Effects of Intercropping on the Life Cycle of the Turnip Root Fly (*Delia floralis*)

Behaviour, Natural Enemies and Host Plant Quality

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Abstract

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The turnip root fly (*Delia floralis*) is a pest insect in the northern temperate regions of the world. If uncontrolled, it can cause severe problems in the production of brassica crops. This thesis examines how intercropping of cabbage (*Brassica oleracea*) and red clover (*Trifolium pratense*) affects the different life cycle stages of *D. floralis*. Such knowledge about the mechanisms involved is needed for developing intercropping systems with optimal pest reduction.

A field trial was performed in Umeå, northern Sweden (63º45'N; 20º15'E), to study the effects of intercropping on *D. floralis* oviposition behaviour, and the impact of predators and parasitoids on *D. floralis* in the field. Intercropping was found to reduce *D. floralis* oviposition compared with monoculture. Furthermore, analysis of the spatial distribution of eggs within plots showed that the difference in egg numbers was greatest close to the border between the cultivation systems. This indicates that the effect of intercropping can be enhanced if *D. floralis* is provided with an alternative oviposition site. Natural enemies, in this case mainly predators, significantly reduced the final pupal numbers of *D. floralis* but this effect did not differ between the cultivation systems. However, the study showed that it is possible to retain the predation pressure in intercropped systems despite lower predator activity-densities and *D. floralis* egg numbers.

A greenhouse experiment was performed to investigate effects of intercropping on development of *D. floralis* at different larval and intercropping densities and to analyse different aspects of host plant quality in the same system. It was found that *D. floralis* pupal weight decreased in response to both intercropping and larval density. This impaired larval development is likely to be explained by changes in host plant quality, which included decreased biomass, lower root nitrogen levels, higher root fibre content and altered glucosinolate concentrations. Information on plant responses to herbivory in competitive plant systems can be valuable in identifying quality aspects that are negative for insect development, which may further improve pest insect regulation in these systems.

Keywords: Oviposition, border effect, predation, parasitization, glucosinolates, NDF, lignin, induced response.

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Effekter av samodling mellan vitkål och rödklöver på den stora kålflugan (*Delia floralis*)

Beteende, naturliga fiender och värdväxtkvalité

Den stora kålflugan (*Delia floralis*) är en skadegörare på kålväxter som t.ex. vitkål, broccoli och blomkål. Flugan lägger sina ägg i jorden intill plantan, och larverna äter sedan av rötterna, vilket kan hämma plantans tillväxt eller leda till att den dör. Ekologiska grönsaksodlare i Sverige har identifierat en pålitlig och effektiv bekämpning av skadegörare som en viktig del i utveckling av den ekologiska trädgårdsodlingen. Det finns därför ett behov att hitta nya metoder för att minska skador orsakade av *D. floralis*.

Samodling mellan växter kan vara en metod för att minska angrepp av skadegörare i en odling. I den här avhandlingen har jag undersökt hur samodling mellan vitkål och rödklöver påverkar äggläggningen hos *D. floralis*, samt hur effekten av dess naturliga fiender som predatorer och parasitoider som angriper flugans ägg, larver och puppor, påverkas av odlingssystemet.

Studierna av äggläggningsbeteende och naturliga fiender gjordes i ett fältförsök på Röbäcksdalen i Umeå. Jag fann att samodling kraftigt minskade äggläggningen av den stora kålflugan jämfört med vitkål odlad i monokultur. Effekten av samodling var störst nära gränsen till monokulturen, och denna 'gränseffekt' sträckte sig ett par meter in i båda odlingssystemen. Det visar att det är möjligt att ytterligare förbättra effekten av samodling om *D. floralis* har tillgång till en bättre äggläggningsplats. Att kombinera samodling och monokultur kan vara en strategi i utvecklingen av odlingssystem med hög reglering av skadegörare. Naturliga fiender, i det här fallet främst predatorer, hade en god reducerande effekt i fältet, och denna effekt var lika hög i båda odlingssystemen. Försöket visade att det är möjligt att bibehålla en effekt av naturliga fiender trots att både färre predatorer och kålflugeägg återfanns i samodlingen.

I ett växthusförsök undersökte jag hur en ökad klöverdensitet, samt en ökad grad av rotskada orsakad av *D. floralis* larver, påverkar vitkålens kvalité som födoresurs för kålflugan. Kålflugans utveckling hämmades då vitkålen var samodlad med klöver, samt vid konkurrens med andra kålflugelarver. Denna effekt kan förklaras av förändringar i vitkålens kvalité vilket inkluderade en lägre kåltillväxt, lägre näringsinnehåll, ökat fiberinnehåll samt förändrade nivåer av sekundära ämnen, s.k. glukosinolater. Information om vilka växtfaktorer som hämmar insekters utveckling är värdefull för att långsiktigt kunna dämpa tillväxten i en insektpopulation. Sådan kunskap, tillsammans med kunskap om insekters beteende och deras samspel med naturliga fiender, ökar möjligheten att utveckla samodlingssystem med en optimerad effekt på skadeinsekter.

Contents

Appendix

Papers I-IV
This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I.   Björkman, M., Hambäck, P.A. & Rämert, B. 2007. Neighbouring monocultures enhance the effect of intercropping on the turnip root fly (*Delia floralis*). *Entomologia Experimentalis et Applicata* 124, 319-326.

II.   Björkman, M., Hambäck, P.A., Hopkins, R.J. & Rämert, B. Evaluating the Enemies hypothesis in an intercropping system – effects of generalist and specialist natural enemies on the turnip root fly (*Delia floralis*). (Submitted to *Agricultural and Forest Entomology*).

III.   Björkman, M., Hopkins, R.J., Hambäck, P.A. & Rämert, B. Effects of intercropping and herbivore density on the development of the turnip root fly (*Delia floralis*) mediated by host plant quality (Submitted to *Entomologia Experimentalis et Applicata*).

IV.   Björkman, M., Hopkins, R.J. & Rämert, B. Combined effect of intercropping and turnip root fly (*Delia floralis*) larval feeding on the glucosinolate concentrations in cabbage roots and foliage (Submitted to *Journal of Chemical Ecology*).

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Introduction

The turnip root fly, *Delia floralis* Fall. (Diptera: Anthomyiidae), is a specialist pest insect of *Brassica* crops, such as cabbage, cauliflower and broccoli. If uncontrolled, *D. floralis* can cause substantial yield losses in vegetable production. In a recent survey, organic vegetable growers in Sweden identified efficient and reliable pest control as one key factor for the development of organic vegetable production systems (Nilsson, 2007). At present, methods for adequate control of *D. floralis* in organic vegetable production are scarce. There is therefore a need to develop alternative methods for pest control, in order to meet the demands of sustainable and reliable vegetable production.

Increased attention has been given to the potential benefits of enhanced within-field plant diversity as a strategy for pest insect control (Risch, 1983; Vandermeer, 1989). Intercropping is one way to add diversity to a cropping system, and there are many examples where these systems have been shown to suffer from lower yield losses due to insect damage compared with monocultures (Theunissen, Booij & Lotz, 1995; Rämert & Ekbom, 1996). However, the variability in responses by insect herbivores to plant diversification (Andow, 1991) shows that there is a need for better understanding of the mechanisms affecting insect herbivores in diverse systems.

The work in this thesis formed part of the project *Ecology of the Cultivation System – Green Manure as a Multifunctional tool in Vegetable Production*, the aims of which were to develop locally adapted organic vegetable production systems in which green manure use is optimised for integrated management of plant nutrients, pests and product quality, and to evaluate the agronomic and economic performance of vegetable production systems.

Aims of thesis

The main aim of this thesis was to examine different aspects of the effects of intercropping cabbage with red clover on the life cycle of *D. floralis* and to gain knowledge about the mechanisms involved, which is needed for developing intercropping systems with optimised pest reduction. The project was divided into two parts. In a field trial, the pest reduction capacity of intercropping for *D. floralis* was examined. This was done by: (1) Studies of the oviposition behaviour of the flies; and (2) examination of the effect of natural enemies as predators and parasitoids. Studying both these in the same field experiment gave the opportunity to evaluate the importance of each mechanism for pest reduction. In addition, a greenhouse experiment was performed to: (3) Investigate effects on development of *D. floralis* at different larval and intercropping densities; and (4) study the response of the host plants in the same system by analysing the effects on growth and content of nitrogen and carbon, fibre (neutral detergent fibre and lignin) and secondary compounds (glucosinolates).

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Intercropping cabbage with clover was expected to affect the oviposition behaviour of the turnip root fly, the predation and parasitization by natural enemies, and the development of the flies through altered host plant quality. This thesis is based on the following questions:

- Is the oviposition behaviour of *D. floralis* disrupted by the presence of a clover intercrop?

- Does the distance from the adjoining treatment affect the distribution of eggs within the monocultured and intercropped experimental plots?

- Do natural enemies, such as carabids and staphylinids, respond with higher activity-densities in the diverse intercropped treatment?

- Does intercropping lead to higher predation and parasitization rates of *D. floralis*, and does the predation pressure change during the season?

- Is the quality of cabbage (growth, C and N, and fibre) affected by intercropping and herbivore pressure, and is the development of *D. floralis* affected by these changes?

- Is the content of glucosinolates in cabbage foliage and roots affected by intercropping and herbivore pressure, and are there any implications for *D. floralis* development?

Theoretical background

Intercropping theory

Definition of intercropping

Intercropping can be defined as the cultivation of two (or more) plant species simultaneously in the same field. The plant species do not necessarily have to be sown at the same time, and their harvest times may differ, but they should be grown simultaneously for a substantial part of their growth periods (Andrews & Kassan, 1976). There are several different modes of intercropping, ranging from very regular arrangements to situations where the different plant species are intermingled. In *mixed intercropping*, the plants are not arranged in distinct rows, whilst in *row intercropping*, two or more species are cultivated together, but in separate rows. With *strip intercropping,* several rows of one species are alternated with several rows of another species. Finally, in *relay intercropping*, two or more species are grown together during at least part of their life cycles (Andrews & Kassan, 1976). An intercropping system can either contain two or more economically important crops, or a marketable crop combined with a plant species included to improve the productivity of the system. This could for example be a

nitrogen fixing species that at least in a longer perspective may contribute nutrients to the system and act as a soil improver, and also presumably lower infestations of pest insects. Besides the term intercropping, it should be acknowledged that diverse plant systems also may be referred to in terms such as polycultures, mixed cropping, undersowing, living-mulch and companion planting (Tukahirwa & Coaker, 1982; Andow, 1991; Finch, Billiald & Collier, 2003; Dixon *et al.*, 2004; Hooks & Johnson, 2006).

Effects on pest insects in intercropping systems

Vandermeer (1989) divided the mechanisms that might lead to reduced insect attack in intercropping systems into three hypotheses: The Disruptive Crop Hypothesis (1) (which is closely linked to Root´s (1973) Resource concentration hypothesis), in which the intercrop disrupts a specialised herbivorous insect pest from attacking its host; while The Trap Crop Hypothesis (2) states that reduced insect damage can be achieved if the insects are more attracted by an alternative host (Hokkanen, 1991). The third mechanism proposed by Vandermeer (1989) is the Enemies Hypothesis (3), originally developed by Elton (1958) and Root (1973), in which a diverse habitat is believed to attract and retain more enemies of insect pests. Compared with a monoculture, adding more plant species to a system affects herbivores in two major ways. Firstly, the environment of the host plants, *e.g.* neighbouring plants and microclimatic conditions, is altered and secondly, host plant quality, *e.g.* morphology and chemical content, is altered (Langer, Kinane & Lyngkjær, 2007). The simultaneous effect on both environment and quality may complicate comparisons between systems, as several mechanisms affect herbivorous insects at the same time (Bukowinzky *et al.*, 2004). Changes in environment and host plant quality lead to direct effects on the host plant searching behaviour of herbivorous insects, as well as indirect effects on their developmental rates and on interactions with natural enemies.

The mechanisms behind the direct effects of intercropping have been investigated further by Finch & Collier (2000), who developed the theory of Appropriate/inappropriate landings. This theory states that when an herbivorous insect lands on an intercrop plant instead of a host plant, its behavioural sequence is disrupted (Finch & Collier, 2000). These authors suggest that insects use a three-link chain during host selection in which the initial link is governed by volatile host plant chemicals (Nottingham & Coaker, 1985), the central link by visual stimuli (Finch & Collier, 2000) and the final link by non-volatile chemicals (Simmonds *et al.*, 1994). It is in the central link that disruption occurs, as insects are attracted to land on any green surface and avoid landing on bare soil (Kostal & Finch, 1994; Finch & Collier, 2000). When insects make an inappropriate landing, the behavioural sequence is disrupted and they have to 'locate' the host plant all over again.

It has been suggested that the effect of intercropping on herbivore behaviour is exaggerated in small-scale experiments, as insects can move freely between the diverse treatments and the controls (Bergelson & Kareiva, 1987; Bommarco & Banks, 2003). The controls, often a pure stand of host plants, then function as a

trap crop, suffering higher herbivore densities and damage. The response to vegetation diversity varies for insect herbivores (Andow, 1991), and is most likely to be dependent on factors such as breadth of diet (Andow, 1991), insect search mode (Hambäck, Pettersson & Ericson, 2003; Bukowinszky *et al.*, 2005) and life history aspects (Åsman & Ekbom, 2006). When evaluating the responses of a specific insect species to intercropping, one must consider both behavioural responses to intercropping *per se*, and responses to the design used in the particular experiment.

