Investigations into the biology and behaviour of *Thrips tabaci* L.

Joshua Alexander Burnstone

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Table of Contents

List of Tables

List of Figures

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Declaration

The work presented in this thesis is my own work and has not been submitted for a degree at another university.

Some data gathered for this thesis were presented in the following paper:

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Summary

The onion thrips, *Thrips tabaci* (Thysanoptera, Thripidae) is a polyphagous pest of *Allium* crops in the UK and considerable effort and expenditure is employed in its control. Despite this, overall understanding of the biology and behaviour of *T. tabaci* is poor and this project addresses some of these deficiencies in knowledge.

The relationship between *T. tabaci* development and temperature was investigated using linear and non-linear descriptors. The most accurate descriptor was a non-linear logistic curve. A forecasting system was developed to predict population trends in the field using field temperature data to estimate the progression of development over time. It was not possible to predict field population trends accurately and possible reasons for this are discussed.

The effect of temperature and of leaf quality on behaviour was examined. A range of different behaviours were identified, classified and shown to have a direct relationship with both temperature and leaf quality. The potential for such information to help to explain and predict patterns of behaviour seen in the field is discussed.

The diel periodicity of the intra-plant distribution of *T. tabaci* was examined and a clear pattern identified. A high proportion of adults were located on exposed portions of host plants in the early afternoon. An experiment was conducted, focusing on this potential window of vulnerability, using a novel control technique involving irrigation. No significant control of thrips was achieved, but further investigations into the potential of such strategies are recommended.

Field populations of *T. tabaci* were monitored between 2004 and 2008. Throughout this period thrips were most numerous in late summer and overwintered as adults. The monitoring data were examined in light of what has been learnt about *T. tabaci* biology and behaviour in this study. Recommendations are made about future work on forecasting and control.

Chapter 1: Introduction

The pest problem

The onion thrips, *Thrips tabaci* (Thysanoptera, Thripidae) is a polyphagous pest of *Allium* crops in the UK (Garthwaite et al., 1997, Lewis, 1997b, Alford, 1999). Worldwide *T. tabaci* is recognised as a key pest insect of a wide range of different crop plant families ranging from alliums to brassicas and from cotton to fruits including tomatoes and pineapple. In the UK, the focus for *T. tabaci* pest problems has been the *Allium* family where it is now considered, certainly in terms of targeted control strategies, to be the key pest arthropod.

Indeed *T. tabaci* is considered to be such a potentially harmful pest of alliums that considerable effort and expenditure is employed in its control. The problem lies in the method by which *T. tabaci* feeds. Like all thrips, *T. tabaci*, has piercing and sucking mouthparts, consisting of a fleshy proboscis or cone, housing stylets that are used for penetration of and feeding from plant material, in this case leaves (Lewis, 1973a). Feeding by the thrips damages the host plant via direct removal of cell contents. As individual plant cells are killed, scarring of the leaf, in the form of silvering, due to the high visibility of emptied cell cavities, is observed. Despite individual feeding sites being small, the damaged area of the leaf does not recover and becomes larger and more pronounced as the plant grows. This can quickly lead to damage that is visible on the leaf even to the untrained observer.

Plants with obvious thrips feeding damage are considered unacceptable for sale in many cases and therefore the economic impact of a thrips infestation can be severe. In the UK, actual yield loss from extremely heavy infestations on salad onion and leek is rare (information from growers), but does occur occasionally. It is the cosmetic damage caused by *T. tabaci* which is the key problem and the target of the extensive effort expended upon *T. tabaci* control on UK *Allium* crops. In 1995, around 54% of all UK *Allium* crops treated with insecticides were treated for thrips; whereas by 2003, 83% of all *Allium* crops treated with insecticide or nematicide were being treated specifically for *T. tabaci* (Garthwaite et al., 1997, Garthwaite et al., 2003).

Despite this increase in insecticide use, in most cases, the level of control attained by employing traditional chemical strategies is insufficient to overcome the

economic damage caused by *T. tabaci* (Mayer et al., 1987, Gupta et al., 1990, Fournier et al., 1994, Shelton, 1995, Theunissen and Schelling, 1997, Lewis, 1997a, Shelton et al., 1998). This is not necessarily because the thrips are tolerant to the chemical compounds used (Lewis, 1997a), although that is a growing concern for many farmers (Martin et al., 2003, Allen et al., 2005), but because their biology and behaviour allows them to avoid contact with pesticides and because thrips populations can quickly recover from any losses that do occur.

However, the lack of efficacy of insecticides for the control of *T. tabaci* is a widespread problem in Europe and North America (Bocak, 1993, Hoffmann et al., 1995, Liu, 2003). Recent research has been undertaken in the UK, due to increasing numbers of reports of the low efficacy of pyrethroid insecticides for the control of *T. tabaci*. This has revealed extensive and serious resistance in the majority of UK populations sampled to the key insecticide Deltamethrin (DEFRA, 2007a)**.** The combination of the cryptic nature of *T. tabaci* and its increasing resistance to the relatively small arsenal of available pesticides means that more efficient pesticidal control strategies or indeed an alternative to pesticidal control is sorely needed.

Recent research in Europe and North America has concentrated on one of two themes: identifying new or alternative control methods for *T. tabaci* that do not wholly rely upon control by pesticides; and understanding the biology and behaviour of *T. tabaci* so that any chosen control method can be targeted more efficiently against the pest. This PhD project combines aspects of both of these themes in order to improve our knowledge of, and ability to control, *T. tabaci* outbreaks on UK salad onion and leek crops. At this time very little research has been done on *T. tabaci* in the UK and almost none on its role as a pest of salad onion. Although investigations on populations in other geographical locations continue to expand our knowledge of *T. tabaci* in general, the resultant information is not always directly relevant to the understanding of UK populations or the particular situations in which *T. tabaci* becomes a problem on UK *Allium* crops.

Biology and behaviour

Classification and identification

Thrips, known colloquially in Britain as 'Thunderflies' or 'Stormflies' are a group of generally small and sometimes tiny insects. The order Thysanoptera (Table 1.1) contains over 5000 described species worldwide and these display an extraordinarily diverse range of life histories and specialisations. There are two sub-orders of thrips, the Terebrantia, which contains the majority of described species, and the Tubulifera which contains only a single family.

Table 1.1 The classification of *Thrips tabaci*

Order	**Sub-order**	**Family**	**Sub-family**	**Tribe**
Thysanoptera	Terebrantia	Thripidae	Thripinae	Thripini

A typical Terebrantian of temperate regions, *T. tabaci* is a small insect whose larvae range from around 0.5 mm in length to around 1.2 mm in length and whose adults rarely exceed 2 mm. *Thrips tabaci* larvae exhibit very little pigmentation and often appear clear or yellowish. Adult colouring ranges from dark yellow to almost black; male adults are smaller and lighter in colour than females. Larvae may sometimes appear to have a dark line running down their backs, but closer inspection reveals this to be plant material visible in the gut. A study by Murai and Toda (2001) has indicated that the size and pigmentation of adult *T. tabaci* differs significantly between different populations and may be determined further by the environmental conditions in which the thrips are raised. Darker pigmentation and larger body size may be an indication that the thrips experienced a low average temperature during its development.

Reproduction and development

The life stages exhibited by *T. tabaci* are typical of the Terebrantian Thysanoptera. There are four immature stages before adulthood, two of which are active and two of which are inactive. The two active immature stages are termed

larva 1 and larva 2 and the inactive stages, pre-pupa and pupa (Milne and Walter, 1998b).

The two active larval stages ingest all the food required by the thrips for development to the adult stage (Lewis, 1973b). Stage 1 larvae are extremely small, around 0.5 mm in length, and begin to feed very quickly after hatching. The larval diet for both active feeding stages is primarily plant juices, extracted via probing of the leaf surface with piercing and sucking mouthparts and the removal of cell contents. As a result, larvae begin to cause visible plant damage almost immediately after emergence (Lewis, 1973b).

In some situations *T. tabaci* larvae may supplement their diet by feeding upon the eggs of mites, though this is far more common in second stage larvae than the first (Milne and Walter, 1998b). It is unlikely that predation of mite eggs would in many cases significantly reduce time spent feeding upon the plant and indeed Milne and Walter (1998) concluded that it was not a key aspect of *T. tabaci* ecology and merely a result of opportunistic feeding; moreover they questioned whether first stage larvae could complete development to the second stage on a predatory diet. First stage larvae feed constantly from a few minutes after their emergence until they have reached a size that is roughly twice their original length, approximately 1 mm.

In the USA, Edelson and Magaro (1988) identified a direct relationship between the temperature experienced by *T. tabaci* during their development and the time the thrips took to progress through each of their life stages. This was not a new approach since the link between development and temperature had already been investigated by MacGill (1927, 1936), by Harris *et al.* (1936), by Lall and Singh (1968) and also subsequently by Murai (2000). However, Harris *et al.* and Lall and Singh identified only the overall development times from egg to adult at a constant temperature of 30^{o}C (11.2 days) and a mean temperature of 30.8^{o}C (13.9 days) respectively and MacGill addressed temperature as a factor whilst investigating mortality rates of larvae as a result of changing humidity. Although Edelson and Magaro did not look at the larval stages separately, they identified a lower threshold for development of 11.5^{o}C and a trend of faster development with increasing temperature. This study has provided the basis for thrips pest forecasting using day-degree calculations (Collier et al., 2007, Martens and Plovie, 2007). Recently, however, there has been some question about the accuracy, or at the very least, the transferability of their results to other thrips populations (Collier et al., 2007). These

studies and the relationship between temperature and *T. tabaci* development are discussed in greater detail in Chapter 3.

Once the first stage larvae are approximately 1 mm long, they seek out a sheltered area of the leaf to undergo the moulting process. Newly-emerged second stage larvae are generally a little smaller than final first stage larvae, but they go on to feed until they have reached the size of the eventual adult. Following the second larval stage, the thrips move into a two stage period of inactivity, which depending upon the host plant and conditions, usually takes place in the surrounding soil (Lewis, 1973b). The first of these two stages is called the pre-pupa. At this point, wing buds are visible on the immature thrips, which is almost completely immobile, having ceased feeding and excreting completely. The pre-pupa eventually moults into the final immature stage, the pupa, which is totally immobile. Once the thrips has developed fully inside its pupal case, the adult emerges.

Reproduction in *T. tabaci* is predominantly parthenogenetic in UK populations, especially in the warmer environs of greenhouses where males are rarely seen at all (Morison, 1957). Some males are seen in field populations but they are rare and the sex ratios of most populations appear to be heavily balanced in favour of females. This is not an unusual occurrence since in Hawaii the sex ratio of *T. tabaci* has been recorded as 1 male to every 1000 females, and in the Sudan, an even more extreme 1 male to every 3000 females (Lewis, 1973b).van Rijn et al. (1995) found that unmated *T. tabaci* females from a population in the Netherlands produced no male offspring at all compounding the evidence that northern European populations of this species may be thelytokous. Terebrantian females, including those of the species *T. tabaci* have an unusual and unique method for the laying of their eggs. Their ovipositors are sharp and saw-like and are used to cut into the surface of the leaf; eggs are then laid inside the leaf surface with only a small area projecting above it. This provides the egg with a high level of protection from both predators and desiccation and makes *T. tabaci* eggs very difficult to locate.

Populations

Thrips tabaci populations thrive in warm and fairly dry conditions, which not only promote fast larval development but are ideal for flight, the primary means by which the thrips migrate between hosts (Harding, 1961, Kirk, 1997, Lewis, 1997b, Lewis, 1997c).

Murai and Toda (2001) collected *T. tabaci* from two different populations in Northern Japan and discovered significant differences between populations in the size and pigmentation of individual thrips, indicating that they were two distinct strains. Further studies by Brunner *et al.* (2004) into host-associated genetic differentiation in *T. tabaci* revealed a hitherto unimagined series of genetic differences within populations collected from across Europe. Indeed these differences were so pronounced, and the populations and their ecologies so distinct, that Brunner *et al.* (2004) concluded that they were a 'complex of cryptic subspecies'. If distinct populations with such clear differences can occur in relatively close proximity in mainland Europe, then it follows that populations from Europe and America may also exhibit distinct differences, and without further investigation it would seem unwise to directly infer information about one population from the other. A detailed understanding of how temperature affects the development of UK *T. tabaci* populations is lacking and furthermore its importance within the range of factors that could influence development is not as yet fully understood. Many questions as to the nature of British *T. tabaci* populations vis-à-vis their potential for growth, how many generations they produce in a season, their composition etc. remain unanswered at this time.

Behaviour

Temperature also influences the behaviour of *T. tabaci*, and in particular the choice of areas of the plant upon which to feed (Theunissen and Legutowska, 1991b). It is well known that *T. tabaci* adults and larvae have differing preferences for certain areas of a plant and in the case of leek and salad onion, this has major implications for ease of control (Theunissen and Legutowska, 1991b, Sites et al., 1992, Milne and Walter, 1998a). The cryptic behaviour of *T. tabaci* is the main reason why insecticide applications are so unsuccessful, as it is very difficult to target the chemicals. An increased understanding of the behavioural processes underlying the intra-plant distribution of thrips would therefore be highly useful in increasing the efficacy of foliar sprays, particularly if a position of maximum vulnerability could be identified.

Sites et al. (1992) investigated the possibility that the intra-plant distribution of the thrips changed with time of day and was therefore affected by one or more of the physical factors which change with it (temperature, light intensity, humidity etc.).

Thrips in general are known to be particularly vulnerable to desiccation and so hiding at the centre of the plant, where the microclimate is likely to be the most humid, may be a behavioural adaptation. This behaviour also reduces encounters with predators and parasitoids. Sites *et al.* (1992) were able to show that, in midsummer, there was a tendency for thrips to aggregate towards the apical half of leaves in the early afternoon, when temperatures were highest. This may reflect dispersion behaviour, as the thrips climb to higher parts of the host plant to initiate flight. It also highlights the importance of understanding the diel periodicity of the intra-plant distribution of *T. tabaci* for the timing of insecticide sprays.

Dispersal

Thrips tabaci is a comparatively active thrips species with highly nimble larvae and fast moving adults (Lewis, 1973b). Dispersal between plants and between crops is via flight. Thrips in general are poor fliers and *T. tabaci* is no exception (Lewis, 1997c). Long fringed wings that are normally held tight against the body along the dorsal line are extended and beaten, allowing the thrips to lift off from the plant surface. It is thought that thrips have little control of the direction or speed of flight unless the day is particularly still. Srinivasan et al. (1981) noted an uneven distribution of *T. tabaci* within onion crops and indicated that aggregations could be due to behavioural or environmental factors and indeed a limited control of flight and a difficulty in making short, controlled, directed dispersal movements may well be a factor in this. Indeed investigations by den Belder et al. (2002) indicated that thrips numbers were lower in onion fields located in complex landscapes. North and Shelton (1986a) identified July-August as a key flight period for *T. tabaci* in New York State. Collier et al. (2007) indicated that similar patterns may exist in UK populations. This data (collected partially as part of this PhD project) shall be discussed in greater depth in Chapter 6.

Overwintering

The overwintering biology of thrips, has been studied fairly extensively in North America and Europe, where it has been demonstrated that in different locations the species overwinters as either adults, larvae or pupae (North and Shelton, 1986c, Chambers and Sites, 1989, Cho et al., 1995, Lacasa et al., 1995, Jenser et al., 2003, Larentzaki et al., 2007). However it has received little attention in

the UK and indeed no work has been done on the overwintering of *T. tabaci*. Understanding the overwintering habits of this pest and the conditions and factors influencing its colonisation of new hosts in the spring is fundamentally important to any strategy employed for its control.

Current control strategies

Biological control of T. tabaci

Thrips species are attacked by several groups of generalist predators including Coleoptera, Diptera, Neuroptera, Hemiptera and Acari (Waterhouse and Norris, 1989, Kirk, 1997). Potential predators from all of these groups are present in the UK and seem likely to be able to control *T. tabaci* populations to some extent. However Theunissen and Schelling (1996) found very low numbers of natural enemies in leek crops in the Netherlands and so care must be taken when considering the potential effectiveness of such a resource.

There has been some success in controlling thrips species with predators, though mainly in protected crop environments and using augmentative or inundative techniques (Ramakers, 1980, Trjapitzin, 1995, Deligeorgidis et al., 2005). Some hymenopteran parasitoids (the main parasitoids of thrips (Kirk, 1997)) have also been investigated for use as control agents and these too have met with some limited success, even in field experiments (Waterhouse and Norris, 1989). However inundative release of predators under field conditions was shown to be insufficient to control *T. tabaci* populations by Shelton et al. (1998). Nematodes are also known to parasitize thrips species, although little practical work has been done at this time (Loomans et al., 1997, Arthur and Heinz, 2003). Investigations into the use of nematodes for the control of *F. occidentalis* have demonstrated potential, though the results have not been universally successful (Chyzik et al., 1996, Ebssa et al., 2001, Ebssa et al., 2004). Entomopathogenic nematodes were investigated as a potential biological control agent in a recent project in the UK (DEFRA, 2007b). This study showed that the nematodes will survive for several days in droplets of water trapped within the leek sheath. However, it is not known whether such nematodes are able to parasitize nearby thrips or whether they remain 'trapped' in the droplets. Thus there is the potential for further work in this area.

The use of entomopathogenic fungi is another potential method of control (Butt and Brownbridge, 1997). Early work by Samson et al. (1979) and Carl (1975) showed that various species of Entomophthorales could be isolated from thrips populations. However, fungal pathogens have only rarely been deployed against thrips outside of controlled glasshouse conditions, and therefore much more work is required before their potential in field crops is fully understood. Maniania et al. (2003) demonstrated that field plots treated with fungal pathogens exhibited reduction in thrips feeding damage similar to the control gained via insecticidal treatments and in some cases bulb yield was higher in fungal treated plots. However natural enemy levels were also higher in these plots and so the exact extent to which the fungus was controlling the thrips population is questionable.

It has been demonstrated that varietal resistance to *T. tabaci* exists in some cultivars of onion (Coudriet et al., 1979, Shelton et al., 1998, Hamilton et al., 1999), and as such choice of such varieties is an option for growers looking to improve control. Indeed Shelton et al. (1998) found that use of some resistant varieties was more effective in control of *T. tabaci* populations than application of insecticides. The range of commercially available cultivars is large though, and there has been no comprehensive survey of resistance meaning that growers must generally rely upon experience to identify cultivars that not only grow well in the particular conditions of the grower's location but also provide good resistance to *T. tabaci*.

Thrips behaviour has major implications for the effectiveness of biocontrol strategies, just as it does for chemical control strategies. Thrips can exhibit effective defences against predators and may only be vulnerable to certain predators when they are at specific life stages (Ramakers, 1980, Bakker and Sabelis, 1989). Moreover, the cryptic behaviour of thrips may also limit the effectiveness of fungal and nematode control methods.

Cultural control of T. tabaci

Cultural control of *T. tabaci* is an area that appears to hold much potential. Intercropping has been investigated as a method of control in UK onion crops and was found to reduce infestations by up to 50% (Uvah and Coaker, 1984). In Egypt, intercropping with tomato plants in onion and garlic plantations reduced thrips numbers by around 80%, though some yield loss was noticed due to competition with the intercrop (Afifi and Haydar, 1990). Undersowing has shown excellent

potential for the reduction of thrips populations, though again, competition between the crop and companion plants may limit its usefulness (Theunissen and Schelling, 1996). However, intercropped leeks did themselves appear to suffer less damage than monocropped leeks, giving rise to the possibility that inter-specific competition in some way either hardens the plant to attack and therefore reduces the appearance of feeding symptoms or reduces colonisation by the pest (Theunissen and Schelling, 1997). However a review by Finch & Collier (2000) cast doubt on the traditional explanations put forward for the advantages gained through intercropping primarily as none of those hypotheses had been used to produce a general theory of host plant selection as none of them included the influence of visual stimuli in the pests choice of host plant. Instead Finch & Collier put forward their own complete theory of host plant selection by pests which includes cues from volatile plant chemicals, visual stimuli and non-volatile plant chemicals. This theory, termed the 'appropriate/inappropriate landings' theory, would certainly explain why the undersowing and intercropping studies on thrips appeared to be so successful at reducing pest damage.

Harding (1961) showed that the damage caused by thrips populations declined after periods of precipitation. Kirk (1997) stated that periods of heavy rain can reduce thrips populations, because individuals are washed off plant surfaces onto the soil. Investigations by Wardle (1927) indicated that it may be the effect of water on the soil surface and not directly on the pest that may be beneficial to the farmer. Irrigation to reduce thrips populations is already employed by growers in many countries (including to a certain extent by this project's industrial partner, Specialty Produce), and there appears to be a consensus, based upon the experience of these growers, that this is effective.

At this time few studies have been made into the effectiveness of utilising irrigation for the control of thrips species, and very few in the United Kingdom. Wardle (1927) investigated the relationship between the severity of infestation and water applied, but could find no direct relationship between thrips mortality and irrigation. He concluded that caking of the surface soil by applying excessive amounts of water to the crop might prove effective in preventing soil dwelling pupae from successfully emerging successfully. Palumbo *et al.* (2002) investigated the effects of overhead sprinkler irrigation on Western Flower Thrips, *Frankliniella occidentalis* (Thysanoptera, Thripidae), and found that, under certain circumstances,

suppression of thrips populations by up to 50% could be achieved. This was compared unfavourably with the higher levels of control attainable through chemical control strategies.

Irrigation was also investigated as a means of thrips control by Kannan and Mohamed (2001), in this case for the control of *T. tabaci* on onions in the El Rahad scheme in Sudan. Irrigation frequency had a significant effect upon *T. tabaci* populations in the region. Further work to determine the effectiveness of employing irrigation as a means of *T. tabaci* population control in the United Kingdom, and an economic comparison with insecticide strategies, would seem to be most important.

Other cultural techniques such as the use of reflective mulches and crop covers, have been investigated, with encouraging results (Lu, 1990, Benoit and Ceustermans, 1998). Such techniques can, however, be not only costly, but difficult and time-consuming to implement on a large scale.

Project Aims

This summary of the literature has shown that there are several important gaps in our understanding of the biology and behaviour of *Thrips tabaci* in relation to its role as a pest of horticultural crops in the UK. The overall aim of this project was to try and fill some of those gaps in knowledge, and its specific objectives were to:

1. Examine whether the forecasting model developed for *Thrips tabaci* populations in other countries is applicable to UK populations, and if not, suggest alternative systems (Chapter 3)

2. Investigate the effect of temperature and of leaf quality on the behaviour of *Thrips tabaci*, in order to develop the knowledge required to identify and explain windows of vulnerability, which might increase the efficacy of current or novel control methods within an integrated pest management strategy (Chapter 4)

3. Investigate whether there are changes in the intra-plant distribution of *Thrips tabaci* during the day to identify periods of vulnerability to foliar sprays and to test the efficacy of irrigation control programmes based on these results (Chapter 5)

4. Carry out a long term survey of *Thrips tabaci* populations in the field to obtain more information about their population dynamics in the UK, including flight times, overwintering strategies and population development and discuss how all of these relate to our ability to forecast the development of *T. tabaci* infestations effectively (Chapter 6)

Chapter 2: General Techniques

This chapter describes the general techniques employed in this project.

Maintaining a field population of Thrips tabaci

Throughout the life of the project, a field population of *T. tabaci* was maintained in sequentially-planted plots (of a minimum size 16 m x 16 m) of leek (cv. Shelton). A fresh plot was sown or planted in April-May each year in order to provide a constant uninterrupted habitat for *T. tabaci* on site in Wellesbourne. This field population not only provided a site to monitor population development, overwintering and flight activity, but also acted as a source of thrips for natural invasion of other plots, both of leek and of salad onion, that were subjected to more specific treatments or monitoring.

Insect rearing

To ensure a regular supply of *Thrips tabaci* of all life stages for experiments, it was necessary to devise a method for rearing them in controlled environments rather than relying wholly upon field-sourced material.

It was important that the artificially reared *T. tabaci* population was large enough to supply experiments and that it remained healthy. Initially, therefore, populations were established in small greenhouses at Warwick HRI, Wellesbourne. Leek (*Allium ampeloprasum*) and salad onion (*Allium cepa*) plants were grown in Hassy 308 seed trays until they were approximately 15 cm in height. They were then transferred into 16 cm pots at a density of 3 plants per pot. These pots were then packed tightly onto benches within the greenhouses and were infested with *T. tabaci*. Inspections of greenhouse plant material were conducted regularly to monitor the health and development of the thrips population and to scrutinise the condition of the host plants. Fresh plant material was added at intervals and older plants were removed. Fresh thrips were brought in from the field when necessary.

For certain experiments, it was important that the thrips were reared under specific environmental conditions in incubators. The thrips were reared in clear plastic containers (300 ml) closed with fine mesh netting. These were placed in trays in the incubator. A piece of filter paper was placed in the bottom of each container

and infested plant material (leek or salad onion foliage) was placed on top of the filter paper. This rearing method provided a consistent supply of thrips and it was easy to find each life stage within the container. The pre-pupae and pupae were usually found beneath the filter paper at the bottom of the container.

Sampling

During the project it was necessary to assess the size, structure and impact of *T. tabaci* populations on a variety of crop plants and in a variety of locations, so it was important to develop consistent sampling methods.

The cryptic nature and small size of *T. tabaci* makes *in situ* assessments of population size inaccurate, if not impossible. Thus most sampling has been destructive. Unless a specific area of the crop was of interest, or the experimental parameters required the removal of specific plants (within a transect for example), the plants were chosen at random. If the plants were assessed immediately then they were taken to the laboratory in plastic boxes. If, however, they were to be assessed later, they were placed in plastic bags and stored in the dark at approximately 5^{o}C.

In the laboratory, each plant was assessed to estimate the extent of damage to the leaf surface caused by thrips feeding activities. This is the yardstick by which commercial crops are assessed for their marketability. For simplicity, and to ensure consistency, an estimate was made of the overall percentage of each leaf damaged by thrips, to the nearest 10%.

The leaves were then removed from the plant one by one and the numbers of adult and larval *T. tabaci* were recorded using a hand lens and binocular microscope. Because *T. tabaci* females implant their eggs into the leaf surface it was impossible to record egg numbers accurately. Numbers of dead *T. tabaci* and potential predators and parasitoids were also recorded, as was the size, colour and physical appearance of live *T. tabaci* specimens.

Chapter 3: The effect of temperature on the development of *Thrips tabaci*

3.1.0 Introduction

The effect of temperature on the development of *Thrips tabaci* has been investigated several times (MacGill, 1927, MacGill, 1936, Lall and Singh, 1968, Quartey, 1982, Edelson and Magaro, 1988, Murai, 2000). Understanding this relationship may well be key to the development of a robust and reliable forecasting system. The rate at which insects develop has a direct relationship with temperature (Sharpe and DeMichele, 1977). Development rates increase with temperature but there is an upper temperature limit, above which the animal can no longer develop/survive, and a lower limit, the development threshold, below which development ceases. Towards these upper and lower extremes, the relationship between development rate and temperature is non-linear, but in the middle range of temperatures, the curve is generally linear (Sharpe and DeMichele, 1977). The theoretical development threshold is usually calculated from this linear portion of the development rate curve and this is used to estimate the day-degree requirement of particular development stages (Lamb, 1992). The derived development threshold is theoretical and is not necessarily the true development threshold (Collier and Finch, 1985).

Day-degree or accumulated temperature forecasting systems have been used extensively for several pest insect species, particularly when considering specific events such as the start of adult emergence in the spring following winter diapause or the start of egg laying etc. (Finch et al., 1996). However the utility of such forecasts, based on the assumption that the relationship between development rate and temperature is linear, has been questioned (Lamb, 1992, Finch et al., 1996, Briere et al., 1999, Bergant and Trdan, 2006) and indeed Briere et al. (1999) stated that linear models that do not take into account non-linearity at higher and lower temperatures "produce biased results". MacGill (1927) stated that the relationship between development rate and temperature in *T. tabaci* is, as a whole, non-linear.

Collier et al. (2007) demonstrated, using data gathered during this project, together with data from another study, that the widely accepted day-degree model for *T. tabaci* development (van Rijn et al., 1995, Villeneuve et al., 1996, Bergant et al., 2005, Martens and Plovie, 2007), based on the study by Edelson & Magaro (1988),

did not predict population trends on UK crops accurately. Edelson & Magaro (1988) based their day degree calculations on a development threshold obtained via linear regression (as did Murai (2000)).

The aim of this investigation was to address some of the perceived shortcomings of previous studies. The study follows the basic experimental processes used by Edelson & Magaro (1988) and applies them to a UK population. The aims of this were to increase our understanding of the relationship between development and temperature in *T. tabaci* and to identify a possible alternative forecasting method that might be more accurate for UK populations.

3.2.0 Materials and methods

The basic design of the experiment followed, as far as possible, the procedure used by Edelson and Magaro (1988) in their study on the development of *T. tabaci* as a function of temperature.

3.2.1 Thrips

A field population of *Thrips tabaci* was established in 2003 at Warwick HRI, Wellesbourne, through natural infestation. The population was maintained on an insecticide-free plot of leek (cv Shelton). Males appear to be extremely rare in this population although no exact female to male ratio is known. *Thrips tabaci* from this population were removed to the laboratory and reared in plastic containers in incubators maintained at 18.5^{o}C with a photoperiod of L16:D8. Further information on thrips rearing can be found in Chapter 2.

3.2.2 Experimental

Newly-emerged adults were taken from the population established in the incubator and were placed individually in 50 ml plastic containers together with a section of leek leaf and a piece of filter paper to remove any excess moisture. In total, 160 adult thrips were selected in this way and 20 were assigned to each of the 8 different temperature treatments used in the study: 10, 12.5, 15, 17.5, 20, 22.5, 25^{o}C and a treatment carried out in a greenhouse with variable temperatures. Each of the thrips to be studied at a constant temperature was placed in an incubator at that temperature with a photoperiod of L16:D8. The thrips exposed to variable temperatures were placed in a greenhouse at Warwick HRI, Wellesbourne (August 2008) where the temperature in a typical rearing container was monitored with a Rotronic Hygrolog logger.

The sections of leek leaf in each container were removed daily and held at the same temperature as the adult thrips. The date of their exposure to the adults was noted. This leaf material was then monitored daily between 9am and 11am to ascertain both the pre-oviposition period of the adult (the time period between its emergence as an adult and first oviposition) and the egg incubation period.

Freshly-emerged larvae were removed to their own individual 50 ml container and provided with fresh leaf material. They were monitored daily between

9am and 11am for pupation and then adult emergence. Fresh leaf material was provided when necessary. In total 20 individuals were monitored in this manner for each temperature treatment.

Information was therefore gathered, for each adult thrips which emerged successfully, on: the pre-oviposition period of their parent, their own egg incubation period, larval development period and pupal development period. Leek foliage which had not been exposed to thrips was also held in the incubator at 20^{o}C as a control, to ensure that no contamination of the host material had occurred.

3.2.3 Analysis

Data for all life stages and for the overall development time were investigated using both linear and non-linear descriptors. Theoretical development thresholds for each life stage and the overall life cycle were obtained by fitting logistic and Gompertz curves to the available data, and also by extrapolation via linear regression. The results were compared by percentage fit.

All data were analysed using Genstat for Windows (VSN International Ltd.) and Microsoft Excel (Microsoft Corporation).

3.3.0 Results

No thrips emerged from the leek material that had not been exposed to adult thrips in the control cages, indicating that no contamination of the host plant material had occurred outside the experiment.

No recordable development was observed at 10^{o}C, the adults survived just as well at this temperature as at the others; however no larvae emerged from the leaf material exposed to them. Leaf material exposed to adults at 10^{o}C which was then transferred to higher temperatures also produced no larvae. Adults were kept at 10^{o}C for 30 days and then discarded.

The temperatures (in ^{o}C) recorded for the variable temperature experiment in the greenhouse were:

Mean	Maximum	Minimum
16.1^{o}C	31.8^{o}C	5.4^{o}C

Average development times for each of the temperature treatments studied are presented in Table 3.1. As can be seen from the table, a great deal of variability in development times was observed between individuals across the life stages.

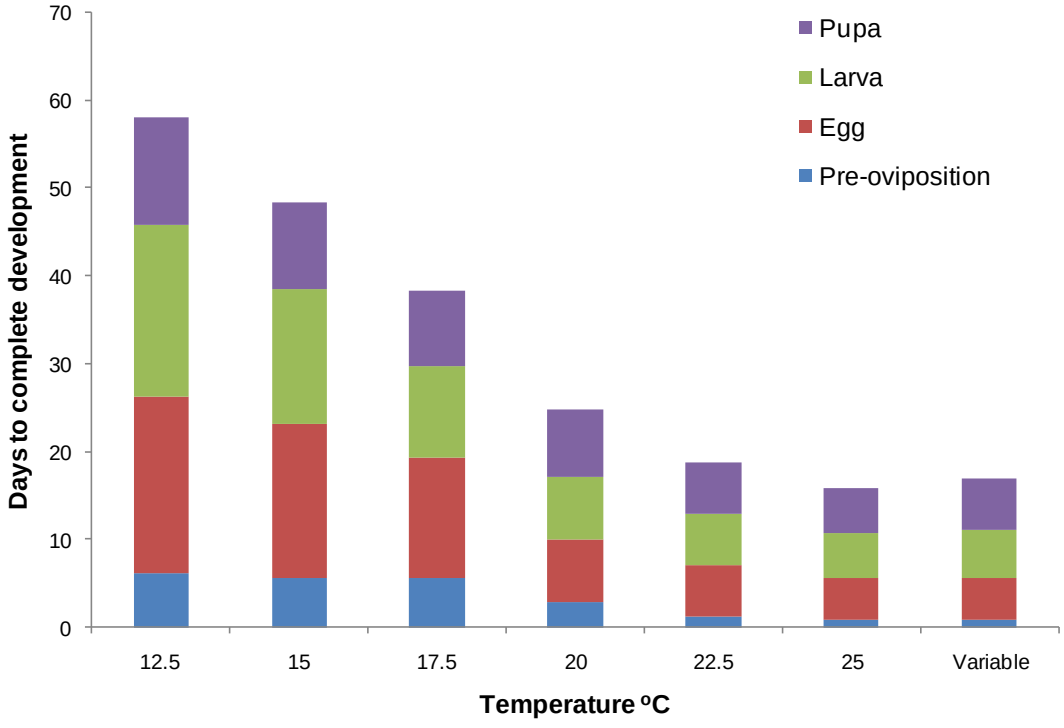
Table 3.1 Average development times in days for each of the 8 temperature treatments. The maximum and minimum numbers of days taken by individual thrips to complete each life stage at each of the temperatures are also shown.

Life Stage	**Temperature ^{o}C**							
	10	**12.5**	**15**	**17.5**	**20**	**22.5**	**25**	**Variable**
Pre-Ovi	-	6.3	5.6	5.6	2.95	1.3	1	1
Max - Min	-	8 - 5	7 - 5	7 - 5	4 - 2	2 - 1	1 - 1	1 - 1
Egg	-	20.05	17.7	13.7	7.05	5.8	4.65	4.6
Max - Min	-	21 - 19	19 - 17	15 - 13	8 - 6	7 - 4	6 - 4	6 - 4
Larva	-	19.6	15.25	10.45	7.2	5.85	5.15	5.5
Max - Min	-	22 - 18	17 - 14	12 - 9	8 - 7	7 - 5	6 - 4	6 - 5
Pupa	-	12.1	9.85	8.65	7.65	5.95	5.15	5.9
Max - Min	-	13 - 11	12 - 9	10 - 7	9 - 7	7 - 5	6 - 4	7 - 5
Overall	-	51.75	42.8	32.8	21.9	17.6	14.95	16

All four individual life stages examined exhibited an influence of temperature on their duration, and this is reflected in the times for overall development seen in Table

3.1. The variation in the duration of the individual life stages over temperature was, however, not consistent. The duration of the pupal stage was least affected by temperature, the average length of the pupal stage at 12.5°C being just over twice the average length at 25°C, whereas the differences in the duration of the other life stages over this temperature range were approximately four times or more. The duration of the pre-oviposition period did not lengthen significantly below 17.5°C, although, as discussed above, oviposition may have ceased entirely by 10°C, whereas the duration of the other life stages continued to lengthen over this temperature range. Figure 3.1 displays these trends graphically and shows the mean overall development times and the contribution of each life stage at the different temperatures.

Figure 3.1 Mean overall development time (in days) and the constituent durations of each life stage for each of the different temperature treatments.



Individuals in the variable temperature experiment developed faster than would have been expected, given the mean temperature (16.1°C) that they experienced.

3.3.1 Development thresholds and development rates

To estimate the development threshold of the thrips population investigated in this study, the data for all life stages and for the overall development time were analysed using both linear and non-linear descriptors. Development thresholds for each of the life stages, and for overall development, calculated from these descriptors are shown in Tables 3.2 to 3.6 as are the percentage fits, by which they can be compared. The following shortened descriptions are used in each table:

- Logistic – A non-linear regression
- Gompertz – An alternative non-linear regression
- Linear – A linear regression whose slope was calculated using all available temperature data
- Linear 3 – A linear regression whose slope was calculated from data collected at 20, 22.5 and 25^{o}C
- SE – Standard error of the calculated development threshold
- LINT – Lower confidence interval
- UINT – Upper confidence interval
- DNF – The regression did not fit

Derived development thresholds for the non-linear descriptors are higher than the linear descriptors for pre-oviposition (Table 3.2). This is to be expected as the non-linear curve flattens out towards the lower extremes. A similar pattern of higher development thresholds being estimated from non-linear regressions in comparison with the linear ones is seen in the other tables, although the standard errors on the linear descriptors are lower for several of the life stages.

Table 3.2 **Pre-oviposition:** Estimated development thresholds and the percentage fit of each of the different descriptors for the pre-oviposition stage.

Regression type	Derived development threshold (^{o}C)	SE	LINT	UINT	% Fit
Logistic	18.59	0.25	18.10	19.07	91.9
Gompertz	18.53	0.22	18.09	18.97	91.9
Linear	12.51	0.39	11.75	13.28	76.2
Linear 3	16.81	0.49	15.84	17.79	72.2

Table 3.3 demonstrates the closeness of the derived development thresholds between the two non-linear regression analyses and the two linear regression analyses respectively, which is a general pattern across the life stages.

Table 3.3 **Egg:** Estimated development thresholds and the percentage fit of each of the different regression types for the egg stage.

Regression type	Derived development threshold (^{o}C)	SE	LINT	UINT	% Fit
Logistic	14.46	0.48	13.52	15.40	91.7
Gompertz	14.37	0.43	13.52	15.23	92.0
Linear	10.54	0.32	9.91	11.18	87.5
Linear 3	10.83	1.23	8.36	13.30	60.7

For the larval stage (Table 3.4), the linear regression analysis calculated from the limited temperature range of 20 – 25^{o}C has a lower percentage fit than any of the other analyses across all life stages.

Table 3.4 **Larva:** Estimated development thresholds and the percentage fit of each of the different regression types for the larval stage.

Regression type	Derived development threshold (^{o}C)	SE	LINT	UINT	% Fit
Logistic	11.92	0.56	10.81	13.02	92.8
Gompertz	11.66	0.50	10.67	12.64	92.8
Linear	9.13	0.29	8.55	9.71	91.5
Linear 3	7.89	1.65	4.59	11.18	57.3

The Gompertz non-linear regression analysis did not fit at all when applied to the pupal life stage independently (Table 3.5) and for this reason it was considered unsuitable as an analytical tool to describe *T. tabaci* development as a function of temperature. Although the standard error and confidence intervals were high for the logistic analysis, the curve did fit the data and to a high accuracy.

Table 3.5 **Pupa:** Estimated development thresholds and the percentage fit of each of the different regression types for the pupal stage.

Regression type	Derived development threshold (^{o}C)	SE	LINT	UINT	% Fit
Logistic	16.54	44.99	-72.54	105.60	86.4
Gompertz	DNF	DNF	DNF	DNF	DNF
Linear	4.00	0.60	2.79	5.20	84.5
Linear 3	9.83	1.24	7.36	12.30	64.4

Table 3.6 **Overall:** Estimated development thresholds and the percentage fit of each of the different regression types for the overall life cycle.

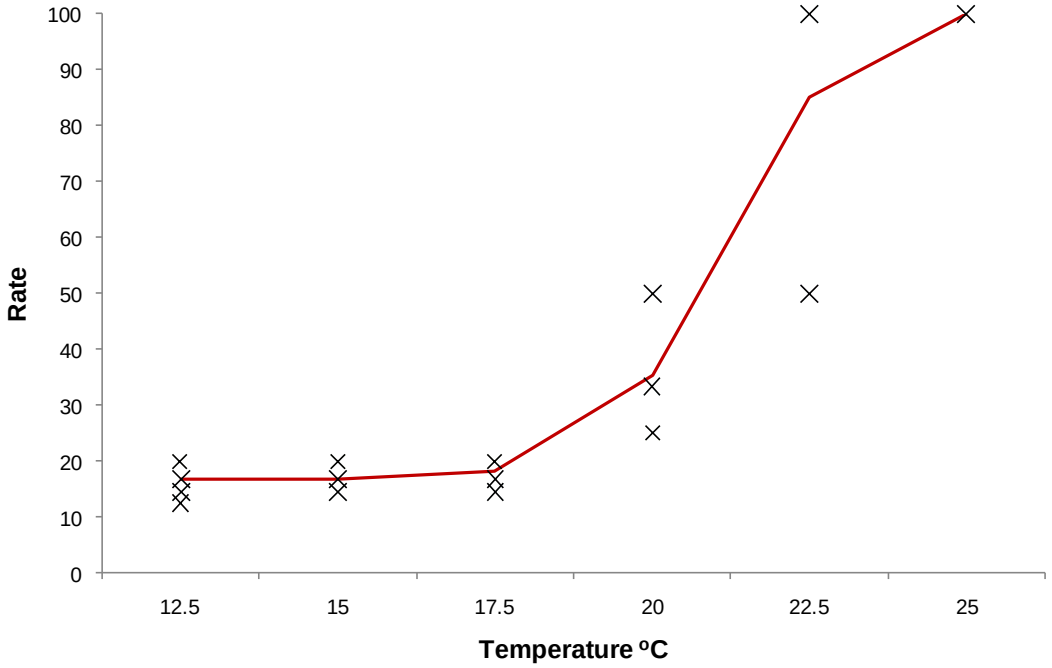
Regression type	Derived development threshold (^{o}C)	SE	LINT	UINT	% Fit
Logistic	12.28	0.31	11.66	12.90	97.6
Gompertz	11.88	0.27	11.33	12.42	97.6
Linear	8.77	0.22	8.33	9.21	95.2
Linear 3	9.28	0.72	7.84	10.72	85.3

The most consistent descriptor and the one that was most accurate in describing each life stage individually, and indeed the overall life cycle (Table 3.6), was the non-linear logistic curve. Linear descriptors were consistently less accurate across all the life stages. The logistic curve fitted has the following equation:

$$A + \frac{C}{\left(1 + EXP\left(-B * (X - M)\right)\right)}$$

In Figures 3.2 to 3.6, the logistic curves estimated for each of the life stages and for the overall life cycle are compared with the recorded rates of development over the entire range of fixed temperatures. Figure 3.2 compares observed development rates for the pre-oviposition life stage with the fitted logistic curve for that life stage.

Figure 3.2 *Thrips tabaci* - observed development rates (percent development per day) and the fitted logistic curve for the pre-oviposition period.



As is clear from Figure 3.2 (and is mirrored in Figures 3.3 to 3.6), there was a general trend for an increase in variability in terms of how the rates differ from each other and how far they depart from the estimated development rate curve as temperatures increase. The reason for this lies in the coarseness of the time intervals used for monitoring development and therefore the increasing influence of minor variations as the overall development time decreases. Figure 3.3 compares observed development rates for the egg stage with the fitted logistic curve for development for that life stage.

Figure 3.3 Observed development rates (percent development per day) and the fitted logistic curve for development of *Thrips tabaci* for the egg stage.

