

# Neighbouring monocultures enhance the effect of intercropping on the turnip root fly (*Delia floralis*)

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## Abstract

Knowledge of insect behaviour is essential for accurately interpreting studies of diversification and to develop diversified agroecosystems that have a reliable pest-suppressive effect. In this study, we investigated the egg-laying behaviour of the turnip root fly, *Delia floralis* (Fall.) (Diptera: Anthomyiidae), in an intercrop-monoculture system. We examined both the main effect of intercropping and the effect on oviposition in the border zone between a cabbage monoculture [*Brassica oleracea* L. var. *capitata* (Brassicaceae)] and a cabbage-red clover intercropping system [*Trifolium pratense* L. (Fabaceae)]. To investigate the border-effect, oviposition was measured along a transect from the border between the treatments to the centre of experimental plots. Intercropping reduced the total egg-laying of *D. floralis* with 42% in 2003 and 55% in 2004. In 2004, it was also found that the spatial distribution of eggs within the experimental plots was affected by distance from the adjoining treatment. The difference in egg-laying between monoculture and intercropping was most pronounced close to the border, where egg-laying was 68% lower on intercropped plants. This difference in egg numbers decreased gradually up to a distance of 3.5 m from the border, where intercropped plants had 43% fewer eggs than the corresponding monocultured plants. The reason behind this oviposition pattern is most likely that flies in intercropped plots have a higher probability of entering the monoculture if they are close to the border than if they are in the centre of a plot. When entering the monoculture, flies can pursue their egg-laying behaviour without being disrupted by the clover. As the final decision to land is visually stimulated, flies could also be attracted to fly from the intercropped plots into the monoculture, where host plants are more visually apparent. Visual cues could also hinder flies in a monoculture from entering an intercropped plot. Other possible patterns of insect attack due to differences in insect behaviour are discussed, as well as the practical application of the results of this study.

## Introduction

There has been a growing concern for sustainability in agriculture and horticulture during the last decades, and two primary reasons for this have been unwanted environmental side-effects of pesticide use and the development of resistance among herbivorous insects (Denholm et al., 2002). As a consequence, research on pest control has increasingly focussed on alternative ways of

reducing damage from pest species. One such alternative is the design and use of diversified pest-suppressive agroecosystems (Wood & Lenné, 1999), such as mixing multiple crops within the same field. To grow more than one plant species within a field gives the possibility to manipulate the spatial dynamics of herbivores, and thereby reduce the damage level. Intercropping is one such strategy, in which the non-host plant disrupts the behaviour of the pest insect, leading to a reduced host-plant acceptance (Finch & Collier, 2000), while another strategy is to use a trap-crop that attracts and retains herbivores outside the cropping area (Hokkanen, 1991).

One problem in the development of efficient diversified systems has, however, been that most studies thus far have

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been done at quite small spatial scales. It has been argued that scale has a direct impact on the effect that a mixed crop has on herbivores. The argument is that diverse host-plant patches achieve lower attack rates only when patches are sufficiently small in size and placed near a more attractive alternative, for example, a pure stand of host plants. Under those circumstances, herbivores could be influenced by a choice situation. Thus, there has been a widespread critique that the effect of diversity is exaggerated and that conclusions are drawn from small-scale experiments that would not be applicable at the larger spatial scales in a real farming situation (Bergelson & Kareiva, 1987; Bommarco & Banks, 2003). While this critique has received considerable support in reviews of field experiments, it merely shows that large intercropping fields may not be the optimal solution for using diversified systems in attempts to reduce pest attack. When using intercrops, it may be necessary to adjust the design of agricultural fields to the behaviour of pest insects and to the scale at which they operate. As the response of insects to plant diversity is variable, depending on factors such as insect search mode (Hambäck et al., 2003; Bukovinszky et al., 2005) and diet breadth (Andow, 1991), it is also likely that the design should vary depending on the species present.