The indirect consequences of intercropping include effects on the natural enemy community. Pest natural enemies, both parasitoids and generalist predators, have proved to be an important factor in biological control, and recent studies have also aimed to translate control efficiency into monetary values, with promising results (Östman, Ekbom & Bengtsson, 2003). Whether the effect of natural enemies is enhanced in diverse habitats is, however, debatable. The Enemies Hypothesis suggests that the effect of natural enemies is enhanced in mixed cropping systems, because these systems provide a variety of microhabitats and alternative prey (Root, 1973). However, The predictions of the Enemies Hypothesis are likely to vary between generalist and specialist natural enemies, as the latter are unlikely to benefit from the presence of alternative prey that should favour generalists. Specialists are expected to accumulate in simpler habitats, where their specific prey usually achieve higher densities and are easier to find (Sheenan, 1986). However, parasitoids utilising flower resources have benefited from more diversified systems (Lavandero *et al.*, 2005). Examinations of the effect of plant diversity on generalist natural enemies have often shown an increased abundance in diverse systems (Booij, Noorlander & Theunissen, 1997; Denno, Finke & Langelotto, 2005). However, there are variations in the responses not only among predator species, but also within the same species when different studies are compared (Tukahirwa & Coaker, 1982; Rämert, 1996a; Armstrong & McKinlay, 1997), and these differences are likely to be explained by factors such as prey density (Bryan & Wratten, 1984), prey preference hierarchies of specific natural enemy species, and habitat preferences (Thiele, 1977).

Besides an alteration in the host plant environment of intercropping systems directly affecting herbivore behaviour, crop plants in intercropping systems often compete with the intercrop for resources such as light, water and nutrients. These factors may have consequences for plant growth (Langer, 1996; Rämert, 1996b), morphology (Hooks & Johnson, 2001) and chemical composition (Stamp *et al.*, 2004; Osier & Jennings, 2007), which in turn could affect host plant finding and acceptance by herbivores (den Belder, Elderson & Vereijken, 2000). Indirectly, this might also change the suitability of the crop plant as a food source for insect herbivores (Simpson & Raubenheimer, 1995), which could have consequences for their development rates (Bukowinszky *et al.*, 2004; Osier & Jennings, 2007). Among plant quality traits found to affect herbivore development are their fibre and nutrient contents (Bethke *et al.*, 1987; Hunt, Drury & Maw, 1992; Hochuli, 1993), which can both be affected by environmental conditions (Widdicombe & Thelen, 2002; Osier & Jennings, 2007), and might therefore be expected to vary between monocultured and intercropped plants.

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Furthermore, plant competition in intercropped systems may affect the allocation of resources to either plant growth or to the maintenance of their defence mechanisms (Herms & Mattson, 1992). In cruciferous plants, the sulphur and nitrogen containing glucosinolates are considered to be an important part of their defence system against herbivores and pathogens (Mithen, 2001; Halkier & Gershenzon, 2006). When plant tissues are damaged, the glucosinolates are hydrolysed by plant myrosinase enzymes, and a wide range of volatile and non-volatile compounds are produced, of which the isothiocyanates (mustard oils) are the best known (Mithen, 2001). These compounds are largely responsible for the characteristic flavours of crucifers and are toxic to generalist herbivores (Giamoustaris & Mithen, 1995; Kliebenstein *et al*., 2002). Specialised herbivores, on the other hand, use glucosinolates and isothiocyanates in their host plant finding and acceptance (Nottingham & Coaker, 1985; van Loon *et al*., 1992; Renwick, 2002). Glucosinolate concentrations change in response to herbivore damage (Koritsas, Lewis & Fenwick, 1991; Bartlet *et al*., 1999; van Dam & Raaijmakers, 2006), but also to environmental stress factors (Yusuf & Collins, 1998; Radovich, Kleinhenz & Streeter, 2005). As plants are rarely subjected to only competition or herbivory, there are likely to be interactive effects which may have consequences for plant quality aspects such as fibre, nutrients and the concentration of glucosinolates, and hence for the development of feeding herbivores.

The turnip root fly - *Delia floralis*

Biology

The turnip root fly (Fig. 1), *Delia floralis* Fallén (Diptera: Anthomyiidae), is considered to be an economically important pest on cruciferous crops in the north temperate region, including the countries of Fennoscandia: Sweden (Lundblad, 1933), Denmark (Jørgensen, 1957; Bromand, 1980), Norway (Andersen *et al*., 1983) and Finland (Varis, 1967), as well as Canada (Brooks, 1951), Scotland (Morison, 1939) and Russia (Vasina, 1927). The fly larvae feed on the root system of their host plant, which can lead to decreased plant growth, or death of the plant. Host plants of *D. floralis* include different varieties of *Brassica oleracea* L., *e.g.* cabbage, cauliflower, kale and broccoli, and *Brassica napus* L., *e.g.* swede and canola (oilseed rape) (Morison, 1939; Brooks, 1951; Broatch & Vernon, 1997).

The turnip root fly shares many of its biological and behavioural traits with its close relative the cabbage root fly, *Delia radicum* L. (Varis, 1967; Baur *et al*., 1996a). The geographical distribution of these two species overlaps, but *D. radicum* has a more southerly distribution (Coaker & Finch, 1971). Where the two species occur together, the proportions of the two species in the total population vary between locations and years (Sundby & Taksdal, 1969; Paper II). When they occur together, the emergence of *D. floralis* seems to be some weeks later than that of *D. radicum* (Varis, 1967; personal observations by the author).

The female turnip root fly lays small white oval eggs 1.10 ± 0.008 mm long (Varis, 1967). The eggs are laid close to the host plant, preferably in crevices in

the soil (Havukkala & Virtanen, 1985). Under laboratory conditions, female flies lay about 55 eggs in the first batch, after which the egg numbers decrease continuously in subsequent batches (Havukkala & Virtanen, 1984). Cage experiments have shown that after emerging from the pupae, the females begin to lay eggs after 8 days on average (Havukkala & Virtanen, 1984), and oviposition then lasts for about 3 weeks (Varis, 1967).

Fig. 1. A turnip root fly, *Delia floralis*, female.

The egg stage lasts about 8 days (Varis, 1967), and after hatching the neonate larvae burrow into the plant roots to feed. Larval development includes three stages. When the larvae are fully developed, after 5-7½ weeks (Varis, 1967), they move down into the soil and pupate at a depth of about 10 cm, but sometimes as deep as 23 cm, from the soil surface (Morison, 1939). The pupal stage is the stage in which the turnip root fly overwinters. *Delia floralis* is considered to be univoltine (Morison, 1939; Brooks, 1951), but in certain places in Denmark two generations have been encountered (Jørgensen, 1957), and in Finland there are reports of at least a partial second generation in warm years (Varis, 1967).

Behaviour

The pre- and post-alightment behavioural process has been investigated for both root fly species (Havukkala & Virtanen, 1985; Kostal & Finch, 1994; Hopkins *et al*., 1996; Städler & Schöni, 1990) and their behaviours seem to be similar. During the host location process, which is completed through oviposition by female flies, a broad spectrum of stimulatory cues operates, and the relative importance of these different cues depends on the specific stage in the behavioural process.

Gravid *D. floralis* females arrive in a brassica field through a series of short (2 m) flights, re-orientating towards the wind between landings (Havukkala, 1987). Volatile host plant compounds, such as the isothiocyanates, elicit up-wind movement of *D. radicum* (Havukkala, 1982; Nottingham & Coaker, 1985), and *D. floralis* has shown similar behaviour in the presence of host plant odour (Havukkala, 1987). In the vicinity of host plants, the importance of visual stimuli has been determined for *D. radicum*, which is attracted to land on green surfaces at a distance of 40-60 cm from the host plant (Prokopy, Collier & Finch, 1983). Havukkala (1987) also assumed that visual stimuli were important for *D. floralis* as the female flies flew directly towards green traps at close range. Leaf area seems to be of greater importance than leaf form in stimulating landing by *D. radicum* (Roessingh & Städler, 1990). Furthermore, plants that are grown on bare

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soil are more attractive than undersown plants, probably because they are more visually conspicuous to the flies (Kostal & Finch, 1994).

After a fly has landed on a host plant, it is suggested that volatile cues enhance its response to the host plant, even if these compounds alone do not induce oviposition (de Jong & Städler, 1999). In addition, contact cues have been shown to be important for the ensuing behaviour and final host acceptance (Simmonds *et al.*, 1994). The non-volatile glucosinolates have long been considered to be the main contact cues for both *D. floralis* and *D. radicum* (Städler, 1978). More recent studies have found non-volatile compounds that are even more stimulating than the glucosinolates as conditioning cues for oviposition (Hurter *et al.*, 1999; Hopkins *et al.*, 1997). Cabbage Identification Factors or CIFs (thia-triazafluorene compounds), have been found on the leaf surface of crucifers in very low concentrations compared to the glucosinolates, which have been found in concentrations about 6×10^4 times higher than that of the CIF compounds (Roessingh *et al.*, 1992; Roessingh *et al.*, 1997). However, glucosinolates alone, for example glucobrassicin (Gouinguené & Städler, 2006), induce oviposition in both *D. floralis* and *D. radicum*. In addition, other factors such as leaf surface waxes may affect the ability of insects to detect oviposition stimulating compounds (Roessingh & Städler, 1990).

Post-alightment behaviour includes a specific sequence of behavioural stages, culminating in oviposition at the base of the plant stem. Havukkala & Virtanen (1985) divided the post-alightment behavioural process for *D. floralis* into six stages: (1) landing, (2) extension of the proboscis and examination of the leaf surface, (3) walking over the leaf, (4) running down the stem, (5) walking on the ground at the base of the stem and (6) oviposition. After making the initial landing on a leaf, *D. radicum* performs short, so-called 'spiral flights' around the plant canopy as part of the exploration process (Kostal & Finch, 1994), and this behaviour has also been observed in *D. floralis* (personal observations by the author). Oviposition behaviour can be aborted at any of the stages described (Havukkala & Virtanen, 1985), but comparison of the behaviour on susceptible and resistant brassica plants has revealed that cues perceived immediately after landing on a leaf (the so-called leaf contact phase) are crucial for acceptance, or rejection, of the plant as a oviposition site (Hopkins *et al.*, 1996, 1999). In the final stage before oviposition, flies also perceive cues emanating from the roots. Female *D. radicum* prefer to oviposit on plants where conspecific larvae have fed for 4-5 days (Baur *et al.*, 1996b). The changes induced by larval feeding were not detected on the leaf surface, which indicates that contact or volatile cues at ground level are important for oviposition. In addition, specific egg-associated compounds, recently identified as CIF compounds, stimulate oviposition by conspecific females (Gouinguené, Poiger & Städler, 1996). These two mechanisms may explain the aggregated oviposition pattern found for *D. radicum* in the field (Mukerji & Harcourt, 1970).

Natural enemies

Carabids are known to feed on immature stages of dipteran pests and have been widely studied for their potential in biological control (Coaker & Williams, 1963; van Dinther & Mensink, 1971; Finch & Elliot, 1992; Finch, 1996). The potential rate of egg consumption varies between species, and depends on factors such as body size. Laboratory experiments have revealed a positive linear relationship between the numbers of eggs eaten and carabid body size within the 2.7 to 10 mm size range. Species of *Agonum*, *Amara*, *Bembidion* and *Harpalus* were among those species that had a high consumption rate in relation to their body size (Finch, 1996). van Dinther and Mensink (1971) found that *Bembidion* spp. were dominant egg predators in cabbage fields, while other groups only consumed eggs occasionally. Larger species (>10 mm), such as *Pterostichus melanarius*, seem to have a low interest in *Delia* eggs (Finch & Elliot, 1994).

Staphylinids have been studied less thoroughly for their ability to predate dipteran eggs, but two *Aleochara* species, *A. bilineata* Gyll. and *A. bipustulata* L. (Coleoptera; Staphylinidae), are known to attack root fly eggs (Coaker & Williams, 1963; Andersen *et al.*, 1983). *Aleochara* adults have the capacity to eliminate a considerable quantity of *D. radicum* eggs, larvae and pupae. According to laboratory studies, individual *A. bilineata* beetles are capable of eating 25 *D. radicum* eggs per day (Langlet & Brunel, 1996) or about 600 eggs during their lifetime (Read, 1962). *Aleochara bilineata* also predates on later developmental stages (Hartfield & Finch, 2003). Both *Aleochara* species also function as parasitoids on root fly pupae, with *A. bilineata* as a specialist attacking mainly *Delia* species (Wishart, 1957; Maus, Mittman & Peschke, 1998), while *A. bipustulata* is considered to be more of a generalist (Maus, Mittman & Peschke, 1998). *Trybliographa rapae* Westw. (Hymenoptera; Cynipidae) is also a common parasitoid of *Delia* spp. It is a larval parasitoid that preferably attacks the early larval instars of its host (Wishart & Monteith, 1954).

