

Increasing vineyard floral resources may not enhance localised biological control of the leafroller *Epiphyas postvittana* (Lepidoptera: Tortricidae) by *Dolichogenidea* spp. (Hymenoptera: Braconidae) parasitoids

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Abstract

In agroecosystems, the efficacy of biological control exerted by many parasitoids is predicted to be enhanced where the availability of floral resources is increased. Such resources may attract parasitoids and enhance their longevity and fecundity. In Hawke's Bay, New Zealand, this prediction was tested by adding varying quantities of potted flowering alyssum (*Lobularia maritima*) (Brassicaceae) to plots containing apple plants (*Malus domestica*) inoculated with larvae of the leafroller, *Epiphyas postvittana* (Lepidoptera: Tortricidae). In two replicated trials, over 90% of the parasitoids from recovered larvae were *Dolichogenidea* spp. (Hymenoptera: Braconidae). In both trials increasing the percentage of alyssum did not result in a corresponding increase in the leafroller parasitism rate. Instead, the primary influence on parasitism rates was due to *Dolichogenidea* spp. dispersing from a nearby orchard. A significant negative correlation was observed in leafroller parasitism as a function of distance from this orchard. A vineyard to the north of the study site also influenced parasitism rates. Our results suggest the orchard was a regional source population for this parasitoid, and the abundance of local resources such as alyssum did not influence parasitoid foraging. At the level of our entire study block, our effective area of resource provision was 0.1%. A level of resource provision higher than that used in this study may be necessary to test for a positive influence on local parasitism rates. From our results, it appears that for parasitoids with relatively high dispersal rates, the availability of local resources may not be as important as a regional source population.

Keywords: Conservation biological control, alyssum, leafroller, *Dolichogenidea* spp., spatial design, dispersal

Introduction

Conservation biological control (CBC) involves manipulating the environment in such a way so as to favour and therefore increase the effectiveness of beneficial

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arthropods (Landis et al. 2000). Such manipulations often include the addition of floral resources within an agroecosystem (Hickman & Wratten 1996; Stephens et al. 1998; Irvin 1999; Berndt 2002; Berndt et al. 2003). The underlying theory for this concept was developed by Root (1973), who proposed the 'enemies' hypothesis. He argued that predators and parasitoids would more effectively control herbivores in diverse rather than simple habitats because of, among other things, access to resources like pollen and nectar. For many adult parasitoids, access to the high nutritional value of these resources has been shown to increase survival and fecundity (Idris & Grafius 1995; Jervis et al. 1996; Jervis & Kidd 1999).

A number of studies across a variety of cropping systems have found evidence that supports the predictions of the enemies hypothesis (Hickman & Wratten 1996; Murphy et al. 1996; Peng et al. 1998; Stephens et al. 1998; Irvin 1999; Nicholls et al. 2000). In his review of this hypothesis, however, Russell (1989) noted that enemy abundance and herbivore mortality was not always enhanced in diverse habitats when compared to simple ones. For example, in vineyards Costello & Daane (1998) measured the effect of ground cover on predator densities, and spiders in particular. Overall, no consistent increase in spider abundance or change in species composition in cover-cropped vineyards was observed. We suggest the underlying mechanisms contributing to observed outcomes may often remain obscure. One such mechanism that requires greater investigation is the propensity for natural enemy movement. This movement is of great significance when attempting to determine the appropriate scale for the enemies hypothesis (Russell 1989).

In New Zealand there has been limited research into parasitoid mobility, both within and between non-contiguous agroecosystems. Parasitoids may be highly mobile and therefore able to forage throughout a perennial system and the surrounding habitat. Where this occurs it may be difficult to determine supporting evidence for the enemies hypothesis, as parasitoids may simply perceive the system as a single polyculture moving freely between treatments (Russell 1989). Recently in Hawke's Bay, New Zealand, a study in a grazed pasture found that the parasitoid, *Dolichogenidea* spp., successfully foraged for hosts to a distance of at least 100 m from a known population reservoir, although parasitism did generally decline as distance increased (Bell 2004). Relating such parasitoid movement to that which might occur within a perennial system like a vineyard is potentially important, especially when examining the enemies hypothesis.

The present study took place in a vineyard, which provided a relatively sterile environment in which to perform resource manipulations due to the limited understory vegetation. The addition of a flowering plant species allowed us to measure the possible influence of floral resources on the parasitism rate of the introduced leafroller, *Epiphyas postvittana* (Walker). Grape vines as well as fruit trees, such as apple, are hosts for *E. postvittana* and its parasitoids. *Dolichogenidea* (= *Apanteles*) *tasmanica* (Cameron) is an early instar, solitary endoparasitoid. An effective natural enemy of leafroller, *D. tasmanica* may parasitise orchard populations at rates of between 25–51% (Dumbleton 1932; Dumbleton 1935). Alyssum (*Lobularia maritima* (L.) Desv. c.v. 'Snow Carpet') was added to the vineyard understory because laboratory trials had shown that over time it enhanced the fecundity of adult *D. tasmanica*, suggesting this non-host feeding parasitoid may be synovigenic (Irvin 1999). Further, in the field the addition of several understory plant species, including alyssum, was found to significantly enhance leafroller parasitism (Irvin 1999).

