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Flower attractiveness and nectar accessibility for *Delia radicum* (Diptera:Anthomyiidae) with implications for the control by *Trybliographa rapae* (Hymenoptera:Figitidae)

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The Master thesis is part of a larger FORMAS financed PhD-project, that studies conservation biological control in a crop rotation system. The parasitoid wasp *T. rapae* and other natural enemies against *Delia* spp. should be favored through intercropping flower strips with e g Brassicaceae crops.

Keywords; conservation biological control, flower attractiveness, nectar accessibility, *Delia radicum*, *Trybliographa rapae*, Hymenoptera, parasitoid wasps, flower strips, selective biodiversity, floral food sources, *Lobularia maritima*, *Anethum graveolens*, *Fagopyrum esculentum*, olfactometer, volatile collection, GC-MS.

Front page picture: A cabbage root fly, *Delia radicum*, feeding on nectar from alyssum, *Lobularia maritima*.

Abstract

Conservation biological control aims at preserving populations of natural enemies in and around crop fields. Resources of floral nectar are important to natural enemies to increase the longevity, fecundity and motivation to seek host insects. Floral nectar for hymenopteran parasitoid wasps is investigated in a literature study, which suggests plant species to include in flower strips. However it is important to ensure that the plant species are selective towards natural enemies and not favor pest insects in addition. The aim of this Master thesis is to study the attraction to and nectar accessibility of dill, *Anethum graveolens* (Apiaceae); buchwheat, *Fagopyrum esculentum* (Polygonaceae) and alyssum, *Lobularia maritima* (Brassicaceae) for the severe crucivorous pest *Delia radicum*. The ambition is ultimately to find plants species selectively suitable as nectar sources for the parasitoid wasp *Trybliographa rapae*.

The three plants species investigated were found to be both attractive and having accessible nectar to *D. radicum*. The flower attractiveness experiments revealed significant attraction, where the preference was *L. maritima* > *A. graveolens* > *F. esculentum*. When given a choice between *L. maritima* (food plant) and cauliflower (host plant), there was a tendency of preference for *L. maritima*. The plant species had accessible nectar and gave a weight increase after 1, 6 and 12 hrs. After 1 h, *L. maritima* and *F. esculentum* gave an equal increase, which was significantly higher than for *A. graveolens*. Volatile collections of the highly attractive *L. maritima* were made and revealed six common compounds; toluene; limonene; 2-ethylhexyl acetate; 2-ethyl-1-hexanol; benzaldehyde; and 2-hydroxy-benzaldehyde. These compounds could be observed in a ratio of 17:1:1:2:2:1.

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Sammanfattning

Naturliga fiender; predatorer och parasitoider, behöver gynnas i odlingslandskapet på olika sätt för att öka deras prestation och reglering av skadegörare. Detta kallas conservation biological control, eller ”bevarandebiologi”. Genom att förse dem med skydd, övervintringsplatser, alternativa värdinsekter eller föda kan man bevara och upprätthålla stabila fiendepopulationer. Födokällor inkluderar alternativa värdinsekter, honungsdagg och växtbaserad föda, vilken kan bestå av pollen, nektar och extrafloral nektar. Nektar är en viktig kolhydratkälla för att öka livslängden, fekunditeten och motivationen att söka värdinsekter hos flera naturliga fiender. De naturliga fiendernas behov kan tillgodoses nära fältet genom till exempel obesprutade blommande fältkanter eller insådda perenna blomsterremsor. För en stabil kontroll av skadegörare över tiden krävs dock minskad habitat fragmentering samt en ökad biologisk mångfald i hela odlingslandskapet.

Blomsterremsor bör bestå av en blandning av annuella och perenna växter med olika blomningstid så att de producerar växtbaserad föda under hela säsongen och flera år framåt. Växtarterna ska väljas med omsorg så att de selektivt gynnar de naturliga fienderna och inte skadeinsekten. Selektiv biodiversitet kan baseras på attraktion till blomdofter, nektartillgänglighet, nektarkvalitet, nektarsmak, insektens näringsbehov och metabolism.

Parasitsteklar är parasitoider och är viktiga naturliga fiender då de lägger ägg i och dödar skadeinsekter. Parasitsteklar äter generellt inte pollen, varför nektar är mycket viktigt för deras överlevnad och parasiteringseffektivitet. Alla växter är inte lämpliga som nektarkällor till parasitsteklar. Även om parasitsteklar attraheras till en växt är det inte säkert att nektarn är tillgänglig. Tillgängligheten begränsas ofta genom skillnader i morfologi hos blomman jämfört med huvudkapselns storlek samt parasitstekelns mundelar. Parasitsteklar har oftast korta mundelar vilket begränsar deras nekarintag till blommor med grunda blomkronor och lättillgängliga nektarier. Bland växter som funnits både attraktiva och tillgängliga för parasitsteklar kan Apiaceae, flockblomstriga växter nämnas, såsom vildmorot, *Daucus carota* och kirskål, *Aegopodium podagraria*.

Parasitstekeln *Trybliographa rapae* (Hymenoptera:Figitidae) är betydelsefull som parasitoid på larverna av blomsterflugor, *Delia* spp. (Diptera:Anthomyiidae), vilka förekommer som allvarliga skadegörare i stjälkar och rötter i grönsaksgrödor. Lilla kålflugan, *Delia radicum*, är en allvarlig skadegörare på korsblommiga grödor, vars larver skadar rotsystemet och orsakar kvalitetsskador och torkstress. Dess värdväxtsök är välstuderat, det är dock inte sökandet efter och utnyttjandet av födokällor. För att kunna mogna ägg i sin kropp behöver kålflugan tillgång till en kolhydratkälla, vilken i fält utgörs av nektar. Detta skapar en konflikt då naturliga fiender även gynnas av nektar.

Syftet med detta Master-arbete är att studera attraktionen till samt nektar-tillgängligheten hos tre utvalda växter för *D. radicum*. Målet är att finna växter som fungerar som en selektiv nektarkälla för *T. rapae* och som kan användas i blomsterremsor i ett samodlingssystem med korsblommiga grödor. Växterna som undersöktes har tidigare visat sig lämpliga för parasitsteklar; dill, *Anethum graveolens* (Apiaceae); bovete, *Fagopyrum esculentum* (Polygonaceae) och strandkrassing, *Lobularia maritima* (Brassicaceae).

Blomattraktionen undersöktes genom tvåvalstest i en olfaktometer, där kålflugan fick välja mellan fuktig luft och blomdoft, eller mellan två olika blomdofter. Även ett tvåvalstest mellan värdväxt och födoväxt utfördes. Nektartillgängligheten för de utvalda växterna testades genom ett viktökningsförsök, där kålflugor fick tillgång till vardera blommande växt samt vägdes med olika intervaller. Slutligen undersöktes den kemiska sammansättningen av doften från *L. maritima*. Detta utfördes genom att adsorbera doften för att sedan desorbera doftuppsamlingen, varefter extraktet analyserades med GC-MS.

Alla tre växtarterna visade sig attraktiva samt hade tillgänglig nektar för *D. radicum*. Alla arterna var signifikant attraktiva, men preferensen var *L. maritima* > *A. graveolens* > *F. esculentum*. Vid val mellan *L. maritima* (födoväxt) and blomkål (värdväxt), tenderade *L. maritima* att föredras. Alla växtarterna gav en viktökning efter 1, 6 och 12 timmar. Efter 1 timme gav *L. maritima* och *F. esculentum* en liknande ökning, vilken var signifikant högre än för *A. graveolens*. Doftuppsamling från *L. maritima* uppvisade sex gemensamma ämnen; toluen; limonen; 2-etylhexyl acetat; 2-etyl-1-hexanol; benzaldehyd samt 2-hydroxy-benzaldehyd. Dessa observerades i förhållandet 17:1:1:2:2:1.

Resultaten diskuteras ur odlingssystemets perspektiv där tillämpningar föreslås.

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1. Introduction

The cabbage root fly, *Delia radicum* (Diptera:Anthomyiidae), is a noxious pest on Brassicaceae crops all over the world (Alford, 1999). Measures to control the pest are conventionally aimed at chemical insecticides. This thesis will deal with a conservation biological control approach, including habitat management to provide important resources to its natural enemy, the parasitoid wasp *Trybliographa rapae* (Hymenoptera:Figitidae). The tritrophic interaction Brassicaceae plant-pest-natural enemy is a well studied system, and similar studies have previously been conducted (Idris & Grafius, 1995; Bigger & Chaney, 1998; Pfiffner et al., 2003; Winkler et al., 2003; Wäckers, 2004; Forehand et al., 2006; Harvey & Wagenaar, 2006; Winkler et al., 2006). This thesis will add new information into the system about *D. radicum* and its food plant preferences.

1.1 Conservation biological control and habitat management

Insect pest management in organic farming excludes the use of chemical insecticides, which means that other methods have to be employed. Practices to favor the arthropod natural enemies, the predators and parasitoids, of the insect pests are one way. Favoring the natural enemies with the intention of increasing their performance is termed conservation biological control, or as defined "Modification of the environment or existing practices to protect and enhance specific natural enemies or other organisms to reduce the effect of pests." (Eilenberg et al., 2001). The enemies are supported by provision of resources such as shelter, overwintering sites, mating sites and food. Sites harboring natural enemies are especially important in annual monocultural cropping systems scarce in vegetational continuity and with a high degree of disturbance by cultural practices (Landis et al., 2000).

One strategy to retain natural enemies over the crop season and crop rotation is to provide alternative hosts to maintain the population when the target pest species is absent. This could be fairly straightforward in generalist predators, such as carabids and spiders, but is more difficult in specialist parasitoids with a narrow host range (Landis et al., 2000), e g. *T. rapae*, a parasitoid on *Delia* spp. (Wishart & Monteith, 1954).

Food sources include alternative hosts, honeydew-producing insects and plant provided food. Plant provided food comprises of pollen, floral nectar and extrafloral nectar. Especially nectar in various forms is important carbohydrate sources for several adult natural enemies to increase longevity, fecundity and motivation to seek hosts (Landis et al., 2000; Wäckers et al., 2007).

Several resources could be satisfied by incorporating them to the crop field area in the form of field margins, perennial flower strips, weed strips, beetle banks or hedgerows. It is important to realize that habitat management demands taking in consideration larger spatial scales and improve the spatial level of the entire landscape. Natural enemies should be encouraged to move between patches of resources, such as crop fields. For this reason, corridors of resources should be provided in the agricultural landscape to decrease habitat fragmentation (Landis et al., 2000; Zehnder et al., 2007; Pfiffner & Wyss, 2004; Tscharntke et al., 2007).

1.1.2 Flower strips

Flower strips should be designed to provide food resources throughout the season to ensure decimating the pests. The strips are ultimately positioned in the field interior of larger fields, or in the field margin of smaller fields, to allow sufficient dispersal of natural enemies over the field (Landis et al., 2000).

Flower strips are recommended to be composed of a mixture of annual, biennial and perennial plant species, and to be sown in strips of 3-10 m width. The plant species should be carefully selected with consideration to promote diversity and abundance of natural enemies, have a protracted flowering period, good longevity and succession on the site, be non-competitive to the crop, and most important to not support pest species. A common used mixture developed in Switzerland is composed of 24 (basic) up to 37 locally adapted plant species (full mixture) and is described by Pfiffner & Wyss (2004). The review also gives details on establishment and management.

Some studies report positive effects (Pfiffner et al., 2003) of floral resources on pest suppression, while other report neutral (Bigger & Chaney, 1998; Forehand et al., 2006) or negative effects (Baggen & Gurr, 1998). Pfiffner et al. (2003) tested a commercial mixture to reveal if proximity to a flower strip enhanced parasitism in cabbage

lepidopteran pests. The parasitism of both caterpillars and eggs of *Mamestra brassicae*, *Pieris rapae* and *Plutella xylostella* were assessed. The field trials showed positive results on parasitism and several parasitoids was also subsequently sampled.

1.1.3 Selective biodiversity

Increased diversity in the agricultural landscape should strive for selectively favor natural enemies otherwise pest problems could increase. When providing food resources for natural enemies there is also the potential risk of a benefit for the pests (Baggen & Gurr, 1998; Baggen et al., 1999; Landis et al., 2000; Winkler et al., 2003). This unfortunate experience was made when selecting food plants for *Copidosoma koehleri* a hymenopteran egg parasitoid of the potato tuber moth, *Phthorimaea operculella*. The moth benefited highly from the plants provided and populations increased close to flower strips (Baggen & Gurr, 1998; Baggen et al., 1999). Winkler et al. (2003) found indications of unintentional benefit to lepidopteran pests, *P. rapae* and *P. xylostella*, in a system with different flowering plant species intended for their parasitoid wasps, *Cotesia glomerata* and *Diadegma semiclausum*.