Development and food quality

The development of *D. floralis* and *D. radicum* has been reported to vary depending on host plant species, resulting in differences in the percentage pupating successfully and the final pupal weight (Finch & Ackley, 1977; Hopkins *et al.*, 1995). The factors affecting *D. floralis* development are relatively unknown, but a high content of root neutral detergent fibre (NDF) may affect *D. floralis* larval growth negatively, leading to lower pupal weights (Hopkins *et al.*, 1995). NDF includes cellulose, hemicellulose and lignin as major components (van Soest, Robertson & Lewis, 1991). Reports on the digestibility of NDF vary between species, but is usually considered to be low (Hochuli, Sanson & Roberts, 1993), and is generally associated with a decrease in host plant quality for herbivorous insects (Hochuli, 1996). The content of NDF is likely to vary between host plants (Hopkins *et al.*, 1995) as is nutrient (Osier & Jennings, 2007) and glucosinolate concentration (Birch *et al.*, 1992; Griffiths, Birch & MacFarlane-Smith, 1994). Although it has not been studied in *D. floralis*, a high nitrogen level is considered to be positive for herbivore development (Bethke *et al.*, 1987; Hunt, Drury &

Maw, 1992). However, the effect of host plant glucosinolate concentrations on the development of crucifer specialists has not shown consistent patterns (Cole, 1997; Agrawal & Kurashige, 2003).

Against this background of knowledge, the present study aimed to investigate how intercropping affects the different stages of the life cycle of *D. floralis*, with the emphasis on behaviour, natural enemies and host plant quality, in order to evaluate the potential of this strategy as a control method for *D. floralis*. A field trial was designed to investigate the relative impact of the effects on *D. floralis* oviposition behaviour and the effects on natural enemies in the same system. A separate experiment was performed to assess the effects of intercropping density and *D. floralis* egg density on host plant quality and the development of *D. floralis*.

Materials and Methods

The thesis comprises of a field trial performed in two successive years and a greenhouse experiment.

Field trial

The aim of the field trial was to study the effect of intercropping on *D. floralis* oviposition, as well as the effects of natural enemies on the fly population. The field trial was located at Röbäcksdalen in Umeå (63º45'N; 20º15'E) and consisted of alternating plots (15 m x 15 m) with cabbage monocultures (*Brassica oleracea* var. *capitata* genotype Castello) and plots with row intercropping of cabbage and red clover (*Trifolium pratense* genotype Betty) (Fig. 2). The red clover was sown in the whole field in the previous season and was incorporated into the field as green manure before the transplanting of the cabbage plants. Strips of red clover, 20 cm wide, were left running through the plots aimed for intercropping. The distance between cabbage rows was 70 cm in both treatments, and within row plant distance was 40 cm. The field trial in 2004 was performed at a distance of approximately 40 m from the field trial of the previous year.

The effect on *D. floralis* oviposition and the effect on the natural enemy community were measured in both study years. In 2003, pilot studies of egg predation, total predation and parasitization were performed, and the methods were modified for the field season of 2004. In both 2003 and 2004, oviposition was examined throughout the oviposition period from early July to the middle of August. This was done with felt egg traps placed on the stem of the cabbage plants (Freuler & Fischer, 1982) and sampled two times a week for egg counts (Papers I & II).
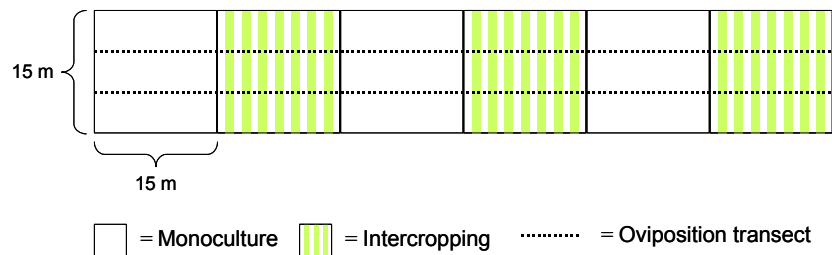
Fig. 2. The two different cultivation systems tested in the field trial at Röbäcksdalen in Umeå. Left, a cabbage monoculture and right, intercropping between cabbage and red clover. Underneath is the design of the field experiment.

During both seasons, the natural enemy community was monitored with pitfall traps. This method is far from problem-free, especially when comparing two treatments that differ in plant complexity (Greenslade, 1964), but no attempt was made here to measure absolute abundance. Thus, the aim was to measure the presence of different species and their activity-densities (Mitchell, 1963). Pitfall traps were emptied two times per week (Paper II) and species of *Carabidae* and *Staphylinidae* were counted and identified to species.

In 2004, a study of egg predation was performed by placing *D. floralis* eggs in the field in a density comparable to a natural egg batch size (30 eggs). Eggs from a fly culture kept at Röbäcksdalen were placed in the field repeatedly during the oviposition period and were recollected in order to count the remaining eggs and examine them for predation marks (Paper II). Total predation was estimated by using predator exclusion barriers (Fig. 3). The resulting pupae inside and outside the barriers were sampled in early autumn (Paper II). Parasitization rates were estimated from pupal samples both in 2003 (40 per plot, presented only in this thesis) and in 2004 (35 per plot, Paper II).

To summarise the overall survival of *D. floralis* in the field, comparisons of oviposition and final pupal numbers in both intercropping and monoculture are presented below.

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Fig. 3. A predator exclusion barrier in the cabbage mono-culture.

Greenhouse experiment

A greenhouse experiment (Fig. 4) was performed to investigate the effects of intercropping and herbivore density on the development of *D. floralis* (Paper III), and the responses of plants with respect to growth and content of fibre, nutrients (Paper III) and glucosinolates (Paper IV). Cabbage plants were grown in monoculture (M) or in one of two clover densities (IC1 & IC2). Eggs of *D. floralis* eggs were inoculated onto 6-week-old plants at the 6-7 true leaf stage in four different densities (0, 10, 20 or 40 eggs), and the fly larvae were able to feed until pupation. After six weeks, the experiment was terminated. Cabbage plants were weighed (aerial parts and roots separately) and plant samples were taken for analyses of total nitrogen and carbon of cabbage roots and shoots, cabbage root NDF (neutral detergent fibre) and lignin (Paper III), as well as the glucosinolate concentrations of cabbage foliage and roots (Paper IV). The pupae were washed out from the soil, counted and weighed (Paper III).

Fig. 4. Overview of the greenhouse experiment.

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Statistical analyses

The effect of cultivation system on total oviposition (Paper I) was analysed with analysis of variance (ANOVA). To investigate the effects of adjoining treatments on the spatial distribution of eggs, an analysis of covariance was performed (ANCOVA). To examine the distance the border effect extended into the plots, a gliding window was used, analysing four distances at a time with an ANCOVA. When a threshold value was found, which indicated the extent of the border effect, the two cultivation systems were analysed separately with linear regressions to examine whether one or both treatments were causing the border effect.

The effect of cultivation system on oviposition with edge effects excluded (Paper II) was analysed with a two-way ANOVA. The egg predation rates over time were first analysed with a nested ANOVA, and then with two-way ANOVAs for each sampling date as a planned comparison. The effects on total predation and parasitization rates were analysed with split plot ANOVAs and the likelihood of the presence of at least one pupa parasitized by *T. rapae* per plant was analysed with GLM (Paper II).

The pitfall trap catches of groups of carabids and staphylinids were analysed with a two-way ANOVA (Paper II), and this analysis was repeated for *Bembidion* spp., *A. bipustulata*, 'other carabids' and 'other staphylinids' separately (Paper II). To compare the activity-densities of individual predators between cultivation systems, we used a blocked Multi-Response Permutation Procedure (MRPP, Zimmerman, Goetz & Mielke, 1985), and an indicator species analysis as a post-hoc test (Dufrene & Legendre, 1997) with the default number of randomisations (1 000) in PC-ORD 4.25 (McCune & Mefford, 1999). The MRPP analysis was only done for 2004 due to a lack of power in the 2003 data (Paper II).

The effects of intercropping and egg density on cabbage growth, fibre and nutrient content and on *D. floralis* pupal weights were analysed with ANCOVAs (Paper III). For the glucosinolate analysis (Paper IV), separate MANOVAs were performed for foliage and root samples. GLM analyses were used to analyse individual glucosinolates, as well as the groups of aliphatic and indole glucosinolates and the total concentrations in cabbage roots and foliage. Correlation analyses were carried out to identify possible correlations between insect development and plant growth, NDF, lignin, carbon and nitrogen content (Paper III), as well as glucosinolate concentrations (presented only in this thesis).

Transformation of data was performed when needed to fulfil assumptions on normality and equal variances. All analyses, except for the MRPP analysis (Paper II), were made using S-PLUS statistical software (Insightful Corp. Seattle, USA. S-PLUS® 6.0).

Results and discussion

Behavioural effects

Quantity and distribution of eggs

Oviposition measurements in the field trial showed that oviposition by *Delia floralis* was reduced considerably in the intercropped plots compared with the monoculture plots in both study years (Papers I & II; Fig. 5). The overall reduction in oviposition in the intercropped plots, compared with the monoculture plots, was 42% in 2003 and 55% in 2004 (Paper I). The duration of the oviposition period extended from early July to the middle of August, with a peak in oviposition around July 20 in both years (Paper II). Furthermore, oviposition in 2004 was around 6 times greater than in 2003.
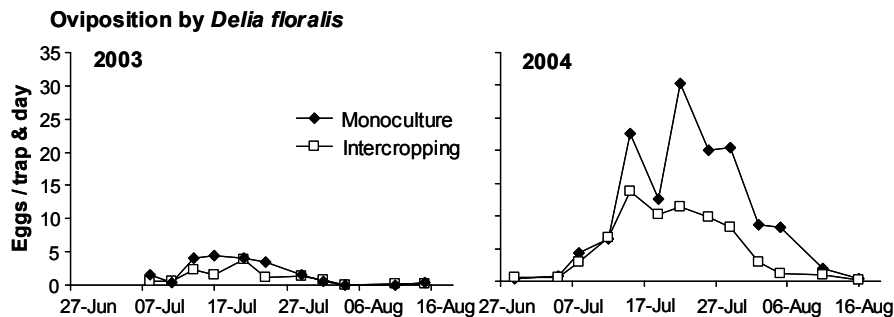
Fig. 5. Oviposition by *D. floralis* during 2003 and 2004 in monoculture and intercropped plots (Paper II).

Analysis of the distribution of eggs within the experimental plots showed a decreased oviposition in intercropped plots and an increased oviposition in monoculture plots close to the border between treatments (Paper I), although this effect was only statistically significant in 2004. Consequently, the difference in oviposition between the monoculture and intercropped plots was greatest close to the border. The difference in egg numbers decreased with distance from the border up to a distance of 3.5 m into the plots (Fig. 6).

The mechanisms behind the reduced oviposition in the intercropped plots in both years are likely to be found in the behaviour of the gravid female flies (Finch & Kienegger, 1997), and in the specific cues used during their oviposition behavioural sequence (Prokopy, Collier & Finch, 1983; Simmonds *et al.*, 1994). In many cases, initial colonisation of intercropped and monoculture treatments is similar, with for example *D. radicum* arriving to a cabbage-clover system (Tukahirwa & Coaker, 1982). Therefore, the odour of clover does not seem to interfere with the host location process pre-alightment, although this has been proposed for certain non-host plant odours (Nottingham, 1987). The main reason

for reduced oviposition in the intercropped plots is therefore likely to be factors operating after the flies arrive in the field.

After flies have arrived in a field, the capacity of a specific plant-intercrop system to lower pest infestations is determined by both the behavioural and biological attributes of specific herbivores. It is suggested that the number of 'appropriate' landings an insect has to make during the behavioural sequence is a key factor determining the value of intercropping for pest control (Finch & Collier, 2000). The ability of a specific insect species to perceive and orientate towards visual and olfactory cues is crucial and may affect the probability of making landing 'mistakes'. In the vicinity of a host plant, vision is the main stimulus eliciting landing on any green surface by *D. radicum* (Prokopy, Collier & Finch, 1983). As *D. radicum* has been shown to perform an average of four so-called 'spiral flights' during its oviposition behavioural sequence (Kostal & Finch, 1994), there is a high risk for behavioural disruption through 'inappropriate landings'. *Delia floralis* females share the general pattern of their host selection behaviour with *D. radicum* (Hopkins *et al.*, 1996; personal observations by the author), and the present study has demonstrated the disruptive capacity of intercropping for *D. floralis* (Papers I & II). The number of host plant contact phases required to achieve oviposition probably varies both between, as well as within, the same species. Thus, a host plant of low quality may need more 'appropriate landings' before being accepted (Finch & Collier, 2000).

Furthermore, an insect's pattern of movement in the vicinity of a host plant, and the specific intercropping system, will determine the number of interactions that occur between the insect and the intercrop, and thus influence the probability of making 'inappropriate landings'. The pattern of movement is, in part, determined by the location of the oviposition site. For example, intercropping seems to have a large effect on insects that oviposit in the soil, such as the cabbage root fly and the turnip root fly (Finch & Kienegger, 1997; Papers I & II), the carrot fly (*Psila rosae* F.) (Rämert & Ekbom, 1996) and the onion fly (*Delia antiqua* Meigen) (Finch, Billiald & Collier, 2003). An important factor influencing the reduction in oviposition may be the interaction with the intercrop during the insect's vertical movement from the host plant foliage down to the soil. This may be one of several factors explaining the reduced effect of intercropping on some leaf ovipositors such as the diamond back moth (*Plutella xylostella* L.) (Finch & Kienegger, 1997) and the leek moth (*Acrolepiopsis assectella* Z.) (Åsman, Ekbom & Rämert, 2001).

