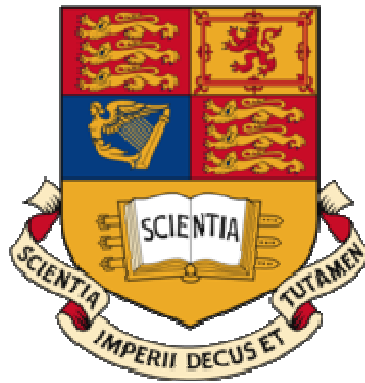


Crops, Insect Pests and Natural Enemies: Effects of Organic and Conventional Fertilisers

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Declaration

The work in this thesis is entirely my own except for the parts listed below:

Chapter 4

The photo-spectrometer analysis of leaf material was carried out by Dr T. Doring of Imperial College, London

Chapter 5

Four of the clip cage experiments were carried out by students of Imperial College, one of whom was working on an undergraduate project. The experimental design and data analysis are my own.

Signed

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Confirmed

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Denis Wright

Abstract

Agricultural intensification can have negative impacts on the environment and there is increasing interest in the use of low intensity or organic agricultural methods to improve sustainability. Fertiliser is an important component of all agricultural systems and can affect the performance of crop pests and their natural enemies. This thesis presents the results from a quantitative review of the literature on both farming system and organic and conventional fertiliser effects on pests and natural enemies. Results from a series of laboratory and field experiments investigating the effects organic and conventional fertiliser on cereal aphids and their natural enemies are reported.

The review demonstrates that crop pests and their natural enemies benefit from organic or low intensity methods and this is evident for natural enemies in farm scale experiments. The effect of organic and conventional fertilisers on arthropod pests is variable although the influence of manures is consistently negative while the effect of plant composts is positive. More studies investigating organic and conventional fertilisers and the response of natural enemies are needed.

Field and laboratory experiments show that conventional fertilisers can benefit cereal aphids but the mechanism behind this response is species specific. *Rhopalosiphum padi* is sensitive to temporal nutrients availability and is influenced by the timing of fertiliser application, while *Metopolophium dirhodum* is responsive to plant morphology with aphids performing better on plants with a high proportion of vegetative matter. The implications of pest performance on fertiliser management strategies are discussed. Parasitoid abundance in the field was not found to be influenced by fertiliser treatment although in the laboratory, indirect effects of fertiliser, mediated through its aphid host, were found to affect parasitoid fitness with larger parasitoids emerging from larger aphids. A positive influence of conventional fertiliser on syrphid oviposition in the field was also apparent.

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Chapter 1

Introduction

1.1 Farming systems

1.1.1 Agricultural intensification

Global land area under agriculture has increased enormously since the industrial revolution. Between 1700 and 1980, cultivated land increased by 466% worldwide (Meyer and Turner, 1992). In more recent years, agricultural production has intensified through the use of high yielding crop varieties and increased chemical fertiliser and pesticide application (Matson *et al.*, 1997). Thus, yields achieved per unit area of agricultural land has risen (Naylor, 1996).

As well as improved yields this agricultural intensification has brought about many environmental issues. The increased application of chemical fertilisers can lead to excess runoff resulting in pollution of water bodies and eutrophication (Matson *et al.*, 1997). High tillage practices can reduce soil organic matter leading to desertification (McLaughlin and Mineau, 1995) and the monocultures and pesticide application associated with modern intensive agricultural methods have resulted in widespread reductions in biodiversity (McLaughlin and Mineau, 1995; Benton *et al.*, 2003). These negative effects can render such intensive agricultural systems unsustainable.

A possible solution to the problems associated with agricultural intensification is the adoption of lower intensity agricultural practices or use of organic farming techniques. By definition, 'low intensity' techniques will reduce pressure on natural resources and the 'organic' label has become ubiquitous with a holistic farming approach. Although organic certification varies worldwide, the use of biological and mechanical practices

are promoted while the use of synthetic chemical inputs is restricted in organic systems (Letourneau and Bothwell, 2008). As a result, inputs of nitrogen, potassium and phosphorus can be reduced by 34-51% in organic systems while reductions in pesticide application can be as much as 97% (Mader *et al.*, 2002). These reduced inputs come at a cost; yields are typically 20% less in organic systems when compared with conventional agriculture (Mader *et al.*, 2002). Nonetheless, globally, organic farming covered 30.4 million hectares in 2006 and this is expected to increase year on year (Willer and Yussefi, 2007) and following EU support, 4% of European agricultural land is certified 'organic' (Abando and Rohner-Thielen, 2007).

Studies have shown that reduced intensity or organic agricultural practices can improve biodiversity in the agroecosystem. In a review of published literature, arthropod richness was found to be greater in cropping systems which employed at least one of several low intensity management practices including reduced pesticide or fertiliser application, minimum tillage, crop rotation or intercropping (Attwood *et al.*, 2008). Furthermore, birds, mammals, arable flora and soil organisms have all been shown to benefit from organic agriculture (Bengtsson *et al.*, 2005; Hole *et al.*, 2005). It is clear that low intensity farming can influence general biodiversity in a positive way but if a more holistic agricultural approach is going to provide a meaningful alternative to conventional agriculture then its impact on pests and natural enemies within the agro-ecosystem needs to be well understood.

1.1.2 Farming systems and crop pests

There is evidence that the relaxed monocultures (Matson *et al.*, 1997) and reduced synthetic fertiliser applications associated with low intensity agricultural systems can reduce pest outbreaks (Altieri and Nicholls, 2003). Host plant resistance and biopesticides such as *Bacillus thuringiensis*, entomopathogenic fungi and baculovirus are available to organic farmers to try and combat pest outbreaks (Zehnder *et al.*, 2007). Examples of low-input or organic systems that show lower pest populations include leaf miners, *Lyriomyza spp.* and white fly, *Bemisia spp.* on tomatoes (Hummel *et al.*, 2002; Bettiol *et al.*, 2004), cereal aphids (Moreby *et al.*, 1994; Reddersen, 1997; Roschewitz *et al.*, 2005) and plant hoppers, *Nulaparvata lugens* and *Sogatella*

furcifera numbers on traditionally cultivated rice (Hidaka, 1997). Yet pest populations in conventional systems can be lower than in low intensity systems, for example western tarnish plant bug, *Lygus hesperus* infestations of strawberries (Rhainds *et al.*, 2002) and lepidopteran and thrip pests of tomatoes (Hummel *et al.*, 2002). A review by Bengtsson *et al.* (2005) found no significant difference between organic and conventional agriculture in terms of pest abundance, while another meta-analytical study found that herbivorous invertebrates were generally more abundant in low intensity cropping systems (Attwood *et al.*, 2008), although this was dependent on the method of analysis.

Clearly there is variation in pest responses to farming practice and this seems to be dependent on the specific pest involved or particular aspects of the cropping system. The variety of crops, pests and management practices makes generalisations difficult. Perhaps effects of farming practice on invertebrate pests needs to be considered on a case by case basis.

1.1.3 Farming systems and crop pest natural enemies

Natural enemies are an important component of the agroecosystem and assist in controlling pest populations. This is true for parasitoids (Sigsgaard, 2002; Lumbierres *et al.*, 2007), aerially dispersing predators (Schmidt *et al.*, 2003) and ground living predators including carabid and staphylinid beetles (Collins *et al.*, 2002; Ostman *et al.*, 2003). Moreover, conservation biocontrol involving habitat manipulation to increase natural enemy abundance is proposed as an effective method of pest suppression (Zehnder *et al.*, 2007). Numerous cases exist where the abundance of invertebrate natural enemies is higher following organic or low intensity cropping. Examples include species of coccinellids, syrphids (Reddersen, 1997), spiders (Schmidt *et al.*, 2005; Oberg, 2007), neuropterans (Berry *et al.*, 1996) and carabids (Clark, 1999; Irmeler, 2003). Predatory species richness is also increased in organic farming systems (Bengtsson *et al.*, 2005) or following low intensity agricultural techniques (Attwood *et al.*, 2008). Caution must be taken however when assuming increased natural enemy diversity will improve pest control (Gurr *et al.*, 2003) as this is not always the case and further work on diversity and pest suppression is needed (Letourneau and

Bothwell, 2008). There are also examples where natural enemy numbers are lower on organic sites, including some staphylinid and carabid species (Shah *et al.*, 2003; Purtauf *et al.*, 2005; Clough *et al.*, 2007) and hymenopteran parasitoids (Moreby *et al.*, 1994).

Synthesised chemical insecticides, which are important factors in the mortality of natural enemies (Hummel *et al.*, 2002), are absent or reduced in organic or low intensity systems. This may cause increased natural enemy abundance. Furthermore, habitat heterogeneity can improve natural enemy abundance, possibly through providing refuge from intra-guild predators or improving access to alternative food sources (Tonhasca, 1993; Langellotto and Denno, 2004). Habitat heterogeneity at multiple spatial and temporal scales can also improve farmland biodiversity (Benton *et al.*, 2003), potentially improving pest control by natural enemies (Gurr *et al.*, 2003). The small field sizes (Drinkwater *et al.*, 1995; Letourneau and Goldstein, 2001) and practices such as intercropping, minimum tillage, beetle and flower banks available to organic or low intensity farmers (Zehnder *et al.*, 2007) may serve to increase agroecosystem habitat heterogeneity. Other practices such as cropping method and fertiliser regime may also be important influences on natural enemy numbers.

1.2 Fertilisers

1.2.1 Introduction

Fertilisers are an essential component of all farming systems. Macronutrients such as nitrogen and potassium are essential in achieving high yields (Mengel *et al.*, 2006; Takahashi and Anwar, 2007) and potassium is important for plant protein production and affects yield (Myers *et al.*, 2005). As a result, the increased outputs following agricultural intensification in recent years have become reliant on high inputs of, typically inorganic, nutrients (Matson *et al.*, 1997). Worldwide, fertiliser consumption increased seven fold from the early 1960s to the early 1990s (Naylor, 1996) and in 2007 over a million tonnes of nitrogen, 200,000 tonnes of phosphate and 300,000 tonnes of potash were applied to British farms alone (DEFRA, 2008b).

Alternatives to synthetic fertilisers exist, indeed these were the only forms of fertiliser available to farmers before the industrial synthesis of nitrogen and processing of phosphorous were mastered in the early 20th century (Manlay *et al.*, 2007). Animal manures (Sieling *et al.*, 2006), plant waste (Montemurro *et al.*, 2006), cover crops (Blumberg *et al.*, 1997) and other animal by-products (Gioacchini *et al.*, 2006; Hasse *et al.*, 2006) are all alternative nutrient sources currently in use.

Nutrients available to the plant from conventional (synthetic) and organic fertilisers differ and levels of nutrients depends on fertiliser type (Cordovil and Cabral, 2001). Organic fertilisers rely on mineralisation of organic nitrogen compounds (Dawson *et al.*, 2008), a process dependent on several soil characteristics including the C:N ratio, pH, soil texture and organic matter content as well as the initial nutrient content of the fertiliser (Gioacchini *et al.*, 2006). The ability of a plant to take up inorganic nutrient ions into the root by selective diffusion is then affected by concentration gradients, electrostatic soil characteristics and can be highly dependent on mycorrhizal symbionts (Hopkins and Huner, 2009). Furthermore the absolute availability of nutrient ions to the plant will be limited by nutrient mineralisation and movement in the soil (Marschner, 2002). This will determine nutrient availability and plant response in organic and conventionally fertilised systems. Although yields are often lower in organically fertilised systems (Mader *et al.*, 2002; Sieling *et al.*, 2006) the soil is generally considered to be healthier due in part to the higher levels of organic matter supplied by many organic fertilisers (Manlay *et al.*, 2007). This organic matter helps maintain soil water capacity and structure as well as minimising erosion and promoting soil biological activity (Matson *et al.*, 1997). The resulting increased microbial diversity and abundance found in organically fertilised soils can increase nitrogen mineralisation potential (Drinkwater *et al.*, 1995). Conversely, reduced soil communities in agricultural systems often render them unable to retain and mediate transfer of excess nutrients resulting in typical nitrogen take up rates of between 40 and 60% (Matson *et al.*, 1997) with the remainder contributing to run-off.

Micronutrients and trace elements can also be higher following application of organic fertiliser when compared with conventional mineral fertilisers (Courtney and Mullen, 2008). Nonetheless, despite the benefits of organic fertilisers, nutrients such as nitrogen are still limited in low-input systems and synchronising nutrient supply with crop demand is difficult (Dawson *et al.*, 2008).

1.2.2 Fertilisers and crop pests

Fertiliser application, mediated through the host plant, can affect insect herbivore performance. For example the aphid, *Aphis gossypii*, was larger and had a higher fecundity on cotton receiving higher doses of nitrogen fertiliser compared with those that received a reduced dose (Nevo and Coll, 2001). While the survival and pupal weight of *L. trifolii* on potted potatoes (Facknath and Lalljee, 2005) and populations of western flower thrips, *Frankliniella occidentalis* on chrysanthemums were increased following nitrogen fertilisation (Chau *et al.*, 2005). Field populations of many pests are also increased following application of nitrogenous fertilisers. This was true for the whitefly, *Bemisia argentifolii* on cotton (Bi *et al.*, 2001) and leaf feeding cereal aphids, *Metopolophium dirhodum* (Honek, 1991b; Hasken and Poehling, 1995; Gash *et al.*, 1996). The improved performance of herbivorous insects following fertiliser application is generally attributed to improvements in host quality, these include increased phloem amino acid concentration (Awmack and Leather, 2002), a more suitable amino acid profile (Weibull, 1987) and higher foliar nitrogen (Facknath and Lalljee, 2005; Prudic *et al.*, 2005). Moreover, a literature survey by Scriber (1984a) demonstrated that in general pest performance correlated positively with plant nitrogen. However, the positive effects of nitrogen on herbivore performance are not ubiquitous. For example, the intrinsic rate of increase of the melon aphid, *Aphis gossypii* was reduced under the highest nitrogen application rates applied to chrysanthemums (Bethke *et al.*, 1998) and the application of fertilisers to barley increased secondary metabolites including gramine and *Schizaphis graminum* performance was reduced (Salas *et al.*, 1990).

It is not only nitrogenous fertilisers that can affect insect herbivore performance but other macronutrients also have an influence. The negative effect of potassium on aphids is well documented, it resulted in reduced reproduction of *Brevicoryne brassicae* and *Myzus persicae* on Brussels sprouts (van Emden, 1966) and the soybean aphid, *Aphis glycines* performed better on potassium stressed plants and this was attributed to increased amino acid concentration in the absence of potassium, known to be an important element in protein production (Myers *et al.*, 2005; Walter and DiFonzo, 2007). Soil application of potassium increased the concentration of

potassium in the leaves and decreased the suitability of potato plants to the leaf miner, *Liriomyza trifolii* (Facknath and Lalljee, 2005). The effects of potassium on pests are not solely nutritional. Host preference, represented by the number of *Rhopalosiphum padi* per tiller soon after colonisation, was higher on barley receiving no potassium fertiliser (Havlickova and Smetankova, 1998). This preference effect was postulated to be a result of potassium deficient plants being more yellow. Potassium effects are not always negative and Shaw *et al.* (1986) found that herbivore response to potassium and phosphorus application to alfalfa was species specific; populations of the alfalfa weevil, *Hypera postica* were higher on fertilised plants but numbers of the potato leaf hopper, *Empoasca fabae* were lower. Clearly fertiliser application is an integral part of the agroecosystem and has a key role to play in pest management.

At this point it is worth considering aphids in more detail because they have been extensively studied with regards to their response to soil nutrients (i.e. following fertiliser application) (Honek, 1991b; Hasken and Poehling, 1995; Gash *et al.*, 1996; Bethke *et al.*, 1998; Nevo and Coll, 2001) and plant nutrition (Weibull, 1987; Salas *et al.*, 1990; Walter and DiFonzo, 2007). Because aphid performance is dependent on and often limited by dietary nitrogen (Awmack and Leather, 2002) it is often assumed that increased plant available nitrogen will improve aphid performance. There are, however, numerous other factors that will determine aphid response to fertiliser. For instance the ability to locate and utilise a sieve element can be influenced by drought, irrespective of the amino acid composition of the phloem. In fact under drought conditions 'phloem quality' was improved but aphid performance was reduced (Hale *et al.*, 2003). Furthermore, work involving artificial diets has shown that there is an optimum ratio of sucrose and amino acids for maximal aphid growth and reproduction and this is not simply the highest amino acid:sucrose ratio (Simpson *et al.*, 1995). Therefore increased availability of phloem free amino acids as a result of improved soil nutrients may not be manifested in improved aphid performance.

Aphids also have strategies that enable them to overcome fluctuations or deficiencies in the quality of their diet. A key component of aphid nutrition is the existence of endosymbiotic bacteria, principally of the genus *Buchnera*. Located in the mycetocytes in the hemocoel, these bacteria synthesise essential amino acids from non-essential amino acids and make them available to the aphid, a process known as

nitrogen upgrading (Prosser *et al.*, 1992; Douglas, 1998). As a result, aphids are able to persist on a diet devoid of essential amino acids (Douglas *et al.*, 2001) and consequently these endosymbionts will have the capacity to buffer aphid dietary requirements and enable them to perform on plants with varying amino acid profiles, a profile that can be determined by fertiliser application (Weibull, 1987). A further adaptation shown by aphids is that of ‘compensatory feeding’. Through the process of compensatory feeding, aphids are not only able to utilise diets with a low concentration of essential amino acids but they can also maximise performance on diets with a lower overall concentrations of amino acids. In an experiment by Prosser *et al.* (1992), the growth rate of *Acyrtosiphon pisum* was similar on diets with varying concentrations of amino acids, this equality in performance was achieved through the increased production of honey dew by aphids on amino acid poor diets. In fact, the amino acid flux through an aphid is a better correlate of performance than the amino acid composition of their diet (Hale *et al.*, 2003).

1.2.3 Organic and conventional fertilisers and crop pests

Given the often pronounced effects of soil nutrients on pest performance and the contrasting nature of nutrient availability following application of conventional fertilisers and organic slow release fertiliser, a dissimilar effect of these fertilisers on invertebrate herbivores can be expected. Altieri and Nicholls (2003) proposed that the use of fast release chemical fertilisers can cause nutrient imbalances in crops, improving pest performance, while the use of organic fertiliser can increase soil biological activity and organic matter resulting in nutrients being released more slowly and thus not enhancing plant nitrogen levels and causing pest outbreaks. Similar ideas led Phelan *et al.* (1996) to propose the ‘mineral balance hypothesis’ which states that the balanced nutrients often found in organically managed soils promote optimum conditions for plant growth and resistance to pests. There is evidence in support of the mineral balance hypothesis, including lower numbers of Colorado potato beetle, *Leptinotarsa decemlineata* on manure fertilised potatoes (Alyokhin *et al.*, 2005) and the preferential oviposition by the European corn borer, *Ostrinia nubilalis* on maize grown in soils with a history of conventional fertiliser management (Phelan *et al.*, 1995). Interestingly, Phelan *et al.* (1995) found the

addition of fertilisers had inconsistent effects on oviposition suggesting management history was more important than short term fertiliser amendments. Further evidence that pest numbers can be lower in organically fertilised systems include the lower population densities of flea beetles, alate aphids and lepidopteron pests on collards fertilised with manure and sludge when compared with those which received chemical fertilisers (Culliney and Pimentel, 1986). The aphid, *Rhopalosiphum maidis* was also less numerous on organically fertilised maize (Morales *et al.*, 2001) and similar findings were made for *Leucinodes orbonalis* on aubergines where the number of larvae per shoot was higher for plants receiving chemical fertiliser when compared with three other organic fertilisers (Sudhakar *et al.*, 1998).

There is also evidence that pest abundance can be higher on organically fertilised plants. Both the cabbage aphid *B. brassicae*, and the diamond backed moth, *Plutella xylostella* were more numerous on cabbage receiving market crop waste in contrast to conventional fertilisers, although the significance of this relationship was dependent on year and whether the waste had been composted prior to application or not (Karungi *et al.*, 2006b). The number of *Rhopalosiphum padi* was higher on barley receiving organic fertilisers compared with conventionally fertilised barley and the organically fertilised barley also had a higher nitrogen content which might explain this effect (Bado *et al.*, 2002). Following the use of living mulches and conventional fertiliser, no significant effect was found on *M. persicae* or *B. brassicae* on broccoli (Costello and Altieri, 1995) and the application of various organic fertilisers did not significantly affect populations of the corn borer, *O. nubilalis* on peppers when compared with those fertilised chemically (Delate *et al.*, 2003). Clearly there is variation in pest responses to the application of both organic and conventional fertilisers and this can be dependent on fertiliser type and soil management history. Furthermore, Altieri and Nicholls (2003) highlight the need for more studies comparing organic and conventional fertiliser effects on pest populations before any generalisations can be made. Importantly many of the studies mentioned do not control for the amount of nutrients added to the system and in many cases, one fertiliser regime may be contributing far more nutrients to the system thus affecting pest response. Evidently there is a need to quantitatively review available literature on the subject whilst further contributions to the data set are vital.

1.2.4 Fertilisers and crop pest natural enemies

In light of the positive and negative impact of fertiliser application on both plants and their invertebrate herbivores, effects on higher trophic levels can be expected.

Predators appear to show mixed responses to fertiliser treatment. In cotton fields receiving variable doses of nitrogen, the numerical response of various pest species was inconsistent, however, natural enemies tended to be more abundant in plots receiving higher doses of nitrogen and this was significant for spiders and big eyed bugs, *Geocoris spp.* (Chen and Ruberson, 2008). In contrast, the suppression of *Cacopsylla pyricola* populations by *Anthocoris nemoralis* on pear trees was not affected by the addition of fertilisers but whether the results from this cage trial on young plants can be related directly to effects in the field is debatable (Daugherty *et al.*, 2007).

Studies of fertiliser effects on predators are rare. Studies involving parasitoids are more common and given that parasitoids rely more directly on the fitness of their host as their sole supply of developmental resources, they may be more responsive to plant fertilisation. The fact that both numerical and physiological effects of fertiliser on parasitoids are apparent highlights this. *Chrysocharis oscinidis*, a parasitoid of *L. trifolii*, showed reduced development times following applications of intermediate levels of nitrogen fertilisers to bean plants and female fecundity correlated with leaf nitrogen (Kaneshiro and Johnson, 1995). Individuals of the aphid parasitoid, *Aphidius colemani* emerging from *M. persicae* reared on plants grown in soil with higher nutrients were larger (Wurst and Jones, 2003) and the egg load of the parasitoid, *Cotesia flavipes* was higher after parasitising the stem borer, *Chilo partellus* which had developed on plants receiving higher doses of nitrogen (Jiang and Schulthess, 2005). Higher numbers of aphid parasitoids were recorded on ryegrass (Krauss *et al.*, 2007) and *Encarsia formosa* parasitizing the whitefly, *Bemisia argentifolii* on poinsettia were more numerous (Bentz *et al.*, 1996) following application of nitrogen fertilisers, although in both cases parasitoids numbers were responding to the increased abundance of their host. It appears tritrophic effects of fertilisers are evident whether mediated through host fitness or abundance.

1.2.5 Organic and conventional fertilisers and crop pest natural enemies

Similar to pest responses, the contrasting nature of organic and conventional fertilisers in terms of nutrient availability and impacts on soil health should convey up the trophic ladder and effect natural enemies. Nonetheless, despite its potential importance, few studies have investigated conventional and organic fertiliser effects on natural enemies. The level of parasitism and predator numbers on cabbage was higher in crops receiving market crop waste compared to conventional fertilisers although numbers of *B. brassicae*, *M. persicae* and *P. xylostella* were also higher on the cabbage fertilised with market crop waste (Karungi *et al.*, 2006b). The percentage parasitism of *B. brassicae* was also increased following compost fertilisation of broccoli (Ponti *et al.*, 2007). Other investigations have found no effect of fertiliser type on natural enemy numbers (Blumberg *et al.*, 1997; Zhang and Drummond, 1998; Yardim and Edwards, 2003). The lack of available research in this area highlights the need to further study tritrophic effects of organic and conventional fertilisers.

1.2.6 Study system

Barley is an important crop in Britain and currently over one million hectares of agricultural land is dedicated to the production of barley in the UK, this has a market value of approximately £882 million (DEFRA, 2008a). Aphids are the principle pest of barley both through direct damage and virus transmission (Mann *et al.*, 1997) and parasitoids are an important cereal aphid natural enemy (Schmidt *et al.*, 2003; Levie *et al.*, 2005). Fertilisers have also been implicated as a contributing factor in the population growth and development of cereal aphid pests (Honek, 1991b; Hasken and Poehling, 1995; Gash *et al.*, 1996; Duffield *et al.*, 1997). These economic and ecological factors make the barley-aphid-parasitoid system ideally suited to fertiliser manipulation experiments. Furthermore, the growth and production similarities and shared pests found between barley and other cereal crops including wheat and oats also highlights the wider relevance of data collected on barley and its associated agriculturally important invertebrates. The ability to grow barley in both the field and laboratory and the ease with which aphids can be cultured are also advantageous.

1.3 Aims and objectives

The aims of this research were to gain a clearer understanding of the effects of different fertilisers on pests and natural enemies at multiple spatial scales and to consider how a better understanding of the tritrophic effects of fertilisers can help in fertiliser decision making.

The objectives of the research described in this thesis were to:

- 1) Quantitatively review the available literature on the effects of low intensity and conventional farming systems on arthropod crop pests and natural enemies and more specifically consider the effects organic and conventional fertilisers have on pests and natural enemies and consider the role these fertilisers play within these farming systems.
- 2) Use a barley - cereal aphid system to investigate the effects of organic slow release and conventional fertilisers on naturally occurring aphid populations and their natural enemies on a field and semi-field scale. In particular the effects of plant morphology and colour on aphid populations were explored.
- 3) Investigate the effects of organic and conventional fertilisers on individual aphid performance and the dynamics of aphid colonies in a controlled environment. The interaction between fertiliser type, application timing and plant age were examined using the barley - cereal aphid system.
- 4) Explore the tritrophic effects of organic and conventional fertilisers using barley cereal aphids and their parasitoid natural enemies, considering both parasitoid host location and fitness in response to different fertilisers.

Chapter 2

The effects of farming systems and fertilisers on pests and natural enemies: a synthesis of current research

2.1 Introduction

The area under organic agriculture is increasing globally (Willer and Yussefi, 2007) due in part to the potential of low input agricultural methods to be more sustainable with fewer negative environmental consequences (Matson *et al.*, 1997; Mader *et al.*, 2002). While, benefits of low intensity agricultural techniques to agroecosystem biodiversity are evident (Bengtsson *et al.*, 2005; Hole *et al.*, 2005; Attwood *et al.*, 2008), possibly more important in terms of agricultural productivity and sustainability is the effect of the farming system on pest and natural enemy performance and abundance. Pests have been shown to be less abundant in low input systems (Ostman *et al.*, 2001; Hummel *et al.*, 2002; Bettiol *et al.*, 2004; Roschewitz *et al.*, 2005) but examples to the contrary also exist (Hummel *et al.*, 2002; Rhainds *et al.*, 2002). Natural enemies also show positive (Reddersen, 1997; Irmiler, 2003; Corrales and Campos, 2004; Oberg, 2007) and negative responses (Moreby *et al.*, 1994; Shah *et al.*, 2003; Purtauf *et al.*, 2005; Clough *et al.*, 2007).

Fertiliser application is an important component of the agroecosystem and can have significant effects on pest populations (Hasken and Poehling, 1995; Bethke *et al.*, 1998; Bi *et al.*, 2001) due in part to changes in plant nutritional quality (Awmack and Leather, 2002). Fertilisers can also affect natural enemies (Kaneshiro and Johnson, 1995; Krauss *et al.*, 2007; Chen and Ruberson, 2008) and contrasting effects of organic and conventional fertilisers on both pests and natural enemies can be

hypothesised. Research in this area is limited and results are variable (Culliney and Pimentel, 1986; Costello and Altieri, 1995; Blumberg *et al.*, 1997; Delate *et al.*, 2003; Yardim and Edwards, 2003; Alyokhin *et al.*, 2005; Karungi *et al.*, 2006a; Ponti *et al.*, 2007). Clearly there is a need to review available research on the effects of both farming system and fertiliser on arthropod pests and natural enemies.

2.1.1 Meta-analysis

Meta-analysis is a recognised analytical tool used to find and quantitatively test scientific hypotheses across groups of related studies (Rosenberg *et al.*, 2000b). While the technique has been used for some time in other scientific disciplines, particularly medicine (Arnqvist and Wooster, 1995), meta-analysis has only been utilised to examine ecological patterns relatively recently (Tonhasca and Byrne, 1994; Koricheva and Larsson, 1998; Langellotto and Denno, 2004; Bengtsson *et al.*, 2005; Frampton and Dorne, 2007). Meta-analysis has its limitations, including research and publication bias (Arnqvist and Wooster, 1995; Gurevitch and Hedges, 1999). Meta-analysis involves defining a control and experimental treatment that is comparable across numerous independent studies. This enables an overall treatment effect to be established that takes into account the magnitude of the effect as well as the level of replication within the independent studies. Confidence limits are given for the treatment effect size enabling the significance of this ecological trend to be tested. Furthermore, categorical meta-analyses can be carried out where studies can be segregated into defined groups enabling the treatment effect to be compared between species, experimental scales or any other variable that more than one study share (Rosenberg *et al.*, 2000b).

2.1.2 Vote-counting

Vote-counting is a method of testing a hypothesis incorporating experimental results from various studies in the primary literature (Hedges and Olkin, 1980). The proportion of studies that demonstrate a significant positive, a significant negative or a non-significant response are statistically compared with respect to the experimental question being asked and thus a conclusion is drawn (Koricheva and Larsson, 1998;

Huberty and Denno, 2004). An alternative vote-counting method involves counting the number of studies which show a positive or a negative response to treatment, irrespective of significance and testing this against a binomial distribution to ascertain whether a negative or positive pattern is significant (Frampton and Dorne, 2007). As with meta-analyses, vote-counting does have its limitations and is often overly conservative in its estimations (Hedges and Olkin, 1980), while high numbers of non-significant studies can reduce the statistical power of a vote-count (Cooper, 1998). Vote-counting is also non-quantitative with respect to a treatment effect size. As long as all these limitations are considered, however, and vote-counting methods are used in conjunction with other multi-study analysis techniques, they can provide a useful tool when testing hypotheses across several related studies to infer broad trends in a treatment effect (Huberty and Denno, 2004; Bengtsson *et al.*, 2005; Attwood *et al.*, 2008).

2.2 Aims and objectives

Agricultural farming systems and fertilisers can have a significant impact on pests and natural enemies, thus the aim of this chapter was to use data from the wider literature to quantitatively examine the effects of organic and conventional farming systems and fertilisers on crop pests and natural enemies in an attempt to understand what factors dictate pest and natural enemy responses to these farming systems and fertilisers.

The objectives of the present study were to use both meta-analysis and vote-counting techniques to determine the effects of farming system on 1) arthropod pests and 2) their natural enemies. How taxonomic group, functional group, experimental scale and pest management regime effect pest and natural enemy responses to farming system was considered. Further objectives of this study were to use meta-analysis and vote-counting techniques to investigate the effects of organic and conventional fertilisers on 3) pests and 4) natural enemies, again considering arthropods by taxonomic and functional groups. The effects of different organic fertilisers on organism responses was also considered.

2.3 Methods

2.3.1 Literature search

A comprehensive search of all available published literature on arthropod pest and natural enemy studies that compared organic and conventional farming systems or fertiliser treatments was made. The scientific literature search engine 'Web of Knowledge' was utilised using the search words 'organic', 'conventional', 'farming system', 'fertiliser/fertilizer', 'pest' and 'natural enemies'. Following the acquisition of relevant research papers, a systematic search of appropriate reference lists was made. As is common with review work, restricting included literature to only those studies that have been published creates the "file drawer" problem (Arnqvist and Wooster, 1995), with many non-significant responses remaining unreported. If the review is to include only research of a publishable standard, however, this problem is unavoidable.

2.3.2 Meta-analysis

2.3.2.1 Methods

To carry out a meta-analysis, a treatment variable needs to be established that is comparable across all studies. In the present case, two levels of farming system or fertiliser treatment were assigned. Treatments were classed as 'organic' or 'conventional'. A response variable for each of these treatments is then necessary to enable the calculation of a treatment effect size. To make a comparison between the two treatments, the information required from a source include the mean, the standard deviation and the level of replication for a particular arthropod under each of the two treatments. An 'effect size' due to treatment for each pest or natural enemy, in this case Hedges' d , can then be calculated. In many instances the mean, standard deviation and sample size for studies were given in the text or data tables. In other cases published graphs were measured using ImageJtm to establish the means. Where the standard deviation was not provided, the standard error and replicate number were

used to calculate the standard deviation. Where details on several individual replicates were given, but no mean was provided, the mean and standard deviation were calculated from the raw data.

For all meta-analyses, Hedges' d , which is an estimate of the standardised mean difference, was used to estimate a treatment effect size for each comparison of 'organic' and 'conventional' farming system or 'organic' and 'conventional' fertiliser application. Hedges' d is calculated as:

$$d = [(X^O - X^C)/S]J$$

Where X^O is the mean for the organic treatments and X^C is the mean for the control treatment. S is the pooled standard deviation and J is a correction factor to correct for bias when sample sizes are small; a problem associated with the older Hedges' g measure of effect size (Rosenberg *et al.*, 2000b). J is calculated as:

$$J = 1 - 3/[4(N^C + N^O - 2) - 1]$$

Where N^O and N^C are the samples sizes for the organic and conventional treatments respectively. The variance of Hedges' d (V_d) is found by:

$$V_d = [(N^C + N^O)/(N^C N^O)] + [d^2/2(N^C + N^O)]$$

For analysis, data points were grouped by categorical variables and incorporated into a random-effects model. Categorical grouping within a random-effects model creates a mixed-effects model and incorporates random variation within a category as well as the fixed differences between categories (Hedges and Vevea, 1998). The use of a mixed-effects model allows the analysis of groups of data that are highly heterogeneous in their response, a phenomenon commonly found in meta-analysis. Mean estimates of Hedges' d were then found for each categorical group within the model and a significant trend was inferred if Hedges' d with 95 % confidence intervals did not incorporate zero. For all calculations of effect sizes and model analysis the statistical programme MetaWin version 2 (2000a) was used.

A prerequisite of any meta-analysis is that each data point is entirely independent. Invertebrate responses were considered independent if they involved separate species on separate crops. If a mean was given for a group of species on a crop, this was considered an independent data point because, despite some overlap, no two groups incorporated exactly the same species. For example, both Clough *et al.* (2007) and Weibull (2003) give data on staphylinids as a whole group on wheat and undoubtedly there would be overlap in what species make up the catches of staphylinids in both studies, but it is impossible to know to what extent and thus the responses from both studies were considered independent enough to be included. Nonetheless, wherever adequate information was given, individual species data was used. If this individual species data also contributed to an organism group response within the same study the group response was discarded if individual species data contributed greater than 50 % of the group response. For example, in the study by Letourneau and Goldstein (2001), parasitoids, for which individual data was given, made up over two thirds of the number of predators and parasitoids combined. Therefore the combined data were dropped from the meta-analysis and data on parasitoids alone was used.

In a limited number of cases, several invertebrate responses to farming system or fertiliser treatments were given in one study, for example fecundity and development time. To avoid non-independence of data points, only one measure was included in the analysis and these were selected based on a hierarchy, with the responses considered more closely associated with pest or natural enemy success in the field given priority. Abundance was prioritised above damage level, followed by fecundity, development time and weight or size. In some studies which looked at several life stages of an invertebrate, the adult response was prioritised. Many studies took place over several years or seasons. Looking at the same species on the same crop but on different years was not considered independent, so the year or season where the mean organic and conventional pest or natural enemy organism response was highest were chosen. Where a control treatment was used, the year with the highest control arthropod response was measured. This system was used because it would incorporate data from possible outbreak years whilst also providing an unbiased method of data selection. Selection criteria such as these have been used in a previous meta-analysis (Tonhasca and Byrne, 1994).

Some exceptions to these data selection criteria exist. In a study on *Chrysoperla carnea* by Corrales and Campos (2004), data on numbers through a single season were given but no cumulative value or mean was provided, so the mean numbers of *C. carnea* at the population peak was chosen as the data reference point. Hidaka's (1997) experiments occurred in two different regions over two years and consequently the region and year where the level of replication was considerably higher, regardless of invertebrate numbers, were used due to increased reliability. Furthermore, in the above study, organic fields were grouped based on how long organic practices had been carried out in the experimental fields. Data from the group of fields where organic practice had been going on longest, 12 years, were used. The studies by Hossain *et al.* (2002) and Hidaka (1997) both considered *Nilaparvata lugens* and *Sogatella frucifera* on rice. Despite the overlap both studies were included in the meta-analysis because Hossain *et al.* (2002) gives data for both species combined while Hidaka (Hidaka, 1997) considers both species separately. It is unclear what contribution each of the species makes to the group response in Hossain and colleagues' (2002) study and due to the differing nature of both the organic and conventional treatments between each of the studies, the responses of these plant hoppers was considered independent. Details of data taken from each study can be found in the Appendix 1 and 2.

2.3.2.2 Farming system meta-analysis

Studies were included in this meta-analysis if they compared conventional farming systems with organic farming systems with respect to arthropod crop pest or natural enemy biology. A treatment was considered 'organic' when the use of synthetic fertilisers or chemical pesticides was not permitted. The treatment did not have to have organic status which imposes many limitations on the land management history. Consequently, many of the treatments involved in the meta-analyses were not termed as 'organic' but 'biorational', 'biological' or 'low intensity' farming methods. The aim of this meta-analysis was to assess the impact of farming system on pests and natural enemies, therefore a variety of organism responses were deemed appropriate if they could be considered a determinant of pest or natural enemy success. Responses included abundance, fecundity, development rate, size and damage. Experiments

performed at any spatial scale, on any crop plant and using any monitoring technique were included, provided they fitted the above criteria.

To establish whether different invertebrate groups respond differently to farming practice, meta-analytical models were divided categorically. Both natural enemies and pests were first examined based on taxonomic family and then functional groups based on the life history characteristics of those species involved. Pests were subdivided based on feeding habit, they were classed as either suckers or chewers. If an individual data point incorporated data on species from more than one group, that data point was then put in a third category called 'mixed'. Natural enemies were classed as parasitoids, predators, spiders or coleopterans. Natural enemy spiders and coleopterans, despite being predators, were kept as separate categories due to the large number of data points contributed and the heterogeneous nature of their data. Once again a 'mixed' category was necessary.

The responses of individual species and the responses of groups of species to a treatment may be divergent. Thus in another analytical model the data points were divided into two categories. A response was termed 'individual' if it involved only the response of one species and 'grouped' if the response incorporated data from more than one species. As well as grouping invertebrate responses categorically, the two treatments, organic and conventional farming systems, were also categorised. The influence of pest control was determined by grouping studies into one of three categories, 'conventional' if pest control was used only in the conventional treatment, 'both' if pest control was practiced in both organic and conventional treatments and 'none' if no pest control was practiced under either of the farming systems. Finally, to examine effects of spatial scale, responses were categorised as either 'farm scale' or 'field scale' based on whether the experiment compared different farms or two treatments had been imposed within one farm or field site.

2.3.2.3 Fertiliser meta-analysis

The impact of organic and conventional fertilisers on pests and natural enemies was tested using a meta-analysis incorporating available studies on comparisons of organic

and conventional fertilisers. As with the meta-analytical models testing farming system effects, fertiliser models were broken down categorically, again based on taxonomic family and functional groups of the test organisms. Additional categorical variables involved dividing treatments based on the organic fertiliser used. Organic fertilisers were classed as ‘manure’ if the fertiliser originated from any form of animal by-product, including animal waste and sewage sludge. If organic fertilisers were derived from any plant material or cover crop they were grouped as ‘compost’. Any fertiliser treatments that involved the input of both animal and plant material were termed ‘mixed’. If an individual study applied two different fertiliser treatments such as the fresh and composted form of a fertiliser (Karungi *et al.*, 2006a), these were considered two separate data points within the analysis because composting is known to alter the composition of a fertiliser (Dawson *et al.*, 2008) and a different effect on a pest or natural enemy might be expected. To test the effect of fertiliser on pests and natural enemies within a farming context, all the studies involved in the farming system meta-analysis and the fertiliser specific studies were incorporated into one data set and categorised based on organic fertiliser inputs followed by a final meta-analysis.

2.3.3 Vote-counting

The study selection criteria for the vote-counting methods were the same as those used for the meta-analysis, hence every data point in the meta-analysis were included in the vote-count. For the vote-count, the inclusion of responses from studies which did not provide a mean, standard deviation or the level of replication on a pest or natural enemy was enabled. Data were included wherever a response direction to organic or conventional treatments were provided and either a p-value was given or the author stated whether the difference between treatments was significant or not. This information was given in graphs, tables and/or in the text. In one case where detailed information on the level of significance was not given the authors’ conclusion was used (Culliney and Pimentel, 1986). In a long term study by Anderson (2000) on various species responses to farming system, data were highly variable and only four species showed consistent responses to treatment. These four species were included in the vote-count and others were ignored.

As with the meta-analyses (Section 2.3.2.2 and 2.3.2.3), pests and natural enemies were divided into feeding guilds and taxonomic groups as well as categorising studies based on pest control practice and spatial scale. For this investigation two vote-counting techniques were carried out, one involving only the response direction (+ or -) and one taking the level of significance into account. For the first analysis, studies were divided into one of two categories; a positive response to organic farming/fertiliser or a negative response. A binomial test was then used to test if the number of positive and negative responses might arise by chance alone at a significance level of $P < 0.05$. If this was not true then the distribution was considered significant in favour of one or other of the treatments. Studies where the difference between treatments was zero were excluded from the test. The second vote-counting method involved dividing included studies into significantly positive, significantly negative or non-significant responses with respect to farming system or fertiliser treatment. For each of the categories within pests and natural enemies, the number of cases falling into each of the three response categories was compared using a chi-squared test. Again if the distribution was unlikely to arise by chance at a level of $P < 0.05$ then there was assumed to be a treatment effect.

2.4 Results

2.4.1 Pests and farming system meta-analysis

Data from 16 different studies including 40 separate pest responses to organic and conventional farming system were involved in the pest response meta-analysis. Thirty-five of the responses involved pest abundance while the remaining five compared levels of pest damage, see Appendix 1 for details. Overall, pests showed a significant positive response to organic farming practices (Fig. 2.1a) and the heterogeneity of these responses was not significant ($Q = 50.79$). Following subdivision of pests into both taxonomic and feeding groups, no significant effect of farming system was found (Fig 2.1b&c). All mean effect sizes were positive except for the Hemiptera and Diptera. In all cases the 95% confidence interval were large but neither the within category or between category heterogeneity was significant for

taxonomic (between $Q = 8.37$, within $Q = 41.01$) or feeding groups (between $Q = 0.01$ within $Q = 48.42$). In correspondence with pests overall, individual pest species responded significantly positively to organic farming and while the response of groups of species was also positive it was not significant (Fig 2.1d), these responses were homogenous (between $Q = 0.98$, within $Q = 49.83$). The effects of organic practices on pests were also significantly positive when experiments were carried out on a farm scale (Fig. 2.1e), this effect was not significant in smaller scale experiments. The between category heterogeneity for experimental scale was significant (between $Q = 3.89^*$, within $Q = 47.70$). Furthermore, whether pest control was practiced on conventional sites only or both conventional and organic sites did not significantly influence pest responses to farming system (Fig 2.1f). Within and between category heterogeneity was not significant in this instance (between $Q = 0.21$, within $Q = 48.13$).

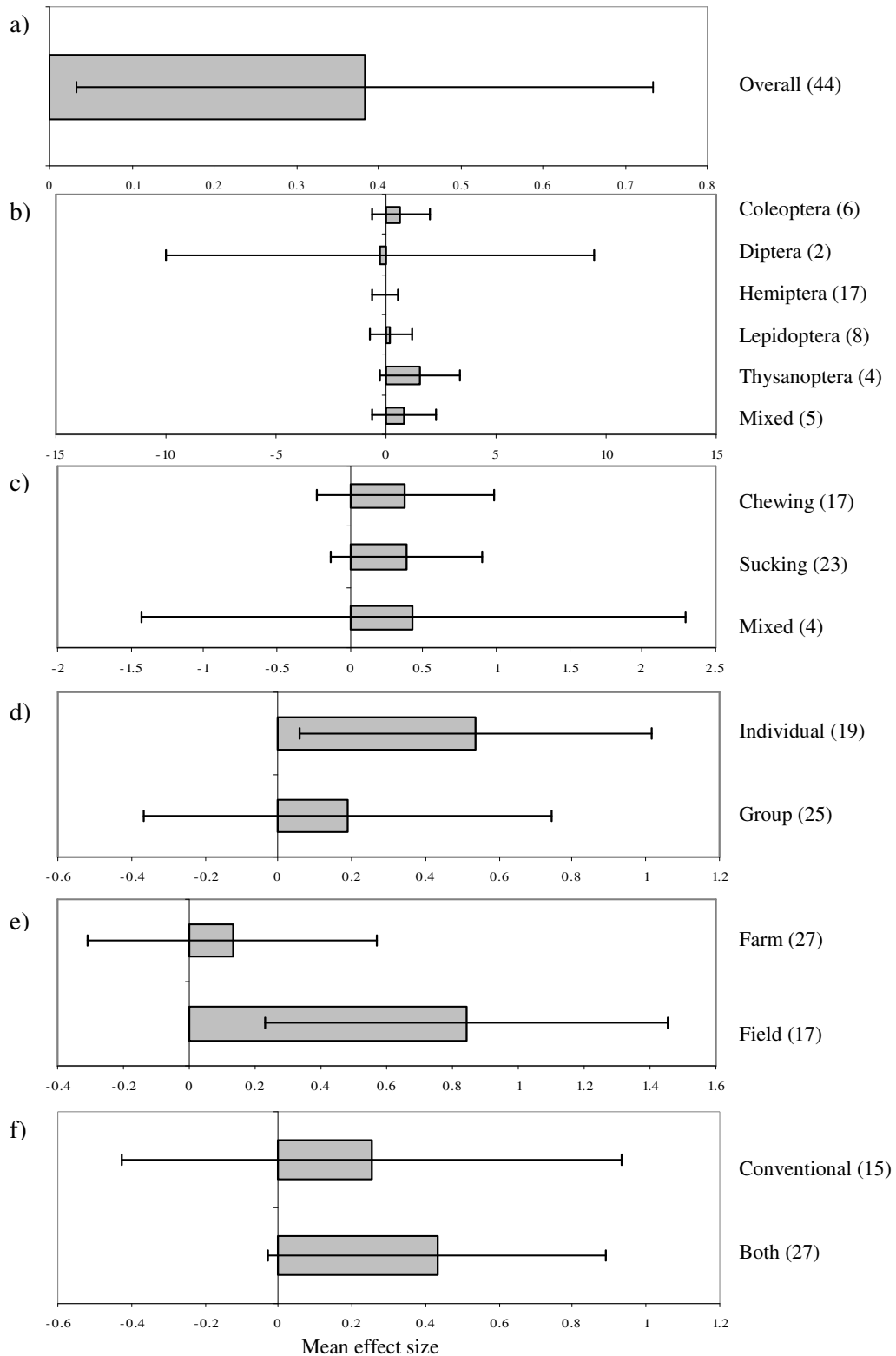


Fig. 2.1 Mean effect size of organic farming system on pest responses following analysis using categorical random effects models, error bars represent 95% confidence intervals for (n) responses. a) Overall pest response and responses categorised by b) taxonomic group, c) feeding guild, d) individual or group response, e) experimental spatial scale and f) presence of pest management.

2.4.2 Natural enemies and farming system meta-analysis

A total of 24 studies comparing natural enemy responses under organic and conventional farming systems contained sufficient information to enable an effect size to be calculated. Within these studies, 54 independent species or group responses to farming system were suitable for the meta-analysis. All studies compared abundance of natural enemies between treatments apart from two which looked at natural enemy condition and one which examined parasitoid impact, measured as percentage parasitism. Details of each independent response can be found in Appendix 2.

When data from all studies were combined, arthropod natural enemies showed a significant positive response to organic farming systems (Fig. 2.2a). With a mean effect size of 0.33, natural enemy numbers, impact or performance, depending on the measured response, was on average over 30% greater under organic treatments. For the data set as a whole, heterogeneity was high ($Q = 81.32^{**}$) and significant. When the data set was divided into taxonomic subgroups, all categories showed a positive mean effect size in response to organic farming except the Coleoptera which showed a slight negative response (Fig. 2.2b). Due to large 95% confidence intervals for the taxonomic categories, none of these effect sizes were significant and the within category heterogeneity was high and significant (between $Q = 7.92$, within $Q = 73.53^{**}$). The response of natural enemy functional groups was similar to that of taxonomic groups (Fig. 2.2c), with all categories showing positive effect sizes except for the coleopterans, again within category heterogeneity was significant (between $Q = 6.56$, within $Q = 76.32^{**}$). When a natural enemy response was taken for a group of species, the mean effect size was far more positive and significant when compared with studies examining individual species, which showed only a slight non-significant positive mean effect of organic farming (Fig. 2.2d). The within category heterogeneity comparing individuals and groups was significant (between $Q = 1.49$, within $Q = 78.97^{**}$).

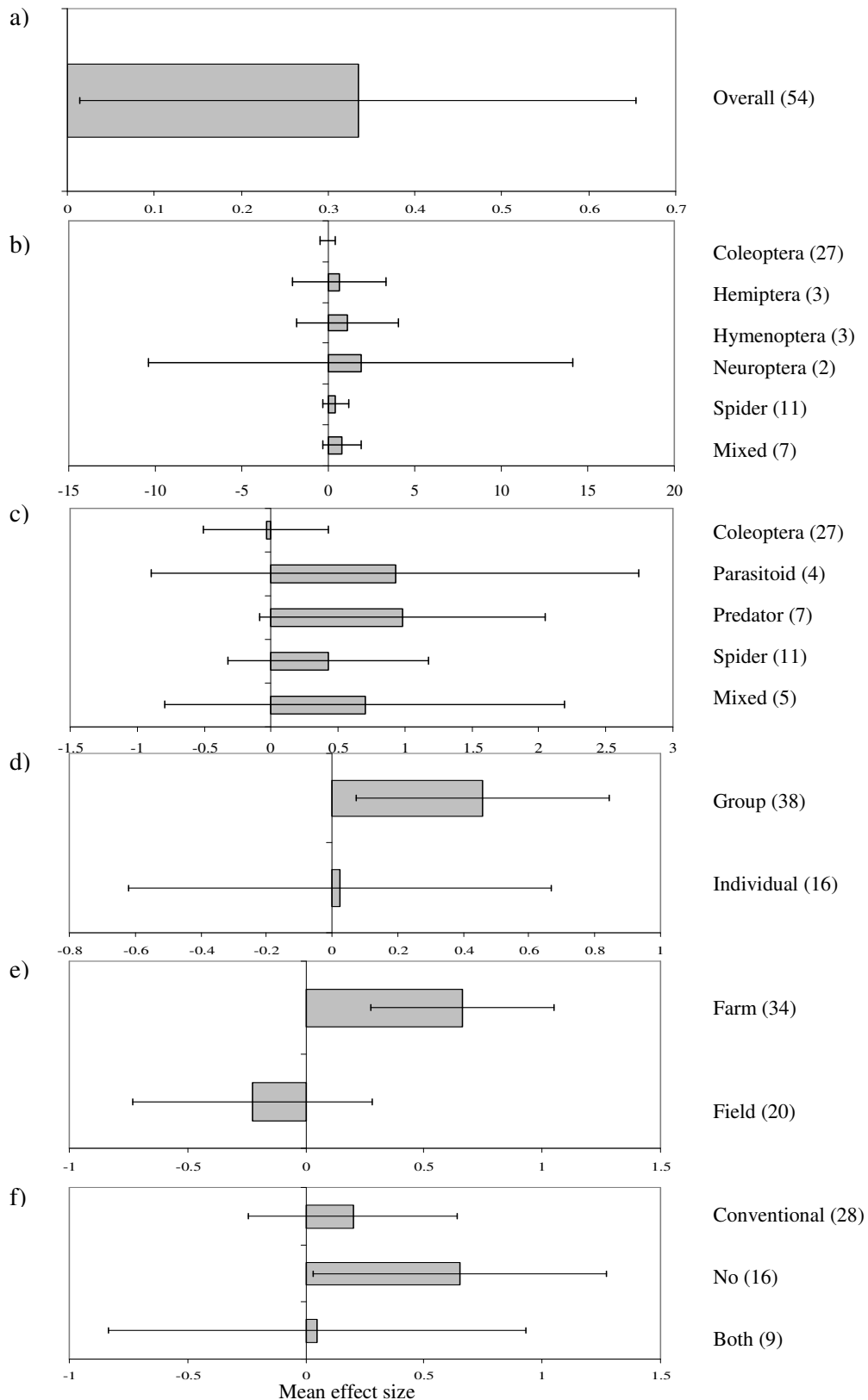


Fig. 2.2 Mean effect size of organic farming system on natural enemy responses following analysis using categorical random effects models, error bars represent 95% confidence intervals for (n) responses. a) Overall natural enemy response and responses categorised by b) taxonomic group, c) functional group, d) individual or group response, e) experimental spatial scale and f) presence of pest management.

The scale of the experiments had an impact on the measured natural enemy response, with a significant positive mean effect size shown by natural enemies in farm scale studies (Fig. 2.2e). Field scale studies showed an opposing response although this was not significant. Both within ($Q = 80.64^{**}$) and between ($Q = 8.32^{**}$) category heterogeneity was significant for experimental scale. The mean effect of organic farming on natural enemy responses was positive regardless of whether pest control was practiced under one, both or neither of the experimental treatments. This positive response was only significant, however, when there was no pest control in either treatment (Fig. 2.2f). For this model, within category heterogeneity was significant (between $Q = 2.12$, within $Q = 79.17^{**}$).

2.4.3 Pests and fertiliser meta-analysis

Ten studies compared the effects of organic and conventional fertilisers on pest performance on crop plants. Responses to treatment included abundance, development time, damage and oviposition preference. Seventeen independent responses of pests on different host plants under different fertiliser treatments were used for the meta-analyses (see Appendix 3). The meta-analysis involving both studies which compared farming system and those which compared only fertiliser treatments involved 57 responses from 25 studies.

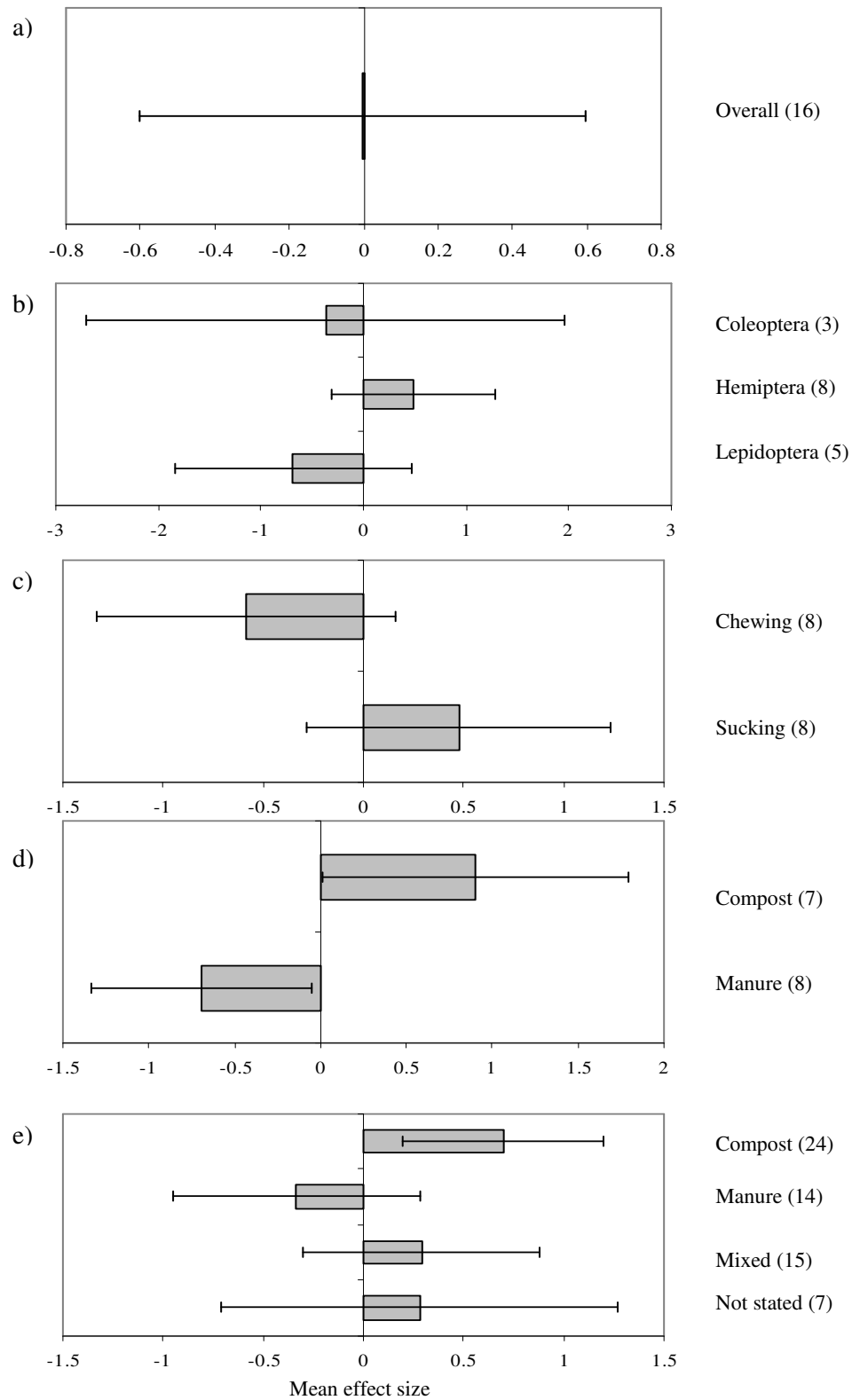


Fig. 2.3 Mean effect size of organic fertiliser treatments on pest responses following analysis using categorical random effects models, error bars represent 95% confidence intervals for (n) responses. a) Overall pest response and responses categorised by b) taxonomic group, c) feeding guild and d) organic fertiliser type. e) Shows mean effect sizes of different organic fertiliser types on pest responses from all farming system and fertiliser studies combined.

Overall there was no significant mean effect of organic fertilisers on arthropod pests (Fig. 2.3a). Although the response of chewing and sucking pests differed, there were no significant treatment effects on mean pest responses to organic or conventional fertiliser treatments when considered by taxonomic group (Fig. 2.3b) or feeding guild (Fig 2.3c). The data for these three random-effects models were all homogenous except for between category variation in the model examining feeding guilds (Overall: $Q = 12.76$, taxonomic: between $Q = 5.28$, within $Q = 12.82$, feeding guild: between $Q = 5.56^*$, within $Q = 14.03$). There were contrasting responses of pests in manure versus conventional fertiliser studies and compost versus conventional fertiliser studies with mean negative and mean positive responses respectively, to the organic fertiliser type (Fig 2.3d). Response heterogeneity was significant between but not within categories (between $Q = 12.33^{***}$, within $Q = 10.17$). When all studies involved in comparing pest responses to organic and conventional farming system and those studies examining the effect of fertiliser were combined and categorised by fertiliser treatment, again pest responses in studies using compost and manure fertilisers were contrasting and the response was significantly positive for studies using composts (Fig. 2.3e). In this case responses were homogenous (between $Q = 7.60$, within $Q = 60.75$).

2.4.4 Natural enemies and fertiliser meta-analysis

Eleven natural enemy responses to fertiliser treatments from five studies were involved in the meta-analysis. Eight responses involved natural enemy abundance and five measured natural enemy impact represented by percentage parasitism (see Appendix 4). The meta-analysis incorporating both fertiliser and farming system studies involved 63 data points from 29 studies.

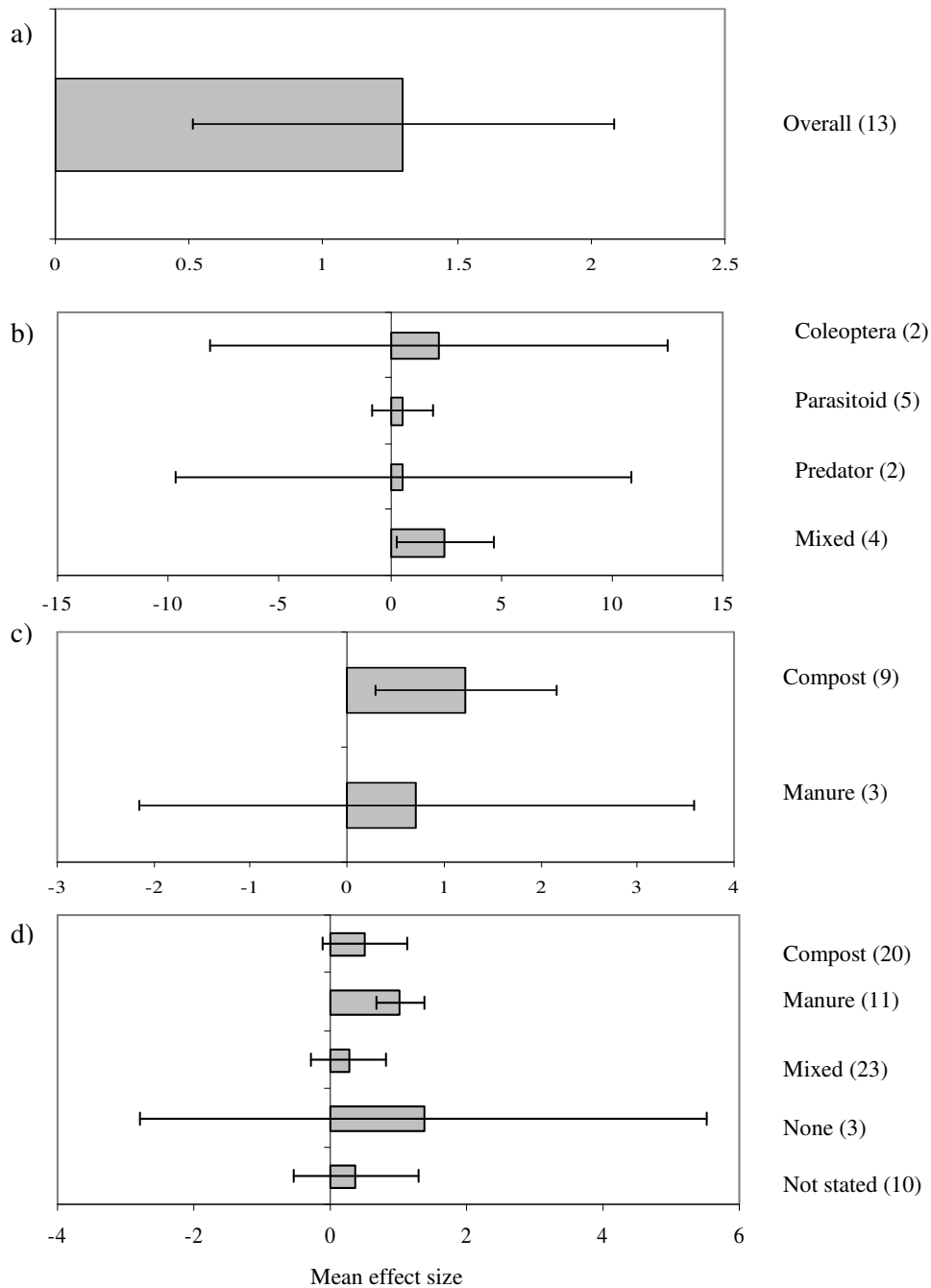


Fig. 2.4 Mean effect size of organic fertiliser treatments on natural enemy responses following analysis using categorical random effects models, error bars represent 95% confidence intervals for (n) responses. a) Overall pest response and responses categorised by b) taxonomic group and c) organic fertiliser type. d) Shows mean effect sizes of different organic fertiliser types on natural enemy responses from all farming system and fertiliser studies combined.

There was a significant positive effect of organic fertilisers on natural enemy responses which was homogenous ($Q = 17.18$) (Fig. 2.4a). When natural enemies were categorised by functional group, the responses shown by all categories was again positive although only significant for the mixed category (Fig. 2.4b). Neither

the within ($Q = 15.09$) or between category heterogeneity ($Q = 0.43$) was significant for functional groups. When organic fertilisers were categorised by type, both categories show a positive response in favour of organic fertilisers which was significant in studies involving compost (Fig. 2.4c). The between category heterogeneity was significant for this model (between $Q = 12.33^{**}$, within $Q = 10.17$). When both farming system and fertiliser studies were combined into one meta-analysis, mean effect sizes were positive for all fertiliser categories including those studies where no fertiliser was applied to the crops involved (Fig. 2.4d). Responses were homogenous both within ($Q = 60.75$) and between ($Q = 7.60$) categories for this model. Only those studies which used manure as an organic fertiliser showed a significant positive mean effect of organic agriculture on natural enemy responses.

2.4.5 Pests and farming system vote-count

Of the 76 responses from 24 studies on pest response to organic and conventional farming system, 42 pest groups or pest species showed a positive effect of organic farming while 25 showed a negative effect (Fig. 2.5). This difference was not significant. Following categorisation of responses by feeding guilds, group versus individual responses, experimental scale and pest management regime, there is generally more positive responses to organic practices and this difference is significant for the chewing and group categories of pests. By contrast, there was no difference in the number of positive and negative responses shown by sucking pests or experiments where individual pest species are monitored.

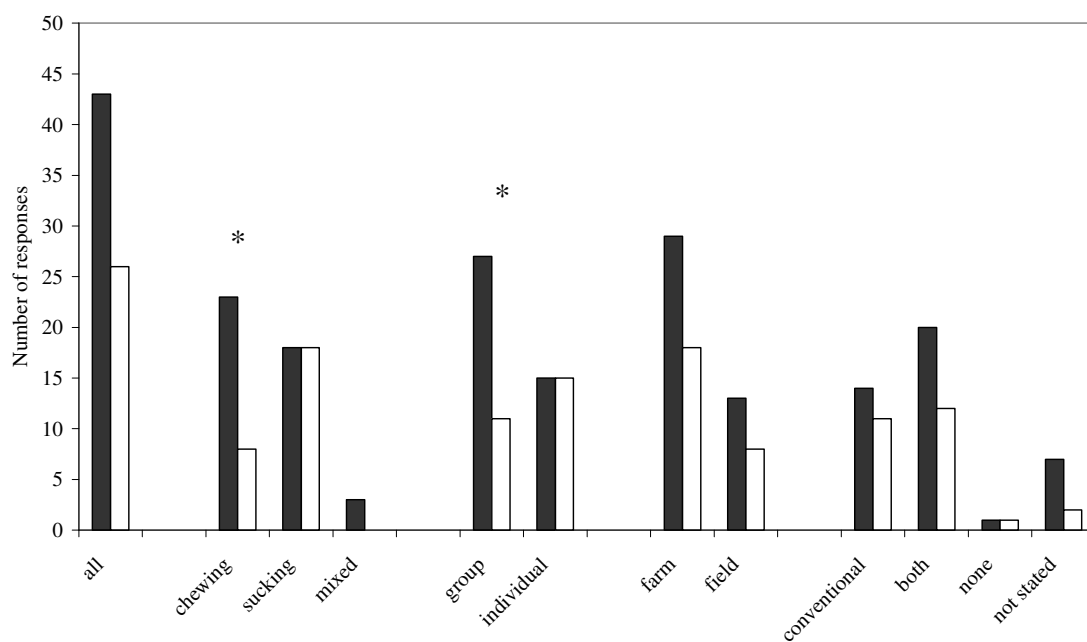


Fig. 2.5 The number of positive (■) and negative (□) pest responses to organic farming system, categorised by feeding guild, individual species or group response, experimental scale and pest management practice. Pairs of bars with asterisks are significantly different (Binomial test, P * < 0.05, ** < 0.01, *** < 0.001).

