasshouse experience different temperatures which might affect *T. tenuis* web-building design (*Random.org, 2017*) (*Figure 8.3*). As the roots of *H. vulgare* can, at full growth, reach 70 cm in length, the containers had a depth greater than this (AHDB, 2015).

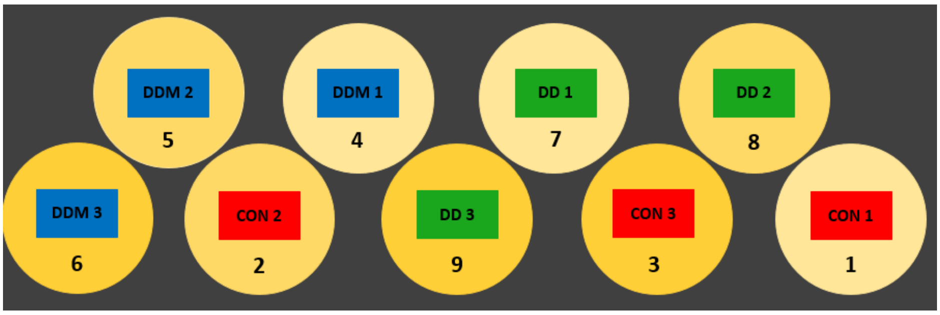


Figure 8.3: Schematic diagram of random arrangement of mesocosm for effects of soil tillage intensity on prey capture by T. tenuis *in mesocosms of* H. vulgare*. (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green).*

To recreate the action of the sub-soiler in the mesocosm, an inverted soil corer, 19” Chrome Tool Probe, was used (*Section 3.1.3.4.*). The implement penetrated to 25 cm in one straight line, down the centre to allow the sub-structure to be loosened. For Direct Drill Managed, penetration reached 20 cm in depth to portray its lightened cultivation in the field. To simulate the action of the disc harrow, a 3 cm diameter circular blade, Saxton TCT Circular Wood Saw Blade (300 mm x 30 x 60 teeth), was used. Teeth represented the notched blades of the Kelly Disc Harrow® used in Cambridge (*Section 3.1.3.4.*). The blade worked the soil by being pressed down to 2 cm depth and then rolled along the entire surface. This final action was the creation of two tramlines with the same circular saw, 15 cm apart, to mimic the seedbed. Direct Drill was imitated in all mesocosms by seeds being placed into the soil at 4 cm depth by a circular screw (Goldscrew® Woodscrews Double Self Countersunk (80 mm diameter)).

An irrigation system (polythene 4 mm piping) was set up with four drip lines in each container to water each mesocosm for five minutes, twice daily, controlled by Galcon DC1 6100®. The four drip lines were placed at opposite points, providing water distribution across the mesocosm. Soil moisture was measured in % water content with a Delta T Devices© HH2 Moisture Meter, moisture required to be in the correct parameters for Hanslope soil series. Available water for cereal crops, for the heavy clay content, noted to be 25% to 40%, between permanent wilting point and field capacity. (Ashman & Puri, 2002; Badalı́kova, 2010; Paul, 2015; Williams, 1979) (*Section 2.2.2., Section 3.1.3.2. & Section 6.3.1*.).

Furrows were identified to support *T. tenuis* activity, in the NIAB fields in Cambridge, by allowing a definite break in the soil to create anchor points (*Section 5.1.6.2.2.).* This was an important addition to the mesocosms to allow the glasshouse trials to mirror field trials (*Figure 8.4a* - *c*). Mean width and depth of the furrows measured in the field after drilling of *H. vulgare* in 2018, were reproduced in the mesocosms using a gardener's trowel.

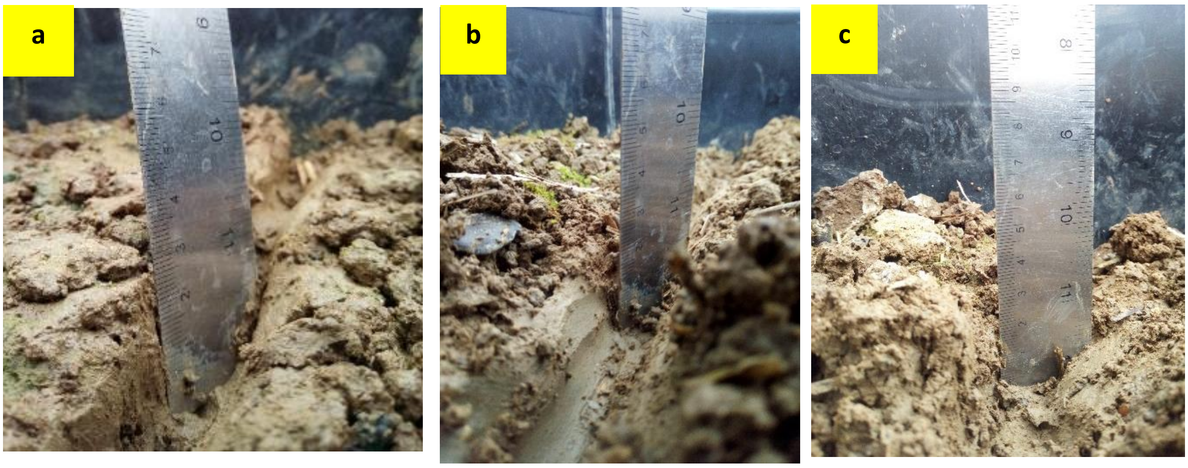


Figure 8.4a - c: Furrow creation in mesocosm for effects of soil tillage intensity on prey capture by T. tenuis *in mesocosms of* H. vulgare*. a = Conventional. b = Direct Drill Managed. c = Direct Drill.*

Straw and upright stubble were included in the mesocosms to further simulate the field. These additions corresponded with data collected from fieldwork, *H. vulgare* 2017 / 2018 season GS 11 - GS 15, of the different tilled areas and were quantified to match the dimensions of the mesocosm (*Figure 8.5a* - *c*) (*Table 5.1.1., Section 5.1.3.1., Page 82*).

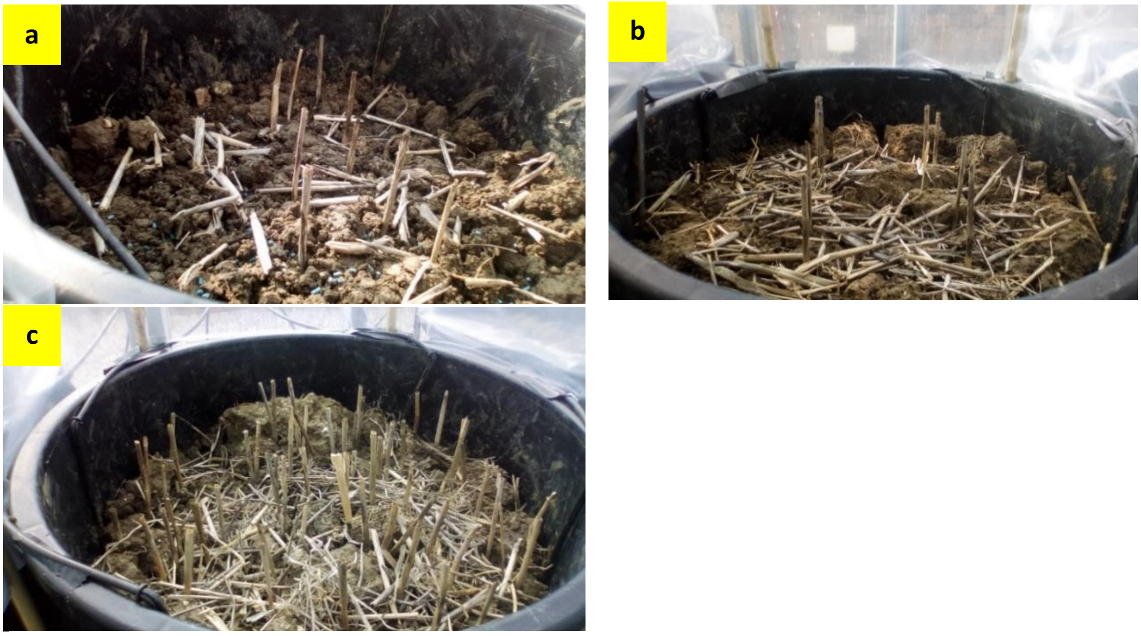


Figure 8.5a - c: Upright stubble and straw of mesocosms. Effects of soil tillage intensity on prey capture by T. tenuis *in mesocosms of* H. vulgare. *a = Conventional. b = Direct Drill Managed. c = Direct Drill.*

Fertiliser is used in the NIAB trials in the form of Omex© Liquid Suspension Fertiliser 3x Solution™. It was important to be consistent with this approach. Soil blocks were collected prior to the season's fertilisation application and thus it was deemed important to add a fertiliser simulation to aid the growth of *H. vulgare,* as in the field. Fertiliser application rate was informed from figures in the RB209, DEFRA Fertiliser Manual (AHDB, 2017). Data chosen related to medium / heavy clay soils with low rainfall (*Section 3.1.2. & Section 3.1.3.2.*) From this, 80 g nitrogen (N), 31 g sulphur (S) and 60 g phosphate (P_2O_5) were required ha^{-1}. Therefore, 1.28 g ammonium nitrate (NH_4NO_3), 1.70 g ammonium phosphate ($(NH_4)_3PO_4$) and 1.94 g ammonium sulphate ($(NH_4)_2SO_4$), formed from combining common salts, was added to each mesocosm before seeds were sown. *H. vulgare* was chosen due to the rapid growth of a spring variety in Field B in Cambridge, where sampling had taken place and analysis of *T. tenuis* activity had occurred in the field (*Sub-Chapter 5.1.*).

The *H. vulgare* seed chosen was Syngenta® Propino™ treated with the triazole fungicide Raxil® Star, active ingredients fluopyram, prothioconazole and tebuconazole. Propino™ is the variety used in the NIAB fields dressed with Redigo Pro®, also a triazole fungicide with active substances of prothioconazole and tebuconazole. In the field, seeds are planted 2 cm apart with a row spacing of 15 cm, giving a mean of 200 seeds m^{-2}, simulated in the mesocosm as in Figure 8.6.

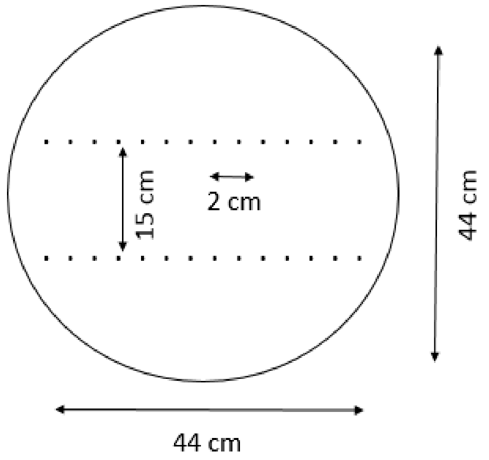


Figure 8.6: Schematic diagram of H. vulgare *seed placement in Mesocosm. Each seed placement represented by a dot. Effects of soil tillage intensity on prey capture by* T. tenuis *in mesocosms of* H. vulgare*.*

Five adult female *T. tenuis* were incorporated into each mesocosm, collected from the same location at Myerscough College as discussed in Method Development of Glasshouse Experiments and habitualised for 48 hours before measurement and entering the experiment (*Section 7.2.1.*). *T. tenuis* dimensions were recorded by the same method discussed in Section 7.2.2.

Five *S. avenae* nymphs, cultivated in the glasshouse (*Figure 7.2b, Section 7.2.3., Page 210*) were chosen which corresponded to the mean *S. avenae* density identified at GS 33 - GS 37 of *H. vulgare* in 2016 / 2017 season of the NIAB fields (*Table 5.1.1.*). Mass of the *S. avenae* nymphs was calculated on the *H. vulgare* leaf as described in Section 7.2.4. The *H. vulgare* leaf, with five nymphs upon it, was placed next to a *H. vulgare* leaf in the mesocosm after seven days when *H. vulgare* reached germination (GS 21). This period simulated when *S. avenae* nymphs may be present in the field with nutritional material in the form of *H. vulgare* tillers emerging.

8.4. Data Collection

Data was collected every seven days throughout the growth of *H. vulgare* until flowering (GS 61), anthesis. Data was recorded weekly to analyse how *T. tenuis* behaviour alters as prey density changes. Temperature was recorded via the smart glasshouse system employed at Myerscough College, the Tom Tech^{Ltd} T200. The thermal screen closed when light fell below 10.0 k lx. Above 80.0 k lx shade screens operated. Further temperature was taken to the nearest 0.1 °C with a Portable Pen Digital Thermometer WT-1B®. Both values were used to validate temperatures recorded.

Threads were observed as bridge threads for rappelling or support threads as webs. Anchor height of any threads to the nearest 0.1 cm and thread length to the nearest 0.1 mm were recorded. Web area was determined by length of all sides and Heron's formula as in fieldwork (*Section 4.3.4.*). In addition, number of *S. avenae* nymphs and adults were counted on *H. vulgare* leaves. Webs were analysed for

S. avenae presence, adult and nymph, and exuviae. The measurements obtained relate to *T. tenuis* activity stated in Table 5.1.2. (*Section 5.1.3.2., Page 83*). Additional variables recorded were *H. vulgare* density and mean *H. vulgare* height to nearest 0.1 cm.

Analysis were split into two definite growth stages of *H. vulgare* (early and late) which follows the analysis presented in fieldwork (*Section 5.1.5.*). Each growth stage lasted three weeks and 'early' incorporated the main growth stages of germination, tillering, flag leaf development and stem elongation (GS 0 - GS 49). 'Late growth' stage relates to when *H. vulgare* underwent ear emergence, milk development of the kernel, dough development and ripening (GS 51 - GS 92) (AHDB, 2018) (*Section 2.2.1.*).

8.5. Cleaning and Subsequent Preparations of Mesocosms

Due to the experiment being trialled twice, the mesocosms required clearing before repeating the methodology. This to allow no *T. tenuis* or *S. avenae* behaviour from the first trial to influence the results of the second trial. All surface material (straw, upright stubble and *T. tenuis* activity) was removed and *H. vulgare* was uprooted. *S. avenae* (alive and deceased) identified through observation and hand searching, were further removed. Insurances were made that all five *T. tenuis* were identified and taken out of the habitat. Each mesocosm was then covered with a cotton muslin square (70 cm x 70 cm of 13.1 g weight) and left for twenty-four hours to allow the contents of the mesocosm to settle and prevent incursion from new animals. Any further *S. avenae* found were removed from the mesocosm (*Section 7.4.2.1.*).

Before the seeding of *H. vulgare* for the second trial, the soil moisture content was analysed using the soil penetrometer Delta T Devices$^{©}$ HH2 Moisture Meter to allow adjustments of the irrigation system for adequate growth parameters of *H. vulgare* (*Section 8.3.*). All soil of the mesocosms were required to be of similar water moisture content. If lower than mean, additional water was applied (by hand spraying) to these mesocosms.

The level of soil nitrate-nitrogen (NO_3-N) was measured in each mesocosm. Filtered samples were analysed by colourimetric testing with the regent 2M potassium chloride (KCl). Samples were read at 420 nm by a Colour Spectrometer INESA™ 721G.

8.6. Statistical Analysis

Statistical analysis for this experiment was by multiple regression models, which, as in Section 5.1.4.2. and Section 6.5.2., used the stepwise backwards elimination method. The responses entered were dependent variables (y-axis variables) of anchor point height and thread length. Explanatory independent variables (x-axis variables), measured weekly, were placed into the models for each response variable. This included plant height, number of plants and temperature inside the mesocosm, for example. The backwards elimination method removed insignificant explanatory variables at the α >0.05, providing a robust regression model. Steps were analysed to assess the position at which a variable was removed. Associated statistics were referenced to negate factors of multicollinearity (VIF) and abnormally high standard error of the coefficients (Bass, 2007; Khan, 2013).

As previously noted, *T. tenuis* mass, cephalothorax length, abdomen length and plant height were explanatory variables that were entered as means (*Section 6.5.2.*). Normality was checked for each stepwise regression model via a residual vs fitted values plot, analysing the pattern of residuals. Large numbers in each model aided to assure normality (Khan, 2013).

A multiple regression model was run on the response of other variables measured, for example cumulative number of *S. avenae* found in the web, without the categorical predictor of soil tillage intensity. This was run to understand which variables held significant regression to the response, regardless to which mesocosm replicating soil tillage intensity the result was found. Parabolas were not graphed due to no categorical predictor grouping the variables (*Section 6.5.2*.).

All data was found to be non-normal through normality testing and analysing distribution on histograms and probability plots (*Section 5.1.4.1*.). Interactions in two-way rank ANOVAs were examined between means of a response (dependant variable) and two categorical factors, soil tillage intensity a factor incorporated into each model, for any significance where P - value was set at the α <0.05. The other categorical factor was either attachment material of the anchor point height or whether the *S. avenae* was found in the web when the response was web area. (Hawkins, 2014; Zuur *et al.,* 2007). As with Section 5.1.4.2. the programme FCSTats V2_1a© was used to find if significance existed in the interaction and Dunn's test applied to understand where the significance occurred (Wheater & Cook, 2000). Again letters to identify significance was understood through the use of the Bonferroni post-hoc test on the rank data in Mintab18©. Correlations were examined between two variables recorded; utilising Spearman's Rank (Rho) statistic for non-normality (Wheater *et al.,* 2011).

8.7. Results

Two trials which ran for six weeks, concluded when anthesis was at heights of 75.9 cm for Direct Drill Managed and 68.3 cm for Conventional. When anthesis occurred in one mesocosm the trial was ended. The set-up for each trial with *S. avenae* as prey was identical. Data was collected every seven days and placed together for all statistical analysis to strengthen trends observed.

Only a small number of bridge threads were identified after seven and fourteen days in a mesocosm mimicking each soil tillage. No other bridge threads were recorded within subsequent monitoring. The bridge threads were not included in the model due to limited data. All measurements represented here were from support threads of webs.

Alate morphs were identified in all soil tillage from week three of sampling. No significant relationship was identified between alate morphs and anchor point height and thread length due to low data entries. From this, they were removed from the dataset. Adult *S. avenae* recorded on leaves and within webs were apterous morphs only. Mass of *S. avenae* nymphs incorporated at the beginning of the trial did not significantly correlate to number of *S. avenae* observed on leaves and in the web at every recording. Therefore *S. avenae* mass of nymphs at the start was not included in the models. The variable of cumulative *S. avenae* in web reports the total biological control potential produced by the spinning of a web in each mesocosm of soil tillage intensity.

The results were split into two definite growth stages of *H. vulgare* (early and late) which follows the analysis presented in fieldwork (*Section 5.1.5. & Section 8.4.*). The analysis of the dependant variables of anchor point height, thread length and web area that explain *T. tenuis* activity are presented in turn.

8.7.1. Summary of results

- Direct Drill showed a significantly lower mean rank anchor point height when attached to upright stubble compared to plant, in Direct Drill and Direct Drill Managed, in early growth stages (*Figure 8.7.*).
- Significant negative correlation was found between number of *S. avenae* on plants, number of plants and mean plant height with anchor point height of early growth stages (*Table 8.3.*).
- Number of plants, *S. avenae* nymphs on plant, cumulative *S. avenae* within web and mean abdomen length had a quadratic regression to anchor point height (*Figure 8.9.*).
- Mean cephalothorax length was significantly positively correlated to anchor point height in both growth stages (*Table 8.3.*). Number of *S. avenae* on plant (nymph and adult) were significantly negatively correlated to anchor point height within early growth (*Table 8.3.*).
- Webs of a greater height within Conventional was a response to a greater capture rate of cumulative *S. avenae* (*Figure 8.9.*).
- Number of Aphididae in web at later growth stages was significantly positively correlated with anchor point height (*Table 8.3.*). This variable was a positive significant predictor, alongside number of plants, for the response cumulative number of *S. avenae* within web (*Table 8.7.*).
- Lower anchor point height was recorded when temperature and cumulative *S. avenae* in web, was at the lower and higher in Direct Drill Managed (*Figure 8.9.*).
- Straw mass was significantly positively correlated to anchor point height within early growth stages (*Table 8.3.*).
- Anchor point height of Direct Drill webs was lower throughout the growth and capture rate of *S. avenae* (*Figure 8.9.*).
- Mean cephalothorax length was significantly positively correlated to thread length within both growth stages (*Table 8.5.*). In Direct Drill Managed a greater mean cephalothorax length, spun smaller webs at later growth stages (*Figure 8.10.*). The same pattern was found for mean abdomen length (*Table 8.5. & Figure 8.10.*).
- Straw mass and thread length were significantly positively correlated in early growth stages (*Table 8.5.*).
- Numbers of plant and mean plant height showed significant negative correlation to thread length in later growth stages (*Table 8.5.*). Number of plants presented weak open downwards parabolas to thread length in Direct Drill Managed and Conventional (*Figure 8.10.*).
- Web area increased with temperature in Direct Drill Managed (*Figure 8.10.*). Web area was larger at lower temperature in Direct Drill (*Table 8.5. & Figure 8.10.*).
- The larger webs of Direct Drill captured no *S. avenae* (*Figure 8.10.*).

8.7.2. Anchor Point Height

Table 8.1: Response of rank anchor point height and factors of soil tillage intensity and anchor point attachment material in early growth stages, effects of soil tillage intensity on prey capture by T. tenuis *in mesocosms of* H. vulgare*. (n = 336). (* relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	34.977	0.001*
Anchor Point Attachment Material	1	27.466	0.001*
Interaction: Soil Tillage Intensity * Anchor Point Attachment Material	2	8.202	0.017*

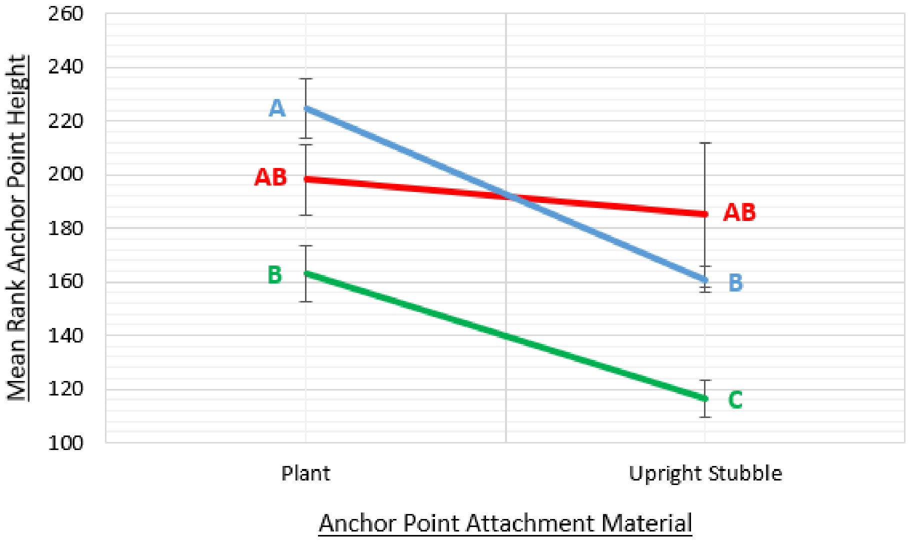


Figure 8.7: Interaction of mean rank anchor point height, soil tillage intensity and anchor point attachment material in early growth stages, effects of soil tillage intensity on prey capture by T. tenuis *in mesocosms of* H. vulgare *(n = 336). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Plant ±s.e.13.177 (n = 51), Conventional Upright Stubble ±s.e.26.848 (n = 10), Direct Drill Managed Plant ±s.e.10.968 (n = 80), Direct Drill Managed Upright Stubble ±s.e.4.703 (n = 6), Direct Drill Plant ±s.e.10.474 (n = 84), Direct Drill Upright Stubble ±s.e.6.991 (n = 105)). (Points that do not share the same letter are significantly different at the p<0.05 level).*

Significance was exhibited within the interaction between mean rank anchor point heights of different soil tillage intensities and the different attachment materials used in the early growth stages (*Figure 8.7. & Table 8.1*.). Heterogeneity was found between mean rank anchor point height of Direct Drill Managed attached to the material of plant and the mean rank anchor point height identified attached to plant for Direct Drill and attached to upright stubble for Direct Drill Managed and Direct Drill.

Adding straw into the above model negated the significant interaction found between plant and upright stubble and therefore, was removed.

Table 8.2: Response of rank anchor point height and factors of soil tillage intensity and anchor point attachment material in late growth stages, effects of soil tillage intensity on prey capture by T. tenuis *in mesocosms of* H. vulgare*. (n = 361). (* relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	1.756	0.416
Anchor Point Attachment Material	2	201.205	0.001*
Interaction: Soil Tillage Intensity * Anchor Point Attachment Material	4	7.651	0.048*

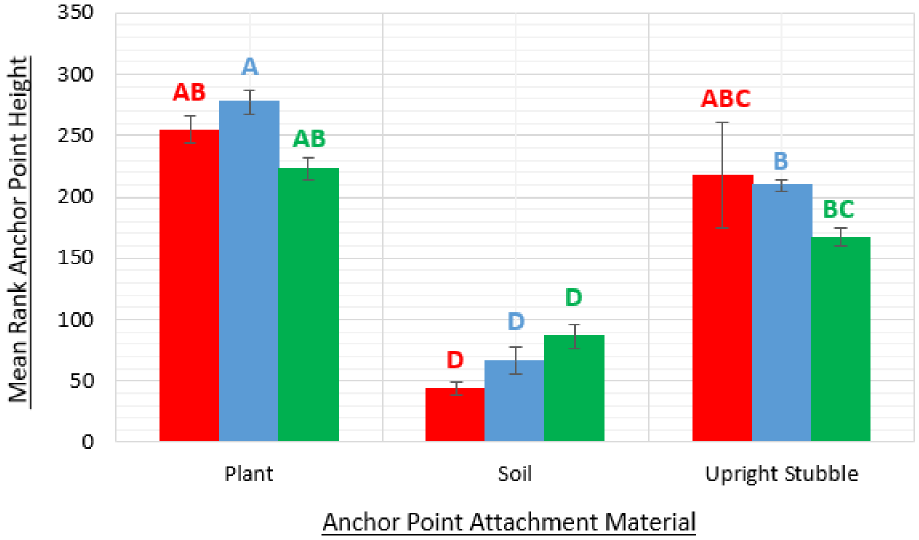


Figure 8.8: Interaction of mean rank anchor point height, soil tillage intensity and anchor point attachment material in late growth stages, effects of soil tillage intensity on prey capture by T. tenuis *in mesocosms of* H. vulgare*. (n = 361). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Plant ±s.e.10.594 (n = 48), Conventional Soil ±s.e.4.831 (n = 42), Conventional Upright Stubble ±s.e.42.978 (n = 5), Direct Drill Managed Plant ±s.e.10.181 (n = 59), Direct Drill Managed Soil ±s.e.11.449 (n = 22), Direct Drill Managed Upright Stubble ±s.e.4.285 (n = 4), Direct Drill Plant ±s.e.9.102 (n = 74), Direct Drill Soil ±s.e.9.670 (n = 36), Direct Drill Upright Stubble ±s.e.6.957 (n = 71)). (Points that do not share the same letter are significantly different at the p<0.05 level).*

Within all soil tillage of differing intensity, the mean rank anchor point measured on the attachment material of *H. vulgare* (plant) was significantly greater than the mean rank anchor points measured for the attachment material of soil (*Figure 8.8. & Table 8.2.*). The mean rank anchor point height attached to the material of plant for Direct Drill Managed was significantly higher than the mean rank anchor point height found attached to upright stubble for the same soil tillage intensity and for Direct Drill.

Table 8.3: Correlations of independent variables measured in the mesocosm, with the dependant variable anchor point height (cm) in early and late growth stages, effects of soil tillage intensity on prey capture by T. tenuis *in mesocosms of* H. vulgare. *(* relates to significant with α <0.05).*

	Early			**Late**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**
Cumulative *S. avenae* in Web	-0.234	0.001*	271	0.037	0.432	443
Furrow Depth (cm)	-0.424	0.001*	271	0.026	0.585	443
Mean Cephalothorax Length (mm)	0.403	0.001*	271	0.179	0.001*	443
Mean Plant Height (cm)	-0.187	0.002*	271	0.186	0.001*	443
Mean *T. tenuis* Mass (g)	0.072	0.237	271	0.156	0.001*	443
Number of Adult *S. avenae* on Plant	-0.081	0.182	271	0.141	0.003*	443
Number of Aphididae Exuviae in Web	0.104	0.087	271	0.269	0.001*	443
Number of Nymph *S. avenae* on Plant	-0.275	0.001*	271	0.146	0.002*	443
Number of Plants	-0.009	0.883	271	0.144	0.002*	443
Number of Upright Stubble	0.127	0.037*	271	-0.137	0.004*	443
Straw Mass (g)	0.424	0.001*	271	0.021	0.601	443
Temperature (^{o}C)	-0.249	0.001*	271	-0.182	0.001*	443

The mean cephalothorax length of *T. tenuis* was significantly positively correlated to anchor point height in the early and late growth stages of *H. vulgare* (*Table 8.3*.). Temperature measured in the mesocosms was significantly negatively correlated to anchor point height in both stages of *H. vulgare* growth (early and late). Mean plant height of *H. vulgare* and number of nymph *S. avenae* recorded on the plant were significantly negatively correlated to anchor point height during early growth stages of *H. vulgare* and significantly positively correlated in the later growth stages. Number of upright stubble was significantly positively correlated against anchor point height during the early growth stages and significantly negatively correlated within the later growth stages. The cumulative number of *S. avenae* recorded within the web and furrow depth was significantly negatively correlated with anchor point height recorded in the early growth stages of *H. vulgare*, whilst straw mass held a significant positive correlation at times when *H. vulgare* was at its early growth stages. Three variables were significantly positively correlated to anchor point height at the later growth stages only. These were mean *T. tenuis* mass, number of adult *S. avenae* found on the *H. vulgare* plant and number of Aphididae exuviae found within the *T. tenuis* web.

Table 8.4: Significant predictors to the response anchor point height (cm), in early and late growth stages, effects of soil tillage intensity on prey capture by T. tenuis *in mesocosms of* H. vulgare. *(n = 712, R^2 - 23.90%). (* relates to significant with α <0.05).*

Continuous Predictor	**Coefficients**	**Standard Error (SE) Coefficients**	***T***	***P***	**VIF**
Cumulative *S. avenae* in Web	-0.0402	0.0128	-3.14	0.002*	4.10
Mean Abdomen Length (mm)	-5.28	2.53	-2.09	0.037*	1.58
Mean Plant Height (cm)	0.1199	0.0303	3.95	0.001*	4.51
Number of Nymph *S. avenae* on Plant	0.003100	0.000725	4.28	0.001*	4.27
Number of Plants	0.447	0.106	4.21	0.001*	2.59
Number of Upright Stubble	-0.0522	0.0145	-3.60	0.001*	1.42
Temperature (°C)	-0.2897	0.0758	-3.82	0.001*	2.50

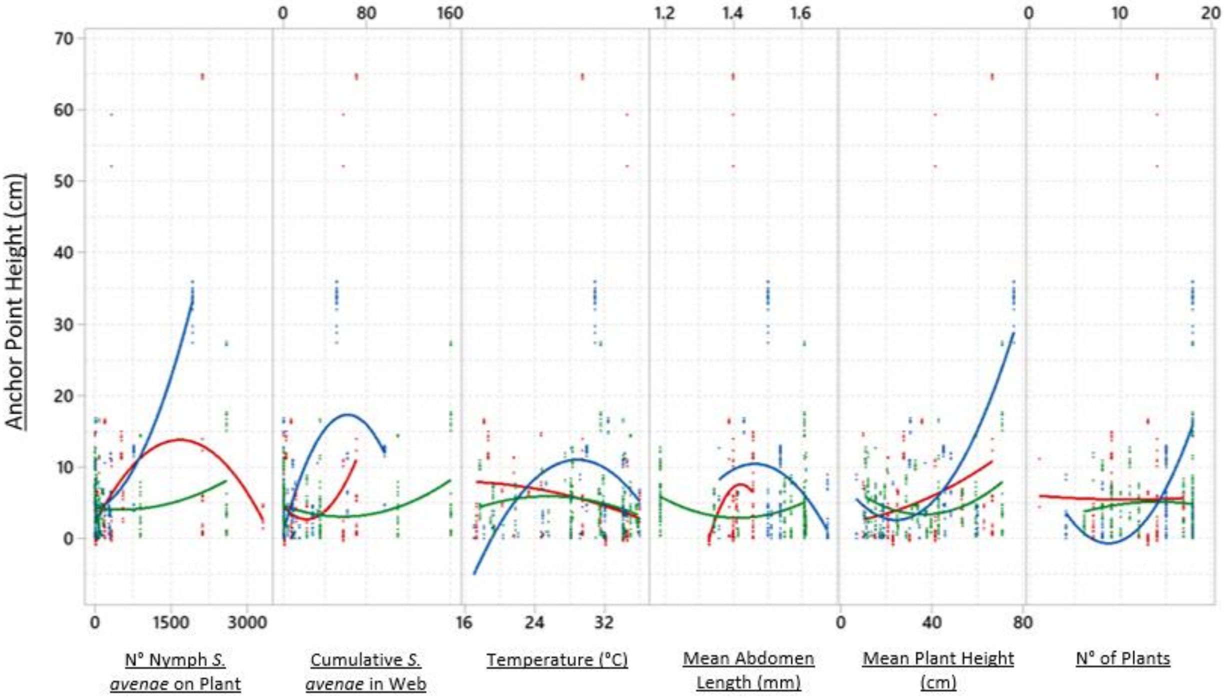


Figure 8.9: Matrix plot with quadratic regression and intercept fitted for anchor point height (cm) with number of S. avenae *nymph on plant, cumulative number of* S. avenae *in web, temperature (°C), mean* T. tenuis *abdomen length (mm), mean plant height (cm) and number of plants in early and late growth stages, effects of soil tillage intensity on prey capture by* T. tenuis *in mesocosms of* H. vulgare. *(n = 712, R^2 - 23.90%). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green).*

For Direct Drill Managed mesocosms, the steep open upward parabola representing anchor point height relationship with number of *S. avenae* nymph found on *H. vulgare* plants, identifies a lower range of data was found within these mesocosms and the higher anchor point height was identified when peak nymph *S. avenae* were recorded (*Figure 8.9.* & *Table 8.4.*). The wide downwards open parabola for Conventional identifies a greater range of data along the x-axis (nymph numbers on the plant) and the maximum vertex, explaining peak anchor point height, was identified mid-range of the nymph numbers recorded. Conventional peaked when the greater cumulative *S. avenae* was recorded in the web, this is due to a steep upwards open parabola established. For Direct Drill Managed, the downward open parabola gave a maximum vertex for anchor point height when sixty-two *S. avenae* were found in the web.

Temperature appears to have affected the Direct Drill Managed mesocosms where a wide-open downwards parabola, shows anchor point height was greater when the temperature reached 25 to 29 ^{o}C. Maximum vertices were established when mean abdomen length was analysed against anchor point heights recorded in the mesocosms for Conventional (at 1.4 mm abdomen length) and Direct Drill Managed (at 1.5 mm abdomen length), the greater anchor point established in Direct Drill Managed.

Direct Drill Managed measured quadratic regression between mean plant height and density of *H. vulgare* against anchor point height. A minimum vertex of anchor point height was established, the greater anchor point height found when mean plant height and number of plants was at its highest.

Weak regression existed in Direct Drill for all continuous predictors against the response.

8.7.3. Thread Length

Table 8.5: Correlations of independent variables measured in mesocosm, with the dependant variable thread length (mm) in early and late growth stages, effects of soil tillage intensity on prey capture by T. tenuis *in mesocosms of* H. vulgare*. (* relates to significant with α <0.05).*

	Early Growth Stage			**Late Growth Stage**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**
Cumulative *S. avenae* in Web	-0.229	0.001*	271	-0.178	0.001*	443
Furrow Width (cm)	0.385	0.001*	271	0.055	0.256	443
Mean Abdomen Length (mm)	0.008	0.892	271	-0.116	0.016*	443
Mean Cephalothorax Length (mm)	0488	0.001*	271	0.142	0.003*	443
Mean Plant Height (cm)	-0.327	0.001*	271	-0.217	0.001*	443
Number of Adult *S. avenae* on Plant	-0.021	0.733	271	-0.136	0.005*	443
Number of Nymph *S. avenae* on Plant	-0.281	0.001*	271	-0.159	0.001*	443
Number of Plants	-0.098	0.108	271	-0.165	0.001*	443
Straw Mass (g)	0.318	0.001*	271	0.020	0.675	443
Temperature (^{o}C)	-0.364	0.001*	271	-0.003	0.948	443

The cumulative number of *S. avenae* within the web, number of nymph *S. avenae* identified in the web and mean plant height were significantly negatively correlated to thread lengths measured at both early and late growth stages of *H. vulgare* (*Table 8.5*.). The opposite was found for mean cephalothorax length, which was significantly positively correlated to the thread lengths measured in the mesocosms in the early and late growth stages. Furrow width and straw mass were significantly positively correlated to thread length in the early growth stages. Temperature in the mesocosms was significantly negatively correlated to thread length at the early growth stages of *H. vulgare*. Thread length at only the later growth stages of *H. vulgare*, was significantly negatively correlated to the mean abdomen length of *T. tenuis*, number of plants and adult *S. avenae* found on the plant.

8.7.4. Web Area

Table 8.6: Significant predictors to the response web area (mm^2) in early and late growth stages, effects of soil tillage intensity on prey capture by T. tenuis *in mesocosms of* H. vulgare. *(n = 172, R^2 - 29.72%). (* relates to significant with α <0.05).*

Continuous Predictor	**Coefficients**	**Standard Error (SE) Coefficients**	***T***	***P***	**VIF**
Cumulative *S. avenae* in Web	-0.01276	0.00152	-8.39	0.001*	4.12
Mean Abdomen Length (mm)	-4.24	2.09	-2.02	0.044*	1.46
Mean Cephalothorax Length (mm)	-0.2164	0.0615	-3.52	0.001*	2.21
Number of Nymph *S. avenae* on Plant	0.007655	0.000926	8.27	0.001*	3.88
Number of Plants	0.0515	0.0241	2.14	0.033*	3.81
Temperature (°C)	-0.0896	0.0207	-4.33	0.001*	3.92

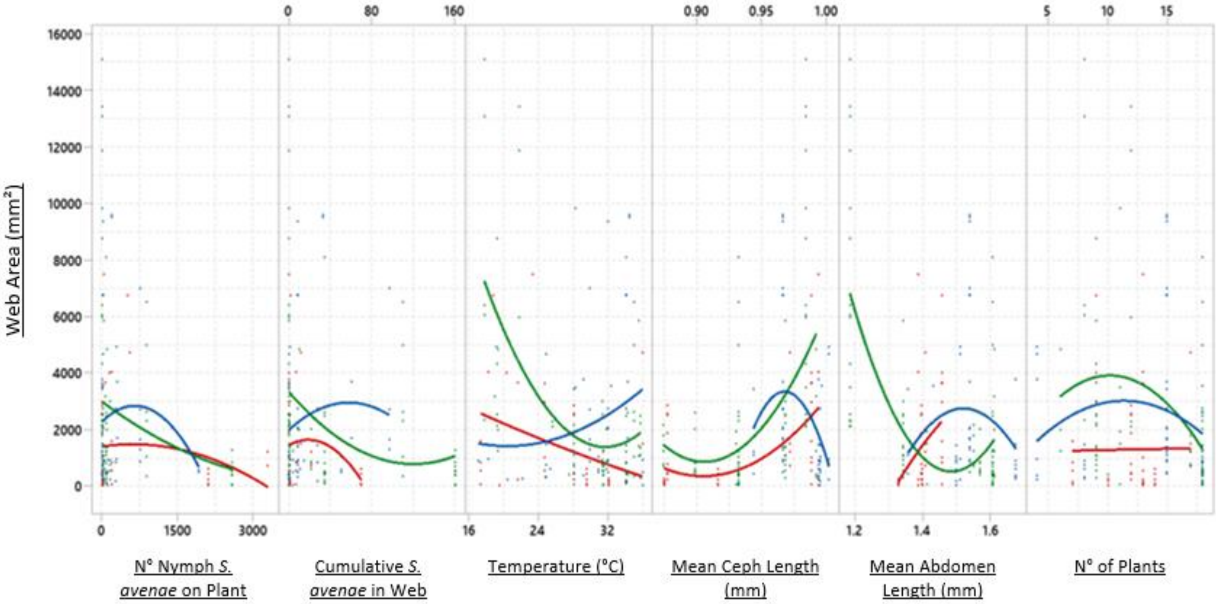


Figure 8.10: Matrix plot with quadratic regression and intercept fitted for web area (mm^2) with number of S. avenae *nymph on plant, cumulative* S. avenae *in web, temperature (°C), mean* T. tenuis *cephalothorax length (mm), mean* T. tenuis *abdomen length (mm) and number of plants in early and late growth stages, effects of soil tillage intensity on prey capture by* T. tenuis *in mesocosms of* H. vulgare. *(n = 172, R^2 - 29.72%). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green).*

An open downward parabola established for Direct Drill Managed, observed the greater web area was found when the number of nymph *S. avenae* recorded on the plant was within the middle of the dataset for this mesocosm (*Figure 8.10. & Table 8.6.*). For the cumulative number of *S. avenae* recorded in the web, the greatest range of this variable was found in the Direct Drill mesocosms with a wide parabola established. Maximum vertices were established in the Conventional and Direct Drill Managed mesocosms when web area was analysed with cumulative *S. avenae* identified in the webs. This explains the greater web area within these mesocosms was recorded when the median cumulative number of *S. avenae* was identified.

A wide downward open parabola was identified for the relationship of web area with the temperature in the mesocosms for Direct Drill. The greater range of temperatures was identified in this soil tillage, the lower web areas were established when the temperature was 29 to 34 °C.

Smaller web areas were measured when cephalothorax length was at its smallest and longest in the mesocosms of Direct Drill Managed. When mean abdomen length was at its smallest, the larger web areas were spun in the Direct Drill mesocosms. Only positive linear regression existed in the Conventional mesocosms for the variable mean abdomen length. The smaller webs were further spun by *T. tenuis* of mean longer and shorter abdomen length in the Direct Drill Managed mesocosms with an open downwards parabola established.

Large data range of number of *H. vulgare* plants was found in all mesocosms of soil tillage. The web areas measured in the mesocosms of Direct Drill Managed and Direct Drill followed similar trends with a maximum vertex found when *H. vulgare* density was nine to thirteen plants.

8.7.5. Other Variables Measured

Table 8.7: Significant predictors to the response cumulative number of S. avenae *within web, in early and late growth stages, effects of soil tillage intensity on prey capture by* T. tenuis *in mesocosms of* H. vulgare. *(n = 54, R^2 - 79.16%). (* relates to significant with α <0.05).*

Continuous Predictor	**Coefficients**	**Standard Error Coefficients (SE Coeff)**	***T***	***P***	**VIF**
Number of Aphididae Exuviae in Web	0.2564	0.0360	7.13	0.001*	2.81
Number of Nymph and Adult *S. avenae* on Plant	0.02334	0.00163	14.36	0.001*	4.21
Number of Plants	2.344	0.469	5.00	0.001*	3.75
Temperature (°C)	0.651	0.2630	2.47	0.001*	1.73

Without the categorical predictor of soil tillage intensity, the variables of number of Aphididae exuviae recorded in the web, temperature, number of *H. vulgare* plants and number of nymph and adult *S. avenae* on *H. vulgare* were all significant predictors to the response of cumulative number of *S. avenae* within the web (*Table 8.7.*). These significant predictors were all significantly positive within the model.

8.8. Discussion

The upright stubble was monopolised as an attachment material in Direct Drill at early growth stages, which follows the trend found in fieldwork sampling (*Figure 8.7. Section 5.1.6.2.1.*). This created a platform for web-weaving away from the soil and straw as an alternative of the plant when the crop was germinating (Harwood *et al.,* 2003; Hogg & Danne 2018; Szymkowiak *et al.* 2007) (*Table 8.3. & Figure 8.7.*). Interestingly, the upright stubble was utilised at a significantly lower height to plant in Direct Drill in early growth stages (*Figure 8.7.*). Chabert & Sarthou (2017) and Hein *et al.* (2019) discuss that the use of a multitude of attachment materials allows a plethora of webs at differing heights to be spun. The use of the upright stubble, in the Direct Drill, offered an extension into the environment of the mesocosm, to allow the plant at higher reaches to become an attachment point. Less upright stubble in the Direct Drill Managed tillage, facilitated the utilisation of the *H. vulgare* at higher tillers than within Direct Drill (Dennis *et al.,* 2015; Fahrig *et al.,* 2011; Henschel & Lubin, 2018) (*Figure 8.7.*).

It was noteworthy that *T. tenuis* were not attaching to the growing plant with greater frequency. *S. avenae,* within the early growth stages, were confirmed to be in the basal layers, thus it appears webs were constructed in lower strata in consequence of this (*Table 8.3.*). Lombaert *et al.* (2006) and Mehrparvar *et al.* (2013) discuss that a colony requires time to establish, nymphs incorporated needing to reach maturity before reproductive potential is reached. *S. avenae* activity appeared to only increase *T. tenuis* web placement height at later growth stages, as colony size increased, pushing *S. avenae* to disperse (*Table 8.3.*).

A similar pattern existed for number of *S. avenae* nymphs on leaves, exhibiting that *S. avenae* population growth was dependant on plant height and density (*Figure 8.9*). This follows, as *H. vulgare* was the only food source available, due to the confined nature of the trial the phloem required for fitness and viability could become a limited resource (Alignier *et al.,* 2014; Ben-Issa *et al.,* 2017; Gagnon *et al.,* 2011; Goggin, 2007). It appears that plant height and density had more influence in creating the higher anchor points for webs (*Figure 8.9.*). This agrees with fieldwork sampling, where vegetation structure appears to have been of greater importance (*Section 5.1.5.2.2*). However, this trend only occurred in the Direct Drill Managed mesocosms (*Figure 8.9.*). It may be that an increased fitness of *T. tenuis* in Direct Drill Managed enabled ease to climb upon *H. vulgare* to reach higher aspects of the mesocosm (Jakob *et al.,* 1996; Jurczyk *et al.,* 2012; Opatovsky *et al.,* 2016; Prenter *et al.,* 2010; Toft, 1989). Direct Drill Managed, a middle habitat, showed the lower utilisation of applied landscape features, upright stubble and furrow dimensions, for example (*Figure 8.8*). The maximum vertex is greater for Direct Drill Managed, in the interaction of abdomen length and anchor point height (*Figure 8.9.*). *T. tenuis* body size interacted with anchor point height, however, there was no clear linear relationship formed. *T. tenuis,* within Direct Drill Managed mesocosms, may have enough resources for an adequate claim of territory for individual web-building (Birkhofer *et al.,* 2007; Janetos, 1984; Opatovsky *et al.,* 2016; Schütt, 1997).

Anderson & Prestwich (1975), Herberstein (2011) and Schmitz (2013) discuss that the hydrostatic fluid pressure pumps of Linyphiidae, which drive leg flexion in muscles of the tibia, are located in the cephalothorax (*Table 8.3*.). Prenter *et al.* (2010) comment that an increase in cephalothorax enables greater flexion to be attained. In fieldwork, larger-bodied *T. tenuis* showed dominance by spinning webs at a greater height, occupying a higher stratum (*Section 5.1.6. & Section 5.3.6*.). Gregori *et al.* (2015) discussed that body size increased Linyphiidae foraging effort. Lichtenstein *et al.* (2016) agreed, commenting that reduced body size decreases personality traits, one such being confidence. However, *T. tenuis* mass was not of importance within early growth stages, as noted earlier *S. avenae* colonies were confined to the lower aspects. It may be here that the difference in mass only had a subtle effect in spinning in the prime web-site. This can be further analysed when anchor point height was low in mesocosms where less cumulative *S. avenae* in the web were found within the first fourteen days (*Figure 8.9*.).

