

ORIGINAL CONTRIBUTION

Herbivore response to habitat manipulation with floral resources: a study of the cabbage root fly

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Abstract

Biological control of pest insects can be improved by providing natural enemies with additional food resources such as floral nectar within the production field. However, herbivores may also benefit from this practice. The aim of this 3-year field study was to investigate if dill and buckwheat, aimed as food resources for natural enemies, could increase the densities of the cabbage root fly, *Delia radicum* L. (Diptera: Anthomyiidae), a severe pest on crucifers. Differences in egg density, numbers of pupae and sex ratio were compared between cabbage plots with or without flowers. Habitat manipulation by intercropping flowering plants with cabbage did not increase the overall *D. radicum* egg density in our 3-year study, and there were no significant differences in egg numbers between treatments in any year. No effect on the fecundity of *D. radicum* was observed, most likely because of the high mobility and feeding behaviour of the female flies, combined with high abundance and diversity of other food sources around the fields during this period. Despite equal egg numbers, fewer pupae were found in plots with flowers than without in one of three studied years. This finding suggests that natural enemies attacking larvae and pupae of *D. radicum* were either more abundant or efficient in cabbage plots with flowers.

Introduction

Vegetable crops in the temperate region of the world are attacked by a broad range of insect pests. The cabbage root fly, *Delia radicum* L. (Diptera: Anthomyiidae), is a severe pest on crucifers (Nair and McEwen 1975). The larvae feed on the roots and stems of host plants, which can result in crop losses of up to 60% in newly planted fields (Finch 1989). Attacks later in the growing season reduce the quality and yield whilst rarely kill the plant (Coaker and Finch 1971). Overwintering takes place in the pupal stage in the soil (Nair and McEwen 1975).

A variety of natural enemies are known to suppress *D. radicum* populations (Hughes and Salter 1959; Finch 1996; Brunel et al. 1999; Eyre et al. 2009). The parasitoid wasp *Trybliographa rapae* Westwood (Hymenoptera: Figitidae) is the most important larval parasitoid of *D. radicum* (Jones 1986) and

parasitism rates may vary between a few per cent up to 60% of the sampled population (Wishart and Monteith 1954; Bromand 1980; Finch 1989).

By improving the conditions for natural enemies within the agroecosystems, a more efficient pest control can be achieved (Wolcott 1942; Altieri and Letourneau 1982; Landis et al. 2000; Gurr et al. 2003; Zehnder et al. 2007). For instance, intercropping with flowers, as a food resource, can increase the abundance and diversity of natural enemies and is suggested as a pest management strategy (Leius 1967; Landis et al. 2000; Frank and Shrewsbury 2004; Lee and Heimpel 2005; Hogg et al. 2011). The positive effects of floral nectar have been intensively studied for numerous Hymenoptera parasitoid species (Jervis et al. 1993; Baggen and Gurr 1998; Lee et al. 2006; Vattala et al. 2006; Brown et al. 2010). Potentially, floral resources may promote high densities of *T. rapae* within the field and thus stabilize

the population of *D. radicum* from one generation to other. However, herbivores may also benefit from floral resources, with negative effects on crop quality and yields (Zhao et al. 1992; Baggen and Gurr 1998; Wäckers et al. 2007). In field, *D. radicum* feed on flowers because carbohydrates are essential for egg maturation and survival (Finch 1971) and long-term aggregation of flies is often found at hedges in the close vicinity of the feeding site (Hawkes 1973). The sex ratio in crop field is biased towards females as males stay at the aggregation site (Hawkes 1972; Nair and McEwen 1975). Intercropping with flowers may increase the realized fecundity of *D. radicum* females and, if flies aggregate in the flower stands, alter the sex ratio within the field (Finch 1971).