When the level of significance is considered, whether looking at all data points combined or following sub-division into feeding guild, grouped versus individual responses, experimental scale or pest management practices, significantly more studies found no significant treatment effect on pest response to organic or conventional farming systems (Fig. 2.6). The only exceptions to this are studies where no pest management was practiced or where pest management practices were unspecified.

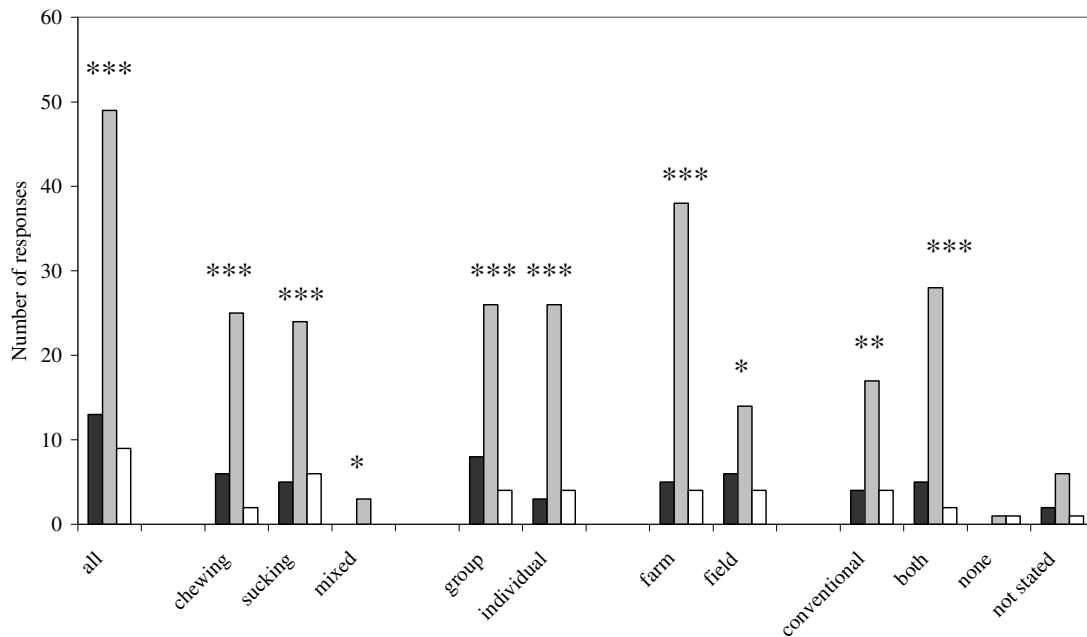


Fig. 2.6 The number of significantly positive (■), significantly negative (□) and non-significant (▒) pest responses to organic farming system, categorised by feeding guild, individual species or group response, experimental scale and pest management practice. Groups of bars with asterisks are significantly different (Chi squared test, $P^* < 0.05$, $P^{**} < 0.01$, $P^{***} < 0.001$).

2.4.6 Natural enemies and farming system vote-count

Thirty-eight separate studies involved suitable treatments and natural enemy responses enabling inclusion in the vote-count. Within these studies information on 139 separate species or groups of species interaction with different crop plants were available. Significantly more natural enemies showed positive responses to organic farming systems (Fig. 2.7). Following functional grouping of natural enemies, all groups showed higher numbers of positive responses to organic farming and this pattern was significant for the predators, spiders and the mixed group.

Significantly more positive responses to organic farming were also found in studies which looked at groups of natural enemies as opposed to individual species responses. Similarly, a large number of positive responses to organic farming system were found in studies that compared farming practice on a farm scale and not within one field site. Although more positive responses to organic practices were found under all pest management comparisons, this was significant only for those studies where pest

management was practiced in both organic and conventional systems and when pest management practice was not specified.

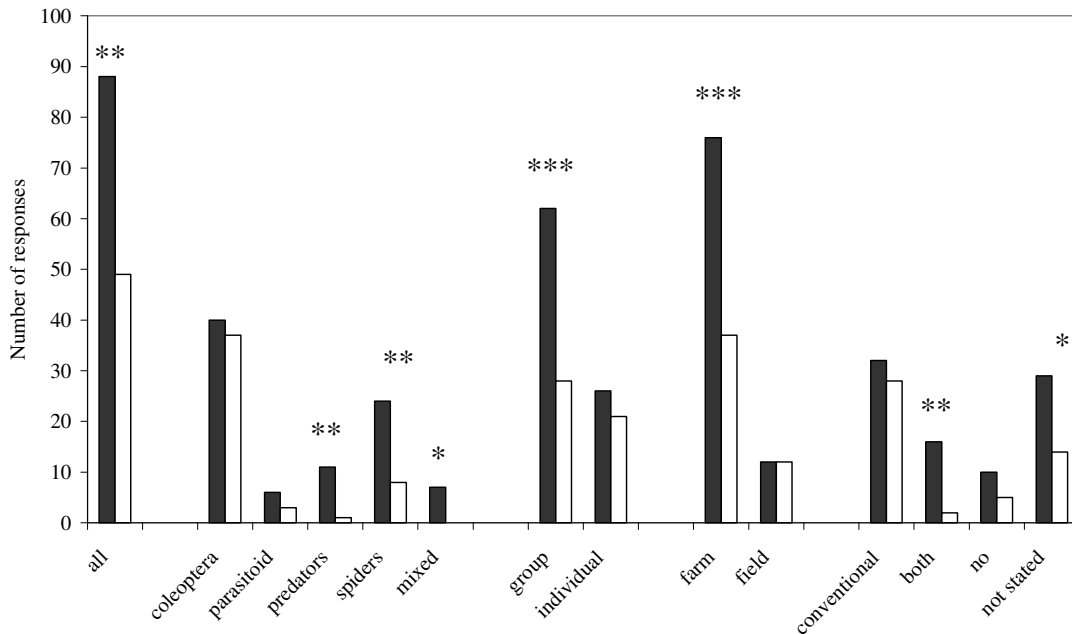


Fig. 2.7 The number of positive (■) and negative (□) natural enemy responses to organic farming system, categorised by functional group, individual species versus group response, experimental scale and pest management practice. Pairs of bars with asterisks are significantly different (Binomial test, $P^* < 0.05$, $** < 0.01$, $*** < 0.001$).

Significant differences between the number of significantly positive, significantly negative and non-significant responses were found when all studies were considered together and in studies involving spiders, coleopterans and mixed natural enemies when functional group categorisation had been implemented (Fig. 2.8). In each case there were a higher number of non-significant responses followed by significantly positive responses. A significant difference in the number of each response type was also found in studies looking at groups of natural enemies and experiments carried out on both a farm and field scale. Non-significant responses were again the most numerous followed by positive responses. With respect to pest management practice, significant differences in numbers of each response category are found in studies where pest control was carried out in both treatments and those studies which did not specify pest management practice. Once more there are more non-significant and positive responses to organic farming.

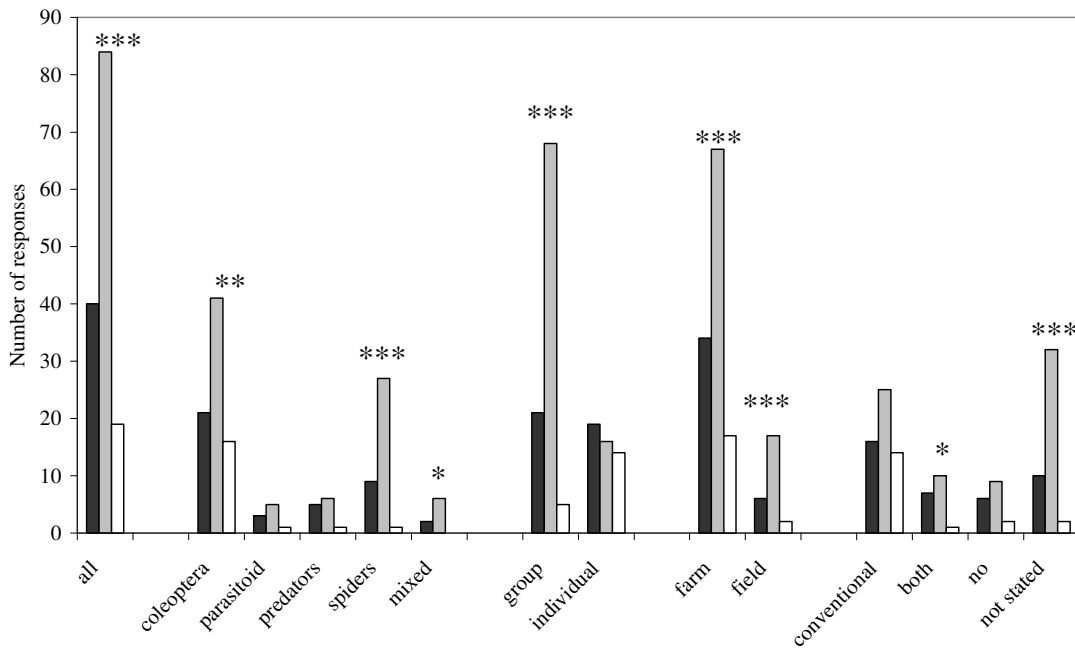


Fig. 2.8 The number of significantly positive (■), significantly negative (□) and non-significant (■) natural enemy responses to organic farming system, categorised by functional group, individual species versus group response, experimental scale and pest management practice. Groups of bars with asterisks are significantly different (Chi squared test, $P^* < 0.05$, $** < 0.01$, $*** < 0.001$).

2.4.7 Pests and fertiliser vote-count

Nineteen individual studies investigating the effects of organic and conventional fertilisers on pest abundance or performance were found. Within these studies information on 40 separate pest-host interactions under different fertiliser treatments were available for the vote-count. Significantly more chewing insects showed a positive response to conventional fertiliser. Sucking pests appeared to show the opposite response but this was not significant (Fig 2.9). The response of pests to organic fertiliser type also differed. In studies using animal waste as an organic fertiliser, significantly more pest species performed better on crops receiving conventional fertilisers. For studies using plant material as organic fertilisers the opposite trend was seen but was not significant. When all studies, including those testing farming management systems, were grouped by organic fertiliser type, the same pattern was found with contrasting responses for manure and compost. This was significant for studies involving manure. Studies using a variety of organic composts and studies where details on fertiliser regime were not provided both

showed a higher number of positive responses to organic treatments, though this was not significant.

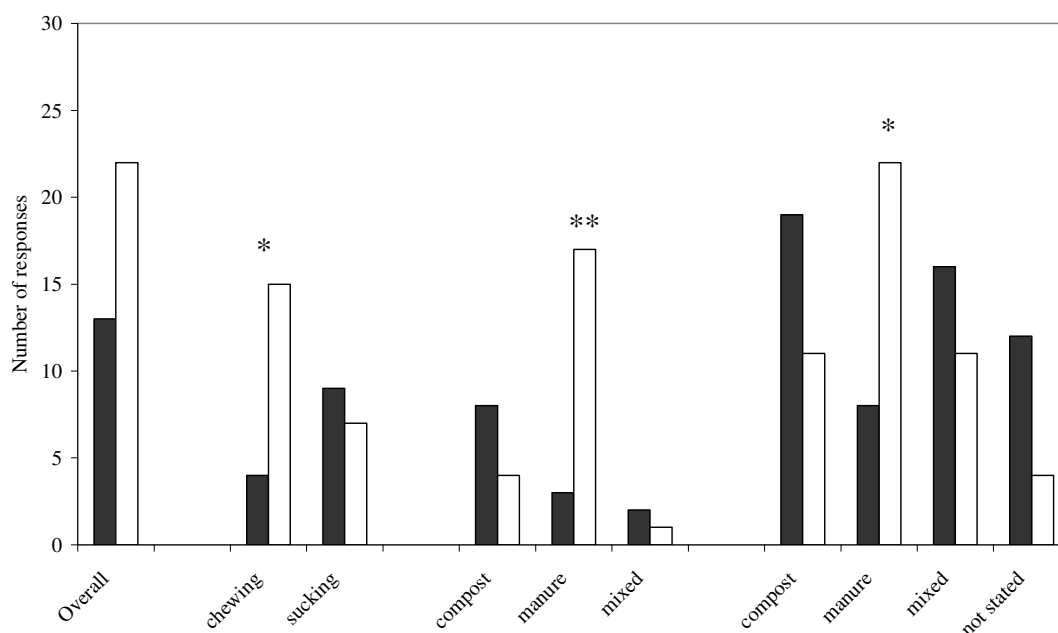


Fig. 2.9 The number of positive (■) and negative (□) pest responses to organic fertilisers categorised by feeding guild and organic fertiliser type. Pest responses to organic fertiliser type from fertiliser and farming system studies are also shown. Pairs of bars with asterisks are significantly different (Binomial test, P * < 0.05, ** < 0.01, *** < 0.001).

When considering the response direction and the level of significance, more studies found pest responses to organic and conventional fertiliser to be either non-significant between treatments or significantly positive in favour of conventional fertilisers (Fig. 2.10). A similar distribution in responses was found for both chewing and sucking pests but was significant for the former only. When manure was used as an organic fertiliser a significant distribution was found, more pest responses were significantly positive or not significant. By contrast, in studies using compost as an organic fertiliser there was no significant difference in the number of responses in each category. Considering the data set as a whole, significantly more studies involving manure fertilisers showed either non-significant or positive responses to conventional fertilisers. Those studies with either mixed fertiliser regimes or where no detail was given on fertiliser treatments showed significantly more non-significant responses to organic treatments.

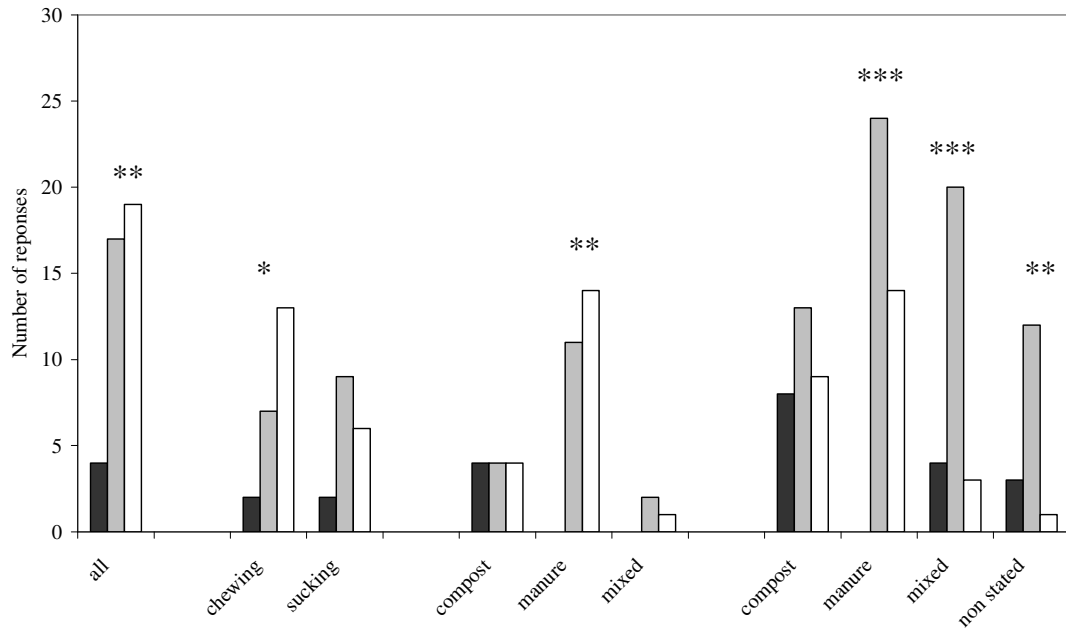


Fig. 2.10 The number of significantly positive (■), significantly negative (□) and non-significant (■) pest responses to organic fertilisers categorised by feeding guild and organic fertiliser type. Pest responses to organic fertiliser type from fertiliser and farming system studies are also shown. Groups of bars with asterisks are significantly different (Chi squared test, $P^* < 0.05$, $** < 0.01$, $*** < 0.001$).

2.4.8 Natural enemies and fertiliser vote-count

Eight studies specifically investigated the effects of organic and conventional fertilisers on arthropod natural enemies; with 22 separate crop-fertiliser-natural enemy interactions. Significantly more positive responses of natural enemies on plants treated with organic fertiliser were found (Fig. 2.11). The number of positive responses to organic fertilisers was greater than the number of negative or non-significant responses for all functional groups and organic fertiliser types, although the low number of studies means none of these distributions were significant. Following the combination of studies investigating farming practice and fertiliser treatments and subsequent division based on organic fertiliser type, higher numbers of positive responses to organic treatments were found in all categories of which manure and not stated were significant.

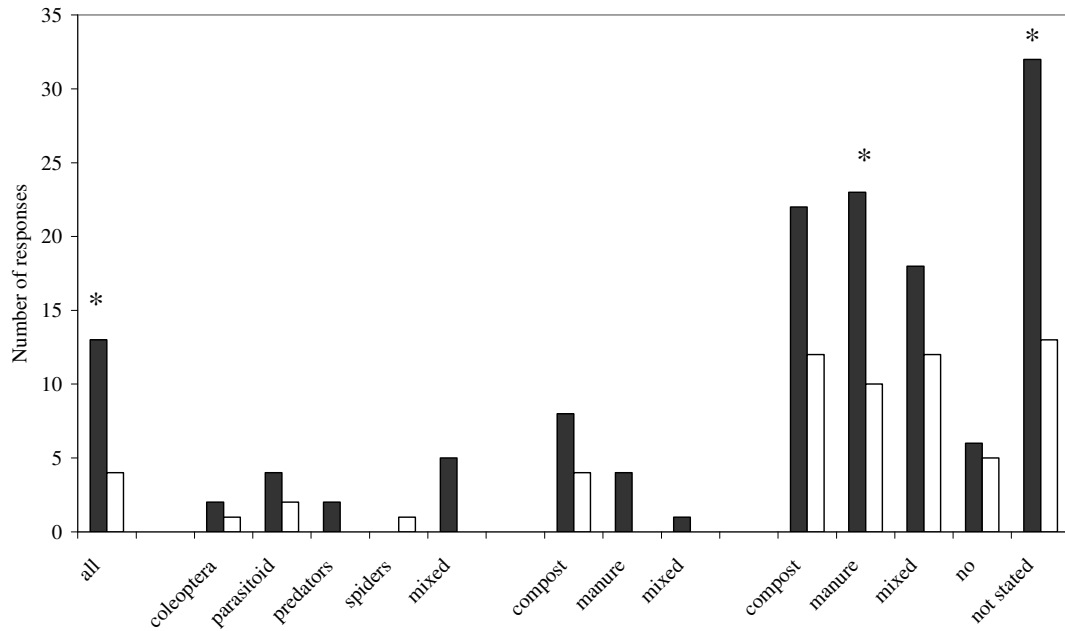


Fig 2.11 The number of positive (■) and negative (□) natural enemy responses to organic fertilisers categorised by functional group and organic fertiliser type. Pest responses to organic fertiliser type from fertiliser and farming system studies are also shown. Pairs of bars with asterisks are significantly different (Binomial test, $P^* < 0.05$, $** < 0.01$, $*** < 0.001$).

Significantly more non-significant natural enemy responses were found when all studies investigating fertiliser effects were combined and when studies investigating parasitoids were considered alone (Fig. 2.12). In studies using compost and manure as organic fertilisers the number of non-significant responses was highest and there were no significantly positive responses to conventional fertilisers. In fact, when the studies investigating fertiliser treatments alone are considered, no significantly positive effects of conventional fertiliser on natural enemies were found. When all studies are considered, both those investigating farming system effects and fertiliser effects, in the compost, mixed and ‘not stated’ groups the response distribution is significantly different from random. In all three categories the number of non-significant responses is highest followed by positive responses to organic treatments.

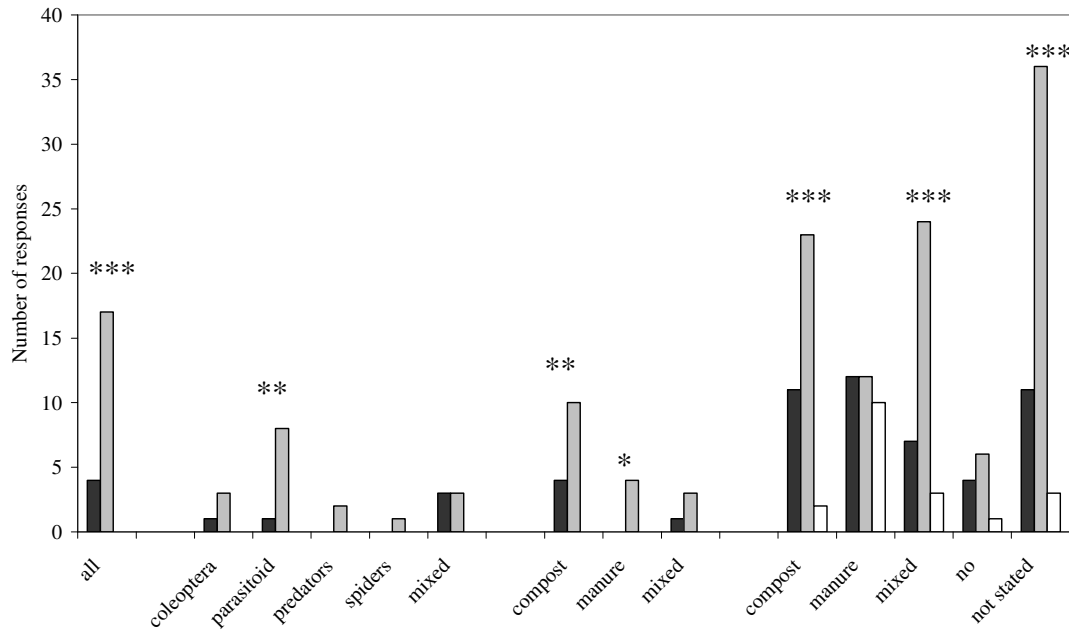


Fig. 2.12 The number of significantly positive (■), significantly negative (□) and non-significant (▒) natural enemy responses to organic fertilisers categorised by functional group and organic fertiliser type. Natural enemy responses to organic fertiliser type from fertiliser and farming system studies also shown. Groups of bars with asterisks are significantly different (Chi squared test, $P^* < 0.05$, $** < 0.01$, $*** < 0.001$).

2.5 Discussion

2.5.1 Pest response to farming system

The response of pests to organic farming systems was consistently positive, reflected by the positive mean effect sizes found in the meta-analysis and high number of positive responses to organic practices in the directional vote-count i.e. organic methods favour pests. This may indicate that conventional pest control strategies, including chemical pesticides, available to conventional farmers are effective in reducing pest populations. Perhaps effective weed control is absent in organic systems and the increased plant diversity contributed by abundant weeds is providing overwintering sites and alternative hosts for many pest species, thus increasing their abundance (Andow and Prokrym, 1990). These findings concur with those made by Attwood *et al.* (2008) who found that pests were generally more abundant in low

intensity agricultural systems although the significance of this relationship was dependent on the method of analysis.

Significant positive effects of organic farming were found when individual pest species were studied and for pests studied in field scale experiments. The fact that this pattern is prominent for individual species responses indicates that it is individual pests in the agroecosystem that are responding to management practice not overall pest abundance. The positive effects of organic agricultural methods on pest responses was only seen in field scale experiments indicating that management practices imposed in an individual field such as application of chemical insecticides, herbicides and crop husbandry, contribute to the reduced occurrence of pests. When experiments were carried out on a farm scale such benefits of organic practices to pests were not seen. The small fields, increased crop diversity and absence of chemical herbicides often found in organic systems may all serve to increase agroecosystem diversity. This increased diversity can increase natural enemy abundance (Ostman *et al.*, 2001; Langellotto and Denno, 2004) and subsequently reduce pest populations. While the directional vote-count tended to correlate with the meta-analysis it is worth noting that when the level of significance is considered, the vast majority of pest responses were non-significant. This demonstrates that while, in the main, pest abundance and performance was improved in organic systems, differences are typically small and whether pests are achieving damage thresholds in the organic systems and not in the conventional systems is questionable. This highlights the benefit of using both meta-analytical and vote-counting techniques in conjunction.

2.5.2 Natural enemy response to farming system

The present meta-analysis suggests a positive effect of organic farming on natural enemy performance and abundance, which is significant when all species are considered together. This is supported by the high number of positive responses to organic farming systems shown by natural enemies in the directional vote-count. Reasons for this might include the absence of chemical insecticides on organic sites, since many are known to have a marked negative impact on natural enemies (McLaughlin and Mineau, 1995; Hummel *et al.*, 2002). Conservation biocontrol

practices such as beetle banks and alternative food sources found on organic farms can also increase natural enemies (Zehnder *et al.*, 2007). When the data set is broken down into functional groups, spiders, predators, and parasitoids show positive mean effect sizes although this is not significant due to large confidence intervals and high within-group heterogeneity. These positive responses concur with findings made by Bengtsson *et al.* (2005) and Attwood *et al.* (2008) who found spiders and predatory insects benefited from organic farming or low intensity farming methods. Hole *et al.* (2005) reviewed the literature on spider abundance between farming systems and arrived at the same conclusion. Data on coleopteran species responses to farming system contradict the patterns of the other functional groups in these meta-analyses with a mean effect size close to zero. Coleopterans are a diverse group with a variety of life history characteristics including specialist and generalist predators (Lovei and Sunderland, 1996). Carabid species abundance with respect to farming management has been found to depend on the habitat preference of the species in question (Doring and Kromp, 2003). Various other work has also found that carabid and staphylinid responses to farming practice are species specific (Helenius, 1990; Krooss and Schaefer, 1998; Shah *et al.*, 2003; Purtauf *et al.*, 2005). The high levels of diversity in the coleopteran group might explain why no consistent effect of farm management on the group was found.

The response of individual natural enemies and groups of natural enemies appear to differ with respect to farming system. Group responses to organic management were significantly positive, while individual species response is variable with a mean effect size close to zero. This may reflect the overall trend found for natural enemies with a general trend towards organic management practices benefitting natural enemies. While, as demonstrated by the coleopterans in particular, individual species responses are more specific and maybe determined by one or a few specific elements of farming practice. Furthermore, for the vote-count 40 of the 49 individual responses concern coleopterans and for the meta-analysis 10 of the 16 responses involve coleopterans and this may be influencing the outcome in both cases. The vote-count and meta-analysis concur with respect to group and individual responses, although the number of non-significant group responses is high.

One striking trend in the data from the meta-analysis and the vote-count is the impact of experimental spatial scale on the response of natural enemies to farming system. When an experiment is carried out on a farm scale, a large significant positive mean effect was observed in favour of organic farming. When experiments are carried out on a smaller scale, however, this trend is reversed, although not significant. This indicates that larger scale management practices found on farms and within the agroecosystem are having a greater impact on natural enemies than those management practices that are imposed within the confines of an individual field site, including pest control practice, fertiliser regime and crop husbandry. Larger scale characteristics associated with organic farms including smaller field sizes, a larger variety of crops and other features such as hedgerows and conservation headlands may all serve to potentially increase habitat heterogeneity in and around the farm. Agroecosystem heterogeneity has been shown to increase abundance of spiders on a field and landscape scale (Sunderland and Samu, 2000). Soybean pest natural enemies also benefited from diversification of the agro-ecosystem through strip intercropping (Tonhasca, 1993). Field and landscape diversification increases natural enemy numbers (Gurr *et al.*, 2003; Langellotto and Denno, 2004) and biodiversity as a whole (Benton *et al.*, 2003) and in comparisons of conventional and organic farms, habitat heterogeneity and key landscape feature have been shown to have a greater impact on natural enemies than the specific farming management practices themselves (Weibull and Ostman, 2003; Purtauf *et al.*, 2005; Roschewitz *et al.*, 2005). Evidence from this meta-analysis and vote-count show that it is features of organic farms and not specific elements of organic or conventional farming practice, that have the primary influence on natural enemies. The number of studies carried out on a farm scale was higher than the number conducted within one field site, however, therefore limiting the strength of this hypothesis.

Results for studies involving pest control on conventional sites only, and studies where control was practiced on both conventional and organic sites show a positive association between organic farming and natural enemy abundance and performance although this is not significant. This demonstrates that whatever pest control procedures are permitted on organic sites are not having a negative effect on natural enemies. These control procedures included *Bacillus thuringiensis*, neem, soaps and other plant extracts. A significant positive effect of organic farming on natural

enemies is found in studies where pest control is absent and this could be in response to higher pest numbers in these studies supporting more natural enemies.

For the most part, results from the natural enemy meta-analysis and the vote-count correlate with the same major trends in the data apparent from both methods. These include an overall positive effect of organic farming on natural enemies although this does not hold for the diverse coleopteran group. Studies on groups of individuals appear to be more responsive to organic systems than individual species and the response of natural enemies in farm scale experiments is highly significant.

2.5.3 Pest response to fertiliser

According to the meta-analysis there was no significant effect of fertiliser on pest responses. This was true across taxonomic groups and feeding guilds. The low number of available data points and resulting large confidence intervals is probably the principle reason no significant pattern was found. Conversely, both vote-count methods tend to show pests performing better, following application of conventional fertilisers. Previous work has shown that plant nutrients and particularly nitrogen can affect pest performance in the sucking insects (Hasken and Poehling, 1995; Kaneshiro and Johnson, 1995; Bethke *et al.*, 1998; Bi *et al.*, 2001; Nevo and Coll, 2001) and many chewing pests ((Scriber, 1984b)cited by Altieri and Nichols (2003)) and this is generally attributed to increased nutritional quality of the host plant (Awmack and Leather, 2002). Therefore, any fertiliser regime that increases plant nitrogen might be expected to affect pest biology and higher nutrient availability in conventionally fertilised crops may be benefitting pest species (Altieri and Nicholls, 2003).

Both the meta-analysis and vote-count show that pests respond differently depending on the organic fertiliser used in each experiment. Pests respond positively to compost application and negatively following application of manure when compared with conventional fertilisers. The divergent responses of pests in manure amended and plant compost amended experiments is interesting. Perhaps manure creates a suitable soil environment for plant growth and resistance to pests. The mineral balance hypothesis states that high organic matter and microbial activity associated with

organically managed soils can optimise plant growth and can make them less susceptible to pest attack (Phelan *et al.*, 1996). Alternatively, manures are known to lose considerable amounts of nutrient post application (Dawson *et al.*, 2008) and lower crop available nutrients may be reflected by reduced pest abundance and performance. It is difficult to make direct comparisons between organic and conventional fertilisers used in the experiments involved in this review because only seven of the 18 studies comparing organic and conventional fertilisers actually match absolute nutrient inputs between treatments and none of those matched studies involved plant composts. Possibly, nutrient inputs from plant sources far outweighed their conventional equivalents and this increased nutrient availability might explain why pest abundance is higher in these cases. Without details on soil nutrients and plant yield this is difficult to confirm. The differing effects of manure and compost on pest responses still holds true even when farming system and fertiliser specific studies are combined. Given the number of other factors involved in determining pest responses to management system, fertiliser type must be making an important contribution and this could be utilised in integrated pest management systems.

2.5.4 Natural enemy response to fertiliser

Due to the very low number of studies involved in comparing organic and conventional fertiliser effects on natural enemies, conclusions are difficult. No measured responses were significantly positively associated with conventional fertilisers and the meta-analysis showed a significantly positive mean effect of organic fertilisers on natural enemies. Plant nutrition can affect parasitoid biology acting indirectly through the host insect (Kaneshiro and Johnson, 1995; Wurst and Jones, 2003) and potentially organically fertilised crops may be providing more suitable prey individuals for the natural enemies, certainly in the case of chewing pests which showed a significant positive response to organic fertilisers. The positive impact of organic fertilisers on natural enemies may be a contributing factor towards the consistently higher numbers of these species found in organic systems.

2.6 Conclusion

Pest responses to farming system are variable and the high number of non-significant responses in the present study suggests that the farming system is not a major factor in determining pest numbers. The vast majority of studies examined pest abundance and this measure was the prioritised response with respect to data collection for this review. Whether abundance represents the true impact of pests on the crop is debatable. A more detailed look at pest impact or resulting yields would go some way to answering this question. The use of conventional fertilisers on the whole impacted positively on invertebrate pests, certainly in the case of chewing insects according to the vote-count. This demonstrates careful use of conventional fertilisers is needed and that pest response depends on the biology of the primary pests of a crop. Furthermore, the use of plant composts or manures as the organic fertiliser had very different affects on pest responses. It would appear that the use of manures has a consistent negative affect on pests and could potentially be very useful to organic and conventional farmers alike. Again the affect of this fertiliser on yield and the impact of pests on the crop in question would need to be studied in more detail.

The belief that organic farming can increase natural enemy numbers through reduced use of broad spectrum insecticides and habitat manipulation is supported by the present study. All groups of natural enemies, except the coleopterans, consistently show a positive response to organic agriculture in both the meta-analyses and vote-counts. That this positive impact is more pronounced at a farm scale indicates that larger scale characteristics of organic agriculture are facilitating natural enemies. Habitat heterogeneity is known to promote natural enemy abundance (Ostman *et al.*, 2001; Gurr *et al.*, 2003; Roschewitz *et al.*, 2005) and may be a contributing factor. Perhaps if farm characteristics and landscape features are the major determinant of natural enemy success then these key features could be manipulated in conventional agriculture to improve pest control, thus reducing the need for insecticide application. The positive effects of organic fertilisers found in this study may help to explain why natural enemies respond positively to organic practices.

Literature review papers can be affected by the criteria used for study selection and specific data collection. The similarity between the conclusion made by this review and others on a similar subject (Bengtsson *et al.*, 2005; Hole *et al.*, 2005; Attwood *et al.*, 2008; Letourneau and Bothwell, 2008), specifically that pest responses to organic agriculture are variable but in some cases positive in organic systems while on the whole natural enemies benefit from organic practices, lends weight to the conclusions made. This review also serves to highlight the potential importance fertilisers play within a farming context in determining pest and natural enemy populations, although it does emphasise a gap in the research, predominantly with regards to natural enemies and the impact of organic and conventional fertilisers.

Chapter 3

The effects of organic and conventional fertilisers on cereal aphids and parasitoids in the field

3.1 Introduction

Barley is a key crop in Britain (DEFRA, 2008a) and aphids are its major pest through direct damage and virus transmission (Mann *et al.*, 1997). Parasitoids are an important natural enemy of aphids, playing a key role in population suppression (Schmidt *et al.*, 2003; Levie *et al.*, 2005). The cereal-aphid-parasitoid system is an ideal system to manipulate to observe fertiliser effects on pests and natural enemies in the field. With much work already carried out on the impacts of synthetic fertiliser on cereal aphid populations (Honek, 1991b; Hasken and Poehling, 1995; Gash *et al.*, 1996; Duffield *et al.*, 1997), a comparison between conventional and organic fertiliser is relevant, particularly when the expanding organic movement is considered.

The principle aphid species found on cereal crops, including barley in Britain are *M. dirhodum*, *S. avenae* and *R. padi* (Leather, 1989; Mann *et al.*, 1997; Larsson, 2005). The rose-grain aphid, *Metopolophium dirhodum* is holocyclic and overwinters on *Rosa spp.*, although in western Europe it has a tendency to overwinter parthenogenetically utilising numerous grasses and cereals (Blackman and Eastop, 2000). Primarily a leaf feeding aphid (Watt, 1979), *M. dirhodum* is predominantly a pest of spring cereals (Mann *et al.*, 1997) hence its prevalence in central Europe where spring sown cereals are common (Honek, 1991a). *Metopolophium dirhodum* transmits barley yellow dwarf virus and when populations exceed the damage threshold of 15 aphids per tiller direct yield reductions can occur (Oakley and Walters, 1994).

The grain aphid, *Sitobion avenae*, is monoecious and holocyclic although anholocyclic overwintering is common in milder winters. *S. avenae* will utilise many Gramineae species as hosts (Blackman and Eastop, 2000) and is a major pest of winter cereals in Northern Europe. Colonisation occurs in early summer with populations often reaching damaging numbers towards ear ripening, a growth stage on which it performs best (Walters and Dixon, 1982) and when significant yield reductions can occur (Larsson, 2005). Although prophylactic control measures are sometimes practiced to reduce the impacts of *S. avenae*, outbreaks are historically sporadic and irregular (Mann *et al.*, 1986).

By comparison, the bird-cherry oat aphid *Rhopalosiphum padi*, is somewhat less abundant in the UK where it exists as a pest due to its ability to transmit barley yellow dwarf virus. In mainland Europe and particularly Scandinavia numbers can get much higher and significant direct feeding damage can be caused (Leather, 1989).

Rhopalosiphum padi is heteroecious and holocyclic and in Europe its primary host is *Prunus padus* with numerous secondary hosts including major cereals and pasture grasses (Blackman and Eastop, 2000). *Rhopalosiphum padi* preferentially feeds on the stem of its secondary hosts (Leather and Dixon, 1981) and often arrives on cereal crops early in spring (Leather, 1989) confounding its role as an important virus vector.

Previous work on cereal aphids and the effects of organic and conventional farming are limited, with inconsistent conclusions. A farm scale experiment by Roschwitz *et al.* (2005) found significantly reduced aphid numbers on organically managed farms but also found that landscape complexity was equally, or more important than farm management in determining the abundance of some aphid species. Moreby (1994) by contrast, found higher numbers of aphids in organically managed cereals. Another farm scale investigation of cereal aphid populations found no significant differences between organic and conventionally managed wheat or barley (Ostman *et al.*, 2001). Smaller field scale experiments are also contradictory with respect to cereal aphids, with fewer *R. padi* found on organic barley (Helenius, 1990) but increased numbers of *S. avenae* and *M. dirhodum* on organic wheat (Poveda *et al.*, 2006).

Numerous studies have investigated the effects of fertiliser application on pest performance but historically the vast majority have been carried out on a small scale.

In fact Letourneau (1988) found only 10% of such studies involved field scale experiments and questions whether conclusions drawn from pot experiments will hold true in the wider environment. More recently field studies on fertiliser effects on cereal aphids have become more numerous (Honek, 1991b; Gash *et al.*, 1996; Duffield *et al.*, 1997). Field studies on organic and conventional fertiliser on cereal aphid populations independent of other management practices, however, are rare (Bado *et al.*, 2002).

Natural enemies including parasitoids can benefit from the use of organic agricultural methods. The effect of organic fertilisers on parasitoids, however, remains largely unstudied. Organic composts have apparently improved parasitoid abundance and their impact on pests in broccoli and sorghum on a field scale (Blumberg *et al.*, 1997; Ponti *et al.*, 2007) but data on the impact of manures in the absence of insecticide treatments and other management practices on cereal crops are unavailable. With so little work on field comparisons of fertilisers and their impacts on pests and natural enemies the present field trial is highly relevant.

Farm manure is a readily available fertiliser across the world and is an important source of nitrogen in many integrated, organic and low input systems (Dawson *et al.*, 2008). Despite their generally lower nitrogen availability, organic fertilisers can increase soil organic matter and release nitrogen throughout the growing season (Montemurro *et al.*, 2006) while also increasing soil pH and stimulating microbial activities (Mader *et al.*, 2002), all of which are properties essential for maintaining a healthy soil ecosystem. Conventional fertilisers have been shown to increase aphid abundance in cereals (Honek, 1991b; Hasken and Poehling, 1995). If the use of slow release organic fertilisers could mitigate these effects on pests while not impacting negatively on yield then their use may be highly beneficial in cereal production.

3.2 Aims and objectives

Fertilisers can influence plants, pests and natural enemies in a number of ways and so this experiment aimed to investigate the trophic effects of organic and conventional fertilisers on a crop, pest and natural enemy system on a field scale.

The objectives of the present field experiment were to measure how the application of conventional fertilisers and composted horse manure affect 1) barley growth and yield, 2) aphid population density and 3) aphid parasitoid natural enemies on a field scale.

3.3 Materials and methods

3.3.1 Field sites and farming practice

Two 0.25 ha field sites were established at Silwood Park, Ascot, Berkshire, UK (51.4086N, 0.6495S); one in Silwood Bottom and one in Four Acre Field. Both sites, whilst not regularly cultivated, have had cereals grown on them in the past and both sites are rotovated annually to maintain their grassland status (Fig. 3.1).



Fig. 3.1 Silwood Park barley field sites in a) Four Acre Field and b) Silwood Bottom soon after barley germination, summer 2006.

The soils found throughout Silwood Park are free-draining, acid, sandy soils of the Bagshot Series (Crawley, 2005). To gain baseline soil nutrient data and determine the physical characteristics of both field sites, soil samples were taken on 12/8/2008. Four, 30 cm cores along a 50 m transect were extracted from each field site. The transects were located alongside each field site but in a position where no fertiliser

had been applied for at least three years. The samples were homogenised, kept cool and analysed by NRM Analysis Ltd (Bracknell) (Table 3.1).

Table 3.1 The physical and chemical characteristics of soil from Silwood Bottom and Four Acre Field study sites at Silwood Park.

	Soil characteristic	Unit	Field site	
			Silwood Bottom	Four Acre Field
Chemical	Available P	mg/l	40	19
	Available K	mg/l	106	88
	Available Mg	mg/l	50	55
	Nitrate	mg/kg	4.10	1.86
	Ammonium	mg/kg	1.06	1.24
	pH		6.1	5.2
Physical	Sand 2.00-0.063mm	%w/w	76	71
	Silt 0.063-0.002mm	%w/w	15	18
	Clay <0.002mm	%w/w	9	11
	Organic matter	%w/w	2.6	4.0
	Dry matter	%	83.7	77.4
	Textural class		Sandy loam	Sandy loam

Prior to planting, both sites were treated with a blanket covering of glyphosate (Round-up ProTM) at 5 l/ha on 26/4/2006 to minimise the impact of weeds in the subsequent crop. Glyphosate was applied using a rotary atomiser with a spray volume of 10 l/ha with a flow rate of 0.115 l/min.

Both sites were then rotovated on 3/5/2006 prior to barley seed plant on 5/5/2006 and 6/5/2006. Feed barley (cv. Doyen, Sherborne Processing Ltd, Dorset) was spread evenly by hand at a seed density of approximately 500 seeds/m². This is a particularly high seed density to compensate for loss due to pest and low germination rate in the absence of seed drilling. Soil was then turned by hand to cover any exposed seed and the crop was allowed to grow under natural conditions without further weed control or watering.

3.3.2 Fertiliser treatments

Both field plots were divided into six subplots, 12 in total, each measuring 25 m x 16.5 m. Half of these plots were randomly selected and assigned either organic or conventional fertiliser treatments within a semi-Latin square framework ensuring each fertiliser type was represented at least once in each column and row of each field site. This allowed for variations in gradient, soil type, proximity to the field edge as well as wind and weather effects (Fig 3.2). Each of these subplots was then further randomly subdivided into two smaller plots measuring 12.5 m x 16 m, one plot receiving a high dose of fertiliser while the other received a low dose. This experimental set up created a semi-randomised factorial split-plot design with three experimental factors all of which had two levels, fertiliser type (organic or conventional), fertiliser dose (high or low) and field site (Silwood Bottom and Four Acre Field). Replication at the highest factor level was 12.

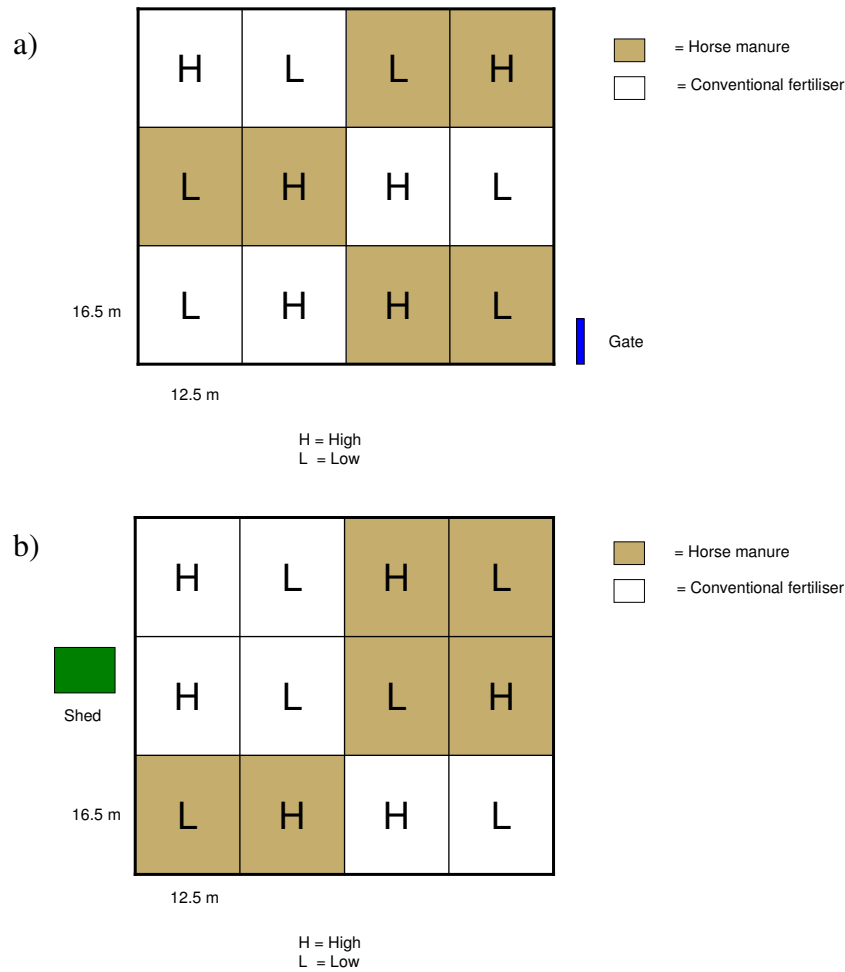


Fig 3.2 Fertiliser treatment layout in a) Four Acre Field and b) Silwood Bottom

Prior to the experiment a conservative estimate of the macro-nutritional content of horse manure was made to enable comparable doses of nitrogen, phosphorous and potassium to be applied to the field plots by organic and conventional means. The horse manure used in this experiment was supplied by a local farmer and had been well composted with the addition of some straw bedding material. Previous studies have tested horse manure and found various percentage ratios of nitrogen, phosphorous and potassium. Dong *et al.* (2006) found levels of 0.7:0.2:0.7, while nitrogen levels of 1.9% were found by Ferreras *et al.* (2006), both referring to the fresh weight. The latter compost also had additional rabbit manure added. Following analysis of horse manure composted with straw, fresh weight percentages of 2.5:1.4:1.3 were found by Levy and Taylor (2003). Composted manure without any bedding material appears rather different with a ratio of 5.5:0.6:1.7, measured by Siddiqui (2004). The DEFRA fertiliser recommendation handbook states that

partially composted fresh weight cattle, pig, sheep and duck manures contain ratios of nitrogen, phosphorous and potassium ranging from 0.6 - 0.7, 0.35 - 0.7 and 0.3 - 0.8 respectively (DEFRA, 2000). The above research shows then that nitrogen and potassium are consistently higher than phosphorous in composted horse manure and the lowest percentage contents found in composted manures fall below 1% for nitrogen, phosphorous and potassium. For these reasons and considering the storage and bedding material involved, the horse manure used in this experiment was assumed to have an N:P:K content of 0.6:0.3:0.6. This ratio was used when making fertiliser dose rate calculations.

All 12 organic plots had composted horse manure applied evenly across the plot by hand between 27/11/2005 and 5/12/2005. The six high dose plots received 760 kg each and the six low dose plots received 380 kg. Conventionally fertilised plots were treated by hand when barley was at growth stage 12 (Tottman and Broad, 1987) between 17/5/2006 and 18/5/2006. High dose plots received terranitram, super phosphate and potassium sulphate levels of 10.4 kg, 10 kg and 7.5 kg, respectively. Low dose plots received 5.2 kg of terranitram, 5 kg of super phosphate and 3.75 kg of potassium sulphate. The resulting N:P:K levels for high dose input plots were 180:90:180 kg per hectare and for low dose plots amounts were 90:45:90 kg per hectare for both organic and conventionally fertilised plots.

3.3.3 Plant and yield measurements

The number of tillers and growth stage of all plants involved in the aphid counts was recorded using five growth categories based on important stages in barley development; more than one leaf (GS12-20), tillering (GS20 – 29), stem elongation (GS30- 48), ear emergence (GS49 – 55) and post inflorescence (GS55+) (Tottman and Broad, 1987).

At the end of the growing season, when all the barley was fully ripe a yield measurement was taken (1/8/2006 and 2/8/2006). Yield collection involved the random placement of three, 1 m² quadrats in each of the 24 plots. The ears were then removed from all barley plants within the quadrat and the number of ears collected in

each quadrat was recorded. After 48 h in a 60°C oven, the total dry weight of barley ears per m² quadrat was determined enabling a relative yield per hectare to be calculated.

3.3.4 Aphid survey

Aphid counts were carried out every 3-4 days throughout the barley growing season, starting soon after barley emergence on 24/5/2006 and finishing prior to harvest on 19/7/2006. For each count, one of the two field sites was randomly selected as the starting site, either the first or last plot on that site was then selected randomly as the first plot to be observed. Within each plot, 10 whole plants were isolated randomly along a transect, which had been randomly orientated down one of the two diagonals of the plot. The species and number of all aphids on each plant was recorded.

Whether the aphid was apterous (wingless) or alate (winged) was also noted. The relative measure of aphid populations on tillers and plants was taken as 'aphid days'. Aphid days is a measure commonly used to investigate aphid populations on plants (Hansen, 2000; Ostman *et al.*, 2001), with one aphid day representing one aphid on one plant or tiller for one day.

3.3.5 Parasitoid survey

Parasitoid surveys were carried out in parallel with aphid counts on the same randomly selected plants. The number of aphid mummies found was recorded. A subsample of mummies was also collected and stored in Ependorf tubes for identification, none however survived to emerge.

3.3.6 Statistical analysis

A factorial one-way ANOVA was carried out to determine the effect of fertiliser treatment on barley yield, tiller number and ear weight. The factor levels, fertiliser type, dose and site were included in the model. Tiller number is a mean derived from data collected on count days 10 to 14, when all plant were at post tillering developmental stages. Therefore, this represents a mean maximum tiller number.

Using a BoxCox test (Crawley, 2007) and following visual inspection of the distribution of the data, tiller number was log transformed and yield was square root transformed prior to analysis. Ear weight required no transformation. Throughout the results any reported site effects are from the simplest model that still retains the three main factors. Fertiliser type and dose effects are taken from the minimum adequate models.

To analyse fertiliser effects on the mean number of *M. dirhodum* aphid days per tiller a factorial one-way ANOVA was carried out with the factors fertiliser type, dose and site and their interactions. The same ANOVA model was used to investigate the effects of treatment on *M. dirhodum* aphid days per plant.

To investigate the influence of tiller number and ear weight on *M. dirhodum* aphid days per plant, linear regressions were carried out. Again the values for mean tiller number were derived from data collected on counts 10 to 14 and tiller number was log transformed before analysis.

The number of alate *M. dirhodum* counted per tiller was summed through the season due to the low numbers encountered. Fertiliser type, dose and site effects were analysed using ANOVA. Due to positive skew in the data and zero counts, alate *M. dirhodum* number per tiller was $\log+0.1$ transformed.

For the incidence counts of *M. dirhodum* in the barley plots, the response variable was taken as the proportion of the ten plants sampled in each plot with aphids present. Data for incidence counts were then analysed using a factorial analysis of deviance with binomial errors for proportion data. A separate analysis of deviance was carried out for each of the 14 count days with binomial or quasibinomial error structures used depending on dispersion.

To assess the effects of fertiliser treatment on parasitism, the cumulated number of parasitoid mummies per tiller was used in an ANOVA model with type, dose and site effects. A linear regression between cumulated mummies per tiller and cumulated aphids per tiller was also carried out. To normalise the vector, following visual inspection of the data and the BoxCox test, cumulated parasitoid mummies per tiller

was square root transformed prior to analysis. All statistical calculations were undertaken using the statistical program 'R' version 2.7.1 (Ihaka and Gentleman, 1996).

3.4 Results

3.4.1 Barley

Fertiliser type, organic or conventional, was found to significantly influence both plant tiller number and ear weight. Following analysis of variance, significant fertiliser type effects were found. Greater tiller numbers (Type: $F_{1,21} = 14.15$, $P < 0.01$; Dose: $F_{1,20} = 4.19$, $P = 0.054$) and ear weights (Type: $F_{1,20} = 11.49$, $P < 0.01$; Dose: $F_{1,20} = 0.29$, $P = 0.06$) occurred in conventionally fertilised plots (Fig. 3.3). There were also significant site effects on tiller number ($F_{1,20} = 28.21$, $P < 0.001$) and ear weight ($F_{1,20} = 5.22$, $P < 0.05$), both were significantly higher at Silwood Bottom.

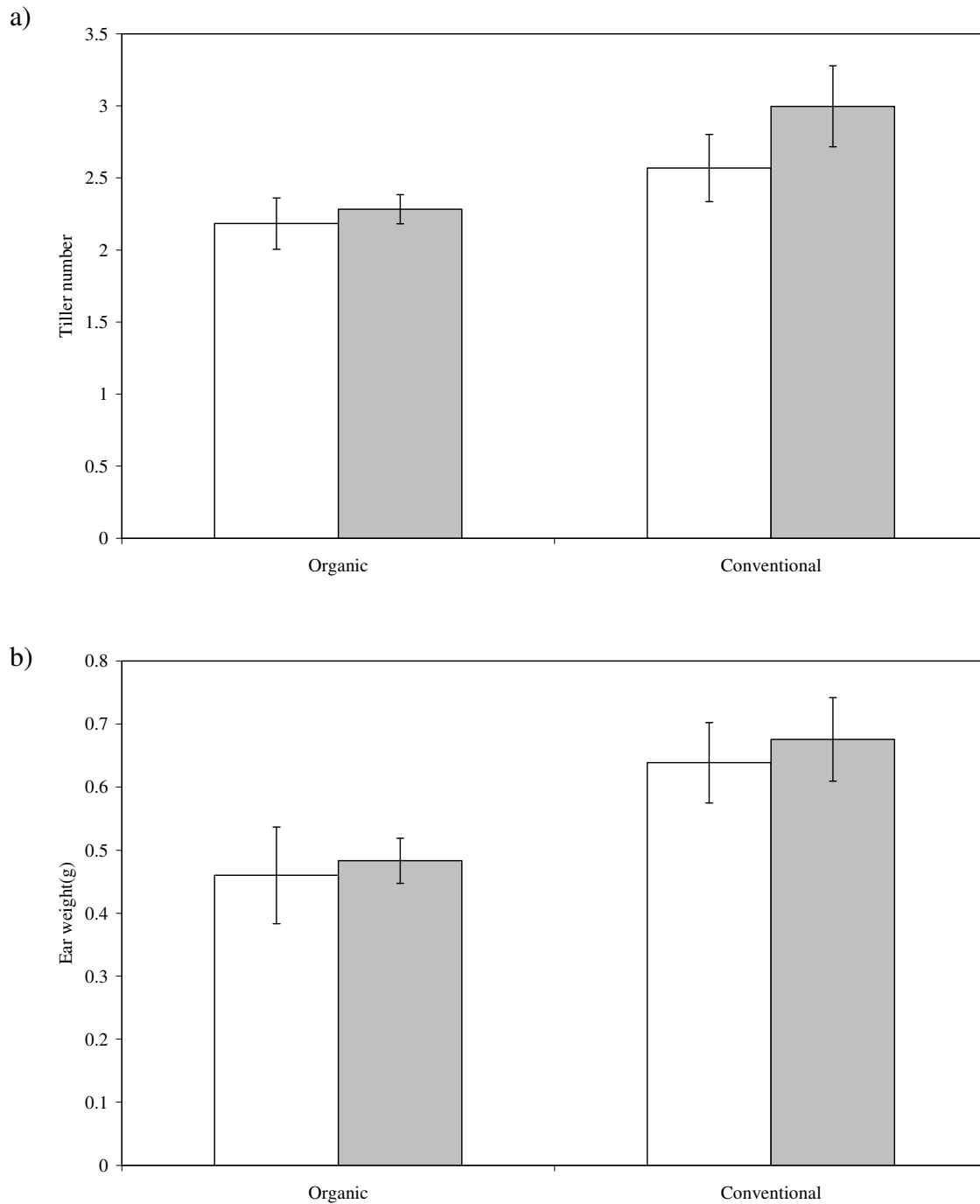


Fig. 3.3 a) Tiller number and b) ear weight of barley grown using conventional and organic fertiliser treatments at a high (■) and low (□) dose (mean \pm SEM).

Yield in tonnes/ha varied considerably between plots following this field trial, however, total yield per hectare was significantly greater in conventionally fertilised plots (Type: $F_{1,21} = 7.85$, $P < 0.05$; Dose: $F_{1,20} = 0.64$, $P = 0.43$) (Fig. 3.4). A significant site effect was also apparent ($F_{1,20} = 5.11$, $P < 0.05$) with consistently higher yields achieved in plots located at Silwood Bottom.

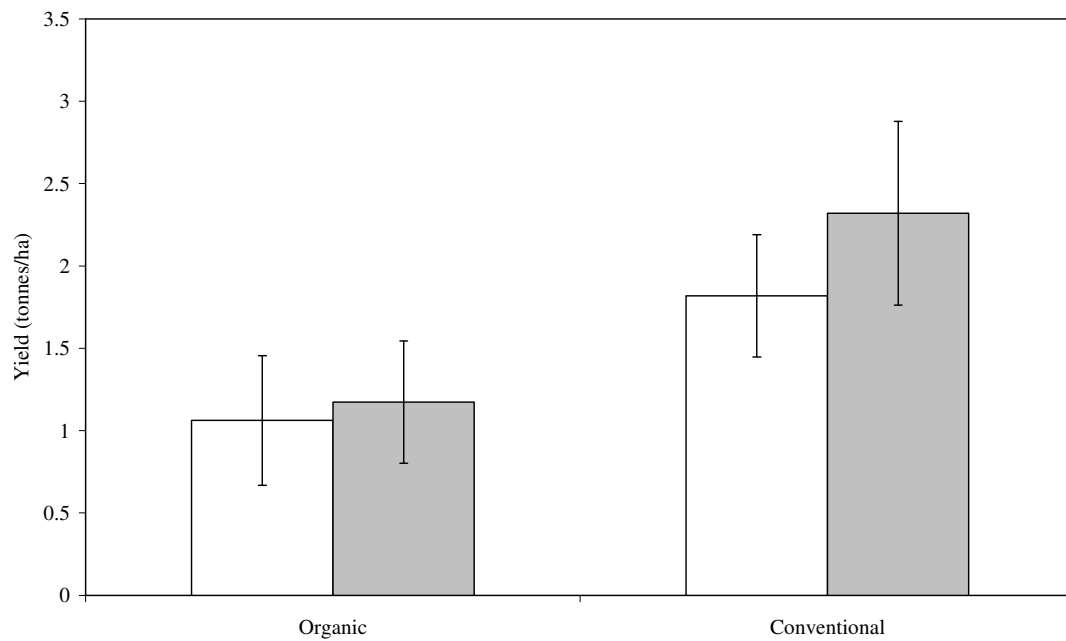


Fig. 3.4 Yield of barley in tonnes per hectare grown under organic and conventional fertiliser treatments at a high (■) and low (□) dose (mean \pm SEM).

Barley development occurred in parallel under all treatments with growth categories such as germination, awn appearance and inflorescence occurring at a similar time in all plots (Fig. 3.5). The non-linear nature of these growth categories makes it difficult to compare treatments statistically.

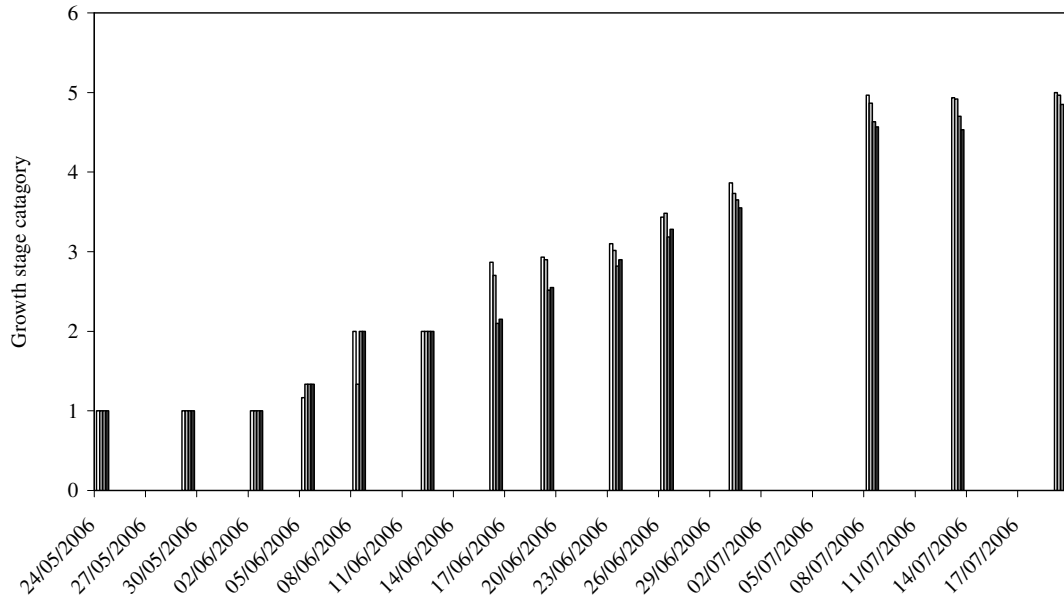


Fig. 3.5 Mean growth stage of barley grown under organic and conventional fertiliser treatments at a high and low dose. Conventional high (□), conventional low (○), organic high (■) and organic low (■).

3.4.2 Aphids

Three principal aphid species were identified on the barley crop during the two month barley field trial. *Metopolophium dirhodum* was by far the most common making up over 90% of all aphids counted with 1906 individuals recorded. Twenty-three *R. padi* and 96 *S. avenae* were identified whilst 71 individuals belonged to other aphid species.

Due to low numbers of other species, only data on *M. dirhodum* abundance is investigated for the remainder of this chapter. *Metopolophium dirhodum* populations in the barley field sites clearly change throughout the growing season (Fig. 3.6).

Mean aphid number per tiller increased steadily for 25 days following the first count on 24/5/2006, there was then a rapid population increase until the 23/6/2006 when the population crashed to almost no aphids present by the 19/7/2006, the final day of counting.

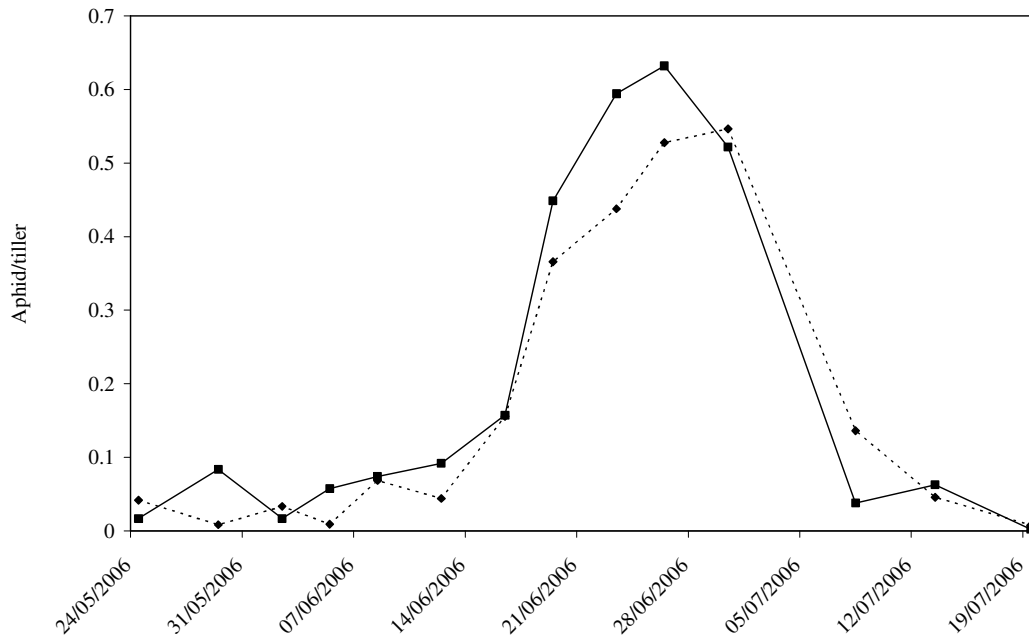


Fig. 3.6 Mean *Metopolophium dirhodum* per barley tiller grown under organic (dashed line) and conventional fertiliser (solid line) treatments.

Although numbers were greater under conventional fertiliser treatments at the population peak, there was no significant fertiliser type, dose or site effect on *M. dirhodum* aphid days per tiller (Type: $F_{1,22} = 0.37$, $P = 0.55$; Dose: $F_{1,22} < 0.05$, $P = 0.83$; Site: $F_{1,20} = 0.057$, $P = 0.81$) (Fig. 3.7a). When the mean number of *M. dirhodum* aphids days per plant was considered there were significantly greater numbers on conventionally fertilised plants (Type: $F_{1,21} = 10.09$, $P < 0.01$; Dose: $F_{1,21} = 0.76$) (Fig. 3.7b). A significant site effect was also found, with greater numbers of aphid days per plant at Silwood Bottom ($F_{1,20} = 6.12$, $P < 0.05$).

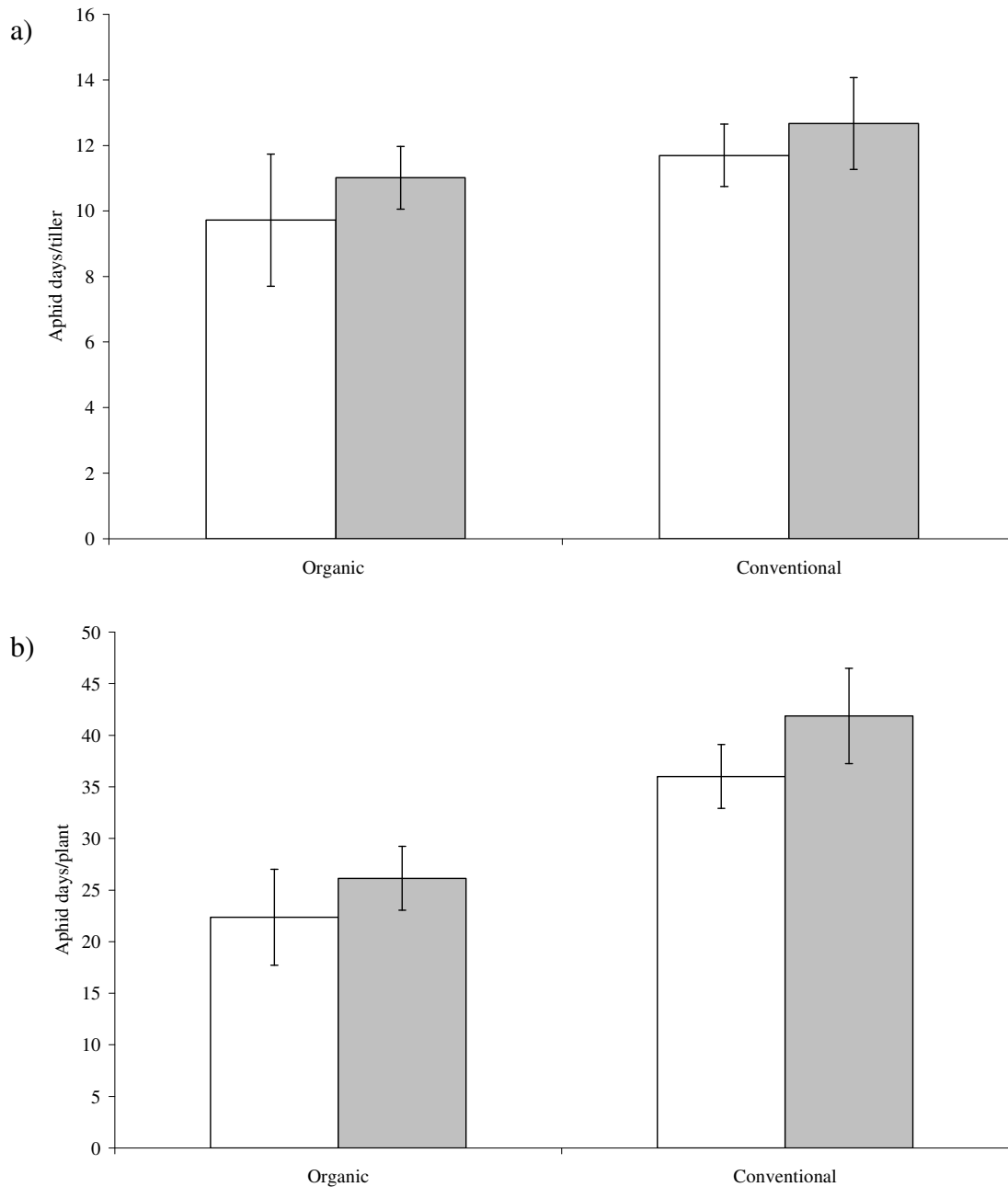


Fig. 3.7 *Metopolophium dirhodum* aphid days a) per tiller and b) per plant on barley grown under organic and conventional fertiliser treatments at a high (■) and low (□) dose (mean \pm SEM).