Selectivity between insects could be based on flower attractiveness and food accessibility (Patt et al., 1997; Wäckers, 2004), feeding response (Wäckers, 1999), nectar quality (Vattala et al., 2006), nutritional requirements and metabolic efficiency (Hausmann et al., 2005). Ultimately there is a trade off between the net benefits to the herbivore compared to the natural enemy.

1.1.4 Floral food sources for hymenopteran parasitoids

Hymenopteran parasitoids usually require a carbohydrate energy source during their adult stage, such as floral nectar, to increase longevity (Idris & Grafius, 1995; Baggen & Gurr, 1998; Vattala et al., 2006), (lifetime) fecundity (Idris & Grafius, 1995; Baggen & Gurr, 1998; Winkler et al., 2006) and motivation to seek hosts (Wäckers, 1994; Winkler et al., 2006). Consequently, provision of nectar plants in the agroecosystems can increase the effectiveness of biological control programs. Nevertheless, not all nectar plants are appropriate for hymenopteran parasitoids (Wäckers & Steppuhn, 2003; Wäckers, 2005).

The suitability of a nectar plant is determined by its availability, apparency, accessibility and nutritional composition. The availability of nectar can vary in time and

space. Floral nectar (and pollen) is only available during the period of flowering, while extrafloral nectar is also present during vegetative stages of plant growth. The apparency and detectability of floral nectar is determined by olfactory and visual cues, such as flower odor and color (Wäckers, 2005). Even if a floral nectar source is available and subsequent detected, it is not a guarantee that it is accessible to the insect. Accessibility is most often restricted by the morphology of the flower compared with the morphology of the insect mouthparts (Patt et al., 1997). The generally short mouthparts of hymenopteran parasitoids limits feeding to flowers with shallow corollas and easily accessible nectaries (Jervis et al., 1993; Wäckers, 2005). However some have elongated mouthparts specialized to reach concealed nectar in tubular flowers (Jervis, 1998).

Floral nectar is mainly composed of carbohydrates, amino acids, proteins, lipids, vitamins and secondary plant metabolites (Wäckers, 2005). The composition determines the nutritional suitability (Hausmann, et al., 2005; Vattala et al., 2006), feeding stimulation (Romeis & Wäckers, 2000) and gustatory response (Wäckers, 1999). The sugar concentration ranges commonly between 20 to 40%. Carbohydrates common in floral nectars include sucrose, fructose and glucose, and in lower amounts raffinose, galactose, mannose and xylose. The preference for the different sugars can vary between insect groups (Schoonhoven et al., 2005b; Wäckers, 2005).

The importance of floral nectar has been demonstrated in several studies. In a semi-field experiment, Winkler et al. (2006) found that food deprived *D. semiclausum* parasitized significantly ($P<0.001$) less host (*P. xylostella*) than parasitoid wasps offered flowering *Fagopyrum esculentum* as nectar source. Accordingly the reproductive lifespan was increased if offered nectar, from 0.8 days (hungry) to 28 days (fed). In the absence of food, parasitoids would spend more time food foraging and less time for host searching.

The food sources actually used in field by hymenopteran parasitoids have been investigated (Wäckers & Steppuhn, 2003; Steppuhn & Wäckers, 2004; Lee et al., 2006; Hogervorst et al., 2007). Origin of sugars consumed by parasitoids can reveal the importance of sugar sources for specific insects in field, whether floral nectar or honeydew. The sugar profile and ratio can conclude the nutritional state and use of a specific food source (Wäckers & Steppuhn; 2003; Steppuhn & Wäckers, 2004; Lee et al., 2006; Hogervorst et al., 2007). Since crops usually lack nectar honeydew can be an

important food complement in agricultural systems, although it is suggested to be nutritionally inferior to nectar (Wäckers, 2005). *Aphidius* spp., parasitoids of aphids, in wheat fields were found to consume a large part of its diet, over 50%, on honeydew (Hogervorst et al., 2007). Honeydew can contain specific sugars synthesized by the insect, such as the trisaccharides melezitose and erlose and the disaccharides trehalose and trehalulose (Wäckers, 2005).

Pollen is primarily a source of amino acids and proteins, with protein levels ranging from 2.5-61% (Wäckers, 2005). Direct pollen-feeding by hymenopteran parasitoids is not common, although records occur. Jervis et al. (1993) found no proof of pollen feeding when dissecting flower-visiting wasps. However there are parasitoid wasps that show specialization for pollen-feeding (Jervis, 1998).

1.1.4.1 Flower attractiveness; fragrance, color and hunger state

Plants attract insects by conspicuous flowers with bright color and prominent fragrance to get pollinated. In return the insects receive nectar and pollen as food. Flower attractiveness is a combination of many factors, among them flower color and flower fragrance (Schoonhoven et al., 2005a). It has been suggested that parasitoids and many other insects have an innate preference for yellow, as well as innate responses to constituents of floral odors (Wäckers, 1994).

1.1.4.1.1 Flower fragrance

Flower fragrances consist of a blend of volatile compounds from different chemical classes. Odors from flowers mainly originate from three chemical groups; fatty acid derivates, benzenoids and isoprenoids. The fatty acid derivates are further subdivided into saturated and unsaturated hydrocarbons, aldehydes, alcohols, ketones and esters. The benzenoids include compounds constituting a C_6 aromatic ring with hydroxyl groups and other functional groups, and could encompass e g. aldehydes, alcohols and esters. Isoprenoids constitute of four major groups: monoterpenes, sesquiterpenes, diterpenes and irregular terpenes (Knudsen et al., 1993; Ouellette, 1998; Schoonhoven et al., 2005a). Compounds could also contain nitrogen and/or sulphur, as the glucosinolates and their

hydrolysis product the isothiocyanates (and nitriles) found mainly in cruciferous plants (Schoonhoven et al., 2005a; Bones & Rossiter, 2006).

A large review by Knudsen et al. (1993) comparing numerous studies of volatile collections of floral scents found several common compounds with records from many plant genera. These include for benzenoids; benzaldehyde, benzyl alcohol, phenylethyl alcohol, benzyl acetate, methyl benzoate and methyl 2-hydroxybenzoate. For isoprenoids; 1,8-cineole, geraniol, limonene, linalool, myrcene, *trans*-β-ocimene, α-pinene, β-pinene, caryophyllene and α-farnesene. For fatty acid derivates; 1-hexanol, (Z)-3-hexenol, (Z)-3-hexenyl acetate, which are all 'green leaf volatiles' (GLV). These common flower and plant components are suggested to relate to innate responses in generalist foraging insects (Wäckers, 1994).

Released mainly from damaged leaves, but also through the stomata, the GLV:s are common in the bouquet around plants, although not typical floral odor constituents. The ratio of the GLV:s in the odor from a plant species can permit an insect to find its host plant. If the plant is damaged the release ratio of GLV:s and other compounds is altered. The odor profile will be different if the damage is mechanical or caused by a herbivore. Herbivore induced odors will attract the natural enemies of the herbivore, which is called induced indirect defense (Schoonhoven et al., 2005a).

Floral scents within a species have been found to vary with the individual plant or flower, pollination history, irradiation, nutrition and diurnal pattern (Knudsen et al., 1993; Schoonhoven et al., 2005a; Schoonhoven et al., 2005b).

Wäckers (2004) investigated plant species with respect to their attractiveness on three different parasitoid wasp species. *Origanum vulgare*, *Galium mollugo*, *Aegopodium podagraria* and *Leucanthemum vulgare* were all found attractive to *Heterospilus prosopidis*, although only *A. podagraria* had accessible nectar. *Pimpla turionellae* was attracted to *O. vulgare* and *G. mollugo*, where *O. vulgare* resulted in weight gain. *C. glomerata* was not attracted to any of the plants tested, and only *A. podagraria* provided nectar. *D. carota* did not elicit any response on attractiveness, but had accessible nectar to *P. turionellae*. Attractiveness and accessibility was thus not necessarily linked. *Vicia sepium* allowed weight gain, mainly due to extrafloral nectaries, which are easily accessed.

1.1.4.1.2 Flower color

Many insects have an innate visual preference for yellow (Wäckers, 1994), which is a common flower color. Jönsson et al. (2005) found two pollen beetle parasitoids (*Phradis interstitialis* and *Tersilochus heterocerus*) to be significantly attracted to yellow, when given a choice between yellow and green. When combined with flower odors from oilseed rape, *Brassica napus*, the attraction was even more pronounced for *T. heterocerus*, a species preferring older larvae occurring in flowering rape. In contrast, Idris & Grafius (1997) did not observe color preference in flower choice by *Diadegma insulare* offering choice between several yellow flowers, including *B. napus*, and white flowers.

1.1.4.1.3 Physiological state of the insect

The physiological state of a parasitoid wasp influences its foraging decisions. Physiological states include food deprivation (Wäckers, 1994; 2005), age, mating status and egg load (Jervis et al., 1993; Wäckers, 2005). The level of attraction to flower odors and color as well as the motivation to seek host is influenced by the feeding history of the parasitoid. When a starved parasitoid is fed there is a shift from food foraging to host foraging.

Wäckers (1994) found that sugar-deprived individuals of the parasitoid wasp *Cotesia rubecula* were more attracted to yellow than fed parasitoids. Food-deprived parasitoids made more landings on yellow targets than sugar-fed parasitoids. Following landing the food-deprived showed an intense searching behavior with scraping of the mouth parts. The majority of the time spent on the yellow target was used for food foraging. When both fed and starved parasitoids were given a choice between rape flowers and uninfested rape leaves, both groups chose the flowers. However, when given a choice between flower odors and odors from host-infested leaves, starved parasitoids chose flowers while fed parasitoids chose infested leaves.

It is common in investigations of food preference, that the insect in question is starved in order to increase to magnitude of the response (Wäckers, 1994; Patt et al., 1997). Hungry insects are more likely to respond to food odors than fed insects (Wäckers, 1994).

1.1.5 Floral nectar accessibility; morphology of flower and insect

Nectar accessibility is determined by the morphology of the insect and the flower. Theoretical accessibility is obtained by measurements of the corolla depth (to nectaries) and corolla opening (at narrowest part) of the flower compared to measurements of the head width and length of parasitoid mouthparts (Jervis et al., 1993; Winkler et al., 2003; Vattala et al., 2006). Accessibility could also be established by empirical experiments (Idris & Grafius, 1995; Patt et al., 1997; Winkler et al., 2003; Wäckers, 2004). There is not always a fit between theoretical and actual nectar accessibility (Winkler et al., 2003), why experiments should be conducted to be certain.

Vattala et al. (2006) investigated the parasitoid wasp *Microctonus hyperodae* with respect to nectar accessibility and nectar quality of selected plant species. Of the tested species, only *F. esculentum* and *Coriandrum sativum* increased parasitoid longevity (relative to water). *Phacelia tanacetifolia* and *Lobularia maritima* provided no accessible nectar, because the head width of the parasitoids restricted the nectar utilization.

Patt et al. (1997) observed and measured nectar accessibility for the parasitoid wasps *Edovum puttleri* and *Pediobius foveolatus* on a range of flower species and artificial flowers with disparate nectarium positions; exposed, partially exposed, partially hidden and hidden. The investigation found exposed nectaries, mostly Apiaceae, to be most beneficial to the parasitoids. The slightly larger *P. foveolatus* could also access partly hidden nectaries. This was suggested to be because the larger wasp is stronger and can thus separate flower structures. The pattern was similar both for real and artificial flowers. The searching behavior was also evaluated with consideration of odor using scented (honeywater) and unscented (sucrose solution) artificial flowers. The result revealed that food location is easier when visual cues are aided by odor cues.

Idris & Grafius (1995) found a correlation between longevity compared to flower corolla opening width. The wider the opening, the better longevity of the parasitoid *D. insulare*.

Some parasitoids could access nectar by chewing into flower bases or separating the petals by kicking, which was observed for *D. insulare* by Idris & Grafius (1997). The behaviors could circumvent disparate insect and flower morphologies. The wasp also displayed learning behavior. Food experienced wasps tended to continuously choose

flowers increasing the longevity and fecundity. These flowers were more frequently visited than species that affected the wasp negatively. Also longer time was spent on beneficial flowers (Idris & Grafius, 1997).

1.1.6 Suitable plant species for hymenopteran parasitoids

Some plant species reoccur in several studies. *P. tanacetifolia* provides both pollen and nectar and is beneficial to many insects, but has a deep corolla which makes the nectar inaccessible to others (Baggen et al., 1999; Landis et al., 2000). Small parasitoids can exploit deep corollas such as *Phacelia* spp. (Baggen et al., 1999) as well as narrow corollas such as Asteraceae (Jervis et al., 1993).