To increase the predictability and reliability of crop diversification as a tool for reducing pest damage, it is necessary to understand the mechanisms underlying herbivore population responses to diversified agroecosystems (Potting et al., 2005). For annual cropping systems in particular, this implies studies of herbivore movement and host-finding behaviour (Risch, 1983). One approach could be to investigate the behaviour of pest insects at the border between a more and a less suitable host-plant patch. The spatial distribution of insect attack rates on both sides of the border between patches can reveal information about the distance at which the behaviour is affected by a choice situation. In this study, we investigated how intercropping cabbage [*Brassica oleracea* L. var. *capitata* (Brassicaceae)] with red clover [*Trifolium pratense* L. (Fabaceae)] affects oviposition of the turnip root fly, *Delia floralis* (Fall.) (Diptera: Anthomyiidae), compared to a cabbage monoculture. We also wanted to examine how oviposition is affected in a choice situation between the two cultivation systems. To investigate the border-effect, egg-laying was measured along a transect from the border between the treatments to the centre of the experimental plots.

## Materials and methods

### Insects

The focal species in this study, the turnip root fly (*D. floralis*) and its congener the cabbage root fly (*Delia radicum* L.), are herbivores on cruciferous crops. The cabbage root

fly has been frequently studied for its potential to be controlled by intercropping (Theunissen et al., 1995; Finch & Kienegger, 1997; Lehmus et al., 1999; Dixon et al., 2004). The two species have similar biology and behaviour and react upon the same or related stimuli (Varis, 1967; Baur et al., 1996a). One major difference is that *D. floralis* is univoltine while *D. radicum* can have as many as four generations per year, depending on location (Varis, 1967).

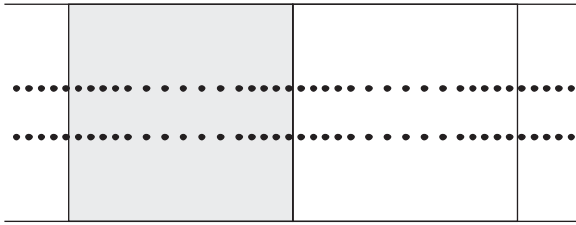
The root fly complex in our study area in the north of Sweden consists mainly of *D. floralis*, but *D. radicum* is also present. Results from pupal examination at the end of the 2003 season showed that 91% of the root fly population consisted of turnip root flies, while cabbage root flies made up the remaining 9%. In 2004, the corresponding values were 98 and 2% (M Björkman unpubl.). Because it was not possible to distinguish the eggs by sight, the two species were not separated in egg counts.

### Field layout

We studied the oviposition behaviour of the turnip root fly (hereafter referred to as *D. floralis*) in an experimental intercropping system in Röbbäcksdalen, Umeå, in the north of Sweden (63°45'N, 20°15'E) in 2003 and 2004. The field trial consisted of plots of cabbage (*B. oleracea* var. *capitata* genotype Castello) grown in monoculture and plots of cabbage grown with a red clover (*T. pratense* genotype Betty) intercrop. Plot size was 15 × 15 m (225 m<sup>2</sup>) and plots were placed in a row with alternating treatments. There were three replicates of each treatment in 2003, creating a field of 15 × 90 m. In 2004, there were four replicates of each treatment, creating a field of 15 × 120 m. The red clover was sown the season before the experiment to ensure that it would be already present at the beginning of the egg-laying season. In the monocultures, all clover was incorporated in the soil in early June as green manure, while in the intercropped plots, strips with red clover of 20 cm were left with 50 cm in between for the cabbage plants. The strips ran parallel to the border between treatments. Four-week-old cabbage plants with 4–5 true leaves were transplanted in between the strips in the second week of June. In both treatments, the distance between cabbage rows was 70 cm and plant distance within rows was 40 cm. Each plot contained 20 rows of cabbage plants with 40 plants in each row. During the growing season, the clover was mown on two occasions in 2003 and one in 2004, maintaining its height at 25–30 cm. At the end of the egg-laying season, in the first week of August in 2003 and second week of August in 2004, the clover was cut down to the ground.

### Measurement of egg-laying

To study the effects of intercropping and distance from the border on egg-laying, woolen egg traps (Freuler & Fischer,



**Figure 1** Detail of the field layout with an intercropped plot (grey) and a monoculture (white). The dotted lines represent the two transects for egg-laying measurements with traps on every plant in the border area and traps on every second plant in the centre of the plots.

