

TRITROPHIC INTERACTIONS BETWEEN CRUCIFERS, APHIDS AND HYMENOPTERAN PARASITIDS

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ABSTRACT

During the 1970s, educational institutions were affected by political, economic, and social changes. This study was conducted in a rural area of Malawi, where the primary schools were under government control. The study was conducted in a rural area of Malawi, where the primary schools were under government control. The study was conducted in a rural area of Malawi, where the primary schools were under government control.

*This thesis is dedicated to all the members of my family. my mother for her sacrifices. wife
Hauwa and my three loving sons Kitenda, Lubanga and Kimuda*

ABSTRACT

Studies on tritrophic interactions involving three cultivars of common cabbage, *Brassica oleracea* var *capitata*, with varying levels of susceptibility to aphids, cv Minicole, (green-leaved) partially resistant with antibiosis mechanisms, Ruby Ball, (red-leaved) with antixenosis factors, and Derby Day (green-leaved), susceptible, were conducted with two aphid species, *Myzus persicae* (Sulzer), a generalist, and *Brevicoryne brassicae* (L.), a crucifer specialist and two hymenopteran parasitoids, *Aphidius colemani* (Viereck) and *Diaeretiella rapae* (McIntosh).

Investigations on the olfactory response of *A. colemani* in a four-way olfactometer showed that odours influenced *A. colemani* response to varying degrees. The odours of the cabbage cultivar on which the parasitoid had been reared was preferred over the odours of the other cultivars. Parasitoids gave a significant response to the volatiles of the cultivar on which they developed when tested against water. Overall, parasitoid responses increased when plant to plant comparisons were made as compared with plant to water controls, and again the magnitude of parasitoid response to odours depended on cultivar with Derby Day and Minicole preferred over Ruby Ball. However, when provided with a choice between odours of infested plants, parasitoids did not show a significant preference for the cultivar on which they were reared.

Laboratory studies were conducted to determine the effects of plant cultivar and aphid species on the performance of *A. colemani*. Significantly greater aphid populations were found on Derby Day regardless of the presence or absence of parasitoids, compared with Minicole or Ruby Ball. Minicole had the greatest proportion of aphids parasitised and Derby Day the least. A significantly lower percentage of emerged parasitoids was recorded on Minicole for both aphid species compared with Derby Day and Ruby Ball. The total development time of female parasitoids reared on *M. persicae* did not differ significantly between Minicole and Derby Day but was significantly faster on Ruby Ball. Sex ratios, size and longevity of both male and female parasitoids on either host were not significantly influenced by cultivar.

Field studies showed that cultivar and plant growth stage rather than fertiliser influenced aphid infestation and parasitism. In 1998, Ruby Ball was least colonised by aphids in early stage of plant growth, while Minicole had the greatest aphid infestation. Similarly in early season of 1999, Ruby Ball was least colonised but aphid densities were greatest on Derby Day followed by Minicole. In both years, from mid to late stages of plant growth, the lowest aphid infestation and the highest level of parasitism was observed on Minicole. *Brevicoryne brassicae* was the dominant species and had greater rate of parasitism compared with *M. persicae* during the early part of the season. *Diaeretiella rapae* was the major parasitoid and was found earlier than *Aphidius* sp. There was evidence of a beneficial interaction between the degree of plant resistance and biological control at the early and mid stages of plant growth. The implications of the results are discussed in relation to the integrated management of these aphids.

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1

INTRODUCTION

1.1 Aphid problems in agriculture

Aphids are regarded as the most important insect pests of agriculture in temperate zones (Minks and Harrewijn, 1987; Cole, 1997a). Their distribution is global but predominantly temperate with the northern temperate regions reporting the highest pest status (Dixon, 1998). Aphids influence plant growth by feeding on its sap, decreasing its turgor, and therefore reducing the availability of nutrients and water to the plant growth points. The damage caused by aphids may be through direct feeding on the phloem, or indirectly through production of honeydew which contaminates the leaf surface, and transmission of viruses (Minks and Harrewijn, 1987).

Aphids are common pests in the United Kingdom of cereals, sugar beet, potatoes, beans, vegetables, fruits and vegetable produce. Most species are highly host specific except for the broadly polyphagous peach-potato aphid, *Myzus persicae* Sulzer (Dixon, 1987). The high specificity of most aphid species is attributed to their specific diet requirements, as the phloem sap which they feed on has a strictly defined composition which differs among the different plant species (Dixon, 1987; Cole, 1994).

Aphid problems in field-grown vegetables are restricted to a few vegetables and aphid species, of which some cause damage almost every season, whilst others seldom occur in sufficiently large numbers to be injurious (Theunissen, 1989). The most economically important species are: *Brevicoryne brassicae* (L.) in cruciferous crops (Hughes, 1963; Gabrys *et al.*, 1997), *Myzus persicae*, *Nasonovia ribis-nigri* (Mosley) and *Pemphigus bursarius* (L.) in leafy vegetables such as lettuce and endive, and *M. persicae* and *Acyrtosiphon pisum* (Harris) in beetroot and pea respectively (Theunissen, 1989).

The cabbage aphid, *B. brassicae* is a cosmopolitan pest and one of the most damaging and consistently present on cabbage crops in temperate zones (Hughes, 1963; Singh *et al.*, 1994; Cole, 1997b). It is the primary aphid pest on cabbage in the United Kingdom with a limited host range, principally of cruciferae (Wearing, 1972). Another serious pest of cabbage, *M. persicae*, has a host range which include sugar beet, potatoes and chrysanthemums (van Emden *et al.*, 1969; Blackman, 1974; Chambers, 1994). Damage to cruciferae by these aphid species is sporadic but often serious and follows a contrasting pattern, *M. persicae* feeding predominantly on old leaves while *B. brassicae* prefers the young leaves (Wearing, 1972; Gabrys *et al.*, 1997).

Under field conditions, aphid infestations and the resultant crop damage are usually kept under check by various mortality factors (Hughes, 1963; Hasken and Poehling, 1994). Damage by aphids can also be minimised through intercropping. However, at the lower aphid levels that are normally accepted in commercial fields, the intercropping effect would not be large enough to obtain a sufficient degree of cabbage aphid control (Theunissen, 1989). Manipulation of water levels and the plant nutrition status can also reduce aphid damage (Wearing, 1972; Dodd and van Emden, 1979). When aphid populations reach alarming levels and in such situations where infestations threaten to cause economic yield losses, both *M. persicae* and *B. brassicae* must be controlled by the use of suitable aphicides (Foster *et al.*, 1998).

In many parts of the temperate zone, use of natural enemies in reducing aphids (Mackauer and Way, 1976) has not been generally effective except in some cases in greenhouses (Ramakers, 1989; Chambers, 1994). Likewise, host-plant resistance has had only limited success in the management of aphid populations (van Emden and Wratten, 1991). However, these methods of control have been investigated largely independently and mostly in a (ditrophic) pest-natural enemy or plant-pest context, respectively (Price, 1986; Verkerk and Wright, 1996; Verkerk *et al.*, 1998b). Because of the high number of chemical applications needed for controlling aphids, chemical control has considerably raised the production costs (Trumble, 1982) and the situation has been aggravated by over 20 aphid species, including *M. persicae* and *B. brassicae* developing resistance to insecticides (Minks and Harrewijn, 1987; Foster *et al.*, 1998). There, thus, may be considerable benefits

in a more integrated approach. For instance, in aphid systems where natural enemies alone are not sufficiently effective, improvement in their efficacy through host-plant manipulation is both possible and highly desirable (van Lenteren, 1991). There is, therefore, a need to examine these effects in a tritrophic (plant-pest-natural enemy) system to exploit positive interactions in the management of aphids.

1.2 Aim of the present study

Manipulation of tritrophic interactions to enhance parasitism through the use of infochemicals and plant characteristics is crucial in the sustainable management of *B. brassicae* and *M. persicae* in cruciferous systems. The aim of the present study was to investigate tritrophic interactions between cultivars, aphid species and their parasitoids under laboratory and field conditions.

One of the most crucial consequences of pest management involving more than one method of control is that interactions between these methods can occur (van Emden, 1981). Studies by Thomas and Waage (1996) have shown the potential benefits of such interactions in pest management. It is now known that the nutritional quality of plants used as resource by a herbivore not only affects the physiology and behaviour of the herbivore, but also affects the quality of the herbivore as a resource for the natural enemy. Natural enemies also base their foraging decisions from these plant-herbivore trophic levels and the chemical information emanating from them mediates their searching behaviour (Vet and Dicke, 1992; Takabayashi and Dicke, 1996; Vet *et al.*, 1998; Dicke, 1999). For example, studies on the oviposition behaviour of the polyphagous aphid parasitoid *Aphidius colemani* (Viereck) showed that its preference for certain hosts was influenced by genetic and epigenetic (conditioning) factors (Messing and Rabasse, 1995). Natural enemy activity has also been found to be influenced by differences in plant nutritional status and levels of susceptibility of the host plant to aphids (Wyatt, 1970; Mohammed and van Emden, 1989; Gowling and van Emden, 1994).

A major concern regarding the use of parasitoids for pest control is the possible antagonistic interaction with host-plant resistance (van Emden, 1978; Price, 1986; Hare, 1992; Souissi and Le Ru, 1998a). For example, studies by van Emden (1978) showed that due to low levels of glucosinolate in a variety of brussels sprout partially resistant to *B. brassicae*, the parasitoid *Diaeretiella rapae* (M'cIntosh) did not settle on that variety as readily as on one that was more susceptible. As a result of the reduced mortality from *D. rapae*, aphid numbers on the partially resistant variety eventually overtook those on the susceptible variety.

Negative interactions may also be caused by plant physical factors which can impede natural enemy effectiveness, for example, leaf toughness, cuticle thickness, trichomes and plant architecture (Price, 1986) or by secondary plant chemicals (Hare, 1992). The nutritional substrate offered by the host plant or herbivore can influence parasitoid fitness through reduced growth rates, greater development time and mortality. It can also lead to decreased fecundity and longevity (Bergman and Tingey, 1979; Reed *et al.*, 1991; Godfray, 1994; Souissi and Le Ru, 1997; Souissi *et al.*, 1998b).

1.3 Specific objectives

1) To examine the olfactory response of *Aphidius colemani* (Hymenoptera: Aphidiidae) to odours by testing odours from:

- (i) plant and non-plant odours;
- (ii) cultivars of varying levels of resistance (without aphids)
- (iii) infested and non infested plants
- (iv) cultivars of varying levels of resistance (with aphids)

2) To determine the extent to which cultivars with varying degrees of resistance to cruciferous aphids influence the performance of *A. colemani*

3) To evaluate under field conditions the interaction between plant cultivars and fertiliser on aphid infestation and parasitism by using:

- (i) a range of cultivars of varying susceptibility to aphids;
- (ii) different levels of fertiliser

In this thesis, background information on the biology and ecology of *B. brassicae* and *M. persicae* and the methods of aphid control is given in Chapter 2. Chapter 3 deals with laboratory studies on the olfactory response of *A. colemani* to cabbage and cabbage-aphid odours under different plant and plant-pest combinations. Presented in Chapter 4 is a laboratory investigation on the extent to which cultivars of varying levels of resistance to cruciferous aphids influence the performance of *A. colemani*. In Chapter 5, field investigations were carried out on the tritrophic interactions between cultivars with different resistance and fertiliser levels, cruciferous aphids and parasitoids. Finally, in a general discussion in Chapter 6, the results obtained in the study are reviewed in relation to other studies on the potential for manipulating tritrophic interactions in pest management.

2

LITERATURE REVIEW

2.1 Introduction

A substantial amount of research work has been carried out in an effort to control aphids in temperate regions (Minks and Harrewijn, 1989). It is, however, evident from these studies that research on aphids in general and cruciferous aphids in particular, has not been focused on an integrated control approach. Plant breeders have mainly emphasised the intrinsic defence mechanisms, while, biological control specialists have largely focused on extrinsic mechanisms (Price, 1986). Although research on tritrophic interactions relating to arthropod herbivores has expanded rapidly (Price *et al.*, 1980; Boethel and Eikenbary, 1986; Thomas and Waage, 1996) there have been relatively few studies on crop-based systems (Price, 1986; Hare, 1992; van Emden, 1995) and rigorous studies linking laboratory and field experiments in this context are lacking (Verkerk *et al.*, 1998a). The studies reported here aim at obtaining some of this information.

2.2 Biology of *Brevicoryne brassicae* and *Myzus persicae*

The biology of both *B. brassicae* and *M. persicae* is characterised by the short duration of nymphal development and a high reproductive rate (Hughes, 1963; Blackman, 1974; Dickson, 1994), influenced by such factors as temperature, light intensity, and the nature and conditions of the host plant (Blackman, 1974; Hardie and vaz Nunes, 1994). On suitable host plants, many aphids species, including *B. brassicae* and *M. persicae*, have very high rates of population development (Blackman, 1974; Dixon, 1998). The basis of the rapid increase in population is an extreme form of viviparity whereby embryonic development begins within the unborn nymph (Kennedy and Stroyan, 1959; Hughes, 1963; Dixon, 1990). Because of the "telescoping of generations" resulting from rapid embryonic and nymal development, both *B. brassicae* and *M. persicae* and other aphid species have

exceptional rates of multiplication (Hughes, 1963; Dixon, 1998). It is this high rate of multiplication that makes aphids potentially very serious pests of crops (Minks and Harrewijn, 1987; Dixon, 1994).

2.3 *Brevicoryne brassicae* and *Myzus persicae* ecology: life cycle and dispersal

Aphids in general have adapted well to hosts that are seasonal in occurrence and extremely diverse in growth patterns (Dixon, 1998). They have evolved extensive variation in form and life cycle patterns for exploitation of resources of short-lived host plants through a complex system of polyphenism, each form having a different function (Hughes, 1963; Dixon, 1998). It is this system of alternative polyphenism that ensures their survival (Kennedy and Stroyan, 1959; Dixon, 1998). For example, *B. brassicae* and *M. persicae* produce both sexual morphs as well as parthenogenetic forms. The sexual forms are produced at the approach of winter (apterous, oviparous female and alate male) except for *M. persicae* which can remain parthenogenetic in winter (van Emden *et al.*, 1969; Blackman, 1974). The oviparae lay their eggs on the aerial part of the plant which in spring hatch into the parthenogenetic stem mothers, which produce first generation nymphs (Hughes, 1963; Gabrys *et al.*, 1997).

Winged aphids of both species develop in a colony as a response to climatic conditions, over-crowding or changes in the nutritional status of the host, particularly when the nitrogen content is low (Kennedy and Stroyan, 1959; Blackman, 1974; Dixon, 1994). The development and dispersal of winged aphids enables these insects to colonise fresh and more suitable plants on which the apterous existence can be resumed. This dispersal subsequently affects their natural enemies.

Dispersal of alate aphids usually starts during the first hours of adult life. However, alates may not leave host plants that are highly favourable (Kennedy and Stroyan, 1959; Dickson, 1998). Initial take-off by the bean aphid is a positive response to short-wave length light and once air-borne, the aphids are transported by convective currents (Hughes, 1963; Nottingham *et al.*, 1991). Because of the host-selection process in aphid flight, primary dispersal results in the partial contraction of alate populations on suitable host plants

(Kennedy *et al.*, 1959; Pickett *et al.*, 1992). On a new host, generations of wingless progeny are produced until seasonal changes, overcrowding, or a decline in host quality trigger the production of new alates which disperse and initiate the next cycle (Blackman, 1974; Dixon, 1990).

2.4 Host location and selection by *Brevicoryne brassicae* and *Myzus persicae*

Aphids discover their host plants with extreme collective efficiency. However, host plant location consists of random dispersal and repeated alightment by large numbers of highly active migrants most of which die in the process (Schneider, 1962; Ward *et al.*, 1998). The process of host plant location begins with the termination of alate dispersive flight, especially when convective air movements stops, and descent towards the ground (Schneider, 1962; Pickett *et al.*, 1992). In the field, they land preferentially on leaves reflecting a greater proportion of long-wave length energy (Dixon, 1998). Aphids respond to visual cues of which colour is a good indicator of the nutritive status of the plant but a poor indicator of a plants taxonomic status (Kennedy *et al.*, 1961; Dixon, 1998). The attractiveness of green and particularly yellow to aphids ensures that aphids alight on nutritionally suitable plants, as both highly nutritious young and senescent foliage tend to be yellower than the nutritionally poorer mature leaves (Kennedy *et al.*, 1961; van Emden *et al.*, 1969; Dixon, 1998).

On alighting, aphids probe the host plant. This may be followed by rejection of the plant and take-off, or by settling to feed and reproduce (Johnson, 1953; Kennedy 1965; Bones *et al.*, 1991). The quality of the food available to an aphid is important in determining its size, survival and reproductive rate (Kennedy *et al.*, 1950; Bones *et al.*, 1991). High quality food is usually available to aphids feeding on actively growing or senescing plants or parts of plants and often declines rapidly when plants cease growing. This is because nitrogen concentrations are normally greater in the phloem sap of plants that are growing, flowering or senescent as most nutrients are translocated to these parts. Thus, the food of aphids shows marked variations in quality in space and in time. That is, between different parts of a plant and between different stages in the seasonal growth cycle of a plant (Dixon, 1998). This probing stage, therefore, has tremendous potential for the manipulation of the host

plant in the control of aphids (van Emden *et al.*, 1969; Cole, 1997a). The monitoring, and the subsequent behavioural decision to leave or stay explains the strong host discrimination by aphids (van Emden and Way, 1973; Cole, 1997b). Thus, *B. brassicae* tends to avoid red cabbage varieties at the early selection stage although such varieties tend to be more suitable for the later multiplication of the aphid (Radcliffe and Chapman, 1965; Singh and Ellis, 1993).

The requirements for host selection by individual aphid species appear to be very characteristic, so that each species not only has a particular range of host plants, but also preferred feeding sites on the plant. *Myzus persicae*, for example, is not very discriminating between plants in taxonomic terms, but highly discriminating in plant physiological terms (Kennedy and Stroyan, 1959; van Emden, 1966; Cole, 1997b), while *B. brassicae* is highly specific taxonomically (van Emden *et al.*, 1969). The final settlement on the host plant is, therefore, dependent on the recognition of those plant characteristics that favour subsequent aphid multiplication (van Emden *et al.*, 1969; Cole, 1997b).