Jervis et al. (1993) conducted a large study in which they observed inflorescences of many plants in several habitats and recorded presence of parasitoid wasps as well as food searching behavior and nectar consumption. Apiaceae plants were concluded to be both highly attractive and eliciting feeding behaviors in many Hymenoptera families. The study also mentions *Angelica sylvestris*, *Daucus carota*, *Heracleum sphondylium* and *Oenanthe crocata* to be attractive. *T. rapae* were found on these species except *D. carota*. All wasps searching for food at Apiaceae were also observed consuming nectar. *H. sphondylium* have also been found beneficial for wasps in other studies (Winkler et al., 2003).

Plant species belonging to Apiaceae have rather easily accessible exposed or partially exposed nectaries and is especially suitable for parasitoid wasps (Jervis et al., 1993; Patt et al., 1997). Species that have been investigated with regards to positive accessibility are given in table 1. Many of the Apiaceae mentioned are crop plants, adding additional benefit to intercropping. Plant species belonging to other plant families have also been successfully used (table 1). It should be mentioned that buchwheat, *F. esculentum*, have been found to have a sugar quality especially suitable for parasitoids (Vattala et al., 2006).

Brassicaceae plants could potentially aid additional attraction for parasitoids attacking cruciferous pests. Plants studied include *Brassica kaber*, *Barbarea vulgaris* (Idris & Grafius, 1995) and alyssum, *L. maritima*, in which the nectar accessibility could be restricted for some parasitoid species (Patt et al., 1997; Vattala et al., 2006). Bordering

the crop with canola, *Brassica napus* (Landis et al., 2000) could also be beneficial for some parasitoids. Jervis et al. (1993) did not record many parasitoid visits to the Brassicaceae species observed; *Alyssum* sp., *Brassica oleracea* and *B. napus*.

Species belonging to the Asteraceae has proven unsuitable for parasitoids as nectar sources (Patt et al., 1997; Wäckers, 2004), if the insects are not very small, or have specialized mouthparts (Jervis, 1998). The nectaries of Asteraceae are located at the bottom of the narrow tubular corollas of the disc flowers and thus hidden (Jervis et al., 1993; Patt et al., 1997). However species of this family could serve as a pollen source (Patt et al., 1997).

Fabaceae species has proven both unattractive (Jervis et al., 1993; Wäckers, 2004) and having inaccessible nectar (Wäckers, 2004; Vattala et al., 2006), although species with extrafloral nectaries such as *Phaseolus vulgaris* has proven beneficial (Patt et al., 1997).

Table 1. Suitable plant species for hymenopteran parasitoids. Numbers indicate literature reference; 1 = Idris & Grafius, 1995; 2 = Patt et al., 1997; 3 = Baggen & Gurr, 1998; 4 = Winkler et al., 2003; 5 = Wäckers, 2004; 6 = Vattala et al., 2006; 7 = Lee et al., 2006; 8 = Winkler et al., 2006.

Species		**Family**	**References**
dill	*Anethum graveolens*	Apiaceae	2,3,4
coriander	*Coriandrum sativum*	Apiaceae	2,3,6
carrot	*Daucus carota*	Apiaceae	1,2,4,5
ground elder	*Aegopodium podagraria*	Apiaceae	5
parsnip	*Pastinaca sativa*	Apiaceae	2
bupleurum	*Bupleurum rotundifolia*	Apiaceae	2
fennel	*Foeniculum vulgare*	Apiaceae	2
parsley	*Petroselinum crispum*	Apiaceae	2
angelica	*Angelica archangelica*	Apiaceae	2
ammi	*Ammi majus*	Apiaceae	2
buchwheat	*Fagopyrum esculentum*	Polygonaceae	4,6,7,8
borage	*Borago officinalis*	Boraginaceae	3
common figwort	*Scrophularia nodosa*	Scrophulariaceae	1

1.2 The crucivore Delia radicum

The cabbage root fly, *Delia radicum*, is a major pest of cruciferous crops causing severe damage to the root systems of the plants. The infestations primarily cause wilt and reduce harvest, but also cause quality damage in root crops such as Swedish turnip and radish (Alford, 1999). Increasing consumer demand and banned insecticides have accentuated the need for organic pest management methods for controlling *D. radicum*.

1.2.1 Host plant finding and acceptance

Many investigations have been done on *D. radicum* assessing both behavioral steps (Kostal, 1993; Kostal & Finch, 1994; Finch & Collier, 2000; Finch et al., 2003; Morley et al., 2005) and chemical cues (Roessingh et al., 1992; Baur et al., 1996; Hurter et al., 1999; Marazzi et al., 2004; Gouinguené & Städler, 2006a) involved in host plant finding and acceptance. Investigations have been done using both classical observation methods and electrophysiological techniques. The later has often been conducted using tarsal recordings to assess the function and response of sensilla (e. g. Roessingh et al., 1992; Baur et al., 1996; Hurter et al., 1999; Marazzi et al., 2004; Gouinguené & Städler, 2006a). Researchers have concluded that non volatile glucosinolates present on leaf surfaces of host plants acts as major oviposition stimulants by contact chemoreception (Roessingh et al., 1992; Hurter et al., 1999; Marazzi et al., 2004; Gouinguené & Städler, 2006a). In addition a non-glucosinolate, CIF (cabbage identification factor; 1,2-dihydro-3-thia-4,10,10b-triaza-cyclopenta[.a.]fluorene-1-carboxylic acid), has been found to be important (Baur et al., 1996; Hurter et al., 1999; Marazzi et al., 2004; Gouinguené & Städler, 2006a). The volatile isothiocyanates act as cues mediating host plant finding by odor chemoreception (Nottingham, 1988).

It is suggested that the host plant acceptance is based on ‘appropriate/inappropriate landings (Finch & Collier, 2000), and that the final decision to ovipositit is made after several host plant encounters in where the fly accumulates enough host plant stimuli to be induced to lay (Kostal & Finch, 1994). The behaviors observed to acquire this stimuli is hops, walks and spiral flights (Kostal & Finch, 1994; Morley et al., 2005) The non-host plants are rather arrestants than repellants or deterrents, since the fly spends more time on

non-hosts than hosts (Morley et al., 2005). The arrestment is caused by the green color of the leaves and not from odor or taste (Finch et al, 2003).

1.2.2 Floral nectar food sources

Conversely, little attention has been given during recent times to the requirements, finding and utilization of food plants (Finch & Coaker, 1969a; Finch, 1971; 1974). *D. radicum* have been found to require carbohydrate energy to mature the first batch of eggs (Finch & Coaker,1969a). To mature the second or more batches of eggs, proteins are needed in addition (Finch, 1971). Flies of the second generation caught in field revealed that only 3% had fed from protein sources, thus being able to mature a second batch of eggs. Clearly the potential fecundity is not always met under field conditions (Finch, 1971). If proteins are provided to a standard carbohydrate diet under laboratory conditions a dramatically increase in fecundity is seen (Finch & Coaker, 1969a; Finch & Coaker, 1969b). The feeding activity is reported to peak at 2-3 days after emergence (Finch & Coaker, 1969b). *Delia* spp. are able to disperse thousands of meters in flight (Finch & Skinner, 1975), and can thus exploit food sources far away.

Anthomyiidae flies have been observed feeding on flowers of wild cherry and seed brassicas during late spring (Finch & Coaker,1969a). Miles (1950) suggested that there might be an association between fly egg laying activity and the flowering of fruit trees. The activity is also seen to be stimulated by warm and sunny weather.

Finch & Coaker (1969a) investigated flower utilization of *D. radicum*. In early summer (first generation flies) *Anthriscus sylvestris* gave an increase in fecundity compared to control 0.1 M sucrose solution. In late summer (second generation flies) several plants tested gave at least as good fecundity as the control; *Plantago lanceolata*, *Rubus fruticosus*, *Lamium album* and the grasses *Holcus lanatus* and *Phleum pratense*. Higher fecundity than control was achieved with *H. sphondylium* and *Crataegus monogyna*, and the grasses, *Dactylis glomerata* (best of all plants tested) and *Lolium perenne*. The naturally occuring carbohydrates sucrose, glucose, fructose, maltose, melezitose, mannitol and sorbitol gave a high fecundity as well as good longevity when provided to *D. radicum* (Finch & Coaker, 1969a).

Finch (1974) analyzed the nectar quality of the plant species previously showed beneficial to *D. radicum*. The nectar of *A. sylvestris* and *L. album* were found to contain mainly fructose and sucrose. Species present later in the season, *H. sphondylium* and *R. fruticosus* instead contained fructose and glucose. The anthers of the grasses *H. lanatus* and *D. glomerata* also contained the later mentioned sugars. The pollen of the grasses in addition contained inositol.

The number of flowers in an umbel from *A. sylvestris* required for *D. radicum* to lay the first batch of eggs were established to be only 2 flowers per day per fly (Finch, 1971).

1.2.3 Biology

The cabbage root fly occurs in two-three generations in northern Europe per year. The emergence of the first generation adults depends upon temperature and occurs in April-May (Alford, 1999). The mating occurs at the earliest 3 days after emergence (Swailes, 1961), and egg laying starts in 5-7 days after emergence (Finch & Coaker, 1969b). Females have been found to lay on average 80 eggs under laboratory conditions and live for around 20-30 days (Swailes, 1961), but reports exists of several hundreds eggs per female (Finch & Coaker, 1969b). The higher the weight of the puparium, the higher the fecundity of the emerged female fly (Finch & Coaker, 1969b). The eggs are laid in the soil by the stems of the host plant, or on the lower leaves and hatch in 3-7 days. The larva then feeds during 3-4 weeks and undergoes three larval stages before pupating in the close vicinity to the host plant. The last generation enters diapause and overwinter as pupae within puparia (Alford, 1999). In the next season all flies terminate diapause. In both generations it is found to exist an early and a late phenotype differing in emergence time. The strategy is to ensure survival of the species even if annual variations of environmental conditions occur. The late emerging type is found to have a longer developmental time than the early (Fournet et al., 2004). The late emergers have also been found to require more day-degree accumulation before diapause is terminated (Block et al., 1987).

1.2.4 Related species

The genus *Delia* (Diptera:Anthomyiidae) consists in the Nearctic region of approximately 162 species, of which many species also occur all over the temperate world (Griffiths, 1991). The flies appear greyish with size and appearance as the house-fly, *Musca domestica* (Alford, 1999). The *Delia* spp. flies are hard to differentiate in the adult stage, although they can be distinguished based on male genitalia (Darvas & Szappanos, 2003). Brooks (1951) gives keys for identification of some economic species based on adult, larvae and eggs. The species are most easily distinguished as larvae or puparium based on the morphology of posterior tubercles. The genus has several synonymous names, including *Erioischia*, *Leptohylemyia*, *Hylemya*, *Hylemyia*, *Phorbia* and *Chortophila*, where the species also has changed their specific names several times during the years (Finch, 1989; Wood, 1989)

The following species occur as economical pests of crops over the world. *D. radicum*, cabbage root fly, and *D. floralis*, turnip root fly, both attack the roots of Brassicaceae crops. *D. antiqua*, onion fly, is a pest on onion bulbs. *D. coarctata*, wheat bulb fly, feed on cereals. *D. echinata*, spinach stem fly attack spinach. These mentioned species are considered to be true primary phytophages. Other species occur as secondary saprophages utilizing the entrances of different injuries. These include the two been seed flies *D. florilega* and *D. platura*, which can occur in cabbage, onions, germinating beans and other large seeds (Finch, 1989; Alford, 1999).

1.2.5 Natural enemies

There are a range of organisms controlling *D. radicum* populations under field conditions. The parasitoid wasp *T. rapae* is an important natural enemy of *Delia* spp. Other species of significance are the parasitoid and egg and larvae predatory beetles *Aleochara bilineata* and *A. bipustulata* (Coleoptera: Staphylinidae) (Wishart & Monteith, 1954). Other generalist egg predators such as *Bembidion* spp. and *Agonum* spp. (Coleoptera:Carabidae) could consume considerable amounts (Prasad & Snyder, 2004). During humid years several entomopathogenic fungi could reduce the fly population. Species that should be mentioned include *Metarhizium anisopliae*, *Beauveria bassiana* (Bruck et al., 2005) and *Entomophthora muscae* (Thomsen & Eilenberg, 2000).

1.3 The hymenopteran parasitoid Trybliographa rapae

The hymenopteran wasp *T. rapae* is one of the most important natural enemies against *D. radicum* and other *Delia* spp. Parasitation in field can be considerable. Some investigations have found 10 % (Neveu et al., 1996) but others as much as 45% parasitation rate (Wishart & Monteith, 1954). To obtain high parasitation rates it is important to favor the wasp by providing food and shelter in close proximity to crucifer crop fields, as described previously.