An explanation of the greater difference in egg density near the border between the intercropped and monoculture plots (Fig. 6) may be that the flies in parts of the intercropped plots close to the border have a higher probability of entering the monoculture than flies in the centre. When flies enter the monoculture plots, they can oviposit without disruption from the clover. In addition, as the final choice to decide where to land is based on visual cues (Prokopy, Collier & Finch, 1983), the visual stimulus of a host plant growing with a background of bare soil (Kostal & Finch, 1994) might further motivate flies to stay in, or fly into, the monoculture.

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The border effect was most pronounced in the intercropped plots (Paper I). The more homogeneous egg distribution in the monoculture is probably explained in part by increased mobility of the flies in this treatment. In an intercropping situation, *D. radicum* spends considerable periods of time inactive on non-host plant leaves (Morley, Finch & Collier, 2005). For *D. floralis* and *D. radicum*, the time spent on the foliage of a non-host plant (Morley, Finch & Collier, 2005) or a resistant plant (Hopkins *et al.* 1996, 1999) has been shown to be longer than the time spent on a host plant, and such inactive periods may contribute to the reduced oviposition by *D. floralis* in intercropping systems (Morley, Finch & Collier, 2005). However, the arresting effect of contact with non-host plants or resistant cultivars does not seem to be general for all species, as the cabbage moth (*Mamestra brassicae* L.) and the leaf mining fly (*Liriomyza trifolii* Burgess), for example, spend less time on non-preferred host plants or non-host plants compared with host plants (Bethke & Parella, 1985; Rojas, Wyatt & Birch, 2000).
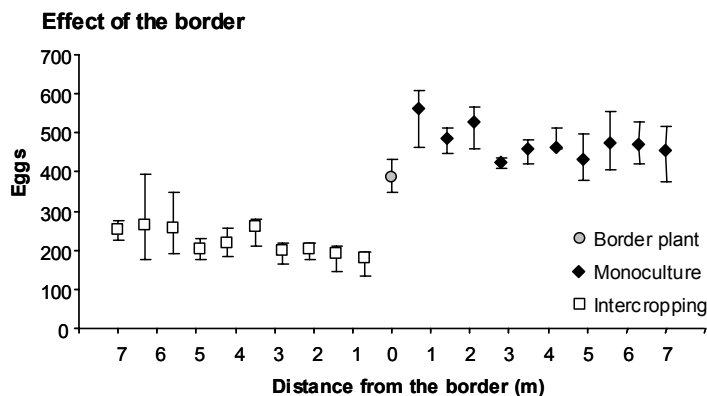

Fig. 6. The effect on *D. floralis* oviposition of distance from the border between intercropped and monoculture plots in 2004 (Paper I).

Besides behavioural factors, life history aspects such as the insect's response to host plant deprivation may also influence the magnitude of the reduction in attack in intercropping systems. Insects deprived of a preferred resource may accept a previously unacceptable resource, as with ovipositing checkerspot butterflies (*Euphydryas editha*) (Singer, 1982). If insects become less discriminating in response to failed oviposition attempts and if deprived individuals have the ability to postpone oviposition, as shown for the leek moth (Åsman & Ekbom, 2006), the effect of plant diversity may decrease with time. Whether *D. floralis* becomes less discriminating with time is still unknown, but it is not unlikely that the border effect found in this field trial may have been enhanced because deprived females finally encountered a suitable host plant.

Some caution is needed when interpreting results from studies of intercropping, as the cultivation system often leads to interspecific competition, which in turn can lead to physiological differences between intercropped and monocultured plants (Bukovinszky *et al.*, 2004). For example, it has been shown that plant size can

have an effect on preference for *D. radicum* in a choice situation (Kostal & Finch, 1994) and that increased leaf area stimulates more landings (Prokopy, Collier & Finch, 1983). In the field trial reported here, the intercropped cabbage actually performed slightly better at the beginning of the oviposition period (Rämert *et al.*, unpublished data). Hence, if *D. floralis* had been attracted to larger plants, this would rather have reduced the difference in oviposition between the treatments. At the beginning of August, the cabbage in the monoculture started to outgrow the intercropped cabbage. At this stage the main proportion of the eggs had already been laid, so the effect of plant size appears to have been less important in this experiment. Other aspects of host plant quality that may have importance for ovipositing females, such as morphological aspects or glucosinolate levels, were not measured during the oviposition period.

Similarly to several other studies of intercropped systems, final crop yield suffered from reductions through competition with the intercrop, and cabbage yield was reduced by approximately 38% in the intercropped plots (Rämert *et al.*, unpublished data). As the primary aim of this field trial was to examine the potential of intercropping for pest control, the measures for reducing competition were few (Papers I & II). For a practical use of intercropping systems, account must be taken of both the pest disruptive capacity of the cropping system and minimising competition with the main crop. These goals may both be achieved through careful consideration of choice of crop and intercrop species, as well as practical measures to prevent competition, *e.g.* through root pruning of the intercrop (Båth *et al.*, submitted).

Effects *on* and *of* natural enemies

Effects on natural enemy activity-densities

The species caught in the pitfall traps were subdivided into four groups: *Bembidion* spp., *Aleochara bipustulata*, 'other carabids' and 'other staphylinids'. This subdivision was based on their numbers and known potential as predators of root fly eggs (Coaker & Williams, 1963; van Dinther & Mensink, 1971; Andersen *et al.*, 1983; Finch & Elliot, 1992; Finch, 1996; Langlet & Brunel, 1996). In both years, the activity-densities of carabid beetles were higher in the monoculture. This result was explained largely by species of the *Bembidion* family (mainly *B. quadrimaculatum* L., *B. bruxullense* Wesmael and *B. lampros* Herbst), which were caught predominantly in the monoculture plots. The effect of cultivation system on *Bembidion* spp. was somewhat stronger in 2003. The numbers of 'other carabids' caught did not differ between the cultivation systems. The distribution of other individual carabid species between cultivation systems was similar between the years, and the MRPP analysis of the 2004 data showed that only *Pterostichus niger* Scall. was caught more often in the intercropped plots than in the monoculture. In addition, species such as *Calathus melanocephalus* L., *Trechus secalis* Paykull and *P. melanarius* Ill. dominated the pitfall trap catches in the intercropped plots. *Aleochara bipustulata* was the dominant staphylinid species in both years and was captured almost exclusively in the monoculture (Paper II). Furthermore, the effect of cultivation system on *A. bipustulata* activity-densities

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was stronger in 2004. The group of 'other staphylinids' responded with a higher activity-density in the intercropped plots in 2003, while trap catches for 2004 were similar in the two treatments. Similar patterns were observed in the species distribution of 'other staphylinids' between years. In 2004, *Aloconota gregaria* Er. and *Anotylus rugosus* F. were trapped more frequently in the monoculture plots. Only *Oxypoda umbrata* Gyll. and *Mocyta orphana* Er. had higher activity-densities in the intercropped plots, even though *M. fungi* Grav. tended to have a similar response.

Even though the majority of studies have found increased predator densities in diversified systems (Andow, 1991), there is undoubtedly a large variation in the response of different carabids and staphylinids towards diversification (Tukahirwa & Coaker, 1982; McKinlay, 1993; Rämert, 1996a; Armstrong & McKinlay, 1997; Booij, Noorlander & Theunissen, 1997). The responses to increased vegetation diversity are probably based on the habitat preferences of different species (Thiele, 1977), but may also be influenced by the explicit design of the systems studied (Bommarco & Banks, 2003). Because the design of this field trial meant that different treatments were adjacent to one another, it is likely that the differences in activity-densities are a result of a redistribution of the natural enemy community at this site. Some insects may have inhabited both treatments, for example *Pterostichus melanarius*, which has been shown to forage in monocultures during the night but to remain in intercropped areas during the day (Chapman, Armstrong & McKinlay, 1999).

The temporal dynamics of carabid and staphylinid activity-densities in 2004 showed that the increases in numbers of *A. bipustulata* and *Bembidion* spp. occurred mainly during the early part of the summer, while there were only small differences in the activity-densities of the remaining species throughout the season (Paper II). *Bembidion* spp. and *A. bipustulata* were treated separately in this study because of their high numbers and their potential as predators on *Delia* spp. As the responses of *Bembidion* spp. and *A. bipustulata* where most apparent early in the season when egg densities were fairly low and egg numbers where similar in both cultivation systems, it seems likely that the main effect on these species was a response to other habitat factors, and to a lesser extent to *D. floralis* egg densities. This conclusion is further supported by the strong respons in *Bembidion* spp. in 2003 when egg densities were relatively low (Paper II).

Predation and parasitization

The specific studies of total predation and egg predation indicated that the predation pressure was similar in the two cultivation systems. If there was any trend at all, it was towards a higher predation pressure in the monoculture, which was especially apparent from the experiment using the predator exclusion barriers. Comparison of pupal numbers inside and outside the barriers gave an estimate of 41% mortality due to predation in the monoculture and 21% in the intercropped treatment (Paper II; Fig. 7). Pilot studies on egg predation in 2003 indicated that there was no difference between the cultivation systems in egg predation rates, and this was confirmed in the field trial in 2004. During 2004, there were no consistent

patterns in differences in predation levels between the two cultivation systems, or between predator activity-densities and egg predation rates during the season (Paper II).

Overall, parasitization rates were low in both 2003 (monoculture 6.3%, intercropped 2.3%) and 2004 (monoculture 5.3%, intercropped 4.6%) and did not differ between the cultivation systems. *Trybliographa rapae* was the main species of parasitoid. A small number of pupae parasitized by *Gnotus* spp. or by *Aleochara bipustulata* were also found. In 2004, when pupal numbers were high, there was a density-dependent response between numbers of pupae per plant and the likelihood of at least one pupa being parasitized by *T. rapae*. This pattern was similar in both cultivation systems. Parasitization by *A. bipustulata* is likely to have been underestimated because a closer inspection of pupae suggested that *A. bipustulata* had already hatched at the time of sampling.
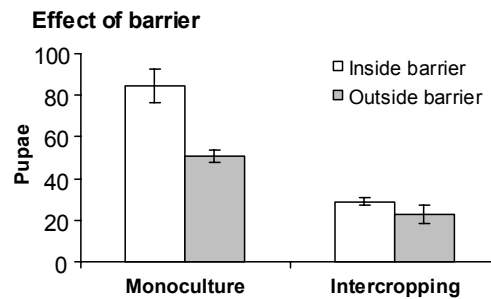
Effect of barrier

Fig. 7. Comparison of pupal numbers inside and outside barriers (mean ± SEM) in monoculture and intercropping (Paper II).

Predictions made by the Enemies Hypothesis of a greater effect of natural enemies in diverse systems (Root, 1973) have been both confirmed (Letourneau & Altieri, 1983) and contradicted (Andow & Risch, 1985), while in the present field trial the effects of both predators and parasitoids were similar (Paper II). Similarly, an earlier study using predator exclusion barriers did not reveal any differences in egg predation pressure due to vegetation diversity (Tukahirwa & Coaker, 1982), and our study suggests that this lack of effect persists into the pupal stage. For the predation studies, the lack of effect could be explained by comparable differences between systems in predator activity-densities and *D. floralis* egg numbers, creating similar predator:egg ratios. The applicability of the Enemies Hypothesis to specialist natural enemies has been questioned, as they are expected to accumulate where prey densities are higher (Sheenan, 1986). The low parasitization rates by *T. rapae* in this field trial did not show any density-dependent effects, although these were found previously by Jones & Hassell (1988) (Paper II). The similar parasitization rates in monoculture and intercropped plots confirm earlier studies, which found no effect of plant diversity on the host finding efficiency of *T. rapae* (Hartfield, Nethercleft & Finch, 1999).

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Survival of D. floralis in the field

Even though oviposition differed significantly between the two cultivation systems in both study years, pupal numbers differed only in 2004 (Table 1). The pupa:egg ratio, which may be regarded as a measure of survival, was similar between cultivation systems in 2004. This further confirms that there was similar predation pressure in both the monoculture and intercropped plots during this season. In 2003, survival seems to have differed between systems, as pupal numbers were similar. As they were not measured in 2003, differences in predation pressure between treatments cannot be excluded, and the stronger effect of treatment on *Bembidion* spp. in this year (Paper II) may have led to stronger predation pressure in the monoculture, which could have resulted in similar numbers of pupae in the two systems. However, this result also raises questions about the abiotic factors affecting survival rates in the two systems. The immature stages of *D. floralis* and *D. radicum* are sensitive to high temperatures and desiccation (Vodinskaya, 1928; Coaker & Finch, 1971; Mukerji, 1971), which is considered to contribute to their high overall mortality (Mukerji, 1971). The mean temperature during the period of peak oviposition was approximately 3 ºC higher in 2003 than in 2004, which may have led to higher survival in the intercropped plots as a result of a more stable microclimate in terms of temperature and humidity (Potts, 1990; Bodreau, 1993; Fininsa, 2001). Furthermore, even though both egg and pupal numbers are likely to have been underestimated in this study, the pupa:egg ratio indicates that only a minority of *D. floralis* eggs survive to the pupal stage.