Two webs, in Direct Drill Managed, were woven between *H. vulgare* tillers at 12 - 14 cm in height where low numbers of nymphs were identified (*Table 8.3.*). The experiment had run for fourteen days with zero *S. avenae* counted within the two webs. The greatest number of nymphs found on the plant at this time was thirty, with sheet webs capturing twenty-two *S. avenae*, counted in a Direct Drill mesocosm. Webs here were woven in between the soil, upright stubble and plants at a lower height (*Figure 8.9*.). It appears something was driving *T. tenuis* to spin webs at a greater height in Direct Drill Managed mesocosms, even though they were unsuccessful in prey capture. Perhaps it was the absence of *S. avenae* that drove *T. tenuis* of a greater abdomen to ascend higher. Blamires *et al.* (2013), Houser *et al.* (2016) and Segoli *et al.* (2004) note that in times of low food availability, foraging, creation of the extended phenotype, increased inactivity in search distance extended for a profitable web-site in prey capture.

S. avenae can be identified as occupying all strata of *H. vulgare* leaf, as time continued, phloem access became a limited resource as the population grew (Sanders & Platner, 2007; Valenzuela & Hoffman, 2014) (*Figure 8.11a & b*.). At the greatest number of nymph *S. avenae* (n = 3312) at week six, the anchor point height was the lowest found in a Conventional mesocosm (*Figure 8.9. & Figure 8.11b*.). This was due to three new webs formed in the basal stratum which together caught ten further *S. avenae*. This identified that the webs were a success which discords with Gómez *et al.* (2016), Kovac *et al.* (2009) and Roberson *et al.* (2016), who discuss the benefit of web-spinning within higher tillers to intercept a greater prey abundance. It appears that the size of the *S. avenae* colony became a limiting factor and thus the propensity to drop increased, falling into underlying sheet webs (Alford *et al.,* 2016; Ma & Ma, 2012; Mansion-Vaquié *et al.,* 2020). The greatest difference between adult and nymph numbers were identified in Direct Drill and Direct Drill Managed mesocosms, here nymph numbers were considerably greater at week five and six of the trial (*Figure 8.9*.). This explains a high population of *S. avenae* in early developmental stages, first instars, where ecdysis may not have commenced (Buriro *et al.,* 2006; Price *et al.,* 2011; Watanabe *et al.,* 2018; Winder *et al.,* 2013) (*Section 2.2.6.1*.). In time, if the trial had continued and *S. avenae* reached later instars, exuviae could have fallen into webs. Furthermore, *S. avenae* propensity to drop may have increased due to over-crowding (Agabiti *et al.,* 2016; Brabec *et al.,* 2014).

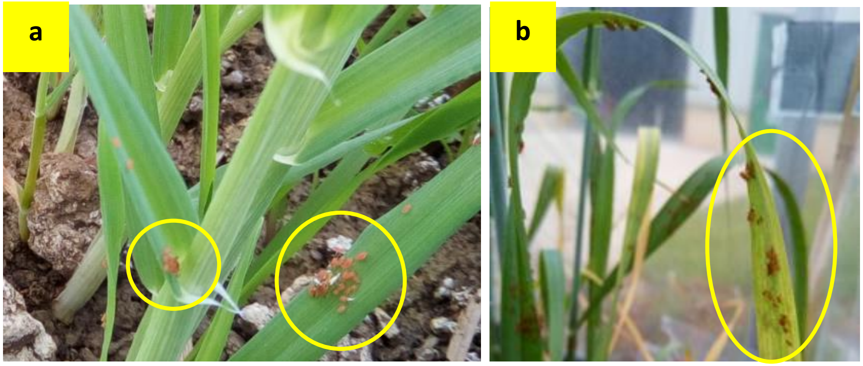


Figure 8.11a & b: S. avenae *nymphs and apterous adults on* H. vulgare *leaves. (*S. avenae *circled in yellow). Effects of soil tillage intensity on prey capture by* T. tenuis *in mesocosms of* H. vulgare. *a = Direct Drill. Lateral view. b = Conventional. Elevated view.*

T. tenuis appear to be creating webs of a greater height within Conventional mesocosms due to a response of greater capture rate of cumulative *S. avenae* (*Figure 8.9.)*. This agrees with research by Diehl *et al*. (2013), Feber *et al.* (1998) and Harwood *et al.* (2004) who showed that *T. tenuis* movement was determined by prey selection of Aphididae. However, Aphididae are known to occupy all heights of an *H. vulgare* leaf where addition phloem source may be reached (Goggin, 2007; Mestre *et al.*, 2018; Parry, 2013, Watanabe *et al.,* 2018) (*Figure 8.11a & b*). The cumulative *S. avenae* in the web held no significant correlation in the later growth stages to anchor point height. It appeared that *S. avenae* were caught at any height, perhaps aided by no disturbances (wind and rain) in the mesocosms. Qin *et al.* (2015), Rodríguez & Gamboa (2000) and Welch *et al.* (2013) explain that *S. avenae* movement in a web can cause small ripples in the silk which stimulate *T. tenuis* sensory receptors, heightened when deprived of climatic disturbances. This may prompt web construction near a web with *S. avenae* capture and initiate a positive feedback system.

The number of adults on leaves was less than nymphs, which was as expected with asexual reproduction (Price *et al,* 2011; Rispe *et al.,* 1996). The apterous morphs, though noted by Zhang *et al.* (2016) to move in an awkward staggered way, are more likely to ascend to greater heights of the tiller to begin a colony in an isolated territory (Gish, 2012; Oliver *et al*., 2007) (*Table 8.3*.). Moreover, fecundity requires high energy consumption, thus encouraging the feeding of new growth higher within the canopy (Brabec *et al.,* 2014; Paulmann *et al.,* 2018).

Muratori *et al.* (2008) and Oelbermann & Scheu (2002) describe that exuviae in web cannot directly portray a predator and prey relationship. It is assumed that exuviae presence is evidence of juvenile development of *S. avenae* within the upper aspects of the plant (Oelbermann & Scheu, 2002; Pekár, 2000). With *S. avenae* found in webs alongside Aphididae exuviae, it appears webs were spun at the appropriate location for prey capture, especially in later growth stages (Jurczyk *et al.,* 2012; Kasumovic & Jordan, 2013) (*Table 8.3. & Table 8.7*.). Parry (2013), describing additional plant material, offers phenotypic factors that can aid fecundity with *S. avenae* (*Table 8.7*.). Of interest, in later growth stages *S. avenae* abundance achieved web-building at a greater height within the mesocosm. Bell *et al.* (2002) and Toft (1987) discuss that at times of great food availability, *T. tenuis* are prompted to gorge, this relaxing *T. tenuis* and additionally, if fed a continuous diet of Aphididae, will over time develop an adverse taste to this prey. This perhaps explained why not all Aphididae could be consumed in the web and were able to be recorded. Negating a driving urge of starvation is explained to dissuade a *T. tenuis* into ascension (Toft, 1987; Toft, 1995; Toft, 2002). However, Toft (1987) and Toft (2002) describe the aversion lasts for approximately two days. With the current experiment lasting six weeks, *T. tenuis* may indeed have been responsive to prey stimuli and inclined to reach upper strata of the *H. vulgare*, later within the experiment, to ascertain new territories (*Table 8.3*.).

The lower anchor point height was found when the temperature and cumulative *S. avenae* in web, was at its lower and higher point in Direct Drill Managed (*Figure 8.9*.). *S. avenae* are notably sensitive to extreme temperatures, above the optimal (Buriro *et al.,* 2006; Mehrparvar *et al.,* 2013; Newman, 2004). While thermo-regulation pathways allow survival during times of heat stress, Jeff & Leather (2014) and Ma & Ma (2012) discussed that growth and viability of Aphididae are likely to be impaired. At points within this trial, temperature reached >34 °C in all soil tillage simulations. This temperature is noted to be in excess of *S. avenae* optimum for successful parthenogenesis and dispersal (Chen *et al.,* 2000; Jeff & Leather, 2014; Newman, 2005). Low anchor point at times of high temperatures may relate to higher levels of *S. avenae* dropping from *H. vulgare* leaves (*Table 8.3*.). Alford *et al.* (2016) and Ma & Ma (2012) discuss propensity to drop increases as a response to heat stress, an outcome of diverting energy to reduce internal body temperature. Within Direct Drill Managed, two higher webs >10 cm were constructed when temperature was noted as 34.3 ^{o}C. at week five, with thirteen *S. avenae* noted within the web. Predator success was identified in this web placement. Angilletta *et al.* (2004) and Franken *et al.* (2018) are in accord, explaining Linyphiidae 'sit and wait' strategy provides a general sedentary existence which assists with the regulation of internal temperature. Energy can, therefore, be further freely used to ascend to greater heights. Increased height allows access to possible advantageous web-sites (Borges & Brown, 2001; Dennis *et al.,* 2001; Diehl *et al.,* 2013; Prenter *et al.,* 2010).

It can be viewed that the increase in straw mass in Direct Drill and Direct Drill Managed, if only small, may have influenced *S. avenae* movement upwards and their reproductive potential in early growth stages (Kennedy & Connery, 2005; Kennedy *et al.,* 2010; Summers *et al.,* 2004) (*Table 8.3.*). Straw presence was highlighted to be a reason of *S. avenae* persistence in the Conventional area when *T. tenuis* behaviour was understood in areas of symptomatic BYDV *H. vulgare* (*Section 6.6.2*.). Straw, in the mesocosms, may have covered lower aspects of the stem within the early crop growth stages, pushing *S. avenae* further up the stem and thus acquiring phloem of higher nutritional content (Goggin, 2007; Summers *et al.,* 2004). Webs were spun at a greater height to intercept *S. avenae* residing in the upper tillers (*Table 8.3*.). *S. avenae* reproduce *in situ*, and if an apterous morph is higher on a plant, so it follows that its offspring will also have access to nutritional phloem (Goggin, 2007; Lombaert *et al.,* 2006; Price *et al.,* 2011). As *H. vulgare* went into later growth stages, straw held no influence on web placement. As plant height increased and plant growth held a greater green canopy, the higher strata provided higher levels of landscape complexities pushing *T. tenuis* activity upwards (*Figure 8.9*.). El-Nabawy *et al.* (2016), Entling *et al.* (2011) and Öberg (2007) comment that the web placement is often a product of landscape orientation.

Anchor point height of Direct Drill webs was generally low throughout the population growth of *S. avenae* (*Figure 8.9*.). It appears that *T. tenuis* chose to remain web-spinning in the lower aspects of the Direct Drill mesocosm. This was shown by Buri *et al.* (2016), Davey *et al.* (2013) and Rybak (2007) to be the preferred anchor location of *T. tenuis* where optimal conditions are employed, with plentiful resources and low intra-specific competition. It appears that the greater level of fitness of *S. avenae* was observed in Direct Drill, thus a plentiful resource located at the base of the mesocosm. The requirement not to ascend to create a web at a greater height, identified as unnecessary energy expenditure, an element that a Linyphiidae is persistently aiming to keep balanced with energy reaped (Alderweireldt, 1994; Bonte *et al.,* 2008; Ford, 1977; Harwood & Obrycki, 2007; Qin *et al.,* 2015).

Increased flexion of a larger cephalothorax can allow silk threads to be spun more rapidly and with greater ease (Bonte *et al.,* 2008; Craig, 2003; Harmer *et al.,* 2011; Spagna & Peattie 2012) (*Table 8.5. & Figure 8.10*.). Direct Drill Managed shows an anomaly when *T. tenuis* with a greater mean cephalothorax length, spun webs of a small length towards the end of the experiment (*Figure 8.10*.). The same pattern occurred for mean abdomen length (*Table 8.5. & Figure 8.10*.). This contradicts findings of Craig (1987), Houser *et al.* (2016), Nentwig & Heimer (1987), Segoli *et al.* (2004) and Toft

(1987) who comment that larger-bodied *T. tenuis* may spin webs of greater area to enforce dominance and enhance prey capture capability. However, here vegetation complexity may be more important at determining web area, the orientation of anchor materials observed from spatial modelling by Downie *et al.* (2000) and Prieto-Benítez & Méndez (2011) to be fundamental in allowing the development of a web. This observation was identified in field sampling, as the growth of *H. vulgare* progressed (*Section 5.1.6.2.2.*). The static environment of mesocosms provides a plethora of potential web-sites equating to low tendency to compete, where fitness level of a *T. tenuis* may be disregarded. Environmental factors are a key parameter when reviewing a potential web-site (Blake *et al.,* 2013; Schütt, 1997; Tew & Hesselberg, 2017; Welch *et al.,* 2011).

Aphididae presence was noted on the straw, an occurrence explained by Barro (1991) and Dupuis *et al.* (2017) to be due to Aphididae' poor optic ability. This makes them unable to discriminate between a tussock of straw residue and growing plant, moreover, able to visually ascertain the difference between bare soil and crop. The greater threads spun in between straw may have been *T. tenuis* orienteering its web, to traverse across large areas of the straw residue (*Table 8.5.*). As stem elongates further in later *H. vulgare* growth, the presence of the straw residue diminishes as a colony ascends the plant (Dupuis *et al.,* 2017; Kennedy & Connery, 2005; Kennedy *et al.,* 2010; Summers *et al.,* 2004). In Conventional mesocosms, large horizontal sheet webs were spun across the length of the furrow, which discords with Blake *et al.* (2013) and Platen *et al*. (2013) who stated that *T. tenuis* prefers a web above the ground and will not actively seek to anchor to soil (*Table 8.5.*). Alderweireldt (1994) and Samu *et al*. (1996) discuss the positive use of soil for attachment if another material was limited, again transcribing the use of the soil when a physical feature created there reveals an anchor point. The use of a furrow, as an anchor material for web-spinning, was favoured in Conventional in times of fieldwork due to drought stressed *H. vulgare* exhibiting poor growth (*Section 5.1.5.2.3.*).

Number of plants was shown to interact with thread length due to micro-habitat heterogeneity, it appears that number of plants drove the establishment of a greater range of thread lengths within webs (Dennis *et al.,* 2015; Öberg *et al.,* 2008; Poggio *et al.,* 2013; Thorbek & Topping, 2005) (*Table 8.5., Figure 8.10.*). It may be that the arrangement of the tillering of the plants as they developed allowed spinning of different webs of varying thread lengths (*Figure 8.12.*). This is supported by Beals (2006), Sunderland & Samu (2000) and Warui (2004) who, through modelling plant physiognomy and Linyphiidae behaviour, identified that different spacing between anchor materials increased web-building potential. There was little interaction for web area and number of plants within the Conventional mesocosms (*Figure 8.10.*). Therefore, the greater furrow width accessible for anchorage, due to the reduced straw mass and upright stubble, were provided in the Conventional mesocosms (*Figure 8.8.*).

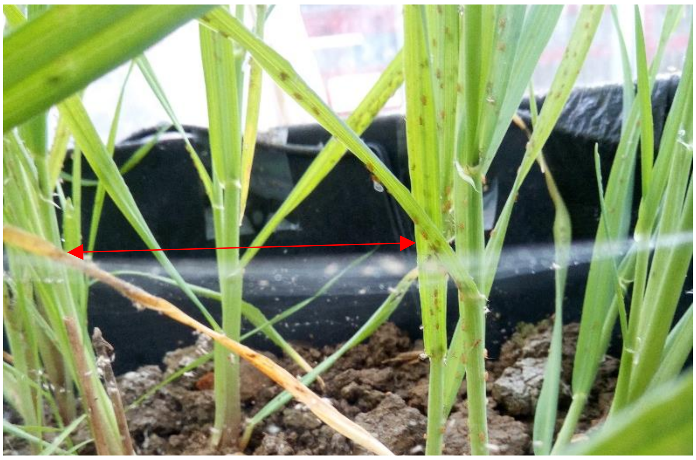


Figure 8.12: Sheet web woven across H. vulgare *in Direct Drill Managed mesocosm. Effects of soil tillage intensity on prey capture by* T. tenuis *in mesocosms of* H. vulgare*. Lateral view. (Red arrow = 112.7 mm).*

At increased growth stages, stem elongation causes structural weakness and therefore causes bending, drawing a canopy closer together (AHDB, 2018; Mornhinweg, 2011). It may be that the change in orientation decreased thread length and thus web size (*Table 8.5*.). Krafft & Cookson (2012) and Lyons *et al.* (2018) discuss that a web is a configuration of the environment presented.

At greater temperatures, within later growth stages, in the Direct Drill Managed mesocosms, web area was increasing as temperature reached its maximum (*Figure 8.10*.). For adult Linyphiidae, compensation at high temperatures is less costly than the thermo-regulation process of *S. avenae* thus, they can yield silk with the tension required (Angilletta *et al.*, 2004; Pekár, 2000; Suter, 1981; Welch *et al.,* 2011). Egg sac incubation and juvenile development during Linyphiidae life history where extreme temperatures (<15 °C and >30 °C) were found to impeded growth rate (Bonte *et al.,* 2008; Thorbek & Bilde, 2004; Vanacker *et al.,* 2001). Web area was larger at times of the lower temperature in Direct Drill (*Table 8.5. & Figure 8.10.*). This was driven by several webs >8,000 mm^2 noted at 17.7°C-19.1°C. These webs were woven in the basal layer of the mesocosm within the last two weeks of the experiment. The similar trend for temperature and cumulative *S. avenae* (which is in time order) identified that temperature could be driving *S. avenae* parthenogenesis rate, which agrees with earlier discussions, where temperature was a limiting factor in the Aphididae life cycle (Honek *et al.* 2018; Jeff & Leather, 2014) (*Table 8.7., Figure 8.10. & Section 5.1.6.2.2*.). Poor canopy growth in density and height of *H. vulgare* was noted where low *S. avenae* abundance was found, which suggested that Aphididae success depended on a narrow range of phenotypic elements, with poor phloem availability as one of these (Dorokhov *et al.,* 2014; Parry, 2013; Reddy *et al.,* 2009) Greater open space in the canopy may have allowed prey to be ensnared at a lower height (Badenhausser, 2020; Rosas-Ramos *et al.,* 2018). Furthermore, low *S. avenae* abundance most likely to reside in the basal layer if new canopy growth is failing (Davis *et al.,* 2015; Ma & Bechinski, 2008).

The maximum vertex of web area was reached midway through its cumulative *S. avenae* capture in Conventional and Direct Drill Managed, perhaps related to subtleties in *H. vulgare* orientation, as growth developed more than *S. avenae* availability (*Figure 8.10.*). Alderweireldt (1994) and Herrmann *et al.* (2010) showed that small disparities in micro-habitat (mesocosm), may alter web dimensions. Less cumulative *S. avenae* were captured within Conventional than other mesocosms, however the greater number of nymph *S. avenae* were identified within Conventional (*Figure 8.10.*). Borges & Brown (2001), Heiling & Herberstein (1998) and Toft (1987) explain that thread length describes the size of the web, whereas anchor point height is a function of the web's location, thus anchor point height would result from an interaction with *S. avenae* in web more than thread length (Gómez *et al.,* 2016; Roberson *et al.,* 2016; Stenchly *et al.,* 2011). The action of web-spinning is discussed by Harwood *et al.* (2004) and Jurczyk *et al.* (2012) as not 100% fool-proof, as *T. tenuis* may have anticipated *S. avenae* capture.

Dispersal of alate morph *S. avenae,* allowed morphs to reach all areas of the *H. vulgare.* Blackledge & Eliason (2007) and Kasumovic & Jordan (2013) discuss that web-spinning follows prey, with webs of shorter thread lengths woven into small areas of the mesocosm, exploiting pockets of heightened *S. avenae* activity (*Figure 8.10.*). Generally smaller webs were spun in Direct Drill mesocosms as greater cumulative *S. avenae* were recorded in the web (*Figure 8.10.*). This agrees with the above statement, with the greater *S. avanae* explanation of growth identified in a Direct Drill mesocosms. Webs were spun at an appropriate location to enforce predator dynamics (Clark *et al.,* 2004; Marc & Canard, 1997; Stenchly *et al.,* 2011; Tahir & Butt, 2009). The extended phenotype of webs therefore woven in the vicinity of a fecund colony of *S. avenae* (Asin & Pons, 2001; Klüken, 2008; Watanabe *et al.,* 2018).

With such extreme differences in *S. avenae* numbers (nymph = 10 to 3312) at the end of the experiment, it can be understood why number of nymphs found in the mesocosms significantly altered the web area that *T. tenuis* spun (*Figure 8.10.*). In Direct Drill Managed, a small data range existed for number of *S. avenae* identified on the vegetation compared to that of Conventional and Direct Drill. With *S. avenae* mass not holding any significant correlation, parthenogenesis rate may be slowed, fitness or low rate of instar development perhaps faltered. *S. avenae* were bred in the glasshouse where there was no interaction with an alternative colony (*Section 7.4.2.*). This may have led to excessive in-breeding where weaker genetic traits were amplified (Goggin, 2007; Jeff & Leather, 2014; Mehrparvar *et al.,* 2013). The large webs for Direct Drill Managed, were spun when number of nymphs on the plant was 888 (*Figure 10.11.*). These webs, woven at high aspects of the plant, caught no *S.*

avenae, only exuviae were recorded. The greater number of webs (n = 22) were identified in the Direct Drill Managed mesocosms at this stage, week five of the experiment. It appears much web-construction had occurred here in different spatial arrangements offered by the landscape heterogeneity of the mesocosm. Only thirty-five nymphs were caught in the webs in week four which showed little pest suppression occurring, *T. tenuis* not able to capitalise on the outlay of a woven web. *T. tenuis* required cues of *S. avenae* presence from small vibrations within the *H. vulgare* (Blackledge *et al.,* 2011; Glover, 2013; Hesselberg & Vollrath, 2006; Tew & Hesselberg, 2017). Number of plants was high (n = 18) and thus, it is hypothesised that *S. avenae* were able to disperse amongst the abundance of green material available and be less inclined to show wing polymorphism or drop, both stimuli for web-spinning (Kraft & Cookson, 2012).

8.9. Final Discussion - Effects of Soil Tillage Intensity on Prey Capture by *T. tenuis* in Mesocosms of *H. vulgare*

The use of straw, upright stubble and furrow dimensions, key to the difference in soil tillage, made little difference to *T. tenuis* activity throughout the growth of *H. vulgare* with both prey species. However, straw and upright stubble was shown to affect the placement of *S. avenae* in Direct Drill tillage and higher webs spun in this mesocosm because of this. This relates to both aims of this Chapter, one and four, discussed in Section 8.2.1. Direct Drill had little variation within the response variables. Web location was confined to the basal stratum of the habitat, identifying this may be the preferred location of *T. tenuis* when competition is low and resources plentiful. Low variation in anchor point height and thread length in Direct Drill showed that greater prey abundance led to increased accessibility to resources. Here both aims of this Chapter have been met (*Section 8.2.1*.)

It has been identified that *T. tenuis* dimensions do not directly relate to *T. tenuis* fitness, and thus the capability to ascend to greater heights and spin longer webs. It has been clear though that cephalothorax length may be a key parameter to understand an increase in energy output for *T. tenuis*, with leg movement controlled in this body segment. Interestingly, no *T. tenuis* rappelling was recorded. Exploratory behaviours appear to be limited, with the commencement of web-building beginning almost instantaneously. High web occupation expressed adequate capability of the web for prey capture, interception of prey was expected and a positive to biological control potential directed to the first aim (*Section 8.2.1*.).

The population growth of *S. avenae* differed in the mesocosms, temperature and fecundity observed as the main factors. This showed differences in web anchor height due to differences in cues intercepted by *T. tenuis*. Anchor point height followed prey movement, *T. tenuis* ability to spin webs of appropriate location enhanced prey capture and addressed the fourth aim of Section 8.2.1.

Chapter Nine

9.0. Effects of Primary and Secondary Cultivation on *T. tenuis* Behaviour Under Controlled Experimental Conditions: A Mesocosm Experiment

9.1. Introduction

After primary and secondary cultivation in the field, it was noted that landscape features differed on a large scale between the three intensities of soil tillage (*Section 5.1.5.1.2.*). Observations further noted differences in *T. tenuis* web-building and migratory behaviour within Conventional, Direct Drill Managed and Direct Drill. This was discussed as primarily due to landscape heterogeneity in the form of soil clods (Conventional) and the upright stubble and straw (Direct Drill). Direct Drill Managed, at times of cultivation, was shown to support low *T. tenuis* activity, thought to be due to increased landscape homogeneity with decreased straw and upright stubble abundance and lack of soil clod formation (*Section 5.1.6.1.2. & Section 5.1.6.1.3.*). To explore *T. tenuis* interaction with the landscape provided at cultivation in greater depth, it was useful to replicate the field habitats for the different cultivation intensities in a controlled experiment.

9.2. Aims and Specific Objections

9.2.1. Aims

This experiment was designed specifically to address Research Aim 2 (*Section 1.2.*, Page 2).

2. Identify any differences in extended phenotypes of *T. tenuis* within tillage practices, e.g. web dimensions and bridge thread length.

9.2.2. Specific Objectives

- Assess *T. tenuis* performance by measuring size and location of extended phenotypes and quantify bridging in the different landscape heterogeneity created by replicating primary and secondary cultivation of the different tillage intensities.
- Analyse whether body size of *T. tenuis* influences activity.

9.3. Methodology

This experiment used the mesocosms described in Chapter Eight. As noted in Section 7.4.2.1, all contents apart from the soil was cleared. *S. avenae* and *T. tenuis* were removed along with landscape features in *H. vulgare*, upright stubble and straw mass.

9.3.1. Primary Cultivation

To produce a surface that mimicked the field cultivations of Conventional and Direct Drill Managed, thought was given of how to represent the conditions left after the cultivators, within a mesocosm setting (*Section 3.1.3.4.*). The soil in the Conventional and Direct Drill Managed mesocosms (used in the previous Chapter) were cultivated once with a soil corer to replicate primary cultivation of the field (*Section 8.3.*). To recreate the action of the sub-soiler, the same process was used as in the mesocosms growing *H. vulgare*, an inverted soil corer, was penetrated to 25 cm for Conventional and 20 cm for Direct Drill Managed (*Section 8.3.*).

The twenty-nine soil clods, for Conventional, and twenty-six, for Direct Drill Managed, were formed with the garden trowel and by hand after cultivation with the soil corer (*Section 7.4.2.2.*). Greater clod heights were found within the Conventional area than Direct Drill Managed, due to greater depth of soil cultivation (*Figure 5.1.3, Section 5.1.5.1.2., Page 91*).

The corresponding mean straw mass, and total upright stubble was calculated from the sample plots of *H. vulgare*, 2017 / 2018 season after primary cultivation (*Figure 9.1a & b*) (*Table 5.1.1., Section 5.1.3.1., Page 82*). The upright stubble of Direct Drill had not been disturbed by the cultivator in the field and therefore remained in the crop rows (*Section 3.1.3.4.*). This was important to replicate in the mesocosms as discussed previously in the fieldwork within the time of primary cultivation, the orientation of the upright stubble could be key to promoting attachment to the upright stubble and subsequent web-building (*Section 5.1.6.1.2.*).

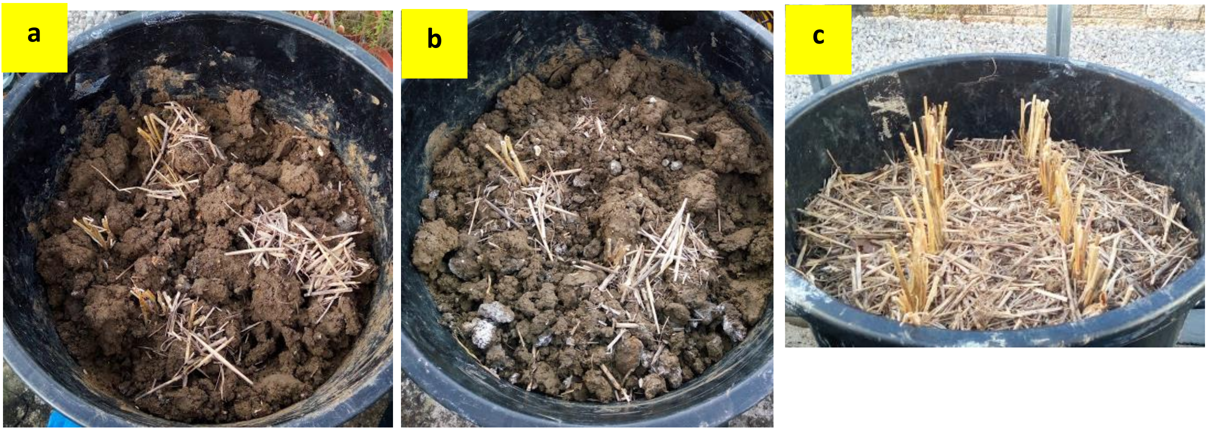


Figure 9.1a - c: Set-up of mesocosm of primary cultivation for effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment. a = Conventional. b = Direct Drill Managed. c = Direct Drill.*

Three adult female *T. tenuis* were measured, had mass determined and were placed into each mesocosm in the same manner as previous glasshouse trials (*Section 7.2.1. & Section 8.3.*). Three animals equate to the mean number of *T. tenuis* recorded per unit area of *H. vulgare* 2017 / 2018, twenty-four hours after primary cultivation (*Table 5.1.1.*).

The mesocosms were set as in Figure 9.2a - c with random placement as identified for previous mesocosm trials (Random.Org, 2018) (*Figure 8.3., Section 8.3., Page 228*). Plastic film, 60 µm thick, was attached over the surface with the use of tape, (3M Venture™ 921CW All Weather Translucent Tape) with care given to ensure no plastic creased or was damaged. One hundred pin prick-sized holes were zig-zagged across the surface to provide ventilation (*Figure 9.2a-c*). The trial ran for four days to ensure *T. tenuis* could explore their new environment and allow a web to be constructed in the best location. Extending the trial beyond four days was deemed irrelevant as all initial potential web construction should have commenced (Benjamin & Zschokke, 2003; Blackledge *et al.,* 2009; Segoli *et al.,* 2004; Zschokke & Herberstein, 2005).

Figure 9.2a - c: Set-up of mesocosm primary cultivation for effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment. a = Random sequence of Mesocosms. b = Direct Drill Managed enclosed. C = Direct Drill enclosed.*

9.3.2. Secondary Cultivation

This trial was set up in a similar way as the mesocosms of primary cultivation (*Section 9.3.1.*) but using similarities of variables relating to secondary cultivation. Data for variables relate to measurements collected from *H. vulgare* of the 2017 / 2018 season after secondary cultivation (*Table 5.1.1.*).

No change occurred in the Direct Drill mesocosms to replicate zero-till of the field (*Figure 9.3c*). All straw and upright stubble was removed from Conventional and Direct Drill Managed mesocosms. The mesocosms were cleaned of *T. tenuis* activity in thread spinning and web-building, extra care was taken to check the Direct Drill mesocosms for webs without disturbing the integrity of the landscape of the mesocosm (*Section 7.4.2.1.*).

Soil cultivation was carried out to mimic the disc harrow of secondary cultivation as in mesocosms which grew *H. vulgare* in the previous experiment (*Section 8.3*.). The disc harrow was simulated again with the use of a Saxton™ TCT Circular Wood Saw Blade (300 mm x 30 x 60 teeth) at a depth of 2 cm.

Twenty-nine clods were incorporated for Conventional and twenty-four for Direct Drill Managed (*Section 7.4.2.2. & Figure 9.3a & b*). Straw mass and total upright stubble incorporated into Conventional and Direct Drill Managed related to field data collected from this sampling period in 2017 / 2018 season (*Figure 5.1.1. & Figure 9.3a-c*). Three female *T. tenuis* (relating to mean number found in the field in this sampling period) were collected from g-vac and placed into the terrarium for twenty-four hours (*Section 7.2.1*.). *T. tenuis* were measured as in all previous glasshouse trials (*Section 7.2.2., Section 8.3. & Section 9.3.1.)* and then placed into each habitat. The trial ran for four days.

Figure 9.3a-c: Set-up of mesocosm secondary cultivation for effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment. a = Conventional. b = Direct Drill Managed. c = Direct Drill.*

9.4. Data Collection

Data collected included anchor point height and material used for attachment, web dimensions of support thread length and web area, and whether the web was occupied. These measurements related to *T. tenuis* activity, as discussed in the fieldwork methodology of Table 5.1.2. (*Section 5.1.3.2., Page 83*). As the focus of this trial was *T. tenuis* web-building activity in the landscape created after primary and secondary cultivation, anchor point height was measured against materials of the mesocosm that had become attachment sites. Temperature was taken to the nearest 0.1 °C with a Portable Pen Digital Thermometer WT-1B®immediately after the 'unveiling' of each mesocosm, taking care not to disrupt any web-building activity.

9.5. Statistical Analysis

Statistical analysis was carried out with Minitab18©. A Principal Component Analysis (PCA) was run to examine the power of variables on the results and associations formed. The two variables that were noted to have had the greater influence on the data, from the first and second component, were identified and placed into a scatter plot (Hawkins, 2014; Khan, 2013).

All data in this glasshouse experiment (primary and secondary) was found to be normal through normality testing (*Section 5.1.4.1.*). One-way ANOVA was applied to understand if any significant difference existed between the means of independent variables measured from the three different areas of soil tillage intensities (Conventional, Direct Drill Managed and Direct Drill) (Zuur *et al.,* 2007). As data was tested as normal, the multiple comparison test used was Tukey. Pearson's (r) testing was applied for correlation analysis.

Multiple regression models were built using the stepwise backward elimination method discussed previously in Section 5.1.4.2. & Section 6.4. The regression model identified which continuous and categorical predictors held significant influence over a measured response (anchor point height, thread length and web area) (Wheater *et al.,* 2011). Steps were analysed to understand which predictors were removed from the model and how this strengthened the model's reliability. The R^2 (adj) value is reported to identify how well the data of the response fits the values given within the model (Bass, 2007; Khan, 2013).

For both multiple regression and two-way ANOVA, the Variance Inflation Factors (VIF) and standard error of the coefficient was considered. A term with a VIF >5 was removed from the model as this indicated multicollinearity within the term, where a term can be readily predicted from use of the other predictors in the model. This can disrupt any real influence on the response. The standard error of the coefficient was evaluated, a high value signalled high deviation was present from the coefficient, this lowering the validity of the coefficient (Hawkins, 2014; Khan, 2013).

9.6. Results

All anchor point heights and thread lengths relate to support threads that were within webs. Only eight bridge threads were identified in the primary cultivation trial and six with the secondary cultivation trial and held no significance between soil tillage intensities.

9.6.1. Summary of Results

Primary Cultivation

- Mean abdomen length and mean soil clod height influenced the variance of data in different directions in the first principal component of the PCA (*Figure 9.4*).
- Mean abdomen length, straw mass, and straw and upright stubble as attachment materials, influenced anchor point height (*Figure 9.6. & Table 9.2*.). Direct Drill held the significantly higher anchor point height and longer thread length (*Figure 9.5*. & *Figure 9.7*.).
- Thread length was significantly positively correlated to mean cephalothorax length (*Table 9.3*.).

Secondary Cultivation

- Number of upright stubble and temperature held significant positive regression to anchor point height within webs (*Table 9.5. & Figure 9.9*.). Soil and straw, as attachment materials, were significantly negative predictors to the response anchor point height (*Table 9.5*.).
- Mean web area held the most influence over the data within the Conventional mesocosms. Direct Drill mesocosms were affected the most by number of upright stubble (*Figure 9.8*.).
- Web area was significantly positively correlated to temperature and mean *T. tenuis* mass (*Table 9.6*.).

9.6.2. Primary Cultivation

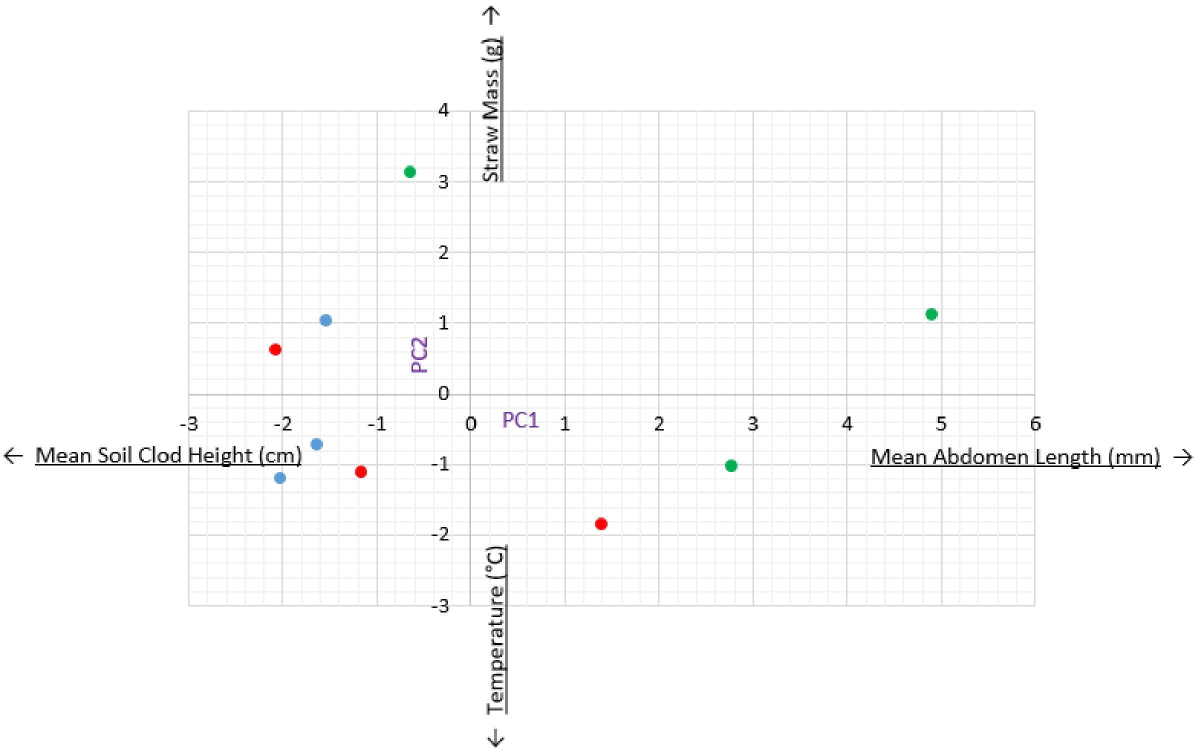


Figure 9.4: PCA of variables measured in primary cultivation along the first two principal components and variables correlating to each component. Effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment. (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green).*

Table 9.1: The variance in data for primary cultivation explained by principal component 1 and principal component 2 and associated eigenvalues for the variables which held the most influence within the data in each component. Effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment.*

	Principal 1	**Principal 2**
Variance	47.1%	19.7%
Variables	**Eigenvalue**	**Eigenvalue**
Mean Abdomen Length (mm)	0.355	
Mean Soil Clod Height (cm)	-0.207	
Straw Mass (g)		0.316
Temperature (°C)		-0.409

Mean soil clod height affected data in the opposite direction to mean abdomen length of *T. tenuis*, it appeared to have had greater influence over the data collected in the Conventional and Direct Drill Managed mesocosms than mean abdomen length (*Figure 9.4. & Table 9.1.*). The opposite was found for the data within the Direct Drill mesocosms where mean abdomen length influenced the data away from mean soil clod height. Straw mass appeared to have affected the datasets of Direct Drill the most.

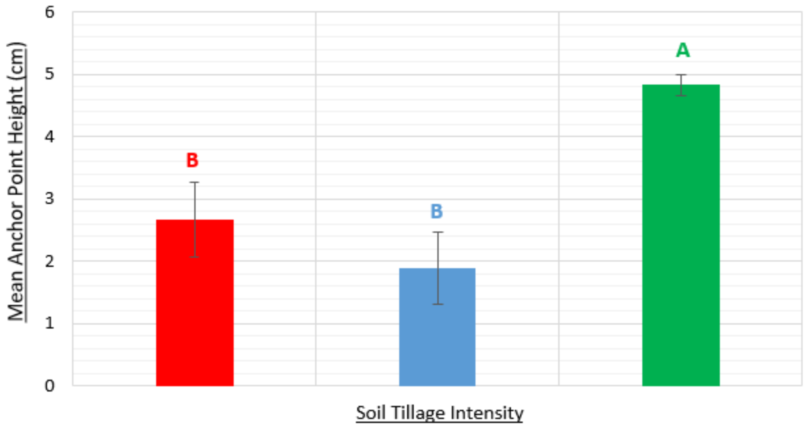


Figure 9.5: Mean anchor point height (cm) for soil tillage intensity in primary cultivation. Effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment. (n = 130, P - 0.001). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green) Conventional ±s.e.3.604 (n = 35), Direct Drill Managed ±s.e.1.413 (n = 64), Direct Drill ±s.e.3.70 (n = 41)). (Bars that do not share a letter are significantly different at the p<0.05 level).*

Mean anchor point height was significantly higher in the Direct Drill Mesocosms at 4.8 cm compared to 2.6 cm for Conventional and 1.9 cm for Direct Drill Managed (*Figure 9.5*).

Table 9.2. Significant predictors to the response anchor point height (cm) in primary cultivation. Effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment. (n = 130, R-sq - 61.36%). (* relates to significant with α <0.05).*

Continuous Predictor	**Categorical Predictor**	**Coefficients**	**Standard Error Coefficients**	***T***	***P***	**VIF**
Mean Abdomen Length (mm)		6.03	1.68	3.60	0.001*	2.03
Straw Mass (g)		0.01773	0.00794	2.23	0.027*	2.45
	Attachment Material					
	Soil	-1.954	0.506	-3.86	0.001*	2.12
	Straw	-3.705	0.599	-6.19	0.001*	1.85
	Upright Stubble	2.724	0.709	3.85	0.001*	1.60

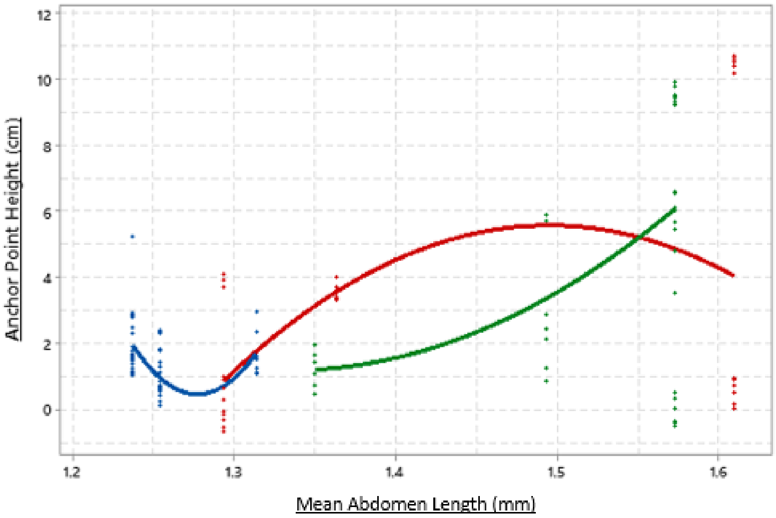


Figure 9.6: Matrix plot with quadratic regression and intercept fitted for anchor point height (cm) with mean abdomen length (mm) in primary cultivation. Effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions. (n = 130, R-sq - 61.36%). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green).*

The continuous predictors of mean *T. tenuis* abdomen length and straw mass significantly positively influenced the response (*Table 9.2.*). The categorical predictor of attachment material of the anchor point further significantly influenced anchor point height described for the materials of straw, upright stubble, and soil. Straw and soil a significant negative predictor. A shallow and wide parabola exists for mean abdomen length for Direct Drill and Conventional, identifying a general trend where a small range of anchor point heights were recorded over a large range of values for the x variables (*Figure 9.6.*). For the mean *T. tenuis* abdomen length from the Conventional mesocosms, the parabola is open downwards giving a maximum vertex (anchor point height) reached at an abdomen length of 1.5 mm. Straw mass held the same value within each soil tillage intensity respectively, thus was not present on the graph.

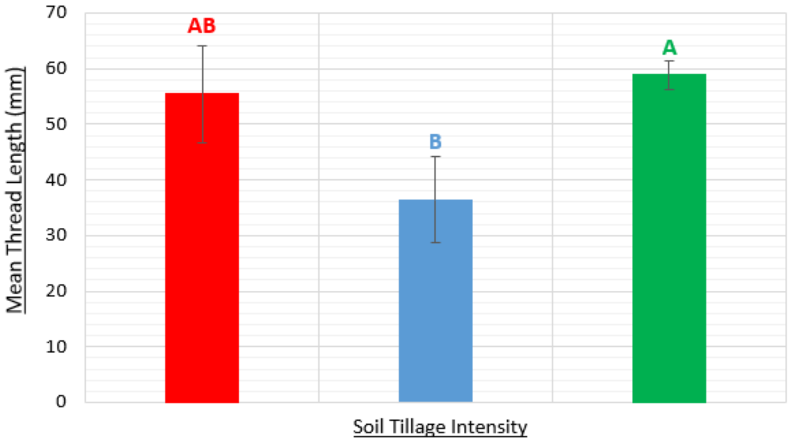


Figure 9.7: Mean thread length (mm) in primary cultivation. Effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment. (n = 130, P - 0.005). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green) (Conventional ±s.e.8.6670 (n = 35), Direct Drill Managed ±s.e.2.634 (n = 64), Direct Drill ±s.e.7.722 (n = 41)). (Bars that do not share a letter are significantly different at the p<0.05 level).*

Direct Drill mesocosms showed a significantly longer mean thread length, 3.4 mm greater than Conventional and 12.5 mm greater than Direct Drill Managed (*Figure 9.7*). Direct Drill Managed mean thread length was significantly shorter than Direct Drill.

Table 9.3: Correlations of independent variables measured in mesocosm, with the dependant variable thread length (mm) in primary cultivation. Effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment. (n = 130). (* relates to significant with α <0.05).*

	(r)	***P***	**df**
Mean Abdomen Length (mm)	0.320	0.001*	128
Mean Cephalothorax Length (mm)	0.277	0.001*	128
Straw Mass (g)	0.184	0.035*	128

Length of support threads was significantly positively correlated against mean *T. tenuis* abdomen and cephalothorax length placed into the mesocosms, and straw mass incorporated into the mesocosms.

9.6.3. Secondary Cultivation

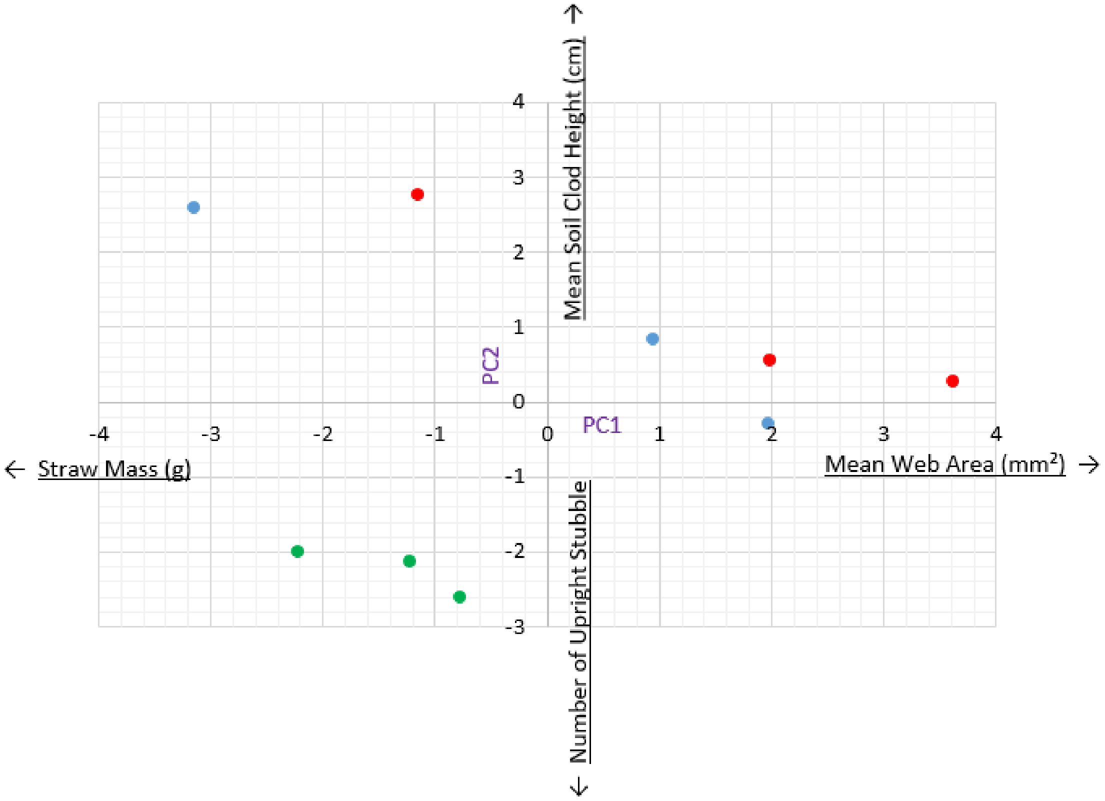


Figure 9.8: PCA of variables measured in secondary cultivation along the first two principal components and variables correlating to each component. Effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment. (Conventional = Red, Direct Drill Managed = Blue and Direct Drill = Green).*

Table 9.4: The variance in data for secondary cultivation explained by principal component 1 and principal component 2 and associated eigenvalues for the variables which held the most influence within the data in each component. Effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment.*

	Principal 1	**Principal 2**
Variance	45.6%	35.2%
Variables	**Eigenvalue**	**Eigenvalue**
Mean Web Area (mm^2)	0.394	
Straw Mass (g)	-0.206	
Mean Soil Clod Height (cm)		0.356
Number of Upright Stubble		-0.435

Data recorded within the Direct Drill mesocosms was affected the greatest by number of upright stubble (*Figure 9.8. & Table 9.4.*). It appears that mean web area held more influence over the data recorded within the Conventional mesocosms than mean soil clod height. Straw mass was holding influence over the Direct Drill mesocosms more than the other two soil tillage intensities.