1982) were put around the stem base of cabbage plants along two transects throughout the field. On the first five rows counted from the border between the monoculture and the intercropping, the traps were put in every row to get a more accurate estimate of the border-effect. In the centre of each plot, traps were put on every second plant, which resulted in five centrally placed traps. A total of 30 egg traps were placed in each plot, 15 in each transect (Figure 1). Studies have indicated that flies prefer to lay eggs on moderately damaged plants (Baur et al., 1996b), and a continuous removal of eggs from the same plants when egg traps were collected could give an inaccurate estimate of oviposition rates. To ensure that experimental plants were not without larval attack, oviposition rates in a transect were alternately estimated in two neighbouring rows of cabbage. The egg traps were collected for egg counting twice a week during the peak of the egg-laying seasons and once a week during the beginning and the end of the egg-laying seasons. Oviposition was measured from 1 July to 15 August in 2003 and from 24 June to 16 August in 2004. For the analysis of the effect of intercropping on egg-laying per plant, the total number of eggs laid during the season was used. An analysis of variance (ANOVA) was used to analyse the effect of intercropping on total egg-laying. Prior to the analysis of the spatial-distribution pattern, we pooled the data for all dates and for the two transects within a plot in order to reduce the variability due to single egg-laying events. This pooling was also motivated by preliminary statistical analyses, which found no significant effects of date on egg-laying patterns. To investigate the effect of adjoining treatments on the spatial distribution of eggs, we performed an analysis of covariance (ANCOVA) on the number of eggs per plant with treatment, block, and distance from the treatment border as independent variables. The cabbage rows situated directly on the border were excluded from the analysis, as they could not be attributed to either treatment, having clover on one side and bare soil on the other. Hence the first true intercropped

and monocultured cabbage plant row in each plot were situated at a distance of 0.7 m from the border. The plant rows closest to the centre of the plots were situated at a distance of 7.0 m from the border. As the field consisted of six plots in 2003 and eight in 2004, five and seven borders were available for analysis each year, respectively. The outermost traps at the end of each transect were excluded from the analysis regarding the spatial distribution of eggs because they did not border onto another plot.

All data were  $\log_e$  transformed before analysis. The statistical analyses were done using S-PLUS statistical software (S-PLUS® 6.0, Insightful Corp., Seattle, WA, USA).

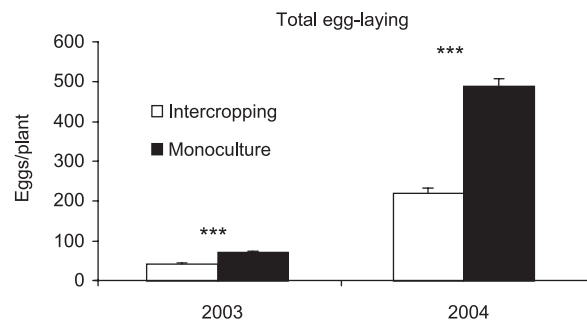
## Results

### Effect of intercropping on total egg-laying

The number of eggs per plant was higher in the cabbage monoculture than in the cabbage-clover intercrop both in 2003 (ANOVA:  $F = 19.26$ , d.f. = 1,  $P < 0.001$ ) and in 2004 (ANOVA:  $F = 212.32$ , d.f. = 1,  $P < 0.001$ ; Figure 2). There was also a considerable difference in egg-laying between years. The mean number ( $\pm$  SEM) of eggs per plant in 2003 ( $n = 3$ ) was  $73 \pm 5$  in the monoculture and  $42 \pm 6$  in intercropped plots, while the corresponding values for 2004 ( $n = 4$ ) were  $489 \pm 24$  and  $220 \pm 25$  eggs per plant. This means that intercropping reduced oviposition with 42% in 2003 and 55% in 2004.

### Border-effect

The ANCOVA showed only a treatment effect for 2003, while there was an interaction between treatment and distance from the border for 2004 (Table 1). The absence of interaction effect for 2003 seem to be due to a high variability, associated with lower egg density, as the pattern in the intercropped plots was visually similar for 2003 and 2004 (Figure 3). We therefore focussed the remaining



**Figure 2** Mean ( $\pm$  SEM) total number of *Delia floralis* eggs per plant for 2003 and 2004. Data was  $\log_e$  transformed before analyses with analysis of variance, and the figures show back-transformed values (\*\* $P < 0.001$ ).