Table 1. *Egg and pupal numbers sampled in 2003 and 2004 (mean ± SEM) and the pupa:egg ratio*

	2003			2004		
	Eggs	Pupae	Pupa:Egg	Eggs	Pupae	Pupa:Egg
Monoculture	76 ± 7	7 ± 3	0.09	471 ± 13	51 ± 5	0.09
Intercropping	47 ± 8	8 ± 2	0.20	246 ± 26	22 ± 3	0.08

Host plant quality and *D. floralis* development

Cabbage N, C, NDF and lignin

In the greenhouse experiment, there was a strong negative effect on the final weight of cabbage plants of competition through both increasing clover density and increasing egg number. This was reflected in both the aerial parts and the roots of the cabbage (Paper III). In addition, plant competition and larval feeding also resulted in higher levels of NDF (neutral detergent fibre) and lignin in the roots of the intercropped cabbage plants. There was also an interactive effect of intercropping and larval density on the lignin content, which was explained by an increase with larval density in the roots of intercropped plants, while the content was unchanged in roots of monocultured plants (Paper III; Fig. 8). The nitrogen content was higher in the roots of monoculture cabbage compared with

intercropped plants, while the amount of carbon was higher in the roots of intercropped cabbage. Both the nitrogen and carbon levels in cabbage roots increased with *D. floralis* egg density, while their content in the foliage was unaffected either by intercropping or feeding by root flies (Paper III).

The negative effects of intercropping on the growth of cabbage and on the root:shoot ratio are predictable consequences of inter-specific plant competition for mutual resources such as light and nutrients (Theunissen, Booij & Lotz, 1995; Agele, Iremiren & Ojeniyi, 1999; Bonifas *et al*., 2005). The effects of nutrient availability were presumably more important in this study, considering the higher root:shoot ratio in intercropped cabbage plants (Bonifas *et al*., 2005). The higher nitrogen content of roots from the monoculture also points in this direction (Paper III), and the impaired cabbage growth due to larval feeding confirms the detrimental effect of root flies, especially on small brassica crop plants.

The increase in the NDF and lignin contents of cabbage roots due to feeding by *D. floralis* corresponds to the response found in the roots of kale, rape and swede (Hopkins *et al*., 1995) and may be caused by two different processes: (1) *D. floralis* may choose to feed on the parts of roots that have a lower fibre content (Hopkins *et al*., 1995); or (2) the damage caused by feeding larvae may induce a plant response that increases the fibre content of the roots. Plants may respond by lignification when wounded or attacked by pathogens (Rittinger, Biggs & Pierson, 1987; Moerschbacher *et al*., 1990; Li *et al*., 2007), and an induced response to larval feeding damage may be one explanation for the pronounced increase in lignin content at high egg densities (Fig. 8).
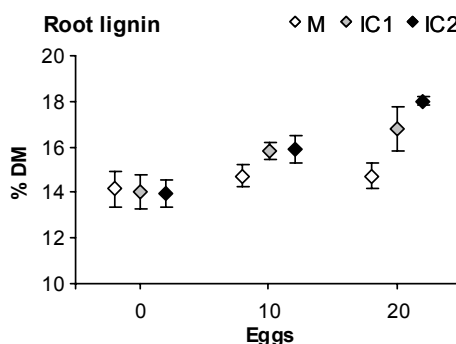

Fig. 8. Effects of intercropping density and *Delia floralis* egg density on the content of lignin in cabbage roots (% of root dry matter, DM) (M = monoculture, IC1 = low clover density, IC2 = high clover density).

Glucosinolate concentrations

The analysis of glucosinolate content of the foliage and roots of the cabbage plants revealed a total of nine different glucosinolates, consisting of five aliphatic and four indole glucosinolates (Table 2). All were present in both the foliage and roots of cabbage plants in all treatments (Paper IV). Both intercropping and *D. floralis*

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egg density affected the concentrations of glucosinolates in cabbage. Of the glucosinolates in the foliage, several decreased in concentration as a response to intercropping, and this resulted in a total decrease in the concentration of indole glucosinolates. The strongest responses in individual glucosinolates were for gluconapin, glucobrassicin and hydroxyglucobrassicin (Paper IV). The responses to insect root damage were less pronounced, with a slightly significant decrease in the concentration of the aliphatic glucosinolate progoitrin and the indole glucosinolate neoglucobrassicin. The total glucosinolate content of the cabbage foliage was not significantly affected by either clover competition or by the damage caused to the roots of the plants by *D. floralis*, even though there were strong tendencies towards a reduction (Paper IV; Fig. 9). Root glucosinolates responded more strongly to both intercropping and egg density and the responses of individual root glucosinolates were complex and, on occasions, non-linear. Most root glucosinolates decreased in response to clover competition, with the exception of the indole methoxyglucobrassicin, which increased, and neoglucobrassicin, which was unchanged. The total concentrations of indole glucosinolates in the roots increased in response to *D. floralis* damage. The aliphatic gluconsinolates decreased in damaged intercropped roots, but only at high egg densities. In monoculture roots, a decrease in concentration of aliphatic glucosinolates was only observed at low egg densities, which caused a non-linear response. However, there were exceptions to this pattern for individual glucosinolates within each group (Paper IV).

Table 2. *Different glucosinolates found in foliage and root samples of cabbage*

	Scientific name	Trivial name
Aliphatic	2-propenyl	Sinigrin
	3-butenyl	Gluconapin
	3-[methylsulphinyl] propyl	Glucoiberin
	2[R]-2-hydroxy-3-butenyl	Progoitrin
	4-[methylsulphinyl] butyl	Glucoraphanin
Indole	Indol-3-ylmethyl	Glucobrassicin
	1-methoxyindol-3-ylmethyl	Neoglucobrassicin
	4-hydroxyindol-3-ylmethyl	Hydroxyglucobrassicin
	4-methoxyindol-3-ylmethyl	Methoxyglucobrassicin

The decreased concentrations of several glucosinolates in the cabbage foliage suggest that cabbage plants in competition with another species, and cabbage plants subjected to root herbivory, do not manage to allocate the same resources as unchallenged plants to sustain levels of leaf defence compounds. Lower concentrations of defence compounds have been shown previously in competing plants (Cipollini & Bergelson, 2001; Stamp *et al*., 2004), and may lead to increased herbivory on these plants (Cipollini & Bergelson, 2002). However, as several glucosinolates have been identified as oviposition and feeding stimulants (Roessingh *et al*., 1992; van Loon *et al*., 1992; Simmonds *et al*., 1994;

Gouinguené & Städler, 2006), a decrease in the concentration of these compounds as a result of plant competition could lead to less attractive host plants in intercropping systems, at least for crucifer specialists such as *D. floralis*.

The responses of root glucosinolate concentrations in this study correspond to responses identified in previous studies of damage-induced changes in glucosinolate concentrations. In previous studies, the concentration of indole-based glucosinolates in roots tended to increase in response to root herbivory (Birch *et al*., 1992, 1996; Griffiths, Birch & MacFarlane Smith, 1994; Hopkins *et al*., 1998; van Dam & Raajimakers, 2006), whilst a damage-induced change in the total amount of root glucosinolates seemed to depend on a balance between a relative increase in indole glucosinolates and a decrease in aliphatic glucosinolates (Birch *et al*., 1992; Hopkins *et al*., 1998). The additional stress provided by competition from the clover intercrop caused interactive effects on *e.g.* the total root glucosinolate level, which was reduced in intercropped treatments at higher egg densities, while the levels in monoculture treatments were fairly constant (Fig. 9). Thus, competition with clover appears to have impaired the ability of the cabbage plants to maintain root glucosinolate levels in the presence of high *D. floralis* infestations (Paper IV).
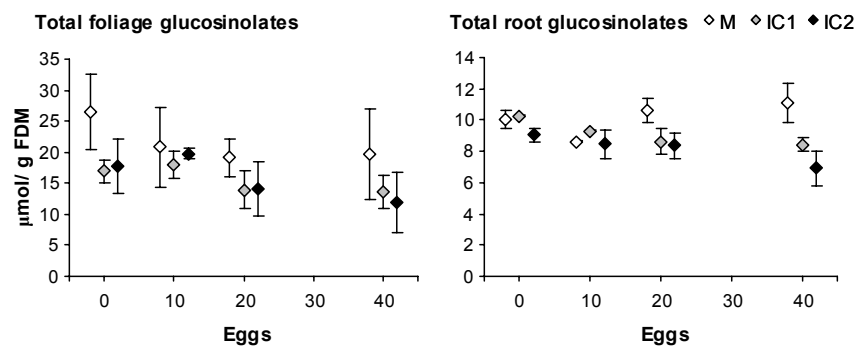
Fig. 9. Changes in root aliphatic glucosinolates concentrations (μmol g^{-1} freeze-dried matter, FDM) in monoculture and in the two clover intercropping densities at an increasing *D. floralis* egg density (M = monoculture, IC1 = low clover density, IC2 = high clover density).

It is clear from the results of this study that individual glucosinolates may not respond uniformly to herbivory or plant competition, within the usual division of glucosinolates into aliphatic, aromatic and indole based glucosinolates. This was shown, for example, for the indole methoxyglucobrassicin, which was the only indole glucosinolate that increased in intercropped roots. In addition, the responses of a specific group of compounds based on chemical structure may be dominated by a few compounds, or sometimes a single compound. In this study, the sinigrin and glucobrassicin dominating in foliage and the sinigrin and neoglucobrassicin in roots had a major influence on the responses of their specific structural groups. As the responsiveness to specific glucosinolates can vary by several orders of magnitude for both *D. floralis* and *D. radicum* (Roessingh *et al*., 1992, Simmonds

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et al., 1994), the dominant compound may not be the most stimulating one from the herbivore point of view. It is therefore relevant to consider these compounds on an individual level (Paper IV).

Development of D. floralis

In the greenhouse experiment, the development of *D. floralis* was affected both by feeding on intercropped cabbage plants and by sharing their food source with conspecific larvae, which resulted in lower pupal weights (Fig. 10).
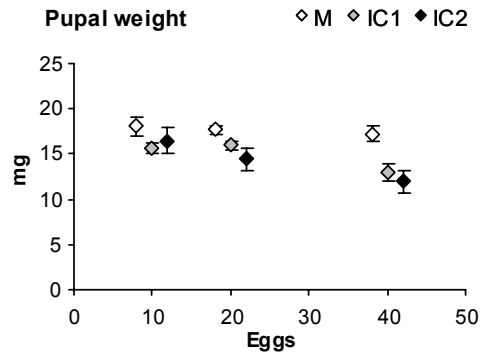

Fig. 10. Effects of intercropping density and *D. floralis* egg density on the final pupal weights (mg) of *D. floralis* (M = monoculture, IC1 = low clover density, IC2 = high clover density).

Evaluation of the factors resulting in reduced pupal weight is complicated, as all of the aspects of quality that were measured were changing at the same time, and due to two different causes; interspecific competition between the cabbage host plants and the clover intercrop, and feeding by *D. floralis* larvae. Reduced food availability for small intercropped roots or through competition with other larvae is one possible cause for reduced larval growth (Paper III). A previous study (Hopkins *et al.*, 1993) showed that intraspecific competition between feeding *D. floralis* larvae led to reduced pupal weights. The positive correlation found here between pupal weight and root weight (Paper III) indicates that a limited food source is a possible cause for impaired larval development in the intercropped treatments.

Other aspects of quality that may have affected larval growth include a high nitrogen concentration, which may have benefited *D. floralis* larvae feeding on the more nutrient-rich monoculture roots (Bethke *et al.*, 1987; Hunt, Drury & Maw, 1992) (Paper III). In contrast, a higher NDF and lignin content in intercropped and insect-damaged roots may have reduced larval growth (Hopkins *et al.*, 1995), as illustrated by the negative correlation between pupal weight and root NDF and lignin (Paper III).

The aggregated oviposition pattern observed for species such as *D. radicum* and *D. antiqua* (Mukerji & Harcourt, 1970; Judd & Borden, 1992), suggests that their larvae may benefit from mutual feeding. Since *D. radicum* prefers to oviposit on

plants with moderate damage rather than undamaged or heavily infested plants (Baur, Kostal & Städler, 1996), there is a possibility that intra-specific interactions may lead to a survival advantage. However, an enhanced survival at high egg densities, expressed as the percentage of individuals forming pupae successfully, was not found in this experiment (Paper III).