The risk of promoting herbivores can be reduced by choosing food plants, identified in laboratory and field studies, as being more suitable for natural enemies, whilst being less suitable for herbivores (Patt et al. 1997; Baggen and Gurr 1998; Landis et al. 2000). The selection of food plants should therefore be based on such studies (Baggen et al. 1999; Winkler et al. 2010). In an earlier laboratory and greenhouse study, we tested the attraction, accessibility and longevity of *D. radicum* and *T. rapae* on different flowers (Nilsson et al. 2011). On the basis of the results, we selected buckwheat [*Fagopyrum esculentum* Moench (Polygonaceae)] and dill [*Anethum graveolens* L. (Apiaceae)] to be further evaluated as food resources for *T. rapae* in a field study. Although dill and buckwheat were less attractive and resulted in less weight gain than some of the other flowers tested, they still improved the longevity of *D. radicum* females as compared to the control treatment where flowers and buds were removed from the plants. Hence, there is a risk that this habitat manipulation strategy may be counterproductive in the field and result in crop losses. However, discrepancy between laboratory and field studies is not uncommon (Jervis et al. 1992). Plants that have been found utilized, as nectar resource by the studied insect, in laboratory may e.g. not be visited in field (Jervis et al. 1992; Wäckers 2005) or do not have accessible nectar in field because of nectar depletion of other nectar feeding insects (Winkler et al. 2009). For instance, Winkler et al. (2010) found that the longevity of the herbivore *Plutella xylostella* L. (Lepidoptera: Plutellidae) increased on three plants in a laboratory study, whilst these plants had no effect on herbivore densities in the field.

The objective of this 3-year field study was to investigate the impact of intercropped floral resources on the pest insect *D. radicum*. The study

examined the following: (i) whether egg densities are higher on cabbage plants intercropped with flowers; (ii) whether intercropping influences the number of eggs that develop into pupae; and (iii) whether floral resources affect the sex ratio of *D. radicum* within the field as this gives an indication if the field population of *D. radicum* aggregates within the field.

Materials and Methods

Field layout

This study was conducted at Torslunda research station, Öland, south-east Sweden (56°37'N, 16°30'E), in 2008, 2009 and 2010. Activity of *Delia* spp. was monitored in 16 experimental plots (21 × 10 m), half of which had a flower and a grass strip and half only a grass strip (control) (fig. 1). This was to achieve a comparison between cabbage plots with a green vegetation strip, with or without flowers. The plots consisted of 20 crop rows (9.75 m long) on each side of the flower/control strip (i.e. a total of 40 rows per plot) and were divided into four randomized blocks, because of altered design in 2009. Each plot was located in the same place every year, and plots were separated by at least 40-m open soil to reduce insect movement between plots. The experimental field was organically managed according to International Federation of Organic Agriculture Movements (IFOAM), without synthetic pesticides and fertilizers. Weeds were removed by hand before flowering within plots, and field edges were cut regularly throughout all seasons. The area between plots was harrowed weekly. Mean monthly precipitation and temperature in the south-east of Sweden in 2008, 2009 and 2010 are given in table 1.

During 2008 and 2010, all plots were planted with cabbage plants (i.e. there were double replicates within each block), whilst half the plots were planted with onions in 2009 to monitor the population of the onion fly *Delia antiqua* Meigen (Diptera: Anthomyiidae) and how natural enemies are affected by crop rotation. Few *D. antiqua* eggs were found, and the results are therefore not discussed here. The effects of floral resources and crop rotation on natural enemies of *D. radicum* were investigated in a separate study (U. Nilsson, L.-M. Rännbäck, M. Björkman, P. Anderson, B. Rämert, unpublished data).