Table 9.5: Significant predictors to the response anchor point height (cm) in secondary cultivation. Effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment. (n = 230, R-sq - 29.98%). (* relates to significant with α <0.05).*

Continuous Predictor	**Categorical Predictor**	**Coefficients**	**Standard Error Coefficients**	***T***	***P***	**VIF**
Number of Upright Stubble		0.03119	0.00599	5.21	0.001*	2.82
Temperature (°C)		0.332	0.115	2.89	0.004*	1.17
	Attachment Material					
	Straw	-1.640	0.391	-4.19	0.001*	1.95
	Soil	-1.165	0.274	-4.25	0.001*	1.81

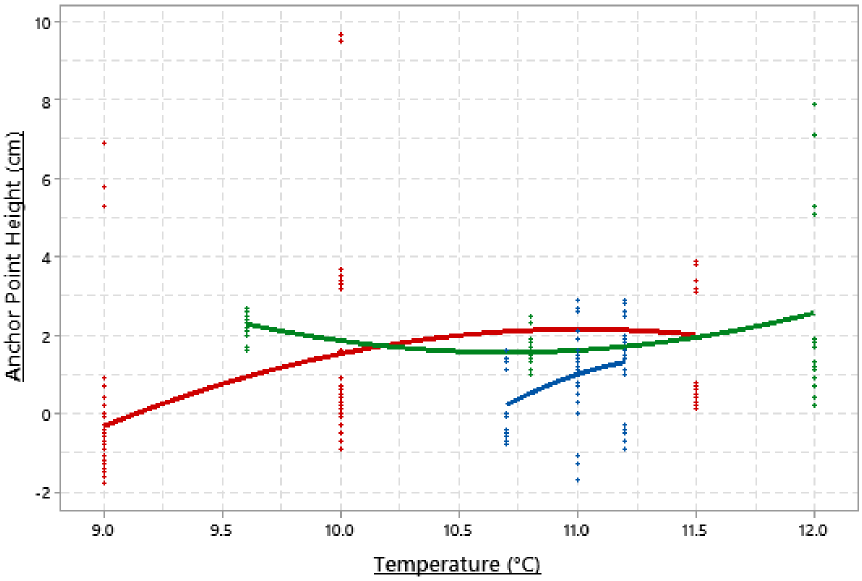


Figure 9.9: Matrix plot with quadratic regression and intercept fitted for anchor point height (cm) with temperature (°C) in secondary cultivation. Effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment. (n = 230, R-sq - 29.98%). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green).*

Number of upright stubble and temperature were both significantly positive in a regression model when the response was anchor point height of support threads (*Table 9.5*.). The attachment materials of soil and straw both held significant negative regression. The weak open upwards parabola for Conventional explains the higher anchor point height was established when temperature was not at is highest (*Figure 9.9*.). For Direct Drill, like with Direct Drill Managed, the greater temperature found the higher anchor point height, though the regression was weak.

No graphical representation is found for the predictor of number of upright stubble due to the same number of upright stubble placed into each mesocosm representing soil tillage intensity.

Table 9.6: Correlations of independent variables measured in mesocosm, with the dependant variable web area (mm^2) in secondary cultivation. Effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment. (n = 41) (* relates to significant with α <0.05).*

	(r)	***P***	**df**
Mean *T. tenuis* Mass (g)	0.497	0.001*	39
Temperature (°C)	0.213	0.001*	39

Both temperature and mean *T. tenuis* mass were significantly positively correlated to web area (*Table 9.6.*).

No regression model for thread length or web area could be attained due to extreme values in the standard error of the coefficients.

9.7. Discussion

9.7.1. Primary Cultivation

T. tenuis abdomen length had a key role in web construction, in design and location within the individual mesocosms (*Figure 9.4. & Figure 9.6.*). The abdomen of *T. tenuis* is where the spinnerets are organised and silk is produced and spun into threads (Saravanan, 2006). When *H. vulgare* was grown in the mesocosms, the larger the abdomen of the female *T. tenuis,* the more able to exert strain onto the thread when it is laid producing a longer stable thread, able to anchor securely at a greater height (Brunetta & Craig, 2010; Saravanan, 2006) (*Section 8.7.2.*). The second, third and fifth-longest mean abdomens were randomly placed into the Direct Drill mesocosms, the mesocosms containing the greater straw mass (*Figure 9.3c., Figure 9.4., Figure 9.6 & Table 9.2.*). The increased straw mass on the soil surface, provided greater anchor point height potential for threads in Direct Drill than the soil clods of the other soil tillage intensities where some soil features were below surface height (*Figure 9.5.*). This agreed with Diehl *et al.* (2013) and Thomson & Hoffmann (2007) who identified that an increase in straw mulch led to higher Linyphiidae abundance due to the straw use as a shelter. All anchor points connected to straw in Direct Drill were part of a small web concealed by straw, which may indicate that *T. tenuis* was taking refuge with no apparent prey availability (*Figure 9.10.*). This followed the trend measured in the field where straw was used as refugia within primary cultivation (*Section 5.1.6.1.2.*). Therefore, greater anchor point height may not be due to increased abdomen length of the female *T. tenuis* but simply the availability of material used to establish threads.

Figure 9.10: Sheet web created in the straw and upright stubble of Direct Drill in primary cultivation. Effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment. Lateral view. (Yellow arrow = 21.1 mm).*

Increased landscape features (straw mass and upright stubble) allowed longer support threads and subsequently larger webs to be anchored higher within the Direct Drill Mesocosms (*Table 9.3. & Figure 9.7.*). These webs were anchored to the plastic container, as well as the straw and upright stubble. The plastic container can be viewed as an extension to the mesocosms where the presence of the straw and stubble allowed the container to be utilised further. This supports the idea that landscape heterogeneity can increase Linyphiidae silk weaving output through the creation of differing anchor points in height and material (Badenhausser *et al.,* 2020; Miyashita *et al.,* 2012; Öberg & Ekbom, 2006; Thorbek & Topping, 2005). Indeed, the limited number of upright stubble and straw mass incorporated into the Conventional mesocosms allowed large support threads to be spun at a greater height attached from the apex of the stubble to the side of the container (*Figure 9.4.*). Furthermore, two different strata of web anchorage were identified against mean abdomen length in the Conventional mesocosms (*Figure 9.6.*). The *T. tenuis* with greater abdomen length was found under the web attached to upright stubble in Conventional, further referencing the point that larger abdomen lengths aid a *T. tenuis* into ascension. The remaining two *T. tenuis* in this mesocosm were found to be <0.20 mm smaller. Houser *et al.* (2016), Řezáč & Řezáčová (2019) and Thorbek & Bilde (2004) note that female *T. tenuis* are highly competitive and a small increase in body size can produce an act of dominance, utilisation of the upright stubble as the prime web-site for potential prey capture when no stimuli of prey was present in the mesocosms.

Increased flexion from a larger cephalothorax has allowed longer thread lengths to be spun (Huber, 2004; Prenter *et al.,* 2010) (*Table 9.3.*). The effect of a larger cephalothorax was viewed in the previous glasshouse experiment where *S. avenae* was incorporated into a growing *H. vulgare* crop (*Section 8.7.2.*).

The soil features of the mesocosms, appear to have influenced data recorded in the opposite direction than abdomen length (*Figure 9.4*.) This led to the attachment material of soil holding a significant term in influencing anchor point height (*Figure 9.5*.). *T. tenuis* as a 'sit and wait' predator' do not forage along a soil surface, thus are behaviourally adapted to avoid construction of a web flush with the soil surface or within a crevice, opting for a web-site higher within the habitat. This allows aerial prey, that fall into webs in a higher degree than ground-dwelling prey, chance to intercept the web (Harwood *et al.,* 2003; Harwood & Obrycki, 2005; Pfister *et al.,* 2015) (*Section 2.1.3.1*.). The result may relate to the fact that the mean lowest abdomen length*,* was incorporated into the Direct Drill Managed mesocosm which held the least straw and upright stubble for potential anchor points (Wise 2006). It is likely that intra-specific completion, led *T. tenuis* of smaller mass to create webs in less attractive web-sites closer to the soil surface, anchoring threads to soil to avoid cannibalism (Romero & Harwood, 2010; Wise, 2006).

9.7.2. Secondary Cultivation

Anchor point height was not significant between mesocosms representing soil tillage intensities, which was a different result from the time of secondary cultivation in the field (*Section 5.1.5.1.3*.). This was an unusual result as through fieldwork and within the previous mesocosm trial of *H. vulgare* with *S. avenae*, anchor point showed a significant difference to subtle alterations in landscape complexity (*Section 5.1.6.1.3. & Section 8.7*.). The upright stubble and straw through these earlier trials and in the field, were shown to significantly influence anchor point height when the field was cultivated or in early growth stages of crop, providing key anchor materials (Harmer *et al.,* 2011; Moya-Laraño, *et al.,* 2008; Schütt, 1997; Szymkowiak *et al.,* 2007). It appears that in each mesocosm replicating soil tillage intensity, the architecture of landscape features was of enough intricacy to provide an abundance of attachment opportunities at various heights (*Table 9.5*.). Aaserud (2005), Dennis *et al.* (2001) and Glover (2013) describe that an attractive web-site is formed from an abundance of possible anchor sites, the material form of which is of less importance if an abundance exists.

Soil features appear to have more influence over *T. tenuis* web-building within the secondary cultivation, than the primary cultivation (*Figure 9.11a & b*). This suggested an increase in soil clod height created a suitable habitat for *T. tenuis,* allowing a greater height difference to be gained between soil surface and top of soil clod (*Table 9.5*.). Sunderland & Samu (2000) identified that *T. tenuis* occupied holes in the soil up to 9.5 cm in diameter. Conventional held the greater mean soil clod height, therefore driving the placement of mean soil clod height in principal component one (*Figure 9.8*). The difference in height may allow *T. tenuis* to construct a web, to occupy a solitary space and be at a suitable height above the surface to allow for 'sit and wait' predation (Alderweireldt, 1994;

Bell *et al.,* 2001; Harwood *et al.,* 2003; Harwood & Obrycki, 2005). Interestingly, straw held a negative coefficient in the regression model explaining the response of anchor point height (*Table 9.5*.). This is an unusual result, with at times of fieldwork the straw residue increasing height of anchorage by providing an additional layer (*Section 5.1.6.1*.). This was due to negative values of anchor point heights attached to straw found in the Conventional mesocosms, straw residue naturally falling into crevices revealed by the formation of the soil clods. Campbell *et al.* (2020) and Pfingstmann *et al.* (2019) note that Linyphiidae are highly sensitive to difference in material composition for anchorage. *T. tenuis* perhaps choosing to attach to soil and straw to manipulate spinning silk in favourable orientations, straw residue noted to offer extensions into an area.

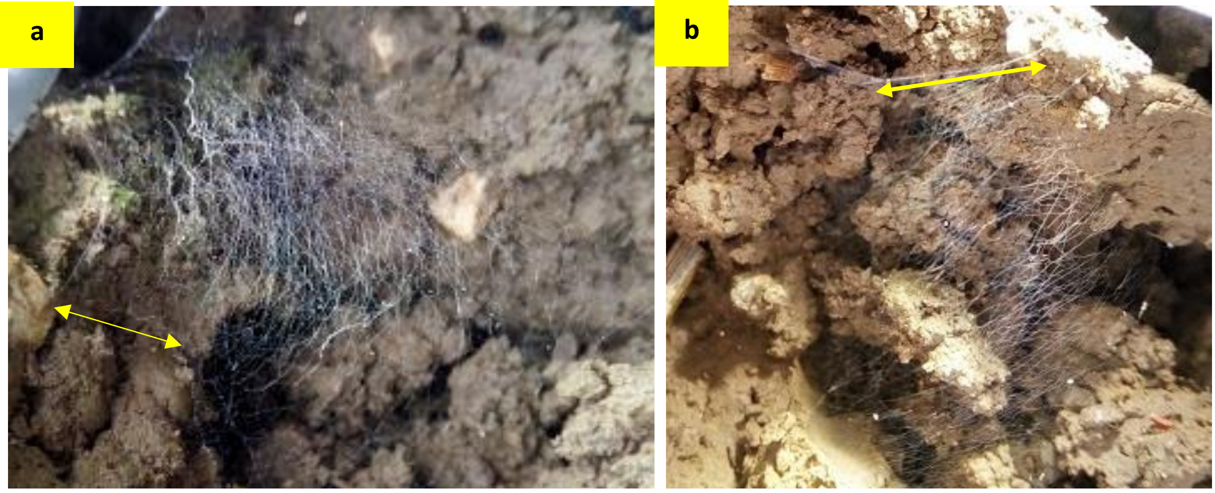


Figure 9.11a & b: Sheet webs created in between soil clods of Conventional mesocosms in secondary cultivation. Effects of primary and secondary cultivation on T. tenuis *behaviour under controlled experimental conditions: a mesocosm experiment. Elevated view. (a: Yellow arrow 33.3 = mm b: Yellow arrow = 30.2 mm).*

Unlike primary cultivation mesocosms, the greatest mean web area was identified in Direct Drill Managed and Conventional (*Figure 9.8*.). Smaller webs were created in the Direct Drill mesocosms of secondary cultivation, the majority at the base of the upright stubble attached to the surrounding straw. This agrees with web creation identified in field Direct Drill plots (*Section 5.1.5.1.4*.). In the Conventional and Direct Drill Managed mesocosms, the materials available for anchorage were observed to be of a greater distance apart, which may have resulted in the larger webs. The thread length increased as *T. tenuis* spun thread from one potential anchor point to the next (Rusch *et al.,* 2016; Schellhorn *et al.,* 2014). This explained the greater mass of straw in Direct Drill pulling data away from the web area (*Figure 9.8*.). The opportunity to allow webs of a greater area to be spun may be beneficial in an agricultural setting. The larger surface area to ensnare ground-dwelling prey may assist Linyphiidae to remain *in-situ* until a crop is seeded (Birhofer *et al.,* 2008; Jansen *et al.,* 2013; Oxbrough *et al.,* 2006)

The absence of larger *T. tenuis* webs amongst the soil clods of the primary mesocosm, may have been due to the short mean abdomen length placed into the Direct Drill Managed mesocosms, preventing long threads being strained correctly to yield a high abundance of silk at one time (De Meester & Bonte, 2010; Vollrath *et al.,* 2001). Level of fitness, not measured, for *T. tenuis* incorporated in both mesocosm trials may correspond to whether a *T. tenuis* is able to spin a large web between anchor points of a certain distance (Vollrath *et al.,* 2001).

There was no significance identified between thread lengths and web area between the mesocosms of differing soil intensity. It appears that in each secondary cultivation simulation; *T. tenuis* were spinning webs of differing dimensions in a multitude of spatial orientations available. In Direct Drill Managed, five threads < 10 mm were identified in between a small amount of upright stubble within the mesocosm. These were identified as rappel threads and exhibited possible web-site searching by a *T. tenuis* (Bonte *et al.,* 2008; De Meester & Bonte, 2010). It may be possible that the upright stubble was a preferred web-site, though after exploration it was viewed that the limited stubble present could not support a web (Horváth *et al.,* 2015; Rusch *et al,* 2016). No webs were observed solely amongst the upright stubble of the Conventional and Direct Drill Managed mesocosms of secondary cultivation. The energy of rappelling here appears to have been at a cost with no web established (Bonte, 2013). Knight & Vollrath (2002) and Kraft & Cook (2012) discuss webs spun with ease are that which fluidly glide across material of similar height and structure.

Increased mass of *T. tenuis* was an indicator of positive nutritional content before the *T. tenuis* was incorporated. This may mean that the *T. tenuis* had a higher degree of energy at its disposal to produce a larger web (Ford, 1977; Harwood *et al.,* 2003; Segoli *et al.,* 2004) (*Table 9.6*.). *T. tenuis* mass was not significantly different amongst the mesocosms. It was observed that the mean higher mass was placed into a Conventional and a Direct Drill Managed mesocosms where the large webs were spun amongst the soil clods. It may have been that the energy for increased nutritional content, allowed webs to be spun in a landscape lacking in anchor point sites. Thread length was required to yield more strength, as stretched in distance between anchor points (Blackledge & Eliason, 2007; De Meester & Bonte, 2010; Harwood *et al.,* 2003; Vollrath *et al.,* 2001).

Temperature recorded ranged from 9 to 12 °C, it appears that a small difference in temperature affected the thread length that was spun and the anchor point height of the thread (*Table 9.5., Table 9.6. & Figure 9.9.*). Hesselberg & Vollrath (2012) and Shehata *et al.* (2019) identified that a small increase in temperature can ease the strain required for major ampullate silk to be extended to the correct tension for proteins to dis-form and organise into functional units (Craig, 2003; Tokareva *et al.,* 2014) (*Figure 2.3a, Section 2.1.2.1., Page 10*). Additionally, Japyassú & Laland (2017), Stenchly *et* *al.* (2011) and Tokareva *et al.* (2014) discuss that, if a greater yield of piriform silk can be obtained, attachment discs, which anchor thread to substrate, can be laid in a greater thickness (*Figure 2.3c, Section 2.1.2.1., Page 11*). Thus, the anchor point of the thread will be attached with increased security, allowing longer silk to be held tightly at a greater height. Temperature has been shown to ease energy commitment required to yield piriform silk (Craig, 2003; Humphreys, 1991; Vollrath *et al.,* 2001; Zhang & Tso, 2016).

9.8. Final Discussion - Effects of Primary and Secondary Cultivation on *T. tenuis* Behaviour Under Controlled Experimental Conditions: A Mesocosm Experiment

The clear difference was the material favoured by *T. tenuis* for anchor points, and subsequent web construction. In primary cultivation, the increased number of upright stubble and straw mass enabled the highest *T. tenuis* activity in web construction, to be in the Direct Drill mesocosms. For the secondary cultivation trial, the soil physical features in the clods provided the material for most anchor points. Both points meet the research aim of this Chapter (*Section 9.2.1*.).

The running themes through both cultivation mesocosms, identify that the different tilled environments provide different landscape heterogeneity, in the materials available for anchor points. If appropriate materials are provided for successful web construction, *T. tenuis* of differing dimensions use material provided in different ways. This may be due to low nutritional content or temperature which may alter ability to extend silk to the correct degree to lay a support thread from one potential anchor point to the next.

Chapter Ten

10.0. *T. tenuis* Behaviour with Different Soil Tillage Intensities and Different Abundances of Cereal Aphididae: A Microcosm Experiment

10.1. Introduction

To support information gained from field sampling, it was deemed beneficial to carry out an experiment on *T. tenuis* behaviour that incorporated different densities of a cereal Aphididae. Within early and later growth stages for *H. vulgare*, 2017 / 2018 season of fieldwork, it was seen that web-building may have been driven by increased prey density in all soil tillage intensities (*Table 5.1.1., Section 5.1.3.1., Page 82, Section 5.1.6.2.1. & Section 5.1.6.2.2.*). Therefore, this trial was set-up to investigate whether *T. tenuis* activity is influenced to a higher degree by cereal Aphididae population size, or the level of intensity of soil tillage applied. In this experiment, *T. aestivum* was used as the cereal crop (*Section 7.5.2.1.*).

10.2. Aims and Specific Objectives

10.2.1. Aims

This experiment was set-up to address Research Aims 1, 2, and 3 (*Section 1.2., Page 2*).

1. Identify the potential biological control by *T. tenuis* of Aphididae within different intensities of tillage in an arable crop.
2. Identify any differences in extended phenotypes of *T. tenuis* within tillage practices, e.g. web dimensions and bridge thread length.
3. Understand whether *T. tenuis* behaviour is stimulated by the presence of Aphididae.

10.2.2. Specific Objectives

Specific objectives were to:

- Quantify *M. dirhodum* abundance in each microcosm to explore reproductive fitness of *M. dirhodum* in the microcosms mimicking differing intensities of soil tillage.
- Measure *T. tenuis* behaviour in web-building and rappelling and relate this to *M. dirhodum* density and location.
- Observe *T. tenuis* prey capture ability by measuring *M. dirhodum* abundance in webs.
- Analyse if *T. tenuis* body dimensions affect its web-building and bridging behaviour.

10.3. Methodology

To permit observations at an appropriate scale, smaller arenas were desirable. Therefore mesocosms (*Chapter 8.0. & Chapter 9.0.*) were replaced with more appropriate microcosms. These were created using flowerpots with dimensions of 19 cm circumference and 15 cm height. Soil used was Hanslope series, collected from the corresponding soil tillage areas of the NIAB fields and added to a height of 11.5 cm in the microcosms before any simulated tillage was applied (*Section 3.1.3.4.*).

Note, *T. aestivum* was chosen for this experiment as both *T. aestivum* and *H. vulgare* were examined in the field. However, due to similarities re *T. tenuis* behaviour, only fieldwork relating to *H. vulgare* has been presented (*Section 7.5.2.1.*).

Soil tillage was carried out on Conventional and Direct Drill Managed microcosms with small equipment (trowel and small domestic rotating disc) and applied twice at different depths to simulate primary (10 cm) and secondary cultivations (8 cm) (*Section 3.1.3.4.*). Furrows were made after simulating tillage, of the dimensions corresponding to fieldwork of *T. aestivum* 2017 / 2018 season after secondary cultivation and *T. aestivum* seeds drilled. Furrows were created after the soil had been tilled (*Figure 10.1.*).

Figure 10.1: Furrows implemented in microcosms after secondary tillage and seeds have been drilled. T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment. Top Row = Direct Drill. Middle Row = Conventional. Bottom Row = Direct Drill Managed.*

Straw and stubble corresponding to data collected in *T. aestivum* 2017 / 2018 season GS 11 - GS 15 of the different tilled areas were incorporated into the pots (*Figure 10.2.*). *T. aestivum* used was FrontierLTD Cordinally™, seeds were collected from the NIAB trial field in the 2016 / 2017 season and dressed with Redigo Pro® (Bayer), a triazole fungicide with active substances of prothioconazole and tebuconazole. Seeding was 15 cm apart horizontally, and 2 cm apart vertically, in rows, as used in the field. The experiment was set up in August 2018.

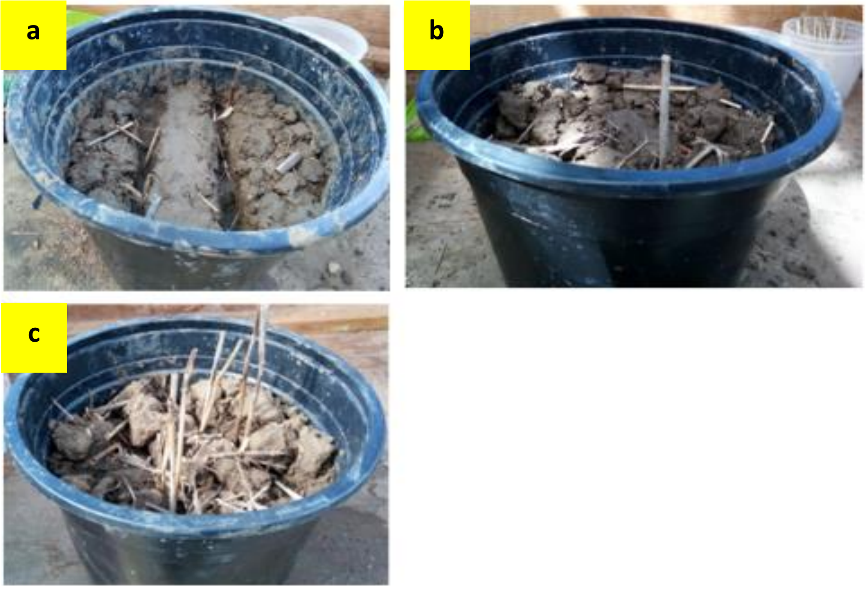


Figure 10.2a - c: Addition of straw and upright stubble in microcosms. T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment. a = Conventional. b = Direct Drill Managed. c = Direct Drill.*

The experiment ran until one *T. aestivum* plant within a microcosm reached 40 cm in height (GS 41 - GS 45). *T. aestivum* has a slow growth rate compared to *H. vulgare* and anthesis would not have occurred until the following spring after a period of over-wintering (AHDB, 2018). Data from fieldwork of *T. aestivum* in 2016 / 2017 and 2017 / 2018 seasons showed no significant differences in *T. tenuis* activity with the different tillage areas after a height of 40 cm. It was therefore determined that data collected after a height of 40 cm would add no further information to this investigation.

Thin polythene sheet (60 µm thick) was wrapped around the outside of the pots and attached externally to bamboo canes (*Figure 10.3. & Figure 10.4.*). The sheet reached 70 cm above the top of the pot to allow for adequate *T. aestivum* growth. An upper surface was created with a fine mesh (holes 0.28 mm x 0.79 mm), preventing movement of Aphididae out of the microcosm, if alate morphs were produced. A small window (5 x 5 cm) was inserted into the plastic to allow *T. tenuis* to be incorporated into the centre of the microcosm and Aphididae to be placed under the emerging crop. Corresponding to data collected in a *T. aestivum* 1m^2 sample at GS 11 - GS 15, three female *T. tenuis* were placed into each microcosm, after a period of twenty-four hours in the terrarium and body dimensions measured (*Section 7.2.1 & Section 7.2.2.*).

Microcosms were maintained in a glasshouse, but an irrigation system was not deemed necessary due to their small habitats. A plant tray, kept watered to the level of the base of the pot, was sufficient to maintain soil moisture in the correct parameters (*Figure 10.4., Section 2.2.2. & Section 8.3.*).

Figure 10.3: Direct Drill microcosm with polythene. T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment.*

Figure 10.4: Set-up of T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment.*

As with the mesocosm experiment incorporating *S. avenae,* Aphididae nymphs had masses determined on small pieces of pre-weighed *T. aestivum* and placed into the microcosms after one plant had emerged (GS 21) in one microcosm mimicking each soil tillage intensity (*Section 7.2.4. & Section 8.3.*). The piece of *T. aestivum* was laid next to the highest plant emerging to give each *M. dirhodum* nymph the greater chance of survival (Bonkowski *et al.,* 2001).

Twenty-seven microcosms were prepared, nine relating to each soil tillage intensity. Three microcosms from each tillage had no *M. dirhodum*, three had two *M. dirhodum* and three had six *M. dirhodum* nymphs incorporated (*Figure 10.5a & b & Section 7.5.2.2.*). The numbers one to twenty-seven were placed into a random number generator to identify a sequence (Random.Org, 2018). The microcosms were placed into that sequence on the workbench from left to right (*Figure 10.5a & b*).

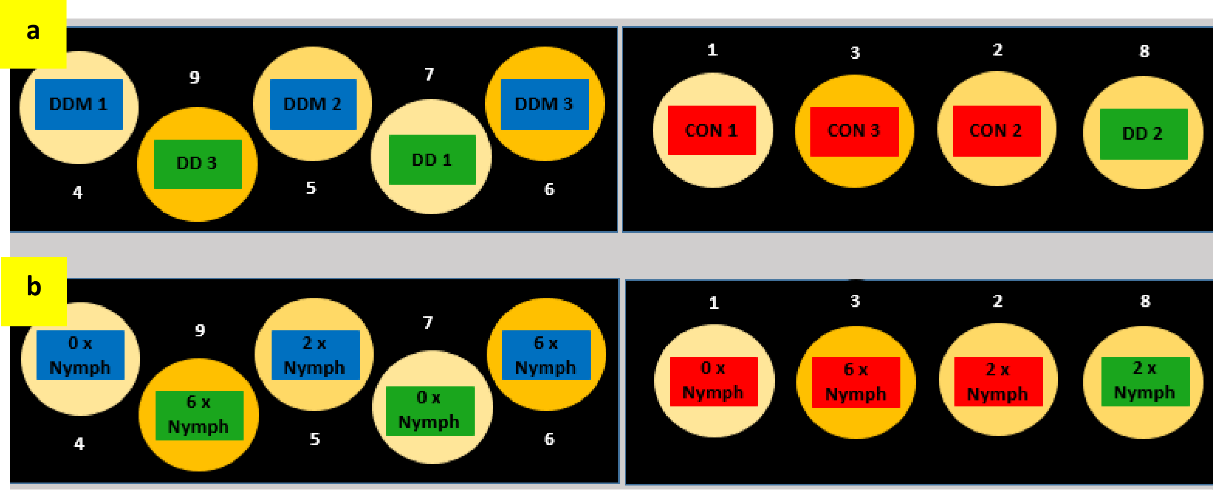


Figure 10.5a & b: Schematic diagram showing arrangement of T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment. a = Soil tillage intensity. b = Number of* M. dirhdoum *nymphs placed into each microcosm at the start of the trial. (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green).*

10.4. Data Collection

All measurements were recorded at the end of the experiment when one *T. aestivum* plant in each soil tillage intensity reached a height of 40 cm. Data collection followed the pattern of the previous glasshouse experiments and fieldwork with thread length to the nearest 0.1 mm and height of anchor point to the nearest 0.1 cm measured (*Table 5.1.2., Section 5.1.3.2., Page 83, Chapter 8.0. & Chapter 9.0.*). Complex web structures were divided into shapes for area calculation using Heron's formula (*Section 4.3.4.*). Web occupation was recorded to assess web-site selection. Number of *M. dirhodum* nymphs and adults were counted on the crop to establish fecundity. Webs were analysed for *M. dirhodum* presence, adult and nymph, and exuviae identified which sought to analyse prey capture ability of *T. tenuis* in each microcosm. Temperature of microcosms was recorded every seven days to the nearest 0.1 °C with a Portable Pen Digital Thermometer WT-1B™. Mean temperature was calculated for each microcosm.

10.5. Statistical Analysis

A PCA was run to examine the association between variables and where the most influence lay in the dataset. The first two principal components are reported (Bass, 2007; Khan, 2013).

After normality testing and analysing pattern of distribution with a histogram and probability plot, the data was concluded as non-normal (*Section 5.1.4.1.*). Therefore two-way rank ANOVAs assessed differences in means of variables measured within the different treatments of soil, the anchor point attachment material utilised and Aphididae abundance incorporated into the microcosms (Hawkins, 2014; Zuur *et al.,* 2007). FCSTats V2_1a© was used to find significance with Dunn's post-hoc test (Wheater & Cook, 2000). Bonferroni post-hoc test on the rank data, run on Mintab18©, found the letters to represent the significance (*Section 5.1.4.2.*). Spearman's Rank (Rho) correlation examined whether a significant, positive or negative, relationship existed between variables measured when normality was not present. Software used was Minitab18© (Bass, 2007; Wheater *et al.,* 2011).

A stepwise backwards method was utilised to create multiple regression models, in Minitab18©, analysing significance in the independent variables to the response of dependant variables recorded (anchor point height, thread length and web area). The formation of this regression model followed that created in Section 6.4. for BYDV occurrence in the field. Significance was gained at $\alpha < 0.05$. Associated statistics were reviewed to assess the model's validity (R^2(adj), VIF, standard error of co-effcients and F - value), as with previous fieldwork and experimental chapters (*Section 5.1.4.2., Section 6.4. & Section 8.4.*). Parabolas were established in matrix plots. Multiple regression was further used to understand the significant predictors to the response variable mean mass of *M. dirhodum* nymphs added into microcosms, outside of soil tillage intensity (Bass, 2007; Khan, 2013; Wheater *et al.,* 2011).

10.6. Results

Results are split into two main sections, firstly data collected after the germination of *T. aestivum* (signified as GS 21), before *M. dirhodum* nymphs were incorporated, and secondly at the end of the experiment when the growth of *T. aestivum* reached a height of 40 cm within a microcosm representing each soil tillage intensity. This was to assess *T. tenuis* early predatory behaviour before prey was incorporated into the microcosm.

The results follow the dependant variables measured (anchor point height, thread length and web area) which express *T. tenuis* activity within the microcosms. The anchor point heights and thread lengths represented within these results relate to support threads (threads inside webs) only. This is because, before the addition of *M. dirhodum*, bridge threads were only identified in the microcosms of Conventional tillage. At the end of the experiment, five bridge threads were identified (three in Direct Drill Managed and two in Conventional). This data was removed from the results.

The interaction plots, for the two-way rank ANOVAs, displaying the response of anchor point height with the categorical factor of attachment material for the anchor point, was run twice. Firstly, with the additional categorical factor of soil tillage intensity and secondly with the categorical factor of number of *M. dirhodum* nymphs placed into the microcosms at the beginning of the experiment (zero, two and six). This was to understand if the number of prey within the microcosm affected the height at which a material was used as an anchor point, alongside analysing the use of attachment materials within the microcosms of differing soil tillage intensities.

In the multiple regression models, the data was categorised by the number of *M. dirhodum* placed into the microcosms at the start of the experiment. Soil tillage intensity was represented by the features of landscape heterogeneity within each soil tillage microcosm, number of upright stubble, straw mass, upright stubble height and furrow dimensions. The model, therefore, represents both categorical factors of soil tillage intensity and number of *M. dirhodum* nymphs added. *T. tenuis* body dimensions (abdomen length, cephalothorax length and mass) and plant height from each microcosm were incorporated as means into the model (*Section 5.1.4.2. & Section 6.4.*).

10.6.1. Summary of Results

After Germination (GS 21) and Before the Addition of *M. dirhodum*

- Upright stubble, attachment material, within the Direct Drill and Direct Drill Managed tillage held a significantly higher mean rank anchor point height than found attached to plant and soil in each soil tillage intensity (*Figure 10.6.*).

After Addition of *M. dirhodum* and End of Trial

- Significantly higher mean rank anchor point was in Direct Drill microcosms, with two *M. dirhodum* added (*Figure 10.8.*). Upright stubble, attachment material, when two *M. dirhodum* were added held the significantly higher mean rank anchor point height (*Figure 10.10.*).
- Number of *M. dirhodum* on plant was a significant predictor to mean mass of *M. dirhodum* nymphs (*Table 10.12*.). Anchor point height was higher when adult *M. dirhodum* numbers were low for two *M. dirhodum* (*Figure 10.11.*).
- Significant lower mean rank anchor point height with zero *M. dirhodum* was found in Conventional tillage (*Figure 10.8.*).
- Anchor point height was significantly positively correlated to number of adult and nymph *M. dirhodum* recorded within web and on plant (*Table 10.7.*).
- Mean rank thread length was significantly longer in Conventional and with six *M. dirhodum* and Direct Drill with two *M. dirhodum* than for zero *M. dirhodum* of all soil tillage intensities (*Figure 10.12.*).
- Direct Drill with two *M. dirhodum* captured the greater number of nymphs (*Figure 10.7.*).
- Mean abdomen length was significantly positively correlated to thread length (*Table 10.10*.). Mean *T. tenuis* mass was significant to the response mean mass of *M. dirhodum* nymphs (*Table 10.12*.).
- Lower anchor point heights occurred when three *T. tenuis* occupied webs than two (*Figure 10.11*.).
- Mean abdomen length was significantly positively correlated to anchor point height (*Table 10.7*.).
- Thread lengths increased as more Aphididae exuviae entered webs (*Figure 10.13*.). Thread length and web area were significantly positively correlated to number of Aphididae exuviae found in the web and number of nymph *M. dirhodum* recorded in web (*Table 10.10. & Table 10.11*.).
- Thread length increased when a lower number of adult *M. dirhodum* were recorded on plant with two *M. dirhodum* incorporated (*Figure 10.13*.).
- Thread length was positively significantly correlated to temperature (*Table 10.10*.). For two *M. dirhodum,* anchor point height generally decreased as temperature increased (*Figure 10.11*.).
- Number of plants was positively correlated to thread length and web area (*Table 10.10. & Table 10.11*.). Number of plants influenced the PCA in the opposite direction than number of nymph *M. dirhodum* within the web (*Figure 10.7*.).
- Six *M. dirhodum* held similar anchor point height when mean plant height was at the lower and higher height (*Figure 10.11*.).
- Number of adult *M. dirhodum* on plant held greater influence than nymphs on plant. Number of nymphs in web influenced data greater than adults in web (*Figure 10.7. & Figure 10.11*).
- Mean cephalothorax length was significantly negatively correlated to thread length (*Table 10.10.*).

10.6.2. After Germination (GS 21) and Before the Addition of *M. dirhodum*

Table 10.1: Response of rank anchor point height and factors of soil tillage intensity and anchor point attachment material. After germination (GS 21) and before the addition of M. dirhodum. T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment (n = 65). (* relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	9.762	0.007*
Anchor Point Attachment Material	2	0.773	0.679
Interaction: Soil Tillage Intensity * Anchor Point Attachment Material	4	42.915	0.001*

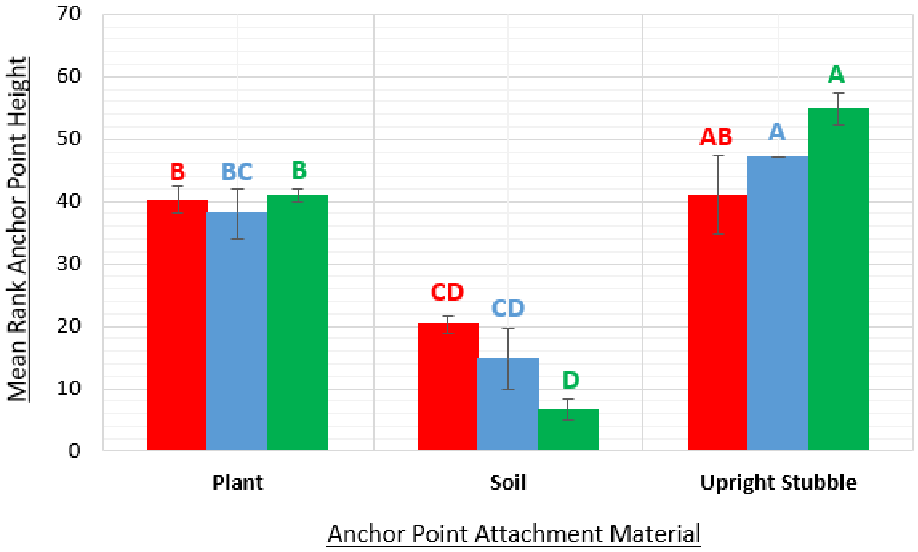


Figure 10.6: Interaction of mean rank anchor point height, soil tillage intensity and anchor point attachment material. After germination (GS 21) and before the addition of M. dirhodum. *Microcosm experiment of* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae (n = 65). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Plant ±s.e.2.173 (n = 16), Conventional Soil ±s.e.1.438 (n = 15), Conventional Upright Stubble ±s.e.6.323 (n = 7), Direct Drill Managed Plant ±s.e.4.002 (n = 2), Direct Drill Managed Soil ±s.e.4.955 (n = 4), Direct Drill Managed Upright Stubble ±s.e.0 (n = 1), Direct Drill Plant ±s.e.0.997 (n = 2), Direct Drill Soil ±s.e.1.673 (n = 9), Direct Drill Upright Stubble ±s.e.2.487 (n = 9)). (Means that do not share the same letter are significantly different at the p<0.05 level).*

There was a significant difference for the interaction between the mean rank anchor point height, attachment material used and soil tillage intensity (*Figure 10.6. & Table 10.1.*). Mean rank anchor point height for Direct Drill and Direct Drill Managed attached to upright stubble was significantly higher than the mean rank anchor point height measured attached to the *T. aestivum* plant and soil within all three different soil tillage intensities. Significant difference in mean rank anchor point existed between the attachment material of upright stubble within Conventional and the material of soil for each soil tillage intensity.

Straw was not included in the model due no anchor points attached to this material within the Conventional mesocosms.

10.6.3. After Addition of *M. dirhodum* and End of Trial

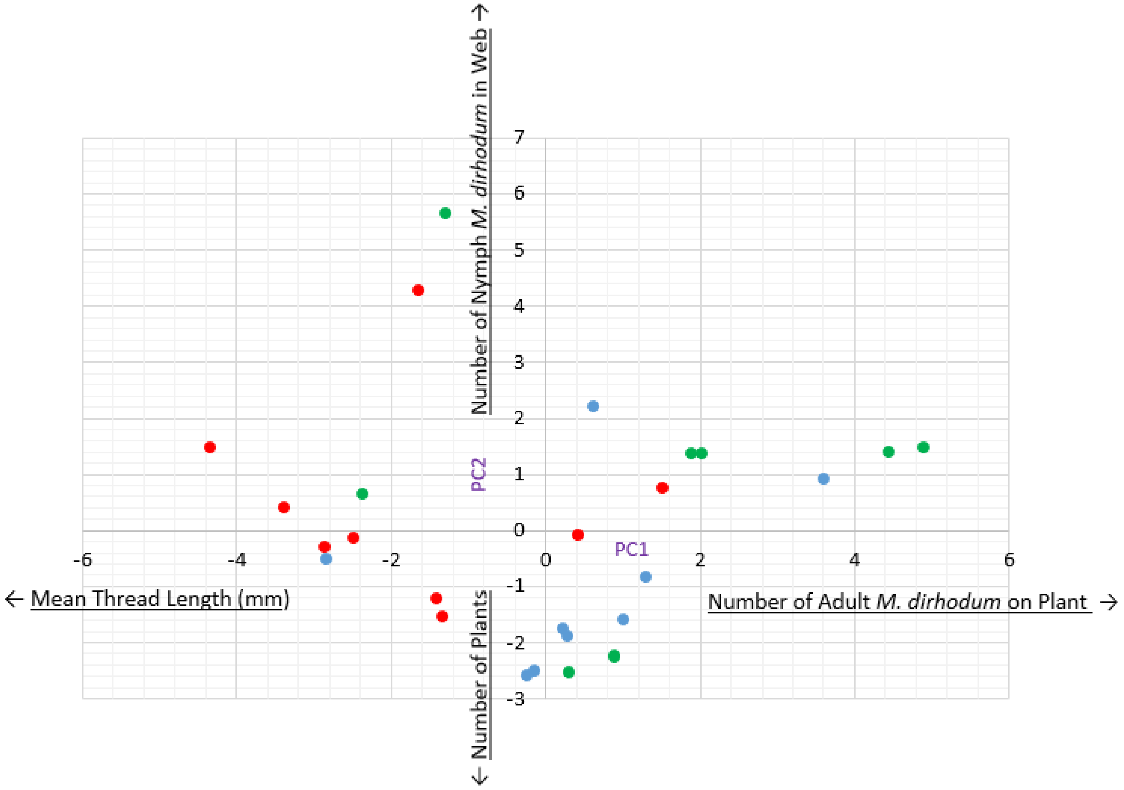


Figure 10.7: PCA of variables measured, along the first two principal components and variables correlating to each component. After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment. (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green).*

Table 10.2: The variance in data explained by principal component 1 and principal component 2 and associated eigenvalues for the variables which held the most influence within the data in each component. After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment.*

	Principal 1	**Principal 2**
Variance	26.5%	20.3%
Variables	**Eigenvalue**	**Eigenvalue**
Number of Adult *M. dirhodum* on Plant	0.394	
Straw Mass (g)	-0.298	
Number of Nymph *M. dirhodum* in the web		0.365
Number of Plants		-0.136

The data collected in the Direct Drill microcosms was influenced most by the number of adult *M. dirhodum* on the *T. aestivum* plant, while for the microcosm of Direct Drill Managed, the number of *T. aestivum* plants affected the data recorded the most (*Figure 10.7. & Table 10.2.*). In contrast, mean thread length appeared to have had the greatest influence on data recorded in the Conventional microcosms.

10.6.3.1. Anchor Point Height

Table 10.3: Response of rank anchor point height and factors of soil tillage intensity and number of Aphididae placed in microcosm. After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment (n = 1303). (* relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	37.556	0.001*
Number of Aphididae Placed in Microcosm	2	6.789	0.049*
Interaction: Soil Tillage Intensity * Number of Aphididae Placed in Microcosm	4	77.857	0.001*

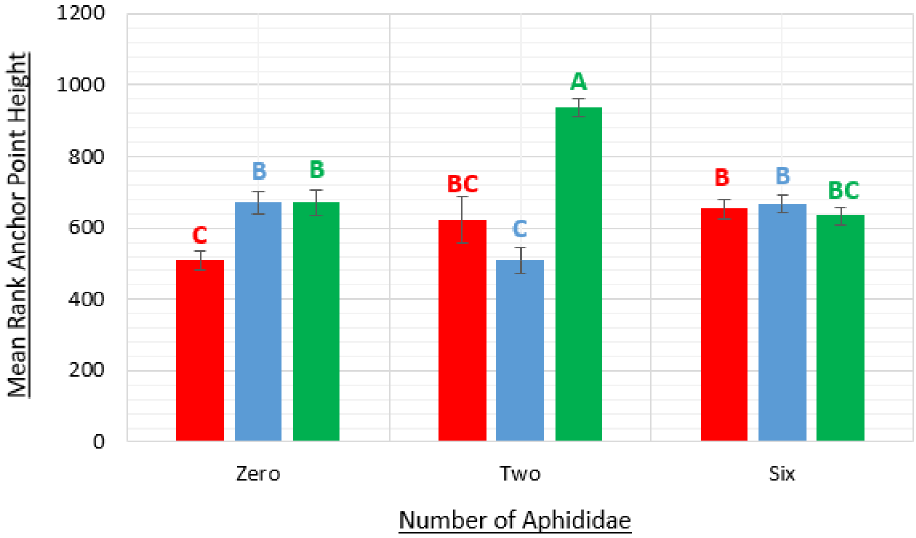


Figure 10.8: Interaction of mean rank anchor point height, soil tillage intensity and number of Aphididae placed in microcosm. After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment (n = 1303). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Zero ±s.e.26.424 (n = 168), Conventional Two ±s.e.63.064 (n = 42), Conventional Six ±s.e.28.242 (n = 178), Direct Drill Managed Zero ±s.e.29.506 (n = 126), Direct Drill Managed Two ±s.e.36.819 (n = 130), Direct Drill Managed Six ±s.e.24.790 (n = 199), Direct Drill Zero ±s.e.34.731 (n = 130), Direct Drill Two ±s.e.23.571 (n = 140), Direct Drill Six ±s.e.25.515 (n = 190). (Means that do not share the same letter are significantly different at the p<0.05 level).*

The mean rank anchor point height found in the Direct Drill microcosms with two *M. dirhodum* added at the beginning of the experiment was significantly higher than all other mean rank anchor point heights measured in the experiment (*Figure 10.8. & Table 10.3.*). Conventional with zero *M. dirhodum* showed a significantly lower mean rank anchor point height than that found in the Direct Drill and Direct Drill Managed soil tillage with zero *M. dirhodum* incorporated and when six *M. dirhodum* were placed into Conventional and Direct Drill Managed tillage.