Metopolophium dirhodum aphid days per plant showed a significant positive correlation with the mean number of tillers in post tillering barley ($F_{1,22} = 34.80$, $P < 0.001$) (Fig. 3.8a) and there was also a significant positive correlation between *M. dirhodum* aphid days per plant and ear weight ($F_{1,22} = 14.57$, $P < 0.001$) (Fig. 3.8b).

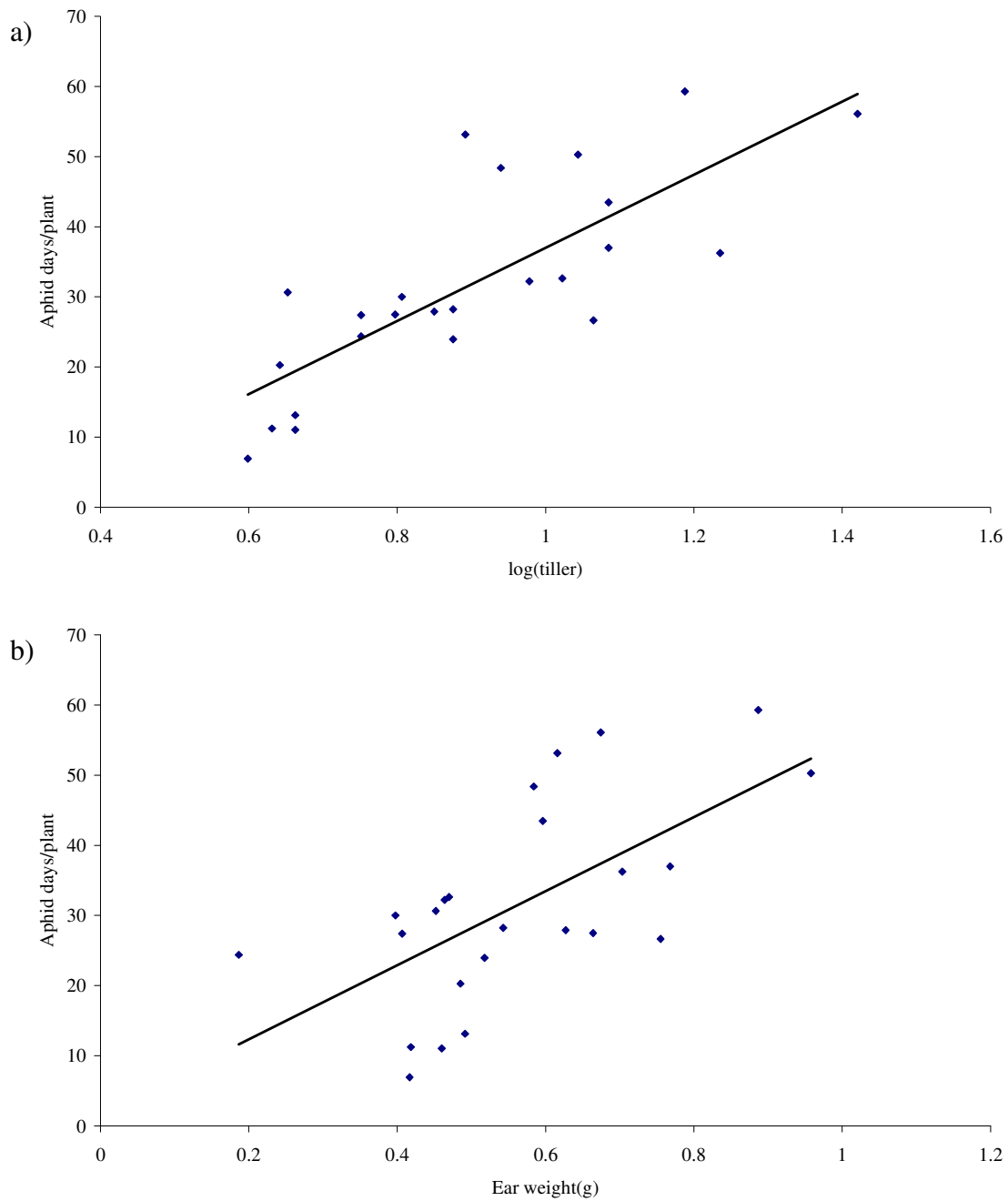


Fig. 3.8 Relationship between aphid days per plant, a) tiller number ($y = 52.10x - 15.12$, $R^2 = 0.61$) and b) ear weight ($y = 52.81x + 1.80$, $R^2 = 0.40$) of spring barley.

The numbers of alate *M. dirhodum* followed closely that of total *M. dirhodum* numbers found through the season (Fig. 3.9). There was however, no significant effect of either fertiliser type ($F_{1,22} = 0.03$, $P = 0.86$), dose ($F_{1,22} = 0.08$, $P = 0.78$) or site ($F_{1,20} = 1.83$ $P = 0.19$) on the cumulative number of alates per tiller.

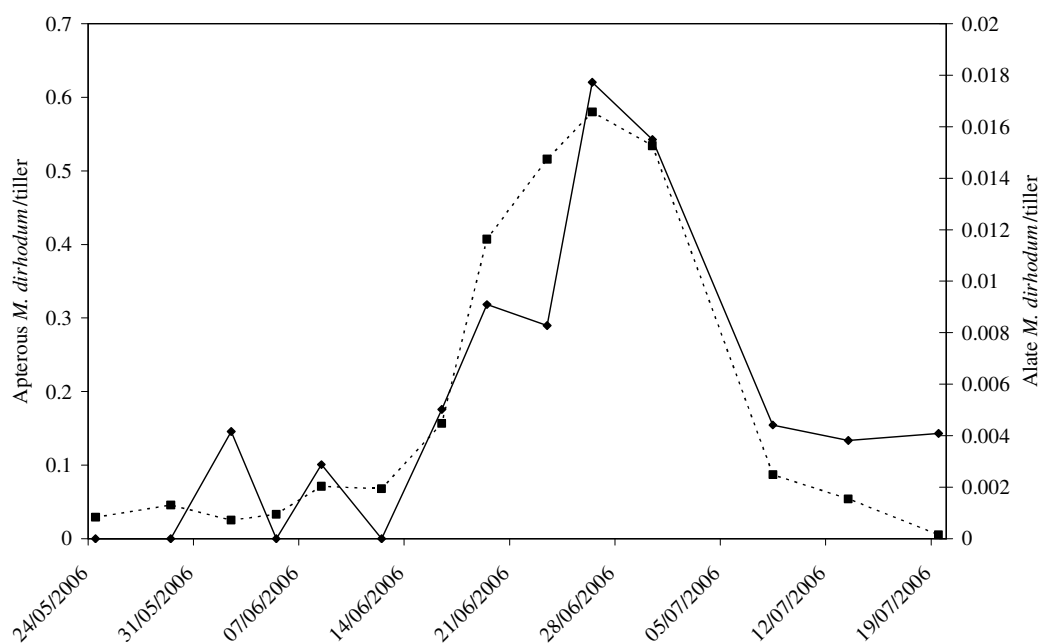


Fig. 3.9 Mean apterous (dashed line) and alate (solid line) *Metopolophium dirhodum* numbers per barley tiller.

On 10 of the 14 count days, more plants in the conventionally fertilised plots were infested by *M. dirhodum*. On 13/6/2006 (Type: $Z_{1,19} = 2.43$, $P < 0.05$; Dose: $Z_{1,19} = -0.84$, $P = 0.40$), 24/6/2006 (Type: $T_{1,20} = -2.998$, $P < 0.01$; Dose: $T_{1,20} = -2.52$, $P < 0.05$) and 27/6/2006 (Type: $T_{1,20} = -4.16$, $P < 0.001$; Dose: $T_{1,20} = -2.23$, $P < 0.05$) this difference was significant (Fig. 3.10). On these three count dates there was also a significant site effect, with Silwood Bottom showing greater levels of infestation (13/6/2006: $Z_{1,19} = -2.05$, $P < 0.05$; 24/6/2006: $T_{1,20} = -3.00$, $P < 0.01$; 27/6/2006: $T_{1,20} = -2.48$, $P < 0.05$). On 13/6/2006 there is a significant interaction between site and dose ($Z_{1,19} = -2.16$, $P < 0.05$).

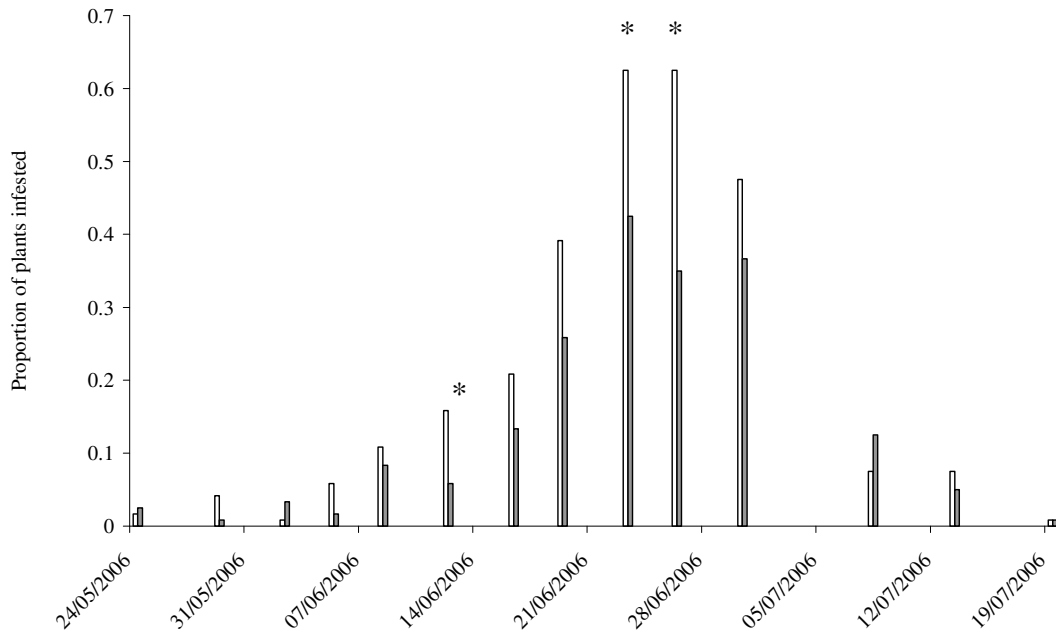


Fig. 3.10 Proportion of infested barley plants grown under organic (■) and conventional (□) fertiliser treatments at the 14 count dates. Pairs of bars with ‘*’ are significantly different ($P < 0.05$).

3.4.3 Parasitoids

There was no significant main treatment effects on the number of parasitoid mummies per tiller (Type: $F_{1,22} = 0.83$, $P = 0.37$; Dose: $F_{1,20} = 0.014$, $P = 0.91$; Site: $F_{1,19} = 0.24$, $P = 0.63$) although a significant dose:site interaction was found ($F_{1,19} = 7.10$, $P < 0.05$). When the total number of mummies counted per plot and the total number of aphids were compared, a significant, positive correlation was found ($F_{1,22} = 140.40$, $P < 0.01$) (Fig. 3.11).

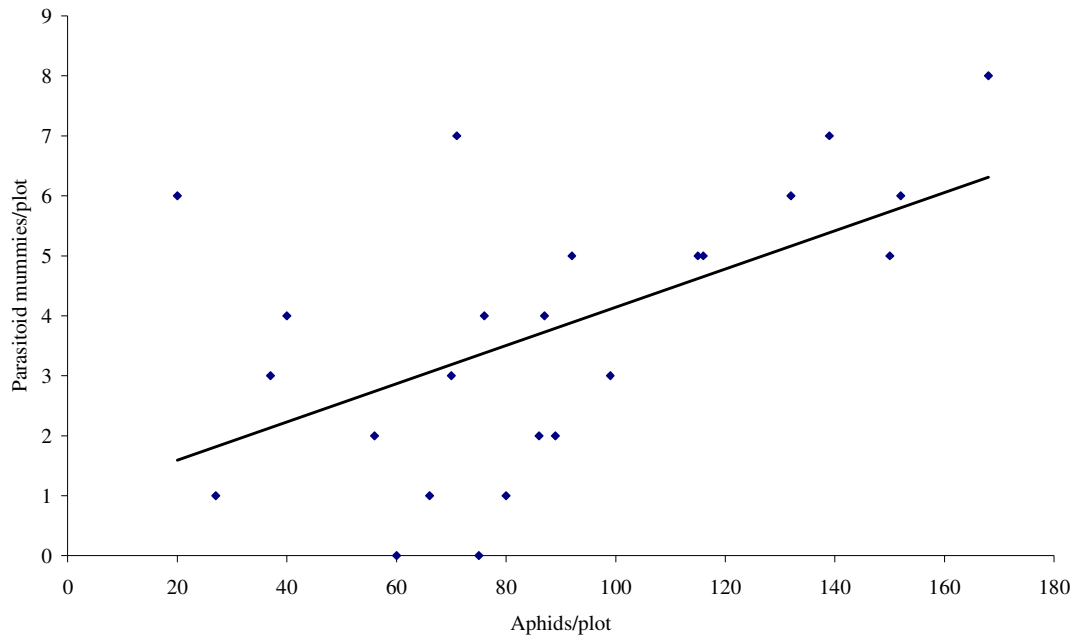


Fig. 3.11 Relationship between total aphid numbers and total parasitoid mummy number in all plots ($y = 0.03x + 0.96$, $R^2 = 0.86$).

3.5 Discussion

3.5.1 Barley

In the present study, barley ear weight, plant tiller number and subsequent yield in tonnes/ha were significantly greater in conventionally fertilised plots leading to the conclusion that barley plants benefit from the application of conventional fertiliser and are more vigorous when compared with plants fertilised with horse manure. Nitrogen losses can be as much as 25% following application of manure and composting is known to reduce the availability of mineral nitrogen (Dawson *et al.*, 2008). Conventional fertilisers on the other hand are associated with abundant mineral nutrients (Mengel *et al.*, 2006) and levels of ammonia are high immediately after application of conventional fertilisers (Gioacchini *et al.*, 2006). The lower levels of plant accessible nutrients such as ammonia (Sieling *et al.*, 2006) under organic treatments at the early stages of barley growth, when the majority of nitrogen is absorbed by the plant (Montemurro *et al.*, 2006), may have resulted in the lower plant yields.

In the present field trial, tiller numbers and ear weights were higher in plots receiving high doses of organic and conventional fertilisers when compared with low doses of each of the fertiliser types, although this relationship was not significant. 180 kg and 90 kg of nitrogen are both relatively high doses to apply to sandy soils and would be recommended only if the 'Soil Nitrogen Supply Index' were at the lower end of the scale (DEFRA, 2000). Conventionally fertilised plots may have been nearly saturated with nitrogen at the low dose and consequently no significant increase in plant yield above this dose was recorded.

Tiller numbers and ear weights were higher in the field plot located in Silwood Bottom. This probably reflects the higher soil nitrogen, phosphorous and potassium found at this site (Table 3.1). Nitrogen, phosphorous and potassium are all important for plant growth. Nitrogen is the most important nutrients for yield (Mengel *et al.*, 2006), phosphorous improves root growth (Kristoffersen *et al.*, 2005) and potassium also impacts positively on yield (Jouany *et al.*, 1996).

Plant developmental rate was apparently unaffected by treatment in this field trial. This contradicts findings by Helenius (1990) who found that organically fertilised barley developed more slowly than conventionally fertilised plants and this was attributed to nutrient stress under the organic treatment. Nitrogen application can also slow plant development in some cases (Hasken and Poehling, 1995). In the present trial, nutritional stress due to excessive or inadequate macronutrients may not have been experienced by barley plants, so no effect on development rate was apparent.

3.5.2 Aphids

Metopolophium dirhodum numbers per plant were found to be significantly greater in conventionally fertilised plots of barley and aphid numbers correlated positively with plant tiller number and ear weight. The 'plant vigour hypothesis' (Price, 1991) predicts positive associations between insect pest performance and plant vigour. This theory is supported by work on *Agromyza nigripes* on *Holcus lanatus* (Bruyn *et al.*, 2002). Aphids have also been observed performing better on more vigorous

unstressed tomato plants (Inbar *et al.*, 2001) and *M. dirhodum* were more abundant on more vigorous chlorophyll rich plants (Honek and Martinkova, 2002).

An alternative to the plant vigour hypothesis is the ‘plant stress hypothesis’ proposed by White (1969) as a potential ecological generalisation. The theory states that herbivores are more successful on less vigorous or more stressed plants due in part to an increased availability of nitrogenous compounds (White, 1984). Stressed plants are also less able to produce defence chemicals making them more suitable for herbivores (Koricheva and Larsson, 1998). Clearly there is some contradiction when considering the effects of plant health or vigour on insect herbivores with evidence supporting both theories (Price, 1991; Koricheva and Larsson, 1998).

The results from the present study conform to the plant vigour hypothesis given that increased numbers of aphids were found on more vigorous plants in this trial. Analogous results were found by Honek (1991b) following experiments on wheat and barley grown with different levels of conventional nitrogen fertiliser. Honek (1991b) concluded that the higher *M. dirhodum* populations found following high doses of fertiliser was a response to greater resource allocation to leaf material and above ground biomass shown by barley receiving high doses of fertiliser. Similar conclusions were made by Helenius (1990) who found organically fertilised barley supported far fewer *R. padi* due to reduced leaf area, reduced above ground biomass and retarded growth when compared with conventionally fertilised plants.

Given that the number of aphid days per tiller was not significantly affected by fertiliser treatment and the highly positive correlation between aphids per plant and tiller number, the increased scouting of a larger habitat area created by the higher number of tillers may have resulted in the higher aphid numbers encountered in the conventionally fertilised plots. However, considering the equal seed density in organically and conventionally fertilised plots, the number of aphids per unit area of field will still have been greater in conventional plots.

There was a significant site effect on *M. dirhodum* aphid days per plant; numbers were higher in Silwood Bottom. This could be a result of the increased tiller numbers and ear weights found in Silwood Bottom resulting in greater aphid numbers but there

may also be spatial variation in aphid distribution between the two field sites. The habitat surrounding Silwood Bottom may have increased aphid numbers on a landscape scale; landscape heterogeneity is known to influence aphid abundance (Ostman *et al.*, 2001).

The greater number of aphids on conventionally fertilised plants could be a result of increased plant vigour, resulting in improved nutritional quality of host plants or simply an increase in the amount of plant material scouted in conventionally fertilised plots. Another explanation could be that aphids are preferentially landing on conventionally fertilised plants.

There was no difference in the number of *M. dirhodum* alates found between treatments during this study, this is surprising considering the number of host location cues used by aphids and the potential for fertiliser to influence these cues. Aphids are known to select suitable host plants using visual stimuli (Powell *et al.*, 2006) and *Myzus persicae* and *B. brassicae* have been shown to alight preferentially on plants emitting a higher long/short wavelength ratio (Schoonhoven *et al.*, 2005). Many cereal aphids show a preference for yellow colours (Havlickova and Smetankova, 1998; Doring and Chittka, 2007). Olfactory cues including green leaf volatiles, alkanes and terpenoids are also known to play a role in host location (Pickett *et al.*, 1992) and when *R. padi* spring migrants feed on cereals a volatile is released which attracts other migrating individuals promoting aggregation (Pettersson *et al.*, 1994). Host selection to maximize offspring performance has been demonstrated in *R. padi* with preference shown for healthy trees as an oviposition site (Leather, 1986). Alate and apterous aphids vary in their response to certain plant volatiles reflecting the different requirements of each morph in the life history of aphids (Quiroz and Niemeyer, 1998). Fertiliser can affect chlorophyll content and leaf colour (Fox *et al.*, 1994) and potentially plant volatile profile. It is reasonable to assume then that an effect of fertiliser on host selection is probable.

The short lifespan of migrant aphids following deposition of young nymphs or fast take-off following laying may be the reason there was no difference in the number of *M. dirhodum* alates found between treatments during this study. Indeed, alate numbers appear to correlate directly with apterous numbers, suggesting that many of

the alates found developed on the barley and were induced by plant growth stage, nutrition or aphid crowding (Holst and Ruggle, 1997), rather than alighting from the wider environment. Number of alates would then not represent any form of preference by *M. dirhodum* for barley grown under particular fertiliser treatments. The low density of aphids makes the crowding stimulus on alate production unlikely in this case so the effect of crowding can probably be disregarded.

Another proxy for aphid preference may be the number of separate colonies, in this case infested plants, which are found in a particular plot. A high number of colonies might reflect a greater number of founding aphids landing and reproducing in one plot more than another suggesting some form of preference. This was the case for this field trial with significantly more separate *M. dirhodum* colonies, reflected by incidence counts in conventionally fertilised plots. Alates might be preferentially depositing nymphs on barley with a more suitable nutritional content (Leather, 1986) or plants producing a preferred volatile profile (Pickett *et al.*, 1992), possibly determined by fertiliser application.

Caution must be taken when using colony number as an indicator of selective preference because density mechanisms mediated by aphid produced chemicals are known to cause non-settled individuals to move and locate new hosts (Ninkovic *et al.*, 2003). This would result in a large number of plant colonisations simply because neighbouring plants were becoming crowded. This situation of local colonisation would occur under one treatment more than another if that treatment, in this case conventional fertiliser, increased the reproductive rate of the aphid population by promoting favourable plant nutrition. Nonetheless, the peak number of aphids per plant reached a mean of little over 2.5 aphids in this field trial with numbers per plant rarely in excess of 10 and never above 16 aphids per plant; well below a density where crowding effects might be expected and dispersal on foot would occur. Incidence counts should thus be an accurate proxy of aphid preference.

3.5.3 Parasitoids

Increased abundance of natural enemies in low intensity or organic agriculture has been found (Bengtsson *et al.*, 2005) and this includes parasitoids (Drinkwater *et al.*, 1995; Berry *et al.*, 1996; Ostman *et al.*, 2001). Which aspects of farming practice are contributing to this improved biocontrol is less clear.

Parasitoids use semiochemical and physical cues to locate hosts including plant volatiles and host semiochemicals (Powell *et al.*, 1998; Schworer and Volkl, 2001; Kalule and Wright, 2004). The link between plant nitrogen and parasitoid performance mediated through the host has been demonstrated in a number of experiments (Kaneshiro and Johnson, 1995; Wurst and Jones, 2003; Jiang and Schulthess, 2005; Krauss *et al.*, 2007). Thus, increased nutrient availability following conventional fertiliser application might influence the impact of parasitoids in the current field trial.

The results from the present study showed no evidence that fertiliser affected parasitoid abundance or impact. This was reflected by the insignificant effects of fertiliser on mummy numbers per tiller. Drawing conclusions on parasitoid impact or determining percentage parasitism from field counts of mummy numbers can be misleading (Driesche *et al.*, 1991). A truer percentage parasitism estimate would be achieved by collecting and rearing a portion of the aphid field population (Sigsgaard, 2002; Lumbierres *et al.*, 2007).

Parasitoid mummy numbers correlated with aphid populations. This pattern is indicative of density dependent levels of parasitism and similar parasitoid population distributions were found by Karungi (2006a) and Pareja *et al.* (2007). Parasitoids are commonly attracted to plant-aphid volatiles (Takabayashi *et al.*, 1998) and have been shown to preferentially forage on damaged plants (Powell *et al.*, 1998). This would explain why more aphid mummies were found in plots where higher aphid numbers were encountered. The low numbers of parasitoids encountered however, makes it difficult to draw conclusions on fertiliser effects on parasitism.

3.6 Conclusion

Due to the different nutrient dynamics of organic and conventional fertilisers, barley tiller number, ear weight and subsequent yield per hectare were significantly greater following conventional fertilisation. Much of the nutrients in horse manure may not have been available to the plant in the immediate growing season and often nutrients from manure is utilised during the season after initial application (Sieling *et al.*, 2006). Moreover, modern varieties of cereal are bred for rapid uptake and utilisation of soil nutrients, so the slow release nature of horse manure may deem it an unsuitable alternative fertiliser for cereal production, at least in the immediate season.

Whether through increased aphid developmental rate, preferential selection by alates or simply larger available habitat, the increased aphid number on conventionally fertilised plants found in this trial appear to be mediated through fertiliser effects on plant tiller number and ear weight. If tiller number and ear weight are considered proxies of plant vigour then the results from this experiment agree with the plant vigour hypothesis (Price, 1991). Despite higher aphid numbers per tiller in conventionally fertilised plots at the peak aphid populations, this difference was not significant with respect to *M. dirhodum*. Aphid control damage thresholds refer to aphids per tiller (Oakley and Walters, 1994; Larsson, 2005) and so impact on yield at least with regards to *M. dirhodum* was not significantly higher in conventional plots. Fertiliser effects on aphid populations may only become apparent when aphid populations are high and close to the damage threshold which is 15 aphids per tiller for *M. dirhodum* (Oakley and Walters, 1994). In other studies, significant fertiliser effects on cereal aphid abundance have only been found in years when aphids were numerous (Gash *et al.*, 1996; Duffield *et al.*, 1997).

Parasitism was low in this field trial so conclusions are difficult. Parasitoid mummy numbers, however, did correlate with aphid numbers but was seemingly unaffected by fertiliser treatment.

This field trial demonstrates that fertiliser has a role to play in determining the number of aphid pests found in organic and conventional cereal farming systems and may go

some way to explaining why organic cereal farms are often found to suffer from fewer aphid pests (Helenius, 1990; Ostman *et al.*, 2001; Roschewitz *et al.*, 2005).

Nevertheless, if yield per unit area is the measurement by which a farmer is judged, the benefits of conventional fertiliser on cereal growth cannot be denied. This field trial is valuable because there is a clear lack of field scale experiments comparing slow release and conventional fertilisers.

Chapter 4

The effects of organic and conventional fertilisers on cereal aphids and their natural enemies in a semi-field trial

4.1 Introduction

Aphids are major pest of cereals in Britain (Carter *et al.*, 1980). The most harmful to spring sown cereals include the rose-grain aphid, *M. dirhodum* (Mann *et al.*, 1997), grain aphid, *S. avenae* (Larsson, 2005) and the bird-cherry oat aphid, *R. padi* (Leather *et al.*, 1989). All cause direct feeding damage (Watt and Wratten, 1984; Duffield *et al.*, 1997; Larsson, 2005; Riedell *et al.*, 2007) and are known virus vectors, particularly for the damaging Barley Yellow Dwarf Virus (Mann *et al.*, 1997).

Fertiliser application can affect aphid populations by altering host plant quality. Nitrogen application influences barley morphology, increasing vegetative growth and crop density and this has been found to result in higher *M. dirhodum* populations (Honek, 1991b). Variations in the number of *R. padi* on barley has also been attributed to fertiliser effects on stand characteristics (Helenius, 1990). Fertilisers can also influence the nutrient quality of plants for aphid pests by altering the amino acid composition of phloem sap. Nitrogen application improved the quality of barley phloem sap for *R. padi* (Weibull, 1987), but conversely, application of potassium reduced phloem quality for the soybean aphid (Walter and DiFonzo, 2007). Furthermore, fertiliser application can affect plant resistance to aphids by altering concentrations of important secondary metabolites such as gramine and indole alkaloids in barley (Salas *et al.*, 1990).

As well as affecting host nutritional quality and aphid population growth, fertilisers may also influence aphid host location and preference. Aphid pre-alighting behaviour is determined by a photo-tactic response with landing behaviour modified by plant volatiles (Pickett *et al.*, 1992; Powell *et al.*, 2006). Colour, determined by the spectral reflectance of light, is influential in aphid landing even when non-plant material such as coloured water traps are used (Doring *et al.*, 2008). The co-evolution theory, that the bright colours displayed by deciduous trees in Autumn are there to warn potential parasites of the poor quality of the host due to investment in defence chemicals (Archetti and Brown, 2004), is dependent on colour perception and preference by tree pests. Aphids, including the autumn migrants of the cereal aphids, are pests of many trees which they use as a primary hosts. *Rhopalosiphum padi* is postulated to prefer more suitable *Prunus padus* trees owing to their green leaf colour (Archetti and Leather, 2005). Mineral fertilisation of winter wheat significantly affects plant nitrogen concentration, which in turn correlates with leaf chlorophyll measurements (Fox *et al.*, 1994; Montemurro *et al.*, 2006). The amount of leaf chlorophyll will determine leaf colour and therefore may have an effect on aphid host location and subsequent populations.

Olfactory cues including green leaf volatiles, alkanes and terpenoids have been shown to be important in aphid host location (Pickett *et al.*, 1992) with green leaf volatiles and aldehydes particularly important to alate morphs of the cereal aphid *R. padi* (Quiroz and Niemeyer, 1998). An effect of fertiliser on cereal plant volatiles could influence aphid host selection. Fertiliser regime can also influence cereal development (Helenius, 1990) with nitrogen application sometimes associated with slowed plant maturation (Hasken and Poehling, 1995). *Sitobion avenae* preferentially lands on older wheat plants (Walters and Dixon, 1982) whilst *R. padi* settled more readily on younger oat leaves (Leather *et al.*, 1989). An indirect effect of fertiliser, mediated through effects on plant development, on host preference could be hypothesised.

Whether through influences on host location, selection or performance once alighted; conventional fertiliser application and particularly nitrogen can result in larger cereal aphid populations (Honek, 1991b; Hasken and Poehling, 1995; Gash *et al.*, 1996; Duffield *et al.*, 1997). Organic and conventionally fertilised soils are very different in

terms of their nitrogen availability, soil micro-nutrients and soil chemistry and biology (Sieling *et al.*, 2006; Courtney and Mullen, 2008; Dawson *et al.*, 2008). Thus, corresponding effects of organic and conventional fertilisers on aphid colonisation and abundance is likely. Cereal aphid populations in organic and conventional systems are variable (Moreby *et al.*, 1994; Ostman *et al.*, 2001; Roschewitz *et al.*, 2005; Poveda *et al.*, 2006) and few studies exist where fertiliser effects on aphids in the field, independent of other management practices, are tested (Helenius, 1990; Bado *et al.*, 2002).

Parasitoids are important natural enemies of cereal aphids and this has been demonstrated in the field (Dean *et al.*, 1981; Sigsgaard, 2002; Schmidt *et al.*, 2003; Lumbierres *et al.*, 2007) and laboratory cage experiments (Fuentes-Contreras and Niemeyer, 2000). Simulation modelling has also shown parasitoids can be effective at suppressing populations of *M. dirhodum*, *R. padi* and *S. avenae*, provided parasitoid numbers are high early in the season (Holst and Ruggle, 1997). Cereal aphid parasitoids found in Europe include *Aphidius ervi*, *Aphidius rhopalosiphii*, *Aphidius matricariae*, *Diaretiella rapae* and *Praon volucre* (Lumbierres *et al.*, 2007), with *A. ervi* and *A. rhopalosiphii* of particular importance (Sigsgaard, 2002). Exclusion experiments have demonstrated the importance of other cereal aphid natural enemies including aerially dispersing coccinellids, syrphids and midges and terrestrial polyphagous predators such as spiders (Schmidt *et al.*, 2003). The impact of terrestrial predators including carabids and staphylinids however, was dependent on aphid colony proximity to suitable alternative habitats (Collins *et al.*, 2002).

Fertiliser application can have a multi-trophic effect and influence natural enemies. Numbers of *A. rhopalosiphii* (Krauss *et al.*, 2007), development of *Chrysocharis oscinidis* (Kaneshiro and Johnson, 1995) and the egg load of *Cotesia flavipes* (Jiang and Schulthess, 2005) were all affected following application of fertilisers. Effects of fertiliser on other natural enemies have also been found, including coccinellids (Morales *et al.*, 2001), syrphids and spiders (Karungi *et al.*, 2006a). Natural enemies are often found to be more abundant in low input or organic systems (Bengtsson *et al.*, 2005; Hole *et al.*, 2005; Attwood *et al.*, 2008), but the extent to which this is influenced by fertiliser regime, independent of other management practices, is unknown.

4.2 Aims and objectives

Fertilisers can affect plants in numerous ways and these effects can influence higher trophic levels. The present experiment aimed to investigate how different fertiliser treatments affect the morphological characteristics of barley and how differences in these characteristics then influence populations of pests and natural enemies.

The objectives of this experiment were to 1) investigate the effects of organic slow release and conventional fertilisers on barley growth characteristics including yield, morphology and leaf colour. 2) The indirect effects of these fertilisers, mediated through effects on the plant host, on naturally occurring cereal aphids populations was investigated. 3) Finally, the abundance of different natural enemies with respect to fertiliser applications was also studied.

4.3 Materials and methods

4.3.1 Field sites and farming practice

The field trial took place in the summer of 2007 and 2008 at two field plots, Silwood Bottom and Four Acre Field, located at Silwood Park, Berkshire (see Table 3.1 for soil physical and chemical characteristics). An initial field trial was attempted that was comparable to the 2006 experiment (Chapter 3) varying only in plot size and fertiliser treatments. However, due to very dry conditions in April and considerable pest pressure, the barley crop failed to establish. To overcome pest and soil moisture problems an alternative experiment was setup, one which involved large pots placed in the field. Pots with a 10 litre capacity were filled with field soil and 80 spring barley seeds were hand planted evenly in each pot. Pots were individually surrounded by chicken wire to prevent access by birds and rabbits (Fig. 4.1) and slug pellets (Metaldehyde) were applied to each pot after planting. Barley was then allowed to grow under natural conditions and was watered only after extended periods

without rain. Twice through the growing season pots were hand weeded, once prior to tillering and again during stem elongation.



Fig. 4.1 Individual pot from the 2008 field trial from Silwood Bottom.

In 2007, barley seeds (cv. Doyen) were planted on the 24/5 and 25/5. Five fertiliser treatments were involved and each was replicated eight times, four times in each field site. Pots were placed in a five by four grid with 10 m spacing between pots in each of the field sites. This spacing was used because pots were placed in the centre of larger plots of barley, plots which were setup as part of an initial field trial attempt which subsequently failed to establish. Fertiliser treatments were randomly assigned to each pot using a semi-Latin square design to eliminate climatic and spatial variation.

Barley seed planting took place on 10/4 and 11/4 in 2008 and seven fertiliser treatments were involved. Each treatment was replicated 12 times and again replicates were split evenly between the two field sites, Silwood Bottom and Four Acre Field. Pots were laid out in a six by seven grid with 0.5 m spacing between pots (Fig. 4.2). As with the 2007 trial, fertiliser treatments were randomly assigned to each pot using a semi-randomised Latin-square design. Each treatment occurred once in each of the six rows within each field site.



Fig. 4.2 Field pot layout for season 2008 in Four Acre Field.

4.3.2 Fertiliser treatments

In 2007, five fertiliser treatments were applied to field pots, two organic, two conventional and a control. The first organic treatment was chicken manure pellets containing nitrogen, phosphorus and potassium and was supplied by ‘Greenvale, North Yorkshire’. The second organic fertiliser was hoof and horn meal supplied by ‘Monro Horticulture, Goodwood, West Sussex’ which contained only nitrogen. With the application of ammonium nitrate (Terranitram), potassium sulphate and super phosphate, two conventional fertiliser treatments were established to match the total nutrients input supplied by the two organic fertilisers. Finally, the control treatment involved the addition of no fertilisers. All fertiliser treatments were matched with regards to the amount of nitrogen added to the pot, which was the equivalent to 100 kg per hectare. The amount of phosphorus and potassium were also matched for the chicken manure and conventional(cm) treatments, 67 kg per hectare of both phosphorus and potassium were applied. The hoof and horn fertiliser treatment was applied as a ‘base’ dressing at the time of seed planting. All other fertiliser treatments were ‘top’ dressed when barley was at the two leaf stage (GS12) (Table 4.2).

Seven fertiliser treatments were used in 2008; these included the five fertiliser treatments involved in 2007 replicated exactly plus two new treatments. One was chicken manure which was ‘base’ dressed at the time of planting and the other was a ‘top’ dressing of hoof and horn meal at the two leaf stage. As in 2007, all nutrient application was matched for corresponding treatments (Table 4.2).

Table 4.2 The percentage nutrient content of fertilisers used, the amount of nitrogen, phosphorus and potassium added under each treatment and the mass of fertiliser required to supply these nutrient doses. The year each treatment was used and the timing of fertiliser application are also shown.

Treatment	2007	2008	Application method	% content	Active ingredient (g)			Mass of fertiliser added (g)
					N:P:K	N	P	
Control	+	+	-	0:0:0	0	0	0	0
Chicken manure (seed)		+	Base	4.5:3:3	2	1.3	1.3	44
Chicken manure (two-leaf)	+	+	Top	4.5:3:3	2	1.3	1.3	44
Hoof and horn (seed)	+	+	Base	13:0:0	2	0	0	15
Hoof and horn (two-leaf)		+	Top	13:0:0	2	0	0	15
Conventional(cm)	+	+	Top	34.5:18:48	2	1.3	1.3	N – 6 P – 7.2 K – 2.7
Conventional(hh)	+	+	Top	34.5:0:0	2	0	0	N – 6 P – 0 K – 0

4.3.3 Aphid survey

Regular aphid counts were made throughout the growing seasons. A count involved randomly selecting a pre-determined number of individual barley plants within each pot and recording the number and species of all aphids on that plant, whether the aphid was apterous or alate was noted. Plants were selected using a 0.5 m transect marked at regular intervals depending on how many plants were being selected. The transect was randomly orientated across the pot and the plants nearest the regular marks on the transect were selected for the count. When all the plants along the transect had been examined the transect was reoriented by 90° and another series of counts was made. This second transect orientation was only carried out when 10 plants were being examined. The field site and pot where the count began were selected randomly on each count date.

In 2007, 10 separate counts were made, starting on 11/6 and ending on 07/08. The first four counts involved scouting every plant in each pot. For subsequent counts the number of plants scouted was dropped to 10 and then seven and five randomly selected plants in each pot because older plants are more labour intensive to scout for aphids. Eight counts were made in 2008 between 7/5 and 23/6. For all counts in 2008, 10 plants were randomly selected from each pot.

4.3.4 Natural enemy survey

For every plant involved in the aphid count, the number of natural enemies was recorded. In 2007, the number of parasitoid mummies was recorded. In 2008, in addition to recording mummy numbers, syrphid larvae and pupae and coccinellid larvae were counted. Parasitoid mummies were recorded throughout the season and syrphid and coccinellid numbers were taken from 10/6/2008 onwards, this incorporated peak syrphid and coccinellid abundance.

4.3.5 Plant and yield measurements

The tiller number and development stage of all plants involved in the aphid and natural enemy counts was recorded. Barley development stage was scored according to the decimal scale established by Tottman and Broad (1987). At the end of the growing season when barley plants had ripened in the field a yield measure per pot was taken.

Yield measurement involved removing all ears from barley plants in each pot and drying them for 48 h in a 60°C oven. Given that each pot had a surface area of 0.2 m², multiplying the total ear weight from one pot by 50,000 gave a relative yield per hectare. In addition to a yield count, final plant biomass was recorded. This involved randomly selecting three plants from each pot at the time of yield collection, removing roots and all above ground material and drying in an oven at 60°C for 48 h. Once the plant material was dry, the ears, tillers and roots were separated and weighed. A mean plant ear, tiller and root dry mass was established per pot by averaging data from the three plants collected per pot.

In 2008, additional plant recordings were made. On four dates during the season (22/5, 4/6, 23/6 and 17/7) five random leaf samples were collected from each pot, with only the second leaves down from the primary leaf taken. This leaf was chosen because it enabled consistent comparisons between plants and this leaf was fully developed. The length and mid point width of each of these leaves were recorded. By multiplying the leaf length and mid-leaf width, an estimate of total leaf area was established. The colour of two, randomly selected, leaves from each pot was measured using a photo-spectrometer. This provided a percentage reflectance at wavelengths between 300 and 700 nm for each leaf sample. From the reflectance data a relative aphid attractivity value could be established based on the model developed by Doring *et al.* (2008). The model uses the ratio of blue, green and UV light reflected by a sample to determine its attractivity to aphids. The model is considered to be appropriate for most aphid species and given that the model was based on aphid catch data for which *R. padi* was the most numerous, its relevance to the cereal aphids involved in this study is high.

4.3.6 Statistical analysis

Fertiliser treatment, site and row effects on barley yield, tiller number, individual ear mass, plant ear mass, stem mass, root mass and leaf areas were analysed using ANOVA. Data from 2007 and 2008 were analysed separately. Fertiliser treatment, site and row effects were included in the models as main effects with the addition of a treatment:block interaction. F and P values as well as the corresponding degrees of freedom for site and row effects were taken from the model containing all main effects, the model was then simplified removing all non-significant factors to determine F and P values for fertiliser treatment effects. In the cases where a significant fertiliser effect was found, significant differences between treatment means were determined using a Tukey honest significant difference test. Additional analysis of data was carried out where fertiliser treatments were logically grouped. The first model involved grouping fertilisers as conventional, organic or controls. A second model involved grouping treatment based on when the fertiliser was applied, either as a top dressing, a base dressing or control, which involved the addition of no fertiliser. Again ANOVA followed by a Tukey test was carried out.

In order that data was normally distributed, data on tiller numbers from 2007 and 2008 was log transformed before analysis, root mass from plants grown in 2007 and 2008 was also log transformed. In addition, both stem weight and individual plant yield was log transformed prior to analysis of the 2008 data. Decisions on transformations were based on graphical examination of the data and the BoxCox test (Crawley, 2007). Model diagnostic plots were also used to confirm the suitability of appropriate transformations.

The significance of collection date on mean barley leaf attractivity was tested using an ANOVA. The initial model included fertiliser treatment, site and date effects and all their interactions, row effects were also included in the model. The difference between mean attractivity on each count date was tested using a Tukey test. To determine fertiliser treatment effects on leaf attractivity, each collection date was analysed separately. As with previous models examining barley growth and yield, site and row effects were included in the model. Similarly, fertiliser treatments were grouped by fertiliser type and application timing in additional models. Once again differences between treatment means were examined using a Tukey test. Leaf attractivity is a bounded proportional response, with an attractivity index of 1 equating to maximal attractivity and 0 representing no attractivity, accordingly attractivity index was arcsine transformed prior to analysis.

To examine the effect of fertiliser treatment on aphid populations, aphid days per tiller was used as a response. One aphid day per tiller represents the presence of one aphid on one tiller for one day (Hansen, 2000). The three most abundant aphid species were analysed separately and then all aphid numbers were combined to look at total aphid days per tiller. ANOVA models were used to determine treatment effects on aphid days and once again site and row effects were included in the model. Following initial analysis of fertiliser treatment effects, fertiliser grouping was carried out as before. Initial inspection of the data revealed aphid day responses were not normally distributed. The BoxCox (Crawley, 2007) test in conjunction with graphical examination of data distribution using histograms was used to select the most appropriate transformation for the data. In 2008, *M. dirhodum*, *R. padi* and total aphids days were square root transformed. *Sitobion avenae* aphid days was log +0.1 transformed. For 2007 data, the aphid days per tiller for the three species considered

separately were log+0.01 transformed. When all the aphids counted were considered together a log transformation was most appropriate.

The effect of fertiliser treatment on alate numbers was tested using an ANOVA, structured the same way as previous models. Alate numbers per tiller were very low and so the number of alates per tiller was accumulated over the season to create the response, cumulative alates per tiller, which was then used as the response variable for the analysis.

The correlation between barley biomass allocation and aphid numbers per unit biomass of plant material was tested using linear regression analyses. The response, aphid days per gram, was established by dividing the number of aphid days calculated per plant in each pot by the mean total plant biomass found for plants at the end of the season in the corresponding pot. The proportion of above ground biomass allocated to vegetative growth was then established as the proportion of the combined stem and ear weight made up by stem and leaf material for each plant. This proportion was arcsine transformed before analysis. In 2007, both *M. dirhodum* and *S. avenae* aphid days per gram data were log +0.1 transformed and *R. padi* was log +0.01 transformed. *Metopolophium dirhodum* data was square root transformed in 2008 whilst *S. avenae* was log+0.1 transformed and *R. padi* was log+1 transformed. Transformation decisions were made according to the BoxCox test and visual interpretation of data distribution. Model diagnostic plots were used to confirm appropriate transformations.

Treatment effects on parasitoid mummy numbers were tested using ANOVA involving the same treatment variables and model simplification as for aphid and plant data. The parasitoid response was an accumulated mummy number per tiller through the season. In both 2007 and 2008, this response was log +0.01 transformed. Linear regression analysis was carried out to examine the correlation between aphid numbers and parasitoid mummy numbers. For this analysis both aphid and mummy numbers per tiller were accumulated. Zero parasitoid mummy counts were removed from the data set prior to analysis so both variables became normally distributed following transformation. In 2007 and 2008, accumulative mummy numbers were log transformed and in 2007 aphid numbers were also log transformed. In 2008, aphid numbers required no transformation.

The same ANOVA model used in previous analysis was used to examine the effects of treatment and treatment groups on per tiller numbers of syrphid eggs, syrphid larvae and pupae. Both syrphid response vectors were log +0.1 transformed prior to analysis. To examine the correlation between transformed egg, larvae and pupae data and aphid numbers, linear regressions were carried out. Prior to analysis the aphid days per tiller variable was square root transformed. All statistical analyses were carried out on 'R' version 2.7.1 (Ihaka and Gentleman, 1996).

4.4 Results

4.4.1 Barley

4.4.1.1 Barley yield

In 2007 and 2008 the effect of fertiliser treatment on yield was significant (Tables 4.3 & 4.4). In 2007 the conventional(hh) treatment produced significantly greater yields than the control and chicken manure fertilised pots. In 2008, both hoof and horn treatments and the conventional treatments produced significantly larger yields than the control. Following grouping of the fertiliser treatments, conventionally fertilised pots produced larger yields than the controls in 2007 and 2008. In 2008, the organic yields were also significantly larger than the control but significantly lower than the conventional treatments. A significant effect of timing was found in 2008 with both seed and top dressed treatments producing greater yields than the control. A significant site effect on yield was found in 2008, with yield significantly greater in Silwood Bottom than those achieved in Four Acre Field.

Table 4.3 Effect of fertiliser treatment on barley growth and yield in 2007. Results for individual fertiliser treatments and treatments grouped by fertiliser type and application timing are given. Row and site effects are also shown. Means are displayed \pm SEM. Means within each column with different letters are significantly different (Tukey, $P < 0.05$).

		Yield (tonnes/ha)	Tiller number	Ear mass (g)	Plant yield (g)	Stem mass (g)	Root mass (g)
Treatment	Control	1.76 \pm 0.35 a	3.57 \pm 0.62 a	0.91 \pm 0.08	3.14 \pm 0.56 a	2.76 \pm 0.53 a	0.120 \pm 0.03
	cm(top)	2.11 \pm 0.24 a	4.05 \pm 0.41 a	1.03 \pm 0.07	4.02 \pm 0.41 ab	4.43 \pm 0.69 ab	0.22 \pm 0.05
	hh(base)	2.40 \pm 0.54 ab	4.75 \pm 0.67 ab	0.98 \pm 0.10	4.79 \pm 1.01 ab	6.06 \pm 0.76 ab	0.40 \pm 0.12
	Con(cm)	2.83 \pm 0.23 ab	6.47 \pm 0.73 b	1.03 \pm 0.09	5.89 \pm 1.24 ab	6.83 \pm 1.24 b	0.46 \pm 0.09
	Con(hh)	3.84 \pm 0.44 b	5.43 \pm 0.61 ab	1.12 \pm 0.06	6.92 \pm 0.79 b	6.46 \pm 0.72 b	0.40 \pm 0.09
	df	4,27	4,34	4,32	4,31	4,31	4,31
	F	4.76	3.54	0.88	3.15	4.21	2.26
	P	< 0.01	< 0.05	0.49	< 0.05	< 0.01	0.09
Type	Control	1.76 \pm 0.35 a	3.57 \pm 0.62 a	0.91 \pm 0.08	3.14 \pm 0.56 a	2.76 \pm 0.53 a	0.120 \pm 0.03
	Org	2.26 \pm 0.27 a	4.40 \pm 0.44 ab	1.01 \pm 0.06	4.4 \pm 0.51 a	5.24 \pm 0.54 ab	0.31 \pm 0.06
	Con	3.33 \pm 0.29 b	5.95 \pm 0.54 b	1.08 \pm 0.05	6.40 \pm 0.72 b	6.65 \pm 0.69 b	0.43 \pm 0.06
	df	2,29	2,36	2,34	2,33	2,33	2,33
	F	7.05	6.55	1.41	5.85	7.31	3.59
	P	< 0.01	< 0.01	0.26	< 0.01	< 0.01	< 0.05
Timing	Control	1.76 \pm 0.35	3.57 \pm 0.62 a	0.91 \pm 0.08	3.14 \pm 0.56	2.76 \pm 0.53 a	0.20 \pm 0.03
	Top	2.93 \pm 0.24	5.32 \pm 0.39 b	1.06 \pm 0.04	5.61 \pm 0.54	5.91 \pm 0.55 b	0.36 \pm 0.05
	Base	2.40 \pm 0.54	4.75 \pm 0.67 ab	0.98 \pm 0.10	4.79 \pm 1.00	6.06 \pm 0.76 b	0.40 \pm 0.12
	df	2,29	2,36	2,34	2,33	2,33	2,33
	F	2.77	3.77	1.40	2.68	5.24	1.25
	P	0.078	< 0.05	0.26	0.08	< 0.05	0.3
Row	df	6,20	6,27	6,25	6,24	6,24	6,24
	F	0.92	1.83	0.60	1.15	2.13	0.7
	P	0.5	0.13	0.73	0.36	0.09	0.65
Site	df	1,20	1,27	1,25	1,24	1,24	1,24
	F	2.06	0.01	0.66	1.14	0.08	1.60
	P	0.17	0.94	0.42	0.30	0.78	0.22

Table 4.4 Effect of fertiliser treatment on barley growth and yield in 2008. Results for individual fertiliser treatments and treatments grouped by fertiliser type and application timing are given. Row and site effects are also shown. Means are displayed \pm SEM. Means within each column with different letters are significantly different (Tukey, $P < 0.05$).

		Yield (tonnes/ha)	Tiller number	Ear mass (g)	Plant yield (g)	Stem mass (g)	Root mass (g)
Treatment	Control	3.38 \pm 0.24 a	1.85 \pm 0.06 a	1.04 \pm 0.04	2.27 \pm 0.15	1.51 \pm 0.12 ab	0.11 \pm 0.01
	cm(base)	4.19 \pm 0.20 ab	2.33 \pm 0.13 b	1.10 \pm 0.03	2.54 \pm 0.23	1.65 \pm 0.17 ab	0.12 \pm 0.013
	cm(top)	4.12 \pm 0.28 ab	2.22 \pm 0.11 ab	1.05 \pm 0.03	2.47 \pm 0.19	1.65 \pm 0.18 ab	0.12 \pm 0.013
	hh(base)	4.75 \pm 0.38 b	2.76 \pm 0.21 bc	1.06 \pm 0.06	2.93 \pm 0.40	2.12 \pm 0.30 ab	0.13 \pm 0.016
	hh(top)	4.49 \pm 0.27 b	2.18 \pm 0.08 a	1.06 \pm 0.03	2.14 \pm 0.12	1.37 \pm 0.098 a	0.10 \pm 0.010
	Con(cm)	4.93 \pm 0.30 b	3.28 \pm 0.14 c	0.99 \pm 0.03	2.58 \pm 0.23	2.16 \pm 0.19 b	0.10 \pm 0.011
	Con(hh)	4.91 \pm 0.42 b	3.23 \pm 0.17 c	1.03 \pm 0.03	2.56 \pm 0.23	2.03 \pm 0.18 ab	0.12 \pm 0.014
	df	6,69	6,75	6,70	6,70	6,76	6,70
	F	5.03	21.68	1.13	0.796	2.95	1.05
	P	< 0.001	< 0.001	0.36	0.58	< 0.01	0.4
Type	Control	3.38 \pm 0.24 a	1.85 \pm 0.06 a	1.04 \pm 0.04	2.27 \pm 0.15	1.51 \pm 0.12 a	0.11 \pm 0.01
	Org	4.39 \pm 0.14 b	2.37 \pm 0.07 b	1.07 \pm 0.02	2.52 \pm 0.13	1.70 \pm 0.10 a	0.12 \pm 0.01
	Con	4.92 \pm 0.26 c	3.25 \pm 0.11 c	1.01 \pm 0.02	2.57 \pm 0.16	2.09 \pm 0.13 b	0.11 \pm 0.01
	df	2,73	2,79	2,80	2,81	2,80	2,80
	F	12.98	52.19	2.08	0.44	4.92	0.41
	P	< 0.001	< 0.001	0.13	0.65	< 0.001	0.66
Timing	Control	3.38 \pm 0.24 a	1.85 \pm 0.06 a	1.04 \pm 0.04	2.27 \pm 0.15	1.51 \pm 0.12	0.11 \pm 0.01
	Top	4.61 \pm 0.16 b	2.73 \pm 0.10 b	1.02 \pm 0.02	2.44 \pm 0.10	1.80 \pm 0.09	0.11 \pm 0.01
	Base	4.47 \pm 0.20 b	2.55 \pm 0.13 b	1.08 \pm 0.03	2.74 \pm 0.23	1.88 \pm 0.17	0.13 \pm 0.01
	df	2,73	2,79	2,78	2,81	2,81	2,78
	F	9.03	13.14	1.57	0.81	0.95	1.19
	P	< 0.001	< 0.001	0.21	0.45	0.39	0.31
Row	df	10,59	10,65	10,60	10,60	10,66	10,60
	F	0.62	1.48	0.78	1.06	1.11	0.77
	P	0.79	0.17	0.65	0.41	0.37	0.66
Site	df	1,59	1,65	1,60	1,60	1,66	1,60
	F	34.05	18.56	27.55	0.41	4.24	6.7
	P	< 0.001	< 0.001	< 0.001	0.52	< 0.05	< 0.05

4.4.1.2 Barley morphology

Tiller number was significantly greater under conventional(cm) treatments than control and chicken manure treatments in 2007 (Table 4.3). In 2008, tiller numbers achieved by barley under both conventional treatments was significantly greater than control, chicken manure(base) and hoof and horn(top) treatments (Table 4.4). The chicken manure(base) and hoof and horn(base) treatments also resulted in greater tiller numbers than the control. Following grouping of fertiliser treatments, conventional fertilisers resulted in a significantly greater number of tillers than controls in 2007, while in 2008, tiller numbers followed that of yield with controls

producing significantly fewer tillers than organic fertiliser, which in turn achieved fewer tillers than conventional fertilisers. In both years, top and base dressed fertilisers resulted in greater numbers of tillers than controls; this was significant in 2008 for both top and base dressed fertilisers and top dressed fertiliser in 2007. Once again, a significant site effect was found in 2008 with barley plants growing in Silwood Bottom having significantly greater tiller numbers.

No significant effect of fertiliser treatment on individual ear weight was found in either year, although a significant site effect was recorded in 2008. In 2008, a significant interaction effect of treatment and site was observed ($F_{6,60} = 2.40$, $P < 0.05$) (Table 4.4).

In 2007, barley plants grown with the conventional(cm) treatment produced larger individual plant yields than control plants. Following grouping of fertiliser treatments, conventionally fertilised plants produced larger individual plant yields than both organically fertilised plants and control plants (Table 4.3). Neither fertiliser treatment, site or row had a significant effect on individual plant yield in 2008, although a significant interaction effect of treatment and site was found ($F_{6,60} = 3.71$, $P < 0.05$) (Table 4.4).

Stem mass was significantly affected by fertiliser treatments in both 2007 and 2008 (Tables 4.3 & 4.4). In 2007, both conventional treatments resulted in significantly greater stem biomass than control treatments. In 2008, the conventional(cm) resulted in greater stem biomass than the top dressed hoof and horn fertiliser treatment. In 2007 and 2008, following fertiliser treatment grouping, conventional fertiliser treatments resulted in greater stem mass than control and organic treatments. In 2008 this difference was significant, but in 2007 conventional treatments were only significantly different from control treatments. A significant fertiliser timing effect on stem mass was found in 2007 and a significant site effect in 2008.

Barley root mass was comparable between all fertiliser treatments, however in 2007 conventionally fertilised plants produced bigger roots than control plants. In 2008 there was also a significant site effect, with bigger roots found on plants grown at

Silwood Bottom. A significant interaction effect of treatment and site was found in 2008 ($F_{6,76} = 2.57$, $P < 0.05$) (Table 4.4 & 3.4).

Barley leaf area was affected by fertiliser treatment (Table 4.5). Leaves collected on the 4/5/2008 were significantly larger from pots receiving the conventional(cm) treatment than hoof and horn top dressed pots. Leaves in conventionally fertilised pots had a significantly larger area than those grown in organic and control pots. On 21/05/2008 there was no significant effect of fertiliser treatment on leaf area. On the 23/6/2008 and 17/7/2008 leaves in pots receiving conventional(cm) and conventional(hh) fertiliser treatments were significantly larger than leaves from barley under all other treatments. Following treatment grouping, leaves in conventionally fertilised pots were bigger than organic and control pots. Barley receiving top dressed fertiliser also produced leaves with a larger surface area than barley in control pots (Table 4.5).

Table 4.5 Effect of fertiliser treatment on barley leaf area in 2008. Results for individual fertiliser treatments and treatments grouped by fertiliser type and application timing are given. Row and site effects are also shown. Means are displayed \pm SEM. Means within each column with different letters are significantly different (Tukey, $P < 0.05$).

		04/05	21/05	23/06	17/07
Treatment	Control	8.74 \pm 1.13 a	9.31 \pm 0.33	6.12 \pm 0.73 a	6.18 \pm 0.76 a
	cm(base)	9.57 \pm 1.16 ab	9.73 \pm 0.34	7.51 \pm 0.85 a	7.36 \pm 0.95 a
	cm(top)	9.22 \pm 1.05 ab	8.63 \pm 0.30	6.65 \pm 0.53 a	7.22 \pm 0.61 a
	hh(base)	9.86 \pm 1.20 ab	9.53 \pm 0.42	7.93 \pm 0.70 a	8.11 \pm 0.78 a
	hh(top)	8.88 \pm 1.095 a	9.10 \pm 0.58	6.52 \pm 0.51 a	6.65 \pm 0.64 a
	Con(cm)	11.67 \pm 1.06 b	9.39 \pm 0.40	11.03 \pm 0.85 b	10.69 \pm 0.91 b
	Con(hh)	10.92 \pm 0.85 ab	9.85 \pm 0.46	11.07 \pm 0.81 b	11.01 \pm 0.56 b
	df	6,76	6,76	6,76	6,76
	F	3.66	1.42	19.76	17.25
	P	< 0.01	0.22	< 0.001	< 0.001
Type	Control	8.74 \pm 1.13 a	9.31 \pm 0.33	6.12 \pm 0.73 a	6.18 \pm 0.76 a
	Org	9.38 \pm 0.55 a	9.25 \pm 0.21	7.15 \pm 0.33 a	7.33 \pm 0.37 a
	Con	11.30 \pm 0.67 b	9.62 \pm 0.30	11.05 \pm 0.57 b	10.85 \pm 0.52 b
	df	2,80	2,80	2,80	2,80
	F	10.12	0.77	54.63	48.34
	P	< 0.001	0.47	< 0.001	< 0.001
Timing	Control	8.74 \pm 1.13	9.31 \pm 0.33	6.12 \pm 0.73 a	6.18 \pm 0.76 a
	Top	10.17 \pm 0.52	9.24 \pm 0.33	8.82 \pm 0.47 b	8.89 \pm 0.44 b
	Base	9.71 \pm 0.82	9.63 \pm 0.27	7.72 \pm 0.54 ab	7.73 \pm 0.61 ab
	df	2,80	2,80	2,80	2,80
	F	2.41	0.83	6.81	8.00
	P	0.09	0.44	< 0.01	< 0.001
Row	df	10,66	10,66	10,66	10,66
	F	0.91	0.72	1.19	0.72
	P	0.53	0.70	0/31	0.70
Site	df	1,66	1,66	1,66	1,66
	F	162.52	36.51	108.48	124.69
	P	< 0.001	< 0.001	< 0.001	< 0.001

4.4.1.3 Barley leaf colour

The pattern of spectral reflectance from leaves at all four count dates was comparable; peaks occurred at approximately 570 nm (Fig. 4.3), this is the yellow/green area of the visual spectrum. Barley grown under control and organic fertiliser treatments had consistently higher reflectance between 540 and 600 nm than plant grown with conventional fertilisers, which indicates that plants under these treatment are more yellow. The reflectance peak at 570 nm was also higher on 17/7/2008 than the three earlier dates indicating that leaves are more yellow at the end of the season (Fig. 4.3d).

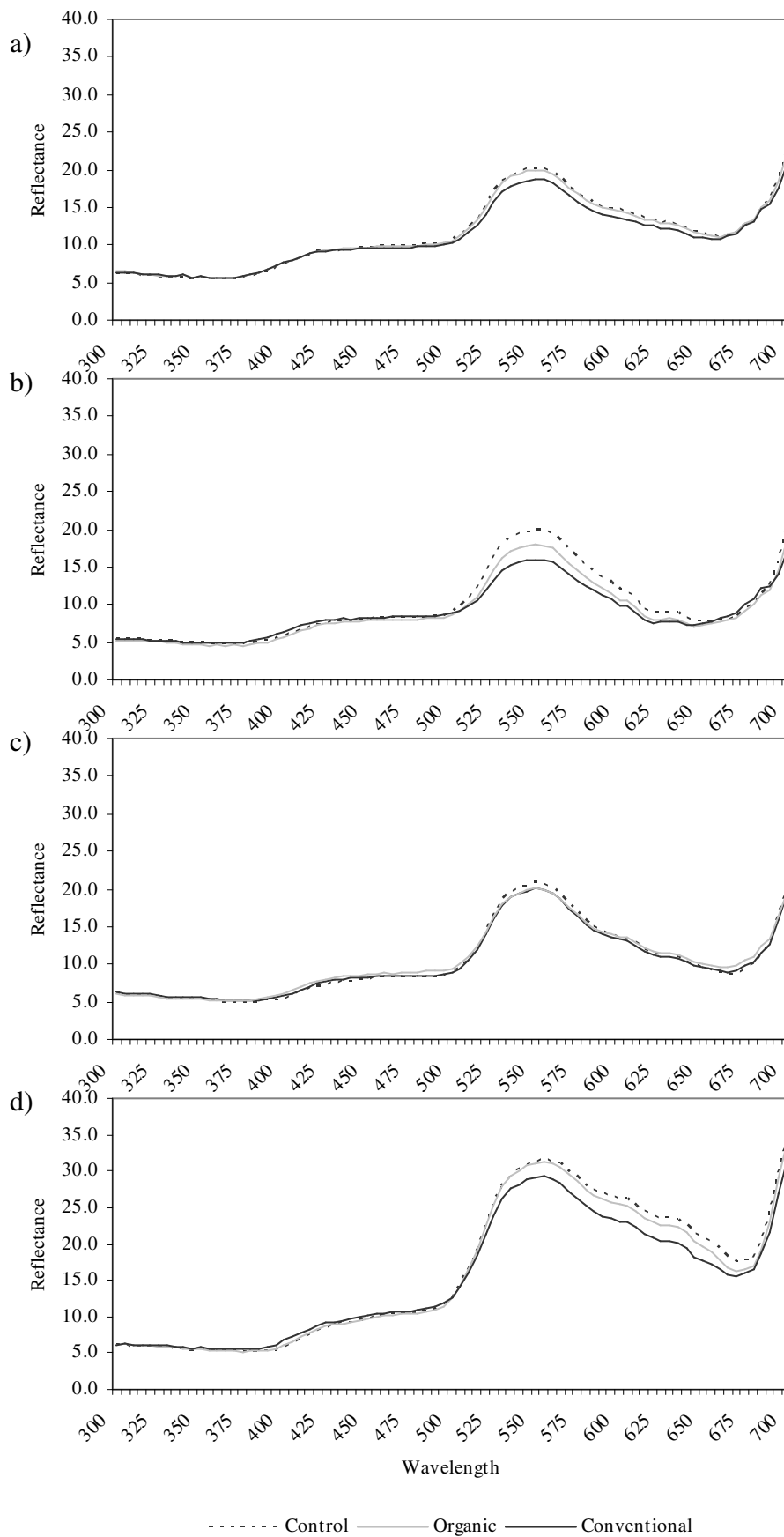


Fig. 4.3 Leaf spectral reflectance at four dates during the growing season of barley grown under three fertiliser regimes. a) 22/5/2008, b) 4/6/2008, c) 23/6/2008, d) 17/7/2008.

The attractiveness index of barley leaves under all fertiliser treatments increased through the season (Fig. 4.4). Mean attractiveness at each of the four dates was significantly different from all other dates ($F_{3,270} = 679.15$, $P < 0.001$). There were also significant fertiliser treatment effects on attractiveness at all four dates.

On 22/5/2008, control, hoof and horn(top) and chicken manure(top) treatments resulted in significantly higher attractiveness than conventional(cm) treatments ($F_{6,76} = 4.33$, $P < 0.001$) (Fig. 4.4). Attractivity in control treatments was also significantly higher than the conventional(hh) treatment. A significant site effect was found ($F_{1,66} = 47.09$, $P < 0.001$) and following grouping of fertiliser treatments, barley grown with conventional fertilisers was found to have a significantly lower attractiveness index than both organically fertilised and control barley ($F_{2,80} = 11.03$, $P < 0.001$).

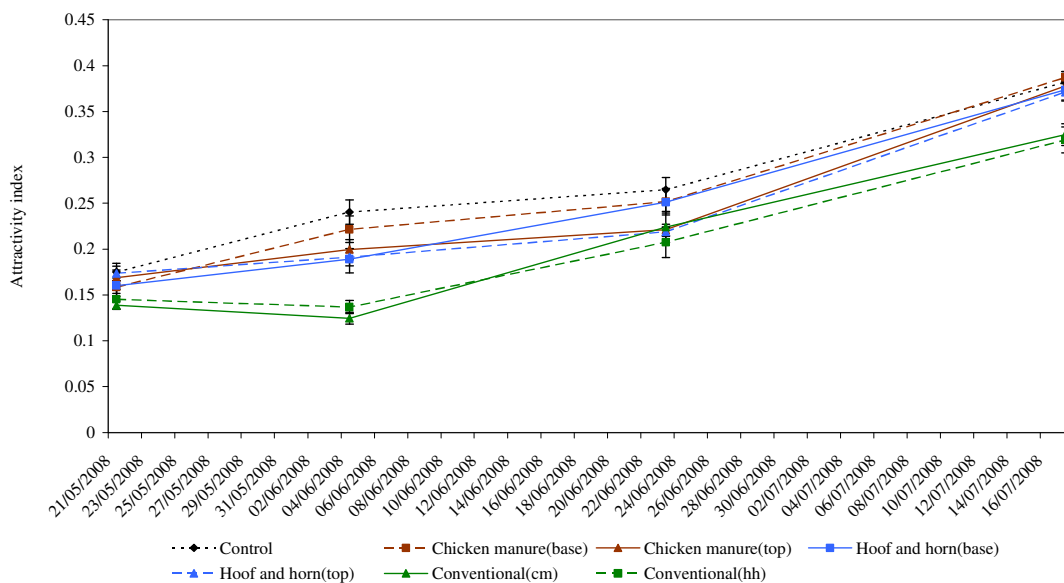


Fig. 4.4 Attractivity index of leaves through the growing season from barley grown under seven different fertiliser treatments (means \pm SEM).