1.3.1 Host insect finding and acceptance

T. rapae find its host by odor perception of volatiles released from both the larvae damaged plant and the larvae. Neveu et al. (2002) found that *T. rapae* females were attracted to infested turnip plants, but not to uninfested. All the plant parts of the infested plants were attractive, even the leaves which were not in contact with *D. radicum*. This is proof for a systemic induced indirect deference in turnip when infested by the fly larvae. Artificially damaged plants were not attractive, however artificially damaged plants treated with crushed *D. radicum* larvae were attractive (Neveu et al., 2002). In the subsequent ovipositor probing significantly more *T. rapae* females probed on infested compared to uninfested swede, and the host searching was also longer on infested swede (Brown & Anderson, 1999). Intercropping cabbage with white clover does not affect host finding by *T. rapae* compared to cabbage monoculture (Langer, 1996).

The host finding and probing is mediated by chemical cues which are sensed by the antenna respectively the ovipositor. These structures have several sense cells, the sensilla, which perceive the chemical signal and forward it to the central nervous system. The morphology and function of these sensilla were investigated by Butterfield & Anderson (1994) for the antenna and by Brown & Anderson (1998) for the ovipositor.

Three types of sensilla are present on the antenna. The sensilla have different distribution along the antennae, as well as function; mechanoreceptors, thermo-hygroreceptors and olfactory chemoreceptors (Butterfield & Anderson, 1994).

The sensilla present on the ovipositor are of two types. One type serves two functions; both thermosensitivity and gustatory (taste) to feel the temperature and taste of

the host. The other type has a mechanoreceptive function, to mediate the movement through the plant tissue at oviposition (Brown & Anderson, 1998).

As seen, the function and morphology of the odor perception apparatus has been investigated in sense of host finding and oviposition, but not yet in the finding of food plants.

1.3.2 Floral nectar food sources

The nutritional requirements of the hymenopteran parasitoid *T. rapae* of nectar, and the accessibility to different flower structures, has not been much investigated. In rearing, *T. rapae* is often provided by acacia honey (Neveu et al., 1996), honey (Kacem & Nenon, 2003) or "sugar" (Butterfield & Anderson, 1994; Brown & Anderson, 1999). Jervis et al. (1993) recorded flower-visiting and nectar consumption by *T. rapae* on *Angelica sylvestris*, *H. sphondylium* and *O. crocata*, all Apiaceae with easily accessible nectaries.

The parasitoid is long-lived and as other parasitoids requires energy to support life and to increase fecundity. It is important to provide nectar sources in close vicinity to or within the field, since *T. rapae* is reported to be a poor flyer (Wishart & Monteith, 1954).

1.3.3 Biology

Mating may occur soon after emergence and the subsequent oviposition can occur within a few hours. The wasp is proovigenic, which means that the females contain mature eggs upon emergence. At oviposition the female insert the ovipositor directly into the plant tissue, or follows the larvae through its burrow (Wishart & Monteith, 1954). *T. rapae* can parasitize *D. radicum* down to a depth of 4 cm, but *D. radicum* occurs also deeper in the soil (Hemachandra et al., 2007). *T. rapae* is a koinobiont parasitoid, which host larvae continue to feed and develop after parasitism, in contrast to idiobiont parasitoids which kill their host instantly (Kacem & Nenon, 2003). The first larval stage of the parasitoid lasts until formation of host puparium. After entering the third instar, the larvae gnaws through the host pupae but still reside within the puparium and starts the destructive feeding of the host. The feeding continues through the last instar until only the cuticula of the host remains. Diapause occurs in the last instar in the host puparium. Pupation then follows and subsequent emergence of the adult, where males emerge first (Wishart & Monteith, 1954).

All larval stages of *D. radicum* can sustain *T. rapae* larval development, although fastest development (50±1 days; from egg to adult) is provided by third instar in 20°C, 60% RH and 16L:8D (Neveu et al., 1996; Neveu et al., 2000). Development is also more rapid at higher temperatures (Kacem et al., 1999). The third instar increases wasp body size compared to earlier instars (Neveu et al., 2000). When offered a choice, the wasp prefers to oviposit in the third instar. The host plant has been found to influence the size of female wasp progeny (Kacem & Nenon, 2003). Detailed requirements in culture of *T. rapae* are given by Neveu et al. (1996) and Kacem et al. (1999).

The host phenotype (early or late emerging types) of *D. radicum* influences the development of *T. rapae*. The development time is longer and the survival better in the late host phenotype. However, the host phenotype does not influence the emergence pattern of the parasitoid. The emergence occurs similar to the host in two peaks (Fournet et al., 2004).

Foliar herbivory by *Pieris brassicae* (Lepidoptera: Pieridae) on *Brassica nigra* were seen to affect *D. radicum* and in accordance *T. rapae* negatively (Soler et al., 2007). The survival of both insects decreased to below 50 %. The survived parasitoids emerged smaller than those on herbivore free plants. Increased levels of indole glucosinolates were found in the roots of leaf infested plants, whereas the level of some other glucosinolates was not altered. Parasitoid intra-guild interaction with *Aleochara* sp. (Coleoptera: Staphylinidae) occurs. *Aleochara* sp. can hyperparasitize puparium in which *T. rapae* has already oviposited, thus killing the *T. rapae* larvae (Wishart & Monteith, 1954).

Trybliographa has as other Figitidae a characteristic raised cup on the disc of the scutellum, which is large in this genus. The wasp is approximately 5 mm in size and shiny black. The sexes are most easily separated by antenna morphology. The female antenna consists of 13 segments (scape, pedicel and 11 flagellar segments) where the last segment is club-shaped, whereas the male antenna consists of 15 segments. (Quinlan, 1978; Brown & Anderson, 1998). The ovipositor is reported to be 2.9 mm long (Brown & Anderson, 1998). Morphology of egg and all four larval instars is described by Wishart & Monteith (1954). In Britain, 11 species of the genus exists, some of which insect host range are largely unknown. Some of the species besides *T. rapae* are also reported to develop in *Delia* spp. of economic importance (Quinlan, 1978).

Aim

The aim of this Master thesis is to study the attraction to and nectar accessibility of three selected plant species for the severe crucivorous pest *D. radicum*. The ambition is ultimately to find plants species selectively suitable as nectar sources for its natural enemy, the beneficial parasitoid wasp *T. rapae*, to use in flower strips in an intercropping system with cruciferous crops.

For the experiments the following annual species were chosen based on previous experience in their suitability for hymenopteran parasitoids; dill, *A. graveolens* (Apiaceae); buchwheat, *F. esculentum* (Polygonaceae) and alyssum, *L. maritima* (Brassicaceae).

2. Methods and Materials

2.1 Rearing of Delia radicum

The rearing of the cabbage root flies was modified from Finch & Coaker (1969b). The adult flies were kept in cages (33x33x33 cm) in a rearing cabinet at 19°C and 16L:8D for mating and egg production, or at 19°C for 18L:6D for experiments. Food was provided twice a week as a mixture of honey, dry yeast (Kronjäst, Jästbolaget) and milk powder (Semper) spread thin on a Petri dish. In addition water and honey water were supplied in small cups protected by a lid with a dental cotton roll inserted. A Petri dish (92 x 16 mm) with moist coarse sand (1.2-2 mm, Rådasand) and a piece of Swedish turnip were offered as an ovipositing site in each rearing cage. Every 3-4 days, the eggs were collected by flotation. The eggs were then carefully rinsed into a pot of 3 l half-filled with moist coarse sand (0.8-1.2 mm, Rådasand). A medium-sized Swedish turnip was subsequently placed on the sand, and more sand was filled around the turnip. The pots were placed in room temperature for 4-5 weeks until completed larval development and subsequent pupation. The pupae were collected by flotation and embedded in moist vermiculite in Petri dishes (92 x 16 mm). The pupae dishes were incubated in cages and moistened daily. After emergence the male and female flies were separated. The flies were only provided with water in order to starve them. For the experiments feeding-inexperienced females of 2-3 days of age were used.

2.2 Plants

The following plants were grown for subsequent experiments; buchwheat, *F. esculentum* (Polygonaceae); dill, *A. graveolens* (Apiaceae); alyssum, *L. maritima* (Brassicaceae) and cauliflower, *B. oleracea* var. *botrytis* cv. 'Vito' (Brassicaceae). The plants were sown weekly in 1-1.5 l pots with fertilized soil (Yrkesplantjord, Kronmull, Weibulls Trädgård), and cultivated in a greenhouse chamber at 22°C, 75 % RH and 16L:8D with light provided by a 400W high pressure sodium lamp. Fertilization was done every second week with standard fertilizer. From sowing to flowering it took 5 weeks for *L. maritima*, 4-5 weeks for *F. esculentum* and 10 weeks for *A. graveolens*. In addition *B. oleracea* var. *botrytis*, was cultivated singly and was grown for 12-14 weeks before used when having approximately 10 true leaves. For experiments, plants free from visible damage were chosen.

2.3 Data analysis

Analysis of the data was done in Minitab Statistical Software release 15.1.1.0. Flower attractiveness was evaluated by two-tailed binomial distribution ($P < 0.05$), testing whether fly choice of a flower odor was significantly higher or lower than 50 %. The data of weight increase in the nectar accessibility experiments was analyzed by ANOVA General Linear Model. The weight increase after 1 h was subjected to Tukey Simultaneous Test. Tables were produced in Microsoft Excel.

2.4 Flower attractiveness

Flower attractiveness of *D. radicum* was evaluated in two-choice experiments with an Y-tube olfactometer, where the set up and method was modified from Jönsson et al. (2005). The Y-shaped glass tube had 220 mm long arms with an inner diameter of 15 mm. To avoid random choices a piece of black tube (2 cm) was placed around the glass before the bifurcation to calm the flies. White fabric surrounded the Y-tube to avoid visual distraction.

The air was initially passed through a 250 ml gas-wash bottle with activated charcoal to eliminate any odors and humidified by passing through a similar bottle with tap water. The airflow rate reaching the arms was 0.8 L/min, adjusted by two flow meters. The

experiments were performed in a bioassay room with 24°C, 60% RH and illumination provided by a 400W mercury-vapor lamp giving approximately 1300 lux at the Y-tube.

The attraction to the emitted odors of the following plants was tested compared to control; *F. esculentum*, *A. graveolens* and *L. maritima*. In two-choice experiments, the following plants were compared: *L. maritima* vs. *A. graveolens* and *F. esculentum* vs. *A. graveolens*. A comparison was also done for *L. maritima* vs. cauliflower to assess if there was a preference for food over ovipositing site.

The relative amounts of flowers used from each plant species were quantified visually to match that of an umbel from *A. graveolens*. Flowering stalks from undamaged plants were cut with a razor blade and wrapped in moist cotton. The cotton was wrapped with parafilm to prevent smell of damaged tissue (Wäckers, 2004). For the experiments using cauliflower, the entire pot with plant was taken. Then the pot and soil were covered with thin aluminium foil to eliminate any soil odour. The plants were put in a 35 x 43 cm (or 45 x 55 cm when cauliflower was used) cooking bag (Melitta) and connected to the Teflon tubings transferring the odours to the arms. Moist cotton wrapped in parafilm put in a cooking bag was used as control. When initiating an experiment the olfactometer set up ran for 20-30 minutes until the Y-tube was saturated with odour before introducing an insect.

Flies used in the experiments were unmated, food inexperienced, 2(-3) days old females only provided with water after emergence. For the experiments with *L. maritima* vs. cauliflower the following fly treatments were used; 2-3 days old, unmated and starved; 2-3 days old, unmated and fed honey water, and finally 6-11 days old, mated and fed honey water. The insect material was confined in plastic tubes (12 x ø 2.5 cm) stopped in both ends by cotton before the experiment. The insects were allowed to acclimatize for one hour in the bioassay room before the onset of the trials.

The female insects were introduced into the Y-tube 21 cm from the bifurcation. The observation started as soon as the insect moved 5 cm into the Y-tube. A choice was recorded when the insect had walked 5 cm into one of the arms and remained there for at least 30 s. All in all, the insects had 5 min to make a choice; otherwise they were recorded as non-responders and excluded from the data. Flies not exhibiting normal grooming behaviour upon perceiving the odor were also excluded.

After 10-15 replications the olfactometer arms were shifted to avoid any position effect. At this point the plant material was renewed. Between each experimental day all glass ware were burn for 8 h at 350°C to remove odours. The Teflon tubes were for the same purpose rinsed in 70% ethanol.

Each experiment was carried out over several weeks, so the fly as well as plant batches were varied. Since the conditions were held constant data from different experimental occasions could be pooled for statistical analysis.

2.5 Nectar accessibility

Nectar accessibility of the three plant species, *L. maritima*, *A. graveolens* and *F. esculentum*, to *D. radicum* was tested by enclosing a female fly with a flowering plant and measure the fly's change in weight.

A few days before the start of the experiments the plants were divided and replanted. Once again, the relative amounts of flowers present on each plant species were quantified visually to match that of an umbel from *A. graveolens*.