Table 10.4: Response of rank anchor point height and factors of soil tillage intensity and anchor point attachment material. After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment (n = 541). (* relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	6.868	0.032*
Anchor Point Attachment Material	2	147.749	0.001*
Interaction: Soil Tillage Intensity * Anchor Point Attachment Material	4	50.107	0.028*

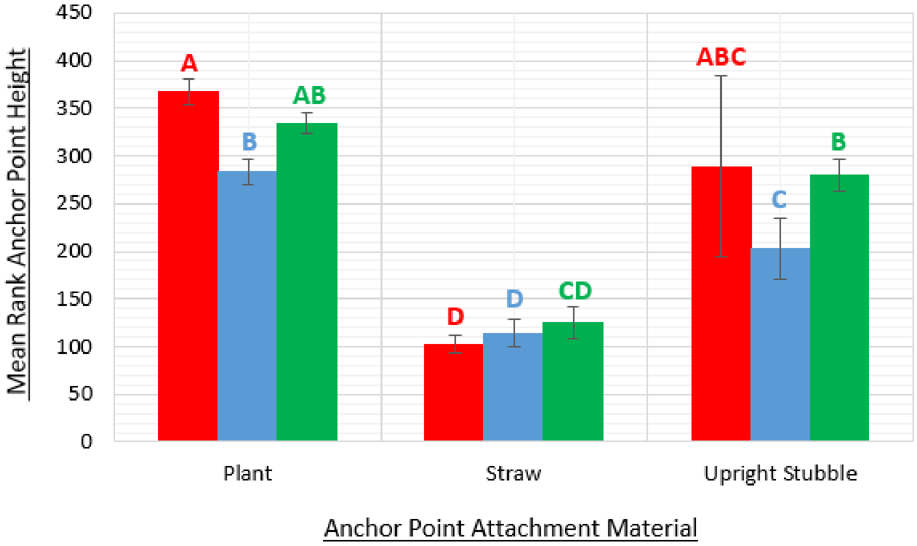


Figure 10.9: Interaction of mean rank anchor point height, soil tillage intensity and anchor point attachment material. After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment (n = 541). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Plant ±s.e.13.983 (n = 77), Conventional Straw ±s.e.9.020 (n = 25), Conventional Upright Stubble ±s.e.94.650 (n = 4), Direct Drill Managed Plant ±s.e.13.423 (n = 133), Direct Drill Managed Straw ±s.e.14.462 (n = 41), Direct Drill Managed Upright Stubble ±s.e.32.512 (n = 20), Direct Drill Plant ±s.e.11.559 (n = 132), Direct Drill Straw ±s.e.16.572 (n = 42), Direct Drill Upright Stubble ±s.e.16.591 (n = 67)). (Points that do not share the same letter are significantly different at the p<0.05 level).*

The mean rank anchor point height found on the attachment material of the *T. aestivum* plant was significantly higher within all soil tillage intensities than that found upon the attachment material of straw (*Figure 10.9. & Table 10.4.*). A mean rank anchor point height, found within Conventional tillage, was significantly higher than found in the Direct Drill Managed microcosms when the attachment material was the *T. aestivum* plant. Heterogeneity was identified between the mean rank anchor point height of Direct Drill Managed and Direct Drill attached to upright stubble.

Table 10.5: Response of rank anchor point height and factors of number of Aphididae placed in microcosm and anchor point attachment material. After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment (n = 541). (* relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Number of Aphididae Placed in Microcosm	2	12.584	0.036*
Anchor Point Attachment Material	2	129.235	0.001*
Interaction: Number of Aphididae Placed in Microcosm * Anchor Point Attachment Material	4	77.759	0.010*

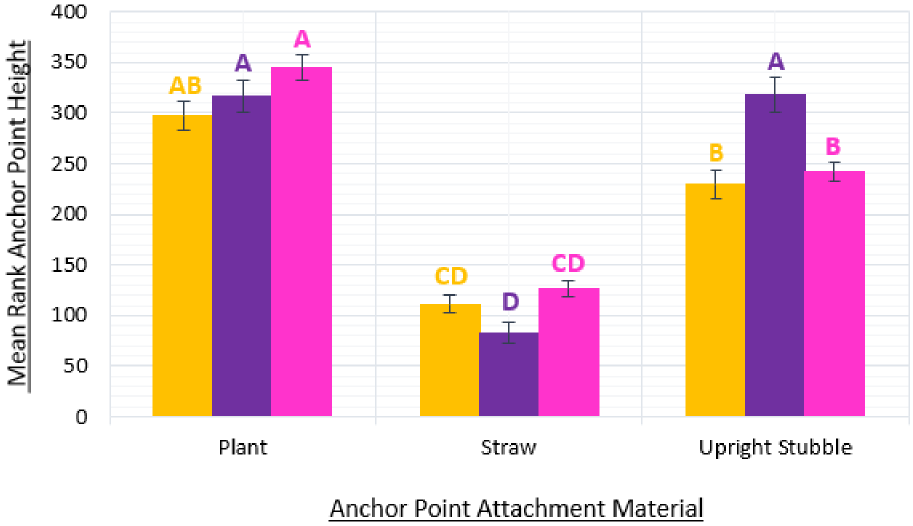


Figure 10.10: Interaction of mean rank anchor point height, numbers of Aphididae placed in microcosms and anchor point attachment material. After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment (n = 541). (Zero Aphididae = Orange, Two Aphididae = Purple, Six Aphididae = Pink) (Zero Plant ±s.e.14.182 (n = 107), Zero Straw ±s.e.9.145 (n = 29), Zero Upright Stubble ±s.e.14.143 (n = 18), Two Plant ±s.e.15.400 (n = 99), Two Straw ±s.e.9.774 (n = 17), Two Upright Stubble ±s.e.17.304 (n = 29), Six Plant ±s.e.12.001 (n = 136), Six Straw ±s.e.8.140 (n = 62), Six Upright Stubble ±s.e.9.725 (n = 44)). (Points that do not share the same letter are significantly different at the p<0.05 level).*

The shape of the interaction plot of Figure 10.10., follows the similar trend as that represented in Figure 10.9. The mean rank anchor point height identified on the attachment material of *T. aestivum* plant was significantly higher with all numbers of *M. dirhodum* applied, than the mean rank anchor point heights calculated attached to the materials of straw (*Figure 10.10. & Table 10.5*.). When that attachment material was upright stubble the mean rank anchor point height was significantly higher when two *M. dirhodum* were placed into the microcosms, compared to when zero and six *M. dirhodum* were incorporated.

Table 10.6: Significant predictors to the response anchor point height (cm). After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment (n = 1303, R-sq - 14.81%). (* relates to significant with α <0.05).*

Continuous Predictor	**Coefficients**	**Standard Error Coefficients (SE Coeff)**	***T***	***P***	**VIF**
Mean Plant Height (cm)	-0.05194	0.0224	7.56	0.001*	2.36
Number of Adult *M. dirhodum* on Plant	-0.002763	0.000766	3.61	0.001*	2.12
Number of Nymph *M. dirhodum* in Web	0.1102	0.0124	8.29	0.001*	1.82
Number of *T. tenuis* in Web	0.2306	0.0979	2.36	0.019*	1.60
Temperature (°C)	-0.2117	0.0582	-3.64	0.001*	1.63

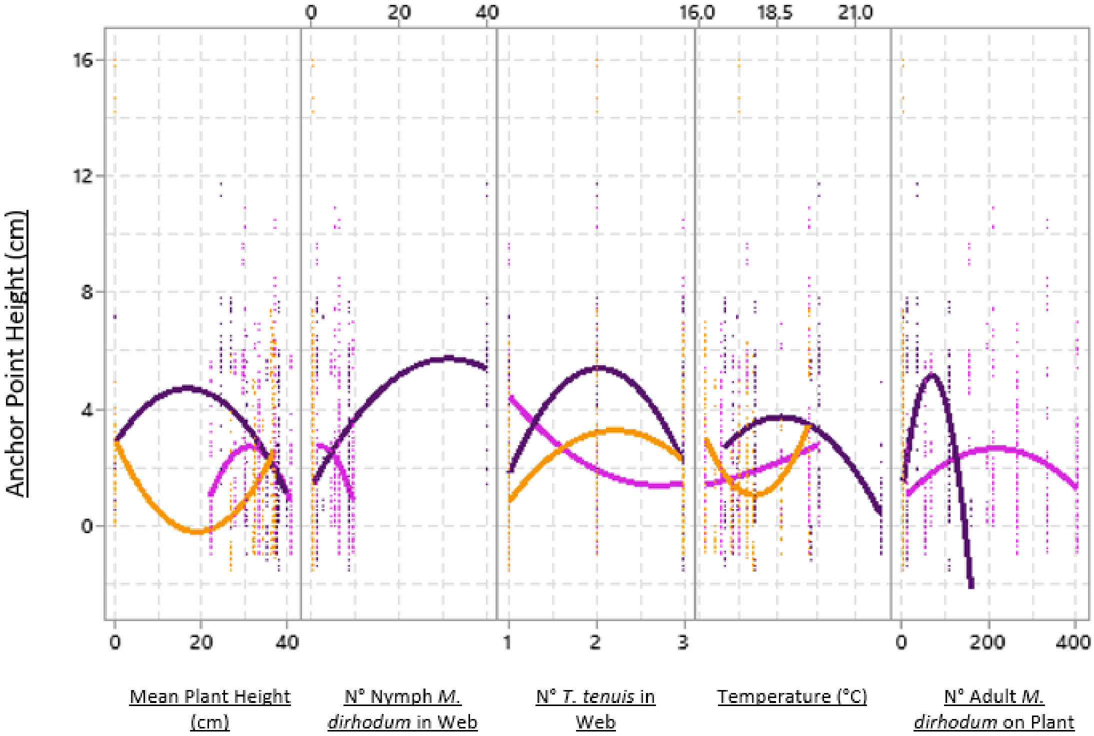


Figure 10.11: Matrix plot with quadratic regression and intercept fitted for anchor point height (cm) with mean plant height (cm), number of nymph M. dirhodum *in web, number of* T. tenuis *in web, temperature (°C) and number of Adult* M. dirhodum *on* H. vulgare *plant. After addition of* M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment. (Zero Aphididae = Orange, Two Aphididae = Purple, Six Aphididae = Pink) (n = 1303, R-sq - 14.81%).*

With zero Aphididae within the microcosm, an open upwards parabola was formed with a minimum vertex, the lower anchor point height was recorded when the mean plant height was midway within the dataset (*Figure 10.11. & Table 10.6.*). With two Aphididae placed into microcosms, the opposite of an upward open parabola resulted, where the greater anchor point height was reached when mean plant height was around 19 cm. Similar anchor point heights were recorded when mean plant height was at the lower and higher height recorded in microcosms of six *M. dirhodum*.

Number of *M. dirhodum* nymphs found within the web, containing six Aphididae, held a small data range, visualised by the narrow downward facing parabola. This combined with a maximum vertex, identified the higher anchor point was reached when there were low *M. dirhodum* nymph numbers observed within the web. The wide parabola, with a weak trend of quadratic regression, shows number of adult *M. dirhodum* on the plants held little influence over anchor point height with the same number of Aphididae incorporated. Number of nymph *M. dirhodum* found in webs and number of adult *M. dirhodum* found on the plant, were shown to have a strong relationship with anchor point height when two Aphididae were added. Trends for both variables was a downward-facing parabola with maximum vertexes.

The highest anchor point height was determined when two *T. tenuis* were recorded underneath sheet webs in microcosms containing zero and two *M. dirhodum*, identified by maximum vertices. A wide-open upwards parabola for the microcosm with six *M. dirhodum* explains a different relationship, where the anchor point height peaked when one *T. tenuis* was recorded underneath a sheet web.

Opposite relationships were displayed when anchor point height was analysed against temperature in the microcosms beginning with zero and two *M. dirhodum* nymphs. Following the trend, the higher anchor point heights of both microcosms occurred at a similar temperature. However, the lower anchor point height was found at a higher temperature within the microcosms of two *M. dirhodum*.

Table 10.7: Correlations of independent variables measured in the microcosms with the dependant variable anchor point height (cm). After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment. (* relates to significant with α <0.05).*

	(Rho)	***P***	**n**
Furrow Depth (cm)	-0.165	0.001*	1303
Mean *T. tenuis* Abdomen Length (mm)	0.082	0.023*	1303
Mean *T. tenuis* Cephalothorax Length (mm)	-0.061	0.027*	1303
Mean Upright Stubble Height (cm)	0.163	0.001*	1303
Number of Adult *M. dirhodum* in Web	0.224	0.001*	1303
Number of Adult *M. dirhodum* on Plant	0.150	0.001*	1303
Number of Aphididae Exuviae in Web	0.230	0.001*	1303
Number of Nymph *M. dirhodum* in Web	0.156	0.001*	1303
Number of Nymph *M. dirhodum* on Plant	0.161	0.001*	1303
Number of Upright Stubble	0.165	0.001*	1303
Straw Mass (g)	0.163	0.001*	1303

Anchor point height was significantly positively correlated to mean abdomen length of *T. tenuis* placed into the microcosms, mean upright stubble height, number of upright stubble, number of adult and nymph *M. dirhodum* counted in the web and on the plant, number of Aphididae exuviae recorded in the *T. tenuis* webs and straw mass (*Table 10.7*.). The opposite was found for the variables of mean *T. tenuis* cephalothorax length and furrow depth, which were significantly negatively correlated to anchor point heights measured.

10.6.3.2. Thread Length

Table 10.8: Response of rank thread length and factors of soil tillage intensity and number of Aphididae placed in microcosms. After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment (n = 1278). (* relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	8.773	0.001*
Number of Aphididae Placed in Microcosm	2	37.477	0.001*
Interaction: Soil Tillage Intensity * Number of Aphididae Placed in Microcosm	4	43.224	0.001*

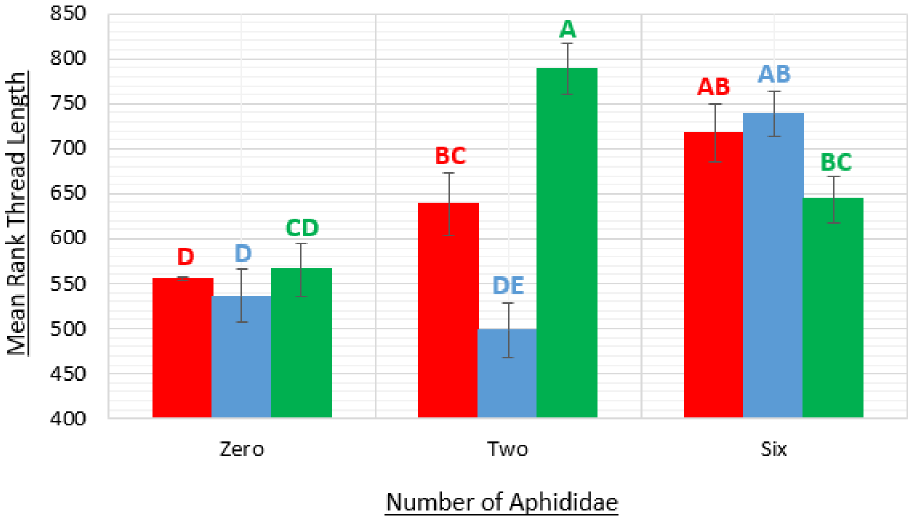


Figure 10.12: Interaction of mean rank thread length, soil tillage intensity and number of Aphididae placed in the microcosms. After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment (n = 1278). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Zero ±s.e.2.002 (n = 166), Conventional Two ±s.e.34.283 (n = 42), Conventional Six ±s.e.32.447 (n = 161), Direct Drill Managed Zero ±s.e.28.853 (n = 130), Direct Drill Managed Two ±s.e.30.035 (n = 122), Direct Drill Managed Six ±s.e.24.550 (n = 199), Direct Drill Zero ±s.e.28.695 (n = 130), Direct Drill Two ±s.e.28.404 (n = 140), Direct Drill Six ±s.e.26.055 (n = 188). (Means that do not share the same letter are significantly different at the p<0.05 level)).*

For Conventional and Direct Drill Managed, where six *M. dirhodum* were added, and Direct Drill, with two *M. dirhodum* incorporated, the mean rank thread length identified was significantly longer than when zero *M. dirhodum* were added for all soil tillage intensities. Further the mean rank thread length from Direct Drill Managed microcosms for two *M. dirhodum* was significantly shorter than that measured in all other microcosms of soil tillage intensity of two and six *M. dirhodum* incorporated (*Figure 10.12. & Table 10.8.*).

Table 10.9: Significant predictors to the response thread length (mm). After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment (n = 1278, R-sq - 21.32%). (* relates to significant with α <0.05).*

Continuous Predictor	**Coefficients**	**Standard Error Coefficients (SE Coeff)**	***T***	***P***	**VIF**
Number of Adult *M. dirhodum* on Plant	-0.10848	0.00938	-11.57	0.001*	3.55
Number of Aphididae Exuviae in Web	0.1697	0.0116	14.49	0.001*	3.77

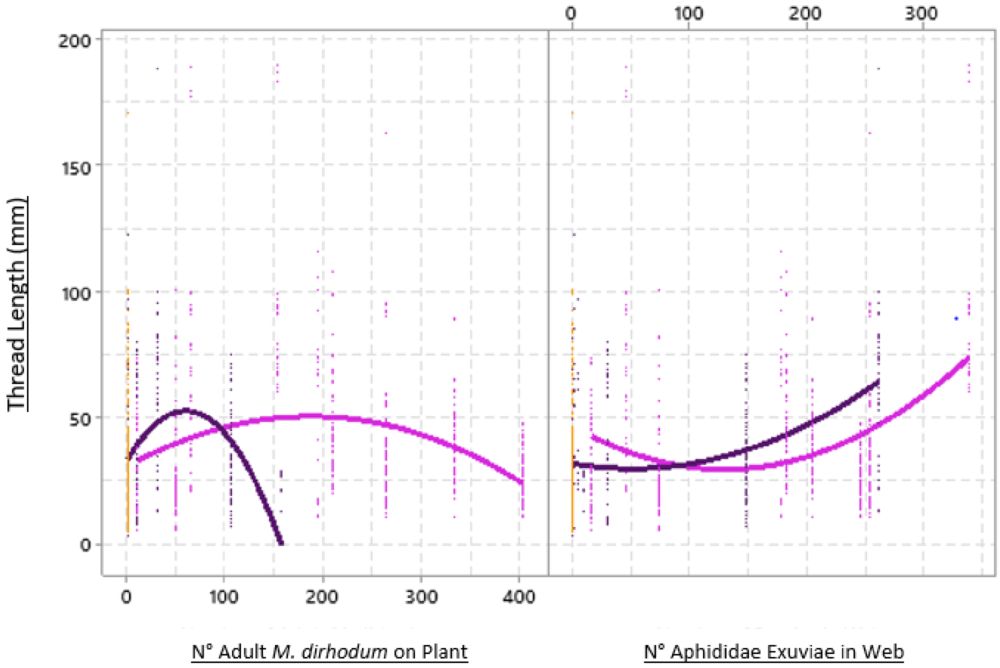


Figure 10.13: Matrix plot with quadratic regression and intercept fitted for thread length (mm) with number of adult M. dirhodum *on the* H. vulgare *plant and number of Aphididae exuviae in web. After addition of* M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment (Zero Aphididae = Orange, Two Aphididae = Purple, Six Aphididae = Pink) (n = 1278, R-sq - 21.32%).*

For the number of adult *M. dirhodum* identified on the plant within the microcosms, the relationship with thread length showed open downwards parabolas for microcosms containing two and six *M. dirhodum* at the beginning of the experiment (*Figure 10.13. & Table 10.9*.). The maximum vertex for both parabolas identified the longest thread length was shown when the number of adult *M. dirhodum* on the plant was mid-range of the data. Microcosms with two *M. dirhodum* added held a smaller range of data for the x-axis (number of adult *M. dirhodum* on plant).

Weak regressive relationships were identified against thread length and the number of Aphididae exuviae found within the web when both two and six *M. dirhodum* nymphs were added. The upwards parabola in both cases explained the longer thread length found when the greater number of Aphididae exuviae were counted within the web.

Table 10.10: Correlations of independent variables measured in the microcosms with the dependant variable thread length (mm). After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment. (* relates to significant with α <0.05).*

	(Rho)	***P***	**n**
Mean Mass of *M. dirhodum* Nymphs (g)	0.107	0.001*	1278
Mean *T. tenuis* Abdomen Length (mm)	0.111	0.001*	1278
Mean *T. tenuis* Cephalothorax Length (mm)	-0.091	0.001*	1278
Number of Adult *M. dirhodum* in Web	0.242	0.001*	1278
Number of Adult *M. dirhodum* on Plant	0.210	0.001*	1278
Number of Aphididae Exuviae in Web	0.275	0.001*	1278
Number of Nymph *M. dirhodum* in Web	0.158	0.001*	1278
Number of Nymph *M. dirhodum* on Plant	0.223	0.001*	1278
Number of Plants	0.105	0.001*	1278
Temperature (°C)	0.102	0.001*	1278

Only one variable was found to be significantly negatively correlated to thread length, mean cephalothorax length of the *T. tenuis* added into the microcosms (*Table 10.10.*). Mean mass of *M. dirhodum* nymphs added, number of *T. aestivum* plants, mean abdomen length of *T. tenuis*, temperature, number of adult and nymph *M. dirhodum* on plant and in web and number of Aphididae exuviae in web were significantly positively correlated to thread lengths measured within the microcosms.

10.6.3.3. Web Area

Table 10.11: Correlations of independent variables measured in the microcosms with the dependant variable web area (mm^2). After addition of M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment. (* relates to significant with α <0.05).*

	(Rho)	***P***	**N**
Number of Adult *M. dirhodum* on Plant	0.135	0.015*	325
Number of Aphididae Exuviae in Web	0.191	0.001*	325
Number of Nymph *M. dirhodum* in Web	0.218	0.001*	325
Number of Nymph *M. dirhodum* on Plant	0.152	0.006*	325
Number of Plants	0.152	0.006*	325
Straw Mass (g)	0.151	0.009*	325

Web area measured was significantly positively correlated to number of adult and nymph *M. dirhodum* recorded on the *T. aestivum* plant and number of nymph *M. dirhodum* and Aphididae exuviae found in the web, number of *T. aestivum* plants and straw mass placed into each microcosm (*Table 10.11.*).

10.6.3.4. Overall - Concerning Data Outside of Soil Tillage Intensity

Table 10.12: Significant predictors to the response mean mass of M. dirhodum *nymphs (g) added into microcosms. After addition of* M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment (n = 27, R-sq - 41.91%). (* relates to significant with α <0.05).*

Continuous Predictor	**Coefficients**	**Standard Error Coefficients (SE Coeff)**	***T***	***P***	**VIF**
Mean *T. tenuis* Mass (g)	0.570	0.155	3.68	0.013*	1.00
Number of Nymph and Adult *M. dirhodum* on Plant	0.000001	0.000001	2.67	0.001*	1.00

The number of adult and nymph *M. dirhodum* found on *T. aestivum* and mean mass of the *T. tenuis* placed into the microcosms were both significant predictors to the response mean mass of *M. dirhodum* nymphs placed into the microcosms (*Table 10.12*.). Both variables held significant positive regression to mean mass of *M. dirhodum* nymphs. The model is not grouped by any categorical predictor due to the mean *M. dirhodum* mass assigned randomly to each microcosm replicating soil tillage intensity.

10.7. Discussion

10.7.1. After Germination (GS 21) and Before the Addition of *M. dirhodum*

The mean anchor point height was found to be significantly greater in Direct Drill and Direct Drill Managed microcosm attached to upright stubble than plant, before the addition of *M. dirhodum* (*Figure 10.6.*). Over three-quarters of anchor points of support threads at this stage were to upright stubble in the Direct Drill treatments. This clearly related to the zero-till of Direct Drill when the field was sampled out of crop (*Section 5.1.5.1.3.*). The upright stubble provided anchorage for support threads and agrees with Dennis *et al*. (2001) and Welch *et al.* (2013) who described the need for an increase in landscape heterogeneity for increased web-spinning, even at a micro-scale. This is an opposite trend to Figure 8.7. in the experimental Chapter focusing on replicating the field, where Direct Drill held the significant lower height on upright stubble (*Section 8.7.2., Page 236*). The plant had established tillers in the early growth stages of the mesocosms, thus stubble was found to be a platform to enable higher reaches of the plant to be utilised. At this stage in this experiment *T. aestivum* growth had only established.

Alternative materials in plant and soil were shown to be of influence on anchor point height (*Figure 10.6*). Bell *et al.* (2002), Bonte *et al.* (2011) and Thorbek (2003), describe the use of soil depressions by *T. tenuis*, as a less favourable alternative to above-ground features, such as upright stubble. However, a web was spun in the furrow of Direct Drill Microcosms. With the absence of prey, it of interest, why a prominent web was woven across the furrow. These microcosms ran from late in August 2018 to September, so it may be that fecundity level in *T. tenuis* was high, thus a female may have exhibited signs of expected courtship. A reproduction window in Linyphiidae is shown to correlate with crop harvest and usually lasts for two weeks (Maklakov *et al.,* 2003; Welch *et al.,* 2013). A web is required to be spun to exert dominance over a male and allow courtship to commence. This can occur without a male present in the vicinity, as it is expected that females draw the males in with the use of pheromones (Gregori *et al.,* 2015; Maklakov *et al.,* 2003; Prenter *et al.* 2010) (*Section 2.1.3.4*).

10.7.2. After Addition of *M. dirhodum* and End of Trial

A Direct Drill microcosm with two *M. dirhodum* nymphs incorporated held the significantly highest mean anchor point height (*Figure 10.8.*). This increase in anchor point height appeared to be due to the presence of upright stubble (*Table 10.7. & Figure 10.10.).* Stubble shown to provide a rigid vertical platform for robust anchoring (Hogg & Danne 2018; Szymkowiak *et al.,* 2007). The use of stubble as an anchorage structure is low compared to the utilisation it received when no plant was present (*Figure 10.9. & Figure 10.10*.). This accords with fieldwork in later growth stages, where the use of the stubble was of less importance due to the plethora of anchor materials in the crop (*Section 5.1.6.2.2*.). Bell *et al.* (2002) and Stenchly *et al*. (2011) noted that Linyphiidae have little preference over anchor material, with its organization of greater importance.

Gómez *et al.* (2016) and Opatovsky *et al.* (2016) commented that webs spun at a higher level, is a response to increased Aphididae abundance. It was shown that an increased number of *M. dirhodum* nymphs, allowed greater reproduction potential (*Table 10.12*.). Brabec *et al.* (2014) and Parry (2013) comment that Aphididae rapid population growth is due to each female's ability for parthenogenesis. However, anchor point height appeared to peak when adult *M. dirhodum* numbers were noted as low for two *M. dirhodum* (*Figure 10.11*). Honek *et al.* (2018) and Winder *et al.* (2013) identify *M. dirhodum* as a crop canopy Aphididae, that prefers the underside of higher tillers, where an increased food source, phloem, is likely to exist. There were approximately four hundred more *M. dirhodum* nymphs within the Direct Drill six *M. dirhodum* microcosms than with two *M. dirhodum* added. Lombaert *et al*. (2006) and Winder *et al.* (2014) show that in times of overcrowding, cereal Aphididae are driven to relocate, usually by the production of an alate morph. However, even at low abundance, the confined nature of the microcosm restricted movement, thus promoting the use of whole *T. aestivum* leaf (*Figure 10.14a & b*). Therefore, when a cereal Aphididae occupation exists at all levels of a crop, the lower areas of a microcosm were the favourable positions for web location with the use of lower substrate (*Figure 10.9*.). This observation fits with work by Bell *et al.* (2002), Davey *et al*. (2013) and

Sutherland & Samu (2000) and where *T. tenuis* was found at the base of a crop, shown to allow aerial prey interception and access a degree of shelter from the vegetation.

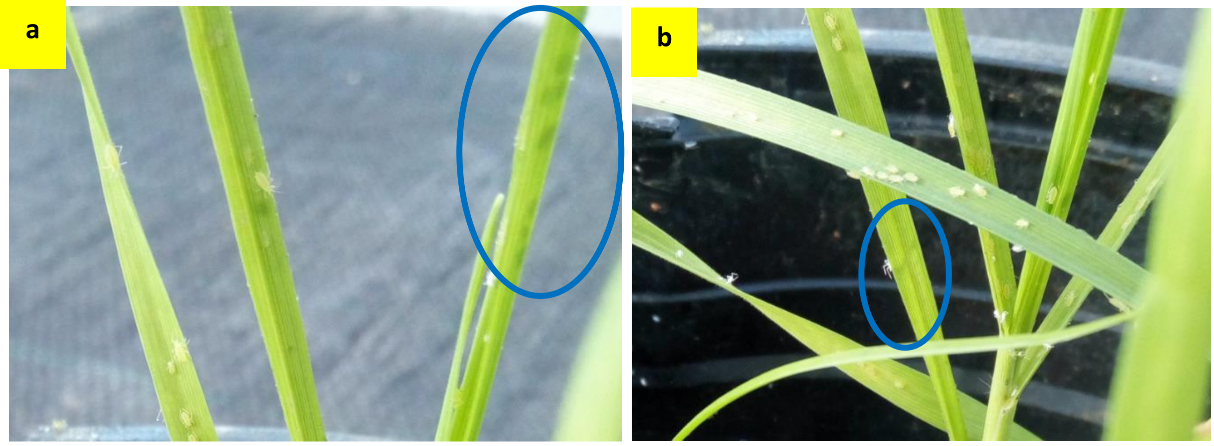


Figure 10.14a & b: M. dirhodum *nymphs and adults depicted on the leaves of the* T. aestivum *tillers (Blue circle identifies* M. dirhodum *on other side of leaf). Direct Drill 9c. Six* M. dirhodum *nymphs. After addition of* M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment. Lateral view.*

Where zero *M. dirhodum* nymphs were incorporated, the significant lower anchor point height recorded was due to the use of the furrow, which was at a greater depth within the Conventional treatment (*Figure 10.8.*). The use of the furrow was seen to be utilised from field sampling at time of poor soil moisture (*Section 5.1.6.2.2.).* This negates the above comment where *T. tenuis* were shown to spin their webs above ground. It may be that throughout the experiment no cues were collected of available aerial, above ground prey. Glover (2013) and Uetz (1990) suggest that *T. tenuis* process cues from the local habitat to sense prey, movement in vegetation and its density. Lubin *et al.* (2011), Mclachlan and Wratten (2003) and Öberg *et al.* (2008) discuss the capture of ground-dwelling prey within a sheet-web. It may be the construction of a web close to the soil surface allowed entrapment of small prey, Collembola (springtails) and Thysanoptera (thrips), that may have been residing in the soil collected from the NIAB fields (Liu *et al.,* 2013a; Shayler, 2005).

It can be observed that prey may be driving anchor placement of a web, specifically within microcosms containing two *M. dirhodum* (*Figure 10.11. & Table 10.7*.). This would agree with fieldwork of *H. vulgare* in early and late growth stages (*Section 5.1.6.2.1. & Section 5.1.6.2.2*.). Ryndock *et al.* (2011), discussing anchor point availability during woodland restoration, and Uetz (1990), commenting on prey interaction, discuss that anchor point height is a key decision in establishing successful prey capture. It appears that increasing anchor point height has allowed webs to collect a higher degree of *M. dirhodum* prey.

Interestingly, mean thread length was significantly longer in Conventional microcosm with six *M. dirhodum* and Direct Drill with two *M. dirhodum* added than zero (*Figure 10.12.*). In Conventional, this was due to large webs spanning across half of the microcosm, attached to the rim of the plastic container and materials in the centre of the microcosm (*Figure 10.8. & Figure 10.15*). In Direct Drill, large webs were woven between plant and upright stubble. The webs within Direct Drill with two *M. dirhodum* captured the greater number of nymphs within the web, shown to influence this variables placement within the first principal component (*Figure 10.7.*). It seems that the greater web areas identified in Conventional six microcosms, were created by female *T. tenuis* of a larger body size (*Table 10.10.*). This follows where the greater mean *T. tenuis* mass was significant in the model representing mean mass of *M. dirhodum* nymphs (*Table 10.12.*). A *T. tenuis* with a greater body size and mass can communicate a higher level of fitness by weaving longer silk threads for a larger web, which was identified by Bonte *et al.* (2008) and Harmer *et al.* (2011) to be an energy-draining process (*Figure 10.15*). By occupying half of the microcosm, it can be seen that this web construction removed web-site opportunities for other *T. tenuis* within the microcosm, thus an act of intra-specific competition (Bianchi *et al.,* 2017; Harwood *et al.,* 2003; Pekár, 2000; Samu *et al.,* 1996), possibly driven by the timing of the experiment as discussed earlier. Possibly a response to greater mean *M. dirhodum* mass, accelerating parthenogenesis rate (*Table 10.12.*).

Figure 10.15: Large web spanning from plastic to crop. Conventional 2c. Six M. dirhodum *nymphs. After addition of* M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment. Elevated view. (Yellow arrow = 50.1 mm).*

Webs constructed were observed to have been successful in prey capture, however, abandonment for a new web-spinning location had also clearly occurred. The frequency of web-building stated by an individual *T. tenuis* was therefore shown. Alderweireldt (1994), Benjamin *et al.* (2002), Harmer *et al.* (2011) and Segoli *et al.* (2004) explain that *T. tenuis* have an inherent instinct to constantly search for a possibly more productive web-site, in terms of prey capture. At the end of this experiment, *T.*

tenuis showed a greater web occupancy rate per area than found from field sampling (*Section 5.1.5*.). However, it can be noted that within the microcosms there was no other location to reside.

It is of relevance that a *T. tenuis* was not occupying a web in some microcosms. The lower web occupancy was identified within the Conventional microcosm of all *M. dirhodum* nymphs incorporated and was higher in Direct Drill with zero and two *M. dirhodum* added (*Figure 10.11*.). The lower anchor point heights of webs occupied, were attached to straw in the Direct Drill mesocosms, which incorporated the greater straw mass (*Figure 10.9. & Figure 10.10*.). Straw was used as an anchorage material; however, no web was completely spun into the straw. Within fieldwork, it was shown in times of soil cultivations that the straw of the Direct Drill cultivation provided a refuge and a possible source of ground-dwelling prey (Diehl *et al.* 2013; Nyffeler & Sunderland, 2003; Schmidt *et al.* 2008b) (*Section 5.1.6.2.1.*). It can be seen within the microcosms that little refugia was required, due to the enclosed nature of the trial and *T. tenuis* were accessing prey of *M. dirhodum* in microcosms where nymphs were incorporated. It may have simply been due to intra-specific interactions of *T. tenuis* driving web occupancy. Some larger female *T. tenuis* were observed to have been added to Conventional microcosms, however smaller-bodied *T. tenuis* were also incorporated to some Conventional, as the addition of *T. tenuis* was random. Bonte *et al.* (2011), Gan *et al.* (2015) and Toft (1989) discuss Linyphiidae web take-over with *T. tenuis* exerting greater fitness and dominance through increased size. Corcobado *et al.* (2010) and De Mas *et al.* (2009), noted female *T. tenuis* have a greater degree of inter-gender competition than males. Therefore, females of lower abdomen mass may be required to opt for a web-site in lower strata or was searching for a new location when the experiment was terminated (*Table 10.7*.).

The exuviae showed whether *T. tenuis* changed the dimensions of web-spinning due to the potential stimulus that *M. dirhodum* presence could initiate (Lichtenstein *et al.,* 2016; Rodríguez & Gamboa, 2000) (*Figure 10.13*.). Within all tillage intensities, webs seemed to be spun to locate *M. dirhodum* within the same way. Thread lengths only began to increase as more Aphididae exuviae became available and greater numbers fell into the web (*Figure 10.13*.). Exuviae found in webs were viewed as the growth rate of *M. dirhodum*, with higher exuviae observed relating to increased developmental rate from nymph to adult (Beck & Toft, 2000) (*Section 2.2.6.2.*). The greatest number of Aphididae exuviae was identified in the Direct Drill mesocosm with two *M. dirhodum* and Conventional with six *M. dirhodum (Figure 10.16. & Figure 10.17.)*. This corresponds with the pattern of the greater thread length identified within these two microcosms (*Figure 10.12., Table 10.10. & Table 10.11*.). The webs woven here provided potential biological control, situated at the nucleus of parthenogenesis activity (Birkhofer *et al.,* 2018; Campbell *et al.,* 2020).

Figure 10.16: M. dirhodum *caught in sheet web along with exuviae. (*M. dirhodum *circled in yellow) Direct Drill 6b. Six* M. dirhodum *nymphs. After addition of* M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment. Lateral view.*

Figure 10.17: M. dirhodum *caught in sheet web along with exuviae. (*M. dirhodum *circled in yellow). Conventional 3c. Two* M. dirhodum *nymphs. After addition of* M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment. Elevated view. (Red arrow = 54.1 mm).*

The smaller webs of the Direct Drill and Direct Drill Managed microcosms had not appeared to capture a greater number of *M. dirhodum* than the large webs of Conventional with six *M. dirhodum* nymphs (*Figure 10.7., Figure 10.18., Table 10.10, Table 10.11. & Table 10.12*.). This is a different result to that found in fieldwork with early growth stages (*Section 5.1.6.2.1*.). Moreover, discords with Dennis *et al.* (2015) and Gómez *et al.* (2016) who discuss the advantage of smaller webs to manipulate location in response to prey, low energy expenditure further allowing rapid construction. Glover (2013), Harwood *et al.* (2003) and Obrycki & Harwood (2005) who comment that webs of low energy cost may be a compromise; however, they harness a greater return due to ease of successive web-building. Web-site optimal possibly altered as the population of *M. dirhodum* grew. Jurczyk *et al*. (2012), Pekár (2000) and Toft (1987) comment on the fine balance between the choice of web location and its desired effect. Thread length peaked when number of adults recorded was lower on *T. aestivum* when two *M. dirhodum* were placed into the microcosms (*Figure 10.13*.). Larger webs perhaps spun to hold a greater surface area under the crop canopy, to enable greater potential contact of *M. dirhodum* to the fibrils of the sheet web. Blackledge & Eliason (2007) and Kraft & Cookson (2012) explain that any aspect of a webs surface area has an opportunity to entrap prey, this seen in the case of Conventional with six *M. dirhodum*. A positive aspect to the biological control a web can exert (Campbell *et al.,* 2020).

Figure 10.18: Small sheet web woven within crop and upright stubble, only containing exuviae. Direct Drill 9c. Two M. dirhodum *nymphs. After addition of* M. dirhodum *and end of trial.* T. tenuis *behaviour with different soil tillage intensities and different abundances of cereal Aphididae: a microcosm experiment. Lateral view. (Yellow arrow = 33.3 mm).*

Brabec *et al.* (2014) and Parry (2013) comment that Aphididae rapid population growth is due to each female's ability for parthenogenesis. Adult and nymph *M. dirhodum* numbers on leaves were greater in Direct Drill with six *M. dirhodum* nymphs incorporated (*Table 10.12*.). This identifies that within Direct Drill microcosms the reproductive capacity of *M. dirhodum* was greater than Direct Drill Managed and Conventional with six *M. dirhodum* nymphs added. Brabec *et al.* (2014) and Parry *et al.* (2006) explain that temperatures outside *M. dirhodum* optimum range can affect fecundity, however, temperatures ranging from 16.2 - 21.1 °C are acceptable conditions for reproduction of a clone to be triggered (*Figure 10.11*.). With no associations identified between number of *M. dirhodum* on leaves and the structure of the mesocosm relating to soil treatment, the fitness of *M. dirhodum* was greater in the Direct Drill microcosms. Moreover, Asin & Pons (2001) and Rispe *et al.* (1996) explain that due to the nature of parthenogenesis producing clones, reproductive fitness can be inherently low if genetic dispersal is low. With the Aphididae cultivated in house, different levels of fitness of nymphs may have occurred (*Section 7.2.3*.).

Vollrath *et al.* (2001) identify that warmer temperatures allow *T. tenuis* to accomplish the required tension for thread spinning with the requirement of less energy (Craig, 2003; Hesselberg & Vollrath, 2012) (*Table 10.10*.). This may have allowed longer threads to span within an environment, although, Bonte *et al.* (2011) have discussed the high energy cost associated with yielding greater silk in one action. It appears the temperature presented *T. tenuis* with optimum conditions for greater web-spinning. For two *M. dirhodum,* anchor point heights decreased when the temperature inside the microcosm was measured at over 19 °C, however, for zero *M. dirhodum,* the anchor point peaked at similar temperatures (*Figure 10.11.*). With Brabec *et al.* (2014) and Klüken (2008), finding that *M. dirhodum* reproductive potential increased with temperature (decreasing after optimal reached), irregularly there was no significant correlation identified between temperature and number of *M. dirhodum* on the plant and *M. dirhodum* nymphs within the web. Interestingly, *T. tenuis* were spinning webs at the basal stratum of the microcosm when *M. dirhodum* were feeding on the more recent growth of *T. aestivum,* the tillers that created the upper canopies. With plant height and density performing at the higher end of the scale with six *M. dirhodum,* than the other microcosms, the *T. tenuis* had a level of vegetation complexity to spin a web between. It appeared that the *M. dirhodum* density was weaker within this microcosm with two *M. dirhodum* incorporated (*Figure 10.11.*), lower abundances residing in the lower levels of the *T. aestivum*, where there was little competition for the phloem content of the main *T. aestivum* stem (Reynolds & Reynolds, 2009). Perhaps *T. tenuis* cognitive abilities had sensed prey at the lower levels and constructed webs over the depressions in the soil to find adequate anchorage (Kraftt & Cookson, 2012).

Number of plants was positively correlated to thread length and web area (*Table 10.10. & Table 10.11.*). This result discords with Dennis *et al*. (2001), Gómez *et al.* (2016) and Stenchly *et al.* (2011) when increased plant physiognomy related to small webs woven between adjacent stems. Within the microcosms, the developing *T. aestivum* appeared to provide the greater plant material within the upper levels, tillers at later growth stages extending outwards (AHDB, 2015; Holopainen-Mantila, 2015; McFarland *et al.,* 2014). With the additional growth provided by greater plant densities, it is curious why *T. tenuis* were spinning webs of a greater size. Benjamin & Zschokke (2004) and Toft (1987) describe that support threads are expected to expend more energy as they are generally spun marginally thicker to allow attachment points visualised to be met. Krafft & Cookson (2012) discuss that a sheet-weaving spider does not fully comprehend the complete architecture of the web they are weaving until the structure is complete. Eberhand *et al.* (2019) discuss that web-weaving is a learning process where the complex cognitive behaviour to web propensity leads to a multitude of variations to be comprehended before each thread is laid. It may be that the larger webs were constructed at the earlier growth of *T. aestivum*, *T. tenuis* here, weaving webs in an environment of lower landscape complexity, to process the spatial orientation of the environment.

Number of plants further influencing the PCA in the opposite direction than number of nymph *M. dirhodum* within the web (*Figure 10.7.*). Poorer growth of *T. aestivum* was noted within the Conventional microcosms (*Figure 10.7.*). Even though moisture was measured in correct percentages for clay, fissures had occurred in the soil, which produced poor germination. Conventional tillage microcosms were the worst affected, theorised to be because an increase in bulk density impeding moisture permeability due to the greatest tillage intensity (Knight *et al.,* 2012; Morris *et al.,* 2010)

(*Section 2.2.2.*). Though this micro-habitat held a small area for soil tillage intensity to be represented. Direct Drill, with two *M. dirhodum,* held the most biological control success with the lower number of plants than Direct Drill Managed (*Figure 10.7.*). Increased levels of biological control, via web capture, may have been due to the low density of the plant material. Thus, allowing cues of the *M. dirhodum* (in sight and vibrations) to be accepted and webs woven in the vicinity of the prey. From here, *M. dirhodum* having removed their stylets from the stem, may have dropped directly into a web, and become entangled in the flagelliform silk (Brunetta & Craig, 2010; Craig, 2003; Segoli *et al.,* 2004). Kraftt & Cookson (2012) state that Linyphiidae entrap mobile prey, thus a web must efficiently be set in the location where vibrations of prey movement are displayed, the *M. dirhodum* of this microcosm had dispersed along the length of the stem perhaps ascending to tillers due to limited plant material.

Six *M. dirhodum* were shown to hold similar anchor point heights of *T. tenuis* webs when plant height was the lower and higher end of the scale (*Figure 10.11.*). The common theme within the contributing microcosms was low numbers of adult and nymph activity recorded. Mansion-Vaquié *et al*. (2020) show that apterous morphs of low density are not inclined to migrate, food is in plentiful supply in lower reaches of the *T. aestivum*. Parthenogenesis occurs at any aspect of plant if nutrition is sufficient, thus *M. dirhodum* appear not to have dispersed from the origin of the colony, at the base of the stem (Agabiti *et al.,* 2016; Mansion-Vaquié *et al*., 2020) (*Section 2.2.6.2.*). Low webs did indeed capture some *M. dirhodum*, an energy source captured with little energy expenditure of ascending the crop (Craig, 2003; Hesselberg & Vollrath, 2012).

Adult *M. dirhodum* upon the vegetation held a greater effect than nymphs recorded on the vegetation, however, the number of nymphs in the web was a significant term but not number of adults ensnared within the web (*Figure 10.7., Figure 10.11. & Figure 10.13.*). More nymphs were captured by *T. tenuis,* which disagrees with Parry (2013) and Parry *et al*. (2006), who discuss that nymphs have a low propensity to drop due to the stylus anchored to vegetation to allow continuous feeding. Overall, there was a greater population of nymphs than adults upon the vegetation which explains how more nymphs were captured by *T. tenuis*, overcrowding initiating dropping behaviour, or driving dispersal to higher tillers of *T. aestivum* with greater flexibility to subdue stylus penetration depth of the Aphididae (Parry 2013; Price *et al.,* 2011; Summers *et al.,* 2004). The parameters of the microcosm in vegetation and low disturbance ensured the process of parthenogenesis producing nymph clones at a steady rate (Goggin, 2007; Westwood & Stevens, 2010). The fecundity rates were not equally representative; for example, 405 adults *M. dirhodum* and 639 nymphs were recorded in a Direct Drill mesocosm and 264 adults and 594 nymphs for another Direct Drill mesocosm both containing six *M. dirhodum* at the outset. It appears that *T. tenuis* activity was more sensitive to the positioning of adult *M. dirhodum* within the microcosms, *T. tenuis* known to have poor cognitive ability, the macrosetae (fine hairs) of *T. tenuis* able to respond to the greater vibration cues presented by larger Aphididae that are laboured in movement (Bradley, 2013; Eberhard *et al.,* 2019; Macfadyen *et al.,* 2019; Zhang & Tso, 2016) (*Section 2.1.1*.). In the field of a cereal crop it would be beneficial if capture rate of nymph Aphididae was greater, to remove Aphididae of early generation before parthenogenesis may occur (Asin & Pons, 2001). The climatic disturbances noted in the field, void in the microcosms, have shown to aid capture of nymphs within a sheet web (*Section 5.1.6.2.3*.).

As discussed in previous chapters, a larger cephalothorax increases flexion to be able to spin longer threads at a faster rate (Anderson & Prestwich, 1975; Prenter *et al.,* 2010) (*Section 8.5.2.*) However, the *T. tenuis* with the smaller cephalothorax length were placed into the mesocosms that held plant densities >9, it appears that the number of plants with mesocosms that incorporated *M. dirhodum,* held the greater influence over thread length than body dimension of *T. tenuis* (*Table 10.10*.). The habitats are of a much smaller scale than that of a field setting. The fundamental use of increased leg flexion has held little consequence to *T. tenuis* within a small environment with no external disturbances to disrupt silk-weaving.

10.8. Final Discussion - *T. tenuis* Behaviour with Different Soil Tillage Intensities and Different Abundances of Cereal Aphididae: A Microcosm Experiment

Prey abundance has been shown in all treatments to drive increased web-spinning in height and area. This is beneficial to the bio-control potential of *T. tenuis*, and explains if prey is available, the power that webs can bring to allow prey entrapment. This follows aim number one and three of this Chapter concerning *T. tenuis* relationship with implementing biological control (*Section 10.2.1*.).

The elements of number of upright stubble and height corresponding to the different soil tillage intensities have been of low influence on *T. tenuis* ability to spin webs at certain orientations. This meeting the second aim analysing *T. tenuis* action against soil tillage intensity (*Section 10.2.1*.). Within this experiment, prey appears to have over-ridden landscape heterogeneity of each microcosm, however, these microcosms are of a much smaller scale than that of a field setting. The fundamental nature of the soil tillage appears to be of little consequence to *T. tenuis* within a small environment where prey is abundant and addresses aim number one, noted in Section 10.2.1.

Discussing the second aim of Section 10.1.2., the furrow appears to be utilised at times of *T. tenuis* intra-specific competition. However, it appears that furrow presence was enough to provide an adequate web-site, regardless of dimensions. Additionally, it was identified that Direct Drill Managed is a mid-habitat, offering features of straw mass, upright stubble abundance, which sits between Conventional and Direct Drill. This ‘midway’ tillage seems to be limited in driving *T. tenuis* activity within this glasshouse experiment.