For leaf samples collected on 4/6/2008, a significant fertiliser treatment, site, row and treatment:site interaction effect on attractiveness was found (fertiliser treatment: $F_{6,60} = 27.01$, $P < 0.001$; site: $F_{1,60} = 52.68$, $P < 0.001$; row: $F_{10,60} = 2.34$, $P < 0.05$; treatment:site: $F_{6,60} = 2.77$, $P < 0.05$) (Fig. 4.4). Both conventional treatments resulted in leaves with significantly lower attractiveness than all organic treatments and the control. The chicken manure(top) treatment and both hoof and horn treatments had significantly lower attractiveness than control barley. Following grouping of

fertiliser treatments, control plants were found to have a greater attractivity than organically fertilised plants which in turn had a greater attractivity than conventionally fertilised barley ($F_{2,68} = 64.43$, $P < 0.001$). A significant effect of fertiliser timing was also found, with control plants showing greater attractivity than base fertilised plants which showed greater attractivity than top dressed plants ($F_{2,78} = 22.07$, $P < 0.001$).

On 23/6/2008, significant fertiliser treatment and site effects were found as well as a significant treatment:site interaction effect (fertiliser treatment: $F_{6,70} = 3.90$, $P < 0.01$; site: $F_{1,60} = 9.40$, $P < 0.01$; treatment:site: $F_{6,60} = 4.76$, $P < 0.001$) (Fig. 4.4). Barley grown under control treatments had a greater attractivity index than barley grown under the conventional(hh) treatment. When fertiliser treatments had been grouped, conventionally fertilised barley had a lower attractivity than control barley ($F_{2,78} = 6.17$, $P < 0.01$). Barley fertilised with a top dressing had a lower attractivity than control or base fertilised barley ($F_{2,78} = 9.53$, $P < 0.001$).

No significant site, row or interaction effects were found on 17/7/2008. A significant fertiliser treatment effect was found; barley grown under both conventional fertiliser treatments showed significantly lower attractivity than all other treatments ($F_{2,77} = 7.16$, $P < 0.001$) (Fig. 4.4). A similar pattern was found following grouping of fertiliser treatments. Conventionally fertilised barley had a lower attractivity than organically fertilised or control barley ($F_{2,81} = 21.40$, $P < 0.001$). Barley fertilised with a top dressing also had a lower attractivity than control and base fertilised barley ($F_{2,81} = 6.62$, $P < 0.01$).

4.4.2 Aphids

4.4.2.1 Aphid abundance

In 2007, 1378 *M. dirhodum*, 918 *R. padi* and 354 *S. avenae* were counted. One hundred and ninety aphid individuals were made up of other species. In 2008, *R. padi* were the most numerous aphids found with 5322 individuals counted followed by *M. dirhodum*, 2955 individuals and *S. avenae*, 464 individuals, 172 aphids from other

species were counted. Aphid abundance in both years showed rapid population growth early in the season followed by a dramatic fall later on (Fig. 4.5a, b).

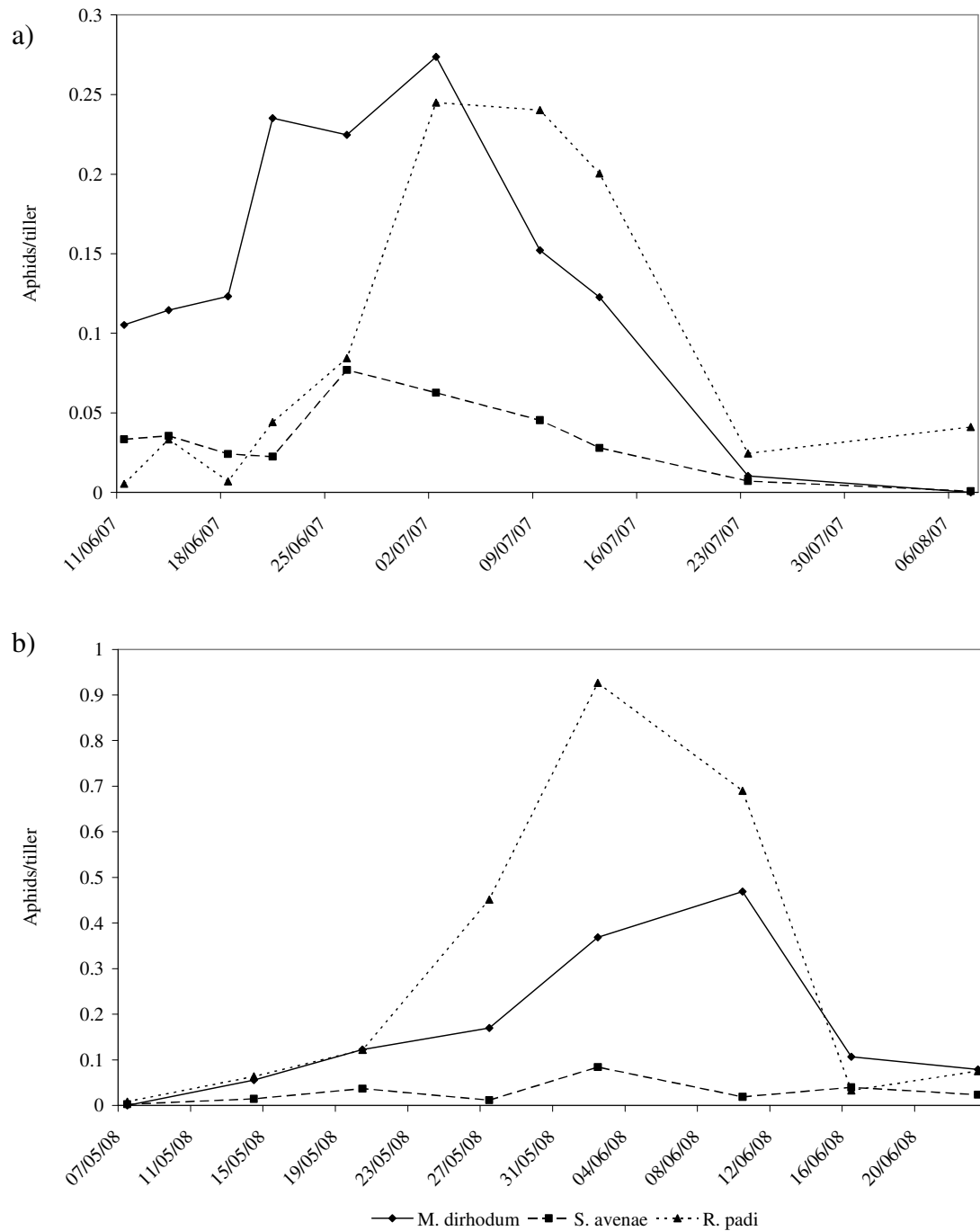


Fig. 4.5 Mean number of *Metopolophium dirhodum*, *Sitobion avenae* and *Rhopalosiphum padi* per spring barley tiller in the summer of a) 2007 and b) 2008.

In 2007, aphid numbers were very variable between pots, with a maximum aphid days per tiller of more than 88 found in one pot and a minimum of less than one aphid day per tiller found in three other pots. There were no consistent treatment effects on

aphid numbers. No significant effects of fertiliser, site or row on aphid days per tiller for either of the three most numerous aphid species or when all aphids were considered together was found (*M. dirhodum*: $F_{4,35} = 0.26$, $P = 0.90$; *S. avenae*: $F_{4,35} = 1.82$, $P = 0.15$; *R. padi*: $F_{4,35} = 1.07$, $P = 0.39$; All: $F_{4,35} = 0.45$, $P = 0.77$). Following grouping of fertiliser treatments into control, organic and conventional treatments (Fig. 4.6) and grouping them based on fertiliser timing, no significant effect of fertiliser was found (Type: *M. dirhodum*: $F_{2,37} = 0.078$, $P = 0.92$; *S. avenae*: $F_{4,37} = 0.13$, $P = 0.88$; *R. padi*: $F_{4,37} = 1.54$, $P = 0.23$; All: $F_{4,37} = 0.53$, $P = 0.59$; Timing: *M. dirhodum*: $F_{4,37} = 0.056$, $P = 0.95$; *S. avenae*: $F_{4,37} = 0.26$, $P = 0.62$; *R. padi*: $F_{4,37} = 0.66$, $P = 0.52$; All: $F_{4,37} = 0.41$, $P = 0.67$).

In 2008, when aphid species were considered separately no significant fertiliser treatment effect on aphid days per tiller was found (*M. dirhodum*: $F_{6,77} = 0.57$, $P = 0.76$; *S. avenae*: $F_{6,76} = 1.04$, $P = 0.40$; *R. padi*: $F_{6,77} = 2.01$, $P = 0.07$) although a significant site effect on *S. avenae* aphid days was apparent ($F_{1,66} = 9.88$, $P < 0.01$), with more aphids found in Four Acre Field. Fertiliser treatment grouping by fertiliser type yielded no significant effects on individual species aphid days per tiller (*M. dirhodum*: $F_{2,81} = 0.55$, $P = 0.58$; *S. avenae*: $F_{2,80} = 0.01$, $P = 0.99$; *R. padi*: $F_{2,81} = 1.98$, $P = 0.14$). When all aphid species were considered together, an initial fertiliser treatment effect on aphid days per tiller was not found ($F_{6,77} = 2.20$, $P = 0.052$) but when treatments were grouped, the number of aphid days was greater under conventional treatments than both control and organic treatments (Fig. 4.6). The difference between organic and conventional treatments was significant ($F_{2,81} = 3.78$, $P < 0.05$). When fertiliser treatments were grouped by timing of application, numbers of *R. padi* and all aphids considered together, were significantly affected (*R. padi*: $F_{2,81} = 4.93$, $P < 0.05$; All: $F_{2,81} = 5.81$, $P < 0.01$). *Rhopalosiphum padi* and all aphids together were more abundant following top dressing of fertilisers. This was not the case for *M. dirhodum* and *S. avenae* (*M. dirhodum*: $F_{2,81} = 0.10$, $P = 0.91$; *S. avenae*: $F_{2,80} = 0.13$, $P = 0.87$).

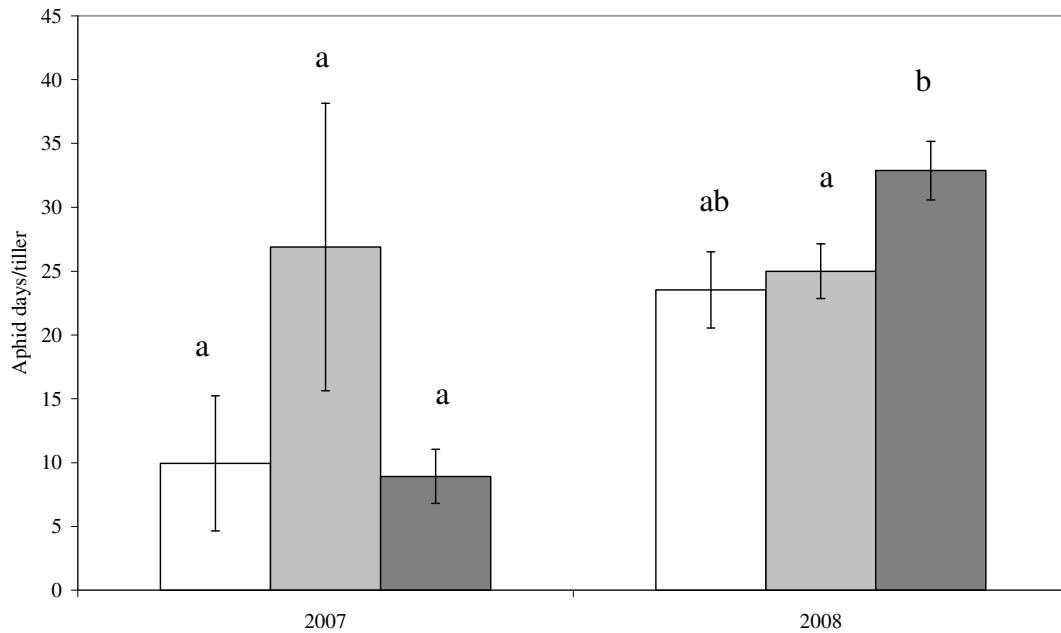


Fig. 4.6 Aphid days per tiller on barley grown under control (□), organic (■) and conventional (■) fertiliser treatments in 2007 and 2008 (mean \pm SEM). Means within each year with different letters are significantly different (Tukey, $P < 0.05$).

The number of alate aphids per tiller peaked early in the season before the peak in total aphid number (Fig. 4.7a, b). In 2007, the cumulative number of alates per tiller was low and similar between treatments and there was no significant effect of treatment or grouped treatments (Fertiliser treatment: $F_{4,34} = 1.71$, $P = 0.17$; Type: $F_{2,36} = 0.44$, $P = 0.64$; Timing: $F_{2,36} = 1.92$, $P = 0.16$). A significant effect of site was found with greater numbers of alate aphids per tiller found on barley in Four Acre Field when compared with Silwood Bottom ($F_{1,28} = 4.30$, $P < 0.05$). In 2008, once more, a greater number of alates was found in Four Acre Field ($F_{1,66} = 4.81$, $P < 0.05$), although no treatment effect was apparent (Fertiliser treatment: $F_{6,76} = 0.30$, $P = 0.93$; Type: $F_{2,80} = 0.12$, $P = 0.12$; Timing: $F_{2,70} = 0.37$, $P = 0.69$).

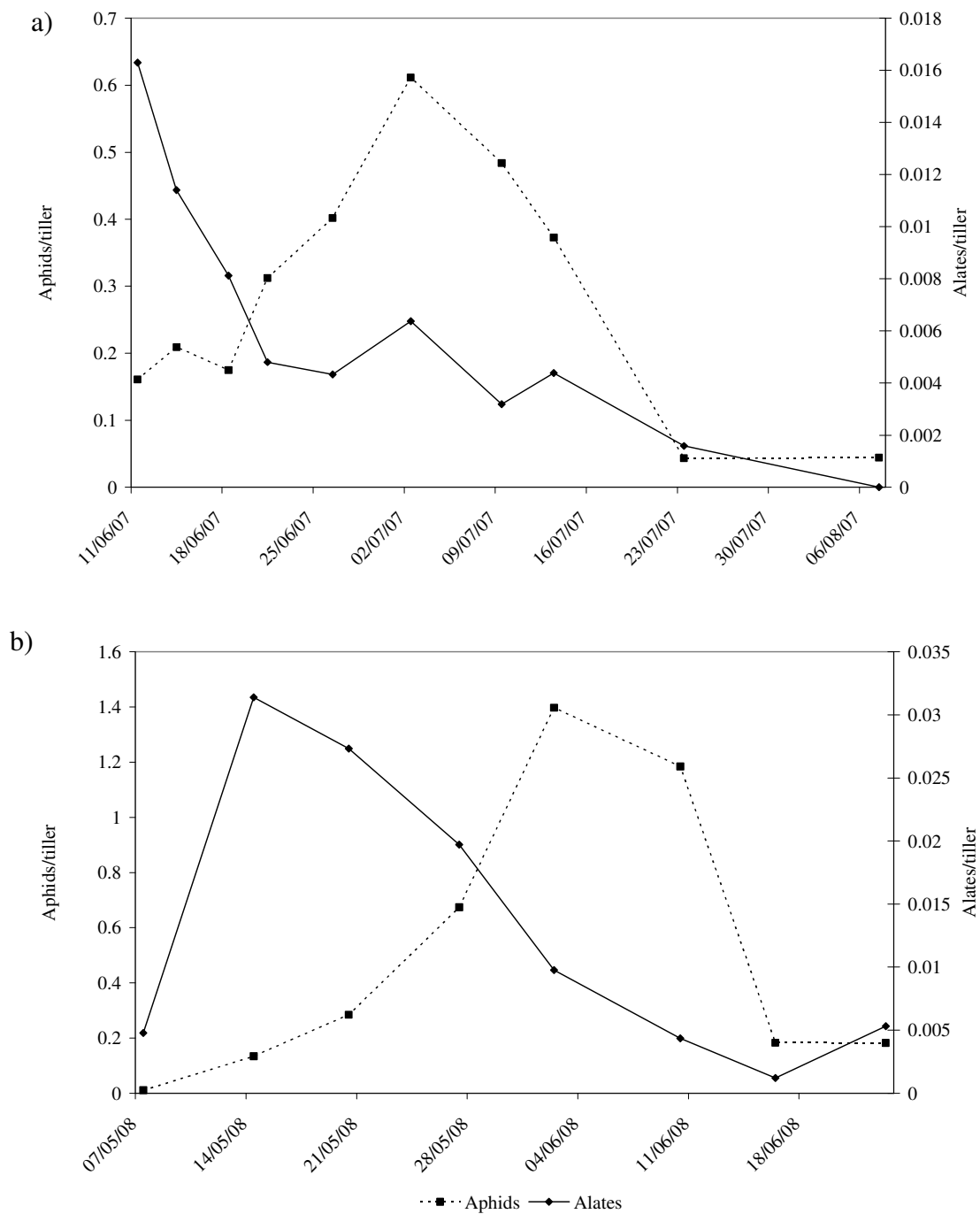


Fig. 4.7 Number of alate aphids and total number of aphids per tiller on spring barley in a) 2007 and b) 2008.

4.4.2.2 Barley morphology and aphid abundance

In 2007, there was no significant correlation between *M. dirhodum*, *R. padi* and *S. avenae* aphid days per unit biomass and the proportion of above ground barley biomass dedicated to vegetative growth and not ear production (*M. dirhodum*: $F_{1,35} =$

0.003, $P = 0.96$; *R. padi*: $F_{1,35} = 0.59$, $P = 0.45$; *S. avenae*: $F_{1,35} = 0.93$, $P = 0.34$) (Fig. 4.8a). In 2008, the positive correlation between the proportion of vegetative biomass and *M. dirhodum* per unit biomass was significant (Fig. 4.8b) but there was no significant correlation for *R. padi* and *S. avenae* (*M. dirhodum*: $F_{1,82} = 4.80$, $P < 0.05$; *S. avenae*: $F_{1,82} = 0.32$, $P = 0.58$; *R. padi*: $F_{1,82} = 1.07$, $P = 0.30$) (Fig. 4.8b).

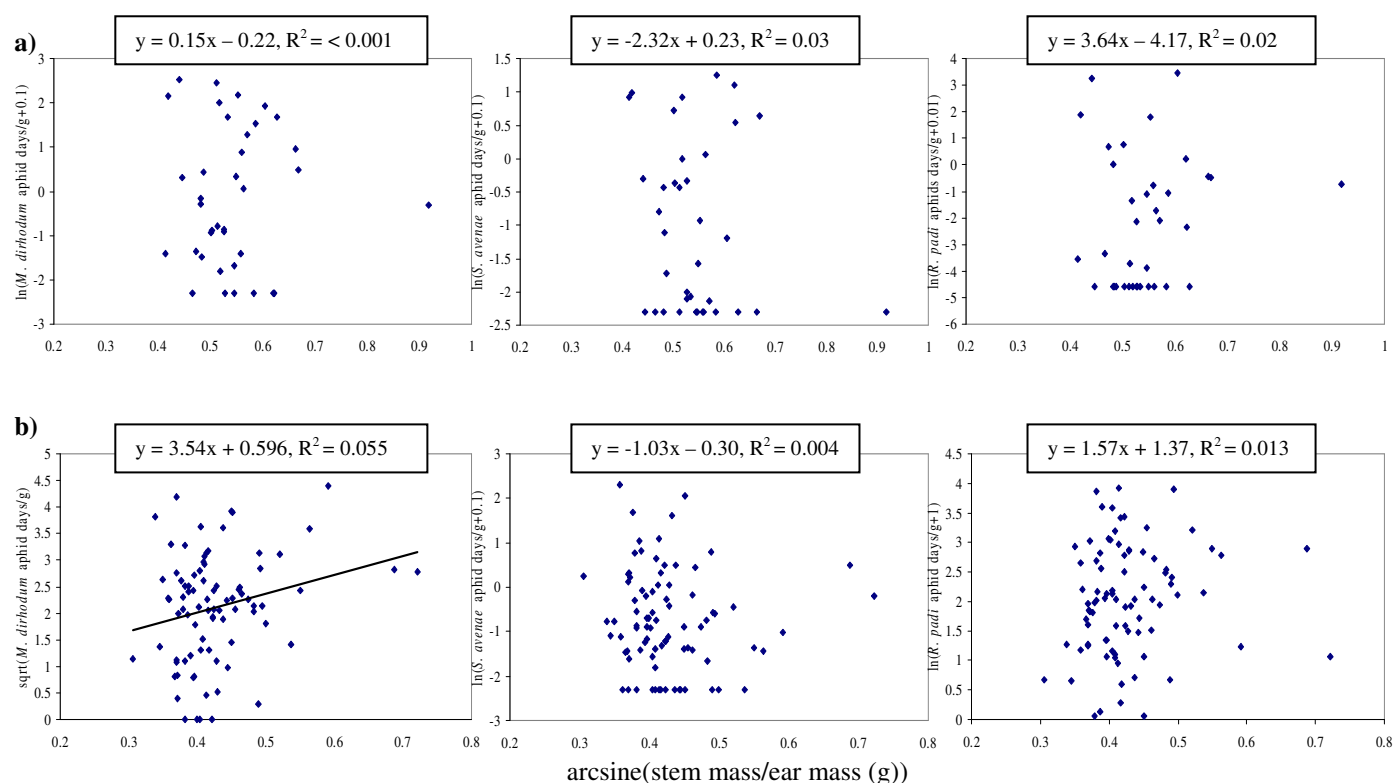


Fig. 4.8 Correlation between *Metopolophium dirhodum*, *Sitobion avenae* and *Rhopalosiphum padi* aphid days per gram of barley dry matter and the proportion of above ground barley biomass made up of vegetative plant material in a) 2007 and b) 2008.

4.4.2.3 Barley leaf colour and aphid abundance

The total number of aphid days per tiller is negatively correlated with leaf attractivity according to the attractivity index on all four leaf collection dates (Fig. 4.9). This negative correlation is significant for leaves collected on 17/7/2008 (22/5/2008: $F_{1,82} = 1.89$, $P = 0.17$; 4/6/2008: $F_{1,82} = 2.00$, $P = 0.16$; 23/6/2008: $F_{1,82} = 1.61$, $P = 0.21$; 17/7/2008: $F_{1,82} = 5.29$, $P < 0.05$). Following linear regression analysis between aphid days and the mean attractivity index through the growing season, a significant negative correlation was found again ($F_{1,82} = 5.24$, $P < 0.05$) (Fig. 4.10).

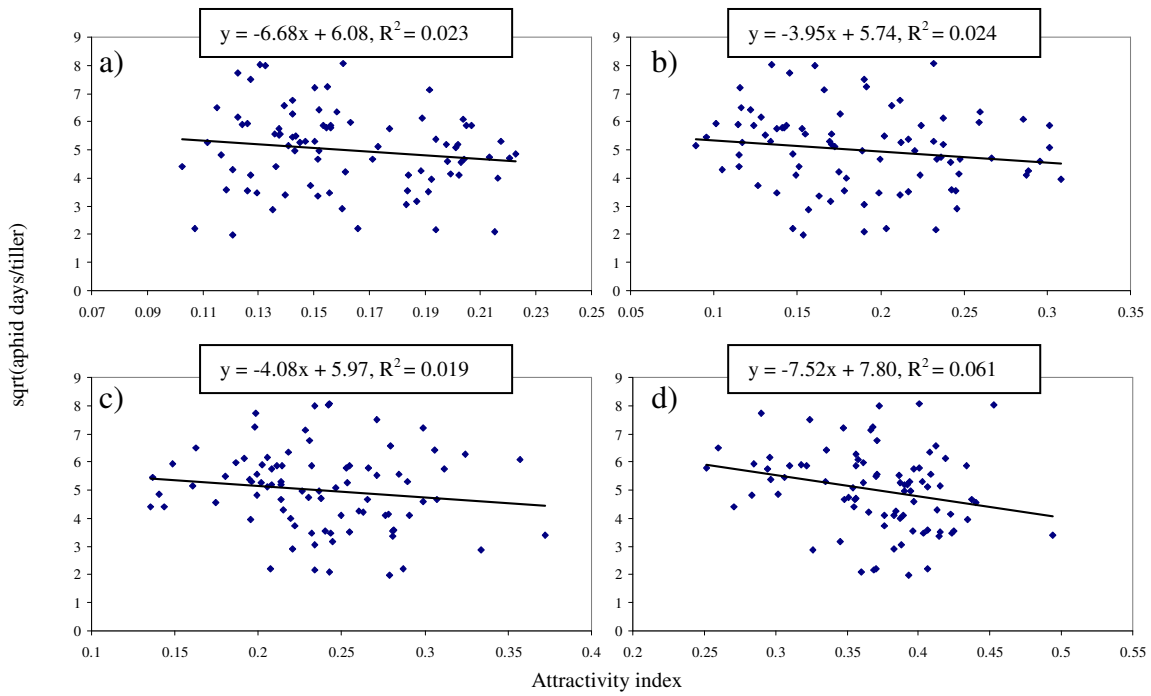


Fig. 4.9 Correlation between aphid days per tiller and leaf attractivity according to the leaf attractivity index on a) 22/5/2008, b) 4/6/2008, c) 23/6/2008 and d) 17/7/2008.

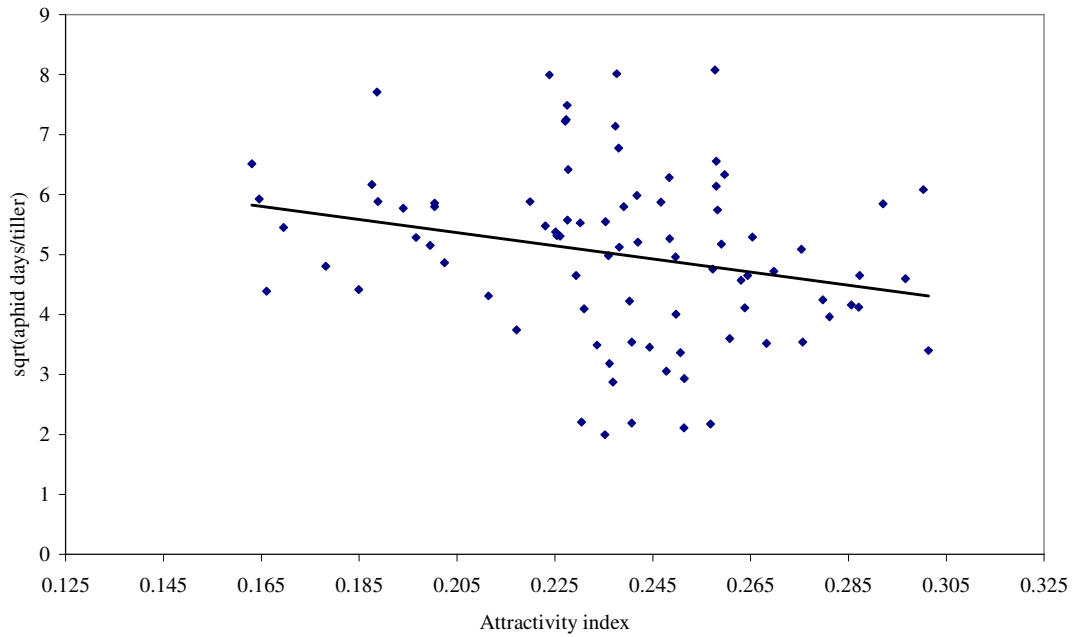


Fig. 4.10 Correlation between mean leaf attractivity through the season and aphid days per tiller ($y = -10.93x + 7.604, R^2 = 0.06$).

4.4.3 Natural enemies

4.4.3.1 Parasitoids

Twenty-seven aphid mummies were encountered through the season in 2007; 78 mummies were found in 2008. Peak parasitoid mummy numbers occurred soon after peak aphid numbers in both years. Despite differing aphid numbers between years, the peak number of parasitoid mummies was comparable in 2007 and 2008 (Fig. 4.11).

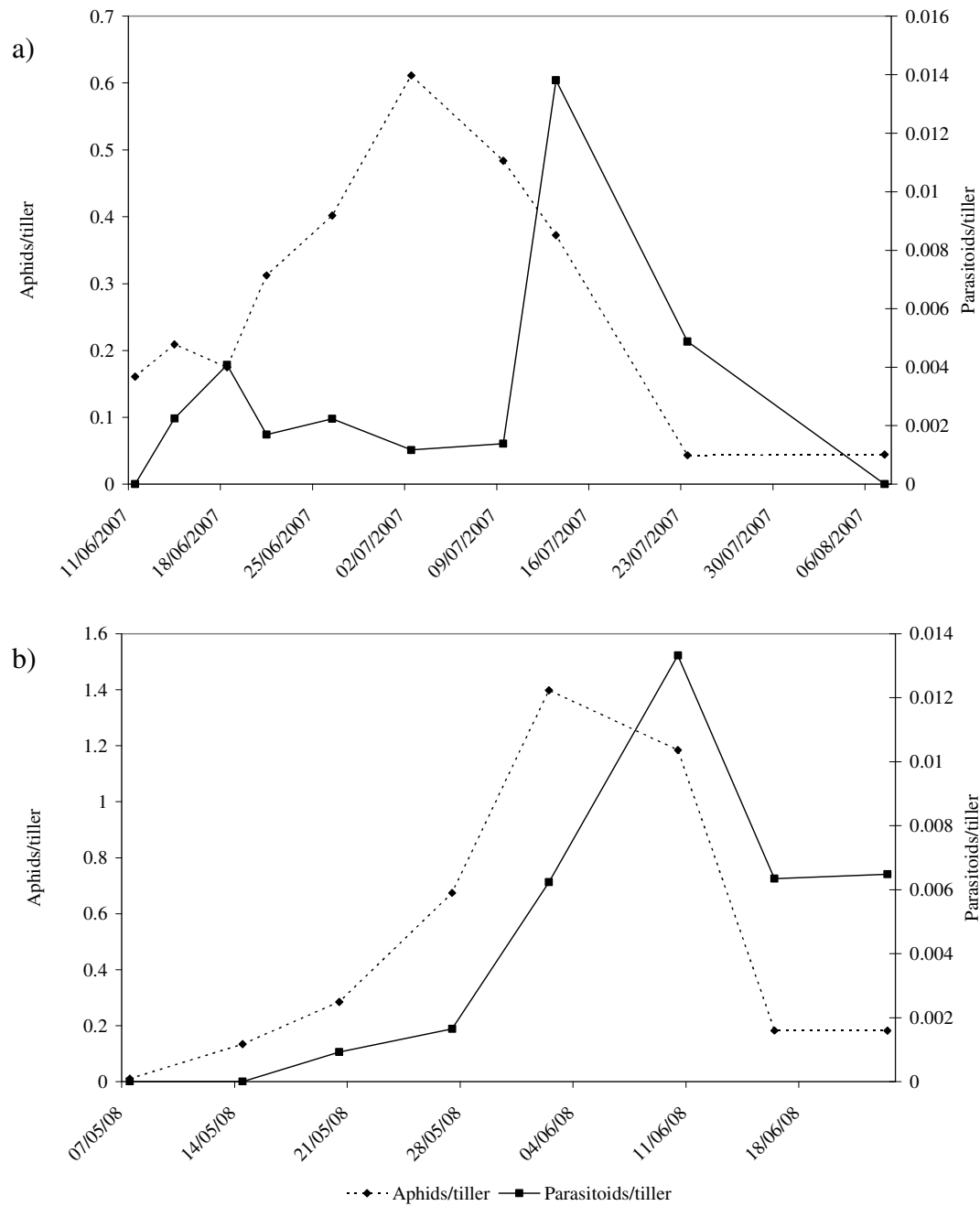


Fig. 4.11 The number of aphids per tiller and parasitoid mummies per tiller through the barley growing season in a) 2007 and b) 2008.

There was no significant effect of fertiliser treatment on cumulative mummy numbers per tiller in 2007 (Fertiliser treatment: $F_{4,35} = 0.14$, $P = 0.97$; Type: $F_{2,37} = 0.26$, $P = 0.77$; Timing: $F_{2,37} = 0.16$, $P = 0.85$) or in 2008 (Fertiliser treatment: $F_{6,76} = 1.11$, $P = 0.36$; Type: $F_{2,80} = 0.28$, $P = 0.76$; Timing: $F_{2,80} = 2.07$, $P = 0.13$). There was a significant site effect in 2008, with more parasitoid mummies found in Silwood Bottom ($F_{1,66} = 14.40$, $P = < 0.001$). Mummy numbers did correlate positively with

aphid numbers in 2007 and 2008 (Fig. 4.12), this correlation was significant in 2007 (2007: $F_{1,12} = 6.73$, $P < 0.05$; 2008: $F_{1,39} = 1.06$, $P = 0.31$).

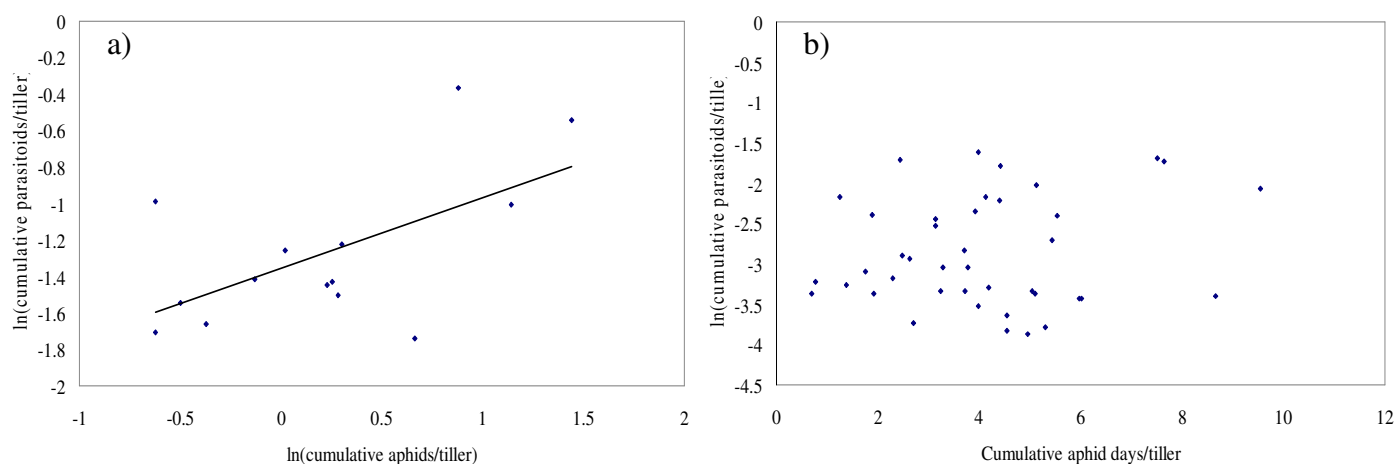


Fig. 4.12 Correlation between cumulative parasitoid mummy numbers and aphid numbers per tiller excluding zero counts in a) 2007 ($y = 0.39x - 3.12$, $R^2 = 0.36$) and b) 2008.

4.4.3.2 Syrphids and coccinellids

At peak abundance, 199 syrphid eggs and 117 syrphid larvae and pupae were counted in 2008. The peak in syrphid larvae and syrphid egg numbers occurred on the 11/6/2008, approximately one week after the peak in aphid numbers. There was a significant effect of fertiliser treatment ($F_{6,77} = 2.48$, $P < 0.05$) on syrphid egg number per tiller at peak abundance (Fig. 4.13). There were significantly more eggs per tiller in barley grown under the conventional(hh) treatment than the chicken manure(base) treatment. Following grouping of fertiliser treatment, a significant effect of fertiliser type was also found with significantly greater egg numbers under conventional treatments by comparison with organic or control treatments ($F_{2,81} = 5.41$, $P < 0.01$) (Fig. 4.13). No significant effect of fertiliser timing was found on syrphid egg numbers ($F_{2,81} = 2.72$, $P = 0.07$). The number of syrphid larvae and pupae was not affected by fertiliser treatment, type or timing (Treatment: $F_{6,77} = 1.23$, $P = 0.30$; Type: $F_{2,81} = 0.91$, $P = 0.41$; Timing: $F_{2,81} = 0.95$, $P = 0.39$).

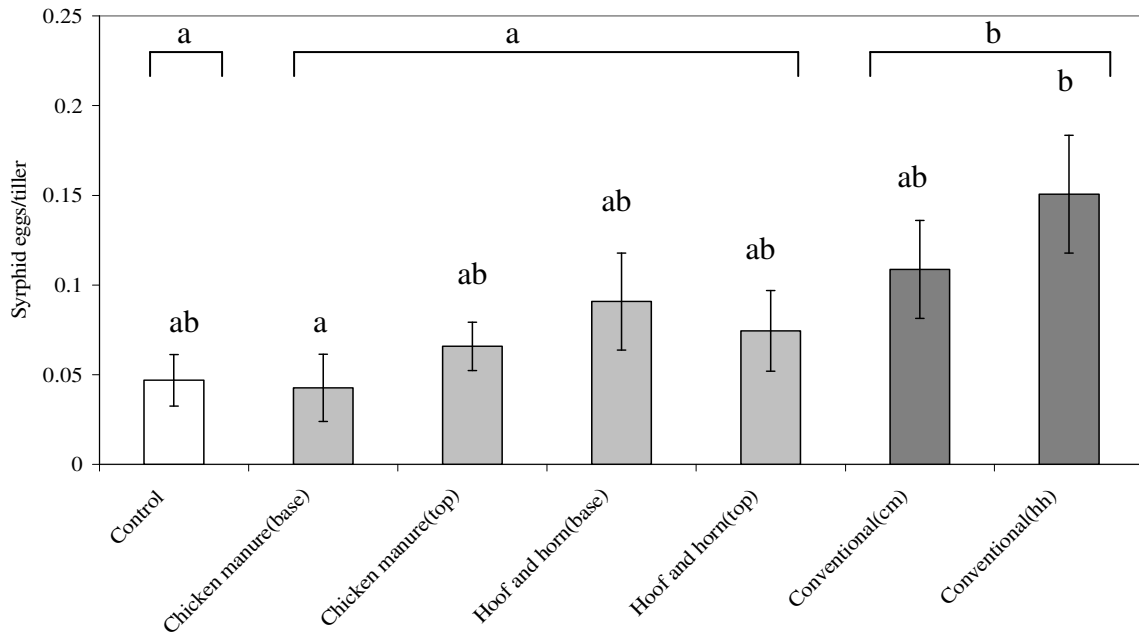


Fig. 4.13 Peak number of syrphid eggs per tiller on barley grown under different fertiliser treatments (mean \pm SEM). Bars and groups of bars with different letters are significantly different (Tukey, $P < 0.05$).

A significant positive correlation was found between the peak number of syrphid eggs per tiller and the number of aphid days per tiller ($F_{1,82} = 4.16$, $P < 0.05$) (Fig. 4.14). No significant correlation was found between aphids and syrphid larvae and pupae ($F_{1,82} = 3.02$, $P = 0.09$).

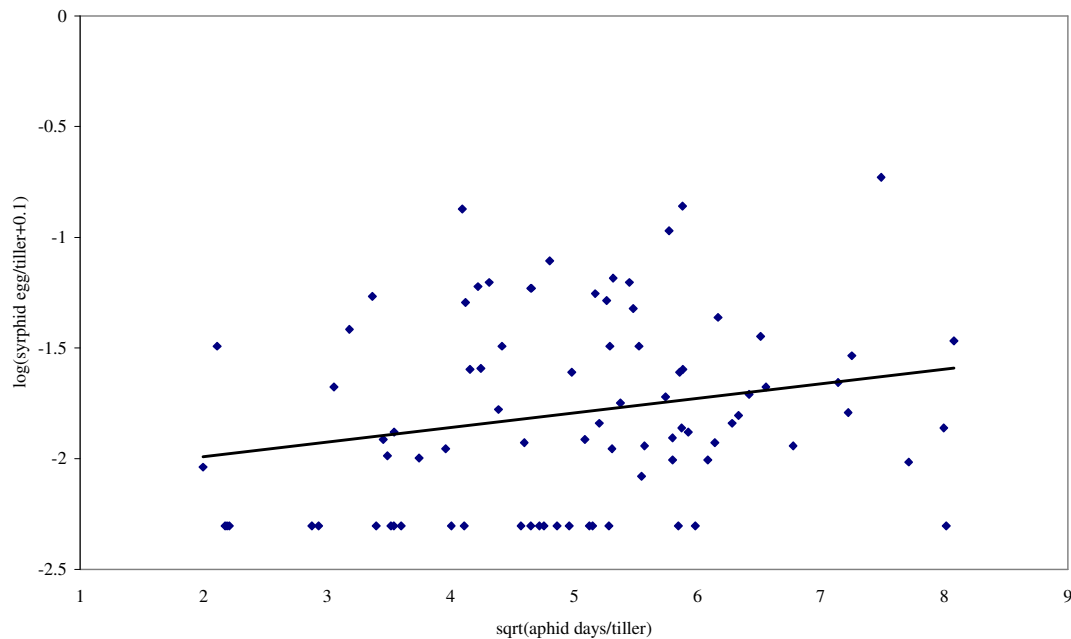


Fig. 4.14 Correlation between peak syrphid egg number per barley tiller and aphid days per tiller ($y = 0.066x - 2.12$, $R^2 = 0.05$).

At peak coccinellid abundance, 22 larvae and three adults were encountered but this was not adequate for statistical analysis.

4.5 Discussion

4.5.1 Barley

4.5.1.1 Barley yield

Barley yield achieved in 2007 was consistently lower than that achieved in 2008. The primary reason for this was because, due to intensive pest pressure, fewer plants established per pot in 2007. This dramatically reduced the overall potential yield. Furthermore, due to the experimental problems which occurred in 2007, barley involved in this trial was planted over a month later than in 2008. Sowing date is known to be an important determinant of yield, with early sowing typically resulting in higher yields (Conry, 1995). Indeed in both 2007 and 2008 yields were low when compared to yields achieved in modern barley agriculture (DEFRA, 2008a), again probably a result of late sowing date.

Yield (tonnes per ha) was greater in conventionally fertilised pots when compared with organically fertilised pots, which in turn were higher than control pots in both 2007 and 2008. This pattern becomes particularly apparent when fertiliser treatments were grouped as conventional, organic and control. This hierarchy in yield production was highly significant in 2008. Both conventional and organic fertiliser have been shown to improve yields in cereals due to increased nitrogen availability. This is true for both manures (Sieling *et al.*, 2006) and horn meal (Juroszek *et al.*, 2004). The availability of nutrients from organic slow release fertilisers is dependent on nitrogen mineralisation (Dawson *et al.*, 2008) and the rate of mineralisation is determined by the carbon:nitrogen ratio, soil pH, soil structure and soil organic matter (Gioacchini *et al.*, 2006) and is often limiting in organic systems. In contrast, soil mineral nitrogen, such as ammonia, is very high immediately after application of conventional fertilisers (Gioacchini *et al.*, 2006). Given that the majority of nutrient

uptake in barley occurs early in the season (Montemurro *et al.*, 2006) and modern varieties are bred to respond well to conventional fertilisers (Dawson *et al.*, 2008) it is not surprising that yields were higher in conventionally fertilised pots. In Europe, cereal yields in organic systems are typically 60-70% that of conventional systems (Mader *et al.*, 2002) and fertiliser regime may be an important factor.

It is worth noting that as for chicken manure, hoof and horn application resulted in lower yields than conventional fertilisers. However, the difference between conventional and hoof and horn treatments was not significant in either 2007 or 2008. A soil incubation experiment revealed that temporal nutrient availability between horn meal and chicken manure was different and horn meal resulted in higher rye grass yields in a pot experiment (Cordovil and Cabral, 2001). Moreover, in a field trial, soil mineral nitrogen was higher in horn meal amended soils than those amended with cow manure and it was concluded that organically bound nitrogen was more readily available from horn meal than cow manure (Hasse *et al.*, 2006). This experiment indicates that nutrient release from hoof and horn meal is better synchronised with barley demand than chicken manure irrespective of the timing of application. Similar findings were reported by Cordovil and Cabral (2001) with differing nutrient release rates and subsequent Ryegrass growth under the same two fertilisers.

The present study indicated that it is barley tiller number that is more important in determining yield than ear weight. This is demonstrated by the significant effects of fertiliser treatments on tiller numbers while individual ear weight is unaffected. Nitrogen is important for cereal tiller production (Honek, 1991b; Duffield *et al.*, 1997) and higher nitrogen availability early in plant development in conventionally fertilised pots may have promoted tillering.

In 2008, a significant effect of field site on yield was found. Soil structure was very similar between sites but the base levels of nitrate, potassium and phosphorus were all higher in Silwood Bottom (Table 3.1), probably resulting in the higher yields found there.

4.5.1.2 Barley morphology

Resource distribution in barley plants was significantly affected by fertiliser treatments in this study. In 2008, there was no significant effect of fertiliser on individual plant yield but vegetative biomass represented by stem mass was higher in conventional pots when compared with both organic and control pots. Furthermore, on three of the dates measured, leaf area was higher in conventional pots than either organic or control pots. Therefore the application of conventional fertilisers promotes vegetative growth in barley, whilst ear production is not so affected. This is probably due to increased nitrogen availability following the application of conventional fertilisers. Increasing nitrogen inputs in the field have been shown to result in increased cereal biomass and larger leaves, whilst ear weights were not affected (Honek, 1991b). Total barley leaf area per tiller was also increased following fertiliser application (Duffield *et al.*, 1997). Honek (1991a) found that barley in nutrient rich soil invested more resources in leaf materials and tillers, whilst barley in nutrient poor soil invested more resources in ear production. Given that early nitrogen application increases vegetative growth (Dawson *et al.*, 2008), the contrast in temporal availability of nitrogen between organic and conventional fertilisers explains the different morphologies of barley grown under different fertiliser regimes. Controlled application of nitrogen fertilisers to minimise vegetative growth whilst maintaining yields is a potential asset in cereal agriculture (Duffield *et al.*, 1997). Although it must be remembered that nitrogen accumulated in plant vegetative tissues is an important source of grain nitrogen at ripening (Montemurro *et al.*, 2006).

4.5.1.3 Barley leaf colour

The leaf attractivity index is based on the measured leaf wavelength spectra (Doring *et al.*, 2008). It incorporates the amount of light reflected by the leaf in the blue, green and UV regions of the spectrum and quantifies this as a relative attractivity to aphids. This measure was used because it enables direct statistical comparisons between leaf spectral reflectance and does not rely on arbitrary quantification of leaf yellowness or greenness by the observer. A high attractivity index found in this study would be interpreted as yellow by the human eye (pers comm., T. Doring, 2008).

Throughout the growing season in the present study, barley plants had a consistently higher attractivity index, or were yellower, in control pots. This was followed by plants in organic and then conventional pots. Leaf reflectance was particularly divergent on 4/6/2008. The differences in leaf colour probably represent the difference in nutrient, and particularly nitrogen, availability between fertiliser treatments. In winter wheat, nitrogen application, leaf nitrogen content and leaf chlorophyll, measured by a SPAD Chlorophyll Meter, were all positively correlated (Fox *et al.*, 1994). Given that chlorophyll makes up the green component of leaf material, this dictates that nitrogen availability determines leaf colour. Many studies have shown that crop nitrogen content is consistently higher in conventionally fertilised systems when compared to organic systems (Altieri and Nicholls, 2003). This would result in consistently greener leaves in conventionally fertilised systems where soil nutrients are more readily available to the plant; a result found in the present study.

4.5.2 Aphids

4.5.2.1 Aphid abundance

In 2007, aphid numbers were very low and variation between pots was high, subsequently no significant treatment effects were found. In 2008, aphid numbers were again relatively low when compared with the economic injury level of seven aphids per tiller at the population peak for *S. avenae* on wheat (Larsson, 2005), a control threshold of 137 aphid days per tiller for *R. padi* on spring barley (Hansen, 2000) and a damage threshold of 15 aphids per tiller for *M. dirhodum* on spring cereals (Oakley and Walters, 1994). There was, however, a significant effect of fertiliser treatment on aphid days per tiller with numbers significantly greater in conventionally fertilised pots when compared with organically fertilised pots. Nitrogen availability can alter phloem amino acid composition which can affect cereal aphid performance. *Rhopalosiphum padi* intrinsic rate of increase was lower on nitrogen restricted barley (Weibull, 1987; Ponder *et al.*, 2000) and apterous *R. padi* on wheat receiving high doses of ammonium nitrate were more fecund (Khan and Port, 2008). Aphid feeding behaviour is also affected by phloem nitrogen content (Ponder

et al., 2001). Increased aphid numbers following nitrogen application in the field have been found in numerous studies (Honek, 1991b; Gash *et al.*, 1996; Duffield *et al.*, 1997). The increased availability of nitrogen early in the season following application of conventional fertilisers in the present study may have improved the nutritional quality of barley phloem sap. This may have improved aphid population growth, resulting in larger aphid populations through the season, represented by greater numbers of aphid days per tiller.

Rhopalosiphum padi appears particularly responsive to the temporal availability of nutrients given that there is a significant fertiliser application timing effect on this species alone; aphid days was positively associated with top dressed fertilisers. There are highly soluble components of organic fertiliser, such as ammonia, that can be considered as accessible to the plant as conventional fertilisers (Sieling *et al.*, 2006) even if they do not constitute such a large proportion of total nutrients. Gioachini *et al.* (2006) found nitrate levels increased rapidly following application of slow release organic fertilisers. High levels of available nitrogen immediately after application of both organic and conventional fertilisers may have contributed to the response shown by *R. padi*.

4.5.2.2 Barley morphology and aphid abundance

In 2008, *M. dirhodum* per unit plant mass correlated positively with plant biomass allocation to stems and leaves. No such significant effect was found for *R. padi* and *S. avenae*. In fact, in both years *S. avenae* was negatively correlated with the proportion of stem and leaf mass. *Metopolophium dirhodum* is a leaf feeding aphid (Watt, 1979) and a positive response to resource allocation to the leaves and stem would be expected. Honek (1991a) and Honek and Martinkova (2002) have found that *M. dirhodum* numbers are higher on wheat and barley with bigger leaves. In another study, the increased number of *M. dirhodum* following fertiliser application was attributed to changes in barley morphology (Honek, 1991b). The same effects of morphology on *S. avenae* was not found and this was because, in concurrence with this study, fertiliser treatment and soil nutrients did not effect ear growth (Honek,

1991b; Honek, 1991a) which is the preferred feeding site of *S. avenae* (Watt, 1979; Walters and Dixon, 1982).

4.5.2.3 Barley leaf colour and aphid abundance

Pre-alighting behaviour in aphids is photo-tactic (Powell *et al.*, 2006) and yellow is considered to be an attractive colour, relative to green, brown and red (Doring and Chittka, 2007). Thus, the model proposed by Doring *et al.* (2008) establishes an attractivity index with the most attractive reflectance spectrum to an aphid appearing yellow to the human eye. Experimental evidence has found many cereal aphid species to be attracted to yellow stimulus, including *Rhopalosiphum maidis*, *Schizaphis graminum* and *S. avenae*, with *R. padi* showing varied responses (Doring and Chittka, 2007). The increased colonisation of barley by *R. padi* in potassium deficient soils was attributed, in part, to an alate preference for yellow leaves (Havlickova and Smetankova, 1998).

Results from the present study demonstrate a negative correlation between leaf attractivity or yellowness and aphid populations represented as aphid days per tiller. If aphid visual preference dictated aphid numbers then these findings would contradict current theory. Many other factors determine aphid populations however, including the nutritional quality of the host. High foliar nitrogen resulted in increased aphid numbers (Bado *et al.*, 2002) and leaf chlorophyll content correlates with *M. dirhodum* abundance in wheat, barley and oats (Honek and Martinkova, 2002). Both chlorophyll and nitrogen content, a major component of chlorophyll (Fox *et al.*, 1994), would make leaves appear more green and explain why in the present study higher aphid populations are found on plants with a lower attractivity index. Furthermore, aphid host selection is not determined solely by colour. Olfactory cues are important to landing (Pickett *et al.*, 1992; Quiroz and Niemeyer, 1998) and the decision to remain and reproduce is gustatory, where primary metabolites are often important cues (Powell *et al.*, 2006). The preference for yellow plants shown by aphids is surprising given that green plants are of greater nutritional value. An evolutionary relic may be the reason, the attractiveness of yellow may actually be a result of aphids evolving to avoid brown un-nutritious leaves (Doring and Chittka, 2007).

Nevertheless the attractiveness of yellow plants has implications for pest management. Although not seen in the present study due to the low number of alate aphids, the yellower leaves produced by control and organically fertilised barley may be more attractive to aphids, which is of particular importance when virus vectors are considered. Reflex probes are made soon after landing and will determine whether the aphid will stay and reproduce and viruses can be transmitted even if the aphid decides the host is unsuitable for reproduction (Powell *et al.*, 2006). The organically fertilised cereals may prove more attractive to alate virus vectors and will be more readily infected with the virus even if aphid populations are lower because the host is morphologically or nutritionally less suitable and the aphid does not remain to establish a colony. This is important because viruses considerably reduce yield in spring sown cereals (Mann *et al.*, 1997).

4.5.3 Natural enemies

4.5.3.1 Parasitoids

Results from the present study indicate no significant effect of fertiliser on parasitoid numbers although the number of mummies encountered was very low. Mummy numbers counted in this trial appeared to match that of aphid numbers with a time lag but it is difficult to infer the impact of parasitoids on an aphid population from mummy counts alone. A more accurate method is to determine percentage parasitism by rearing through a portion of the aphid population (Sigsgaard, 2002; Lumbierres *et al.*, 2007). Dean *et al.* (1981) stresses the importance of collecting and rearing both aphids and mummies from field populations if impact is to be inferred. Collecting aphid sub-populations was not possible in the present study given the low numbers of aphids encountered and removal of part of the population would have influenced subsequent population development within the confines of one plant pot.

In the present work, a positive correlation was found between mummy numbers and aphid numbers and given that parasitism is density dependent (Pareja *et al.*, 2007) and parasitoids search longer on host infested plants and respond to host induced volatiles (Schworer and Volkl, 2001), it is unsurprising that parasitoid numbers were higher on

plants infested with more aphids. Soil nutrient effects on parasitoid numbers mediated through fertiliser effects on host numbers has been found in other studies (Wurst and Jones, 2003; Krauss *et al.*, 2007).

Fertiliser can affect not just parasitoid abundance, but also their development and reproduction. Increasing nitrogen inputs can increase size, reduce development time (Kaneshiro and Johnson, 1995) and increase egg load (Jiang and Schulthess, 2005). Although these effects were not measured during this study, other effects of fertiliser on plant morphology and colour suggest an increased availability of nitrogen in plants in conventionally fertilised pots and it could be hypothesised that parasitoids emerging from conventionally fertilised pots, although not more numerous, may be fitter. Further experimentation would be needed to confirm this.

4.5.3.2 Syrphids and coccinellids

Syrphid egg numbers were affected by fertiliser treatment; greater numbers of eggs were found in conventionally fertilised pots. Aphidophagous syrphid oviposition site selection can be classed as primarily aphidozetic, where egg laying is determined by characteristics of the host colonies, or phytozetic, where oviposition is determined by features of the host plant (Chandler, 1968). *Episyrphus balteatus* was found to preferentially lay eggs near young colonies of aphids characterised by more first instar nymphs and fewer alates (Kan, 1988). The increased number of eggs on the conventionally fertilised barley found in the present study may reflect fertiliser effects on aphid colony structure. Due to increased availability of nutrients, aphid colonies may have been growing more rapidly and were the preferred oviposition site for female syrphids. Certainly there were few aphid colonies that resembled the well developed, unfavoured colonies involved in Kan's (1988) experiment and thus a positive correlation between egg and aphid numbers was found.

Fertiliser effects on barley characteristics may have also been important in determining syrphid egg density given that plant colour and structure were dependent on fertiliser treatment. The preference of a dense moist canopy for female syrphid oviposition was the proposed cause of high numbers of eggs under high fertiliser

treatments in wheat (Hasken and Poehling, 1994 cited by Hansken and Poehling (1995)). Increased tiller number and leaf area will have created a denser canopy in the conventionally fertilised pots involved in the present study and affected syrphid egg laying accordingly.

4.6 Conclusion

Barley plant morphology, leaf colour and subsequent yield were all significantly affected by fertiliser treatment. Plants were greener, had more vegetative mass and produced larger yields following application of conventional fertilisers. This reflects the increased availability of plant nutrients from these fertilisers when compared with organic slow release fertilisers. Barley is a fast growing annual which assimilates considerable nutrients early in the season (Montemurro *et al.*, 2006). The release of much of the nutrients from organic fertilisers is often delayed until the next season (Sieling *et al.*, 2006). Organic fertilisers can also influence soil quality by improving structure, moisture content and buffer pH (Phelan *et al.*, 1995) as well as affecting micro nutrients (Courtney and Mullen, 2008). These benefits of organic fertilisers may not have been observed given that fertilisation in the present study was only carried out for one season. If these contrasting fertiliser had been maintained for several seasons the yield gap between the organic and conventional treatments may have diminished.

Aphid numbers were greater in conventionally fertilised pots probably due to increased nitrogen availability to their plant hosts. The basis of the positive response of aphids to nitrogen appeared to be dependent on species. *Metopolophium dirhodum* was influenced by fertiliser effects on plant morphology, while *R. padi* was affected by the temporal availability of nutrients, reflected by the significant fertiliser application timing effect. This has implication for the control of both of these species. Canopy management of cereals (Duffield *et al.*, 1997) through the use of organic or carefully timed application of conventional fertiliser may reduce the abundance of *M. dirhodum*. Application of organic slow release fertilisers before planting may help control *R. padi* outbreaks by minimising nutrient availability at critical periods in aphid population growth. Fertiliser application decisions will then depend on what

aphid species is the primary pest of crops in that locality or in that year. The low number of aphids encountered during this field trial may have masked some effects of fertiliser on abundance. The limits of inferring fertiliser effects on aphids when populations are low are highlighted by studies from Gash (1996) and Duffield (1997). It would be interesting to see what happens in outbreak years when nutrients are more limiting or aphid population were above the damage threshold and having significant impacts on yield. Moreover, the effects of fertiliser on aphid preference, mediated through leaf colour, might be observed with higher numbers of immigrating alates.

The abundance of parasitoids appears to be determined by aphid abundance and not directly by fertiliser application. This link between parasitoid and aphid abundance has been recorded before (Wurst and Jones, 2003; Krauss *et al.*, 2007; Pareja *et al.*, 2007). The increased impact or abundance of parasitoids recorded in low input systems (Drinkwater *et al.*, 1995; Berry *et al.*, 1996; Hossain *et al.*, 2002; Hummel *et al.*, 2002) may be a result of increased pest abundance and it may not be due to contrasting fertiliser regimes but other management practices or landscape effects (Roschewitz *et al.*, 2005). Fertiliser effects on either plant biology or aphid colony development appear to influence syrphid oviposition which will in turn influence the level of control achieved by these species. Manipulating the cereal canopy through correct fertiliser application may promote control by syrphids but the correlation between syrphids and aphids may dictate that abundant syrphids in conjunction with scarce aphid populations cannot be achieved. Syrphids will, however, oviposit in the absence of a host (Kan, 1988) indicating plant characteristics alone can be important for phytozetic species.

Chapter 5

The effects of organic and conventional fertilisers on the performance of the cereal aphids *Rhopalosiphum padi* and *Metopolophium dirhodum* in the laboratory

5.1 Introduction

Metopolophium dirhodum and *R. padi* are important aphid pests of barley (Mann *et al.*, 1997). Cereal aphid abundance in the field has been shown to be affected by fertiliser treatment, with increases in conventional nitrogen application resulting in larger aphid populations; this is true for both *M. dirhodum* (Hasken and Poehling, 1995; Duffield *et al.*, 1997) and *S. avenae* (Honek, 1991b; Gash *et al.*, 1996). Reasons include changes in plant structure and improved nutritional quality of host plants following fertiliser application. Numerous studies have shown that plant nutrition affects cereal aphid performance in the laboratory, through differences in plant age (Leather and Dixon, 1981; Weibull, 1987; Zhuo and Carter, 1992) or location of aphid feeding on the cereal plant (Watt, 1979; Leather and Dixon, 1981). Studies investigating the direct effects of fertiliser on cereal aphid performance in controlled environments are less numerous. *Rhopalosiphum padi* was found to perform poorly on plants under reduced nitrogen inputs in the laboratory (Ponder *et al.*, 2000; Khan and Port, 2008).

Organic fertilisers often contain low proportions of plant available nutrients initially but instead release nutrients slowly through the plant growing season (Montemurro *et al.*, 2006). Conversely, conventional fertilisers contain high levels of inorganic

nutrients which are readily available to the plant (Mengel *et al.*, 2006). The timing of the application of both these fertiliser types will therefore be important for barley growth and for the response of aphids to fertiliser treatments. In the field, aphid numbers have been reported to be lower on organically fertilised barley plots when compared with those fertilised conventionally (Helenius, 1990; Bado *et al.*, 2002). However, in neither of the above studies were the organic and conventional fertilisers matched with respect to the total amount of nutrient added. There is a need therefore, to compare the effects of organic and conventional fertilisers on cereal plants and their aphid hosts while controlling for the amount of nutrients added to the system. Carrying out experiments in the absence of environmental variation and considering fertiliser effects alone is important in trying to understand the impact of plant nutrients on arthropod pests.

Numerous measures of relative aphid performance exist, including mean relative growth rate (MRGR), adult weight, development time, fecundity, longevity, intrinsic rate of increase (r_m) (Awmack and Leather, 2007) and reproductive potential (Leather, 1988). These measures have been used to determine effects of temperature (Zhuo and Carter, 1992), host growth stage and feeding position (Watt, 1979; Leather and Dixon, 1981) on cereal aphid performance. This information is useful when establishing resistant varieties of cereals (Leszczynski *et al.*, 1989) or attempting to model aphid populations in the field (Zhuo and Carter, 1992) which is crucial information for effective pest control. Some performance measures more accurately predict aphid fitness than others. Mean relative growth rate correlated significantly with seven-day fecundity and r_m for *R. padi* (Leather and Dixon, 1984), while adult weight showed no such relationship, although this correlation was dependent on host (Leather, 1989). For many other aphid species, adult weight and fecundity do correlate (Leather, 1988). The accuracy of determining potential fecundity by counting un-laid nymphs in adults is dependent on the reproductive biology of the aphid species (Leather, 1988) and the use of r_m does not accurately predict fitness in all aphid species (Awmack and Leather, 2007). Nonetheless, when it is too time consuming or impractical to allow an aphid population to grow to capacity in the laboratory, relative measures of aphid performance must be used.

5.2 Aims and objectives

The aim of this study was to investigate whether different fertilisers and the timing of their application influences the performance of different cereal aphid species and whether the response of these species is dependent on what parameter is used to quantify their performance.

The objectives of this series of experiments were to: 1) Investigate how organic and conventional fertilisers and host plant age affect *Metopolophium dirhodum* performance in a controlled environment. 2) Investigate how different aphid performance measures differ in their response to treatment effects. 3) Investigate how host plant age and the timing of fertiliser applications interact to affect two different aphid species, *M. dirhodum* and *R. padi*. 4) Investigate the effect of fertiliser type and timing on barley growth.

5.3 Materials and methods

5.3.1 Experiment 1: Effects of barley growth stage and fertiliser treatment on *Metopolophium dirhodum* in a high nutrient base compost

5.3.1.1 Potting procedure

Spring barley (cv. Doyen) was grown in seed trays containing John Innes seed compost supplied by 'Wyevale®, Sunningdale, Berkshire'. When the barley had reached the two leaf growth stage, plants were transferred to fertiliser amended plant pots measuring 11 cm across the top and 9 cm deep. Pots also contained John Innes seed compost. Until aphid experimentation began, barley was grown in a controlled temperature glasshouse with day and night temperatures of $20\pm 5^{\circ}\text{C}$ and $14\pm 5^{\circ}\text{C}$ respectively, and a 16:8 h day:night regime. Plant pots were kept in water trays, base

watered regularly and soil was not allowed to dry out. For aphid experimentation, pots were transferred to a controlled temperature (CT) room.

5.3.1.2 Aphid culture

Before experiments began, *M. dirhodum* stock cultures were reared on spring barley grown in John Innes seed compost. Cultures were maintained in a CT room at 20°C with a 16:8 h day:night regime at 70% humidity. The original holocyclic *M. dirhodum* clone was taken from long standing aphid cultures at Rothamsted Research, Harpenden, Hertfordshire.

5.3.1.3 Fertiliser treatments

The experiment consisted of five fertiliser treatments: two organic, two conventional and a control. The first organic treatment involved chicken manure (cm) fertiliser containing nitrogen, potassium and phosphorus supplied by 'Greenvale®'. The second organic treatment was hoof and horn meal (hh) fertiliser containing nitrogen and supplied by 'Monro Horticulture LTD, Goodwood, West Sussex'. Two conventional treatments were established to match the nutrient content of both the hoof and horn and chicken manure treatments (Table 5.1). For the conventional fertiliser treatment equivalent to the chicken manure (conventional(cm)), nitrogen, potassium and phosphorous were applied as ammonium nitrate, potassium sulphate and super phosphate. For the conventional fertiliser treatment equivalent to hoof and horn (conventional(hh)), ammonium nitrate alone was applied. Fertiliser was applied to individual pots containing John Innes seed compost and thoroughly mixed in before transplantation of barley plants. Control pots remained un-amended. See Table 5.1 for details of the amount of fertiliser applied for each treatment. Ten barley plants were transplanted to 10 pots for each of the five treatments.

Table 5.1 Experiment 1 - The percentage nutrient content of the fertilisers used, the amount of nitrogen, phosphorus and potassium added under each treatment and the mass of fertiliser required to supply these nutrient doses.

Treatment	% content	Active ingredient (g)			Mass of fertiliser added (g)
	N:P:K	N	P	K	
Control	0:0:0	0	0	0	0
Chicken manure	4.5:3:3	0.5	0.33	0.34	11
Hoof and horn	13:0:0	0.5	0	0	3.8
Conventional(cm)	34.5:18:48	0.5	0.33	0.34	N – 1.45 P – 1.8 K – 0.7
Conventional(hh)	34.5:0:0	0.5	0	0	N – 1.45 P – 0 K – 0

5.3.1.4 Clip cage procedure

Four separate clip cage experiments were carried out to measure the effect of fertiliser treatment on *M. dirhodum* on barley. Plants starting at four different growth stages were used; the three leaf stage (GS13), early tillering (GS21), early stem elongation (GS31) and flag leaf emergence (GS40+). All growth stages were measured according to the decimal code of Tottman and Broad (1987). For each experiment 10 clip cages (MacGillivray and Anderson, 1957) on 10 plants for each of the five fertiliser treatments were used. Round clip cages made from Perspex and muslin with a diameter of 3 cm were attached to canes using a rubber band and then clipped to the first leaf down from the lead leaf on the primary tiller of each plant. One alate *M. dirhodum* aphid was taken from the stock culture and placed in each clip cage. After 24 h the cage was checked and if the alate had deposited any nymphs on the leaf then one was randomly selected as the experimental aphid. All other nymphs and the alate were then removed from the cage. If no nymphs were produced by the alate, the alate was replaced and the clip cage was left undisturbed for a further 24 h before being checked again.

Following establishment of the experimental nymph, clip cages were visited every 24 h to measure aphid progress. Five separate measures of aphid performance were taken; seven-day fecundity, intrinsic rate of increase, total reproductive output, mean nymph weight and adult weight.

Seven-day fecundity was determined by counting the number of nymphs produced by each aphid from day two to day eight of aphid reproductive age; the sum total of these nymphs equates to the seven-day fecundity. Day one nymphs were not counted because the length of time the experimental aphid had been producing offspring within the first 24 h period was unknown.