Female flies used for the experiment were unmated, food inexperienced and 2(-3) days old. Each fly was weighed on a micro balance (Mettler AT250, Stathmos) before enclosing them individually with an intact plant. The flies were subsequently weighed individually after 1h, 6h, 12h, 24h and 48h to record the change in weight. The plants were not changed over the experimental period, since the plants were assumed to reassimilate nectar.

The experiment was repeated on three occasions, denoted experiment 1, 2 or 3. In every occasion each plant species were replicated five times. Three control treatments were included; honeywater + water, water or nothing. Every control treatment was replicated 1-2 times on every occasion. Unfortunately the experiments were not performed exactly similar every week, since the method was developed. During experiment 1, all treatments were contained in plastic boxes (18 x 18 x 11.5 cm) ventilated at one side (8 x 4 cm) and at the lid (8 x 8 cm), except for *A. graveolens*, where the umbels were contained in plastic boxes (31x 22x 12 cm) ventilated by mesh (ø 10.5 cm). In experiment 2, a bag (50 x 40 cm) of fine mesh with a small opening (4 cm) at the top (for fly handling) were put around each plant, except for the controls and *L. maritima*,

which were contained in the above mentioned boxes. In the final experiment 3, the mesh bags were put around all treatments, but for *L. maritima* and all controls, the bottom part of the plastic boxes were kept. The experiments were performed in a greenhouse at 22°C, 75 % RH and 16L:8D. Artificial light was provided by a 400 W high pressure sodium lamp.

2.6. Volatile collection

Volatile collections were made from *L. maritima* to identify its odor profile and to obtain extracts to use in electrophysiological recordings. The method was modified from Jönsson & Anderson (1999).

L. maritima was chosen since it showed to be both extremely attractive as well as had accessible nectar, in previous experiments with *D. radicum*. *L. maritima* plants were either newly in blossom or fully flowering. Two methods were tested to see which gave the less contaminated profile. The plant to be sampled was either carefully pulled out from the soil in the pot or kept in the pot. If pulled out soil was rinsed from the roots and the plant was put in tap water in a 250 ml Ehrlenmeyer flask. If kept in the pot, the pot and the soil was wrapped in aluminium thin foil.

Adsorbent filters were prepared by filling Teflon tubings (ø 1/8" ~ 3 mm) with Tenax GR 60/80 (Supelco), stopped by thick walled Teflon and polypropylene wool. The filters where then rinsed with 2 x 0.5 ml pentane puris p.a., and dried with nitrogen gas.

The flowering plant was subsequently enclosed in a 35 x 43 cm polyacetate cooking bag (Melitta), which was wrapped tightly with tape. A glass tube with charcoal and glass fiber stoppers was included for purification of the inlet air. At the top of the cooking bag a hole was cut and Teflon tubings with the adsorbent filters inserted. A reversed aquarium pump (2 l min^{-1}) was connected to the filters by silicon rubber tubings with adjustable valves. The flow rates through the filters were measured and adjusted by the valves to an equal flow of approximately 100 ml air min^{-1}. One pair of filters consisted of control, while the other two pairs where connected to respective odor source. The volatile collection where carried out under laboratory conditions during 3 hours at approximately 11-14 or 12-15 hours.

The adsorbent filters where subsequently desorbed with 400 µl pentane *puris p.a.* (Fluka, Buchs, Switzerland) into 2 ml glass screw top vials (with rubber septa) with 400 µl microvolume glass inserts (Agilent Technologies). A testing GC-MS run showed the concentrations of the samples to be too low. The samples where then concentrated by evaporation in a fume hood for approximately one hour until approximately 30-40 µl remained in the tapered bottom of the insert. The obtained extracts where kept at –20ºC until analysis by GC-MS.

2.7. Combined Gas Chromatography and Mass Spectrometry (GC-MS)

The extracts from the volatile collection of *L. maritima* was analysed by GC-MS (quadrupole) system by autoinjection (7683B Agilent Technologies, Palo Alto, CA, USA) of 2 µl at 225ºC, and splitless injection for 30 s. The GC (6890N Agilent Technologies) consisted of a fused silica capillary column (30m x 0,25mm) coated with DB-wax (df = 0,25 µm) (J&W Scientific, Folsom, CA, USA). The temperature program for the GC was 30ºC for 3 minutes, followed by an increase of 10ºC/min until 225ºC. The mobile phase was helium at velocity 35 cm/s. The transfer line was temperature programmed to 200°C for 20 minutes, followed by an increase of 10°C/ minute, to 225ºC, to follow the temperature program of the GC oven. The MS (5975 Mass Selective Detector, Agilent Technologies) scanned the region *m/z* 29-330 generated at 70 eV with full scan after 4 minutes. Between samples, the syringe was rinsed 20 times with respectively acetone and subsequently hexane. The chemical compounds were identified by analysis on the Hewlett-Packard MS data program StandAlone (G1701AA, version A.03.00) by comparison of mass spectra from known compounds in the libraries of NIST05, WILEY175 and the own constructed library, KE1995, based on samples from our own collection of reference compounds.

3. Results

3.1 Flower attractiveness

All the nectar plant species tested in the two-choice experiments were shown to be significant attractive to *D. radicum* compared to the control of moist air; *F. esculentum* ($p = 0.023$); *A. graveolens* ($p = 0.003$) and *L. maritima* ($p = 0.001$). The percentages of non-responders were 35% for *F. esculentum*, 5% for *A. graveolens*, and 15% for *L. maritima* (table 2).

A comparison was also made of the preference when given a choice between two nectar plants. When selecting between *F. esculentum* and. *A. graveolens*, the latter was significantly ($p = 0.022$) more attractive than the former. Given a choice between *L. maritima* and *A. graveolens* yielded significant more attraction ($p = 0.001$) to *L. maritima*. The percentages of non-responders in these experiments were 19% and 13% respectively (table 2).

A comparison was also done between *L. maritima* and *B. oleracea* var. *botrytis* to assess if there was a preference for food over ovipositing site. Three experiments were done; 2-3 days old, unmated and starved; 2-3 days old, unmated and fed, and finally 6-11 days old, mated and fed. In all experiments, more flies chose *L. maritima* than cauliflower, however the attraction for the nectar plant was not significant, except for the last experiment ($p = 0.019$). The percentages of non-responders were 22%, 48% and 0% respectively (table 2).

Table 2. Attraction of *D. radicum* females to nectar plants. Stars indicate level of significance of the attraction difference between the plants; significance at the * 5 %, ** 1% and *** 0.1% levels respectively. ns = not significant. Letters denote treatments; a = 2-3 days old, unmated and starved; b = 2-3 days old, unmated and fed; c = 6-11 days old, mated and fed.

	Plant	Air/Plant	No choice	% No choice	N	p-value
F. esculentum	30	14	24	35	44	0.023*
A. graveolens	31	11	2	5	42	0.003**
L. maritima	33	1	6	15	34	0.001***
A. graveolens vs. F. esculentum	11	2	3	19	13	0.022*
L. maritima* vs. *A. graveolens	35	7	6	13	42	0.001***
***L. maritima* vs. cauliflower**	8	6	4	22	14	0.791^{ns} a
	11	5	15	48	16	0.21^{ns} b
	15	4	0	0	19	0.019* c

3.1.1 Behavioral observations

During the two-choice tests with the olfactometer some behaviors were observed linked to the plant species. Flies normally exhibited a grooming behavior of antennae, wings, rear end and mouthparts, in response to flower odor irrespective of the plant species.

When *L. maritima* was encountered the flies groomed themselves unusual intensively. The searching for the odor source was rapid and all flies but one chose the flower over control. In the tubes the flies walked fast to the arm with flower odor as they tasted the glass with their mouthparts. Probing with the mouthparts also occurred for the other species but not as prevalent. *A. graveolens* elicited a rather quick response, although not as quick as for *L. maritima*. For the highly attractive *L. maritima* and *A. graveolens* some flies that first chose control realized their mistake and subsequently ran into the arm with flower odor.

For *F. esculentum* the response was not equally enthusiastic. Several flies turned around in the tube, as if they were repelled, as evident by the high proportion of non choosing flies. The flies that did make a choice took a long time to do that.

3.2 Nectar accessibility

The weight increase at 1 h was significantly different between the plant species ($p = 0.019$) but also compared to which day it was performed ($p = 0.017$). For 6 hrs the tested days was significant different ($p = 0.038$), but not the plant species tested ($p = 0.12$). After 12 hrs there was no difference according to plant species ($p = 0.17$) or day ($p = 0.28$).

The weight increase at 1 h was subjected to Tukey Simultaneous Test to reveal which plant species that was different from each other. A significant difference were seen between *L. maritima* compared to *A. graveolens* ($p = 0.045$), but not compared to *F. esculentum* ($p = 0.67$). However the weight increase of *F. esculentum* was significant different from *A. graveolens* ($p = 0.022$).

In some experiments, flies died or escaped, why data on *A. graveolens* and *F. esculentum* were excluded from occasions 1 and 2 respectively. Also readings were missing for some of the hours for various reasons. The statistical analysis was only done for increase after 1, 6 and 12 hrs, because after 12 hrs flies decreased in weight and died. The three experiment occasions were analyzed together (table 3, figure 1).

The initial weight of the flies was randomized and varied from 4.75 – 12.33 mg. The large span ranged from the fact that the few emerging flies needed to be used. A tendency could be seen that heavier flies increased more in weight than small ones.

The three control treatments (table 4) were not included in any statistical analysis or comparison with plant nectar, since the data was too small. The controls were instead used as an internal check of the fly quality. On average flies provided with water were seen to increases slightly in weight, but not as much as control flies provided with honeywater + water. Flies provided with neither water nor food rapidly lost weight, dehydrated and died.

Table 3. Average weight increase and Standard deviation (SD). Bold indicate Least square of means (L) and Standard error of mean (SE). Values from B2 and D1 are excluded. A = *L. maritima*, B = *F. esculentum* and D = *A. graveolens.* 1, 2, 3 denotes experiment occasion. The n-value is 5 flies at every occasion at 1, 6 and 12 hrs, except for A1 and D3, which were 4 flies.

	1 h	SD/SE	**6 h**	SD/SE	**12 h**	SD/SE	**24 h**	**48 h**
A1	0.3075	0.145			0.8375	0.928	0.9825	0.545
A2	3.1	1.125	3.342	1.455			2.768	2.038
A3	1.274	0.984	1.104	0.819	0.466	0.722	0.404	-0.2233
AL	**1.584**	**0.3066**	**2.223**	**0.4232**	**0.664**	**0.3803**		
B1	1.372	1.758			1.952	1.773	2.944	2.982
B3	1.712	1.005	1.734	0.919	1.17	0.722	1.458	0.955
BL	**2.019**	**0.3975**	**2.419**	**0.6731**	**1.561**	**0.3597**		
D2	0.726	0.866	1.29	1.731			-0.05	
D3	0.87	0.880	0.895	1.330	0.15	1.299	1.06	1.525
DL	**0.335**	**0.3992**	**1.038**	**0.4475**	**0.444**	**0.6261**		

Table 4. Average weight increase for the control (C) treatments. 1, 2, 3 denotes experiment occasion. Letters denote food treatment; a = nothing, b = water, c = honeywater + water. The n-values was 1-2 flies at every occasion.

	1 h	**6 h**	**12 h**	**24 h**	**48 h**
C1a	-0.85		-0.83	-1.32	-3.01
C2a	0.2	-1.25		-3.88	all dead
C3a	-0.325	-1.155	-1.745	-2.52	all dead
C1b	0.42		0.39	0.93	0.81
C2b	-1.24	0.88		-0.86	all dead
C3b	-0.675	0.425	-1.035	0.315	0.02
C1c	0.58		4.07	1.77	2.04
C2c	3.1	3.19		3.01	2.17
C3c	0.25	0.815	1.45	2.255	1.66

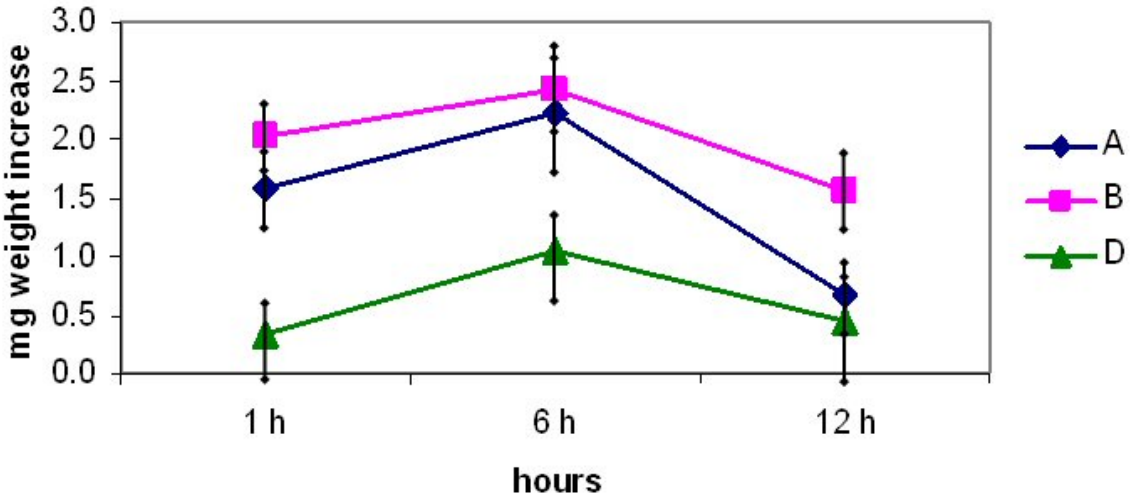

Figure 1. Least square of means for weight increase. Values from B2 and D1 are excluded. A = *L. maritima*, B = *F. esculentum* and D = *A. graveolens.*

3.3 Volatile collection

Ten volatile collections from four different days of *L. maritima* were analyzed, including plants both newly in blossom or more fully flowering. No correlation between the quantity of volatiles and the amount of flower material used was found when visually comparing the abundance values. The plants either remained in the pot (covered with aluminium thin foil) where it was grown, or was put in tap water in an Ehrlenmeyer flask. No differences could be observed between the pot and the flask with regards to contamination profile. Contaminants, mostly phthalates, were present in both methods.