Chapter Eleven

11.0. Choice Chambers for *T. tenuis* Selection of Upright Stubble and Furrow With or Without the Presence of Aphididae

11.1. Introduction

The glasshouse experiments so far described, placed *T. tenuis* into meso/microcosms where one factor was assessed, e.g. in landscape heterogeneity and/or Aphididae abundance (*Chapter 8.0. - Chapter 10.0.*). The experiment described in this Chapter took elements from the differing soil intensities and offered *T. tenuis* a choice of these elements under controlled conditions. The premise was that, results could potentially identify which elements have the greatest influence over *T. tenuis* decisions in web-site location and design.

There were four trials within this glasshouse experiment. As the abundance of upright stubble and furrow dimensions had been shown to enhance *T. tenuis* capacity for web-building (*Section 5.1.5.*), this was further tested in choice chambers, where *T. tenuis* could utilise upright stubble of certain heights and densities and furrows of specific dimensions. From fieldwork and previous glasshouse experiments, the presence of Aphididae (*M. dirhodum* and *S. avenae*) had been shown to influence web-site selection. It was therefore appropriate to incorporate prey into the choice chambers, as the foundation of this research was to understand how the conditions in arable agriculture could affect *T. tenuis* prey capturing ability. *M. dirhodum* were incorporated into the choice chambers alongside the presence of upright stubble and furrow to investigate whether *T. tenuis* alters its web construction decisions if Aphididae are detected.

11.2. Aims and Specific Objectives

11.2.1. Aims

This research sought to address Aims 2, 3 and 4 from Section 1.2., Page 2.

2. Identify any differences in extended phenotypes of *T. tenuis* within tillage practices, e.g. web dimensions and bridge thread length.
3. Understand whether *T. tenuis* behaviour is stimulated by the presence of Aphididae.
4. Comprehend if a certain level of landscape heterogeneity affects *T. tenuis* ability to predate.

11.2.2. Specific Objectives

- Locate *T. tenuis,* web-site and bridge thread in the choice chamber and determine the position of *M. dirhodum* (if incorporated), to assess which factors are of influence.
- Evaluate web area, anchor point height and bridge thread length and relate to elements in the choice chamber.
- Assess the effects of specified *T. tenuis* (number, gender, and body size) on the utilisation of features in the choice chambers.

11.3. Selection of Upright Stubble With or Without the presence of Aphididae

11.3.1. Selection of Upright Stubble Without the presence of Aphididae

11.3.1.1. Introduction

The first two trials took the element of upright stubble and confined this variable into a choice experiment, where *T. tenuis* had a choice to utilise the upright stubble for web-building. This was to ascertain if upright stubble led to promotion of web-site selection and web-building.

11.3.1.2. Methodology

Each trial was conducted in a choice chamber (a plastic box: 28 (l) x 16 (w) x 14 (h) cm) with 15 small holes (diameter 1.5 mm) drilled into the lid for ventilation. Each choice chamber was divided into two equal halves. Straw mass (g), corresponded to the mean amount collected in sample plots of the different soil tillage from growth stages (GS) 31 - GS 33, *H. vulgare* 2017 / 2018 cropping season, as in Section 8.3., and was placed in both halves of the choice chamber (*Table 5.1.1., Section 5.1.3.1., Page 82*). In each choice chamber, upright stubble, corresponding to the same fieldwork data was placed only on one side (*Figure 11.1a & b*). This gave *T. tenuis* the option to inhabit and construct webs on upright stubble amongst straw or on straw alone. The arrangement (clusters) of the upright stubble simulated the stubble arrangement found in the plots of the different soil tillage intensities, using the same methodology from the field trial of addition of upright stubble on cultivated land (*Section 5.2.3.*).

One trial consisted of a choice chamber representing one of the three soil tillage intensities (Conventional, Direct Drill Managed or Direct Drill) incorporating a given abundance of *T. tenuis*, run at the same time. There were five treatments of *T. tenuis*: 1 x Female; 1 x Male; 1 x Female and 1 x Male; 2 x Female; and 2 x Male, replicated three times (n = 15 chambers) (*Section 7.6.2.3.*). Animals were measured according to the methodology established for all glasshouse experiments, after stabilising in the terrarium (*Section 7.2.1. & Section 7.2.2.*). *T. tenuis* were added simultaneously, if two incorporated, at the centre of the choice chambers. Each trial ran for twenty-four hours, commencing at midday.

Figure 11.1a & b: Set-up of choice chambers of selection of upright stubble trials. a = Direct Drill. b = Direct Drill Managed. (Upright stubble circled in yellow).

11.3.2. Selection of Upright Stubble With the Presence of Aphididae

11.3.2.1. Introduction

This trial involved upright stubble and incorporated *M. dirhodum*. The addition was to investigate if prey availability influenced *T. tenuis* behaviour alongside upright stubble, or if it was a more dominant factor.

11.3.2.2. Methodology

Choice chambers were set up as in Section 11.3.1.2. except that *T. tenuis* incorporated had been starved for twenty-four hours in Petri dishes with three sticks and a small piece of moist cotton wool (*Section 7.6.2.4*.).

M. dirhodum were cultivated on *H. vulgare* from initial stock acquired from The Rothamsted Institute (*Section 7.2.3*.). Two adult apterous morph *M. dirhodum* were added into each choice chamber corresponding to data collected from GS 55 - GS 61 *H. vulgare* 2016 / 2017 season, when temperatures in the field were optimal for parthenogenesis (*Table 5.1.1. & Section 5.1.6.2.1*.). The two Aphididae were placed into the centre of the habitat at the same time and then the unit sealed (*Section 7.6.2.5*.).

11.4. Selection of Furrow With or Without the Presence of Aphididae

11.4.1. Selection of Furrow Without the Presence of Aphididae

11.4.1.1. Introduction

Two further trials concerned the addition of another landscape feature identified from the field, a furrow, constructed in the soil for a seedbed. Differing depths and widths of a furrow were identified in each soil tillage intensity. It was, therefore, an important element to be investigated, as in earlier glasshouse trails (*Chapter 8.0. & Chapter 10.0.*). As with upright stubble, trials were run with no Aphididae to discover how the depth and width of a furrow might influence web-site selection.

11.4.1.2. Methodology

The principle was identical to the previous choice chambers with selection of upright stubble, but with the choice element of the furrow, which was only established on one half of the choice chamber (*Section 11.3.1.2.*). It was noted that Direct Drill tilled area had a furrow, even if not as defined as the other tilled areas, due to the previous crop seedbed being undisturbed from the lack of cultivation. Soil used in this trial was Hanslope Series soil taken from the corresponding tilled areas from NIAB Field B (*Figure 3.5b, Section 3.1.3.3., Page 51*). As in mesocosm trials, the dimensions of the furrows used related to data gathered after secondary cultivation and direct drilling of *H. vulgare* cropping season 2017 / 2018 (*Figure 11.2.a - c*) (*Table 5.1.1. & Section 8.3.*).

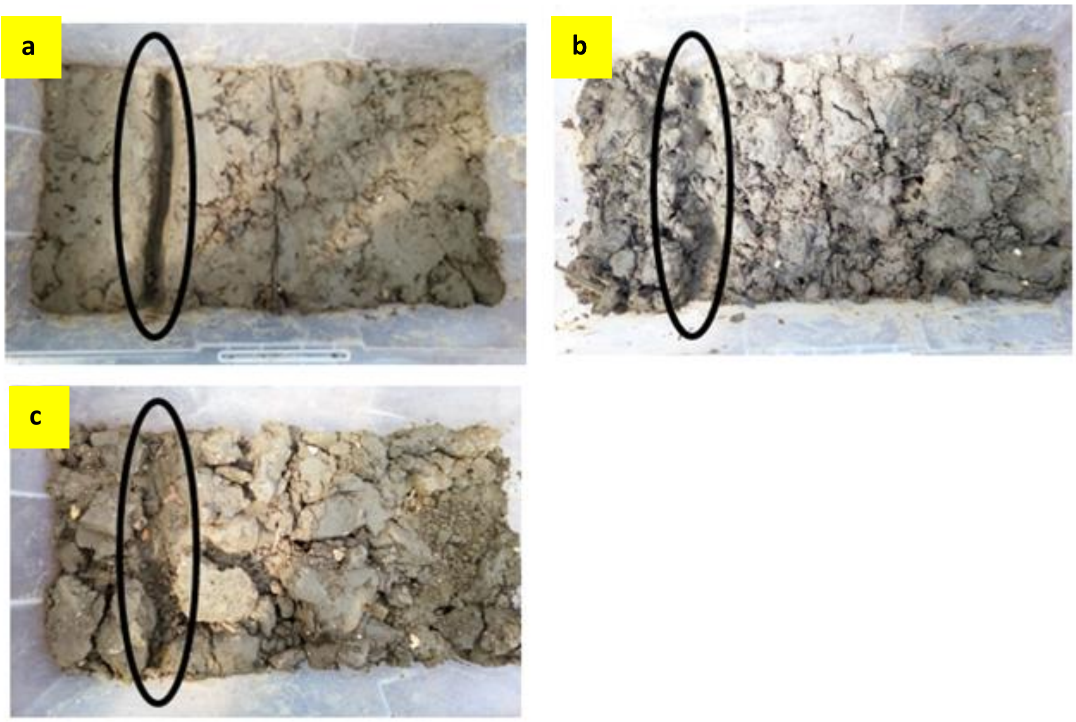


Figure 11.2a - c: Set-up of choice chambers of selection of furrow trials (Furrow circled in black). a = Conventional. b = Direct Drill Managed. C = Direct Drill.

To replicate the field as closely as possible, upright stubble and straw mass were incorporated into both sides of the trial. The same amount of each equalled that of the choice chamber for selection of upright stubble allowing any potential relationship to be identified between both choice chambers trials. This was to explore whether there is a preference for *T. tenuis* web construction in either upright stubble or an incision into the soil (*Figure 11.3a - c*).

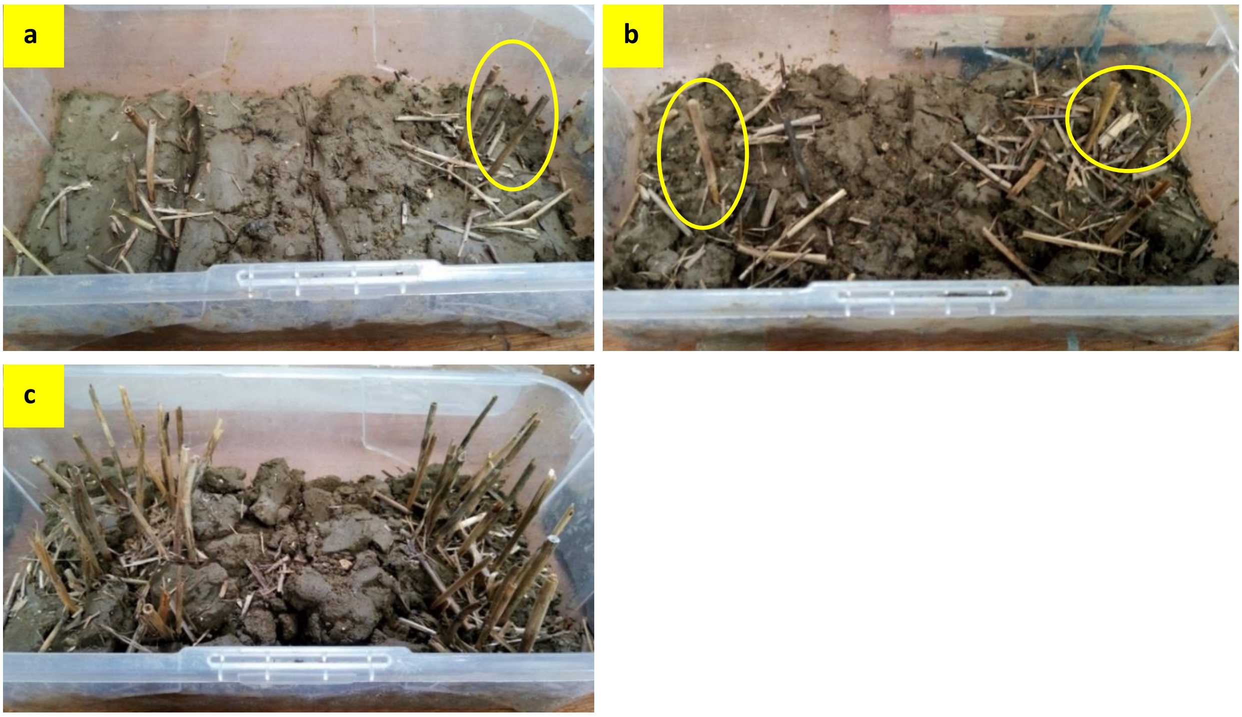


Figure 11.3a - c: Set-up of choice chambers of selection of furrow trials with the addition of straw and upright stubble. (Upright stubble circled in yellow). a = Conventional. b = Direct Drill Managed. c = Direct Drill.

No food source was added for this duration. The same combination of *T. tenuis* (by gender and numbers) in each soil tillage intensity, as in choice chambers for upright stubble with and without Aphididae was incorporated (five treatments of *T. tenuis* with three replicates of soil tillage) and run for twenty-four hours, commencing at midday (*Section 11.3.1.1. & Section 11.3.2.1.*).

11.4.2. Selection of Furrow With the Presence of Aphididae

11.4.2.1. Introduction

It was important that the choice chambers for furrow selection also incorporated the choice element of prey (Aphididae). This allowed comparison between the choice chamber trials for selection of upright stubble and furrow against Aphididae, which enabled predator dynamics and biological control potential to be further understood.

11.4.2.2. Methodology

Another set of trials were carried out with the addition of two adult apterous *M. dirhodum* added into the centre of each choice chambers. Each *T. tenuis* was starved, as in choice chambers selection of upright stubble with Aphididae (*Section 11.3.2.2.*).

11.5. Data Collection

Data recorded after twenty-four hours included measuring anchor point height and thread length in and out of webs (support and bridge threads respectively). The material that each thread was anchored to was also noted. Web area was calculated with the thread length in webs along with internal distances placed into Heron's formula, identical to fieldwork sampling (*Section 4.3.4.*). Data was gathered separately from each side of the choice chambers. Any information recorded (e.g. bridge thread) crossing the centre of the choice chambers was discounted.

In addition, the final position of *T. tenuis* in the habitat, (stubble or non-stubble / furrow or non-furrow), was recorded. This was related to how *T. tenuis* interacts with landscape heterogeneity and / or presence of prey (in the form of *M. dirhodum*). In trials incorporating Aphididae, the location of *M. dirhodum*, by side of chamber, was recorded and whether this was in the same side as *T. tenuis* noted.

As *T. tenuis* have been noted to have a preference to construct webs at a certain time of the day, (early morning), the hours of daylight were recorded for each trial to determine if this influenced web-building activity (Krol *et al.,* 2018) (*Section 2.1.3.1.*). Temperature was measured to the nearest 0.1 °C with a Portable Pen Digital Thermometer WT-1B®, as soon as the trial ended and the choice chamber was opened, taking care not to disturb any *T. tenuis* activity.

11.6. Statistical Analysis

A three-way log-linear analysis was run to cross-tabulate categorical data. Three categorical variables were incorporated; soil tillage intensity with corresponding sides (Conventional, Direct Drill Managed and Direct Drill and stubble and non-stubble, for example), number and gender of *T. tenuis* placed into the choice chambers and position of *T. tenuis* at the end of the trial (side of choice chamber). In the trials without Aphididae, there were two terms within the latter variable, stubble side / non-stubble side, and furrow side / non-furrow side. In the choice chamber where Aphididae were incorporated there were four terms, stubble side Aphididae / stubble side no Aphididae / non-stubble side Aphididae / non-stubble side no Aphididae. The same configuration was also used for furrow-related choice chambers. Any significant relationships were recorded, hierarchical level of significance in terms of the level of interaction. If the higher hierarchical level was identified, odds ratios were calculated for a specific question, for example odds ratio that a *T. tenuis* would be found in the side of an Aphididae. Normality was tested through analysing if the expected results were identical to the outcome calculated from the model. The chi-square likelihood of ratio (χ^2 = (1)) in goodness of fit should be significant at the beginning of the analysis (χ^2 (0) = 0 and P - 0.001) to confirm the expected model is a good fit for the data presented, from here terms can be removed to identify the highest order of interaction. The model was then seen to fit normal parameters. Software used for the log-linear analysis was IBM® SPSS Statistics© 25 (Field, 2009).

The basis of log-linear analysis is to analyse the frequency that observations occur in each cross-classification category (a classification category being a *T. tenuis* ending in the side of the choice chamber of Conventional tillage of non-stubble when one male was incorporated at the start of the experiment), also known as exploratory variables (Menard, 2010; Tansey *et al.,* 1996). Log-linear models were chosen over logistic regression as all variables in the design were categorical / discrete and nominal, log-linear analysis performs well in this situation due to the nature of this test an extension of the chi-square test (Menard, 2010; Ranganathan *et al.,* 2017; Upton, 1991). There was further no clear distinction between the dependant variable (frequency counts) and explanatory variables, the spider had equal chance to end in either side of the choice chamber in each soil tillage intensity, thus, no special status was assigned to the variables. Every input was independent of one another (Menard, 2010; Tansey *et al.,* 1996). Log-linear analysis is based on Poisson distribution (probability of an event occurring in a given space and time), useful here as each observation was independent and not dependant on the sample size, whereas logistic regression is based on bi-nominal distribution where there are only two possible outcomes (Field, 2009; Ranganathan *et al.,* 2017; Upton, 1991; Wheater *et al.,* 2011).

Due to the principle of log-linear analysis to respond to frequency of observations a frequency plot represents the outcomes of the model, frequency a *T. tenuis* will end up in one side of the choice chamber of a particular soil tillage intensity and of a particular number and gender of *T. tenuis* incorporated into the experiment (Field, 2009; Menard, 2010). Understanding assumptions, reliability in expected frequencies is a given, due to more than two exploratory variables utilised in this experiment, allowing 20% of cells (counts) to have a frequency less than 5 (Field, 2009; Menard, 2010; Tansey *et al.,* 1996).

Minitab18© was utilised to perform normality testing (Anderson-Darling and Ryan-Joiner for clarification) alongside visual interpretation of histograms and probability plots (*Section 5.1.4.1.*). The hypothesis was rejected (P - value α <0.05) on all data in this experimental Chapter. Correlations were carried out with the Spearman's rank (Rho) test to understand if any significant correlations were found within the variables measured (Bass 2007, Wheater *et al.,* 2011).

Two-way rank ANOVAs examined if there were any significant relationships between the response variable (anchor point height and thread length) and two categorical factors, a factor represented in every model was soil tillage intensity and side of choice chamber (e.g. Conventional stubble side etc). The other categorical factor was either: the attachment material used for an anchor point or whether the response variable belonged to a thread inside or outside a web. As with other experimental Chapters where data was non-normal, degrees of freedom (df) and sums of squares (SS) were identified and placed into FCSTats V2_1a© to be able to assign significance if it existed. Mean rank values were tested with the multiple comparison Dunn's test to locate where the significance lay within the samples. The Bonferroni test, through Minitab18©, allowed letters to be assigned to the samples when graphed (Hawkins, 2014; Wheater & Cook, 2000) (*Section 5.1.4.2*.).

General linear models (GLM) were used to establish interactions between the response variables (anchor point height and thread length) that were measured alongside the factors of number and gender of *T. tenuis* that were added into the choice chambers (e.g. one male, two male etc) and the soil tillage intensity. *T. tenuis* (in number and gender) were nested into the soil tillage intensity and the side of selection (e.g. Conventional stubble etc), where activity was recorded. Nesting allowed all combinations of the factor (number and gender of *T. tenuis*) to be analysed within their co-ordinating factor of soil tillage intensity / side of choice chamber. The fixed factors of soil tillage intensity / side of choice chamber and number and gender of *T. tenuis* (nested) were each mutually exclusive. No two-way rank ANOVA could be modelled on these variables due to not all sides of the choice chambers utilised by *T. tenuis* in each trial. Analysis was carried out on support threads only, the key to predator dynamics to understand differences in the size and location of webs spun. Normality was assured using a residual plot, where residuals were close to the trend line, and residuals versus order plot, where no cyclic pattern was established. Both indicate variables are independent of one another (Bass, 2007; Field, 2009; Wheater & Cook, 2000; Wheater *et al.,* 2011; Zuur *et al.,* 2007). Outliers were removed where normality could not be ascertained.

11.7. Results

The results are set out into four sections following each set of trials. Selection of upright stubble with and without Aphididae (*M. dirhodum*) and selection of furrow with and without Aphididae. Within each section, the dependant variables of anchor point height and length for threads inside and outside of webs were analysed. Web areas were measured in all sides of the choice chambers with each trial; however, no statistical significance could be identified. Thread length found inside webs (of support threads) is a representation of web area. Within each section where Aphididae (*M. dirhodum*) were included in the trials, dependant variables measured in correlations and general linear models, refer to the side where *M. dirhodum* was recorded and to support threads of webs only. *T. tenuis* response to *M. dirhodum* presence was the key factor to be analysed in these trials and the web is a direct response to potential prey capture.

The term 'soil tillage intensities' within this glasshouse experiment refers to the six sides in the selection of stubble. These are Conventional (stubble and non-stubble), Direct Drill Managed (stubble and non-stubble), Direct Drill (stubble and non-stubble). The same holds for the furrow experiment; Conventional (furrow and non-furrow) for example.

11.7.1. Summary of Results

Selection of Upright Stubble Trials Without the Presence of Aphididae

- The greater frequency of *T. tenuis* was found in the stubble side (*Figure 11.4.*) The same sides showed a significantly higher mean, found for the attachment material of upright stubble (*Figure 11.6.*). Conventional and Direct Drill stubble sides showed a significantly higher mean rank anchor point of support threads (*Figure 11.5.*). Number of upright stubble was significantly positively correlated to anchor point height of support threads (*Table 11.3.*)
- Conventional non-stubble side exhibited significant longer mean rank bridge thread length (*Figure 11.9.*). Straw mass was significantly positively correlated to anchor point height of support threads (*Table 11.3.*). Significantly longer mean length of support threads was shown in Conventional stubble side with two male *T. tenuis* (*Figure 11.10.*).
- The highest mean anchor point height was found in Direct Drill stubble side when one female and one male and two females were incorporated (*Figure 11.7. & Figure 11.8.*)
- Cephalothorax length was significantly positively correlated to anchor point outside of webs and thread length of support webs (*Table 11.3. & Table 11.5.*).
- Sunlight duration was significantly negatively correlated to length of bridge and support threads (*Table 11.5.*).

Selection of Upright Stubble Trials With the Presence of Aphididae

- Number and gender of *T. tenuis* incorporated into the choice chambers significantly affected the side where *T. tenuis* was found at end of trial (*Figure 11.11*.).
- Straw mass was significantly positively correlated to anchor point height and length of support threads (*Table 11.6. & Table 11.7.*).
- Direct Drill stubble showed significantly higher anchor point height at side with *M. dirhodum*, when one male *T. tenuis* was incorporated (*Figure 11.12*.). Number of upright stubble was significantly positively correlated to anchor point height of support threads (*Table 11.6*.).

Selection of Furrow Trials Without the Presence of Aphididae

- Mean rank higher anchor point height was found attached to the material of upright stubble than straw and soil for Conventional and Direct Drill furrow and non-furrow sides (*Figure 11.13*. & *Figure 11.14*.).
- Furrow depth held significant negative correlation with anchor point height of bridge threads (*Table 11.12.*). Whereas, furrow width and depth were significantly positively correlated to length of bridge threads (*Table 11.13.*).
- Mean anchor point height outside of webs in Conventional furrow was significantly lower than that of the Direct Drill (*Figure 11.16*.). Significantly higher mean anchor point height of support threads was calculated for Direct Drill non-furrow and Direct Drill Managed furrow side (*Figure 11.15*.).
- Temperature and sunlight duration were significantly positively correlated to the anchor point height and length of support threads (*Table 11.12. & Table 11.13*.).

Selection of Furrow Trials With the Presence of Aphididae

- Significance was identified in the three-way interaction for the log-linear analysis (*Figure 11.17. – Figure 11.22.*). Odds ratios for *T. tenuis* sharing the side of *M. dirhodum,* after twenty-four hours, was low for all soil tillage intensities.
- Significant mean anchor point height, side of *M. dirhodum,* was recorded in Direct Drill non-furrow with one and two male *T. tenuis* in the chamber (*Figure 11.23. & Figure 11.24.*).
- Anchor point height of support threads was significantly negatively correlated to furrow dimensions and significantly positively correlated to number of upright stubble (*Table 11.14.*).

11.7.2. Selection of Upright Stubble Trials Without the Presence of Aphididae

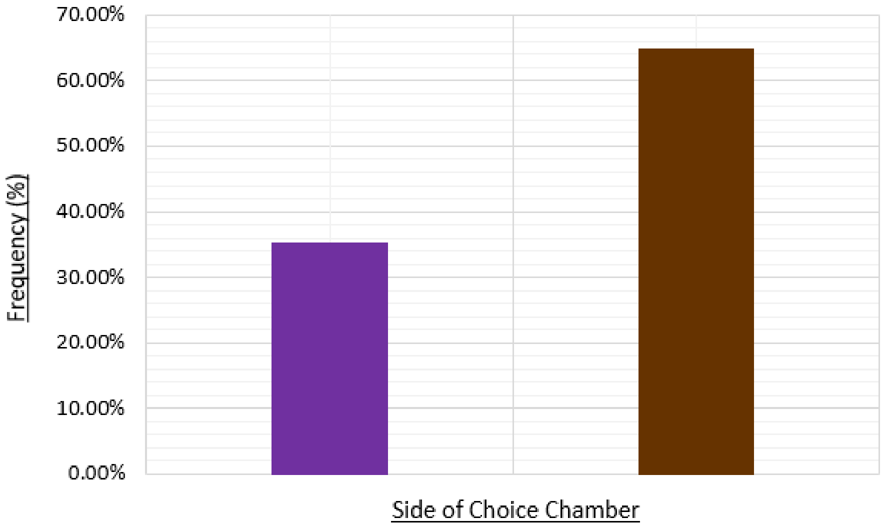


Figure 11.4: Frequency plot showing the frequency (%) of T. tenuis *end position, in the non-stubble side or stubble side. Choice chambers of selection of upright stubble trials without Aphididae. (χ^2 = (1) - 95.71, P - 0.001) (Non-Stubble Side = Purple, Stubble Side = Brown).*

The three-way log-linear analysis produced a final model where the main effect, the lowest order hierarchical level, was significant and was retained in the model. Backward elimination of orders of interaction noted the end position of *T. tenuis* to be the main effect where the significance lies. No interaction between the three categorical terms was significant. Difference between the end positions of *T. tenuis* in the non-stubble side or stubble side was significant regardless of treatment or gender (*Figure 11.4.*). A greater frequency of *T. tenuis* was noted to be within the stubble side (64.30%) than the non-stubble side (35.70%) when the trial ended.

11.7.2.1. Anchor Point Height

Table 11.1: Response of rank anchor point height inside webs (of support threads), factors of soil tillage intensity and side of choice chamber. Choice chambers of selection of upright stubble trials without Aphididae (n = 223). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	1.603	0.449
Side of Choice Chamber	1	13.791	0.001*
Interaction: Soil Tillage Intensity * Side of Choice Chamber	2	3.498	0.174

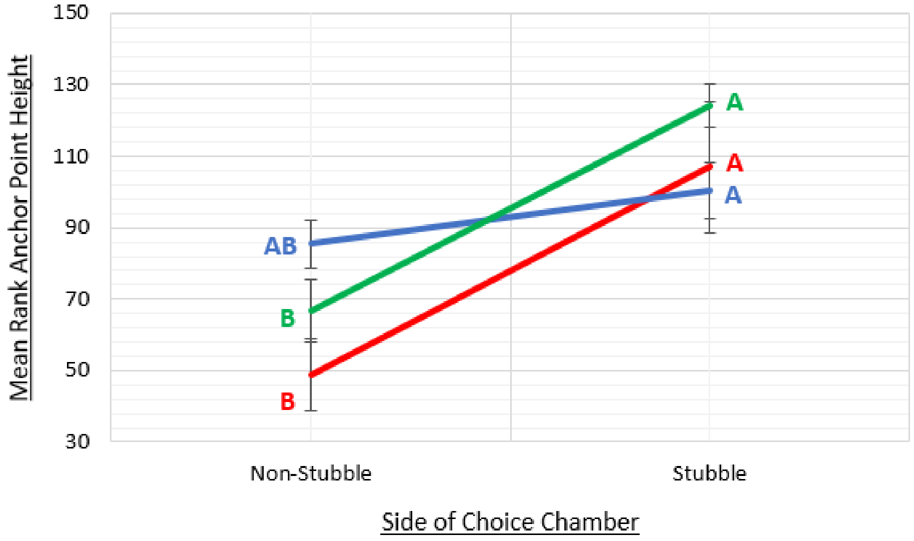


Figure 11.5: Interaction of mean rank anchor point height inside webs (of support threads), soil tillage intensity and side of choice chamber. Choice chambers of selection of upright stubble trials without Aphididae (n = 223). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Non-Stubble ±s.e.10.075 (n = 16), Conventional Stubble ±s.e.18.457 (n = 27), Direct Drill Managed Non-Stubble ±s.e.6.701 (n = 18), Direct Drill Managed Stubble ±s.e.7.837 (n = 49), Direct Drill Non-Stubble ±s.e.8.761 (n = 8), Direct Drill Stubble ±s.e.6.068 (n = 105)). (Points that do not share the same letter are significantly different at the p<0.05 level).

Significance in the response of mean rank anchor point height of support threads with the side of the choice chamber was found (*Figure 11.5*. & *Table 11.1*.). Homogeneity was found in the mean rank anchor point height between the sides of choice chamber representing Direct Drill Managed. The Conventional and Direct Drill stubble side held a significantly higher mean rank anchor point height inside of webs than that found in the non-stubble side of the same soil tillage intensities.

Table 11.2: Response of rank anchor point height inside webs (of support threads) and factors of soil tillage intensity of stubble side and anchor point attachment material. Choice chambers of selection of upright stubble trials without Aphididae (n = 169). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	3.341	0.188
Anchor Point Attachment Material	1	33.785	0.001*
Interaction: Soil Tillage Intensity * Anchor Point Attachment Material	2	2.910	0.233

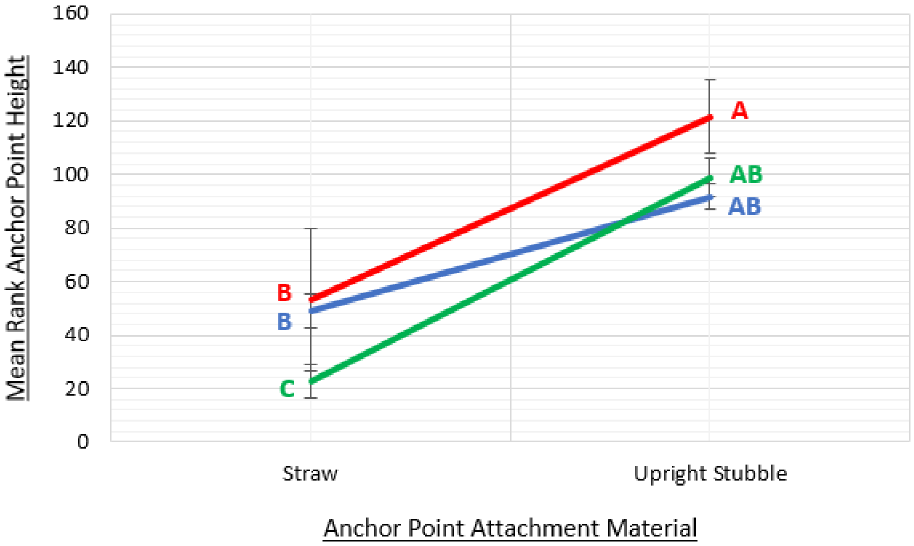


Figure 11.6: Interaction of mean anchor point height inside webs (of support threads) and factors of soil tillage intensity of stubble side and anchor point attachment material. Choice chambers of selection of upright stubble trials without Aphididae (n = 169). (Conventional = Red, Direct Drill Managed Blue, Direct Drill = Green). (Conventional Straw ±s.e.26.536 (n = 6), Conventional Upright Stubble ±s.e.13.633 (n = 9), Direct Drill Managed Straw ±s.e.6.220 (n = 11), Direct Drill Managed Upright Stubble ±s.e.4.795 (n = 93), Direct Drill Straw ±s.e.6.360 (n = 25), Direct Drill Upright Stubble ±s.e.7.060 (n = 25)). (Points that do not share the same letter are significantly different at the p<0.05 level).

The Conventional and Direct Drill choice chambers held a mean rank anchor point height, utilising the attachment material of upright stubble, that was significantly higher than the mean rank anchor point height attached to straw (*Figure 11.6. & Table 11.2.*).

The non-stubble sides were discounted due to straw the only attachment material within these sides.

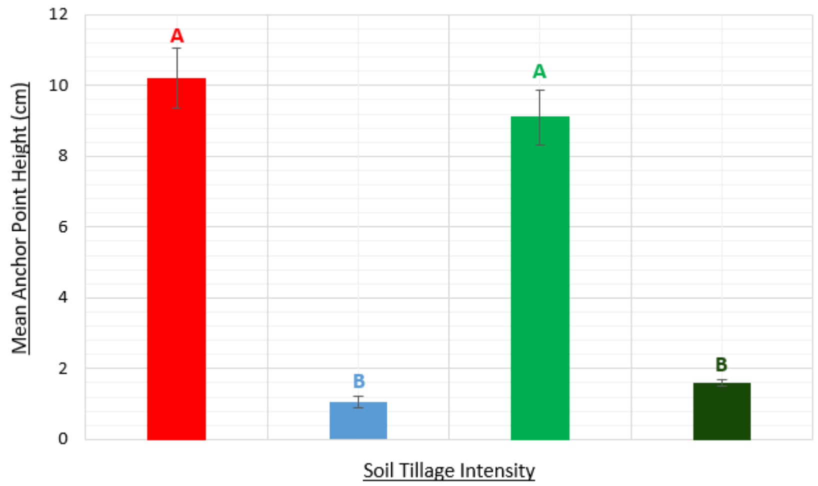


Figure 11.7: Mean anchor point height (cm) inside webs (of support threads) of soil tillage intensities with 1 x female and 1 x male T. tenuis*. Choice chambers of selection of upright stubble trials without Aphididae. (n = 256, df - 13, F - 8.55, R-sq - 35.36%, P - 0.001). (Conventional Stubble = Red, Direct Drill Managed Stubble = Blue, Direct Drill Stubble = Green, Direct Drill Non-Stubble = Dark Green,). (Conventional Stubble ±s.e.2.512 (n = 12), Direct Drill Managed Stubble ±s.e.0.149 (n = 3), Direct Drill Stubble ±s.e.1.165 (n = 39), Direct Drill Non-Stubble ±s.e.0.084 (n = 6)). Bars that do not share the same letter are significantly different at the p<0.05 level).*

Significance was found within the mean anchor point heights of support threads recorded within the different sides of soil tillage intensities when one female and one male *T. tenuis* were incorporated into the choice chamber (*Figure 11.7.*). The Conventional stubble side, mean anchor point height inside webs of 10.2 cm, and Direct Drill stubble, mean of 9.1 cm, showed significantly higher mean anchor point heights of support threads than that of Direct Drill non-stubble side (mean of 1.6 cm) and Direct Drill Managed stubble side (mean of 1.0 cm).

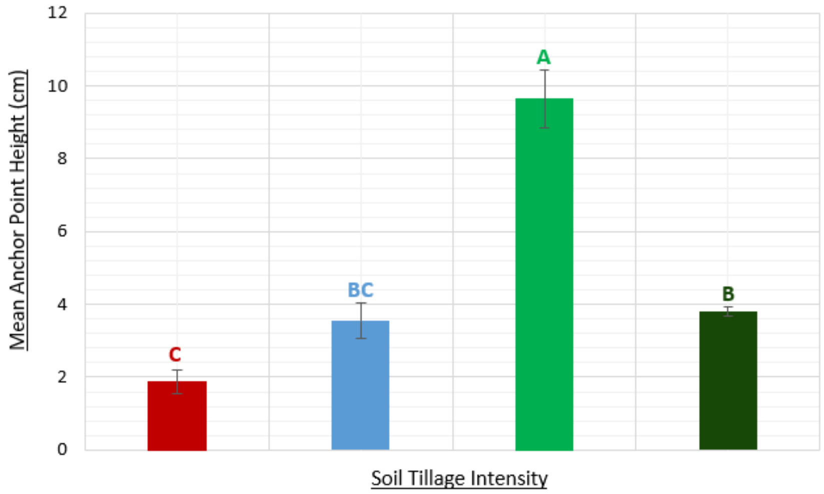


Figure 11.8: Mean anchor point height (cm) inside webs (of support threads) of soil tillage intensities with 2 x female T. tenuis*. Choice chambers of selection of upright stubble trials without Aphididae. (n = 256, df - 13, F - 8.55, R-sq - 33.36%, P - 0.001). (Conventional Non-Stubble = Dark Red, Direct Drill Managed Stubble = Blue, Direct Drill Stubble = Green, Direct Drill Non-Stubble = Dark Green). (Conventional Non-Stubble ±s.e.0.321 (n = 7), Direct Drill Managed Stubble ±s.e.0.489 (n = 8), Direct Drill Stubble ±s.e.0.793 (n = 21), Direct Drill Non-Stubble ±s.e.0.118 (n = 7)). Bars that do not share the same letter are significantly different at the p<0.05 level).*

Significant difference was established between the mean anchor point heights inside webs and the sides of soil tillage intensity for two female *T. tenuis* (*Figure 11.8.*). The Direct Drill stubble side held the anchor point height 9.6 cm which was the significantly higher. Conventional non-stubble side exhibited the significantly lower mean anchor point height (mean 1.9 cm) to that measured in Direct Drill stubble and non- stubble side.

Table 11.3: Correlations of independent variables measured in choice chambers, with the dependant variable anchor point height (cm) inside and outside of web. Choice chambers of selection of upright stubble trials without Aphididae. (relates to significant with α <0.05).*

	Inside Web			**Out of Web**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**
Mean Abdomen Length (mm)	0.369	0001*	256	-0.104	0.124	64
Mean Cephalothorax Length (mm)	0.025	0.690	256	0.276	0.027*	64
Number of Upright Stubble	0.303	0.001*	256	0.207	0.027*	64
Straw Mass (g)	0.200	0.001*	256	-0.023	0.858	64
Sunlight Duration (mins)	0.157	0.013*	256	-0.534	0.001*	64
Temperature (°C)	0.306	0.001*	256	-0.373	0.002*	64

Mean abdomen length of *T. tenuis* placed into the choice chamber, straw mass, sunlight duration of the experiment, temperature inside the choice chamber and number of upright stubble were found to be significantly positively correlated to anchor point heights measured inside webs (of support threads) (*Table 11.3*.). Only mean cephalothorax length of *T. tenuis* and number of upright stubble were found to be significantly positively correlated to anchor point outside of web (of bridge threads), whereas temperature and sunlight duration recorded were significantly negatively correlated to anchor point heights of bridge threads.

11.7.2.2. Thread Length

Table 11.4: Response of rank thread length outside of webs (of bridge threads) and factors of soil tillage intensity and side of choice chamber. Choice chambers of selection of upright stubble trials without Aphididae (n = 43). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	8.806	0.012*
Side of Choice Chamber	1	0.033	0.857
Interaction: Soil Tillage Intensity * Side of Choice Chamber	2	2.430	0.297

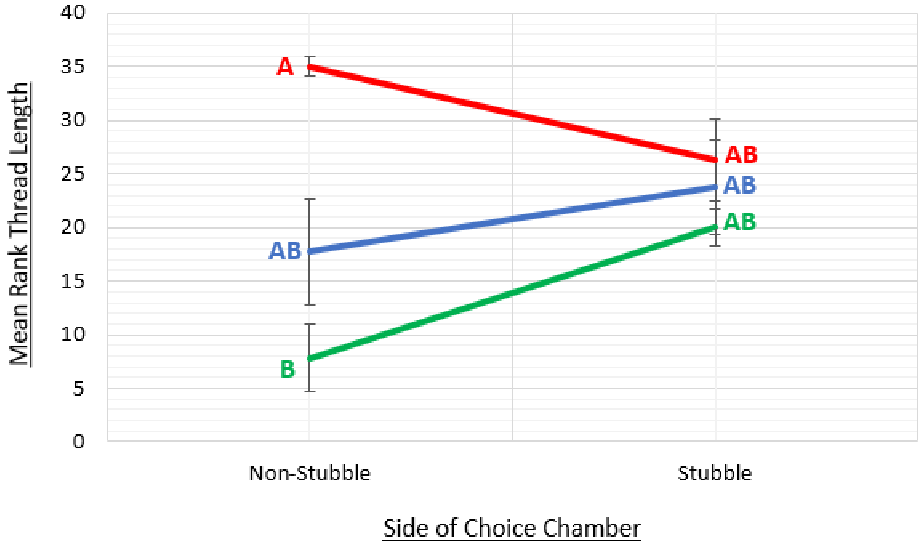


Figure 11.9: Interaction of mean rank thread length outside of webs (of bridge threads), soil tillage intensity and side of choice chamber. Choice chambers of selection of upright stubble trials without Aphididae (n = 43). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Non-Stubble ±s.e.0.894 (n = 3), Conventional Stubble ±s.e.3.797 (n = 9), Direct Drill Managed Non-Stubble ±s.e.7.993 (n = 7), Direct Drill Managed Stubble ±s.e.4.377 (n = 10), Direct Drill Non-Stubble ±s.e.3.164 (n = 3), Direct Drill Stubble ±s.e.1.716 (n = 11)). (Points that do not share the same letter are significantly different at the p<0.05 level).

The Conventional non-stubble side held the significantly longer mean rank thread length of bridge threads, than that found in the Direct Drill non- stubble side (*Figure 11.9*. & *Table 11.4*.). There was no significance within the interaction of mean rank thread length, soil tillage intensity and side of choice chamber the mean was found in.

No significance was identified in all terms in a two-way rank ANOVA for mean rank thread length of support threads.

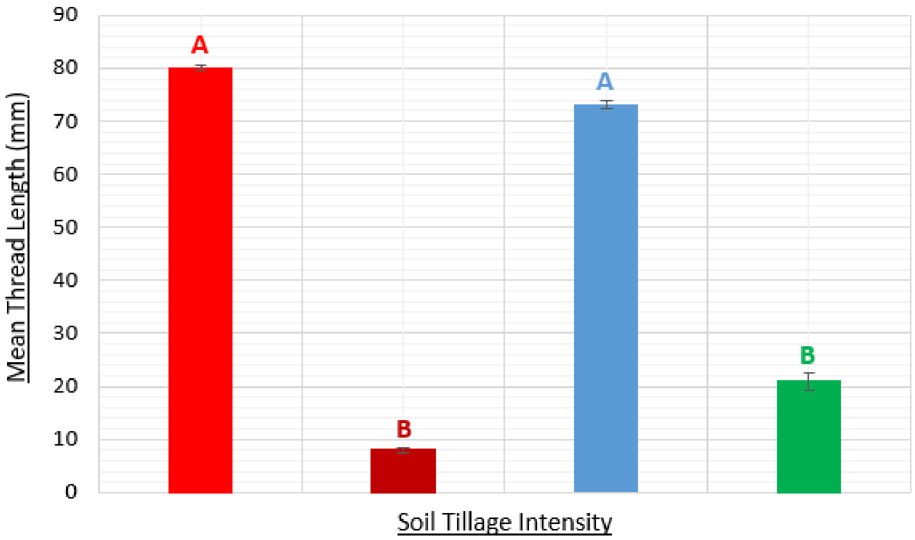


Figure 11.10: Mean thread length (mm) inside webs (of support threads) of soil tillage intensities with 2 x male T. tenuis*. Choice chambers of selection of upright stubble trials without Aphididae. (n = 234, df - 13, F - 11.34, R-sq - 41.36%, P - 0.001). (Conventional Stubble = Red, Conventional Non-Stubble = Dark Red, Direct Drill Managed Stubble - Blue, Direct Drill Stubble = Green). (Conventional Stubble ±s.e.0.521 (n = 7), Conventional Non-Stubble ±s.e.0.442 (n = 7), Direct Drill Managed Stubble ±s.e.8.892 (n = 7), Direct Drill Stubble ±s.e.0.653 (n = 21). Bars that do not share the same letter are significantly different at the p<0.05 level).*

Significant heterogeneity within mean thread length only existed when two male *T. tenuis* were placed into the choice chamber (*Figure 11.10*.). The Conventional stubble side with a mean of 80.1 mm and Direct Drill Managed stubble side, 73.2 mm mean thread length, both held the significantly longer mean thread lengths inside webs. Conventional non-stubble and Direct Drill stubble side held the significantly lower.

Table 11.5: Correlations of independent variables measured in choice chambers, with the dependant variable thread length (mm) inside and outside of web. Choice chambers of selection of upright stubble trials without Aphididae. (relates to significant with α <0.05).*

	Inside Web			**Out of Web**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**
Mean Cephalothorax Length (mm)	0.255	0.001*	234	0.137	0.392	42
Straw Mass (g)	0.010	0.873	234	-0.423	0.005*	42
Sunlight Duration (mins)	-0.323	0.001*	234	-0.379	0.013*	42

Mean cephalothorax length of *T. tenuis* was significantly positively correlated to lengths of support threads (*Table 11.5*.). The opposite was found for straw mass and thread length outside of webs which showed significant negative correlation. Sunlight duration was significantly negatively correlated to both the lengths of support threads and bridge threads.

11.7.3. Selection of Upright Stubble Trials With the Presence of Aphididae

The log-linear analysis model for the choice chambers of selection of upright stubble with Aphididae states the second level of hierarchy is significant. The model stops here and the three-way interaction between the categorical variables is not retained. The term involved in the significant two-way interaction is the number and gender of *T. tenuis* incorporated and the end position of *T. tenuis* (stubble side or non-stubble side, with or without Aphididae) (*Figure 11.11.*).