2.5 Approaches to the control of *Brevicoryne brassicae* and *Myzus persicae* infestations

Serious crop injury by the aphids stems from the fact that large populations may develop and feed on delicate growing parts of plants. Damage to crop plants is three-fold : i) mechanical injury to plants (Kennedy and Stroyan, 1959), ii) withdrawal of plant sap (Schepers, 1989), and iii) transmission of plant viruses (Schepers, 1989). Among cruciferous aphid species, *B. brassicae* is considered the most harmful due to its feeding habits (Schepers, 1989; Gabrys *et al.*, 1997). It has a preference to young and tender growing parts of the plant, where it forms large colonies on the underside of leaves. The leaves ultimately become lumpy with curling edges and yellow spots and photosynthesis is reduced (Schepers, 1989). *Myzus persicae*, on the other hand, tends to feed on older leaves (Wearing, 1972), where its visible effects are negligible (van Emden *et al.*, 1969; Costello and Altieri, 1995).

In temperate zones, the occurrence of suitable environmental conditions leads to heavy build up of aphid populations. This results in serious injury to crops and in some instances to extensive spread of plant virus diseases (Theunissen, 1989; Schepers, 1989). In such situations, economic crop losses are averted largely by the application of insecticides (Dewar and Read, 1991; Thomas *et al.*, 1992).

2.5.1 Chemical control of cruciferous aphids

In instances where aphid outbreaks have continued to threaten yield losses of economic proportions, chemical control has retained a central role as the only method by which immediate crop losses have been averted (Singh *et al.*, 1994). Pirimicarb and demeton-s-methyl are now the most commonly used insecticides in the UK (Foster *et al.*, 1998). However, chemical control has numerous draw-backs.

Insecticide application involves direct cost outlays that may not be justified by the value of the crop (Foster *et al.*, 1998). Thus, in the control of *B. brassicae* and *M. persicae* on cabbage, chemical control of the aphids may not be economical due to the repeated number of applications required for effective control (Trumble, 1982; Thomas *et al.*, 1992). Frequent application of insecticides can also result in some phytotoxicity in *Brassica* spp. (Schepers, 1989) and the development of resistance (Dewar *et al.*, 1992). Finally, increased applications will lengthen pesticide residual activity hence endangering the health of consumers (Schepers, 1989).

When chemical insecticides are used to control aphids on cabbage, such compounds, particularly in foliar sprays, are known to pose serious hazards to pollinators, parasites and predators by affecting both their diversity and population density (Powell *et al.*, 1985; Gamal *et al.*, 1992). This may have serious consequences since the pests are often kept under check by a healthy population of natural enemies (Kennedy and Stroyan, 1959; Hasken and Poehling, 1994). Pest resurgence may also occur in situations where chemical and biological control methods are antagonistic (Suss, 1983) and from possible stimulation of aphid reproduction under certain sub-lethal concentration of insecticides (Henry *et al.*, 1988). The over-dependence of farmers on chemicals as the centre-piece for the control of

aphids, has culminated in the increasing incidence and severity of insecticide resistance (Devonshire, 1989; Dewar *et al.*, 1992). This is particularly true for *M. persicae* where a number of resistance mechanisms have been identified to organophosphates (OP), pyrethroids and carbamates (Foster *et al.*, 1998). Studies in the UK have demonstrated that up to 20% of *M. persicae* were highly resistant to insecticides (Devonshire, 1989; Moores *et al.*, 1994).

It is evident, therefore, that because of the costs involved in chemical control, the adverse effects on natural enemies, and the development of insecticide resistance, a more integrated (multitrophic) approach to the control of aphids on cabbage is desirable and needs to be investigated.

2.5.2 Host plant resistance in aphid management

Painter (1951) defined resistance of plants to insect attack as the relative amount of heritable qualities possessed by the plant which influence the ultimate degree of damage done by the insect. However, plant resistance is relative and can be measured only by comparison with other genotypes. Due to its variability, it can be modified by physical, chemical and biological factors (Auclair, 1989).

Three mechanisms account for plant resistance to insect damage: (i) non-preference or antixenosis, where plants are unattractive or unsuitable for colonisation or oviposition by an insect, (ii) antibiosis, where the insect life history is adversely affected through reduced growth, reproduction or survival when a resistant host plant is used for food and (iii) tolerance, which enables the host plant to grow and reproduce itself or repair an injury to a marked degree in spite of supporting a population approximately equal to that damaging a susceptible host (Painter, 1951).

The multiplication of aphids and the development of an infestation are highly dependent on either genetically inherent characteristics of the plant or environmental factors (van Emden *et al.*, 1969; van Emden, 1991; Wellings and Ward, 1994). Basic plant characteristics that may impart resistance or susceptibility to aphids can be morphological, such as variation in

foliage size, shape, colour, pubescence, and biochemical, including, the nutritional composition of the plant, especially proportion of essential nutrients (Auclair, 1989; Cole, 1997a). For example, "glossy" (or non-waxy) leaved varieties of Brussels sprouts are resistant to *B. brassicae* but are more susceptible than waxy varieties to *M. persicae* (Way and Murdie, 1965). The degree of waxiness is a crucial factor in determining the resistance or susceptibility of Brussels sprouts to these insects. In brassicas, the intrinsic rate of increase of *B. brassicae* but not of *M. persicae* has been correlated with phloem amino acid concentrations (Cole, 1997b).

Plant characteristics may also include allelochemic factors, such as allomones (repellents, oviposition and feeding deterrents) and kairomones. It is evident that utilisation of some of these traits in combination with other control measures could have positive attributes in pest management (Shepard and Dahlman, 1988; Thomas and Waage, 1996; Gould, 1998; Cortesero *et al.*, 2000).

The use of host plant resistance for the management of aphids in Brassica crops has been met with varying degree of success. For instance, seasonal shifts in the resistance of commercial varieties of cabbage to *B. brassicae* have been reported, with the susceptibility of red cabbage varieties to host selection by alate increasing with the season (Radcliffe and Chapman, 1966). Studies by van Emden (1966) and van Emden *et al.* (1969) showed that *M. persicae* responds more to changes in the nutritional status of cabbage compared with *B. brassicae*. Its fecundity being correlated to increase in soluble nitrogen in the leaves and a decrease in potassium. In Brussels sprouts, resistance to aphids has been linked to soluble nitrogen concentrations (van Emden and Bashford, 1969) and specific leaf amino acids (van Emden, 1972). On the other hand, mustard oil has been found to be an important prerequisite to colonisation of cruciferae by *B. brassicae* (van Emden, 1978) while antixenosis and antibiosis have been identified as defence mechanism against *B. brassicae* in cabbage cultivars Ruby Ball and Minicole, respectively (Singh and Ellis, 1993; Ellis *et al.*, 1996).

The above studies clearly demonstrate the importance of plant characteristics in imparting resistance or susceptibility to aphids in cruciferae. More importantly, some of these characteristics could be effectively exploited as components of an integrated control

practice for cabbage.

2.5.3 The natural control of aphid pests

The build-up of damaging populations of cruciferous and other aphid pests on crops is normally prevented by heavy aphid mortality caused by adverse weather conditions (Blackman, 1974) and by natural enemies (Kennedy and Stroyan, 1959). Intraspecific competition and the production of dispersing alates also influence the development and subsequent decline of aphid populations on crops (Schneider, 1962; Kelm, 1988).

The three groups of aphid natural enemies are predators, insect parasitoids and entomopathogenic fungi. Predators and parasitoids have been the most intensively studied (Minks and Harrewijn, 1989). Attempts have been made to use fungi as control agents despite the technical problems inherent to handling this difficult material (Ramakers, 1989). Recently, it has become increasingly clear that fungi can be effective in managing aphid populations. *Pandora neoaphidis* (Entomophthorales: Entomophthoraceae) is now a major pathogen of aphids (Feng *et al.*, 1991; Elkassabany *et al.*, 1992) and has been found to be a major limiting factor for *Diuraphis noxia* (Kurdjumov) population growth (Basky and Hopper, 2000). Aphids are also preyed upon by a wide range of predators, including birds, arachnids, and insects mainly in the orders Coleoptera, Diptera, Hemiptera, and Neuroptera (Frazer, 1988; Minks and Harrewijn, 1989; Hasken and Poehling, 1995). Of these, the Coleoptera are the most common and intensively studied predators of aphids (Frazer, 1988).

From numerous studies of predation of aphids, mainly in temperate regions, it has been established that coccinellids (Coleoptera: Coccinellidae) are one of the most effective group of aphid predators (Frazer, 1988). The most important characteristics of these predators are their diversity, abundance and power of dispersal and their great feeding capacity since both adults and larvae feed on aphids (Frazer, 1988). Syrphids have also been reported to be effective in reducing aphid populations in various farming systems (Hasken and Poehling, 1994). Despite the extensive work on predators as natural control factors of aphids, their significance in aphid population dynamics is poorly known, and the specific features of the

aphid-predator relationships that are used to judge efficiency in predators need to be examined by rigorous field testing (van Lenteren, 1991). More importantly, unlike parasitoids, the life cycles of even specialised aphid predators are rarely closely linked to those of the aphids preyed upon (Carver, 1989). This, in effect, reduces their efficiency.

Two hymenopterous families, Aphidiidae and Aphelinidae, constitute the majority of parasitoids of aphids. In addition, there are a few species from other hymenopteran families and some species of the gall midges (Diptera: Cecidomyiidae). (Mackauer and Chow, 1986). In all cases of successful biological control of aphids, the control agents have been parasitoids and these, with one exception, are all members of the family Aphidiidae (Carver, 1989; van Lenteren, 1991), a highly specialised family of solitary endoparasitoids (Stary, 1988a; Hagvar and Hofsvang, 1991) of which more than 400 species are known (Stary, 1998a). In this family, the genera *Aphidius* Nees, *Diaeretiella* Stary, *Ephedrus* Haliday, *Lysiphlebus* Forster, *Praon* Haliday and *Trioxys* Haliday, are regarded as the most important in the management of aphid populations (Stary, *et al.*, 1988b; van Steenis, 1995). Crucially, these parasitoids have an obligatory, co-evolved and conspicuous relationship with aphids (Carver, 1989).

Diaeretiella rapae, is the main parasitoid of *B. brassicae*, a world wide pest on crucifers in Europe (Kelm, 1988), North America (Lopez and van Driesche, 1989; Sheehan and Shelton, 1989a) and Africa (Bahana and Karuhize, 1986), and has been reported to reduce the population of *B. brassicae* by some significant proportions (Hughes, 1963; Kelm, 1988; Lopez *et al.*, 1990). *Aphidius colemani* on the other hand, has been used in biological control programmes on *M. persicae* in many parts of the world (Fernandez and Nentwig, 1997). This parasitoid is widely distributed in Asia, southern Europe, Africa, South America and Australia and is broadly oligophagous on Aphididae (Stary, 1975; van Steenis, 1995).

Successful biological control programmes have been reported against aphids in greenhouses, where parasitoids of the genus *Aphidius* have been used for control of *M. persicae* for more than 20 years (Shijko, 1989; van Steenis, 1995). Notable among these has been the use of *Aphidius matricariae* (Haliday), and *A. colemani* (Viereck) (Ramakers,

1989; Fernandez and Nentwig, 1997). *Aphidius matricariae* has been successful in the management of *M. persicae* on cucumber in the Netherlands (van Lenteren and Woets, 1988; van Steenis, 1993) and on chrysanthemum in the United Kingdom (Wyatt, 1985). *Aphidius colemani* has also been reported as an effective control agent for *M. persicae* on chilli and egg-plant grown in greenhouses in India and on cucumber in the Netherlands (Easwaramoorthy *et al.*, 1976; van Steenis, 1995).

Some level of success has been observed in the field control of the woolly aphid, *Eriosoma lanigerum* (Hausmann) with the aphelinid, *Aphelinus mali* Haldeman (Carver, 1989). Hughes (1989) also reported eight substantial successes of biological control of aphids in the open field constituting 30% of the adequately documented attempts. Of the eight, six were due to Aphidiidae.

Successful biological control in the greenhouses has been attributed to a number of factors. Under greenhouse conditions, most aphid species reproduce only parthenogenetically and do not show host-plant alternation. This, in combination with the favourable environment, leads to higher rates of aphid multiplication than in the field. Early and massive inundative releases of parasitoids achieves timely control of the aphids as their low reproductive rates is compensated for by their high numbers (Ramakers, 1989; van Lenteren, 1991).

A number of factors are responsible for the limited influence of natural enemies on aphids under field conditions. For instance, their potential rates of natural increase is much lower than that of the aphids. Secondly, natural enemies often arrive too late after aphid settlement. Thirdly, the complex life cycles of aphids and host-plant alternation leads to temporal disruptions of the aphid-parasite interaction (Ramakers, 1989).

2.6 Tritrophic aspects

Considerable attention has focused recently on the potential of tritrophic interactions as fundamentally important concepts of integrated pest management (Boethel and Eikenbary, 1986; van Emden, 1986; Price, 1986; Wright and Verkerk, 1995; Verkerk *et al.*, 1998a). However, detailed studies on crop based tritrophic systems have not received much

attention (Boethel and Eikenbary, 1986; Price, 1986; van Emden and Wratten, 1991; Verkerk *et al.*, 1998a). Such studies are essential in finding out what role the plant plays in supporting the action of natural enemies and how this role might be manipulated for the benefit of natural enemies (van Edmen, 1986; van Lenteren, 1991; Verkerk *et al.*, 1998a).

A very important feature of tritrophic systems is that members of alternate trophic levels may act in a mutualistic manner (Price, 1986). In order to understand tritrophic systems in crucifers and other crops, an integration of not only the knowledge on each trophic level but of the different kinds of factors that mediate interactions is essential (Price, 1986). Such factors involve interactions mediated by semiochemicals (Nordlund, 1981). Another crucial factor that needs to be considered is the closely allied area of chemically mediated interactions, involving plant nutritional and resistance factors of a less obvious semiochemical nature (Price, 1986; Stadler and Mackauer, 1996; Bottrell *et al.*, 1998; Cortesero *et al.*, 2000).

The importance of tritrophy is reflected in the searching behaviour of natural enemies of herbivores. Information from plants is crucial in their searching processes as their responses to different information sources brings them closer to the herbivore (Vet and Dicke, 1992; Dicke, 1996; Powell *et al.*, 1998). Chemical information is crucial in these processes and a positive interaction results where parasitoids use chemical cues in host habitat and host location. These information conveying chemicals have been termed “infochemicals” (Vet and Dicke, 1992) and may originate from the host plant or chemicals released as a result of interactions between the herbivore and its food plant or the herbivore host itself (Lewis and Martin, 1990; Dicke, 1999).

A number of studies have demonstrated the importance of chemical information in the foraging behaviour of parasitoids (Turlings *et al.*, 1989; Tumlinson *et al.*, 1992; Du *et al.*, 1996; Vet *et al.*, 1998). It has been reported for example, that some cruciferous plants when attacked by the herbivore can release enzymes which rapidly convert inactive mustard oils to volatile parasitoid-attracting derivatives (Whitman, 1988). These findings raise the prospect of application of natural enemy-attracting chemicals to plants for the enhancement of biological control (Verkerk *et al.*, 1998a). Other prospective areas for manipulation

include: enhancement of searching efficiency of natural enemies, using natural enemies response to allelochemicals as a selection criterion in control programmes and breeding of plant cultivars which have high emission rates of natural enemy-attracting synomones (Dicke *et al.*, 1990; Bottrell *et al.*, 1998)

Relatively little is known about the role of chemical cues in the foraging behaviour of aphid parasitoids (Hymenoptera: Braconidae and Aphidiinae) when compared with the foraging behaviour of parasitoids attacking lepidopteran hosts (Du *et al.*, 1996). Nevertheless, studies by Read *et al.* (1970) and van Edmen (1986) showed that host-plant volatiles were important cues for foraging aphid parasitoids. For example, the specialist crucifer aphid, *B. brassicae* uses sinigrin as a cue for finding host plants, but its parasitoid, *D. rapae* uses allyl-isothio-cyanates produced by the plant to find the plant and then the aphid (Read *et al.*, 1970). Different aphid parasitoids appear to vary in their responses to cues originating from the different trophic levels in the system (Du *et al.*, 1996). There is a need, therefore, to investigate the response of the other major aphid parasitoid, *A. colemani*, to cues emanating from a cabbage system.

Differences in plant nutrition and levels of susceptibility of host plants to aphids are known to influence natural enemy activities. Studies by van Emden and Wearing (1965) and van Emden (1966), for example, showed that the abundance of *B. brassicae* and *M. persicae* on Brussels sprouts could be depressed by a high potassium/good irrigation regime and such 'cultural' resistance would be compatible with the action of natural enemies under field conditions (van Emden and Wearing, 1965). Studies by Mohammed and van Edmen (1989) also showed that the mean weight of the generalist aphid species, *M. persicae* was reduced by 14% on Brussels sprout receiving low fertiliser inputs hence affecting parasitism. Other studies by Stadler and Mackauer (1996) showed that changes in the fitness (development time and offspring growth potential) of the parasitoid *Ephedrus californicus* (Baker) were mediated by plant quality.

van Emden and Wearing (1965) were the pioneers of the notion that partial plant resistance, in combination with natural enemies, may give economic levels of control for some agricultural insects pests. Follow up studies have shown some interesting results. For example, Wyatt (1970) found parasitism of *M. persicae* to be higher on partially resistant genotypes of chrysanthemums as compared with the susceptible genotypes. In Wyatt's study, biological control of aphids by *A. matricariae* was only effective when aphid resistant varieties were used. Similarly, Starks *et al.* (1972) documented a positive interaction by showing that the aphidiid, *Lysiphlebus testaceipes* (Cresson) had a greater depressive effect on the aphid *Schizaphis graminum* (Rondani) when a resistant barley variety was used compared with a susceptible variety. Obrycki *et al.* (1983) and Obrycki and Tauber (1984) also demonstrated the benefits of using both biological control and plant resistance in pest management. In the latter studies, it was shown that potato clones bearing moderate rather than high levels of glandular pubescence had compatible and complementary effects with parasitoids and predators in the management of aphids. Breeding of cultivars with moderate densities of glandular trichomes was therefore recommended in the development of integrated pest management programmes for potatoes (Obrycki, 1986). Further studies have documented a complementary relationship between host-plant resistance and biological control (Kuo, 1986; Ofuya, 1995; Farid *et al.*, 1998b).

Partial plant resistance may also be beneficial to the third trophic level in that by reducing the intrinsic rate of increase of the prey, the duration of their availability to natural enemies is increased (Feeny, 1976). Studies by Gowling and van Emden (1994) on wheat showed that partially resistant cultivars increased the likelihood of aphids falling off such plants as compared with the susceptible cultivars. The resulting increased mobility and chance of aphids falling off plants would be likely to increase the rate of predation and parasitism on and off the plants.

Attempts to develop aphid-resistant cultivars (Auclair, 1989) has led to the identification of antixenosis and antibiosis resistance mechanisms (Section 2.5.2) in some cabbage cultivars. For example, antixenosis is an important resistance mechanism in the red-leaved cabbage, Ruby Ball, while the green-leaved Minicole, posses a degree of partial resistance (antibiosis) (Singh and Ellis, 1993; Ellis *et al.*, 1996). There is, however, not much information on the

effect of this resistance on the aphid parasitoids and their biological activity.