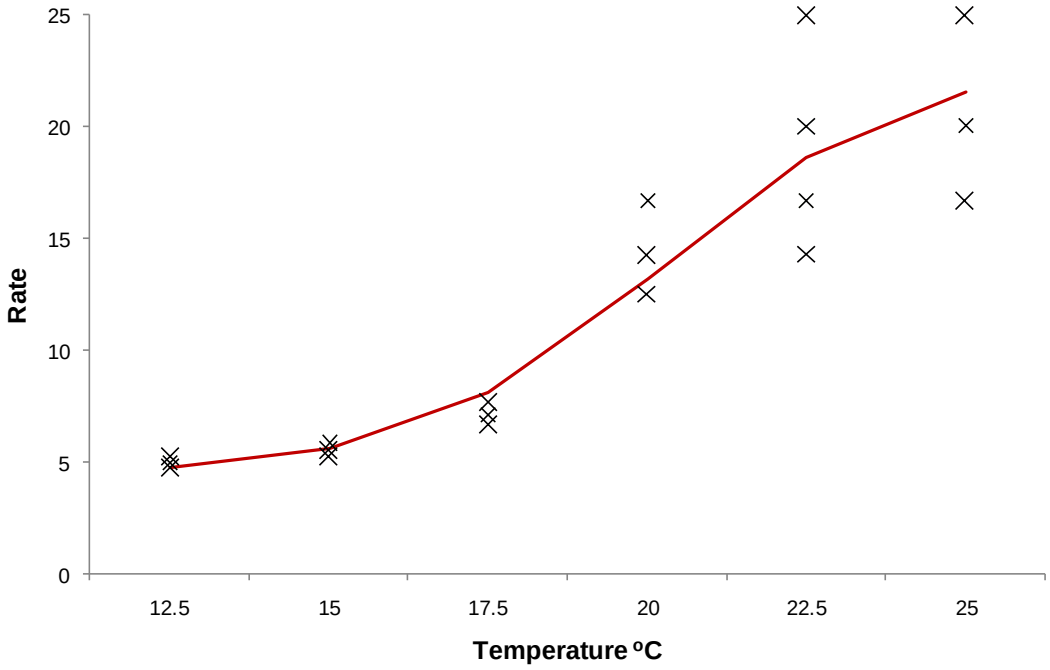


Figure 3.4 compares observed development rates for the larval stage with the fitted logistic curve for development.

Figure 3.4 Observed development rates (percent development per day) and the fitted logistic curve for development of *Thrips tabaci* for the larval stage.

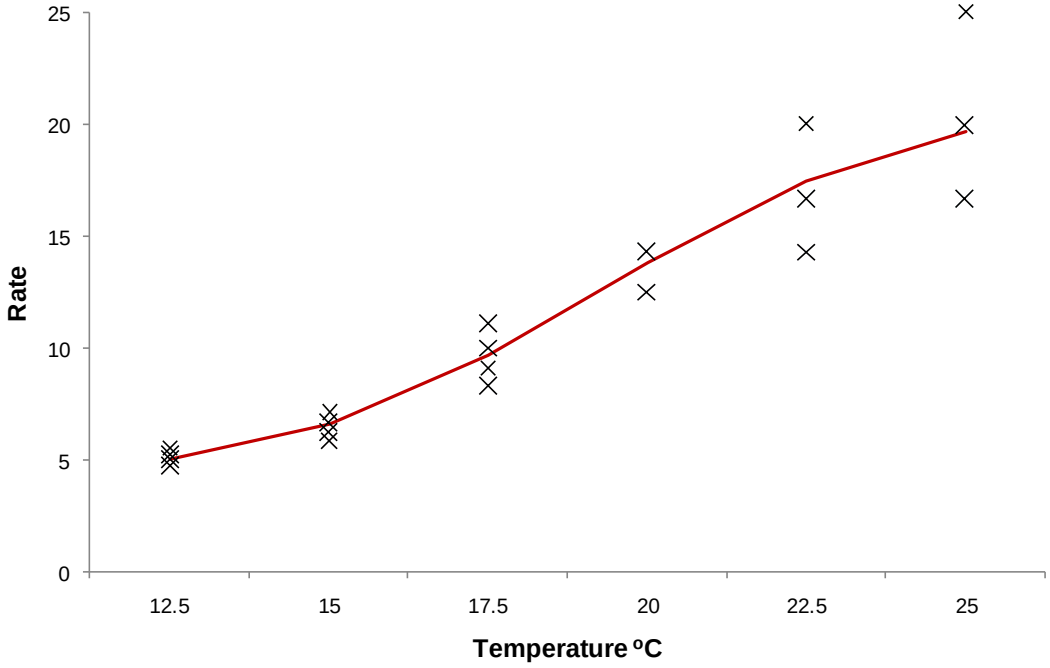


Figure 3.5 compares observed development rates for the pupal stage with the fitted logistic curve for development.

Figure 3.5 Observed development rates (percent development per day) and the fitted logistic curve for development of *Thrips tabaci* for the pupal stage.

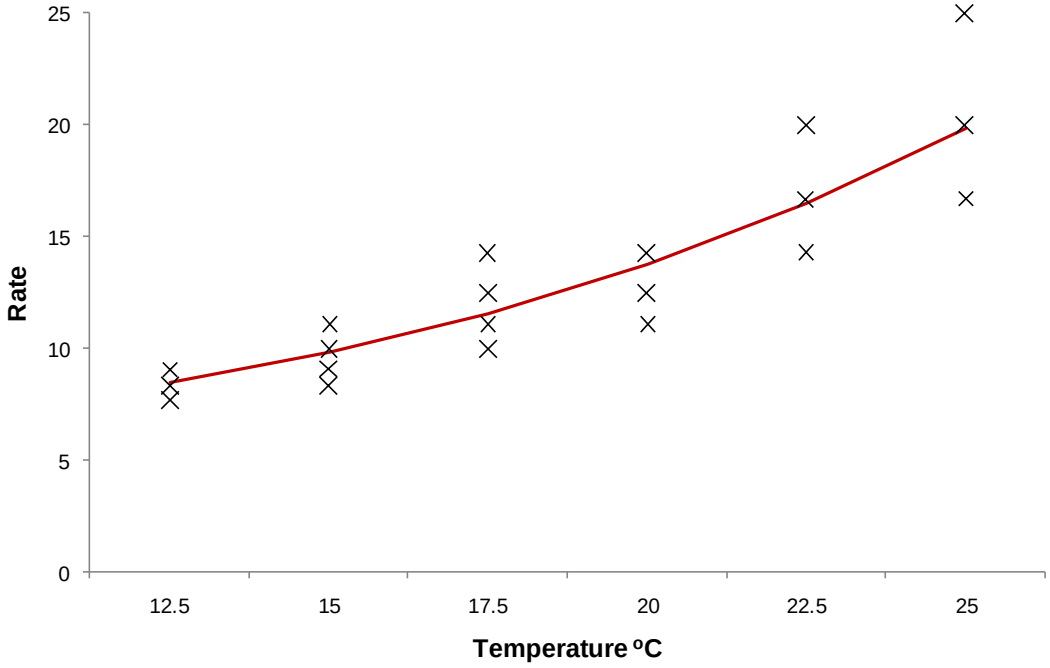
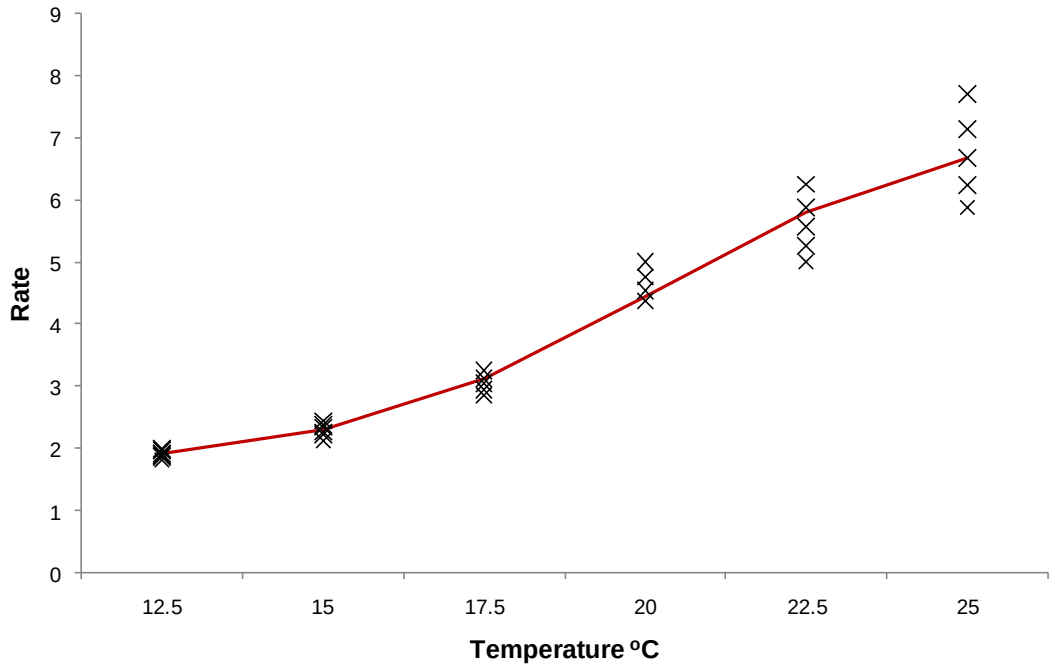


Figure 3.5 shows the greatest deviance from the normal logistic shape and demonstrates that the relationship between development and temperature is not fixed across the life of the insect. Figure 3.6 compares observed development rates for the entire life cycle with the fitted logistic curve.

Figure 3.6 Observed development rates (percent development per day) and the fitted logistic curve for development of *Thrips tabaci*.



The overall development threshold , which is estimated to be 12.28°C, does not differ very greatly from that calculated by Edelson & Magaro (1988), which was 11.5°C. The estimated overall development thresholds for both studies are lower than the thresholds estimated for some of the individual life stages.

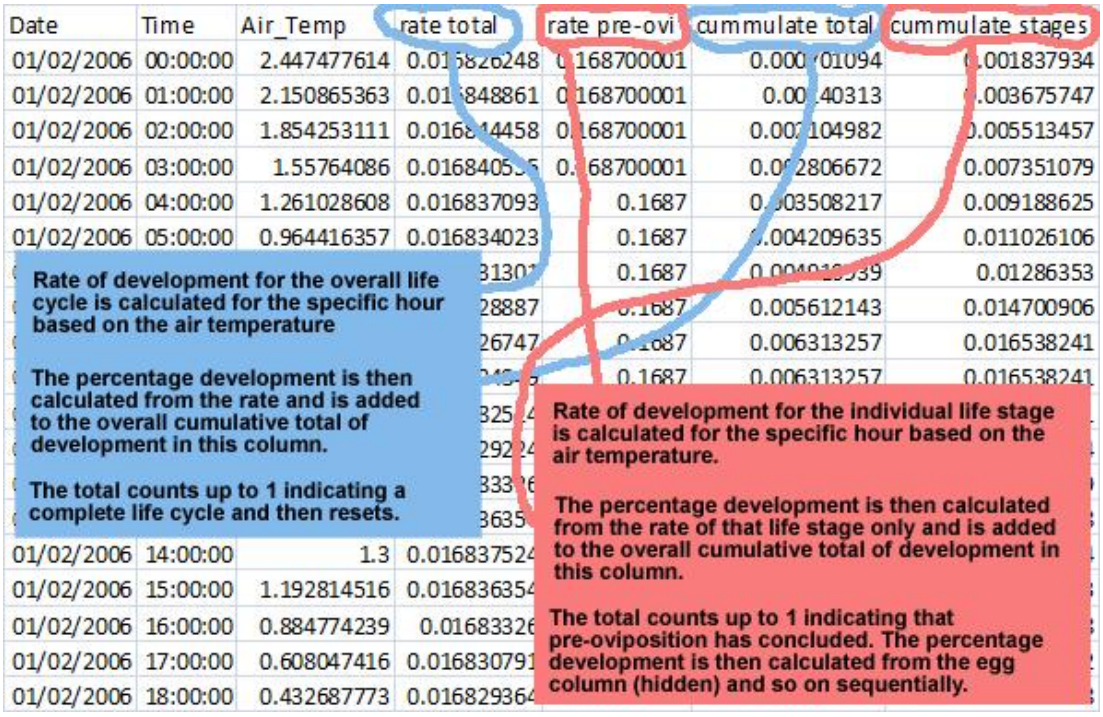
3.3.2 Population forecasting

In order to predict population trends in the field by application of the logistic equations developed in section 3.3.1 it was necessary to work out a system whereby field temperature data could be used to estimate the progression of development over a particular time frame. Field daily temperature data for Warwick HRI, Wellesbourne were converted to 'estimated hourly temperatures' using the modified Parton & Logan (1981) equation developed by Phelps et al. (1993). An Excel spreadsheet was set-up to estimate development of an 'average' thrips based on the corresponding hourly temperature data. Each life stage was addressed individually and sequentially, using its particular development rate, estimated previously. The spreadsheet was used to estimate the percentage of each development stage completed each hour and to calculate a cumulative total. Once a total of 100% had been accumulated for a particular stage, it was assumed that the 'insect' would move into the next stage. Using this approach it was possible to apply 'global'

development thresholds, that would apply to all life stages, by altering the spreadsheet so that it did not accumulate development from periods (hours) during which the temperature was lower than the given threshold. It was possible, therefore, to investigate how application of such a development threshold affected the predictions of thrips development derived from the system.

Figure 3.7 is a screenshot taken from the Excel spreadsheet and illustrates some of its function. Several columns have been hidden in this image in order to reduce clutter.

Figure 3.7 A screenshot taken in Microsoft Excel® showing the spreadsheet by which field population development was estimated.



The following series of graphs illustrate the application of this forecasting method to field temperatures recorded at Warwick HRI, Wellesbourne, over a single year in 2006. Further discussion regarding the other years of the study are in the chapter on field studies, Chapter 6, and the full range of graphs for all years is in the appendix. All estimations of development rates were derived from the logistic curves fitted to the data.

The red line in each graph represents the accumulated development of the thrips population over its entire life cycle addressing each life stage sequentially and taking

into account the estimated development rates for each stage. Between 0 and 1 is the pre-oviposition period, between 1 and 2 is egg development, between 2 and 3 larval development and between 3 and 4 pupal development. Once the series reaches 4 it resets and the next generation is calculated, again beginning from the pre-oviposition period and moving forward. This continues until the end of the year. As the development rates were calculated from sample means, the point at which the series transfers between one life stage and the next is the point at which approximately half of the population would have developed to that point.

To compare this method of forecasting development with one based solely on a single development rate representing the entire life cycle, a second series is presented on each graph, represented by a blue line. This second series re-sets on completion of a generation at 1 instead of 4.

Figure 3.8 displays forecasted development and generation times for *T. tabaci* at Warwick HRI, Wellesbourne in 2006 based on hourly temperature data and with a development threshold of 12.28^{o}C, as estimated by logistic regression (Table 3.6).

Figure 3.8 Forecasted development and generation times of *T. tabaci* at Warwick HRI, Wellesbourne in 2006 from hourly temperature data. Combined (single development rate) and Individual (separate life stage development rates calculated sequentially) forecasted series. Development threshold 12.28^{o}C.

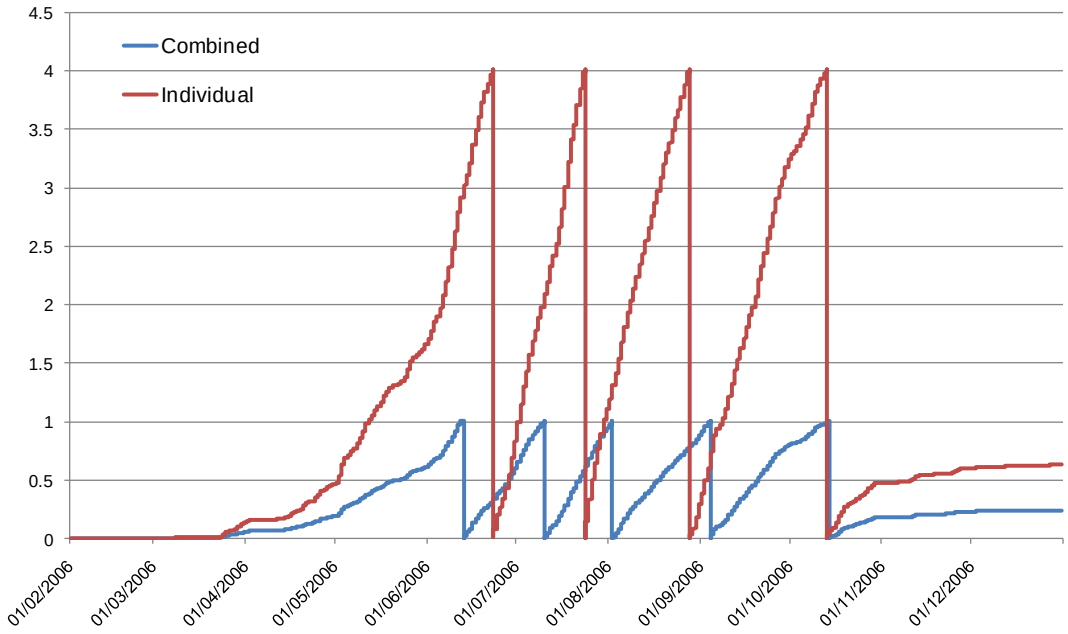
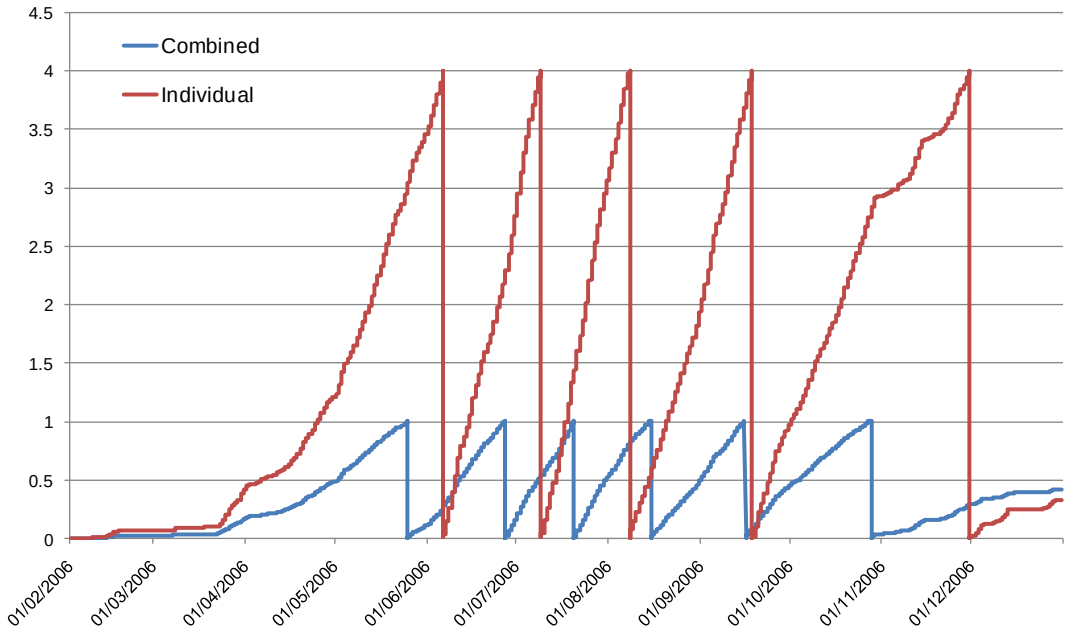


Figure 3.8 shows that there is a discrepancy when comparing forecasts based on the development rates of the individual life stages and those based on the whole life cycle. The series based on the complete life cycle not only predicts earlier generations, but a total of 5 generations over the year, compared with the forecast based on individual life stages, which predicts 4 generations. Figure 3.9 shows the progression of development and the number of generations using a development threshold of 8.77^{o}C as estimated by linear regression (Table 3.6).

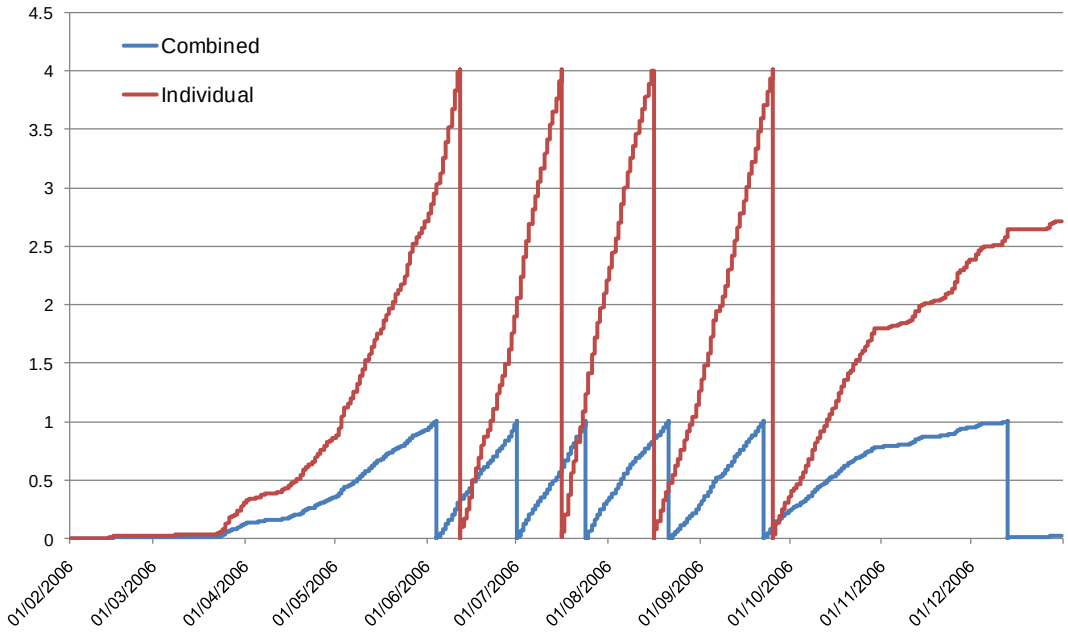
Figure 3.9 Forecasted development and generation times of *T. tabaci* at Warwick HRI, Wellesbourne in 2006 from hourly temperature data. Combined (single development rate) and Individual (separate life stage development rates calculated sequentially) forecasted series. Development threshold 8.77^{o}C



As can be seen from a comparison of Figures 3.8 and 3.9, a reduction in the development threshold affected the forecasts in different ways and to different degrees. Forecasting the time at which 50% of the initial generation has reached maturity is not greatly affected, the difference being approximately 10 days. However this first generation is developmentally active for a far longer period when using a lower development threshold. This is a reflection of the extended period of cool weather experienced in the early months of the year. It is in forecasting subsequent generations that the difference in development thresholds is most telling, in particular in the total number of generations and the extent to which they continue the cycle into the autumn and winter period.

Figure 3.10 shows how these development patterns appear if a threshold temperature of 10^{o}C, roughly half way between that calculated from the linear and the logistic regressions, is applied.

Figure 3.10 Forecasted development and generation times of *T. tabaci* at Warwick HRI, Wellesbourne in 2006 from hourly temperature data. Combined (single development rate) and Individual (separate life stage development rates calculated sequentially) forecasted series. Development threshold 10^{o}C



A detailed investigation of the accuracy of this forecasting method, and of the effect of using different development thresholds in the spreadsheet is presented in Chapter 6, where forecast population development is compared with population data recorded in the field at Warwick HRI, Wellesbourne between 2004 and 2008.

3.4.0 Discussion

This study followed broadly the methods laid down by Edelson & Magaro (1988) for the gathering of the raw data, as their method was logical and designed to simulate as closely as possible feeding conditions that immature thrips might experience in the field. Murai (2000) relied upon rearing the insects on artificial honey solutions and pollen, a factor which may have affected recorded development times.

A recent study has shown that the method derived from the data collected by Edelson & Magaro is inaccurate when predicting trends in UK populations (Collier et al., 2007). There are a number of reasons why each of the major investigations of thrips development available in the literature, including that of Edelson & Magaro, have not led to a forecasting system that could be used reliably in the UK.

Linear vs non-linear

Edelson & Magaro (1988) based their day degree calculations on a development threshold obtained via linear regression, a method whose accuracy has been called into question (Lamb, 1992, Finch et al., 1996, Briere et al., 1999). Recent studies have shown it is possible to develop forecasting models based on non-linear relationships between development rate and temperature. For example, Phelps et al. (1993) and Finch et al. (1996) demonstrated that forecasting models based on linear and non-linear descriptions of the relationship between rate of development and temperature were accurate for predicting field population trends for several major pest species in the UK.

In this study, the non-linear logistic curve was the most consistent descriptor and the one that was most accurate for describing each life stage individually, and indeed the overall life cycle (Tables 3.2 – 3.6). Linear descriptors were consistently less accurate across all the life stages and would appear to be inferior methods of describing the relationship between development and temperature. It was for this reason that the forecasting system developed in this study was based on non-linear descriptions of the temperature-development relationship.

Limited temperature ranges

The accuracy of a development threshold can be questioned further if it is derived not only by linear regression, but also from a limited range of temperatures. Edelson & Magaro's (1988) development threshold was calculated from data collected at just four constant temperatures between 17.5 and 27.5^{o}C, a range that stopped a full 6^{o}C above their estimated threshold. Sharpe & DeMichelle (1977) stated that it was at the temperature extremes, i.e. those temperatures closest to the development threshold and the upper limit, where the relationship between development and temperature was the least linear. By not investigating temperatures closer to the theoretical development threshold, it is difficult to predict how the increase in non-linearity seen towards this extreme may have affected the true threshold temperature.

In this study, the linear regressions calculated from the limited temperature range of 20 – 25^{o}C had a lower percentage fit than any of the other analyses across the entire range of life stages, indicating that this is a relatively inaccurate method of describing *T. tabaci* development as a function of temperature. Linear extrapolations estimated from experiments at a limited range of temperatures may indicate a development threshold that is lower than the true threshold.

An alternative method for determining the development threshold

No larvae emerged from leaf material exposed to adults at 10^{o}C. This would tend to indicate that oviposition was inhibited at 10^{o}C, although, as it was not possible to make a comprehensive survey of the leaf surface for evidence of egg laying, egg mortality cannot be ruled out as a reason for the lack of larval emergence. In either case, 10^{o}C appears to be a baseline temperature below which the thrips are unable to complete their life cycle. This is not to say that none of the life stages were capable of development at this temperature, some may have been, but time did not allow for further investigations into this question. Of course obtaining an accurate development threshold or base temperature for the thrips to complete their life cycle is critical to the development of accurate forecasting systems for the pest. As discussed in Chapter 6, none of the methods utilised so far for identifying that threshold, including the ones used in this study, may be accurate enough to predict population patterns under field conditions with confidence. In terms of simplicity, perhaps the most straightforward method of improving on these

estimates would be to repeat observations at temperatures closer and closer to the baseline until an exact temperature, below which the thrips were unable to complete their life cycle was identified. However, there are two problems with such an approach. Firstly, the closer the observation temperature gets to this baseline temperature, the longer the thrips will take to reach maturity, and this might be an inordinately long time, making experiments extremely difficult to sustain. Secondly, such an approach is demonstrably crude in that it addresses the development of the insect as a whole, whereas in this study it has been shown that each life stage has a unique temperature-development relationship.

Whole life cycle development threshold vs individual life stage thresholds

Edelson & Magaro (1988) estimated a threshold temperature of 11.5^{o}C for development of *T. tabaci* from measurement of the complete life-cycle, including the pre-oviposition period. They separated the life-cycle into three phases: pre-oviposition, egg to larva and larva to adult. However the threshold temperatures for these three separate stages were not used in the final estimation of an overall development threshold temperature and indeed the thresholds for the individual stages differed markedly from the final threshold temperature of 11.5^{o}C. The thresholds for each of the three phases also differed markedly, with a threshold of 15.7^{o}C for the pre-oviposition period, compared with 10.2^{o}C for development from larva to adult. With such different development thresholds for the separate phases, doubt is cast on the potential accuracy of the overall development threshold.

In the present study, the threshold of 12.28^{o}C for overall development does not differ very greatly from the threshold of 11.5^{o}C estimated by Edelson & Magaro (1988), but is quite different from Quartey's (1982) estimation of 7.4^{o}C, although the latter study did not include the pre-oviposition period or egg development in its remit. What is important to note is that both this study and that of Edelson & Magaro (1988) estimated a threshold for overall development that is lower than the thresholds for some of the individual life stages; the pre-oviposition and egg stages in the case of Edelson & Magaro's study (which did not address pupae and larvae separately) and the pre-oviposition, egg and pupal stages in the case of the present study. Not all life stages have the same relationship with temperature; they each have their own requirements and should be addressed individually. This is illustrated well in Figures 3.2 – 3.6 which show that very different development rate curves were

estimated for each life stage. A single threshold for the entire life cycle may be too crude a method for understanding or predicting development as a function of temperature. This is especially true if it is derived from data in which some life stages were not addressed individually but combined (Edelson & Magaro) or when some life stages were not tested at all (Quartey).

The relationship between temperature and development in *T. tabaci* could be more accurately modelled by addressing each life stage individually and sequentially in terms of the development rate rather than by accumulation of day degrees for the entire life cycle as a whole. The forecasting method developed in this chapter utilises these ideas and applies them to temperatures recorded in the field.

Geographical location

Edelson & Magaro (1988) undertook their investigation in the United States, in Texas, and their population of *T. tabaci* was sourced from that location. Honêk (1996) demonstrated, in his survey of the development of over 335 insect species, that geographical origin has a significant effect on the thermal requirements for insect development. This geographical effect can be observed in development thresholds and the sum of effective temperatures (SET), the number of day-degrees above the development threshold required to complete development. Honêk reported a clear relationship between geographical origin and the development threshold of a population, with increasing latitude (going north from the equator) associated with a decrease in the development threshold. This trend was apparent for all development stages investigated (eggs, larvae, pupae and overall development time). It is possible that UK populations of *T. tabaci* are simply better adapted for development at lower temperatures than Texan populations and have a different development threshold and consequent day-degree requirement, than those *T. tabaci* to be found in Texas.

For some time it has been known that there are large differences between populations of *T. tabaci*. For example, sex ratios differ considerably amongst geographically distinct populations (Morison, 1957, Lewis, 1973b). Jenser et al. (2001) demonstrated that populations of *T. tabaci* subsisting on two different host species, onion and tobacco, had significant genetic differences. Genetic analysis conducted by Toda & Murai (2007) confirmed that there are at least two distinct groups of *T. tabaci* population according to the COI gene phylogenetic tree. Brunner et al. (2004) in their study on host-associated genetic differentiation in *Thrips tabaci*

identified what they termed as a "complex of at least three taxa" making up the thrips populations in a relatively small geographic area in the northern Mediterranean. They suggested that what has traditionally been considered a single species, *Thrips tabaci*, may in fact be a complex of different species or sub-species which may share common origins and certainly morphological features but between which the flow of genetic material has halted. If such is the case, it is clear that the application of development thresholds and day-degree requirements estimated from one population to another, even over short geographical distances, may be an unsound practice. Compounding this is the variation in sex ratios found globally (possibly another reflection of sub-species dispersion) which will inevitably have an impact on all aspects of population growth and development. None of the investigations into the development of *T. tabaci* and its relationship with temperature to be found in the literature have given any explanation as to the sexual make-up of the population from which the test insects were sourced. Males appear to be extremely rare in the population at Warwick HRI, Wellesbourne although no exact female to male ratio is known.

In conclusion

The current accepted method for forecasting *Thrips tabaci* populations used by Villeneuve et al. (1996) and Martens and Plovie (2007) is based on Edelson & Magaro's (1988) estimate of the development threshold and the day-degree requirement for development by *T. tabaci* that is derived from that. However, as shown above, the accuracy of a forecasting method based on a threshold temperature derived 1) for a full life cycle and 2) by linear regression is questionable when the individual life stages have demonstrably different development thresholds and development rates. For this reason a forecasting system was developed that both took into account the non-linearity of the relationship between temperature and development in *Thrips tabaci* but also the changing nature of this relationship over the different life stages.

The accuracy of this new forecasting system will be investigated in detail in Chapter 6. However it must be noted that even with this perhaps more rigorous and logical way of addressing development of *T. tabaci* as a function of temperature, potential pitfalls abound. Firstly, as with all such forecasting systems derived from means, individual variability may decrease the accuracy of forecasts. In this case

variability is evident across the life stages, and the extent to which individual development times varied was significant (Table 3.1). Secondly, the relative coarseness of the time intervals used for recording mean that minor variations between individuals are potentially magnified when examining higher temperatures and therefore shorter overall life cycles. This problem could be minimised by recording more frequently, though it would always exist in theory, yet this might prove difficult without significantly improved resources. Thirdly, studies of this nature address the relationship between development and temperature at fixed temperature intervals and the insects do not experience continually varying temperatures as they would do in the field. The extent to which temperature increases and decreases affect development rates is therefore hard to determine. This is illustrated by the test conducted under variable temperatures in the greenhouse, in which development was much faster than might be expected if expressed in terms of the mean temperature the thrips experienced (Figure 3.1). Finally although temperature is considered to be the factor determining the rate of thrips development, field conditions are generally more variable than those to which the thrips were exposed in the laboratory. Indeed, especially early in the year, when the initial generations might have to develop on overwintered crops, the availability of good quality food sources and a host of other factors may also affect development time.

For these reasons, forecasting of *T. tabaci* populations in the field, no matter how accurately the threshold temperature is estimated, will remain a difficult challenge.

Chapter 4: The activity and behaviour of *Thrips tabaci*

4.1.0 Introduction

The onion thrips, *Thrips tabaci* (Thysanoptera, Thripidae) is a major pest of *Allium* crops in the UK and is the key arthropod pest of both leek and salad onion (Lewis, 1997b, Garthwaite et al., 2003). Many growers have little confidence in their ability to control thrips populations with the control methods available to them currently, particularly during periods of high infestation. Although recent research has demonstrated increasing levels of pesticide resistance in UK populations, (DEFRA, 2007a), control with chemical pesticides has, according to growers, always been poor. The problem lies with the cryptic nature of *T. tabaci* (Theunissen and Legutowska, 1991b) and the difficulties that growers have in ensuring that pesticides reach their intended target. There are several adaptive advantages to the cryptic behaviour of *T. tabaci*: they are small and therefore vulnerable to desiccation, and by hiding within the deeper foliage they probably minimise their encounters with predators and parasitoids. This does, however, make thrips control very difficult, since it is hard to target a pest that spends so much of its time in locations that are virtually inaccessible to foliar sprays. One way to maximise their contact with foliar sprays is to determine whether there are periods when *T. tabaci* move onto the upper parts of the leaves, where they will be more exposed. Sites et al. (1992), in their study on the diel periodicity of thrips dispersion, identified a diurnal periodicity in the intra-plant distribution of thrips on onion plants, with a distinct peak in numbers on the exposed upper leaf area in the early afternoon, when temperatures were highest. A greater knowledge of the activity and behaviour patterns of *T. tabaci* and of how these are affected by temperature, amongst other factors, may help growers to predict periods of high vulnerability.

There is little published material on the behaviour of thrips, apart from investigations into the more socially complex colonial *Hoplothrips* species, such as those conducted by Crespi (Crespi, 1986, Crespi, 1988), and a few studies examining more specific behaviours such as Whitaker and Kirk's (2004) investigations into the effect of photoperiod on walking, feeding and oviposition in *Frankliniella occidentalis* (Pergande). Koschier and colleagues (2002, 2003, 2007) have conducted a series of investigations testing the effect of plant volatiles and essential

oils on a variety of behaviours by both *T. tabaci* and *F. occidentalis* and she is now attempting to observe and classify the full range of *T. tabaci* behaviours (H. Koschier, personal communication). As part of this effort Riefler and Koschier (2009) have recently published an investigation into behavioural patterns of *T. tabaci* on leek and cucumber. However, at present there is no published list of behaviours exhibited by any of the leaf feeding thrips species and nothing is known about how these behaviours are affected by environmental influences such as temperature, or how such influences affect overall levels of activity.

The aim of this study was to investigate the effect of temperature and of leaf quality on the behaviour of onion thrips, including the behaviours exhibited, the frequency of behaviours, behavioural sequences and overall levels of activity. An understanding of the influence of these factors on thrips behaviour may help to identify and predict windows of vulnerability, potentially increasing the efficacy of current or novel control methods within an integrated pest management strategy.

4.2.0 Materials and methods

4.2.1 Thrips

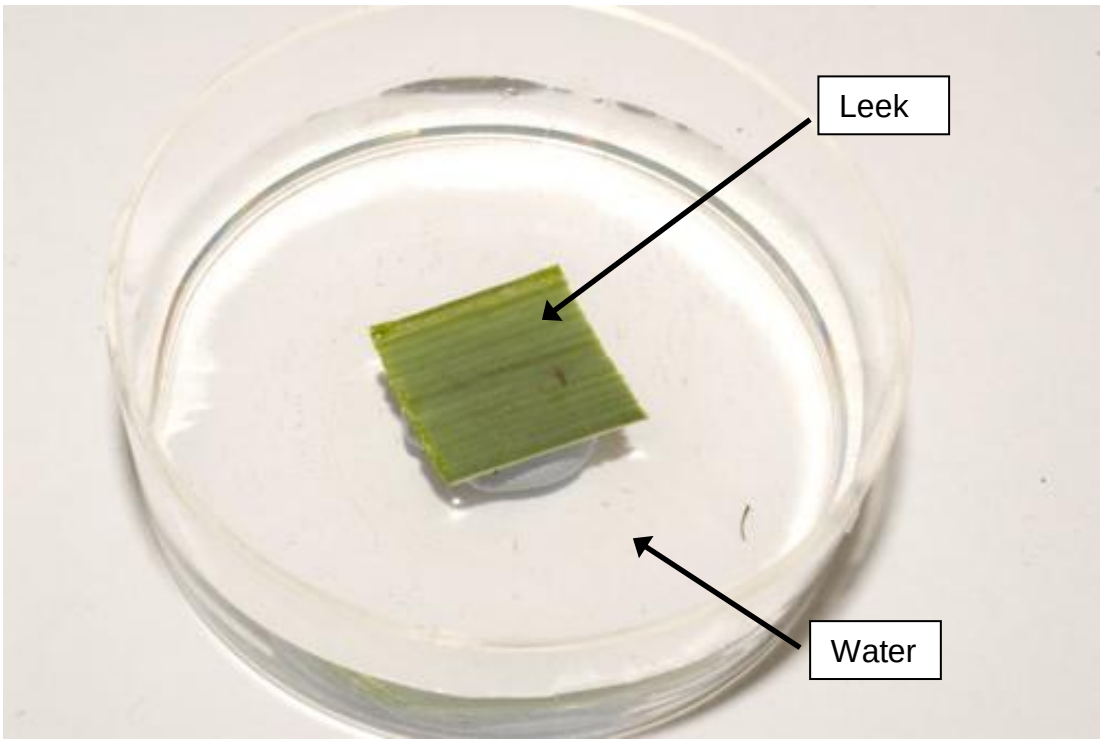
A field population of *T. tabaci* was established in 2003 at Warwick HRI, Wellesbourne, through natural infestation. The population was maintained on an insecticide-free plot of leek (cv Shelton). *Thrips tabaci* from this population were removed to the laboratory and reared in plastic containers in incubators maintained at 18.5^{o}C with a photoperiod of L16:D8. Further details of thrips rearing and other general materials and methods can be found in Chapter 2.

The thrips were observed at a range of constant temperatures by placing them in a Sanyo growth chamber (model MLR-351). This incubator has a glass wall, so that it is possible to observe the thrips without opening the door and thereby altering the internal temperature. The thrips were prepared by placing them at the test temperature 24 hours prior to the start of the observation period.

4.2.2 Observation Cage Design

The arenas used to observe thrips behaviour were based in part on a design used by Elisabeth Koschier in her recent attempts to classify and organise thrips behaviours (personal communication). Each arena consisted of a 1 cm x 1 cm piece of fresh leek foliage (cv Shelton from a greenhouse culture) supported above the centre of a 30 mm diameter plastic Petri dish using a small piece of Blu-Tac® (Figure 4.1). The piece of leek foliage was surrounded by water to prevent the thrips walking away.

Figure 4.1 The arena used to observe thrips behaviour.



4.2.3 Observation and recording

For each test, a single thrips was removed from the rearing cage, using a fine paintbrush, and placed within the observation arena, where it was left to acclimatise for 1 minute. The thrips was then observed for a period of 5 minutes, during which its behaviours were recorded. The observation period commenced when the thrips first changed its behaviour (e.g. from resting to walking). The time spent engaged in each behaviour, and the sequence of behaviours, were recorded. The observation period was terminated after 5 minutes or sooner if the thrips took flight or fell off the leaf square. Fifty individual thrips were observed at each temperature.

4.2.4 Temperatures

In order to survey as wide a range of temperatures as possible and to ensure that range reflected closely what might be experienced by *Thrips tabaci* in the field, 9 temperatures between 5 and 35^{o}C were evaluated. These were 5, 7.5, 10, 12.5, 15, 20, 25, 30 and 35^{o}C.

4.2.5 Leaf quality assessments

To assess the effect of leaf quality on behaviour, the experiment was repeated, by making observations of thrips behaviour at 20^{o}C on dry leek foliage, rotten leek foliage and a non-host species (oak). 'Reproducible' treatments were achieved in the following ways:

- Control treatment: The data gathered previously using fresh leek foliage at 20^{o}C were used.
- Dry leaves: Fresh leek foliage was cut and allowed to dry in an incubator for 10 days.
- Rotten leaves: Fresh leek foliage was cut and allowed to rot in a humid environment within a box for 5 days.
- Non-host species: Fresh Oak (*Quercus robur)* leaves were used.

4.2.6 Categorising behaviour

A number of distinct behaviours were observed through the course of the experiment and these were grouped into categories prior to statistical analysis of the data. The categories were:

1. **Resting** – containing non-active behaviours
2. **Walking** – containing all walking related behaviour
3. **Searching** – including any exploratory behaviours
4. **Feeding** – including leaf probing and pre-feeding behaviours
5. **Grooming** - including body flexing and wing and antennal cleaning
6. **Defecation**
7. **Flight** – an action which ended the observation period
8. **Exiting arena** – any action that brought the observation period to an end prematurely but that did not involve flight.

Behaviours within categories 1-6 did not result in the termination of the 5 minute observation period. However, if categories 7 or 8 were witnessed, then the observation period was terminated, as these behaviours resulted in the thrips leaving

the experimental arena. In addition, the first six categories describe behaviours whose duration is variable, whereas categories 7 and 8 describe instantaneous events.

4.2.7 Data Analysis

The time a thrips spent engaged in a single behaviour 'event' and the total time each thrips spent in each behaviour across the entire observation period were analysed using Residual Maximum Likelihood (REML). The data were analysed excluding the final behaviours of an observation session. If these times had been included then the average time spent in these behaviours would have been an underestimate. As both flight and falling off the leaf are instantaneous events, no 'time' information exists for them and therefore they are excluded from this analysis. The total time a thrips was observed before it took flight was also analysed using REML, excluding those thrips which did not fly. To establish whether there was a statistically significant difference between the different temperatures in the likelihood that a thrips would fly, a binomial test for the equality of two proportions was used.

To investigate the sequence of behaviours observed, and to establish whether any patterns were present, two transition matrices were created. The first of these was based on a 5-second interval and was used to establish the number of times a thrips moved between any two behaviours (the 5-second time period allowing transitions within a single behavioural category). The second matrix investigated the proportion of thrips which moved between any two behaviours at the different temperatures.

All data were analysed using Genstat for Windows (VSN International Ltd.) and Microsoft Excel (Microsoft Corporation).

4.3.0 Results

4.3.1 Behaviours Observed

A more detailed description of the behaviours observed in each of the categories follows:

1. **Resting** – This category was ascribed to periods which contained no observed active behaviours. This was typified by extended periods of motionlessness. These periods were sometimes, albeit rarely, interrupted by individual antennal grooming sweeps, whereby a single antenna was swept along the foreleg. These events were not classified as an interruption of the resting period as this particular minor behaviour was engaged in commonly during many of the other behaviours and does not compare with the serious investment in grooming activities displayed by the behaviours grouped in category 5. Resting typically occurred in rough or undulating areas of the arena surface and the thrips tended to align their bodies with these ridges or troughs.

2. **Walking** – Walking speed varied greatly between individuals, but each individual tended to move at roughly the same speed throughout the period of observation. It was not possible to measure walking speed by eye and, as there were no easily distinguishable variants, for example simply slow or fast movements, the decision was made to group all walking speeds into a single category. Further variations existed related to whether the thrips walked in a straight line or in long turns. These two variants were often observed during the same walking event and so are grouped in this category as well. There was very little noticeable edge-influenced behaviour; the thrips did not simply walk around the edge of the arena, but constantly traversed it, turning around or following the edge for short periods upon reaching it.

3. **Searching** – This category contains two behaviours that were generally engaged in only briefly and infrequently by the thrips. The first of these was a behaviour that was undertaken by thrips that also engaged in feeding

behaviours during the period of observation. Distinctive side to side head movements, often accompanied by one or more sideways steps, appeared to reflect sampling of the leaf for an appropriate feeding site via the sweeping of the antennae across the leaf surface. The second behaviour in this category could reflect a more thorough enactment of similar behaviour, as the thrips turned on the spot, often through 360^{o} or 720^{o}. However, as this behaviour was always enacted in a single direction and at a much higher speed than the previous behaviour, it could also indicate that the thrips use vision to decide upon a direction of travel (walking often followed this behaviour). In either case it was classified as an exploratory behaviour and so placed in this category.