There was a positive correlation between the concentration of aliphatic glucosinolates in the cabbage roots and pupal weight. This was because pupal weight was positively correlated with concentrations of the individual glucosinolates iberin, sinigrin and napin. This also resulted in a positive correlation between pupal weight and the total concentration of glucosinolates. Plants with high levels of glucosinolates at harvest produced heavier pupae. There was no correlation between pupal weight and the concentration of indole glucosinolates. Within the indole group, there were variable patterns of correlation between pupal weight and individual glucosinolate concentrations. Pupal weight was positively correlated with hydroglucobrassicin, but negatively correlated with methoxy-glucobrassicin (Fig. 11).
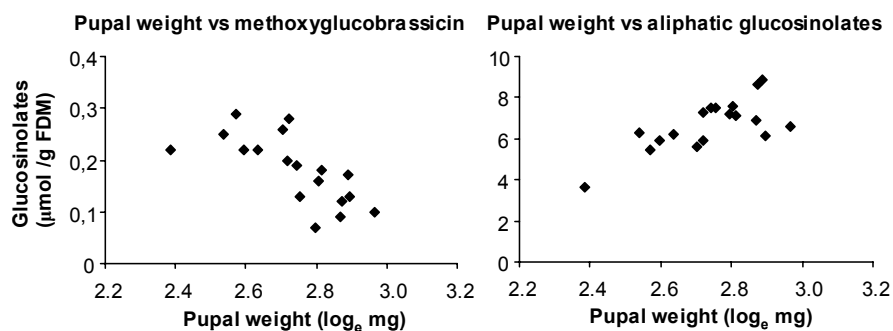
Fig. 11. Correlation results for pupal weights and methoxyglucobrassicin and the group of aliphatic glucosinolates.

The negative correlation between pupal weight and the concentration of methoxyglucobrassicin is the only indication that glucosinolates would provide a defence against feeding by *D. floralis* larvae. However, this needs to be investigated further, as the results of this experiment do not say anything about the glucosinolate profile or the concentration of individual glucosinolates during the larval feeding period, especially as glucosinolates seem to have both a fast induction response and turnover rate (Martin & Müller, 2007).

In the Brassicaceae, the glucosinolate-myrosinase complex has been called the "mustard oil bomb" for its defence properties (Ratzka *et al*., 2002), but several specialist insects have evolved strategies for disarming this defence mechanism. The diamond back moth (*P. xylostella*) prevents the formation of toxic hydrolysis products arising from this plant defence system by producing an enzyme that desulphates glucosinolates in the gut of the feeding larva (Ratzka *et al.*, 2002). The larva of the small white butterfly (*Pieris rapae* L.) redirects the glucosinolate hydrolysis reaction from the formation of toxic isothiocyanates to the formation of

harmless nitriles, through a specific gut protein (Wittstock *et al.*, 2004). However, these disarming strategies do not always seem effective, since the glucosinolate-myrosinase system has also reduced feeding in cruciferous specialists such as *P. xylostella* and *Phyllotreta cruciferae* Goeze (Siemens & Mitchell-Olds, 1996) and decreased growth in *P. rapae* (Agrawal & Kurashige, 2003). However, it should be noted that other studies have found no such effect (Hopkins, Ekbom & Henkow, 1998; Traw & Dawson, 2002; Travers-Martin & Müller, 2007).

It is not known whether, and how, *D. floralis* or *D. radicum* are affected specifically by the glucosinolates in their diet or their specific strategy used for coping with the glucosinolate-myrosinase system. The mechanisms for plant antibiotic resistance causing developmental differences on different crucifers (Finch & Ackley, 1977; Hopkins *et al.*, 1995) most likely depend on both structural and chemical traits, in which the glucosinolate profile may play a significant role.

Conclusions and applications

The development of intercropping as a pest management strategy must be based on knowledge of the behaviour and biology of the target pest. Based on this knowledge, there is increased potential for the successful development of locally adjusted intercropping systems for optimal pest reduction. This thesis shows that intercropping of cabbage and red clover has the potential to reduce oviposition by the turnip root fly, *Delia floralis*, compared with cabbage monoculture. In addition, the border effect found shows that the effect of intercropping can be enhanced if *D. floralis* is provided with an alternative oviposition site, in this case a monoculture that functions as a trap crop. This implies that a cropping design in which intercropping and monoculture are combined would be comparable to a push-pull strategy, where location of a resource is made difficult (push), whilst at the same time providing the pest with an attractive alternative (pull).

This thesis further shows that natural enemies, in this case mainly predators, have the potential to reduce the population of *D. floralis* in the field. Even though the difference in effects of natural enemies was similar in both cultivation systems, this study nonetheless shows that there is potential to retain predation pressure in the intercropping system, despite lower predator activity-densities. As a combination of intercropping and monoculture may be a strategy to enhance the effect on *D. floralis* oviposition, it is promising that the effect of predation was comparable between cultivation systems. For the development of systems where diversity is used for pest reduction and spatial manipulation of attacks, it is probable that measures directed towards enhancing the natural enemies at farm level are more important than intercropping per se for enhancing the effect of natural enemies in the field.

A high level of clover competition not only reduced cabbage biomass, but also led to altered plant quality with respect to root fibre and root nitrogen content. In addition, competition altered the glucosinolate profile of both cabbage foliage and roots. Adding *D. floralis* herbivory to this system had further and sometimes interactive effects on cabbage growth, structure and chemical content, and these competition and herbivory induced changes had negative consequences for *D. floralis* development. Although the competitive conditions in this experiment far exceeded an acceptable field situation, the results provide further insight into plant responses in complex systems. Knowledge of plant responses to herbivory in these systems may be useful in identifying mechanisms that affect herbivores negatively.

To conclude, intercropping and trap cropping are often seen as opposing strategies for pest control, but the results in this thesis show that a combination may lead to an enhanced effect on pest insect behaviour. This could provide the potential to protect a more susceptible crop through intercropping, while using a more tolerant plant species as a trap crop. Knowledge of insect responses in these systems is still needed, and a future challenge will be to integrate such knowledge in diversification strategies for pest reduction. Consideration must be given to choice of intercrop species for optimal disruption and the integration of a trap crop into the system for manipulation of attack distribution. Furthermore, long-term studies on effects on natural enemy populations in diverse agroecosystems are scarce, so further studies are essential for the development of diverse systems for optimal pest reduction of predators and parasitoids. Although effects of competition may be minimised in intercropping systems through choice of intercrop species or mechanical management, plant-plant interactions will occur and consequently affect herbivores in these systems, both in their host plant search, host plant acceptance and subsequent development. This may be important for the long-term effects on pest insect dynamics in these systems, but there are still questions to be answered regarding plant resistance mechanisms and the responses by herbivores to these.

References

Agele, S.O., Iremiren, G.O. & Ojeniyi, S.O. 1999. Effects of plant density and mulching on the performance of late-season tomato (*Lycopersicon esculentum*) in southern Nigeria. *Journal of Agricultural Science* 133, 397-402.

Agrawal, A.A. & Kurashige, N.S. 2003. A role for isothiocyanates in plant resistance against the specialist herbivore *Pieris rapae*. *Journal of Chemical Ecology* 29: 1403-1415.

Andersen, A., Hansen, Å.G., Rydland, N. & Øyre, G. 1983. Carabidae and Staphylinidae (Col.) as predators of eggs of the turnip root fly *Delia floralis* Fallén (Diptera, Anthomyiidae) in cage experiments. *Zeitschrift für angewandte Entomologie* 95: 499-506.

Andow, D.A. & Risch, S.J. 1985. Predation in diversified agroecosystems: Relations between a coccinellid predator *Coleomegilla maculata* and its food. *Journal of Applied Ecology*, 22, 357-372.

Andow, D.A. 1991. Vegetational diversity and arthropod population response. *Annual Review of Entomology* 36: 561-86.

Andrews, D.J. & Kassan, A.H. 1976. The importance of multiple cropping in increasing food supplies. In: *Multiple Cropping*. R.I. Papendick, P.A. Sanchez & G.B. Triplett (eds.). *Asa Special Publication Number 27*. American Society of Agronomy. pp 1-10.

Armstrong, G. & McKinlay, R.G. 1997. The effect of undersowing cabbages with clover on the activity of carabid beetles. *Biological Agriculture and Horticulture* 15, 269-277.

Åsman, K., Ekbom, B. & Rämert, B. 2001. Effect of intercropping on oviposition and emigration behavior of the leek moth (Lepidoptera: Acrolepiidae) and the diamondback moth (Lepidoptera: Plutellidae). *Environmental Entomology*, 30, 288-294.

Åsman, K. & Ekbom, B. 2006. Responses of ovipositing moths to host plant deprivation: life history aspects and implications for intercropping. *Agricultural and Forest Entomology* 8, 213-219.

Bartlet, E., Kiddle, G. Williams, I. & Wallsgrove, R. 1999. Wound-induced increases in the glucosinolate content of oilseed and forage rape and their effect on subsequent herbivory by a crucifer specialist. *Entomologia Experimentalis et Applicata* 91, 163-167.

Båth, B., Kristensen, H.L. & Thorup-Kristensen, K. Root pruning for reduction of root competition increased crop growth and N uptake in an intercropping system. Submitted manuscript.

Baur, R., Kostal, V. & Städler, E. 1996. Root damage by conspecific larvae induces preference for oviposition in cabbage root flies. *Entomologia Experimentalis et applicata*, 80, 224-227.

Baur, R., Birch, A.N.E., Hopkins, R.J., Griffiths, D.W., Simmonds, M.S.J. & Städler, E. 1996a. Oviposition and chemosensory stimulation of the root flies *Delia radicum* and *D. floralis* in response to plants and leaf surface extracts from resistant and susceptible *Brassica* genotypes. *Entomologia Experimentalis et Applicata* 78, 61-65.

Baur, R., Kostal, V., Patrian, B. & Städler, E. 1996b. Preference for plants damaged by conspecific larvae in ovipositing cabbage root flies: Influence of stimuli from leaf surface and roots. *Entomologia Experimentalis et Applicata* 81, 353-364.

Bergelson, J. & Kareiva, P. 1987. Barriers to movement and the response of herbivores to alternative cropping patterns. *Oecologia* 71, 457-460.

Bethke, J.A. & Parella, M.P. 1985. Leaf puncturing, feeding and oviposition behavior of *Liriomyza trifolii*. *Entomologia Experimentalis et Applicata* 39, 149-154.

Bethke, J.A., Parrella, M.P., Trumble, J.T. & Toscano, N.C. 1987. Effect of tomato cultivar and fertilizer regime on the survival of *Liriomyza trifolii* (Diptera: Agromyzidae). *Journal of Economic Entomology* 80, 200-203.

Birch, A.N.E., Griffiths, D.W., Hopkins, R.J., MacFarlane Smith, W.H. & McKinlay, R.G. 1992. Glucosinolate responses of swede, kale, forage and oilseed rape to root damage by turnip root fly (*Delia floralis*) larvae. *Journal of the Science of Food and Agriculture* 60, 1-9.

Birch, A.N.E., Griffiths, D.W., Hopkins, R.J. & MacFarlane Smith, W.H. 1996. A time-course study of chemical and physiological responses in Brassicas induced by turnip root fly (*Delia floralis*) larval feeding. *Entomologia Experimentalis et Applicata* 80, 221-223.

Bodreau, M.A. 1993. Effect of intercropping beans with maize on the severity of angular leaf-spot of beans in Kenya. *Plant Pathology* 42, 16-25.

Bommarco, R. & Banks, J.E. 2003. Scale as modifier in vegetation diversity experiments: effects on herbivores and predators. *Oikos* 102, 440-448

Bonifas, K.D., Walters, D.T., Cassman, K.G. & Lindquist, J.L. 2005. Nitrogen supply affects root:shoot ratio in corn and velvetleaf (*Abutilon theophrasti*). *Weed Science* 53, 670-675.

Booij, C.J.H., Noorlander, J. & Theunissen, J. 1997. Intercropping cabbage with clover: Effects on ground beetles. *Biological Agriculture and Horticulture* 15, 261-268.

Broatch, J.S. & Vernon, R.S. 1997. Comparison of water pan traps and sticky traps for monitoring *Delia* spp. (Diptera: Anthomyiidae) in canola. *Canadian Entomologist* 129, 979-984.

Bromand, B. 1980. Investigations on the biological control of the cabbage root fly (*Hylemya brassicae*) with *Aleochara bilineata*. *SROP/WPRS Bulletin* 3(1), 49-62.

Brooks, A.R. 1951. Identification of root maggots (Diptera: Anthomyiidae) attacking cruciferous garden crops in Canada, with notes on biology and control. *The Canadian Entomologist* 3, 109-120.

Bryan, K.M. & Wratten, S.D. 1984. The responses of polyphagous predators to prey spatial heterogeneity: aggregation by carabid and staphylinid beetles to their cereal aphid prey. *Ecological Entomology* 9, 251-259.

Bukovinszky, T., Tréfás, H., van Lenteren, J.C., Vet, L.E.M. & Fremont, J. 2004. Plant competition in pest-suppressive intercropping systems complicates evaluation of herbivore responses. *Agriculture, Ecosystems and Environment* 102, 185-196.

Bukovinszky, T., Potting, R.P.J., Clough, Y., van Lenteren, J.C. & Vet, L.E.M. 2005. The role of pre- and post- alighting detection mechanisms in the responses to patch size by specialist herbivores. *Oikos* 109, 435-446.

Chapman, P.A., Armstrong, G. & McKinlay, R.G. 1999. Daily movements of *Pterostichus melanarius* between areas of contrasting vegetation density within crops. *Entomologia Experimentalis et Applicata* 91, 477-480.

Cipollini, D.F. & Bergelson, J. 2001. Plant density and nutrient availability constrain constitutive and wound-induced expression of trypsin inhibitors in Brassica napus. *Journal of Chemical Ecology* 27, 593-609.