In consideration of the above limitations in the management of *B. brassicae* and *M. persicae*, the present study was instituted to investigate multitrophic interactions between cabbage cultivars of different characteristics, aphid species and their parasitoids under laboratory and field conditions.

3

OLFACTORY RESPONSE OF *Aphidius colemani* TO CABBAGE AND CABBAGE-APHID ODOURS

3.1 Introduction

Parasitoids go through a series of behavioural responses to locate and successfully parasitise their hosts, categorised as host habitat location, host location, host acceptance, host suitability (Doutt, 1959) and host regulation (Vinson, 1975). Vinson (1984) classified the first three steps as the "host selection process" which involves habitat preference, potential host community location, host location, host examination, ovipositor probing, ovipositor drilling and oviposition.

Chemical orientation is crucial in all these stages and the olfactory cues eliciting the searching process during host foraging may originate from the plant upon which the herbivore-host is feeding, the host itself, other organisms associated with the host, or chemicals released as a result of interactions between the host and its plant food (Vinson, 1981; Lewis and Martin, 1990; Vet and Dicke, 1992). The utility of chemical information depends upon its reliability and detectability (Vet and Dicke, 1992). Therefore, the information value of odour stimuli from the herbivore-host and host-plant is important to aid the parasitoid in selecting a suitable host (Reed *et al.*, 1995).

An indirect defence mechanism of plants is to promote the effectiveness of natural enemies of the herbivore (Price *et al.*, 1980). There is growing evidence that plants are actively involved in the release of chemical signals that attract natural enemies of the herbivore (Vet and Dicke, 1992), especially among parasitoids attacking lepidopteran hosts. Comparatively little is known on aphid parasitoids (Du *et al.*, 1996) although Read *et al.* (1970) and van Emden (1986) have shown that host-plant volatiles are important cues for foraging aphid parasitoids species and different parasitoids appear to vary in their response

to cues originating from the different trophic levels in the system (Du *et al.*, 1996).

Volatiles from different cultivars of a crop may influence the number of parasitoids responding to the chemical cues. For example, olfactometer studies by Wickremasinghe and van Emden (1992) showed a high attraction of parasitoids to an aphid resistant-variety of wheat compared with a susceptible one. This synergism between partial resistance and biological control may stem partly from the effects of the host plant on the response of the parasitoid (Wickremasinghe and van Emden, 1992). Attempts to develop aphid resistant cabbage cultivars have led to the identification of antixenosis and antibiosis resistance mechanisms in some cabbage cultivars. For example, antixenosis is an important resistance mechanism in the red-leaved cabbage, Ruby Ball, while the green-leaved Minicole, exhibits antibiosis (Singh and Ellis, 1993; Ellis *et al.*, 1996). There is, however, no information on the interaction between these cabbage cultivars and the parasitoid *A. colemani*.

The present study investigated the host-location behaviour of *A. colemani* in a tritrophic system involving cabbage cultivars with different levels of susceptibility to *M. persicae*. The following questions were asked. 1) Do *A. colemani* females respond to plant volatiles? 2) If so, does the response vary with cultivar? 3) Does the response of *A. colemani* to volatile cues vary between infested and non-infested plants? 4) Is the response of *A. colemani* to volatiles from infested plants influenced by plant susceptibility?

3.2 Materials and methods

3.2.1 Plants

Three cabbage cultivars, Derby Day and Minicole (Elsoms Seeds, Spalding, UK) and Ruby Ball (Nickerson Seeds, Lincoln, UK) were used in all the experiments. The cultivars were chosen because of their different levels of resistance to *B. brassicae* and *M. persicae*. Derby Day is considered highly susceptible to both aphid species while, Minicole has been shown under certain conditions to possess a degree of partial resistance (antibiosis) to *B. brassicae* (Ellis *et al.*, 1996). The third cultivar, Ruby Ball is considered partially resistant with antixenosis factors to *B. brassicae* (Singh and Ellis, 1993). Plants were sown in pots

and maintained for the first 2-3 weeks in the greenhouse. All the plants used in the experiments were at the 7-8 leaf stage (30-35 days-old) and were maintained in a controlled environment ($20 \pm 2^{\circ}\text{C}$ and $65 \pm 3\%$ rh, 16:8 L:D photoperiod). In experiments where infested plants were required, a mixed population of 100 aphids was placed carefully on each of the three varieties at the 6-7 leaf stage using a Camel brush. Aphids were given 10 to 14 days to spread over the leaves before the start of the experiments.

3.2.2 Insect culture

All insect cultures were maintained in a controlled environment at $20 \pm 2^{\circ}\text{C}$ and $65 \pm 3\%$ rh under a 16:8 L:D photoperiod. Illumination was provided by a 50W circular fluorescent lamp 20cm above the cages. *Myzus persicae* (MpSIL colony) was established at Silwood Park in March, 1996 from a sub-population of a *M. persicae* clone which has been maintained for over ten years at the Institute of Arable Crops Research (IARC), Rothamsted Harpenden, UK). The insects were cultured on each of the three host plant cultivars for several generations, fresh plants being offered every two weeks.

3.2.3 Parasitoids

Aphidius colemani was supplied by Biological Crop Protection Limited, Wye, UK. All parasitoids were reared continuously on the cabbage cultivars, Derby Day, Minicole and Ruby Ball in perspex cages for over six generations.

3.2.4 Olfactometer

A 4-way olfactometer was used, similar to that designed by Pettersson (1970). It had a central chamber with orifices at the four corners through which air was drawn in, creating four potential odour fields, and a central orifice where mixing of the airflow from the arms occurred. A constant airflow was maintained through each of the four quadrats, a pump placed on the floor drawing air into the olfactometer chamber which was then vented out through a tube. The distribution of the airflow was confirmed by a smoke test prior to the beginning of the experiments.

Parasitised aphids (mummies) were removed from their respective cabbage plants and placed in small vials. Upon emergence, female parasitoids were mated within 24 hours and fed on honey solution (50% w/v). All parasitoids used in the tests were 2 days-old and naive, having had no exposure to aphids or plants since emergence. Test materials were put into opposing arms of the olfactometer, with distilled water in the other two arms to act as controls (Vet *et al.*, 1983). The only exception was when the plant was tested against distilled water. In this case, the other two arms were left blank. Therefore, all experiments were designed as binary choice tests, i.e., parasitoids were given a simple choice between test material odours and control. The test materials consisted of the three cabbage cultivars either infested with aphids or uninfested. Each binary test was replicated five times with each replicate consisting of 10 females. The choice tests conducted are depicted in Table 3.1.

Table 3.1. Choice tests conducted in a four arm olfactometer (5 x 10 female parasitoids per test) with a) water b) non-infested plants c) infested and non-infested d) infested plants.

Plant parasitoid source ^a	Odour source ^b
a)	
Minicole	Minicole vs water
Ruby Ball	Ruby Ball vs water
Derby Day	Derby Day vs water
b)	
Derby Day	Derby Day vs Ruby Ball
Ruby Ball	Ruby Ball vs Minicole
Minicole	Minicole vs Ruby Ball
Ruby Ball	Ruby Ball vs Derby Day
Derby Day	Derby Day vs Minicole
Minicole	Minicole vs Derby Day
c)	
Ruby Ball	Ruby Ball + aphid vs Minicole
Minicole	Minicole + aphid vs Ruby Ball
Derby Day	Derby Day + aphid vs Ruby Ball
Ruby Ball	Ruby Ball + aphid vs Derby Day
Minicole	Minicole + aphid vs Derby Day
Derby Day	Derby Day + aphid vs Minicole
d)	
Ruby Ball	Ruby Ball + aphid vs Minicole + aphid
Minicole	Minicole + aphid vs Ruby Ball + aphid
Derby Day	Derby Day + aphid vs Ruby Ball + aphid
Ruby Ball	Ruby Ball + aphid vs Derby + aphid
Minicole	Minicole + aphid vs Derby Day + aphid
Derby Day	Derby Day + aphid vs Minicole + aphid

^a Plant host on which the parasitoid developed (was reared)

^b Control was distilled water in most of the tests

Experiments were conducted at 20-22°C under a light intensity of 0.04W/m² (420-680nm) (Young *et al.*, 1987). Parasitoids to be tested were introduced singly into the olfactometer exposure chamber through the exit port so that they were exposed to all four odours in a relatively limited area. Once in the chamber, the parasitoids were given 5 minutes to make their choice between the four air fields. If the parasitoid did not cross any of the choice lines (the sides of the square in the chamber) within the given time, it was considered a 'no response' and the insect was discarded.

A parasitoid was noted as having made a choice when it entered a treatment arm and stayed there for at least 20 seconds. A small number of females (maximum 2 out of 50 tested) entered the control arms and were not included in the analysis. In order to remove any directional bias in the chamber, the olfactometer was reversed after five parasitoids in each replicate had been tested (Morgan and Hare, 1998). When all ten parasitoids had been tested, the odour sources were removed and the olfactometer was cleaned with 70% ethanol.

3.2.5 Data analysis

Results were analysed using a Chi-square test (χ^2). A significant value of χ^2 denoted a deviation in the response of aphids between the odours which was significantly ($P < 0.05$) greater than the expected due to chance. The χ^2 values for heterogeneity between replicates (χ^2 n-1 df) were also calculated. A statistically significant overall (χ^2 1 df) was only accepted if accompanied by a non-significant heterogeneity (χ^2 n-1 df) ($P > 0.05$) (Gomez and Gomez, 1984).

3.3 Results

Odours influenced parasitoid responses in the olfactometer although to varying degrees. The odour of the cabbage plant was always preferred over water. This response appeared to be greater for Derby Day and Minicole compared with Ruby Ball (Table 3.2).

Table 3.2. Olfactory response of female *Aphidius colemani* to different cabbage cultivars and water.

Parasitoid source	Test material A vs B	Mean % reacting to		χ^2 (1 df)	χ^2 (n-1 df)
		A	B		
Minicole	Minicole vs water	48	10	12.5***	3.3
Ruby Ball	Ruby Ball vs water	42	14	7.0**	3.5
Derby Day	Derby Day vs water	48	10	12.5***	2.7

*** $P < 0.001$, ** $P < 0.01$

When the three cabbage cultivars were paired in all possible combinations and the parasitoid sources alternated, varying degrees of parasitoid response to plant odours were obtained. In the majority of cases, the total parasitoid response ($A + B$) was greater when plant to plant host comparisons were made (Table 3.3) compared with plant to water tests (Table 3.2). Comparisons between Derby Day and Minicole, with Derby Day as the source of parasitoids revealed a significantly greater ($P < 0.05$) response to the odour of Derby Day (Table 3.3). When Minicole as the source of parasitoids was tested against Derby Day, the parasitoids showed a significant preference ($P < 0.01$) for odours from Minicole. However, in instances where Ruby Ball as a parasitoid source was tested against either Derby Day or Minicole, no significant differences ($P > 0.05$) in response were obtained (Table 3.3).

Table 3.3. Response of female *Aphidius colemani* to volatiles of different cabbage cultivars.

Parasitoid source	Test material A vs B	Mean % reacting to		χ^2 (1 df)	χ^2 (n-1 df)
		A	B		
Ruby Ball	Ruby vs Minicole	40	26	1.5	1.4
Derby Day	Derby vs Ruby	46	8	13.4***	1.9
Minicole	Minicole vs Ruby	50	8	15.2***	2.3
Minicole	Minicole vs Derby	54	16	10.3**	1.8
Derby Day	Derby vs Minicole	46	20	5.1*	1.6
Ruby Ball	Ruby vs Derby	44	24	3.0	3.1

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

There was a marked increase in total parasitoid response to volatiles in the Minicole vs Ruby Ball and Derby Day vs Ruby Ball tests with the introduction of infested plants as test materials (Table 3.4) compared with the same but non-infested cultivars (Table 3.3). As in previous tests, parasitoid preferred the cultivar on which they had developed (Table 3.4). In all cases, parasitoids showed a strong preference for infested plants, most notably when infested Derby Day was tested against non-infested Ruby Ball and when infested Minicole was tested against non-infested Ruby Ball (Table 3.4).

Table 3.4. Olfactory response of *Aphidius colemani* to infested and non-infested cultivars.

Parasitoid source	Test material A vs B	Mean % reacting to		χ^2 (1 df)	χ^2 (n-1 df)
		A	B		
Ruby Ball	Ruby + aphid vs Minicole	44	20	4.5*	1.4
Minicole	Minicole + aphid vs Ruby	54	18	9.0**	2.2
Derby Day	Derby + aphid vs Ruby	60	12	16***	2.1
Ruby Ball	Ruby + aphid vs Derby	48	22	4.8*	1.5
Minicole	Minicole + aphid vs Derby	58	10	17***	1.5
Derby Day	Derby + aphid vs Minicole	50	22	5.5*	1.5

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

When both cabbage cultivars were infested with aphids, in most cases the parasitoid response was not significantly ($P > 0.05$) influenced by parasitoid source (Table 3.5). The exception was when Minicole was tested against Ruby Ball. *Aphidius colemani* gave the weakest response to plant-host volatiles when Ruby Ball as the parasitoid source was tested (Table 3.5).

Table 3.5. Response of *Aphidius colemani* to infested cabbage cultivars of varying levels of resistance to cruciferous aphids.

Parasitoid source	Test material A vs B	Mean % reacting to		χ^2 (1 df)	χ^2 (n-1 df)
		A	B		
Ruby Ball	Ruby + aphid vs Minicole + aphid	48	30	2.1	2.0
Derby Day	Derby + aphid vs Ruby + aphid	38	22	2.2	2.8
Minicole	Minicole + aphid vs Ruby + aphid	44	20	4.5*	2.1
Ruby Ball	Ruby + aphid vs Derby + aphid	36	22	1.7	1.9
Minicole	Minicole + aphid vs Derby + aphid	44	26	2.3	4.5
Derby Day	Derby + aphid vs Minicole + aphid	46	28	2.2	1.6

* $P < 0.05$

3.4 Discussion

Results from the olfactometer clearly demonstrated that *A. colemani* females respond to plant and plant-herbivore odours. Parasitoids responded strongly to the odour of the host plant, particularly the host plant on which they had been reared and responded weakly to water. Such response could increase the parasitoids searching efficiency in the field since they would orient towards host plants. In their search for hosts, parasitoids may exploit volatile cues from the uninfested plant (Nordlund *et al.*, 1988; Souissi, 1999). Overall, the magnitude of the responses suggests that Derby Day and Minicole were preferred by the parasitoids compared with Ruby Ball.

Responses to plant volatiles have been detected for a number of aphid parasitoids using olfactometers (Read *et al.*, 1970; Powell and Zhang, 1983; Wickremasinghe and van Emden, 1992) and these volatiles have been found to be the source of attraction for parasitoids (Powell and Zhang, 1983; Nordlund *et al.*, 1988; Vet and Dicke, 1992). For example, female *D. rapae* locate the habitat of potential host aphids by an olfactory response to volatile chemicals released by aphid host plants (Read *et al.*, 1970). Studies by Sheehan and Shelton (1989b) showed that *D. rapae* flew upwind in response to collard odour, but less so to potato.

Wickremasinghe and van Emden (1992) found volatile compounds from uninfested wheat leaves to be attractive to the aphid parasitoid, *Aphidius rhopalosphi* De Stefani Perez. The odour of the plant on which the parasitoid had been reared was preferred over the odours of other plant cultivars. The present study shows that *A. colemani* also has a preference for the cultivar on which it had been reared but that the magnitude of its response can differ with cultivar.

In contrast, studies by Bouchard and Cloutier (1985) could not detect a response of *Aphidius nigripes* Ashmead to plant volatiles of cut uninfested potato and barley while, Reed *et al.* (1995) did not observe a response of *D. rapae* to uninfested cabbage and wheat leaves. However, Bouchard and Cloutier and Reed *et al.* used plant parts (leaves) in their studies whereas in the present study whole cabbage plants were used. It is possible that in

A. nigripes the absence of reaction to plant volatiles might have resulted from the volatile mixture emanating from the plants following cutting (Visser and Nielsen, 1977). Thus, there could be differences in the quality and quantity of volatiles emanating from plant parts (leaves) and whole plants.

The variable responses of *A. colemani* to the different cultivars could be reflected in the strength of odour cues emitted by the different host plants. *Aphidius colemani* reared on Minicole or on Derby Day gave consistently strong responses while Ruby Ball-reared *A. colemani* in the majority of cases gave the weakest response. It is possible that the cultivars, due to their phenotypic and genotypic differences, emit a blend of volatiles that differ both quantitatively and qualitatively which could account for the choice or response of the parasitoids. The present results are in agreement with those of Souissi (1999), who showed that the parasitoid, *Apoanagyrus lopezi* De Santis discriminated between cassava varieties on the basis of their odours. The increase in response of *A. colemani* when host plants were eventually tested against each other, from the relatively low response obtained when tested against water underlines the importance of plant cues in host location of this parasitoid. It is also possible that the presence of host plant volatiles may sometimes help the parasitoid in rejection of unsuitable hosts as exemplified by the low response to water.

Plant odours, unless linked directly to the presence of the parasitoids herbivore host, are not very reliable beyond the location of appropriate habitats in which to forage (Du *et al.*, 1996). Herbivore induced volatiles (infested plant volatiles), on the other hand, are more reliable and detectable host location cues for parasitoids (Turlings *et al.*, 1990; Vet and Dicke, 1992). The infested cabbage plants in the present study stimulated a very strong response by *A. colemani* as compared with non-infested plants, results that are consistent with studies by other workers. For example, Wickeremasinghe and van Emden (1992) showed that the six parasitoids species in their study showed an odour preference for the plant-aphid combination over the host plant alone. Similarly, studies by Guerrieri *et al.* (1993) showed that flight by *Aphidius ervi* Haliday females was oriented more to the bean-aphid complex than to the aphid or plant alone.

Morgan and Hare (1998) have shown that insect damage may enhance production of plant volatile attractants. In the present study it was clear that although *A. colemani* responds to both non-infested and infested plant volatiles, its response was boosted by the presence of the herbivore host on the plant. This suggests that production of volatiles already present in the plants increased with herbivore feeding hence the increase in response by *A. colemani*.

The inability of parasitoids to show a significant preference for cultivars among infested plants (Table 3.5) of varying levels of susceptibility and more importantly, for the cultivars on which they had been reared raises important questions. It would be expected that cultivars with varying levels of susceptibility would elicit different cues since they succumb differently to aphid feeding and the resultant damage. Vet and Dicke (1992) have shown that the value of plant information depends on the level of infestation. The higher the infestation, the more reliable the information to the parasitoids. On the basis of the previous tests, it might have been expected that the parasitoid would show a significant preference for the cultivar on which it was reared. It is possible, therefore, that *A. colemani* requires a certain level of aphid infestation to be able to discriminate between infested cultivars, a level which was not realised in the present study. Another possible reason for the non-preference could be that plant cues *per se* are not as important to *A. colemani* in the presence of the herbivore compared with a combination of plant-herbivore cues. The same could apply in the case of parasitoid rearing history.