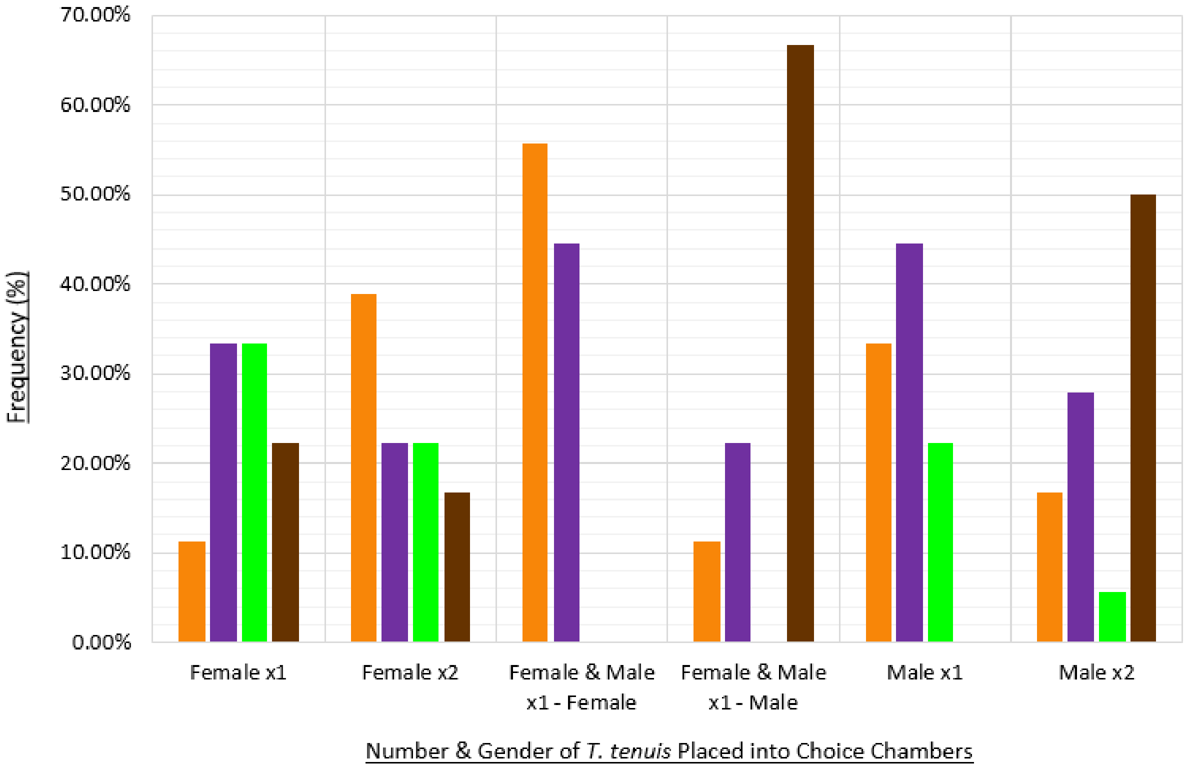


Figure 11.11: Frequency plot showing the frequency (%) of the T. tenuis *end position, in the non-stubble side or stubble side, with or without Aphididae, grouped by number and gender of* T. tenuis *incorporated into each choice chamber. Choice chambers of selection of upright stubble trials with Aphididae. (χ^2 = (1) - 31.255, P - 0.007). (Non-Stubble Side Aphididae = Orange, Non-Stubble Side No Aphididae = Purple, Stubble Side Aphididae = Light Green, Stubble Side No Aphididae = Brown).*

The interaction displays the greatest frequency of female *T. tenuis* end position, when one female was incorporated, was shared by the side of non-stubble without Aphididae and stubble with Aphididae (*Figure 11.11.*). All sides were chosen when two female *T. tenuis* were incorporated, the greatest being the non-stubble side with Aphididae. Female, when added with a male *T. tenuis*, only frequented the non-stubble side, with and without Aphididae. The male *T. tenuis* when added with a female, was found in the greatest frequency of the side of stubble without Aphididae. With one male *T. tenuis*, no males were found in the side of stubble without Aphididae, the greatest frequency being non-stubble side without Aphididae. The side of stubble without Aphididae held the greatest frequency and the stubble with Aphididae the lowest, when two male *T. tenuis* were added.

11.7.3.1. Anchor Point Height

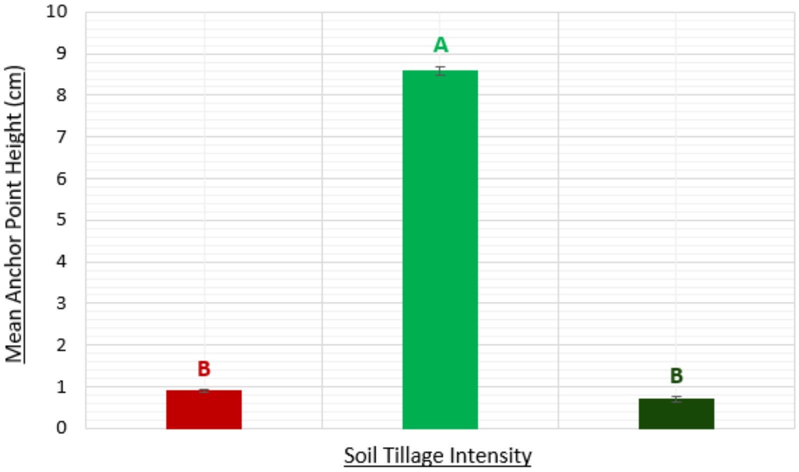


Figure 11.12: Mean anchor point height (cm) inside webs (of support threads) where M. dirhodum *was recorded of soil tillage intensities with 1 x male* T. tenuis*. Choice chambers of selection of upright stubble trials with Aphididae. (n = 79, df - 8, F - 3.68, R-sq - 43.45%, P - 0.015). (Conventional Non-Stubble = Dark Red, Direct Drill Stubble = Green, Direct Drill Non-Stubble = Dark Green). (Conventional Non-Stubble ±s.e.0.045 (n = 4), Direct Drill Stubble ±s.e.0.101 (n = 7), Direct Drill Non-Stubble ±s.e.0.082 (n = 6)). (Bars that do not share the same letter are significantly different at the p<0.05 level).*

Significance existed in mean anchor point height inside webs when one male was added, at the side of the *M. dirhodium,* in the Conventional non-stubble side and the Direct Drill stubble and non-stubble sides only (*Figure 11.12*.). A mean anchor point height found within the Direct Drill stubble side was significantly higher than that of Conventional and Direct Drill non-stubble sides.

Table 11.6: Correlations of independent variables measured in choice chambers, with the dependant variable anchor point height (cm) inside web (of support threads), side of M. dirhodum*. Choice chambers of selection of upright stubble trials with Aphididae. (* relates to significant with α <0.05).*

	(Rho)	***P***	**n**
Mean Cephalothorax Length (mm)	0.229	0.044*	79
Number of Upright Stubble	0.564	0.001*	79
Straw Mass (g)	0.301	0.001*	79

Anchor point inside the web, where *M. dirhodum* was identified, was significantly positively correlated to mean cephalothorax length of *T. tenuis*, straw mass and number of upright stubble (*Table 11.6.*).

11.7.3.2. Thread Length

Table 11.7: Correlations of independent variables measured in choice chambers, with the dependant variable thread length (mm) Inside web (of support threads), side of M. dirhodum*. Choice chambers of selection of upright stubble trials with Aphididae. (* relates to significant with α <0.05).*

	(Rho)	***P***	**n**
Number of Upright Stubble	0.243	0.033*	79
Straw Mass (g)	0.326	0.004*	79

Length of support threads was significantly positively correlated to the amount of straw mass and number of upright stubble (*Table 11.7.*).

11.7.4. Selection of Furrow Trials Without the Presence of Aphididae

11.7.4.1. Anchor Point Height

Table 11.8: Response of rank anchor point height inside webs (of support threads) and factors of soil tillage intensity of furrow side and anchor point attachment material. Choice chambers of selection of furrow trials without Aphididae (n = 184). (relates to significant with α <0.05).*

Categorical Predictor	df	*H*	*P*
Soil Tillage Intensity (Furrow Side)	2	0.962	0.918
Anchor Point Attachment Material	2	121.802	0.001*
Interaction: Soil Tillage Intensity * Anchor Point Attachment Material	4	15.778	0.022*

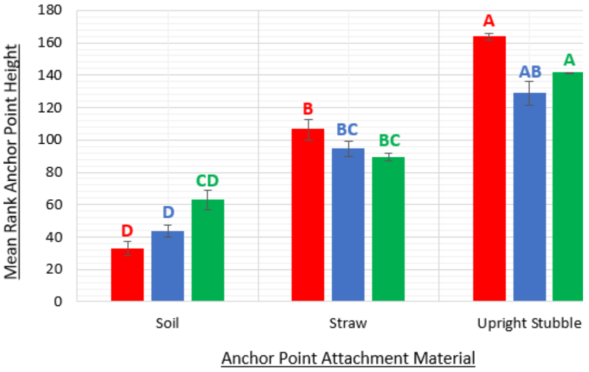


Figure 11.13: Interaction of mean rank anchor point height inside webs (of support threads), soil tillage intensity of furrow side and anchor point attachment material. Choice chambers of selection of furrow trials without Aphididae (n = 184). (Conventional Furrow = Red, Direct Drill Managed Furrow Blue, Direct Drill Furrow = Green). (Conventional Soil ±s.e.4.208 (n = 23), Conventional Straw ±s.e.6.230 (n = 3), Conventional Upright Stubble s.e±.2.082 (n = 6), Direct Drill Managed Soil ±s.e.3.730 (n = 49), Direct Drill Managed Straw ±s.e.4.695 (n = 4), Direct Drill Managed Upright Stubble ±s.e.7.358 (n = 21), Direct Drill Soil ±s.e.6.121 (n = 13), Direct Drill Straw ±s.e.2.607 (n = 5), Direct Drill Upright Stubble ±s.e.0.400 (n = 60)) (Points that do not share the same letter are significantly different at the p<0.05 level).

Table 11.9: Response of rank anchor point height inside webs (of support threads) and factors of soil tillage intensity of non-furrow side and anchor point attachment material. Choice chambers of selection of furrow trials without Aphididae (n = 128). (relates to significant with α <0.05).*

Categorical Predictor	df	*H*	*P*
Soil Tillage Intensity (Non-Furrow Side)	2	6.268	0.043*
Anchor Point Attachment Material	2	52.786	0.001*
Interaction: Soil Tillage Intensity * Anchor Point Attachment Material	4	12.662	0.013*

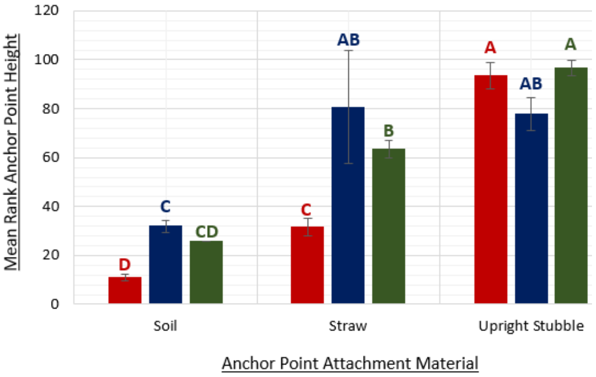


Figure 11.14: Interaction of mean rank anchor point height inside webs (of support threads), soil tillage intensity of non-furrow side and anchor point attachment material. Choice chambers of selection of furrow trials without Aphididae (n = 128) (Conventional Non-Furrow = Dark Red, Direct Drill Managed Non-Furrow Dark Blue, Direct Drill Non-Furrow = Dark Green). (Conventional Soil s.e.±1.323 (n = 16) Conventional Straw s.e.±3.408 (n = 5), Conventional Upright Stubble s.e.±0.418 (n = 17), Direct Drill Managed Soil ±s.e.2.595 (n = 26), Direct Drill Managed Straw ±s.e.22.928 (n = 3), Direct Drill Managed Upright Stubble s.e.6.715 (n = 12), Direct Drill Soil ±s.e.0 (n = 1), Direct Drill Straw ±s.e.3.589 (n = 10), Direct Drill Upright Stubble ±s.e.3.267 (n = 38)). (Points that do not share the same letter are significantly different at the p<0.05 level).

The mean rank anchor point height of support threads, found on the attachment material of upright stubble of Conventional and Direct Drill furrow side, was significantly higher than the mean rank anchor point height recorded when the attachment material was straw and soil for the furrow side of choice chambers representing all three soil tillage intensities (*Figure 11.13. & Table 11.8.*).

Significant was found in the interaction of anchor point attachment material and soil tillage intensity (*Figure 11.14. & Table 11.9.*). Mean rank anchor point height, of support threads, attached to upright stubble within the non-furrow side was significantly higher than the mean rank anchor point height attached to soil for all soil tillage intensities and attached to straw for Conventional and Direct Drill.

Table 11.10: Response of rank anchor point height inside web (of support threads) and factors of soil tillage intensity and side of choice chamber. Choice chambers of selection of furrow trials without Aphididae (n = 392). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	64.118	0.001*
Side of Choice Chamber	1	12.488	0.012*
Interaction: Soil Tillage Intensity * Side of Choice Chamber	2	2.436	0.296

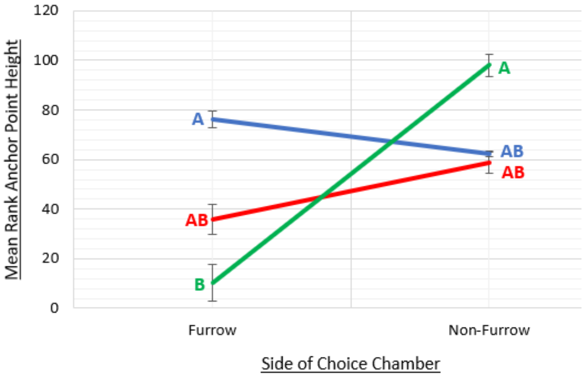


Figure 11.15: Interaction of mean rank anchor point height inside web (of support threads), soil tillage intensity and side of choice chamber. Choice chambers of selection of furrow trials without Aphididae (n = 392). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Furrow ±s.e.20.950 (n = 44), Conventional Non-Furrow ±25.103 (n = 54), Direct Drill Managed Furrow ±s.e.15.380 (n = 98), Direct Drill Managed Non-Furrow ±s.e.23.871 (n = 47), Direct Drill Furrow ±s.e.26.271 (n = 96), Direct Drill Non-Furrow ±s.e.35.322 (n = 53)). (Points that do not share the same letter are significantly different at the p<0.05 level).

Table 11.11: Response of rank anchor point height outside of web (of bridge threads) and factors of soil tillage intensity and side of choice chamber. Choice chambers of selection of furrow trials without Aphididae (n = 109). (relates to significant with α <0.05).*

Categorical Predictor	**df**	***H***	***P***
Soil Tillage Intensity	2	13.779	0.001*
Side of Choice	1	10.173	0.001*
Interaction: Soil Tillage Intensity * Side of Choice Chamber	2	15.827	0.001*

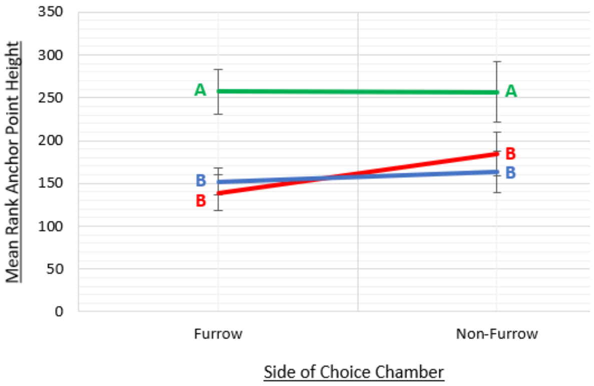


Figure 11.16: Interaction of mean rank anchor point height outside of web (of bridge threads), soil tillage intensity and side of choice chamber. Choice chambers of selection of furrow trials without Aphididae (n = 109). (Conventional = Red, Direct Drill Managed = Blue, Direct Drill = Green). (Conventional Furrow ±s.e.6.008 (n = 20), Conventional Non-Furrow ±4.364 (n = 44), Direct Drill Managed Furrow ±s.e.3.331 (n = 3), Direct Drill Managed Non-Furrow ±s.e.0.997 (n = 2), Direct Drill Furrow ±s.e.7.589 (n = 12), Direct Drill Non-Furrow ±s.e.4.634 (n = 28)). (Points that do not share the same letter are significantly different at the p<0.05 level).

The mean rank anchor point height of support threads calculated within the Direct Drill Managed furrow side and Direct Drill non-furrow side, were significantly higher than the mean anchor point height of Direct Drill of the furrow side (*Figure 11.15. & Table 11.9.*).

Interaction was significant with mean rank anchor point height of bridge threads in Direct Drill of both sides of the choice chamber, the means significantly higher than that recorded in Conventional and Direct Drill Managed furrow and non-furrow sides (*Figure 11.16. & Table 11.10.*).

Table 11.12: Correlations of independent variables measured in choice chambers, with the dependant variable anchor point height (cm) inside and outside of web. Choice chambers of selection of furrow trials without Aphididae. (relates to significant with α <0.05).*

	Inside Web			**Out of Web**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**
Furrow Depth (cm)	-0.201	0.001*	392	-0.326	0.001*	109
Number of upright stubble	0.365	0.001*	392	0.218	0.023*	109
Straw Mass (g)	0.365	0.001*	392	0.218	0.023*	109
Sunlight Duration (mins)	0.229	0.001*	392	0.363	0.001*	109
Temperature (°C)	0.332	0.001*	392	0.190	0.052	109

Anchor point heights of support threads and bridge threads were significantly negatively correlated to furrow depth (*Table 11.12*.). Whereas, straw mass, sunlight duration and number of upright stubble were significantly positively correlated to both anchor point heights. Anchor point heights of support threads were significantly positively correlated to the temperature measured in the choice chamber.

11.7.4.2. Thread Length

Table 11.13: Correlations of independent variables measured in choice chambers, with dependant variable thread length (mm) inside and outside of web. Choice chambers of selection of furrow trials without Aphididae. (relates to significant with α <0.05).*

	Inside Web			**Out of Web**		
	(Rho)	***P***	**n**	**(Rho)**	***P***	**n**
Furrow Depth (cm)	-0.030	0.577	353	0.329	0.007*	67
Furrow Width (cm)	0.038	0.482	353	0.294	0.017*	67
Sunlight Duration (mins)	0.362	0.001*	353	0.203	0.052	67
Temperature (°C)	0.395	0.001*	353	0.221	0.051	67

Sunlight duration of the experiment and temperature recorded within the choice chamber were significantly positively correlated with length of support threads (*Table 11.13.*). Furrow width and depth were found to be significantly positively correlated to length of bridge threads.

11.7.5. Selection of Furrow Trials With the Presence of Aphididae

The three-way log-linear analysis produced a final model that retained all effects in two and three-way interactions. Due to the hierarchical nature of the log-linear model, the highest order interaction (treatment x gender x end position of *T. tenuis*) was significant, and all other two-way interaction were ignored. To break down this effect, odds ratios were performed for the end position of *T. tenuis* variable for each treatment. Emphasis was placed on the effect of the soil tillage intensity due to this being the key interaction studied in the fieldwork (*Chapter 5.0.*). The odds ratio of choosing Aphididae was also included as this factor displays predatory response by *T. tenuis*, enabling biological control.

The odds ratios indicated that for Conventional soil tillage intensity the odds that a *T. tenuis* would go towards a side with Aphididae was 0.636, Direct Drill Managed 0.571 and Direct Drill 0.525. This result suggests that soil tillage intensity had little effect on the choice of *T. tenuis* for the side with Aphididae. Further, the low odds ratio (<1) explains Aphididae had little impact in the end position of *T. tenuis*. The significance appears to lie in the interaction of the number and gender of *T. tenuis* incorporated into the choice chamber.

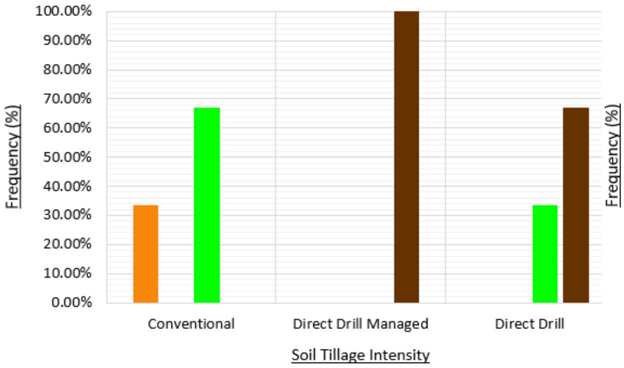


Figure 11.17: Frequency (%) of the T. tenuis *end position of 1 x Female* T. tenuis *in choice chambers of selection of furrow trials with Aphididae grouped by soil tillage intensity. (χ^2 = (1) = 52.900, P - 0.006) (Non-Furrow Side Aphididae = Orange, Furrow Side Aphididae = Light Green, Furrow Side No Aphididae = Brown).*

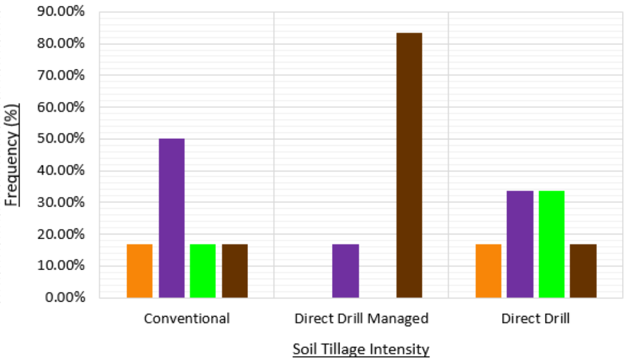


Figure 11.18: Frequency (%) of the T. tenuis *end position of 2 x Female* T. tenuis *in choice chambers of selection of furrow trials with Aphididae grouped by soil tillage intensity. (χ^2 = (1) = 52.900, P - 0.006) (Non-Furrow Side Aphididae = Orange, Non-Furrow Side No Aphididae = Purple, Furrow Side Aphididae = Light Green, Furrow Side No Aphididae = Brown).*

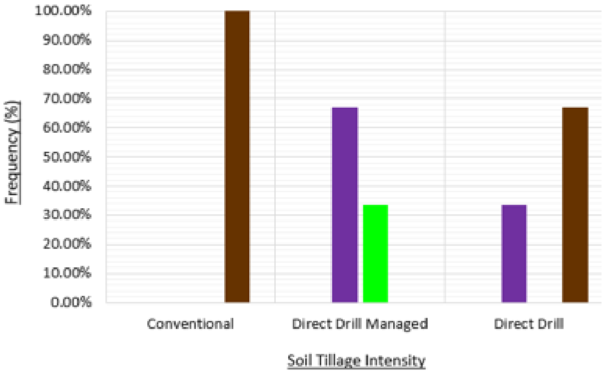


Figure 11.19: Frequency (%) of the T. tenuis *end position of female* T. tenuis *in 1 x female and 1 x male in choice chambers of selection of furrow trials with Aphididae grouped by soil tillage intensity. (χ^2 = (1) = 52.900, P - 0.006) (Non-Furrow Side No Aphididae = Purple, Furrow Side Aphididae = Light Green, Furrow Side No Aphididae = Brown).*

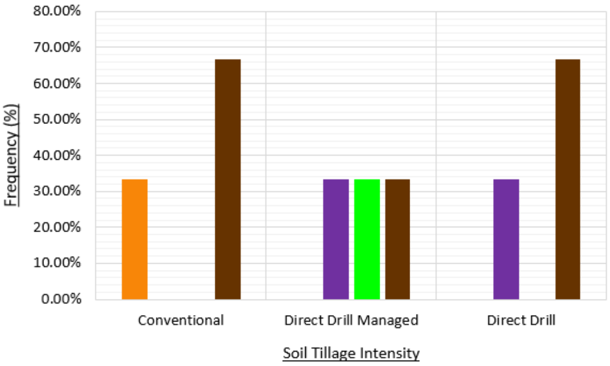


Figure 11.20: Frequency (%) of the T. tenuis *end position of male* T. tenuis *in 1 x female and 1 x male in choice chambers of selection of furrow trials with Aphididae grouped by soil tillage intensity. (χ^2 = (1) = 52.900, P - 0.006) (Non-Furrow Side Aphididae = Orange, Non-Furrow Side No Aphididae = Purple, Furrow Side Aphididae = Light Green, Furrow Side No Aphididae = Brown).*

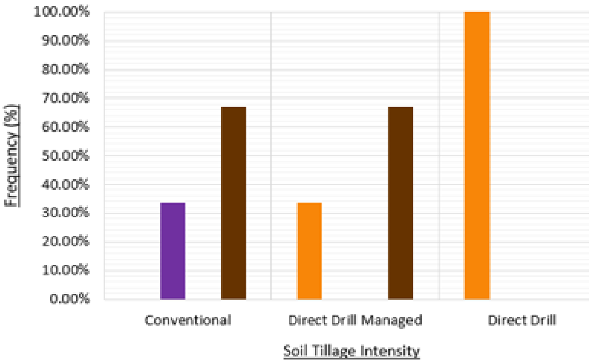


Figure 11.21: Frequency (%) of the T. tenuis *end position of 1 x male* T. tenuis *in choice chambers of selection of furrow trials with Aphididae grouped by soil tillage intensity. (*χ^2 *= (1) = 52.900, P - 0.006) (Non-Furrow Side Aphididae = Orange, Non-Furrow Side No Aphididae = Purple, Furrow Side No Aphididae = Brown).*

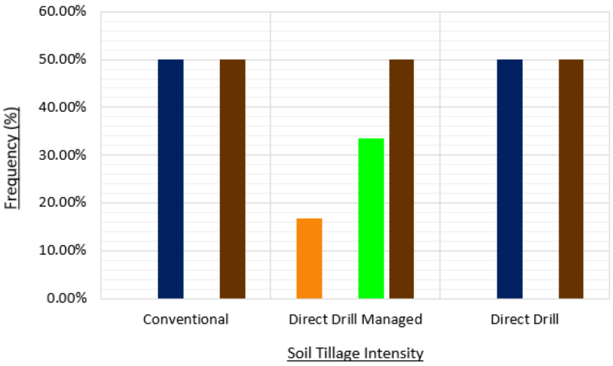


Figure 11.22: Frequency (%) of the T. tenuis *end position of 2 x male* T. tenuis *in choice chambers of selection of furrow trials with Aphididae grouped by soil tillage intensity. (*χ^2 *= (1) = 52.900, P - 0.006) (Non-Furrow Side Aphididae = Orange, Non-Furrow Side No Aphididae = Purple, Furrow Side Aphididae = Light Green, Furrow Side No Aphididae = Brown).*

Figure 11.17. describes female *T. tenuis* were found in the furrow side with Aphididae and non-furrow side with Aphididae in the soil tillage Conventional, when one female was incorporated. In Direct Drill Managed, all female *T. tenuis* were found in the furrow side without Aphididae. For Direct Drill, the female *T. tenuis* were only found in the furrow side, the greatest frequency being the side without Aphididae.

When two female *T. tenuis* were incorporated into the treatment of Conventional and Direct Drill, *T. tenuis* were found in both sides of the choice chambers with and without Aphididae (*Figure 11.18.*). The greatest frequency for Conventional was non-furrow side without Aphididae, for Direct Drill the furrow side with Aphididae and non-furrow side without Aphididae. For Direct Drill Managed the greatest frequency for end position of *T. tenuis* was the furrow side without Aphididae.

Only the furrow side without Aphididae was found to be the end position of female *T. tenuis* in Conventional, when one male and one female *T. tenuis* were placed into the choice chamber (*Figure 11.19.*). This side held the greatest frequency for Direct Drill under the same conditions of one of both female and male *T. tenuis*. The greatest frequency for Direct Drill Managed was the non-furrow without Aphididae.

In Conventional, the greatest frequency was found in the side of furrow with no Aphididae, for male when one male and one female were added (*Figure 11.20.*). Males were found in non-furrow side with Aphididae in this soil tillage intensity treatment. All sides, except the non-furrow with Aphididae held a male at the end of the trial in Direct Drill Managed, therefore sharing an identical frequency. For Direct Drill of this category, the greatest frequency was furrow without Aphididae, with another male being in the non-furrow side without Aphididae only.

When one male was inserted into the choice chambers, the greatest frequency of end position for Conventional was the furrow side without Aphididae (*Figure 11.21.*). The same was observed for Direct Drill Managed, however, a male was found in the non-furrow side with Aphididae, whereas in Conventional, a male was in the non-furrow side without Aphididae at the end of the trial. The frequency of 100% identifies that all the male *T. tenuis* in the Direct Drill treatment were in the non-furrow side with Aphididae.

With two males incorporated, a frequency of 50% males for furrow and non-furrow side without Aphididae, were found in these two sides in Conventional and Direct Drill (*Figure 11.22.*). For Direct Drill Managed, 50% of male *T. tenuis* were found in the furrow without Aphididae side. Male *T. tenuis* were also located in the furrow and non-furrow side with Aphididae, the greatest frequency of these categorical variables held by the furrow side.

11.7.5.1. Anchor Point Height

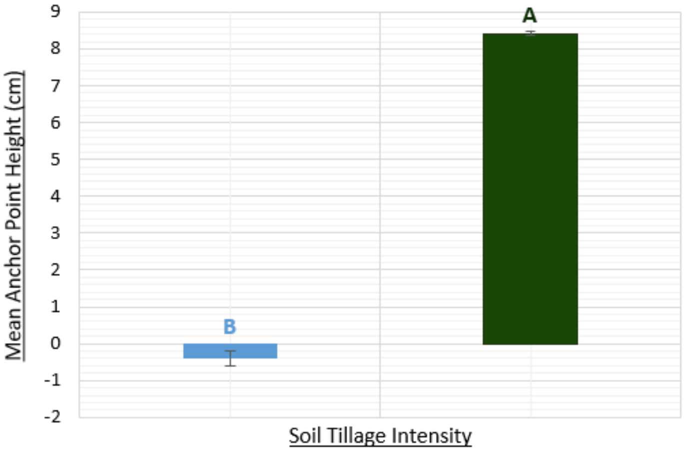


Figure 11.23: Mean anchor point height (cm) inside web (of support threads) where M. dirhodum *was recorded of soil tillage intensities with 1 x male* T. tenuis*. Choice chambers of selection of furrow trials with Aphididae. (n = 149, df - 9, F - 21.62, R-sq - 63.69%, P - 0.001) (Direct Drill Managed Furrow = Blue, Direct Drill Non-Furrow = Dark Green). (Direct Drill Managed Furrow ±s.e.0.058 (n = 3), Direct Drill Non-Furrow ±s.e.0.919 (n = 12). Bars that do not share the same letter are significantly different at the p<0.05 level).*

When one male *T. tenuis* were placed into the choice chamber significant difference was identified within the mean anchor point height of support threads found in Direct Drill Managed furrow and Direct Drill non-furrow sides (*Figure 11.23.*). The mean anchor point height of 8.4 cm, for Direct Drill non-furrow side was significantly higher than the mean anchor point height found in the Direct Drill Managed furrow side of -0.4 cm.

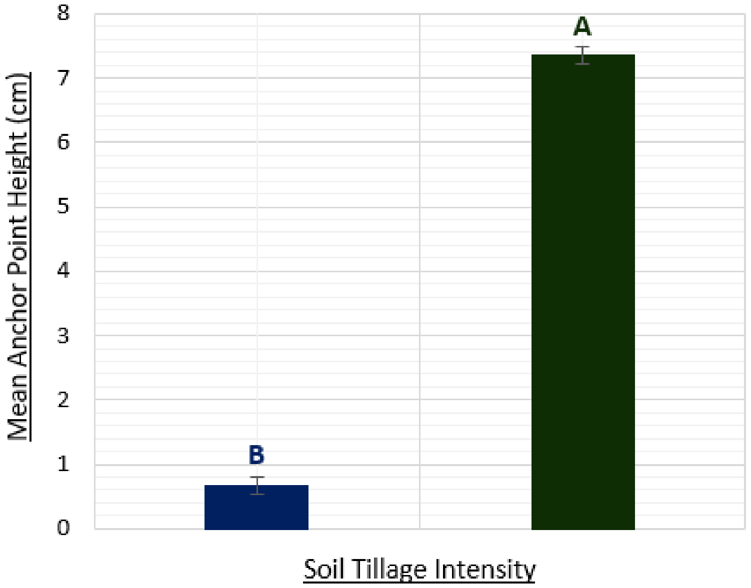


Figure 11.24: Mean anchor point height (cm) inside web (of support threads) where M. dirhodum *was recorded of soil tillage intensities with 2 x male* T. tenuis. *Choice chambers of selection of furrow trials with Aphididae. (n = 149, df -9, F - 21.62, R-sq - 63.69%, P - 0.001). (Direct Drill Managed Non-Furrow = Dark Blue, Direct Drill Non-Furrow = Dark Green). (Direct Drill Managed Non-Furrow ±s.e.0.145 (n = 3), Direct Drill Non-Furrow ±s.e.0.628 (n = 14). Bars that do not share the same letter are significantly different at the p<0.05 level).*

The mean anchor point height of support threads in the Direct Drill non-furrow side, 7.4 cm, was significantly higher than the mean found in the Direct Drill Managed non-furrow area, 0.6 cm (*Figure 11.24.*). This recorded a difference in mean anchor point height of 6.8 cm.

Table 11.14: Correlations of independent variables measured in choice chambers, with the dependant variable anchor point height (cm) inside web (of support threads) where M. dirhodum *was recorded. Choice chambers of selection of furrow trials with Aphididae. (* relates to significant with α <0.05).*

	(Rho)	***P***	**n**
Furrow Depth (cm)	-0.324	0.001*	149
Furrow Width (cm)	-0.346	0.001*	149
Number of Upright Stubble	0.353	0.001*	149
Straw Mass (g)	0.353	0.001*	149

Two variables were found to be significantly positively correlated to anchor point heights found inside webs of the side where the *M. dirhodum* was recorded: straw mass and number of upright stubble (*Table 11.14.*). The furrow depth and width were found to be significantly negatively correlated to anchor point height of support threads.

No significance existed for thread length of support threads where *M. dirhodum* was recorded and dependant variables measured.

11.8. Discussion

11.8.1. Selection of Upright Stubble Without the Presence of Aphididae

The incorporation of the upright stubble influenced *T. tenuis* abundance and web-building more than rappelling (*Figure 11.4. & Figure 11.6.*). Further, the significant higher mean anchor point within webs was found in the side where stubble was present for Conventional and Direct Drill (*Figure 11.5. & Figure 11.25.*). This is an unusual result with previous findings in the field suggesting at times of no crop, upright stubble allowed short-range dispersal by providing stepping-stones of a high aspect, key to facilitating rapid dispersal. As discussed earlier, anchoring to the apex of structures to facilitate the extension of the abdomen (Bonte *et al.,* 2008; De Meester & Bonte, 2010; Simmoneau *et al.* 2016) (*Section 5.1.6.1.2. & Table 11.3.*). Very few bridge threads were identified in the increased number of upright stubble of the Direct Drill stubble side. This could be concerned with spatial scales, the choice chambers offering a much-reduced spatial scale than the main field, therefore less opportunity given for short range exploration (Bonte *et al.,* 2011; Halley *et al.,* 1996; Tscharntke *et al.,* 2011). Similar sized trials from work by Benjamin *et al.* (2002), Segoli *et al.* (2004) and Zschokke & Herberstein (2005), with adequate attachment sites for web commencement, identified little prior exploration by rappelling of the habitat. It was recorded in times of cultivation in the field and before the addition of the *M. dirhodum* in the microcosms analysing different Aphididae abundance, that upright stubble has supported web-building allowing a site of increased sturdy anchorage (Armendano & González, 2011; Bianchi *et al.,* 2017) (*Section 5.1.5.1.3. & Section 10.5.2.*).

Figure 11.25: Use of upright stubble for web-building in the stubble side of 1 x female in Direct Drill. Choice chambers of selection of upright stubble trials without Aphididae. Elevated view. (Red arrow = 19.2 mm).

The mean thread length within the Convention non-stubble side, was significantly longer than that of Direct Drill Managed and Direct Drill (*Figure 11.9.*). There was only the landscape factor of straw within these sides, the only bridge thread found was attached to pieces of straw residue, the web found within this area was further attached to the straw. It appears rappelling behaviour traversing the straw, directly led to web construction (*Table 11.3.*). This identifies a greater return on the energy output for spinning the bridge threads (Bonte 2013; De Meester & Bonte, 2010; Harmer *et al.,* 2011; Zhang *et al.,* 2016). However, when two males were incorporated into the mesocosms the greater thread length within webs was identified in the stubble side of the Conventional tillage (*Figure 11.10.*) Within these choice chamber, the two males were within the different sides. One male spun a web of a larger area within the straw and upright stubble, while the other male constructed a small web within the straw only. This could signal intra-specific competition with males requiring definite territory for sanctuary and spinning of sperm webs. Eichenberger *et al.* (2009) and Entling *et al*. (2011) describe that intra-specific competition of Linyphiidae can arise due to differences in body size, Sexual Sized Dimorphism (SSD), the male *T. tenuis* within the stubble holding an abdomen length 0.41 mm larger (*Section 2.1.2.2.*).

There was no significant difference in the interaction of gender and number of *T. tenuis* with soil treatment and its final position. This can be observed as surprising, as the addition of another *T. tenuis* to the choice chambers could be seen to alter the way materials are utilised within. Downie *et al.* (2000) showed clear divisions in space between web-sites when a male and female *E. atra* were combined into a microcosm. Glover (2013), identifying similar results, explained division to be due to threat of competition. However, in this trial, the end position of *T. tenuis* was shared eight out of nine times for the trial of two males, and every trial when a male and female were incorporated. This is viewed unusual as *T. tenuis* are noted to be a solitary arachnid, territorial of a space assigned for web-building (Janetos, 1984; Opatovsky *et al.,* 2016; Toft 1987). It can be noted that 66.67% of this sharing was found on the stubble side within all soil tillage intensity treatments (*Figure 11.4.*). The strength of the upright stubble proved an extensive material for web-building at a greater height (*Figure 11.7., Figure 11.8. & Table 11.3.*). With Harwood *et al.* (2004) and Sereda *et al.* (2012) commentating on *T. tenuis* fierce competition for key web-sites, it appears that the addition of the upright stubble was creating a suitable location and offering the ideal web-building site in the choice chambers. *T. tenuis* can be observed to utilise a small web-building site, explaining that webs may be built in close proximity and still allow *T. tenuis* to hold dominance over a territory (Černecká, *et al.,* 2017; Halley *et al.,* 1996; Oxbrough *et al.,* 2006) (*Figure 11.8.*). Di-Rienzo & Aonuma (2018) and Japyassú & Laland (2017) describe that the extended phenotype of the web allows a definition of the habitat, and a highly defendable territory erected.

In the mesocosm trial analysing *T. tenuis* activity with soil tillage intensity and *S. avenae* (*Section 8.7.2. & Section 8.7.3.*) and the mesocosm trial with primary cultivation (*Section 9.6.2*.), it was shown that a small increase in cephalothorax length allowed a greater energy output to be reached, to spin larger threads and ascend higher (Anderson & Prestwich, 1975; Coddington, 2005; Prenter *et al.,* 2010; Rodríguez-Gironés *et al.,* 2010). A difference in cephalothorax length may have influenced the final position of *T. tenuis* to reside higher in the stubble side from investigative rappelling, spinning larger webs (*Table 11.3. & Table 11.5*.). However, the choice chamber's features were small in size, therefore perhaps an ability to a greater energy output in increase leg flexion would create little difference if larger distances and heights were not available to be attained. This may be the reasons why abdomen length was not significantly correlated to thread length, which had been shown previously (*Section 8.7.3. & Section 10.6.3.2.*). Perhaps the random assignment of *T. tenuis* into the different replicates of the trial did not allow any correlations to prevail, for example, the *T. tenuis* of the longest and smallest abdomen was placed into the Direct Drill Managed choice chamber, where the level of landscape heterogeneity was the same. This identified the strength of the available materials to dictate the dimensions and orientations of a web.

Sunlight duration was negatively correlated to length of bridge and support threads (*Table 11.5*.), which was surprising, with Król *et al.* (2018) describing *T. tenuis* as most active after day-break, to claim territory and avoid predation. Within this experiment, no threat of predation existed. Though the *T. tenuis* would not identify the absence of prey within the first response, especially when the experiment commenced at midday. An experiment running for twenty-four hours is recorded by Janetos (1984), Segoli *et al.* (2004), Sensenig *et al.* (2010) and Toft (2002) as enough time to spin a web in a confined area. Temperature of the choice chambers was shown to have had no significance to web-weaving. Though temperature was measured as 18 to 21 °C, shown by Craig (2003) and Hesselberg & Vollrath (2012), an optimum for yielding greater expanse of thread at a low energy cost. The conditions were enclosed environments, where the physical disturbance was low to non-existent and may have removed the significance that temperature may have had on web construction and need for thermo-regulation of *T. tenuis* (Humphreys, 1991; Simonneau *et al.,* 2016; Suter, 1981). Mader *et al*. (2017) and Pedley & Dolman (2014) comment that the results of physical disturbance can alter competition for a web-site, due to additional variables of shelter and protection required.

11.8.2. Selection of Upright Stubble With the Presence of Aphididae

It is of interest that the number and gender of *T. tenuis* incorporated into the choice chambers was shown to significantly affect the side where *T. tenuis* chose to be at the end of the trial (*Figure 11.11*.). It appears that the addition of *M. dirhodum* created this interaction, as this was the only change between this choice chambers and the previous (*Section 11.7.2.*).

Five out of nine females chose the same side as the males. It could not be identified which gender spun any web recorded first, however it is clear the *T. tenuis* in these choice chambers were prepared to share a small amount of space. As noted in the previous trial, with little physical disturbance, both *T. tenuis* can attain a solitary web-site in a small space (Černecká, *et al.,* 2017; Halley *et al.,* 1996; Štokmane & Spuņģis *et al.,* 2016) (*Section 11.8.1*.). Males and females were found in the non-stubble sides without *M. dirhodum*, this was surprising as these sides were void of prey abundance and plethora of attachment sites, two elements shown by Alderweireldt (1994), Dennis *et al.* (2015) and Romero & Harwood (2010) to drive *T. tenuis* abundance (*Figure 11.11*.). Prenter *et al.* (2010), Rundus *et al.* (2011) and Watson (1993) discuss the movement of male *T. tenuis* to locate a female for copulation, however, the current trials were carried out in July, shown to be early for courtship in the life history of *T. tenuis* (Bell *et al.,* 2002; Kasumovic & Jordon, 2013). The temperature identified in the choice chamber, higher than would be observed in the field, may induce courtship behaviour due to increasing *T. tenuis* metabolic rate (Jiao *et al.,* 2009; Keil & Watson, 2010, Herberstein 2011; Hesselberg & Vollrath, 2006). From this information it can be hypothesised that the females constructed the webs first, this gender the dominate web-builder (Bonte *et al.,* 2008; Thomas & Jepson, 1999). If this was the case, then it could be questioned why the non-stubble side was chosen if no Aphididae were present. This side appeared not to present any benefits to the web-spinning (in food availability, shelter, or increased anchor height). It may be that a factor outlined the non-stubble side as a potential web location due to its sparse nature, *T. tenuis* are often driven to pioneer a disturbed landscape. However, this is unlikely with no previous experience of the habitat, Buchholz & Hartmann (2008), Halley *et al.* (1996) and Nyffler & Sunderland (2003) suggested that this pioneer ability comes from learnt behaviour of previous vegetation complexity. It may be that the small nature of the habitat reduced the spatial effect of the low structural heterogeneity (Horváth *et al.* 2015; Mclachlan & Wratten, 2003; Miyashita *et al.,* 2012; Villard & Metzger, 2014).

All sides were chosen when two female *T. tenuis* were incorporated, the greatest being the non-stubble side with Aphididae (*Figure 11.11*.). This can show that Aphididae may have been easier to identify without the stubble. With poor vision of distant objects, removal of obstructing features may allow the vibrant green of *M. dirhodum* to be received by the eyesight of female *T. tenuis* (Herberstein, 2011; Lichtenstein *et al.,* 2016; Young & Wanless, 2009). Preston-Mafham & Preston-Mafham (1996) and Young & Wanless (2009) showed that the contrast in colour aids reception of the Linyphiidae optic system. Cues from movement in straw, may be transmitted in clear pathways to *T. tenuis* receptors without stubble acting to perhaps impede this motion. The two trials of one and two female *T. tenuis* explained that straw may be key to understanding why the *M. dirhodum* chose to reside in the straw during the trial (*Table 11.6. & Table 11.7.*). This disagrees with Kennedy *et al.* (2010) and Summers *et al.* (2004) who suggested that straw aided Aphididae capture due to pushing the Aphididae to a higher stratum within a habitat. Within the choice chamber, low landscape architecture overall and lack of vegetation, may have allowed the straw to become an attractive dwelling for the *M. dirhodum*. Hesler & Berg (2003) and Schmidt *et al.* (2004) explain that crop residue provided a suitable habitat for Aphididae in times of no crop, explained as due to offering shelter whilst searching for an alternative food source.

With only one male *T. tenuis,* the greatest frequency of end position was in the non-stubble side without Aphididae (*Figure 11.11. & Figure 11.26.*). With *M. dirhodum* not located on the stubble, it appeared likely that the greater density of stubble in the Direct Drill side influenced *T. tenuis* decision to construct a web at a higher level (*Figure 11.12. & Table 11.6*.). Krafft & Cookson (2012) explain a web architecture is not foreseen, rather Linyphiidae rely on sensory guidance from the surrounding structures to complete a web, the upright stubble clusters in Direct Drill providing easily identifiable cues in each step of web-building.

Figure 11.26: Use of straw for web-building in the non-stubble side of 1 x male in Direct Drill. Choice chambers of selection of upright stubble trials with Aphididae*. Elevated view. (Abdomen Length = 1.59 mm, Cephalothorax length = 1.02 mm).*

In only three out of the nine choice chambers, two male *T. tenuis* were identified on the same side, each in the side without Aphididae (*Figure 11.11*.). There appeared to be a factor preventing the predator dynamics of male *T. tenuis*, especially when starved. Bell *et al*. (2002) and Harwood *et al.* (2003) explain that *T. tenuis* can endure times of extended starvation, thus, this may not have altered the predator capacity of a *T. tenuis* starved for twenty-four hours, plus time within the terrarium previous (*Section 7.2.1.*). Sunderland *et al.* (1986) agreed, describing a heightened response to prey capture was shown to increase after seven days of starvation. With the mass of the Aphididae not significant to the end position of the *T. tenuis*, an increase in the mass of *M. dirhodum* did not alter the intensity of cues in movement, which may have allowed a greater response from *T. tenuis*. However, three *M. dirhodum* were caught in the webs woven into the straw, one in the non-stubble side and two in the stubble side when two female *T. tenuis* were incorporated. It appeared that the predatory ability was greater in female *T. tenuis* in this circumstance than males. Gavish-Regev *et al*. (2009) and Mansour & Heimbach (1993) both detailed that female Linyphiidae have a higher success in a greater degree of prey capture over males. Corcobado *et al*. (2010) and De Meester & Bonte (2010) identified that female Linyphiidae require a greater amount of energy, thus are prone to act on received evidence of prey.

11.8.3. Selection of Furrow Without the Presence of Aphididae

The implantation of the furrow of differing dimensions for the soil tillage simulations or arrangement of *T. tenuis* added into the trial in numbers and gender, held no effect over the final position of the *T. tenuis* once the trial ended. This suggests that in all soil tillage intensities, both sides of the choice chambers, with or without the furrow, held enough vegetation complexity for adequate web-building to be identified. Indeed, all materials of both sides provided attachment points for support threads (Lyons *et al.,* 2018; Mestre *et al.,* 2018; Rusch *et al.,* 2016) (*Figure 11.13., Figure 11.14., Figure 11.27., Figure 11.28. & Table 11.12.*).

Figure 11.27: Use of soil for web-building in the non-furrow side of 1 x female in Conventional. Choice chambers of selection of furrow trials without Aphididae. Elevated view. (Red arrow = 23.4 mm).

Figure 11.28: Use of upright stubble and straw for web-building in the furrow side of 1 x female in Direct Drill. Choice chambers of selection of furrow trials without Aphididae. Elevated view. (Red arrow = 11.2 mm).

Webs and rappel threads were shown to be made at all locations and heights across all sides of each choice chamber, regardless of soil tillage intensity treatment (*Figure 11.15., Figure 11.16., Figure 11.27. & Figure 11.28.*). This agrees with Borges & Brown (2001), Lowe *et al.* (2014), Platen *et al.* (2017) and Sunderland & Samu (2000) who describe that if a high abundance of possible anchor materials exists, and these are in a spatial arrangement to allow threads to be woven between, the possibility for potential web-spinning of differing heights and areas is great. It appears that definite strata of web building commenced, with significance found of mean rank anchor point height between the attachment materials of soil and upright stubble (*Figure 11.13. & Figure 11.14*.). With upright stubble accessible in all choice chambers, it is of interest that some webs were woven into the soil and straw, when the strength of the upright stubble material was shown in the previous trial and by Bianchi *et al.* (2017) and Blake *et al.* (2013) to be a functional web-building structure (*Figure 11.15. & Section 11.7.3.1*.). It was established that within most choice chambers representing soil tillage intensity, number of webs exceeded that of the *T. tenuis* incorporated into the choice chamber, expressing web abandonment had taken place. The small webs woven into the structures of the habitats are likely to be of low energy consumption and thus more readily vacated (Henschel & Lubin, 2018; Rodríguez-Gironés *et al.* 2010). It is reported that a starving *T. tenuis* that has identified limited cues to possible prey may choose to construct a new web of a different aspect in a rapid time frame to intercept potential stimuli of prey (Kraftt & Cookson, 2012). Though, the *T. tenuis* had only been without food for two days (in the artificial habitat and choice chamber), any prolonged period without any prey, stimuli is noted to heighten the predatory response (Japyassú & Laland, 2017) (*Section 7.2.1*.).