Identified compounds with a match quality over 80%, in comparison with the mass spectra from known compounds in the reference libraries, are found in table 5. Of these six compounds were present in all ten samples; toluene, limonene, 2-ethylhexyl acetate, 2-ethyl-1-hexanol, benzaldehyde and 2-hydroxy-benzaldehyde.

Some of the six compounds were also present in the blank control collections, but in lower abundance; toluene, limonene, 2-ethyl-1-hexanol and benzaldehyde. Other compounds were not found at all in the blanks; 2-ethylhexyl acetate and 2-hydroxy-benzaldehyde. If a compound was present in the blank collection in equal or higher amounts than in the volatile collection, it was assumed to be a contaminant and thus excluded. The excluded compounds were; 2-pentanone, methyl isobutyl ketone, 3-ethoxy-propanoic acid ethyl ester and 2,4-bis(1,1-dimethylethyl)-phenol.

Table 5. Compounds found in volatile collection from *L. maritima*. RT and match quality are averages. Bold indicate compounds found in all 10 collections. B = benzenoid, I = isoprenoid, FA = Fatty acid derivate, N = nitrogen containing, S = sulphur containing, GLV = Green leaf volatile. *Hydrolysis product of glucosinolates (Bones & Rossiter, 2006). Numbers indicate literature reference; 1 = Knudsen et al., 1993; 2 = Bergström et al., 1992; 3 = Jönsson et al., 2005; 4 = Jönsson & Anderson, 2007; 5 = Blande et al., 2007; 6 = Gouinguené & Städler, 2006; 7 = Bones & Rossiter, 2006; 8 = Gürbüz et al., 2006; 9 = Pinto et al., 2007; 10 = Alissandrakis et al., 2007.

	RT	times found	match quality	class
benzene	4.507	2	86	B (1)
toluene	**6.357**	**10**	**93**	B (1)
ethylbenzene	7.954	7	92	B (1)
1,2 or 1,3-dimethyl-benzene (xylene)	~8.433	9	95	B (1)
limonene	**9.216**	**10**	**91**	I, (1, 2, 3, 4)
4-hydroxy-4-methyl-2-pentanone	11.727	2	83	FA (1, 6)
2-ethylhexyl acetate	**12.018**	**10**	**91**	FA (8)
4-isothiocyanato-1-butene (3-butenyl isothiocyanate)	12.993	2	89	N, S* (4, 5)
2-ethyl-1-hexanol	**13.435**	**10**	**83**	FA, GLV (1)
benzaldehyde	**13.909**	**10**	**96**	B (1, 2, 3, 4)
acetophenone	15.501	6	90	B (1)
2-hydroxy-benzaldehyde	**15.832**	**10**	**92**	B (1)
phenyl methanol (benzyl alcohol)	18.003	2	94	B (1, 2)
phenylethyl alcohol	18.391	1	86	B (1, 2, 3, 4)
benzyl nitrile	18.555	2	92	B, N* (7,9,10)
4-methoxy-benzaldehyde	19.588	6	94	B (1, 2)

The six common compounds were subjected to further comparisons. In table 6 the abundances put in area units are given for the compounds in the ten collections. The abundance is also visualized in figure 2. Toluene has the highest abundance of all compounds. The other five compounds have lower abundances that are similar to each other. Calculations of average abundance values and subsequent ratio calculation gave a ratio of 17:1:1:2:2:1 between toluene: limonene: 2-ethylhexyl acetate: 2-ethyl-1-hexanol: benzaldehyde: 2-hydroxy-benzaldehyde. The ratio was calculated from limonene put to the value 1 since limonene had a stable and low occurrence. The abundance average and the ratio should be seen as ruff calculations, since the standard deviation is rather high.

Collections 1-3 were seen to have gas chromatograms and abundance of compounds deviating from the other collections, and be of a different quality, and were thus excluded from the calculations. As seen from the standard deviations in table 6 and from figure 2, the variation of abundance is high in toluene, but lower for the other compounds. If collections 1-3 were included, the standard deviation and thus variation would be high for all compounds.

Table 6. All abundance values (=area units) have been divided by 10^6. Collections 1-3, collected at the same day, withdrawn from calculations because of deviation. RT = Average retention time. a = newly in blossom, b = fully flowering, p = pot, v = vase. X, y, z, o have been collected at the same occasions.

	toluene	**limonene**	**2-ethylhexyl acetate**	**2-ethyl-1-hexanol,**	**benzaldehyde**	**2-hydroxy-benzaldehyde,**
1apx	35.01	2.24	34.66	41.47	12.69	7.93
2apx	57.72	3.36	40.52	49.72	24.57	12.48
3bvx	34.31	1.25	6.96	8.80	21.88	8.94
4bpy	8.35	0.27	0.16	0.30	0.75	0.11
5bvy	64.47	7.52	6.50	12.01	11.91	4.38
6bvy	42.27	3.60	3.81	6.10	10.70	3.80
7apz	16.02	0.42	2.07	2.67	1.34	0.45
8apz	7.86	0.15	1.24	1.42	0.42	0.16
9bvo	33.78	0.42	1.08	2.03	0.71	0.11
10bvo	43.20	0.59	1.35	2.41	1.46	0.28
Average	**30.85**	**1.85**	**2.32**	**3.85**	**3.90**	**1.33**
StDev	21.12	2.78	2.16	4.02	5.09	1.90
Ratio	**17**	**1**	**1**	**2**	**2**	**1**
RT	6.357	9.216	12.018	13.435	13.909	15.832

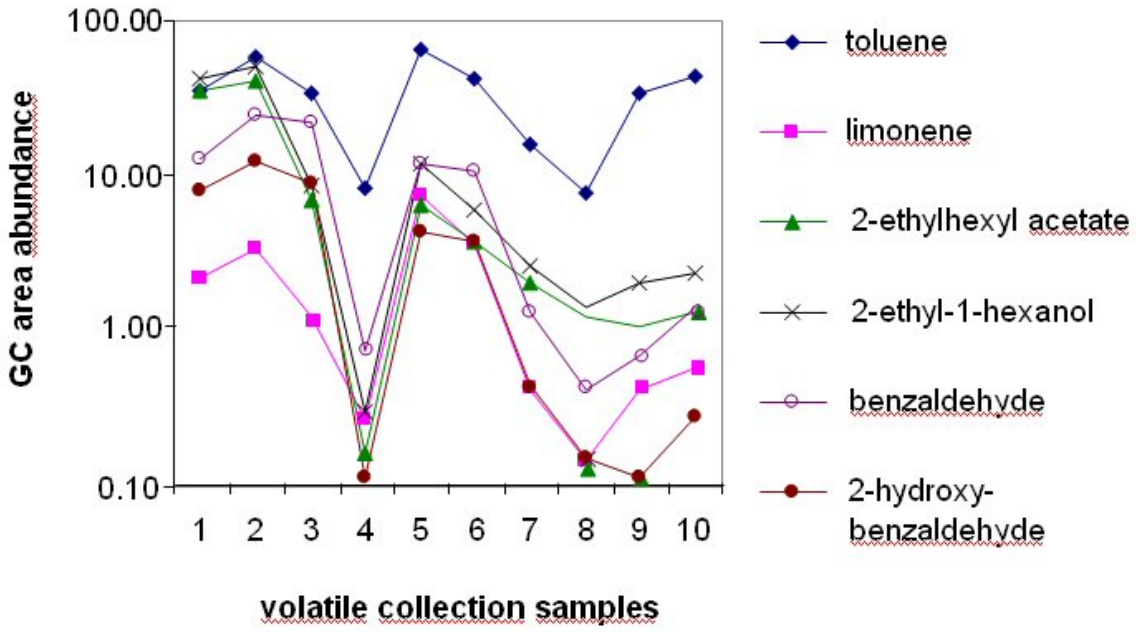

Figure 2. Abundance (=area units) of compounds in 10 volatile collections from *L. maritima*. The abundance values have been divided by 10^6 and log 10 transformed. Samples 1,2,7 and 8 comes from plants newly in blossom. For further information of the collections, see table 6.

4. Discussion

The three plants species investigated were found to be both attractive and having accessible nectar to *D. radicum*. In conclusion for the flower attractiveness experiments all nectar plants tested were significantly attractive, at different significance levels, to *D. radicum*, but when given a choice, the preference is *L. maritima* > *A. graveolens* > *F. esculentum*. When given a choice between *L. maritima* and cauliflower, there was a tendency of preference for *L. maritima*. In conclusion for the nectar accessibility all plant species gave a weight increase after 1, 6 and 12 hrs. After 1 h, *L. maritima* and *F. esculentum* gave an equal increase, which was significantly higher than for *A. graveolens*.

In the two-choice tests the proportion of non choosing flies for *F. esculentum* was much higher than for *L. maritima* and *A. graveolens*. This might suggest that the odor from *F. esculentum* is not so attractive, or slightly repellent. The potential mild repellency was also evident by the behavior in response to the odor which was not as enthusiastic as for *L. maritima* and *A. graveolens*. In contrast, providing the flies with *F. esculentum* resulted in a large weight increase in the nectar accessibility experiments, which was even higher than for *A. graveolens*. This could be explained by *F. esculentum* perhaps having a larger nectar production than *A. graveolens*. Since the attraction of *D. radicum* to *F. esculentum* were not so high, it might serve as a selective food plant to *T. rapae*, provided it is attractive and accessible to the wasp. *F. esculentum* has been found to be beneficial to other parasitoids (Winkler et al., 2003; Lee et al., 2006; Vattala et al., 2006; Winkler et al., 2006).

D. radicum of different physiological states (age, hunger state, mating status) were given a choice between *L. maritima* and cauliflower, both Brassicacae, to assess if there was a preference for food over ovipositing site. In all experiments, the flies chose *L. maritima* over cauliflower but the attraction was not significant, except for in the last experiment. It was surprising, since the last experiment comprised of flies well fed, presumably mated and in the right age for ovipositing. The n-value of the attractiveness experiments with *L. maritima* vs. cauliflower was low, and in some cases the number of non choosing flies was high. The experiments should be repeated before any certain conclusions can be made. It is possible that *L. maritima* were more attractive due to a

higher dose of emitted odors. Volatile collections could be made on both plant species to quantify release rates of e g. isothiocyanates, and then find the right amounts of plant material to test against each other.

In the nectar accessibility experiments, insects of similar pupal weights should have been used if possible, since there was a tendency in the data that larger flies fed more. Pupal weight is related to the size of the emerged fly, were large pupae gives large flies (Finch & Coaker, 1969b). If more emerged flies had been available when the experiments were conducted more control treatments could have been done. The weight increases of the treatments should then have been statistically compared to all of the controls. A control treatment with plants without flower could also have been made, as done by Wäckers (2004) and Baggen & Gurr (1998). Perhaps the nectar plants should have been changed at some point in the experiment. The decreasing weight after 12 h indicate that the nectar resource was consumed, and not reassimilated and starving of the flies occurred. Further longevity and fecundity tests could be conducted to see the effects of different nectar sources. The standard deviation and standard error of mean of the data were high, which should be bared in mind. Even if the variation was large it could still be concluded that all the plants offered to *D. radicum* gave a weight increase.

The head and mouthpart morphology of the two insects differs. *D. radicum* has a larger head than *T. rapae* and also more elongated mouthparts (pers. observations). However the elongated mouthparts could compensate for the larger head, and thus the same nectar sources could theoretically be accessed. Measurements of the fly and wasp heads was not done in this study, although it would be interesting to compare theoretical with actual accessibility for literature values of measurements on commonly used nectar plants as done by Winkler et al. (2003).