The results reported in the present study raise practical considerations for the management of cruciferous aphids. Firstly, it is clear that *A. colemani* responds to plant volatiles. Secondly, by responding strongly to cues from infested plants, which is an indication of herbivore presence, *A. colemani* is able to overcome the reliability-detectability problem. This in turn enhances its efficiency as a control agent. Finally, the study highlights the importance of cultivar in influencing the olfactory response of *A. colemani*. In most cases, the parasitoid preferred the cultivar on which it had been reared on to other cultivars hence suggesting that parasitoids were "conditioned" on the respective cultivar (Hopkins, 1917; Messing and Rabasse, 1995). This emphasises the importance of parasitoid rearing history and its effect on *A. colemani* response to odours. However, where all the plants are infested (Table 3.5) the importance of parasitoid rearing history on biological control may

not be so straightforward in the field unless there are very large differences in infestations between the cultivars.

The efficiency of *A. colemani* as a control agent could be enhanced by utilising a number of factors. For example, plant volatiles attractive to parasitoids can be enhanced through plant breeding (Lewis and Nordlund, 1985; Powell and Wright, 1988; Cortesero *et al.*, 2000). Exploiting parasitoid learning through pre-release conditioning with the target insect/plant combination is another promising method of enhancing the effectiveness of mass produced natural enemies (Tessa, 1998). There is therefore, a need for identification and evaluation of these factors to achieve better levels of pest management.

4

EFFECT OF CABBAGE CULTIVARS WITH VARYING LEVELS OF RESISTANCE TO APHIDS ON THE PERFORMANCE OF *Aphidius colemani*

4.1 Introduction

Natural enemies of phytophagous insects function and develop in multitrophic systems (Price *et al.*, 1980). Consequently, their behaviour and physiology which determine their fitness or performance, are influenced by both the plant (first trophic level) and the phytophagous (herbivore) host (Vinson, 1976; Reed *et al.*, 1991). The effect of the plant may be manifested directly by their physical and chemical characteristics on the parasitoid, for example, foliage morphology and volatile or toxic substances may directly influence natural enemy activity (Price, 1986; Hare, 1992), or indirectly by altering the nutritional properties or behaviour of the host or parasitoid (Bergman and Tingey, 1979; Campbell and Duffey, 1981; Orr *et al.*, 1985). Herbivores of poor quality may act on the survival and fitness of the parasitoid through their influence on parasitism, parasitoid size, fecundity and development time (Reed *et al.*, 1991; Godfray, 1994).

Most studies on the management of aphid populations have focused either on the relationship between plants and herbivores or on the relationship between herbivores and natural enemies (van Lenteren, 1991; Verkerk *et al.*, 1998b). The former studies have contributed to the understanding of plant-aphid relationships and to the development of aphid-resistant cabbage varieties. For example, antixenosis is an important resistance mechanism to *B. brassicae* in the red-leaved cultivar, Ruby Ball, while the green-leaved Minicole, exhibits antibiosis to *B. brassicae* (Singh and Ellis, 1993; Ellis *et al.*, 1996). Biological control agents have also been applied in the management of cruciferous aphids with some degree of success. Notable among these is the solitary endoparasitoid, *A.*

colemani which is used for the biological control of *M. persicae* in protected cropping systems in the United Kingdom (Fernandez and Nentwig, 1997; Tessa, 1998). However, due to the independent nature of these studies, the level of success attained in the management of aphid populations has remained low (Mackauer and Way, 1976; van Emden and Wratten, 1991).

The need for the integration of studies on host-plant resistance and natural enemies has been emphasised by van Emden (1986) and some studies have found biological control and host-plant resistance to be complementary in the management of aphid populations (Starks *et al.*, 1972; Salto *et al.*, 1983; Kuo, 1986; Ofuya, 1995; Farid *et al.*, 1998b). In contrast, Reed *et al.* (1992) found that the development time of *D. rapae* was prolonged when it developed on Russian wheat aphid, *Diuraphis noxia* Mordvilko reared on resistant wheat with antibiotic factors compared with the susceptible one.

It is evident that depending on the level and category of resistance, plants can have a positive or negative effect on parasitoids (Tingle and Copland, 1988; van Emden, 1991; Hare, 1992) and understanding the interactions that may arise from plant-aphid-parasitoid system is crucial in developing a pest management system for these insects. Olfactometer studies in Chapter 3 have shown that the response of *A. colemani* to cabbage plants is influenced by cultivar and this is probably a function of qualitative and quantitative differences in odours emitted by the different cultivars. The present study aimed to determine the extent to which cultivars, characterised by different levels of resistance to *M. persicae* and *B. brassicae*, influence the performance of this parasitoid.

4.2 Materials and methods

4.2.1 Interactions between cultivar, *Myzus persicae* and *Aphidius colemani*

4.2.1.1 Plants

Three cabbage cultivars, Derby Day and Minicole (both green-leaved) and Ruby Ball (red-leaved) were used. The cultivars were chosen because of their different levels of resistance to aphids as described in Section 3.2.1. Twenty plastic pots measuring 8.5cm in diameter were used to plant each cultivar with one plant per pot. Seeds were sown on a Levingtons Multipurpose Compost® medium (Fisons, UK) and the plants were maintained in the greenhouse. When plants were at the 7-8 leaf stage (30-35 days old), they were transferred to a controlled environment room (20 ± 2 °C, $65 \pm 3\%$ rh, and 16:8 L:D photoperiod). One potted plant of each cultivar was placed in a 50 x 50 x 50 cm perspex cage which had two opposing sides made of fine netting to allow for ventilation. Illumination was provided by 50W circular fluorescent lamps placed 20 cm above the cage. All experiments were conducted under the same controlled environment conditions.

4.2.1.2 Insects

Myzus persicae used in the study was obtained from the MpSIL colony. The insects were then cultured on each of the three cultivars in perspex cages for several generations fresh plants being offered every two weeks. All insect cultures were maintained under the conditions described above.

4.2.1.3 Parasitoids

The *A. colemani* colony used in the study was maintained on *M. persicae* on the three cultivars Derby Day, Minicole and Ruby Ball and by the time the study was initiated, the parasitoids had completed approximately 15-17 generations. The colony was maintained in a controlled environment as described above in 50 x 50 x 50 cm cages.

4.2.1.4 Experimental procedure

Myzus persicae of mixed age was placed carefully on the two upper-most leaves of each cultivar using a camel-hair brush. Thirty aphids were placed on each leaf. The aphids had been reared previously on the respective cultivar for several generations, i.e., *M. persicae* reared on Derby Day was placed on Derby Day. The plants were left undisturbed for 5 to 7 days to allow for free distribution of aphids on the plants and for honeydew production, a kairomone for the parasitoids (Bouchard and Cloutier, 1984). At this stage, the experiment was split into two sets, with and without parasitoids: Five cages, each cage consisting three cultivars constituted a replicate. The experiment was repeated four times.

In the aphid + parasitoid treatment, a newly emerged (<24h-old) female parasitoid was confined with a male parasitoid in a glass vial for 2 hours to allow for mating. After mating, six female parasitoids, with one pair of females originally reared on *M. persicae* on Derby Day, and the other two pairs on Minicole and Ruby Ball, respectively, were put together in a stoppered glass vial (3 cm diameter) and introduced into the cage in between the three cultivars. Five cages, each cage consisting of three cultivars constituted a replicate. The experiment was repeated four times, giving a total of 60 plants. After 24 hours, all the parasitoids were removed and the plants were examined for mummified aphids after five days.

4.2.1.4.1 Effect of cultivar on aphid population growth and parasitism

Counts of aphid numbers in the aphid only and aphid + parasitoid cages were made after nine days, when no new mummies could be found. Since the initial aphid populations were the same in both sets, aphid suppression due to parasitoids (expressed as a percentage) was determined by subtracting the aphids + parasitoids, from the aphids only, divided by the aphid only population. The total number of aphids killed due to parasitoid feeding was determined by counting the number of mummies formed. An aphid was considered a mummy when its exoskeleton had become whitish-brown in colour. Percentage parasitism was calculated as a proportion of the total aphid density. Mummy to aphid ratios were derived from the formula of Kausalya *et al.* (1995) as: mummy : aphid ratio = $m : a + m$.

where the total number of mummies = m and total number of aphids (alive and parasitised) = $(a + m)$.

4.2.1.4.2 Parasitoid emergence

Mummies were placed individually in glass vials and held in a constant environment room until parasitoid emergence. The number of adult parasitoids emerging was expressed as a proportion of the total number of mummies. This parameter reflects immature mortality of *A. colemani*.

4.2.1.4.3 Developmental parameters

Parasitoid development time was determined for parasitoids emerging from aphids on each plant. Egg to pupa days were calculated from the parasitoid release day (day 0) to mummy formation, while pupa to adult days were counted from mummy formation to wasp emergence.

4.2.1.4.4 Sex ratio, size and longevity

The sex of the parasitoids was determined by the shape of terminal end of the abdomen. Wasp size was assessed as total body length, using a microscope with an eyepiece graticule to measure from the head to the distal end of the abdomen. Adult longevity was studied by placing parasitoids (<24 hours old) in Petri dishes (9 cm in diameter) and supplied with cotton wicks moistened with 30% honey-water solution. The cotton wicks were moistened daily and changed every two days to prevent fungal growth.

4.2.2 Interactions between cultivar, *Brevicoryne brassicae* and *Aphidius colemani*

4.2.2.1 Experimental procedure

A *B. brassicae* clone (BbHRI) used in the study was obtained from Horticulture Research International, Wellesbourne, UK. The cabbage cultivars Ruby Ball, Minicole and Derby Day were grown as described in Section 4.2.1.1. *Brevicoryne brassicae* were cultured on each of the three cultivars for several generations under controlled environment. Fresh plants were offered every two weeks. *Aphidius colemani* used in the study were maintained on *M. persicae* on each of the three cultivars. The experimental set-up was as in Section 4.2.1.4.

4.2.3 Effect of parasitoid source on parasitism of *Brevicoryne brassicae* and *Myzus persicae*

In order to assess the effect of parasitoid rearing history on parasitism of the two aphid species, *B. brassicae* and *M. persicae* were maintained on cv. Minicole for several generations. *Aphidius colemani* used in this study was maintained on *B. brassicae* and *M. persicae* for one generation on Minicole. The experimental procedure was as described above except only one cultivar was used. The number of mummies formed and the number of emerged parasitoids was recorded.

4.2.4 Data analysis

Data was subjected to one-way ANOVA using the MSTAT-C (MSTAT-C, 1990) software package after the appropriate transformations. Percentage data was subjected to arcsine or square root ($\sqrt{X+0.5}$) transformations. Variance in aphid counts were stabilised with the $\log(X+1)$ transformation (Trumble, 1982). When the F-values were significant, ($P < 0.05$), the means were compared using Fisher's least significant difference (LSD) test. T-tests were carried out to assess if there were significant differences between a group of means, assuming equal variances. Correlation analyses were also carried out to assess the relationship between sex and development time, size and longevity of *A. colemani*.

4.3 Results

4.3.1 Interactions between cultivar, *Myzus persicae* and *Aphidius colemani*

4.3.1.1 Effect of cultivar on aphid population growth and parasitism

There were significant differences in aphid infestation between cultivars in both the aphid only and aphid + parasitoid treatments. Greater aphid populations ($P < 0.01$) were found on Derby Day regardless of the presence or absence of parasitoids (Table 4.1). There was, however, a marked decrease in aphid population with the introduction of parasitoids, especially on Minicole where the aphid population was suppressed by 38%. Aphid suppression was least on Derby Day (Table 4.1).

Table 4.1. Mean number of *Myzus persicae* on three cabbage cultivars with aphids only and aphids + the parasitoid *Aphidius colemani*.

Cultivar	Aphids only ^a	Aphids	Mean %
		+ parasitoids	suppression ^b
Ruby Ball	270 ($2.4 \pm 0.2b$)	195 ($2.3 \pm 0.2b$)	27
Minicole	240 ($2.4 \pm 0.1b$)	150 ($2.2 \pm 0.2b$)	38
Derby Day	360 ($2.6 \pm 0.1a$)	295 ($2.5 \pm 0.1a$)	18

^a Mean $\pm$ S.E. log. transformed values within columns followed by same letter are not significantly ($P > 0.05$) different (LSD Test); $N = 4$.

^b % suppression = non-transformed values of: (Aphid only - Aphid + parasitoids / Aphids only) $\times 100$.

Aphid mortality due to parasitoids was not significantly ($P>0.05$) influenced by cultivar (Table 4.2). The mummy to aphid ratios were, however, higher on Minicole and Ruby Ball compared with Derby Day. The proportion of aphids parasitised was significantly ($P<0.05$) influenced by cultivar with Minicole having the highest proportion and Derby Day the lowest (Table 4.2).

Table 4.2. Influence of cultivar on parasitism of *Myzus persicae* by *Aphidius colemani*.

Cultivar	Mean no. of mummies/plant ^a	Mean no. of aphids/plant	Mummy : aphid ratio ^b	Mean proportion parasitised ^c
Ruby Ball	71 ($1.9 \pm 0.2a$)	195 ($2.3 \pm 0.2b$)	1:3	$39 \pm 5.5ab$
Minicole	68 ($1.8 \pm 0.1a$)	150 ($2.2 \pm 0.2b$)	1:2	$45 \pm 5.7a$
Derby Day	74 ($1.9 \pm 0.1a$)	295 ($2.5 \pm 0.1a$)	1:4	$30 \pm 3.5b$

^a Mean $\pm$ S.E. log. transformed values within columns followed by same letter are not significantly ($P>0.05$) different (LSD Test); N = 4.

^b Ratios derived from non-transformed data.

^c Mean $\pm$ S.E. arcsine transformed values within a column followed by same letter are not significantly ($P>0.05$) different (LSD Test).

4.3.1.2 Parasitoid emergence

The number of adult parasitoids emerging from mummies was not significantly different ($P>0.05$) between cultivars (Table 4.3). However, parasitoids growing on hosts reared on Ruby Ball and Derby Day had a significantly ($P<0.05$) greater emergence rate compared with parasitoids growing on Minicole (Table 4.3).

Table 4.3. Mean number of mummies, number of emerged parasitoids and percentage emergence of *Aphidius colemani* from *Myzus persicae* reared on Ruby Ball, Minicole and Derby Day.

Cultivar	Mean no. of mummies/plant ^a	Number of emerged parasitoids	Mean % emergence ^b
Ruby Ball	71 (1.9 ± 0.2a)	64 (1.8 ± 0.2a)	90 (72 ± 6.3a)
Minicole	68 (1.8 ± 0.1a)	48 (1.7 ± 0.1a)	71 (57 ± 4.2b)
Derby Day	74 (1.9 ± 0.1a)	59 (1.8 ± 0.1a)	80 (66 ± 7.2a)

^a Mean ± S.E. log. transformed values within columns followed by same letter are not significantly ($P>0.05$) different (LSD Test); $N = 4$.

^b Mean ± S.E. arcsine transformed values within a column followed by same letter are not significantly ($P>0.05$) different (LSD Test).

4.3.1.3 Developmental parameters

Development time of immature parasitoids varied with cultivar and sex. The overall development time of the female parasitoids did not differ significantly ($P>0.05$) between Minicole and Derby Day but was significantly ($P<0.05$) shorter on Ruby Ball (Table 4.4). Development for females at the egg-pupa and pupa-adult stages was faster on Ruby Ball (Table 4.4).

The total duration of immature parasitoid development for males showed a significant ($P<0.01$) variation between cultivars. Males developed faster on aphids on Ruby Ball compared with Minicole (Table 4.4). The parasitoid took significantly ($P<0.05$) longer to develop to the pupal stage when on *M. persicae* reared on Minicole compared with Ruby Ball or Derby Day (Table 4.4).

Table 4.4. Duration of development of female and male *Aphidius colemani* in *Myzus persicae* reared on different cabbage cultivars.

Cultivar	Sex	Developmental parameters (days)		
		Egg-pupa	Pupa-adult	Egg-adult
		Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE
	Female			
Ruby Ball		7.5 $\pm$ 0.2c	5.3 $\pm$ 0.3b	12.8 $\pm$ 0.4b
Minicole		7.8 $\pm$ 0.1b	6.2 $\pm$ 0.4a	14.0 $\pm$ 0.4a
Derby Day		8.1 $\pm$ 0.2a	6.0 $\pm$ 0.3a	14.1 $\pm$ 0.2a
	Male			
Ruby Ball		7.6 $\pm$ 0.3b	4.9 $\pm$ 0.2a	12.5 $\pm$ 0.4b
Minicole		8.5 $\pm$ 0.3a	5.4 $\pm$ 0.4a	13.9 $\pm$ 0.3a
Derby Day		7.7 $\pm$ 0.4b	5.1 $\pm$ 0.4a	12.8 $\pm$ 0.5ab

For each sex, values within columns followed by the same letter are not significantly ($P > 0.05$) different (LSD test); $N = 4$.

Overall, the total development time of males was shorter (12.8 ± 0.5) than that of females (14.1 ± 0.2), $t_{19} = 7.49$; $P = 0.0001$ when developing on Derby Day. The development times of males and females were not significantly different on Ruby Ball and Minicole ($t_{19} = 1.9$; $P = 0.07$ and $t_{19} = 1.4$; $P = 0.08$).

4.3.1.4 Sex ratio, size and longevity

The sex ratio of the progeny was consistently female biased with more females emerging from hosts of all cultivars (Table 4.5). Parasitoid body size or longevity did not vary significantly ($P > 0.05$) with cultivar for both sexes. (Table 4.5).

Table 4.5. Sex ratio, size and longevity of *Aphidius colemani* in *Myzus persicae* reared on different cabbage cultivars.

Cultivar	Sex	Sex ratio (%)	Total body size (Mean $\pm$ SE; mm)	Average longevity of adult parasitoids $\pm$ SE (days)
Female				
Ruby Ball		57	2.14 $\pm$ 0.04a	7.1 $\pm$ 0.9a
Minicole		53	2.10 $\pm$ 0.04a	6.9 $\pm$ 0.8a
Derby Day		58	2.22 $\pm$ 0.06a	8.0 $\pm$ 0.7a
Male				
Ruby Ball		43	1.84 $\pm$ 0.02a	5.0 $\pm$ 0.7a
Minicole		47	1.88 $\pm$ 0.04a	5.8 $\pm$ 0.3a
Derby Day		42	1.86 $\pm$ 0.05a	6.0 $\pm$ 0.6a

For each sex, values within columns followed by the same letter are not significantly ($P > 0.05$) different (LSD test); $N = 4$.