T. tenuis dimensions showed no significant correlation to *T. tenuis* silk-spinning behaviours suggesting no competition existed between *T. tenuis* of differing body dimensions when two *T. tenuis* were incorporated. Heiling & Herberstein (1998) and Prenter *et al.* (2010) explain that body dimensions may not measure *T. tenuis* fitness. This was noted to be the case in the mesocosms following *T. tenuis* activity over *H. vulgare* growth, where larger webs were spun from low averages of body length and mass (*Section 8.7.4.).* However, with no log-linear analysis model established for the sides chosen by the different *T. tenuis* of the trial, the probability of fitness having an effect is shown to be void.

Several rappel threads were observed traversing across the furrow (*Table 11.13*.). This was shown to be greatest in Conventional, where the furrow was at a greater depth (*Figure 11.29. & Table 11.12*.). It appeared that furrow depth influenced rappelling more than width, a different result to field sampling, when soil of poor moisture availability allowed furrows to widen (*Section 5.1.6.2.2.).* This was an unexpected result concerning rappelling, which usually commences higher within a habitat, laying bridge threads onto sturdy structures, additional height allowing rapid dispersal with little obstruction (Blandenier, 2014; Bonte *et al.,* 2016; Hogg & Danne, 2018; Szymkowiak *et al.,* 2007). It may be that there was less upright stubble within the Conventional trial and thus an exploration of the furrow may have been occurring before web-spinning (*Figure 11.16*.). Rosa *et al.* (2019) commented that Linyphiidae are sensitive to changes in physical properties of soil and the subsequent features promoted, for example, soil of high bulk density altering landscape features such as seedbed (furrow). Linyphiidae were further identified to be attracted to increase Aluminium (lll) ion (Al^{+3}) within soil through the sense of smell, the soil of Hanslope contains high Al^{+3} due to the cation exchange capacity (Cranfield University, 2017; Paul, 2015; Rosa *et al.,* 2019) (*Section 2.2.2*.). Thus, the furrow in Conventional may have been an attractive web-site in a habitat low in landscape complexity.

Figure 11.29: Use of furrow sides for attachment sites for a bridging thread in the furrow side of 1 x female in Conventional. Choice chambers of selection of furrow trials without Aphididae. Lateral view. (Red arrow = 7.3 mm).

Temperature range inside the choice chambers of this trial was 17.3 - 19.6 °C. It was generally identified that the higher temperatures allowed webs to be spun to a greater area and a higher height as discussed earlier (*Table 11.12. & Table 11.13., Section 11.8.1.*). The greatest web areas were spun at times of two male *T. tenuis* and two female *T. tenuis* when the temperatures were recorded at 19.2 °C and 19.6 °C, respectively. It was identified in earlier discussions, that higher temperatures allowed a higher degree of energy to be expelled into thread spinning, due to low thermo-regulation required (Bonte & Saastamoine, 2013; Humphreys, 1991) (*Section 8.8*.). At the temperatures discussed in these choice chambers, thermo-regulation would not be a requirement (Schütt, 1997; Suter, 1981). However, Harmer *et al.* (2011) and Zhang & Tso (2016) commented that a small increase in temperature reduces the tensile stress needed to yield the correct loading capacity for the major ampullate silk (Blackledge *et al.* 2009; Craig 2003; Saravanan, 2006) (*Figure 2a, Section 2.1.2.1., Page 10*). This allows greater distances to be spun, with the requirement of less energy and ability to obtain the structural stability needed for a support thread of a web.

11.8.4. Selection of Furrow With the Presence of Aphididae

When one female *T. tenuis* was added to the choice chamber, differences were identified in all soil tillage intensity treatments in the end position chosen by the individual *T. tenuis* (*Figure 11.17.*). This is interesting due to no competition existing in these choice chambers; therefore, the whole habitat is a potential area for web construction, no disturbance (physical or intra-specific) affecting this decision. However, the presence of the furrow appeared to attract the single female *T. tenuis* (*Figure 11.17.*). *M. dirhodum* presence does not seem to have influenced web-building in Direct Drill Managed and Direct Drill (*Figure 11.17*.). The complexity of an environment has been shown to curb cues of a prey's whereabouts (Kraft & Cookson, 2012). This point is heightened as *M. dirhodum* were apterous and therefore no aerial movement occurred with the habitats. Moreover, Gravesen (2008) suggested bare soil can promote *M. dirhodum* locomotion and apterous morphs were identified commuting along furrows. It can be identified that the complexity of the habitat with the addition of the soil and upright stubble on both sides, suppresses any stimuli that may be accessed by the female *T. tenuis* (Schütt, 1997; Spears, 2012; Štokmane & Spuņģis, 2016; Welch *et al.,* 2013) (*Figure 11.3a* - *c*).

When two female *T. tenuis* were incorporated, the dynamics changed within the choice chamber, all potential of the habitat for web-building was thought to be shared at the outset of this trial (*Figure 11.18.*). It was expected that more areas of the choice chamber would be thus utilised. It was therefore surprising that female *T. tenuis* were found in the greatest frequency sharing the furrow side without Aphididae in Direct Drill Managed (*Figure 11.18*.). With only three upright stubble incorporated into Direct Drill Managed, the furrow can be observed as perhaps a much-needed increase in attachment points for threads in the landscape (*Figure 11.3b*). In Conventional, both female *T. tenuis* did occupy webs, where a *M. dirhodum* was within a web of the furrow side (*Figure 11.18*.). The low landscape heterogeneity in the Conventional treatment may have allowed cues of *M. dirhodum* presence to have been interpreted. It may take additional *T. tenuis* to intercept cues of prey availability, due to none found in webs of one female *T. tenuis* trial. Even though *T. tenuis* have been described as territorial species, highly defending a key web-site, Glover (2013), Harwood *et al*. (2004), Japyassú & Laland (2017) and Sunderland & Samu (2000) identified that a high abundance of Linyphiidae is a cue that the area habituated may be of high prey availability. Gan *et al*. (2015), Samu *et al.* (1996) and Toft (1989) describe web take-over usually occurs as an act of dominance where fundamentally the previous building of this web was at a key location. This was identified in field sampling when many Linyphiidae webs were found in one sampling area in the early growth stages of *H. vulgare* (*Section 5.1.6.2.1.*). This may have been what was occurring within habitats of the current trials, low physical disturbance decreasing a need to compete, a female *T. tenuis* followed the example of another whose decision to reside in a side may have been due to receiving a stimulus from *M. dirhodum*.

Only the furrow side without Aphididae was found to be the end position of female *T. tenuis* in Conventional, when a male and female were added (*Figure 11.19.*). The greatest frequency for the males of the same choice chamber were found to be at the same side (*Figure 11.20.*). Indeed, in two replicates out of three, males and females were shown to be occupying the same side of furrow with no Aphididae. The addition of the furrow provided additional attachment sites with less upright stubble and straw incorporated. One male did build a web in the side without a furrow, the side where the *M. dirhodum* were located. *M. dirhodum* was found in the web in this location. It can be hypothesised that the prey did dissuade the *T. tenuis* from locating the web of greater vegetation complexity within the furrow side. De Meester & Bonte (2010), Harwood *et al.* (2004) and Thomas *et al.* (2003) discuss that females expel a greater amount of energy to act on prey cues, however, Japyassú & Laland (2017), Romero & Harwood (2010) and Willemart & Lacava (2017) identified no difference in the capability of interpreting a stimulus of prey capture between genders. Perhaps the male of this choice chambers was of higher fitness and this heightened reaction time to respond to prey (Gregori *et al.,* 2015; Harwood & Obryck, 2005; Jeperson & Toft, 2003; Peng *et al.,* 2013).

For Direct Drill Managed, one female and one male did access the *M. dirhodum* furrow side in the same choice chambers (*Figure 11.19. & Figure 11.20.*). No female or male *T. tenuis* was found sharing a web which described that courtship was not taking place. The question is whether *T. tenuis* were responding to the greater availability of anchor points or the availability of prey in the form of *M. dirhodum*. This is difficult to establish as male and female have been seen to share the same side without the presence of *M. dirhodum* in the previous choice chambers (*Section 11.7.2.*). However, a small exuviae lying in the female *T. tenuis* web suggests the web was placed near to *M. dirhodum* activity. As observed in earlier fieldwork, exuviae were a sign of a near presence of Aphididae (Beck & Toft, 2000; Muratori *et al.,* 2008) (*Section 5.1.6.2.1.*). Female and male *T. tenuis* were, however, viewed not to be reacting to the addition of *M. dirhodum,* when in most replicates, they were found inhabiting sides that did not contain Aphididae (*Figure 11.19. & Figure 11.20.*). This is incorporated into the low odds ratio of all soil treatments, that a *T. tenuis* would choose the side of an Aphididae. This was the case for female and male *T. tenuis* within the Direct Drill choice chamber, where only the side without Aphididae, were shown to house the *T. tenuis* at the end of the trial (*Figure 11.19. & Figure 11.20.*). The complexity of the Direct Drill areas may allow the cues of *M. dirhodum* to be hidden to the *T. tenuis* as discussed earlier in this trial. The furrow is still key within Direct Drill, in times where above-ground vegetation may be shown to be adequate (*Figure 11.19. & Figure 11.20.*). Alderweireldt (1994) and Samu & Sunderland (2000) discussed the use of soil for a *T. tenuis* web in times of other structures providing potential anchor points. However, Bell *et al.* (2002) and Landsman & Bowman (2017) explained the orientation of structures, physiognomy, is a driver for enhancing web-building abundance. It may be that the random orientation of the upright stubble may suit web-spinning, due to the slight increase in distance between the stubble due to the furrow (*Figure 11.3c*).

When one male was present in the choice chambers, the greatest frequency of end position for Conventional and Direct Drill Managed was the furrow side without Aphididae. (*Figure 11.21.*). It appeared that the presence of *M. dirhodum* may not have been intercepted, again linking to the low odds ratio. This is clear when literature and previous findings suggest *T. tenuis* are primarily driven to construct webs in areas of higher prey abundance (Pfingstmann *et al.,* 2019; Pompozzi *et al.,* 2019; Rosas-Ramo *et al.,* 2018) (*Section 5.1.5.2.4. & Section 10.6.3.1.*). It may be the furrow, increasing the complexity of the vegetation was a learnt cue from the field environment that prey is possibly more likely in an area of increased landscape features (Glover, 2013; Willemart & Lacava, 2017). One male in Conventional chose the non-furrow side without the *M. dirhodum,* which negates the previous statement (*Figure 11.21.*). Only bridge threads were identified in this choice chamber, woven between the straw. It may be that an exploration of the habitat was occurring and perhaps the fitness of this male *T. tenuis* was such that it was able to expel energy for web-site exploration. The male was generally low mass and abdomen length, although these two dimensions did not show any significance to *T. tenuis* silk-spinning behaviour. As described earlier in the choice chambers of selection of upright stubble, fitness cannot be described directly by body dimensions measured, fitness being related to genetic traits and environmental factors (Higgins, 1993; Jakob *et al.,* 1996; Jurczyk *et al.,* 2012; Opatovsky *et al.,* 2016) (*Section 11.8.1.*). Indeed, Prenter *et al.* (2010) discussed that a male with a smaller mass could lay threads at a faster, more energy-efficient pace. For Direct Drill Managed and Direct Drill, males were found in the furrow side with Aphididae, linking the significant lower mean anchor point height for the furrow in Direct Drill Managed (*Figure 11.21., Figure 11.23. & Table 11.14.*).

As stated earlier, it can be questioned as to whether *M. dirhodum* was the driving factor in the decision to create a web in the furrow side for Direct Drill Managed and Direct Drill. The *M. dirhodum* was identified dead within the straw residue away from the web at termination of the trial of Direct Drill Managed. Exuviae of *M. dirhodum* were shown to be attached to splinter in an upright stubble, it may be that this was a cue to create a web within. Hatano *et al.* (2008) and Muratori *et al.* (2008) identified Aphididae exuviae in the field can often act as a cue to Aphididae existence. However, the web was anchored to the soil of the furrow. A greater web height would be expected if above ground prey were identified, a position frequented by *T. tenuis* (Bell *et al.,* 2002; Davey *et al.,* 2013; Harwood & Obrycki, 2005). It can be identified that the inclusion of a greater number of potential anchor sites offered, obscured the exuviae presence. Within the Direct Drill habitat, it could be that the need for the furrow had been negated by the additional material added into the choice chamber. Additionally, no *M. dirhodum* were identified in the webs, though webs were spun at a greater height attached to the top of stubble, perhaps a response to a stimulus of the prey (Diehl *et al.* 2013; Feber *et al.* 1998; Oelbermann & Scheu, 2009; Schütt, 1997) (*Table 11.14*.). Conceivably, if the trial had been extended, the capture of the apterous *M. dirhodum* may have occurred, Willemart & Lacava (2017) explaining that *T. tenuis* foraging ability sharpens as habitat becomes familiar.

When two male *T. tenuis* were put into the trial, low utilisation of the sides containing *M. dirhodum* was found (*Figure 11.22.*). This clearly explains their presence went unnoticed, again expressing the increased capacity for females to entrap prey (De Meester & Bonte, 2010; Lichtenstein *et al.,* 2016; Watson, 1993; Welch *et al.,* 2016). There appeared to be no element of competition within six out of the nine trials (with all soil tillage simulations). *T. tenuis* were found occupying the same side of the choice chambers. This may display the behaviour noted earlier, where the propensity to web-build in an area was due to following the choice of web-site location by another *T. tenuis* (*Section 11.8.2*.). This is described as 'mass action' by Bianchi *et al.* (2017) and Entling & Tscharntke (2011), where Linyphiidae are driven into an area due to the cue of an increasing Linyphiidae density emerging. This may have inspired the anchor point heights to be higher within the non-furrow side of Direct Drill (*Figure 11.24.*). Two males here were under webs of differing strata attached to upright stubble where *M. dirhodum* was identified, however, neither web contained *M. dirhodum*. It appears that if high densities of one species exists, competition occurs for occupancy of the stratum (Janetos, 1984; Miyashita *et al.,* 2012). This difference in strata for web occupation, in times of increased Linyphiidae abundance, was also observed within sampling of hedgerows (*Section 5.3.6.1*.).

In one choice chamber of Direct Drill Managed, two male *T. tenuis* shared the furrow side where *M. dirhodum* was noted, with a *M. dirhodum* found in the web woven half-way into the upright stubble, occupied by one male *T. tenuis* (*Figure 11.22.*). In another Direct Drill Managed choice chamber, a *M. dirhodum* was within the web of a male *T. tenuis* in the non-furrow side. From the evidence of web capture, it can be viewed that the appropriate web-site was established and its location may have been deliberately placed in response to a cue by *M. dirhodum* (Mark & Canard, 1997; Pekár, 2000; Welch *et al.,* 2016). The low straw mass and number of upright stubble may have enabled prey to be identified. However, in the field, increased vegetation complexity is often a cue to *T. tenuis* that prey may be in abundance, phytophagous pests requiring vegetation for a food source (Glover, 2013; Mansion-Vaquié *et al.,* 2020; Rodríguez & Gamboa, 2000). The mechanics of the choice chambers are different from the field, when in general terms a simplified landscape of the field is offered to the *T. tenuis* here (*Figure 11.3a - c*.). Additionally, with no vegetation in the trial, other stimuli for prey occurrence was required, primarily in movement (Benhadi-Marín *et al.,* 2019; Schellhorn *et al.,* 2014; Welch *et al.,* 2013). Interestingly, low attachment for the webs were chosen when there were no definite breaks in the soil to offer suitable anchorage and upright stubble was present (*Figure 11.24.*).

It may be vibrations of *M. dirhodum* within the soil surface, movements laboured, alerted *T. tenuis* to their presence, *T. tenuis* sensitive to subtle differences in vibration patterns (Japyassú & Laland 2017; Willemart & Lacava, 2017).

It can be observed, that the selection of furrow choice chambers showed significance in interactions of soil tillage intensity, the differing *T. tenuis* incorporated and the end position of the *T. tenuis*, when in the selection of upright stubble trial only the latter two variables showed significant interaction (*Section 11.7.3. & Section 11.7.5.*). It would be thought that the addition of upright stubble in both areas of the choice chambers, the furrow the only difference, would negate the differences between soil tillage intensities further. It may be simply that the greater movement of Aphididae occurred. Even though prey capture was limited, expressed in low odds ratios, 50% more Aphididae were captured in the selection of the furrow trial. Perhaps, the *M. dirhodum* were responding to the habitat of the furrow with a higher level of fitness and development rate due to the increasingly complex environment. Mehrparvar *et al.* (2013) discussed phenotypic plasticity in cereal Aphididae. This is where environmental factors may offer alternative phenotypes, higher level of alate morphs which in turn increases fecundity rate. One factor described is vegetation complexity. This is agreed by Lombaert *et al.* (2006) and Parry (2013), where vegetation complexity offers protection for increased Aphididae movement and subsequently wing polymorphism. Whereas in the upright stubble trial the *M. dirhodum* appeared to be confined to the straw, in the furrow trial *M. dirohodum* was located at various heights and locations within the habitat (*Figure 11.30.*). Mehrparvar *et al.* (2013) and Parry *et al.* (2006) stated that environmental factors may take several generations to alter fitness and offer alternative phenotypes, however, a choice chambers of increased small-scale landscape heterogeneity seemed to alter *M. dirhodum* activity.

Figure 11.30: M. dirhodum *and exuviae at a high level on plastic within choice chambers in the furrow side of 2 x female in Direct Drill. Choice chambers of selection of furrow trials with Aphididae. Lateral view. (*M. dirhodum *circled in yellow).*

11.9. Final Discussion - Selection of Upright Stubble or Furrow With or Without the Presence of Aphididae

It was interesting to see that in all stubble trials a side was chosen and only three instances had to be rejected in the furrow trial due to *T. tenuis* occupying a central position. It appeared that *T. tenuis* were keen to occupy a definite space.

Throughout the selection of upright stubble and furrow, landscape heterogeneity appeared to be more important at driving *T. tenuis* occupation and web-spinning than the incorporation of *M. dirhodum* addressing the three aims noted for this Chapter (*Section 11.2.1.*). This was clearly shown with more *T. tenuis* activity occurring in the furrow side with and without Aphididae and low odds ratios in favour of choosing the Aphididae side.

The results of this trial are not conclusive in determining that in a choice between landscape heterogeneity, prey abundance has a decreased priority. The decision not to follow *M. dirhodum* and the low capture observed, may mean more time was required. This could allow the cues of prey to be gained by the *T. tenuis* and thus a reaction would result in movement to locate prey which would require more time. *T. tenuis* require a period of learning before web commencement to collect information on the architecture of the landscape and where possible prey may lie. The two *M. dirhodum* may not have provided enough signals of their presence. Perhaps a greater quantity of a prey stimulus was needed to be processed by *T. tenuis*.

One surprising finding was the sides of the choice chambers shared where two *T. tenuis* were incorporated into the trial, especially on learning *T. tenuis* will defend a high profitable web-site. This may show the power of 'mass action' which is an element that supports the biological control potential of this Linyphiidae and refers to the third aim mentioned in Section 11.2.1. The influence can be shown in the number and gender of *T. tenuis* having a significant interaction of the log-linear analysis model of selection of furrow with Aphididae. However, it was noted that it would be beneficial if *T. tenuis* power of biological control could suppress pest abundance at times of lower densities.

Soil tillage intensity was shown to have a very limited effect (in the upright stubble, straw mass and furrow dimensions) on the decision of a *T. tenuis* to choose a particular side with or without Aphididae, clearly meeting the second and fourth aims for this experiment (*Section 11.2.1.*). It may be that the small size of the choice chambers reduced the spatial effect that the elements of the increased landscape complexity of Direct Drill had in the field (*Section 5.1.5.*). Due to the much-reduced scale of the choice chambers to the field, landscape heterogeneity was present in all soil tillage intensity simulations regardless of the amount of upright stubble, straw mass or furrow dimensions.

Chapter Twelve

12.0. DNA Bar-Coding of Aphididae in *T. tenuis* Gut Contents and Linyphiidae Web

12.1. Introduction

To further understand the prey capturing ability of *T. tenuis* and Linyphiidae within the field, it was thought that the technique of DNA bar-coding could allow predator-prey interactions to be measured at a molecular level. DNA bar-coding offers a definitive answer as to whether a *T. tenuis* has encountered a prey species. This can therefore be used to support field observations of prey abundance in webs and measurements of web area for example.

This Chapter consists of two parts. The first sought to determine if prey DNA could be found in the gut of *T. tenuis* collected from the areas of differing tillage intensities and how the results could aid further understanding of *T. tenuis* prey capturing ability. The second concentrated on whether Aphididae DNA could be retrieved from Linyphiidae webs collected within Conventional, Direct Drill Managed and Direct Drill areas of the NIAB fields.

12.2. Aims and Specific Objections

12.2.1. Aims

This part of the research sought to address Aims 1 and 5 (*Section 1.2., Page 2*).

1. Identify the potential biological control by *T. tenuis* of Aphididae and *S. mosellana* within different intensities of tillage in an arable crop.
5. Quantify *T. tenuis* biological control by comparing Aphididae and *S. mosellana* DNA presence in *T. tenuis* gut and Linyphiidae webs with Aphididae and *S. mosellana* populations within different intensities of tillage.

12.2.2. Specific Objectives

Specific objectives were to:

- Analyse *T. tenuis* gut content and Linyphiidae webs for presence of crop pests, in the form of cereal Aphididae and *S. mosellana*, and relate results to *T. tenuis* interaction with prey.
- Sample *T. tenuis* from each area of differing soil tillage intensity to indicate if level of intensity affects *T. tenuis* and Linyphiidae web-building behaviour towards prey capture.

12.3. DNA Bar-Coding to Analyse *T. tenuis* Gut Contents for Aphididae

12.3.1. Introduction

DNA bar-coding involving DNA extraction and Polymerase Chain Reaction (PCR) was used to gain verification of *T. tenuis* prey interactions from the different soil tillage intensities in the *H. vulgare* and *T. aestivum* fields that were utilised in field sampling (*Section 4.3.12.2. & Sub-Chapter 5.1.*). Results from *T. aestivum* are represented here, alongside *H. vulgare,* due to abundance of *S. mosellana* adults found to be greater within the *T. aestivum* sampling of 2017 / 2018 (NIAB Field A) (*Table 3.1., Section 3.1.3.3., page 50*). *S. mosellana* larval survival rate was higher upon *T. aestivum* grains. The ear of *T. aestivum* able to shield larvae from environmental disturbance to a greater degree than that of *H. vulgare* (AHDB, 2016; Oakley *et al.,* 2005) (*Section 2.2.6.3*.). The damage of larval feeding in cereals is costly in grain deterioration and it would be useful if *T. tenuis* acts as a biological control to *S. mosellana* (Elliott *et al.,* 2011 & Knight *et al.,* 2012) (*Section 2.2.6.4*.). Gut content of *T. tenuis* was analysed for the presence of a specific short genetic marker which belonged to a particular Aphididae or S. *mosellana* (Birkhofer *et al.,* 2014; Davey *et al.,* 2013; Furlong, 2015; Symondson *et al.,* 2013) (*Section 2.3.3.*).

12.3.2. Methodology

12.3.2.1. Sample Collection

T. tenuis were collected from g-vac sampling of random plots in fieldwork. This action was carried out after all other fieldwork was complete. *T. tenuis* were sampled from GS 11 - GS 15 to GS 87 - GS 91 for *H. vulgare* and GS 11 - GS 15 to GS 71 - GS 74 for *T. aestivum,* in 2017 / 2018 cropping season (*Table 5.1.1., Section 5.1.3.2., Page 82*). Two female adult *T. tenuis* were collected at each sample, due to their greater prey demands and increased activity in web-spinning to entrap prey (*Section 2.1.3.2.*).

The digestion process for *T. tenuis* is complete within a six hour time frame per prey item consumed, however Davey *et al.* (2013), Harwood *et al.* (2004) and Powell *et al.* (2004) comment that between two to four hours of digestion of Aphididae is the optimal time period for molecular analysis to detect the Aphididae DNA markers within the *T. tenuis* gut. It was felt that direct freezing of the *T. tenuis* field samples was paramount to impede the digestion process and preserve any protein markers of *S. avenae*, *M. dirhodum* and *S. mosellana* within the gut (Eitzinger *et al.,* 2013). *T. tenuis,* once collected, were thus placed into 1.5 ml microcentrifuge tubes and into a freezer box containing ice. This was to preserve the samples on the four-hour journey from the field to the laboratory.

12.3.2.2. DNA Extraction

T. tenuis DNA was extracted using Qiagen DNeasy Blood & Tissue Kit™. *T. tenuis* were placed in 1.5 ml microcentrifuge tubes and the process of lysis of cells begun by the addition of 200 µl of Phosphate Buffered Saline Solution (PBS Buffer) and *T. tenuis* mechanically broken down with the action of a mini pestle (Cold Spring Harbour Laboratory, 2015; Wagner *et al.,* 2016) (*Section 2.3.3.*). Macías-Hernández *et al.* (2018) identified all parts of a Linyphiidae body contain some quantity of a consumed Aphididae antigen in the later stages of digestion. This is due to the Linyphiidae expelling digestive enzymes externally, meaning feeding is in liquid form. This, and a branched gut forming diverticula (pockets), allows ingested liquid to be present in appendages as well as the central body (Davey *et al.,* 2013; Eberhard, 2006; Macías-Hernández *et al.,* 2018; Nyffeler & Sunderland, 2003). It has been identified however, that DNA from prey ingested was extracted in greater concentration within the abdomen and the cephalothorax of an arachnid and limited DNA was extracted from the appendages (Davey *et al.,* 2013; Macías-Hernández *et al.,* 2018). Legs of *T. tenuis* were the hardest element to break down and took considerable time. Therefore, if the tissues and cells of the *T. tenuis* cephalothorax and abdomen were fully incorporated in the solution, the sample was moved onto the next stage of DNA extraction even if legs remained. ATL (tissue-cell lysis) Buffer and Proteinase K were then added to aid further lysis. The samples were periodically heated to 56 °C in a heat block as denaturing may occur at a higher temperature, and vortexed for 15 seconds. This process lasted until most cells of the *T. tenuis* cephalothorax and abdomen were broken down and entered solution.

The next steps involved precipitation of DNA with 200 µl absolute ethanol and AL (cell lysis) Buffer. The samples were centrifuged at 8,000 rpm (rotation per minute) for 1 minute. The supernatants were then transferred to mini-spin columns where two separate washes were used to clean the DNA, centrifuging the first at 8,000 rpm for 1 minute and then the second wash at 13,000 rpm for 3 minutes. The exuded buffer was then pipetted directly onto the mini-spin column and further centrifuged at 8,000 rpm for 1 minute. The supernatant collected was the extracted DNA.

12.3.2.3. DNA Amplification

Generic and specific cereal Aphididae primers were structured from Chen *et al.* (2000) (*Section 2.3.3.*). Specific primers that were manufactured were for the main cereal Aphididae prevalent in the UK and therefore the NIAB fields, *M. dirhodum* and *S.avenae* (*Figure 12.1a & b, Section 5.1.5.*). *S. mosellana* primer design, Cecid-F4 and Cecid-R4, was referenced from King *et al.* (2012), who screened several invertebrates for multi-plex PCR. The primers, segments of mitochondrial COII (Cytochrome c-oxidase subunit II), were transported dry and rehydrated with PCR water to a specified level. A negative control (PCR water) and positive control (Aphididae and *S. mosellana* DNA) were incorporated into each PCR.

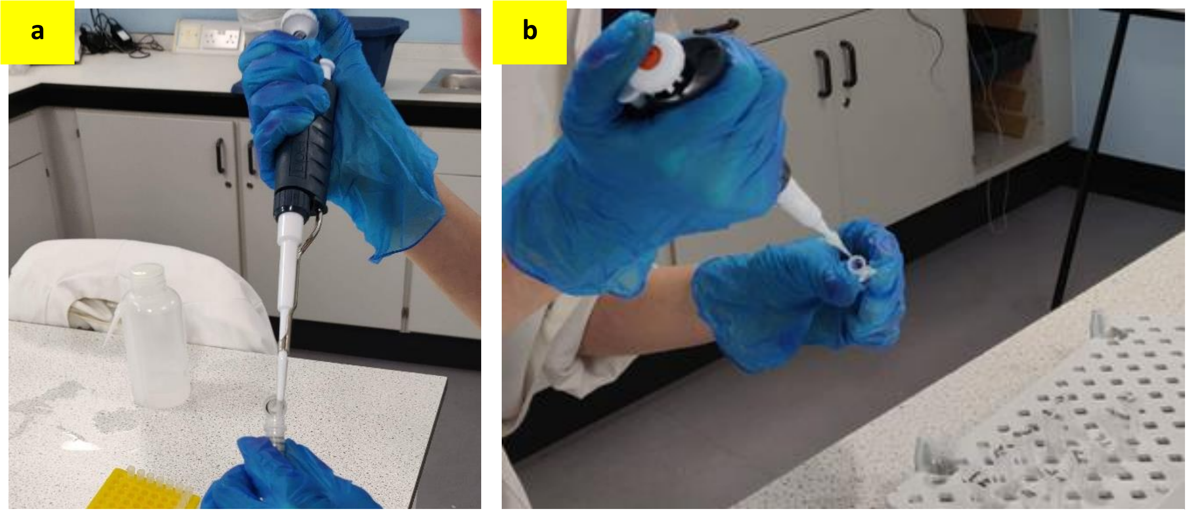


Figure 12.1a & b: M. dirhodum *forward primer 0.2 µl pipetted with use of Gilson® Pipetman P2™ (0.1 - 2.0 µl).*

12.3.2.4. Bar-Coding DNA

TAE (Tris/Acetate/EDTA) 0.5 M buffer was added to electrolysis trays after agarose gel had set. The disassociation of ions aided movement of the current and further provided an environment of constant pH maintaining the integrity of the amplicon (PCR product) (Collins, 2018) (*Figure 12.2a*). Thermo Scientific™ 6X DNA Loading Dye was added to amplicons (*Figure 12.2b*). Genomic DNA sequences obtained were read in 2% agarose gel for clarification under UV light box (Powell *et al,* 2004). DNA sequence length was read to nearest kilo-base pair (kbp). Nucleotide base pairs were read to identify presence of specific Aphididae mtDNA (mitochondrial DNA) COII sequence (Chen *et al.,* 2000; Cold Spring Harbour Laboratory, 2015; Powell *et al.,* 2004; Vink *et al.,* 2011) (*Section 2.3.3*.).

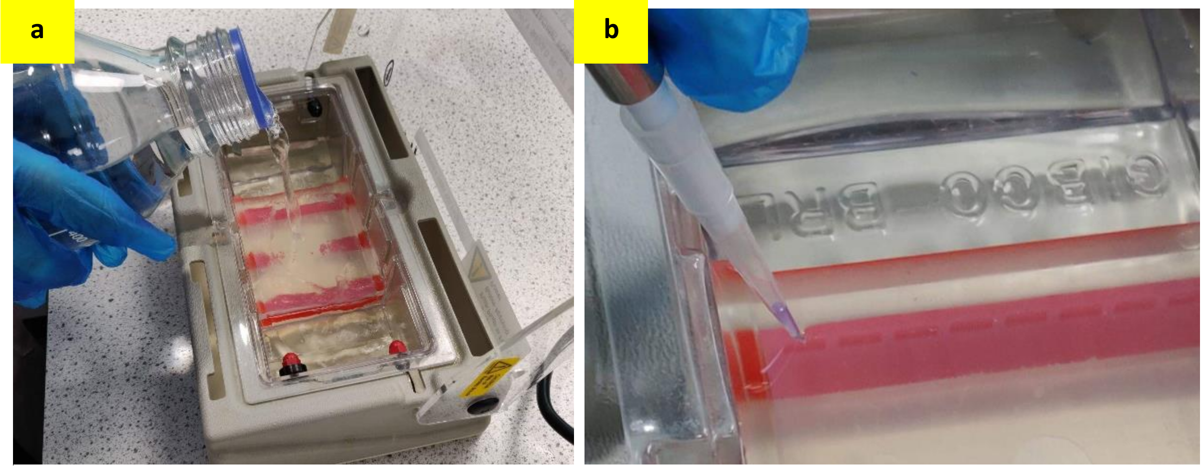


Figure 12.2a & b: Procedure for DNA Bar-coding. a = TAE Buffer solution added to electrolysis tray to assist movement of DNA. b = 9 µl Amplicon (PCR product) with loading buffer loaded into wells of agarose gel.

Two rows of bands appeared on the agarose gel. This was due to the loading dye used, allowing the presence of DNA at different bp (base pairs) widths to be tracked on the agarose gel (*Section 2.3.3.*). The different rates of movements, due to the electric current of electrophoresis, of two chemicals (Bromophenol Blue and Xylene Cyanol) allowed this to occur. The low bp of Aphididae and *S. mosellana* is tracked through the faster moving of the two chemicals: Bromophenol Blue (ThermoFisher Scientific, 2017).

12.3.2.5. Primer Verification

T. tenuis identification was verified with primers designed by Folmer (1994), to amplify the DNA of mitochondrial cytochrome c subunit I from diverse metazoan invertebrates. The forward primer was LCO01606 and reverse primer HCO2042 (*Section 2.3.3*.). Live *T. tenuis*, frozen for an hour were used to verify the specific *T. tenuis* primer.

Dead adult samples of *S. avenae* and *M. dirhodum* were acquired from the Rothamsted institute and were frozen on arrival to verify the primers. The samples were amplified first with the generic Aphididae primer to confirm this primer and then amplification occurred using the relevant specific Aphididae primer. It was seen that faint bands came from *S. avenae* in the generic and specific primers. Live samples of the Aphididae for DNA extraction had been identified to yield higher quality DNA (Chen *et al.,* 2000; Telesnicki *et al.,* 2012; Wagner, 2016). Live samples of alate morph adult *S. avenae* and *M. dirhodum* were obtained from the Insectary at the Rothamsted institute (*Section 7.2.3*.). *S. mosellana* specimens were collected live from the *T. aestivum* field. The Aphididae were placed into the freezer for immediate death for one hour, the *S. mosellana* frozen in-field, and DNA then extracted. The bands from gel-electrolysis on the killed samples were clearer and in the correct band length verifying the primers.

Due to DNA bar-coding, here analysing the presence of Aphididae and *S. mosellana* within the gut of *T. tenuis,* it was important to verify the generic and specific Aphididae and *S. mosellana* primers when the prey were within the gut. *T. tenuis* were starved in a sealed Petri dish for twenty-four hours and then five *S. avenae, M. dirhodum* and *S. mosellana* adults were added to a specific dish (*Figure 12.3a - c*). The Petri dish was checked daily. When it was clear an Aphididae / *S. mosellana* had been eaten by evidence of remains in the web or the removal of an Aphididae / *S. mosellana* from the dish, the *T. tenuis* was frozen and DNA bar-coding procedure was applied.

Figure 12.3a - c: Female T. tenuis *given an Aphididae for feed primer verification. (12.3b = Aphididae circled in yellow, 12.3c = Aphididae remains circled in yellow. 12.3a & c =* T. tenuis *circled in blue).*

12.3.2.6. Adaptations to Methodology

Primer dimers were identified early on in gel-electrophoresis (*Figure 12.4a & b*). This is an effect where the band has smudged within the gel. Primer dimers occur when molecules from the primer hybridize because of the complimentary base pairs that are contained within the primer. The hybridisation competes against the primer reagents from attaching to the base pairs to replicate the samples DNA (Brownie *et al.,* 1997; Ye *et al.,* 2017) (*Section 2.3.3.*).

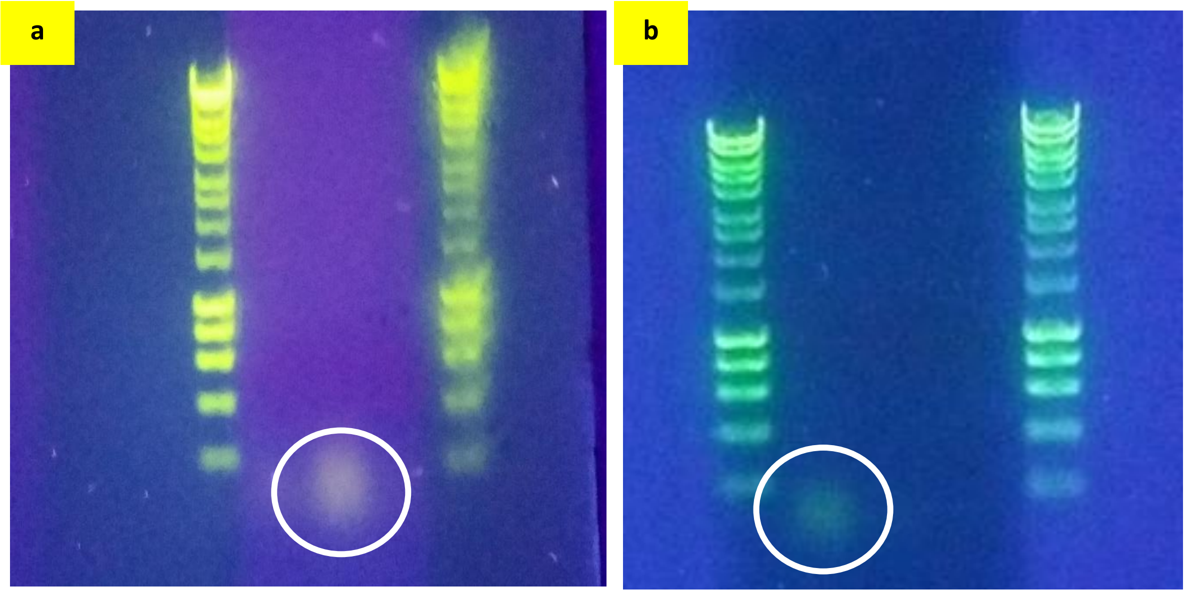


Figure 12.4a & b: Primer dimer on agarose gel for DNA Bar-coding (primer dimer identified circled in white).

To combat primer dimer, the annealing temperature was increased. This increases the bond between the primer molecules making it more difficult for them to dissociate and thus be free to hybridize. Three annealing temperatures (55 °C, 57 °C and 59 °C) were assessed to produce results with less primer dimers (Brownie *et al.,* 1997; Ye *et al.,* 2017).

Smearing occurred, which may have been due to the over-filling of the wells or the agarose gel being too thick. The voltage in electrophoresis may have been too high, which caused proteins to be pushed too hard through the gel causing smearing. Agarose was set to incorporate wells of a greater size; this was to aid with ease of PCR product application and to gain clearer positive bands. Less PCR mix was placed into the wells, (9 µl instead of 10 µl), and voltage was set at 70 V instead of 100 V for the electrophoresis for this and the subsequent PCR (Brownie *et al.,* 1997).

The PCR with the annealing temperature of 57 °C exhibited the clearest results with a band being present for the two Aphididae tested with the specific and generic primers, with little primer dimer. This gave evidence that lowering electrophoresis voltage and placing less liquid into the wells aided prevention of smearing and reduced primer dimers (*Section 2.3.3.*).

12.3.3 Results

12.3.3.1. Summary of Results

- Verification for the *S. avenae* and *M. dirhodum* primer was identified. *S. mosellana* primer was not verified.
- *S. avenae* was found in the guts of a *T. tenuis* collected from a Conventional and Direct Drill Managed sample at GS 33 - GS 37 of *H. vulgare*.

Figure 12.5: Agarose gel with M. dirhodum *Primer in* T. tenuis *gut.*

Wells reading from left to right on gel - T. tenuis *sampled from: -*

1. *Conventional GS 11 - 15.* H. vulgare
2. *Direct Drill Managed GS 11 - 15.* H. vulgare
3. *Direct Drill GS 11 - 15.* H. vulgare
4. *Conventional GS 33 - 37.* H. vulgare
5. *Conventional GS 33 - 37.* H. vulgare
6. *Direct Drill Managed GS 33 - 37.* H. vulgare
7. *Direct Drill Managed GS 33 - 37.* H. vulgare
8. *Direct Drill GS 33 - 37.* H. vulgare
9. *Direct Drill GS 33 - 37.* H. vulgare
10. *Conventional GS 61 - 65.* H. vulgare
11. *Direct Drill Managed GS 61 - 65.* H. vulgare
12. *Positive Control*
13. *Negative Control*

A band was present in the correct band width for *M. dirhodum* (301 bp) for the positive control (Chen *et al.,* 2000) (*Figure 12.5.*). No band appeared for the negative control. From these results, no *M. dirhodum* DNA was present in the gut of the *T. tenuis* collected from the different soil tillage intensities in *H. vulgare* at different growth stages.

Figure 12.6: Agarose gel with S. avenae *Primer in* T. tenuis *gut.*

Wells reading from left to right on gel - T. tenuis *sampled from: -*

1. *Conventional GS 11 - 15.* H. vulgare
2. *Direct Drill Managed GS 11 - 15.* H. vulgare
3. Direct Drill *GS 11 - 15.* H. vulgare
4. *Conventional GS 33 - 37.* H. vulgare
5. Conventional *GS 33 - 37.* H. vulgare
6. *Direct Drill Managed GS 33 - 37.* H. vulgare
7. *Direct Drill Managed GS 33 - 37.* H. vulgare
8. *Direct Drill GS 33 - 37.* H. vulgare
9. *Direct Drill GS 33 - 37.* H. vulgare
10. *Conventional GS 61 - 65.* H. vulgare
11. *Direct Drill Managed GS 61 - 65.* H. vulgare
12. *Positive Control*
13. *Negative Control*

S. avenae appeared to be present in the gut of a *T. tenuis* in Conventional and Direct Drill Managed GS 33 - GS 37 of the *H. vulgare* 2017 / 2018 cropping season (*Figure 12.6.*). The band is matched with the positive control and aligns with the bp of *S. avenae* (bp 281) (Chen *et al.,* 2000). No band appears for the negative control. No other *T. tenuis* sampled appeared to contain *S. avenae* in the gut.

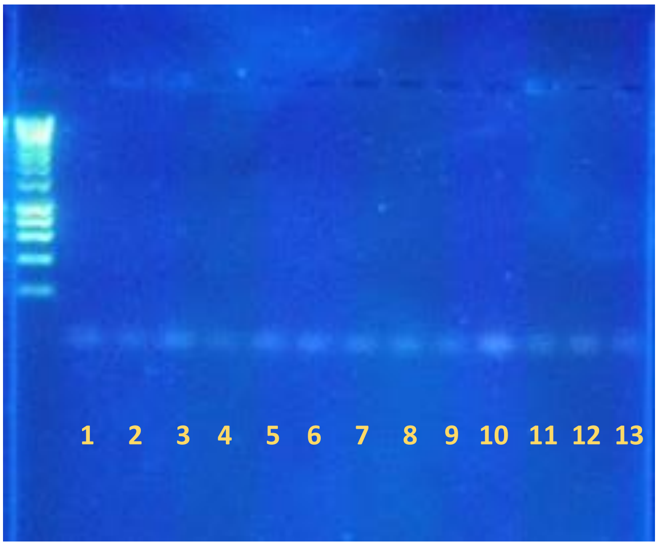


Figure 12.7: Agarose gel with S. mosellana *Primer in* T. tenuis *gut.*

Wells reading from left to right on gel - T. tenuis *sampled from: -*

1. *Conventional GS 31 - 33.* T. aestivum
2. *Conventional GS 31 - 33.* T. aestivum
3. *Direct Drill Managed GS 31 - 33.* T. aestivum
4. *Direct Drill GS 31 - 33.* T. aestivum
5. *Conventional GS 33 - 37.* H. vulgare
6. *Direct Drill Managed GS 33 - 37.* H. vulgare
7. *Direct Drill GS 33 - 37.* H. vulgare
8. *Conventional GS 47 - 51.* T. aestivum
9. *Conventional GS 47 - 51.* T. aestivum
10. *Direct Drill Managed GS 47 - 51.* T. aestivum
11. *Direct Drill 47 - 51.* T. aestivum
12. *Positive Control*
13. *Negative Control*

There was no band present in the positive sample (*Figure 12.7.*). It is concluded that the primers were not correctly specified to identify *S. mosellana* or that the positive sample did not yield enough DNA to be amplified.

12.3.4. Discussion

Only *S. avenae* was identified in the gut of *T. tenuis* in the Conventional and Direct Drill Managed tillage from GS 33 - GS 37 of the *H. vulgare* 2017 / 2018 season (*Figure 12.6.*). This related to fieldwork where the greater number of *S. avenae,* collected by the g-vac and in webs, at this time was found in the Conventional and Direct Drill Managed areas (*Section 5.1.5.2.1.*). It appears that biological control in these soil cultivations had taken place and *T. tenuis* had consumed *S. avenae* that were captured within the webs (Oelbermann & Scheu, 2009; Nyffeler & Sinderland, 2003; Schmidt & Tscharntke, 2005; Welch *et al.,* 2016). The Conventional area is of key importance as this is the area where BYDV was identified from GS 61 - GS 65 and confirmed from samples at GS 87 - GS 91 (*Section 6.1. & Section 6.5.1.*). The *T. tenuis* sampled came from an area 1.3 m from *H. vulgare* with early symptomatic signs of BYDV. Perhaps the *S. avenae* consumed by the *T. tenuis* was a vector of the viral infection and the predator dynamics of *T. tenuis* prevented this *S. avenae* from inoculating another *H. vulgare* plant (Burio *et al.,* 2006; Falks & Duffus, 1981; Moore *et al.,* 2011).

It is surprising however, that not more cases of *T. tenuis* consuming *S. avenae* and *M. dirhodum* were identified by the appearance of a band (*Figure 12.5. & Figure 12.6.*). It would be expected that a greater degree of *T. tenuis* consumed *S. avenae* and *M. dirhodum* within these time periods, having understood *T. tenuis* capability for positive biological control of cereal Aphididae through the literature (Bell *et al.,* 2002; Chapman *et al.,* 2013; Schmidt *et al.,* 2004; Toft, 1987). Toft (1987) and Welch *et al.* (2016) suggest Linyphiidae will tolerate high consumption of Aphididae even though they are of poor taste and nutritional quality to the Linyphiidae palate. However, as noted in the 2017 / 2018 season for both cereals, temperatures were unusually high which were shown to affect *S. avenae* and *M. dirhodum* fecundity and dispersal rate (Alford *et al.,* 2016; Brabec *et al.,* 2014; Jeffs & Leather, 2014; Parry, 2013) (*Section 5.1.6.2.2*.). This concluded in low numbers identified. Perhaps in times of greater *S. avenae* and *M. dirhodum* abundance, greater cases of consumption by *T. tenuis* would have been observed.

Bands of the agarose gel for the presence of *S. avenae* in *T. tenuis* gut could have been sharper, identifying purification of the DNA (*Figure 12.6.*). This could be implemented by further ethanol precipitation, further precipitating the *S. avenae* DNA nucleic acids out of solution (Chen *et al.,* 2000; Vink *et al.,* 2011). This may have allowed bands to be of a higher definition. In turn, this may have allowed traces of *S. avenae* that were within the *T. tenuis* gut, after nearly complete digestion and assimilation into cellular proteins, to have been amplified by the primer as a faint band after gel-electrophoresis. However, with no faint indication of a band in the original gel, it is unlikely that DNA purification will have yielded any different results, only creating sharper bands already present (Furlong, 2015; Harper *et al.,* 2005; Pommeresche *et al.,* 2013).

In terms of biological control, the extended phenotype of the web is a great asset to the potential Linyphiidae can bring to lower pest prey abundance (Blackledge *et al.,* 2011; Gregori *et al.,* 2015; Japyassú & Laland, 2017). The web is a vehicle to allow prey capture and therefore removal from the local ecosystem without the need of consumption by *T. tenuis*. This allows recordings of web contents to be placed against the PCR results of gut analysis for a combined biological control effect. Therefore, it appears that in GS 33 - GS 37, Conventional and Direct Drill Managed supported a higher degree of biological control of *S. avenae* than Direct Drill. However, at this GS, it appears due to a greater abundance of *S. avenae* being within these areas and not relevant to soil tillage intensity (*Section 5.1.6.2.1*.).