Cipollini, D.F. & Bergelson, J. 2002. Interspecific competition affects growth and herbivore damage of *Brassica napus* in the field. *Plant Ecology* 162, 227-231.

Coaker, T.H. & Williams, D.A. 1963. The importance of some Carabidae and Staphylinidae as predators of the cabbage root fly, *Erioischia brassicae* (Bouché). *Entomologia Experimentalis et Applicata* 6, 156-164.

Coaker, T.H. & Finch, S. 1971. The cabbage root fly, *Erioichia brassicae* (Bouché). *Report of the National Vegetable Research Station for 1970*, pp. 23-42.

Cole, R.A. 1997. The relative importance of glucosinolates and amino acids to the development of two aphid pests *Brevicoryne brassicae* and *Myzus persicae* on wild and cultivated brassica species. *Entomologia Experimentalis et Applicata* 85, 121-133.

Degen, S. & Städler, E. 1996. Influence of natural leaf shapes on oviposition in three phytophagous flies: A comparative study. *Entomologia Experimentalis et Applicata* 80, 97-100.

de Jong, R. & Städler, E. 1999. The influence of odour on the oviposition behaviour of the cabbage root fly. *Chemoecology* 9, 151-154.

den Belder, E., Elderson, J. & Vereijken, G. 2000. Effects of clover on host plant selection by Thrips tabaci adults in leek. *Entomologia Experimentalis et Applicata* 94, 173-182.

Denno, R.F., Finke, D.L. & Langelotto, G.A. 2005. Direct and indirect effects of vegetation structure and habitat complexity on predator-prey and predator-predator interactions. In: *Ecology of Predator-Prey Interactions.* Barbosa, P. & Castellanos, I. (eds.). Oxford University Press, New York, pp. 211-239.

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Dixon, P., Coady, J.R., Larsson, D.J. & Spaner, D. 2004. Undersowing rutabaga with white clover: Impact on *Delia radicum* (Diptera: Anthomyiidae) and its natural enemies. *The Canadian Entomologist* 136, 427-442.

Dufrene, M. & Legendre, P. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67, 345-366.

Elton, C.S. 1958. *The Ecology of Invasions by Plants and Animals*. Methuen and Co., London, England. 209 pp.

Finch, S. & Ackley, C.M. 1977. Cultivated and wild host plants supporting populations of the cabbage root fly. *Annals of Applied Biology* 85, 13-22.

Finch, S. & Elliot, M.S. 1992. Carabidae as potential biological agents for controlling infestations of the cabbage root fly. *Phytoparasitica* 20(Suppl.), 67-70.

Finch, S. & Elliot, M.S. 1994. Predation of cabbage root fly eggs and larvae by carabid ground beetles – fact or fantasy? *IOBC/WPRS Bulletin* 17(8), 109-114.

Finch, S. 1996. Effect of beetle size on predation of cabbage root fly eggs by ground beetles. *Entomologia Experimentalis et Applicata* 81, 199-206.

Finch, S. & Kienegger, M. 1997. A behavioural study to help clarify how undersowing with clover affects host plant selection by pest insects of brassica crops. Entomologia *Experimentalis et Applicata* 84, 165-172.

Finch, S. & Collier, R.H. 2000. Host-plant selection by insects - a theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants. *Entomologia Experimentalis et Applicata* 96, 91-102.

Finch, S. & Billiald, H. & Collier, R.H. 2003. Companion planting – do aromatic plants disrupt host-plant finding by the cabbage root fly and the union fly more effectively than non-aromatic plants? *Entomologia Experimentalis et Applicata* 109, 183-195.

Fininsa, C. 2001. *Epidemiology of Bean Common Bacterial Blight and Maize Rust in Intercropping*. PhD thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Freuler, J. & Fischer, S. 1982. Description d'un piège à oeufs pour la mouche du chou, *Delia brassicae* Wiedemann. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 55, 77-85.

Giamoustaris, A. & Mithen, R. 1995. The effect of modifying the glucosinolate content of leaves of oilseed rape (*Brassica napus* ssp. *oleifera*) on its interactions with specialist and generalist pests. *Annals of Applied Biology* 126, 347-363.

Gouinguené, S.P.D & Städler, E. 2006. Comparison of the egg-laying behaviour and electrophysiological responses of *Delia radicum* and *Delia floralis* to cabbage leaf compounds. *Physiological Entomology* 31, 382-389.

Gouinguené, S.P.D, Poiger, T. & Städler, E. 2006. Eggs of cabbage root fly stimulate conspecific oviposition: Evaluation of the activity and determination of an egg-associated compound*. Chemoecology* 16, 107-113.

Greenslade, P.J.M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology* 33, 301-310.

Griffiths, D.W., Birch, A.N.E. & MacFarlane Smith, W.H. 1994. Induced changes in the indole glucosinolate content of oilseed and forage rape (*Brassica napus*) plants in response to either turnip root fly (*Delia floralis*) larval feeding or artificial root damage. *Journal of the Science of Food and Agriculture* 65, 171-178.

Halkier, B.A. & Gershenzon, J. 2006. Biology and biochemistry of glucosinolates. *Annual Review of Plant Biology* 57, 303-333.

Hambäck, P.A., Pettersson, J. & Ericson, L. 2003. Are associational resistance species specific? *Functional Ecology* 17, 87-93.

Hartfield, C. & Finch, S. 2003. Releasing the rove beetle *Aleochara bilineata* in the field as a biological agent for controlling the immature stages of the cabbage root fly, *Delia radicum*. *IOBC WPRS Bulletin* 26(3), 127-133.

Hartfield, C., Nethercleft, M. & Finch, S. 1999. The effect of undersowing *Brassica* crops with clover on host finding by *Trybliographa rapae* and *Aleochara bilineata*, two parasitoids of the cabbage root fly, *Delia radicum*. *IOBC WPRS Bulletin* 22(5), 117-124.

Havukkala, I. 1982. Odour source finding behaviour of *Delia brassicae* in the field. *Proceedings of the 5th International Symposium on Insect-Plant Relationships*, NL-Wageningen, pp. 397-399.

Havukkala, I. & Virtanen, M. 1984. Oviposition of single females of the cabbage root flies *Delia radicum* and *D. floralis* (Diptera, Anthomyiidae) in the laboratory. *Annales Agriculturae Fenniae* 50, 81-84.

Havukkala, I. & Virtanen, M. 1985. Behavioural sequence of host selection and oviposition in the turnip root fly *Delia floralis* (Fall.) (Anthomyiidae). *Zeitschrift für angewandte Entomologie* 100, 39-47.

Havukkala, I. 1987. Odour source finding behaviour of the turnip root fly, *Delia floralis* (Fall.) (Dipt., Anthomyiidae) in the field. *Journal of Applied Entomology* 104, 105-110.

Herms, D.A. & Mattson, W.J. 1992. The dilemma of plants – to grow or defend. *Quarterly Review of Biology* 67, 283-335.

Hochuli, D.F., Sanson, G.D. & Roberts, B. 1993. Approximate digestibility of fibre for two locusts. *Entomologia Experimentalis et Applicata* 66, 187-190.

Hochuli, D.F. 1996. The ecology of plant/insect interactions: implications of digestive strategy for feeding by phytophagous insects. *Oikos* 75, 133-141.

Hokkanen, H.M.T. 1991. Trap cropping in pest management. Annual *Review of Entomology* 36, 119-138.

Hooks, C.R.R. & Johnson, M.W. 2001. Broccoli growth parameters and level of head infestations in simple and mixed plantings, impact of increased flora diversification. *Annals of Applied Entomology* 138, 269-280.

Hooks, C.R.R. & Johnson, M.W. 2003. Population densities of herbivorous lepidopterans in diverse cruciferous cropping habitats: Effects of mixed cropping and using a living mulch. BioControl 51, 485-506.

Hopkins, R.J., Griffiths, D.W., Birch, A.N.E., McKinlay, R.G. & Hall, J.E. 1993. Relationship between turnip root fly (*Delia floralis*) larval development and the sugar content of swede (*Brassica napus* ssp. *rapifera*) roots. *Annals of Applied Biology* 122, 405-415.

Hopkins, R.J., Birch, A.N.E., Griffiths, D.W., Morrison, I.M. & McKinlay, R.G. 1995. Changes in dry matter, sugar, plant fibre and lignin contents of swede, rape and kale roots in response to turnip root fly (*Delia floralis*) larval damage. *Journal of the Science of Food and Agriculture* 69, 321-328.

Hopkins, R.J., Wright, F., McKinlay, R.G. & Birch, A.N.E. 1996. Analysis of sequential behaviour patterns: The oviposition decision of the turnip root fly, *Delia floralis*. *Entomologia Experimentalis et Applicata* 80, 93-96.

Hopkins R.J., Birch, A.N.E., Griffiths, D.W., Baur, R., Städler, E. & McKinlay, R.G. 1997. Leaf surface compounds and oviposition preference of turnip root fly *Delia floralis:* The role of glucosinolate and nonglucosinolate compounds. *Journal of Chemical Ecology* 23, 629-643.

Hopkins, R.J., Ekbom, B. E. & Henkow, L. 1998. Glucosinolate content and susceptibility for insect attack of three genotypes of *Sinapis alba* L. *Journal Chemical Ecology* 24, 1203-1216.

Hopkins, R.J., Griffiths, D.W., Birch, A.N.E. & McKinlay R.G. 1998. Influence of increasing herbivore pressure on modification of glucosinolate content of swedes (*Brassica napus* spp. *rapifera*). *Journal of Chemical Ecology* 24, 2003-2019.

Hopkins, R.J., Wright, F., Birch, A.N.E. & McKinlay, R.G. 1999. The decision to reject an oviposition site: Sequential analysis of the post-alighting behaviour of *Delia floralis*. *Physiological Entomology* 24, 41-50.

Hunt, D.W.A., Drury, C.F. & Maw, H.E.L. 1992. Influence of nitrogen on the performance of Colorado potato beetle (Coleoptera: Chrysomelidae) on tomato. *Environmental Entomology* 21, 817-821.

Hurter, J. Ramp, T, Patrian, B, Städler, E., Roessingh, P., Baur, R., de Jong, R., Nielsen, J.K., Winkler, T., Richter, W.J., Müller, D. & Ernst, B. 1999. Oviposition stimulants for the cabbage root fly isolated from cabbage leaves. *Phytochemistry* 51, 377-382.

Jones, T.H. & Hassell, M.P. 1988. Patterns of parasitism by *Trybliographa rapae*, a cynipid parasitoid of the cabbage root fly, under laboratory and field conditions. *Ecological Entomology* 13, 309-317.

Jørgensen, J. 1957. Den store kålflue (*Chortophila floralis* Fall.) *Beretning fra Statens forsøgsvirksomhed i plantekultur* 533, 657-712.

Judd, G.J.R. & Borden, J.H. 1992. Aggregated oviposition in Delia antiqua (Meigen): A case for mediation by semiochemicals. *Journal of Chemical Ecology*, 18, 621-635.

Kliebenstein, D., Pedersen, D., Barker, B. & Mitchell-Olds, T. 2002. Comparative analysis of quantitative trait loci controlling glucosinolates, myrosinase and insect resistance in Arabidopsis thaliana. *Genetics*, 325-332.

Koritsas, V.M., Lewis, J.A. & Fenwick, G.R. 1991. Glucosinolate responses of oilseed rape, mustard and kale to mechanical wounding and infestation by cabbage stem flea beetle (*Psylliodes chrysocephala*). *Annals of Applied Biology* 118, 209-221.

Kostal, V. & Finch, S. 1994. Influence of background on host plant selection and subsequent oviposition by the cabbage root fly (*Delia radicum*). *Entomologia Experimentalis et Applicata* 70, 153-163.

Langer, V. 1996. Insect-crop interactions in a diversified cropping system: Parasitism by *Aleochara bilineata* and *Trybliographa rapae* of the cabbage root fly, *Delia radicum*, on cabbage in the presence of white clover. *Entomologia Experimentalis et Applicata* 80, 365-374.

Langer, V., Kinane, J. & Lyngkjær, M. 2007. Intercropping for pest management: The ecological concept. In: *Ecologically Based Integrated Pest Management*. Koul, O. & Cupreus, G.W. (eds.), Cabi Publishing, Wallingford, UK. 462 pp.

Langlet, X. & Brunel, E. 1996. Preliminary results on predation by *Aleochara bilineata* Gyll. (Coleoptera: Staphylinidae). *IOBC WPRS Bulletin* 19(11), 162-172.

Lavandero, B., Wratten, S., Shishehbor, P. & Worner, S. 2005. Enhancing the effectiveness of the parasitoid *Diadegma semiclausum* (Helen): Movement after use of nectar in the field. *Biological Control* 34, 152-158.

Letorneau, D.K. & Altieri, M.A. 1983. Abundance patterns of a predator, *Orius tristicolor* (Hemiptera: Anthocoridae), and its prey, *Frankliniella occidentalis* (Thysanoptera: Thripidae): Habitat attraction in polycultures versus monocultures. *Environmental Entomology* 12, 1464-1469.