Longevity of adult female parasitoids was strongly correlated with the total development time of the immature parasitoid ($r = 0.55$; $P = 0.001$) the same applied for the males although the relationship was less strong ($r = 0.30$; $P = 0.06$) (Table 4.6). Longevity for both females and males was correlated with adult size ($r = 0.43$; $P = 0.01$ and $r = 0.30$; $P = 0.06$, respectively). Adult female size was strongly correlated to the development time of the parasitoids ($r = 0.61$; $P = 0.001$) but less for males ($r = 0.36$; $P = 0.04$) (Table 4.6).

Table 4.6. Correlations ($Y = a + bx$) between development time, adult size and longevity of males (M) and females (F) of *Aphidius colemani* developing in *Myzus persicae*.

Nature	a	b	r	P
Time(M) vs Size (M)	1.50	0.03	0.36	0.04
Time(M) vs Longevity(M)	1.00	0.35	0.30	0.06
Time(F) vs Size (F)	1.19	0.07	0.61	0.001
Time(F) vs Longevity(F)	-1.97	0.68	0.55	0.001
Size (M) vs Longevity (M)	-2.35	4.27	0.35	0.05
Size (F) vs Longevity (F)	0.69	3.08	0.43	0.01

N = 60.

4.3.2 Interactions between cultivar, *Brevicoryne brassicae* and *Aphidius colemani*

4.3.2.1 Effect of cultivar on aphid population growth and parasitism

The aphid population was significantly ($P < 0.01$) greater on Derby Day in both the aphid only and aphid + parasitoid treatments compared with the other cultivars (Table 4.7). The effect of *A. colemani* on aphid population growth was greatest on Minicole, with a 25% reduction in aphid population, while the least effect was on Derby Day (Table 4.7).

Table 4.7. Mean number of *Brevicoryne brassicae* on three cabbage cultivars with aphids only and aphids + the parasitoid *Aphidius colemani*.

Cultivar	Aphids only ^a	Aphids + parasitoids	Mean % suppression ^b
Ruby Ball	335 (2.5 ± 0.1b)	268 (2.4 ± 0.2b)	20
Minicole	310 (2.5 ± 0.1b)	233 (2.4 ± 0.1b)	25
Derby Day	400 (2.6 ± 0.2a)	355 (2.5 ± 0.1a)	11

^a Mean ± S. E. log. transformed values within columns followed by same letter are not significantly ($P>0.05$) different (LSD Test); N = 4.

^b% suppression = untransformed values of: (Aphid only - Aphid + parasitoids/Aphids only) × 100.

Although aphid mortality, as exhibited by number of mummies formed, did not differ significantly ($P>0.05$) between cultivars, greater mummy to aphid ratios were observed on Minicole and Ruby Ball which had lower aphid populations compared with Derby Day (Table 4.8). When aphid mortality was analysed as a proportion of the total aphid population, significant ($P<0.05$) differences in parasitism were observed between Minicole and Derby Day with *B. brassicae* raised on Minicole having the greatest mortality (Table 4.8).

Table 4.8. Influence of cultivar on parasitism of *Brevicoryne brassicae* by *Aphidius colemani*.

Cultivar	Mean no. of mummies/plant ^a	Mean no. of aphids/plant	Mummy: aphid ratio ^b	Mean proportion parasitised ^c
Ruby Ball	39 (1.6 ± 0.1a)	268 (2.4 ± 0.2b)	1:7	3.9 ± 0.3ab
Minicole	43 (1.6 ± 0.1a)	233 (2.4 ± 0.1b)	1:5	4.3 ± 0.4a
Derby Day	39 (1.6 ± 0.1a)	355 (2.5 ± 0.1a)	1:9	3.3 ± 0.3b

^a Mean ± S.E. log. transformed values within columns followed by same letter are not significantly ($P > 0.05$) different (LSD Test); $N = 4$

^b Ratios derived from non-transformed data.

^c Mean ± S.E. $\sqrt{X+0.5}$ transformed values within a column followed by same letter are not significantly ($P > 0.05$) different (LSD Test).

4.3.2.2 Parasitoid emergence

The number of adult parasitoids emerging from mummies was not significantly different ($P > 0.05$) between cultivars (Table 4.9). However, parasitoids growing on hosts reared on Derby Day and Ruby Ball had a significantly greater ($P < 0.05$) emergence rate compared with parasitoids growing on Minicole (Table 4.9).

Table 4.9. Mean number of mummies, number of emerged parasitoids and percentage emergence of *Aphidius colemani* from *Brevicoryne brassicae* reared on Ruby Ball, Minicole and Derby Day.

Cultivar	Mean no. of mummies/plant ^a	Number of emerged parasitoids	% emergence ^b
Ruby Ball	39 ($1.6 \pm 0.1a$)	28 ($1.5 \pm 0.2a$)	72 ($59 \pm 2.8a$)
Minicole	43 ($1.6 \pm 0.1a$)	28 ($1.5 \pm 0.1a$)	65 ($53 \pm 4.7b$)
Derby Day	39 ($1.6 \pm 0.1a$)	31 ($1.5 \pm 0.2a$)	79 ($63 \pm 4.5a$)

^a Mean $\pm$ S.E. log. transformed values within columns followed by same letter are not significantly ($P>0.05$) different (LSD Test); $N=4$.

^b Mean $\pm$ S.E. arcsine transformed values within a column followed by same letter are not significantly ($P>0.05$) different (LSD test).

4.3.2.3 Developmental parameters

Total development time of the female parasitoids was significantly ($P<0.05$) influenced by the cultivar on which *B. brassicae* was reared on and was shortest on Ruby Ball compared with Minicole (Table 4.10). Development from egg-pupa period was significantly ($P<0.05$) faster on Ruby Ball compared with Minicole (Table 4.10). For males, however, the effect of cultivar on the egg-pupa, pupa-adult, and total development time of immature parasitoids was not significant ($P>0.05$) (Table 4.10).

Table 4.10. Duration of development of female and male *Aphidius colemani* in *Brevicoryne brassicae* reared on different cabbage cultivars.

Cultivar	Sex	Developmental parameters (days)		
		Egg-pupa	Pupa-adult	Egg-adult
		Mean $\pm$ SE	Mean $\pm$ SE	Mean $\pm$ SE
	Female			
Ruby Ball		8.7 $\pm$ 0.1b	5.2 $\pm$ 0.1a	13.9 $\pm$ 0.2b
Minicole		9.0 $\pm$ 0.2a	5.2 $\pm$ 0.2a	14.2 $\pm$ 0.1a
Derby Day		8.8 $\pm$ 0.2ab	5.2 $\pm$ 0.2a	14.0 $\pm$ 0.1ab
	Male			
Ruby Ball		8.3 $\pm$ 0.2a	5.4 $\pm$ 0.3a	13.7 $\pm$ 0.2a
Minicole		8.6 $\pm$ 0.2a	5.2 $\pm$ 0.2a	13.8 $\pm$ 0.1a
Derby Day		8.4 $\pm$ 0.3a	5.2 $\pm$ 0.2a	13.6 $\pm$ 0.2a

For each sex, values within columns followed by the same letter are not significantly ($P > 0.05$) different (LSD test); $N = 4$.

Development was faster for males (13.6 $\pm$ 0.2) compared with (14.0 $\pm$ 0.1) for females, $t_{19} = 3.5$; $P = 0.002$ on Derby Day and also faster for males (13.8 $\pm$ 0.1) compared with (14.2 $\pm$ 0.1) for females, $t_{19} = 5.8$; $P = 0.001$) on Minicole.

4.3.2.4 Sex ratio, size and longevity

The sex ratio was consistently female biased with more females emerging from hosts of all cultivars Derby Day (Table 4.11). Adult parasitoid size or longevity was not significantly ($P > 0.05$) influenced by the cultivar on which *B. brassicae* was reared for both sexes (Table 4.11).

Table 4.11. Sex ratio, size and longevity of *Aphidius colemani* in *Brevicoryne brassicae* reared on different cabbage cultivars.

Cultivar	Sex	Sex ratio (%)	Total body size (Mean $\pm$ SE; mm)	Average longevity of adult parasitoids $\pm$ SE (days)
	Female			
Ruby Ball		56	2.20 $\pm$ 0.03a	6.3 $\pm$ 0.2a
Minicole		55	2.18 $\pm$ 0.04a	6.6 $\pm$ 0.3a
Derby Day		53	2.18 $\pm$ 0.03a	7.4 $\pm$ 0.3a
	Male			
Ruby Ball		44	1.94 $\pm$ 0.03a	5.7 $\pm$ 0.2a
Minicole		45	1.91 $\pm$ 0.02a	6.8 $\pm$ 0.4a
Derby Day		47	1.89 $\pm$ 0.01a	5.9 $\pm$ 0.2a

For each sex, values within columns followed by the same letter are not significantly ($P > 0.05$) different (LSD test); $N = 4$.

Longevity of adult females was correlated with the development time of immature females ($r = 0.40$; $P = 0.05$). This correlation was however less strong for males ($r = 0.22$; $P = 0.09$) (Table 4.12). Longevity of both females and males was correlated with adult size ($r = 0.46$; $P = 0.04$ and $r = 0.31$; $P = 0.08$, respectively). The correlation between adult size and development time of immature parasitoids was not strong for both the females and males ($r = 0.38$; $P = 0.06$ and $r = 0.20$; $P = 0.15$ respectively) (Table 4.12).

Table 4.12. Correlations ($Y = a + bx$) between development time, adult size and longevity of males (M) and females (F) of *Aphidius colemani* developing in *Brevicoryne brassicae*.

Nature	a	b	r	P
Time (M) vs Size (M)	1.80	0.01	0.20	0.15
Time (M) vs Longevity (M)	1.30	0.06	0.22	0.09
Time (F) vs Size (F)	1.42	0.05	0.38	0.06
Time (F) vs Longevity (F)	-2.73	0.67	0.40	0.05
Size (M) vs Longevity (M)	-0.83	3.63	0.31	0.08
Size (F) vs Longevity (F)	-0.41	3.28	0.46	0.04

N= 60.

Assessment of the effect of individual aphid species on the overall performance of *A. colemani* showed marked variations between species. When pooled across cultivar, it was observed that *A. colemani* performed better when *M. persicae* was the host (Table 4.13). The number of mummies formed were significantly ($P < 0.01$) higher on *M. persicae* compared with *B. brassicae*. Similarly, parasitoids emerged into adults in significantly ($P < 0.01$) greater numbers when *M. persicae* was the host (Table 4.13).

Table 4.13. The mean number of aphids parasitised (mummies), number of emerged parasitoids and percent emergence of *Aphidius colemani* when *Myzus persicae* and *Brevicoryne brassicae* were exposed to *Aphidius colemani* which had been reared on *Myzus persicae* for 15 generations.

Aphid species	No. of mummies/plant	No. of emerged parasitoids	Mean % emergence
<i>M. persicae</i>	71 ($1.9 \pm 0.1a$)	57 ($1.8 \pm 0.1a$)	80 ($65 \pm 5.7a$)
<i>B. brassicae</i>	40 ($1.6 \pm 0.1b$)	29 ($1.4 \pm 0.2b$)	72 ($59 \pm 4.2b$)

Mean $\pm$ S.E. log. and arcsine transformed values (in parentheses) within columns followed by same letter are not significantly ($P > 0.05$) different by t-test.

4.3.3 Effect of parasitoid source on parasitism of *Brevicoryne brassicae* and *Myzus persicae*

There was no significant ($P > 0.05$) difference in the number of mummies formed on both *B. brassicae* and *M. persicae* when *A. colemani* was reared on *M. persicae* (Table 4.14). Similarly, the number of mummies formed did not differ statistically ($P > 0.05$) between aphid species when *B. brassicae* was the source of the parasitoid (Table 4.14). The number of parasitoids emerging into adults was significantly ($P < 0.05$) greater on *M. persicae* compared with *B. brassicae* when *M. persicae* was the source of the parasitoid. However, when *A. colemani* was reared on *B. brassicae*, the number of parasitoids which emerged into adults was not significantly ($P > 0.05$) influenced by aphid species (Table 4.14).

Table 4.14. The mean number of aphids parasitised (mummies), number of emerged parasitoids and percent emergence of *Aphidius colemani* when *Myzus persicae* and *Brevicoryne brassicae* were exposed to the parasitoid reared on each aphid species for one generation.

Parasitoid source	Aphid species	No. of mummies/plant	No. of emerged parasitoids	Mean % emergence
<i>M. persicae</i>				
	<i>M. persicae</i>	66 ($1.8 \pm 0.1a$)	45 ($1.7 \pm 0.1a$)	68 ($56 \pm 3.8a$)
	<i>B. brassicae</i>	47 ($1.7 \pm 0.1a$)	34 ($1.5 \pm 0.2b$)	72 ($58 \pm 4.9a$)
<i>B. brassicae</i>				
	<i>M. persicae</i>	55 ($1.7 \pm 0.2a$)	36 ($1.6 \pm 0.1a$)	66 ($54 \pm 3.4a$)
	<i>B. brassicae</i>	51 ($1.7 \pm 0.1a$)	33 ($1.5 \pm 0.1a$)	64 ($53 \pm 4.2a$)

Mean $\pm$ S.E. log. and arcsine transformed values (in parentheses) within columns followed by same letter are not significantly ($P>0.05$) different by t-test.

4.4 Discussion

The results show that cultivars and to some extent aphid species affected the performance of *A. colemani*. These effects were a result of differences in suppression of aphid populations, proportion parasitism, parasitoid emergence, development time and size and longevity of adult parasitoids. Suppression of *M. persicae* and *B. brassicae* was greatest on the partially resistant cultivars, Minicole and Ruby Ball, as compared with the susceptible Derby Day. This, therefore, shows that the first trophic level, (cultivar) can influence the third trophic level (parasitoid) and that parasitoids can decrease damage to plants by lowering aphid populations (Reed *et al.*, 1991). In the aphid only and the aphid plus parasitoid combinations, the number of aphids on Minicole and Ruby Ball was always below that of Derby Day. Ellis *et al.* (1996) had earlier shown that Derby Day was substantially more susceptible than Minicole when estimated on the basis of percentage infestation levels and number of colonies formed.

Although the number of mummies formed for both aphid species was not dependant on cultivar, the mummy to aphid ratios and the proportion parasitism was always greater on Minicole as compared with the other cultivars. This could be partly attributed to the lower aphid population on Minicole relative to the other cultivars, aphids on Minicole being available for parasitism by for a longer period (Fenny, 1976). This beneficial interaction between a resistant cultivar and biological control has been reported by several workers (Obrycki *et al.*, 1983; Salto *et al.*, 1983; Kuo, 1986; Nwanze *et al.*, 1998).

In the present study, the percentage of parasitoids which emerged into adulthood was a reflection of the mortality rate of *A. colemani* immature stages. Percentage parasitoid emergence was greatest on Ruby Ball when *M. persicae* was the host and greatest on Derby Day with *B. brassicae* as the host. The significantly lower parasitoid emergence on Minicole in both aphid species could be a characteristic of a nutritionally unfavourable host (Campbell and Duffey, 1979; van Emden, 1991), since plants provide nutrients directly and indirectly to the third trophic level (Price, 1986). The greater rate of parasitoid emergence on Derby Day and Ruby Ball is probably an indication of their nutritional superiority over Minicole. Minicole is partially resistant to *B. brassicae* with antibiosis factors, whereas

Ruby Ball is partially resistant due to antixenosis primarily mediated by avoidance of alates in the field and Derby Day is highly susceptible to both aphid species. It is possible that the antibiosis factors in Minicole contributed to the low parasitoid emergence through cultivar-mediated effects on the aphids (Orr *et al.*, 1985). Herzog and Funderburk (1985) and Barbosa (1988) have shown that plant allelochemicals involved in plant resistance can be toxic to parasitoids within their hosts and that parasitoids may be more sensitive than their hosts to plant secondary chemicals (Campbell and Duffey, 1979; Duffey *et al.*, 1986).

Cultivar effects on parasitoid biology was also evident in the development time of immature parasitoids. Overall, immature females developed faster into adults when reared on Ruby Ball regardless of aphid species. These differences in development time could be a reflection of host suitability. Once a host is accepted for oviposition, and an egg is deposited, the successful development of the parasitoid into an adult depends on host suitability (Hagvar and Hofsvang, 1991).

Aphids continue to feed and grow after parasitisation (Cloutier and Mackauer, 1979; Sequeira and Mackauer, 1992). As a consequence, the amount of nutritional resources available to the immature parasitoid depends on host growth after parasitisation and not by host size at oviposition (Sequeira and Mackauer, 1992). The changes in parasitoid development time and offspring growth potential therefore, are mediated by "bottom up" factors associated with the first trophic level (plant) that, in turn, affect the second trophic level (aphid) (Mackauer and Kambhampati, 1984; Stadler and Mackauer, 1996). The longer development time of *A. colemani* on Minicole could therefore, be due to plant effects (antibiosis). Changes in insect life history due to antibiosis resistance are usually manifested in increased development time and increased mortality (Painter, 1951). The quality of food consumed by a herbivore therefore, is of great importance as it modifies its quality as food for the parasitoid hence affecting its development (Souissi and Le Ru, 1998a). Similar results have been reported by Campbell and Duffey (1979) where the larval development time of the parasitoid *Hypostor exiguae* (Viereck) in its host *Heliothis zea* (Boddie) was increased significantly when hosts were reared on artificial diet containing the tomato antibiotic agent α -tomatine. Similar effects of this antibiosis resistance mechanism have been reported in a wheat-aphid-parasitoid system (Reed *et al.*, 1992). The

development time of the immature stages of *Aphelinus asychis* (Walker) was also substantially prolonged when it developed in *M. persicae* fed on a diet deficient in sugar and iron (Zohdy, 1976).

The development time of males tended to be shorter than that of females on all cultivars for both aphid species indicating protandry (Godfray, 1994). Males which emerge before females stand a greater chance of mating with one or several females (Wiklund and Fagerstrom, 1977). Because *A. colemani* is female biased as shown in this study, the males which emerge may have the opportunity to mate with many females. However, in solitary parasitoids, the male wasp may have to search for the female over a long range when the parasitoids scatter or when the emergence sites are greatly separated from each other (Kawaguchi and Tanaka, 1999). It is probable that in a field situation, males may have difficulty in finding females when there are large differences in their development times as exhibited by parasitoids reared on Derby Day.