White cabbage plants (*Brassica oleracea* var. *capitata* f. *alba* cv. Castello L.) were planted on 19 May 2008, 14 May 2009 and 25 May 2010. Onion plants (*Allium cepa* cv. Hytech Eco L.) consisting of five to

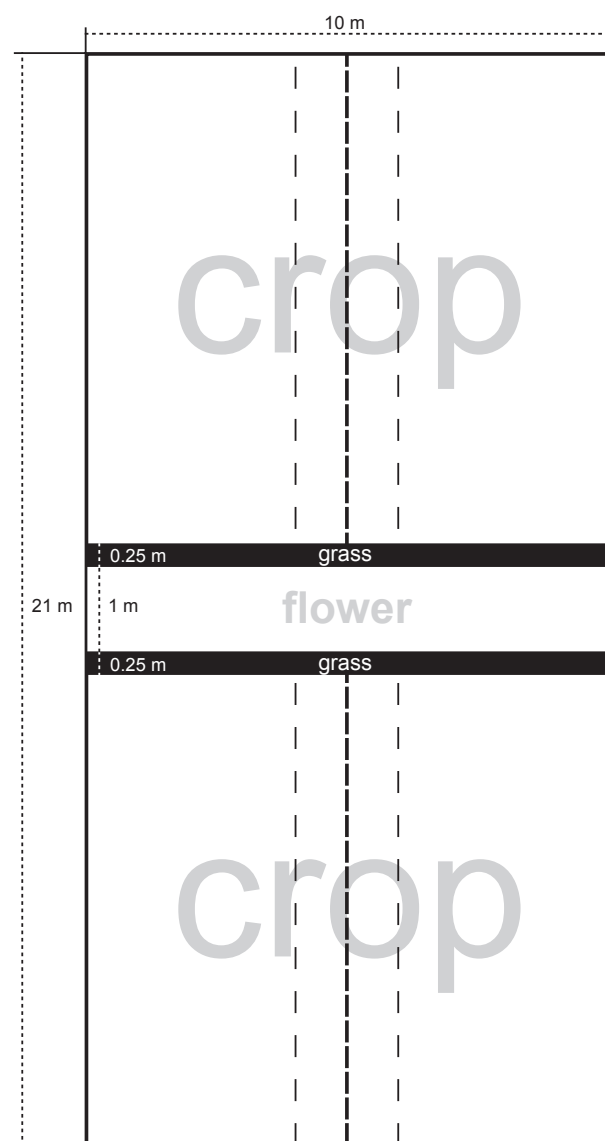


Fig. 1 Layout of the experimental plot. Flower strips are replaced with grass in control plots. Thin dashed lines represent egg sampling transects, whilst the thick dashed line indicates the soil sampling transect.

seven seedlings per pot were transplanted on 13 May 2009. The space between cabbage rows and between cabbage plants within rows was 50 cm. Onion plants were spaced at 50 cm between rows and 18 cm within rows.

Buckwheat and dill were sown in the middle of plots (1 × 10 m wide strip) with flower strip treatments (fig. 1). This was performed on two different occasions to prolong the flowering period: 3 June and 17 June 2008, 27 May and 17 June 2009 and 2 June and 17 June 2010. Flowering started in week 28 in 2008, week 28 in 2009 and week 27 in 2010

Table 1 Mean monthly temperatures and precipitation in the south-east of Sweden in 2008, 2009 and 2010

Year	Month	Temperature (°C)	Precipitation (mm)
2008	May	11.0	26
	June	14.9	22
	July	17.2	44
	August	16.1	117
2009	May	10.9	49
	June	13.7	50
	July	17.4	52
	August	16.6	40
2010	May	9.4	68
	June	14.3	25
	July	19.1	125
	August	16.8	48

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and lasted throughout the egg sampling period for all years. On each side of the flowering strip, a 25-cm strip of perennial grass [*Dactylis glomerata* L. (Poaceae)] was hand-sown on 15 May 2008 and then left during the entire 3-year study. Flowering heads of the grass were removed, as *D. radicum* can utilize this as a food resource (Finch and Coaker 1969). During winter, *D. glomerata* provides suitable overwintering sites for epigeal predators such as carabids and staphylinids (MacLeod et al. 2004). *D. glomerata* was also sown in the middle of control plots (1.5 × 10 m) on 19 May 2008, 6 November 2008 and 5 November 2009 and was cut to 6 cm height during season and ploughed down in autumn as we did not want to provide overwintering sites for epigeal predators in the control plots.