However, theoretical nectar accessibility does not mean that an insect actually will exploit a nectar source, if it not proven attractive. Attractiveness is also a source of differentiation between insects, which should be further investigated for *D. radicum* and *T. rapae*. A plant species unattractive to *D. radicum* could prove attractive to *T. rapae* and vice versa. Electrophysiological studies could be conducted with both species to reveal their responses to common plant odor compounds. Olfaction clearly plays an important role in host finding in both *D. radicum* and *T. rapae* (see sections 1.2.1 and

1.3.1), but the odor guided orientation to food flower nectar sources has not been investigated as much as for host finding.

Besides flower attractiveness and nectar accessibility (Wäckers, 2004) it is also important to investigate and find differences in color preferences (Wäckers, 1994) and nutritional requirements (Wäckers, 1999; Vattala et al., 2006) to find food plants that only favor the wasp. The carbohydrates that could be utilized by *D. radicum* have already been investigated (Finch & Coaker, 1969a), which also should be tested for *T. rapae*.

Jervis et al. (1993) recorded flower-visiting and nectar consumption by *T. rapae* on the Apiaceae *Angelica sylvestris*, *H. sphondylium* and *O. crocata*. *H. sphondylium*, as well as *Anthriscus sylvestris*, has unfortunately also been established to be a highly nutritive source for *D. radicum* (Finch & Coaker, 1969a; Finch, 1971). *D. radicum* are also suggested to utilize pollen from grasses as evident by Finch & Coaker (1969a), which means that *D. radicum* have bountiful sources in the field. These examples stress the importance of finding key elements for natural enemies and carefully weigh which plants to include in a flower strip.

It is very important to consider the flying abilities of both species when planning flower strips, since *D. radicum* is a good flyer (Finch & Skinner, 1975) while *T. rapae* is a poor flyer (Wishart & Monteith, 1954). *D. radicum* could explore nectar sources far away from the field, why it is important to favor *T. rapae* as much as possible in the field. It is also important to design flower strips for *T. rapae* that flowers throughout the entire flight period of the wasp.

Another way of supporting *T. rapae* is to sustain the wasp population even when *D. radicum* is not present. This can be done by planning crop rotations to allow the parasitoid access to host flies, such as *D. antiqua* on onions (Nilsson, 2008). *Delia* spp. without economic importance exists (Griffiths, 1991), which host plants could be kept in borders or flower strips (Nilsson, 2008).

The volatile collections of *L. maritima* disclosed six common compounds; toluene; limonene; 2-ethylhexyl acetate; 2-ethyl-1-hexanol; benzaldehyde; and 2-hydroxy-benzaldehyde. These compounds could be observed in a rough ratio of 17:1:1:2:2:1. The volatile profile constitute of compounds of which some are common in flower fragrance; benzaldehyde, benzyl alcohol, phenylethyl alcohol and limonene (Knudsen et

al., 1993). The attractive response of *D. radicum* to *L. maritima* might be provided by a common floral odor component, a ratio of several common floral odor components, crucifer unique compounds, a ratio of GLV:s or a combination of the mentioned. Since there was no time for electrophysiological studies (coupled gas chromatography electroantennodetection, GC-EAD) no specific compound in *L. maritima* could be identified as especially attractive for *D. radicum*.

The variations of abundance for some of the compounds released by *L. maritima* were high. A high or low variation in abundance for compounds, and the ratio between compounds, is a manner for insects to recognize a desired plant. The herbivores and the natural enemies will sense subtle changes in the ratio of certain compounds, both from the leaves and the flower. Different release ratios mediate insects in their host finding and foraging decisions. Compounds from the leaves could e. g. tell if the plants is infested or not, and aid in the decision whether an insect should oviposit/search for host insect. The scent of the flowers could e. g. reveal if pollinated or not and thus give information about the nectar production.

Typical compounds from cruciferous plants were found in four of the collections; 4-isothiocyanato-1-butene (3-butenyl isothiocyanate) and benzyl nitrile. Certainly the two compounds are present in all the plants tested although they were probably accentuated because of accidentally breaking some leaves, since both are hydrolysis product of glucosinolates (Bones & Rossiter, 2006). Isothiocyanates and benzyl nitrile could probably also be released through stomata of intact plants in low amounts (Schoonhoven, et al., 2005a). These low amounts could perhaps accentuate the attraction of *D. radicum* to *L. maritima*, since isothiocyanates are well known to attract *D. radicum* (Nottingham, 1988). The compounds would also be released upon damage by feeding *D. radicum* larvae, and thus probably attract *T. rapae* (Neveu et al., 2002). The compound 3-butenyl isothiocyanate have been found in the headspace of oilseed rape infested by pollen beetles (Jönsson & Anderson, 2007). Blande et al. (2007) found this compound when turnip was infested by aphids, and the parasitoid *Diaeretiella rapae* was significantly attracted to it.

The result of the volatile collection should be seen as a rough estimate. If more time had been available the identity should have been more established. Since the extracts originally were intended for coupled gas chromatography electroantennodetection (GC-

EAD), no internal standard was used to quantify the compounds. The identity of the compounds should further have been established by run of synthesized compounds on a GC with same column as the GC-MS. The retention order should also have been concluded by comparison to Kovats index. Further, collections should also have been made from *L. maritima* without flowers to reveal which compounds mainly originate from the leaves. Collections could also have been made under more greenhouse-like conditions instead of the laboratory conditions used here.

The high attractiveness of *L. maritima* to *D. radicum* found in the two-choice tests, and the presence of isothiocyanates mediating host-finding and glucosinolates allowing host-plant acceptance, could indicate the potential of *L. maritima* as a dead-end trap crop. A dead-end trap crop is a highly attractive plant that deceives the insect to oviposit but fail to support the offspring (Shelton & Badenes-Perez, 2006). The small root system of *L. maritima* would probably fail to develop larvae. *L. maritima* and other Brassicaceae spp. interesting to investigate should in this manner lure *D. radicum* to oviposit, but could also have the additional advantage of benefiting and attracting natural enemies. *Brassica kaber* and *Barbarea vulgaris* have shown to increase longevity and fecundity of *D. insulare* (Hymenoptera:Ichneumonidae) under field conditions (Idris & Grafius, 1995) and could be tested for attraction to *D. radicum* as dead-end trap crops.

The compound 4-hydroxy-4-methyl-2-pentanone found in *L. maritima* headspace have been found released from germinating beans, *Phaseolus vulgaris*, and mediated ovipositing as well as electrophysiological response in the polyphagous *Delia platura* (Gouinguené & Städler, 2006b), also reported from cruciferous crops (Alford, 1999). *L. maritima* could thus potentially also attract and deceive this species if used as a dead-end trap crop.

The mechanism behind dead-end trap cropping is that female herbivores tend to oviposit in the vicinity of nectar food plants, which will provide optimal foraging and save energy. If the same plant can be used as both food plant and ovipositing site an even higher benefit is gained. This could result in oviposition on plants which is not optimal as host plants for the larval offspring (Shelton & Badenes-Perez, 2006; Wäckers et al., 2007).

Several investigations have been carried out on the effects of floral nectar supplements on parasitoid wasps in the tritrophic interaction of Brassicaceae crop – pest – natural enemy – system (Idris & Grafius, 1995; 1997; Bigger & Chaney, 1998; Pfiffner et al., 2003; Winkler et al., 2003; 2006; Wäckers, 2004; Harvey & Wagenaar, 2006; Lee et al., 2006). The findings from this thesis and subsequent work in the project should be implemented for the manipulation of this trithrophic system. Finally and ultimately conservation biological control approaches for all crucivore pests should be considered from the findings of other similar studies and combined to select nectar plants selectively suitable for several natural enemies, including hymenopteran parasitoids.

5. References

Alford, D.V. (1999), *A textbook of Agricultural Entomology*, Blackwell Science, Cambridge, p.197-202.

Alissandrakis, E., Tarantilis, P.A., Harizanis, P.C., Polissiou, M. (2007), Comparison of the volatile composition in thyme honeys from several origins in Greece**.** *Journal of Agricultural and Food Chemistry*, 55: 8152-8157.

Baggen, L.R., Gurr, G.M. (1998), The influence of food on *Copidosoma koehleri* (Hymenoptera:Encyrtidae), and the use of flowering plants as a habitat management tool to enhance biological control of potato moth, *Phthorimaea operculella* (Lepidoptera:Gelechiidae), *Biological control*, 11: 9-17.

Baggen, L.R., Gurr, G.M., Meats, A. (1999), Flowers in tri-trophic systems: mechanisms allowing selective exploitation by insect natural enemies for conservation biological control, *Entomologia Experimentalis et Applicata*, 91: 155-161.

Baur, R., Birch, A.N.E., Hopkins, R.J., Griffiths, D.W., Simmonds, M.S.J., Städler, E. (1996), Oviposiotion and chemosensory stimulation of the root flies *Delia radicum* and *D. floralis* in response to plants and and leaf surface extracts from resistant and susceptible *Brassica* genotypes, *Entomologia Experimentalis et Applicata*, 78: 61-75.

Bigger, D.S., Chaney, W.E. (1998), Effects of *Iberis umbellata* (Brassicaceae) on insect pests of cabbage and on potential biological control agents, *Environmental Entomology*, 27: 161-167.

Bergström, G., Birgersson, G., Groth, I., Nilsson, L.A. (1992), Floral fragrance disparity between three taxa of Lady´s slipper *Cypripedium calceolus* (Orchidaceae), *Phytochemistry*, 31: 2315-2319.

Blande, J.D., Pickett, J.A., Poppy, G.M. (2007), A comparison of semiochemically mediated interactions involving specialist and generalist *Brassica*-feeding aphids and the braconid parasitoid *Diaeretiella rapae*, *Journal of Chemical Ecology*, 33: 767-779.

Block, W., Turnock, W.J., Jones, T.H. (1987), Cold resistance and overwintering survival of the cabbage root fly, *Delia radicum* (Anthomyiidae), and its parasitoid, *Trybliographa rapae* (Cynipidae), in England, *Oecologia*, 71: 332-338.

Bones, A.M., Rossiter, J.T. (2006), The enzymic and chemically induced decomposition of glucosinolates, *Phytochemistry*, 67: 1053-1067.

Brooks (1951), Identification of the root maggots (Diptera:Anthomyiidae) attacking cruciferous garden crops in Canada, with notes on biology and control, *The Canadian Entomologist*, 83: 109-120.

Brown, P.E., Anderson, M. (1998), Morphology and ultrastructure of sense organs on the ovipositor of *Trybliographa rapae*, a parasitoid of the cabbage root fly, *Journal of Insect Physiology*, 44: 1017-1025.

Brown, P.E., Anderson, M. (1999), Factors affecting ovipositor probing in Trybliographa rapae, a parasitoid of the cabbage root fly, *Entomologia Experimentalis et Applicata*, 93: 217-225.

Bruck, D.J., Snelling, J.E., Dreves, A.J., Jaronski, S.T. (2005), Laboratory bioassays of entomopathogenic fungi for control of *Delia radicum* (L.) larvae, *Journal of Invertebrate Pathology*, 89: 179-183.

Butterfield, A., Anderson, M. (1994), Morphology and ultrastructure of antennal sensilla of the parasitoid, *Trybliographa rapae* (Westw.) (Hymenoptera: Cynipidae), *International Journal of Insect Morphology and Embryology*, 23: 11-20.

Darvas, B., Szappanos, A. (2003), Male and female morphology of some central European *Delia* (Anthomyiidae) pests, *Acta Zoologica Academiae Scientiarum Hungaricae*, 49: 87-101.

Eilenberg, J., Hajek, A., Lomer, C. (2001), Suggestions for unifying the terminology in biological control, *Biocontrol*, 46: 387-400.

Finch, S. (1971), The fecundity of the cabbage root fly *Erioischia brassicae* under field conditions, *Entomologia Experimentalis et Applicata*, 14: 147-160.

Finch, S. (1974), Sugars available from flowers visited by the adult cabbage root fly, *Erioischia brassicae* (Bch.) (Diptera, Anthomyiidae), *Bulletin of Entomological Research*, 64: 257-263.

Finch, S. (1989), Ecological considerations in the management of *Delia* pest species in vegetable crops, *Annual Review of Entomology*, 34: 117-137.

Finch, S., Coaker, T.H. (1969a), Comparison of the nutritive values of carbohydrates and related compounds to Erioischia brassicae, *Entomologia Experimentalis et Applicata*, 12: 441-453.

Finch, S., Coaker, T.H. (1969b), A method for the continuous rearing of the cabbage root fly *Erioischia brassicae* (Bch.) and some observations on its biology, *Bulletin of Entomological Research*, 58: 619-627.

Finch, S., Skinner, G. (1975), Dispersal of the cabbage root fly. *Annals of Applied Biology*, 81: 1-19.