4. **Feeding** – This category is straightforward as it contained two behaviours, leaf probing and feeding itself. Leaf probing was identified as the periods before full feeding commenced, when a thrips repeatedly moved its head up and down, bringing its stylet into contact with the leaf surface. The thrips commonly made several probes before commencing full feeding.

5. **Grooming** - This category contains a diverse range of behaviours. By far the most common of these was wing combing and body flexing. This involved flexing of the abdomen in order to adjust the position of the wing setae, preparing them for flight.

   Apart from wing grooming, it was not uncommon to see antennal grooming taking place. This involved the use of the front legs to comb down the antenna, generally a left comb followed in quick succession by a right followed by a left etc. The left leg would comb the left antenna and the right leg the right antenna. This sequence often occurred for several seconds and included several dozen grooming sweeps of each antenna. Individual antennal grooming sweeps often occurred whilst the thrips was engaged in other behaviours. These events typically lasted less than half a second and did not interrupt the main behaviour and so are not counted in this category.

6. **Defecation** – This category contains a single behaviour which was typified by a very distinctive bending of the thrips' abdomen. Individuals would bend

their abdomens downwards so the tip was facing the leaf surface and then excrete a small dark droplet of faecal matter. Thrips sometimes dragged the tip of the abdomen along the leaf to dislodge the droplet and sometimes stabbed downwards directly with the abdomen tip to plant the droplet on the leaf surface

7. **Flight** – Thrips spread their wings and launch very quickly, the process taking typically less than a second. For the purposes of this experiment, therefore, this behaviour was treated as instantaneous, as no measurement of the duration of the flight was attempted.

8. **Exiting Arena** – Rarely, an observation period had to be curtailed because the subject left the arena before the end of the 5 minute observation period. If the thrips did not fly from the leaf and merely fell into the surrounding water, it was classified in this category. As this was not a true behaviour in itself, and exhibited no discernable trends based on any recorded factor, it was not considered further in the analysis.

Not all behaviour categories were observed at all temperatures; Table 4.1 summarises the behaviours undertaken at each temperature.

Table 4.1 Behavioural categories observed at each temperature (**O** = behaviour observed, **A** = behaviour absent)

	Temperature ^{o}C								
	5.0	7.5	10.0	12.5	15.0	20.0	25.0	30.0	35.0
resting	O	O	O	O	O	O	O	O	O
walking	O	O	O	O	O	O	O	O	O
searching	A	O	O	O	O	O	O	O	O
feeding	A	O	O	O	O	O	O	O	O
grooming	A	O	O	O	O	O	O	O	O
defecating	A	A	A	O	O	O	O	O	O

The number of instances when the different behaviours were observed across the temperatures is summarised in Table 4.2. There was a general increase in the number of behaviours observed as temperatures were increased.

Table 4.2 Total numbers of instances of each behaviour and the overall total number of observed behaviours at each temperature.

Temp ^{o}C	resting	walking	searching	feeding	grooming	defecation	Total
5	73	49	0	0	0	0	122
7.5	80	90	14	4	22	0	210
10	155	158	14	4	24	0	355
12.5	51	136	57	23	61	5	333
15	61	155	30	15	86	23	370
20	24	203	75	59	105	25	491
25	27	197	58	13	122	49	466
30	43	239	72	27	163	66	610
35	69	171	55	17	72	38	422

Table 4.3 shows the mean number of times a thrips engaged in each of the various behaviours at each temperature.

Table 4.3 Mean number of instances of each behaviour per thrips.

Temp ^{o}C	resting	walking	searching	feeding	grooming	defecation	Total
5	1.5	1.0	0	0	0	0	2.5
7.5	1.6	1.8	0.3	0.1	0.4	0	4.2
10	3.1	3.2	0.3	0.1	0.5	0	7.2
12.5	1.0	2.7	1.1	0.5	1.2	0.1	6.6
15	1.2	3.1	0.6	0.3	1.7	0.5	7.4
20	0.5	4.1	1.5	1.2	2.1	0.5	9.9
25	0.5	3.9	1.2	0.3	2.4	1.0	9.3
30	0.9	4.8	1.4	0.5	3.3	1.3	12.2
35	1.4	3.4	1.1	0.3	1.4	0.8	8.4

4.2.1 Time spent engaged in a behaviour

As this test was attempting to identify variability in the duration of individual behavioural events between the different temperatures, the fixed model term of interest was the interaction between temperature and behaviour (temperature.behaviour). The F-test in Table 4.4 shows that the main effects of temperature and behaviour were both highly significant, as indeed was the model term temperature.behaviour.

Table 4.4 F-test showing the main effects of temperature and behaviour and the interaction between temperature and behaviour.

Fixed Term	F statistic	Degrees of Freedom	Probability Value
temperature	11.55	290.8	<0.001
behaviour	52.81	2538.9	<0.001
temperature.behaviour	3.72	2552.9	<0.001

A $\log_{10}$ transformation was required to improve the normality of these data and Table 4.5 shows the mean values for the interaction between temperature and the duration of each behaviour on this scale.

Table 4.5 Time per behavioural event: Means for the interaction between temperature and behaviour on a $\log_{10}$ transformed scale (time per behavioural event).

Temperature	Behaviour					
	resting	**walking**	**searching**	**feeding**	**grooming**	**defecating**
5	1.478	1.251	-	-	-	-
7.5	1.468	1.433	0.927	1.069	1.091	-
10	1.2	1.341	0.765	1.172	1.048	-
12.5	1.395	1.43	1.071	1.166	1.152	1.088
15	1.355	1.301	1.113	1.133	1.009	1.349
20	0.917	1.272	0.975	0.996	0.921	1.312
25	0.998	0.99	0.999	0.989	0.904	1.288
30	1.221	1.112	0.857	0.925	1.075	1.401
35	1.255	1.294	0.93	0.925	1.198	1.277

Table 4.6 shows the standard error of the difference (SED) for the same level of factor and indicates a good level of consistency between individuals in the duration of a behaviour at each temperature and this is true across all the behaviours.

Table 4.6 Standard error of the difference for the mean value of the interaction between temperature and behaviour on a $\log_{10}$ transformed scale.

	Temperature ^{o}C	**Behaviour**
Average:	0.1005	0.1039
Maximum:	0.2162	0.2712
Minimum:	0.04054	0.049

Table 4.7 shows the means for the interaction between temperature and the duration of each behaviour, back transformed from the $\log_{10}$ scale to a time scale (seconds).

Table 4.7 Back-transformed means for the relationship between temperature and the duration of each behaviour (seconds).

Temperature ^{o}C	Behaviour					
	resting	**walking**	**searching**	**feeding**	**grooming**	**defecating**
5	30.06	17.83	-	-	-	-
7.5	29.35	27.1	8.45	11.71	12.33	-
10	15.84	21.9	5.82	14.87	11.18	-
12.5	24.85	26.93	11.76	14.65	14.2	12.24
15	22.63	20.02	12.98	13.59	10.21	22.36
20	8.26	18.69	9.43	9.9	8.34	20.52
25	9.94	9.76	9.97	9.74	8.01	19.39
30	16.64	12.95	7.19	8.41	11.88	25.19
35	17.98	19.67	8.51	8.41	15.77	18.91

This information and the trends it reveals are illustrated in Figures 4.2-4.7. The mean time a thrips spent resting declined from 5 to 20^{o} and then began to increase again to 35^{o} (Figure 4.2).

Figure 4.2 Back-transformed means for the effect of temperature on the length of an individual resting behaviour.

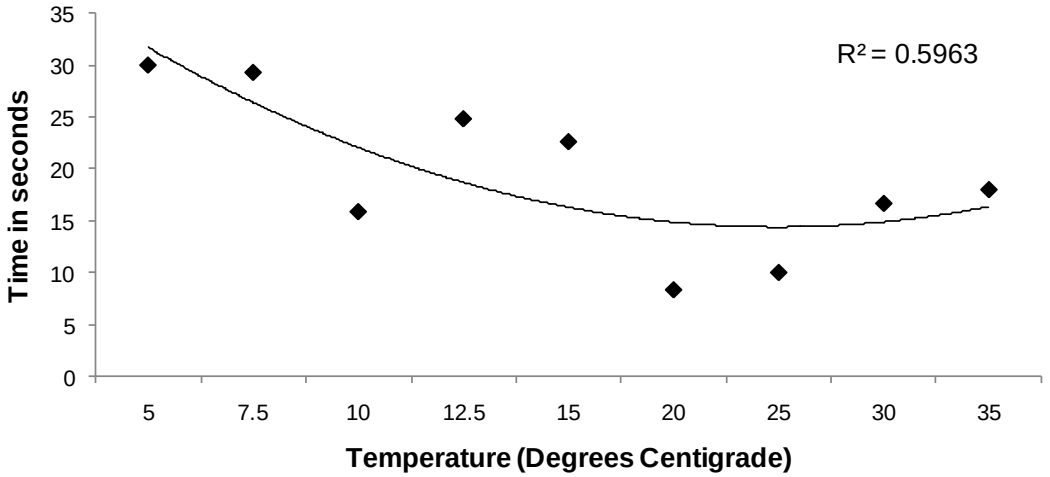


Figure 4.3 shows that walking events followed a similar pattern as resting behaviours, with a general decrease in duration between 7.5 and 25^{o}C, and then an increase to 35^{o}C.

Figure 4.3 Back-transformed means for the effect of temperature on the length of an individual walking behaviour.

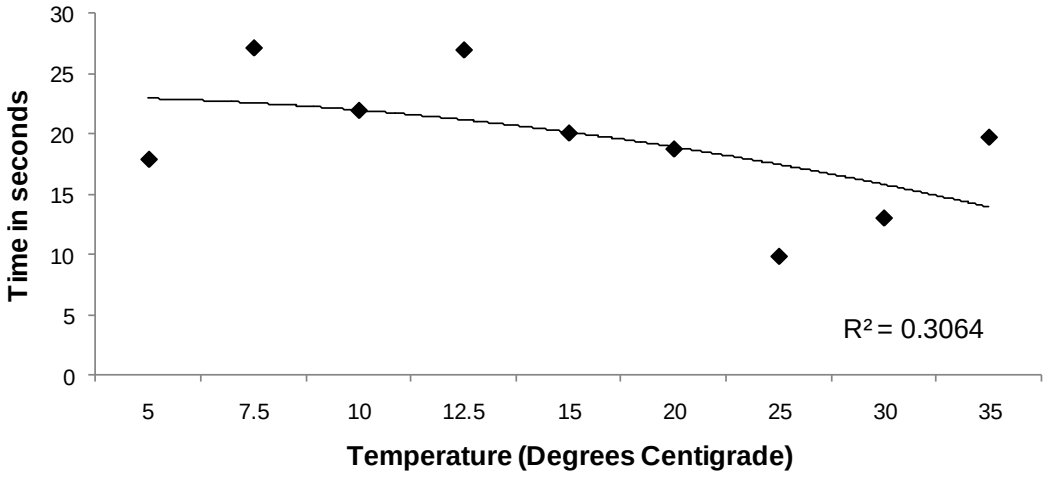


Figure 4.4 shows that searching behaviours did not occur at all at 5°C and their average length remained under 10 seconds at all but 12.5°C and 15°C.

Figure 4.4 Back-transformed means for the effect of temperature on the length of an individual searching behaviour.

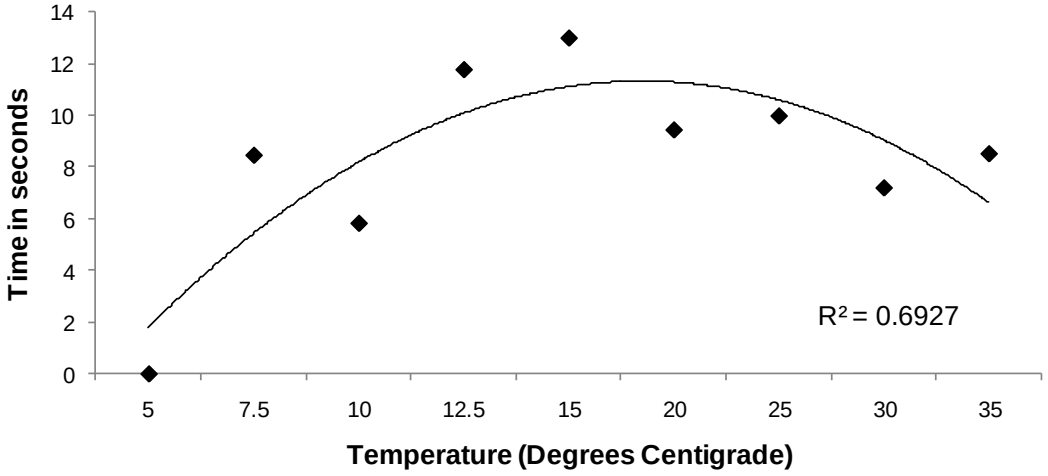


Figure 4.5 shows that feeding did not occur at all at 5°C, was at its maximum at 10°C, and then gradually declined as temperatures increased above that.

Figure 4.5 Back-transformed means for the effect of temperature on the length of an individual feeding behaviour.

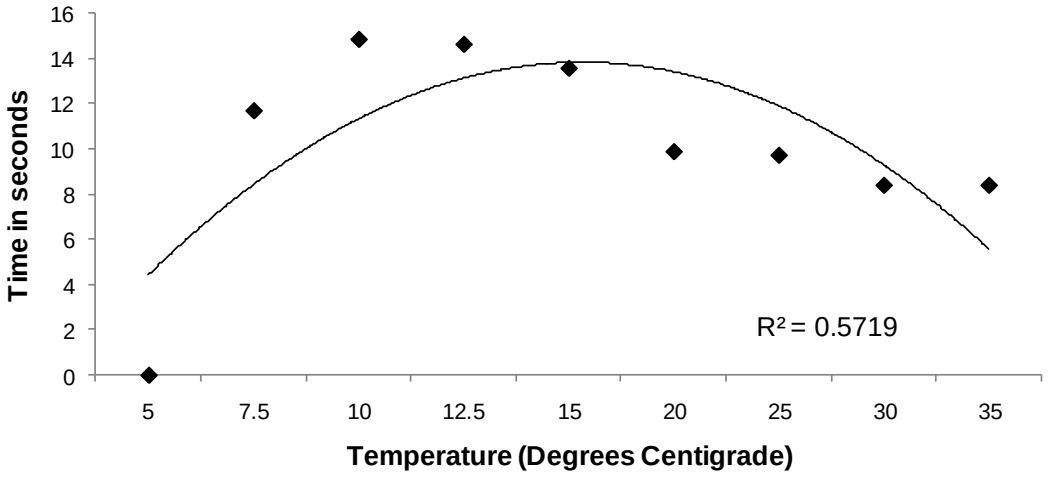


Figure 4.6 shows that grooming did not occur at all at 5^{o}C.

Figure 4.6 Back-transformed means for the effect of temperature on the length of an individual grooming behaviour.

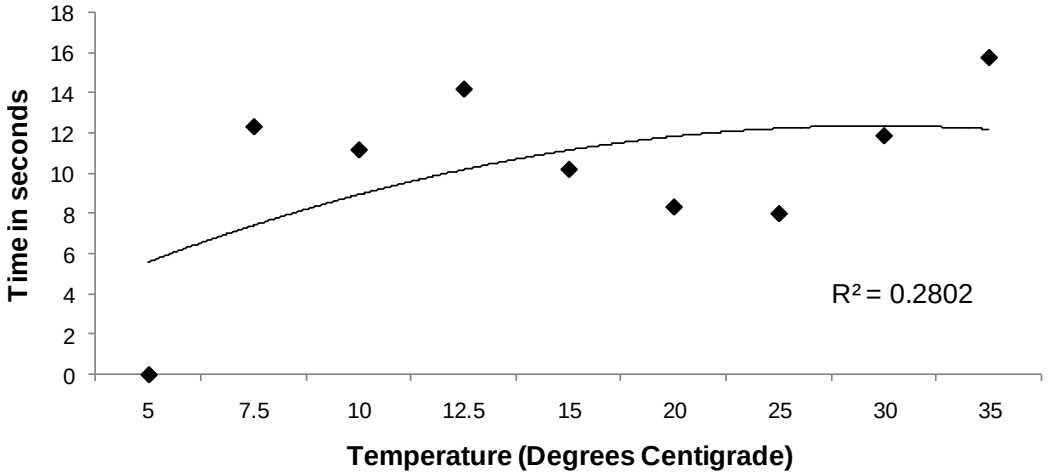
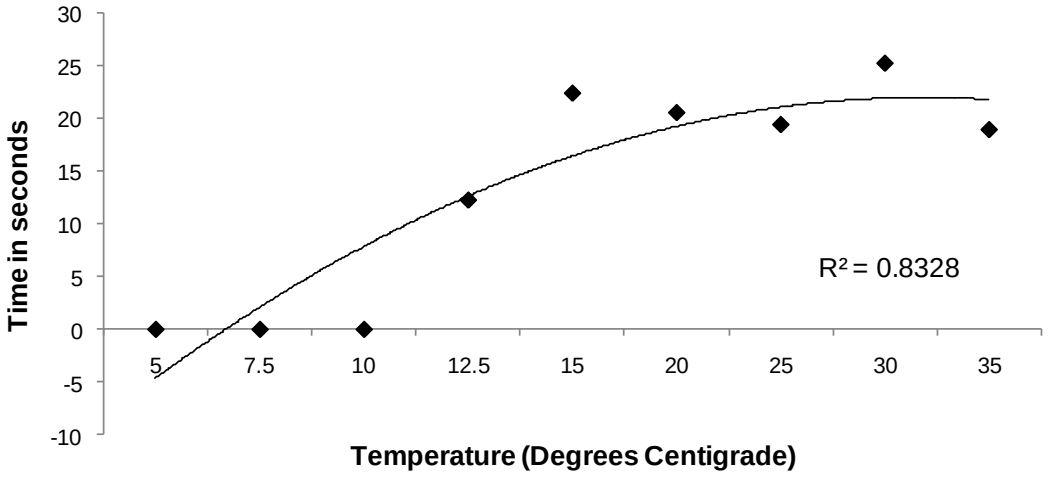


Figure 4.7 shows that defecation was not observed at all below 12.5^{o}C. Between 15^{o}C and 35^{o}C its average duration remained fairly constant.

Figure 4.7 Back-transformed means for the effect of temperature on the length of an individual defecation behaviour.



As the model for the above analysis included both temperature and behaviour as terms it was not possible to extract the overall time spent at each temperature because not all behaviours occurred at each temperature. In order to extract this information, the model was refitted with temperature as a fixed effect and again a $\log_{10}$ transformation was used. Table 4.8 shows both the $\log_{10}$ transformed overall mean times and the back-transformed overall mean times in seconds. The mean duration of a behaviour generally decreased as the temperature increased up to 25^{o}C and then increased again as the temperature was increased further.

Table 4.8 Predicted means for the time engaged in a behaviour at the different temperatures on a $\log_{10}$ transformed scale and back-transformed in seconds.

	Temperature ^{o}C								
	5	7.5	10	12.5	15	20	25	30	35
$\log_{10}$	1.357	1.340	1.227	1.266	1.213	1.087	1.001	1.100	1.198
Seconds	22.74	21.90	16.88	18.44	16.35	12.22	10.02	12.63	15.79

As well as the duration of each behavioural event, the overall time a thrips engaged in a particular behaviour across each observation session was analysed. The resultant F-test is displayed in Table 4.9 and shows that the main effects of

temperature and behaviour and the interaction term of temperature.behaviour were all highly significant.

Table 4.9 F-test showing the main effects of temperature and behaviour and the interaction between temperature and behaviour.

Fixed Term	F statistic	Degrees of Freedom	Probability Value
temperature	3.17	276.9	0.002
behaviour	41.50	876.8	<0.001
temperature.behaviour	2.80	895.9	<0.001

Once again a $\log_{10}$ transformation was required to improve the normality of these data and the resultant means are presented in Table 4.10.

Table 4.10 Means for the interaction between temperature and behaviour on the $\log_{10}$ transformed scale (total time per behavioural category).

Temperature ^{o}C	Behaviour					
	resting	walking	searching	feeding	grooming	defecating
5	1.778	1.426	*	*	*	*
7.5	1.689	1.733	1.12	1.306	1.219	*
10	1.682	1.863	0.963	1.349	1.218	*
12.5	1.516	1.763	1.37	1.229	1.429	1.296
15	1.616	1.863	1.333	1.241	1.239	1.62
20	1.029	1.847	1.325	1.339	1.313	1.799
25	1.119	1.538	1.367	1.083	1.277	1.69
30	1.436	1.72	1.154	1.107	1.556	1.611
35	1.561	1.764	1.281	1.042	1.519	1.644

Table 4.11 shows the standard error of differences for the same level of factor.

Table 4.11 Standard error of differences for the means of the interaction between temperature and behaviour on the log10 transformed scale.

	Temperature	Behaviour
Average:	0.1585	0.1546
Maximum:	0.3463	0.3933
Minimum:	0.09457	0.09193

Once the means were back-transformed to seconds, some clear trends were evident. These are illustrated in Figures 4.8-4.14. The time spent resting decreased from 5°C to 20°C, but increased above 20°C (Figure 4.8).

Figure 4.8 Back-transformed means for the effect of temperature on overall time spent resting.

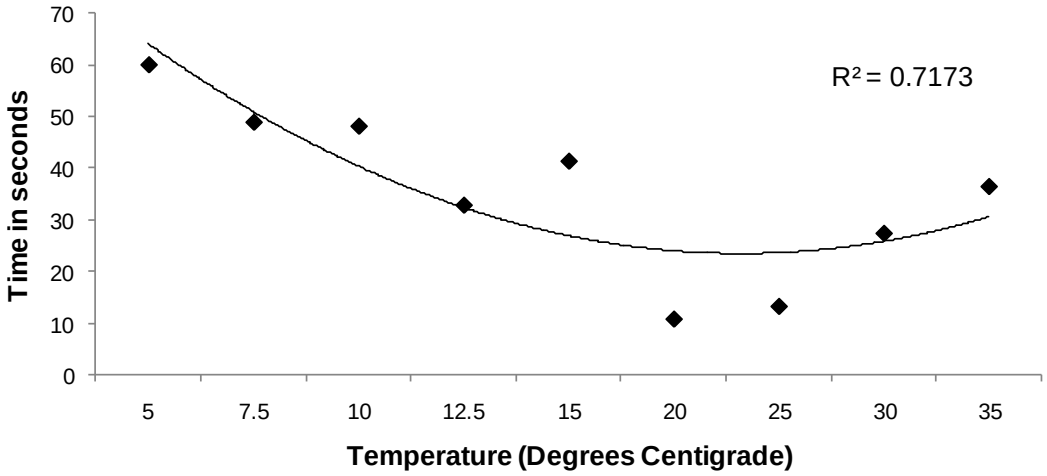


Figure 4.9 shows that in general, the time spent walking fluctuated across the temperatures but did not show any clear trends, though thrips spent the least time walking at 5°C.

Figure 4.9 Back-transformed means for the effect of temperature on overall time spent walking.

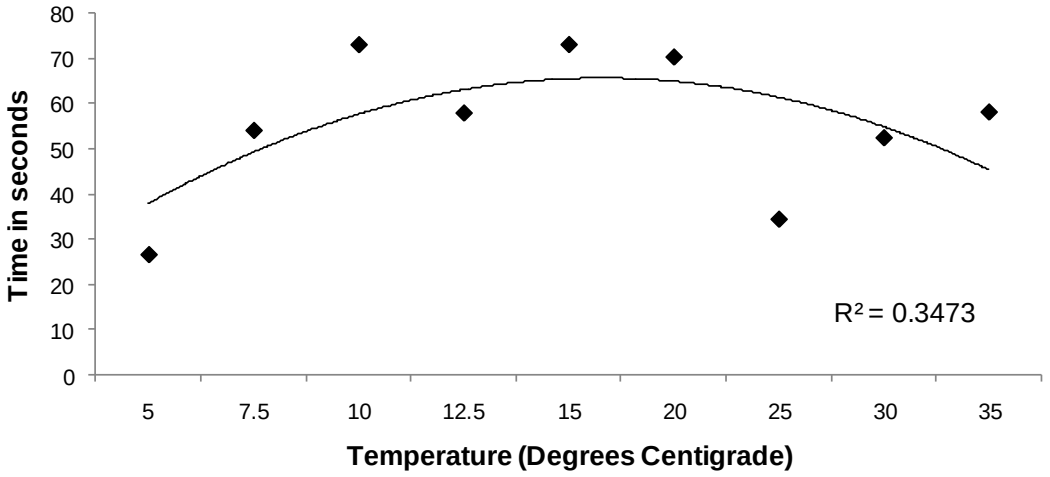


Figure 4.10 shows that searching behaviours were most prominent above 12.5^{o}C and that they did not occur at all at 5^{o}C.

Figure 4.10 Back-transformed means for the effect of temperature on overall time spent searching.

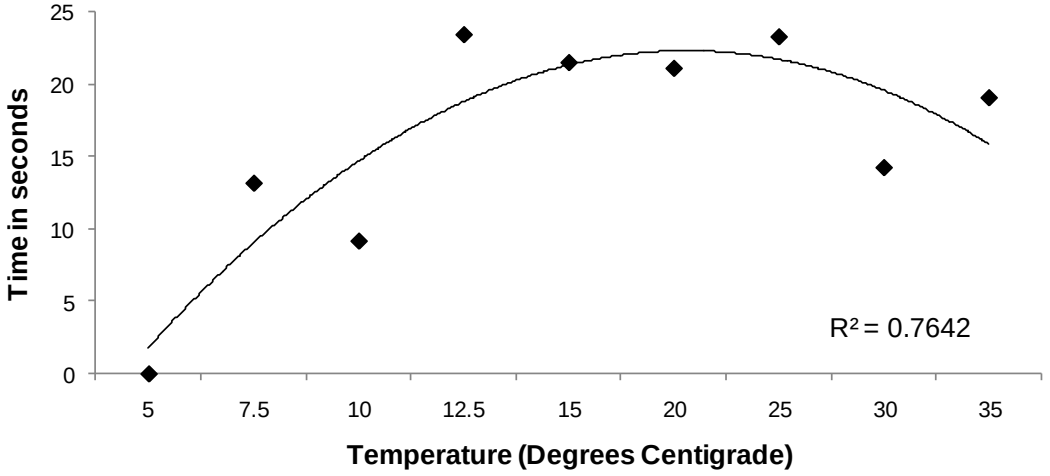


Figure 4.11 shows that time spent feeding was fairly consistent between 7.5 and 20^{o}C declining slightly above that temperature. No feeding was observed at 5^{o}C.

Figure 4.11 Back-transformed means for the effect of temperature on overall time spent feeding.

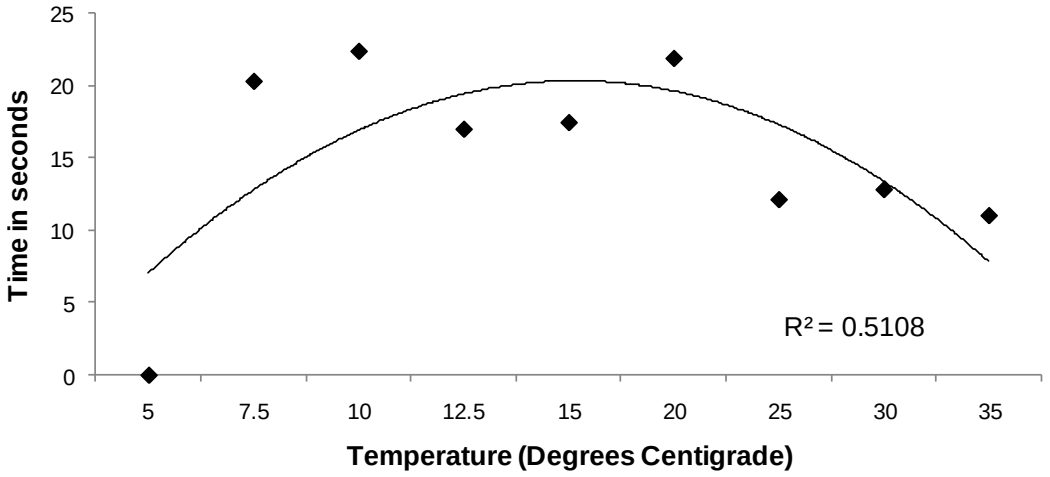


Figure 4.12 shows that as temperatures increased between7.5 and 35^{o}C the time spent grooming increased. No grooming was observed at 5^{o}C.

Figure 4.12 Back-transformed means for the effect of temperature on overall time spent grooming.

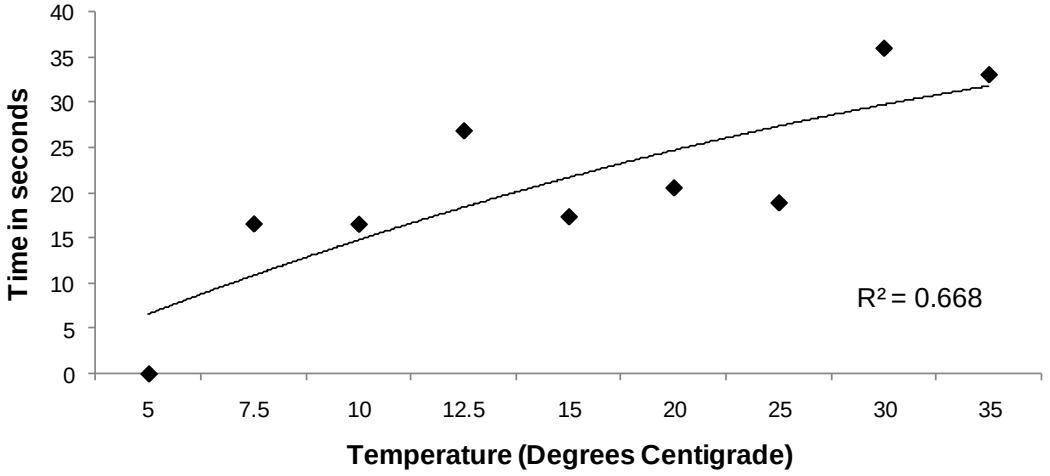
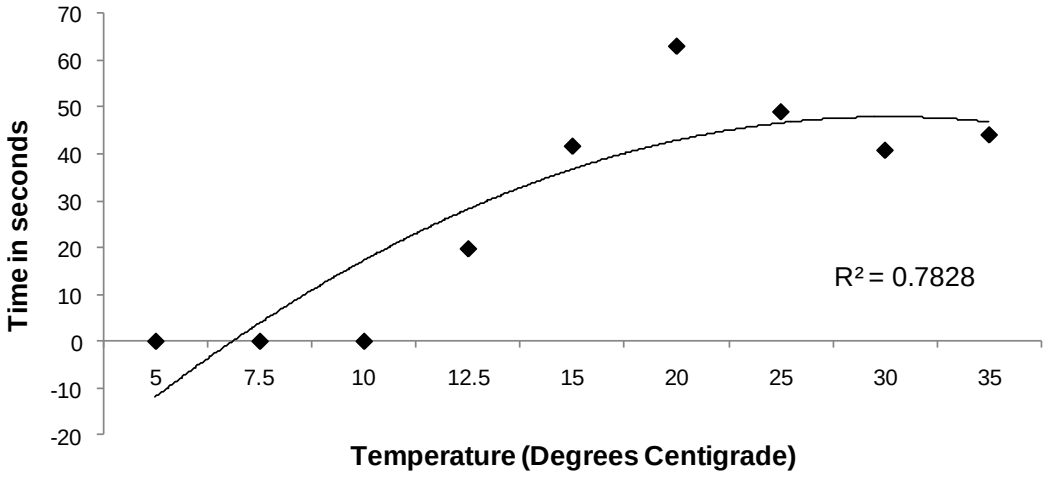


Figure 4.13 shows a clear peak in the time spent defecating, at 20^{o}C. No defecation was observed between 5 and 10^{o}C.

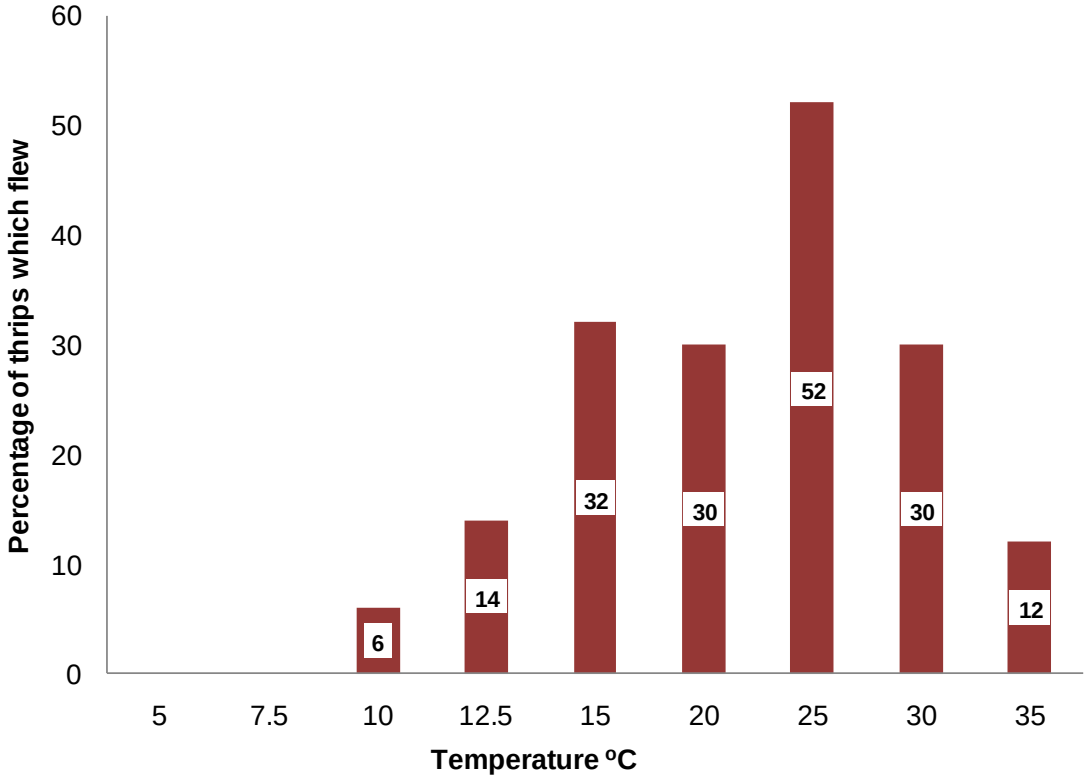
Figure 4.13 Back-transformed means for the effect of temperature on overall time spent defecating.



4.3.2 Flight Behaviour

Flight is the one key behaviour that is not represented in the previous analyses, as it is an instantaneous behaviour and so cannot be analysed for duration. Figure 4.14 shows the percentage of the 50 thrips which flew at each temperature.

Figure 4.14 The percentage of thrips which flew at each temperature.



A binomial test for the equality of two proportions was used to compare the proportions of thrips which flew at each temperature. The proportion which flew at each of the temperatures was compared individually with the proportion which flew at each of the other temperatures to test whether there was any significant difference. Table 4.12 gives the p-values for these comparisons (the 5^{o}C observations are excluded as no flights were made).

Table 4.12 The p-values for a binomial test of the equality of the proportions of thrips which flew at each temperature.

7.5	1.000							
10	0.079	0.079						
12.5	0.006	0.006	0.182					
15	<0.001	<0.001	<0.001	0.032				
20	<0.001	<0.001	0.002	0.053	0.829			
25	<0.001	<0.001	<0.001	<0.001	0.043	0.025		
30	<0.001	<0.001	0.002	0.053	0.829	1.000	0.025	
35	0.012	0.012	0.290	0.786	0.016	0.027	0.001	0.027
	7.5	**10**	**12.5**	**15**	**20**	**25**	**30**	**35**

The values in Table 4.12 agree with a generalised linear model (GLM) assuming a Bernoulli distribution and logit link function indicating a normal distribution of flights across the temperature range.

4.3.3 Leaf quality assessments

Not all behaviour categories were observed on all leaf types; Table 4.13 summarises the behaviours undertaken on each leaf type.

Table 4.13 Behavioural categories observed on each leaf type (**O** = behaviour observed, **A** = behaviour absent)

	Leaf types			
	Normal	Dry	Rotten	Oak
resting	O	O	O	O
walking	O	O	O	O
searching	O	O	A	A
feeding	O	O	A	A
grooming	O	O	O	O
defecating	O	O	O	O

Although all behaviour categories were observed on dry leaves, there was a significant reduction, in several categories, in the number of times behaviours were observed compared with normal leaves. Similar patterns were seen on rotten leek and on oak leaves. Records of the number of instances when the different behaviours were observed across the leaf types is summarised in Table 4.14.

Table 4.14 Total numbers of instances of each behaviour and the overall total number of observed behaviours on each leaf type.

Leaf type	**resting**	**walking**	**searching**	**feeding**	**grooming**	**defecation**	**Total**
Normal	24	203	75	59	105	25	491
Dry	17	88	6	2	52	4	169
Rotten	10	67	0	0	46	4	127
Oak	6	70	0	0	36	1	113

Table 4.14 reveals a very significant curtailment of the number of behaviours engaged in over the observation periods. On average a thrips on normal leaves could be expected to engage in 9.82 behaviours in 5 minutes. This number of behaviours was reduced to 3.38 on dry leaves, 2.54 on rotten leaves and just 2.26 on oak leaves.

4.3.5 Time spent engaged in a behaviour (leaf quality)

As this test was attempting to identify variability in the duration of individual behavioural events between the different leaf types, the fixed model term of interest was the interaction between leaf type and behaviour (leaftype.behaviour). The F-test in Table 4.15 shows that the effect of leaf type was statistically significant and the effects of behaviour and the model term leaftype.behaviour were highly significant.

Table 4.15 F-test showing the main effects of leaf type and behaviour and the interaction between leaf type and behaviour.

Fixed term	F statistic	Degrees of Freedom	Probability Value
leaftype	3.28	112.7	0.023
behaviour	13.39	537.7	<0.001
leaftype.behaviour	4.14	581	<0.001

Once again a $\log_{10}$ transformation was required to improve the normality of these data and Table 4.16 shows the mean values for the interaction between leaf type and the duration of each behaviour on this scale.

Table 4.16 Time per behavioural event: Means for the interaction between leaf type and behaviour on a $\log_{10}$ transformed scale (time per behavioural event).

Leaf type	Behaviour					
	resting	walking	searching	feeding	grooming	defecating
Normal	0.949	1.289	0.999	0.999	0.951	1.353
Dry	1.719	1.358	0.852	0.89	1.118	1.051
Rotten	1.461	1.287	-	-	1.431	0.996
Oak	0.904	1.514	-	-	1.08	1.24

Table 4.17 shows the means for the interaction between leaf type and the duration of each behaviour, back transformed from the $\log_{10}$ scale to a time scale

(seconds). This table reveals marked variation in the duration of different behaviours on the different leaf types.

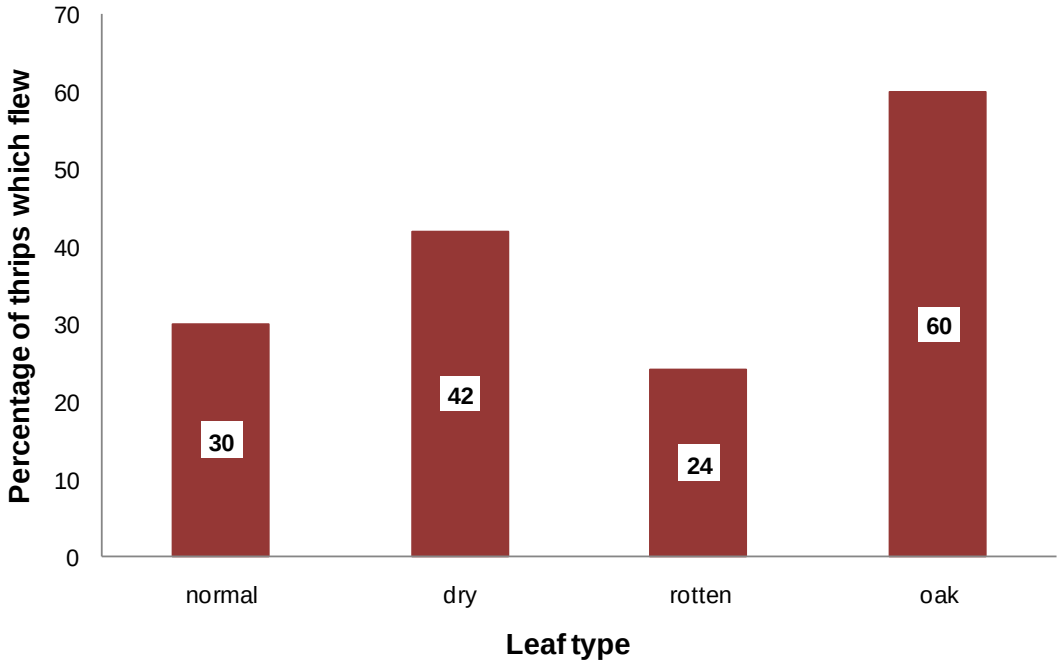
Table 4.17 Back-transformed means for the interaction between leaf type and behaviour (seconds).

Leaf type	Behaviour					
	resting	**walking**	**searching**	**feeding**	**grooming**	**defecating**
Normal	8.9	19.44	9.98	9.98	8.93	22.55
Dry	52.4	22.79	7.11	7.76	13.12	11.24
Rotten	28.9	19.37	-	-	26.99	9.91
Oak	8.01	32.69	-	-	12.02	17.4

4.3.6 Flight behaviour (leaf quality)

Flight is the one key behaviour that is not represented in the previous analyses, as it is an instantaneous behaviour and so cannot be analysed for duration. Figure 4.15 shows the percentage of the 50 thrips which flew from each leaf type. Both thrips on dry leaves and those on oak leaves flew more often than on normal healthy leek leaves, and indeed those on oak were twice as likely to fly.

Figure 4.15 The percentage of thrips which flew from each leaf type.



4.3.7 Transition Matrices

Two transition matrices were calculated for each temperature. The first matrix represents the number of times any thrips moved from activity i (row) to activity j (column). Transitions within activities were possible as transitions are based on a 5-second interval. A thrips which remained in the same activity for 11-15 seconds therefore had 2 transitions within that activity.

The second matrix for each temperature gives the proportion of thrips which moved directly between activity i (row) and activity j (column). For example, at 10^{o}C there were 24 transitions from the behaviour 'feeding', out of which 1 was to 'resting', 3 to 'walking' and 20 remained 'feeding'. These 24 counts were pooled from all the thrips at 10^{o}C. Row 4 (feeding) of the second half of Table 4.19 (10^{o}C) therefore has 0.42 (1/24) in the resting column, 0.125 (3/24) in the walking column and 0.833 (20/24) in the feeding column. The descriptions of behaviours are abbreviated in the tables and the abbreviations are:

RST: Resting
WLK: Walking
SRC: Searching
FED: Feeding
GRM: Grooming
DEF: Defecating
FLI: Flight
FAL: Fall

Rows 7 and 8 in each matrix contain only zeroes as behaviours 7 and 8 are absorbing states which means that once a thrips enters these behaviours it cannot exit them again or transition within them, they are instantaneous. Rows containing only * symbols are behaviours that did not occur at all at those temperatures and so are not considered. These four tables are included in the main text to illustrate the changes in association between behaviours that is observed across the temperature spectrum, the rest of this series of tables are in the appendix.

Table 4.18 illustrates the paucity of observed behaviours at 5^{o}C and shows that the vast majority of transitions are accounted for within the single behaviour of resting.

Table 4.18 Transition matrices for 5^{o}C, showing the number of times thrips moved from one activity to another (1st matrix) and the proportion of thrips which moved between activities (2nd matrix).