Assessing adult flies

Yellow-coloured pan traps (20 cm in diameter) combined with a 20-cm-high plexi-glass window were used to assess the abundance and sex ratio of adult *D. radicum* flies in the field (Kostal and Finch 1996). Traps (two per plot) were filled with water and a few drops of a surface detergent and placed either next to the flower/control strip or 7 m away from the strip, within the cabbage crop. All traps were clearly visible from above. In 2008, one control and one flower plot were assessed in each of four blocks from 25 July to 15 August. All 16 plots were assessed in 2010 from 15 July to 14 August. Traps were exposed weekly in the field for 48 h. Caught *Delia* spp. flies were counted, sexed and species-determined following the characteristics described by Darvas and Szapannos (2003).

Assessment of egg-laying

Eggs of *D. radicum* were sampled weekly from the soil around cabbage and onion plants according to a procedure described by Hughes and Salter (1959). Each sample measured 7 days of egg-laying activity. Samples were collected from plants along two transects across the plot throughout the season (fig. 1). The same plant was thereby only sampled every second week as *D. radicum* favour to oviposit on host plants already damaged by conspecific flies (Baur et al. 1996). Weekly sampling with removal of eggs from the same plant could therefore have underestimated the oviposition rates in the field (Björkman et al. 2007).

During 2008, a total of 20 soil samples were taken in each plot (10 on each side of the strip). The number of samples was reduced to 10 for 2009 and 2010 (five on each side of the strip) to minimize the sampling effort whilst still maintaining a sufficient degree of accuracy. Sampling started on the plant closest to the strip and thereafter every second plant for 2008 and every fourth plant for 2009 and 2010.

Soil samples were placed in a plastic beaker and stirred with water three times, as the eggs floated on the surface of the water film. The water was poured into a fine sieve, and the eggs were collected and species-determined following the egg characteristics described by Brooks (1951). Egg-laying was measured between 3 June and 19 August 2008, 2 June and 18 August 2009 and 3 June and 10 August 2010.

Estimation of pupal density

The numbers of *D. radicum* pupae around cabbage plants were monitored in soil samples that included the root systems of the plant. Twenty plants were sampled along a transect across the plot (fig. 1) on 13 October 2008, 7 September 2009 and 30 August 2010. Samples were collected and prepared following a method described in detail by Björkman et al. (2010). Fly pupae were species-determined according to Brooks (1951). Both damaged and intact pupae were counted. Damaged pupae included pupae with signs of predation and parasitized pupae. Data on predation and parasitization are presented elsewhere (U. Nilsson, L.-M. Rännbäck, M. Björkman, P. Andersson, B. Rämert, unpublished data).

Statistical analysis

Egg-laying and pupal data were transformed by $\log_{10}(1 + n)$ to achieve a normal distribution and

equal variance for the residuals. The analysis was limited to data from the weeks when the second generation of *D. radicum* egg-laying coincided with full flowering (weeks 28–32 for all years).

A split plot model (PROC MIXED with Satterthwaite's option, SAS) was used to assess the differences in egg-laying for each of the study years separately. Factors included in the model were as follows: treatment, week, block (random factor), week \times treatment, with treatment as main plot factor and week as split plot factor.

A t-test was used to test whether the crop rotation regime, with planting of onions in 2009, had any effect on the number of *D. radicum* eggs found on cabbage plants in 2010. Comparisons of the mean number of eggs per plant (within the weeks 28–32) were made between plots that were planted with onion and those planted with cabbage the previous year.