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 onion fly more effectively than non-aromatic plants?, *Entomologia Experimentalis et Applicata*, 109: 183-193.

Forehand, L.M, Orr, D.B., Linker, H.M. (2006), Evaluation of a commercially available beneficial insect habitat for management of Lepidoptera pests, *Journal of Economic Entomology*, 99: 641-647.

Fournet, S., Astier, N., Cortesero, A.M., Biron, D.G. (2004), Influence of a bimodal emergence strategy of a Dipteran host on life-history traits of its main parasitoids, *Ecological Entomology*, 29: 685-691.

Gouinguené, S.P.D., Städler, E. (2006a), 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., Städler, E. (2006b), Oviposition in *Delia platura* (Diptera, Anthomyiidae): The role of volatile and contact cues of bean, *Journal of Chemical Ecology*, 32: 1399-1413.

Griffiths, G.C.D. (1991), *Flies of the Nearctic region*, *Volume VIII: Cyclorrhapha II (Schizophora: Calyptratae), Part 2: Anthomyiidae, Number 7 and 8*, E. Schweizerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller), Stuttgart, p. 953-1048 and 1049-1240.

Gürbüz, O., Rouseff, J.M., Rouseff, R.L. (2006), Comparison of aroma volatiles in commercial Merlot and Cabernet Sauvignon wines using gas chromatography-olfactometry and gas chromatography-mass spectrometry, *Journal of Agricultural and Food Chemistry*, 54: 3990-3996.

Harvey, J.A., Wagenaar, R. (2006), Development of the herbivore *Pieris rapae* and its endoparasitoid *Cotesia rubecula* on crucifers of field edges, *Journal of Applied Entomology*, 130: 465-470.

Hausmann, C., Wäckers, F.L., Dorn, S. (2005), Sugar convertibility in the parasitoid *Cotesia glomerata* (Hymenoptera:Braconidae), *Archives of Insect Biochemistry and Physiology*, 60: 223-229.

Hemachandra, K.S., Kuhlmann, U., Mason, P.G., Holliday, N.J. (2007), Spatial patterns of *Trybliographa rapae* parasitism of *Delia radicum* larvae in oilseed rape and cauliflower, *Journal of Applied Entomology*, 131: 338-346.

Hogervorst, P.A.M., Wäckers, F.L., Romeis, J. (2007), Detecting nutritional state and food source use in field-collected insects that synthesize honeydew oligosaccharides, *Functional Ecology*, 21: 936-946.

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

Idris, A.B., Grafius, E. (1995), Wildflowers as nectar sources for *Diadegma insulare* (Hymenoptera:Ichneumonidae), a parasitoid of diamondback moth (Lepidoptera:Yponomeutidae), *Environmental Entomology*, 24: 1726-1735.

Idris, A.B., Grafius, E. (1997), Nectar-collecting behavior of *Diadegma insulare* (Hymenoptera:Ichneumonidae), a parasitoid of diamondback moth (Lepidoptera:Plutellidae), *Environmental Entomology*, 26: 114-120.

Jervis, M., Kidd, N.A.C., Fitton, M.G., Huddleston, T., Dawah, H.A. (1993), Flower-visiting by hymenopteran parasitoids, *Journal of Natural History*, 27: 67-105.

Jervis, M. (1998), Functional and evolutionary aspects of mouthpart structure in parasitoid wasps, *Biological Journal of the Linnean Society*, 63: 461-493.

Jönsson, M., Anderson, P. (1999), Electrophysiological response to herbivore-induced host plant volatiles in the moth *Spodoptera littoralis*, *Physiological Entomology*, 24: 377-385.

Jönsson, M., Anderson, P. (2007), Emission of oilseed rape volatiles after pollen beetle infestation; behavioural and electrophysiological responses in the parasitoid *Phradis morionellus*, *Chemoecology*, 17: 201-207.

Jönsson, M., Lindkvist, A., Anderson, P. (2005), Behavioural responses in three ichneumonid pollen beetle parasitoids to volatiles emitted from different phenological stages of oilseed rape, *Entomologia Experimentalis et Applicata*, 115: 363-369.

Kacem, N., Neveu, N., Nénon, J.P. (1999), Time for development of *Trybliographa rapae*, an endoparasitoid of the cabbage root fly *Delia radicum*, at four constant temperatures, *IOBC/WPRS Bulletin*, 22: 125.

Kacem-Haddjel-Mrabet, N., Nenon, J.-P. (2003), Effect of the host-plant on the biological characteristics of *Trybliographa rapae* W. (Hymenoptera: Figitidae), endoparasitoid of the cabbage root fly *Delia radicum* L. (Diptera: Anthomyiidae), *IOBC/WPRS Bulletin*, 26: 135-140.

Knudsen, J.T., Tollsten, L., Bergström, L.G. (1993), Floral scents – a checklist of volatile compounds isolated by head-space techniques, *Phytochemistry*, 33: 253-280.

Kostal, V. (1993), Physical and chemical factors influencing landing and oviposition by the cabbage root fly on host-plant models, *Entomologia Experimentalis et Applicata*, 66: 109-118.

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.

Lee, J.C., Andow, D.A., Heimpel, G.E. (2006), Influence of floral resources on sugar feeding and nutrient dynamics of a parasitoid in the field, *Ecological Entomology*, 31: 470-480.

Landis, D.A., Wratten, S.D., Gurr, G.M. (2000), Habitat management to conserve natural enemies of arthropod pests in agriculture, *Annual Review of Entomology*, 45: 175-201.

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.

Marazzi, C., Patrian, B., Städler, E. (2004), Secondary metabolites of the leaf surface affected by sulphur fertilization and perceived by the cabbage root fly, *Chemoecology*, 14: 87-94.

Miles, M. (1951), Factors affecting the behaviour and activity of the cabbage root fly (*Erioischia brassicae* Bché), *Annals of Applied Biology*, 38: 425-432.

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.

Neveu, N., Kacem, N., Nénon, J.-P. (1996), A method for rearing *Trybliographa rapae* W. on *Delia radicum* L., *IOBC/WPRS Bulletin*, 19: 173-178.

Neveu, N., Krespi, L., Kacem, N., Nénon, J.-P. (2000), Host-stage selection by *Trybliographa rapae*, a parasitoid of the cabbage root fly *Delia radicum*, *Entomologia Experimentalis et Applicata*, 96: 231-237.

Neveu, N., Grandgirard, J., Nenon, J.P., Cortesero, A.M. (2002), Systemic release of herbivore-induced plant volatiles by turnips infested by concealed root-feeding larvae *Delia radicum* L., *Journal of Chemical Ecology*, 28: 1717-1732.

Nilsson, U. (2008), Personal communication with PhD-student, Department of Plant Protection Biology, Swedish University of Agricultural Sciences, Alnarp.

Nottingham, S.F. (1988), Host-plant finding for oviposition by adult cabbage root flies, *Delia radicum*, *Journal of Insect Physiology*, 34: 227-234.

Ouellette, R.J. (1998), *Organic chemistry – a brief introduction*, 2nd edition, Prentice Hall, New Jersey, 559 pp.

Patt, J.M., Hamilton, G.C., Lashomb, J.H. (1997), Foraging success of parasitoid wasps on flower: interplay of insect morphology, floral architecture and searching behavior, *Entomologia Experimentalis et Applicata*, 83: 21-30.

Pinto, D.M., Nerg, A.-M., Holopainen, J.K. (2007), The role of ozone-reactive compounds, terpenes, and green leaf volatiles (GLVs), in the orientation of *Cotesia plutellae***,** *Journal of Chemical Ecology*, 33: 2218-2228.

Pfiffner, L., Wyss, E. (2004), Use of sown wildflower strips to enhance natural enemies of agricultural pests, In: Gurr, G.M., Wratten, S.D., Altieri, M.A. (eds), *Ecological engineering for pest management – advances in habitat manipulation for arthropods*, CABI Publishing, Wallingford, pp. 165-185.

Pfiffner, L., Merkelbach, L., Luka, H. (2003), Do sown wildflower strips enhance the parasitism of lepidopteran pests in cabbage crops?, *IOBC/WPRS Bulletin*, 26: 111-116.

Prasad, R.P. & Snyder, W.E. (2004), Predator interference limits fly egg biological control by a guild of ground-active beetles, *Biological Control*, 31: 428-437.

Quinlan, J. (1978), *Hymenoptera Cynipoidea Eucoilidae, Handbooks for the Identification of British Insects Vol. VIII, Part 1 (b)*, Royal Entomological Society of London, London, 58 pp.

Roessingh, P., Städler, E., Fenwick, G.R., Lewis, J.A., Kvist Nielsen, J., 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.

Romeis, J., Wäckers, F.L. (2000), Feeding responses by female *Pieris brassicae* butterflies to carbohydrates and amino acids, *Physiological Entomology*, 25: 247-253.

Schoonhoven, L.M., van Loon, J.J.A., Dicke, M. (2005a), Plant chemistry: endless variety, In: Schoonhoven, L.M., van Loon, J.J.A., Dicke, M., *Insect-plant biology*, 2nd ed, Oxford University Press, New York, pp. 48-98.

Schoonhoven, L.M., van Loon, J.J.A., Dicke, M. (2005b), Insects and flowers: mutualism par excellence, In: Schoonhoven, L.M., van Loon, J.J.A., Dicke, M., *Insect-plant biology*, 2nd ed, Oxford University Press, New York, pp. 306-335.

Shelton, A.M., Badenes-Perez, F.R. (2006), Concepts and applications of trap cropping in pest management, *Annual Review of Entomology*, 51: 285-308.

Soler, R., Bezemer, T.M., Cortesero, A.M., van der Putten, W.H., Vet, L.E.M., Harvey, J.A. (2007), Impact of foliar herbivory on the development of a root-feeding insect and its parasitoid, *Oecologia*, 152: 257-264.

Steppuhn, A., Wäckers, F.L. (2004), HPLC sugar analysis reveals the nutritional state and the feeding history of parasitoids, *Functional Ecology*, 18: 812-819.

Swailes, G.E. (1961), Laboratory studies on mating and oviposition of *Hylemya brassicae* (Bouché) (Diptera:Anthomyiidae), *The Canadian Entomologist*, 93: 940-943.

Thomsen, L., Eilenberg, J. (2000), *Entomophthora muscae* resting spore formation *in vivo* in the host *Delia radicum*, *Journal of Invertebrate Pathology*, 76: 127-130.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., van Nouhuys, S., Vidal, S. (2007), Conservation biological control and enemy diversity on a landscape scale, *Biological Control*, 43: 294-309.

Vattala, H.D., Wratten, S.D., Phillips, C.B., Wäckers, F.L. (2006), The influence of flower morphology and nectar quality on the longevity of a parasitoid biological control agent, *Biological Control*, 39: 179-185.

Winkler, K., Wäckers, F., Valdivia, L., Larraz, V., van Lenteren, J. (2003), Strategic use of nectar sources to boost biological control, *IOBC/WPRS Bulletin*, 26: 209-214.

Winkler, K., Wäckers, F., Bukovinszkine-Kiss, G., van Lenteren, J. (2006), Sugar resources are vital for *Diadegma semiclausum* fecundity under field conditions, *Basic and Applied Ecology*, 7: 133-140.

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

Wood, A.M. (1989), *Insects of economic importance: a checklist of preferred names*, CAB International, Wallingford, p.45, 141.

Wäckers, F.L. (1994), The effect of food deprivation on the innate visual and olfactory preferences in the parasitoid *Cotesia rubecula*, *Journal of Insect Physiology*, 40 (8): 641-649.

Wäckers, F.L. (1999), Gustatory response by the hymenopteran parasitoid *Cotesia glomerata* to a range of nectar and honeydew sugars, *Journal of Chemical Ecology*, 25: 2863-2877.

Wäckers, F.L. (2004), Assessing the suitability of flowering herbs as parasitoid food sources: flower attractiveness and nectar accessibility, *Biological Control*, 29: 307-314.

Wäckers, F.L. (2005), Suitability of (extra-)floral nectar, pollen, and honeydew as insect food sources, In *Plant-Provided Food for Carnivorous Insects*, ed. F.L. Wäckers, P.C.J. van Rijn, and J. Bruin, Cambridge University Press, Cambridge, p. 17-74.

Wäckers, F.L., Steppuhn, A. (2003), Characterizing nutritional state and food source use of parasitoids collected in fields with high and low nectar availability, *IOBC/WPRS Bulletin*, 26: 203-208.

Wäckers, F.L., Romeis, J., van Rijn, P. (2007), Nectar and pollen feeding by insect herbivores and implications for multitrophic interactions, *Annual Review of Entomology*, 52: 301-323.

Zehnder, G., Gurr, G.M., Kühne, S., Wade, M.R., Wratten, S.D., Wyss, E. (2007), Arthropod pest management in organic crops, *Annual Review of Entomology*, 52: 57-80.