Li, H., Kuo, J. Barbetti, M.J. & Sivasithamparam, K. 2007. Differences in the responses of stem tissues of spring-type *Brassica napus* cultivars with polygenic resistance and single dominant gene-based resistance to inoculation with *Leptosphaeria maculans*. *Canadian Journal of Botany* 85, 191-203.

Lundblad, C. 1933. Kålflugorna. *Statens Växtskyddsanstalt* 3. 103 pp.

Martin, N. & Müller, C. 2007. Induction of plant responses by a sequestering insect: Relationship of glucosinolate concentration and myrosinase activity. *Basic and Applied Ecology* 8, 13-25.

Maus, C., Mittman, B. & Peschke, K. 1998. Host records of parasitoid *Aleochara* Gravenhorst species (Coleoptera: Staphylinidae) attacking puparia of cyclorrhapheous Diptera. *Deutsche Entomologische Zeitschrift* 45, 231-254.

McCune, B. & Mefford, M.J. 1999. *Multivariate Analysis of Ecological Data, version 4.25*, MjM Software Design, Oregon.

McKinlay, R.G. 1994. Effect of intercropping swedes with clover on the level of cabbage root fly damage and numbers of carabid ground beetles. *IOBC WPRS Bulletin* 17(8), 168-172.

Mitchell, B. 1963. Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank). II. Studies on populations of adults in the field, with special reference to the technique of pitfall trapping. *Journal of Animal Ecology* 32, 377-392.

Mithen, R.F. 2001. Glucosinolates and their degradation products. *Advances in Botanical Research* 35, 213-262.

Moerschbacher, B.M., Noll, U., Gorrichon, L. & Reisener, H. 1990. Specific inhibition of lignification breaks hypersensitive resistance of wheat to wheat stem rust. *Plant Physiology* 93, 465-470.

Morison, G.D. 1939. The turnip root fly (*Phorbia floralis* Fallen) in northern Scotland. In: *Proceedings 7th International Congress of Entomology, Berlin* 1938, pp. 2576-2584.

Morley, K., Finch, S. & Collier, R.H. 2005. Companion planting – behaviour of the cabbage root fly on host plants and non-host plants. *Entomologia Experimentalis et Applicata* 117, 15-25.

Mukerji, M.K. & Harcourt, D.G. 1970. Spatial pattern of the immature stages of *Hylemya brassicae* on cabbage. *The Canadian Entomologist* 102, 1216-1222.

Mukerji, M.K. 1971. Major factors in survival of the immature stages *Hylemya brassicae* (Diptera: Anthomyiidae) on cabbage. *The Canadian Entomologist* 103, 717-728.

Nilsson, U., 2007. Ekologisk Odling av Grönsaker, Frukt och Bär. Hinder och Möjligheter för Framtida Utveckling. *Ekologiskt Lantbruk,* 49. 52 pp.

Nottingham, S.F. & Coaker, T.H. 1985. The olfactory response of cabbage root fly *Delia radicum* to the host plant volatile allylisothiocyanate. *Entomologia Experimentalis et Applicata* 39, 307-316.

Nottingham, S.F. 1987. Effects of non-host plant odors on anemotactic response to host-plant odor in female cabbage root fly, *Delia radicum*, and carrot rust fly, *Psila rosae*. *Journal of Chemical Ecology* 13, 1313-1317.

Osier, T.L. & Jennings, S.M. 2007. Variability in host-plant quality for the larvae of a polyphagous insect folivore in midseason: The impact of light on three deciduous sapling species. *Entomologia Experimentalis et Applicata* 123, 159-166.

Östman, Ö., Ekbom, B. & Bengtsson, J. 2003. Yield increase attributable to aphid predation by ground-living polyphagous natural enemies in spring barley in Sweden. *Ecological Economics* 45, 149-158.

Potts, M.J. 1990. Influence of intercropping in warm climates on pests and diseases of potato, with special reference to their control. *Field Crops Research* 25, 133-144.

Prokopy, R.J., Collier, R.H. & Finch, S. 1983. Visual detection of host plants by cabbage root flies. *Entomologia Experimentalis et Applicata* 34, 85-89.

Radovich, T.J.K., Kleinhenz, M.D. & Streeter, J.G. 2005. Irrigation timing relative to head development influences yield components, sugar levels, and glucosinolate concentrations in cabbage. *Journal of the American Society for Horticultural Science* 130 (6), 943-949

Rämert, B. 1996a. The influence of intercropping and mulches on the occurrence of polyphagous predators in carrot fields in relation to carrot fly (*Psila rosae* (F.)) (Diptera., Psilidae) damage. *Journal of Applied Entomology*, 120, 39-46.

Rämert, B. 1996b. Intercropping as a strategy for reducing damage to carrots caused by the carrot fly, *Psila rosae*. *Biological Agriculture and Horticulture*, 13, 359-369.

Rämert, B. & Ekbom, B. 1996. Intercropping as a management strategy against carrot rust fly (Diptera: Psilidae): A test of enemies and resource concentration hypothesis. *Population Ecology* 25, 1092-1099.

Ratzka, A., Vogel, H., Kliebenstein, D.J., Mitchell-Olds, T. & Kroymann, J. 2002. Disarming the mustard oil bomb. *PNAS*, 99, 11223-11228.

Read, D.C. 1962. Notes on the life history of *Aleochara bilineata* Gyll. (Coleoptera: Staphylinidae), and on its potential value as a control agent for the cabbage root maggot, *Hylemya brassicae* Bouché (Diptera: Anthomyiidae). *The Canadian Entomologist*, 94, 417-424.

Renwick, J.A. 2002. The chemical world of crucivores: Lures, treats and traps. *Entomologia Experimentalis et Applicata* 104, 35-42.

Risch, S.J. 1983. Intercropping as cultural pest control: prospects and limitations. *Environmental Management* 7, 9-14.

Rittinger, P.A., Biggs, A.R. & Peirson, D.R. 1987. Histochemistry of lignin and suberin deposition in boundary layers formed after wounding in various plant species and organs. *Canadian Journal of Botany* 65, 1886-1892.

Roessingh, P. & Städler, E. 1990. Foliar form, colour and surface characteristics influence oviposition behaviour in the cabbage root fly *Delia radicum*. *Entomologia Experimentalis et Applicata* 57, 93-100.

Roessingh, P., Städler, E., Fenwick, G.R., Lewis, J.A., Nielsen J.K., Hurter, J. & Ramp, T. 1992. Oviposition and tarsal chemoreceptors of the cabbage root fly are stimulated by

glucosinolates and host plant extracts. *Entomologia Experimentalis et Applicata* 65, 267-282.

Roessingh, P. Stadler, E. Baur, R. Hurter, J. & Ramp, T. 1997. Tarsal chemoreceptors and oviposition behaviour of the cabbage root fly (*Delia radicum*) sensitive to fractions and new compounds of host-leaf surface extracts. *Physiological Entomology* 22, 140-148

Rojas, J.C., Wyatt, T.D. & Birch, M.C. 2000. Flight and oviposition behavior toward different host plant species by the cabbage moth, *Mamestra brassicae* (L.) (Lepidoptera: Noctuidae). *Journal of Insect Behaviour* 13, 247-254.

Root, R. 1973. Organisation of a plant-arthropod association in simple and diverse habitats. The fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43, 95-124.

Sheenan, W. 1986. Response by specialist and generalist natural enemies to agrosystem diversification: A selective review. *Environmental Entomology* 15, 456-461.

Siemens, D.H. & Mitchell-Olds, T. 1996. Glucosinolates and herbivory by specialists (Coleoptera: Chrysomelidae, Lepidoptera: Plutellidae): Consequences of concentration and induced resistance. *Environmental Entomology*, 25, 1344-1353.

Simmonds, M.S.J., Blaney, W.M., Mithen, R., Birch, A.N.E. & Lewis, J. 1994. Behavioural and chemosensory responses of the turnip root fly (*Delia floralis*) to glucosinolates. *Entomologia Experimentalis et Applicata* 71, 41-57.

Simpson, S.J. & Raubenheimer, D. 1995. The geometric analysis of feeding and nutrition: A user´s guide. *Journal of Insect Physiology* 7, 545-553.

Singer, M.C. 1982. Quantification of host preference by manipulation of oviposition behaviour in the butterfly *Euphydryas editha*. *Oecologia* 52, 230-235.

Städler, E. 1978. Chemoreception of host plant chemicals by ovipositing females of *Delia* (*Hylemya*) *brassicae*. *Entomologia Experimentalis et Applicata* 24, 511-520.

Städler, E. & Schöni, R. 1990. Oviposition behavior of the cabbage root fly, *Delia radicum* (L.), influenced by host plant extracts. Journal of Insect Behavior 3, 195-209.

Stamp, N., Bradfield, M., Li, S. & Alexander, B. 2004. Effect on competition on plant allometry and defence. *American Midland Naturalist* 151, 50-64.

Sundby, R.A. & Taksdal G. 1969. Surveys of parasites of *Hylemyia brassicae* (Bouché), and *Hylemyia floralis* (Fallén) (Diptera, Muscidae) in Norway. *Norsk entomologisk tidsskrift* 16, 97-106.

Theunissen, J., Booij, C.J.H. & Lotz, L.A.P. 1995. Effects of intercropping white cabbage with clovers on pest infestation and yield. *Entomologia Experimentalis et Applicata* 74, 7-16.

Thiele, H.U. 1977. *Carabid Beetles in Their Environments. A Study on Habitat Selection by Adaptations in Physiology and Behaviour*. Springer-Verlag, New York. 369 pp.

Travers-Martin, N. & Müller, C. 2007. Specificity of induction responses in *Sinapis alba* L. and their effects on a specialist herbivore. *Journal of Chemical Ecology* 33, 1582-1597.

Traw, B.M. & Dawson, T.E. 2002. Reduced performance of two specialist herbivores (Lepidoptera: Pieridae, Coleoptera: Chrysomelidae) on new leaves of damaged black mustard plants. Environmental Entomology 31: 714-722.

Tukahirwa, E.M. & Coaker, T.H. 1982. Effect of mixed cropping on some insect pests of brassicas: Reduced *Brevicoryne brassicae* infestations and influences on epigeal predators and the disturbance of oviposition behaviour in *Delia brassicae*. *Entomologia Experimentalis et Applicata* 32, 129-140.

van Dam, N.M. & Raaijmakers, C.E. 2006. Local and systemic induced responses to cabbage root fly larvae (Delia radicum) in *Brassica nigra* and *B. oleracea*. *Chemoecology* 16, 17-24.

Vandermeer, J. 1989. *The Ecology of Intercropping*. Cambridge University Press, Cambridge, USA. 237 pp.

van Dinther, J.B.M. & Mensink, F.T. 1971. Use of radioactive phosphorus in studying egg predation by carabids in cauliflower fields. *Medeilingen van de Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent* 36, 283-293.

van Loon, J.J.A., Blaakmeer, A., Griepink, F.C., van Beek, T.A., Schonooven, L.M. & de Groot, A. 1992. Leaf surface compound from *Brassica oleracea* (Cruciferae) induces oviposition by *Pieris brassicae* (Lepidoptera: Pieridae). *Chemoecology* 3, 39-44.

van Soest, P.J., Robertson, J.B. & Lewis, B.A. 1991. Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *Journal of Dairy Science* 74, 3583-3597.

Varis, A. 1967. Studies on the biology of the cabbage root fly (*Hylemya brassicae* Bouché) and the turnip root fly (*Hylemya floralis* Fall.). *Annales Agriculturae Fenniae* 6, 1-13.

Vasina, A.N. 1927. The cabbage fly (*Hylemyia brassicae* Bché and *Hylemyia floralis* Fall.). Trud. OpuitnoIssl. Uch. Stanz. Zashsch. Rast. Vred. Mosk. Zem. Otd. 63-89. (Ref. *Review of Applied Entomology* 16: 412-414).

Vodinskaya, K.I. 1928 On the biology and ecology of *Hylemyia brassicae* Bché and *Hylemyia floralis* Fall. *Review of Applied Entomology* 17: 141-142.

Widdicombe, W.D. & Thelen, K.D. 2002. Row width and plant density effect on corn forage hybrids. *Agronomy Journal* 94, 326-330.

Wishart, G. & Monteith, E. 1954. *Trybliographa rapae* (Westw.) (Hymenoptera: Cynipidae), a parasite of *Hylemya* spp. (Diptera: Anthomyiidae). *The Canadian Entomologist* 86, 145-154.

Wishart, G. 1957. Surveys of Parasites of *Hylemya* spp. (Diptera: Anthomyiidae) that attack cruciferous crops in Canada. *The Canadian Entomologist* 89, 450-454.

Wittstock, U., Agerbirk, N., Stauber, E.J., Olsen, C.E., Hipler, M., Mitchell-Olds, T., Gershenzon, J. & Vogel, H. 2004. Successful herbivore attack due to metabolic diversion of a plant chemical defense. *Proceedings of the National Academy of Sciences of the United States of America* 101, 4859-4864.

Yusuf, S.W. & Collins, G.G. 1998. Effect of soil sulphur levels on feeding preference of *Brevicoryne brassicae* on Brussels sprouts. *Journal of Chemical Ecology* 24: 417-424.

Zimmerman, G.M., Goetz, H. & Mielke, P.W. 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. *Ecology* 66, 606-611.

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