Treatment differences in *D. radicum* egg and pupal density between and within years were evaluated using a split plot model (PROC MIXED with Satterthwaite's option, SAS). All plots were used in 2008 and 2010 because the t-test showed no significant difference in egg-laying of *D. radicum* between plots planted with onion or cabbage the year before, for 2010. Plots that were planted with onions were excluded from the analysis for 2009. The following factors were included in the model: block (random factor), treatment, year and year \times treatment, with treatment as main plot factor and year as split plot factor. Mean number of eggs/pupae per plant in 2009 was divided by two to compensate for half the number of cabbage plants being planted that year. The differences in pupal density for single years and single treatments were also analysed (using LSMEANS with PDIF and SLICE in SAS).

Differences in sex ratio, defined as a proportion of caught adult females, between treatments were analysed separately for 2008 and 2010. Data for each plot were summed across the sampling weeks and arcsine-transformed before analysis (PROC GLM, SAS), with block and treatment as factors. The overall difference between the number of females and males caught in the field was analysed using separate Wilcoxon signed-rank tests for 2008 and 2010, i.e. catches were totalled over the treatments. This could be performed because the GLM analysis did not show any treatment effects in sex ratio for 2008 or 2010.

The significance level of $P < 0.05$ was used for all tests. Statistical analyses were performed using Minitab 16 (Minitab 2010) and SAS 9.2 (SAS 2010).

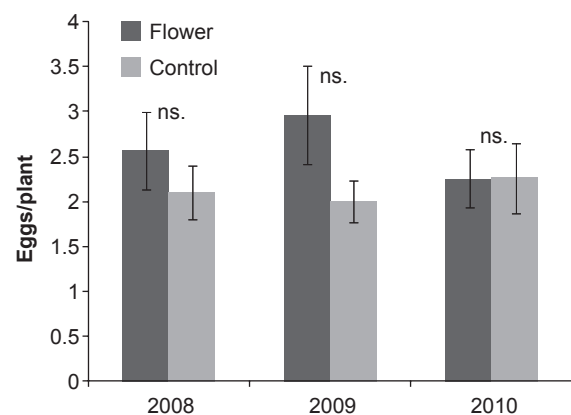


Fig. 2 Average number of *Delia radicum* eggs per cabbage plant (\pm SEM) in flower and control treatments between weeks 28 and 32 in 2008–2010. Egg values are compensated for half the number of planted cabbage plants in 2009. Figure shows back-transformed values. ns = no significant treatment difference, $P > 0.05$ (PROC MIXED, SAS).

Results

Effect of floral resources on egg-laying

There was no effect of floral resources on the egg-laying densities of the second generation of *D. radicum* across the whole seasons for all years (2008: $P = 0.442$; 2009: $P = 0.511$; 2010: $P = 0.921$) (fig. 2). In addition, there was no interaction between treatment and sampling week (2008: $P = 0.450$; 2009: $P = 0.615$; 2010: $P = 0.602$). Overall egg-laying (i.e. flower and control treatment) of *D. radicum* differed significantly between sampling weeks for all years (2008: $P < 0.001$; 2009: $P = 0.008$; 2010: $P < 0.001$). Egg-laying peaked in week 32 in 2008 and in week 30 in 2009 and 2010 (fig. 3).

Floral resources did not increase egg densities of *D. radicum* when treatment effects were compared over all 3 years ($P = 0.240$) and egg-laying was not significantly different between years ($P = 0.906$). In addition, there was no interaction between treatment and year ($P = 0.960$).