**Table 1** The effect on egg-laying of *Delia floralis* of treatment, distance from border (0.7–7.0 m), and the interaction between treatment and distance from border

		d.f.	Mean square	F
2003	Treatment	1	2.27	5.10*
	Distance	1	0.51	1.15
	Block	4	0.96	2.14†
	Treatment × distance	1	0.01	0.02
	Residuals	66	0.45	
2004	Treatment	1	8.35	99.32***
	Distance	1	0.10	1.20
	Block	6	0.38	4.53***
	Treatment × distance	1	0.68	8.09**
	Residuals	94	0.08	

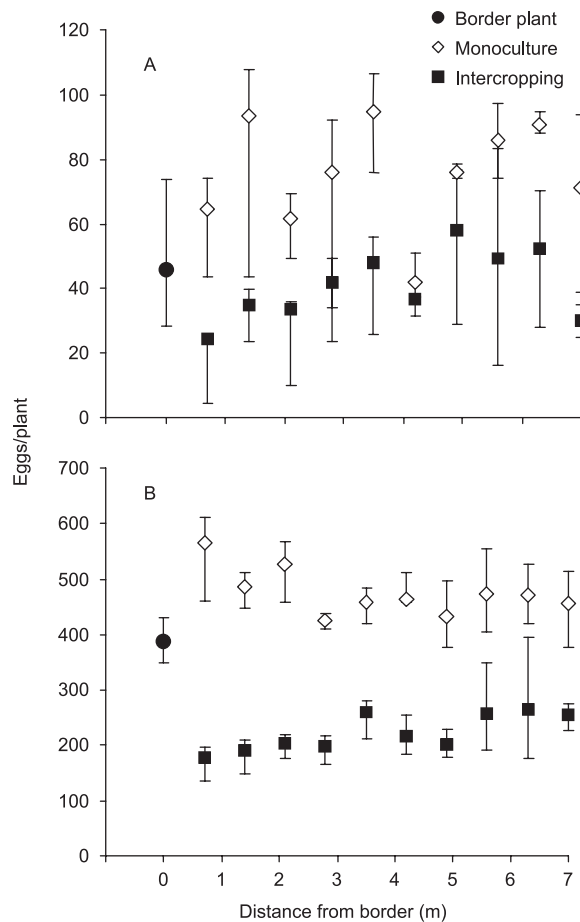
†P<0.1, \*P<0.05, \*\*P<0.01, and \*\*\*P<0.001.

analysis on 2004, where the data were sufficient for a more detailed analysis. A visual inspection of the oviposition pattern showed that the interaction occurred due to a reduced egg-laying with distance from the treatment border in the monoculture, while egg numbers increased with distance from the border in intercropped plots (Figure 3). This effect appeared to occur mainly in the first few meters from the treatment border. To estimate at which distance from the border the interaction appeared, a gliding window was used as follows. The ANCOVA was repeated, using four distances each time, from the border towards the centre. This analysis showed that the interaction between treatment and distance from border was strongest for the window 1.4–3.5 m ( $F = 4.3$ , d.f. = 1,  $P < 0.045$ ). At greater distances, the interaction was gradually reduced, suggesting that 3.5 m from the border is a threshold value for this effect. Based on this result, the data was divided into two intervals, 0.7–3.5 m and 3.5–7.0 m, which were analysed separately (Table 2). An interaction between treatment and distance from the border was found in the interval 0.7–3.5 m, but not for the interval 3.5–7.0 m. This shows that the interaction found in previous analyses can be explained by egg distribution on the plants up to 3.5 m from the treatment border. To analyse if the interaction effect in the border zone occurred because of a distance effect in both or in only one of the treatments, we performed linear regressions on the number of eggs per plant up to 3.5 m from the border for each treatment separately. These analyses showed that the number of eggs increased with distance from the border in the intercropped plots [slope =  $0.13 \pm 0.06$  (mean  $\pm$  SE)]. In the monoculture, there was a strong tendency of egg numbers decreasing with distance from the border (slope =  $-0.06 \pm 0.04$ ; Table 3). This border-effect corresponds to a reduction in

the mean number ( $\pm$  SEM) of eggs per plant in the monoculture from  $564 \pm 85$  at the border to  $457 \pm 29$  at 3.5 m from the border, which is a relative decrease of 23%. The corresponding increase in egg numbers in the intercropped plots was from  $179 \pm 29$  at the border to  $258 \pm 39$  at 3.5 m from the border, which is a relative increase of 31%. Overall, 68% fewer eggs were laid on intercropped plants at the border compared with 43% at a distance of 3.5 meters from the treatment border.