The intrinsic rate of increase (r_m) is a measure of future population growth rate and incorporates both development rate and fecundity (Wyatt and White, 1977). To establish the r_m for the experimental aphids, the number of nymphs produced by each aphid was counted for the number of days that it took for the experimental aphid to reach reproductive age. This combined with the developmental rate in days can be used to calculate r_m using the following formula:

$$r_m = 0.738(\log_e dD)/d$$

Where D is the number of days to reach reproductive age and d is the number of offspring produce in D days (Wyatt and White, 1977).

Aphid total reproductive output is a measure of the total biomass produced by an experimental aphid in seven-days. Nymphs produced by experimental aphids were collected each day and weighed to the nearest microgram on a 'Sartorius micro-balance®'. As with seven-day fecundity, nymphs were collected only from days two to eight given the indefinite period of reproduction in day one and the variable and possibly unrepresentative nature of the first few nymphs produced by an aphid (Dixon *et al.*, 1993). The sum weight of the nymphs collected is the total reproductive output.

Mean nymph weight was determined by dividing the total nymph weight collected for each daily cohort by the number of nymphs in that cohort. The mean of these weights from day two to eight equates to the mean nymph weight.

Finally, to establish adult weight, at the end of each experiment the experimental aphid was collected and weighed on a micro-balance. All clip cage experiments were laid out in a fully randomised block and undertaken in a CT room at 20°C with a

constant light:dark regime of 16:8 h. Any experimental aphids that died or were lost during the experiment were excluded from all analysis.

5.3.1.5 Statistical analysis

An ANOVA model was used to determine any growth stage effects and any consistent fertiliser effects across all growth stages on the five measures of aphid performance. Reproductive output, r_m , nymph weight and adult weight are all continuous responses and were normally distributed. Despite being non-continuous, inspection of the data found seven-day fecundity to be normally distributed and model checking confirmed that seven-day fecundity require no transformation. If no fertiliser effects were found in the initial model, separate analyses were carried out for each of the four growth stages. To establish significant differences between fertiliser and growth stage means, a Tukey honest significant difference test was performed. Results for reproductive output, r_m , and adult weight are presented as graphs and results for seven-day fecundity and mean nymph weight are referred to in the text.

Following initial analysis of fertiliser treatment effects if no significant response was found, the treatments were logically grouped, first into organic, conventional and control and then into fertiliser or no fertiliser treatments. The blocked groups were analysed using a Tukey test.

Fertiliser treatment effects on barley tiller numbers were compared using an ANOVA followed by a Tukey test. Tiller numbers from plants at each of the four growth stages were analysed separately. Tiller number is a discontinuous response variable but inspection of the data and model checking showed no transformation was needed.

The correlation between adult weight, nymph weight and r_m , and between adult weight and total reproductive output were examined using linear regression analyses. For these analyses, data from all four clip cage experiments was combined. All statistical analyses were carried out using the statistical programme 'R' version 2.7.1 (Ihaka and Gentleman, 1996).

5.3.2 Experiment 2: Effect of barley growth stage, fertiliser treatment and time of application on *Metopolophium dirhodum* and *Rhopalosiphum padi* performance

5.3.2.1 Potting procedure

Spring barley (cv. Doyen) plants were grown from seed in fertiliser amended plant pots measuring 9 cm by 11 cm. The compost used was produced by 'Monro Horticulture' and was composed of 55% sand, 30% loam and 15% peat. Plants were kept in a controlled light and temperature glasshouse until experimentation as in Experiment 1. Twelve barley plants were grown under each of the five fertiliser treatments.

5.3.2.2 Aphid culture

Metopolophium dirhodum aphids were taken from stock cultures (see Experiment 1). *Rhopalosiphum padi* cultures were maintained on spring barley plants grown in John Innes seed compost in CT rooms as for *M. dirhodum*. The holocyclic *R. padi* clone was taken from long running cultures at Rothamsted Research.

5.3.2.3 Fertiliser treatments

The five fertilisers treatments used in Experiment 2 were the same as those used for Experiment 1: chicken manure, hoof and horn and their conventional equivalents and a control. The amounts of each fertiliser applied was different to that of Experiment 1, see Table 5.2 for details. Dose rates for experiment 2 were based on applying 100kg N/ha and considering the surface area of the pots. The dose rates in experiment 1 were considerably higher and, based on results from initial trials, were designed to elicit a response in plants and aphids even in a high nutrient compost base. To investigate whether the timing of fertiliser application affects aphid performance, two fertiliser application methods were used. One involved grinding up measured quantities of each fertiliser in a pestle and mortar and mixing this with the compost

substrate in pots prior to planting. The second application method involved grinding up fertilisers but the application of these was made to the surface of each pot when the barley plant was at the two leaf stage (GS12). Twelve plants under each fertiliser treatments and at both application methods were grown.

Table 5.2 Experiment 2 - The percentage nutrient content of the fertilisers used, the amount of nitrogen, phosphorus and potassium added under each treatment and the mass of fertiliser required to supply these nutrient doses.

Treatment	% content	Active ingredient (g)			Mass of fertiliser added (g)
	N:P:K	N	P	K	
Control	0:0:0	0	0	0	0
Chicken manure	4.5:3:3	0.2	0.13	0.13	4.35
Hoof and horn	13:0:0	0.2	0	0	1.5
Conventional(cm)	34.5:18:48	0.2	0.13	0.13	N – 0.57 P – 0.72 K – 0.27
Conventional(hh)	34.5:0:0	0.2	0	0	N – 0.57 P – 0 K – 0

5.3.2.4 Clip cage procedure

The objective of Experiment 2 was to investigate the effects of organic and conventional fertilisers on aphid performance and whether this is dependent on host plant growth stage or the timing of fertiliser application. Separate clip cage experiments were carried out on barley starting at the early tillering (GS21) and early stem elongation (GS31) stages under each of the fertiliser application methods. The first application method involved applying fertiliser with the seed at planting, hence forth referred to as ‘seed applied’. The second application method involved application of fertilisers to the surface of plant pots when barley was at the two leaf stage of development, referred to as ‘two-leaf applied’ from now on. To investigate whether aphid response to fertiliser application time and plant age is species specific, *R. padi* and *M. dirhodum* were tested in separate clip cage experiments at growth stage 21. At growth stage 31 both species were studied on the same plants in different clip cages and on different leaves.

The seven-day fecundity, r_m and adult weight were all measured using the same methods as described for Experiment 1. The reproductive output and mean nymph weight were calculated differently due to time constraints. Nymphs were not collected on each consecutive day of the experiment. Instead nymphs were collected and weighed on the third and seventh day of reproduction. A mean nymph weight could then be calculated and a theoretical reproductive output established. Third and seventh day nymphs were chosen because they would represent nymphal weights early and later in the reproductive age of the experimental aphids. Preliminary work had shown that nymph weights on the third and seventh day correlated significantly with overall mean nymph weight over seven days. All experiments were again carried out in fully randomised blocks in CT rooms at 20°C with a light:dark regime of 16:8 h.

5.3.2.5 Plant performance

As well as examining the performance of different aphid species under different fertiliser treatments and application methods, the response of the experimental barley plants was also measured. The tiller number of barley plants at the end of the clip cage experiment on stem elongating (GS31) barley was recorded. Plant material was then collected and dried for 48 h in a 60°C oven and above ground plant material was weighed to establish plant biomass.

5.3.2.6 Statistical analysis

Clip cage experiments involving each fertiliser application method, barley plant age and aphid species were analysed separately. Tukey tests following ANOVA were used to determine significant differences between treatment means for all aphid performance parameters as in Experiment 1. Similarly to Experiment 1, reproductive output, r_m and adult weight are presented as graphs whilst seven-day fecundity and mean nymph weight are referred to in the text. Effects of fertiliser treatments on plant tiller number and biomass were also compared using ANOVA followed by a Tukey test. Initial inspection revealed positive skew in the plant data, therefore both plant biomass and tiller number were log transformed before analysis. All statistical

analyses were carried out using the statistical programme 'R' (Ihaka and Gentleman, 1996).

5.4 Results

5.4.1 Experiment 1: Effects of barley growth stage and fertiliser treatment on *Metopolophium dirhodum* in a high nutrient base compost

5.4.1.1 *Metopolophium dirhodum* performance

An effect of barley growth stage on seven-day fecundity was found ($F_{3,156} = 8.70$, $P < 0.001$), with seven-day fecundity significantly lower for *M. dirhodum* on GS13 than either GS21 or GS31 barley. Mean nymph weight was also affected by growth stage ($F_{3,156} = 10.10$, $P < 0.001$) with significantly lower weights found at GS13 and GS40 when compared with GS21 and GS31. The same effect of growth stage on total reproductive output was found ($F_{3,156} = 11.80$, $P < 0.001$) (Fig. 5.1a), with significantly lower values for GS13 and GS40 compared with GS21 and GS31. There was a significant growth stage effect on intrinsic rate of increase ($F_{3,156} = 2.72$, $P < 0.05$) (Fig. 5.1b) but this yielded no significant differences between growth stage means according to the Tukey test. Adult weights followed the same pattern as both mean nymph weight and total reproductive output ($F_{3,150} = 8.03$, $P < 0.001$) with weights on barley at GS21 and GS31, significantly greater than weights on GS13 and GS40 (Fig 5.1c).

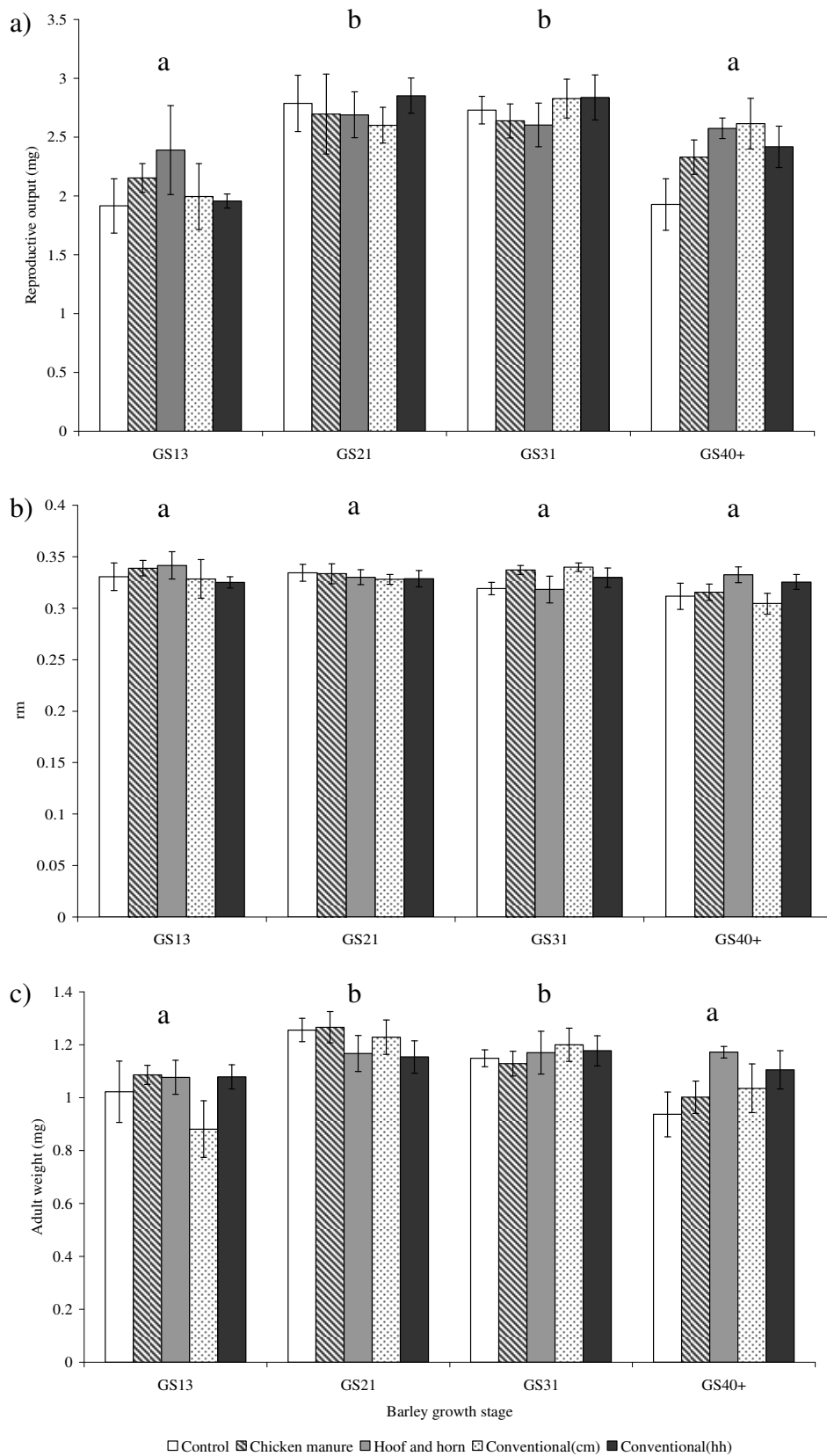


Fig. 5.1 The a) Total reproductive output b) Intrinsic rate of increase and c) adult weights of *Metopolophium dirhodum* on barley plants at four growth stages grown under five fertiliser treatments (mean \pm SEM). Growth stages with different letters are significantly different (Tukey, $P < 0.05$).

There were no significant effects of fertiliser treatment on the intrinsic rate of increase (Fig. 5.1b) or adult weight (Fig. 5.1c). Significant fertiliser effects were however, found for seven-day fecundity, total reproductive output (Fig. 5.1a) and mean nymph weight. At GS40, aphids on plants receiving fertiliser treatments had significantly higher seven-day fecundity than aphids on control plants ($F_{1,36} = 6.17, P < 0.05$). Organic and conventional fertilisers also showed significantly higher total reproductive outputs than the control treatment at GS40 ($F_{2,36} = 4.24, P < 0.05$) (Fig 5.1a). On barley at GS40, aphids produced larger nymphs on plants receiving conventional fertilisers than those on control plants ($F_{2,36} = 3.34, P < 0.05$).

5.4.1.2 Plant performance

There were significant fertiliser effects on barley tiller numbers at growth stages 21, 31 and 40 (Fig. 5.2). The conventional(cm) treatments resulted in significantly higher tiller numbers than the hoof and horn and conventional(hh) treatments at GS21 ($F_{4,45} = 5.22, P < 0.01$). All fertiliser treatments resulted in significantly higher tiller numbers than the control plants at GS31 ($F_{4,45} = 7.94, P < 0.001$). The same was true at GS40+ ($F_{4,45} = 11.63, P < 0.001$) with the addition of one more significant effect, the number of tillers found on plants receiving the conventional(cm) treatments were significantly higher than the number of tillers found on plants receiving hoof and horn fertiliser.

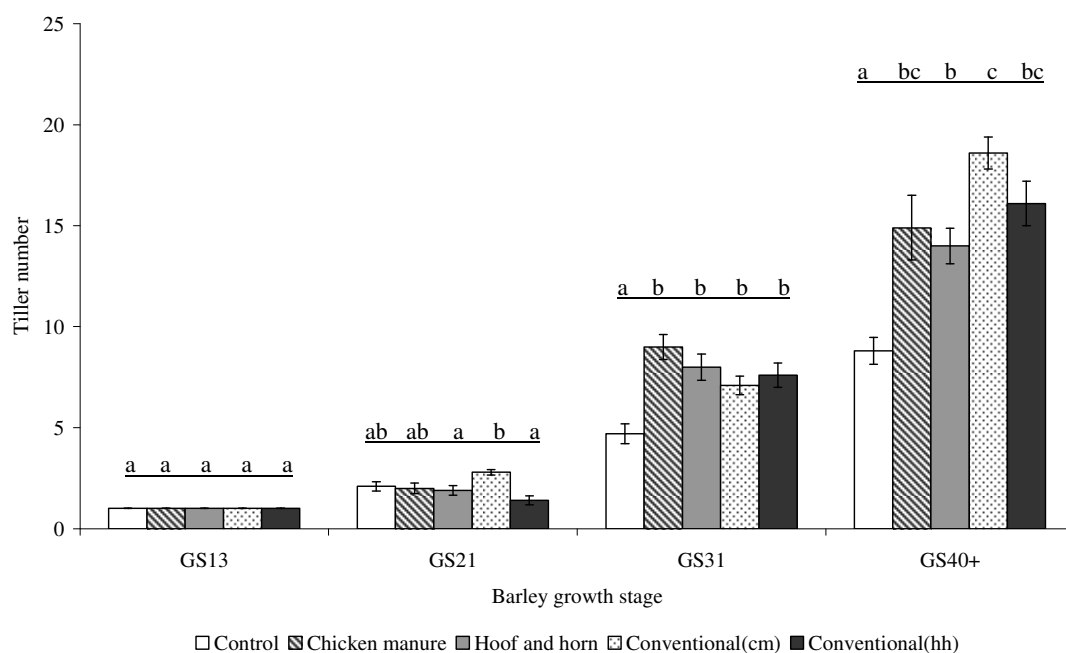


Fig. 5.2 Barley tiller numbers under five fertiliser treatments at four growth stages at the start of each clip cage experiment (means \pm SEM). Fertiliser treatments with different letters are significantly different within each growth stage block (Tukey, $P < 0.05$).

5.4.1.3 Aphid performance measures

Both adult weight ($R^2 = 0.24$, $F_{1,156} = 48.61$, $P < 0.001$) and nymph weight ($R^2 = 0.081$, $F_{1,162} = 14.27$, $P < 0.001$) correlated positively and significantly with r_m (Fig. 5.3 & 5.4). Adult weight was also significantly positively correlated with total reproductive output ($R^2 = 0.45$, $F_{1,156} = 126.3$, $P < 0.001$) (Fig. 5.5).

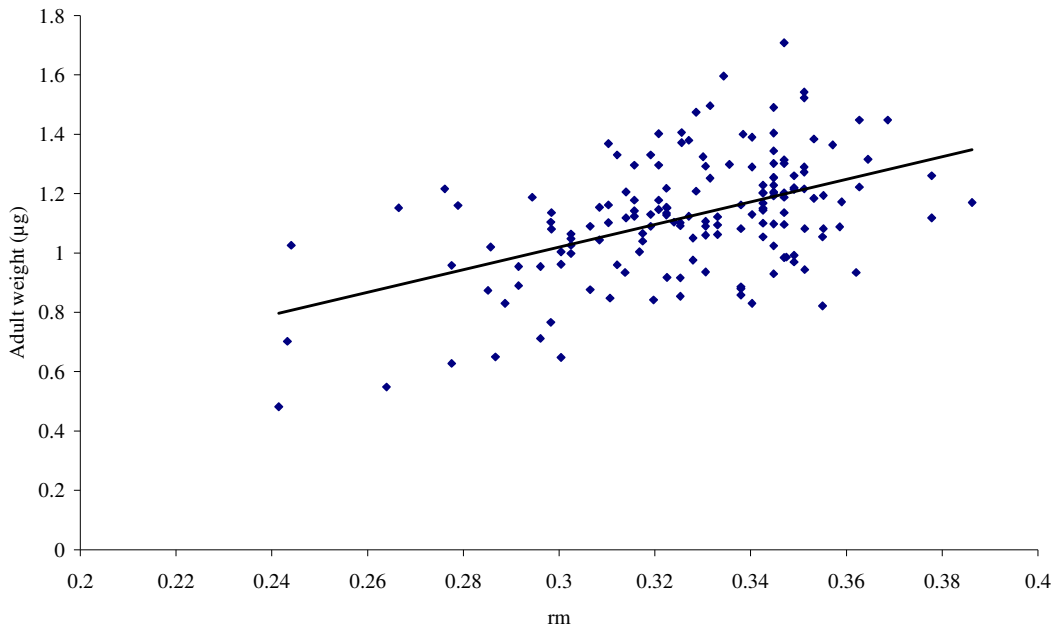


Fig. 5.3 Relationship between *Metopolophium dirhodum* adult weight and intrinsic rate of increase (r_m) on spring barley ($y = 0.81x + 0.12$, $R^2 = 0.24$).

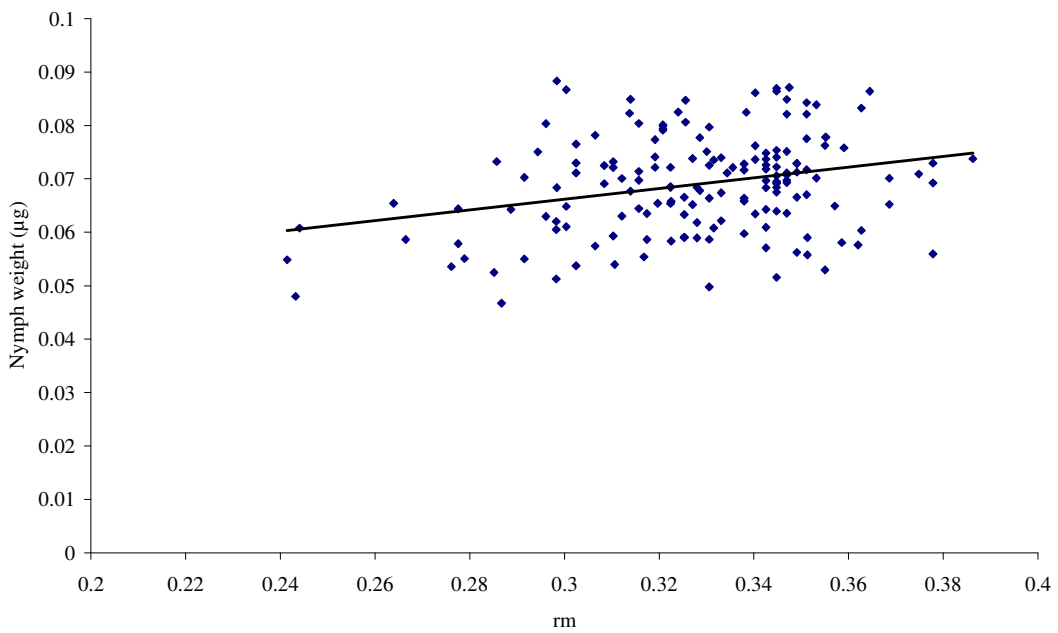


Fig. 5.4 Relationship between *Metopolophium dirhodum* nymph weight and intrinsic rate of increase (r_m) on spring barley ($y = 0.1x + 0.04$, $R^2 = 0.081$).

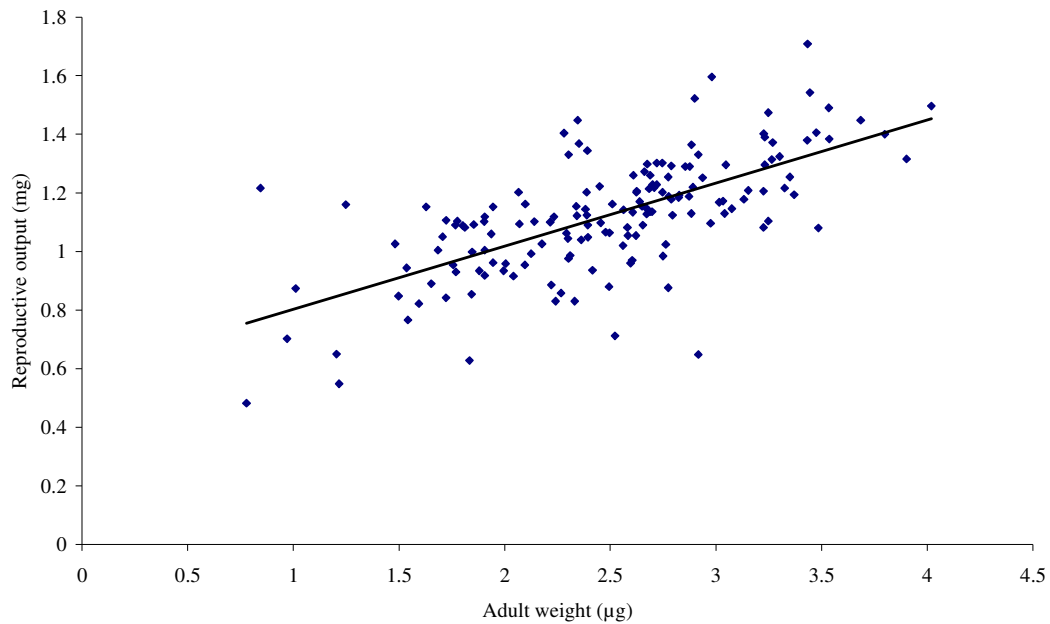


Fig. 5.5 Relationship between *Metopolophium dirhodum* adult weight and reproductive output on spring barley ($y = 0.21x + 0.59$, $R^2 = 0.45$).

5.4.2 Experiment 2: Effect of barley growth stage, fertiliser treatment and time of application on *Metopolophium dirhodum* and *Rhopalosiphum padi* performance

5.4.2.1 *Metopolophium dirhodum* performance

Reproductive output was significantly affected by fertiliser treatment (Fig. 5.6) at GS31 both for seed and two-leaf applied fertilisers but no significant effect at GS21 was observed (two-leaf applied: $F_{4,41} = 1.94$, $P = 0.12$; seed applied: $F_{4,39} = 2.05$, $P = 0.11$). At GS31 following seed application of fertilisers the reproductive output of *M. dirhodum* on conventional(cm), conventional(hh) and hoof and horn fertiliser treatments were significantly greater than the control ($F_{4,48} = 10.21$, $P < 0.001$). The conventional(cm) treatment was also significantly greater than the chicken manure treatment. At GS31 following two-leaf application of fertilisers, *M. dirhodum* reproductive output under the two conventional treatments was significantly greater than the control. The chicken manure treatment was significantly greater than the control while the hoof and horn treatment was not. The hoof and horn treatment was significantly lower than the conventional(cm) treatment ($F_{4,44} = 8.29$, $P < 0.001$).

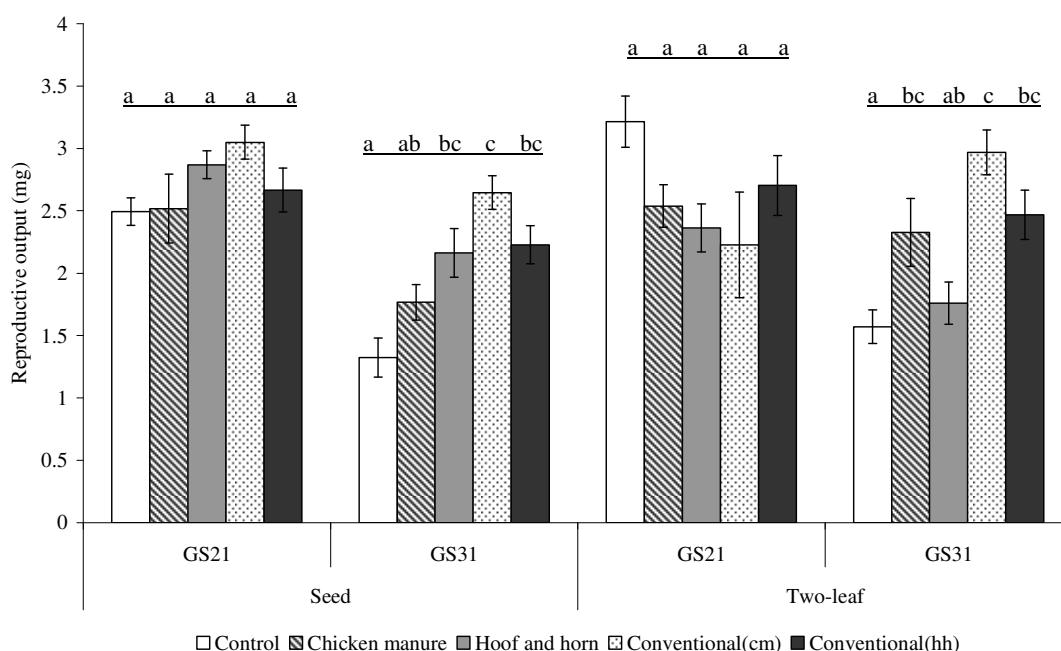


Fig. 5.6 The reproductive out put of *Metopolophium dirhodum* on barley receiving five fertiliser treatments at two growth stages and at two fertiliser application times (mean \pm SEM). Different letters denote significant differences between fertiliser treatments (Tukey, $P < 0.05$).

The effect of growth stage, fertiliser treatment and application method on seven-day fecundity follows that of reproductive output (GS21 seed applied: $F_{4,39} = 2.13$, $P = 0.10$; GS21 two-leaf applied: $F_{4,41} = 2.25$, $P = 0.08$; GS31 seed applied: $F_{4,48} = 7.46$, $P < 0.001$; GS31 two-leaf applied: $F_{4,44} = 8.01$, $P < 0.001$) with one exception. At GS31, following two-leaf application of fertilisers, the seven-day fecundity of *M. dirhodum* under the conventional(hh) treatment was significantly different from those under hoof and horn treatments.

There was no significant effect of fertiliser treatment on r_m at GS21 following seed application of fertiliser ($F_{4,39} = 0.64$, $P = 0.63$). Following two-leaf application at GS21, both conventional treatments were significantly lower than the control ($F_{4,41} = 3.25$, $P < 0.05$) (Fig. 5.7). At GS31, r_m on the conventional treatments was greater than under the controls. Following seed application this difference is significant for conventional(cm) ($F_{4,48} = 3.85$, $P < 0.01$). For two-leaf application, a significant difference in r_m was found between conventional(hh) and the control treatments ($F_{4,44} = 3.90$, $P < 0.01$) (Fig. 5.7).

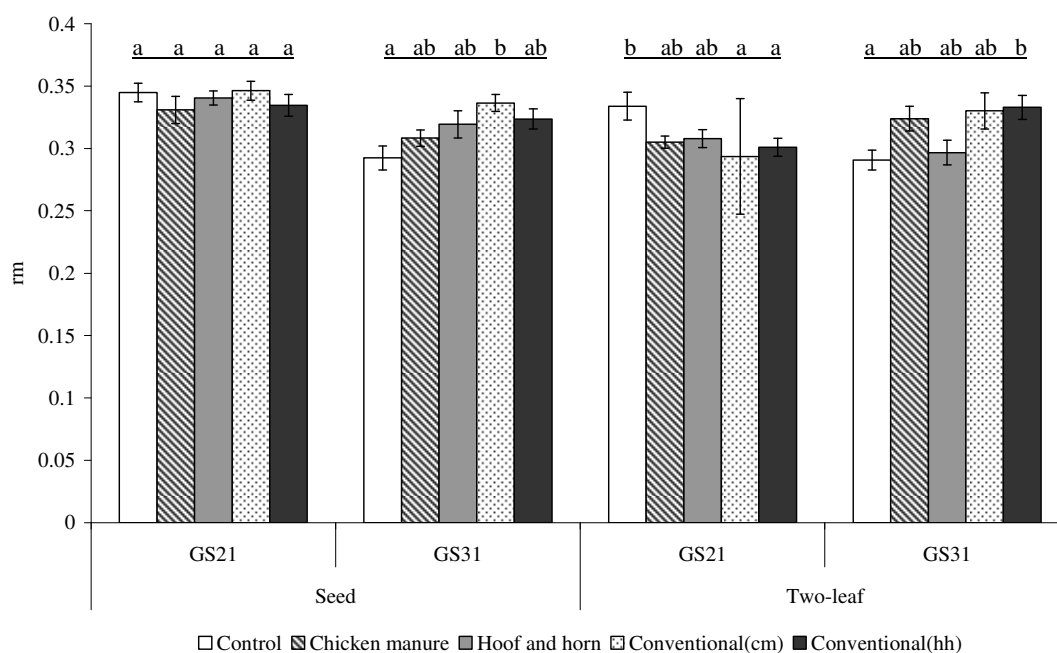


Fig. 5.7 The intrinsic rate of increase (r_m) of *Metopolophium dirhodum* on barley receiving five fertiliser treatments at two growth stages and at two fertiliser application times (mean \pm SEM). Different letters denote significant differences between fertiliser treatments within each growth stage block (Tukey, $P < 0.05$).

There was no significant fertiliser effects on the weight of adult aphids at GS21 following seed ($F_{4,39} = 0.91$, $P = 0.47$) and two-leaf ($F_{4,41} = 1.58$, $P = 0.20$) application of fertilisers (Fig. 5.8). Following seed application, at GS31 all fertiliser treatments gave greater mean adult weights than the control and this was significant for both the conventional(cm) and the hoof and horn treatments ($F_{4,48} = 3.20$, $P < 0.05$). Significant effects were also found at GS31 for two-leaf applied fertilisers ($F_{4,44} = 4.38$, $P < 0.01$) and in this case aphid weights on both the conventional treatments were significantly greater than on the controls (Fig. 5.8).

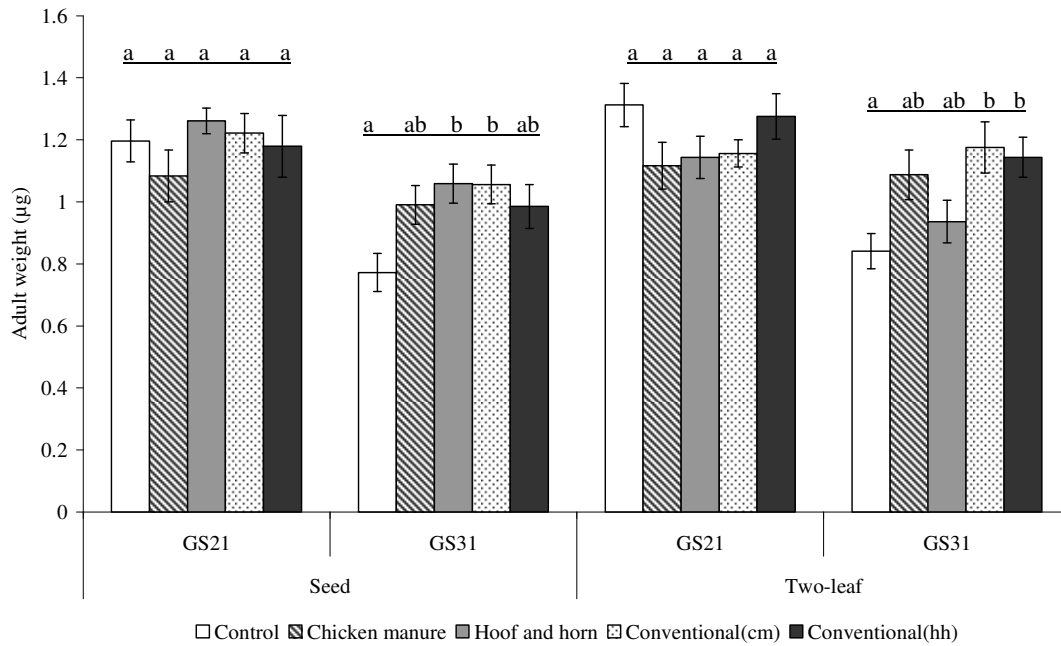


Fig. 5.8 The adult weight of *Metopolophium dirhodum* on barley receiving five fertiliser treatments at two growth stages and at two fertiliser application times (mean \pm SEM). Different letters denote significant differences between fertiliser treatments within each growth stage block (Tukey, $P < 0.05$).

5.4.2.2 *Rhopalosiphum padi* performance

At growth stage 31, following two-leaf application of fertilisers, *R. padi* reproductive output under both conventional fertiliser treatments was significantly greater than the control; reproductive output under the conventional(hh) treatment was also significantly greater than under both organic treatments ($F_{4,36} = 13.64$, $P < 0.001$) (Fig. 5.9). There were no significant fertiliser effects on aphid reproductive output at either growth stage when fertiliser was seed applied (GS21: $F_{4,45} = 0.90$, $P = 0.47$; GS31: $F_{4,38} = 2.36$, $P = 0.07$) and at GS21 when fertiliser was two-leaf applied ($F_{4,36} = 0.19$, $P = 0.94$) (Fig. 5.9).

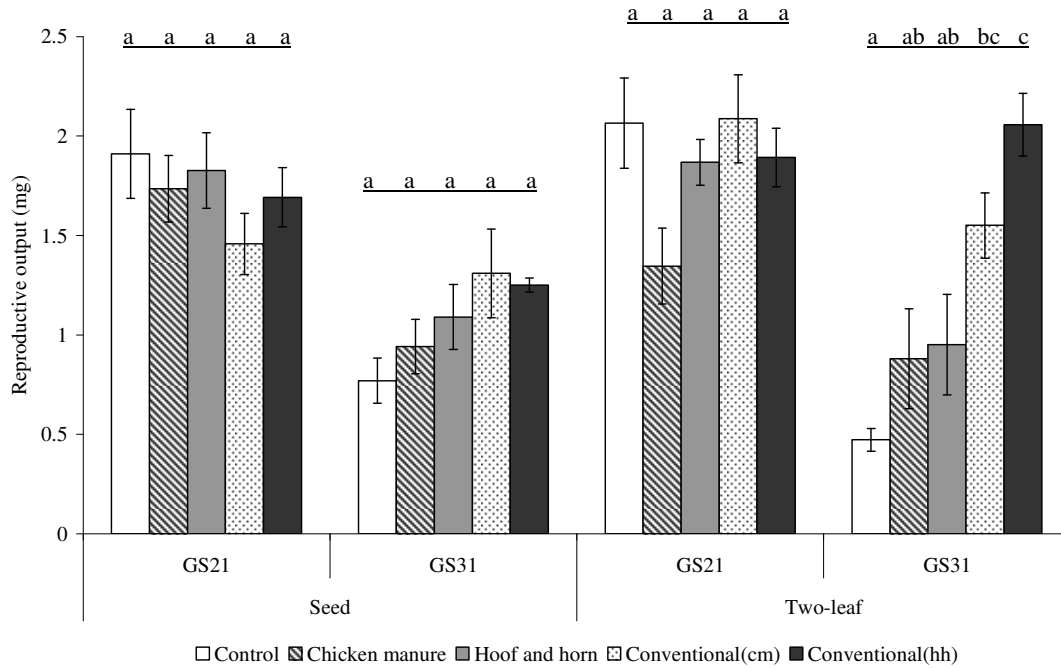


Fig. 5.9 The reproductive output of *Rhopalosiphum padi* on barley receiving five fertiliser treatments at two growth stages and at two fertiliser application times (means \pm SEM). Different letters denote significant differences between fertiliser treatments (Tukey, $P < 0.05$).

The effect of fertiliser treatment on the seven-day fecundity was the same as the effect of fertiliser treatment on reproductive output in terms of which treatments were significantly different from which (GS21 seed applied: $F_{4,45} = 1.41$, $P = 0.25$; GS21 two-leaf applied: $F_{4,36} = 1.88$, $P = 0.13$; GS31 seed applied: $F_{4,38} = 2.91$, $P < 0.05$; GS31 two-leaf applied: $F_{4,36} = 9.99$, $P < 0.001$). The only significant effects of fertiliser treatment on the intrinsic rate of increase on barley were at growth stage 31 when fertiliser had been applied at the two-leaf stage (GS21 seed applied: $F_{4,45} = 0.88$, $P = 0.48$; GS21 two-leaf applied: $F_{4,36} = 0.84$, $P = 0.51$; GS31 seed applied: $F_{4,38} = 2.38$, $P = 0.07$; GS31 two-leaf applied: $F_{4,36} = 11.90$, $P < 0.001$) (Fig. 5.10). In this case, the intrinsic rate of increase of *R. padi* was significantly greater on both conventional treatments when compared with the control and furthermore, the intrinsic rate of increase on conventional(hh) treatments was significantly greater than on both organic treatments.

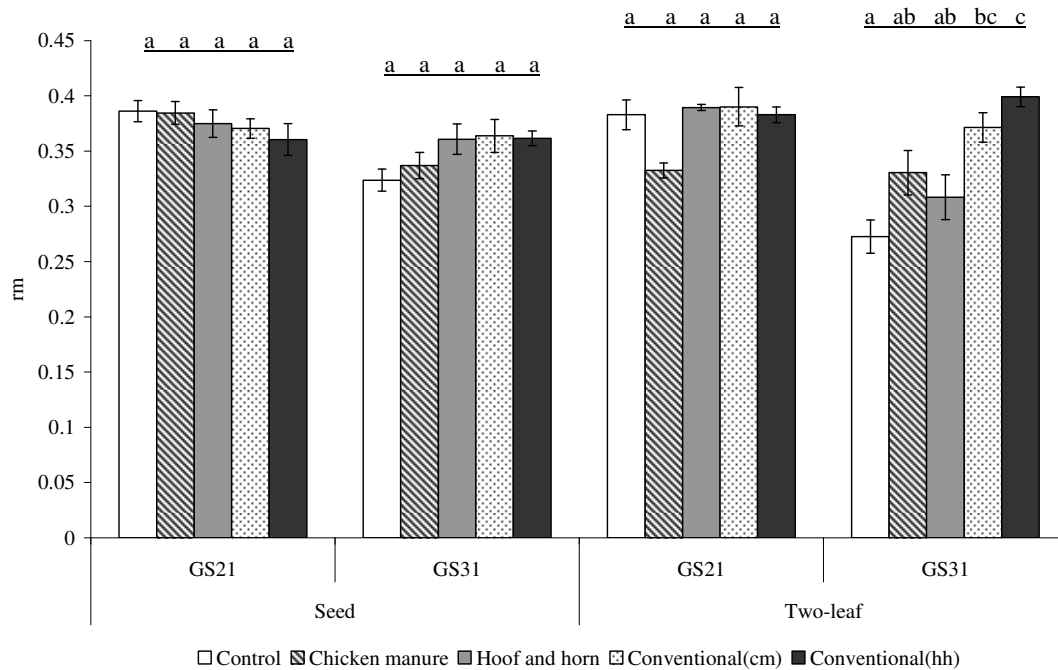


Fig. 5.10 The intrinsic rate of increase (r_m) of *Rhopalosiphum padi* on barley receiving five fertiliser treatments at two growth stages and at two fertiliser application times (mean \pm SEM). Different letters denote significant differences between fertiliser treatments within each growth stage block (Tukey, $P < 0.05$).

Irrespective of fertiliser application timing, adult weight was not significantly affected by fertiliser at growth stage 21 (seed applied: $F_{4,45} = 1.81$, $P = 0.14$; two-leaf applied: $F_{4,36} = 1.60$, $P = 0.20$) (Fig. 5.11). At GS31, when fertiliser was seed applied, adult aphids were significantly heavier under conventional fertiliser treatments than the control treatment ($F_{4,38} = 4.40$, $P < 0.01$) (Fig. 5.11). When the fertiliser treatment was two-leaf applied and aphids were reared on plants at GS31 ($F_{4,36} = 12.99$, $P < 0.001$), again both conventional treatments resulted in significantly greater adult weights than the control and adult weight under the conventional(hh) treatment was significantly greater than under both organic treatments (Fig. 5.11).

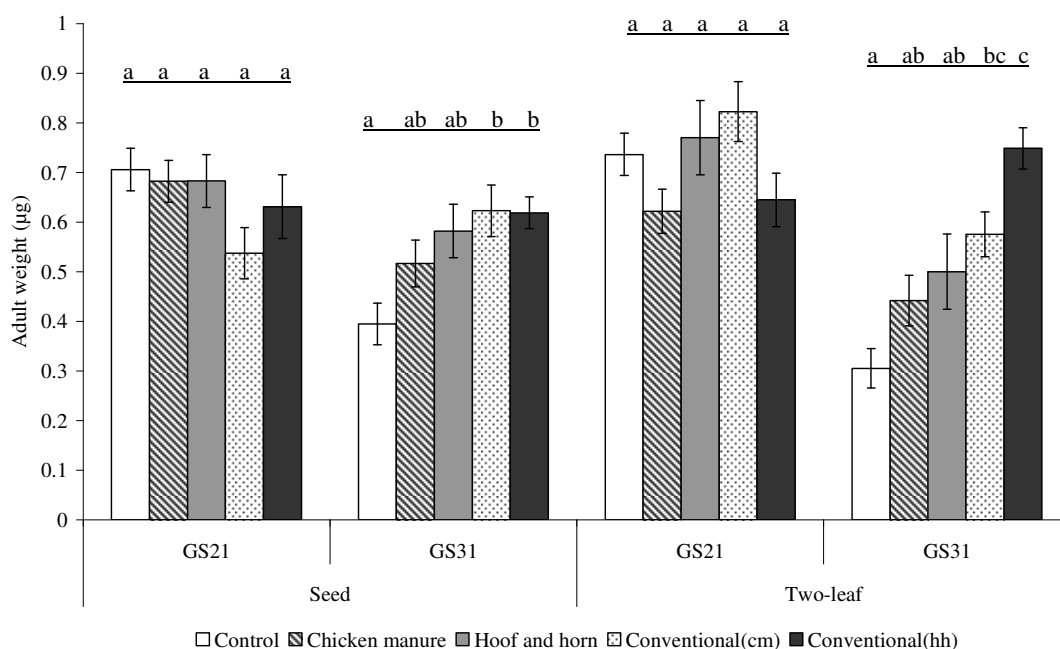


Fig. 5.11 The adult weight of *Rhopalosiphum padi* on barley receiving five fertiliser treatments at two growth stages and at two fertiliser application times (mean \pm SEM). Different letters denote significant differences between fertiliser treatments within each growth stage block (Tukey, $P < 0.05$).

5.4.2.3 Plant performance

Seed application of fertilisers resulted in significantly greater numbers of tillers on barley plants receiving both conventional treatments and the hoof and horn organic treatment when compared with plant grown under control nutrient conditions ($F_{4,55} = 7.98$, $P < 0.001$) (Fig. 5.12). When fertilisers were applied at the two-leaf stage, both conventional fertiliser treatments resulted in greater tiller numbers than the control treatments and both organic treatments ($F_{4,55} = 31.87$, $P < 0.001$) (Fig. 5.12). Tiller numbers under the hoof and horn treatment were also significantly greater than the control.

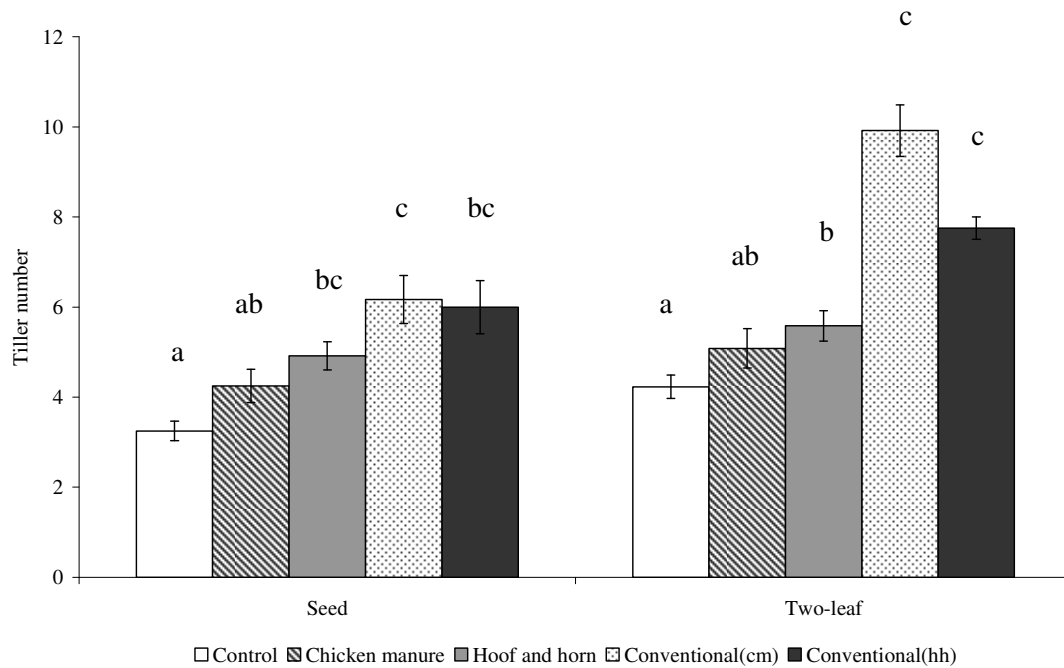


Fig. 5.12 Barley tiller number under five fertiliser treatments with two application methods (mean \pm SEM). Fertiliser treatments with different letters are significantly different with in each growth stage block (Tukey, $P < 0.05$).

Effects of fertiliser application on barley biomass after application of fertilisers with the seed, mirrored the response of tiller number ($F_{4,55} = 7.36$, $P < 0.001$) (Fig. 5.13); conventional and hoof and horn treatments produced significantly larger plants than the control. Plants grown with the conventional(cm) treatment were also larger than plants receiving chicken manure fertiliser. When fertiliser was applied at the two-leaf stage, all fertiliser treatments resulted in larger plants than the control treatment ($F_{4,55} = 25.03$, $P < 0.001$) (Fig. 5.13). Both conventional treatments also resulted in larger plants than chicken manure treatments. The conventional(cm) treatment resulted in significantly larger plants than either the conventional(hh) or the hoof and horn treatments.

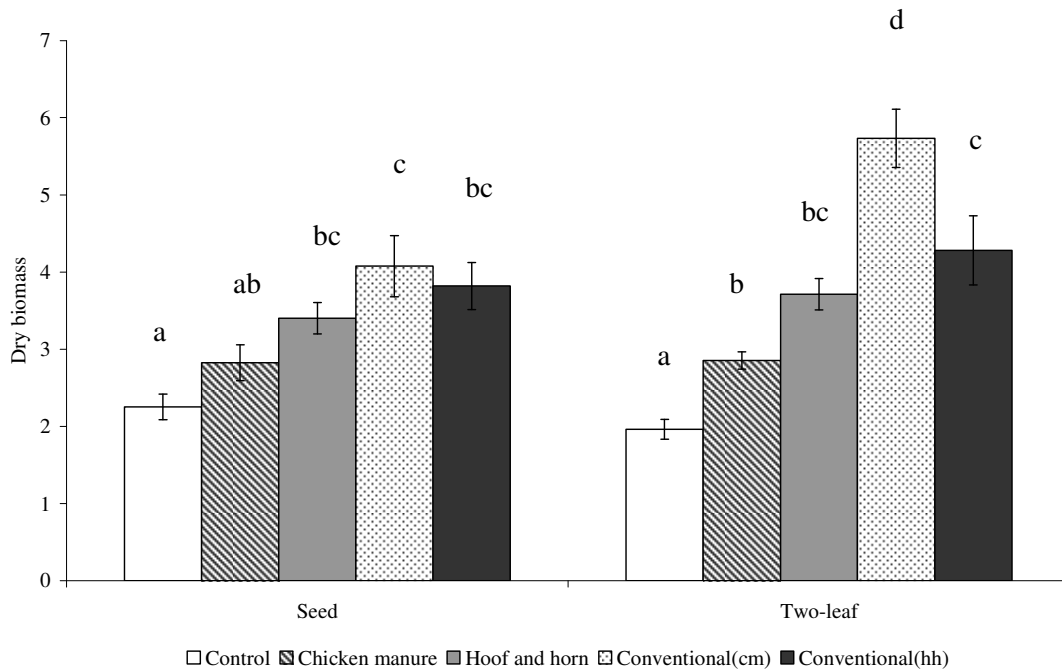


Fig. 5.13 Barley above ground biomass under five fertiliser treatments with two application methods (mean \pm SEM). Fertilisers with different letters are significantly different within each growth stage block (Tukey, $P < 0.05$).

5.5 Discussion

5.5.1 Experiment 1: Effects of barley growth stage and fertiliser treatment on *Metopolophium dirhodum* in a high nutrient base compost

5.5.1.1 *Metopolophium dirhodum* performance

Reproductive output and adult weight were both significantly lower for *M. dirhodum* reared on young three leaf barley and older plants (post flag leaf emergence) when compared with tillering plants and plants going through stem elongation. Growth stage effects on the performance of cereal aphids measured as adult weights, seven-day fecundity or r_m have been found before for *S. avenae* (Watt, 1979), *R. padi* (Leather and Dixon, 1981; Leather *et al.*, 1989) and *M. dirhodum* (Zhuo and Carter, 1992). For *M. dirhodum*, Zhuo *et al.* (1992) found that development time was reduced and fecundity was greater on booting wheat when compared with flowering

wheat. Three of the growth stages used in this experiment were considerably younger than booting or flowering and demonstrate that there are also growth stage effects on younger barley. Given that *M. dirhodum* is primarily a leaf colonising aphid (Watt, 1979), its performance on the vegetative growth stages of barley is important.

Reasons for improved performance of *M. dirhodum* on tillering and stem elongating barley may be due to temporal changes in availability of amino acids, important for aphid development and fecundity (Rahbe *et al.*, 1988; Simpson *et al.*, 1995; Ponder *et al.*, 2000). Given that the overall amino acid content of phloem sap varies with barley age (Weibull, 1987), an effect of plant age on aphid performance might be expected. Interestingly, amino acid concentration was found to be higher in seedlings and stem elongating plants than those that were tillering (Weibull, 1987). With *M. dirhodum* reproductive output and adult weight lower on seedlings it might be the amounts of certain essential amino acids that is important, not the overall concentration.

Alternatively, barley defence chemicals such as the indole alkaloid, gramine can be higher in younger barley leaves grown in a high nutrient conditions (Salas *et al.*, 1990). Gramine has a negative effect on cereal aphid performance (Pickett *et al.*, 1992) and might be why *M. dirhodum* performed less well on younger leaves.

An effect of fertiliser on aphid performance was only found on the oldest barley plants involved in the experiments. Given that no significant difference was found between organic and conventional fertilisers suggests that it might be overall nutrients in the pot plant system that is affecting aphid performance. Plants in control plots may have used all available nutrients after a sustained period in a closed soil system. Moreover, the absence of any difference between the control and fertiliser treatments earlier in plant development implies that there were ample nutrients supplied by the John Innes seed compost, causing saturation and allowing maximal growth of all barley plants. The high number of tillers attained by control plants when compared with tiller numbers achieved by cereals in the field during this study and others (Riedell *et al.*, 2007) supports this.

5.5.1.2 Plant performance

Plant growth was affected by fertiliser with significantly higher tiller numbers at GS31 and GS40+ in fertilised pots, indicating that nitrogen application does indeed promote tillering (Honek, 1991b; Duffield *et al.*, 1997). The increasing tiller numbers after GS31, however, suggests uncharacteristic barley growth resulting in abnormally high tiller numbers. Cereals will typically stop tillering after GS30. This tillering throughout development could indicate unrealistically high nutrient availability in the pots. This experiment serves to highlight the need to use appropriate composts when studying plants nutrients in pots. Ideally plant growth should match that which might be expected in the field.

5.5.1.3 Aphid performance measures

Adult weight and nymph weight correlate positively with r_m and this relationship between size and measures of fecundity has been found in other cereal aphid species including *R. padi* (Leather and Dixon, 1981), *S. avenae* (Watt, 1979) and is the trend in general for aphids (Leather, 1988). These results indicate that using adult or nymph weight may be a useful proxy of *M. dirhodum* fitness given that these measures are far less time consuming than calculating the r_m or seven-day fecundity of experimental aphids.

The use of r_m as a measure of aphid performance has other limitations. Development time has a considerable influence on r_m and if a treatment does not affect development rate then effects on r_m may not be seen. Additionally, r_m relies on aphids producing 95% of their offspring in the number of days it takes them to reach reproductive age (Wyatt and White, 1977) and does not account for longevity (Awmack and Leather, 2007). Adult *M. dirhodum* can live and reproduce as adults for up to 15 days (Zhuo and Carter, 1992) and this might explain why barley age effects on r_m were not seen, but for seven-day fecundity, adult weight, total reproductive output and nymph weight, plant age effects were in evidence. Given that there were significant effects of growth stage on the adult weight and the reproductive output of *M. dirhodum* but not the r_m suggests that r_m may be a conservative or an inappropriate measure of *M. dirhodum*

performance. Reproductive output is useful because it incorporates fecundity as well as nymphal weights.

5.5.2 Experiment 2: Effects of barley growth stage, fertiliser treatment and time of application on *Metopolophium dirhodum* and *Rhopalosiphum padi* performance

5.5.2.1 Aphid performance on tillering barley (GS21)

The only significant effect of fertiliser on aphids reared on tillering barley occurred when fertilisers were two-leaf applied. In this instance, *M. dirhodum* intrinsic rate of increase was lower on plants receiving conventional fertilisers when compared with control plants.

Negative effects of potassium on aphid performance have been reported (Havlickova and Smetankova, 1998; Myers *et al.*, 2005; Walter and DiFonzo, 2007) but reduced performance following nitrogen application is less common, although examples do exist (White, 1984). It is possible that plant resistance chemicals are altered by fertiliser application. For example, concentrations of the alkaloid peramine, known to be toxic to aphids, is increased following fertiliser application to Ryegrass (Krauss *et al.*, 2007). Gramine, another alkaloid which negatively affects cereal aphids, is also increased following the application of nutrients to barley plants (Salas *et al.*, 1990), although it is worth noting that in Salas' (Salas *et al.*, 1990) experiment the nutrient added was potassium nitrate and although the author attributed changes in plant chemistry to levels of nitrate, the potassium may well have been having an effect on the secondary metabolites.

Alternatively, poor aphid performance on young fertilised barley could be an example in support of the plant stress hypothesis (White, 1969; White, 1984) with unfertilised plants suffering nutrient stress, potentially increasing plant soluble nitrogen (White, 1984) and aphids benefitting accordingly. These findings have implications on the pest status of cereal aphids. If an aphid species is a pest early in cereal growth, such as *R. padi* which colonises young spring cereals particularly in Scandinavia and

central Europe (Leather *et al.*, 1989), then the addition of fertilisers, organic or conventional, will not promote early population growth. For those species that cause economic damage later in cereal development, such as *S. avenae* (Larsson, 2005), response to fertilisers in young plants is of less importance.

5.5.2.2 *Metopolophium dirhodum* performance on stem elongating barley (GS31)

Metopolophium dirhodum reproductive output at GS31 was positively affected by seed and two-leaf application of conventional fertilisers when compared with the control treatments. This follows with previous research showing that nitrogen deficiency in plants can alter phloem amino acid composition and concentration (Weibull, 1987; Ponder *et al.*, 2000) which can affect aphid performance (Simpson *et al.*, 1995). The response of *M. dirhodum* on plants going through stem elongation (GS31) to the application of organic fertiliser was dependent on fertiliser type and timing of application. Reproductive output was significantly improved by hoof and horn fertiliser following seed application and by two-leaf applied chicken manure when compared to control treatments. This may be a result of changes in the temporal availability of mineral nutrients, particularly nitrogen. Initial nitrogen mineralisation is more rapid for chicken manure than hoof and horn but between 21 and 67 days incubation in sandy soils, mineral nutrient release from hoof and horn is consistently higher than chicken manure (Cordovil and Cabral, 2001). This would explain why *M. dirhodum* performance is improved soon after chicken manure application but the positive response of aphids to hoof and horn fertiliser is delayed.

The performance of *M. dirhodum* could thus be manipulated by careful timing of organic fertiliser application. Mineral nutrients becomes available as organic nutrients are broken down (Dawson *et al.*, 2008) and if this could be timed so as not to cause excess free amino acids in plant tissue when it might benefit aphid population growth, possible outbreaks might be prevented. The effect of organic fertiliser timing on plant growth and yield must also be considered.

5.5.2.3 *Rhopalosiphum padi* performance on stem elongating barley (GS31)

During plant stem elongation (GS31), conventional fertilisers improved *R. padi* reproductive output when compared with the control treatments only when fertiliser was applied at the two-leaf stage. Following two-leaf and seed application of organic fertilisers no such effect was observed. This positive response of *R. padi* to late applied conventional fertilisers suggests that this species is particularly responsive to pulses in available nutrients associated with conventional fertilisers causing nutrient imbalances in plants (Altieri and Nicholls, 2003). The application of conventional nitrogen fertiliser to sandy soils in pots shows immediately high levels of ammonia when compared to organic fertilisers (Gioacchini *et al.*, 2006). From these results it would appear that the use of organic fertilisers and their characteristically slow release of nutrient (McLaughlin and Mineau, 1995; Dawson *et al.*, 2008) or early application of conventional fertilisers could reduce *R. padi* outbreaks. Again the effects of these fertiliser practices on yield would need to be considered.

5.5.2.4 Plant performance

Tillering is important for cereal yield because tiller number dictates the number of ears a plant will produce. Plant biomass is also linked to yield given that nutrients are remobilised from vegetative tissues at ripening and redistributed to ear growth (Montemurro *et al.*, 2006). For the purposes of this experiment it was assumed that plants which attained a larger biomass would be expected to achieve a comparable increase in yield if they had been allowed to grow to ripening. Both conventional fertilisers improved barley tillering and subsequent biomass and this was particularly true for the conventional(cm) treatment. This positive response to nitrogen, phosphorous and potassium rather than nitrogen alone was expected given that nitrogen is an important nutrient for cereal crop yield (Mengel *et al.*, 2006) but plant responses to nitrogen are often dependent on levels of soil phosphorus (Takahashi and Anwar, 2007) and potassium (Hasse *et al.*, 2006). Whether applied with the seed or at the two-leaf stage, hoof and horn fertiliser achieved a similar biomass as conventional(hh) and was significantly different to the control. Plants grown with

chicken manure had reduced biomass and were only significantly different to the control following later application of fertiliser at the two-leaf stage. Chicken manure treatments were also consistently lower than both conventional treatments. Results would suggest then that barley performed better following hoof and horn application when compared to chicken manure. Perhaps peaks in hoof and horn mineralisation coincided better with barley requirement than peaks in chicken manure mineralisation, particularly after application with the seed; matching nutrient release with plant need is of major importance when using organic fertilisers (Dawson *et al.*, 2008). Results of this kind were found for pot grown ryegrass with synthetic fertiliser application achieving higher yield than hoof and horn which in turn gave higher yield than chicken manure (Cordovil and Cabral, 2001).

5.6 Conclusion

Barley benefitted from the application of conventional fertilisers when compared with organic fertilisers or the absence of fertiliser. The importance of phosphorous and potassium for maximal growth is also highlighted by this study. The effect of host plant age on the performance of *M. dirhodum* is confirmed and that it is apparent in younger plants is also shown.

The present study shows that which measure of aphid performance is used may influence the interpretation of aphid fitness. Intrinsic rate of increase (r_m) was found to be a conservative estimate of aphid performance, one which ignores any effect of treatment on weight, an important correlate of aphid success (Watt, 1979; Leather and Dixon, 1981; Leather, 1988). Nonetheless, adult and nymph weight were found to correlate with r_m . Reproductive output proved to be highly responsive to fertiliser treatments probably because it confounded the effects of fecundity and larval weight and for this reason may be a more accurate representation of aphid fitness.

The responses of the two aphid species to fertiliser application appear divergent with *R. padi* responding positively to later application of conventional fertilisers, while the timing of fertiliser application appeared to effect *M. dirhodum* to a lesser extent.

Rhopalosiphum padi are possibly more sensitive to temporal availability of soil nutrients while the performance of *M. dirhodum* matches that of plant growth, as has been found in the field (Honek, 1991 a, b). Application of controlled release fertilisers may help to reduce *R. padi* outbreaks but if *M. dirhodum* performance is strongly linked to plant growth then any controlled fertiliser measure to reduce *M. dirhodum* outbreaks might be expected to have the same negative effect on yield. Controlled fertiliser application to manage the canopy of winter wheat to reduce the incidence of *M. dirhodum* was found not to be effective (Duffield *et al.*, 1997) indicating that *M. dirhodum* abundance may have again been linked to yield which was comparable between canopy managed and control plots.

Chapter 6

Effect of organic and conventional fertilisers and plant age on *Metopolophium dirhodum* colonies

6.1 Introduction

The rose-grain aphid, *Metopolophium dirhodum*, is a holocyclic aphid species that overwinters on *Rosa* spp. Its Summer hosts include numerous species of grasses and cereals (Blackman and Eastop, 2000). *Metopolophium dirhodum* is a pest of spring cereals in Britain and is a vector of cereal viruses including Barley Yellow Dwarf Virus (Mann *et al.*, 1997). It is particularly abundant in central Europe where it is the major pest of spring cereals (Honek, 1991a).

Application of fertiliser has been shown to significantly affect field populations of *M. dirhodum* with increased application of ammonium nitrate associated with increased aphid populations. This is attributed to increases in cereal leaf area and canopy density (Honek, 1991b; Gash *et al.*, 1996; Duffield *et al.*, 1997). Nitrogen fertiliser effects on phloem amino acid concentration have also been shown to affect cereal aphid performance (Weibull, 1987; Ponder *et al.*, 2000) although not for *M. dirhodum* specifically. Effects of other macronutrients, including potassium, on aphid populations (Havlickova and Smetankova, 1998; Walter and DiFonzo, 2007) and development are also apparent in cereal and soybean aphids (Myers *et al.*, 2005). It is important to understand fertiliser effects on aphid populations and consider ways in which pest outbreaks might be controlled through guided use of fertilisers as part of an integrated pest management system.

Following application of conventional and organic slow release fertilisers, soil nutrient availability is different (Gioacchini *et al.*, 2006) and these differences can be

manifested as variations in yield (Sieling *et al.*, 2006) or contrasting nutrient levels in plant material (Altieri and Nicholls, 2003). Given that plant nutrients can influence pest performance (White, 1984; Awmack and Leather, 2002) an effect of fertiliser type on aphid performance can be hypothesised and has been demonstrated in the earlier chapters of this thesis. Differences in populations of cereal aphids in the field following treatment with conventional and organic slow release fertilisers have been found (Helenius, 1990; Bado *et al.*, 2002; Poveda *et al.*, 2006). Experiments comparing the effects of conventional and organic slow release fertilisers on cereal aphids in a controlled environment, however, are absent.

Many studies investigating the effects of host plant quality or age on aphid performance involve the use of clip cages to monitor the performance of an individual aphid (Watt, 1979; Zhuo and Carter, 1992; Walter and DiFonzo, 2007). The use of such restrictive methods aid in the observation of individual aphids but may themselves influence the performance of the experimental aphid. For example: 1) frequent disturbance of aphids housed in clip cages can adversely affect performance. *Rhopalosiphum padi* development time was increased and weight was reduced when aphids were reared in clip cages and compared with un-caged individuals (Awmack and Leather, 2007). 2) Restricting an experimental aphid to one organ of a host plant may also be detrimental. This is true for both *R. padi* and *S. avenae* given that their performance is significantly affected by the organ of the host plant on which they feed (Watt, 1979; Leather and Dixon, 1981). 3) Variations in the suitability of sites within the plant may exist. For example, the within plant distribution of *M. dirhodum* was determined by variations in levels of leaf chlorophyll with aphids preferentially inhabiting leaves with increased amounts of chlorophyll (Honek and Martinkova, 2002). This within plant movement to maximise fitness would be restricted by the use of clip cages.

Using relative measures of aphid performance such as intrinsic rate of increase (r_m) (Leszczynski *et al.*, 1989; Zhuo and Carter, 1992; Ponder *et al.*, 2000; Khan and Port, 2008) and mean relative growth rate (MRGR) (Leather and Dixon, 1984; Weibull, 1987; Cabrera *et al.*, 1995) to infer future population growth can be useful. They save time and enable rapid collection of data. In some cases however, it can be important to observe actual population development over successive generations rather than

speculate based on the performance of individual aphids. This is true for a number of reasons: 1) Intra-specific interactions can influence individual aphids. Pre-infestation of barley by the cereal aphid, *Schizaphis graminum*, increased phloem proline concentration, reduced water potential and leaf chlorophyll and these effects contributed to the reduced MRGR and increased development times of aphids reared on the plants after initial infestation (Cabrera *et al.*, 1995). Nutritional enhancement of the host by large numbers of aphids following alteration of phloem amino acid composition can also be advantageous to other individuals of the same species (Sandstrom *et al.*, 2000). 2) Inter-specific interactions between aphids can also occur. The performance of *R. padi* and *S. avenae* were reduced when colonies of both species were reared on the same plant. Competition for the shared phloem nutrient resource was believed to be the cause, although the numerical effects of the second species and the influence of the presence of the second species, irrespective of numbers, was not differentiated (Gianoli, 2000). 3) An 'induced response' can occur where aphid infestation causes a defensive reaction in the host plants affecting subsequent aphid development, sensitivity to induced response was found for *R. padi* on wheat (Gianoli, 1999). 4) As well as density dependent effects on aphid performance, it may require observation of an aphid for successive generations for a treatment effect to become apparent. Conditions of maternal rearing significantly affected the offspring of both *Aphis gossypii* (Nevo and Coll, 2001) and *R. padi* (Leather, 1989).