Effect of floral resources on pupal density

The abundance of *D. radicum* pupae varied significantly between all years ($P < 0.001$) with the lowest abundance found for 2008. In both flower and control treatments, the abundance of pupae increased from the first year to last experimental year (flower: $P = 0.001$; control: $P < 0.001$). A significant interaction between treatment and year was found ($P = 0.003$). In 2009, there were almost three times

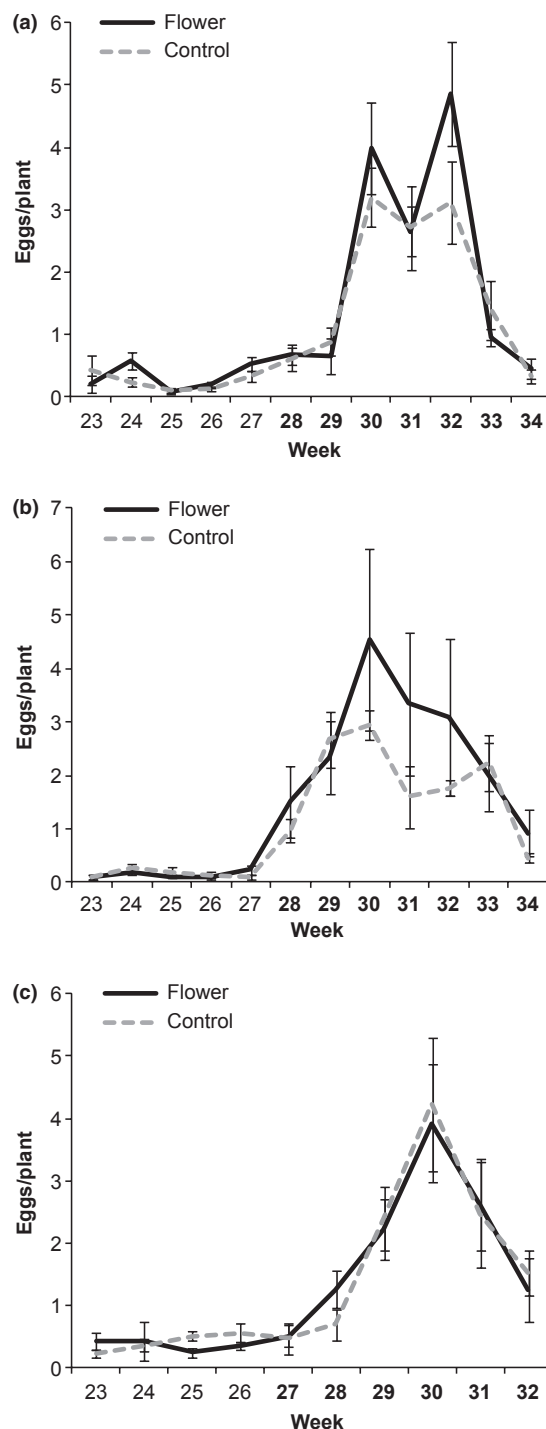


Fig. 3 Average number of *Delia radicum* eggs per cabbage plant (\pm SEM) and week in flower and control treatments in (a) 2008, (b) 2009 and (c) 2010. Average number of eggs per plant in 2009 is compensated for that half the number of cabbage plants was planted this year, $n = 8$ per week in 2008 and 2010 whilst $n = 4$ for 2009. Italic and bold week numbers represent the period when buckwheat and dill flowered.

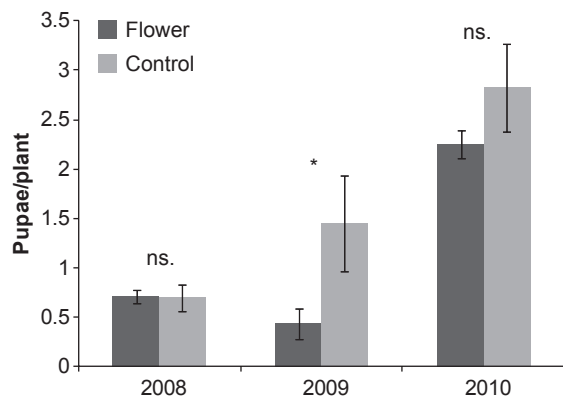


Fig. 4 Average number of *Delia radicum* pupae per cabbage plant (\pm SEM) in flower and control treatments in 2008–2010. The number of pupae in 2009 is compensated for half the number of planted cabbage plants. Figure shows back-transformed values. ns = no significant treatment difference, $P > 0.05$; * $P < 0.05$, asterisk indicates significant difference based on test of effect slices on least square means.

as many pupae in the control as in the flower treatment ($P < 0.001$) whilst no significant difference between treatments was found for other years (2008: $P = 0.875$; 2010: $P = 0.198$) (fig. 4).