## Discussion

This study has shown that intercropping strongly reduces the egg-laying of the turnip root fly, *D. floralis*. Overall, oviposition rates were reduced by 42–55% in intercropped plots compared to monocultures. Furthermore, in the



**Figure 3** Numbers of *Delia floralis* eggs per plant (means  $\pm$  SEM) from the border between the treatments to the centre of the experimental plots in (A) 2003 and (B) 2004. Notice that the left-most marker show the plants on the border.

**Table 2** The effect of distance from the adjoining treatment on the egg-laying of *Delia floralis* for the interval 0.7–3.5 m and 3.5–7.0 m in 2004

		d.f.	Mean square	F
0.7–3.5 m	Treatment	1	5.44	68.81***
	Distance	1	0.07	0.85
	Block	6	0.31	3.87**
	Treatment × distance	1	0.62	7.79**
	Residuals	58	0.08	
3.5–7 m	Treatment	1	0.46	4.98*
	Distance	1	0.01	0.08
	Block	6	0.15	1.64
	Treatment × distance	1	0.01	0.11
	Residuals	40	0.09	

\* $P < 0.05$ , \*\* $P < 0.01$ , and \*\*\* $P < 0.001$ .

study year with high egg-laying (2004), the spatial distribution of eggs within the experimental plots was strongly affected by distance from the adjoining treatment. This effect was not significant in the year with low egg-laying, but this could be due to the large variability. The difference in egg numbers between monoculture and intercropping was most pronounced close to the border and then gradually reduced up to a distance of 3.5 m from the border. When comparing border plants, egg-laying was reduced by 68% in intercropped plots, while the reduction was only 43% when comparing plants at a distance of 3.5 m from the border. The border-effect was mainly explained by the egg distribution in the intercropped plots.

The underlying mechanisms that lead to the difference in egg-laying between treatments and the border-effect are likely to be found in the behaviour of gravid female flies. Gravid *D. floralis* females are attracted to host plants and arrive after a series of short upwind flights, landing and reorientating into the wind between flights (Havukkala,

**Table 3** The effect of distance from the adjoining treatment on the egg-laying of *Delia floralis* for the interval 0.7–3.5 m for the treatments separately in 2004

		0.7–3.5 m		
		d.f.	Mean square	F
Monoculture	Distance	1	0.14	2.98 <sup>†</sup>
	Block	6	0.53	1.88
	Residuals	27		
Intercropping	Distance	1	0.54	4.29*
	Block	6	0.25	1.98
	Residuals	25	0.13	

<sup>†</sup> $P < 0.1$  and \* $P < 0.05$ .

1987). Tukahirwa & Coaker (1982) showed in a laboratory study that similar numbers of female cabbage root flies, *D. radicum*, arrived at trays containing a *Brassica* host plant and a clover companion plant as at trays containing only the *Brassica* host plants. It is therefore reasonable to assume that non-host plant odour does not act as a repellent and that the initial number of gravid females of *D. floralis* attracted to the field in our study is equal for both the intercropped and monocultured plots. The total reduction in oviposition as well as the border-effect is thus likely to be an in-field effect.

According to the theory of appropriate/inappropriate landings (Finch & Collier, 2000), which was originally motivated from studies on cabbage herbivores, damage levels are lower in intercropping systems due to a disruption of the oviposition behaviour. This happens when insects land on a companion plant instead of on a host plant, at the beginning or during the egg-laying process. A recent study of the behaviour of *D. radicum* after landing on host plants and non-host plant showed that the time spent on non-host plants was almost four times as long as the time spent on host plants (Morley et al., 2005). The conclusion was that the companion plants 'produce their disruptive effect by arresting the flies on inappropriate (non-host) plants for long periods' and that flies that land initially on clover have to start the oviposition process all over again. Studies of the post-alighting behaviour of *D. floralis* have similarly shown that cues received immediately after the insect lands on a plant (the so-called leaf contact phase) are most important for the decision to continue the oviposition process (Hopkins et al., 1996; Hopkins et al., 1999). *Delia floralis* spent approximately twice as long in the leaf contact phase on resistant host plants that were later rejected than on host plants accepted for continued oviposition behaviour. This indicates that *D. floralis* behave in a similar way to *D. radicum* on non-suitable host plants, and that the same behavioural mechanism can explain the reduction in egg-laying found in this study.