Whether monitored in isolation or as part of a colony over several generations, the impact of an aphid on a crop may not be determined by individual characteristics of that aphid but the characteristic of the aphid colony as a whole. The production of different morphs for example, including alates, can determine population development and subsequent pest status. This is particularly true for *M. dirhodum* where, following field observations, the production of alate morphs was proposed as a major factor influencing maximum populations achieved (Howard and Dixon, 1992). The importance of alate production on cereal aphid population decline was also demonstrated by simulation modelling (Holst and Ruggie, 1997). Therefore, observing treatment effects on aphids for the duration of colony development is important.

Host plant age significantly affects aphid performance and this is true for *R. padi* (Leather and Dixon, 1981), *M. dirhodum* (Watt, 1979; Zhuo and Carter, 1992) and *S. avenae* (Watt, 1979). The age of spring cereals on which *M. dirhodum* arrives in the field dictate the size of the peak aphid numbers achieved (Honek and Martinkova, 2004). Fertiliser type can also affect aphid field populations (Helenius, 1990; Bado *et al.*, 2002; Poveda *et al.*, 2006). Therefore it is important to understand the interaction between fertiliser type and aphid arrival time on the development of aphid populations if fertiliser regime might be used as part of an integrated system to minimise aphid pest outbreaks.

6.2 Aims and objectives

Given the limitations on the use of relative measures of aphid performance and the importance of population development in the pest status of aphids this experiment aimed to determine how the application of different fertilisers influences the development of an aphid colony and how the age of the host plant on which a colony develops affects its response to different fertilisers.

The objectives of this investigation were to: 1) determine the effects of different fertiliser treatments on barley growth comparing both organic and conventional supplies of nitrogen, phosphorus and potassium added to field soil. 2) Examine the effects of fertiliser on population growth characteristics of *Metopolophium dirhodum* colonies on barley in a controlled environment. These growth characteristics were colony population growth, the fecundity of the founding aphid, the fitness of subsequent generations and the induction of alates. 3) Investigate how the age of the host plant on which an aphid begins reproduction interacts with fertiliser type to influence these colony characteristics.

6.3 Materials and methods

6.3.1 Potting procedure

Spring barley (cv. Doyen) was grown individually from seeds in plant pots which were 9 cm in diameter and 11 cm deep. The plant pots were filled with top soil taken from Four Acre Field located at Silwood Park, Berkshire (see Table 3.1, Chapter 3, for Four Acre Field soil structure and chemistry). Plant pots were placed in individual water trays and watered regularly to ensure soil never dried out. For the duration of the experiment the plants were grown in a controlled temperature glasshouse with a light:dark regime of 16:8 h and day and night temperatures of $20\pm 5^{\circ}\text{C}$ and $14\pm 5^{\circ}\text{C}$, respectively.

6.3.2 Fertiliser treatments

The experiment consisted of five fertiliser treatments; two organic, two conventional and a control involving the addition of no fertiliser. The first organic treatment was chicken manure (cm) fertiliser. The second organic treatment was hoof and horn meal (hh) fertiliser. Two conventional treatments were established to match the nutrient content of both the hoof and horn (conventional(hh)) and chicken manure (conventional(cm)) treatments (see Table 5.2, Chapter 5 for details of fertiliser nutrient content, the amounts added to each pot and to see the materials and methods for fertiliser suppliers). Fertilisers were ground up using a pestle and mortar and applied to the surface of each pot when barley was at the two leaf stage (GS12) according to Tottman and Broad (1987). Control pots remained un-amended. For each of the three experiments, 10 plants were grown under each of the five treatments.

6.3.3 Colony establishment

Three separate experiments were carried out, each on barley plants at different growth stages. Each experiment took place in a separate time block. For the first experiment *Metopolophium dirhodum* colonies were started on barley plants at the two leaf

growth stage (GS12), here on referred to as ‘young’ barley. The second experiment began on ‘middle aged’ barley which had developed one tiller (GS19) and for the third experiment colonies were established on ‘old’ tillering barley (GS20-25). Colony establishment involved placing one alate *M. dirhodum* in a clip cage and attaching this to the second leaf down from the primary leaf of each of the 50 barley plants involved in each experiment. After 12 h the clip cage was checked and all but one nymph and the alate aphid were removed from the leaf. If no nymph had been produced the alate was replaced and the clip cages were checked every few hours until a nymph was present. Following nymph establishment the clip cages were taken off the plants and, to prevent aphid escape, the plants were covered with a transparent micro-perforated bag measuring 38 cm by 90 cm (bags were supplied by ‘Asianet Uk Ltd’, Leicester). The individual nymphs were then allowed to move freely throughout the host plant and develop and reproduce. Plants under each treatment were oriented randomly in the glasshouse in one, fully randomised, experimental block and the plants remained in the controlled temperature glasshouse throughout the experiments (Fig. 6.1).

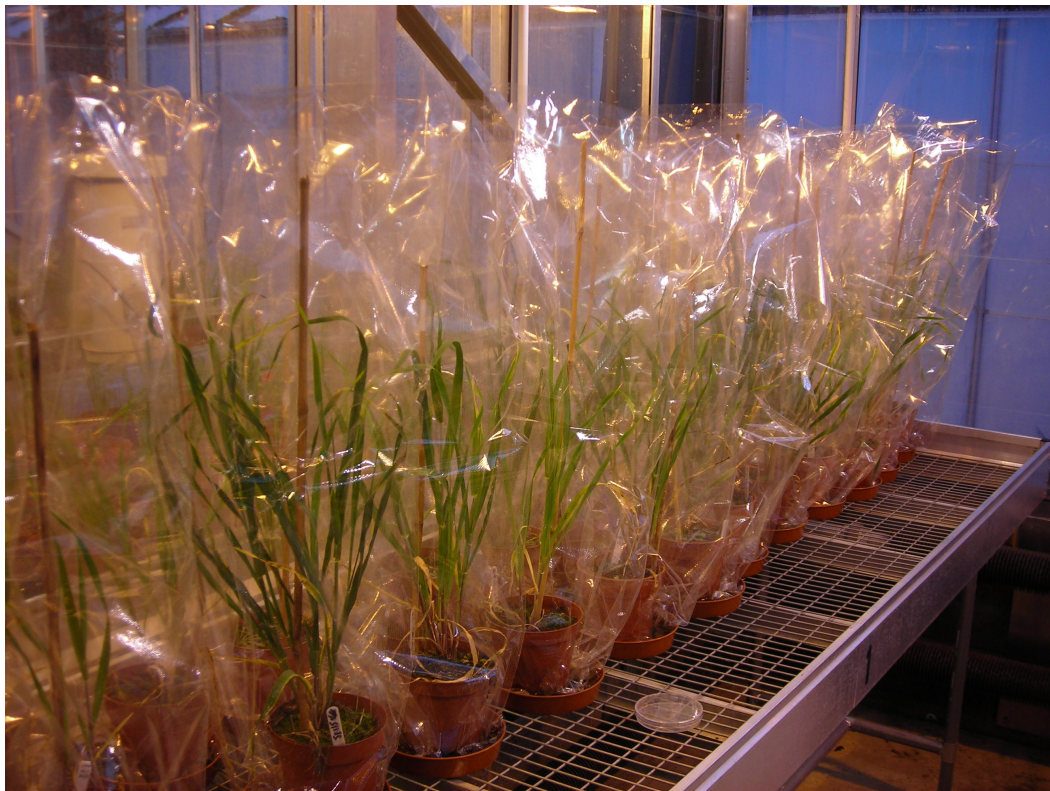


Fig. 6.1 Barley plants and aphid colonies surrounded by micro perforated bags in the controlled temperature glasshouse.

6.3.4 Colony measurements

The development of aphid colonies was observed for a period of 26 days from the establishment of the first nymph. Several measures of colony performance were taken including aphid population growth and population maximums. Aphid performance measures of the founding aphid and of subsequent generations were taken as well as determining the colonies readiness to produce alate morphs. To measure colony growth, the number of individual aphids on each plant was recorded every three or four days for the duration of the experiment. To determine maximum population sizes, the total number of aphids on each plant at the end of the 26 day period was counted. To establish the fitness of the founding nymph a measure of seven-day fecundity was used, seven-day fecundity was recorded from the day when the first nymph was produced by the founding aphid. To investigate generational effects of treatment, on the final day of each experiment, three randomly selected apterous fifth instar nymphs were removed from the barley plants and weighed on a Sartorius micro-balance to establish mean adult fresh weight. Finally, to determine the readiness of a colony to produce alate morphs, on the final day of the experiment the number of apterous and alate fifth instar nymphs were recorded.

6.3.5 Plant measurements

At the end of each 26 day experiment the barley plants were removed from the soil and placed in a 60°C oven for 24 h. The above ground biomass and root mass of each plant were separated and weighed. The growth stage of each plant was also recorded.

6.3.6 Statistical analysis

Fertiliser treatment effects on both above ground biomass and root mass were analysed using ANOVA followed by a Tukey honest significant difference test to determine differences between means, working to $P < 0.05$. Fertiliser treatment effects on biomass were examined for each growth stage separately. Following the BoxCox test and visual examination of the data, log transformation of root mass data

and square root transformation of above ground biomass were most appropriate prior to analysis.

A generalised linear model was used to determine barley growth stage effects on final aphid population size. The model included both growth stage and fertiliser treatment effects. The aphid response was a 'count' and data proved to be overdispersed so a quasipoisson error structure was used. Significant differences between means were established using t values presented by the model. Fertiliser treatment effects on aphid numbers on day 1, 8, 12, 15, 19, 22 and 26 of colony development were examined using generalised linear models with quasipoisson errors due to overdispersion. Once again, significant differences between treatment means were determined using t values.

Generalised linear models were used to determine the significance of correlations between final day aphid colony size and above ground biomass for young middle aged and old barley plants. Once more, above ground biomass was square root transformed prior to analysis to normalise the data.

To investigate growth stage effects on primary aphid seven-day fecundity and adult weight, an initial ANOVA model including both growth stage and fertiliser treatment effects as well as their interactions was used. Following model simplification, a Tukey test was carried out to investigate significant effects between each of the three growth stages. For fertiliser treatment effect on both seven-day fecundity and adult weight, growth stages were analysed separately using ANOVA, again the Tukey test was used to establish significant differences between means. The responses, seven-day fecundity and adult weight, were both normally distributed so no transformation was necessary.

On the 26th day of colony development the number of fifth instar aphids was counted. The proportion of individuals with wings was then established. This proportionate response was arcsine transformed before fertiliser treatment effects on the proportion of alates was investigated using an ANOVA. Due to low numbers of alates on young and middle aged barley, only alate data on older barley was statistically analysed. To determine significant differences between treatment means a Tukey test was carried

out. To test fertiliser type effects on alate production a second ANOVA model was carried out where treatments were grouped as organic, conventional or control. The significance of the correlation between alate number and above ground biomass was established using a linear regression. Once again the proportion of alate aphids was arcsine transformed. Following a BoxCox test and visual examination of the data, above ground biomass was square root transformed. For all statistical analyses the programme 'R' version 2.7.1 was used (Ihaka and Gentleman, 1996).

6.4 Results

6.4.1 Plants

At the end of the experiment on 'young' barley, plants reached growth stages between GS30 and GS32 with no apparent effect of treatment. Middle aged plants were between GS32 and GS34 and old plants were between GS36 and GS49 at the end of each experiment, again with no effect of treatment on growth stage apparent.

Within each age category there were significant fertiliser treatment effects on above ground biomass. For young barley the application of both conventional treatments and the hoof and horn treatment resulted in significantly larger plants than the control ($F_{4,39} = 4.15$, $P < 0.01$) (Fig. 6.2). No significant effect of treatment on the root mass of young plants was found ($F_{4,39} = 1.19$, $P = 0.33$).

For middle aged barley, above ground biomass was greater under all fertiliser treatments when compared with the control. The conventional(cm) treatment also resulted in significantly greater above ground biomass than the chicken manure and hoof and horn treatments ($F_{4,43} = 28.43$, $P < 0.001$) (Fig. 6.2). Root mass achieved under all fertiliser treatments was significantly bigger than the root mass achieved by control barley ($F_{4,43} = 10.21$, $P < 0.001$).

In older plants, the above ground biomass was greater under all fertiliser treatments when compared with control plants. Additionally the conventional(hh) treatment

resulted in a greater above ground biomass than the chicken manure treatment. Barley fertilised with the conventional(cm) treatment also produced a greater above ground biomass than all other fertiliser treatments ($F_{4,45} = 39.83$, $P < 0.001$) (Fig. 6.2). All fertiliser treatments resulted in greater root mass than controls for older plants ($F_{4,45} = 13.86$, $P < 0.001$).

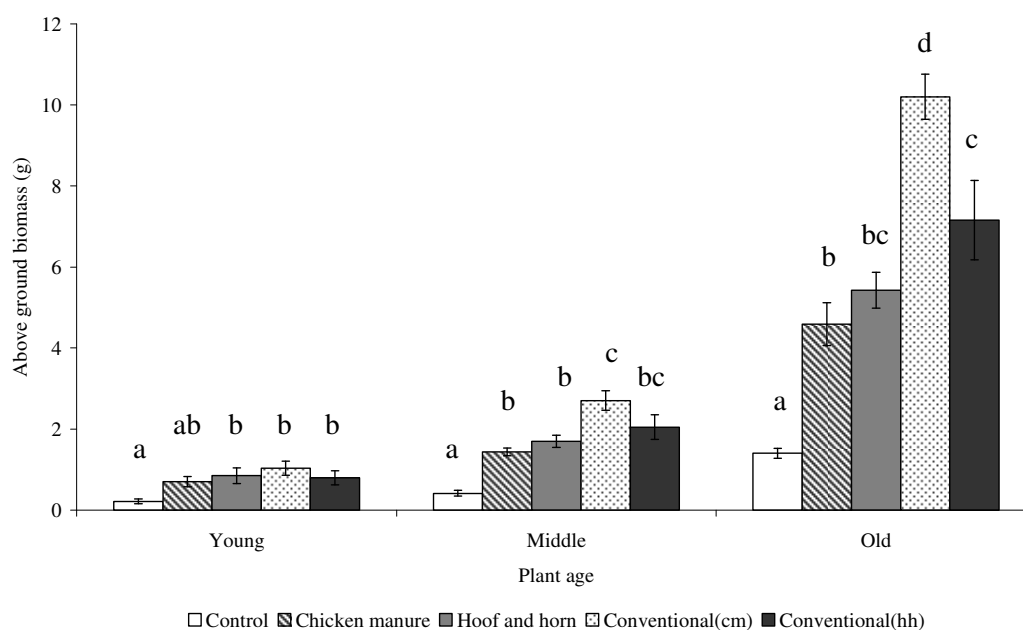


Fig. 6.2 Above ground biomass of barley at three different growth stages grown under five fertiliser treatments (mean \pm SEM). Bars with different letters within each growth category are significantly different (Tukey, $P < 0.05$).

6.4.2 Aphid populations

Aphid populations increased exponentially under all fertiliser treatments, regardless of barley growth stage at colony establishment (Fig. 6.3). The aphid populations achieved after 26 days were significantly affected by the age of the plant the colony was established on. The aphid numbers reached on young plants were significantly lower than numbers reached on middle aged ($t_{2,101} = 6.30$, $P < 0.001$) and old plants ($t_{2,101} = 9.74$, $P < 0.001$). Numbers reached on middle aged barley were significantly lower than numbers on old barley ($t_{2,101} = 4.00$, $P < 0.001$).

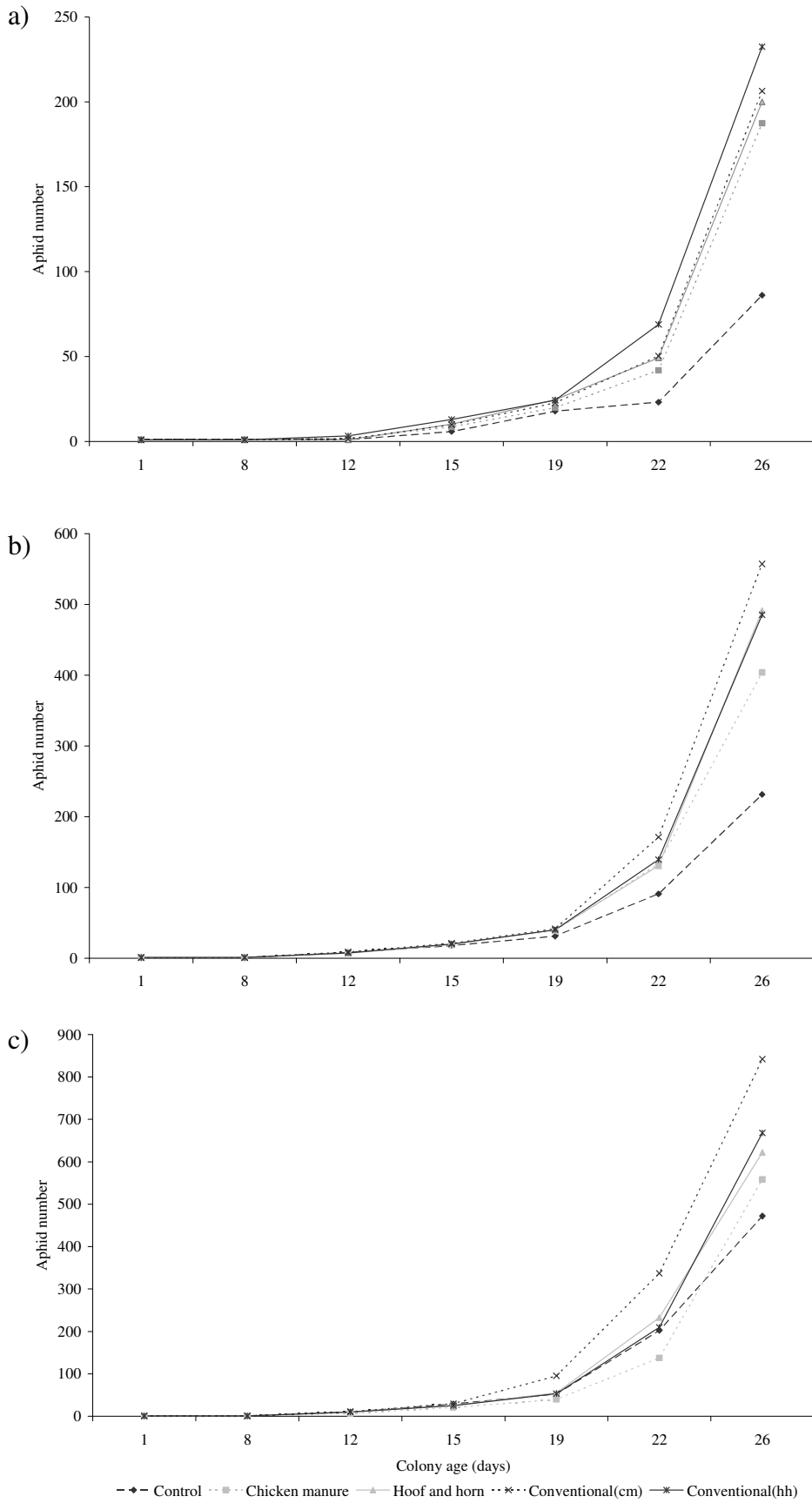


Fig. 6.3 *Metopolophium dirhodum* population growth following colony establishment on barley at growth stages a) 12, b) 19 and c) 22-25 under five fertiliser treatments.

For colonies established on barley at GS12 or 'young' barley, numbers of aphids throughout aphid population growth were greater on barley receiving the conventional(hh) treatment when compared with other treatments. Populations on control barley were also lower than other fertiliser treatments (Fig. 6.3a). Significant fertiliser treatment effects were found on day 12 and day 15. On both days, aphid numbers on barley which received the conventional(hh) treatment were significantly greater than control barley (Table 6.1).

In colonies established on middle aged barley at growth stage 19, aphid populations were greater on all fertiliser treated plants when compared with the control. The conventional(cm) treatment resulted in the highest populations (Fig. 6.3b). Significant effects of fertiliser treatment were found on day 19, 22 and 26. On day 19 populations on the conventional(hh), conventional(cm) and hoof and horn treated plants were significantly greater than populations on control plants. On day 22, only the conventional(cm) treatment resulted in greater aphid numbers than the control. On day 26, all fertiliser treatments resulted in greater aphid numbers than on control barley (Table 6.1).

At the later stages of colony development, the conventional(cm) treatment resulted in consistently greater aphid numbers than other treatments when aphid colonies were established on old barley at growth stages 22 - 25 (Fig. 6.3c). Significant effects of fertiliser treatments were observed on day 15 when both control and conventional(cm) treatments resulted in greater aphid numbers than the chicken manure treatment. On day 19 and 20, the conventional(cm) treatment resulted in greater aphid numbers than all other treatments. On day 26 aphid populations on barley receiving the conventional(cm) treatment were significantly larger than on the control and chicken manure treated barley (Table 6.1).

Table 6.1 *Metopolophium dirhodum* colony size (mean \pm SEM) at different colony ages on barley grown under five fertiliser treatments. Colonies were established on barley at three growth stages. Means for the five fertiliser treatments within each growth stage column with different letters are significantly different (t test, $P < 0.05$). Days with significant treatment effects are in bold.

Growth stage	Treatment	Colony age in days						
		1	8	12	15	19	22	26
GS12	Control	1 \pm 0a	1 \pm 0a	1 \pm 0a	5.8 \pm 1.39a	17.8 \pm 2.31a	23.2 \pm 4.22a	86.2 \pm 25.48a
	cm	1 \pm 0a	1 \pm 0a	1.71 \pm 0.47ab	8.57 \pm 1.78ab	19.86 \pm 3.12a	41.86 \pm 12.76a	187.29 \pm 53.69a
	hh	1 \pm 0a	1 \pm 0a	1 \pm 0ab	10.17 \pm 1.64ab	24.5 \pm 2.03a	49.17 \pm 15.32a	200 \pm 41.21a
	Con(cm)	1 \pm 0a	1 \pm 0a	1.44 \pm 0.44ab	9.89 \pm 1.36ab	22.67 \pm 2.30a	50.33 \pm 20.54a	206.33 \pm 66.67a
	Con(hh)	1 \pm 0a	1 \pm 0a	3.22 \pm 1.01b	12.89 \pm 2.44b	24.22 \pm 3.72a	68.78 \pm 18.67a	232.44 \pm 61.95a
GS19	Control	1 \pm 0a	1 \pm 0a	8.1 \pm 1.00a	18 \pm 1.61a	31.1 \pm 2.11a	91.1 \pm 19.14a	231.2 \pm 40.02a
	cm	1 \pm 0a	1 \pm 0a	8 \pm 1.46a	20 \pm 1.37a	38.83 \pm 2.48ab	133.17 \pm 26.60ab	403.83 \pm 55.76b
	hh	1 \pm 0a	1 \pm 0a	7 \pm 2a	19 \pm 3.62a	40 \pm 6.07b	130.8 \pm 48.08ab	491.2 \pm 121.41b
	Con(cm)	1 \pm 0a	1 \pm 0a	8.86 \pm 1.50a	21.14 \pm 1.71a	41.71 \pm 3.04b	171.14 \pm 30.44b	557.29 \pm 71.44b
	Con(hh)	1 \pm 0a	1 \pm 0a	7.5 \pm 1.20a	20.13 \pm 1.74a	40 \pm 2.27b	139.38 \pm 20.53ab	485.13 \pm 64.84b
GS22-25	Control	1 \pm 0a	1 \pm 0a	10 \pm 1.56a	28.6 \pm 2.24b	52.43 \pm 6.02a	202.29 \pm 24.20a	472 \pm 31.64a
	cm	1 \pm 0a	1 \pm 0a	6.67 \pm 1.61a	20.67 \pm 3.53a	39.67 \pm 4.99a	137.5 \pm 31.5a	558.33 \pm 115.52a
	hh	1 \pm 0a	1 \pm 0a	10.33 \pm 1.43a	25.33 \pm 2.07ab	54.89 \pm 6.80a	232.33 \pm 35.45a	622.44 \pm 60.52ab
	Con(cm)	1 \pm 0a	1 \pm 0a	10.86 \pm 1.93a	29.86 \pm 2.03b	95.43 \pm 58.66b	336.86 \pm 58.66b	841.86 \pm 82.89b
	Con(hh)	1 \pm 0a	1 \pm 0a	9.86 \pm 1.68a	24.86 \pm 2.20a	53.14 \pm 43.88a	209.57 \pm 43.88a	668.14 \pm 94.34ab

A positive correlation was found between aphid colony size on the 26th day of colony development and barley above ground biomass (Fig. 6.4). This correlation was significant for young ($t_{1,34} = 4.30$, $P < 0.001$), middle aged ($t_{1,34} = 5.31$, $P < 0.001$) and old barley plants ($t_{1,34} = 2.54$, $P < 0.001$).

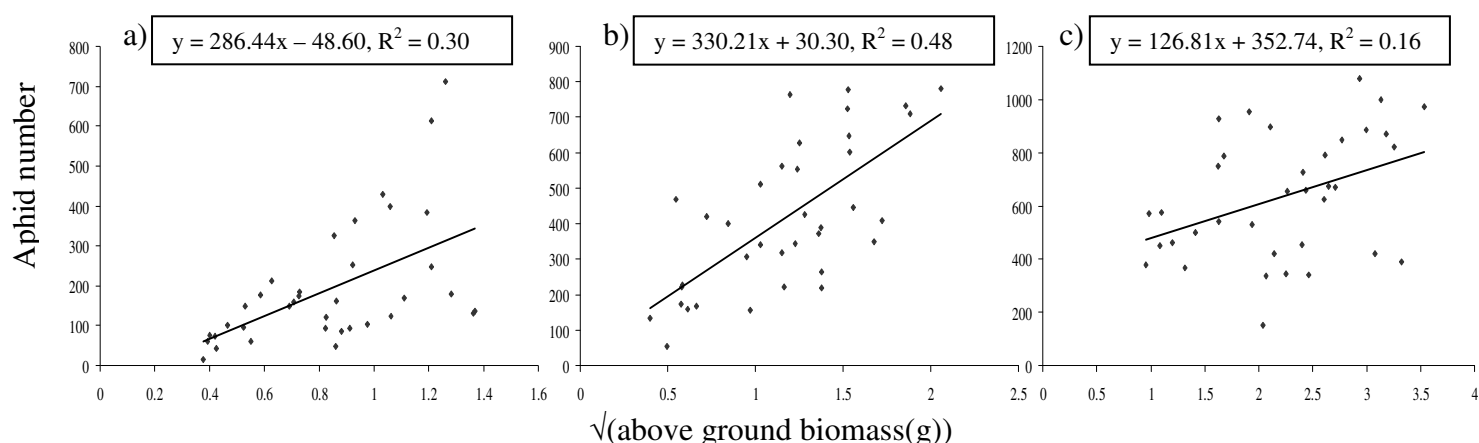


Fig. 6.4 The correlation between final *Metopolophium dirhodum* population size and above ground biomass for a) young, b) middle aged and c) old barley.

6.4.3 Aphid performance measures

The seven-day fecundity achieved by the primary aphid was significantly affected by the age of the plant on which the aphid was reared. The fecundity of aphids reared on young barley was significantly lower than the fecundity of aphids reared on middle aged barley, which in turn was lower than the fecundity of aphids reared on old barley ($F_{2,103} = 25.45$, $P < 0.001$) (Fig. 6.5). Irrespective of barley host age, aphid seven-day fecundity was not significantly affected by fertiliser treatment (young: $F_{4,31} = 0.96$, $P = 0.44$; middle: $F_{4,30} = 0.99$, $P = 0.43$; old: $F_{4,34} = 0.10$, $P = 0.98$).

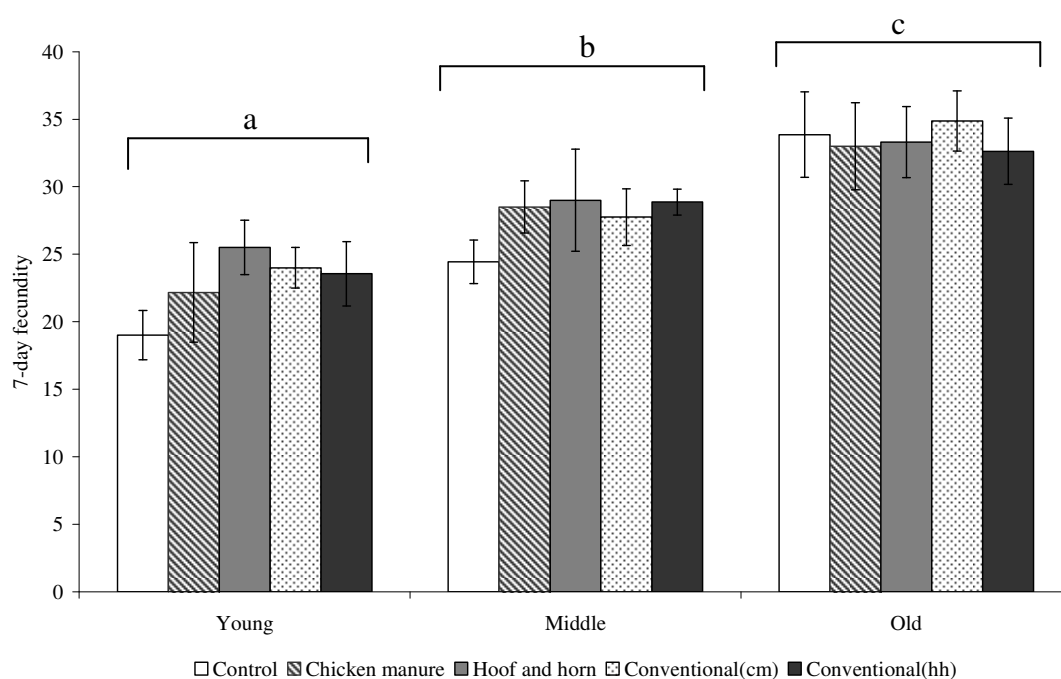


Fig. 6.5 The seven-day fecundity of *Metopolophium dirhodum* reared on young, middle aged and old barley grown with five fertiliser treatments (mean \pm SEM). Barley ages with different letters are significantly different (Tukey, $P < 0.05$).

The fresh weight of fifth instar *M. dirhodum* aphids was significantly less for aphids from colonies reared on older plants by comparison with those reared on middle aged plants ($F_{2,110} = 3.27$, $P < 0.05$) (Fig. 6.6). There were significant effects of fertiliser treatment on the adult weight of aphids from colonies reared on all ages of barley plants. Fifth instar nymphs from colonies reared on young plants weighed significantly less on control barely when compared with those fertilised with chicken manure, hoof and horn and the conventional(cm) treatments. Fifth instar nymphs from conventional(cm) fertilised young barley also weighed significantly more than

fifth instar nymphs from conventional(hh) fertilised young barley ($F_{4,32} = 6.91$, $P < 0.001$) (Fig. 6.6). When considering barley at the middle growth stages, fifth instar nymphs from control barley had significantly less mass than all other fertiliser treatments ($F_{4,27} = 7.62$, $P < 0.001$) (Fig. 6.6). As with aphids from middle aged barley, fifth instar nymphs from control barley had a lower mass than nymphs from both conventional and the hoof and horn fertiliser treatments in colonies on old barley. In contrast, however, the control and chicken manure treatments were not significantly different in old barley ($F_{4,43} = 6.91$, $P < 0.001$) (Fig. 6.6).

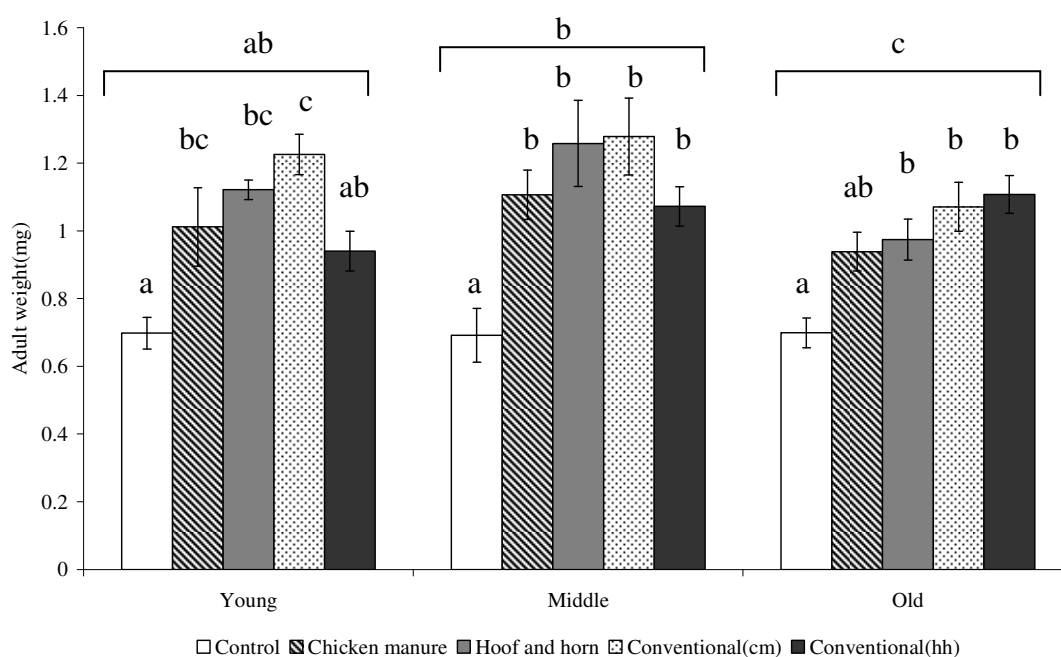


Fig. 6.6 The adult fresh weight of *Metopolophium dirhodum* reared on young, middle aged and old barley grown with five fertiliser treatments (mean \pm SEM). Barley ages and fertiliser treatments within age groups with different letters are significantly different (Tukey, $P < 0.05$).

6.4.4 Alates

The number of alates produced in colonies of aphids reared on young and middle aged barley was low and variable and could not be statistically analysed. There was a significant effect of fertiliser treatment on the proportion of adult aphids that were alate in colonies reared on the older barley plants ($F_{4,43} = 6.91$, $P < 0.001$) (Fig. 6.7). The proportion of alates in colonies reared on control barley was significantly higher than those reared on barley fertilised with the conventional(hh) treatment. Following grouping of treatments into organic, conventional and control treatments, the

proportion of alates under the control treatment was higher than both the organic and conventional treatments ($F_{2,33} = 5.09$, $P < 0.05$).

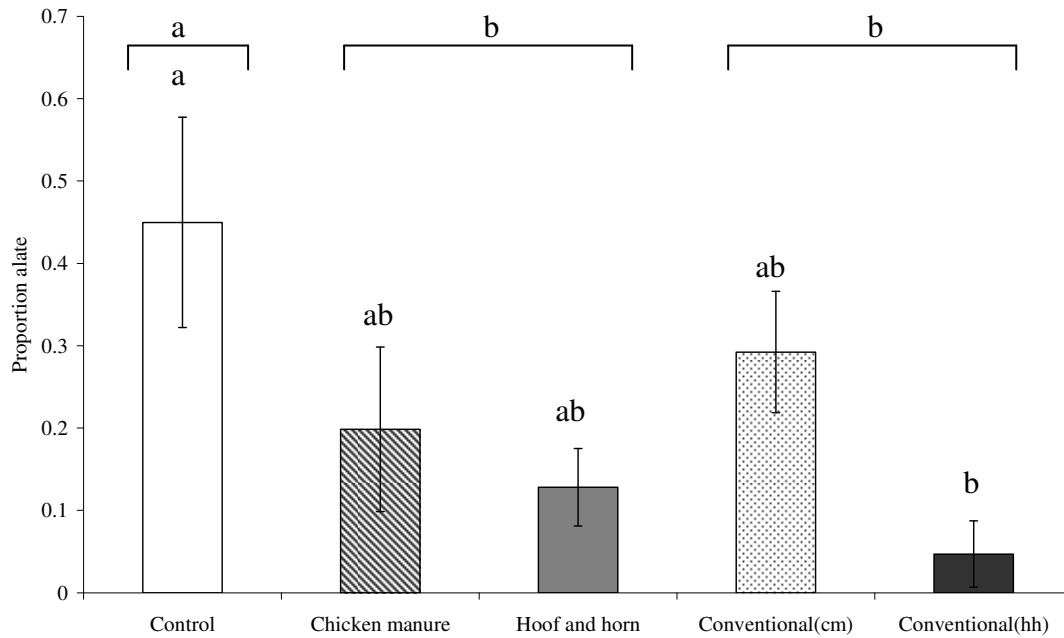


Fig. 6.7 The proportion of alate fifth instar *Metopolophium dirhodum* from colonies reared on barley under five fertiliser treatments (mean \pm SEM). Bars and groups of bars with different letters are significantly different (Tukey, $P < 0.05$).

The proportion of alates produced by aphid colonies reared on older plants was negatively correlated with above ground barley biomass (Fig. 6.8). This negative correlation was very close to significant ($F_{1,34} = 3.99$, $P = 0.054$).

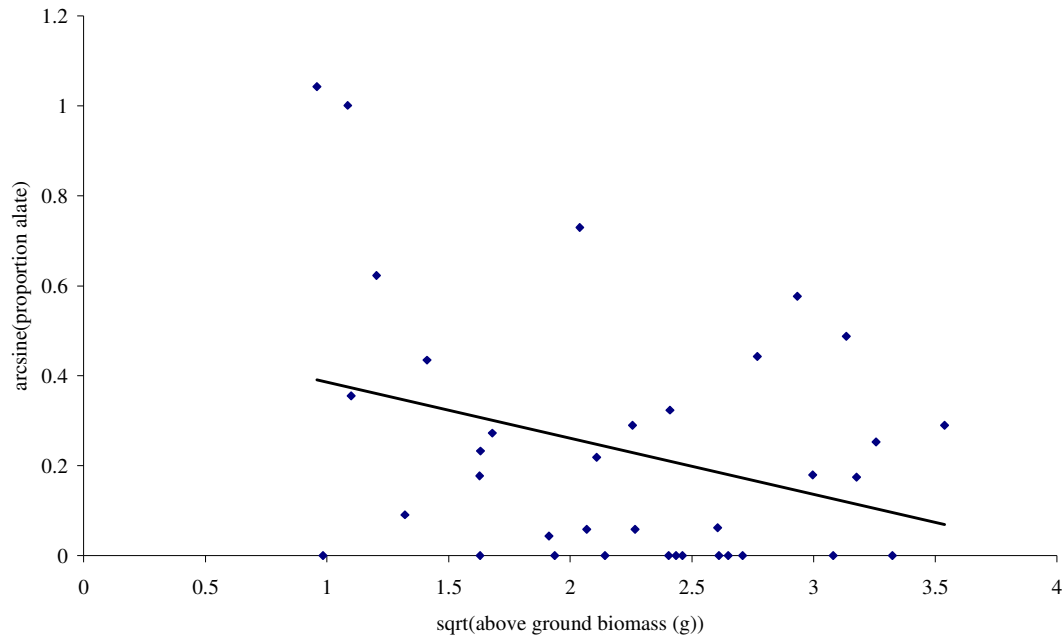


Fig. 6.8 The correlation between the proportion of alate *Metopolophium dirhodum* fifth instar nymphs that were alate and the above ground biomass of the barley plant on which colonies were reared ($y = -0.12x + 0.51$, $R^2 = 0.11$).

6.5 Discussion

6.5.1 Plants

At all the growth stages tested, barley plants grown in soil amended with fertilisers had a larger above ground biomass than control barley. Root mass was also larger in fertilised plots for middle aged and older barley plants. This demonstrates the benefits of fertiliser, and particularly nitrogen, given that two of the fertiliser treatments contained only nitrogen (hoof and horn and conventional(hh)), to cereal growth (Mengel *et al.*, 2006). Fertiliser effects on above ground biomass were evident even in the youngest barley plants weighed, although the difference between control barley and those grown with chicken manure was not significant. This indicates that nutrient release from the fertiliser treatments is sufficient for maximal barley growth early in development despite the different nutrient release rates of chicken manure, hoof and horn and conventional fertilisers (Cordovil and Cabral, 2001). Organic fertilisers contain mineral nutrients (Sieling *et al.*, 2006) and levels of

nitrate can be high soon after application of organic slow release fertilisers (Gioacchini *et al.*, 2006). These nutrients combined with the basal nutrients already in the field soil used for this experiment may have been adequate for early plant growth.

For middle aged and older barley the differences between fertiliser treatments on above ground barley biomass became apparent. This is particularly evident for the conventional(cm) treatment, where biomass under this treatment was significantly greater than under the two organic treatments at both the middle and older growth stages. The conventional(cm) treatment supplies mineral nitrogen, potassium and phosphorus in the form of ammonium nitrate, potassium sulphate and super phosphate. These mineral forms of nutrients are all readily accessible to the plant (Mengel *et al.*, 2006). Nutrient release from organic fertiliser, however, relies on mineralisation by bacteria and is water and temperature dependent (Dawson *et al.*, 2008) and these processes may have been inadequate in this experimental system. Indeed, matching nutrient supply with demand is a major limitation in low input systems (Dawson *et al.*, 2008). Given that the conventional(cm) produced larger plants than the conventional(hh) treatment, which contained no potassium or phosphorous, also highlights the importance of one or both of the other macro nutrients for plant growth. The response of cereals to nitrogen has been shown to be dependent on the application of phosphorus in phosphorus deficient systems (Takahashi and Anwar, 2007). This may be particularly apparent in pot grown plants where access to nutrients is restricted by the small pot size. These results highlight the benefits of conventional fast release fertiliser to cereal growth and that access to all the major nutrients is important.

6.5.2 Aphid populations

Aphid populations reached significantly higher numbers when reared on older barley plants compared with younger plants. Growth stage can affect cereal aphid fecundity (Watt, 1979; Leather and Dixon, 1981; Leather, 1989) although growth stage did not affect survival and relative growth rates of *M. dirhodum* on wheat in the field or laboratory (Howard and Dixon, 1992). Effects of growth stage on *M. dirhodum*

development time, reproductive period and fecundity was found by Zhou and Carter (1992), although this experiment was carried out on booting plants (GS41-49) and plants going through anthesis (GS60-69) which is older than plants involved in this study. The older plants in the present study had significantly larger root systems than younger plants and so will have had access to more nutrients including nitrogen (Dawson *et al.*, 2008). Nitrogen availability can determine phloem amino acid composition and leaf nitrogen, thus improving aphid development and fecundity (Weibull, 1987; Ponder *et al.*, 2000; Nevo and Coll, 2001). This may be the reason for larger aphid populations on older plants.

In the youngest plants, early aphid population growth was affected by fertiliser treatment with significantly higher numbers of aphids found on conventional(hh) fertilised plants. This may represent the high accessibility of nutrients from this conventional fertiliser (Dawson *et al.*, 2008) improving aphid growth and fecundity relative to the control. Given that the other conventional treatment did not improve fecundity in such a way may be indicative of the negative effects of potassium on aphid performance (Myers *et al.*, 2005; Walter and DiFonzo, 2007) since, unlike the conventional(cm) treatment, the conventional(hh) treatment does not contain potassium. Final aphid populations were not significantly different between treatments. This may indicate that early in plant development the nutritional quality of barley under different fertiliser treatments may not be divergent enough to elicit a response in aphid populations despite an effect on plant growth.

On middle aged barley plants final aphid numbers were higher under all fertiliser treatments when compared with the control. Access to nutrients can benefit both plants (Mengel *et al.*, 2006) and aphid populations (Nevo and Coll, 2001; Khan and Port, 2008) and such trophic benefits of nutrients are evident in this study. Interestingly at this growth stage fertiliser type does not appear to be affecting aphid populations while the effect on plant growth is significant. It could be that aphid populations are below a certain size and following tillering of barley an abundance of leaf material is available. Thus, despite plants being significantly different in size under different fertiliser treatments, enough nutritionally rich leaves to support maximal aphid population growth may still be available to mobile nymphs under all fertiliser treatments. The within-plant distribution of *M. dirhodum* is known to be

determined by levels of individual leaf chlorophyll (Honek and Martinkova, 2002) and results from this study may be indicative of within-plant dispersal of this species to maximise fitness.

Only the conventional(cm) treatment is significantly different from the control with respect to final aphid number on the older plants and this treatment is also significantly different from the chicken manure treatment. The difference between this and the response shown by aphids on middle aged plants suggests some form of temporal nutrient availability from the fertiliser is having an effect on aphid population growth. This has resulted in greater aphid populations relative to the control for all the fertiliser treatments but only on middle aged plants, aphid populations under most of the fertiliser treatments were not different from the control for older plants. A pulse of nutrients may be taken up by the plants some time after fertiliser application, either when plant roots are more developed or more nutrients have been made available through mineralisation of organic compounds (Dawson *et al.*, 2008). This may be true particularly for the organic fertilisers.

The conventional(cm) treatment resulted in larger plants at all ages involved in the experiment and on older plants aphid populations were significantly larger under this treatment. *Metopolophium dirhodum* is a leaf feeding aphid and its performance in the field is strongly correlated with the allocation of plant resources to leaf growth (Honek, 1991b; , 1991a; Honek and Martinkova, 2002). The large above ground biomass of conventional(cm) fertilised barley reflects the large amount of tiller and leaf material these plants possessed and explains why the aphid populations they supported were so large. The significant positive correlation between above ground biomass and aphid populations found on plants of all ages support this proposed effect of resource allocation on *M. dirhodum* performance.

6.5.3 Aphid performance measures

Metopolophium dirhodum, like other cereal aphids, is affected by host age (Watt, 1979; Leather and Dixon, 1981; Leather, 1989). It would appear that performance is maximised on tillering plants represented by the improved fecundity of the founding

nymph on the older plants and the smaller fifth instar nymphs found at the end of the same experiment when plants are post tillering.

The effect of fertiliser on aphid performance in the present study, whether mediated through plant vigour or temporal availability in phloem nutrients, appears to become apparent in aphid populations only over more than one generation. This is reflected by the lack of a treatment effect on seven-day fecundity. An effect of treatment on adult weight was apparent with significantly larger fifth instar adults, a correlate of fecundity in many aphid species (Leather, 1988), on barley under all fertiliser treatments when compared with controls for all plant ages. Analogous results were found for the cotton aphid, *Aphis gossypii*, on cotton, where parent host nutritional quality had a greater effect on aphid reproduction than the nutritional quality of its own host (Nevo and Coll, 2001). This importance of parent nutrition is probably due to the telescoping of generations found in aphid species where an aphid can complete two thirds of its development before it is born and already contains many embryos that will determine its fecundity (Dixon, 1998). These generational responses demonstrate that measuring the effects of treatment on the response of a single generation of an aphid may not expose effects important to subsequent population growth.

Potentially, the use of seven-day fecundity as a measure of aphid fitness in the present study was inadequate and not sensitive enough to detect fertiliser treatments effects. *Metopolophium dirhodum* longevity can be as great as 15 days but at 20°C, 81% of nymphs are produced in the first eight days (Zhuo and Carter, 1992) and thus seven-day fecundity will have included the period of maximal reproduction and should accurately predict *M. dirhodum* fecundity.

6.5.4 Alates

The proportion of alates produced on young and middle aged barley plants was low compared with colonies reared on older plants. Alate production is affected by host age (Howard and Dixon, 1992) and tactile stimulation associated with crowding (Dixon, 1998). The younger host age and smaller colony sizes involved in the

experiments on the young and middle aged plants explains why fewer alates were produced.

On older plants the proportion of adult aphids that were alate was largest in control plants and, following grouping of treatments, this was significantly different from the proportion of alates from both organic and conventional fertiliser treatments. This morph allocation reflects the poor quality and small size of the control plants and the near significant negative correlation between plant biomass and the proportion of alates supports this. There was no difference in the proportion of alates found between the four other fertiliser treatments, this may reflect the antagonistic effect of contributing stimuli. While host quality, reflected by plant size, was lower under organic treatments, so were aphid population sizes leading to a reduction in crowding stimuli. The production of alates is a major restraint on localised aphid population growth in cereal aphids (Holst and Ruggle, 1997) and this is true for field population of *M. dirhodum* (Howard and Dixon, 1992). Moreover, the fecundity of alates is lower than that of apterous individuals (Cannon, 1984; Llewellyn and Brown, 1985). Therefore, although the potential for dispersal was higher on the control, low nutrient plants, overall colony fitness and the size of potential populations was lower.

6.6 Conclusion

Results from the present study highlight the importance of fertilisers to plant growth and reveals that in some cases nutrient supply from conventional chemical fertilisers can benefit barley growth more than slow release organic fertilisers. This is reflected by the low plant growth under the chicken manure treatment. Furthermore, the importance of potassium and phosphorus to barley growth is in evidence although comparisons between results from this experiment and those found in Chapter 4 show that plant response to potassium and phosphorus may be dependent on the amount of soil plants have access to.

With respect to fertiliser treatment effects on aphids, *M. dirhodum* response was only apparent over more than one generation given that no effect on the fecundity of the

founding aphid was found and this has implications for short term experiments. The maximum number of aphids reached in each colony was higher on fertilised plants, particularly for those fertilised with the conventional(cm) treatment. These plants were also larger indicating that plant and aphid vigour correlate. The readiness to produce alates found on control plants could potentially keep aphid populations below the damage threshold of 15 *M. dirhodum* per tiller (Oakley and Walters, 1994) in the field, although control plants were probably unsuitable in terms of potential yield given that they were very small. It is of note however, that the production of *M. dirhodum* alates in pot and field grown plants is different and alates are produced more readily in the field (Howard and Dixon, 1992).

The interaction between fertiliser type and plant age signify that there are effects of both temporal nutrient availability and plant vigour on aphid performance but that *M. dirhodum* populations are ultimately determined by plant growth. Consequently, controlling outbreaks of this species through the use of slow release fertilisers may be inappropriate given that plant growth appears to be more responsive to fertiliser type than aphid populations.

Chapter 7

The effects of organic and conventional fertilisers on the fitness and host preference of the parasitoid, *Aphidius ervi*

7.1 Introduction

The natural enemies of insects living on crops can benefit from organic or low input farming systems (Bengtsson *et al.*, 2005; Hole *et al.*, 2005) and this is supported by the research synthesis in Chapter 2. This benefit has been attributed to reduced input of chemical insecticides (Hummel *et al.*, 2002) and increases in landscape heterogeneity associated with organic systems (Ostman *et al.*, 2001; Purtauf *et al.*, 2005). Parasitoids are important natural enemies of many crop pests, including cereal aphids (Sigsgaard, 2002; Schmidt *et al.*, 2003; Levie *et al.*, 2005), but their impact in organic and conventional cereal systems has been little studied. Percentage parasitism of cereal aphids by chalcid and ichneumonid wasps was found not to be significantly affected by farming system in Germany (Roschewitz *et al.*, 2005). Conversely, brachonids and ichneumonids were found in significantly higher numbers in conventionally managed winter wheat in Southern England (Moreby *et al.*, 1994). It is clear that many farming practices can influence the third trophic level (McLaughlin and Mineau, 1995), to which natural enemies belong, but the impact of fertilisers and more specifically, organic and conventional fertilisers, on parasitoid natural enemies is not well understood.

Fertilisers mediated through the plant and insect host might be expected to influence a parasitoid and its impact on a pest and this could act at two distinct levels. The first level refers to host location efficiency and preference and will determine the level of parasitism experienced by a pest population. The second level concerns the suitability

of the host once it has been located by the parasitoid. This will influence parasitoid survival and determine the fitness of subsequent generations. Indirect effects of fertiliser on both host location and host suitability will influence the level of pest control a parasitoid might achieve.

In terms of host location, whether pest induced or not, plant volatiles are important for the location of habitats where a parasitoid host might be present (Powell *et al.*, 1998; Schworer and Volkl, 2001). Plant volatiles include alkanes, terpenoids, aldehydes and green leaf volatiles (Quiroz and Niemeyer, 1998), the influence of fertiliser on these is unknown. Plant structure, in terms of size, heterogeneity and connectivity, is also a determinant of parasitoid host location efficiency (Andow and Prokrym, 1990; Gingras *et al.*, 2002) and can again be influenced by fertilisers. Nitrogen application promotes tillering and vegetative biomass production in cereals for example (Honek, 1991b; Mengel *et al.*, 2006). Variations in parasitoid abundance in response to fertiliser application were found in the field (Krauss *et al.*, 2007) and laboratory (Bentz *et al.*, 1996), although in both cases parasitoid numbers correlated with pest abundance, highlighting the importance of host population density in host location and subsequent parasitism (Pareja *et al.*, 2007).

Fertiliser effects at the second level, host suitability, are also apparent. Increased nitrogen availability following the application of fertilisers has been found to improve the fitness of emerging parasitoids. Parasitoids showed an increased fecundity, reduced development times (Kaneshiro and Johnson, 1995), increased adult size (Wurst and Jones, 2003) and increased egg load (Jiang and Schulthess, 2005) in response to increased soil nutrients.

Few studies have made direct comparison between organic and conventional fertilisers and the impact they have on parasitoids. Percentage parasitism by *Diaretiella rapae* was significantly higher in compost fertilised broccoli when compared with broccoli which had received inorganic fertilisers (Ponti *et al.*, 2007). The increased parasitism of aphids on organic versus conventional fertilised cabbage was dependent on the season and the type of organic fertiliser used (Karungi *et al.*, 2006b). Blumberg *et al.* (1997) found higher parasitoid numbers following inorganic nitrogen fertilisation of sorghum but parasitism of aphids on maize was not

significantly affected by organic or inorganic nutrient sources (Morales *et al.*, 2001). These studies however, did not consider parasitoid fitness and were carried out in the field with uncontrolled host population sizes. Moreover, in most cases organic and inorganic fertiliser doses were not matched with regards to the amount of nutrients added to the experimental system.

7.2 Aims and objectives

Fertilisers can have tritrophic effects and these effects can influence host location and parasitoid fitness. The aim of this experiment was to investigate whether different fertiliser treatments, mediated through the plant-host complex, influence parasitoid fitness and whether parasitoids show a preference for more suitable hosts.

The objectives of this investigation were to: 1) use a choice experiment to determine the effects of two organic and two conventional fertiliser treatments on host location and preference by the parasitoid *Aphidius ervi* for the cereal aphid *Metopolophium dirhodum* on barley and 2) determine fertiliser treatment effects on the fitness of *A. ervi*. In each case the effect of fertiliser on both plant and aphid performance was also considered. 3) A further objective was to consider the implications of fertiliser application on parasitoids in the agro-ecosystem in terms of pest suppression.

7.3 Materials and methods

7.3.1 Potting procedure

Spring barley (cv. Doyen) was grown in fertiliser amended pots. Fertiliser treatments included the organic fertilisers, chicken manure and hoof and horn meal. For both organic treatments a conventional equivalent was established (conventional(cm) and conventional(hh)) where absolute nutrient inputs were the same as the organic treatments. A fifth treatment involving the addition of no fertilisers was used as a

control (see Table 5.2, Chapter 5 for fertiliser doses). Fertiliser was applied to the pots prior to planting (see materials and methods Chapter 5, Experiments 2 for details).

7.3.2 Aphid colony establishment

When barley plants were at growth stage 20 (Tottman and Broad, 1987), one alate *M. dirhodum* was put in a clip cage (MacGillivray and Anderson, 1957) attached to the primary leaf of each plant. The clip cage was then checked after 24 h and if a nymph had been produced the alate and all other nymphs were removed. If no nymph had been produced, clip cages were then checked every few hours until a nymph was present. Following nymph establishment the clip cage was taken off the plant and the plant was covered with a transparent micro perforated bag measuring 38 cm by 90 cm to prevent aphid escape. The individual nymph was then allowed to develop and reproduce on the host plant. Host plants with developing aphid colonies were stored in a controlled light and temperature glasshouse with a light:dark regime of 16:8 h and day and night temperatures of $20\pm 5^{\circ}\text{C}$ and $14\pm 5^{\circ}\text{C}$, respectively. After two weeks, aphid colonies were checked and nymphs were removed at random to create colonies of 30 individuals on each barley plant. Nymphs that were removed were of various instars to maintain the colony age structure so the proportion of first, second, third and fourth instars was comparable to the original colony. The founding fifth instar aphid was removed so the aphid colony would not continue to increase in number in the short term. Any colonies where the founding aphid had been lost, died or had moulted into an alate adult were excluded from the subsequent experiment. Plants supporting colonies of 30 aphids were transferred to a constant temperature (CT) room for the parasitoid release experiment.

7.3.3 Parasitoid release procedure

All plants involved in the parasitoid release experiment were at growth stage 31 or 32. Prior to parasitoid release the tiller number of each plant was recorded. One plant supporting 30 aphid nymphs from each of the five fertiliser treatments was randomly selected and placed in a clear Perspex chamber measuring 100 cm by 60 cm by 60 cm. At random each plant was placed equidistant around a 9cm Petri dish containing a

piece of cotton wool soaked in honey solution to act as a food source for introduced parasitoids (Fig. 7.1). Ten male and 20 female *Aphidius ervi* parasitoids were then released in the centre of the Perspex chamber and left for 48 h. Parasitoids were supplied by Syngenta Bioline (www.syngenta-bioline.co.uk) and had been cultured on the bean (*Vicia faba*) and pea aphid (*Acyrtosiphon pisum*) system and so were considered naïve to the *M. dirhodum* and spring barley system. Prior to release, each group of 10 male and 20 female parasitoids had been housed in a small plastic boxes, measuring 10 cm by 10 cm by 20 cm, with access to 10% honey solution for 24 h at 20°C to ensure all *Aphidius ervi* females had been mated. The number of successful aphid colonies on plants grown under the various fertiliser treatments enabled the release experiment to be replicated eight times. Availability of release chambers dictated that experiments had to be carried out in two temporal blocks. Block one involved releases one to five and block two involved releases six to eight. Experiments were carried out in a CT room with a light dark regime of 16:8 h at a constant temperature of 20°C.

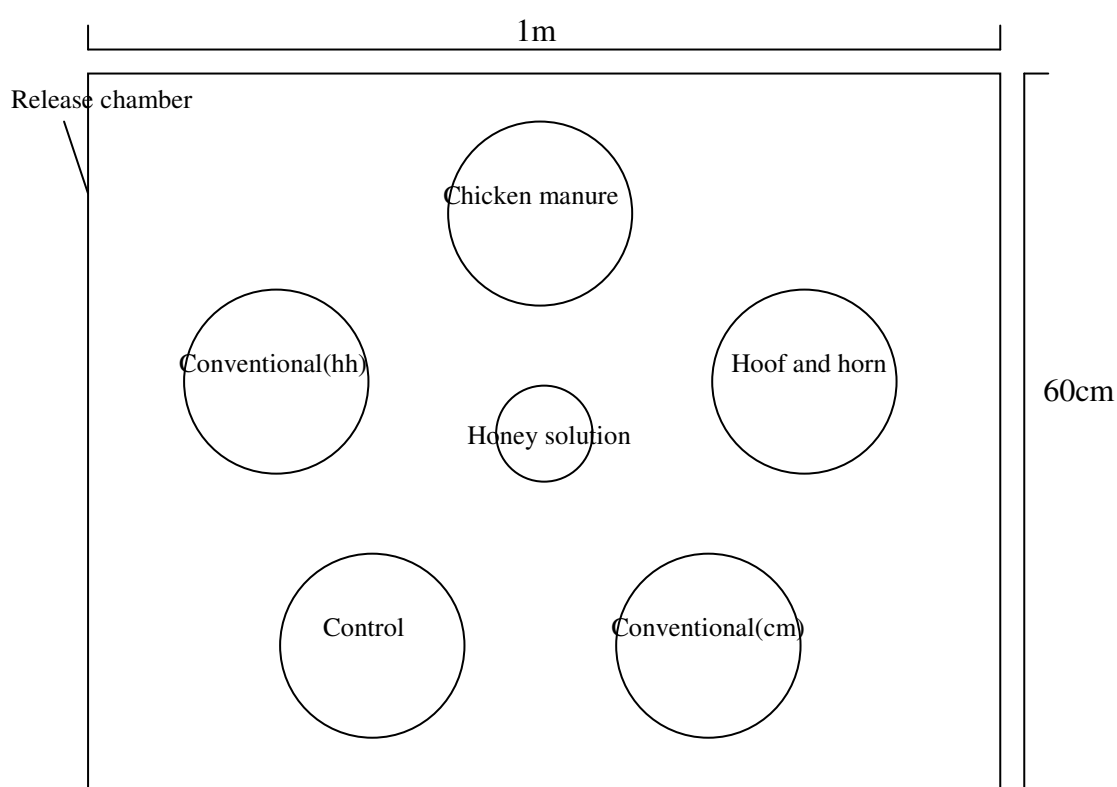


Fig. 7.1 Diagram of the experimental setup for the parasitoid release experiments showing barley plants grown with the five fertiliser treatments (chicken manure, hoof and horn, conventional(cm), conventional(hh) and control). The treatment positions were randomised for each replicate.

7.3.4 Measuring percentage parasitism

Following the 48 h exposure to *A. ervi*, barley plants and their aphid colonies were removed from the Perspex release chamber and transferred individually to Perspex and muslin boxes measuring 100 cm by 20 cm by 20 cm. The aphid colonies were then allowed to continue developing in the CT room. Given that *A. ervi* requires approximately 160 day degrees to develop from egg to aphid mummy (Sigsgaard, 2000), colonies were checked after nine days and the number of aphid mummies on each plant was recorded and collected. Taking into account the original aphid colony size of 30, this number of mummies was then used to calculate percentage parasitism.

7.3.5 Aphid measurements

At the time of mummy counting and removal, four randomly selected, fifth instar, reproductively active aphids were taken from each colony. The fresh weight of each adult was then taken using a Sartorius micro-balance. These data were then used to calculate a mean aphid weight per plant.

7.3.6 Measuring parasitoid sex ratio and size

Following collection, all parasitoid mummies were transferred to glass vials sealed with muslin and stored in a CT room at 20°C until emergence. Newly emerged individuals were transferred to Eppendorf tubes containing industrial methylated spirit (IMS) for storage. Once all parasitoids had emerged and been preserved, individuals were sexed and the length of the hind tibia of each parasitoid was measured under a binocular microscope. This information allowed parasitoid sex ratios and relative size to be inferred.

7.3.7 Statistical analysis

Fertiliser treatment effects on tiller number were analysed using an ANOVA with differences between means examined using a Tukey honest significant difference test.

Prior to analysis, barley tiller number was log transformed after initial inspection of the data revealed tiller number to be positively skewed.

Analysis of variance was used to analyse treatment effects on aphid weights and male and female parasitoid hind tibia lengths. The aphid weight for each plant was determined by taking the mean weight from the four aphids collected from that plant. Similarly, hind tibia length was a mean taken from all male or female parasitoids emerging from one plant. The initial model examined aphid weight and parasitoid tibia length against three experimental factors; block, replicate and fertiliser treatment. Block consisted of two levels representing the two separate temporal blocks in which the experiments were carried out. Replicate represents the eight individual release experiments carried out in the two temporal blocks; five cage releases in the first temporal block and three in the second. Fertiliser treatment consisted of the two conventional, two organic and control fertiliser treatments. Due to non-orthogonal data, interaction effects were not included in the model. If no significant effect of block or replicate was found then the model was simplified to include only fertiliser treatment effects and means were compared using a Tukey test. If no significant treatment effects were found then the fertiliser treatment levels were logically grouped. First to three levels, organic : conventional : control, and if no significant effect was found then fertiliser treatments were further grouped into two levels, fertiliser : control.

Block, replicate and fertiliser treatment effects on percentage parasitism were compared using ANOVA. As it is necessary to normalise the data, percentage parasitism was arcsine transformed prior to analysis. Due to non-orthogonal data, interactions were not included in the model. If block and replicate effects on percentage parasitism were found to be non-significant they were removed from the model, leaving only the fertiliser treatment effects. If still no significant effects were found, as with previous models, fertiliser treatments were grouped, first into three levels and then into two. Comparison of means was undertaken with a Tukey test.

Parasitoid sex ratios were analysed using a generalised linear model with quasibinomial errors because the response variable was a bounded proportion and data was found to be overdispersed. Again, block, replicate and fertiliser treatment

factors were included in the model. Similarly to previous models, interaction effects were not included. Once more if no initial fertiliser treatment effects were found then treatments were logically grouped. Significant differences between fertiliser treatment means were calculated from t values given by the model.

The correlation between male and female parasitoid hind tibia length and adult aphid weight was tested using linear regression analysis. Mean aphid weight and mean hind tibia length from each separate plant was taken as an individual data point. All statistical analysis was carried out using the statistical software 'R' version 2.7.1 (Ihaka and Gentleman, 1996).

7.4 Results

7.4.1 Plant performance

There was a significant effect of fertiliser treatment on barley tiller number ($F_{4,35} = 20.08$, $P < 0.001$) (Fig. 7.2), there were no significant effects of block ($F_{4,28} = 2.25$, $P = 0.14$) or replicate ($F_{6,28} = 1.16$, $P = 0.24$). The tiller numbers of barley plants grown under both conventional fertiliser treatments were significantly greater than the tiller numbers of control barley plants and barley grown using chicken manure fertiliser. The conventional(cm) treatment resulted in significantly greater tiller numbers than the hoof and horn and conventional(hh) treatments.

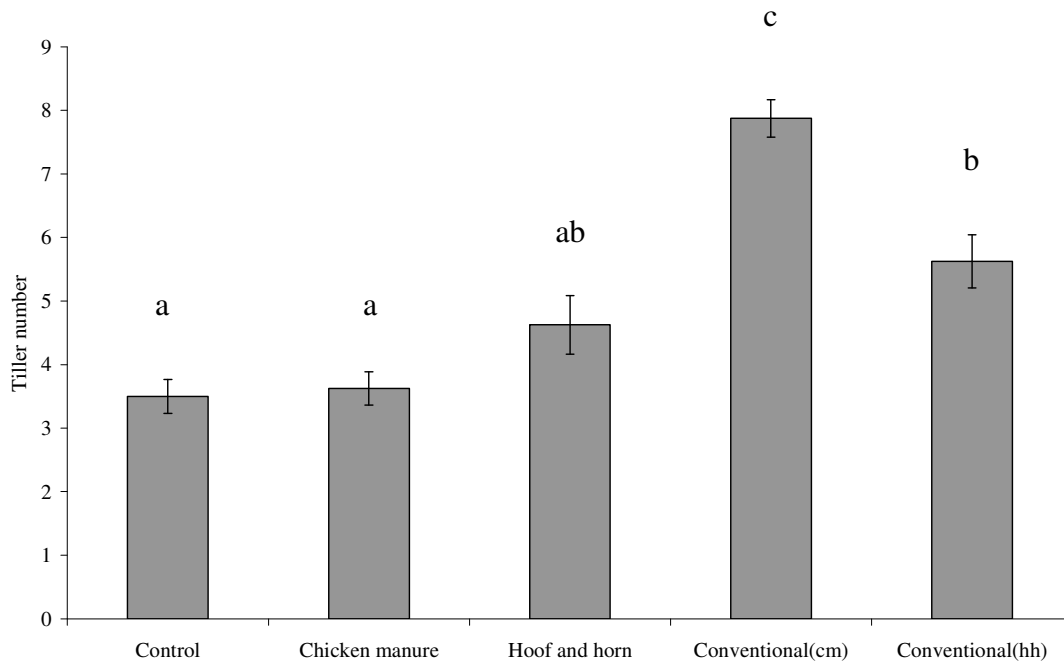


Fig. 7.2 Tiller number of barley plants grown under five fertiliser treatments (mean \pm SEM). Treatments with different letters are significantly different (Tukey, $P < 0.05$).

7.4.2 Aphid performance

No significant effects of experimental block ($F_{1,28} = 1.38$, $P = 0.25$) or replicate ($F_{7,28} = 2.28$, $P = 0.06$) on aphid weight were found. Significant fertiliser treatment effects on aphid weights were, however, apparent ($F_{4,35} = 9.72$, $P < 0.001$) (Fig. 7.3). Both conventional fertiliser treatments resulted in significantly larger aphids than the control treatment. Aphid weights under the conventional(cm) treatment were also significantly greater than aphid weights under both organic fertiliser treatments.