The tendency towards a higher proportion of emerging females is very important in biological control. The further the sex ratio turns in favour of females, the more effective the parasitoids may become in controlling aphids because only females cause mortality (Hagen and van den Bosch, 1968). The number of emerged females may also be a more important value than the number of emerged parasitoids (Fernandez and Nentwig, 1997). The female ratios obtained in the present study (53% to 58%) are greater than the 47% reported for *Aphidius* sp. on *M. persicae* (Hofsvang and Hagvar, 1975b), but lower than the 90% reported for *A. colemani* on *B. brassicae* (Elliott *et al.*, 1994).

The size of emerging parasitoids is largely determined by the amount and quality of food consumed by the larvae. Size, therefore, is a significant indicator of host suitability (Godfray, 1994). It has also been shown that female fitness increases with adult size (King, 1988), since larger individuals may have a higher potential fecundity (Rosenheim and Rosen, 1991; Godfray, 1994) and better searching capacities (Visser, 1994). Similarly, male adult size may influence their ability to locate females (Godfray, 1994).

The present study shows that the various resistant factors inherent in the cabbage cultivars did not significantly influence the size of both the male and female adult parasitoids that emerged from either aphid species. However, studies by Verkerk *et al.* (1998b) reported a sensitivity of the predator, *Aphidoletes aphidimyza* (Rondani) to factors related to the partially resistant cultivars, Minicole and Ruby Ball. In the last study, a significant growth retardation (shorter predator body length) of predator larvae was noted while feeding on both aphid species on cvs. Minicole and Ruby Ball compared with Derby Day.

In the present work, the longevity of both the female and male parasitoids was not influenced by cultivar when they emerged from either aphid species. It is, however, known that the longevity of Aphidiidae depends among others, on temperature, relative humidity and quality and quantity of food (Hagen and van den Bosch, 1968). Since it is only the quality and quantity of food which was variable, having kept the other factors constant, it is evident that the food available to the immature parasitoid did not influence adult longevity. Similar observations were made by Hofsvang and Hagvar (1975a) who reported a non-significant effect of host plants on the longevity of *Aphidius ervi* Haliday and *Aphidius plantensis* Brethes. In contrast, Zohdy (1975) found that the average longevity of female *A. asychis* was lowest when reared on *M. persicae* which was fed on deficient diets hence showing that the composition of the diet offered to *M. persicae* had an indirect effect on the longevity of the parasitoid.

While cultivar was an important factor in influencing the performance of *A. colemani*, it was also evident that the performance of the parasitoid differed with aphid species. In the majority of cases, *A. colemani* performed better when feeding on *M. persicae* compared with *B. brassicae*. These differences may be attributed to the parasitoid rearing history and its effect on *A. colemani* response (see Chapter 3). *Aphidius colemani* used in the study had been reared on *M. persicae* for over 15 generations prior to the experiment. It is possible therefore, that the parasitoids were conditioned on this aphid species (Hopkins 1917; Pungertl, 1984; Chow and Mackauer, 1991; Messing and Rabasse, 1995). For example, van Steenis (1993) found that *A. colemani* performed better, measured in terms of mummy production, on the host species on which they were reared than on the other host species. When the present study tested for evidence of conditioning by using *A.*

colemanni reared for one generation on *M. persicae* and *B. brassicae*, the differences in performance were not significant despite the parasitoid showing a preference for *M. persicae*. This suggests that the performance of *A. colemanni* is to a large extent, dependant on its rearing history.

The present study shows that among the key parameters responsible for the performance of *A. colemanni* as a biocontrol agent, aphid suppression, proportion parasitism, parasitoid emergence into adulthood and development time were significantly influenced by cultivar. Minicole (with antibiosis factors) in particular, had a negative effect on development time of the immature parasitoids and on their emergence into adults (survival) whereas Ruby Ball (with antixenosis factors) did not exhibit any negative effects. It has been suggested (Auclair, 1989) that growth of plants with strong antibiosis and antixenosis qualities may impose selective pressures that lead to development of aphid biotypes which could possibly have some impact on the third trophic level as well. Since the third trophic level is of vital importance, as indicated by the protective influence of the parasitoids in this study, the effect of cultivar should be taken into consideration as an important factor in the success of the parasitoid. A choice has to be made between cultivars with antixenotic factors which may not be as efficient in suppressing aphid populations but have no negative effect on parasitoid development, and those with antibiotic factors which suppress aphid populations but with a negative effect on parasitoids. The present work examined the effects of cultivars under laboratory conditions. Field studies are required in order to fully understand the implications of these observations (van Emden, 1986).

5

TRITROPHIC INTERACTIONS BETWEEN CABBAGE CULTIVARS WITH DIFFERENT RESISTANCE AND FERTILISER LEVELS, CRUCIFEROUS APHIDS AND PARASITOIDS UNDER FIELD CONDITIONS

5.1 Introduction

Plant cultivar, fertiliser treatment and plant age have each been shown to influence the fecundity, population density and the relative growth rate of aphids (Radcliffe and Chapman, 1965; van Emden and Bashford, 1969; Cole, 1997b), and subsequent control measures (Mohamed and van Emden, 1989). For example, resistance to aphids in Brussels sprout cultivars has been linked to soluble nitrogen concentrations (van Emden and Bashford, 1969). In brassicas, the intrinsic rate of increase of *B. brassicae* but not *M. persicae* has been correlated with phloem amino acid concentrations (Cole, 1997b). Plant nutrition has also been found to influence the activity of aphid natural enemies (Mohamed and van Emden, 1989).

The compatibility of plant resistance and biological control has been examined for several plant-herbivore (pest)-natural enemy complexes (Price *et al.*, 1980; Salto *et al.*, 1983; van Emden and Wratten; Ofuya, 1995; Verkerk *et al.*, 1998a). In some cases, these methods of control have been found to be complementary. For example, plant resistance may slow the rate of increase of a pest population, thus allowing biological control agents to provide effective control (Starks *et al.*, 1972; Nwanze *et al.*, 1998). In other cases, plant resistance mechanisms have been shown to hinder the effectiveness of natural enemies (Campbell *et al.*, 1990; Hare, 1992).

Although antixenosis and antibiosis have been identified as defence mechanisms against aphids in the cultivars Ruby Ball and Minicole, respectively (Singh and Ellis, 1993; Ellis *et al.*, 1996), the effect of this resistance on the aphid parasitoids under field conditions is not known. This is crucial because the effects of these resistance factors are also likely to be manifested in the third trophic level, that is, on natural enemies. The results reported in Chapter 4 show that these cabbage cultivars influenced parasitism and biological characteristics of the parasitoid, *A. colemani* under laboratory conditions. However, plant growth stage, seasonal synchrony of aphid and natural enemy abundance, and abiotic factors in the field may contradict results from such laboratory studies (Obrycki and Tauber, 1984). In this study, field tritrophic studies were conducted to evaluate the effect of different cabbage cultivars with varying levels of resistance and with different rates of fertiliser treatment on cruciferous aphids and their parasitoids for the length of the growing season.

5.2 Materials and methods

5.2.1 Establishment of field experiments

Field experiments were established at Silwood Park, Berkshire, in the summers of 1998 and 1999. Three cabbage cultivars, Derby Day, Minicole and Ruby Ball, whose resistance levels have been described in Chapter 3 were used. Seeds of each cultivar were sown separately in 7 cm square plastic trays in the greenhouse using Levingtons Multipurpose Compost® (Fisons, UK). The plants were later transplanted in the field at the 7-8 leaf stage. The experiment was a 3 x 2 factorial, in a randomised complete block design with a split plot arrangement replicated four times. The main plot factor consisted of the three cabbage cultivars. Two fertiliser levels comprised the sub-plot factor: a blanket fertiliser application of NPK at the recommended rate of 95kg N, 78kg P, 78kgK/hectare applied in the fertiliser plots monthly for a period of 3 months and no fertiliser application. A buffer zone of two metres separated the fertilised and unfertilised blocks. Plots measured 2.8 x 2.1 m, each consisting of eight 1.5 m long rows, with cabbage being planted at a spacing of 40 x 30cm. One seedling was planted per hill. Plots were kept free of weeds by regular hand weeding.

5.2.1.1 Effect of cultivar and fertiliser on aphid incidence

In order to assess the influence of the cabbage cultivars and fertiliser on the aphid load and species composition, plants from the inside six rows of each plot were sampled for aphids at weekly intervals by a stratified random sampling plan. One week after the first aphids had alighted on the plants, three plants per plot were scored for number of aphids as a measure of antixenosis; the aphid preference for settling on plants (Singh *et al.*, 1994). On each subsequent sampling occasion, all plants in the sample rows were inspected thoroughly and plants with five or more aphids recorded as infested. Sampling dates are presented as days after transplanting (DAP). The dates corresponded to the following plant growth stages: early stage (28-35 DAP), mid stage (42-49 DAP) and late stage (56-63 DAP). Three leaves were removed from three plants in the sample rows (van Emden, 1963) and the number of apterous aphids and alates per leaf counted.

5.2.1.2 Effect of cultivar and fertiliser on levels of parasitism

Assessment of the number of aphids parasitised (mummy abundance) was carried out on the same plants used for estimating aphid abundance. Mackauer and Chow (1986) did not recommend the use of mummies to assess the impact of parasitoids because mummies accumulate over time. To avoid this problem, only mummies without emergence holes (full mummies) were included in the analyses. This distinction allows for assessment of newly parasitised aphids in situations where sampling is conducted on a regular basis (Fernandes *et al.*, 1998). Sample leaves were taken to the laboratory and emerging parasitoids counted.

5.2.2 Statistical analysis

From the data collected, the abundance of aphids and their species composition as influenced by cultivar and fertiliser during the study period was obtained and tabulated. Variance in aphid counts was stabilised with the $\log(X+1)$ transformation (Taylor, 1970; Trumble, 1982) and the data was analysed using the MSTAT-C software package. Data for each sampling date and year was analysed separately. FACTOR was used to perform the

factorial analyses (MSTAT-C, 1990) to assess if there were any significant differences in the number and type of aphids on the three cabbage cultivars with and without fertiliser. Mean separation was carried out using Fisher's least significant difference (LSD) test. The abundance of mummies on each sampling date on the different cabbage treatments was also determined. Two-way ANOVA was carried out after the appropriate transformations to assess the significance of variation in parasitism as influenced by cultivar levels of resistance and fertiliser. Multiple regression analyses were also carried out to assess the relationship between parasitism and aphid populations and to partition the contribution of the respective aphid species on overall aphid mortality due to parasitism. The two aphid species were treated as multiple variables. The slope (b) of the two parasitised aphid species allowed for the assessment of the contribution of each species to total aphid mortality during different stages of crop development. The t statistic was used to test whether slope estimates differed significantly from zero, indicating a difference in relative contribution between the two aphid species to total aphid mortality (Gomez and Gomez, 1984). The level of parasitism expressed as mummy to aphid ratios, was calculated as in Section 4.2.1.4.1.

5.3 Results

5.3.1 Effect of cultivar and fertiliser levels on total aphid infestation and parasitism

In the majority of cases, aphid infestation was influenced by cultivar rather than by fertiliser. In the early stages of plant growth in the 1998 season (28-35 DAP), aphid infestation was significantly ($P < 0.01$) greater on Minicole while Ruby Ball was the least colonised. In 1999, however, Derby Day suffered the greatest infestation compared with the other cultivars (Table 5.1). The number of mummies formed per plant was not significantly ($P > 0.05$) influenced by cultivar. Ruby Ball had the greatest mummy to aphid ratio in both seasons and Minicole the lowest. Proportionately, parasitism was significantly ($P < 0.01$ and $P < 0.05$ in 1998 and 1999, respectively) greater on Ruby Ball compared with other cultivars (Table 5.1). Ruby Ball had the least aphid colonisation and greatest parasitism levels at the early stages of plant growth (Table 5.1), but as the season progressed, aphid infestation became less on Minicole.

Aphids feeding on Minicole also had significantly ($P < 0.05$) greater levels of parasitism in the mid-stage of plant growth compared with the other cultivars (Table 5.2). In the 35-42 DAP period of 1999, for example, the aphid population on Ruby Ball with fertiliser plots increased by 2.1-fold and the mummy population increased by 1.1-fold, while in Ruby Ball without fertiliser plots, the aphid population increased by 2.1-fold and the mummy population by 1.3-fold. In the Minicole plots, the aphid population increased by 1.9-fold and the mummy population by 1.8-fold in the fertiliser plots, and by 1.7 and 2.2-fold, respectively, in plots without fertiliser (Tables 5.1 and 5.2).

In late season Ruby Ball, which had earlier supported the lowest aphid population had the same aphid population as the susceptible cultivar, Derby Day (Table 5.3). Significantly ($P < 0.05$) lower aphid infestations and greater ($P < 0.05$) levels of parasitism were found on Minicole in 1999 compared with other cultivars (Table 5.3).

Table 5.1. Effects of cabbage cultivar and fertiliser application on total aphid infestation and parasitism in the early stages (28-35 days after transplanting) of plant growth in field trials in 1998 and 1999^e.

Treatment	Mean no of mummies/plant	Mean no. of aphids/plant	Mummy : aphid ratio ^d	Mean proportion parasitism ^e
1998				
Min-fert ^a	18 (1.3 ± 0.2a)	190 (2.3 ± 0.2a)	1:11	3.12 ± 0.15b
Min+fert ^b	17 (1.3 ± 0.1a)	200 (2.3 ± 0.1a)	1:12	3.06 ± 0.47b
Derby-fert	18 (1.3 ± 0.2a)	180 (2.2 ± 0.2ab)	1:10	3.25 ± 0.75b
Derby+fert	15 (1.2 ± 0.1a)	150 (2.2 ± 0.2ab)	1:10	3.32 ± 0.78b
Ruby-fert	26 (1.4 ± 0.1a)	85 (1.9 ± 0.2b)	1:3	5.73 ± 0.93a
Ruby+fert	17 (1.3 ± 0.1a)	70 (1.9 ± 0.1b)	1:4	4.95 ± 0.59a
1999				
Min-fert	20 (1.3 ± 0.2a)	125 (2.1 ± 0.1a)	1:6	4.11 ± 0.23b
Min+fert	26 (1.4 ± 0.2a)	138 (2.1 ± 0.2a)	1:5	4.46 ± 0.60ab
Derby-fert	38 (1.5 ± 0.2a)	155 (2.2 ± 0.3a)	1:4	5.08 ± 0.33ab
Derby+fert	35 (1.5 ± 0.1a)	195 (2.2 ± 0.2a)	1:6	4.47 ± 1.20ab
Ruby-fert	30 (1.5 ± 0.2a)	98 (2.0 ± 0.2a)	1:3	5.57 ± 0.46a
Ruby+fert	32 (1.5 ± 0.2a)	105 (2.0 ± 0.2a)	1:3	5.55 ± 0.30a

^a Without fertiliser.

^b With fertiliser.

^c For each year, mean ± S.E. log. transformed values (in parentheses) within columns followed by same letter are not significantly ($P > 0.05$) different.

^d Ratios derived from non-transformed data.

^e Transformed proportion data ($\sqrt{x + 0.5}$).

Table 5.2. Effects of cabbage cultivar and fertiliser application on total aphid infestation and parasitism in the mid-stages (42-49 days after transplanting) of plant growth in field trials in 1998 and 1999^c.

Treatment	Mean no. of mummies/plant	Mean no. of aphids/plant	Mummy : aphid ratio ^d	Mean proportion parasitism ^e
1998				
Min-fert ^a	35 (1.6 ± 0.1a)	250 (2.3 ± 0.2c)	1:7	3.94 ± 0.54a
Min+fert ^b	40 (1.6 ± 0.2a)	260 (2.4 ± 0.1bc)	1:6	3.99 ± 0.31a
Derby-fert	40 (1.6 ± 0.1a)	360 (2.6 ± 0.1ab)	1:9	3.37 ± 0.49a
Derby+fert	48 (1.7 ± 0.2a)	450 (2.7 ± 0.1a)	1:9	3.31 ± 0.30a
Ruby-fert	28 (1.4 ± 0.1b)	250 (2.3 ± 0.1c)	1:9	3.33 ± 0.27a
Ruby+fert	27 (1.4 ± 0.1b)	280 (2.5 ± 0.2abc)	1:10	3.27 ± 0.29a
1999				
Min-fert	44 (1.6 ± 0.1a)	210 (2.3 ± 0.2b)	1:5	4.60 ± 0.16a
Min+fert	47 (1.7 ± 0.1a)	262 (2.4 ± 0.1ab)	1:6	4.26 ± 0.26ab
Derby-fert	46 (1.7 ± 0.1a)	341 (2.6 ± 0.1a)	1:7	3.79 ± 0.21ab
Derby+fert	53 (1.7 ± 0.2a)	435 (2.6 ± 0.1a)	1:8	3.53 ± 0.54b
Ruby-fert	39 (1.6 ± 0.2a)	205 (2.3 ± 0.2b)	1:5	4.33 ± 0.78ab
Ruby+fert	36 (1.6 ± 0.1a)	225 (2.4 ± 0.1ab)	1:6	4.11 ± 0.63ab

^a Without fertiliser.

^b With fertiliser.

^c For each year, mean ± S.E. log. transformed values (in parentheses) within columns followed by same letter are not significantly ($P > 0.05$) different.

^d Ratios derived from non-transformed data.

^e Transformed proportion data ($\sqrt{x + 0.5}$).

Table 5.3. Effects of cabbage cultivar and fertiliser application on total aphid infestation and parasitism in the late stages (56-63 days after transplanting) of plant growth in field trials in 1998 and 1999^c.

Treatment	Mean no. of mummies/plant	Mean no. of aphids/plant	mummy: aphid ratio ^d	Mean proportion parasitism ^e
1998				
Min-fert ^a	60 (1.8 ± 0.1a)	400 (2.6 ± 0.1a)	1:7	3.84 ± 0.10a
Min+fert ^b	66 (1.8 ± 0.1a)	370 (2.6 ± 0.1a)	1:6	4.31 ± 0.46a
Derby-fert	48 (1.7 ± 0.2a)	450 (2.7 ± 0.1a)	1:9	3.31 ± 0.31a
Derby+fert	61 (1.8 ± 0.1a)	400 (2.6 ± 0.1a)	1:7	3.97 ± 0.59a
Ruby-fert	60 (1.8 ± 0.1a)	460 (2.7 ± 0.2a)	1:8	3.63 ± 0.31a
Ruby+fert	58 (1.8 ± 0.3a)	450 (2.7 ± 0.2a)	1:8	3.71 ± 0.59a
1999				
Min-fert	58 (1.8 ± 0.2a)	290 (2.5 ± 0.2b)	1:5	4.49 ± 0.80a
Min+fert	51 (1.7 ± 0.1a)	275 (2.5 ± 0.2b)	1:5	4.37 ± 0.31a
Derby-fert	46 (1.7 ± 0.1a)	470 (2.7 ± 0.1a)	1:10	3.19 ± 0.29b
Derby+fert	41 (1.6 ± 0.2a)	390 (2.6 ± 0.1ab)	1:10	3.28 ± 0.44b
Ruby-fert	53 (1.8 ± 0.1a)	355 (2.6 ± 0.2ab)	1:7	4.01 ± 0.66ab
Ruby+fert	44 (1.6 ± 0.2a)	370 (2.6 ± 0.1a)	1:8	3.53 ± 0.81ab

^a Without fertiliser

^b With fertiliser

^c For each year, mean ± S.E. log. transformed values (in parentheses) within columns followed by same letter are not significantly ($P > 0.05$) different.