	RST	**WLK**	**SRC**	**FED**	**GRM**	**DEF**	**FLI**	**FAL**
RST	2494	32	0	0	0	0	0	0
WLK	40	424	0	0	0	0	0	0
SRC	0	0	0	0	0	0	0	0
FED	0	0	0	0	0	0	0	0
GRM	0	0	0	0	0	0	0	0
DEF	0	0	0	0	0	0	0	0
FLI	0	0	0	0	0	0	0	0
FAL	0	0	0	0	0	0	0	0

	RST	**WLK**	**SRC**	**FED**	**GRM**	**DEF**	**FLI**	**FAL**
RST	0.987	0.013	0	0	0	0	0	0
WLK	0.086	0.914	0	0	0	0	0	0
SRC	*	*	*	*	*	*	*	*
FED	*	*	*	*	*	*	*	*
GRM	*	*	*	*	*	*	*	*
DEF	*	*	*	*	*	*	*	*
FLI	0	0	0	0	0	0	1	0
FAL	0	0	0	0	0	0	0	1

Table 4.19 illustrates that an increase in temperature to 10^{o}C is associated with an increase in the range of behaviours displayed. Despite this the majority of transitions are still accounted for within the behaviours of resting and walking.

Table 4.19 Transition matrices for 10°C, showing the number of times thrips moved from one activity to another (1st matrix) and the proportion of thrips which moved between activities (2nd matrix).

	RST	WLK	SRC	FED	GRM	DEF	FLI	FAL
RST	1248	107	7	4	13	0	0	2
WLK	115	1028	6	0	10	0	2	7
SRC	6	8	11	0	0	0	0	0
FED	1	3	0	20	0	0	0	0
GRM	10	11	1	0	77	0	1	0
DEF	0	0	0	0	0	0	0	0
FLI	0	0	0	0	0	0	0	0
FAL	0	0	0	0	0	0	0	0

	RST	WLK	SRC	FED	GRM	DEF	FLI	FAL
RST	0.904	0.077	0.005	0.003	0.009	0	0	0.001
WLK	0.098	0.88	0.005	0	0.009	0	0.002	0.006
SRC	0.24	0.32	0.44	0	0	0	0	0
FED	0.042	0.125	0	0.833	0	0	0	0
GRM	0.1	0.11	0.01	0	0.77	0	0.01	0
DEF	*	*	*	*	*	*	*	*
FLI	0	0	0	0	0	0	1	0
FAL	0	0	0	0	0	0	0	1

Table 4.20 illustrates that in the middle temperature ranges, where the insects appear most active, there are clear associations between behaviours and that some behavioural sequences are more prominent than others.

Table 4.20 Transition matrices for 20°C, showing the number of times thrips moved from one activity to another (1st matrix) and the proportion of thrips which moved between activities (2nd matrix).

	RST	WLK	SRC	FED	GRM	DEF	FLI	FAL
RST	61	11	3	4	2	3	0	0
WLK	12	1153	46	35	71	13	5	4
SRC	2	37	147	11	11	7	0	0
FED	0	29	10	176	9	0	1	0
GRM	3	69	7	4	189	2	9	1
DEF	2	19	0	0	0	156	0	0
FLI	0	0	0	0	0	0	0	0
FAL	0	0	0	0	0	0	0	0

	RST	WLK	SRC	FED	GRM	DEF	FLI	FAL
RST	0.726	0.131	0.036	0.048	0.024	0.036	0	0
WLK	0.009	0.861	0.034	0.026	0.053	0.01	0.004	0.003
SRC	0.009	0.172	0.684	0.051	0.051	0.033	0	0
FED	0	0.129	0.044	0.782	0.04	0	0.004	0
GRM	0.011	0.243	0.025	0.014	0.665	0.007	0.032	0.004
DEF	0.011	0.107	0	0	0	0.881	0	0
FLI	0	0	0	0	0	0	1	0
FAL	0	0	0	0	0	0	0	1

In Table 4.21 it can be seen that as temperatures increase to 35°C there is an increased time spent in resting and walking behaviours, as was seen also at the low end of the temperature range. Sequences that are common at 20°C, such as transitions between walking and grooming are rarer and this is accompanied by a major increase in transitions within the resting behaviour, indicating a general reduction in activity.

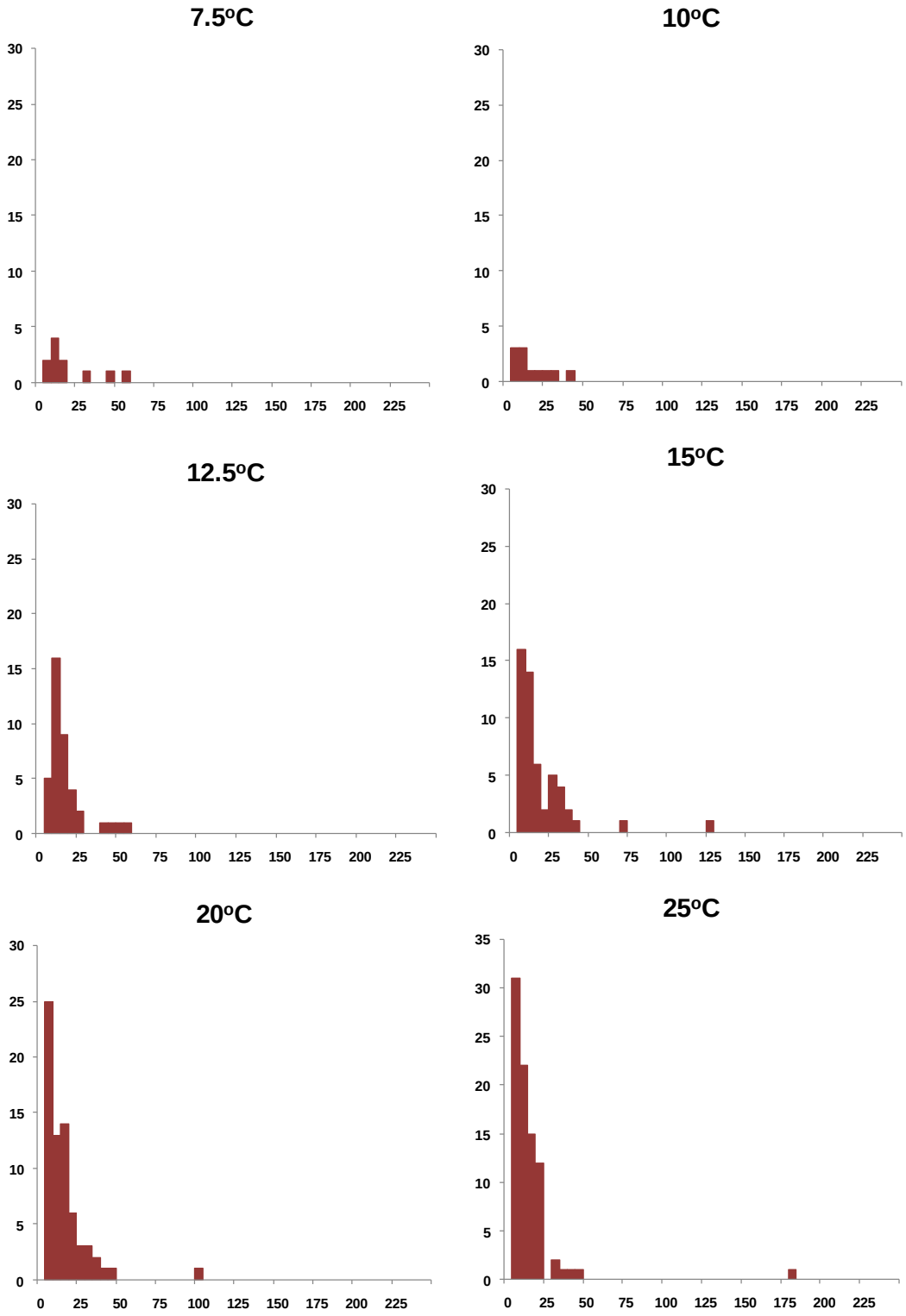
Table 4.21 Transition matrices for 35°C, showing the number of times thrips moved from one activity to another (1st matrix) and the proportion of thrips which moved between activities (2nd matrix).

	RST	WLK	SRC	FED	GRM	DEF	FLI	FAL
RST	583	38	6	4	5	1	0	0
WLK	38	1289	29	8	50	20	6	2
SRC	8	36	90	2	1	5	0	0
FED	3	6	5	19	2	1	0	0
GRM	5	45	8	1	252	8	0	0
DEF	5	17	2	1	9	168	0	0
FLI	0	0	0	0	0	0	257	0
FAL	0	0	0	0	0	0	0	94

	RST	WLK	SRC	FED	GRM	DEF	FLI	FAL
RST	0.915	0.06	0.009	0.006	0.008	0.002	0	0
WLK	0.026	0.894	0.02	0.006	0.035	0.014	0.004	0.001
SRC	0.056	0.254	0.634	0.014	0.007	0.035	0	0
FED	0.083	0.167	0.139	0.528	0.056	0.028	0	0
GRM	0.016	0.141	0.025	0.003	0.79	0.025	0	0
DEF	0.025	0.084	0.01	0.005	0.045	0.832	0	0
FLI	0	0	0	0	0	0	1	0
FAL	0	0	0	0	0	0	0	1

The transition matrices reveal some interesting patterns of behaviour. One of these is the large number of transitions between ‘grooming’ and ‘walking’ observed at temperatures above 7.5°C. Figure 4.16 illustrates how the length of time the thrips spent engaged in grooming prior to walking behaviours changed with temperature.

Figure 4.16 Times spent grooming prior to walking at the different temperatures (Y axes are number of instances of the behaviour, X axes are time spent engaged in the behaviour in seconds).



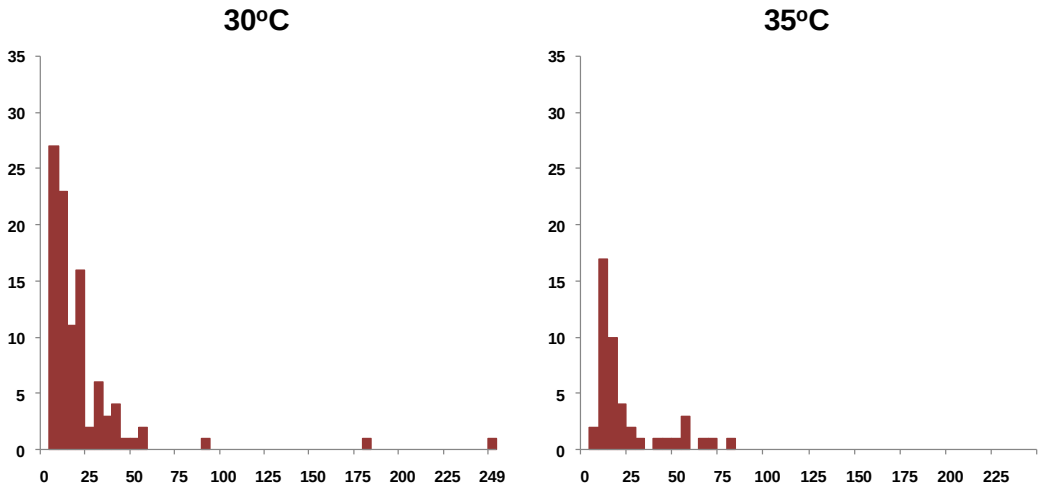
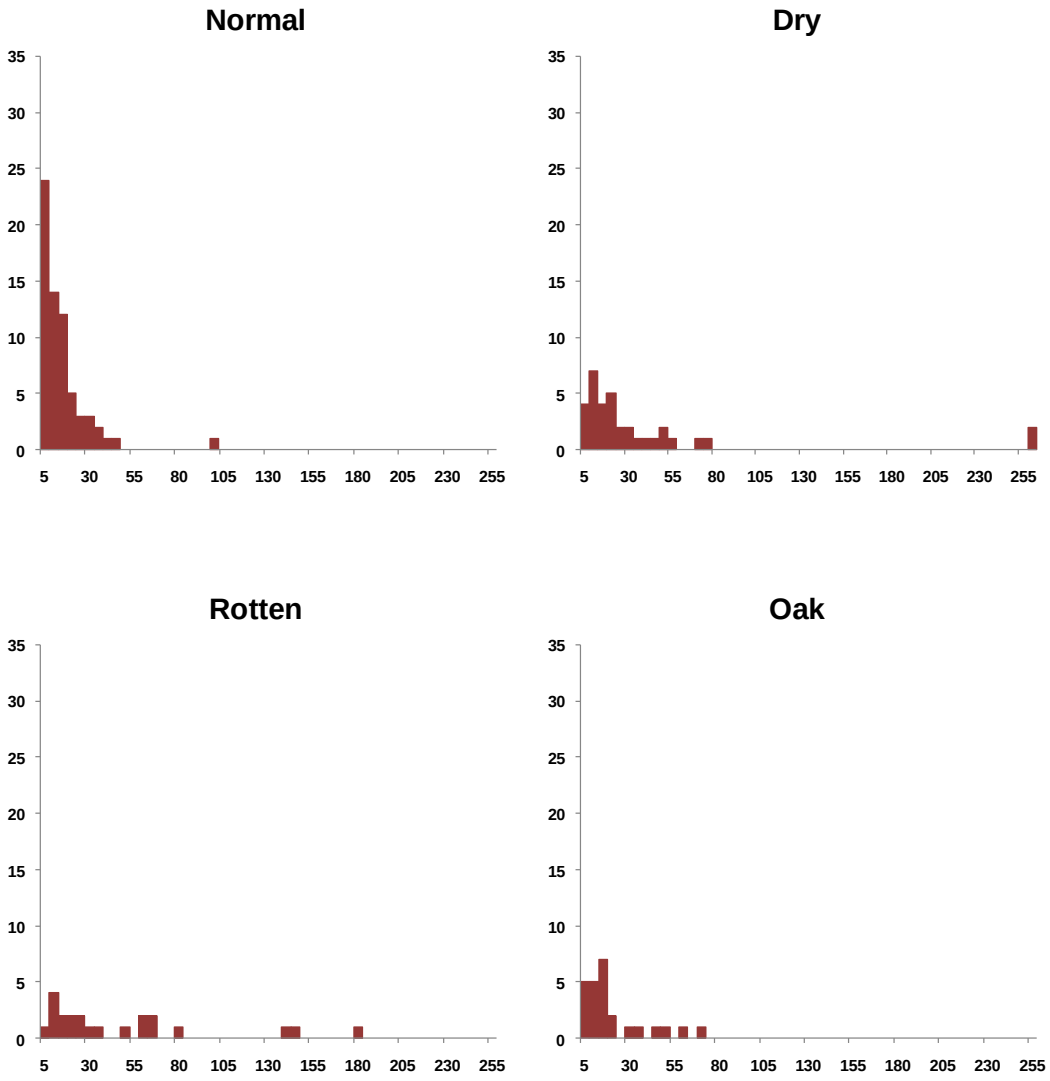


Figure 4.16 shows a clear trend of increasing association between the behaviour categories grooming and walking as temperatures increase up to 25^{o}C and a decline as temperatures further increase thereafter. The number of instances of the behavioural sequence increase, as do the average length of the behaviours.

Transition matrices were also calculated for the leaf quality assessments. Here patterns of association were highly variable indicating a decoupling of normal behavioural sequences when faced with sub-optimal feeding conditions. Figure 4.17 illustrates how the length of time the thrips spent engaged in grooming prior to walking behaviours changed with leaf type. The transition matrices are in the appendix.

Figure 4.17 Times spent grooming prior to walking on the different leaf types (Y axes are number of instances of the behaviour, X axes are time spent engaged in the behaviour in seconds).



4.4.0 Discussion

In this study a range of different behaviours exhibited by *T. tabaci* have been identified, classified, and their relationship with temperature investigated. The discussion will address these various aspects of the investigation in order.

4.4.1 Behaviour categories

The categories used to classify behaviours in this study contained a wide variety of often quite separate behaviours.

1. **Resting** – As resting was a low energy behaviour which was observed in the absence of more active behaviours, it was considered, for the purposes of this study, to be the default behaviour of *T. tabaci*. Thrips engaging in resting behaviours showed a clear preference for rough or undulating areas of the arena surface. Although each arena was as flat as possible, the squares were all cut from living leek tissue and so some variations and inconsistencies in the leaf surface were unavoidable. Thrips tended to align their bodies with ridges or troughs, most probably as an example of thigmotactic behaviour. The reasons why a thrips may be resting are many and not easily definable on a case by case basis. For example a thrips resting during a period of food digestion does not appear any different from a thrips that may be resting due to environmental constraints. They may be resting because conditions such as temperature are unsuitable for other behaviours, or it may be that they are exhibiting a diel periodicity in their behaviours as Whittaker and Kirk (2004) observed in *F. occidentalis* and as is discussed for *T. tabaci* in Chapter 5 of this thesis.

2. **Walking** – The rationale behind grouping all walking speeds into the same category was that the enactment of the behaviour itself was more important than the relative vigour with which it was executed; particularly as variation in speed between thrips seemed to be well represented across the temperature scale. The lack of edge-influenced walking behaviour displayed across the temperatures suggests that the size of the arena was not an important factor when it came to external influences on behaviour.

3. **Searching** – Easily definable searching behaviours were rarely observed at any of the temperatures and it is therefore difficult to glean a great deal of information about them. Care should be taken, though, when observing these behaviours, not to confuse side-to-side head movements, which were categorised here as searching behaviours, with the superficially similar movement of the head observed during antennal cleaning. Hunter and Ullman (1994) associated scraping of the antennae with the foreleg with leaf sampling and therefore searching and feeding in the species *F. occidentalis*. However the behaviours observed by Hunter and Ullman in *F. occidentalis* cannot be related directly to those observed here in *T. tabaci*. The behaviour in *F. occidentalis* associated with searching for suitable feeding locations involved not only scraping the antennae with the forelegs but scraping of the forelegs and antennae on the leaf surface, aspects of behaviour which were not observed in *T. tabaci*. Moreover the antennal scraping observed in *T. tabaci* was also observed in individuals whose antennae had become stuck together, a not uncommon side effect of them being moved by paintbrush (and which of course was excluded from data collection periods). Obviously in such a situation the behaviour was unquestionably related to grooming.

4. **Feeding** – The thrips commonly made several leaf probes before commencing full feeding. Leaf probing did not always lead to commencement of full feeding behaviour and in these cases it can be speculated that the thrips for one reason or another rejected the feeding site as unsuitable

5. **Grooming** – Ellington (1980) discussed the wing grooming behaviour of thrips in his study on the wing mechanics of *Thrips physapus* and reported that it consists of the sharp flexing upwards of the thrips' abdomen which allows its abdominal setae to fix the wing cilia into their flight positions. Ellington reported seeing this behaviour enacted anything up to a dozen times before the thrips was ready to fly. The extended periods of body flexing observed in this experiment often contained many more than a dozen instances of this behaviour, but they did retain the close link with flight

preparation, as the behaviour often, but not always, preceded flight. Another common wing grooming behaviour involved using the back leg to bend the wing away from the body and then run down the length of it, most probably to ensure good maintenance of the cilia and to ensure they were all sitting correctly and in the closed, or non-flight ready position. Ellington mentioned that *T. physapus* often gives its wings a 'thorough combing' post flight, probably for much the same reason. As the thrips had all been introduced to the arena using a brush, it is possible that the wing cilia may have been dislodged from their normal position in this process, provoking this behaviour.

4.4.2 Temperature and behaviour

One of the primary aims of this experiment was to observe how the behaviours exhibited by *T. tabaci* would change, both in type and execution, across a range of temperatures that would be commonly experienced by UK populations. It was for this reason that the temperature range of 5 to 35^{o}C was chosen, a range of temperatures that thrips could be expected to experience in the spring to autumn period in the field.

Unquestionably, thrips behavioural repertoires do change in concordance with prevailing environmental conditions. Like all animals they are constrained by the necessities of survival and reproduction and must make trade-offs to ensure they are successful in both endeavours. As discussed in Chapter 6, *T. tabaci* populations overwinter as adults in the UK and these adults do not exhibit the same range of behaviours as spring or summer adults. Overwintering adults do not reproduce for example. However although E. Koschier (personal communication) is working on one, the current lack of a complete or even partial survey of *T. tabaci* behaviours makes the definition of differences in behavioural repertoires particularly difficult. This study has shown that the behaviours exhibited by *T. tabaci* do change with temperature (Table 4.1), and this may be a good explanation of the trigger for the changes that are obviously occurring seasonably in field populations. And yet this is not the only influence, for indeed the study on diel periodicity in intra-plant distribution of *T. tabaci* in Chapter 5 and the study by Whittaker and Kirk (2004) both show an influence of time of day on the behaviours observed and perhaps more

importantly patterns of activity. A complex of factors is no doubt at work here, temperature, photoperiod and many other environmental factors playing their part.

Low temperatures may represent a physical barrier to behaviours for example; flight muscles might be too cold to contract. In such a case, each behaviour would be controlled by a threshold temperature, below which the thrips would be incapable of enacting it. For example the threshold temperature for flight in *T. tabaci* appears, from the information gathered in this study, to be close to 10^{o}C. The body temperature of insects is labile (Heinrich, 1974) and can be influenced by both the animal and its environment. Heinrich (1974) noted that apart from the flower-visiting insects and those that spend much of their time on the wing, the body temperatures of many groups of insects would not be appreciably higher than the ambient temperature. Insects that do maintain a higher temperature than their environment commonly do so by muscle movement and rarely keep it much above the minimum required for muscle function. Thermoregulation in all insects is hampered by the limitations of a small body size and therefore the rapidity with which generated heat is lost to the surrounding environment. When considering *T. tabaci*, these factors are particularly pertinent, they are indeed small insects and ones that spend little appreciable time generating heat through high energy flight activities; indeed we know the Thysanoptera as a whole to be weak and inconsistent fliers (Lewis, 1997c). For the majority of the time then it is clear that we can expect the body temperature of *T. tabaci* to closely track that of its surrounding environment. If such is indeed the case, then it is not a stretch to consider that during periods of low environmental temperature, *T. tabaci* will be physically incapable of engaging in some of its behaviours.

Alternatively the change in behavioural repertoires over temperature can be considered in the light of optimality and prioritisation. Models pertaining to the optimality of individual behaviours, or groups of such, are well established in the literature and are perhaps best represented by the works of Emlen (1966) and MacArthur and Pianka (1966) and the review by Pyke et al. (1977) on optimal foraging theory. However, such models do not generally address the situation under discussion here, i.e. how behaviours change due to environmental factors, but rather how behaviours change in order to optimise, whether it be the collection, maintenance or quality of, a currency; whether that be energy, heat, nutrients or mates etc. Most models of optimality in behaviour therefore address the choices

made by an animal, to feed on one leaf or another for example, rather than how those behaviours are affected by changes in their environment.

As most studies on behaviour focus on optimisation of the various currencies animals require, it is interesting to consider *T. tabaci* behaviours in such a light. Of course the majority of studies, and indeed models pertaining to behaviour, assume that only one currency is optimised at a time, for example, intake of nutrients. However at no time in its life cycle will *T. tabaci* be capable of concentrating solely upon the maximisation of a single currency whilst ignoring all other needs. Defence against predation, nutrient and energy gathering and successful reproduction are just some of the factors that will remain constantly important to an individual throughout its adult life. Such problems have been considered before (Sih, 1980) and indeed it is clear that compromises are made, optimisation of a single currency never being dominant to the complex of behaviours that will keep an animal alive. In order to understand what drives the variation in behavioural repertoire seen in *T. tabaci* over temperature, behaviours must be considered not in terms of pure optimisation for a fixed goal, but prioritisation of optimisation for a complex of changing goals. Lima and Bednekoff (1999) demonstrated just such a change in prioritisation of optimisation while investigating how animals must vary their allocation of feeding and anti-predation behaviours across a range of different risk situations. Perhaps the key to understanding this complex of changing goals lies in identifying what is the critical currency for the thrips at any one time. Traditional optimality models have rarely established whether the currency assumed to be being optimised is in fact the critical one to the animal (Price, 1997), and indeed the critical currency may change so frequently that identification of such may be all but impossible on a practical basis.

On a fundamental level then it is clear that external influences including temperature must have an effect on the way thrips prioritise their behaviours. Changing environmental conditions force thrips to adapt their behaviours to the requirements of short term survival and developmental needs. At the temperature extremes it may well be that the behaviours which maximise survival chances become more dominant to the detriment of the rest of the behavioural suite as the threats of, for example, desiccation or starvation increase. It may therefore be the case that the restricted behavioural repertoire seen in this experiment at the lower

temperatures represents a reprioritisation of behaviours by the thrips in order to cope with the specific environmental stress of extremely low temperatures.

A discussion of behaviours by temperature follows.

Lower temperature range (5-10^{o}C)

The variation in behavioural repertoires seen across this lower temperature range illustrates the direct effect that temperature has on *T. tabaci* behaviour. The increasing variety of behaviours exhibited with increasing temperature as shown in Table 4.1 further confirms the existence of threshold temperatures for particular behaviours, and the occurrence of those thresholds within the 5 to 10^{o}C range. These trends are consistent with some of the observations made of *T. tabaci* populations in the field as discussed in Chapter 6. At the extreme end of the range, at 5^{o}C, thrips spend the majority of their time inactive or simply walking, which corresponds closely to observations of overwintering adults Chapter 6, section 6.3.2. One explanation is that they are reducing energy expenditure to weather a period of poor environmental conditions, yet maintaining locomotive capability to ensure they can continue to avoid danger and seek shelter. The presence of feeding behaviours at 7.5^{o}C and the absence of flight may mirror the short feeding period seen on overwintering hosts in spring before migration to fresh hosts for reproduction. Certainly an individual capable of beginning nutrient and energy gathering earlier and at lower temperatures than its peers would convey a competitive advantage upon its first generation progeny, and indeed variation was seen, as not all individuals engaged in these behaviours at 7.5 and 10^{o}C (Table 4.3). The small numbers of individuals flying at 10^{o}C is a further indication of the variation in the capabilities of individual thrips to take advantage of prevailing environmental conditions.

The increasing number of observed behaviours as temperature increased and the generally increasing length of those behaviours indicates that overall activity levels increased with temperature. Less time spent inactive and more time in active behaviours dependent on higher temperatures, such as flight and feeding, reveals a direct effect of temperature on energy expenditure by the thrips. Although the observations in this study did not include damage inflicted on the leaf square arena by the thrips, it is likely that as activity levels and energy expenditure increases, the damage potential of the individual will also increase.

Middle temperature range (12.5-20^{o}C)

Engagement in the full behavioural repertoire at 12.5^{o}C indicates that the absolute low temperature thresholds for *T. tabaci* behaviours are being exceeded at this point. This middle range of temperatures may represent the thermal niche for this population of *T. tabaci* in that it defines their physiological and metabolic optima, a theory of the influence of temperature espoused by Magnuson et al. (1979) in their work addressing temperature as an ecological resource. Magnuson et al. (1979) suggested that temperature should be viewed in the way that ecologists have previously viewed more obvious 'resources' such as food, and that individuals whose 'temperature resource' is optimal will be able to conduct important biological processes such as growth most efficiently. As with the lower temperature range, much variation between individuals and their ability to exploit prevailing temperature conditions remains at 12.5^{o}C, only half are feeding at this temperature for example. This is an indication that if 12.5^{o}C is indeed within the temperature niche that *T. tabaci* requires for optimum efficiency, it is a niche which varies with individuals and that this temperature is perhaps its lowest extreme. This is a view supported by the frequency with which behaviours occurred at this temperature, though active behaviours were much more common than at 10^{o}C they remained much less frequent than at the rest of the middle temperature range. A reason for defecation being the behaviour which has the highest threshold could be that it is only at these higher temperatures that the digestive systems of the thrips are acting normally, and so even though feeding occurs at lower temperatures, digestive transit and faecal matter processing may be significantly extended.

If 12.5^{o}C perhaps represents the lower limit of *T. tabaci's* optimal temperature niche, then 20^{o}C must be at its centre. This was the only temperature at which the mean number of feeding events per thrips exceeded 1 and it also represents the lowest number of observed resting periods. The crop damage potential for this population of *T. tabaci* therefore peaks at 20^{o}C and indeed as is discussed in Chapter 3 their generation time is low at this temperature. Flight activity essentially doubles over this temperature range and is another indication that activity levels are still increasing up to 20^{o}C. This temperature corresponds closely with what might be expected in the field in the mid-summer months when populations are high and damage to crops is often significant.

High temperature range (25-35^{o}C)

Activity levels peak at 30^{o}C, with the highest number of individual behaviours observed by the thrips. Yet at this point the influence of high temperature restrictions on behaviour are already becoming evident in the reduced number of observed feeding events and in the increasing time spent resting. Indeed by 35^{o}C, these trends are quite marked. It may well be that, for example, the increasing danger of desiccation at these higher temperatures is beginning to restrict behaviours. The peak of flight activity at 25^{o}C, above that of feeding at 20^{o}C, perhaps mirrors the sequence of events seen in the field in late summer as discussed in Chapter 6. In the field, the background level of flight activity of summer populations is dwarfed by a series of large flights observed on particularly warm days in late July and August which may be when healthy adults move off summer hosts in search of potential overwintering ones. The overall reduction in higher energy behaviours observed at 35^{o}C and the increase in resting behaviours is most likely to be the beginning of a trend that would be exposed if further higher temperature observations had been made. Indeed if the temperature range was extended above 20^{o}C, as much as it is extended below, perhaps behavioural repertoire restrictions such as those seen at extremely low temperatures would become evident also.

Thrips tabaci can most certainly survive and continue to function at a range of temperatures. However this study has revealed that temperature appears to restrict behaviour, except within a fairly narrow range around 20^{o}C. Above and below this temperature, the time spent engaged in active behaviours reduces fairly quickly and is mirrored by an increase in 'default' resting behaviours, suggesting that the environment is no longer optimal for the thrips.

4.4.3 Leaf quality and behaviour

Field observations at Warwick HRI conducted between 2005 and 2008 (discussed in Chapter 6) indicated that there was some influence of plant quality on the inter-plant distribution of thrips with a clear preference for young and fresh plants over older plants or those in poorer condition. This experiment was undertaken to further investigate this phenomenon, and the potential effect of plant quality, on thrips behaviour. The data obtained show a clear correlation between what has been observed in the field and this experiment. Thrips exposed to leek

foliage of varying quality behaved very differently. On rotten leaves the thrips' behavioural repertoire was seriously curtailed, they did not engage in any feeding-related behaviours at all. Although both types of feeding-related behaviour, were observed on dry leaves, the number of instances was so low that in fact they might be considered insignificant (Table 4.14). The fact they were observed at all lends weight to the argument that, as discussed in section 4.4.2, thrips are capable of engaging in all their behaviours at 20^{o}C but are, in this case, restricted by a secondary factor, the quality of the host plant. Overall changes in observed behaviour were also considerably reduced on the two low-quality samples of leek, again indicating that the host plant was unsuitable. It might be expected that an unsuitable host plant would encourage increased emigration, yet flight activity showed a significant increase only on dry leaves. Rotten leaves induced comparable, though slightly lower, levels of flight activity to healthy leaves. One explanation for this might be that dry leaves represent a more pressing threat to thrips survival than leaves which are merely of poor quality but still moist. Microclimates formed around the leaf surface may be more similar in humidity and temperature on rotten leaves than on dry ones and an increased danger of desiccation may be a more pressing incentive to emigrate.

Behaviours on the oak leaf samples were much as might be expected for a non-host plant. Behavioural repertoires were curtailed, with no feeding or feeding related behaviours at all, and the overall number of instances of behaviour was much lower than on leek leaves. The reason for this, and also the significantly increased incidence of flight activity, which was twice that on healthy leek leaves, is the unsuitability of the host material and the capacity of the animal, at 20^{o}C, to engage in flight behaviour as a means of locating a new host plant. It is highly likely that, if the observation period on oak leaves were to be extended a little longer, all the thrips would have been observed engaging in flight. Riefler and Koschier's (2009) newly published paper on behavioural patterns of *T. tabaci* on leek and cucumber also identifies differences in the amount of time the thrips spent in various behaviours on two different crops, indicating that the host plant environment has a direct influence on behaviours.

4.4.4 Behavioural sequences

There are sequences in the order in which thrips engage in their behaviours and aspects of these behaviours and sequences are influenced by environmental temperature. On a fundamental note, the majority of observed behavioural sequences are what one might expect to see, for example, the high percentage of thrips engaged in wing grooming directly before flight.

Limitations imposed by the size of the dataset required to confidently and robustly identify sequences involving multiple behaviours over extended periods means that only direct sequences of two behaviours were considered here. Despite this, it is clear that temperature has a direct effect on such sequences and how they are expressed. The sequence highlighted in Figure 4.16 illustrates this well. The relationship between two behaviours was not merely an expression of the varying number of behaviours exhibited at the different temperatures, since in many cases, sequences became more or less prominent as temperatures changed. An example is the relationship between grooming and walking, which accounted for only about 16% of transitions at 7.5^{o}C and yet accounted for about 27% at 25^{o}C, a clear growth in association between these behaviours as temperature increased. The reason for this discrepancy may be that certain groups of behaviours are naturally expressed together in order to achieve certain goals. For example, searching must be associated with feeding if nutrient and energy gathering are to be successful. As temperatures change, it may well be that relationships within these behavioural complexes change too. An example would be that as temperatures become more conducive to feeding, then locomotive behaviours will become increasingly associated with searching behaviours so that suitable feeding sites can be located. If such thinking is applied to the observed diel periodicity in intra-plant distribution, for example, as discussed further in Chapter 5 then daily changes in temperature can be seen as the direct instigator of necessary pre-flight locomotion by which the thrips reach suitable positions on the plant for take-off.

4.4.5 Conclusion

This study has demonstrated that both temperature and leaf quality have a direct influence upon the behaviour of *T. tabaci* in terms of which particular behaviours are expressed, the length and frequency of these behaviours and their relationship with one another. As discussed in Chapter 7 the combination of this

information and that of the influence of temperature on thrips' development and generation times goes some way to helping to identify periods when the population may pose the highest potential threat to crops and also when they might be most vulnerable to control.

What is abundantly clear from both this study and the study on development (Chapter 3) is that intra-specific variation is significant. Such intra-specific variation was discussed in terms of separate populations by Mound (1997) in his discourse on the biological diversity of the Thysanoptera. In his review he considered that short term effects such as changes in temperature could have a significant influence upon the body size and colour of *T. tabaci*. Such statements are supported by observations made during this project, as highlighted in Chapter 6. Short term environmental influences also affect behaviour, and indeed, in order to further explain variation in individual physical and behavioural characteristics, it is perhaps necessary to look more closely than the level of the population and to the level of the generation or individual. Wide variation in the ability to cope with, and exploit, disparities in temperature in their environment, may highlight not only genetic variation within the population, but variation in the individual life histories of the animals themselves. It is not unreasonable to consider that variations in the microclimate and food gathering success of immature individuals may have an effect upon the physical and behavioural capabilities of the resultant adult. This would certainly explain some of the variation between individuals and their capabilities and might go some way further to explain the unpredictability of populations and damage under field conditions.

Although the adult thrips used in this study appeared healthy, oviposition was not observed. This would have been a boon as it would have allowed some insight into the influence of temperature on population growth rates. However as Sakimura (1937) observed that an average *T. tabaci* female produced just 80 eggs in her lifetime, in a time period of, on average, 50 days, the lack of such behaviour in this study is not unexpected. The length of the observation period is one aspect of the study that it would certainly be advantageous to alter, if it were to be repeated.

Longer observation periods, although they would seriously increase the time investment required for data gathering, might allow for an increased understanding of how the duration of certain behaviours is affected by temperature. They would also reduce the effect that the curtailment of behaviours (ones that ran over the end

of the 5 minute observation period) had on the amount of data available to analyse the times spent in particular behaviours and for behavioural sequences.

The nature of the arena and the time of day at which data were gathered may provide further limitations to this study. The arena itself was necessarily small so that the thrips could be constantly observed in detail. This small size did not appear to have any direct influence on behaviour, beyond the occasions when the thrips fell off the arena. Edge-following behaviours, which could have had a significant influence, were notable by their absence. It should be pointed out, however, that particularly vigorous individuals at the higher temperatures quickly covered the whole arena and, in so doing, may have been more likely to engage in flight behaviours in order to search out fresh patches. Furthermore the arena was horizontal and not vertical, a restriction imposed by the necessity for close observation and handling, and also by the method in which the thrips were prevented from escaping the host leaf, a water-filled moat. Although in the field, thrips on leek and salad onion are likely to spend the majority of their time orientated vertically on plant leaves, it was considered that the influence of this on behaviour was likely to be associated with factors such as walking direction, rather than walking overall and so was a reasonable compromise. Obviously there may have been some influence of leaf orientation on behaviours such as flight, which, in the field, has been related to the location of the thrips on the host plant (Chapter 5). However, as all the observation periods in this experiment were comparable, observations on the influence of temperature and leaf quality on such behaviours remains valid.

Time of day may have had an influence on the study also. All observations were made during the period between 10am and 5pm and this was uniform across the temperatures. Thrips were kept in a simple L16:D8 light cycle and, obviously, at a constant temperature. However as discussed in Chapter 5, there is a diel periodicity in the intra-plant distribution of thrips and therefore most likely in their expressed behaviours. Although such an influence may have been small, due to the standard environmental conditions, the possibility of some variation due to diel periodicity cannot be ruled out. Therefore if this experiment were to be repeated the observation times should be standardised to rule this out.

Chapter 5: Improving the targeting of thrips control measures

Chapter 5 describes two experiments which, although independent of one another, nevertheless both address the targeting and control of *T. tabaci*. Section 5A addresses the intra-plant distribution of UK *T. tabaci* populations and whether they are influenced in that distribution by the natural cycle of environmental conditions throughout the day. Section 5B then goes on to investigate whether control measures focusing on potential periods of vulnerability identified in the intra-plant distribution of *T. tabaci* can be exploited using a potential novel control technique involving irrigation.

5A: The diel periodicity of the intra-plant distribution of *Thrips tabaci*

5A 1.0 Introduction

The onion thrips, *Thrips tabaci* (Thysanoptera, Thripidae) is a major pest of *Allium* crops in the UK and is the main arthropod pest of both leek and salad onion (Lewis, 1997b, Garthwaite et al., 2003). Recent research has demonstrated increasing levels of pesticide resistance in UK populations, (DEFRA, 2007a). However, according to growers, control using chemical pesticides has always been poor. The problem lies with the cryptic nature of *T. tabaci* and the difficulty growers have in ensuring that control applications reach their intended target. There are several advantages for *T. tabaci* in exhibiting cryptic behaviour; thrips in general are known to be particularly vulnerable to desiccation and so hiding at the centre of the plant, where the microclimate is most humid, is likely to be a behavioural adaptation. Furthermore, hiding within the foliage should minimise their encounters with predators and parasitoids. However, it does pose a difficult question, which is: how can growers target a pest that spends so much of its time in locations virtually inaccessible to foliar sprays? One way would be to improve targeting efficiency by identifying periods of increased vulnerability.

Theunissen and Legutowska (1991b) investigated the intra-plant distribution of *T. tabaci* on leek and established that the majority of the active population was located in the shaft of the plant, where they were least vulnerable to control by chemical sprays or natural enemies. They recommended good forecasting techniques

and improved spray equipment. Forecasting *T. tabaci* generations based on Edelson and Magaro's (1988) paper on the effect of temperature on *T. tabaci* development, has gained favour in some northern European countries and is considered to be a reliable tool in certain areas (Villeneuve et al., 1996, Martens and Plovie, 2007). However, it is not wholly accurate and some discrepancies between predicted population peaks and actual population peaks occur in some seasons (Villeneuve et al., 1999). This forecasting method has not proved to be so reliable for UK populations since Collier *et al*. (2007) were unable to determine a consistent relationship between periods when peak numbers of thrips were captured on sticky traps and accumulated day-degrees.

North and Shelton (1986a) identified a tendency for *T. tabaci* to accumulate on the underside of horizontally orientated cabbage leaves, a behaviour they associated with avoidance of rain. Sites *et al*. (1992) investigated the possibility that the intra-plant distribution of thrips could be affected by time of day, and therefore all the physical factors associated with it (temperature, light intensity, humidity etc.). They were able to show that, in midsummer, there was a tendency for thrips to aggregate on the apical half of leaves in the early afternoon, when temperatures were highest. This may reflect dispersion behaviour, as the thrips climb to higher parts of the host plant to initiate flight. It also highlights the importance of understanding the diurnal periodicity of the intra-plant distribution of *T. tabaci* to improve the timing of insecticide sprays.

In the knowledge that environmental factors such as temperature could influence the intra-plant distribution of *T. tabaci*, a field experiment was done to test the hypothesis that 'the intra-plant distribution of *T. tabaci* is affected by the natural cycle of environmental conditions throughout the day', with the aim of identifying a predictable pattern of distribution which might help to target control measures.

5A 2.0 Material and methods

Plant material

The salad onion varieties White Lisbon [*A.cepa*] and Guardsman [*A.cepa/ A.fistulosum* cross] were direct-drilled into the field at Warwick HRI, Wellesbourne, Warwickshire, UK on 10 May 2006 at a rate of 50 seeds/m. The plot was 8 m in length and 2 x 1.82 m beds wide. Each bed contained 4 rows, two of each variety arranged alternately. Further plots were drilled throughout the summer on 2 June, 30 June, 31 July and 31 August respectively to ensure a constant supply of fresh plant material. The plots were situated close to a leek plot which had been maintained overwinter as a source of *T. tabaci* and upon which a large population of thrips had overwintered.

Sampling

Sampling took place over a series of eight replicate days between 22 June and 17 October 2006. Samples were taken five times a day from the two varieties of salad onion and five plants of each variety, selected at random, were sampled on each occasion. The first sample was taken at dawn and the last at dusk; the remaining three samples were spaced evenly throughout the day (dependent on the times of dawn and dusk) with a mid morning, early afternoon and late afternoon sample in each case. Sampling was destructive and the plants were separated into three sections: stem, basal half of leaves and apical half of leaves. The three sections were sealed in separate plastic bags and taken back to the laboratory for assessment. The numbers of adult and larval *T. tabaci* on each section of each plant were recorded. Dead adults and larvae were ignored.

Data analysis

A generalised linear model (GLM) was fitted separately to the adult and larval data. For both data sets, a GLM assuming a Poisson distribution with a log link function was fitted for the total counts (for each time point). The factors of time, date and variety were used to create the model. Some non-orthogonality was present in the analysis of the adult data; in effect there was some interaction or correlation between the different factors.

All data were summarised using Microsoft Excel (Microsoft Corporation) and analysed using Genstat for Windows (VSN International Ltd.).

5A 3.0 Results

Temperatures

The maximum and minimum temperatures recorded at Warwick HRI, Wellesbourne on each of the eight days of data collection are contained in Table 5.1.

Table 5.1 Maximum and minimum temperatures (^{o}C) for each of the recording days.

Date	Maximum Temperature (^{o}C)	Minimum Temperature (^{o}C)
22/06/2006	18.9	10.1
12/07/2006	25	8.3
26/07/2006	29.9	18.7
09/08/2006	20	14.7
23/08/2006	19.3	13.2
06/09/2006	26.6	16.3
20/09/2006	22	11.8
17/10/2006	16.1	9.1

Adults

The presence of non-orthogonality in these data made it difficult to choose the 'best' model based on the overall statistical significance, as fitting the interaction terms in a different order affected their individual significance. Table 5.2 demonstrates this well since the approximate χ^2 probability value for the position.variety interaction term changed depending on where in the sequence of terms it was fitted.

Table 5.2 Approximate χ^2 probability of the interaction term position.variety when it is fitted in a different order within the GLM.

Model position + time*date*variety + one of the following	Approx Chi pr.
position.variety + position.time + position.date + 3-factor interactions	0.002
position.time + **position.variety** + position.date + 3-factor interactions	0.007
position.date + **position.variety** + position.time + 3-factor interactions	0.128
position.date + position.time + **position.variety** + 3-factor interactions	0.069

The most important interaction term for this study was position.time as this describes the relationship between the location of adult thrips and time of day. As this experiment was designed to investigate this interaction it was important to discover whether it was statistically significant in isolation. Table 5.3 shows an accumulated analysis of deviance table for the GLM and shows the deviance, mean deviance and approximate χ^2 probability for each of the interactions.

Table 5.3 **Adults:** Accumulated analysis of deviance table for the full model. The terms have been fitted based on decreasing mean deviance.