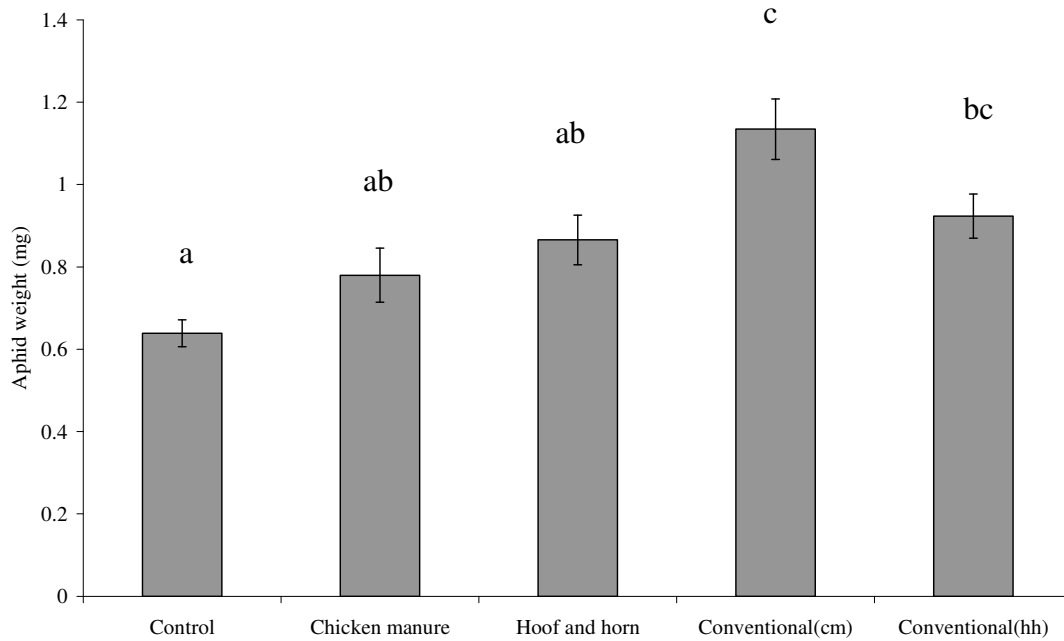


Fig. 7.3 Weight of adult *Metopolophium dirhodum* on barley plants grown under five fertiliser treatments (mean \pm SEM). Treatments with different letters are significantly different (Tukey, $P < 0.05$).

7.4.3 Parasitoid host location

Mean percentage parasitism was between 15% and 30% for all treatments with a maximum and minimum of 57% and 3% found on individual plants (Fig. 7.4.). There were no significant effects of block ($F_{1,28} = 0.74$, $P = 0.40$) or fertiliser treatment ($F_{4,28} = 1.28$, $P = 0.30$) on percentage parasitism. Following analysis of replicate effects on percentage parasitism a significant effect was found ($F_{7,32} = 2.41$, $P < 0.05$) although a Tukey test revealed no one replicate was significantly different from any other.

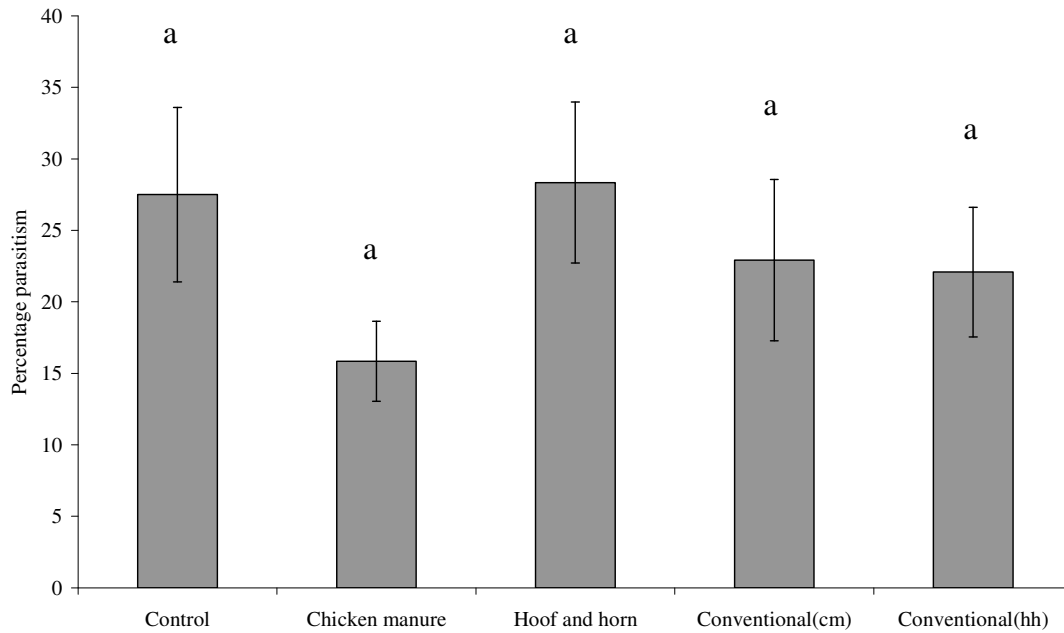


Fig. 7.4 Percentage parasitism of *Metopolophium dirhodum* colonies by *Aphidius ervi* on barley plants grown under five fertiliser treatments (mean \pm SEM). Treatments with different letters are significantly different (Tukey, $P < 0.05$).

7.4.4 Parasitoid host suitability

A total of 280 aphids were parasitised in the present study and of those parasitoids that emerged, 132 were male and 99 were female. Male and female *A. ervi* hind tibia lengths were highest under conventional(cm) treatments and lowest on control plants (Fig 7.5&7.6), although no significant effects of block (male: $F_{1,25} = 0.19$, $P = 0.67$; female: $F_{1,20} = 0.06$, $P = 0.80$), replicate (male: $F_{6,25} = 2.17$, $P = 0.08$; female: $F_{6,20} = 0.67$, $P = 0.68$) or fertiliser treatment (male: $F_{4,32} = 1.69$, $P = 0.18$; female: $F_{4,27} = 1.19$, $P = 0.34$) was found. Following fertiliser treatment grouping, still no significant effects were apparent.

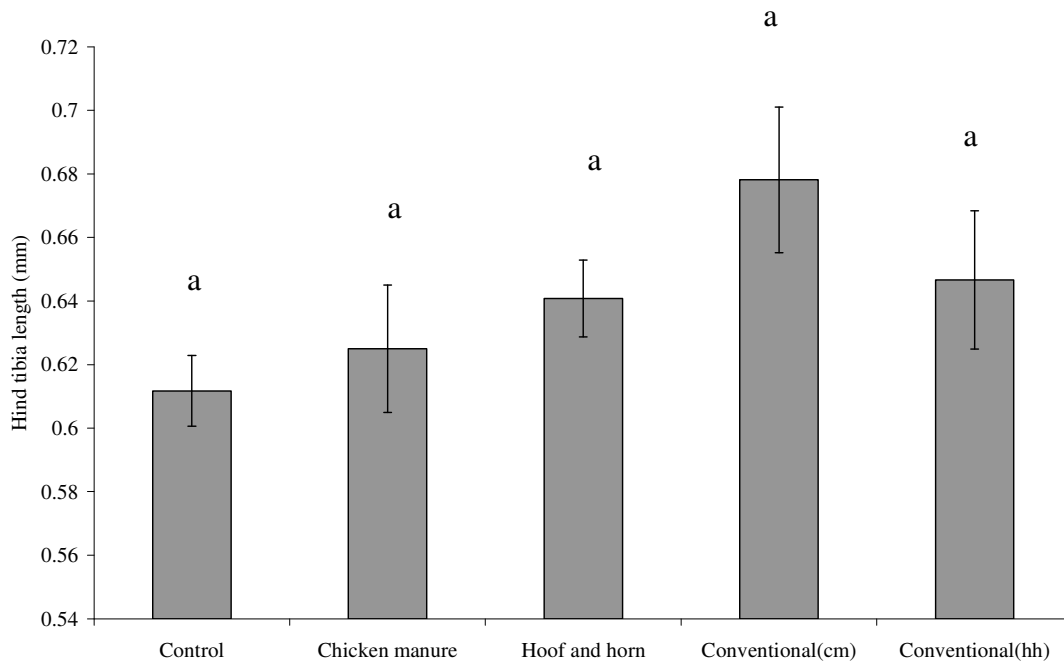


Fig. 7.5 Hind tibia length of male *Aphidius ervi* parasitoids emerging from *Metopolophium dirhodum* aphids reared on barley grown under five fertiliser treatments (mean ± SEM). Treatments with different letters are significantly different (Tukey, $P < 0.05$).

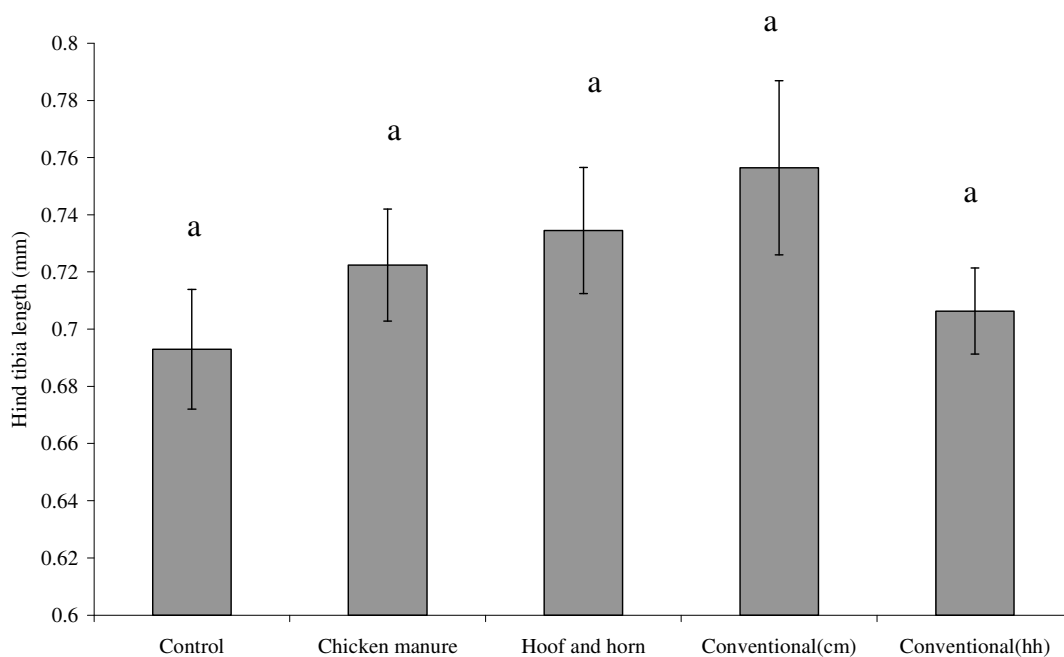


Fig. 7.6 Hind tibia length of female *Aphidius ervi* parasitoids emerging from *Metopolophium dirhodum* aphids reared on barley grown under five fertiliser treatments (mean ± SEM). Treatments with different letters are significantly different (Tukey, $P < 0.05$).

Both male (Fig. 7.7) and female (Fig. 7.8) *A. ervi* hind tibia lengths were significantly positively correlated with adult aphid weight (males: $F_{1,35} = 7.64$, $P < 0.01$; females: $F_{1,30} = 4.40$, $P < 0.05$).

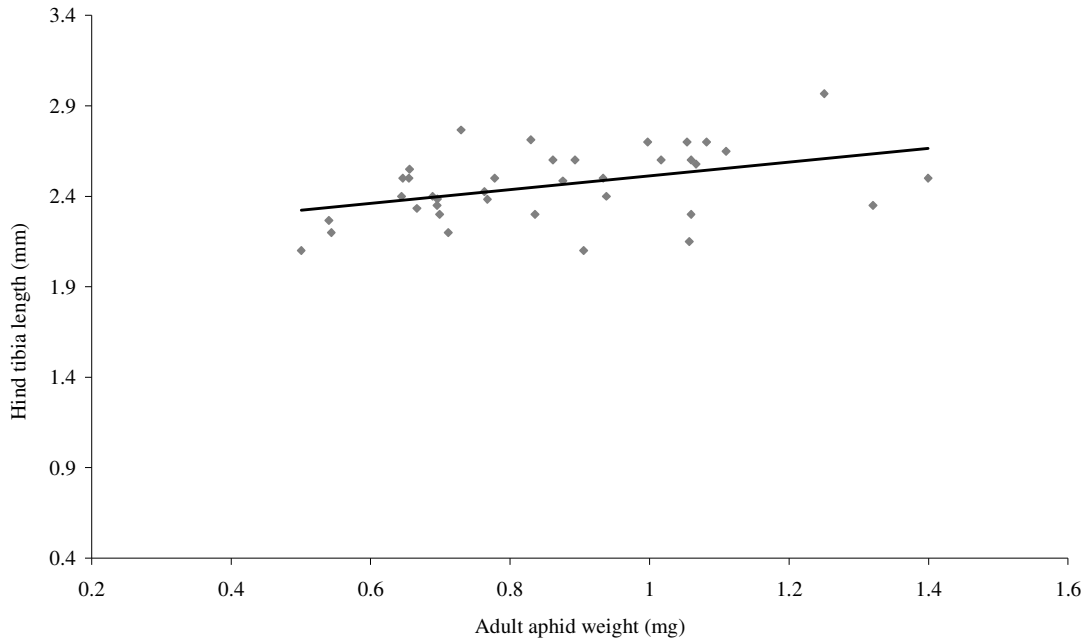


Fig. 7.7 Relationship between male *Aphidius ervi* hind tibia length and *Metopolophium dirhodum* adult weight on barley ($y = 0.37x + 2.13$, $R^2 = 0.16$).

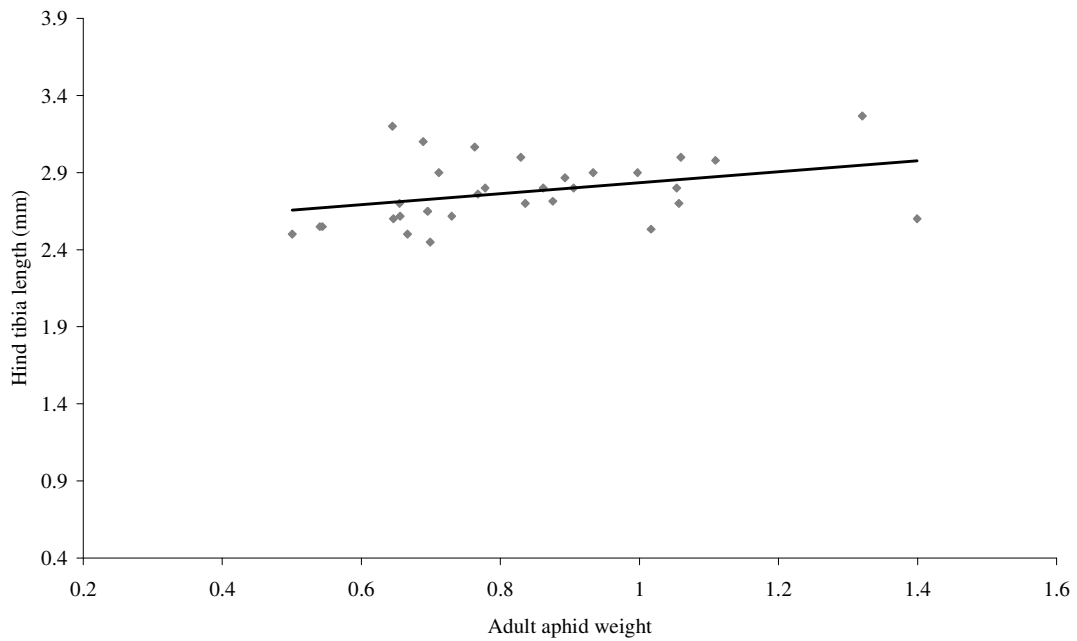


Fig. 7.8 Relationship between female *Aphidius ervi* hind tibia length and *Metopolophium dirhodum* adult weight on spring barley ($y = 0.35x + 2.48$, $R^2 = 0.13$).

The sex ratio represented as the mean proportion of female parasitoids emerging under the five fertiliser treatments ranged from 30% to 50% (Fig. 7.9). This was not significantly affected by block ($F_{11,25} = 0.04$, $P = 1$), replicate ($F_{11,25} = 0.04$, $P = 1$) or

fertiliser treatment ($F_{4,32} = 0.05$, $P = 0.99$), even following fertiliser treatment grouping.

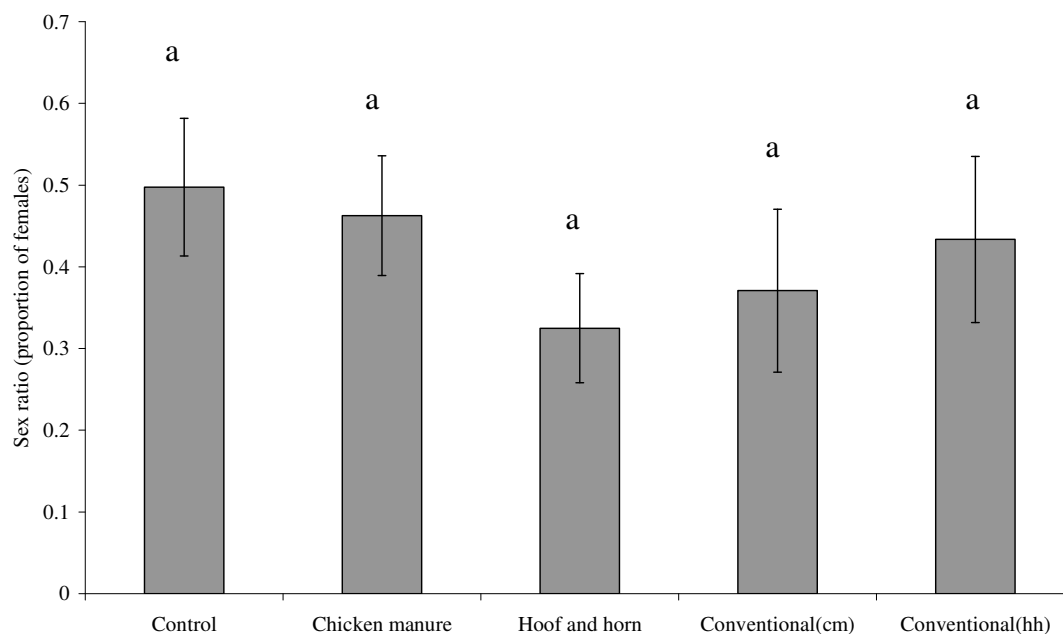


Fig. 7.9 The sex ratio of *Aphidius ervi* parasitoids emerging from *Metopolophium dirhodum* aphids reared on barley grown under five fertiliser treatments (mean \pm SEM). Treatments with different letters are significantly different (Tukey, $P < 0.05$).

7.5 Discussion

7.5.1 Plant performance

Fertiliser treatment had a significant effect on barley tiller number with conventionally fertilised plants producing more tillers than plants grown in the absence of fertilisers. The high level of plant available nutrients, particularly nitrogen, found in conventional fertilisers is known to promote tillering (Honek, 1991b; Duffield *et al.*, 1997). The fact that plant response to nitrogen is dependent on potassium and phosphorous (Hasse *et al.*, 2006; Takahashi and Anwar, 2007) explains why barley receiving the conventional(cm) treatment, which contains sources of nitrogen, phosphorus and potassium, yielded the greatest number of tillers.

7.5.2 Aphid performance

Metopolophium dirhodum adult weight, a correlate of fitness for many aphid species (Leather, 1988), was highest on plants receiving the conventional(cm) treatments. Hoof and horn and conventional(hh) fertilised plants also resulted in significantly larger aphids than the control. Fertiliser application can alter the amino acid composition of phloem sap (Weibull, 1987) and aphid performance is highly dependent on the concentration of certain amino acids in their diet (Simpson *et al.*, 1995). Furthermore, fertiliser can dictate resource allocation in cereal plants and this can influence the performance of cereal aphids, *M. dirhodum* in particular (Helenius, 1990; Honek, 1991b). High plant available nutrients in the soil following application of hoof and horn, conventional(hh) and conventional(cm) fertilisers will have benefited both plants and aphids accordingly. Chicken manure fertilisers may contain a smaller proportion of plant available nutrient or the nutrients may take longer to break down under the action of micro-organisms (Cordovil and Cabral, 2001) resulting in smaller plants and aphids. The low level of available nutrients in the control treatments was reflected by low plant growth and aphid size.

7.5.3 Parasitoid host location

In the present study, aphid colony parasitism was as low as 3% on some plants with means of between 15% and 30%. Given that *A. ervi* can lay as many as 14 eggs an hour (Schworer and Volkl, 2001), sub-maximal parasitism of the aphid colonies was occurring even if parasitism is restricted to certain instars. Furthermore, *A. ervi* host location efficiency or preference was apparently not affected by fertiliser treatment. The aphid colonies had been on the barley host plant in varying numbers for at least two weeks prior to parasitoid release. Given that aphid host infestation for a period of three days by colonies of 10 (Schworer and Volkl, 2001) and 40 aphids (Powell *et al.*, 1998) on bean plants is enough to alter host plant volatile profiles and improve host location by *A. ervi*, the absence of host induced plant volatiles is probably not the reason for low parasitism or the apparent lack of preference shown by *A. ervi* for plants grown under certain fertiliser treatments in this experiment. The plant-host complex the parasitoid *Aphidius colemani* is reared on is highly influential in the host

preference of its offspring in olfactometer work (Douloumpaka and Emden, 2003) and in cage releases (Bilu *et al.*, 2006) and this is attributed to plant and parent derived chemical cues in the mummy of the emerging parasitoid. The parasitoids used in the present study were reared on an entirely different plant-host complex and inefficient host location may explain why aphid colonies experienced low levels of parasitism. In addition, a naïve parasitoid might be less sensitive to slight changes in plant volatile emissions caused by fertilisers and sensitivity to fertiliser treatments was not seen in the present study given that aphid colonies on barley receiving different fertilisers were parasitised equally. Adult *A. ervi* however, have shown increased orientated flight toward a plant-host complex after as little as one minute conditioning on an infested host (Guerrieri *et al.*, 1997). This demonstrates that learning in adult parasitoids could have occurred over the short period of the experiment. Nonetheless, further work involving parasitoids reared on the experimental system may show different effects of fertiliser treatment on host location and preference.

An alternative explanation for the lack of preference shown by *A. ervi* could be that any fertiliser treatment effects on host preference were masked by fertiliser effects on plant structure. Fertiliser application and conventional fertilisers in particular, promoted tillering in the barley plants involved in this experiment. High numbers of tillers will have increased plant complexity and parasitoids such as *Trichogramma nubilale* have been shown to search more intensively (Andow and Prokrym, 1990) and are more effective at host location on simple plant (Gingras *et al.*, 2002). Moreover, the number of aphids per unit area of leaf material was less for plants with higher tiller numbers, namely the conventionally fertilised plants, and so a parasitoid will have had to search more leaf area to locate an aphid or aphid colony. Given that once alighted on a plant, host location by *A. ervi* is carried out on foot (Guerrieri *et al.*, 1997; Schworer and Volkl, 2001), aphid number per unit leaf area may be very important in terms of the frequency of host contact. An experiment where different fertilisers are applied but plant tiller number is controlled for would extricate independent effects of fertiliser on plant volatiles and plant structure.

The significant replicate effect on percentage parasitism may be a result of a few parasitoids introduced into some of the cages which were extremely effective at host location and increased the overall level of parasitism in a cage regardless of fertiliser

treatment. This potential variability in individual parasitoid efficiency is reflected in the high variability found between replicates.

7.5.4 Parasitoid host suitability

The effect of fertiliser treatment on male and female *A. ervi* parasitoid tibia length, a proxy used to represent parasitoid fitness (Wurst and Jones, 2003; Bilu *et al.*, 2006), was not significantly affected by fertiliser treatment. The response of parasitoid size to fertiliser treatment did follow that of aphid weight, with the largest parasitoids emerging from conventional (cm) treatments and the smallest found on control treatments. There was a significant correlation between both male and female tibia length and adult aphid weight showing that plants which produced bigger aphids also produced bigger parasitoids.

These results show a tritrophic effect of fertiliser treatment, with certain treatments resulting in barley with more tillers which result in larger aphids which in turn support larger parasitoids. Tritrophic effects of fertiliser application have previously been reported for ryegrass, cereal aphids and their parasitoids (Krauss *et al.*, 2007); beans, *Liriomyza trifolii* and the parasitoid *Chrysocharis oscinidis* (Kaneshiro and Johnson, 1995); *Bemisia argentifolii* reared on *Euphorbia pulcherrima* and the parasitoid *Encarsia formosa* (Bentz *et al.*, 1996) and sorghum, *Chilo partellus* and the larval parasitoid *Cotesia flavipes* (Jiang and Schulthess, 2005). In all cases both herbivore and parasitoid performance, whether measured as infestation level, percentage parasitism, fecundity, development rate or size, were improved by the application of fertilisers. This was attributed to increased plant biomass (Krauss *et al.*, 2007) or by increases in foliar nitrogen (Kaneshiro and Johnson, 1995; Bentz *et al.*, 1996; Jiang and Schulthess, 2005).

Parasitoid sex ratios remained unaffected by fertiliser treatment and given that female parasitoids were larger than males, and might be expected to be preferentially laid in larger hosts, this was surprising. Perhaps the maintenance of a sex ratio close to 50:50, observed under all fertiliser treatments in this study, is actually the optimum

for *A. ervi* and even given access to more suitable host *A. ervi* will maintain this sex ratio.

7.6 Conclusion

The results from the present study indicate that the performance of *A. ervi*, reflected by its size, is dependent on the fitness of its host and possibly not directly linked to fertiliser treatment. Whichever fertiliser treatment, whether conventional or organic, results in larger aphid hosts will result in larger parasitoids. It is surprising to note then that aphid host preference, represented by percentage parasitism, was not affected by fertiliser treatment or host size. *Aphidius ervi* were not preferentially selecting a more suitable host, a behaviour which has been observed in *A. colemani* (Bilu *et al.*, 2006). The consistent number of female parasitoids found between treatments also suggests that female parasitoids were not preferentially being laid in larger host.

These results have important implications for pest control. The increased abundance of parasitoids sometimes found in organic farming systems (Drinkwater *et al.*, 1995; Berry *et al.*, 1996) is probably not due to organic fertiliser application but other management practices given that fertiliser did not affect percentage parasitism in the present study. In addition, increased aphid numbers and improved fitness following application of conventional fertilisers (Hasken and Poehling, 1995; Duffield *et al.*, 1997; Nevo and Coll, 2001) might be expected to increase parasitoid abundance and fitness in high input systems, as was found by Moreby *et al.* (1994). These results indicate that the use of slow release fertilisers or the considered use of conventional fertilisers in cereal systems to improve the impact of parasitoids in conjunction with reduced aphid infestation would be difficult given that host and parasitoid performance are both inextricably linked, an association reported in other studies (Kaneshiro and Johnson, 1995; Wurst and Jones, 2003; Jiang and Schulthess, 2005; Krauss *et al.*, 2007).

Chapter 8

Discussion

With increasing concern over the environmental costs and unsustainability of agricultural intensification there has been a drive towards promoting low intensity farming practices. This is reflected most overtly by the increasing area of agricultural land that is becoming certified as organic, particularly in Europe.

There has been growing interest in the effects of alternative fertilisation methods as a component of both intensive and low intensity farming systems. The effects of excess fertiliser and thus increased plant nutrients on promoting pest performance has been known for some time, reflected by Scriber's 1984 (cited in Altieri and Nicholls, 2003) N-damage hypothesis. Researchers are now emphasising that improvements in general soil biology through the use of alternative fertilisers might reduce nutrient imbalances in crop plants and promote healthy crop growth in conjunction with the reduced incidence of pests (Altieri and Nicholls, 2003). This is embodied in the mineral balance hypothesis (Phelan *et al.*, 1995). The research described in this thesis has contributed to the knowledge base regarding soil fertility effects on pests and natural enemies by reviewing available research on the subject and undertaking field and laboratory trials to examine fertiliser effect on the cereal, aphid, natural enemy biological system.

The quantitative literature review in Chapter 2 of this thesis demonstrated that farming systems, varying primarily in fertiliser regime and pest management practice, show significant trends in their effects on both pests and natural enemies. These effects were that in the main, pests and natural enemies profited from low intensity or organic management practices. The effects of management practice on natural enemies was more pronounced in farm scale experiments indicating that it is large scale factors associated with low intensity or organic systems that benefits natural

enemies. The strong influence of habitat and vegetation heterogeneity on natural enemies on a local and landscape scale (Gurr *et al.*, 2003; Langellotto and Denno, 2004) may be key factors. The benefits of low intensity methods to arthropod pests were prominent in field scale experiments indicating that pest management, crop husbandry and fertilisation practice implemented on a field scale may be dictating pest response.

The synthesis of current research revealed that despite obvious impacts of large scale low intensity agricultural methods on both pests and natural enemies, effects of fertilisers can be important within the context of an agricultural system. The meta-analysis showed no overall effect of organic or conventional fertilisers on pest responses but the vote-counts indicated a positive effect of conventional fertilisers. This is a case potentially in support of the mineral balance hypothesis (Phelan *et al.*, 1995) and further evidence that readily accessible nutrients following application of conventional fertilisers can influence higher trophic levels.

A significant finding of the research synthesis was that the effects of organic fertilisers derived from plant materials and animal derived products were entirely different with regards to pest response. Manures suppressed pest numbers and performance while the opposite was true for composts. The contrasting influence of manures and composts was still apparent in studies comparing whole management systems; this is testament to its importance. Whether this effect is mediated through influences on plant health or temporal availability of nutrients would need to be tested by considering each example on a case by case basis. Regardless of its underlying reasons, the potential for this effect to be utilised in pest management is profound.

The research synthesis revealed that relatively few studies matched nutrient inputs between organic and conventional treatments and this is a potential limitation in many of these studies. Nutrient must be matched if researchers wish to differentiate between impacts of absolute nutrient inputs and the effects of fertiliser type on soil biology, plant resistance and temporal nutrients availability. Nutrient matching was carried out in the experimental manipulations reported in Chapter 3, 4, 5, 6 and 7 of this thesis.

Both the meta-analytical and vote-counting methods involved in the synthesis showed positive effects of organic fertilisers on natural enemies. Evidently fertiliser may be contributing to the positive effects of low intensity farming methods found on natural enemies, although it is hard to determine what is behind these effects. This study highlights the apparent lack of published research and stresses the need for further work in this area; work contributed to by Chapters 3, 4 and 7 of this thesis.

The experimental work reported in this thesis involved the barley, aphid and parasitoid system and investigated effects of organic and conventional fertilisers on a crop, its pest and their natural enemies. The growth or yield of spring barley was consistently improved following application of conventional fertilisers when compared with organically fertilised plants both in field trails, semi-field trials and glasshouse pot experiments. In the case of the field pot experiment referred to in Chapter 4; this improved yield was attributed primarily to increased tiller numbers. Tiller numbers were also consistently higher following conventional fertiliser application in all glasshouse trials. This difference in plant growth could be a result of increased nutrient availability soon after application of conventional fertilisers. Barley is a fast growing annual crop which takes on a considerable proportion of its nutrient early in growth (Montemurro *et al.*, 2006) and importantly, modern varieties of cereals are bred for increased yield in response to conventional fertilisation (Dawson *et al.*, 2008). Potentially, cereal crops including barley may not be responsive to organic slow release fertilisers rendering such fertilisers unsuitable for this crop, however adequate barley yields have been achieved by mixing both conventional and organic fertilisers (Montemurro *et al.*, 2006).

The beneficial effects of organic fertilisers including increased soil organic matter, microbial activity and subsequent improvements in mineralization potential can be considered cumulative and will increase following application of these fertilisers over several seasons. Therefore the differences in yield found in the present study might be less pronounced or even reversed if fertiliser treatments were implemented over several seasons. Experiments reported in chapters 3, 4 and 6 of this thesis, however, were carried out using a soil which had received little agricultural management with no removal of organic matter, characteristic of agricultural systems. Therefore the organic matter, microbial activity and mineralization potential of this soil can be

considered high, yet differences in yield between organic and conventional treatments were still apparent. One can postulate then that organic fertiliser application over several years would still result in low barley tillering and low yields.

Further work involving slower growing annuals such as brassicas or perennials may not show such significant differences in yield between organic and conventional fertiliser treatments. Slow growing crops, where yield is not so dependent on a nutrient sensitive early growth characteristic such as tillering, may respond better to the slow release nature of organic fertilisers.

One limitation to the methodologies involved in the present experiments involves judging barley yield purely by weight. The difference in yield between organic and conventional treatments might not be so dramatic if the protein content as well as the ear weights were considered. Perhaps the late release of nutrients from organic fertilisers might improve grain protein content and increase yield. This would be a hypothesis to test in further work.

Aphid abundance and species composition were contrasting between the field trials of 2006, 2007 and 2008. The timing of cereal aphid spring migration is dependent on numerous factors including winter temperatures, global radiation and precipitation (Klueken *et al.*, 2009) and there will have no doubt been variation in these critical factors between years. The Rothamsted Insect Survey (www.rothamsted.ac.uk/insect-survey/STAphidBulletin.php) data, based on 16 suction traps in different areas of Britain, shows considerable variation between years in both the number and timing of aphid migration and this includes *M. dirhodum*, *S. avenae* and *R. padi* in 2006, 2007 and 2008. Moreover, the sowing date of barley in each of the three years was different and this will have affected at what barley growth stage immigrant aphids arrived. Given the morphological and growth stage preference of these cereal aphid species (Watt, 1979; Leather and Dixon, 1981; Walters and Dixon, 1982), varying effects of sowing date on subsequent aphid species composition can be expected.

Several ecological theories have relevance when considering the response of aphids to different fertiliser treatments, these include the 'plant vigour hypothesis' (Price, 1991), the 'plant stress hypothesis' (White, 1969), the 'mineral balance hypothesis' (Phelan

et al., 1995) and the 'N-damage hypothesis' ((Scriber, 1984) cited in Altieri and Nicholls, 2003). The plant vigour and plant stress hypotheses are contradictory; one proposes that herbivores will perform better on vigorous, fast growing hosts while the other states that stressed plants are nutritionally more favourable to herbivores and particularly phloem feeders. The N-damage hypothesis suggests a positive correlation between host nitrogen content and herbivore damage while the mineral balance hypothesis states that positive soil functioning will be conveyed to host plants making them better able to resist pests.

The cereal aphids involved in the present study consistently performed better on conventionally fertilised plants when compared with those receiving organic fertilisers or those growing in the absence of fertiliser. For the field trial reported in Chapter 3, the number of *M. dirhodum* days per plant was higher in conventionally fertilised plots. For the field trial discussed in Chapter 4, the number of aphid days per tiller was significantly higher in conventionally fertilised pots when compared with those fertilised organically. Similar findings were made in pot trials carried out in both control temperature rooms (Chapter 5) and glasshouses (Chapter 6 & 7). Aphid performance in clip cages represented by total reproductive output was higher following conventional fertiliser application and this was particularly apparent in the response of *M. dirhodum* to the conventional(cm) treatment and the response of *R. padi* to the late applied conventional(hh) treatment (Chapter 5). The benefits of conventional fertilisers to *M. dirhodum* was further supported by the increased colony sizes (Chapter 6) and larger adult aphids achieved (Chapter 7) under the conventional(cm) treatment. Given the improved plant growth and yields shown by plants receiving the conventional fertiliser treatments, these findings tend to conform to the plant vigour hypothesis. The findings conform only in older plants suggesting the hypothesis may be age dependent, certainly in the case of cereals and cereal aphids. Leaf nitrogen analysis taken from plants at a growth stage when aphids are responding to the application of fertilisers may also demonstrate the relevance of Scriber's' (1984) N-damage hypothesis in this instance.

An interesting finding from this research is how the mechanism of aphid response to fertiliser treatment appears to be species specific. *Rhopalosiphum padi* is sensitive to the timing of fertiliser application. This response is probably caused by temporal

availability of soil mineral nutrients effecting the amino acid composition of phloem sap. This is demonstrated by the significant effect of the timing of fertiliser application on aphid numbers found in the field trial of 2008 (Chapter 4) and the extremely positive response of this aphid to late applied conventional fertilisers in Chapter 5.

The response of *M. dirhodum* on the other hand, is consistently correlated with that of plant growth, and particularly vegetative growth. In Chapters 4, 5 and 6, the performance of *M. dirhodum*, whether measured as aphids per unit dry mass, colony size or reproductive output, correlated with barley vegetative biomass. The experiments did not prove that *M. dirhodum* is not affected by temporal fluctuations in phloem amino acid composition or that *R. padi* is not influenced by plant growth, indeed a strong link between fluctuations in soil nutrients, changes in phloem amino acid content and plant growth would be expected.

Recent advances in techniques for measuring plant phloem amino acids by combining high sensitivity capillary electrophoresis coupled with laser-induced fluorescence detection (Gattolin *et al.*, 2007; , 2008) mean that the quantities of individual amino acids within one sieve element can now be measured from very small quantities of phloem sap. These techniques could be used to observe the temporal change in amino acid composition as well as spatial variation within a crop plant as it grows under the influence of different fertilisers applied at different times. This coupled with observation of aphid performance throughout plant growth may help in the understanding of the effects of temporal nutrient availability and resource allocation to certain plant organs and how this is linked to aphid performance. It is worth noting at this point however, that phloem amino acid composition is not the sole determinant of aphid success. The phloem sap of drought stressed plants can improve in terms of essential and non-essential amino acid concentration, however, the performance of aphids may not correlate with this improvement, as was found for *R. padi* reared on several grass species (Hale *et al.*, 2003). It was concluded that phloem accessibility was as important to aphid success as phloem composition. Aphids also possess endosymbiotic bacteria, these are primarily involved in the provision of essential amino acids and enable aphids to compensate for inadequacies in their diet (Douglas, 1998). Indeed this ability of aphids to compensate for variations in diet quality may explain

some of the null responses to fertiliser treatments found in the field trial of 2006 (Chapter 3), clip cage experiment 1 (Chapter 5) and clip cage experiment 2 on young plants (Chapter 5).

Information on temporal and spatial variations in phloem amino acid composition coupled with the finding from this study would prove useful in minimising pest outbreaks through the use of informed fertiliser application as part of an integrated crop management system. The mineral nutrients in soil varies depending on soil chemistry, soil biology and fertiliser type. Figure 8.1 is a theoretical graph showing soil mineral nutrient availability following application of two different organic fertilisers and the application of conventional fertilisers at two different times. Information is adapted from soil incubation experiments (Cordovil and Cabral, 2001; Gioacchini *et al.*, 2006).

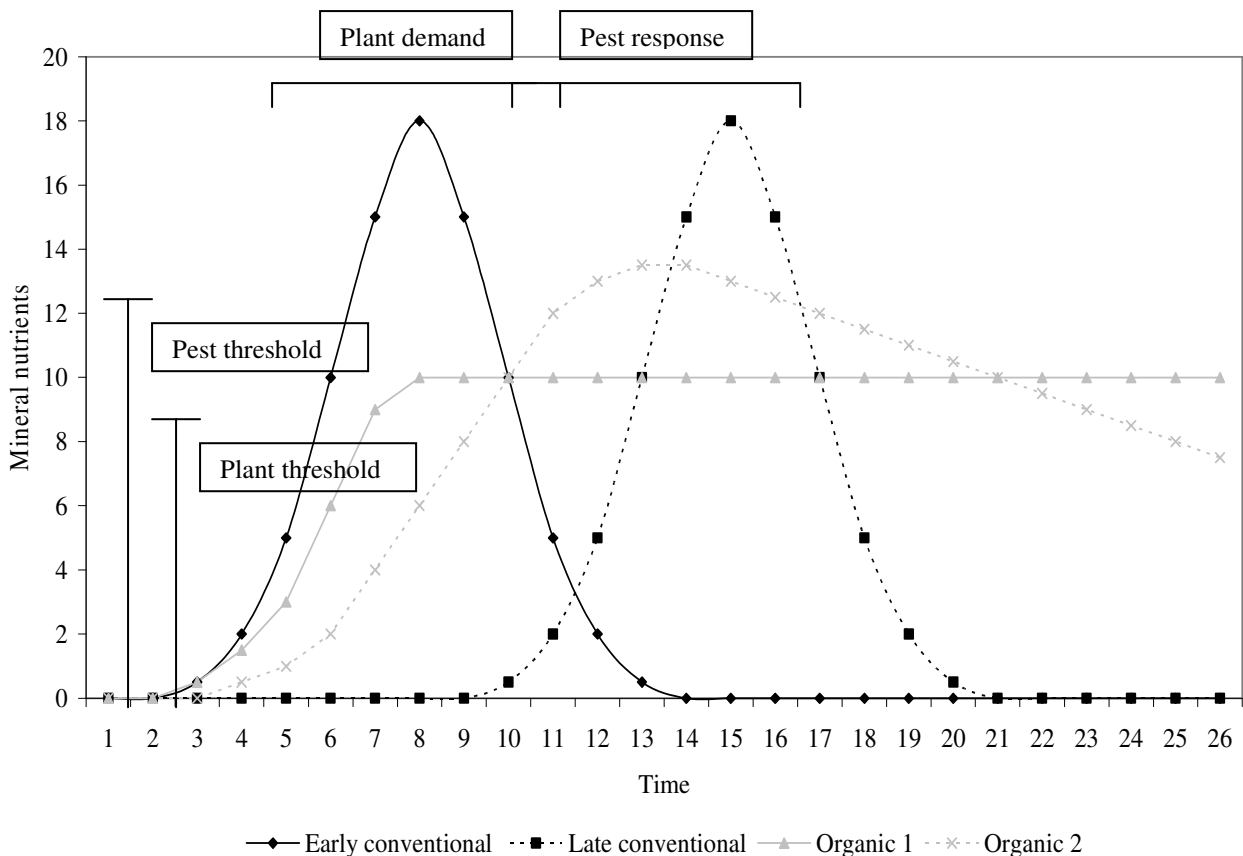


Fig. 8.1 Theoretical levels of soil mineral nutrients following application of two different organic fertilisers or conventional fertilisers at two different times. Theoretical time periods when a plant and a pest will respond positively to mineral nutrients and the threshold in mineral nutrients required to elicit these responses are also shown.

Assuming mineral nutrients are readily available to a crop plant and will improve growth and yield and the demand by plants is dependent on species and varies with growth stage, there is an optimum time to apply either conventional or organic fertilisers so that peaks in mineral nutrient availability coincide with plant demand. This can be represented by a temporal window for plant demand. Benefits to the plant, however, are not the only effects of fertiliser that need to be considered, pest performance is also important because this can impact on yield. So similarly to a temporal window for plant demand there will be a temporal window of pest response (Fig. 8.1). This will be determined by whether the pest is actually present on the crop to respond to fertiliser application and whether the effect of fertilisers on pest numbers or performance is at a time in crop development when economic damage would be caused.

Considering the example of cereal aphids, nutrient uptake by cereals is high early in plant growth with further demand later at ear ripening (Montemurro *et al.*, 2006). Thus, two temporal windows of plant demand exist and peaks in soil mineral nutrients early and late in plant development would be ideal to maximise plant yield. This could be achieved by two applications of conventional fertilisers or a single application of an organic fertiliser, provided the level of mineral nutrients released from the organic fertiliser is adequate for the plant's requirements within each of the temporal windows. The idea of a threshold for mineral nutrients can thus be postulated. Termed the 'plant threshold' in Fig. 8.1, it is the level of nutrients within the temporal window required to achieve the desired plant yield.

The impact of cereal aphids on a cereal crop is dependent on the size of the aphid population achieved and whether this population peak occurs at a time in plant development when yield will be affected (Watt and Wratten, 1984; Larsson, 2005). The size and timing of an aphid population peak will be determined by, among other things, the time of alate arrival on the crop (Honek and Martinkova, 2004) and the nutritional quality of the crop when the aphid is present. For example, a peak in soil mineral nutrients and a resulting pulse in phloem amino acid concentration before aphid arrival on the plant will not be of concern. Nor will a pulse in the nutrition quality of the cereal to an aphid at a point in cereal growth when large aphid populations are less damaging to a crop. For example, at milk development, wheat

can tolerate high numbers of aphids (Watt and Wratten, 1984; Larsson, 2005). Thus, a late pulse in the amino acid concentration within a cereal crop may encourage aphid populations to grow but this proliferation will not affect plant yield. The level of soil mineral nutrients and the corresponding effects on crop nutrition may need to be over a certain threshold for aphid populations to respond in such a way that they achieve pest status, therefore a 'pest threshold' in soil mineral nutrients level also exists (Fig. 8.1).

Considering the example of cereals discussed, as long as soil nutrients are high early and late in cereal growth and low when aphids are pests on the crop and causing damage, then a desirable situation is created. This could be achieved by two applications of conventional fertiliser or the application of an organic fertiliser, provided mineral nutrients levels following application of organic fertilisers are above the plant threshold but below the pest threshold. This would be impossible in practice if, for the particular crop-pest system being considered, the plant threshold was higher than the pest threshold. Application of fertiliser pre tillering and prior to ear ripening is recommended for winter cereals (ICI, 1980), thus slight changes to fertiliser application based on the model (Fig. 8.1) could work in practice without incurring additional cost or reducing a farmer's yield. For spring sown cereals this may be more problematic given that one early application of fertilisers is advised (ICI, 1980).

Among the numerous other factors that will determine the status of pests and resulting crop yields and although somewhat simplistic, this model demonstrates that fertilisers can play an important role in integrated pest management. This effect of fertiliser is dependent on the type of fertiliser used, the time of application and will vary between different crop-pest systems. Consideration of pest and plant demand and response windows and their corresponding thresholds therefore, would prove useful in an integrated cropping system. It must be remembered however, that any adaptation made to agricultural practice based on the principles developed from studies like those reported in this thesis must be applicable within the existing framework within which a farmer must work. Changes to fertilising practice may incur additional costs, costs which must be justified by the potential benefits.

Another interesting outcome of the present research concerns the effects of fertiliser treatment on leaf colour. Aphids were found to perform poorly on yellow plants, however the overwhelming evidence in the wider literature is that aphids prefer to land on yellow plants and this holds true for most aphid species (Doring and Chittka, 2007; Doring *et al.*, 2008). The negative correlation between ‘yellowness’ and aphid performance found in this study seems therefore paradoxical, since aphid host selection to maximise offspring fitness would be expected. The measurement of crop colour and aphid populations in response to fertiliser treatment in this study may be unique and contributes to the ongoing debate on the evolutionary history of aphid colour vision.

Published research on organic and conventional fertiliser effects on natural enemies is rare, as highlighted in Chapter 2. Results from Chapters 3, 4 and 7 of this thesis make a much needed contribution to this body of research. There appeared to be no direct effect of fertiliser on the numerical response of parasitoid mummies in any of the three field seasons. Parasitoid mummy numbers were more related to aphid abundance in 2006 and 2008, which may be an indirect effect of fertiliser. Given the density dependent nature of many pest and natural enemy interactions it will always be difficult to determine the effect of a treatment on the abundance of an organism at the third trophic level if that treatment has a numerical affect on the second trophic level, more refined survey techniques may be required.

Accurate estimation of percentage parasitism is one way of determining the impact of parasitoids on aphids (Dean *et al.*, 1981; Sigsgaard, 2002; Lumbierres *et al.*, 2007) and further work involving fertiliser application and cereal aphids would benefit from collecting subsamples of aphid field populations to correctly establish percentage parasitism and infer parasitoid impact. The data from Chapter 7 did, however, demonstrate the direct link between aphid performance and parasitoid performance and that this is indirectly affected by fertiliser treatment. In short, fitter aphids support fitter parasitoids. This highlights the difficulty in trying to use bottom-up practices such as fertiliser treatments to promote natural enemies without also benefiting the intermediate trophic organisms, namely the herbivore or pest. This is particularly true for parasitoids because the very nature of their biology means that their performance is closely linked with that of the pest.

It may be the case that effects of organic and conventional fertilisers on plants, not mediated through the pest, can be utilised to maximise the impact of parasitoids. Fertiliser effects on plant structure, colour and volatile emissions may prove to be an avenue of research worth pursuing. Olfactometers could be utilised to determine parasitoid response to plant volatiles following application of organic and conventional fertilisers whilst observations of behaviour may shed light on their response to colour or plant structure. Such finding would help with fertiliser decision making if parasitoids were relied on as a key mortality factor in a crop pest population.

While field results on parasitoids were inconclusive, syrphids were found to strongly prefer conventionally fertilised crops as sites for oviposition. The effects of host aphids and plants on aphidophagous syrphid oviposition is well documented (Chandler, 1968; Kan, 1988) and indirect effects of fertilisers on syrphids has been postulated ((Hasken and Poehling, 1994) cited by Hansken and Poehling (1995)). The results from Chapter 4 show that characteristics of cereals might be manipulated by fertiliser application to increase the impact of syrphids on cereal aphid populations. If it was found that the syrphids in this trial were phytozetic and responding primarily to plant cues then this might be straight forward. However, if the response of the syrphids was primarily aphidozetic and dictated by aphid populations on conventionally fertilised plants then fertiliser application to improve syrphid numbers might be difficult without also impacting positively on the aphid population. The mechanisms behind this fertiliser effect on syrphid oviposition would be an interesting area for further research.

In conclusion, this thesis has demonstrated the significant effects of farming system on both pests and natural enemies and that the fertilisers used in these farming systems play an important role in the trophic interactions of many crop, pest and natural enemy systems. The literature review highlights the need for more research on the effects of different fertiliser regimes on pest and particularly natural enemies. This thesis demonstrates the effects different fertilisers have on cereal aphid pests on a field, semi-field and smaller scale. The mechanism behind the response of aphids to fertiliser treatment is species specific and how the use of different fertiliser regimes might improve pest management depending on fertiliser type, crop type and pest species is hypothesised. The effects of fertilisers on both parasitoid fitness and

syrphid oviposition signify the potential importance of fertilisers on top down control of pest species. Improving the impact of natural enemies however, without also improving pest performance may prove to be impossible in practice. It must always be remembered that the primary objective of agriculture is the production of resources and sustainability of these systems is paramount. Fertilisers are an integral part of the management of agricultural systems. Careful regulation of their use could reduce negative environmental impacts while pest and natural enemy populations could be manipulated therefore mitigating the need for excessive insecticidal inputs.

References

- ABANDO, L. L. & ROHNER-THIELEN, E. (2007) *Different Organic Farming Patterns in the EU-25.*, Eurostat, Luxembourg, [Online] available from: http://epp.eurostat.ec.europa.eu/cache/ITY_OFFPUB/KS-SF-07-069/EN/KS-SF-07-069-EN.PDF [Accessed Aug 2008].
- ALTIERI, M. A. & NICHOLLS, C. I. (2003) Soil fertility management and insect pests: harmonizing soil and plant health in agroecosystems. *Soil and Tillage Research* 72: 203-211.
- ALYOKHIN, A., PORTER, G., GRODEN, E. & DRUMMOND, F. (2005) Colorado potato beetle response to soil amendments: A case in support of the mineral balance hypothesis? *Agriculture, Ecosystems and Environment* 109: 234-244.
- ANDERSEN, A. & ELTUN, R. (2000) Long-term developments in the carabid and staphylinid (Col., Carabidae and Staphylinidae) fauna during conversion from conventional to biological farming. *Journal of Applied Entomology* 124: 51-56.
- ANDOW, D. A. & PROKRYM, D. R. (1990) Plant structural complexity and host-finding by a parasitoid. *Oecologia* 82: 162-165.
- ARCHETTI, M. & BROWN, S. P. (2004) The coevolution theory of autumn colours. *Proceeding of the Royal Society, B* 271: 1219-1223.
- ARCHETTI, M. & LEATHER, R. (2005) A test of the coevolution theory of autumn colours: colour preference of *Rhopalosiphum padi* on *Prunus padus*. *Oikos* 110: 339-343.
- ARNQVIST, G. & WOOSTER, D. (1995) Meta-analysis: synthesizing research findings in ecology and evolution. *Tree* 10: 236-240.
- ATTWOOD, S. J., MARON, M., HOUSE, A. P. N. & ZAMMIT, C. (2008) Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? *Global Ecology and Biogeography* 17: 585-599.
- AWMACK, C. S. & LEATHER, S. R. (2002) Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* 47: 817-844.
- AWMACK, C. S. & LEATHER, S. R. (2007) Growth and Development. IN EMDEN, H. V. & HARRINGTON, R. (Eds.) *Aphids as Crop Pests*. CAB International, Wallingford, UK
- BADO, S. G., RODRIQUEZ, S. M. & FOLCIA, A. M. (2002) Aphids (Homoptera: Aphididae) and predatory ladybeetles (Coleoptera: Coccinellidae) abundance variation in a barley crop with different fertilization practices. *IDESIA* 20: 31-42.

- BENGTSSON, J., AHNSTROM, J. & WEIBULL, A. (2005) The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology* 42: 261-269.
- BENTON, T. G., VICKERY, J. A. & WILSON, J. D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution* 18: 182-188.
- BENTZ, J., III, J. R., BARDOSA, P. & FRANCIS, B. (1996) The effect of nitrogen fertilizer applied to *Euphorbia pulcherrima* on the parasitization of *Bemisia argentifolii* by the parasitoid *Encarsia formosa*. *Entomologia Experimentalis et Applicata* 78: 105-110.
- BERRY, N. A., S, D. W., MCERLICH, A. & FRAMPTON, C. (1996) Abundance and diversity of beneficial arthropods in conventional and "organic" carrot crops in New Zealand. *New Zealand Journal of Crop and Horticultural Science* 24: 307-313.
- BETHKE, J. A., REDAK, R. A. & SCHUCH, U. K. (1998) Melon aphid performance on chrysanthemum as mediated by cultivar, and differential levels of fertilization and irrigation. *Entomologia Experimentalis et Applicata* 88: 41-47.
- BETTIOL, W., GHINI, R., GALVAO, J. A. H. & SILOTO, R. C. (2004) Organic and conventional tomato cropping systems. *Scientific Agriculture* 61: 253-259.
- BI, J. L., BALLMER, G. R., HENDRIX, D. L., HENNEBERRY, T. J. & TOSCANO, N. C. (2001) Effect of cotton nitrogen fertilization on *Bemisia argentifolii* populations and honeydew production. *Experimentalis et Applicata* 99: 25-36.
- BILU, E., HOPPER, K. R. & COLL, M. (2006) Host choice by *Aphidius colemani*: effects of plants, plant-aphid combinations and the presence of intra-guild predators. *Ecological Entomology* 31: 331-336.
- BLACKMAN, R. L. & EASTOP, V. F. (2000) *Aphids on the World's Crops*, John Wiley & Sons Ltd, Chichester.
- BLUMBERG, A. J. Y., HENDRIX, P. F. & CROSSLEY, D. A. (1997) Effects of nitrogen source on arthropod biomass in no-tillage and conventional tillage grain sorghum agroecosystems. *Community and Ecosystem Ecology* 26: 31-37.
- BRUYN, L. D., SCHEIRS, J. & VERHAGEN, R. (2002) Nutrient stress, host plant quality and herbivore performance of a leaf-mining fly on grass. *Oecologia* 130: 594-599.
- CABRERA, H. M., ARGANDONA, V. H., ZUNIGA, G. E. & CORCUERA, L. J. (1995) Effect of infestation by aphids on the water status of barley and insect development *Phytochemistry* 40: 1083-1088.
- CANNON, R. J. C. (1984) The development rate of *Metopolophium dirhodum* (Walker) (Hemiptera: Aphididae) on winter wheat. *Bulletin of Entomological Research* 74: 33-46.

- CARTER, N., MCLEAN, I. F. G., WATT, A. D. & DIXON, A. F. G. (1980) Cereal aphids: a case study and review. *Applied Biology* 5: 271-348.
- CHANDLER, A. E. F. (1968) Some host-plant factors affecting oviposition by aphidophagous Syrphidae (Diptera). *Annals of Applied Biology* 61: 415-423.
- CHAU, A., HEINZ, K. M. & JR, F. T. D. (2005) Influences of fertilization on population abundance, distribution, and control of *Frankliniella occidentalis* on chrysanthemum. *Entomologia Experimentalis et Applicata* 117: 27-39.
- CHEN, Y. & RUBERSON, J. R. (2008) Impact of variable nitrogen fertilisation on arthropods in cotton in Georgia, USA. *Agriculture, Ecosystems and Environment* 126: 281-288.
- CLARK, M. S. (1999) Ground beetle abundance and community composition in conventional and organic tomato systems of California's Central Valley. *Applied Soil Ecology* 11: 199-206.
- CLOUGH, Y., KRUESS, A. & TSCHARNTKE, T. (2007) Organic versus conventional arable farming systems: Functional grouping helps understand staphylinid response. *Agriculture, Ecosystems and Environment* 118: 285-290.
- COLLINS, K. L., BOATMAN, N. D., WILCOX, A., HOLLAND, J. M. & CHANEY, K. (2002) Influence of beetle banks on cereal aphid predation in winter wheat. *Agriculture, Ecosystems and Environment* 93: 337-350.
- CONRY, M. J. (1995) Comparison of early, normal and late sowing at three rates of nitrogen on the yield, grain nitrogen and screenings content of Blenheim spring malting barley in Ireland. *Journal of Agricultural Science* 125: 183-188.
- COOPER, H. (1998) *Synthesizing Research: A Guide for Literature Reviews*, Sage Publications, Thousand Oaks, California, USA.
- CORDOVIL, C. & CABRAL, F. (2001) Fertilising value and mineralisation of nitrogen from organic fertilisers (pot and incubation experiment). IN RAHN, C. R., LILLYWHITE, R. D., NEVE, S. D., FINK, M. & RAMOS, C. (Eds.) *International conference on environmental problems associated with nitrogen fertilisation of field grown vegetable crops*. Potsdam, Germany, June 2001, ISHS Acta horticultrae, 139-145.
- CORRALES, N. & CAMPOS, M. (2004) Populations, longevity, mortality and fecundity of *Chrysoperla carnea* (Neuroptera, Chrysopidae) from olive-orchards with different agricultural management systems. *Chemosphere*: 1613-1619.
- COSTELLO, M. J. & ALTIERI, M. A. (1995) Abundance, growth rate and parasitism of *Brevicoryne brassicae* and *Myzus persicae* (Homoptera: Aphididae) on broccoli grown in living mulches. *Agriculture, Ecosystems and Environment* 52: 187-196.

- COURTNEY, R. G. & MULLEN, G. J. (2008) Soil quality and barley growth as influenced by the land application of two compost types. *Bioresource Technology* 99: 2913-2918.
- CRAWLEY, M. (2005) *The Flora of Berkshire*, Bramley Books, Harpenden.
- CRAWLEY, M. J. (2007) *The R Book*, John Wiley and Sons Ltd, Chichester.
- CULLINEY, T. W. & PIMENTEL, D. (1986) Ecological effects of organic agricultural practices on insect populations. *Agriculture, Ecosystems and Environment* 15: 253-266.
- DAUGHERTY, M. P., BRIGGS, C. J. & WELTER, S. C. (2007) Bottom-up and top-down control of pear psylla (*Cacopsylla pyricola*): Fertilization, plant quality, and the efficacy of the predator *Anthocoris nemoralis*. *Biological Control* 43: 257-264.
- DAWSON, J. C., HUGGINS, D. R. & JONES, S. S. (2008) Characterizing nitrogen use efficiency in natural and agricultural ecosystems to improve the performance of cereal crops in low-input and organic agricultural systems *Field Crop Research* 107: 89-101.
- DEAN, G. J., JONES, M. G. & POWELL, W. (1981) The relative abundance of the hymenopterous parasites attacking *Metopolophium dirhodum* (Walker) and *Sitobion avenae* (F.) (Hemiptera: Aphididae) on cereals during 1973-79 in southern England. *Bulletin of Entomological Research* 71: 307-315.
- DEFRA (2000) *Fertiliser Recommendations for Agricultural and Horticultural Crops (RB209)*, The Stationary Office, London.
- DEFRA (2008a) *Agriculture in the United Kingdom, Chapter 5*, [Online] Available from: <http://statistics.defra.gov.uk/esg/publications/auk/2008/default.asp> [Accessed, June, 2009].
- DEFRA (2008b) *The British Survey of Fertiliser Practice, Fertiliser use on Farm Crops from Crop Year 2007*, British Library Cataloguing in Publication Data, London, [Online] Available from: <http://www.defra.gov.uk/farm/environment/land-manage/nutrient/pdf/bsfp2007.pdf> [Accessed, Aug, 2008].
- DELATE, K., FRIEDRICH, H. & LAWSON, V. (2003) Organic pepper production systems using compost and cover crops. *Biological Agriculture and Horticulture* 21: 131-150.
- DIXON, A. F. G. (1998) *Aphid Ecology*, Chapman and Hall, London.
- DIXON, A. F. G., KUNDU, R. & KINDLMANN, P. (1993) Reproductive effort and maternal age in iteroparous insects using aphids as a model group. *Functional Ecology* 7: 267-272.
- DONG, J., HENGDIJK, H., TING-BO, D., BOER, W. D., QI, J. & WEI-XING, C. (2006) Long-term effects of manure and inorganic fertilizers on yield and soil

- fertility for a winter wheat-maize system in Jiangsu, China *Pedosphere* 16: 25-32.
- DORING, T. F., ARCHETTI, M. & HARDIE, J. (2008) Autumn leaves seen through herbivores eyes. *Proceedings of the Royal Society B* 276: 121-127.
- DORING, T. F. & CHITTKA, L. (2007) Visual ecology of aphids - a critical review on the role of colours in host finding. *Arthropod-Plant Interactions* 1: 3-16.
- DORING, T. F. & KROMP, B. (2003) Which carabid species benefit from organic agriculture?- a review of comparative studies in winter wheat cereals from Germany and Switzerland. *Agriculture, Ecosystems and Environment* 98: 153-161.
- DOUGLAS, A. E. (1998) Nutritional interactions in insect-microbial symbioses: Aphids and their symbiotic bacteria *Buchnera*. *Annual Review of Entomology* 43: 17-37.
- DOUGLAS, A. E., MINTO, L. B. & WILKINSON, T. L. (2001) Quantifying nutrient production by the microbial symbionts in a phytophagous insect. *Journal of Experimental Biology* 204: 349-358.
- DOULOUMPAKA, S. & EMDEN, H. F. V. (2003) A maternal influence on the conditioning to plant cues of *Aphidius ervi* Viereck, parasitizing the aphid *Myzus persicae* Sulzer. *Physiological Entomology* 28: 108-113.
- DRIESCHE, R. G. V., BELLOWS, T. S., ELKINTON, J. S., GOULD, J. R. & FERRO, D. N. (1991) The meaning of percentage parasitism revisited: Solutions to the problem of accurately estimating total losses from parasitism *Environmental Entomology* 20: 1-7.
- DRINKWATER, L. E., LETOURNEAU, D. K., WORKNEH, F., BRIGGEN, A. H. C. V. & SHENNAN, C. (1995) Fundamental differences between conventional and organic tomato agroecosystems in California. *Ecological Applications* 5: 1098-1112.
- DUFFIELD, S. J., BRYSON, R. J., YOUNG, J. E. B., SYLVESTER-BRADLEY, S. & SCOTT, R. K. (1997) The influence of nitrogen fertiliser on the population development of the cereal aphids *Sitobion avenae* (F.) and *Metopolophium dirhodum* (Wlk.) on field grown winter wheat. *Annals of Applied Biology* 130: 13-26.
- FACKNATH, S. & LALLJEE, B. (2005) Effect of soil-applied complex fertiliser on an insect-host plant relationship: *Liriomyza trifolii* on *Solanum tuberosum*. *Entomologia Experimentalis et Applicata* 115: 67-77.
- FERRERAS, L., GOMEZ, E., TORESANI, S., FIRPO, I. & ROTONDO, R. (2006) Effect of organic amendments on some physical, chemical and biological properties in a horticultural soil. *Bioresource Technology* 97: 635-640.

- FOX, R. H., PIEKIELEK, W. P. & MACNEAL, K. M. (1994) Using a chlorophyll meter to predict nitrogen fertilizer needs of winter wheat. *Communications in Soil Science and Plant Analysis* 25: 171-181.
- FRAMPTON, G. K. & DORNE, J. C. M. (2007) The effects on terrestrial invertebrates of reducing pesticide inputs in arable crop edges: a meta analysis. *Journal of Applied Ecology* 44: 362-373.
- FUENTES-CONTRERAS, E. & NIEMEYER, H. M. (2000) Effects of wheat resistance, the parasitoid *Aphidius rhopalosiphi*, and the entomopathogenic fungus *Pandora neoaphidis*, on population dynamics of the cereal aphid *Sitobion avenae*. *Entomologia Experimentalis et Applicata* 97: 109-114.
- GASH, A. F., CARTER, N. & BALE, J. S. (1996) The influence of nitrogen fertiliser application on the cereal aphids *Metopolophium dirhodum* and *Sitobion avenae*. In: *Proceedings of the Brighton Crop Protection Conference: Pests and Diseases*. Brighton, UK, 18-21 Nov 1996, British Crop Protection Council, 209-214.
- GATTOLIN, S., NEWBURY, H. J., BALE, J. S., TSENG, H., BARRETT, D. A. & PRITCHARD, J. (2008) A diurnal component to the variation in sieve tube amino acid content in wheat. *Plant Physiology* 147: 912-921.
- GATTOLIN, S., NEWBURY, J., BALE, J., BARRETT, D. & PRITCHARD, J. (2007) Quantitative analysis of amino acids composition in the sap of individual sieve elements of wheat (*Triticum aestivum*). *Comparative Biochemistry and Physiology - Part A: Molecular and Integrative Physiology* 146: 277-278.
- GIANOLI, E. (1999) Within-plant distribution of *Rhopalosiphum padi* on wheat seedlings is affected by induced response. *Entomologia Experimentalis et Applicata* 93: 227-230.
- GIANOLI, E. (2000) Competition in cereal aphids (Homoptera: Aphididae) on wheat plants. *Population Ecology* 29: 213-219.
- GINGRAS, D., DUTILLEUL, P. & BOIVIN, G. (2002) Modelling the impact of plant structure on host-finding behaviour of parasitoids. *Oecologia* 130: 396-402.
- GIOACCHINI, P., RAMIERI, N. A., MONTECCHIO, D., MARZADORI, C. & CIAVATTA, C. (2006) Dynamics of mineral nitrogen in soils treated with slow-release fertilizers. *Communications in Soil Science and Plant Analysis* 37: 1-12.
- GUERRIERI, E., PENNACCHIO, F. & TREMBLAY, E. (1997) Effect of adult experience on in-flight orientation to plant and plant-host complex volatiles in *Aphidius ervi* Haliday (Hymenoptera, Braconidae). *Biological Control* 10: 159-165.
- GUREVITCH, J. & HEDGES, L. V. (1999) Statistical Issues in Ecological Meta-Analyses. *Ecology* 80: 1142-1149.