Effect of floral resources on the sex ratio

Mean weekly trap catches were lower in 2008 than in 2010 (2008: 0.16 females and 0.041 males; 2010: 1.3 females and 0.14 males per trap and week). Significantly, more females than males were found in the field for both of the studied years (2008: $P = 0.046$; 2010: $P = 0.001$), and the sex ratio of *D. radicum* was not influenced by the presence of flowers as compared to the control (2008: $P = 0.423$; 2010: $P = 0.664$) (fig. 5).

Effect of crop rotation on egg-laying in 2010

The crop rotation regime, with onion in 2009, did not have any significant effect on egg-laying by the second generation of *D. radicum* in 2010 ($P = 0.367$).

Discussion

Habitat manipulation by intercropping flowering plants, dill and buckwheat, with cabbage did not elevate the overall *D. radicum* egg density in any of the years, and there were no significant differences in egg numbers between treatments in any years. This indicates that flowers did not enhance *D. radicum* fecundity. There may be several interacting mechanisms that explain this outcome. The sex ratio of

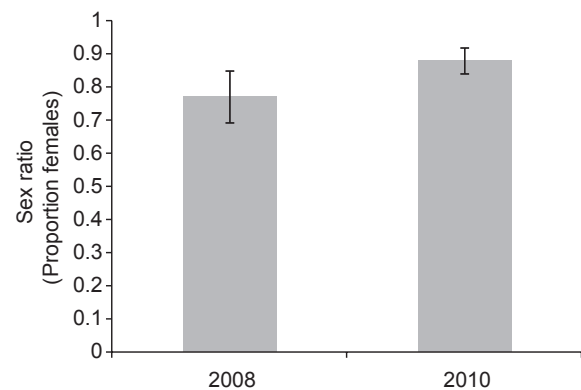


Fig. 5 Mean sex ratio of *Delia radicum* flies (proportion of female flies \pm SEM) in cabbage plots (i.e. plots with floral resources together with control plots) in 2008 and 2010.

adult *D. radicum* in the field was strongly biased towards females in both treatments, and this pattern was consistent for both studied years in the present study. A higher abundance of females within the crop field has been shown in other studies of *D. radicum* (Nair and McEwen 1975), and Hawkes (1972) found that more *D. radicum* flies in a cabbage crop were females than males and a higher proportion of these females were gravid than females at field edges. Flies are attracted to hedges where they forage, mate and mature, and the sex distribution of *D. radicum* at these aggregation sites is closer to 1 : 1 than in field (Coaker and Finch 1971; Hawkes 1972). Aggregation normally occurs in the vicinity of feeding sites and increases the chances of successful mating (Hawkes 1973). The low abundance of males observed indicates that the flowers were not used as a food resource by males and that aggregation did not occur in the field or flower strip.

Furthermore, the females have distinct feeding and oviposition periods that involve attraction to host plants only after feeding and mating (Coaker and Finch 1971). This implies that gravid females, hatched outside the field, may not be more attracted to a production field intercropped with flowers than to a monoculture field as only one of the resources may be relevant during a specific behavioural period. The females may therefore be equally likely to search for food outside the crop as within the field when female flies, as we found indications in our study, must leave the field to mate. In other crucifer herbivores, nectar feeding and egg-laying events are integrated and occur on the same temporal scale (Wäckers et al. 2007). For such insects, combined food and host patches are more attractive as less time has to be spent commuting between resources.