Change	d.f.	Deviance	Mean deviance	Deviance ratio	Approx chi pr.
+ positions + times + dates + varieties + times.dates + times.varieties + dates.varieties + times.dates.varieties	81	1053.6303	13.0078	13.01	<.001
+ positions.dates	14	128.2061	9.1576	9.16	<.001
+ positions.times	8	68.7646	8.5956	8.60	<.001
+ positions.varieties	2	5.3382	2.6691	2.67	0.069
+ positions.times.varieties	8	16.4838	2.0605	2.06	0.036
+ positions.times.dates	56	86.2022	1.5393	1.54	0.006
+ positions.dates.varieties	14	12.2562	0.8754	0.88	0.586
Residual	56	14.3198	0.2557		
Total	239	1385.2012	5.7958		

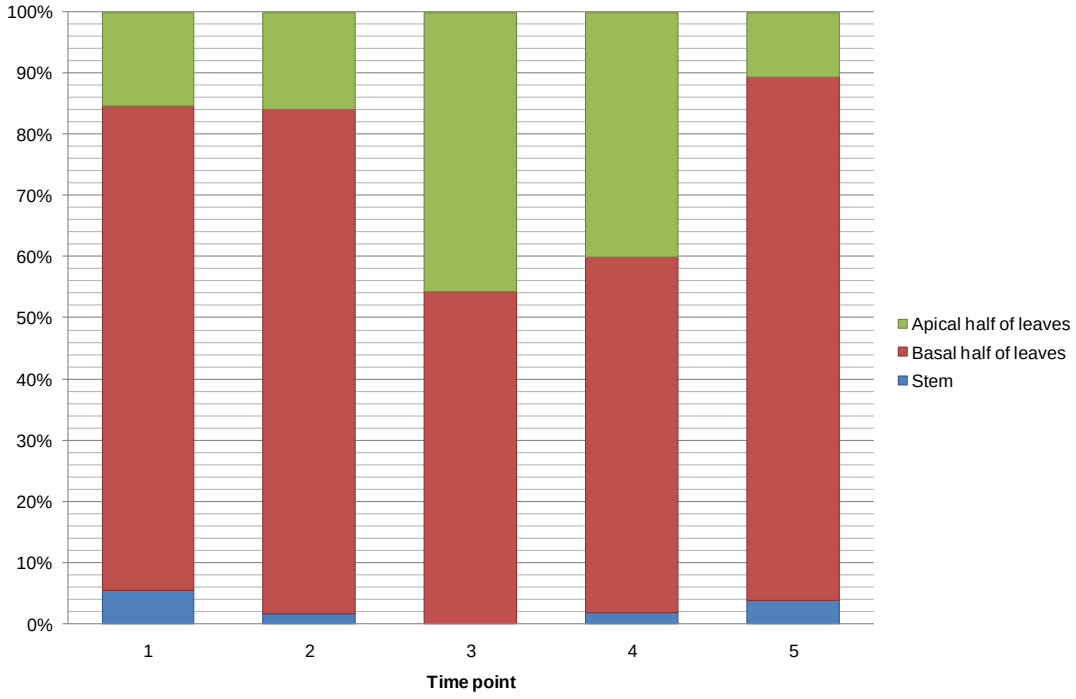
The interaction position.time was highly significant. This means there was a distinct correlation between time of day and the position of *T. tabaci* adults on the plant.

The majority of adults were found on the basal section of the plant throughout the day (Table 5.4). There were hardly any insects on the stem and this was the case across all time points. Time points 3 and 4 were particularly interesting and they correspond to the early and late afternoon sampling times. At these time points there was a clear and statistically significant change in distribution, with a much higher proportion of adults occupying the apical half of the leaves. The level of occupancy of this plant section was 3 to 4 times higher than at any other time of day. Figure 5.1 illustrates this change in distribution.

Table 5.4 Predicted proportions of expected *T. tabaci* adult numbers on the different plant sections at the different times of day.

	Time 1 Dawn	**Time 2** Mid morning	**Time 3** Early Afternoon	**Time 4** late afternoon	**Time 5** Dusk
Apical half of leaves	0.1532	0.1587	0.4575	0.4000	0.1068
Basal half of leaves	0.7928	0.8254	0.5425	0.5818	0.8544
Stem	0.0541	0.0159	0.0000	0.0182	0.0388

Figure 5.1 Predicted percentage of the adult *Thrips tabaci* population occupying different sections of salad onion plants throughout the day.



Inspection of the χ^2 probability for the interactions in the analysis of deviance table (Table 5.2) shows that in addition to the position.time interaction term, the position.date interaction term was also statistically significant. There was, therefore, a difference between the *T. tabaci* distributions observed on the different days of the experiment. There was, however, no statistically significant interaction between the

adult thrips' distribution and variety, indicating that the thrips' distribution was unaffected by the host plant.

Larvae

Table 5.5 shows an accumulated analysis of deviance table for the GLM and shows the deviance, mean deviance and approximate χ^2 probability for each of the interactions.

Table 5.5 **Larvae:** Accumulated analysis of deviance table for the full model. The terms have been fitted based on decreasing mean deviance.

Change	d.f.	Deviance	Mean deviance	Deviance ratio	Approx chi pr.
+ positions + times3 + dates + varieties + times3.dates + times3.varieties + dates.varieties + times3.dates.varieties	81	9834.8358	121.477	121.42	<.001
+ positions.varieties	2	20.8239	10.4119	10.41	<.001
+ positions.dates	14	109.5333	7.8238	7.82	<.001
+ positions.times3	8	24.1458	3.0182	3.02	0.002
+ positions.times3.varieties	8	28.1337	3.5167	3.52	<.001
+ positions.dates.varieties	14	27.6919	1.9780	1.98	0.016
+ positions.times3.dates	56	64.7198	1.1557	1.16	0.199
Residual	56	21.3553	0.3813		
Total	239	10131.2395	42.390		

Unlike the adult data, there was no problem with non-orthogonality in this analysis and different sequences of terms in the model did not alter the significance of the main interactions or effects.

The vast majority of larvae occupied the basal half of the leaves and remained there throughout the day (Table 5.6). This was true across both varieties and for every sampling date during the experiment. Although there was some movement between zones, it was undertaken by very a small percentage of the overall larval population.

Table 5.6 Predicted proportions of expected numbers of *T. tabaci* larvae on the different plant sections at the different times of day.

	Time 1 Dawn	**Time 2** Mid morning	**Time 3** Early Afternoon	**Time 4** late afternoon	**Time 5** Dusk
Apical half of leaves	0.0045	0.0147	0.0157	0.0226	0.0088
Basal half of leaves	0.9761	0.9706	0.9807	0.9662	0.9779
Stem	0.0194	0.0147	0.0036	0.0113	0.0133

5A 4.0 Discussion

Although the majority of adult thrips are to be found on the basal half of the leaves throughout the day, a large proportion of them make a regular and predictable migration to the apical half of the leaves in the early afternoon. This supports the findings of Sites *et al.* (1992) whose studies on *T. tabaci* in Texas identified a comparable shift in intra-plant distribution on warm summer days. In Chapter 4 it is demonstrated that temperature has a direct effect upon the activity and behaviours of *T. tabaci*, including its flight behaviours. The increased warmth experienced during this period of the day is likely to encourage more vigorous activities and will allow behaviours such as flight, which require higher temperatures, to occur. Indeed Sites *et al.* (1992) directly linked this distribution change with flight and also noted a drop in adult density sampled at those times, indicating that a significant proportion of the

population was ‘on the wing’. A decrease in adult density was not observed in this investigation. However, the temperatures experienced were far lower than those observed by Sites *et al.*, and therefore it is likely that the number of adults engaged in flight activity was far lower too. In Chapter 4 it is demonstrated that a temperature of 25^{o}C is required before the percentage of *T. tabaci* which engage in flight activity rises above 50%. Despite this, targeting of control applications in the early afternoon, when the highest proportion of the population is vulnerable, might well lead to an increase in efficacy.

The absence of fluctuations in the distribution of larvae would seem to indicate that daily changes in temperature and other environmental factors have less effect on their activities. There are several reasons for this. Firstly, larvae have much less reason to disperse around the plants than adults since they are not involved in activities such as flight or reproduction and so do not need to search out locations on the plant where these behaviours might be more successful. Moreover, feeding is their main activity, something which would tend to keep them away from the more mature and less succulent areas of the leaf. Secondly, larvae have several pressing reasons to avoid the upper leaf, chiefly the threat of desiccation, but also the increased danger of predation. Sites *et al.* (1992) did not record larval distribution and so no comparison can be made in this case.

One of the main reasons why *T. tabaci* control strategies are ineffective on commercial crops is the lack of accurate information on where and when treatments should be targeted. The intra-plant distribution of *T. tabaci* is crucial to this and this experiment has shown how that distribution fluctuates through the day in a UK population. Based on these data recommendations to growers to focus their spraying efforts in the early afternoon, and to target warmer days when *T. tabaci* is likely to be more active, could be made in order to increase the efficacy of such control measures.

5B: The use of irrigation for the control of *Thrips tabaci*

5B 1.0 Introduction

Conversations with several salad onion growers indicated that they believed that the application of irrigation was a relatively effective method of controlling *Thrips tabaci* populations and that, sometimes, this approach was more effective than the use of insecticides. Harris et al. (1936) also reported dramatic population declines of *T. tabaci* on onion plants following periods of adverse weather including heavy rain and hail. A field experiment was undertaken at Wellesbourne during summer 2006 to test the hypothesis that 'regular overhead irrigation reduces the numbers of adult and larval thrips on salad onion plants'. The four experimental treatments were chosen to cover situations which might occur in a commercial crop or that would be easy to replicate on a commercial scale if required.

5B 2.0 Materials and Methods

Experimental design

The experiment was conducted in the experimental area containing the mobile rain covers at Warwick HRI, Wellesbourne. These covers can be used to protect part of the experimental area from rainfall. The covers move automatically over the 'dry' area when rainfall is detected by a sensor. The sensor is quite sensitive and is activated even in very light rainfall.

Salad onion plants were grown in plots which were subjected to four experimental treatments, each of which was replicated twice:

1: Control – The salad onions were irrigated only when necessary using seep hoses. No overhead irrigation was applied to the plants, although they were exposed to normal rainfall.
2: Dry – The salad onions were protected from rain by the mobile rain covers and were irrigated only by seep hose.
3: Irrigation Morning – The salad onions were irrigated twice weekly between 09:00 and 10:00 using overhead irrigation.
4: Irrigation Afternoon - The salad onions were irrigated twice weekly between 13:00 and 14:00 using overhead irrigation.

The method of irrigation and the amount of water applied were identical for the two irrigation treatments, the only difference being the time of day that water was applied. Water was applied using a spinning sprinkler system which produced fairly large water droplets as might be expected in a commercial situation; 7 mm of water was applied on each occasion and this is close to the amount used by commercial growers. Two application timings were used because there was a suggestion that the intra-plant distribution of thrips may differ during the day and that a change in location might affect their susceptibility to irrigation.

Plant material

The salad onion varieties White Lisbon [*A.cepa*] and Guardsman [*A.cepa/ A.fistulosum* cross] were direct drilled into the field plots on 10 May 2006 at a rate of 50 seeds/m. A total of 8 plots were drilled in two replicates blocks of 4 plots; each block of 4 plots being laid out in a line. Each plot was 8 m in length and 2 x 1.82m beds wide. Each bed contained 4 rows, 2 of each variety arranged alternately. Each block of 4 plots consisted of one of each of the 4 treatments, the positions of which were randomised within the block.

Thrips

The experiment was in a field adjacent to the field in which there was a large plot of leek infested with *T. tabaci*, (this plot is described in Chapter 1 under 'Maintaining a field population of *Thrips tabaci*). Thrips flight activity was monitored using blue sticky traps located between the experimental field and the source plot. These were replaced at weekly intervals and the numbers of adult thrips were recorded. Initial colonisation of the experiment occurred in mid June, which was confirmed by direct examination of the plants.

Recording

During the course of the experiment, thrips numbers were recorded by destructive sampling of plants. Samples were taken on six consecutive weeks beginning on 10 July 2006. Five plants of each variety were selected at random from each of the 8 plots and taken back to the laboratory for assessment. The numbers of adult and larval *Thrips tabaci*, both alive and dead, as well as the numbers of adults of other thrips species were recorded. Before each leaf was discarded it was

examined carefully to estimate the percentage of the leaf surface affected by thrips feeding damage. By 17 July, some plants appeared to be making much better progress than others in terms of their overall size and leaf number and so plant weight was also recorded from that point.

Analysis

The mean numbers of adult thrips per plant and the mean numbers of larvae per plant were analysed using an analysis of variance (ANOVA) for the first 2 weeks' data and an analysis of covariance (ANCOVA) thereafter. In order to improve the underlying assumptions of the analysis, both sets of data were transformed using a square root transformation. The data were analysed using a split plot design with the different irrigation treatments applied to the main plots, which were then split further for variety.

Plant weights were available after week 2 and were analysed using analysis of variance (ANOVA), although no transformation of the data was necessary (weight was used as the covariate in the ANCOVA analyses of population numbers and plant damage after week 2). The data were analysed using a split plot design with the irrigation treatments applied to the main plots, which were then further split by variety.

It was decided that the best way to analyse the leaf damage data was to focus on a single leaf from each plant and the penultimate leaf counting inwards from the outside was chosen (a relatively young fresh leaf whose feeding damage would represent recent activity and not cumulative damage over a potentially lengthy period). The data for the penultimate leaves were also analysed by an analysis of variance (ANOVA) for the first 2 weeks of data and an analysis of covariance (ANCOVA) for the remaining period.

All data were analysed using Genstat for Windows (VSN International Ltd.) and Microsoft Excel (Microsoft Corporation).

5B 3.0 Results

Population sizes

Few corpses of *T. tabaci* were observed on any of the treatments and so these were ignored in the analysis.

Applying plant weight as a covariate to the analysis was not significant in all cases but leaving it out did lead to some drop in significance in a few cases, and so it was left in.

There were no statistically significant interactions between the irrigation treatments and the numbers of adult thrips on the salad onion plants (Table 5.7; Figure 5.2). Essentially no single irrigation treatment had a consistently discernible effect on the numbers of adult *Thrips tabaci* found on plants subjected to that treatment at any point over the entire course of the experiment.

Table 5.7 **Adult numbers:** The p-values associated with the effects of irrigation, variety and the interaction between irrigation and variety on adult *Thrips tabaci* numbers for each week of the experiment. Statistically significant interactions are shown in bold.

	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6
Irrigation treatment	0.555	0.774	0.884	0.333	0.777	0.381
Variety	0.700	0.153	0.325	**<0.001**	0.395	0.316
Irrigation treatment.Variety	0.773	0.317	0.821	0.552	0.167	0.265

However, a highly significant p-value was associated with the numbers of adult thrips found on the two different varieties of salad onion in week 4 of the experiment. An unusually high number of adults was found on plants cv White Lisbon during that week (Figure 5.3), although this difference did not persist in the following weeks. Comparable data for cv Guardsman [A.cepa/ A.fistulosum cross] are shown in Figure 5.4.

Figure 5.2 Mean square root of numbers of adult thrips per plant (both varieties) under each of the four irrigation treatments over the 6 weeks between 10 July 2006 and 27 August 2006.

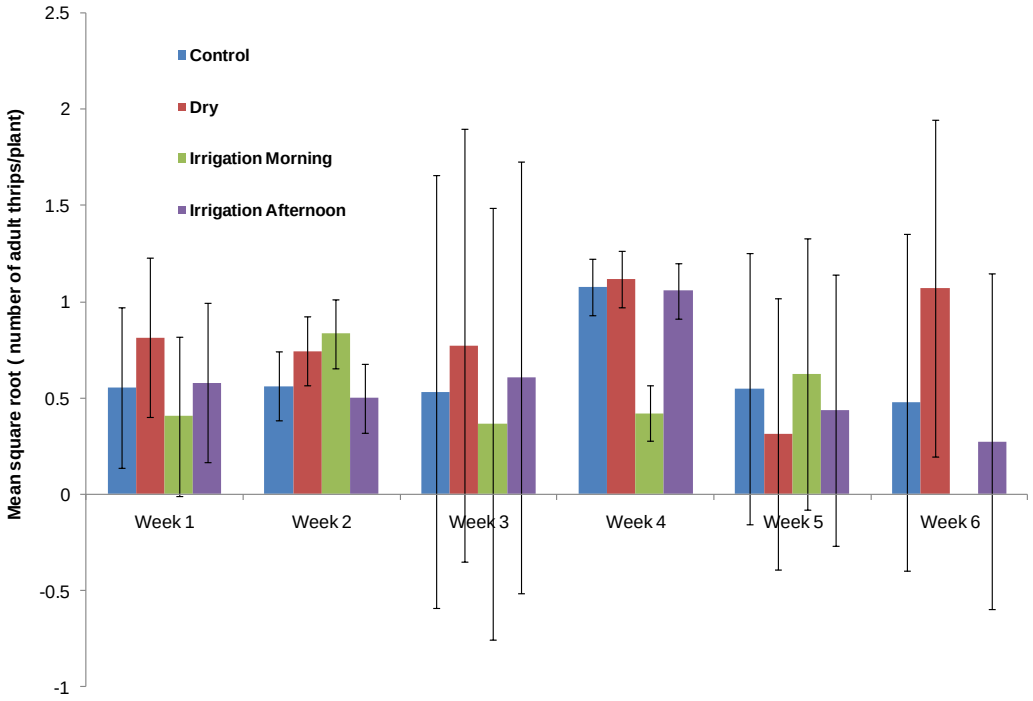


Figure 5.3 Mean square root of numbers of adult thrips per plant cv White Lisbon [A.cepa] under each of the four irrigation treatments over the 6 weeks between 10 July 2006 and 27 August 2006.

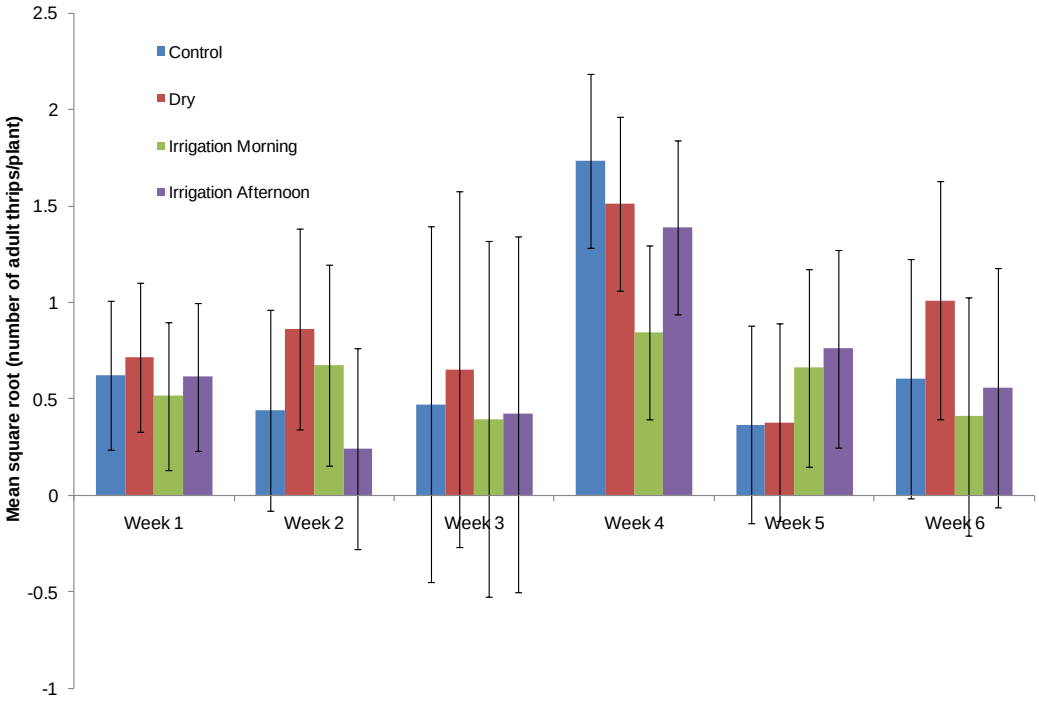
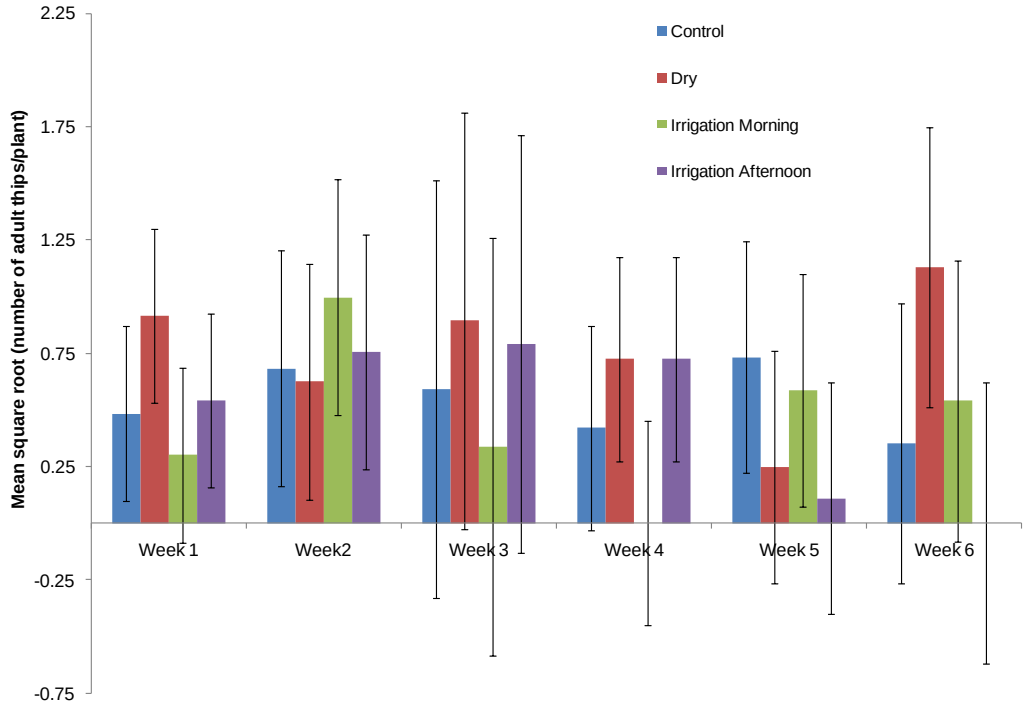


Figure 5.4 Mean square root of numbers of adult thrips per plant cv Guardsman [A.cepa/ A.fistulosum cross] under each of the four irrigation treatments over the 6 weeks between 10 July 2006 and 27 August 2006.



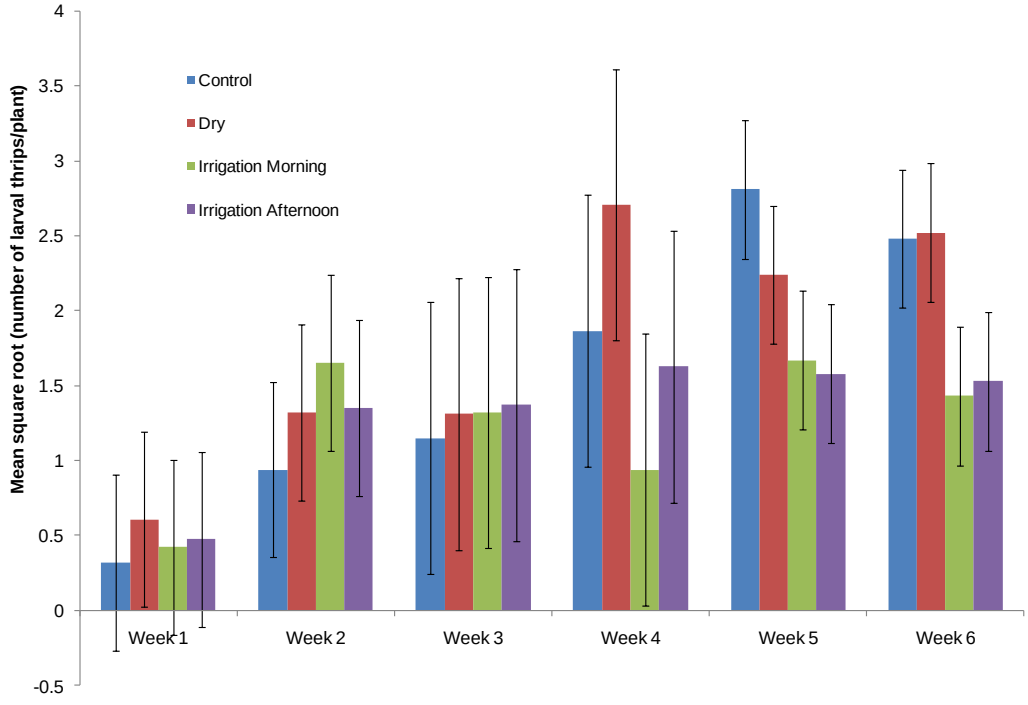
Clearly, neither Figure 5.3 nor Figure 5.4 displays a discernible pattern, either within or between treatments, for adult *T. tabaci* numbers throughout the period of the experiment.

As with the adult *Thrips tabaci* populations, there was no statistically significant interaction between the irrigation treatments and the numbers of larval thrips (Table 5.8; Figure 5.5). Statistically significant interactions were found, however, between larval numbers and variety in week 4 (as with the adult numbers) and between larval numbers and the interaction between irrigation and variety in weeks 1, 2 and 4.

Table 5.8 **Larval numbers:** The p-values associated with the effects of irrigation, variety and the interaction between irrigation and variety on larval *Thrips tabaci* numbers for the plots for each week of the experiment. Significant interactions are shown in bold.

	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6
Irrigation treatment	0.904	0.737	0.855	0.126	0.111	0.108
Variety	0.557	0.201	0.093	**0.002**	0.289	0.140
Irrigation treatment.Variety	**0.045**	**0.009**	0.749	**0.046**	0.375	0.759

Figure 5.5 Mean square root of numbers of larval thrips per plant (both varieties) under each of the four irrigation treatments over the 6 weeks between 10 July 2006 and 27 August 2006.



Plant weight and thrips feeding damage

There were no significant differences in the weight of plants sampled from the different treatments for the full 4 weeks of sampling (Table 5.9). However, a mildly significant interaction was observed between the weight of the sampled plants

and their variety in week 6 (p-value 0.051). The associated means for this sampling date show a mean weight of 48.9g for White Lisbon plants and 58.5g for those of the variety Guardsman.

Table 5.9 **Plant Weights:** The p-values associated with the effects of irrigation, variety and the interaction between irrigation and variety on the weight of plants harvested from the plots for weeks 3, 4, 5 and 6 of the experiment. Statistically ignificant interactions are shown in bold.

	Week 3	Week 4	Week 5	Week 6
Irrigation	0.951	0.746	0.703	0.402
Variety	0.444	0.326	0.069	**0.051**
Irrigation.Variety	0.485	0.929	0.521	0.708

There was no statistically significant association between the level of leaf damage caused by thrips feeding and the irrigation treatment applied to them (Table 5.10). No real pattern of association was seen with variety either as the only statistically significant number was in week 5 and it is notable for being both significant and greatly different from every other week, indicating it is more likely to be due to chance than any other factor.

Table 5.10 **Leaf damage:** The p-values associated with the effects of irrigation, variety and the interaction between irrigation and variety on the visible thrips feeding damage on the leaves of plants sampled each week. Statistically significant interactions are shown in bold.

	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6
Irrigation treatment	0.585	0.834	0.319	0.573	0.375	0.801
Variety	0.872	0.356	0.074	0.098	<**0.001**	0.085
Irrigation treatment.Variety	0.792	0.467	0.436	0.249	0.141	0.624

As with overall leaf damage, there was no statistically significant interaction between the irrigation treatments and the level of damage on the penultimate leaf, as

shown in Figure 5.11. Varietal differences were observed, however, in weeks 3, 4 and 5 and would appear to indicate a higher level of damage to White Lisbon plants than Guardsman.

Table 5.11 **Damage to penultimate leaf:** The p-values associated with the effects of irrigation, variety and the interaction between irrigation and variety on visible thrips feeding damage on the penultimate leaf (counting inwards) of plants sampled each week. Statistically significant interactions are shown in bold.

	Week 1	**Week 2**	**Week 3**	**Week 4**	**Week 5**	**Week 6**
Irrigation treatment	0.614	0.797	0.891	0.176	0.581	0.937
Variety	0.495	0.238	**0.008**	**0.045**	**0.002**	0.261
Irrigation treatment.Variety	0.704	0.662	0.738	**0.042**	0.543	0.298

5B 4.0 Discussion

As there was no statistically significant interaction between the treatments and the numbers of adult or larval *Thrips tabaci,* this experiment does not demonstrate a link between irrigation and thrips control. This does not, however, mean that no link exists and indeed discussions with growers after the conclusion of this experiment have confirmed their belief in the efficacy of irrigation as a control method.

The relatively small scale of the experiment in comparison with commercial crops imposed limitations. Firstly, the experiment was undertaken very close to a source of constantly active thrips, which were vital for initiation of the experiment and ensuring that there was an infestation of thrips on the experimental plots. It is quite possible, however, that the relatively large size of the thrips source in comparison with the experimental plots, and the constant presence of high and unregulated thrips numbers on that plot, led to continuous thrips invasions, enough to mask any control exerted by the various treatments. Furthermore, the small plot sizes (reflecting the size of the areas that could be covered by the mobile covers)

meant that the different treatments were in close proximity to one another, so that thrips could migrate between plots.

Visible leaf damage was the most important measure of the effectiveness of the irrigation treatments in a commercial sense. Here too, no significant differences due to treatment were observed, and this may well have been due to the same factors discussed above. However, varietal differences were seen, in particular when reviewing damage to the penultimate leaf during the latter half of the experiment. As there were no statistically significant differences in thrips numbers over the same period, it seems unlikely that the observed disparity was due to the level of feeding that occurred, but rather the corresponding reaction it caused in the growing plant.

Chapter 6: Field populations of *Thrips tabaci*

6.1.0 Introduction

There are no long term studies of the dynamics of British *Thrips tabaci* populations in the literature and indeed detailed long term studies on populations of any thrips species are rare (Lewis, 1973c). Although studies do exist on several individual aspects of the population dynamics of *Thrips tabaci*, there has been little attempt to marry these diverse investigations in order to identify and understand long term trends in population size. Throughout the course of this project thrips numbers have been monitored on field crops, of leek and salad onion. This was to establish, in particular, how and where thrips spend the winter and to determine whether there is a consistent and potentially predictable pattern to the development of thrips infestations from year to year.

As the results obtained from this study are in large part observational and not the result of tested hypotheses, much of this chapter consists of descriptive analysis of those observations rather than statistical analysis. The data have been examined in the light of trends and conclusions outlined in previous chapters, where individual aspects of thrips biology and behaviour were investigated in replicated experiments. The aim, therefore, has been to expand on the conclusions established in previous chapters and see how well those conclusions, derived from small-scale experiments, describe the trends and patterns seen in field populations over an extended period.

6.2.0 Materials and methods

6.2.1 Thrips

A field population of *Thrips tabaci* was established in 2003 at Warwick HRI, Wellesbourne on an insecticide-free plot of leek (cv. Shelton), for use in another project. Thrips were not introduced to the plot but it was soon colonised by thrips from extant populations in the local area. The plot was left untouched for a full year and was not destroyed until a fresh plot had been established nearby in the following spring. This cycle was repeated throughout the project, with a fresh plot of leek being sown or planted in April-May each year to provide a stable habitat for *T. tabaci* at Wellesbourne.

6.2.2 Plant material

For the most part, plant samples were taken from crops at Warwick HRI, Wellesbourne, although samples were also taken from commercial *Allium* crops in Kent and Lincolnshire. The leek plot grown to maintain the thrips population at Wellesbourne was the main sampling location. In addition, in 2006 and 2007, and also at Wellesbourne, a series of sequentially planted plots of salad onion, containing the varieties White Lisbon [*A.cepa*] and Guardsman [*A.cepa/ A.fistulosum* cross] were monitored. Other crop types were sampled as they were available; no specific plantings were made for this purpose.

6.2.3 Trapping

The flight activity of adult *T. tabaci* was monitored using blue sticky interception traps (Ecospray Limited) set up within, and around, the various crops of interest at a uniform height of 18 inches. The traps were replaced at regular intervals and taken to the laboratory for examination. Thrips adults were identified and counted using a binocular microscope or hand lens. A minimum of 3 traps were set per plot, one in the centre and one at each of the short ends. During certain periods when additional experimentation was occurring, for example when the diurnal periodicity of the intra-plant distribution of *T. tabaci* was being studied, additional traps were placed in experiment plots. Trap numbers were dependent upon plot size, with a trap every 10 metres along the length of the plot. Traps were not in place continuously throughout the experiment, but were *in situ* in the field for 7 days before removal for examination.

6.2.4 Sampling

Plants were sampled destructively and removed to the laboratory for examination. In general, 10 leek or salad onion plants were sampled each week from each available mature plot (this was always one plot for leek but up to 8 for salad onion). Both *T. tabaci* numbers and plant damage were recorded as were obvious trends in thrips size and colour.

To investigate potential thrips overwintering sites, samples were taken from a large variety of crops and vegetation, including hedgerows and fallow fields, and this required a more flexible sampling approach (details of sampling locations in Table 6.1). Mature and established crop plants were sampled destructively, using the same

methodology as for sampling leek and salad onion plants. Hedgerows, grasses and immature cereals were sampled using a D-Vac (Tanaka Pro-Force). Sampling with a D-vac involved walking transects of the target field and taking samples at 10 metre intervals. Locations for transects were chosen at random. D-vac samples were sorted in the laboratory under a binocular microscope. It was not possible to quantify the difference in the sampling potential of D-vac sampling versus destructive sampling, as the two techniques were appropriate for different crop types and sizes. Soil samples were taken from around the bases of leek plants in the long-term monitoring field to check for the presence of overwintering pupae. Soil was taken to a depth of 10cm as this was the depth determined by Deligeorgidis and Ipsilandis (2004) as about the maximum at which *T. tabaci* are found. Soil samples were removed to the laboratory and stored at a temperature of 15^{o}C; they were then checked daily for a period of 3 weeks for adult emergence.

Table 6.1 gives details of the types of crops sampled over winter between 2005 and 2008. Samples were taken monthly in December, January and February for each year. All field sampling locations were within 1km of the leek plot upon which populations were constantly monitored between 2004 and 2008. Hedgerows sampled were all at the margins of the sampled crop fields, hedges were sampled in association with each field sampled.

Table 6.1 Sampling locations and methods used to investigate overwintering of *T. tabaci* at Warwick HRI, Wellesbourne between 2005 and 2008.

Crop type	Type of sampling undertaken	No. of fields sampled	No. of transects conducted per location
Leek	Destructive, Soil	1	3
Winter wheat	Destructive, D-Vac	2	3
Rye	Destructive, D-Vac	1	3
Barley	Destructive, D-Vac	1	3
Fallow fields	D-Vac	2	3
Hedgerows	D-Vac	7	2

To attempt to establish whether overwintering adults were in diapause or simply quiescent, individuals were removed from the field throughout the winter and

placed at constant temperatures in incubators (Sanyo growth chamber model MLR-351). They were then observed at regular intervals to monitor for signs of activity such as feeding. Cages were also monitored for the first eclosion of larvae.

6.3.0 Results and discussion

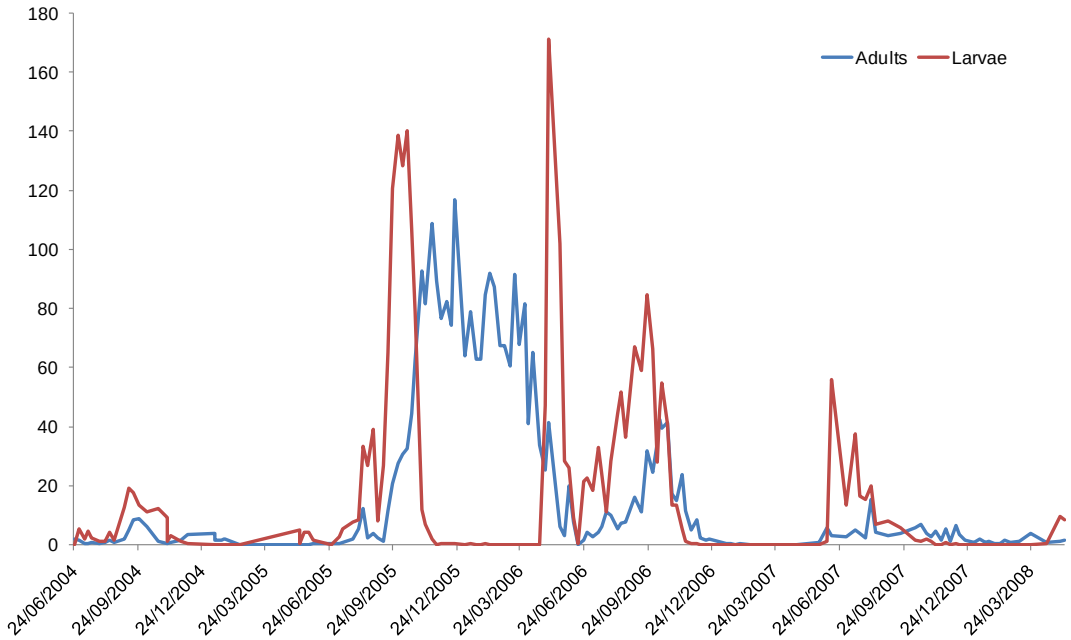
6.3.1 Population size

This section describes the broad trends observed in *Thrips tabaci* population size over the course of the study. The factors driving these trends are discussed and analysed in detail in subsequent sections.

Leek

Figure 6.1 shows the mean numbers of adult and larval *Thrips tabaci* recorded on leek plants at Warwick HRI, Wellesbourne between June 2004 and May 2008.

Figure 6.1 Mean number of adult and larval *Thrips tabaci* per leek plant at Warwick HRI, Wellesbourne between June 2004 and the end of May 2008.



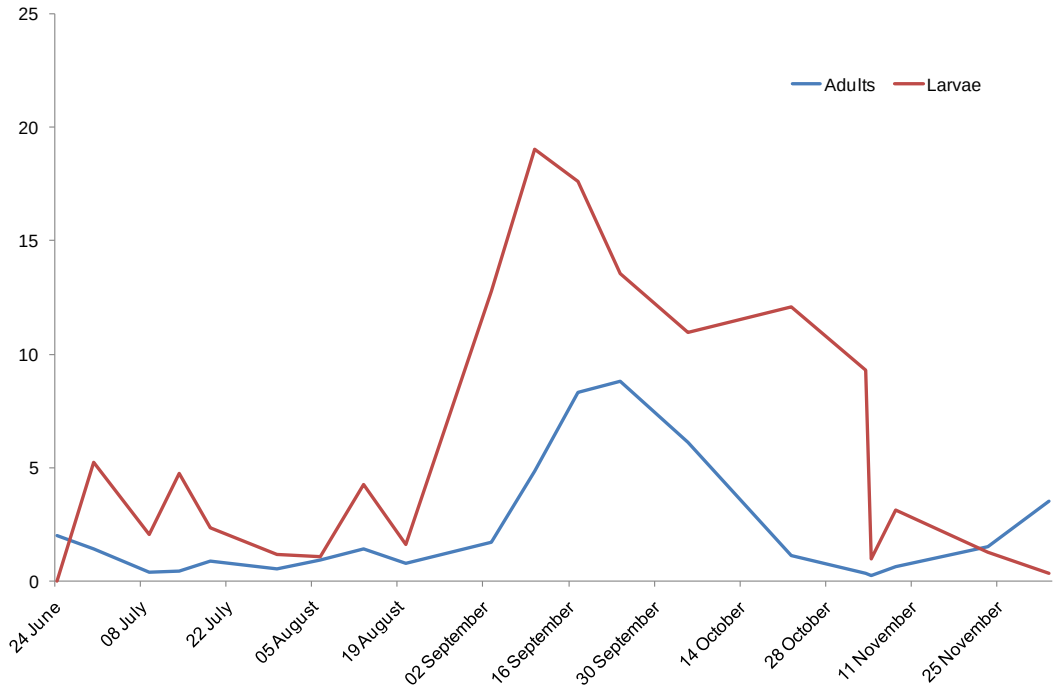
The leek plants were grown in 1.83m wide beds containing 4 rows, each planted at 50 seeds/m. This equates to 1,098,901 plants per hectare:

$$Plants\ per\ hectare = \frac{10{,}000\ square\ metres}{plant\ spacing\ in\ square\ metres} \quad (0.455\ x\ 0.02)$$

The actual number of plants will be somewhat less than this when such things as pathways between plots, plants that failed to germinate, etc. are take into account. Even so, the peak number of approximately 170 *T. tabaci* larvae per plant in the early summer 2006 would equate to a population of approximately 186,000,000 insects per hectare, and this excludes the adults. Although this number seems very large, it is in fact quite moderate compared to population sizes estimated by Lewis (1973c) from published data on US populations, which were as high as 1600 x 10^6 larvae per hectare. Once adults are taken into account as well, this US population would amount to roughly 70 tonnes of biological material per hectare (Lewis, 1973c). Such numbers, although admittedly surprising in their size, give little insight into the real impact of such populations and indeed what such high densities of insects mean in terms of crop yield, plant damage and pest control.

From Figure 6.1 it is clear that population sizes are not uniform between years and as such it is important to examine each year individually. Figure 6.2 shows the mean numbers of adult and larval *Thrips tabaci* recorded on leek plants at Warwick HRI, Wellesbourne between June 2004 and the end of December 2004.

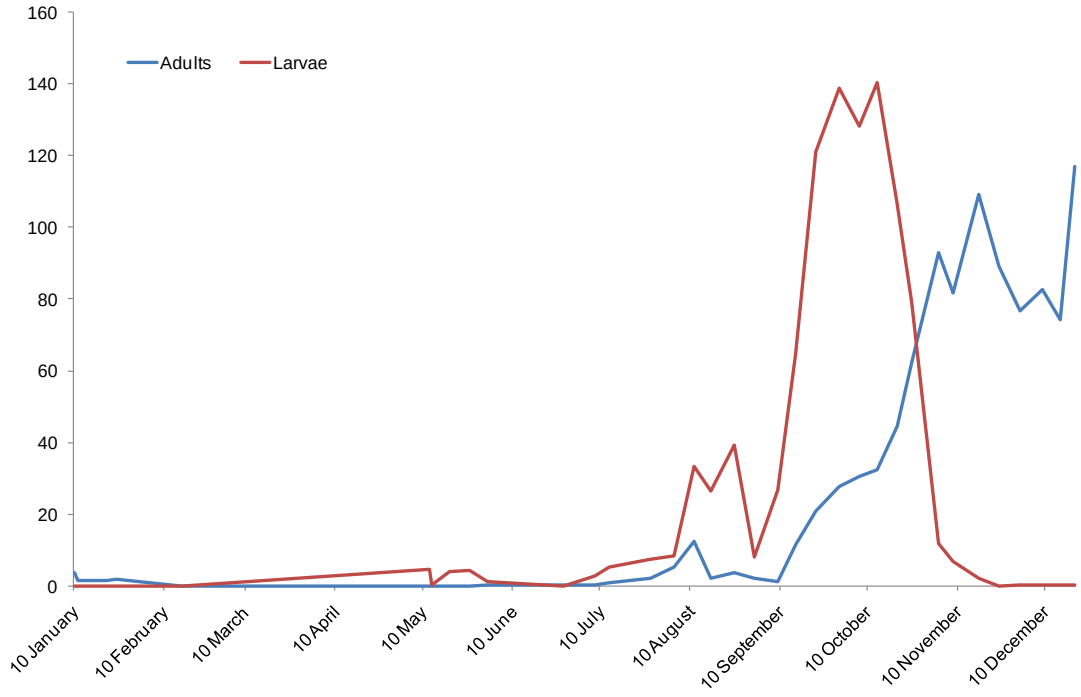
Figure 6.2 Mean number of adult and larval *Thrips tabaci* per leek plant at Warwick HRI, Wellesbourne between June 2004 and the end of December 2004.



It is difficult to identify patterns in the data from 2004. The minor peaks in larval numbers between June and August are almost certainly artefacts of the sampling process, as the overall numbers of insects per plant (5 or below) were very low. As no data were gathered in the spring of 2004, nothing can be said definitively about the date of first larval emergence. Although no larvae were identified on the first sampling date on the 24 June, it is difficult to rule out the presence of larvae before that date, since no samples were available. What is notable, is the dramatic increase in larval numbers and (trailing by a couple of weeks) adult numbers in late August, September and October, and the collapse of the larval population after that. These general trends are mirrored in the successive years. Recorded adult numbers were lower than larval numbers and, especially in the early summer, they do not reflect the fluctuations seen in larval numbers.

Figure 6.3 shows the mean numbers of adults and larvae of *Thrips tabaci* recorded on leek plants at Warwick HRI, Wellesbourne between January 2005 and the end of December 2005.