- GURR, G. M., WRATTEN, S. D. & LUNA, J. M. (2003) Multi-function agriculture biodiversity: pest management and other benefits. *Basic and Applied Ecology* 4: 107-116.
- HALE, B. K., BALE, J. S., PRITCHARD, J., MASTERS, G. J. & BROWN, V. K. (2003) Effects of host plant drought stress on the performance of the bird cherry-oat aphid, *Rhopalosiphum padi* (L.): a mechanistic analysis. *Ecological Entomology* 28: 666-677.
- HANSEN, L. M. (2000) Establishing control threshold for bird cherry-oat aphid (*Rhopalosiphum padi* L.) in spring barley (*Hordeum vulgare* L.) by aphid days. *Crop Protection* 19: 191-194.
- HASKEN, K.-H. & POEHLING, H.-M. (1995) Effects of different intensities of fertilisers and pesticides on aphids and aphid predators in winter wheat. *Agriculture, Ecosystems and Environment* 52: 45-50.
- HASKEN, K.-H. & POEHLING, H. (1994) Some effects of low input agriculture on cereal aphids and aphid specific predators in winter wheat. *Bulletin of the International Organisation for Biological and Integrated Control of Noxious Animals and Plants (IOBC), West Palaearctic Regional Section*: 137-147.
- HASSE, T., SCHULER, C. & HLEB, J. (2006) The effect of different N and K sources on tuber nutrient uptake, total and graded yield of potatoes (*Solanum tuberosum* L.) for processing. *European Journal of Agronomy* 26: 187-197.
- HAVLICKOVA, H. & SMETANKOVA, M. (1998) Effects of potassium and magnesium fertilization on barley preference by the bird cherry oat-aphid *Rhopalosiphum padi* (L.). *Rostlinna Vyroba* 44: 379-383.
- HEDGES, L. V. & OLKIN, I. (1980) Vote-counting methods in research synthesis. *Psychological Bulletin* 88: 359-369.
- HEDGES, L. V. & VEVEA, J. L. (1998) Fixed- and random-effects models in meta-analysis. *Psychological Methods* 3: 486-504.
- HELENIUS, J. (1990) Conventional and organic cropping systems at Suitia VI: Insect populations in barley. *Journal of Agricultural Science in Finland* 62: 349-355.
- HIDAKA, K. (1997) Community structure and regulatory mechanism of pest populations in rice paddies cultivated under intensive, traditionally organic and lower input organic farming in Japan. *Biological Agriculture and Horticulture* 1-4 Entomological Research in Organic Agriculture: 35-49.
- HOLE, D. G., PERKINS, A. J., WILSON, J. D., ALEXANDER, I. H., GRICE, P. V. & EVANS, A. D. (2005) Does organic farming benefit biodiversity? *Biological Conservation* 122: 113-130.
- HOLST, N. & RUGGLE, P. (1997) A physiological based model of pest-natural enemy interactions. *Experimental and Applied Acarology* 21: 325-341.

- HONEK, A. (1991a) Drymass allocation in cereal plants and distribution of *Metopolophium dirhodum* and *Sitobion avenae* (Homoptera, Aphididae). *Acta Entomol Bohemoslov* 88: 103-109.
- HONEK, A. (1991b) Nitrogen fertilization and abundance of the cereal aphids *Metopolophium dirhodum* and *Sitobion avenae* (Homoptera, Aphididae). *Journal of Plant Diseases and Protection* 98: 665-660.
- HONEK, A. & MARTINKOVA, Z. (2002) Factors of between- and within-plant distribution of *Metopolophium dirhodum* (Hom., Aphididae) on small grain cereals. *Journal of Applied Entomology* 126: 378-383.
- HONEK, A. & MARTINKOVA, Z. (2004) Host plant age and population development of a cereal aphid, *Metopolophium dirhodum* (Hemiptera: Aphididae). *Bulletin of Entomological Research* 94: 19-26.
- HOPKINS, W. G. & HUNER, W. P. A. (2009) *Introduction to Plant Physiology, 4th Edition*, John Wiley & Sons, Inc, London.
- HOSSAIN, M. Z., CHOUDHURY, M. H. K., HOSSAIN, M. F. & ALAM, Q. K. (2002) Effects of ecological agriculture on soil properties and arthropod diversity in rice-based cropping systems in floodplain areas in Bangladesh. *Biological Agriculture and Horticulture* 20: 215-227.
- HOWARD, T. M. & DIXON, A. F. G. (1992) The effect of plant phenology on the induction of alatae and the development of populations of *Metopolophium dirhodum* (Walker), the rose-grain aphid, on winter wheat *Annals of Applied Biology* 120: 203-213.
- HUBERTY, A. F. & DENNO, R. F. (2004) Plant water stress and its consequences for herbivorous insects: A new synthesis. *Ecology* 85: 1383-1398.
- HUMMEL, R. L., WALGENBACH, J. F., HOYT, G. D. & KENNEDY, G. G. (2002) Effects of production system on vegetable arthropods and their natural enemies. *Agriculture, Ecosystems and Environment* 93: 165-176.
- ICI (1980) *Growing Cereals* ICI.
- IHAKA, R. & GENTLEMAN, R. (1996) R: a language for data analysis and graphics. *Journal of Computing, Graphics and Statistics* 5: 299-314.
- INBAR, M., DOOSTDAR, H. & MAYER, R. T. (2001) Suitability of stressed and vigorous plants to various insect herbivores. *Oikos* 94: 228-235.
- IRMLER, U. (2003) The spatial and temporal pattern of carabid beetles on arable fields in northern Germany (Schleswig-Holstein) and their value as ecological indicators. *Agriculture, Ecosystems and Environment* 98: 141-151.
- JIANG, N. & SCHULTHESS, F. (2005) The effect of nitrogen fertilizer application to maize and sorghum on the bionomics of *Chilo partellus* (Lepidoptera: Crambidae) and the performance of its larval parasitoid *Cotesia flavipes* (Hymenoptera: Braconidae). *Bulletin of Entomological Research* 95: 495-504.

- JOUANY, C., COLOMB, B. & BOSC, M. (1996) Long-term effects of potassium fertilisation on yields and fertility status of calcareous soils of south-west France. *European Journal of Agronomy* 5: 287-294.
- JUROSZEK, P., DREWS, S., NEUHOFF, D. & KOPKE, U. (2004) Effects of organic fertilisers on the development of weeds and winter wheat. *Journal of Plant Diseases and Protection Special Issue* 19: 611-618.
- KALULE, T. & WRIGHT, D. J. (2004) The influence of cultivar and cultivar-aphid odours on the olfactory response of the parasitoid *Aphidius colmani*. *Journal of Applied Entomology* 128: 120-125.
- KAN, E. (1988) Assessment of aphid colonies by Hoverflies. I Maple aphids and *Episyrphus balteatus* (de Geer) (Diptera: Syrphidae). *Journal of Ethology* 6: 39-48.
- KANESHIRO, L. N. & JOHNSON, M. W. (1995) Tritrophic effects of leaf nitrogen on *Liriomyza trifolii* (Burgess) and an associated parasitoid *Chrysocharis oscinidis* (Ashmead) on bean. *Biological Control* 6: 186-192.
- KARUNGI, J., EKBOM, B. & KYAMANYWA, S. (2006a) Effects of organic versus conventional fertilizers on insect pests, natural enemies and yield of *Phaseolus vulgaris*. *Agriculture, Ecosystems and Environment* 115: 51-55.
- KARUNGI, J., KYAMANYWA, S. & EKBOM, B. (2006b) Comparison of the effect of market crop wastes and chemical soil fertility amendments on insect pests, natural enemies and yield of *Brassica oleracea*. *Annals of Applied Biology* 149: 103-109.
- KHAN, M. & PORT, G. (2008) Performance of clones and morphs of two cereal aphids on wheat plants with high and low nitrogen content. *Entomological Science* 11: 159-165.
- KLUEKEN, A. M., HAU, B., ULBER, B. & POEHLING, H. M. (2009) Forecasting migration of cereal aphids (Hemiptera: Aphididae) in autumn and spring. *Journal of Applied Entomology* 133: 328-344.
- KORICHEVA, J. & LARSSON, S. (1998) Insect performance on experimentally stressed woody plants: A meta-analysis. *Annual Review of Entomology* 43: 195-216.
- KRAUSS, J., HARRI, S. A., BUSH, L., HUSI, R., BIGLER, L., POWER, S. A. & MULLER, C. B. (2007) Effects of fertilizer, fungal endophytes and plant cultivar on the performance of insect herbivores and their natural enemies. *Functional Ecology* 21: 107-116.
- KRISTOFFERSEN, A. O., BAKKEGARD, M. & HOEL, B. O. (2005) Starter fertilizer to spring barley and spring wheat in south-east Norway: Effects on growth and nutrient uptake. *Acta Agricultural Scandinavica Section B - Soil and Plant Science* 55: 252-263.

- KROOSS, S. & SCHAEFER, M. (1998) The effects of different farming systems on epigeic arthropods: a five-year study on the rove beetle fauna (Coleoptera: Staphylinidae) of winter wheat. *Agriculture, Ecosystems and Environment* 69: 121-133.
- LANGELLOTTO, G. A. & DENNO, R. F. (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* 139: 1-10.
- LARSSON, H. (2005) A crop loss model and economic thresholds for the grain aphid, *Sitobion avenae* (F.), in winter wheat in southern Sweden. *Crop Protection* 24: 397-405.
- LEATHER, S. R. (1986) Host monitoring by aphid migrants: do gynoparae maximise offspring fitness? *Oecologia* 68: 367-369.
- LEATHER, S. R. (1988) Size, reproductive potential and fecundity in insects: things aren't as simple as they seem *Oikos* 51: 386-388.
- LEATHER, S. R. (1989) Do alate aphids produce fitter offspring? The influence of maternal rearing history and morph on life-history parameters of *Rhopalosiphum padi* (L.). *Functional Ecology* 3: 237-244.
- LEATHER, S. R. & DIXON, A. F. G. (1981) The effect of cereal growth stage and feeding site on the reproductive activity of the bird-cherry aphid, *Rhopalosiphum padi*. *Annals of Applied Biology* 97: 135-141.
- LEATHER, S. R. & DIXON, A. F. G. (1984) Aphid growth and reproductive rates. *Entomologia Experimentalis et Applicata* 35: 137-140.
- LEATHER, S. R., WALTERS, K. F. A. & DIXON, A. F. G. (1989) Factors determining the pest status of the bird cherry-oat aphid, *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae), in Europe: a study and review. *Bulletin of Entomological Research* 79: 345-360.
- LESZCZYNSKI, B., WRIGHT, L. C. & BAKOWSKI, T. (1989) Effects of secondary plant substances on winter wheat resistance to grain aphid. *Entomologia Experimentalis et Applicata* 52: 135-139.
- LETOURNEAU, D. K. (1988) Soil management for pest control: a critical appraisal of the concepts. In: *Proceedings of the Sixth International Science Conference of IFOAM on Global Perspectives on Agroecology and Sustainable Agricultural systems*. Santa Cruz, 589-600.
- LETOURNEAU, D. K. & BOTHWELL, S. G. (2008) Comparison of organic and conventional farms: challenging ecologists to make biodiversity functional. *Frontiers in Ecology and the Environment* 6: 430-438.
- LETOURNEAU, D. K. & GOLDSTEIN, B. (2001) Pest damage and arthropod community structure in organic vs. conventional tomato production in California. *Journal of Applied Ecology* 38: 557-570.

- LEVIE, A., LEGRAND, M.-A., DOGOT, P., PELS, C., BARET, P. V. & HANCE, T. (2005) Mass release of *Aphidius rhopalosiphi* (Hymenoptera: Aphidiinae), and strip management to control of wheat aphids. *Agriculture, Ecosystems and Environment* 105: 17-21.
- LEVY, J. S. & TAYLOR, B. R. (2003) Effects of pulp mill solids and three composts on early growth of tomatoes. *Bioresource Technology* 89: 297-305.
- LLEWELLYN, M. & BROWN, V. K. (1985) A general relationship between adult weight and the reproductive potential of aphids. *Journal of Animal Ecology* 54: 663-673.
- LOVEI, G. L. & SUNDERLAND, K. D. (1996) Ecology and behaviour of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology* 41: 231-256.
- LUMBIERRES, B., STARY, P. & PONS, X. (2007) Seasonal parasitism of cereal aphids in a Mediterranean arable crop system. *Journal of Pest Science* 80: 125-130.
- MACGILLIVRAY, M. E. & ANDERSON, G. B. (1957) Three Useful Insect Cages. *The Canadian Entomologist* 89: 43-46.
- MADER, P., FLIEBBACH, A., DUBOIS, D., GUNST, L., FRIED, P. & NIGGLI, E. (2002) Soil fertility and biodiversity in organic farming. *Science* 296: 1694-1697.
- MANLAY, R. J., FELLER, C. & SWIFT, M. J. (2007) Historical evolution of soil organic matter concepts and their relationships with the fertility and sustainability of cropping systems. *Agriculture, Ecosystems and Environment* 119: 217-233.
- MANN, B. P., WRATTEN, S. D. & WATT, A. D. (1986) A Computer-Based Advisory System for Cereal Aphid Control. *Computers and Electronics in Agriculture* 1: 263-270.
- MANN, J. A., HARRINGTON, R., CARTER, N. & PLUMB, R. T. (1997) Control of aphids and barley yellow dwarf virus in spring-sown cereals. *Crop Protection* 16: 81-87.
- MARSCHNER, H. (2002) *Mineral Nutrition of Higher Plants, 2nd Edition*, Academic Press.
- MATSON, P. A., PARTON, W. J., POWER, A. G. & SWIFT, M. J. (1997) Agricultural intensification and ecosystem properties. *Science* 277: 504-509.
- MCLAUGHLIN, A. & MINEAU, P. (1995) The impact of agricultural practices on biodiversity. *Agriculture, Ecosystems and Environment* 55: 201-212.
- MENGEL, K., HUTSCH, B. & KANE, Y. (2006) Nitrogen fertilizer application rates on cereal crops according to available mineral and organic soil nitrogen. *European Journal of Agronomy* 24: 343-348.

- MEYER, W. B. & TURNER, B. L. (1992) Human population growth and global land-use/cover change. *Annual Review of Ecology and Systematics* 23: 39-61.
- MONTEMURRO, F., MAIORANA, M., FERRI, D. & CONVERTINI, G. (2006) Nitrogen indicators, uptake and utilization efficiency in a maize and barley rotation cropped at different levels and sources of N fertilization. *Field Crop Research* 99: 114-124.
- MORALES, H., PERFECTO, I. & FERGUSON, B. (2001) Traditional fertilization and its effect on corn insect populations in the Guatemalan highlands. *Agriculture, Ecosystems and Environment* 84: 145-155.
- MOREBY, S. J., AEBISCHER, N. J., SOUTHWAY, S. E. & SOTHERTON, N. W. (1994) A comparison of the flora and arthropod fauna of organically and conventionally grown winter wheat in southern England. *Annals of Applied Biology* 125: 13-27.
- MYERS, S. W., GRATTON, C., WOLKOWSKI, R. P., HOGG, D. B. & WEDBERG, J. L. (2005) Effect of soil potassium availability on soybean aphid (Hemiptera: Aphididae) population dynamics and soybean yield. *Journal of Economic Entomology* 98: 113-120.
- NAYLOR, R. L. (1996) Energy and resource constraints on intensive agricultural production. *Annual Review of Energy and the Environment* 21: 99-123.
- NEVO, E. & COLL, M. (2001) Effect of nitrogen fertilization on *Aphis gossypii* (Homoptera: Aphididae): variation in size, color, and reproduction. *Ecology and Behaviour*: 27-32.
- NINKOVIC, V., AHMED, E., GLINWOOD, R. & PETTERSSON, J. (2003) Effects of two types of semiochemical on population development of the bird cherry oat aphid *Rhopalosiphum padi* in a barley crop. *Agricultural and Forest Entomology* 5: 27-33.
- OAKLEY, J. N. & WALTERS, K. F. A. (1994) A field evaluation of different criteria for determining the need to treat winter wheat against the grain aphid *Sitobion avenae* and the rose-grain aphid *Metopolophium dirhodum*. *Annals of Applied Biology* 124: 195-211.
- OBERG, S. (2007) Diversity of spiders after spring sowing - influence of farming system and habitat type. *Journal of Applied Entomology* 131: 524-531.
- OSTMAN, O., EKBOM, B. & BENGTSSON, J. (2001) Landscape heterogeneity and farming practice influence biological control. *Basic and Applied Ecology* 2: 365-371.
- OSTMAN, O., EKBOM, B. & BENGTSSON, J. (2003) Yield increase attributable to aphid predation by ground-living polyphagous natural enemies in spring barley in Sweden. *Ecological Economics* 45: 149-158.

- PAREJA, M., BROWN, V. K. & POWELL, W. (2007) Aggregation of parasitism risk in an aphid-parasitoid system: Effects of plant patch size and aphid density. *Basic and Applied Ecology* 9: 701-708.
- PETTERSSON, J., PICKETT, J. A., PYE, B. J., QUIROZ, A., SMART, L. E., WADHAMS, L. J. & WOODCOCK, C. M. (1994) Winter host component reduces colonization by bird-cherry-oat aphid, *Rhopalosiphum padi* (L.) (Homoptera, Aphididae) and other aphids in cereal crops. *Journal of Chemical Ecology* 20: 2565-2574.
- PHELAN, L. P., NORRIS, K. H. & MASON, J. F. (1996) Soil management history and host preference by *Ostrinia nubilalis*: evidence for plant mineral balance mediated insect-plant interactions. *Environmental Entomology* 25: 1329-1336.
- PHELAN, P. L., MASON, J. F. & STINNER, B. R. (1995) Soil-fertility management and host preference by European corn borer, *Ostrinia nubilalis* (Hubner), on *Zea mays* L.: A comparison of organic and conventional chemical farming. *Agriculture, Ecosystems and Environment* 56: 1-8.
- PICKETT, J. A., WADHAMS, L. J. & WOODCOCK, C. M. (1992) The chemical ecology of aphids. *Annual Review of Entomology* 37: 67-90.
- PONDER, K. L., PRITCHARD, J., HARRINGTON, R. & BALE, J. S. (2000) Difficulties in location and acceptance of phloem sap combined with reduced concentration of phloem amino acids explain lowered performance of the aphid *Rhopalosiphum padi* on nitrogen deficient barley (*Hordeum vulgare*) seedlings. *Entomologia Experimentalis et Applicata* 97: 203-210.
- PONDER, K. L., PRITCHARD, J., HARRINGTON, R. & BALE, J. S. (2001) Feeding behaviour of the aphid *Rhopalosiphum padi* (Hemiptera: Aphididae) on nitrogen and water-stressed barley (*Hordeum vulgare*) seedlings *Bulletin of Entomological Research* 91: 125-130.
- PONTI, L., ALTIERI, M. A. & GUITIERREZ, A. P. (2007) Effect of crop diversification levels and fertilization regimes on abundance of *Brevicoryne brassicae* (L.) and its parasitisation by *Diaeretiella rapae* (M'Intosh) in broccoli *Agricultural and Forest Entomology* 9: 209-214.
- POVEDA, K., STEFFAN-DEWENTER, I., SCHEU, S. & TSCHARNTKE, T. (2006) Belowground effects of organic and conventional farming on aboveground plant-herbivore and plant-pathogen interactions. *Agriculture, Ecosystems and Environment* 113: 162-167.
- POWELL, G., TOSH, C. R. & HARDIE, J. (2006) Host plant selection by aphids: Behavioural, evolutionary, and applied perspectives. *Annual Review of Entomology* 51: 309-330.
- POWELL, W., PENNACCHIO, F., POPPY, G. M. & TREMBLAY, E. (1998) Strategies involved in the location of hosts by the parasitoid *Aphidius ervi* Haliday (Hymenoptera: Braconidae: Aphidiinae). *Biological Control* 11: 104-112.

- PRICE, P. W. (1991) The plant vigour hypothesis and herbivore attack. *Oikos* 62: 244-251.
- PROSSER, W. A., SIMPSON, S. J. & DOUGLAS, A. E. (1992) How and aphid (*Acyrtosiphon pisum*) symbiosis responds to variation in dietary nitrogen. *Journal of Insect Physiology* 38: 301-307.
- PRUDIC, K. L., OLIVER, J. C. & BOWERS, M. D. (2005) Soil nutrient effects on oviposition preference, larval performance, and chemical defence of a specialist insect herbivore *Oecologia* 143: 578-587.
- PURTAUF, T., ROSCHEWITZ, I., DAUBER, J., THIES, C., TSCHARNTKE, T. & WOLTERS, V. (2005) Landscape context of organic and conventional farms: Influences on carabid beetle diversity. *Agriculture, Ecosystems and Environment* 108: 165-174.
- QUIROZ, A. & NIEMEYER, H. M. (1998) Olfactometer-assessed responses of aphid *Rhopalosiphum padi* to wheat and oat volatiles. *Journal of Chemical Ecology* 24: 113-124.
- RAHBE, Y., FEBVAY, G., DELOBEL, B. & BOURNOVILLE, R. (1988) *Acyrtosiphon pisum* performance in response to the sugar and amino acid composition of artificial diets, and its relation to lucerne varietal resistance. *Entomologia Experimentalis et Applicata* 48: 283-292.
- REDDERSEN, J. (1997) The arthropod fauna of organic versus conventional cereal fields in Denmark. *Entomological Research in Organic Agriculture*: 61-71.
- RHAINDS, M., KOVACH, J. & ENGLISH-LOEB, G. (2002) Impacts of strawberry cultivar and incidence of pests on yield and profitability of strawberries under conventional and organic management systems. *Biological Agriculture and Horticulture* 19: 333-353.
- RIEDEL, W. E., OSBORNE, S. L. & JARADAT, A. A. (2007) Crop mineral nutrient and yield responses to aphids or *barley yellow dwarf virus* in spring wheat and oats. *Crop Science* 47: 1553-1560.
- ROSCHEWITZ, I., HUCKER, M., TSCHARNTKE, T. & THIES, C. (2005) The influence of landscape context and farming practices on parasitism of cereal aphids. *Agriculture, Ecosystems and Environment* 108: 218-227.
- ROSENBERG, M. S., ADAMS, D. C. & GUREVITCH, J. (2000a) *Metawin 2*, Statistical Software for Meta-analysis. 2.1.4 ed. Sunderland, Massachusetts, USA, Sinauer Associates.
- ROSENBERG, M. S., ADAMS, D. C. & GUREVITCH, J. (2000b) *Metawin*, Statistical Software for Meta-Analysis, Version 2, Sinauer Associates, Inc, Sunderland, Massachusetts. USA.
- SALAS, M. L., CORCUERA, L. J. & ARGANDONA, V. H. (1990) Effect of potassium nitrate on gramine content and resistance of barley against the aphid *Schizaphis graminum*. *Phytochemistry* 29: 3789-3791.

- SANDSTROM, J., TELANG, A. & MORAN, N. A. (2000) Nutritional enhancement of host plants by aphids - a comparison of three species on grasses. *Journal of Insect Physiology* 46: 33-40.
- SCHMIDT, M. H., LAUER, A., PURTAUF, T., THIES, C., SCHAEFER, M. & TSCHARNTKE, T. (2003) Relative importance of predators and parasitoids for cereal aphid control. *Proceeding of the Royal Society* 270: 1905-1909.
- SCHMIDT, M. H., ROSCHWITZ, I., THIES, C. & TSCHARNTKE, T. (2005) Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *Journal of Applied Ecology* 42: 281-287.
- SCHOONHOVEN, L. M., LOON, J. J. A. V. & DICKE, M. (2005) *Insect-Plant Biology*, Oxford University Press, Oxford, UK.
- SCHWORER, U. & VOLKL, W. (2001) Foraging behaviour of *Aphidius ervi* (Haliday)(Hymenoptera: Braconidae: Aphidiinae) at different spatial scales: Resource utilization and suboptimal weather conditions. *Biological Control* 21: 111-119.
- SCRIBER, J. M. (1984a) Host-plant suitability. IN BELL, W. J. & CARDE, R. T. (Eds.) *Chemical Ecology of Insects*. Chapman and Hall Ltd, London, UK
- SCRIBER, J. M. (1984b) Nitrogen nutrition of plants and insect invasion. IN HAUCK, R. D. (Ed.) *Nitrogen in crop protection*. American Society of Agronomy, Madison, USA
- SHAH, P. A., BROOKS, D. R., ASHBY, J. E., PERRY, J. N. & WOIWOD, I. P. (2003) Diversity and abundance of the coleopteran fauna from organic and conventional management systems in southern England. *Agricultural and Forest Entomology* 5: 51-60.
- SHAW, M. C., WILSON, M. C. & RHYKERD, C. L. (1986) Influence of phosphorus and potassium fertilization on damage to alfalfa, *Medicago sativa* L., by the alfalfa weevil, *Hypera postica* (Gyllenhall) and potato leafhopper, *Empoasca fabae* (Harris). *Crop Protection* 5: 245-249.
- SIDDIQUI, Z. A. (2004) Effects of plant growth promoting bacteria and composted organic fertilizers on the reproduction of *Meloigogyne incognita* and tomato growth. *Bioresource Technology* 95: 223-227.
- SIELING, K., BRASE, T. & SVIB, V. (2006) Residual effects of different N fertilizer treatments on growth, N uptake and yield of oilseed rape, wheat and barley. *European Journal of Agronomy* 25: 40-48.
- SIGSGAARD, L. (2000) The temperature-dependent development and parasitism of the cereal aphid parasitoids *Aphidius ervi*, *Aphidius rhopalosiphii* and *Praon volucre*. *Entomologia Experimentalis et Applicata* 95: 173-184.
- SIGSGAARD, L. (2002) A survey of aphids and aphid parasitoids in cereal fields in Denmark, and parasitoids' role in biocontrol. *Journal of Applied Entomology* 126: 101-107.

- SIMPSON, S. J., ABISGOLD, J. D. & DOUGLAS, A. E. (1995) Response of the pea aphid (*Acyrtosiphon pisum*) to variation in dietary levels of sugar and amino acids: the significance of amino acid quality. *Journal of Insect Physiology* 41: 71-75.
- SUDHAKAR, K., PUNNAIAH, K. C. & KRISHNAYYA, P. V. (1998) Influence of organic and inorganic fertilizers and insecticides on the incidence of shoot and fruit borer, *Leucinodes orbonalis* Guen. infesting binjal. *Journal of Entomological Research* 22: 283-286.
- SUNDERLAND, K. & SAMU, F. (2000) Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. *Entomologia Experimentalis et Applicata* 95: 1-13.
- TAKABAYASHI, J., SATO, Y., HORIKOSHI, M., YAMAOKA, R., YANO, S., OHSAKI, N. & DICKESS, M. (1998) Plant effects on parasitoid foraging: differences between two tritrophic systems. *Biological Control* 11: 97-103.
- TAKAHASHI, S. & ANWAR, M. R. (2007) Wheat grain yield, phosphorus uptake and soil phosphorus fraction after 23 years of annual fertilizer application to an Andosol. *Field Crop Research* 101: 160-171.
- TONHASCA, A. (1993) Effects of agroecosystem diversification on natural enemies of soybean herbivores. *Entomologia Experimentalis et Applicata* 69: 83-90.
- TONHASCA, A. & BYRNE, D. N. (1994) The effect of crop diversification on herbivorous insects: a meta-analysis approach. *Ecological Entomology* 19: 239-244.
- TOTTMAN, D. R. & BROAD, H. (1987) Decimal code for growth stages of cereals. *Annals of Applied Biology* 110: 683-687.
- VAN EMDEN, H. F. (1966) Studies on the relations of insect and host plant. A comparison of the reproduction of *Brevicoryne brassicae* and *Myzus persicae* on Brussels sprout plants supplied with different rates of nitrogen and potassium. *Entomologia Experimentalis et Applicata* 9: 444-460.
- WALTER, A. J. & DIFONZO, C. D. (2007) Soil potassium deficiency affects soybean phloem nitrogen and soybean Aphid Populations. *Environmental Entomology* 36(1): 26-33.
- WALTERS, K. F. A. & DIXON, A. F. G. (1982) The effect of host quality and crowding on the settling and take-off of cereal aphids. *Annals of Applied Biology* 101: 211-218.
- WATT, A. D. (1979) The effect of cereal growth stage on the reproductive activity of *Sitobion avenae* and *Metopolophium dirhodum*. *Annals of Applied Biology* 91: 147-157.
- WATT, A. D. & WRATTEN, S. D. (1984) The effects of growth stage in wheat on yield reductions caused by the rose-grain aphid *Metopolophium dirhodum*. *Annals of Applied Biology* 104: 393-397.

- WEIBULL, A.-C. & OSTMAN, O. (2003) Species composition in agroecosystems: The effect of landscape, habitat, and farm management *Basic and Applied Ecology* 4: 349-361.
- WEIBULL, J. (1987) Seasonal changes in the free amino acids of oats and barley phloem sap in relation to plant growth stage and growth of *Rhopalosiphum padi* *Annals of Applied Biology* 111: 729-737.
- WHITE, T. C. R. (1969) An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology* 50: 905-909.
- WHITE, T. C. R. (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* 63: 90-105.
- WILLER, H. & YUSSEFI, M. (2007) *The World of Organic Agriculture, Statistics and Emerging Trends 2007*, IFOAM, Bonn, Germany, [Online] Available from: <http://orgprints.org/10506/01/willer-yussefi-2007-p1-44.pdf> [Accessed, Aug, 2008].
- WURST, S. & JONES, H. (2003) Indirect effects of earthworms (*Aporrectodea caliginosa*) on an above ground tritrophic interaction. *Pedobiologia* 47: 91-97.
- WYATT, I. J. & WHITE, P. F. (1977) Simple estimation of intrinsic increase rates for aphids and tetranychid mites. *Journal of Applied Ecology* 14: 757-766.
- YARDIM, E. N. & EDWARDS, C. A. (2003) Effects of organic and synthetic fertilizer sources on pest and predatory insects associated with tomatoes. *Phytoparasitica* 31: 324-329.
- ZEHNDER, G., GURR, G. M., KUHNE, S., WADE, M. R., WRATTEN, S. D. & WYSS, E. (2007) Arthropod pest management in organic crops. *Annual Review of Entomology* 52: 57-80.
- ZHANG, J. & DRUMMOND, F. A. (1998) Effect of crop habitat and potato management practices on the population abundance of adult *Harpalus rufipes* (Coleoptera: Carabidae) in Maine. *Journal of Agricultural Entomology* 15: 63-74.
- ZHUO, X. & CARTER, N. (1992) Effects of temperature, feeding position and crop growth stage on the population dynamics of the rose grain aphid, *Metopolophium dirhodum* (Hemiptera: Aphididae). *Annals of Applied Biology* 121: 27-37.

Appendix 1

Pest meta-analysis data set

Study	Year	Experimental design	Variable	Duration (years)	Response year	Cultivated or not?	Within study difference	Crop	Pest control	Conventional pest control	Dynamic pest control	Beneficial level	Organic fertilizer	Organic fertilizer categories	Pest information	Taxonomic order	Species	Life stage	Response	Response unit	Statistical information	Statistical test	Statistical test from	Statistical test to	n - conventional	n - organic	Mean - conventional	Mean - organic	SD - conventional	SD - organic	Reversal	Effect size - Hedges J	Variance - d						
Abraham	2006	field	fertilizer	3	1	no		potato	conventional or organic	mineral fertilizer, not used	mineral	showing	Coleoptera	<i>Leptogastera arvensis</i>	adult	abundance	number/row plant	table	SE from table	18	18	0.20	0.14	0.10	0.07	0	0	0.02	0.14	0.00	0.00	0.00	0.00	0.00	0.00				
Karungi	2006	field	fertilizer	3	1	no		bean	conventional or organic	composted market crop waste	compost	lacking	Hemiptera	<i>Aphis fabae</i>	all	abundance	number/row plant	table	SE from table	4	4	2.64	2.91	0.26	0.26	0	0	0.90	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00			
Karungi	2006	field	fertilizer	3	2	no		tomato	conventional or organic	composted market crop waste	compost	lacking	Hemiptera	<i>Aphis fabae</i>	all	abundance	number/row plant	table	SE from table	4	4	2.94	2.94	0.26	0.26	0	0	0.90	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
Karungi	2006a	field	fertilizer	3	2	no		carrot	conventional or organic	composted market crop waste	compost	lacking	Hemiptera	<i>Brevicoryne brassicae</i> , <i>Myzus persicae</i>	all	abundance	aphid/plant	table	SE from table	4	4	15.27	61.91	0.04	0.04	20.54	0.04	2.558	0.908										
Karungi	2006a	field	fertilizer	3	2	no		carrot	conventional or organic	composted market crop waste	compost	showing	Lepidoptera	<i>Plutella maculipennis</i>	larvae	abundance	larvae/plant	table	SE from table	4	4	2.39	4.00	0.80	0.80	1.40	0.80	0.816	0.485										
Karungi	2006a	field	fertilizer	3	2	no		carrot	conventional or organic	composted market crop waste	compost	showing	Lepidoptera	<i>Plutella maculipennis</i>	eggs/adult	abundance	eggs/adult	table	SE from table	4	4	2.39	4.00	0.80	0.80	1.40	0.80	0.816	0.485										
Karungi	2006a	field	fertilizer	3	3	no		spec. fertilizer	conventional or organic	fish market crop waste	compost	showing	Lepidoptera	<i>Plutella maculipennis</i>	larvae	abundance	larvae/plant	table	SE from table	4	4	2.50	3.58	1.60	1.26	0	0	0.621	0.526										
Larsen	1994	laboratory	fertilizer	1	1	no		spec. fertilizer	conventional or organic	sewage sludge	manure	lacking	Hemiptera	<i>Trialeurodes vaporariorum</i>	egg/adult	abundance	days	table	SE from table	12	12	22.09	24.82	6.61	6.61	0.0	0.0	0.000	0.1										
Larsen	1994	laboratory	fertilizer	1	1	no		spec. fertilizer	conventional or organic	sewage sludge	manure	showing	Lepidoptera	<i>Trialeurodes vaporariorum</i>	egg/adult	abundance	development time	table	SE from table	40	40	22.00	23.84	1.14	1.14	0	0	0.007	0.064										
Monaco	2001	farm	testifier	2	2	no		tomato	conventional or organic	manure	manure	lacking	Hemiptera	<i>Trialeurodes vaporariorum</i>	all	abundance	number/row plant	test	SE from test	9	9	19.18	9.14	10.89	7.03	0	0	0.603	0.24										
Monaco	1995	laboratory	fertilizer	1	1	yes		fertilizer	conventional or organic	fish manure	manure	showing	Lepidoptera	<i>Trialeurodes vaporariorum</i>	egg	abundance	oviposition preference	graph	SE from graph	5	5	29.34	159.08	122.89	15.54	0	0	0.246	0.838										
Monaco	1995	laboratory	testifier	1	1	yes		testifier	conventional or organic	composted manure	manure	showing	Lepidoptera	<i>Trialeurodes vaporariorum</i>	egg	abundance	oviposition preference	graph	SE from graph	3	3	29.34	163.83	122.89	64.44	0	0	0.219	0.814										
Paul	2003	field	fertilizer	2	1	no		banana	conventional or organic	manure	compost	showing	Coleoptera	<i>Colaspis ovalis</i>	larvae	abundance	% damage/connection	table	SE from table	2	3	6.90	7.60	2.26	1.92	0	0	0.240	0.036										
Tarun	2003	field	testifier	2	1	no		tomatoes	conventional or organic	composted cattle manure	manure	lacking	Hemiptera	<i>Macropodaphis euphorbiae</i> , <i>Myzus persicae</i>	all	abundance	season average/plant	table	SE from table	4	4	16.23	17.41	6.12	6.04	0	0	0.541	0.501										
Tarun	2003	field	fertilizer	3	2	no		tomatoes	conventional or organic	composted cattle manure	manure	showing	Coleoptera	<i>Epiria</i> spp.	egg	abundance	season average/plant	table	SE from table	4	4	3.78	4.00	1.06	1.06	0	0	0.178	0.502										
Andrew	1996	farm	testifier	1	1	no		maize	conventional or organic	plant compost	compost	showing	Lepidoptera	<i>L. disparis</i>	larvae	abundance	larvae/day	table	SE from table	2	2	4.98	9.98	1.98	1.98	0	0	0.054	0.261										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Hemiptera	Aphididae species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Thysanoptera	Thripidae species	all	abundance	number/25 leaves	graph	SD from graph	6	6	0.00	19.52	6.00	6.33	0	0	0.0582	0.723										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25 leaves	graph	SD from graph	6	6	6.12	42.86	3.57	17.86	0	0	2.831	0.622										
Bettel	2004	field	farming system	1	1	yes		spec. fertilizer	conventional or organic	compost, biofertilizer, dolomite	compost	lacking	Lepidoptera	Lepidoptera species	all	abundance	number/25																						

Appendix 2

Natural enemy meta-analysis data set

Study	Year	Environment	Variable	Duration	Response	Certified organic?	Within study difference	Crop	Dist. control	Conventional/pest control	Organic/pest control	Fertiliser level	Organic fertiliser	Functional group	Taxonomic order	Species	Lifestage	Response	Response unit	Statistical test	Mean	Variance taken from	n - conventional	n - organic	Mean - conventional	Mean - organic	SD - conventional	SD - organic	Reversal	Effect size - d	Variance - d
Kanungo	2006	field	fertiliser	3	1	no	species, fertilizer	bean	no	no	conventional + organic	composted market crop waste	compost	parasitoid	Hymenoptera	parasitoid species	all	impact	% parasitism	table	SE from table	4	4	9.00	15.00	5.46	10.14	0.2407	0.8289		
Kanungo	2006	field	fertiliser	3	1	no	species, fertilizer	bean	no	no	conventional + organic	composted market crop waste	compost	predator	Hymenoptera	Ooencyrtus, aphelinids, arachnids	all	abundance	number/100 plants	table	SE from table	4	4	9.33	8.34	0.99	3.24	0.00	2.81	0.0000	0.5610
Kanungo	2006	field	fertiliser	3	1	no	species, fertilizer	bean	no	no	conventional + organic	fresh market crop waste	compost	parasitoid	Hymenoptera	parasitoid species	all	impact	% parasitism	table	SE from table	4	4	9.00	17.38	5.46	9.56	0.0000	0.9161	0.5548	
Kanungo	2006	field	fertiliser	2	2	no	species, fertilizer	carabge	no	no	conventional + organic	composted market crop waste	compost	mixed	no	coccinellids, syrphids, arachnids	all	abundance	number/25 leaves	table	SE from table	4	4	3.13	10.60	8.80	0.64	0.0000	8.9666	5.5289	
Kanungo	2006	field	fertiliser	2	1	no	species, fertilizer	carabge	no	no	conventional + organic	composted market crop waste	compost	mixed	no	parasitoid species	all	abundance	% parasitism	table	SE from table	4	4	11.30	6.28	4.28	4.54	0.0000	0.5101	0.5101	
Kanungo	2006	field	fertiliser	2	1	no	species, fertilizer	carabge	no	no	conventional + organic	composted market crop waste	compost	mixed	no	predator species	all	abundance	number/7 plants	table	SE from table	4	4	0.83	5.00	0.64	2.20	0.0000	2.5005	0.8927	
Kanungo	2006	field	fertiliser	2	1	no	species, fertilizer	carabge	no	no	conventional + organic	composted market crop waste	compost	mixed	no	predator species	all	impact	% parasitism	table	SE from table	4	4	0.83	8.00	0.64	1.80	0.0000	0.5111	0.4130	
Kanungo	2006	field	fertiliser	2	1	no	species, fertilizer	carabge	no	no	conventional + organic	composted market crop waste	compost	mixed	no	predator species	all	abundance	number/3 plants	table	SE from table	4	4	0.83	2.25	0.64	1.48	0.0000	1.0853	0.5733	
Morales	2001	field	fertiliser	2	2	no	maize	maize	no	no	conventional + organic	compost, dry cow manure	compost	colletor	Coleoptera	coccinellid species	all	abundance	number/plant	test	SE from test	9	9	0.04	0.08	0.01	0.02	0.0000	3.3348	0.5311	
Morales	2001	field	fertiliser	1	1	no	maize	maize	no	no	conventional + organic	compost	compost	colletor	Coleoptera	<i>Chrysomelids</i>	all	abundance	% parasitism	table	SE from table	9	9	0.20	8.20	1.20	3.90	0.0000	1.5533	0.2733	
Yadum	2003	field	fertiliser	2	1	no	species	tomatoes	no	no	conventional + organic	composted cattle manure	compost	predator	Hemiptera	antibiotics	all	abundance	season average/plant	table	SE from table	4	4	0.52	0.57	0.22	0.24	0.0000	0.1889	0.5021	
Yadum	2003	field	fertiliser	2	1	no	species	tomatoes	no	no	conventional + organic	composted cattle manure	compost	predator	Coleoptera	coccinellids	all	abundance	season average/plant	table	SE from table	4	4	0.04	0.20	0.08	0.18	0.0000	0.9909	0.5626	
Yadum	2003	field	fertiliser	2	1	no	species	tomatoes	no	no	conventional + organic	composted cattle manure	compost	predator	Coleoptera	coccinellids	all	abundance	season average/plant	table	SE from table	4	4	0.13	0.54	0.12	0.50	0.0000	0.9806	0.5601	
Bentall	2004	field	farming system	1	1	yes	species	tomato	insecticide	mixed	conventional + organic	compost, biofertiliser, dolomite lime, superphosphate	compost	predator	Neuroptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	6	6	2.45	6.94	1.58	3.39	0.0000	1.5666	0.4356	
Bentall	2004	field	farming system	1	1	yes	species	tomato	insecticide	mixed	conventional + organic	compost, biofertiliser, dolomite lime, superphosphate	compost	predator	Neuroptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	6	6	2.45	6.94	1.58	3.39	0.0000	1.5666	0.4356	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5	0.81	1.19	0.31	0.36	0.0000	0.5223	0.4523	
Clark	1999	field	farming system	1	1	no	species	tomato	insecticide	stem extract	conventional + organic	chicken manure	compost	colletor	Coleoptera	cycloperla species	all	abundance	number/25 leaves	graph	SE from graph	5	5								

Appendix 3

Pest vote-count data set

Study	Year	Author	Experiment	Variable	Duration (years)	Response	Certified organic?	Within study difference?	Crop	Conventional pest control	Organic pest control	Fertiliser	Organic fertiliser	Organic fertiliser group	Pest information	Response	Response direction, organic	Reversals	Significant?				
Primary author	Year	Year	Experimental	Variable	Duration (years)	Response	Certified organic?	Within study difference?	Crop	Conventional pest control	Organic pest control	Fertiliser	Organic fertiliser	Organic fertiliser group	Functional group	Taxonomic group	Species	Lifestage	Response unit	Response direction, organic	Reversals	Significant?	
Alvthin	2008	2008	field	fertiliser	3	5	no	no	potato	no	no	conventional + organic	manure + synthetic	manure	feeding	Coleoptera	<i>Leptosterna decemlineata</i>	adult	abundance	number/unt crop	-	+	yes
Blumberg	1997	1997	field	fertiliser	1	1	no	no	barley	no	no	conventional + organic	composted plant material	compost	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	adult	abundance	number/5 plants	+	+	yes
Costello	1995	1995	field	fertiliser	2	1	no	no	species	no	no	conventional + organic	green manure, p. K	compost	sucking	mixed	cicadellidae, miridae, lycgids, elaterids, gryllids, phalangids, Lepidoptera	all	abundance	biomass/m2	-	+	yes
Callaway	1986	1986	field	fertiliser	1	1	no	no	broccoli	no	no	conventional + organic	chicken manure, rice hull compost	mixed	sucking	Hemiptera	<i>Myzus persicae</i>	adult	abundance	aphid/leaf	+	+	no
	1986	1986	field	fertiliser	1	1	no	no	species	no	no	conventional + organic	cow manure	manure	sucking	Coleoptera	<i>Phytolera cruceator</i> , <i>Phytolera stotata</i>	adult	abundance	number/leaf area	+	+	yes
	1986	1986	field	fertiliser	1	1	no	no	species	no	no	conventional + organic	cow manure	manure	sucking	Hemiptera	<i>Lipaphis erysimi</i> , <i>Myzus persicae</i> , <i>Brevicoryne brassicae</i>	adult	abundance	number/leaf area	+	+	yes
	1986	1986	field	fertiliser	1	1	no	no	species	no	no	conventional + organic	cow manure	manure	sucking	Lepidoptera	<i>Pieris rapae</i> , <i>Plutella xylostella</i>	final larval instar	abundance	number/leaf area	+	+	yes
	1986	1986	field	fertiliser	1	1	no	no	species	no	no	conventional + organic	chicken manure	manure	sucking	Coleoptera	<i>Phytolera cruceator</i> , <i>Phytolera stotata</i>	adult	abundance	number/leaf area	+	+	yes
	1986	1986	field	fertiliser	1	1	no	no	species	no	no	conventional + organic	sludge	manure	sucking	Hemiptera	<i>Lipaphis erysimi</i> , <i>Myzus persicae</i> , <i>Brevicoryne brassicae</i>	adult	abundance	number/leaf area	+	+	yes
	1986	1986	field	fertiliser	1	1	no	no	species	no	no	conventional + organic	sludge	manure	sucking	Lepidoptera	<i>Pieris rapae</i> , <i>Plutella xylostella</i>	final larval instar	abundance	number/leaf area	+	+	yes
	1988	1988	field	fertiliser	1	1	no	no	species	no	no	conventional + organic	fresh cow manure	manure	sucking	Lepidoptera	<i>Plutella xylostella</i>	larvae	abundance	number/leaf area	-	+	no
	1988	1988	field	fertiliser	1	1	no	no	species	no	no	conventional + organic	fresh cow manure	manure	sucking	Lepidoptera	<i>Plutella xylostella</i>	larvae	abundance	number/leaf area	-	+	no
	1988	1988	field	fertiliser	1	1	no	no	species	no	no	conventional + organic	fresh cow manure	manure	sucking	Lepidoptera	<i>Pieris rapae</i>	larvae	abundance	number/leaf area	-	+	no
	1988	1988	field	fertiliser	1	1	no	no	species	no	no	conventional + organic	collard	manure	sucking	Coleoptera	Beet beetles	adult	abundance	number/leaf area	-	+	no
	1995	1995	laboratory	fertiliser	1	1	no	no	rice	no	no	conventional + organic	poultry manure, rapeseed meal, straw	mixed	sucking	Hemiptera	<i>Sogatella fructifera</i>	adult	abundance	number/energy	+	+	no
	1995	1995	laboratory	fertiliser	1	1	no	no	species	no	no	conventional + organic	poultry manure, rapeseed meal, straw	mixed	sucking	Hemiptera	<i>Nilaparvata lugens</i>	all	survival	% survival	+	+	yes
	2006	2006	field	fertiliser	3	1	no	no	bean	no	no	conventional + organic	composted market crop waste	compost	sucking	Hemiptera	<i>Aphis fabae</i>	larvae	abundance	number/unt plant	+	+	no
	2006	2006	field	fertiliser	3	1	no	no	bean	no	no	conventional + organic	fresh market crop waste	compost	sucking	Hemiptera	<i>Aphis fabae</i>	larvae	abundance	number/unt crop	+	+	no
	2006a	2006a	field	fertiliser	3	2	no	no	species, fertilizer	no	no	conventional + organic	composted market crop waste	compost	sucking	Hemiptera	<i>Brevicoryne brassicae</i> , <i>Myzus persicae</i>	all	abundance	aphid/plant	+	+	yes
	2006a	2006a	field	fertiliser	3	2	no	no	species, fertilizer	no	no	conventional + organic	fresh market crop waste	compost	sucking	Hemiptera	<i>Brevicoryne brassicae</i> , <i>Myzus persicae</i>	all	abundance	aphid/plant	+	+	yes
	2006a	2006a	field	fertiliser	3	2	no	no	species, fertilizer	no	no	conventional + organic	fresh market crop waste	compost	sucking	Hemiptera	<i>Brevicoryne brassicae</i> , <i>Myzus persicae</i>	all	abundance	aphid/plant	+	+	yes
	2006a	2006a	field	fertiliser	3	3	no	no	species, fertilizer	no	no	conventional + organic	fresh market crop waste	compost	sucking	Lepidoptera	<i>Plutella xylostella</i>	larvae	abundance	larva/plant	+	+	yes
	1994	1994	laboratory	fertiliser	1	1	no	no	species	no	no	conventional + organic	sewage sludge	manure	sucking	Lepidoptera	<i>Trichoplusia ni</i>	development	days	+	+	yes	
	1994	1994	laboratory	fertiliser	1	1	no	no	species	no	no	conventional + organic	sewage sludge	manure	sucking	Lepidoptera	<i>Trichoplusia ni</i>	development	days	+	+	yes	
	2001	2001	farm	fertiliser	2	2	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	fertiliser	2	1	no	no	species	no	no	conventional + organic	manure	manure	sucking	Hemiptera	<i>Rhopalosiphum padi</i>	all	abundance	number/unt plant	-	+	no
	2001	2001	farm	f																			

Appendix 4

Natural enemy vote-count data set

Study	Experiment details					Pest control		Fertiliser		Pest information		Response		Response direction, organic	Reversals	Significant?						
	Primary author	Year	Experimental	Variable	Duration	Response	Certified organic?	Within study difference	Crop	Conventional	Organic post control	Fertiliser level	Organic fertiliser				Functional group	Taxonomic	Species	Lifestage	Response	Response unit
Iado	2002	field	fertiliser	1	1	no	no	barley	conventional # organic	composted plant material	barley	conventional	Coloptera	Coloptera	coccinellid species	adult	abundance	number/5 rows	-	+	no	
Blumberg	1997	field	fertiliser	1	1	no	no	species	conventional # organic	green manure, P, K	barley	conventional	Coloptera	Hymenoptera	chalcids, Ichneumonids	all	abundance	biomass/m2	-	+	no	
Dalau	2006a	field	fertiliser	2	2	no	no	species, fertiliser	conventional # organic	fresh market crop waste	barley	conventional	Coloptera	spider	spider species	all	abundance	number/m2	-	+	no	
Karungi	2006	field	fertiliser	3	1	no	no	species, fertiliser	conventional # organic	green manure, P, K	bean	conventional	Coloptera	Coloptera	Coleoptera, leucospids, Anan	all	abundance	number/plant	+	+	no	
	2006	field	fertiliser	3	3	no	no	species, fertiliser	conventional # organic	composted market crop waste	bean	conventional	Coloptera	Hymenoptera	parasitoid species	all	impact	% parasitism	+	+	no	
	2006	field	fertiliser	3	1	no	no	species, fertiliser	conventional # organic	composted market crop waste	bean	conventional	Coloptera	Coloptera	coccinellids, syrphids, arachnids	all	abundance	number/10 plants	+	+	yes	
	2006a	field	fertiliser	2	2	no	no	species, fertiliser	conventional # organic	fresh market crop waste	bean	conventional	Coloptera	Hymenoptera	parasitoid species	all	impact	% parasitism	+	+	no	
	2006a	field	fertiliser	2	2	no	no	species, fertiliser	conventional # organic	composted market crop waste	bean	conventional	Coloptera	Hymenoptera	coccinellids, syrphids, arachnids	all	abundance	number/10 plants	+	+	no	
	2006a	field	fertiliser	2	2	no	no	species, fertiliser	conventional # organic	composted market crop waste	cabbage	conventional	Coloptera	Coloptera	aphid parasitoids	all	impact	% parasitism	+	+	no	
	2006a	field	fertiliser	2	2	no	no	species, fertiliser	conventional # organic	composted market crop waste	cabbage	conventional	Coloptera	Hymenoptera	<i>Phaenocarpa</i> parasitoids	all	impact	% parasitism	+	+	no	
	2006a	field	fertiliser	2	1	no	no	species, fertiliser	conventional # organic	composted market crop waste	cabbage	conventional	Coloptera	Coloptera	predator species	all	abundance	number/5 plants	+	+	yes	
	2006a	field	fertiliser	2	2	no	no	species, fertiliser	conventional # organic	fresh market crop waste	cabbage	conventional	Coloptera	Hymenoptera	<i>Phaenocarpa</i> parasitoids	all	abundance	number/5 plants	-	+	no	
	2006a	field	fertiliser	2	1	no	no	species, fertiliser	conventional # organic	fresh market crop waste	cabbage	conventional	Coloptera	Coloptera	predators	all	abundance	number/5 plants	+	+	no	
Morales	2001	field	fertiliser	2	2	no	no	species	conventional # organic	compost, dry cow manure	maize	conventional	Coloptera	Coloptera	coccinellids	all	abundance	number/plant	+	+	yes	
	2001	field	fertiliser	2	1	no	no	species	conventional # organic	compost, dry cow manure	maize	conventional	Coloptera	Coloptera	coccinellids, Dermaptera, spiders	all	abundance	number/plant	+	+	no	
	2001	field	fertiliser	2	1	no	no	species	conventional # organic	compost, dry cow manure	maize	conventional	Coloptera	Hymenoptera	parasitoid species	all	impact	% parasitism	+	+	no	
Ponti	2007	field	fertiliser	1	1	no	no	broccoli	conventional # organic	compost	tomatoes	conventional	Coloptera	Hymenoptera	<i>Dacnusa</i> spp.	adult	impact	% parasitism	+	+	yes	
Yardim	2003	field	fertiliser	2	1	no	no	species	conventional # organic	composted cattle manure	tomatoes	conventional	Coloptera	Hemiptera	anthracid species	egg	abundance	season average/plant	+	+	no	
	2003	field	fertiliser	2	1	no	no	species	conventional # organic	composted cattle manure	tomatoes	conventional	Coloptera	Coloptera	coccinellids	egg	abundance	season average/plant	+	+	no	
	2003	field	fertiliser	2	1	no	no	species	conventional # organic	composted cattle manure	tomatoes	conventional	Coloptera	Neuroptera	Chrysopids	egg	abundance	season average/plant	+	+	no	
Zhang	1998	field	fertiliser	2	1-2	no	no	potato	conventional # organic	compost, manure, conventional	potato	conventional	Coloptera	Coloptera	<i>Harporhiza rufipes</i>	adult	abundance	number/pifall trap	-	+	no	
Anderson	2000	farm	farming system	6	1-6	biological	biological	species	conventional # organic	farmyard manure	barley	conventional	Coloptera	Coloptera	<i>Trechus quadristriatus</i>	adult	abundance	active density	+	+	yes	
	2000	farm	farming system	6	1-6	biological	biological	species	conventional # organic	farmyard manure	barley	conventional	Coloptera	Coloptera	<i>Amara bifrons</i>	adult	abundance	active density	-	+	no	
	2000	farm	farming system	6	1-6	biological	biological	species	conventional # organic	farmyard manure	barley	conventional	Coloptera	Coloptera	<i>Aleochara pinguicula</i>	adult	abundance	active density	+	+	yes	
	2000	farm	farming system	6	1-6	biological	biological	species	conventional # organic	farmyard manure	barley	conventional	Coloptera	Coloptera	carabids	adult	abundance	active density	+	+	yes	
	2000	farm	farming system	6	1-6	biological	biological	species	conventional # organic	farmyard manure	barley	conventional	Coloptera	Coloptera	staphylinids	adult	abundance	active density	+	+	no	
Baselwood	1998	farm	farming system	1	1	ecological	ecological	wheat	conventional # organic	not stated	wheat	conventional	Coloptera	spider	spider	spider	adult	abundance	number/pifall trap	-	+	no
Berry	1996	farm	farming system	1	1	yes	yes	species	conventional # organic	not stated	carrot	conventional	Hymenoptera	parasitoids	parasitoids	all	abundance	mean per/0.1m	+	+	yes	
	1996	farm	farming system	1	1	yes	yes	species	conventional # organic	not stated	carrot	conventional	Coloptera	Coloptera	staphylinids	all	abundance	mean per/0.1m	+	+	yes	
	1996	farm	farming system	1	1	yes	yes	species	conventional # organic	not stated	carrot	conventional	Coloptera	Diptera	syrphids	all	abundance	mean per/0.1m	+	+	no	
	1996	farm	farming system	1	1	yes	yes	species	conventional # organic	not stated	carrot	conventional	Coloptera	spider	<i>Opatium</i> spp.	all	abundance	mean per/0.1m	+	+	no	
	1996	farm	farming system	1	1	yes	yes	species	conventional # organic	not stated	carrot	conventional	Coloptera	spider	Araneae species	all	abundance	mean per/0.1m	+	+	no	
	1996	farm	farming system	1	1	yes	yes	species	conventional # organic	not stated	carrot	conventional	Coloptera	spider	Hemeroptera species	all	abundance	mean per/0.1m	+	+	yes	
	1996	farm	farming system	1	1	yes	yes	species	conventional # organic	not stated	carrot	conventional	Coloptera	spider	Chilopoda species	all	abundance	mean per/0.1m	+	+	no	
Bettal	2004	field	farming system	2	1-2	yes	yes	tomato	conventional # organic	compost, biofertiliser, dolomite lime, superphosphate	tomato	conventional	Neuroptera	Cryptopidae	larvae	larvae	abundance	number/5 leaves	+	+	no	
Bovij	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	-	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional # organic	not stated	pea	conventional	Coloptera	Coloptera	carabids	adult	abundance	number/pifall trap/year	+	+	no	
	1992	farm	farming system	2	1-2	yes	yes	species	conventional													

Appendix 4 continued

Hilala	1997	farm	farming system	2	2	yes	species	rice	insecticide	no	conventional # organic	plant compost, legume residue	compost	spider	spider	Lycaonid species	all	abundance	density	+	+	+	not stated	
	1997	farm	farming system	2	2	yes	species	rice	insecticide	no	conventional # organic	plant compost, legume residue	compost	spider	spider	other species	+	abundance	density	-	+	+	not stated	
Hokkanen	1986	farm	farming system	1	1	biological	species	cabbage	insecticide	no	conventional # organic	composted manure	manure	Coleoptera	Coleoptera	carabids	adult	abundance	number in pitfall traps	+	+	+	+	
	2002	farm	farming system	1	1	ecological farming	species	rice	insecticide	no	conventional # organic	farmyard manure, green manure	mixed	mixed	mixed	carabids	all	abundance	number/20 hills	+	+	+	not stated	
	2002	farm	farming system	1	1	ecological farming	species	rice	insecticide	no	conventional # organic	farmyard manure, green manure	mixed	mixed	parasitoid	Hymenoptera	parasitoids	adult	abundance	number/20 hills	+	+	+	not stated
Hummel	2002	field	farming system	4	2	biologically based	species	tomato	insecticide	BT, soap	conventional # organic	soybean man, mineral	compost	parasitoid	Hymenoptera	parasitoids	all	impact	% parasitism	+	+	+	not stated	
	2002	field	farming system	4	1	biologically based	species	tomato	insecticide	BT, soap	conventional # organic	soybean man, mineral	compost	mixed	mixed	carabids	all	abundance	number/10 terminals	+	+	+	no	
	2002	field	farming system	4	4	biologically based	species	maize	insecticide	BT, soap	conventional # organic	soybean man, mineral	compost	mixed	mixed	coccinellids	all	abundance	number/20 plants	+	+	+	not stated	
Imker	2002	farm	farming system	2	1	ecological farming	species	wheat	insecticide	conventional # organic	conventional # organic	herbes, manure	mixed	predator	Coleoptera	ground beetles	all	abundance	active density	+	+	+	not stated	
Labrie	2003	farm	farming system	2	1	yes	species	orchard	insecticide	soap, plant extract	conventional # organic	not stated	not stated	Coleoptera	Coleoptera	<i>Pterostichus melanarius</i>	adult	abundance	number/pitfall trap	+	+	+	yes	
Letourneau	2001	farm	farming system	1	1	yes	species	tomato	mixed	mixed	conventional # organic	manure, worm casts, compost	mixed	parasitoid	Hymenoptera	parasitoids	all	abundance	number for 5 suctions	+	+	+	yes	
	2001	farm	farming system	1	1	yes	species	tomato	mixed	mixed	conventional # organic	manure, worm casts, compost	mixed	predator	Hemiptera	<i>Jalyus sicchami</i>	adult	abundance	number for 5 suctions	+	+	+	not stated	
	2001	farm	farming system	1	1	yes	species	tomato	mixed	mixed	conventional # organic	manure, worm casts, compost	mixed	predator	Hemiptera	<i>Orius trivittatus</i>	adult	abundance	number for 5 suctions	+	+	+	not stated	
	2001	farm	farming system	1	1	yes	species	tomato	mixed	mixed	conventional # organic	manure, worm casts, compost	mixed	spider	spider	<i>Mezomorpops</i> spp.	adult	abundance	number for 5 suctions	+	+	+	not stated	
	2001	farm	farming system	1	1	yes	species	tomato	mixed	mixed	conventional # organic	manure, worm casts, compost	mixed	predator	Hemiptera	<i>Engylocus modestus</i>	adult	abundance	number for 5 suctions	+	+	+	not stated	
Mahr	2007	farm	farming system	1	1	yes	species	kiwi	insecticide	mineral soap	conventional # organic	not stated	not stated	predator	Dermoptera	<i>Forficula auricularia</i>	adult	abundance	number found in shelter traps	+	+	+	yes	
Melnychack	2005	farm	farming system	1	1	organic inputs	species	cereal	insecticide	no	conventional # organic	not stated	not stated	Coleoptera	Coleoptera	carabids	adult	abundance	mean per pitfall trap	+	+	+	yes	
Moreby	1994	farm	farming system	2	2	yes	species	winter wheat	insecticide	no	conventional # organic	green manure, animal manure	mixed	spider	spider	Araneae	all	abundance	number/0.5m suction	+	+	+	yes	
	1994	farm	farming system	2	2	yes	species	winter wheat	insecticide	no	conventional # organic	green manure, animal manure	mixed	parasitoid	Hymenoptera	Ichneumonidae	all	abundance	number/0.5m suction	-	+	+	no	
	1994	farm	farming system	2	2	yes	species	winter wheat	insecticide	no	conventional # organic	green manure, animal manure	mixed	Coleoptera	Coleoptera	coccinellids	all	abundance	number/0.5m suction	-	+	+	yes	
	1994	farm	farming system	2	2	yes	species	winter wheat	insecticide	no	conventional # organic	green manure, animal manure	mixed	predator	Diptera	Diptera (predatory)	all	abundance	number/0.5m suction	-	+	+	yes	
	1996	farm	farming system	2	1	yes	species	wheat	insecticide	no	conventional # organic	green manure, animal manure	mixed	predator	Hemiptera	predatory species	adult	abundance	number/0.5m	+	+	+	no	
Moreby	1997	farm	farming system	1	2	yes	species	winter wheat	insecticide	no	conventional # organic	green manure, animal manure	mixed	Coleoptera	Coleoptera	carabids	adult	abundance	number/0.5m suction	-	+	+	no	
Oberg	2007	farm	farming system	1	1	yes	species	barley, oats, wheat	no	no	conventional # organic	not stated	not stated	spider	spider	<i>Oedothorax apicatus</i>	all	abundance	active density	+	+	+	yes	
	2007	farm	farming system	1	1	yes	species	barley, oats, wheat	no	no	conventional # organic	not stated	not stated	spider	spider	<i>Mezomorpops</i>	all	abundance	active density	+	+	+	not stated	
	2007	farm	farming system	1	1	yes	species	barley, oats, wheat	no	no	conventional # organic	not stated	not stated	spider	spider	<i>Pardosa agrestis</i>	all	abundance	active density	+	+	+	yes	
	2007	farm	farming system	1	1	yes	species	barley, oats, wheat	no	no	conventional # organic	not stated	not stated	spider	spider	<i>Pardosa palustris</i>	all	abundance	active density	+	+	+	not stated	
O'Sullivan	2002	field	farming system	1	1	yes (not certified)	species	potato	not stated	not stated	conventional # organic	farm yard manure	manure	Coleoptera	Coleoptera	carabids	adult	abundance	number/pitfall trap	+	+	+	no	
Oksanen	2001a	farm	farming system	1	1	yes	species	wheat, barley, oats	insecticide	no	conventional # organic	solid/liquid manure, none	manure	Coleoptera	Coleoptera	<i>Pterostichus melanarius</i>	adult	condition	least square mean residual of size	+	+	+	no	
Pfiffner	2002	farm	farming system	3	1-3	low input	species	winter cereal	no	no	conventional # organic	slurry, manure, compost	mixed	Coleoptera	Coleoptera	carabids	adult	abundance	activity density	+	+	+	not stated	
	2002	farm	farming system	3	1-3	low input	species	winter cereal	no	no	conventional # organic	slurry, manure, compost	mixed	spider	spider	spiders	adult	abundance	activity density	+	+	+	not stated	
Portauf	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Amara phoebea</i>	adult	active density	number/pitfall trap	+	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Carabus auratus</i>	adult	active density	number/pitfall trap	+	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Carabus granulatus</i>	adult	active density	number/pitfall trap	+	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Agrostus mulleri</i>	adult	active density	number/pitfall trap	+	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Psephenus cupreus</i>	adult	active density	number/pitfall trap	+	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Platynus dorsalis</i>	adult	active density	number/pitfall trap	+	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Amara similata</i>	adult	active density	number/pitfall trap	+	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Loricera pilicornis</i>	adult	active density	number/pitfall trap	+	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Civina fovea</i>	adult	active density	number/pitfall trap	+	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Nebria salina</i>	adult	active density	number/pitfall trap	-	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Asaphidion flavipes</i>	adult	active density	number/pitfall trap	-	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Notophilus biguttatus</i>	adult	active density	number/pitfall trap	-	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Amara aeneipes</i>	adult	active density	number/pitfall trap	-	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Pterostichus strenuus</i>	adult	active density	number/pitfall trap	+	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	Coleoptera	Coleoptera	<i>Bembidion tetracolum</i>	adult	active density	number/pitfall trap	+	+	+	yes	
Reddersen	1997	farm	farming system	2	1	yes	species	mixed	insecticide	not stated	conventional # organic	organic matter, undersown	compost	parasitoid	Hymenoptera	Parasitica	adult	abundance	number/0.42m device	+	+	+	no	
	1997	farm	farming system	2	1	yes	species	mixed	insecticide	not stated	conventional # organic	organic matter, undersown	compost	spider	spider	Araneae	adult	abundance	number/0.42m device	+	+	+	no	
	1997	farm	farming system	2	1	yes	species	mixed	insecticide	not stated	conventional # organic	organic matter, undersown	compost	Coleoptera	Coleoptera	carabids	adult	abundance	number/0.42m device	+	+	+	no	
	1997	farm	farming system	2	1	yes	species	mixed	insecticide	not stated	conventional # organic	organic matter, undersown	compost	Coleoptera	Coleoptera	staphylinids	adult	abundance	number/0.42m device	-	+	+	no	
	1997	farm	farming system	2	1	yes	species	mixed	insecticide	not stated	conventional # organic	organic matter, undersown	compost	Coleoptera	Coleoptera	coccinellids	adult	abundance	number/0.42m device	+	+	+	yes	
	1997	farm	farming system	2	2	yes	species	mixed	insecticide	not stated	conventional # organic	organic matter, undersown	compost	predator	Diptera	Eristalidae	adult	abundance	number/0.42m device	+	+	+	yes	
Roskewitz	2005	farm	farming system	1	1	yes	species	wheat	not stated	not stated	conventional # organic	not stated	not stated	parasitoid	Hymenoptera	parasitoids	all	impact	% parasitism	+	+	+	no	
Schmidt	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	spider	spider	<i>Erigone</i> spp.	all	abundance	number (total pitfall)	+	+	+	no	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	spider	spider	<i>Oedothorax</i> spp.	all	abundance	number (total pitfall)	+	+	+	yes	
	2005	farm	farming system	1	1	yes	species	wheat	insecticide	no	conventional # organic	manure	manure	spider	spider	<i>Pardosa</i> spp.	all	abundance	number (total pitfall)	+	+	+	yes	
Shah	2003	farm	farming system	1	1	yes	species	mixed	insecticide	no	conventional # organic	no	no	Coleoptera	Coleoptera	<i>P. melanarius</i>	adult	abundance	mean/pitfall trap	+	+	+	yes	
	2003	farm	farming system	1	1	yes	species	mixed	insecticide	no	conventional # organic	no	no	Coleoptera	Coleoptera	<i>P. madidus</i>	adult	abundance	mean/pitfall trap	+	+	+	yes	
	2003	farm	farming system	1	1	yes	species	mixed	insecticide	no	conventional # organic	no	no	Coleoptera	Coleoptera	<i>A. dorsalis</i>	adult	abundance	mean/pitfall trap	-	+	+	no	
	2003	farm	farming system	1	1	yes	species	mixed	insecticide	no	conventional # organic	no	no	Coleoptera	Coleoptera	<i>P. cupreus</i>	adult	abundance	mean/pitfall trap	+	+	+	no	
	2003	farm	farming system	1	1	yes	species	mixed	insecticide	no	conventional # organic	no	no	Coleoptera	Coleoptera	<i>T. quadrivittatus</i>	adult	abundance	mean/pitfall trap	+	+	+	no	
	2003	farm	farming system	1	1	yes	species	mixed	insecticide	no	conventional # organic	no	no	Coleoptera	Coleoptera	<i>T. signatus</i>	adult	abundance	mean/pitfall trap					