Chapman *et al.* (2010), Greenstone *et al.* (2012), King *et al.* (2012) and Rondoni *et al.* (2018) note that there may be contamination of Aphididae DNA from the g-vac bag relating to previous collections. When collecting samples for *T. tenuis* gut examination in *H. vulgare,* perhaps a fragment of *S. avenae* DNA may have transferred to the body of *T. tenuis* chosen for sampling, with whole body of *T. tenuis* dissolved to acquire adequate DNA (*Section 12.3.2.2*.). The bag from the g-vac was sterilised with Kilco© Virex™ Disinfectant (dilution rate 1:300) at Myerscough College after sampling visits, to remove dirt and permit adequate air flow for the next sampling period (*Section 4.3.12.1*.). However, this will not have removed all traces of DNA, as DNA requires dissociation of proteins with specialist chemical and heat treatment to degrade, and this action cannot be carried out in-field, with the g-vac used to collect specimens for DNA extraction at the end of the experiment (*Section 12.3.2.1*). It was ensured that no Aphididae were captured in acquiring the *T. tenuis* DNA samples due to the g-vac employed for a short duration, though *S. avenae* DNA may have persisted from earlier sampling during the day.

It appears that there was a problem with the known DNA sample, methodology or primer when *T. tenuis* guts were sampled for *S. mosellana* DNA. This was due to no DNA being read for the actual *S. mosellana* sample. The primer does relate to the literature where successful results had been attained. The G (Guanine) C (Cytosine) content was in line for successful intron (area of gene expression) attachment of the primer (Chen *et al.,* 2000; King *et al.,* 2011; Vink & Kean, 2013) (*Section 2.3.3*.). It appears that the problem lay with the *S. mosellana* sample or the procedure that was used. This sample was collected from GS 47 - GS 51 *T. aestivum* 2018. The same methodology was used as with Aphididae and samples were extracted into solution apart from *S. mosellana* wings and legs (*Section 12.3.2.2*.). Using literature to troubleshoot the 'no band' in the positive *S. mosellana* control, it may be that the PCR cycle needed to increase the time for annealing of the primer to the template DNA.

The Tm (melting temperature) of the primer was greater than that for the *S. avenae* or *M. dirhodum* primers. The Tm is the temperature that the DNA strand will separate allowing annealing of the primer into an intron (Von Ahsen *et al.,* 2001). It has been identified that a longer time period of annealing with a greater Tm could allow successful amplicons (an amplification of introns) to be formed, amplified and then *S. mosellana* DNA read by gel-electrophoresis (Vink *et al.,* 2011; Von Ahsen *et al.,* 2001).

12.4. Aphididae DNA Identification in *T. tenuis* and Linyphiidae Webs

12.4.1. Introduction

Further analysis of prey potential was obtained from DNA analysis of Linyphiidae sheet webs. This offers further evidence of biological control from a non-invasive perspective and may allow questions (against results of gut analysis) of surplus killing to be explored and if this may benefit pest control (Sint *et al.,* 2014). DNA of *Latrodectus mactans* (Southern Black Widow Spider), and its prey *Acheta domesticus* (House Cricket), were found on the *L. mactans* web 88 days after prey had been consumed and *L. mactans* removed from the web. Xu *et al.* (2015) successfully amplified *L. mactans* DNA at 257 bp and 311 bp, and presence of *A. domesticus* at 248 bp. The DNA for both species was mtDNA COI, DNA sequence confirmed from NCBI BLAST and BOLD IDS. This identifies the resilience of the DNA captured on the fibrils of the silk threads (Xu *et al.,* 2015). This has the potential to allow the biological control capacity of a Linyphiidae to be analysed long after prey capture.

12.4.2. Methodology

12.4.2.1. Sample Collection

Linyphiidae webs, containing no visible prey or prey exuviae, were collected from early and late growth stages of *H. vulgare* (GS 33 - GS 37 to GS 61 - GS 65) 2017 / 2018 cropping season (*Table 5.1.1.*). Additionally, a web was collected from the areas that were sampled containing BYDV symptomatic *H. vulgare* leaves (*Section 6.1.*). Prey and exuviae that were counted in webs of the sampled areas and used in the datasets were already identified to contribute to biological control and no further analysis was needed. Web areas chosen for DNA sampling were above 50.00 mm^2, to be able to have enough material for DNA analysis. Webs were collected on sterile cotton wool buds sealed in sterile tubes and preserved in an ice container with the *T. tenuis* samples collected, until laboratory provided cold storage of -19°C (*Figure 12.8a & b*) (*Section 12.3.2.1.*).

12.4.2.2. Laboratory Procedure

The laboratory experimental design was based on a method of Xu *et al*. (2015), who modified a DNA extraction process from reptile skins to be able to identify *L. mactans*, along with its prey *A. domesticus* within its web. The DNA extraction process used mtDNA COI / COII (*Section 2.3.3.*).

The sterile cotton wool buds were snipped into 1.5-mL microcentrifuge tubes using scissors sterilised via UV light and 70 % ethanol (*Figure 12.8c*). AL (cell lysis) buffer, 800 µL from the Qiagen DNeasy Blood & Tissue Kit™ that was used in DNA bar-coding of Aphididae within the gut of *T. tenuis* (*Section 12.3.2.2.*). The microcentrifuge tubes were inverted ten to twenty times and incubated for 4 hours at 55 °C (*Figure 12.8b & d*). The sample reached room temperature and then 4 µL of RNase A was added followed by twenty inversions. Samples were incubated at 37 °C for 15 minutes and then brought down to room temperature. A protein precipitation solution of 7.5 M ammonium acetate, 300 µL, was added to each sample and vortexed for 20 seconds followed by incubation in an ice bath for 15 minutes (*Figure 12.8e*). Samples were centrifuged at 14,000 rpm for 3 minutes. Supernatants formed were then placed into sterile 2 mL microcentrifuge tubes and 750 µL of isopropanol, at below freezing temperature, was added. The supernatants were inverted fifty times with centrifugation at 14,000 rpm for 2 minutes. The supernatants were drained and 750 µL of 70% ethanol was added followed by further centrifugation at 14,000 rpm for 3 minutes. All liquids were again drained, and the pellets formed were air-dried in a sterile UV chamber.

For DNA amplification, the DNA pellets were rehydrated using 100 µL of TE buffer (10 mM Tris, 0.1 mM EDTA). The PCR methodology and primers used were identical to that used for the identification of Aphididae in the gut of *T. tenuis* (*Section 12.3.2.3. - Section 12.3.2.5.*).

Presence of *S. mosellana* DNA was not DNA bar-coded within the Linyphiidae webs due to the specific primer not verified at this time.

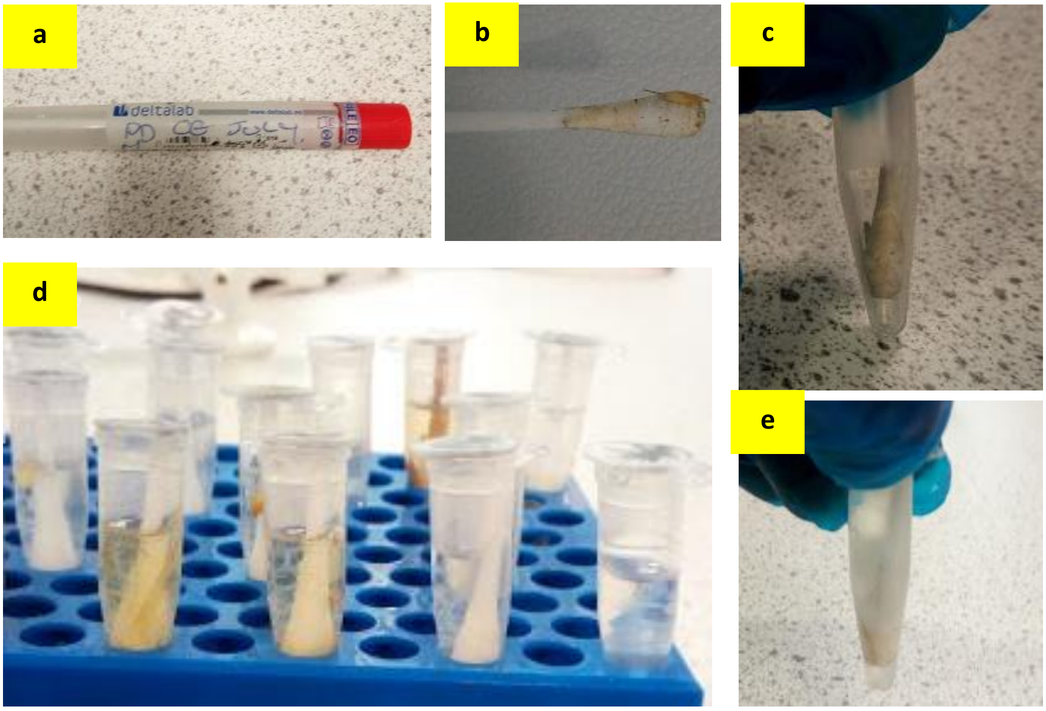


Figure 12.8a - e: Procedure of extracting cereal Aphididae from T. tenuis *and Linyphiidae webs. a = Web from BYDV Sample GS 61 - GS 65,* H. vulgare *2018, collected on a sterile cotton bud. b =Sterile cotton bud with web. c = Sterile cotton bud in microcentrifuge. d = Cotton bud samples after four hours incubation at 55 °C. e = Web precipitated in Ammonia Acetate.*

A negative control, to test for reagent contamination, was a web taken from a female *T. tenuis* that was solitarily within an enclosed Petri dish. No Aphididae were added and present within the enclosure. The positive control for *M. dirhodum,* to ensure primer viability, was a web collected from the microcosm experiment of differing prey abundance, where a *M. dirhodum* adult was observed within the web (*Section 10.6.3*.). The mesocosm experiment provided a positive control for *S. avenae,* where a web containing a *S. avenae* adult was used (*Section 8.7.*). Any visible Aphididae and exuviae were removed prior to examination to ensure any DNA present was located from the web.

12.4.3. Results

12.4.3.1. Summary of Results

- *S.avenae* and *M. dirhodum* primers were both verified.
- Neither *S. avenae* nor *M. dirhodum* DNA were bar-coded on the Linyphiidae web samples.

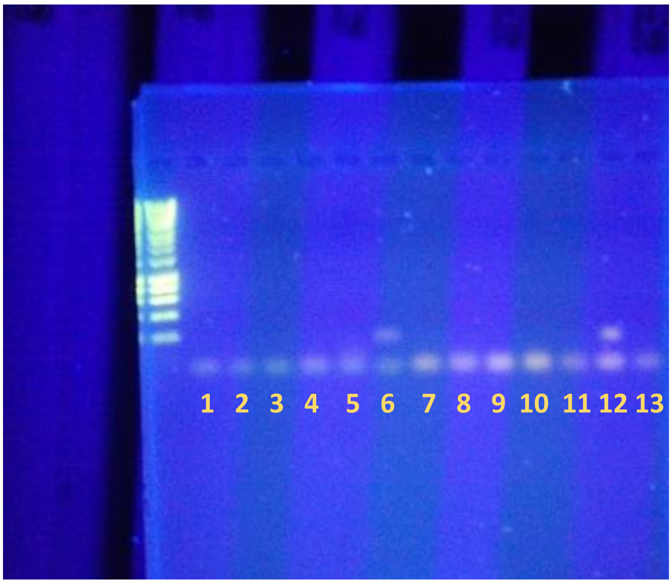


Figure 12.9: M. dirhodum *and* S. avenae *Primer on Linyphiidae web.*

Wells reading from left to right on gel - Web sampled from: -

S. avenae *Primer -*

1. *Conventional GS 61 - 65* H. vulgare
2. *Conventional BYDV GS 61 - 65.* H. vulgare
3. *Conventional BYDV GS 61 - 65.* H. vulgare
4. *Direct Drill Managed GS 61 - 65.* H. vulgare
5. *Positive Control* - S. avenae on Web
6. *Positive Control* - S. avenae
7. *Negative Control*

M. dirhodum *Primer -*

8. *Conventional GS 61 - 65.* H. vulgare
9. *Direct Drill Managed GS 61 - 65.* H. vulgare
10. *Direct Drill GS 61 - 65.* H. vulgare
11. *Positive Control* - M. dirhodum *on Web*
12. *Positive Control* - M. dirhodum
13. *Negative Control*

The positive controls for both *S. avenae* and *M. dirhodum* both have bands at the correct bp, concluding the PCR had produced the correct products (Chen *et al.,* 2000) (*Figure 12.9.*). The negative control incorporated no bands which explains there was no contamination of the reagents.

There was no band present for the positive control of *S. avenae* and *M. dirhodum* in the Linyphiidae sheet web. It appears that no *S. avenae* or *M. dirhodum* DNA upon webs was able to be amplified and read on the agarose gel.

12.4.4. Discussion

No Aphididae DNA could be acquired from the Linyphiidae webs, positive samples or those sampled from the field (*Figure 12.9.*). Revisions to the methodology are required. The original paper used for the methodology above were from large orb webs woven by *L. mactans* (Xu *et al.,* 2015). It seems that the DNA collected from this web may have been in a higher quantity or successfully amplified to that found in the *S. avenae* and *M. dirhodum* placed onto the sheet web. The silk of the flagelliform sheet threads, comprising the centre of the sheet web, where prey is likely to be captured, is fine, the β-helix creating fibrils with little surface area for DNA to be tethered (Pasquet, 2014; Rojas, 2011; Toft 1987) (*Figure 2d., Section 2.1.2.1., Page 11*). Additionally, the disorderly molecular structure with weak bonds may allow the cereal Aphididae DNA to disassociate over a relatively short time frame (Blackledge *et al.,* 2011; Craig, 2003; Harmer *et al.,* 2011; Saravanan, 2006; Xu *et al.,* 2015) (*Section*

2.1.2.1.). Dire webs of starved orb-weaving *L. mactans* are created from viscid threads where the DNA of prey is likely to be left entrapped within a viscid molecule, in higher concentration and with slow dissociation (Blackledge *et al.,* 2011; Craig, 2003; Harmer *et al.,* 2011; Saravanan, 2006; Xu *et al.,* 2015). It is thought that a greater amount of sample of known Aphididae presence on the sheet web may be required for success.

Webs from the field sample and microcosm and mesocosm experiments were collected with small particles of debris consistent with a *H. vulgare* field (plant material, soil) (*Figure 12.8a - e*) (*Section 8.4. & Section 10.4.).* The work involving DNA amplification of *L. mactans* web was carried out under full laboratory conditions (Xu *et al.,* 2015). It may that be that an extra step in the methodology of DNA purification is necessary. This would involve repeating ethanol precipitation (absolute ethanol) and washing the product with 70% ethanol to remove salts and impurities without further re-suspension (Chapman *et al.,* 2013; Chen *et al.,* 2000; Harper *et al.,* 2005; King *et al.,* 2011). From the purified DNA sample, any Aphididae present would allow a primer to insert into an intron and begin amplification.

It is still felt that identifying Aphididae DNA on a Linyphiidae web would be an important step in determining predator dynamics of *T. tenuis* and their biological control potential. Revisions to the methodology are required however, allowing the attainment of DNA from different molecular composition of varying silks and ensuring DNA is free from field contamination when run through PCR.

12.5. Final Discussion - DNA Bar-Coding Aphididae in *T. tenuis* Gut Contents and Linyphiidae Web

Biological control in the realm of gut analysis of *T. tenuis* has been found in an area of soil tillage intensity addressing the first and fifth aims of this Chapter (*Section 12.2.1*.).

Through the above research it is apparent that DNA bar-coding on gut analysis is an important tool alongside observations taken in the field of prey contents of the web. With this, a fuller picture of the predator dynamics of *T. tenuis* and Linyphiidae can be explored.

Chapter Thirteen

13.0. Final Discussion and Recommendations for Integrated Pest Management Plan

This Chapter is divided into three key elements. The first discusses the current research as a whole and the second analyses how it may be developed in the future. The final section looks at recommendations from this research that may aid an Integrated Pest Management Plan for the arable industry, focusing on incorporation of biological control for pest suppression.

13.1. Final Thesis Discussion

This research set out to analyse whether there was a significant difference in the ability of *T. tenuis* to weave webs to facilitate prey capture depending on the intensity of soil tillage on a cereal crop. The fieldwork was a key element to this project and aspects of the results obtained allowed glasshouse trials to be developed.

From the fieldwork, it was identified that Direct Drill Managed and Conventional tillage did eradicate *T. tenuis* abundance and activity immediately after cultivation had taken place (*Section 5.1.5.1.5.*). The predator potential of this Linyphiidae had been removed, though remained relatively undisturbed in Direct Drill. Pioneer abilities of *T. tenuis* and response to survival were identified with much rappelling (threads) measured on the upright stubble immediately after cultivation in Direct Drill and webs were woven in Conventional and Direct Drill Managed areas twenty-four hours later (*Section 5.1.5.1.).* Pioneering ability was further identified in the addition of an upright stubble trial, where a small area of upright stubble induced web construction, when previously no *T. tenuis* or Linyphiidae were observed (*Table 5.2.5., Section 5.2.6., Page 145*).

Soil clods, of greater height, were the key material that gained attachment of support threads in times of cultivation in Conventional and Direct Drill Managed. The action of a sub-soiler (non-inversion technique) clearly upholding Linyphiidae activity (*Section 3.1.3.4*.). Direct Drill Managed, at times of cultivation in the field and later stages of *H. vulgare* growth, provided a landscape with reduced web-spinning observations (*Section 5.1.6.1*.). The lower cultivation depth created a more homogenous landscape than Conventional, with soil clods of lesser variability in height (*Figure 5.1.3., Section 5.1.5.1.2., Page 91*). In secondary cultivation of *H. vulgare,* the landscape was altered, changing the circumstances available for potential web-building. The further breakdown of clods decreased abundance of attachment materials.

The potential for *T. tenuis* as a biological control agent was demonstrated in all soil tillage intensities within the fieldwork and glasshouse trials. A critical finding was greater webs (in area and abundance) capturing *S. avenae* in areas containing BYDV symptomatic leaves and *S. avenae* within the gut of *T. tenuis* collected from the field (*Figure 6.9., Section 6.5.3.3., Page 197, & Figure 12.6., Section 12.3.3., Page 343*). The action of *T. tenuis* here may have removed a vector of BYDV (*S. avenae*) from the micro-habitat and destroyed its potential to affect *H. vulgare*. In all trials, prey appeared to drive *T. tenuis* activity more than conditions created by the intensity of soil tillage. In the microcosm trials, with differing Aphididae abundance and growth of *T. aestivum,* anchor placement of webs appeared to be related to the growth of *M. dirhodum* (*Section 10.6.3.1.*). The highest Shannon-Weiner Diversity Index was calculated in Conventional area of the field, though no significant difference in abundance of prey captured was recorded with each soil tillage intensity (*Figure 5.1.18., Section 5.1.5.2.5., Page 112*). It appeared that prey diversity was low and may have been a consequence of the level of predator dynamics *T. tenuis* could perform.

Throughout this research, measurement of the anchor point height of a bridge thread for rappelling or a support thread for web construction, was a crucial variable. In most of the fieldwork and glasshouse trials, there were significant differences in the anchor point height obtained between the soil tillage intensities. It was clear that the decision of height at which *T. tenuis* anchors a web was principal to the potential prey-capturing ability of the web. Webs of a higher level intercepted no prey within a Conventional area whereas webs at lower strata captured *S. avenae* (*Figure 5.1.16., Section 5.1.5.2.4., Page 109*). An increased anchor point height further allowed webs to capture a greater abundance of *S. avenae* in areas of BYDV symptomatic leaves (*Figure 6.7., Section 6.5.3.2., Page 195*). By measuring anchor point height, it was established that different layers were used in the trial of addition of upright stubble to cultivated land. This trial clearly showed that the different Linyphiidae web-spinning potential between species, occupying different strata, can exert a greater degree of predatory behaviour (*Section 5.2.7.*).

Landscape heterogeneity appeared to be vital to allow the support of Linyphiidae webs. In the trial where upright stubble was added to Conventional cultivated land, this clearly increased the opportunities for web-spinning and rappelling (*Table 5.2.5.*). Use of upright stubble, of the same height within soil tillage intensities, was theorised to promote rappelling, due to a landscape homogeneity effect (*Section 5.2.7.*). Small changes in upright stubble altered *T. tenuis* behaviour in its increased height of the Direct Drill Managed area and showed minor alteration to a landscape affected the propensity to bridge (*Figure 5.2.4b., Section 5.2.3., Page 140*). With the microcosms for *T. aestivum,* the upright stubble at early growth stages (GS) provided additional anchor point material (*Figure 10.6., Section 10.6.2., Page 276*). This was further identified in the mesocosm of primary cultivation, where the upright stubble allowed large webs, using the rim of the plastic container as an attachment site (*Section 9.7.1.*). Upright stubble promoted the idea that increased availability of attachment materials enabled greater web abundance to be spun, increasing predator pressure.

As *H. vulgare* went forward into later GS, *T. tenuis* relied heavily on the plant for thread attachment. The differences created in plant height and density were the main variations and a result of the conditions of the soil tillage intensity involved in web-spinning. This was shown by the greater plant height of Conventional allowing webs at a higher level to be spun and ensnare a greater number of prey (*Figure 5.1.16.*). In the mesocosms with *S. avenae* as prey, where *H. vulgare* growth progressed, the lack of upright stubble and straw in the Conventional mesocosm, which had previously shown to demote *T. tenuis* activity at GS 21, was of no concern as the emerging crop allowed increased anchorage opportunities (*Figure 10.6., & Figure 10.9., 10.6.3.1., Page 279*).

It appeared that layers of landscape heterogeneity were favoured, where straw and upright stubble together supported the creation of *T. tenuis* webs. Both were in greater abundance in Direct Drill area of the field and glasshouse trials. Straw was noted to be a favourable refugia and was further found to increase the height of the ground layer for webs to be spun at a greater height in times of cultivation and early GS (*Table 5.1.3., Section 5.1.5.1.3., Page 92*). Straw was also identified as an area of shelter in the Direct Drill mesocosm of primary cultivation, theorised to be due to no prey availability (*Section 9.6.1*.). In the field, refugia allowed *T. tenuis* and its biological control potential to persist in the micro-habitat. Straw was shown to perhaps aid prey density with *M. dirhodum* observed utilising straw as a habitat in the choice chambers for selection of upright stubble and straw thought to be facilitating *S. avenae* ascension in mesocosms replicating the field (*Table 8.3., Section 8.7.2., Page 238 & Section 11.8.2*.). Straw residue in Conventional tillage of fieldwork (from the non-inversion tillage) may have aided capture of *S. avenae* by ‘pushing’ the Aphididae to a greater height on the crop (*Section 3.1.3.4. & Section 6.6.2*.). The act of soil tillage intensity aiding prey abundance was identified in Direct Drill Managed, where the greater number of *A. myosuroides* were situated (*Section 5.1.6.2.2*.). The lower intensive tillage may have allowed growth of *A. myosuroides* to persist and provide a ‘green-bridge’ for development of a *S. avenae* population (*Section 6.6.2*.).

Throughout this research, furrows were extensively used to support web creation, like the soil clods, the surface of the furrow created an attachment site. For example, high temperatures altered the dimensions of the furrows in in the field of *H. vulgare*, where its use as a web-site was observed (*Section 5.1.6.2.2*.). The furrows, incorporated into the microcosm experiments for prey abundance and selection of furrow with and without Aphididae, were further used extensively in Conventional choice chambers (*Section 10.7.2., Section 11.8.3. & Section 11.8.4.*). Its use appeared to be at times of low plant height and density where the availability of the furrow was attractive for web-spinning, however, little Aphididae prey were captured in the webs anchored to furrows. Capture of ground-dwelling prey may be exerted, though this prey may not be of consequence to the health of the plant, as with cereal Aphididae. To increase the predator pressure on cereal Aphididae and aerial pests such as *S. mosellana,* a web is required to be anchored higher in a habitat than a furrow. The Conventional tillage intensity had not helped this cause in these circumstances, the greater intensity of tillage compacting the Hanslope soil, causing furrows to widen (*Section 2.2.2., Section 3.1.3.4. & Section 5.1.6.2.2*.)

The web, as the extended phenotype, is the territory of *T. tenuis* and its web-site location is crucial to the outcome of the web. With the *T. aestivum* microcosm, holding differing prey abundance and the choice chambers of furrow selection, it was apparent that *T. tenuis* altered web-site location frequently (*Section 10.6.2. & Section 11.8.4*.). The ability to spin a web in many locations is of an advantage to Linyphiidae pest control. It was noted that there were differences to the prey-capturing ability of sheet webs anchored in various orientations. This was identified by smaller webs that held greater *S. avenae* capture in Direct Drill of fieldwork (*Section 5.1.6.2.1*.). These smaller webs had a greater energy return. There is a balance between energy output in web creation and input in prey consumption identified in each soil tillage. Large webs of Conventional field site, spun across plant rows, had no prey capture thus low energy was recuperated (*Figure 5.1.16.*). Keeping *T. tenuis* in energy surplus allowed future webs to be spun.

It has been important to consider how *T. tenuis* sense and respond to prey cues incurred, when understanding their predator dynamics. There were elements where *T. tenuis* appeared to be following Aphididae dispersal through movement of alate morphs in all soil tillage intensities of the field (*Section 5.1.6.2.1*.). Within mesocosms growing *H. vulgare*, *S. avenae* were mostly apterous morphs, their laboured movement meant *H. vulgare* density was used as a signal that prey may be present (*Section 5.1.6.2.2. & Section 8.8.*). In the choice chamber experiment for selection of furrow, it was identified that *T. tenuis* did not respond to *M. dirhodum* due to limited cues. Potential capture rate appeared greater in times of a bare landscape in Conventional, where a small stimulus could be intercepted (*Section 11.8.4.*). In the field, prey was most likely within the vegetation of a higher density, this vegetation a cue that prey may be in the vicinity. It has been noted that prey may have to be in greater abundance to produce effective cues to allow *T. tenuis* to respond. Soil tillage at times of prey abundance (at later GS) did not seem to affect stimuli that prey can produce (*Section 5.1.6.2.2*.).

During a few sampling periods at fallow, low *T. tenuis* or Linyphiidae activity was noted in the Conventional and Direct Drill Managed area (*Section 5.1.6.1.1.*). In the realm of predator dynamics of crop pests, this occurrence was not of a distinct disadvantage, due to low Aphididae migration and *S. mosellana* pupation identified at this stage. As the crop entered later GS, *T. tenuis* ability to capture prey in Conventional was identified when symptomatic BYDV leaves emerged and webs with Direct Drill Managed caught alate *M. dirhodum* (*Section 5.1.6.2.2. & Figure 6.9.*). Additionally, *T. tenuis* from Conventional and Direct Drill Managed areas held DNA evidence of *S. avenae* in the gut (*Figure 12.6.*). It appears that the low *T. tenuis* activity, within periods of fallow, did not translate to poor biological control potential when major crop pests were abundant.

Web occupancy was crucial to ensure that prey was removed from the micro-habitat. Prey can disentangle themselves from the web and escape. *T. tenuis* are required to be present to secure the prey through silk wrapping. A general theme throughout the fieldwork was that more unoccupied webs were found in Conventional tillage (*Section 5.1.6.2.2.*). The lowest web occupancy was seen to be Conventional tillage of *T. aestivum* microcosms when analysing *T. tenuis* behaviour with different abundance of Aphididae (*Section 10.7.2.*). It has been noted that web-site selection requires a time of exploration beforehand to gather information on where the greatest prey capture potential exists and gain protection from inter-specific / intra-specific competition. A period of learning was identified in the choice chamber selection experiments when webs were observed not to be woven at the appropriate location to capture the prey within (*Section 11.8.2. & Section 11.8.4.*).

Rappelling was an important precursor to web-building, to identify a suitable location, however, bridge threads did not relate directly to prey capture. Difference in length of bridge threads in fieldwork showed variations in exploration distances. Long threads were spun over the homogenous landscape of a Conventional area for the trial of addition of upright stubble (*Figure 5.2.8., Section 5.2.6., Page 145*). This identified that greater energy was expended in web-site searching of a landscape that was low in complexity. Rappelling altered in response to prey availability at times when *H. vulgare* was in early and late growth stages in fieldwork, as greater migration occurring when prey was low (*Section 5.1.6.2.1. & Section 5.1.6.2.2.*). Rappelling was limited in the choice chambers for selection of upright stubble or furrow (with and without Aphididae) due to the small spatial scale promoting little area of exploration (*Section 11.8.1. - Section 11.8.4.*). Few prey were captured in this trial, which may have altered if a propensity to bridge had occurred.

Intra-specific relationships outside of the difference in intensity of soil tillage were found to have been an important consideration. Body size of *T. tenuis,* at times held significance to *T. tenuis* activity output. Larger bodied females were shown to be unable to bridge large distances, in the addition of upright stubble trial, due to the gravity hypothesis through SSD (sexual size dimorphism) and thus may have lost prime web-site occupation (*Section 2.1.2.3., & Section 5.2.7.*). Increased cephalothorax length identified a greater ability to spin webs over a larger area and abdomen length allowed a greater strain placed onto silk yield (*Table 8.5., Section 8.7.3., Page 240 & Table 10.10., Section 10.6.3.2., Page 285*). Both factors increased the level of predator dynamics that *T. tenuis* could exhibit. With the selection of the upright stubble choice chambers, it was identified that females and males exhibited predator dynamics in a different manner. The females had an inherent ability to respond to prey cues at an enhanced rate allowing a greater prey capture ability (*Section 11.8.2. & Section 11.8.4.).*

Environmental factors outside of soil tillage have played an important role in both field and glasshouse work. Wind speed in fieldwork altered *T. tenuis* predator dynamics within each soil tillage. Web location lowered due to high wind speed in fieldwork (*Table 5.1.5., Section 5.1.5.1.3., Page 93*). Temperatures altered prey abundance in the mesocosms, replicating field conditions (*Table 8.7., Section 8.7.5., Page 242*). This modified biological control that *T. tenuis* exerted by increasing Aphididae parthenogenesis rate and initiating dropping behaviour of *S. avenae* into webs. Higher temperature enabled *T. tenuis* to ascend higher and yield longer threads with less energy output, the latter due to less tensile stress required to yield the silk (*Figure 8.10., Section 8.7.4., Page 241 & Table 10.10.*). Webs were thus spun more rapidly with higher energy retention to capture potential prey or further web-build.

The hedgerows held high abundance of *T. tenuis* throughout the life cycle of the crop in the field opposite, presenting this area as a crucial reservoir to allow *T. tenuis* to persist (*Figure 5.3.7., Figure 5.3.8., Section 5.3.5.4., Page 168 & Page 169*). Generally, the activity found in the hedgerows did not differ greatly between the intensity of soil tillage that the hedgerows were bordering. This was demonstrated when greater *T. tenuis* abundance was recorded in the hedgerows bordering all soil tillage intensities at times of cultivations (*Figure 5.3.7. & Figure 5.3.8.*). *T. tenuis* were noted to be of greater abundance within the hedgerows when the field was cropped with *H. vulgare* which was of consequence to the biological control capacity *T. tenuis* were able to exert in the main field (*Figure 5.3.8.*). Whether web-occupancy was at the front or rear of the hedgerow was key to understanding migration out of the field. In periods out of crop, where prey abundance had been low in the field, webs were woven at the back of the hedgerow (*Section 5.3.6.1.*). The favoured web-site was shown to be the forefront of the hedgerow at lower strata, potential here for *T. tenuis* to be dispersing in and out of the hedgerow regularly, a positive to pest suppression in the field (*Table 5.3.15., Section 5.3.5.3.2., Page 166*). Hedgerows were shown not to relate directly to *T. tenuis* and Linyphiidae predator dynamics in the field, however, prey capture in the hedgerow (opposite each soil tillage) prevented migration of prey into the crop (*Figure 5.3.5., Section 5.3.5.3.1. Page 165*.).

The fieldwork was the only area that allowed the reproductive potential of *T. tenuis* and the different soil tillage intensities to be explored. This is important, as it promotes a future of biological control candidates in Linyphiidae. There appeared to be no direct relationship between the conditions of the field after tillage and egg sac location. In the hedgerows, egg sacs were littered along the entire length of the hedge, which showed 'bet-hedging' to secure a future generation (*Section 5.3.6.4*.). This was concluded not to be associated with soil tillage intensity; thus, level of soil tillage was found not to be important in establishing the next generation.

13.2. Recommendations for Further Research

The glasshouse trials allowed the cephalothorax length to be measured to 0.01 mm with laboratory equipment, which enabled a greater degree of discrimination to be observed between cephalothorax lengths of *T. tenuis* (*Section 7.2.2*.). From this information, it was observed that a greater cephalothorax facilitated greater thread lengths to be spun and greater heights attained for web-building. Within fieldwork, digital callipers measured cephalothorax length to the nearest 0.1 mm. This permitted little difference between cephalothorax lengths to be obtained as this body segment is smaller than the abdomen (*Figure 2.1, Section 2.1.2., Page 7 & Section 4.3.4.*). At times, where greater height of webs had enabled a higher degree of prey capture, it would have been useful to analyse if a *T. tenuis* of a larger cephalothorax had spun the web or it was a response to prey stimuli (*Figure 5.1.16.*). If this was the case, it may be that the *T. tenuis* was not responding to prey cues, able to expel a greater rate of energy with increased leg flexion potential. For field cephalothorax measurement it would therefore be useful to use an in-field cordless microscope at 40x magnification capable of graticule attachment.

In-field microscopy would be a useful technique to apply to analyse the Aphididae exuviae found within the webs. The exuviae in webs was a useful observation in the field as presence explained that a *T. tenuis* web was constructed in the vicinity of a recent Aphididae colony (*Table 5.1.21., Section 5.1.5.2.4., Page 109*). It was commented within all fieldwork periods that closer analysis of the Aphididae exuviae would have been useful to explore whether the soft Aphididae had been broken down with expelled digestive enzymes and sucked from the outer skin, the feeding method of Linyphiidae (*Section 2.3.3. & Section 12.3.2.1*.). This would allow another element of definite *T. tenuis* predation to be measured. This result could stand with DNA bar-coding for gut analysis to understand where in the field the greatest consumption, element of biological control, of pests was taking place (*Section 12.3*.).

Direct Drill tillage in the centre of the NIAB field trials means that this area is surrounding by hedgerow on only two sides, whereas Conventional and Direct Drill Managed had three (*Figure 4.1., Section 4.2., Page 53*). This at times, theorised to be the reason why Aphididae were seen in greater abundance in the cultivated areas (*Section 6.6.2*.). Climatic conditions were noted to have limited dispersal within the 2017 / 2018 cropping season (*Section 5.1.6.2.2*.). Placement of the Direct Drill area at the edge of the cultivated plot may help to understand if the greater migration from the hedgerows, hypothesised to be directed from the greater hedge surround, is dealt with differently by *T. tenuis*. Perhaps the use of the upright stubble present in the early GS of the crop would allow greater web abundance to be woven, to deal with a prey dispersal event (*Section 5.1.6.2.1*.).

It was identified that rappelling was low in the glasshouse trials, therefore explaining little exploration was required before a suitable location was identified for web-site construction (*Section 8.7., Section 9.6., Section 10.6. & Section 11.8.1. - Section 11.8.4.*). This communicates that the habitat may have been too small a spatial scale to allow accurate representation of the field. It was noted that the landscape heterogeneity scale was lowered, meaning landscape complexity was identified in Conventional with attachment of threads to the sides of the microcosms analysing differing Aphididae prey abundance (*Figure 10.15., 10.7.2., Page 289*). The idea of microcosms is to produce replicable trials allowing results to be examined on a close scale. A recommendation for future work would be to create the microcosms with a material that *T. tenuis* would be unable to anchor threads to. This is of some difficulty, due to the nature of the piriform silk producing the attachment discs and no frictionless materials exist (*Figure 2.3c., Section 2.1.2.1., Page 11*). Graphene coatings may allow low attachment with almost no friction due to the singular-layered structure of carbon atoms; however, this would be at a cost (Hung *et al.,* 2018). Previous literature has favoured Perspex, the surface holding low surface-tension (Howard *et al.,* 2004; Sunderland & Samu, 1996; Toft, 1987). It appears that elimination of the potential of attachment in a glasshouse trial would be difficult.

The idea that *T. tenuis* usually display a learning period before a web-site is selected and the evidence that *M. dirhodum* was on many occasions not intercepted, gives evidence that running the choice chamber experiments (for selection of upright stubble and furrow with Aphididae) for longer would have been beneficial (*Section 11.3.2. & Section 11.4.2*.). A greater time period may allow greater learning and the small stimuli of *M. dirhodum* to be read or the prey location determined by cues in resource availability, and greater capture of *M. dirhodum*. Further, an increased experimental time would allow *M. dirhodum* growth from parthenogenesis, which might promote greater stimuli.

It is still of high consideration that the DNA bar-coding of the gut contents of *T. tenuis,* allowing predator dynamics of this Linyphiidae to be understood, could be utilised alongside fieldwork. It is therefore recommended for future work that the PCR cycle is amended to allow *S. mosellana* to be identified in the gut of *T. tenuis*, as this prey is of high consequence to the yield of cereal crops (*Section 2.2.6.4. & Section 12.3.4.*). The idea of retrieving prey DNA from Linyphiidae webs is important to re-consider and amendments to the methodology need to be trialled (*Section 12.4.*). The advantages of observing prey DNA on a web is its longevity, the DNA detection able to be read after prey consumption and its assimilation within the gut of the Linyphiidae. It is noted that there are advantages in the use of many tools that can be applied to understand the full biological control potential of a Linyphiidae.

13.3. Recommendations for an Integrated Pest Management Plan

The aim of this research was to understand if soil tillage intensity affected the predator dynamics of *T. tenuis* and Linyphiidae within an arable crop. The use of this was to examine the level of biological control to pests that the Linyphiidae can apply in each soil tillage intensity. This was in response to the need to reduce the level of chemical control used due to government bans for environmental concerns or increasing pests acquiring knock down resistance (kdr) (*Section 2.2.6.5.*). The desire was to gain the greatest yield possible of a crop, void of pest damage, with respect to the soil health and ecosystem services. This is of benefit to sustain a large human population and ensure an environment that can continue producing food in the future (Bommarco *et al.,* 2013; Jonsson *et al.,* 2014).

From this research, the choice to use non-inversion techniques for the Conventional and Direct Drill Managed areas has been of great advantage in obtaining Linyphiidae presence in the field after cultivation has occurred (*Section 5.1.6.1.2.*). This was due to crop residues and clods left on the surface providing clear attachment sites for threads spun (*Section 3.1.3.4.*). The information gained at times of soil cultivation identify that the lighter cultivation of Direct Drill Managed held a habitat of lower landscape heterogeneity, thus not able to support a high level of *T. tenuis* or Linyphiidae abundance.

It is vital that yields of the NIAB fields in the trial are considered for this research, as growth of food is the trials primarily goal. From NIAB summery reports of the seasons and Field B where *T. tenuis* activity was measured, there were differences in yield between the different soil tillage (*Figure 3.5b, Section 3.1.3.4., Page 51*). For *H. vulgare* (2016 / 2017 season) the greater yields were identified in Direct Drill Managed (4.92 t ha^{-1}) and Direct Drill (4.71 t ha^{-1}). The yield of Conventional was 3.72 tha^{-1}, over one t ha^{-1} lower than the tillage of Direct Drill Managed (NIAB TAG, 2017). Plant population (plant m^{-2}) followed the pattern of the yield results within the report, and in greater population the landscape heterogenieity increased for spider abundance. At GS 75, head counts of *H. vulgare* found no comparable difference, similar complexity in landscape architechture existed in each soil tillage intensity, for greater probability of web-spinning where crop pests may still be present (NIAB TAG, 2017). *H. vulgare* for 2017 / 2018 season, recorded yields of 5.48 t ha^{-1} for Conventional, 0.52 t ha^{-1} greater than Direct Drill Managed and 1.29 t ha^{-1} greater than the yield of Direct Drill (NIAB TAG, 2018). This equated to a difference in plant population of 43 plant m^{-2} between the Conventional and Direct Drill tillage (NIAB TAG, 2018). The Conventional tillage system for *H. vulgare* had generally greater yields and plant population which is of beneifit to food production and *T. tenuis* web-spinning, where the increase in plant population is likely to provide Linyphiidae with greater opportunities for anchorage sites.

A. myosuroides, at times, appeared to influence greater *T. tenuis* abundance in increased complexity of landscape architecture and had an indirect influence on *T. tenuis* and Linyphiidae propensity to web-spin (*Section 5.1.6.2.2.).* From the NIAB field wide survey, the establishment of *A. myosuroides* had a considerable effect on lowering yields, thus a consequence to food production. The low yield of Conventional for *H. vulgare* in 2016 / 2017 season was due to an aggressive patch of *A. myosuroides* identified in the field edges (NIAB TAG, 2017). It was found, in the field research, that in areas of high plant density, *A. myosuroides* was not used as an attachment point, therefore its removal would be of no consequence to *T. tenuis* behaviour. In *H. vulgare* (2016 / 2017) there was an *A. myosuroides* population of 47 heads m^{-2} in Conventional, 9 heads m^{-2} greater than Direct Drilll (NIAB TAG, 2017) and in 2017 / 2018, *A. myosuroides* population was 151 heads m^{-2} in Direct Drill, 54 heads m^{-2} greater than Conventional (NIAB TAG, 2018). Direct Drill supported a greater density of *A. myosuroides* which concluded to zero-till leaving *A. myosuriodes* to persist (NIAB TAG, 2018) (*Section 3.1.3.4*.).

From NIABTAG 2017 and 2018 report data and *T. tenuis* activity recorded from the fieldwork, it appears that Conventional is a viable soil tillage to allow *T. tenuis* activity to sustain and allow optimum yields to be obtained. Conventional in times of primary cultivation, supported web abundance equalling Direct Drill area twenty-fours hours after cultivation had occurred (*Section 5.1.6.1.2.*). Direct Drill Managed was found to have yields and plant populations in between Conventional and Direct Drill and principally had less *A. myosuriodes* than Direct Drill. This area supported *T. tenuis* activity in later growth stages of *H. vulgare* and therefore is a viable tillage technique to use, however, at times of cultivation very little *T. tenuis* activity was observed (*Section 5.1.6.1.2. & Section 5.1.6.1.3.*). Conventional appears to be the best method of tillage from this research with high yields obtained and *T. tenuis* able to spin webs and capture prey when its presence was noted. However, there are further environmental effects to Direct Drill tillage and at times greater prey was captured with low energy output due to small webs woven at a greater height, noted to be due to a dense crop canaopy (*Section 5.1.6.2.1.*). The NIAB trial has been established for six years, it can take time for breakdown of organic matter from crop residue to improve soil health and microbial build-up to assist in nutrient assimilation (Mbuthia *et al.,* 2015; Shrestha *et al.,* 2015). These factors can potentionally allow greater nutrient availability and accessibility to a growing crop and allow yields to restore in Direct Drill (*Section 2.2.4.*). Perhaps if yields increase along with plant populations in Direct Drill, the effect of zero-till allowing dynamic *T. tenuis* activity, in rappelling and web-spinning, at times of cultivation can translate to greater prey capture in all GS of *H. vulgare*.

A. myosuroides is of much concern for arable farms in this region, its invasive nature able to out compete for resources to thrive while drastically reducing possible crop yields (Jarvis & Woolford, 2017; Melander *et al.,* 2013). *A. myosuroides* reduction is key to reduce pressure on yields of Direct Drill in the NIAB trial. It is noted that the farmer has adopted a sheep grazing regime on fields outside of the NIAB trial as a control measure for *A. myosuroides* (*Section 3.1.1*.). This allows *A. myosuroides* to germinate and be grazed off at early GS before its establishment. Aaserud (2005), Dennis *et al.* (2001) and Mclachlan & Wratten (2003) showed that high Linyphiidae assemblages were established in areas of sheep grazing, more so than mixed livestock or cattle. At times, greater dwarf Linyphiidae were in medium-grazed sheep pastures than found in an arable crop (Downie *et al.,* 2000; Topping & Lövei, 1997). This was commented to be due to the greater landscape heterogenity reached with sheep feeding in a sporadic manner creating vegetation of different heights (Paschetta *et al.,* 2013). Perhaps permitting sheep grazing will allow Direct Drill and Direct Drill Managed tillage (when the field is put to crop) greater potential to support Linyphiidae and produce greater yields through increase in plant populations not pressured by *A. myosuroides* persistance. The 'green-bridge' would also be removed at times of cultivation with low *A. myosuroides* density present and therefore Direct Drill and Direct Drill Managed may support a lesser degree of prey (Dahlin & Ninkovic, 2013.).

During the fieldwork, a higher degree of *T. tenuis* abundance and activity was identified in the hedgerows bordering the field (*Section 5.3.5.4*.). The advantages of a hedgerow with high landscape heterogeneity was noted to allow a generation to persist by offering a reservoir of high bio-diversity and shelter (Schirmel *et al.,* 2016; Ysnel & Canard 2000). At times of fieldwork, it was considered if a greater density of *T. tenuis* were found in the field instead of the shelter habitats, it would be beneficial for biological control, especially in early GS of a crop when a tolerance to damage had not been built (for example tolerance to feeding from vectors of BYDV). Removal of the hedgerows would be of a disadvantage to predator dynamics of Linyphiidae, as the shelterbelt is important for the persistence and continuity of generations (Pfister *et al.,* 2015; Pywell *et al*., 2005). It may be that another slow growing 'companion plant' (companion due to mutualistic benefits) could be grown in the field margins to 'push' *T. tenuis* into the main field. This, known as intercropping, can involve the use of wildflowers such as *Lotus corniculatus* (Birds Foot Trefoil) and *Trifolium pratense* (Wild Red Clover)

(Howard, 2016). These wildflowers are suitable for heavy clay soils, able to persist in times of high surface moisture with the soils' high bulk density permitting low permeability (Ashman & Puri, 2002) (*Section 2.2.2*.). It has been noted that a small increase in landscape heterogeneity is of great appeal to a web-building Linyphiidae (Médiène *et al.,* 2011; Ratnadass *et al.,* 2012). Midega *et al.* (2008) identified, in arable crops, a 'pull' crop increased migration of Linyphiidae into the field and Cook *et al*. (2007) found planting of *Desmodium uncinatum* (Silver Desmodium) at a field edge increased abundance of natural enemies into the main area of a maize field. It is key that a non-invasive native crop is planted into the arable crop not to invade root systems or impede growth of the main crop by obtaining excessive nutrients.

It was noted that a gap of 1 m between the field edge and shelterbelt may be too great to facilitate the rapid dispersal of a ballooning or rappelling *T. tenuis* in and out of a hedgerow. This area within the NIAB trials was noted to be mowed, incorporating limited landscape heterogeneity (*Figure 4.1., Section 4.2., Page 53*). It is understood that this area is used to allow machinery ease of access into the field. It may be beneficial to create 'green-bridges' to aide movement of *T. tenuis* and Linyphiidae into the main field (Baldissera *et al.,* 2004; Feber *et al.,* 2015; Mestre *et al.,* 2018). This may be a small 'corridor' which is not disturbed (mowed), where the grass species are allowed to succeed and provide a linear patch of landscape heterogeneity to connect the field to the sanctuary of the shelterbelt (Horváth *et al.,* 2015; Villard & Metzger, 2014). Rappelling requires upright structures of a height to provide anchorage for the successive bridge threads (Bonte *et al.,* 2008). Two to three 'corridors' each side of the field margin may be sufficient to facilitate movement, perhaps in locations where limited herbicide (glyphosate) drift occurs i.e. corners. It is noted that drift can cause reduced vegetation growth in a margin, defeating the goal of a 'green-bridge' to allow a continuous patch of landscape heterogeneity for increased Linyphiidae web-spinning (Haughton *et al.,* 2001; Hof & Bright, 2010). It is noted the idea of 'green-bridges' within field margins may further encourage early pest, for example Aphididae, migration into the field. However, facilitating Linyphiidae movement before crop germination would encourage biological control upon Aphididae before accelerated parthenogenesis had chance to occur.

The NIAB experiment is of continuing great scientific value in obtaining key information to help guide recommendations for agriculture sustainability in the future. The forward-thinking of Mr. Martin Jenkins and his farming enterprise in Childerly in Dry Drayton, Cambridgeshire, has allowed a large long-term trial to establish and where scientific exploration is encouraged.

13.4. Final Word

One research observation that has been greatly appreciated is the web-spinning ability of Linyphiidae. The mechanisms of silk production in web construction are quite astounding. Webs of Linyphiidae and *T. tenuis* have been recorded woven to a multidude of structures, creating sheet webs of varying dimensions and orientations. The extended phenotype of webs is an incredible feat of natural engineering, which is capable in the appropriate conditions for exerting pressure on pests which cause much damage to arable agricutural industry, reducing the need for chemical control.

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