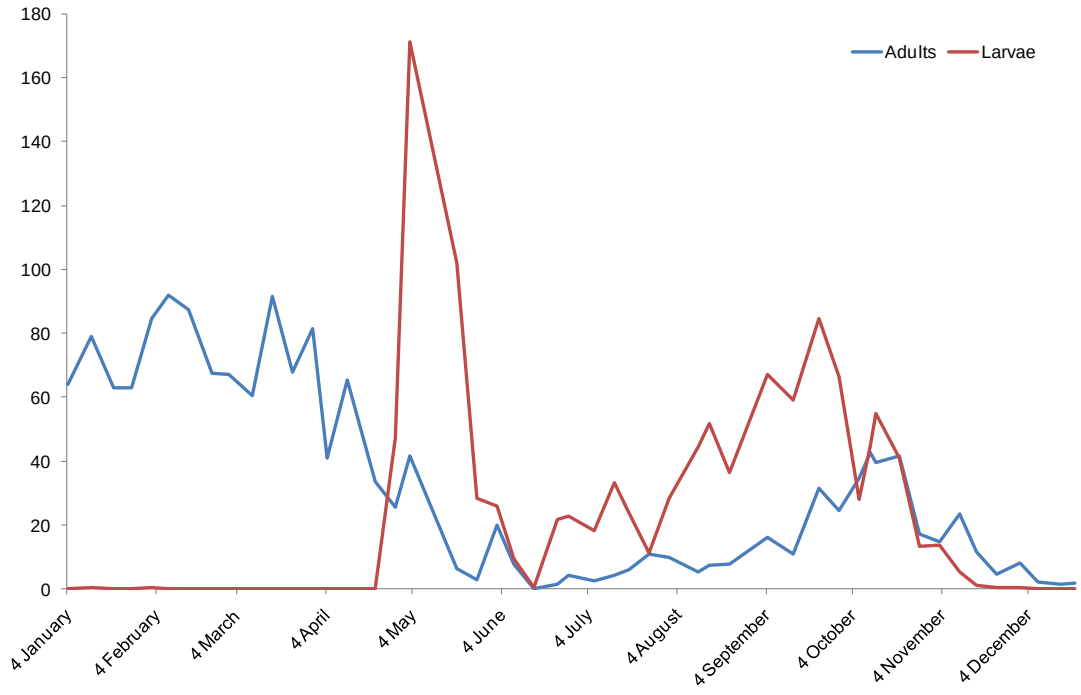
Figure 6.3 Mean number of adult and larval *Thrips tabaci* per leek plant at Warwick HRI, Wellesbourne between January 2005 and the end of December 2005.



Patterns identified in 2004, of an increase in larval numbers and (trailing by a couple of weeks) adult numbers in August, September and October, and the collapse of the larval population after that, were broadly repeated in 2005, although the numbers involved were significantly higher. A more complete picture of the early months of the year indicates that the population remained very low until mid-summer, with no significant population growth until mid July. Indeed adults were completely absent between February and July. However the late summer population boom was the largest of any of the sampling years and the resulting overwintering population of adults was the largest seen throughout the study.

Figure 6.4 shows the mean numbers of adult and larval *Thrips tabaci* recorded on leek plants at Warwick HRI, Wellesbourne between January 2006 and the end of December 2006.

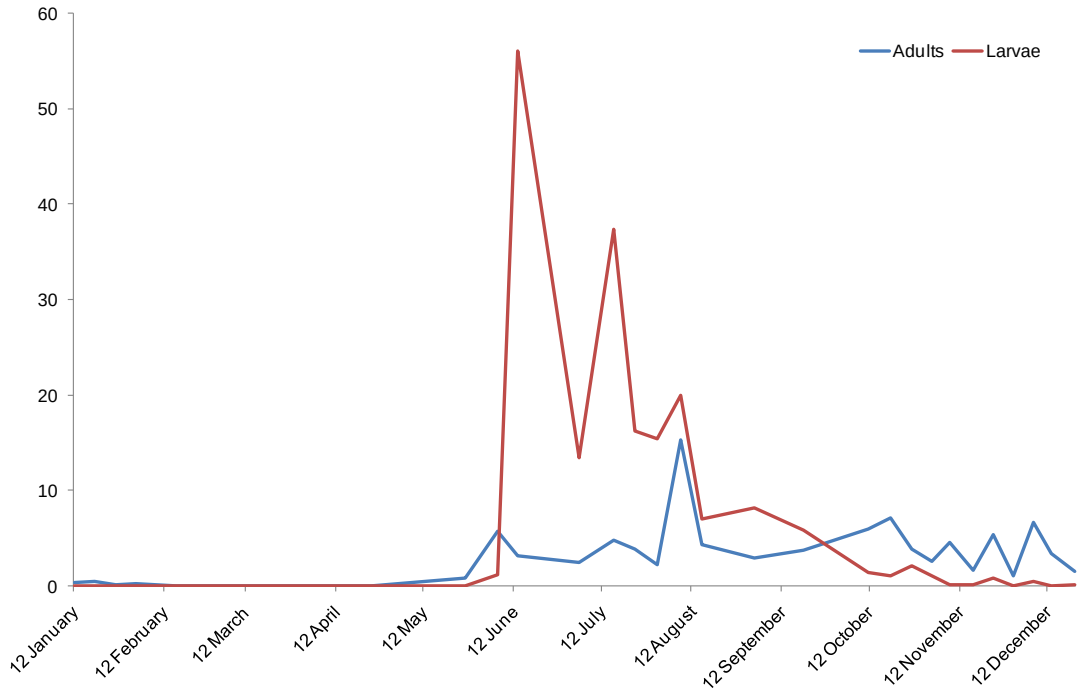
Figure 6.4 Mean number of adult and larval *Thrips tabaci* per leek plant at Warwick HRI, Wellesbourne between January 2006 and the end of December 2006.



The 2006 data represent a departure from the pattern seen in previous years in that a large overwintering population of adult *T. tabaci* remained *in situ* on leek plants between 2005 and 2006. This explains the extremely large larval population that appeared at the end of April 2006. These were the highest recorded numbers of *T. tabaci* larvae at Wellesbourne throughout the study. However the reasons for the collapse in the larval population in May are more complex and such patterns are discussed in detail in later sections. Like previous years, the period of peak population growth was in the late summer, between August and October. Adult numbers built up over this period had declined significantly by early December and, as discussed in subsequent sections, host plant quality may have played some part in this. Adult numbers in the early and mid-summer appear very low and do not reflect some of the population fluctuations seen in larval numbers.

Figure 6.5 shows the mean numbers of adult and larval *Thrips tabaci* recorded on leek plants at Warwick HRI, Wellesbourne between January 2007 and the end of December 2007.

Figure 6.5 Mean number of adult and larval *Thrips tabaci* per leek plant at Warwick HRI, Wellesbourne between January 2007 and the end of December 2007.



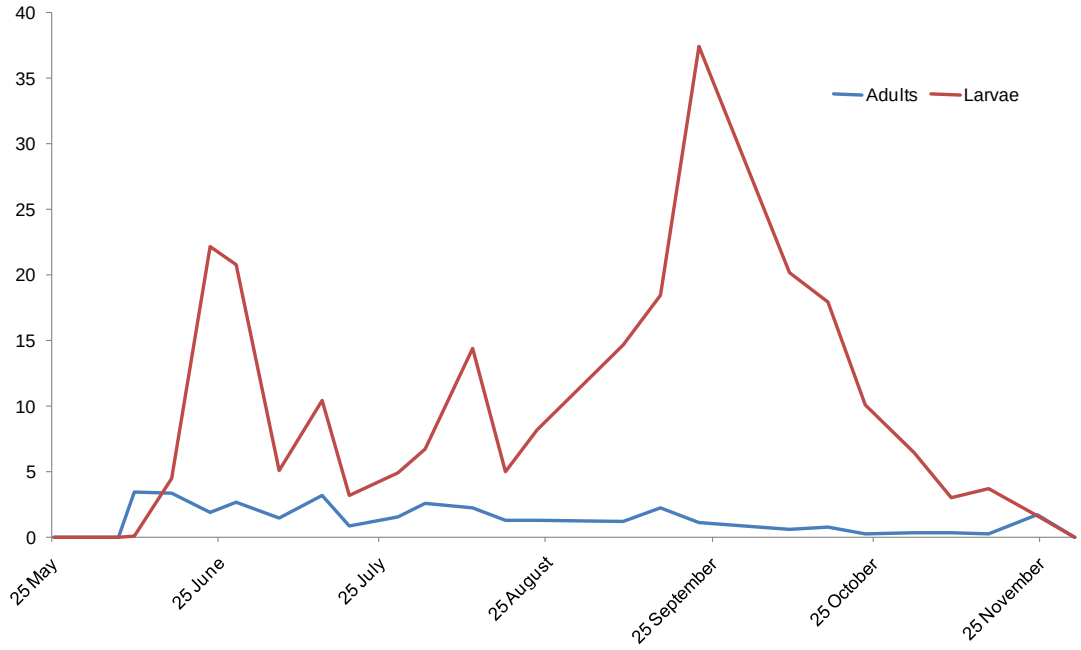
The 2007 data represent well the difficulty in identifying similar year on year trends in the size and development of the *T. tabaci* population. As in the winter of 2004-2005, no thrips remained *in situ* on leek over the winter of 2006-2007. Adult arrivals in late May were new immigrants to the recording plots and the following larval population indicates that they started oviposition immediately and with a high rate of fecundity. Unlike previous years, no late summer population boom was observed in 2007. This could be an aberration, an atypical year, but in order to evaluate this, a more thorough examination of the drivers for population growth and development is required. These factors are discussed in section 6.3.3 onwards.

Salad onion

Populations of *Thrips tabaci* on salad onion in 2006 and 2007 followed broadly the trends seen in populations on leek over the same time period. The overall numbers per plant were much lower than on leek and it is clear that the smaller size and surface area of an average salad onion plant provides a much reduced exploitable habitat.

Figure 6.6 shows the mean numbers of adult and larval *Thrips tabaci* recorded on 2 varieties of salad onion at Warwick HRI, Wellesbourne in 2006.

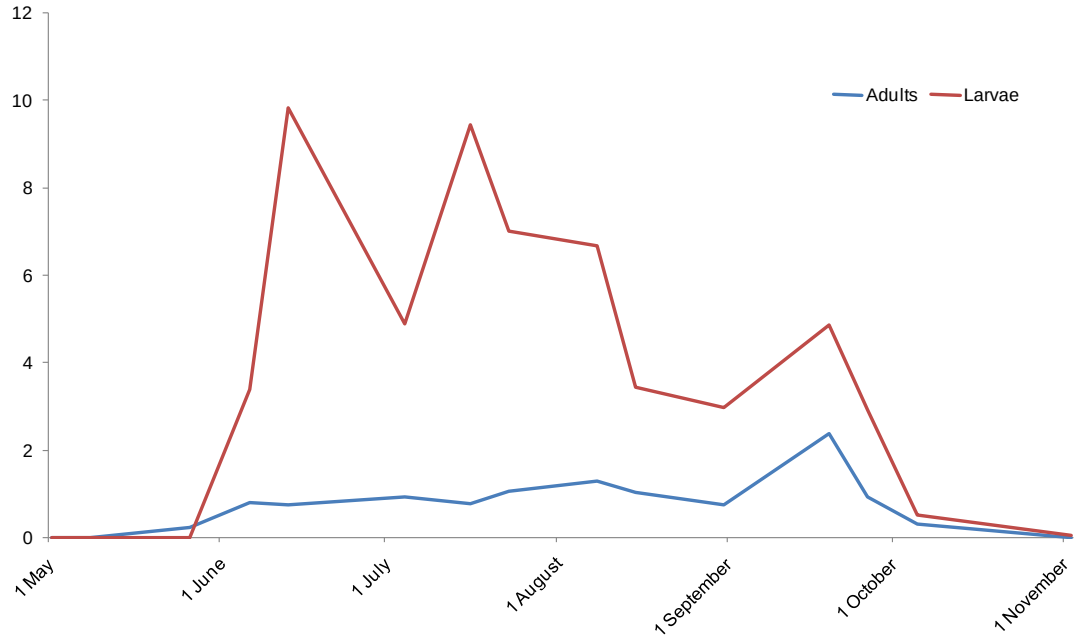
Figure 6.6 Mean number of adult and larval *Thrips tabaci* per plant on both varieties of salad onion plant at Warwick HRI, Wellesbourne in 2006.



There was no evidence of overwintering on salad onions. Population declines in both years were sharp in the autumn after the late summer population boom and thrips were entirely absent from the salad onion plots by early December. The first evidence of adult thrips on the plots in the spring coincided with the first captures of airborne thrips on sticky interception traps. Adult numbers in samples were extremely low in comparison to larvae throughout the year and did not reflect larval trends in population size.

Figure 6.7 shows the mean numbers of adult and larval *Thrips tabaci* recorded on two varieties of salad onion at Warwick HRI, Wellesbourne in 2007.

Figure 6.7 Mean number of adult and larval *Thrips tabaci* per plant on both varieties of salad onion at Warwick HRI, Wellesbourne in 2007.



The 2007 data displayed in Figure 6.7 mirror very closely the patterns seen on leek plants in the same year (Figure 6.5). As with leek plants, the numbers of *T. tabaci* recorded on salad onion in 2007 were far lower than in the previous year and there was no significant late summer population expansion. Although the general patterns of population development were very similar between the two salad onion varieties in both years, the numbers recorded on the two varieties differed greatly in 2006.

Figure 6.8 shows the mean numbers of adult and larval *Thrips tabaci* recorded on salad onion plants cv White Lisbon at Warwick HRI, Wellesbourne in 2006.

Figure 6.8 Mean number of adult and larval *Thrips tabaci* per plant on plants of salad onion cv White Lisbon at Warwick HRI, Wellesbourne in 2006.

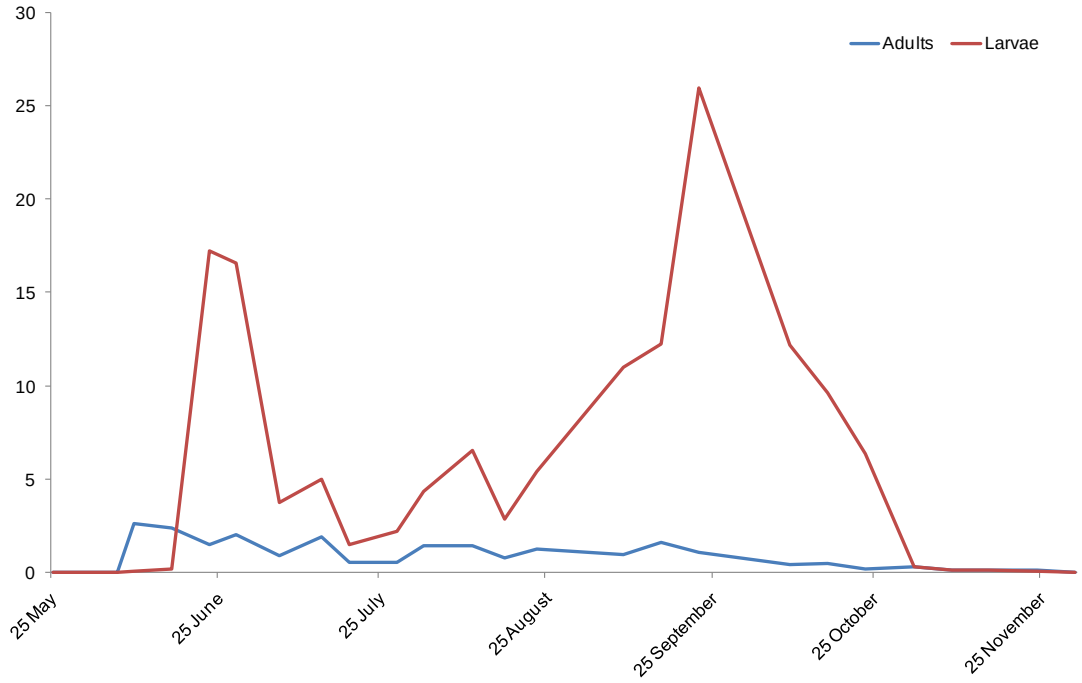
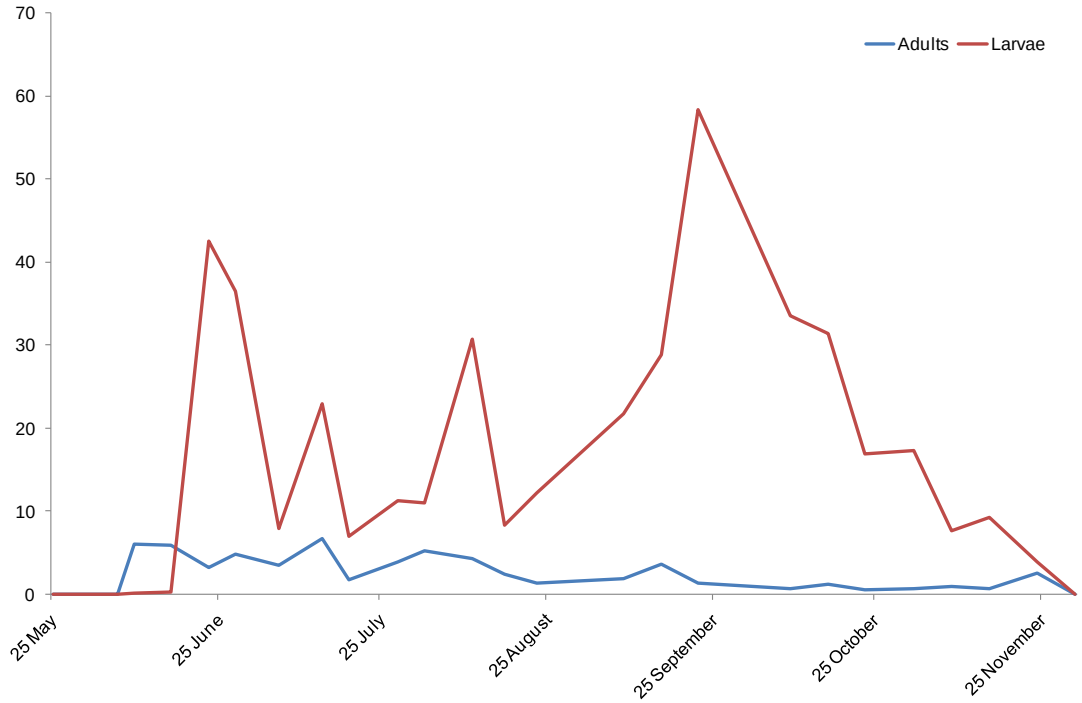


Figure 6.9 shows the mean numbers of adult and larval *Thrips tabaci* recorded on salad onion plants cv Guardsman at Warwick HRI, Wellesbourne in 2006.

Figure 6.9 Mean number of adult and larval *Thrips tabaci* on plants of salad onion cv Guardsman at Warwick HRI, Wellesbourne in 2006.



Figures 6.8 and 6.9 show that the salad onion cv White Lisbon had a population which was roughly half that seen on cv Guardsman throughout 2006, and the population on Guardsman persisted for about a month longer in the late autumn. Guardsman and White Lisbon plants are very similar in size, although some structural differences are apparent, and the plants sampled were from the same plots, which would tend to rule out plant size or physical location as explanations for this phenomenon. It seems likely that Guardsman is a better host for *T. tabaci* in some way. Varietal resistance to *T. tabaci* has been demonstrated in some cultivars (Coudriet et al., 1979, Shelton et al., 1998, Hamilton et al., 1999), though there is no direct evidence to suggest that this is the state of affairs here. In any case, the importance of varietal choice is highlighted in the overall strategy a grower must employ to reduce the potential impact of *T. tabaci* infestations. These varietal differences in population size were not observed in 2007, where the populations on both varieties remained comparable throughout the recording period. In 2007, however, the population sizes on both varieties were much lower and so there would have been less competition for resources.

The trends seen in *T. tabaci* populations on both leek and salad onion are complex and are not uniform year on year. Section 6.3.3 examines what is driving these trends and how closely it is possible to predict them via population forecasting.

6.3.2 Overwintering

Overwintering of *Thrips tabaci* was investigated in the winters of 2005-2006, 2006-2007 and 2007-2008 by destructive plant sampling, use of a D-vac and soil sampling. Samples were taken in fields up to 1km in distance from the leek plots used for population monitoring over the summer, and which were assumed to be the major local source of thrips. The different crops and environments sampled each year were: leek, winter wheat, rye, barley, fallow fields and hedgerows (Table 6.1). Of these, only two were found to harbour *T. tabaci* over the winter months: leek and winter wheat. Numbers of *T. tabaci* recorded on leek over the winter are illustrated in Figures 6.2 to 6.5. In general numbers recorded on winter wheat were far lower than those recorded on leek, it was common to find 3 to 5 thrips per transect of the field. Shelton and North (1986) and Wolfenbarger and Hibbs (1958) also identified wheat as an alternative host for *T. tabaci* and indeed Shelton (1995) hypothesised that winter wheat may be a preferred overwintering host, due to the high survival

rate of *T.* tabaci on that crop. Although *T. tabaci* is known to overwinter in different development stages (North and Shelton, 1986c, Chambers and Sites, 1989, Cho et al., 1995, Larentzaki et al., 2007), no larvae or pupae were found using any of the three sampling techniques over the winter months. It is therefore likely that, in the UK, populations overwinter exclusively as adults. As can be seen in Figure 6.1 adult thrips were most numerous over winter in 2005-2006. This may be because a large population had built up in the autumn of 2005 and the host leek plants were still in a healthy and robust condition; perhaps reducing the proportion of thrips that migrated from them to locate alternate overwintering hosts. Thrips tabaci were more numerous on leek in general and were seen only rarely on winter wheat. The exception to this was the winter of 2006-2007 in which adult numbers declined to zero on leek in the New Year, but adults were still present on winter wheat. This may have been associated with the quality of the leek plants which were in very poor condition by October 2006. As shown in Chapter 4, adult *T. tabaci* that find themselves on inferior plant material will attempt to disperse if conditions are appropriate. Though it is unlikely that thrips were able to move off the plants in the conditions of mid-winter, the poor condition of the plants in late autumn may well have contributed to the sharp decline in numbers during that period, as the thrips dispersed from their summer hosts to locate appropriate overwintering ones.

Overwintering thrips were always found on the middle leaves of leek plants, usually 6 to 7 leaves in from the outside, with almost none being found further out or further in than that. The thrips appeared to be packed together; often in great masses, on these leaves and were clearly inactive, but alive. On several occasions, thrips were survived extreme conditions including being entirely encased in ice, which, when thawed, released the thrips apparently unharmed. Although this seems remarkable, Kirk (1997) noted that several species of thrips are capable of enduring periods of extreme cold. Survival and longevity of overwintered thrips in field conditions is poorly understood and because it would be very difficult to track individual thrips over extended periods in the field, it is likely to remain so. Although there have been studies linking adult longevity with temperature, such as that conducted by Murai (2000), these have been conducted under constant conditions in the laboratory and so little can be extrapolated from them regarding longevity in a complex field environment, particularly with regard to overwintered insects. As shown in Figure 6.4, the only large overwintered adult population

collapsed quickly after the first appearance of spring larvae, indicating that these adults survive long enough only to produce the next generation. The paucity of flight interception trap catches over the same period (Figure 6.17) would indicate that this adult population collapse cannot be put down to emigration from the monitoring plots.

At temperatures above 15^{o}C, individuals were active within hours of removal from the field, and larvae were observed within days, indicating an almost immediate commencement of reproductive activities. This would indicate that the thrips remain inactive and quiescent during the winter months but do not enter full diapause. Leaf damage did not appear to increase significantly over the winter months (Figure 6.21), again indicating that the thrips were inactive. Behavioural experiments conducted on individuals and described in Chapter 4 showed that thrips exposed to extremely low temperatures (5^{o}C) exhibited a much reduced range of behaviours and spent much of their time resting and apparently inactive. This is likely to be a reflection of the state in which thrips are found in the field during the low temperatures of the winter months.

6.3.3 Population dynamics and forecasting

As discussed in Chapter 3, the currently accepted method for forecasting *Thrips tabaci* generation times and population peaks in Europe (Villeneuve et al., 1996, Martens and Plovie, 2007) is based on the day-degree requirement for development of *T. tabaci* estimated by Edelson & Magaro (1988). However Collier et al. (2007) demonstrated, partially using the data gathered for this PhD study, that forecasting systems based on Edelson & Magaro's day-degree calculation were inadequate for *T. tabaci* populations in the UK. As described in Chapter 3, an alternative forecasting system was developed during this project to address the two most serious perceived shortcomings in Edelson & Magaro's study, 1) calculation of a development threshold based on linear extrapolation from a limited range of constant temperatures, and 2) calculation of that threshold based on the entire life cycle rather than taking into account the potentially different development thresholds of the individual life stages. To examine the efficacy of this revised forecasting system, it is important to compare generation times forecasted from recorded field temperatures with 'actual' fluctuations *T. tabaci* numbers seen in the field.

Forecasted populations and actual populations

Figure 6.10 shows the mean numbers of adult and larval *Thrips tabaci* recorded on leek plants at Warwick HRI, Wellesbourne in 2005 and also the times at which approximately 50% of the population was forecast to have completed a generation. The forecast assumes a developmental threshold of 10^{o}C, as this was found to be the cut off point for development in Chapter 3, and has a starting point of the 1st of February, as this is usually around the coldest point of the year.

Figure 6.10 Mean number of adult and larval *Thrips tabaci* per leek plant at Warwick HRI, Wellesbourne in 2005 and the timings of the 4 generations produced by the forecasting system using a developmental threshold of 10^{o}C.

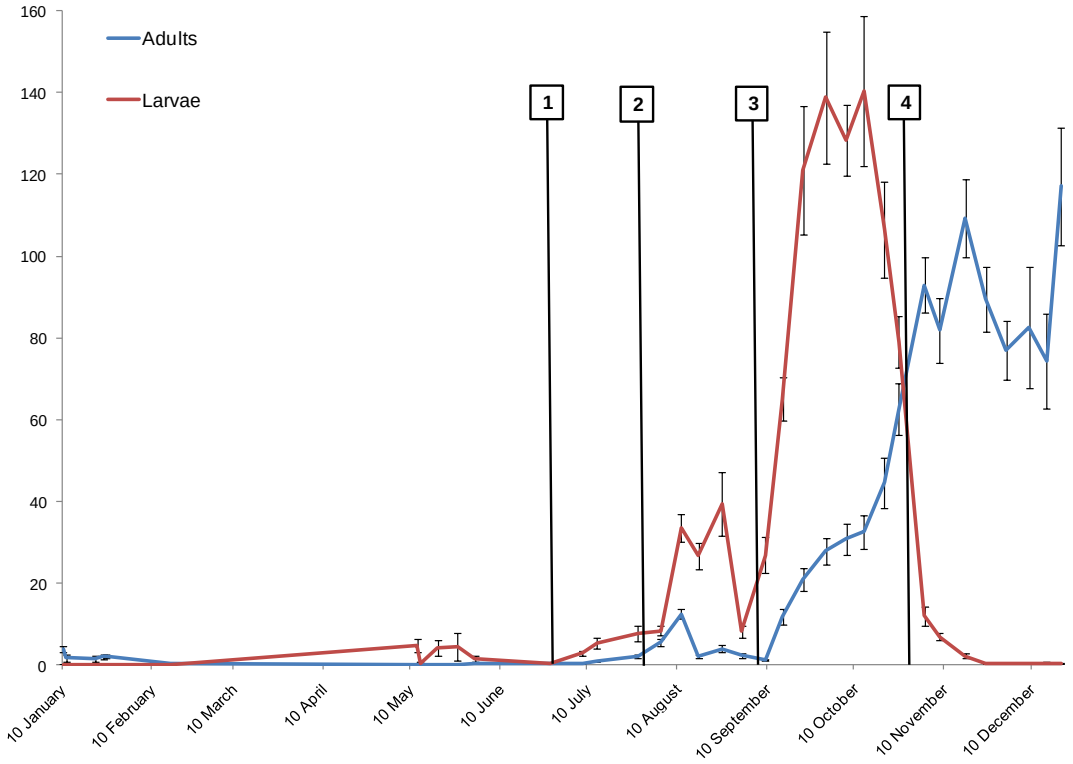
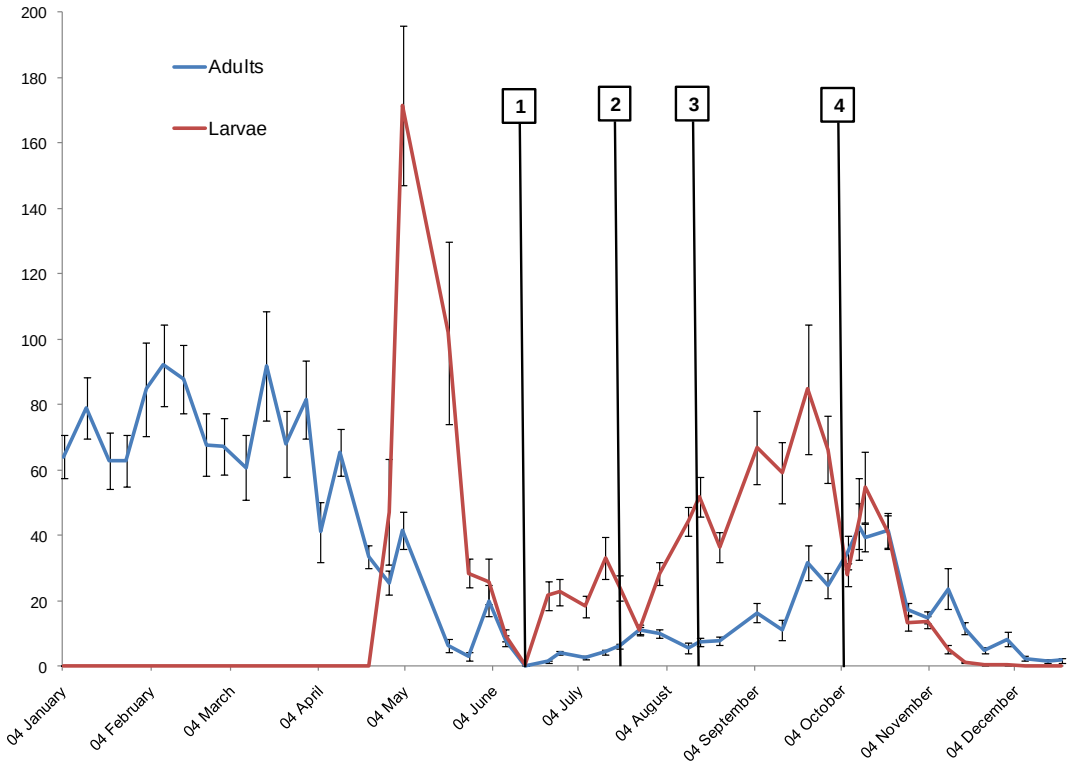


Figure 6.10 demonstrates clear discrepancies between forecast generation times of *T. tabaci* and observed population peaks in the field. Although the forecasting system would indicate that there should be 4 distinct generations through the year it is impossible to reconcile this number of generations with field recordings. This is also the chief failing of forecasting systems derived using

Edelson & Magaro's day-degree calculation (Collier et al., 2007), where predictions of generation times are difficult to marry with actual population peaks.

Figure 6.11 shows the mean numbers of adult and larval *Thrips tabaci* recorded on leek plants at Warwick HRI, Wellesbourne in 2006 and also the times at which approximately 50% of the population was forecast to have completed a generation and reached adulthood. The forecast again assumes a developmental threshold of 10^{o}C, as this was found to be the cut off point for development in Chapter 3, and has a starting point of the 1st of February, as this is usually around the coldest point of the year.

Figure 6.11 Mean number of adult and larval *Thrips tabaci* per leek plant at Warwick HRI, Wellesbourne in 2006 and the timings of the 4 generations produced by the forecasting system using a developmental threshold of 10^{o}C.

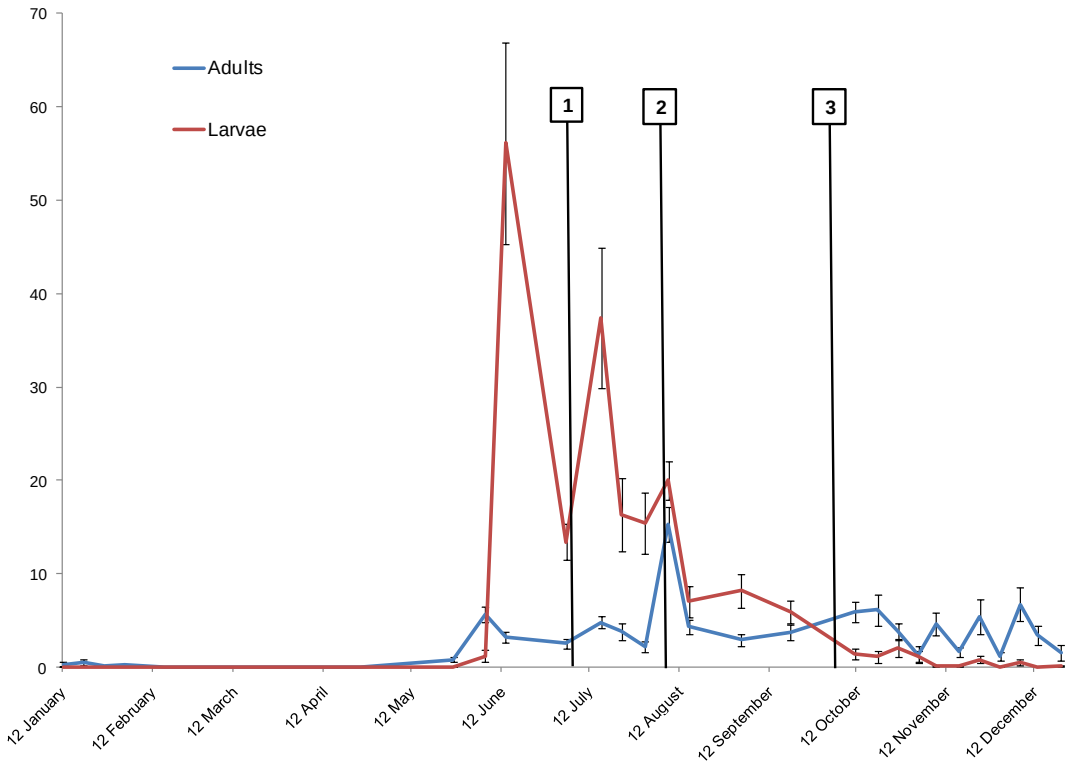


Again the 2006 field data do not tally well with the number of generations and generation times predicted by the forecasting system. Although the 2nd, 3rd and 4th predicted generations coincide somewhat with population increases seen in the field, the complete disconnection between the first observed larval generation and the first forecast generation is such that coincidences later in the year cannot be taken

at face value. Furthermore, the forecast tallies more closely with larval numbers than with adult numbers. As the forecast generation times predict the point at which 50% of the generation has reached adulthood it is fluctuations in the adult population that should be predicted by the forecast dates.

Figure 6.12 shows the mean numbers of adult and larval *Thrips tabaci* recorded on leek plants at Warwick HRI, Wellesbourne in 2007 and also the times at which 50% of the population was forecast to have completed a generation. The forecast assumes a developmental threshold of 10^{o}C, as this was found to be the cut off point for development in Chapter 3, and has a starting point of the 1st of February, as this is usually around the coldest point of the year.

Figure 6.12 Mean number of adult and larval *Thrips tabaci* per leek plant at Warwick HRI, Wellesbourne in 2007 and the timings of the 4 generations produced by the forecasting system using a developmental threshold of 10^{o}C.



The agreement between forecast and observed populations is superficially much greater in 2007 than in either of the previous years. However, closer examination reveals continued serious discrepancies. The 1st and 2nd predicted generations again agree well with larval population peaks, but not with adult

population peaks. Again it is the emergence of successive generations of adults that should be predicted by the forecasting system. Furthermore, the 3rd predicted generation corresponds with no field population peaks at all.

Clearly there is a serious detachment between expected patterns in *Thrips tabaci* population development derived from forecasting systems either based on the original day-degree model, as demonstrated by Collier et al. (2007), or on the new system demonstrated here. In developing this new forecasting system, and as discussed in detail in Chapter 3, it was assumed that the major limitations of the day-degree systems, and the most likely reason that they were ineffective, was their clear lack of accuracy in identifying a developmental threshold relevant to UK populations, and in addition their demonstrable crudeness in addressing the various thrips life stages together, when in fact they are known to have very different developmental rates (Quartey, 1982, Edelson and Magaro, 1988, Murai, 2000). However, as seen in Figures 6.10 to 6.12, this new forecasting system, despite addressing the perceived shortcomings of the older day-degree system, appears to be just as inaccurate.

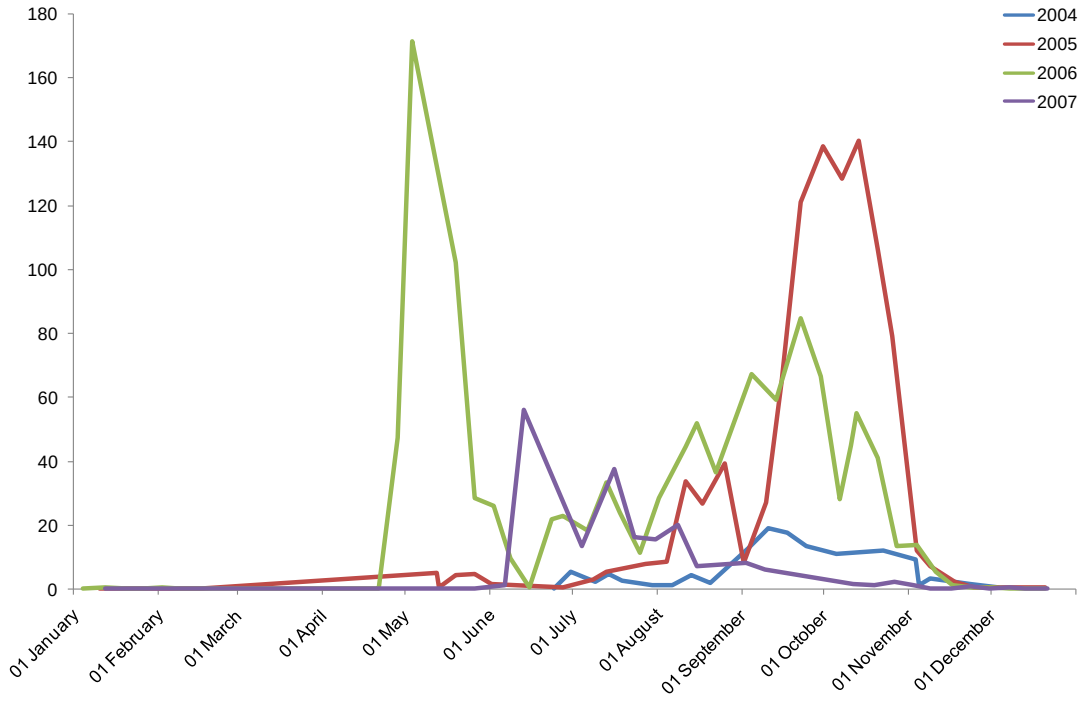
One clear limitation of the system is that because developmental rate is being considered in a non-linear fashion, it is necessary to use an artificial developmental threshold. If one were not used then development would be predicted at extremely low temperatures as the non-linear curve flattens out towards the low end of the temperature range. Clearly this allows for some flexibility on the researcher's part, and indeed it is useful to see how changing the developmental threshold affects population predictions. Eventually though, a representative developmental threshold temperature must be chosen, and 10^{o}C, the temperature at which *T. tabaci* was found to be unable to complete its life cycle in the experiments detailed in Chapter 3, gives a number based, in this case, on recorded data rather than predictions. It is important to note that in the wider investigation of this new forecasting system, other developmental thresholds were tested and applied to the prediction of field population trends using the methodologies described in Chapter 3, and although predicted generation times changed, there was no good match for field population trends using any 'sensible' threshold temperature.

Population and generation patterns

If a pattern of a distinct successive series of generations is exhibited by *T. tabaci* in the UK then it should be possible to identify it by looking at the overall size and adult/larval composition of the field populations examined in this study. However looking at Figures 6.2 to 6.5, such a pattern is not immediately apparent. Indeed although it is possible to identify individual peaks and troughs in some years, which superficially appear to be distinct generations, such trends are isolated and it is not possible to follow a repeating pattern throughout any of the years in which sampling took place, let alone across the entire length of the study. For example, in 2006 and 2007 (Figures 6.4 and 6.5) there is a clear 1st generation in the spring, represented by a very large larval population that develops and declines within a short timescale. In neither of these years is it possible through population size or composition to identify a clear 2nd generation and indeed this distinct 1st generation pattern is not represented in 2004 and 2005 (Figures 6.2 and 6.3) at all. Furthermore, if all the years of the study are looked at together then it becomes clear that there is little in the way of year-on-year repeating patterns in population size and that the population development of *T. tabaci* is very different each year.

Figure 6.13 summarises the mean numbers of *Thrips tabaci* (adults and larvae) recorded on leek plants at Warwick HRI, Wellesbourne for the years 2004 to 2007.

Figure 6.13 Mean numbers (adults and larvae) of *Thrips tabaci* per leek plant at Warwick HRI, Wellesbourne for the years 2004 to 2007.



One general trend that does appear to be present to some extent in three of the study years, 2004, 2005, and 2006 is the increase in population size observed in August and September. This trend is not repeated in 2007. It is possible therefore to observe some apparent trends, but the year-on-year picture is anything but uniform, and it is certainly not possible to track a series of successive generations in any of the years in which field monitoring took place.

6.3.4 Why is forecasting inaccurate?

The explanation for why none of the available forecasting systems, either those based on traditional day-degree calculations or the one formulated for this study, are accurate for predicting population trends in UK *Thrips tabaci* populations is a complex one. The following are all potential reasons for this lack of 'accuracy':

1. Our understanding of the temperature-development relationship is too crude, as it is based entirely upon data derived from fixed-temperature laboratory experiments.

2. Temperature may not in fact be the rate-limiting factor which is defining population growth and development in the field throughout the season.
3. These forecasting models may simply be too limited, a phenological model being inappropriate to properly understand the field trends observed. A full population model may be required to understand such trends.
4. Variation was observed throughout the experiment in the colour and size of *T. tabaci* adults. This was associated with time of year, as was also noted by Sakimura (1937) and Murai and Toda (2001). It is possible that this seasonal variation in physical characteristics is matched by a variation in behaviour or survival strategies which could affect the growth of the population or our ability to record it.
5. Our methods of recording field populations may be inappropriate and may not be giving a complete picture of actual population sizes, population composition or trends of either.

Each of these potential limitations requires some explanation and discussion:

1. Our understanding of the temperature-development relationship is crude

Generation of data on development times and growth rates of *T. tabaci* has been conducted universally under laboratory conditions and has concentrated entirely on the temperature-development relationship (Quartey, 1982, Edelson and Magaro, 1988, Murai, 2000). As was demonstrated in Chapter 3, experiments conducted at variable temperatures produce results that would not be easily predictable when simply looking at the mean temperature that the insects experienced. Indeed what this highlights is that although there is now a good understanding of the relationship between the rates of *T. tabaci* development and various temperatures, as yet little is understood about the effect of changing temperatures on the growth and development of this insect. For example, when and to what extent *T. tabaci* can exploit its available developmental temperature range in an environment where that factor is never constant. Whether, for example, *T. tabaci* requires some 'priming time' when the temperature rises above its developmental threshold before development recommences is a question that has been addressed only very briefly in this study (in investigating whether T. tabaci enter diapause over the winter months, see section 6.3.2), and apparently not at all within the wider

literature. It is the understanding of such processes and relationships which may prove crucial if forecasting systems are to be improved.

2. Temperature may not be the rate-limiting factor

Beyond the obvious limitations of our understanding of the temperature-development relationship is the possibility that it is not this, but other rate-limiting factors that may be paramount in defining growth rates in the field for part or all of the periods that are being examined. Briere et al. (1999) described temperature as "one of the most important factors that influences the developmental rate of arthropods" and Finch et al. (1996) in their review of work done to forecast pest insect attacks in UK horticultural crops stated that "the rates at which insects complete their life cycles depends mainly on temperature". Both statements are undoubtedly true but both also acknowledge that other rate limiting factors exist and are to some degree influential upon developmental rates in the field. It is fairly safe to say that many of the studies available in the literature on arthropod development and growth forecasting, and certainly all those pertaining to *T. tabaci*, have been conducted on the educated assumption that temperature is the key rate-limiting factor in the field rather than any hard data demonstrating that such is actually the case. Of course the field is a much more complicated and dynamic environment than that which is modelled in most laboratory experiments and any number of additional factors may be at work, confusing the picture. Identifying precisely what is the rate limiting factor for development at any one time in the field is not a simple task. If temperature was the key factor limiting development in the field populations examined in this experiment then it might be fair to expect that any forecasts based on the temperature-development relationship studied in the laboratory would be most accurate in predicting events in the early season in the field, when overall temperatures were lower, and therefore temperature-driven development restrictions more severe.