This has been observed for *Pieris brassicae* L. (Lepidoptera: Pieridae), which is more likely to occur in patches containing suitable food and host plants than in patches with only one of these resources (Ohsaki 1979; Zhao et al. 1992). Also, adult *D. radicum* flies can move more than 120 m per day (Finch and Skinner 1975), and this high mobility enables them to forage for food and hosts over a wide area. In addition, crop rotation with onions in the second study year had no effect on the distribution of *D. radicum* eggs, also most likely because of the high mobility of the flies and their need to feed for egg-laying that forces them to redistribute in the field for every new generation (Finch 1989).

Moreover, the proportion of flowering plants within the whole experimental field was small in comparison with open soil and the cabbage crop. The fields were surrounded by private gardens and deciduous forest with a high diversity of flowering plants that could have been utilized as food resources by *D. radicum*. Additionally, there is generally a variety of other food sources available for *D. radicum* flies during July and August. For instance, females can feed on honeydew excreted by aphids, rotten fruit and plant sap (Caesar 1922) and also imbibe free nutrients from the surface of flowering grass (Finch and Coaker 1969). It is therefore likely that early season habitat manipulation with flowering resources could have a greater impact on the fecundity of first generation *D. radicum* females, as there are fewer alternative food resources available in April and May (Finch and Coaker 1969).

As the flower strip plots contained overwintering sites for predators, another explanation for the equal egg numbers found in our treatments would be a higher egg predation rate in these plots. However, no difference in egg predation rates was found (U. Nilsson, L.-M. Rännbäck, M. Björkman, P. Anderson, B. Rämert, unpublished data), and predation is therefore unlikely to explain the results of this study.

Overall, *D. radicum* pupal density was higher in two last years whilst egg densities did not increase in the same period. This suggests that the physical conditions were more favourable for egg hatching or/and larval development or that natural enemies were less abundant or efficient in those years. Eggs and early larval stages are sensitive to dehydration but promoted by high soil humidity (Coaker and Finch 1971; Nair and McEwen 1975). However, weather data showed only small variations in temperature and no pattern in the precipitation that could fully explain the differences observed. In August 2008, there was heavy rainfall but it is not

expected to have negative influence on *D. radicum* pupae. There are indications that plant quality can affect the survival rate of *Delia* spp. larvae (Björkman et al. 2009) but this is unlikely to have differed significantly between years, as crop management was the same and the cabbage plants were similar in size at harvest (U. Nilsson, personal observation). The differences in pupal density between years are thus most likely caused by fluctuations in natural enemy abundance and/or efficiency. Ground beetles and staphylinids can be important predators of immature stages of *D. radicum* (Finch and Elliott 1992; Finch 1996; Kromp 1999; Eyre et al. 2009). The fact that pupal densities increased with time during the study, whilst the provided overwintering sites, in theory would have promoted an increased predator activity points at the complex interactions between natural enemies, pests and alternative prey present in the field (Prasad and Snyder 2004, 2010; Furlong and Zalucki 2010).

In 2009, pupal densities were significantly lower in plots with flowers and this pattern was also evident in 2010, although not significant. A higher predation rate is likely to explain this result as a higher abundance of natural enemies in the vicinity of flowering plants has been reported in numerous studies (White et al. 1995; Stephens et al. 1998; Frank and Shrewsbury 2004; Tylianakis et al. 2004; Lee and Heimpel 2005). For instance, Riechert and Bishop (1990) found significantly higher numbers of spiders and ground beetles in plots bordered with buckwheat plants and linked this to a decrease in pests.

In conclusion, the lack of an effect on the egg-laying of *D. radicum* is most likely because of the high mobility and feeding behaviour of the female flies, combined with high abundance and diversity of other food sources around the fields during this period. The floral resources provided here had an indirect reducing effect on the number of *D. radicum* eggs that developed into pupae in the second study year, most likely because of higher abundance and/or efficiency of natural enemies in these plots. The next step will be to investigate the impact of habitat manipulation on these natural enemies and indirectly on *D. radicum* development.

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