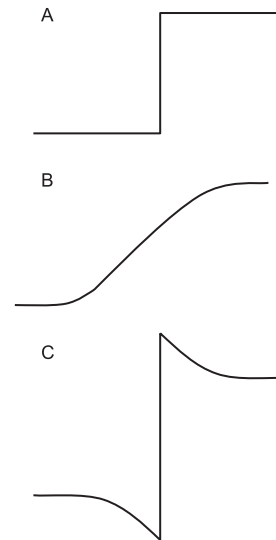
One question remaining is what happens with the fly population after the flies arrive to the field. We did not measure effects of intercropping on root fly abundance in this field trial as it would have interfered with our other goals. However, a study by Tukahirwa & Coaker (1982), focussing on the effect of intercropping on both egg-laying and abundance of *D. radicum*, found that even though intercropping reduced the egg-laying, there was no difference in insect abundance in plots separated by 2 m of bare soil. Intercropping also led to lower damage levels in a study of the carrot rust fly (*Psila rosae*) (Rämert & Ekbom, 1996), but insect abundance was only reduced by intercropping if the intercropped and monocultured plots were adjacent to each other, as in our experiment, or if they were connected

with a 15-m strip of ley vegetation. There was no difference in insect abundance if plots were separated by 15 m of bare soil. The proposed mechanism was that the supposedly higher emigration from intercropped plots was hampered due to a 'barrier' of non-vegetation. This suggests that the border-effect observed in our study may be most strongly expressed when intercropped and monocultured plots are adjacent to each other, facilitating redistribution of flies among plants.

The mechanism most likely to be responsible for the border-effect found in 2004 is that flies in the border zone, but within the intercropping, have a higher probability of crossing the border to lay their eggs than the other way around. This may either be a chance effect due to the behaviour of female flies following unsuccessful host plant finding, or because a neighbouring monoculture provides a clear visual signal for gravid female *D. floralis* in the immediate vicinity of the border. First, a female leaving a non-host plant close to the border will have a higher probability of entering the monocrop than a female leaving a non-host plant in the centre of the plot. When entering the monocrop, they will not be disrupted by non-host plants and can pursue their egg-laying behaviour. Alternatively, Prokopy et al. (1983) concluded that the final choice of landing for *D. radicum* was entirely visual, and that a visually stimulating plant might be detectable from a distance of 40–60 cm. In a choice situation, more than four times as many females of *D. radicum* landed on the *Brassica* plants with a background of bare soil than on *Brassica* plants surrounded by grass (Kostal & Finch, 1994). This is comparable to our results as the cabbage plant closest to the border in the monoculture received about three times as many eggs as the intercropped cabbage closest to the border (Figure 3). If flies in intercropped plots are visually drawn to the monoculture, it is also possible that individuals in the monoculture are reluctant to enter this habitat and thus are reflected by the border (Strayer et al., 2003).

In either case, the stronger border-effect in the intercropping compared with the monoculture probably is a consequence of the higher overall egg loads in the monoculture. Hence, the same number of flies will cause a proportionally larger reduction in density when leaving the intercropping than the increase caused when immigrating into the monoculture. It is also possible that the egg distribution in the monoculture is more spatially homogeneous because the female flies can move more freely between host plants without the risk of landing on the wrong plant, which can have an arresting effect and disrupt the egg-laying behaviour.

Irrespective of the underlying mechanism, it is evident from this study that border-effects should be considered in experiments that examine the effects of diversification, as



**Figure 4** Possible patterns of insect abundance/infestation in the border area between a monoculture (right) and a more diverse habitat, for example intercropping (left), placed next to each other. Alternative (A) shows a lack of border-effect, (B) shows a gradual increase in insect attack in the border area. In alternative (C), the difference in insect attack is maximized close to the border.

is also suggested by a recent review (Bommarco & Banks, 2003). It is, however, important to remember that borders may both increase and decrease rates of herbivory depending on insect behaviour and border structure. Figure 4 shows three theoretical patterns of insect attack at the border between a more and a less suitable host plant patch. Different species may show either (A) no border-effect, or (B) a gradual increase in attack rates across the border area as a result of a herbivore spill-over from a more preferred habitat or random movement behaviours (Turchin, 1998). A third possibility (C) is that the difference in attack rate is maximized close to the border. Here the possible mechanism is, as discussed earlier, an active choice by the herbivores. Considering these alternatives, the importance of plot size becomes evident. With alternative (A), there would be no effect of plot size on the result. With a plot size that is too small to be adjusted for a herbivore responding as alternative (B), the effect of diversification would be underestimated. In the case of turnip root flies, that seem to respond as in (C), a smaller plot size would clearly have caused a larger difference between treatments, using the same design with adjoining treatments as in our experiment.