Table 6.2 compares forecast first larval eclosion of the season with the actual date on which larvae were first recorded in the field. There are two dates in 2008 for first recorded larvae in the field, as an individual larva was seen unexpectedly in February, but seems to have been an anomaly as no other larvae were seen until April.

Table 6.2 Predicted mean (50%) eclosion date for larvae and actual date on which larvae were first recorded in the field.

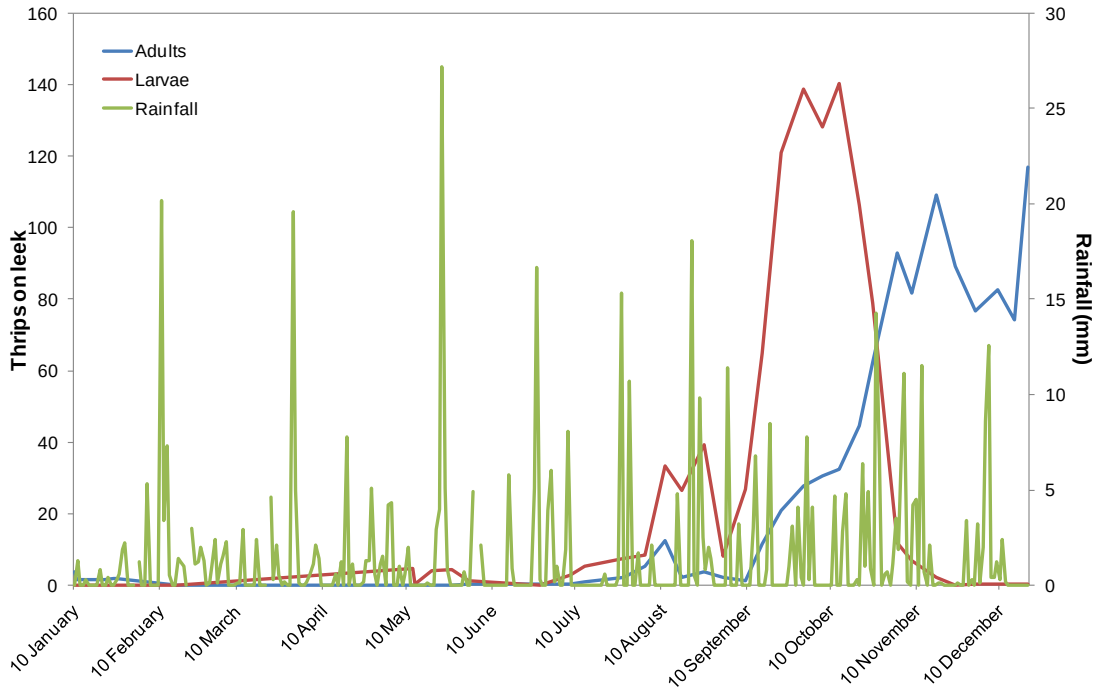
Year	Date of predicted mean (50%) larval eclosion	Date of actual first recorded larvae
2004	19th May	20th June
2005	27th May	12th May
2006	20th May	28th April
2007	10th May	06th June
2008	22nd May	24th February/ 15th April

Even taking into account the 'soft' nature of the predicted dates, they are when approximately 50% of the population is forecast to have eclosed as larvae and so should really represent a period of several days around the stated date, and the relative coarseness of the recording process, in that samples were only taken, on average, every 7 days, it is obvious that predicted and actual eclosion dates have little in common with one another. As all of the currently available forecasting systems for *Thrips tabaci*, including this newly developed one, have been shown to be inaccurate for UK populations, and as the one factor linking all of them is their reliance entirely on temperature as the key predictor, it would seem prudent to consider this as the possible reason for their ineffectiveness. For example, the size of *T. tabaci* populations on cotton in several countries has been shown to be positively correlated with environmental factors such as relative humidity and rainfall (Khan et al., 2008). In order to fully investigate the potential influence of other environmental factors on *T. tabaci* development in the UK it is important to examine them and their relationship with population trends more closely. It is not within the scope of this study to present an in-depth examination of all of the possible alternative factors that may be at work. Nevertheless as data were gathered on rainfall in the field and as the effect of irrigation and rainfall on *T. tabaci* population size has already been examined in some depth (Chapter 5) in this study, the wider influence of this environmental factor will be discussed here.

In Chapter 5 it was demonstrated that, on the small scale, no statistically significant relationship could be observed between levels of irrigation or rainfall and the population size of *T. tabaci*. Despite this, there remains the belief, amongst some

commercial growers, that periods of heavy rain reduce *T. tabaci* numbers, and they are supported in this belief by the work of Harris et al. (1936). Figure 6.14 shows a comparison of the mean numbers of *T. tabaci* observed on destructively sampled leek plants at Warwick HRI, Wellesbourne in 2005 and the corresponding daily rainfall in mm in that location.

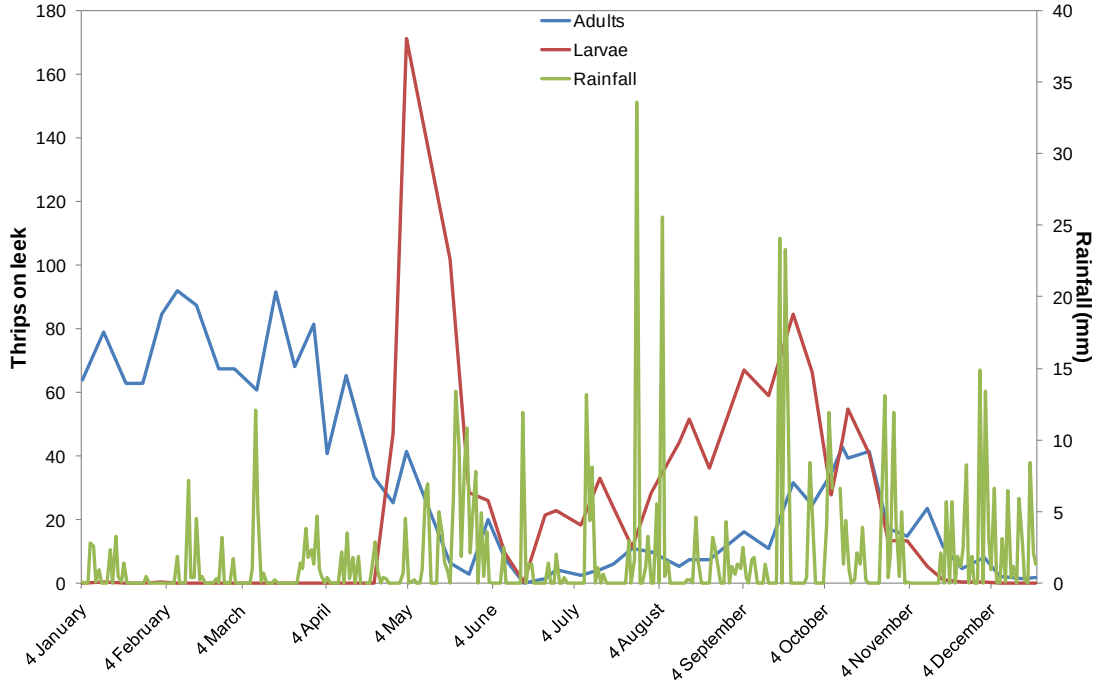
Figure 6.14 Mean number of adult and larval *Thrips tabaci* per leek plant at Warwick HRI, Wellesbourne between January 2005 and the end of December 2005 and the corresponding daily rainfall in mm.



The spring and summer of 2005 were relatively warm and dry at the experimental site in Wellesbourne, Warwickshire. As can be seen in Figure 6.14, only for 3 rainfall events during the year did the daily rainfall exceed 20mm, an arbitrary figure, but one which illustrates that incidences of heavy rainfall over short periods were rare. Despite this, there was little growth in the thrips population in the early summer, and indeed adults were not recorded before late July. If rainfall or temperature were the key barriers to population development at this time it should be expected that population size would have increased quickly over this period. Despite a relatively warm and dry summer this was not, however, the case. Moreover it is very difficult to identify any relationship between periods of rainfall and the size of the population over the entire year. Figure 6.15 shows a comparison of the mean

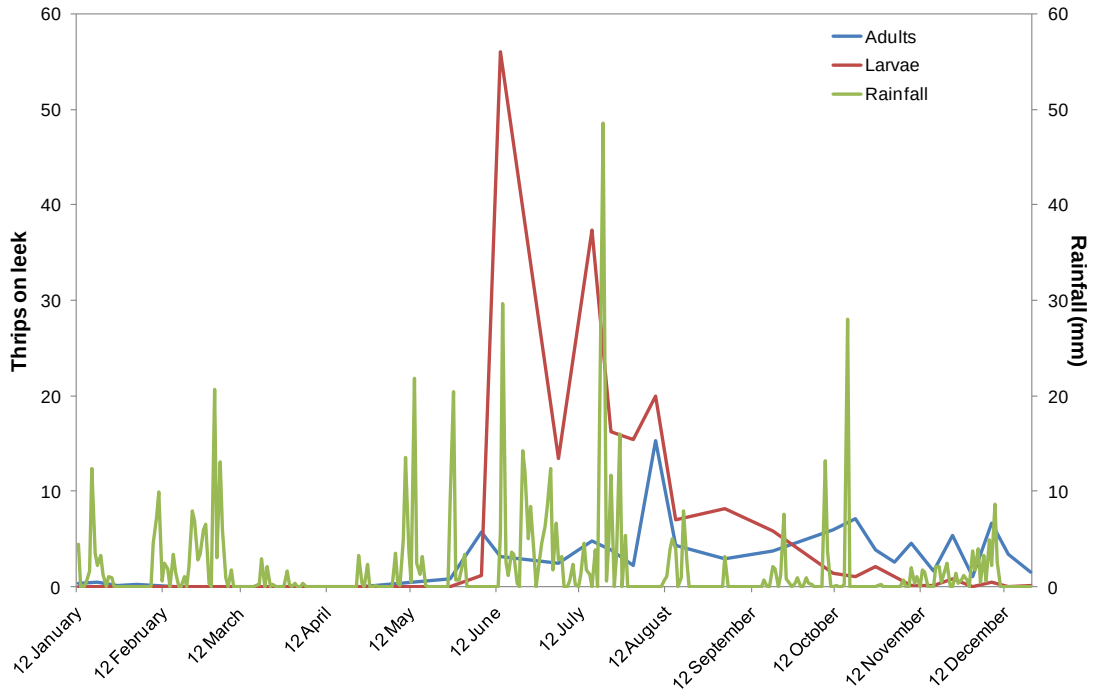
numbers of *T. tabaci* observed on destructively sampled leek plants at Warwick HRI, Wellesbourne in 2006 and the corresponding daily rainfall in mm in that location.

Figure 6.15 Mean number of adult and larval *Thrips tabaci* per leek plant at Warwick HRI, Wellesbourne between January 2006 and the end of December 2006 and the corresponding daily rainfall in mm.



The situation in 2006 is much as that for 2005, it is not possible to see any direct relationship between recorded rainfall and recorded *T. tabaci* population size. Harris et al. (1936) identified a period of heavy rain and hail which corresponded directly with a fall in thrips numbers, as the two occurred simultaneously. The only point when an increase in rainfall, which is in fact minor in this case, appears to correspond directly with a fall in population size is in May and June, and yet this fall in numbers is likely to be related to the maturation of first generation larvae which eclosed in late April. Moreover, other periods of exceptionally high rainfall, like that observed in late July and early August, are in fact accompanied by a general rise in overall thrips numbers. Figure 6.16 shows a comparison of the mean numbers of *T. tabaci* observed on destructively sampled leek plants at Warwick HRI, Wellesbourne in 2007 and the corresponding daily rainfall in mm in that location.

Figure 6.16 Mean number of adult and larval *Thrips tabaci* per leek plant at Warwick HRI, Wellesbourne between January 2007 and the end of December 2007 and the corresponding daily rainfall in mm.



The situation in 2007 is much the same as that for 2005 and 2006, although it is possible to see some periods where high rainfall appears to correspond with a fall in population size, this is not universally the case and indeed rainfall is high during some periods of population expansion.

To gain some more insight into the direct effect of rainfall on *T. tabaci* it would be necessary to have some understanding as to whether and to what extent rainfall causes direct mortality in *T. tabaci*. It has been reported that the key reason for mortality is the physical washing of the insects off the plants and onto the soil where they become stuck or drown, unable to return to the host plant (Harris et al., 1936, North and Shelton, 1986b, Kirk, 1997). Also it has been reported that after rain events the corpses of drowned thrips are easily seen on plant leaves (Kirk, 1997). However direct examination of infested plants exposed to rainfall and irrigation in this study (Chapter 5) recorded neither a significant fall in population size nor a notable increase in corpses on leaves. Corpses on leaves were observed throughout the study and cause of death in these cases is universally difficult to determine. Although some corpses were observed after rainfall or irrigation events, numbers were never particularly higher than background levels. Wardle (1927) suggested that

it was the effect of increased water on the size and health of the host plant that was the important factor rather than the mortality inflicted upon the thrips. Extra water, and therefore increased growth, would reduce the density of thrips per leaf and therefore the overall visual impact of cosmetic damage due to thrips. This may indeed be the case, and in fact discussions with growers have revealed that additional watering prior to harvesting is common practice in order to reduce the visual impact of thrips, especially as the upper leaves are removed during plant processing and quick growth pre-harvesting can effectively 'push' damage up the plant and out of the marketable portion of the crop.

Whether rainfall has a direct effect upon thrips populations or not, and it certainly does not appear so in this case, it is clear that the population size of *T. tabaci* is likely to be influenced by a range of factors and that further investigation of these is required if population development is to be fully understood.

3. The current models are too limited

Though the use of a single predictor, in this case temperature, for the forecasting of *T. tabaci* development is clearly an over-simplification, it is also a necessity for developing a straightforward model that is useful to the end user. The point of forecasting is to predict, with some accuracy, population trends in the pest population by which the grower can most efficiently choose when to apply available control methods. In the case of the system developed here, and described in Chapter 3, the forecast is of mean generation times based on rate of development as modified by temperature and it is expected that these generation times should tally with population peaks observed in the field. It is a purely phenological model. It is important to remember that the forecast itself says nothing about population size, or indeed, in the long run over successive generations, about population composition. Such a population forecast would require both a complete knowledge of existing populations before the start of the modelling process and detailed data on immigration, emigration, fecundity and mortality. There is therefore a clear separation between what this forecasting system, and indeed all other *T. tabaci* forecasting systems, is predicting, namely generation times, and what the important factor actually is for growers looking to control *T. tabaci* populations, which is population size.

The focus in the literature on the modelling of development times, and therefore the forecasting of the timing of successive generations of pests, is clear, and such systems have been proven accurate for a range of insect pests in the UK (Phelps et al., 1993, Finch et al., 1996). However each of those species, for which such a forecasting system is used in the UK, displays a distinct series of generations over the course of the year, a feature which, as has already been discussed, is not apparent in *T. tabaci*. The key to this lack of distinct generations may lie in the relationship between generation time and the fecundity and longevity of the adult insect. The cabbage root fly, *Delia radicum*, and the carrot fly, *Psila rosae*, are examples of two common pest insects for which there exists an efficient and tested temperature-based forecasting model for UK populations (Finch et al., 1996). The forecasts for both species rely upon the knowledge that the insects have a relatively long generation time in comparison with a fairly short 'oviposition window' in which the adults produce eggs. In this way these species exhibit clearly defined successive generations through the season, and the timing of emergence of a new generation can be predicted with some accuracy. This long generation time and short oviposition window is not a feature of *Thrips tabaci* however. As was demonstrated in Chapter 3, the mean generation time for *T. tabaci*, from adult emergence to adult emergence, at 20^{o}C is 21.9 days. Sakimura (1937) recorded that at 21^{o}C the mean pre-oviposition period of newly emerged *T. tabaci* adult females was 3 days, which compares closely to the mean of 2.95 days recorded at 20^{o}C in this project and described in Chapter 3. Sakimura further reported a mean of 50 days as the active oviposition period and 6 days as the mean post-oviposition period. Taking Sakimura's (1937) numbers, an approximate adult lifespan for *T. tabaci* is 60 or so days, 50 of which fall within the period of active oviposition. At a temperature of 18^{o}C, Sakimura calculated that mean egg production is 1.8 eggs/day. Egg production is temperature-dependent and varies between individuals, although younger females tend to be more fecund than older ones. In total at 18^{o}C, the average female produces 80 eggs throughout her oviposition period. As can be seen from these data, *T. tabaci* does not exhibit the traits that make species like *D. radicum* and *P. rosae* so suited to forecasting and targeting by generations, namely long generation times and short 'oviposition windows'. Indeed the mean recorded generation time at 17.5^{o}C is 32.8 days and yet the oviposition window of an adult at 18^{o}C is 50 days. As the oviposition window is longer than the generation time, it is clear that generations

will become almost immediately mixed in the field and that unlike other species, it will not be possible to observe successive generations under field conditions. Add to this the individual variability in development times, which is discussed in Chapter 3, and the variability in fecundity recorded by Sakimura (1937) and it is clear that attempting to monitor *T. tabaci* populations via forecasting of generations may be an impossible task. As corroboration, it should be noted that beyond the initial appearance of larvae in the spring, within a very short time it was possible to see all larval and pupal stages of *T. tabaci* together in the field throughout the season and this was a feature in every year of the study. Such a mix of life stages supports the idea that the population is made up of many series of overlapping generations, rather than a single generation at any given time.

Future forecasting efforts would do well to concentrate on population modelling of *T. tabaci*, rather than simple phenological modelling. An approach more akin to those employed to forecast the population development of viviparous species, such as the numerous pest aphid species, may be required and certainly accurate forecasting is likely to require a more complex model than those that have been employed to date.

4. Seasonal variation in Thrips tabaci may be distorting the picture

Both Sakimura (1937) and Murai and Toda (2001) identified seasonal variation in the size and colour of adult *Thrips tabaci*. In both cases, thrips that developed in cooler conditions were found to be larger and darker in colour than those that developed in mid summer. These observations were also true for the population of *Thrips tabaci* studied at Warwick HRI, Wellesbourne. Mid to late summer adults were often smaller and lighter in colour than adults at other times of the year and this is likely to be due to a combination of factors, including temperature and food quality, which the thrips experienced during development.

As was demonstrated in Chapter 4, the range of behaviours exhibited by *T. tabaci* is directly associated with temperature. It is possible that this range of behaviours will also be affected by the conditions in which a thrips developed, the mid to late summer thrips being perhaps more likely to fly for example. Kirk (1997) noted that seasonal variation in thrips may affect their survival, capacity to migrate and reproductive capability, making the modelling of population dynamics difficult. Physical differences certainly exist and so the possibility of behavioural differences

cannot be ruled out. Further work on this subject would be required for any definitive answer.

5. Monitoring techniques for field populations may be inaccurate.

Two direct monitoring techniques, flight interception trapping and physical counts on plants, and one indirect monitoring technique, plant leaf damage, were used to monitor the size and composition of the *T. tabaci* population at Warwick HRI, Wellesbourne over the course of this study. These techniques have all been used in the literature, either in isolation or together, to estimate *T. tabaci* populations in the field (Suman et al., 1980, Srinivasan et al., 1981, Suman and Wahi, 1981, Shelton and North, 1986, Shelton et al., 1987, Sites and Chambers, 1990, Theunissen and Legutowska, 1991a, Theunissen and Legutowska, 1991b, Fournier et al., 1994, Shelton, 1995). All three techniques have limitations however, and it may be that even when information from all three is combined, it may not be possible to make sufficiently accurate estimates of population size and composition at any one time.

Destructive sampling

Physical counts of the insect in its natural environment are the most fundamental way of measuring its population but are limited in several ways. The physical size and cryptic nature of *T. tabaci*, combined with the physical complexity of the host plants, make *in situ* counts in the field impractical. Indeed Theunissen and Legutowska (1991a) singled out leek and onion as plants whose physical form would make direct visual counts of thrips, to provide a measure of absolute numbers, unreliable. Destructive sampling is therefore necessary, together with the removal of the plants to a laboratory, in order to search for the thrips with the aid of a microscope. This may, however, reduce the accuracy of the resultant count, most specifically, the number of adults observed and therefore the recorded adult-larval composition of the population and in its overall size. Indeed, it appears from close examination of count data that this monitoring system may have been seriously underreporting the number of adult *T. tabaci* present in the field throughout the course of the study. An illustration of this can be seen in Figure 6.3, where it is possible to see the build up of a larval *T. tabaci* population between March and June 2005 in the apparent absence of adults. This is not an isolated case, adult numbers recorded through destructive sampling of host plants appeared low throughout the

course of the study compared with associated larval numbers, and this was further highlighted in several years as large fluctuations in larval numbers were not reflected at all in the adult population. A simple explanation for this phenomenon could be that the method of sampling allows a larger percentage of adults to be lost from, or escape from, the plant before they are recorded than larvae. Adult *Thrips tabaci* have different priorities to larvae, the overriding imperative being to reproduce rather than to grow and develop. Consequently they have different capabilities and were observed to be far more mobile than larvae and they can also fly. More highly mobile adults have a higher likelihood of escaping before being counted and the removal of the plant from the soil, involving the host being moved around sharply is likely to trigger avoidance mechanisms like flight and dropping off the plant, which are less prevalent or absent completely at the larval stage. General observations on the intra-plant distribution of larvae and adults made throughout the study also showed that adults were far more likely to be located on exposed areas of the plant than larvae, areas where they would be more easily dislodged or could more easily escape from during the plant harvesting process. All prudent measures were undertaken to minimise the effect of thrips loss from the plant during destructive sampling, plants were transferred in the field to plastic bags for example, which were also searched for loose thrips, but even so losses incurred in this manner are difficult to quantify. Nevertheless the lack of recorded adult numbers indicates that such losses may have been high, and certainly enough to make population counts based on destructive sampling potentially unreliable. This is especially so since the activity levels of the adults may have had some effect upon the count, in their capacity to escape the plant through flight during the sampling process for example, meaning that losses cannot be presumed to be equivalent across the entire study. However, there remains little alternative to such destructive sampling methodology when making direct counts of *T. tabaci* numbers in the field.

Flight interception trapping

The second direct monitoring technique, flight interception trapping also has its limitations. Thrips flight activity is closely tied to environmental conditions such as temperature (as demonstrated in Chapter 3 and extensively in the literature), humidity and even electric fields (Lewis, 1964, Kahrer, 1992, Kahrer, 1994, Kirk, 1996, Villeneuve et al., 1996, Lewis, 1997c, Kirk, 2004). Furthermore only adults of

T. tabaci are winged and therefore flight interception trapping samples purely the adult portion of the population. Though light blue sticky traps of the kind used in this study have been shown to be useful for monitoring of *T. tabaci* (Trdan et al., 2005), that usefulness applies to monitoring adult numbers at potentially unpredictable intervals, as the drivers behind flight activity remain to some extent obscure, rather than universally of the population size. A good example of this can be seen when reviewing sticky trap catches in 2006 in comparison with *T. tabaci* numbers recorded via destructive sampling, as shown in Figure 6.17.

Figure 6.17 Mean numbers of adult and larval *Thrips tabaci* recorded per salad onion plant and mean numbers recorded on blue sticky traps at Warwick HRI, Wellesbourne in 2006. Error bars represent 1 standard error.

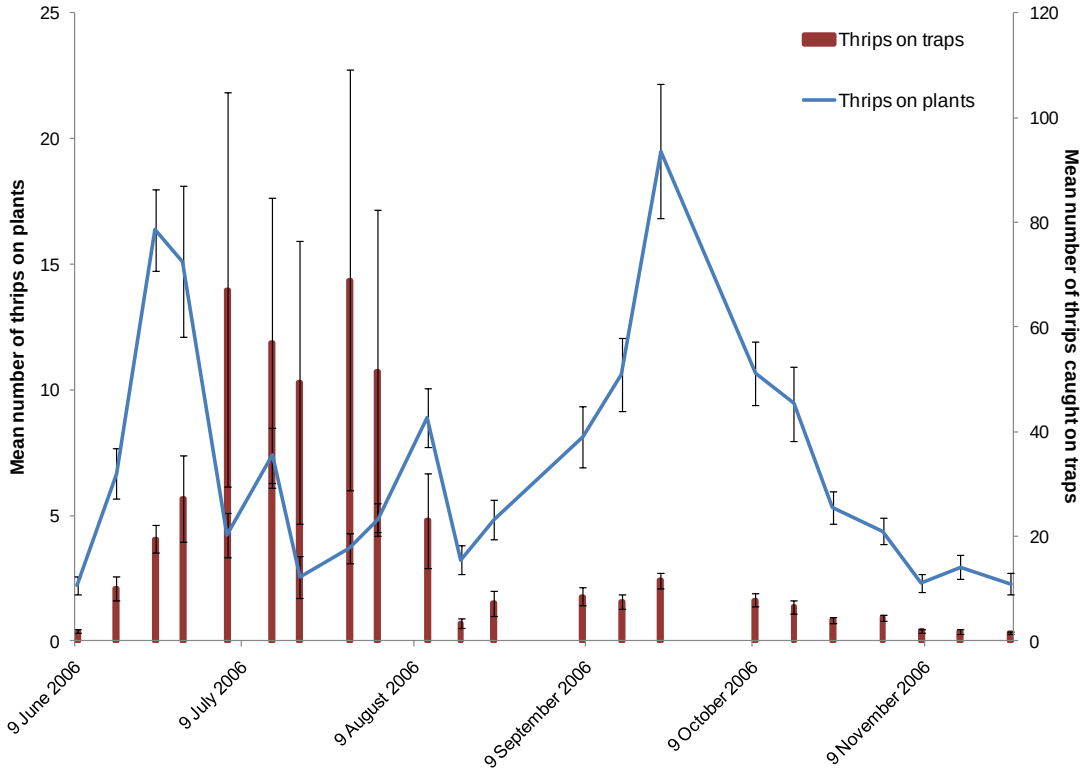
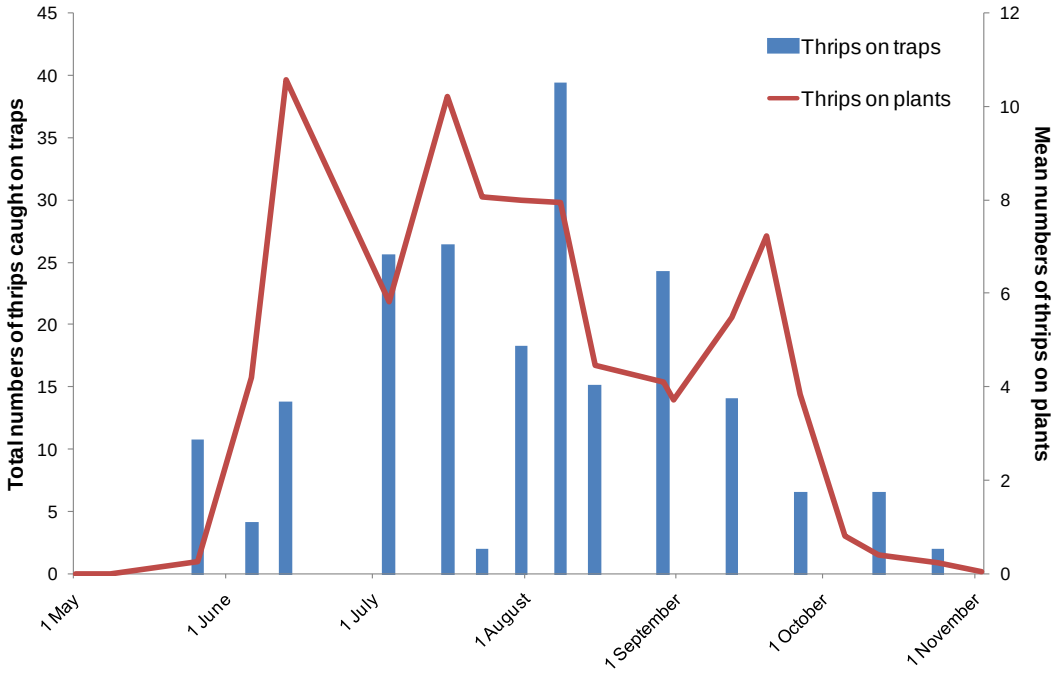


Figure 6.17 demonstrates clearly that high levels of flight activity, and consequently high flight interception trap catches, are not directly associated with population size. Figure 6.18 shows the comparison between sticky trap catches and *T. tabaci* numbers recorded through destructive sampling of salad onion plants in

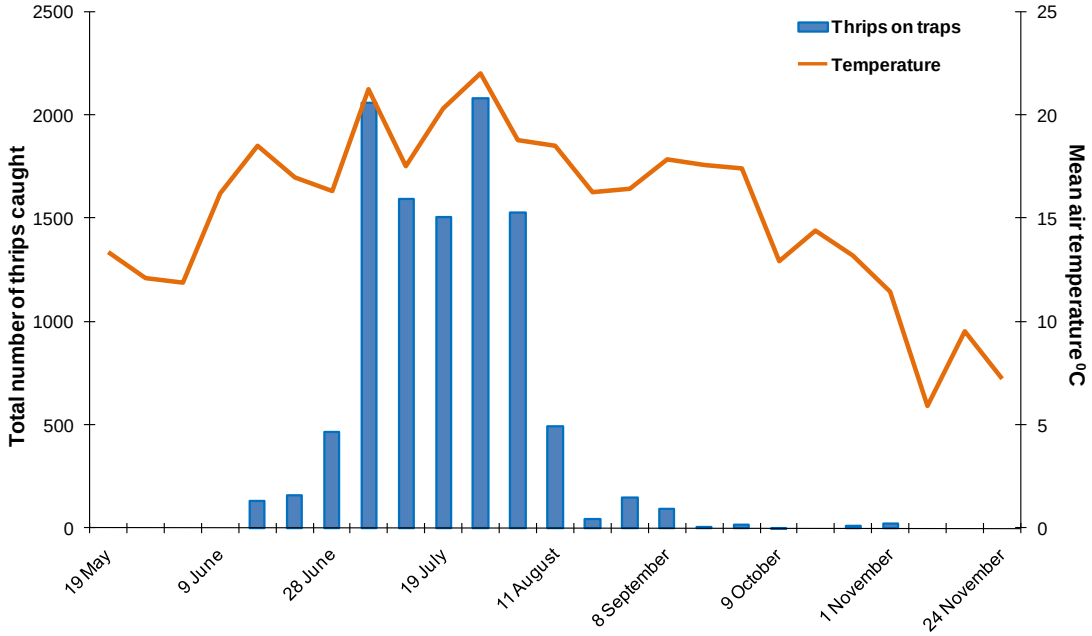
2007, and demonstrates again that there appears to be no direct relationship between the two.

Figure 6.18 Mean numbers of adult and larval *Thrips tabaci* recorded per salad onion plant and total numbers recorded on blue sticky traps at Warwick HRI, Wellesbourne in 2007.



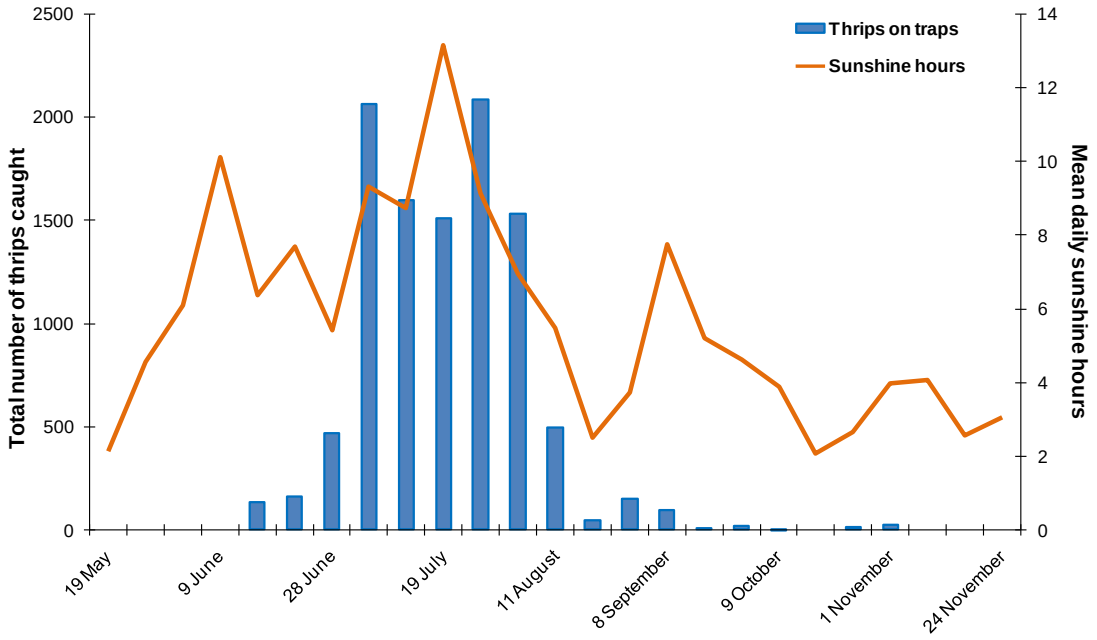
Whether or not destructive sampling is giving an accurate picture of the overall population size, it must certainly give some indication of population trends. Therefore the clear lack of any recorded relationship between numbers of thrips found on plants and those caught on traps over the same period shows quite conclusively that flight interception trapping is an inappropriate method for monitoring *T. tabaci* population size. Indeed, when trap catches are compared with prevailing weather conditions over the same period, it becomes clear that it is these factors, rather than the size of the population which appear to be the main drivers behind flight activity, and therefore sticky trap catches. Figures 6.19 and 6.20 show the relationship between flight interception trap catches and mean air temperature and mean daily sunshine hours at Warwick HRI, Wellesbourne in 2006.

Figure 6.19 Total numbers of adult *Thrips tabaci* recorded on blue sticky traps at Warwick HRI, Wellesbourne in 2006 and the corresponding mean air temperatures.



Flight activity was shown in Chapter 4 to have a direct relationship with temperature, with the majority of flights occurring above 15°C and with activity peaking at around 25°C. Those laboratory-derived figures are borne out when looking at the field flight catches shown in Figure 6.19. Not only is significant flight activity observed only when mean air temperatures are above 15°C, but flights peak when mean air temperatures rise above 20°C. Figure 6.20 further shows that the peak of flight activity corresponds also with the peak of mean daily sunshine hours.

Figure 6.20 Total numbers of adult *Thrips tabaci* recorded on blue sticky traps at Warwick HRI, Wellesbourne in 2006 and the corresponding mean daily sunshine hours.



Flight interception trapping is a useful tool for monitoring adult activity and mass flight events, and as demonstrated by Villeneuve et al. (1996), for monitoring invasions into a particular crop. Flight behaviour in *T. tabaci* itself is still not fully understood though. Although it seems likely that flight activity is driven primarily by environmental conditions, what is clear is that favourable environmental conditions do not always guarantee flights. In Figure 6.19 it can be seen that there were periods in June, August and September of 2006 that were favourable for flight activity in terms of the mean air temperatures and yet very little such activity occurred. Lewis (1964) attributed mass flight events to periods when temperatures are unfavourable for some period allowing a large number of adult thrips to reach a stage at which they are ready to migrate; all those individuals then subsequently flying together when the temperature rises above their flight threshold. This is evidently not the situation in this case. Figure 6.17 demonstrates a wide period of favourable conditions within which there is a limited period of activity. It is possible to speculate on the reasons for this of course, and it certainly merits further investigation. On the one hand, the pattern of flight activity could indeed be driven by environmental conditions, but in a manner not yet fully understood. Other factors

beyond temperature, sunshine hours or rainfall may be at work, or for example, electric fields as discussed by Kirk (2004). Seasonal variations in the thrips themselves, as has been already discussed, may have some influence on the behaviours they demonstrate. The smaller lighter thrips observed in the mid summer, possibly influenced by the conditions they experienced in their immature stages, may be more predisposed to exhibiting behaviours associated with migration, whereas the darker thrips seen in the autumn may be more predisposed to engaging in activities that will help them to survive and overwinter. As discussed in Chapter 4, behaviours exhibited by *T. tabaci* are directly influenced by temperature, and so there may be scope in the future to investigate whether the temperatures and conditions experienced as larvae have some influence on the subsequent physical and behavioural characteristics of the adult thrips.

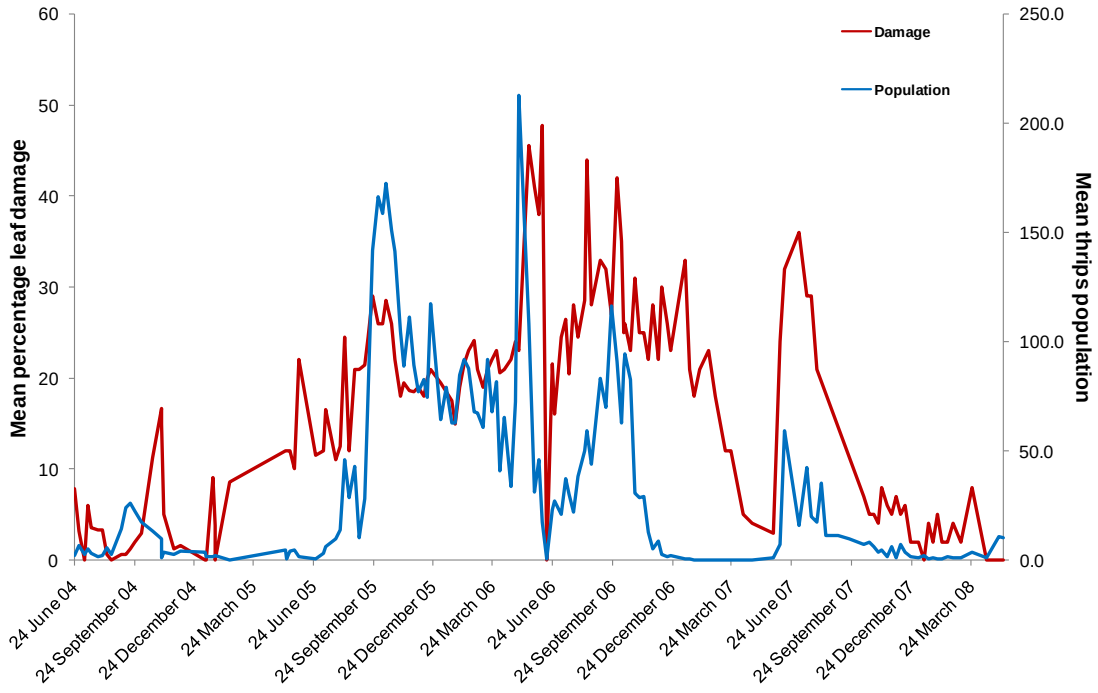
Plant leaf damage

Monitoring visible damage on the leaves of *T. tabaci* host plants was carried out throughout the length of this study. Whenever plants were brought in from the field during the destructive sampling process, each of the leaves was examined individually and assessed for damage as described in Chapter 2. Monitoring leaf damage is an indirect technique as it will naturally be influenced not only by the size of the *T. tabaci* population, but also by the relative intensity of feeding activity. As demonstrated in Chapter 4, feeding behaviours and specifically the frequency at which thrips feed, is influenced directly by temperature, and possibly by other environmental factors as well. As such, feeding damage should be considered in such a light and cannot be used directly to track the development of *T. tabaci* populations. Moreover the appearance of visual damage is a time-delayed process and so visible damage on leaves is likely to reflect the state and feeding activities of the thrips population several days in the past (Theunissen and Schelling, 1997). On top of this is the accumulation of damage. Damage accumulates on leaves at different rates according to the damage inflicted by the population, but may be visually ameliorated by fresh growth in the host plant. Therefore the overall condition of the host plant, its age and the environmental conditions affecting its growth, may all have some influence on the appearance of cosmetic damage visible on the leaf.

Figure 6.21 shows the damage, as a mean percentage of the overall leaf surface, to the penultimate leaf of leek plants and the corresponding population size of *T.*

tabaci recorded by destructive sampling at Warwick HRI, Wellesbourne between 2004 and 2008.

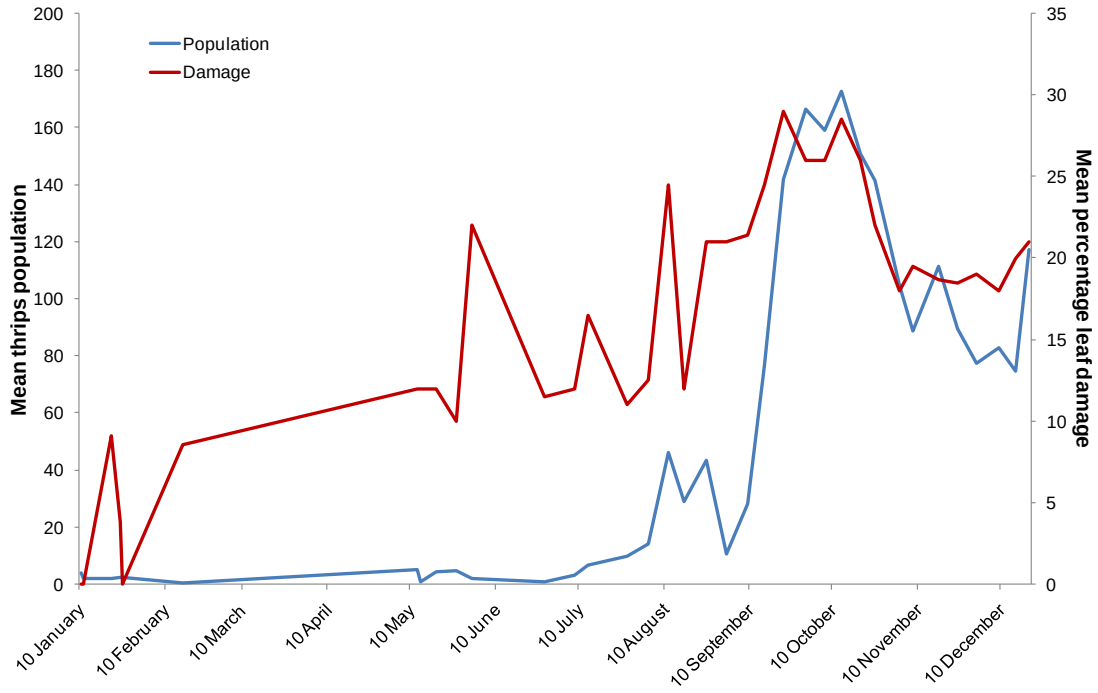
Figure 6.21 Damage, as a mean percentage of the overall leaf surface, observed on the penultimate leaf of leek plants and the corresponding population size (adults and larvae) of *T. tabaci* recorded by destructive sampling at Warwick HRI, Wellesbourne between 2004 and 2008.



Looking at Figure 6.21, it is possible to see that general trends in population size are largely reflected by general trends in cosmetic damage to leaves. Despite this, there were several periods in which damage levels increased quickly on leaves with no apparent corresponding increase in population. Whether this was a reflection of real population fluctuations that were perhaps being underrepresented by direct thrips counts is not known. This is certainly a possibility, and the weaknesses of the destructive sampling process by which direct counts are conducted have already been discussed. Even so, it is not possible to discount the potential influence of accumulated damage. Damage to individual leaves was often extreme and in many cases older leaves had 90%+ of their surface affected. During periods of slow growth, damage to leaves certainly accumulated to a greater extent than in periods where leaves were developing quickly and being replaced by fresh tissue.

Figure 6.22 shows the mean percentage damage of the penultimate leaf of leek plants and the corresponding population size of *T. tabaci* recorded by destructive sampling at Warwick HRI, Wellesbourne in 2005.