^d Ratios derived from non-transformed data.

^e Transformed proportion data ($\sqrt{x + 0.5}$).

5.3.2 Effect of cultivar and fertiliser on incidence and parasitism of *Brevicoryne brassicae* and *Myzus persicae*

In early 1998, *B. brassicae* was the dominant aphid species and it was present in greatest numbers in the Derby Day fertiliser plots while *M. persicae* was most prevalent on Minicole with fertiliser (Table 5.4). Mummy abundance was significantly ($P < 0.05$) greater on Ruby Ball compared with other cultivars. Parasitism of both aphid species was also significantly ($P < 0.05$) greater on Ruby Ball (Table 5.4). By mid-season (42 DAP), Derby Day with fertiliser had the greatest ($P < 0.05$) population of both aphid species (Tables 5.5a and b). Both aphid species had significantly ($P < 0.05$) greater levels of parasitism on Minicole compared with the other cultivars (Tables 5.5a and b). In the late stages of plant growth, aphid infestation was generally low on Minicole in both seasons. In 1998, parasitism of both aphid species was not significantly ($P > 0.05$) different between cultivars. However in 1999, a significantly ($P < 0.05$) greater proportion of *M. persicae* was parasitised on Minicole compared with other cultivars (Tables 5.6a and b).

Table 5.4. Incidence and parasitism of *Brevicoryne brassicae* and *Myzus persicae* on different cabbage cultivars at different fertiliser levels in the early stages of plant growth (28-35 days after transplanting) (1998)^c.

Treatment	Mean no. of mummies/plant	Mean no. of aphids/plant	Mummy: aphid ratio ^d	Mean proportion parasitism ^e
<i>B. brassicae</i>				
Min-fert ^a	13 (1.1 ± 0.1ab)	130 (2.1 ± 0.1ab)	1:10	3.35 ± 0.59bc
Min+fert ^b	8.5 (0.9 ± 0.1b)	131 (2.1 ± 0.2ab)	1:15	2.72 ± 0.38c
Derby-fert	11 (1.1 ± 0.1ab)	141 (2.2 ± 0.2a)	1:13	2.91 ± 0.59c
Derby+fert	8.7 (0.9 ± 0.2b)	116 (2.1 ± 0.2ab)	1:13	2.88 ± 0.46c
Ruby-fert	20 (1.3 ± 0.2a)	75 (1.8 ± 0.2b)	1:4	5.29 ± 0.61a
Ruby+fert	8.8 (0.9 ± 0.2b)	57 (1.8 ± 0.1b)	1:6	4.11 ± 0.30b
<i>M. persicae</i>				
Min-fert	5.2 (0.7 ± 0.2ab)	58 (1.7 ± 0.3ab)	1:11	3.06 ± 0.42bc
Min+fert	4.2 (0.7 ± 0.1ab)	66 (1.8 ± 0.1a)	1:16	2.59 ± 0.19c
Derby-fert	2.8 (0.6 ± 0.2b)	38 (1.6 ± 0.2ab)	1:14	2.79 ± 0.76bc
Derby+fert	2.7 (0.6 ± 0.1b)	31 (1.4 ± 0.3ab)	1:13	2.85 ± 0.54bc
Ruby-fert	5.9 (0.9 ± 0.2a)	27 (1.4 ± 0.1ab)	1:4	4.67 ± 0.78a
Ruby+fert	3.3 (0.7 ± 0.2ab)	22 (1.3 ± 0.1b)	1:7	3.81 ± 0.81ab

^a Without fertiliser.

^b With fertiliser.

^c For each species, mean ± S.E. log transformed values (in parentheses) within column followed by same letter not significantly ($P > 0.05$) different.

^d Ratios derived from non-transformed data.

^e Transformed proportion data ($\sqrt{x + 0.5}$).

Table 5.5a. Incidence and parasitism of *Brevicoryne brassicae* and *Myzus persicae* on different cabbage cultivars at different fertiliser levels in the mid-stage of plant growth (42-49 days after transplanting) (1998)^c.

Treatment	Mean no. of mummies/plant	Mean no. of aphids/plant	Mummy: aphid ratio ^d	Mean proportion parasitism ^e
<i>B. brassicae</i>				
Min-fert ^a	21 (1.3 ± 0.1a)	150 (2.2 ± 0.2b)	1:7	3.90 ± 0.63a
Min+fert ^b	18 (1.2 ± 0.2a)	150 (2.2 ± 0.1b)	1:8	3.76 ± 0.30ab
Derby-fert	21 (1.3 ± 0.2a)	225 (2.4 ± 0.1ab)	1:11	3.08 ± 0.54bc
Derby+fert	22 (1.3 ± 0.1a)	290 (2.5 ± 0.2a)	1:13	2.83 ± 0.30c
Ruby-fert	14 (1.1 ± 0.1a)	174 (2.3 ± 0.1ab)	1:12	2.98 ± 0.56bc
Ruby+fert	12 (1.1 ± 0.1a)	124 (2.2 ± 0.2b)	1:10	3.27 ± 0.59abc
<i>M. persicae</i>				
Min-fert	13 (1.1 ± 0.1a)	100 (2.0 ± 0.2a)	1:8	3.84 ± 0.80a
Min+fert	11 (1.0 ± 0.1ab)	110 (2.0 ± 0.1a)	1:10	3.26 ± 0.39ab
Derby-fert	12 (1.1 ± 0.2a)	140 (2.1 ± 0.1a)	1:12	2.95 ± 0.50ab
Derby+fert	10 (1.0 ± 0.1ab)	140 (2.1 ± 0.1a)	1:14	2.79 ± 0.28b
Ruby-fert	6.1 (0.8 ± 0.1b)	78 (1.9 ± 0.1a)	1:13	2.85 ± 0.46ab
Ruby+fert	8.4 (0.9 ± 0.1b)	120 (2.1 ± 0.1a)	1:14	2.80 ± 0.33b

^a Without fertiliser.

^b With fertiliser.

^c For each species, mean ± S.E. log transformed values (in parentheses) within column followed by same letter not significantly ($P > 0.05$) different.

^d Ratios derived from non-transformed data.

^e Transformed proportion data ($\sqrt{x + 0.5}$).

Table 5.5b. Incidence and parasitism of *Brevicoryne brassicae* and *Myzus persicae* on different cabbage cultivars at different fertiliser levels in the mid-stage of plant growth (42-49 days after transplanting) (1999)^c.

Treatment	Mean no. of mummies/plant	Mean no. of aphids/plant	Mummy: aphid ratio ^d	Mean proportion parasitism ^e
<i>B. brassicae</i>				
Min-fert ^a	40 (1.6 ± 0.1a)	168 (2.2 ± 0.2c)	1:4	4.91 ± 0.22a
Min+fert ^b	41 (1.6 ± 0.1a)	223 (2.4 ± 0.1abc)	1:5	4.37 ± 0.25ab
Derby-fert	39 (1.6 ± 0.1a)	289 (2.5 ± 0.2ab)	1:7	3.72 ± 0.32b
Derby+fert	42 (1.6 ± 0.2a)	348 (2.6 ± 0.1a)	1:8	3.48 ± 0.63b
Ruby-fert	33 (1.5 ± 0.2a)	154 (2.2 ± 0.2c)	1:5	4.54 ± 0.83ab
Ruby+fert	30 (1.5 ± 0.1a)	180 (2.3 ± 0.1b)	1:6	4.16 ± 0.70ab
<i>M. persicae</i>				
Min-fert	4.2 (0.7 ± 0.1b)	42 (1.6 ± 0.1b)	1:10	3.11 ± 0.15a
Min+fert	6.3 (0.9 ± 0.1ab)	39 (1.6 ± 0.1b)	1:6	3.98 ± 0.43a
Derby-fert	7.1 (0.9 ± 0.1ab)	52 (1.7 ± 0.1b)	1:7	3.75 ± 0.72a
Derby+fert	11 (1.1 ± 0.2a)	87 (1.9 ± 0.2a)	1:8	3.83 ± 0.59a
Ruby-fert	6.4 (0.8 ± 0.2b)	51 (1.7 ± 0.1b)	1:8	3.41 ± 0.62a
Ruby+fert	6.2 (0.8 ± 0.1b)	45 (1.7 ± 0.1b)	1:7	3.77 ± 0.58a

^a Without fertiliser.

^b With fertiliser.

^c For each species, mean ± S.E. log transformed values (in parentheses) within column followed by same letter not significantly ($P > 0.05$) different.

^d Ratios derived from non-transformed data.

^e Transformed proportion data ($\sqrt{x + 0.5}$).

Table 5.6a. Incidence and parasitism of *Brevicoryne brassicae* and *Myzus persicae* on different cabbage cultivars at different fertiliser levels in the late stage of plant growth (56-63 days after transplanting) (1998)^c.

Treatment	Mean no. of mummies/plant	Mean no. of aphids/plant	Mummy: aphid ratio ^d	Mean proportion parasitism ^e
<i>B. brassicae</i>				
Min- fert ^a	16 (1.2 ± 0.2a)	179 (2.3 ± 0.2ab)	1:11	3.08 ± 0.24a
Min + fert ^b	20 (1.3 ± 0.2a)	175 (2.2 ± 0.2b)	1:9	3.43 ± 0.30a
Derby - fert	17 (1.2 ± 0.1a)	225 (2.4 ± 0.1a)	1:13	2.86 ± 0.37a
Derby + fert	19 (1.2 ± 0.1a)	180 (2.3 ± 0.1ab)	1:9	3.40 ± 0.31a
Ruby - fert	19 (1.2 ± 0.1a)	225 (2.4 ± 0.1a)	1:12	3.03 ± 0.42a
Ruby + fert	22 (1.3 ± 0.2a)	220 (2.4 ± 0.1a)	1:10	3.29 ± 0.49a
<i>M. persicae</i>				
Min - fert	19 (1.2 ± 0.1a)	220 (2.4 ± 0.1a)	1:12	3.00 ± 0.38a
Min + fert	20 (1.3 ± 0.2a)	195 (2.3 ± 0.1a)	1:10	3.26 ± 0.60a
Derby - fert	18 (1.2 ± 0.2a)	230 (2.3 ± 0.2a)	1:13	2.81 ± 0.46a
Derby + fert	21 (1.3 ± 0.2a)	223 (2.3 ± 0.2a)	1:11	3.06 ± 0.41a
Ruby - fert	17 (1.2 ± 0.2a)	220 (2.4 ± 0.1a)	1:13	2.84 ± 0.25a
Ruby + fert	16 (1.2 ± 0.1a)	175 (2.3 ± 0.1a)	1:11	3.08 ± 0.57a

^a Without fertiliser.

^b With fertiliser.

^c For each species, mean ± S.E. log transformed values (in parentheses) within column followed by same letter not significantly ($P > 0.05$) different.

^d Ratios derived from non-transformed data.

^e Transformed proportion data ($\sqrt{x + 0.5}$).

Table 5.6b. Incidence and parasitism of *Brevicoryne brassicae* and *Myzus persicae* on different cabbage cultivars at different fertiliser levels in the late stage of plant growth (56-63 days after transplanting) (1999)^c.

Treatment	Mean no. of mummies/plant	Mean no. of aphids/plant	Mummy: aphid ratio ^d	Mean proportion parasitism ^c
<i>B. brassicae</i>				
Min- fert ^a	34 (1.5 ± 0.2a)	188 (2.3 ± 0.2b)	1:6	4.29 ± 0.62a
Min + fert ^b	33 (1.5 ± 0.1a)	165 (2.2 ± 0.1b)	1:5	4.51 ± 0.32a
Derby - fert	29 (1.5 ± 0.1a)	272 (2.5 ± 0.1a)	1:9	3.31 ± 0.28a
Derby + fert	25 (1.4 ± 0.2a)	211 (2.3 ± 0.1b)	1:8	3.48 ± 0.38a
Ruby - fert	34 (1.5 ± 0.1a)	196 (2.3 ± 0.2b)	1:6	4.32 ± 0.76a
Ruby + fert	26 (1.4 ± 0.1a)	211 (2.3 ± 0.2b)	1:8	3.55 ± 0.86a
<i>M. persicae</i>				
Min - fert	24 (1.4 ± 0.2a)	102 (2.0 ± 0.1b)	1:4	4.91 ± 0.62a
Min + fert	18 (1.3 ± 0.1a)	110 (2.1 ± 0.1ab)	1:6	4.11 ± 0.30ab
Derby - fert	17 (1.3 ± 0.1a)	198 (2.3 ± 0.1a)	1:12	3.00 ± 0.21c
Derby + fert	16 (1.2 ± 0.2a)	179 (2.3 ± 0.1a)	1:11	3.01 ± 0.51c
Ruby - fert	19 (1.3 ± 0.1a)	159 (2.2 ± 0.2ab)	1:8	3.56 ± 0.57abc
Ruby + fert	18 (1.3 ± 0.2a)	160 (2.2 ± 0.1a)	1:9	3.39 ± 0.70bc

^a Without fertiliser.

^b With fertiliser.

^c For each species, mean ± S.E. log transformed values (in parentheses) within column followed by same letter not significantly ($P > 0.05$) different.

^d Ratios derived from non-transformed data.

^e Transformed proportion data ($\sqrt{x + 0.5}$).

Multiple regression analysis assessed the contribution of the individual aphid species on overall aphid mortality in both seasons. When pooled across cultivar, the regression coefficient or slope (b) varied by aphid species and plant growth stage (Table 5.7). In the early stages of crop development in 1998, the overall aphid mortality depended on *B. brassicae* and *M. persicae* ($t = 3.63$, $P = 0.001$ and $t = 2.73$, $P = 0.012$, respectively; Table 5.7a). In mid-season of 1998, parasitism of *B. brassicae* contributed significantly ($P < 0.001$) to total aphid mortality (Table 5.7b). The mortality of *B. brassicae* in 1998 was a significant predictor ($t = 3.83$, $P < 0.001$) of overall aphid mortality at this stage of plant growth. In 1999, total aphid mortality depended on both *B. brassicae* and *M. persicae* parasitism ($t = 13.1$, $P = 0.0001$ and $t = 3.28$, $P = 0.003$, respectively) although the slope was higher for the former (0.87) compared with the latter (0.19) (Table 5.7b). In the late stages of plant growth (56 DAP), the slope estimates for both aphid species were very low for the 1998 season but were much greater in 1999 especially for *B. brassicae* (Table 5.7c).

The emerging parasitoids found were mainly *D. rapae* and *Aphidius* sp. Their seasonal incidence is presented in Table 5.8. *Diaeretiella rapae* was collected from the field earlier than *Aphidius* sp. and was more abundant. When averaged across years, species determination showed 67% *D. rapae* and 33% *Aphidius* sp. in 1998 and 69% and 31%, respectively, in 1999. *Diaeretiella rapae* was mostly collected from *B. brassicae* mummies while *Aphidius* sp. emerged mainly from *M. persicae* (Table 5.8). *Aphidius* sp. incidence increased with time and peaked in the late stage of plant growth while that of *D. rapae* showed a decline with plant age (Table 5.8).

Table 5.7. Regression analysis of total aphid mortality as influenced by parasitism of *Brevicoryne brassicae* and *Myzus persicae* at early, mid and late stages of plant growth in field trials in 1998 and 1999.

a) Early stage of plant growth (1998)

Dependent variable	Variables in model	Slope (b)	Standard error	t	Probability
Total aphid mortality	<i>B. brassicae</i> mortality	0.40	0.11	3.68	0.001
	<i>M. persicae</i> mortality	0.30	0.11	2.73	0.012

b) Mid stage of plant growth

Dependent variable	Variables in model	Slope (b)	Standard error	t	Probability
1998					
Total aphid mortality	<i>B. brassicae</i> mortality	0.57	0.15	3.83	0.001
	<i>M. persicae</i> mortality	0.31	0.19	1.62	0.118
1999					
Total aphid mortality	<i>B. brassicae</i> mortality	0.87	0.07	13.1	0.0001
	<i>M. persicae</i> mortality	0.18	0.06	3.28	0.003

c) Late stage of plant growth

Dependent variable	Variables in model	Slope (b)	Standard error	t	Probability
1998					
Total aphid mortality	<i>B. brassicae</i> mortality	0.19	0.15	1.29	0.20
	<i>M. persicae</i> mortality	0.14	0.13	1.08	0.29
1999					
Total aphid mortality	<i>B. brassicae</i> mortality	0.84	0.08	11.0	0.0001
	<i>M. persicae</i> mortality	0.17	0.07	2.37	0.03

Table 5.8. The incidence (%) of parasitoids emerging from *Brevicoryne brassicae* and *Myzus persicae* at the various sampling dates in field trials in 1998 and 1999.

Sampling date (DAP) ^a	Aphid species	Parasitoids emerging (%)			
		<i>Diaeretiella rapae</i>		<i>Aphidius</i> sp.	
		1998	1999	1998	1999
	<u><i>B. brassicae</i></u>				
35		80	95	20	05
42		86	89	14	11
49		70	80	30	20
56		60	67	40	33
63		53	60	47	40
	<u><i>M. persicae</i></u>				
35		71	79	29	21
42		66	62	34	38
49		68	64	32	36
56		64	51	36	49
63		49	45	51	55

DAP : days after transplanting

5.4 Discussion

The present study has demonstrated the importance of plant cultivar on aphid incidence and subsequent levels of parasitism. Cultivar-dependent effects were observed on the overall aphid load, species composition and rate of parasitism. However, fertiliser treatment did not appear to influence aphid infestation and parasitism unlike previous reports (van Emden and Bashford 1969; Mohamad and van Emden, 1989). Observations on aphid incidence in the early stages of plant growth seem to suggest that the different cultivar characteristics interfered with aphid colonisation and infestation. Low aphid infestations were observed on the red cabbage cultivar, Ruby Ball, compared with the green cultivars, Minicole and Derby Day. Although no count was made on the number of landing alates, the very low aphid population on Ruby Ball relative to the other two cultivars suggests that it was more resistant to initial aphid colonisation and infestation. Singh and Ellis (1993) had earlier shown that the red coloration in red leaved cabbages was an important resistance mechanism as an antixenosis factor for incoming alates. The susceptibility of Ruby Ball however, increased with time and by mid-season it was more susceptible than Minicole. This suggests a time related shift in resistance (Radcliffe and Chapman, 1965). Furthermore, time of season played a key role in aphid species composition and distribution. *Brevicoryne brassicae* was associated with cabbage from the early stages of crop development fed on tender leaves. *Myzus persicae* was not observed in the field until the third sampling period and fed mainly on older leaves (35 days after transplanting).