A problem when comparing these models with earlier studies on root flies and other insects is that their design does not allow for interpretations of border-effects. This occurs either (i) because insect abundances and attack

rates are not sampled across plot borders, (ii) because most studies lack information about the distribution of plots in relation to each other, or (iii) because the sampling design within plots is not properly described. Strayer et al. (2003) concluded that researchers studying borders must be careful so that the borders defined are truly comparable. This would also be true when comparing studies where borders within the experiments can affect the result.

Some caution is needed when interpreting results from studies of intercropping, as the cultivation system often leads to interspecific competition, which in turn can lead to physiological differences between intercropped and monocultured plants (Bukovinszky et al., 2004). It has, for example, been shown that plant size can have an effect on preference for *D. radicum* in a choice situation (Kostal & Finch, 1994) and that increased leaf area stimulates more landings (Prokopy et al., 1983). This possibility is, however, less likely in this experiment, as the intercropped plants actually performed slightly better at the beginning of the egg-laying season (B Rämert, M Björkman, B Båth, PA Hambäck, A Mårtensson & A Sellstedt, unpubl.). Hence, if *D. floralis* would have been attracted to larger plants, this would rather have reduced the difference in oviposition between the treatments as well as the border-effect. At the beginning of August, the cabbage in the monoculture started to outgrow the intercropped cabbage, but at this stage oviposition decreased anyway and the main portion of the eggs had already been laid. So it is reasonable to assume that the effect of plant size was minimal in this experiment.

#### Practical applications

The results from this study show the potential of intercropping to reduce infestation of the turnip root fly. The pest-reducing effect of intercropping has been shown previously, confirming the benefits of adding an intercrop to the cultivation system, but the observed border-effect implies an additional means to optimize pest reduction. The border-effect observed in this study suggests that the monoculture functioned as a trap-crop (Hokkanen, 1991), but only in the vicinity of the border between the monoculture and intercropping. The information about the spatial scale for this effect, 3.5 m, could provide a basis for developing cropping systems through a combination of intercropping and trapcropping. That undersowing might have to be combined with a trap-crop to be effective in reducing the egg-laying of the cabbage root fly has been proposed in other studies (Kostal & Finch, 1994), and some researchers have stressed that trapcropping has more potential than intercropping (Banks & Ekbom, 1999). We propose using both cultivation systems in combination for optimal effect, comparable to a push–pull strategy (Cook

et al., 2007). By making a resource unattractive, unsuitable, or difficult to locate (push) and at the same time providing the pest with an attractive option (pull), manipulation of the insect pest is possible (Khan et al., 2000). Combining both push and pull has also shown strong evidence for a multiplicative effect (Miller & Cowles, 1990).

To take full advantage of the border-effect found in this experiment, relatively narrow strips of row intercropping, a few meters wide, could be placed right through a monoculture field. For example, it is possible that intercropping could be used to protect a more susceptible crop and at the same time use a more tolerant crop as a trap-crop. Susceptible crops to the cabbage and turnip root fly are, for example, cauliflower (*Brassica oleracea* L. var. *botrytis*) or root vegetables as swede (*Brassica napus* L. var. *napobrassica*), where the flies cause direct damage on the marketable part of the plants.

Once again the importance of research to reveal the underlying mechanisms of herbivore response to diversification is stressed. Besides knowledge about insect movement and host-finding behaviours, it would also be valuable to understand better how insects respond to differences in the architecture of companion plants, in order to find the optimal architecture for disrupting the target pest. Also, research of antixenosis and tolerance of different crops and crop varieties would be useful for finding promising crop combinations that could be used in cultivation systems with optimal pest reduction.

#### Acknowledgements

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