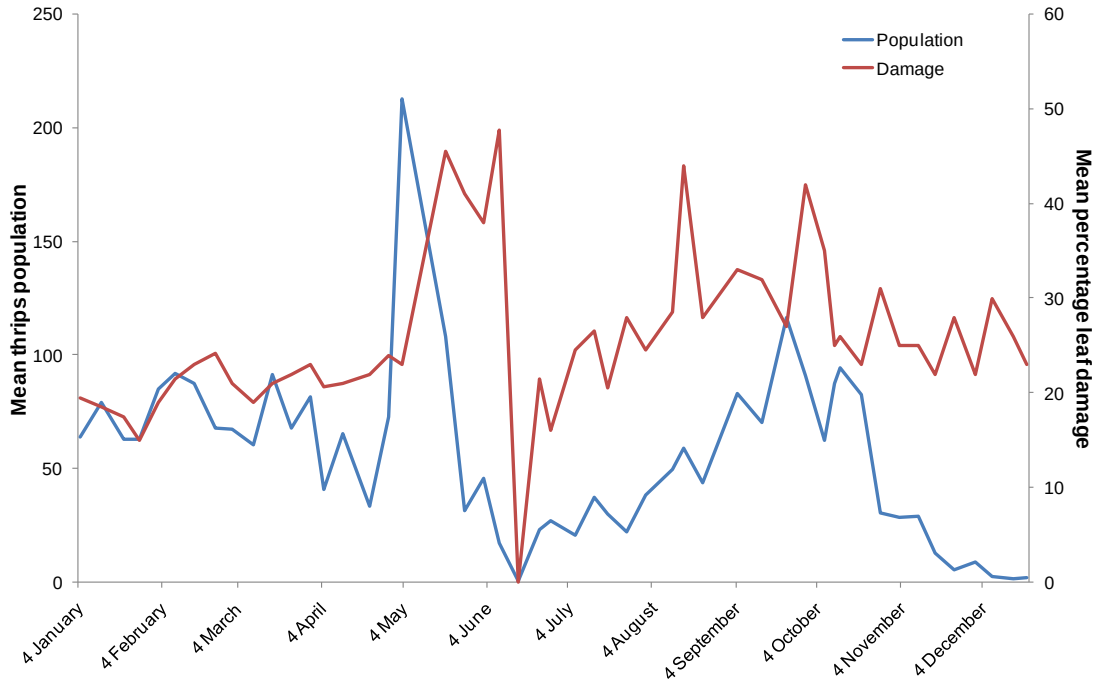
Figure 6.22 Damage, as a mean percentage of the overall leaf surface, observed on the penultimate leaf of leek plants and the corresponding population size of *T. tabaci* (adults and larvae) recorded by destructive sampling at Warwick HRI, Wellesbourne in 2005.



Looking at the relationship between damage and population size in a single year, it is easier to see the discrepancy between the two forms of monitoring. Despite the recorded population size remaining essentially static during the period up to July 2005, the observed damage to host plant leaves grew more quickly and fluctuated more frequently. This may be a reflection of underrepresentation of the population by direct counts, and indeed in this case that would seem the most plausible answer, as no 'stock' of damage from previous high populations had been accumulated by the plants at this stage, and they were growing quickly in the spring, which would tend to ameliorate the level of visible damage inflicted by the population to some extent. Later in the year, damage and population patterns tend to match more closely.

Figure 6.23 shows the mean percentage damage of the penultimate leaf of leek plants and the corresponding population size of *T. tabaci* recorded by destructive sampling at Warwick HRI, Wellesbourne in 2006.

Figure 6.23 Damage, as a mean percentage of the overall leaf surface, observed on the penultimate leaf of leek plants and the corresponding population size of *T. tabaci* (adults and larvae) recorded by destructive sampling at Warwick HRI, Wellesbourne in 2006.



Patterns of population size and damage were closely aligned in 2006, and it is generally possible to see increasing population size reflected in increasing damage for the entire course of the year. Although the population crashed in November and December, the level of damage remained constant. This is to be expected. Damage inflicted by earlier populations is unlikely to be ameliorated in the winter, as plant growth will be negligible to non-existent. Damage suffered in autumn is therefore likely to be visible until the following spring.

Figure 6.24 shows the mean percentage damage of the penultimate leaf of leek plants and the corresponding population size of *T. tabaci* recorded by destructive sampling at Warwick HRI, Wellesbourne in 2007.

Figure 6.24 Damage, as a mean percentage of the overall leaf surface, observed on the penultimate leaf of leek plants and the corresponding population size of *T. tabaci* (adults and larvae) recorded by destructive sampling at Warwick HRI, Wellesbourne in 2007.

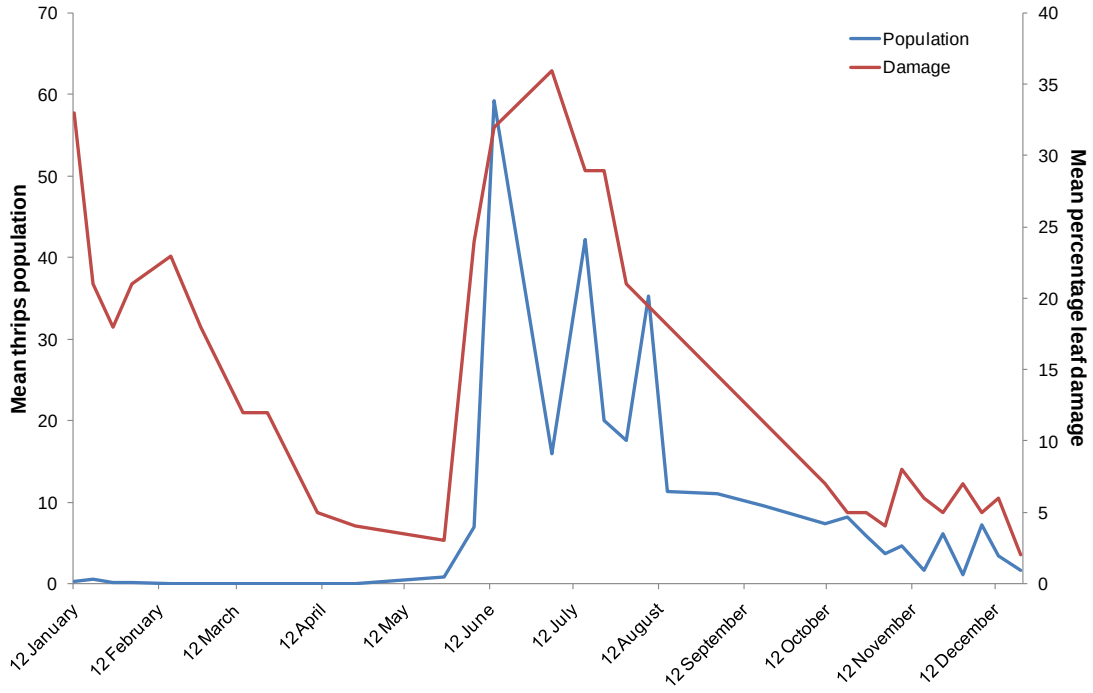


Figure 6.24 clearly shows that the damage inflicted the previous autumn has endured the winter and therefore damage early in the year does not reflect the current population size.

Plant damage is an important monitoring tool for *T. tabaci* and will remain so as it is the yardstick by which the marketability of the crop is measured. Despite this, it must be regarded with some caution as it is not necessarily a reflection of current populations or trends and indeed may be a consequence of population fluctuations over quite extended periods of time. Despite this, damage monitoring does raise some important questions with regard to the accuracy of other monitoring techniques, though of course it has little use in the prediction of future population trends.

It is very difficult to judge in isolation the efficacy of any one monitoring technique for *T. tabaci*. Evidently the cryptic nature, small size and unpredictable behaviours of this pest make it extremely difficult to monitor in any comprehensive way. Nevertheless it has been demonstrated that all three commonly-used monitoring techniques are potentially flawed and that indeed, to some extent, recordings

gathered by each tend method to contradict one other. It may well be that no one technique can be relied upon in isolation to give a clear picture of a thrips population, its size and composition. Indeed even a combination of techniques may be insufficient to give such a clear picture. Whilst so much remains obscure about the nature of *T. tabaci* population dynamics under field conditions, this may continue to be the case.

Chapter 7: Conclusion

Thrips tabaci is a commercially important pest, and its increasing significance as a target for control measures, as illustrated by Garthwaite et al. (1997, 1999, 2003), demonstrates the fact that it is becoming an increasingly burdensome one for UK *Allium* growers. Effective pest control requires knowledge of the target, its biology and behaviour, and therefore its weaknesses, and also control measures, efficient strategies by which knowledge of the pest's weaknesses may be exploited. Only when knowledge of the pest is combined with effective control methods can an integrated pest management strategy be devised and the problem tackled decisively. In the case of *T. tabaci*, both these key facets of effective pest control are deficient. Firstly, forecasting systems developed in other countries to predict the development of *T. tabaci* populations have been shown to be inaccurate when applied to populations in the UK. This, combined with increasing pesticide resistance and the long term decline in available pesticide options, due to increasingly stringent laws and mounting development costs, means that control of *T. tabaci* is perhaps more difficult now than it has ever been.

This project has attempted to address some of the deficiencies in our knowledge of *T. tabaci*. At the beginning of the project four aims were stated:

1. Examine whether the forecasting model developed for *Thrips tabaci* populations in other countries is applicable to UK populations, and if not, suggest alternative systems (Chapter 3)

2. Investigate the effect of temperature and of leaf quality on the behaviour of *Thrips tabaci*, in order to develop the knowledge required to identify and explain windows of vulnerability, which might increase the efficacy of current or novel control methods within an integrated pest management strategy (Chapter 4)

3. Investigate whether there are changes in the intra-plant distribution of *Thrips tabaci* during the day to identify periods of vulnerability to foliar sprays and to test the efficacy of irrigation control programmes based on these results (Chapter 5)

4. Carry out a long term survey of *Thrips tabaci* populations in the field to obtain more information about their population dynamics in the UK, including flight times, overwintering strategies and population development and discuss how all of these relate to our ability to forecast the development of *T. tabaci* infestations effectively (Chapter 6)

These aims will be addressed in order:

1. *Examine whether the forecasting model developed for Thrips tabaci populations in other countries is applicable to UK populations, and if not, suggest alternative systems (Chapter 3)*

Data gathered during this project were used together with data from another study to demonstrate that the forecasting system currently in use in other countries is inaccurate for the prediction of the development of *T. tabaci* populations in the UK (Collier et al., 2007). A potential reason for this discrepancy may be found in Brunner et al.'s (2004) assertion that *T. tabaci* may in fact be a 'complex of cryptic subspecies', and indeed further work investigating variation between geographically separated populations in both biology and behaviour would seem to be necessary.

The accepted method for predicting population development of *T. tabaci* involves using a day-degree or accumulated temperature forecasting system which is based on the assumption that the relationship between development rate and temperature is linear. In Chapter 3 it was demonstrated that in fact this temperature-development relationship is not linear and that the use of linear descriptors to describe it produces inaccurate results. Furthermore, it is only when the differences in developmental rates between the various life stages of *T. tabaci* are taken into account, that a clear picture of the relationship between development and temperature can be seen. A non-linear forecasting model was developed that was accurate in describing development in the laboratory, but this was found to be

inaccurate in predicting field population trends. The reasons for this may potentially lie in the complexity of the field crop environment in comparison to controlled laboratory conditions, and therefore the influence of regulating factors other than temperature. It remains unclear exactly which factors, biotic or abiotic, are influencing population development in the field at any one time. Future work to develop an accurate forecasting system for *T. tabaci* is likely to require further research into these factors and their influence. In the long run accurate forecasting may well require the development of a full population dynamics model rather than a purely phenological one.

2. *Investigate the effect of temperature and of leaf quality on the behaviour of Thrips tabaci, in order to develop the knowledge required to identify and explain windows of vulnerability, which might increase the efficacy of current or novel control methods within an integrated pest management strategy*

At the start of this project, apart from investigations of some specific activities, there was very little published information pertaining to the behaviour of *T. tabaci* (Chapter 4). This study has shown that temperature, leaf quality and host plant species have a direct influence upon the behaviour of *T. tabaci* in terms of the particular behaviours expressed, the length and frequency of these behaviours, and their relationship with one another (agreeing with the findings of Riefler and Koschier (2009)).

The practical applications of such information remain unexploited as it is not possible to accurately predict behaviours of interest such as flight. Further work will have to be undertaken to build on what has been discovered about behaviour in the laboratory. Studies on predicting behaviours such as flight, which may help to increase the efficiency of traditional control methods, are likely to be the most fruitful branch of investigation. Beyond that, though, the understanding of *T. tabaci* behaviour may prove important in assessing the efficiency of novel control measures such as, for example, using plant volatiles to discourage feeding or assessing resistant cultivars. A greater understanding of the behaviour of *T. tabaci* is likely to become ever more important as potential control methods dwindle, due to insecticide resistance or cost, and growers require increased efficiency from those control

methods which remain available to them. Further potential behaviour-influencing factors must be investigated, but these should not be limited to abiotic factors. The influence of the presence of predators, parasitoids and competitors and the effect of crowding and population pressure, for example, are factors that may well influence behaviour, and are illustrative of the potential difficulty of understanding and predicting behaviour in a complex environment.

It is possible that some behavioural patterns seen in the field may be explained by seasonal differences in individual *T. tabaci*. The observed, and as yet not fully explained, seasonal variation in size and colour may reflect different morphs of *T. tabaci* and different morphs might exhibit different behaviours. Summer forms might be more likely to migrate, for example. Further investigation into what causes this seasonal variation is necessary. A direct comparison of behaviours, their frequency and sequences, between these physically different thrips, which are found in different seasons, would demonstrate whether behaviours, such as summer flight patterns, can be partially explained by the biology of the thrips themselves.

3. *Investigate whether there are changes in the intra-plant distribution of Thrips tabaci during the day to identify periods of vulnerability to foliar sprays and to test the efficacy of irrigation control programmes based on these results*

It was possible to demonstrate, in Chapter 5, a clear pattern in the diel periodicity of the intra-plant distribution of *T. tabaci*, in that adults tended to be located higher on the plant during the hottest periods of the early afternoon. This pattern of behaviour supports the observations made in Chapter 4, as behaviours such as flight and feeding are positively correlated with temperature, both of which might be more likely to occur on exposed areas of the plant. Although it was not possible to demonstrate that targeting irrigation at this period of vulnerability was more effective than at other times, this may have been due to the design and scale of the experiment (Chapter 5). Further work could be undertaken to identify other periods of vulnerability and to attempt to exploit the diel periodicity in adult distribution more vigorously. An experiment could be conducted to see whether what

is known about the intra-plant distribution of thrips could be used to target pesticide treatments more effectively.

The question remains as to whether irrigation is a useable strategy for the control of *T. tabaci*, and in order to determine this it will be necessary to investigate the mechanisms of control more closely. Though various methods have been suggested, it is not clear exactly how irrigation causes mortality. A thorough investigation of this process is necessary. Furthermore there remains the possibility that irrigation is positive, more in its effect upon the host plant, in encouraging increased growth and increased health, than in direct control of the pest. A more comprehensive study would include measures of the effects of irrigation on the host as well as the pest.

4. *Carry out a long term survey of Thrips tabaci populations in the field to obtain more information about their population dynamics in the UK, including flight times, overwintering strategies and population development and discuss how all of these relate to our ability to forecast the development of T. tabaci infestations effectively*

The lack of accuracy in forecasting population trends of *T. tabaci* at Wellesbourne between 2004 and 2008 illustrates how little is understood about this important pest. Despite this, several key observations have been made about *T. tabaci* populations in the UK, including the fact that they overwinter as adults and exploit winter wheat as an alternative host. Although it is possible to follow population trends, and in some cases understand them, it is not yet possible to predict population development into the future with any accuracy. Indeed there are many instances in the field where events or trends in population size or behaviour appear to contradict what has been learnt in the laboratory. For example, why thrips flew at one time and not another, when both periods appeared wholly favourable for flight. What is not clear in all respects (as discussed in Chapter 6), is whether the shortfalls in knowledge illustrate a lack of understanding of the complexities of the underlying processes or perhaps a genuine variation in the biology and behaviours of *T. tabaci* itself. Nevertheless, if a greater understanding of this pest, and moreover accurate forecasting, is to be achieved, it will be necessary to address these shortfalls in knowledge decisively.

To move towards a more effective and accurate forecasting system for *T. tabaci,* it seems clear that a change in direction is necessary. The purely phenological models based entirely on the relationship between development and temperature appear wholly unsuited to forecasting infestations of this species. A full population dynamics model which includes all relevant factors would be more appropriate though, of course, significantly more complex. Such factors might include host plant quality and availability, sunshine hours, natural enemies, rainfall and a host of others, both biotic and abiotic. In some cases the influence of these factors is likely to be difficult to determine; extremely low numbers of natural enemies were observed throughout the course of this study for example, suggesting that their influence is unlikely to be significant. Yet circumstantial evidence of an increase in thrips feeding damage (compared with an insecticide-free control treatment) following application of pyrethroid insecticides to leek plants (DEFRA, 2007b), would indicate otherwise. Building a picture that takes into account the full spectrum of factors is likely to be a challenging task and may be specific geographically. It is possible that population forecasting is, in the long run, not the most useful tool for growers and it is the investigation of control strategies and action thresholds which enable growers to target the pest more effectively that will be important. It is difficult, of course, to make the case for being reactive, as modern growers like to plan ahead, and as discussed in Chapter 6, the available monitoring techniques all have potential weaknesses. Nevertheless accuracy is key, especially in these times of limited control options when a grower will perhaps be able to apply insecticides twice or thrice in a season. Spraying in anticipation of an infestation that then never arrives, and then finding that no more control measures are allowed when the infestation does arrive is perhaps worse than waiting until the opportune moment and perhaps suffering some small damage to the crop as a result.

In any case, whether further work is conducted in order to attempt to construct a full population dynamics model, or investigations concentrate on identifying windows of vulnerability to control and exploiting them, it is clear that further investigations into both the biology and behaviour of *Thrips tabaci* will be necessary to fully understand this small yet pernicious pest.

Appendix

Chapter 3: Population development forecasts

Figure A1 Forecasted development and generation times of *T. tabaci* at Warwick HRI, Wellesbourne in 2005 from hourly temperature data. Combined (single development rate) and Individual (separate life stage development rates calculated sequentially) forecasted series. Development threshold 12.28^{o}C.

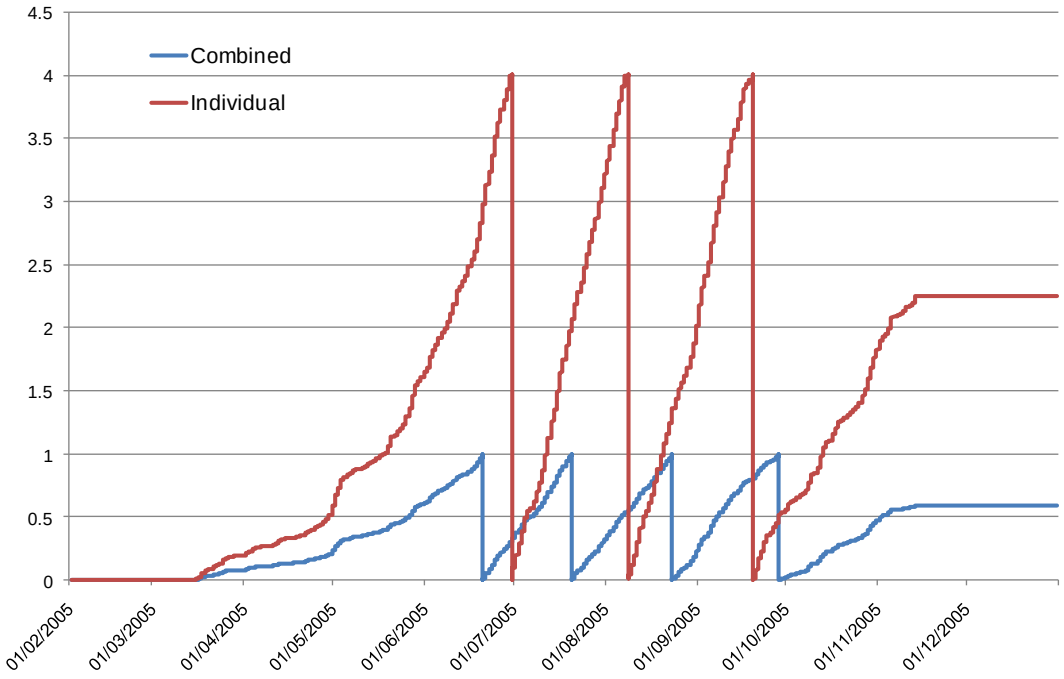


Figure A2 Forecasted development and generation times of *T. tabaci* at Warwick HRI, Wellesbourne in 2005 from hourly temperature data. Combined (single development rate) and Individual (separate life stage development rates calculated sequentially) forecasted series. Development threshold 8.77^{o}C.

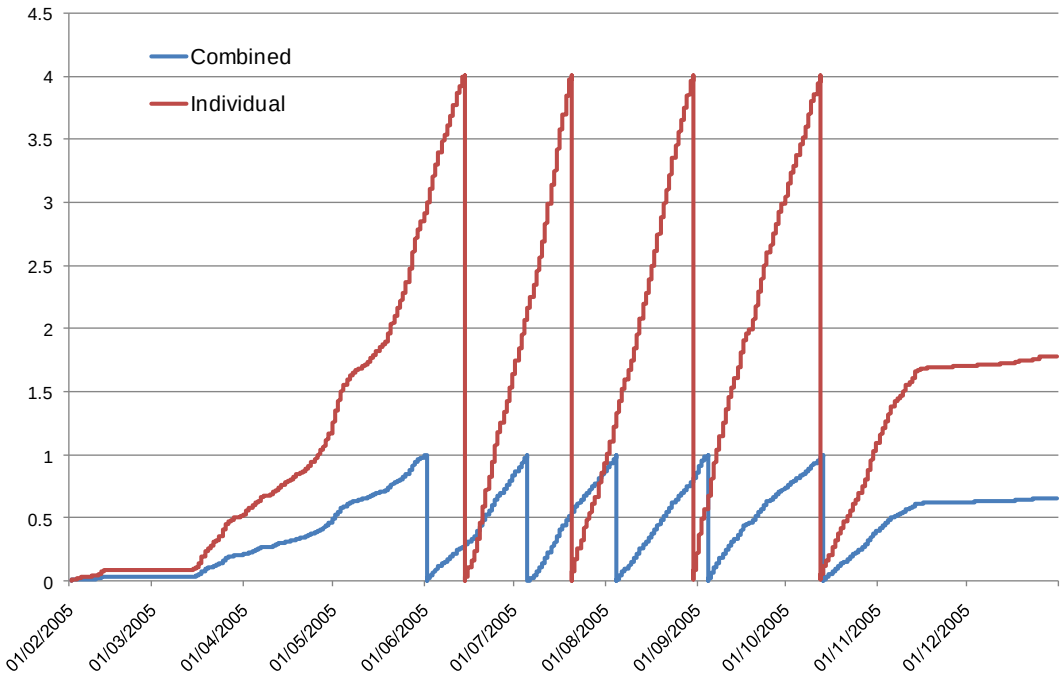


Figure A3 Forecasted development and generation times of *T. tabaci* at Warwick HRI, Wellesbourne in 2005 from hourly temperature data. Combined (single development rate) and Individual (separate life stage development rates calculated sequentially) forecasted series. Development threshold 10^{o}C.

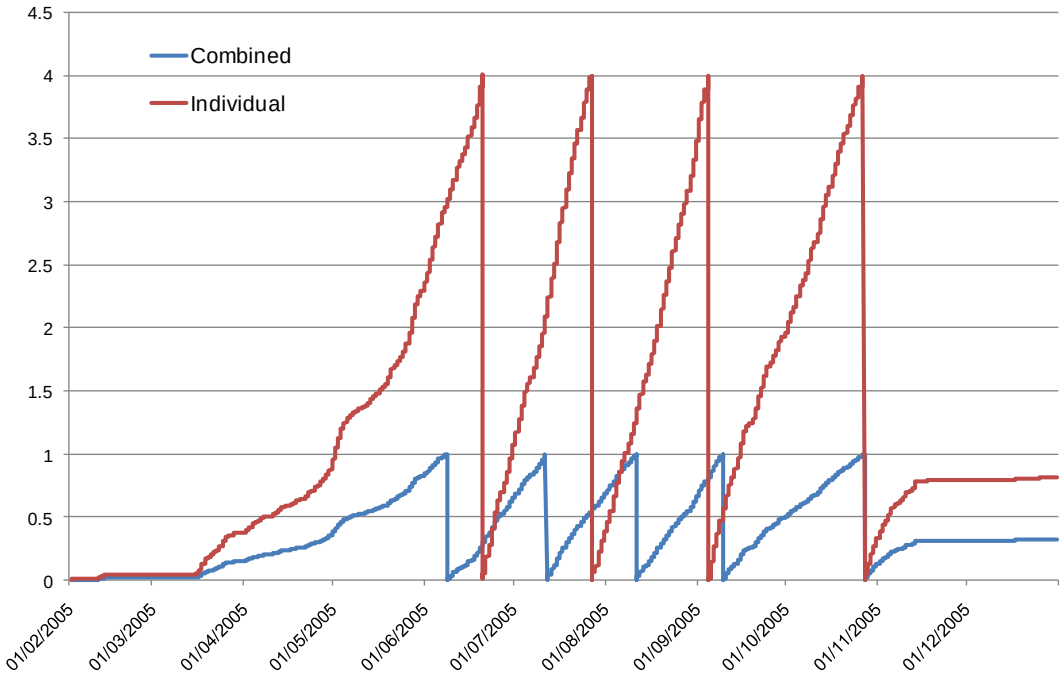


Figure A4 Forecasted development and generation times of *T. tabaci* at Warwick HRI, Wellesbourne in 2007 from hourly temperature data. Combined (single development rate) and Individual (separate life stage development rates calculated sequentially) forecasted series. Development threshold 12.28^{o}C.

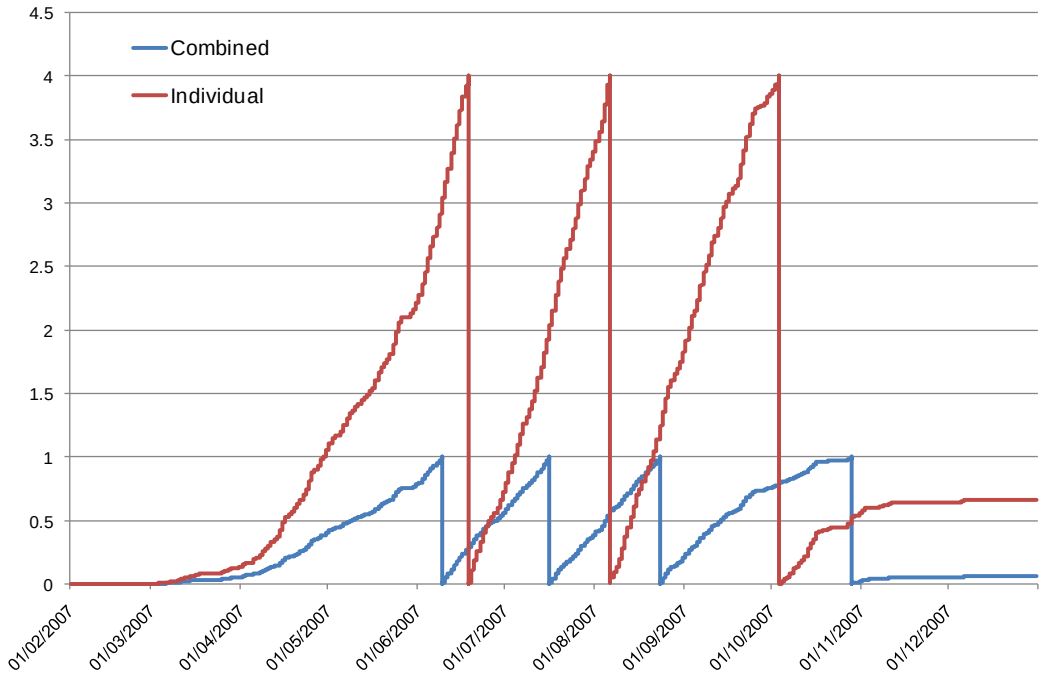


Figure A5 Forecasted development and generation times of *T. tabaci* at Warwick HRI, Wellesbourne in 2007 from hourly temperature data. Combined (single development rate) and Individual (separate life stage development rates calculated sequentially) forecasted series. Development threshold 8.77^{o}C.

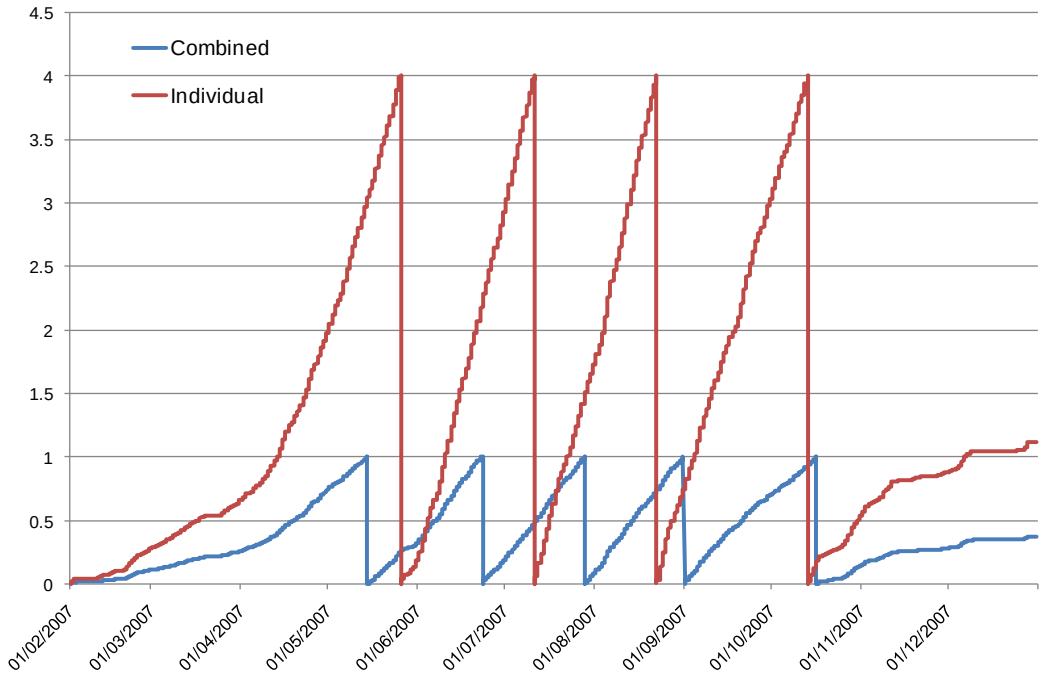
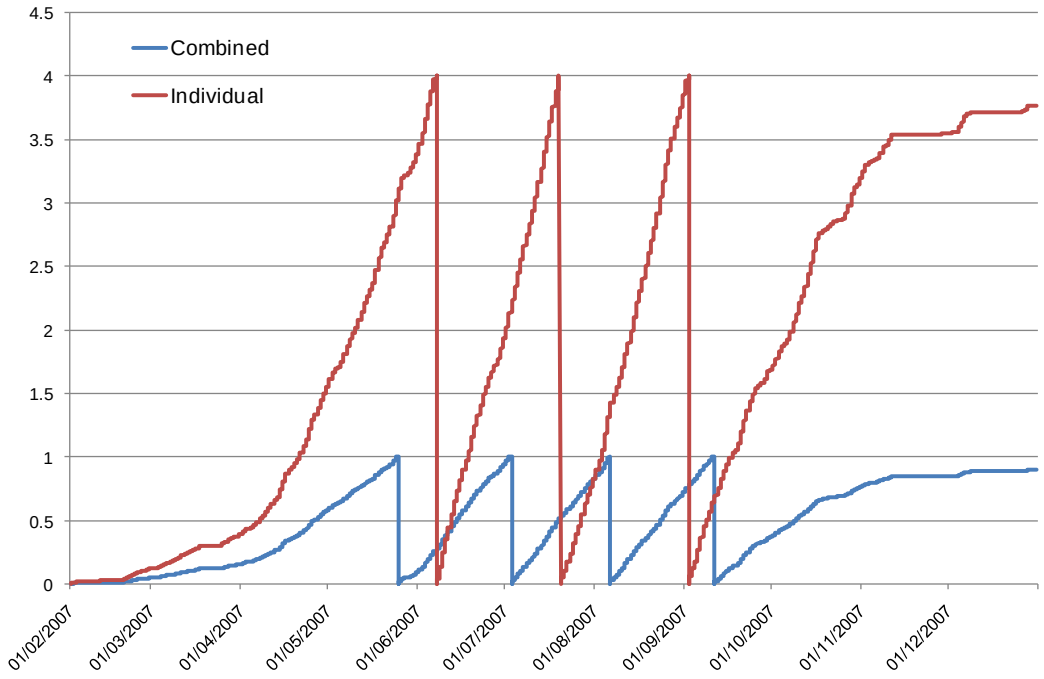


Figure A5 Forecasted development and generation times of *T. tabaci* at Warwick HRI, Wellesbourne in 2007 from hourly temperature data. Combined (single development rate) and Individual (separate life stage development rates calculated sequentially) forecasted series. Development threshold 10^{o}C.



Chapter 4: Transition Matrices

The Tables in this section present the additional transition matrices for those temperatures not shown in Chapter 4. The description of how to interpret the matrices is reproduced here for simplicity. Two transition matrices were calculated for each temperature. The first matrix represents the number of times any thrips moved from activity i (row) to activity j (column). Transitions within activities were possible as transitions are based on a 5-second interval. A thrips which remained in the same activity for 11-15 seconds therefore had 2 transitions within that activity.

The second matrix for each temperature gives the proportion of thrips which moved directly between activity i (row) and activity j (column). The descriptions of behaviours are abbreviated in the tables and the abbreviations are:

RST: Resting
WLK: Walking
SRC: Searching
FED: Feeding
GRM: Grooming
DEF: Defecating
FLI: Flight
FAL: Fall

Rows 7 and 8 in each matrix contain only zeroes as behaviours 7 and 8 are absorbing states which means that once a thrips enters these behaviours it cannot exit them again or transition within them, they are instantaneous. Rows containing only * symbols are behaviours that did not occur at all at those temperatures and so are not considered.

Temperature matrices

Table A1 Transition matrices for 7.5^{o}C, showing the number of times thrips moved from one activity to another (1st matrix) and the proportion of thrips which moved between activities (2nd matrix).

	RST	**WLK**	**SRC**	**FED**	**GRM**	**DEF**	**FLI**	**FAL**
RST	1626	42	4	1	8	0	0	0
WLK	48	1097	8	2	11	0	0	3
SRC	3	10	27	1	0	0	0	0
FED	1	1	2	9	0	0	0	0
GRM	7	11	0	0	49	0	0	0
DEF	0	0	0	0	0	0	0	0
FLI	0	0	0	0	0	0	0	0
FAL	0	0	0	0	0	0	0	57

	RST	**WLK**	**SRC**	**FED**	**GRM**	**DEF**	**FLI**	**FAL**
RST	0.967	0.025	0.002	0.001	0.005	0	0	0
WLK	0.041	0.938	0.007	0.002	0.009	0	0	0.003
SRC	0.073	0.244	0.659	0.024	0	0	0	0
FED	0.077	0.077	0.154	0.692	0	0	0	0
GRM	0.104	0.164	0	0	0.731	0	0	0
DEF	*	*	*	*	*	*	*	*
FLI	0	0	0	0	0	0	1	0
FAL	0	0	0	0	0	0	0	1

Table A2 Transition matrices for 12.5^{o}C, showing the number of times thrips moved from one activity to another (1st matrix) and the proportion of thrips which moved between activities (2nd matrix).

	RST	**WLK**	**SRC**	**FED**	**GRM**	**DEF**	**FLI**	**FAL**
RST	633	23	8	0	7	1	0	0
WLK	29	1313	26	11	41	3	3	4
SRC	7	28	126	7	7	1	0	0
FED	2	10	8	63	1	0	1	0
GRM	3	40	8	3	212	0	3	0
DEF	0	4	0	0	0	9	0	0
FLI	0	0	0	0	0	0	300	0
FAL	0	0	0	0	0	0	0	146

	RST	**WLK**	**SRC**	**FED**	**GRM**	**DEF**	**FLI**	**FAL**
RST	0.942	0.034	0.012	0	0.01	0.001	0	0
WLK	0.02	0.918	0.018	0.008	0.029	0.002	0.002	0.003
SRC	0.04	0.159	0.716	0.04	0.04	0.006	0	0
FED	0.024	0.118	0.094	0.741	0.012	0	0.012	0
GRM	0.011	0.149	0.03	0.011	0.788	0	0.011	0
DEF	0	0.308	0	0	0	0.692	0	0
FLI	0	0	0	0	0	0	1	0
FAL	0	0	0	0	0	0	0	1

Table A3 Transition matrices for 15°C, showing the number of times thrips moved from one activity to another (1st matrix) and the proportion of thrips which moved between activities (2nd matrix).

	RST	WLK	SRC	FED	GRM	DEF	FLI	FAL
RST	481	33	4	2	11	2	2	0
WLK	34	852	18	5	61	15	4	6
SRC	1	17	103	7	2	2	0	0
FED	2	8	2	86	0	1	0	0
GRM	12	52	3	1	190	2	10	0
DEF	5	12	2	0	2	143	0	0
FLI	0	0	0	0	0	0	0	0
FAL	0	0	0	0	0	0	0	0

	RST	WLK	SRC	FED	GRM	DEF	FLI	FAL
RST	0.899	0.062	0.007	0.004	0.021	0.004	0.004	0
WLK	0.034	0.856	0.018	0.005	0.061	0.015	0.004	0.006
SRC	0.008	0.129	0.78	0.053	0.015	0.015	0	0
FED	0.02	0.081	0.02	0.869	0	0.01	0	0
GRM	0.044	0.193	0.011	0.004	0.704	0.007	0.037	0
DEF	0.03	0.073	0.012	0	0.012	0.872	0	0
FLI	0	0	0	0	0	0	1	0
FAL	0	0	0	0	0	0	0	1

Table A4 Transition matrices for 25°C, showing the number of times thrips moved from one activity to another (1st matrix) and the proportion of thrips which moved between activities (2nd matrix).

	RST	WLK	SRC	FED	GRM	DEF	FLI	FAL
RST	146	11	1	0	5	3	1	0
WLK	12	684	40	2	91	30	10	1
SRC	1	28	143	10	7	11	0	0
FED	0	3	7	34	2	1	0	0
GRM	8	86	6	1	194	4	15	0
DEF	5	32	3	0	5	266	0	0
FLI	0	0	0	0	0	0	0	0
FAL	0	0	0	0	0	0	0	0

	RST	WLK	SRC	FED	GRM	DEF	FLI	FAL
RST	0.874	0.066	0.006	0	0.03	0.018	0.006	0
WLK	0.014	0.786	0.046	0.002	0.105	0.034	0.011	0.001
SRC	0.005	0.14	0.715	0.05	0.035	0.055	0	0
FED	0	0.064	0.149	0.723	0.043	0.021	0	0
GRM	0.025	0.274	0.019	0.003	0.618	0.013	0.048	0
DEF	0.016	0.103	0.01	0	0.016	0.855	0	0
FLI	0	0	0	0	0	0	1	0
FAL	0	0	0	0	0	0	0	1

Table A5 Transition matrices for 30°C, showing the number of times thrips moved from one activity to another (1st matrix) and the proportion of thrips which moved between activities (2nd matrix).

	RST	WLK	SRC	FED	GRM	DEF	FLI	FAL
RST	202	19	3	1	6	9	0	0
WLK	23	804	43	18	107	33	2	2
SRC	7	37	95	5	17	4	0	0
FED	1	16	5	39	2	2	0	0
GRM	8	99	11	2	521	15	13	0
DEF	3	37	7	1	10	434	0	0
FLI	0	0	0	0	0	0	0	0
FAL	0	0	0	0	0	0	0	0

	RST	WLK	SRC	FED	GRM	DEF	FLI	FAL
RST	0.842	0.079	0.013	0.004	0.025	0.037	0	0
WLK	0.022	0.779	0.042	0.017	0.104	0.032	0.002	0.002
SRC	0.042	0.224	0.576	0.03	0.103	0.024	0	0
FED	0.015	0.246	0.077	0.6	0.031	0.031	0	0
GRM	0.012	0.148	0.016	0.003	0.779	0.022	0.019	0
DEF	0.006	0.075	0.014	0.002	0.02	0.882	0	0
FLI	0	0	0	0	0	0	1	0
FAL	0	0	0	0	0	0	0	1

Leaf quality matrices

Table A6 Transition matrices for **normal** leaves, showing the number of times thrips moved from one activity to another (1st matrix) and the proportion of thrips which moved between activities (2nd matrix).

	RST	**WLK**	**SRC**	**FED**	**GRM**	**DEF**	**FLI**	**FAL**
RST	61	11	3	4	2	3	0	0
WLK	12	968	46	34	69	13	5	4
SRC	2	37	147	11	11	7	0	0
FED	0	30	10	152	8	0	1	0
GRM	3	66	7	4	168	2	9	1
DEF	2	18	0	1	0	106	0	0
FLI	0	1	0	0	0	0	0	0
FAL	0	0	0	0	0	0	0	0

	RST	**WLK**	**SRC**	**FED**	**GRM**	**DEF**	**FLI**	**FAL**
RST	0.726	0.131	0.036	0.048	0.024	0.036	0	0
WLK	0.01	0.841	0.04	0.03	0.06	0.011	0.004	0.003
SRC	0.009	0.172	0.684	0.051	0.051	0.033	0	0
FED	0	0.149	0.05	0.756	0.04	0	0.005	0
GRM	0.012	0.254	0.027	0.015	0.646	0.008	0.035	0.004
DEF	0.016	0.142	0	0.008	0	0.835	0	0
FLI	0	1	0	0	0	0	1	0
FAL	0	0	0	0	0	0	0	1

Table A7 Transition matrices for **dry** leaves, showing the number of times thrips moved from one activity to another (1st matrix) and the proportion of thrips which moved between activities (2nd matrix).

	RST	**WLK**	**SRC**	**FED**	**GRM**	**DEF**	**FLI**	**FAL**
RST	171	11	0	0	0	0	1	0
WLK	8	846	6	2	40	4	10	2
SRC	1	5	8	0	0	0	0	0
FED	0	2	0	1	0	0	0	0
GRM	1	35	0	0	300	0	10	0
DEF	1	3	0	0	0	15	0	0
FLI	0	0	0	0	0	0	0	0
FAL	0	0	0	0	0	0	0	0

	RST	**WLK**	**SRC**	**FED**	**GRM**	**DEF**	**FLI**	**FAL**
RST	0.934	0.06	0	0	0	0	0.005	0
WLK	0.009	0.922	0.007	0.002	0.044	0.004	0.011	0.002
SRC	0.071	0.357	0.571	0	0	0	0	0
FED	0	0.667	0	0.333	0	0	0	0
GRM	0.003	0.101	0	0	0.867	0	0.029	0
DEF	0.053	0.158	0	0	0	0.789	0	0
FLI	0	0	0	0	0	0	1	0
FAL	0	0	0	0	0	0	0	1

Table A8 Transition matrices for **rotten** leaves, showing the number of times thrips moved from one activity to another (1st matrix) and the proportion of thrips which moved between activities (2nd matrix).

	RST	WLK	SRC	FED	GRM	DEF	FLI	FAL
RST	62	5	0	0	0	0	0	0
WLK	7	580	0	0	33	3	11	0
SRC	0	0	0	0	0	0	0	0
FED	0	0	0	0	0	0	0	0
GRM	1	22	0	0	286	1	8	0
DEF	0	3	0	0	1	14	0	0
FLI	0	0	0	0	0	0	0	0
FAL	0	0	0	0	0	0	0	0

	RST	WLK	SRC	FED	GRM	DEF	FLI	FAL
RST	0.925	0.075	0	0	0	0	0	0
WLK	0.011	0.915	0	0	0.052	0.005	0.017	0
SRC	*	*	*	*	*	*	*	*
FED	*	*	*	*	*	*	*	*
GRM	0.003	0.069	0	0	0.899	0.003	0.025	0
DEF	0	0.167	0	0	0.056	0.778	0	0
FLI	0	0	0	0	0	0	1	0
FAL	0	0	0	0	0	0	0	1

Table A9 Transition matrices for **oak** leaves, showing the number of times thrips moved from one activity to another (1st matrix) and the proportion of thrips which moved between activities (2nd matrix).

	RST	**WLK**	**SRC**	**FED**	**GRM**	**DEF**	**FLI**	**FAL**
RST	3	2	0	0	0	0	0	0
WLK	5	783	0	0	29	0	22	2
SRC	0	0	0	0	0	0	0	0
FED	0	0	0	0	0	0	0	0
GRM	0	25	0	0	147	1	8	0
DEF	0	1	0	0	0	4	0	0
FLI	0	0	0	0	0	0	0	0
FAL	0	0	0	0	0	0	0	0

	RST	**WLK**	**SRC**	**FED**	**GRM**	**DEF**	**FLI**	**FAL**
RST	0.6	0.4	0	0	0	0	0	0
WLK	0.006	0.931	0	0	0.034	0	0.026	0.002
SRC	*	*	*	*	*	*	*	*
FED	*	*	*	*	*	*	*	*
GRM	0	0.138	0	0	0.812	0.006	0.044	0
DEF	0	0.2	0	0	0	0.8	0	0
FLI	0	0	0	0	0	0	1	0
FAL	0	0	0	0	0	0	0	1

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