Radcliffe and Chapman (1965) working with both red and green cabbage cultivars, proposed three factors which may explain the seasonal shifts in relative susceptibility of the red cultivars to aphid infestation: (i) their nutritional susceptibility as host plants, (ii) lack of toxic constituents (antibiosis) and (iii) less parasitism or predation. In the present study, it was confirmed that the nutritional susceptibility of Ruby Ball increased with time. However, the present results on aphid parasitism on Ruby Ball do not agree with the above proposals, as aphids on Ruby Ball did not in most cases show significantly less parasitism than on the other cultivars. Indeed, aphid mortality as depicted by mummy:aphid ratios was greatest on Ruby Ball in the early stages of plant growth. The most plausible reason for this shift in susceptibility could, therefore, be due to lack of toxic constituents (lack of antibiosis) in

Ruby Ball, hence explaining the mid-season breakdown of resistance. Clearly, the alterations in the levels of resistance or susceptibility of the cultivars at different phenological stages influences the plant-aphid-parasitoid relationship.

The low mummy to aphid ratios on Derby Day compared with the other cultivars could be that due to its high susceptibility, the increase in aphid numbers outstripped that of the parasitoids. This in turn may have reduced parasitoid efficiency. In early-mid stage of 1999, for example, the weekly increase in the aphid population on Derby Day was much greater than that of the parasitoid in plots with and without fertiliser. This contrasts sharply with Minicole, where the weekly increase in aphid population was equal to or less than in the parasitoid (Tables 5.1 and 5.2). In the partially resistant Minicole, therefore, parasitoid efficiency was not masked which explains the high mummy to aphid ratios. Thus, it appears that parasitoids were more effective when aphid densities were lower, results that are consistent with those of Farid *et al.* (1998a) who reported that *D. rapae* was more effective at low aphid densities. The present results show a trend towards greater levels of parasitism on cultivars which support lower aphid populations or on which aphid population growth was slower. This supports the hypothesis that any plant condition that lowers the growth rate of an insect herbivore increases the duration of their availability to natural enemies and hence the probability of mortality (Feeny, 1976).

In general, plant growth stage, cultivar and seasonal synchrony of aphid and parasitoids influenced the plant-aphid-parasitoid relationships. In the early stages of crop development, when the plant was more vulnerable to aphid infestation, the antixenotic factors of Ruby Ball complemented the activities of parasitoids by having a significant proportion of dead aphids and favourable mummy to aphid ratios compared with the other cultivars. The present study, therefore, provides evidence of a beneficial interaction between plant resistance and biocontrol at this crucial stage of crop development. This beneficial effect generally declined as the plant became older. However, the partially resistant Minicole, had a more stable complimentary effect from mid season and was able to maintain a high proportion of dead aphids and favourable mummy to aphid ratios throughout the season. In contrast Derby Day, because of its high susceptibility, had the lowest rate of parasitism and mummy to aphid ratios throughout the study period.

Various workers (Wyatt, 1970; Starks, 1972; Kuo, 1986; Ofuya, 1995; Farid *et al.*, 1998b)) have reported complimentary interactions between biological control and host plant resistance since this was first proposed by van Emden and Wearing (1965). The factors that may account for this beneficial interaction have been summarised by van Emden (1991) and include among others, higher pest mortality and increased natural enemy to pest ratios on resistant cultivars. The level of parasitism and the higher mummy to aphid ratios found on Ruby Ball and Minicole at various stages of crop development support these hypotheses.

While cultivar type was crucial in influencing aphid parasitism, it was also evident that differential rates of parasitism occurred between the different aphid species, with *B. brassicae* being more prone to parasitism than *M. persicae*. A number of factors could explain this variance. Firstly, the parasitism levels could be a response to the respective aphid species population densities. Throughout the season, *B. brassicae* populations were generally greater than those of *M. persicae* and this could account for the consistently greater rates of parasitism of the former especially during the early to mid stages of plant growth. It is also possible that *D. rapae* (which had a numerical advantage over the *Aphidius* sp.) showed a preference for *B. brassicae* (Hafez, 1961) hence the differential parasitism observed in the study.

The observed variations in seasonal occurrence of the parasitoids could be another factor for the observed differences in aphid parasitism. In both seasons, *D. rapae* occurred in the field earlier and in greater numbers than *Aphidius* sp. The earlier incidence of *D. rapae* may be important in the suppression of *B. brassicae* in the early stages of crop development when it is the most abundant aphid species. *Brevicoryne brassicae* feeding on cabbage plants is very damaging at this stage as it attacks the newly emerging leaves thereby obstructing head formation (Schepers, 1989). Thus, the compatibility of plant resistance and parasitoid activity becomes particularly relevant at this stage of crop development. The late arrival of *Aphidius* sp. means that numbers of this parasitoid species required to provide effective biological control may develop too late to be of practical value. The lack of synchronisation of the aphids and *Aphidius* sp. is the main reason for this inefficiency. It is evident therefore, that parasitism was influenced by qualitative differences in cultivar and

qualitative and quantitative differences in aphids and parasitoids.

The results reported here are not consistent with earlier studies which showed that enhancing the nutritional status of plants influences herbivore vigour or the subsequent control measures (van Emden and Bashford, 1969; Mohamad and van Emden, 1989). This lack of response to fertiliser treatments was unexpected, given that van Emden and Bashford (1969) found a positive correlation between *M. persicae* and *B. brassicae* fecundity and leaf nitrogen. In the present study, the fertiliser levels may not have been high enough to influence the above factors. Jansson and Smilowitz (1986) also reported that population growth rate for *M. persicae* on potatoes increased with the rate of nitrogen applied while Loader and Damman (1991) found that larvae of the cabbage white butterfly, *Pieris rapae* (L) grew more slowly under low nitrogen conditions and were therefore more susceptible to ground dwelling predators.

The present work has shown that while the parasitoids alone were unable to effect aphid control at the various stages of plant growth, aphid populations could be lowered by parasitoids in combination with partially resistant cultivars. Thus, the wide range of plant resistance in cabbage cultivars is an obvious characteristic to exploit in limiting the increase of cruciferous aphids. For example, the antixenosis factors in Ruby Ball can reduce the initial aphid population allowing time for the parasitoids to act. It is also possible that the relatively low population increase for aphids on Minicole in the mid to late stages of plant growth was due to antibiosis factors. The latter is another factor which can be exploited.

6

SUMMARY AND GENERAL DISCUSSION

6.1 Overview

This study was instituted to investigate tritrophic interactions between different cabbage cultivars, aphid species and their parasitoids under laboratory and field conditions. Interactions arising from such systems could guide in manipulation of aphid management programmes. Results from the study demonstrated the need to consider cultivar as an essential and interactive component of this tritrophic system. Cultivars had an active role in the relationship between parasitoids and aphids and mediated many of the interactions, thereby influencing the level of protection provided by the former. The study identified areas where the plant supports the action of parasitoids and how this role might be manipulated in the management of aphid populations. The major findings of the study are summarised (Section 6.2), prior to consideration of the implications of the findings both in ecological (Section 6.3) and pest management (Section 6.4) contexts.

6.2 Summary of results

Summaries of key findings are given below in the same order as their documentation in the respective chapters of this thesis and are described qualitatively rather than quantitatively.

Olfactometer studies

- ◆ *Aphidius colemani* responded to plant odours and showed a preference for plant odours over water.
- ◆ The magnitude of parasitoid response to odours of uninfested cabbage depended on cultivar with Derby Day and Minicole preferred over Ruby Ball.
- ◆ The strongest parasitoid response was to aphid-infested plants. The odour of the cabbage cultivars on which the parasitoid had been reared was preferred over the other cultivars.

- ◆ When provided with a choice between odours of aphid-infested plants, parasitoids did not show a significant preference for the cultivar on which they had been reared.

Effect of cultivar on the performance of Aphidius colemani

- ◆ Significantly greater aphid populations were found on Derby Day regardless of the presence or absence of parasitoids compared with Minicole or Ruby Ball.
- ◆ Aphid suppression by *A. colemani* was greatest on Minicole and least on Derby Day for both aphid species. Minicole had the greatest proportion of aphids parasitised and Derby Day the least for both aphid species. The mummy to aphid ratios were higher on Minicole and Ruby Ball compared with Derby Day for both aphid species.
- ◆ A significantly lower percentage of emerged parasitoids was recorded on Minicole for both aphid species compared with Derby Day and Ruby Ball.
- ◆ *Aphidius colemani* generally performed better when *M. persicae* was the host.
- ◆ Total development time of female parasitoids varied significantly with cultivar for both host aphid species. Development time for females reared on *M. persicae* did not differ between Minicole and Derby Day but was significantly faster on Ruby Ball. Females reared on *B. brassicae* took significantly longer to develop into adults when on Minicole compared with Ruby Ball.
- ◆ Total development time for male parasitoids reared on *M. persicae* was significantly longer on Minicole compared with Ruby Ball. However, when *B. brassicae* was the host, no significant variations in development time were observed.
- ◆ Sex ratios, size and longevity of both male and female parasitoids were not influenced by cultivar for either aphid species

Tritrophic interactions (field studies)

- ◆ Cultivar and plant growth stage rather than fertiliser were found to influence aphid infestation and parasitism.
- ◆ In 1998, Ruby Ball was the least colonised by aphids in early stage of plant growth, while Minicole had the greatest aphid infestation. Similarly in the early season of 1999, Ruby Ball was least colonised but aphid densities were greatest on Derby Day followed by Minicole.

- ◆ In both years, in the early stages of plant growth, Ruby Ball had the highest mummy to aphid ratios while Minicole had the lowest. In both years, from mid to late stages of plant growth, the lowest aphid infestation and the highest level of parasitism was observed on Minicole.
- ◆ *Brevicoryne brassicae* was the dominant aphid species and had greater rate of parasitism compared with *M. persicae* during the early part of the season.
- ◆ Parasitism by *D. rapae* and *Aphidius* sp. differed in seasonal occurrence and abundance. *Diaeretiella rapae* mummies were found earlier than *Aphidius* sp.
- ◆ There was evidence of a beneficial interaction between the degree of plant resistance and biological control at the early and mid stages of plant growth.

6.3 Ecological aspects

Host plant-mediated processes can potentially contribute to effects on parasitism. Hare (1992) identified four major mechanisms by which host plants may regulate the activities of natural enemies:

- ◆ synomones-in this context, allelochemicals released by the plant which attract natural enemies thus benefiting both parties;
- ◆ sequestration-the ingestion or subsequent conversion of plant secondary chemicals which affect palatability of the herbivorous host to predators;
- ◆ herbivore quality-where plant factors in some way affect the survival, growth, reproduction or fitness of natural enemies;
- ◆ foliar pubescence-plant trichomes which may be detrimental or beneficial to natural enemies.

Price (1986) had earlier identified as many as 12 categories of tritrophic influence. Clearly, in any given tritrophic interaction, more than one process is likely to operate. Two major interactions will be discussed.

6.3.1 Semiochemically-mediated interactions

Semiochemically mediated interactions deal mainly with the ecology of body odour. Chemical messages provided by the plants can influence the third trophic level (Price, 1986). Previous work on crucifers showed that *D. rapae* responded to plant chemical cues to locate plants likely to bear host insects (Read *et al.*, 1970). A major finding of the present study is that another major parasitoid of cruciferous aphids, *A. colemani*, responded to odours from infested and non infested cabbage. Such a response could increase the parasitoids searching efficiency in the field since it would orient towards the host plant hence bringing it closer to the herbivore. Another key finding of this study was on the effect of rearing history on the response of *A. colemani* to plant odours. This aspect of parasitoid behaviour had previously not received adequate attention in some studies (van Emden, 1995; Souissi, 1999). Based on the present results, it is essential that subsequent studies consider this as a crucial aspect in behavioural studies.

6.3.2 Other chemically-mediated interactions: nutritional and resistance factors

The plant may influence the third trophic level through provision of nutrients to the host or through resistance factors which may directly or indirectly affect parasitoid activity (Price, 1986). There was evidence within the cabbage-aphid-parasitoid system that different cabbage cultivars influenced the third trophic level, causing considerable variations in the rate of parasitism for both aphid species. Laboratory studies showed that the partially resistant cultivars Minicole and Ruby Ball, had greater aphid control as exhibited by a greater proportion of aphid parasitised and higher mummy to aphid ratios compared with the susceptible Derby Day. This would imply a compatible or additive effect between biological control and partial plant resistance. However, the lower parasitoid emergence on Minicole compared with the other cultivars raises the possibility for an antagonistic interaction between the plant resistance (antibiosis) and the parasitoid. The longer development time of *A. colemani* on Minicole compared with the other cultivars may also be antagonistic as it may affect the synchronisation between the parasitoid and host aphid. Such effects have been demonstrated in several other systems (Orr *et al.*, 1985; Reed,

1992; Souissi and Re Lu, 1998a). However, that sex ratio and size and longevity of both male and female parasitoid was not affected by cultivar for either aphid species suggests an absence of a strong chemically-mediated antibiosis in Minicole.

The field studies provided a valuable insight into the possibilities of integrating partial plant resistance and biological control in the management of cruciferous aphids. This was evident in the early stages of plant growth when the antixenotic factors of Ruby Ball complemented parasitoid activity, and in the mid stage where the antibiotic factors of Minicole supported the action of parasitoids. The present study therefore, identified two critical stages in plant growth in which partial plant resistance can support the action of parasitoids. However, fertiliser application did not have a significant influence on these interactions at this critical stages of plant growth.

There are relatively few studies in crop-based tritrophic systems which have linked laboratory and field studies (Verkerk, *et al.*, 1998a). However, linking such studies is essential since plant growth stage, synchrony of aphid and natural enemy abundance and abiotic factors in the field may contradict results from the laboratory (Obrycki and Tauber, 1984). In the present study, however, there was good correspondence of laboratory and field studies. For example, observations on the effect of cultivar on parasitism of *M. persicae* and *B. brassicae* on resistant and susceptible cultivars showed similarities in both the laboratory and field experiments. Greater aphid control was observed on the partially resistant cultivars Minicole and Ruby Ball compared with the susceptible Derby Day under both experimental conditions. The importance of this correspondence was however affected by plant growth stage.

The combination of laboratory and field observations allows for more rigorous predictions when considering application of tritrophic studies and the interactions arising therein, to aphid management (Obrycki and Tauber, 1984). Given that aphid control is enhanced by a combination of parasitoids and resistant cultivars, it is essential that this beneficial interaction be manipulated in cabbage management programmes.

6.4 Pest management perspective

Because of the pressure to reduce insecticide use, the future role of non-insecticidal control strategies in the management of aphid populations is expected to increase strongly. The integration of plant resistance and parasitoid action in the management of cruciferous aphids is therefore likely to receive more attention. This is aided by the demonstration of the potential benefits arising from such integration as observed from this study and from other tritrophic systems (Thomas and Waage, 1996; Farid *et al.*, 1998b). Sound knowledge of other key interactions within the tritrophic system could allow for selection of compatible components which could substantially improve on the management of aphids. A key interaction which can be mutually exploited for the benefit of plant and parasitoids is that of chemical communication. Results from the present study and those from other workers show that infested and non-infested plants produce volatile chemicals and that these chemicals are used by natural enemies in host plant and herbivore location (Dicke, 1999). The quality and quantity of volatiles produced may vary with cultivar (Chapter 3) and could subsequently influence the success of the parasitoid as a biological control agent. Therefore, it might be possible to mediate the parasitoids behaviour via plant synomones and increase its effectiveness in controlling the insect pest. By isolating and identifying factors from plants that are attractive to parasitoids, it may be possible to use this knowledge for example, to select and use cultivars that produce high amounts of natural enemy attracting volatiles (van Lenteren, 2000). Combining such traits with partial plant resistance may diminish the need for a high level of plant resistance commonly emphasised in plant breeding (Bottrell *et al.*, 1998). Analysis and testing of volatiles from cabbage cultivars, aphids and cabbage-aphid complexes are therefore needed to determine the relative importance of these infochemicals in host finding processes of these parasitoids.

The present study has demonstrated the importance of cultivar attributes as an interactive component in the cabbage-aphid-parasitoid tritrophic system and is consistent with Feeny's (1976) prediction that natural enemy action is favoured by plants with inherent defenses. More importantly, many of these key plant-mediated interactions can be supplemented by managing other key components of the agro-ecosystem (Verkerk, *et al.*, 1998a). A review by van Emden and Wratten (1991) advocated focusing on a higher ratio of natural enemies

to prey rather than on the absolute numbers of either. This could be achieved by manipulating the third trophic level, the crop plants themselves or other plants both within and outside the crop. Companion plants interplanted with crops can, for example, provide shelter and supplemental food sources for natural enemies (Cortesero, 2000).

The present study has identified some potentially important interactions in the cabbage-aphid-parasitoid system. The beneficial interactions arising from plant resistance and parasitoid activity and the antagonistic interactions due to plant-mediated factors provide important contrasts. The approach which reduces aphid colonisation as observed on Ruby Ball, or which slows down the increase in aphid population (as on Minicole) thus allowing for parasitoids to act should be encouraged. More importantly, factors which antagonise or reduce the effectiveness of parasitoids should be given equal attention.

6.5 Recommendations for future work

Potentially important interactions have been identified in the present study. The study has also exposed information gaps which need to be addressed. The following are suggestions for future work which could guide in the manipulation of tritrophic interactions for sustainable pest management:

Olfactometer studies

1. Does *A. colemani* discriminate between odours of the two aphid species, i.e., *M. persicae* and *B. brassicae*? This information would supplement field observations where it was observed that *Aphidius* sp. emerged more from *M. persicae* than *B. brassicae*. A choice test experiment could be set up in the olfactometer to determine whether there are differences in the parasitoids response to odours when it is exposed to odour sources from *M. persicae* and *B. brassicae*.
2. Does the rearing history of *A. colemani* influence its response to odours from both aphid species? This investigation could be also extended to *D. rapae*.

3. At what aphid densities does *A. colemani* discriminate between odours from infested plants?

Laboratory studies

Laboratory studies are required to investigate long-term effects of antibiosis resistance on parasitoid fitness with special emphasis on development time, emergence and longevity. Cage experiments with *A. colemani* reared on *M. persicae* and *B. brassicae* for several generations after which the parasitoid is released in cages of either aphid species are required.

Field studies

Studies investigating the effect of predators and hyperparasitism on the performance of the major parasitoid species are required.

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