In contrast, alyssum offered no apparent benefit to the fitness of *E. postvittana* (Irvin 1999; Berndt 2002). These factors coupled with ease of planting and abundant flowers, suggest alyssum could be an ideal plant to enhance biological control.

This study set out to address several questions. Firstly, does the provision of flowering alyssum in a vineyard understory influence the parasitism rate of leafroller populations? Secondly, if enhanced parasitism is observed, is the rate of parasitism correlated with the abundance of alyssum flowers? Finally, when establishing this experiment we predicted that an extensive weedy understory in a stone fruit orchard on the western boundary, 30 m from the vineyard study site, might be a suitable population reservoir for parasitoids. Hence, data were analysed to investigate the effect of distance from the orchard on leafroller parasitism among the various treatments in the five replicate rows.

Material and methods

Site description

The experiment was conducted at Dry Creek Vineyard (Delegat's Wine Estate Limited), 16 km west of Havelock North, Hawke's Bay (39°37.94'S 176°44.50'E). This 21-ha vineyard was bordered to the north and to the south by neighbouring vineyards, each of which was 20–30 ha. Dry Creek has been managed under Sustainable Winegrowing New Zealand (SWNZ) since 2000. SWNZ vineyards use sustainable practices, including a reduction in chemical inputs, a pest monitoring regime, together with seeking to maximise the effect of natural enemies on vineyard pest species (Gurnsey et al. 2004). The present study site, the Chardonnay block, was 300 m long (vine spacing 1.8 m) and 300 m wide (row spacing 2.4 m) (9 ha). It was orientated approximately north south. The inter-row sward was a grass-clover mix, which was mowed monthly. A herbicide strip under the vines was maintained through the quarterly use of glyphosate (Roundup®). The combination of herbicide use and mowing appeared to almost completely reduce the presence of flowering plants in the vineyard. No insecticides were applied to the Chardonnay block six weeks before or during this experiment. Several searches were made on the grape vines for *E. postvittana* during the study, but none were observed.

The understory in the vineyards to the north and the south were visually very similar to that of the study site. Fence lines and vehicle tracks around the study site were regularly mowed. Immediately to the east of the study site was a 7-ha Merlot block (also part of Dry Creek Vineyard), which was managed in the same manner as described above. In contrast, the understory in a stone-fruit orchard to the west contained a mixture of grasses and broadleaf species, though the species composition was not determined. The orchard was the only area for several hundred meters in any direction with an abundance of flowering plants, and it was considered likely to contain a significant population of the parasitoid *Dolichogenidea* spp, though we were unable to access the site to sample the insect fauna.

Plant and larval establishment

Larval parasitism was assessed on 2-year-old apple plants (*Malus domestica* Borkh. sibling of 'Pacific Rose' and 'Fiesta') infested with neonate *E. postvittana*. Apple seedlings were transplanted into polythene bags (5 L capacity) in November 2001.

Alyssum seedlings were obtained in November 2002 from Mount Wellington Nurseries, Levin. Because alyssum is small and low growing, two seedlings were transplanted into a single polythene bag (1.2 L capacity). The 240 apple plants and the 2,500 alyssum used in this experiment were planted into a standard, commercially available potting mix containing a slow release fertiliser (Osmocote®). The use of potted plants standardised plant origin, fertiliser and soil conditions. All plants were held outside at The Horticulture and Food Research Institute of New Zealand Limited (HortResearch), Havelock North, until required. A careful inspection indicated that no naturally occurring leafroller larvae were observed on these plants while stored at HortResearch. While at HortResearch a timed irrigation system watered the plants daily for 30-minutes. The apical shoots of the apple plants were pruned in November 2002 to reduce height to ~1.2 m and to promote lateral growth. To control powdery mildew (*Uncinula necator* Burrill), the apple plants were sprayed regularly with a fungicide (Systhane®) between 3 January and 7 March 2003. A bioassay over 4 days at room temperature indicated no significant effects of this compound on neonate *E. postvittana* survival (Bell 2004).

This study used eggs of *E. postvittana* provided by the Insect Rearing Unit at HortResearch, Auckland. Mature eggs were transported from Auckland by overnight courier to HortResearch, Havelock North. Upon arrival, they were placed in an incubator (25°C, RH 65%, photoperiod 16:8 L: D) for 24 h for controlled larval emergence. The neonate larvae were retained within a small screw cap plastic bottle. By tilting and gently tapping the bottle, dislodged larvae would hang by a short silken thread. A fine paintbrush moved through the silk threads made it possible to collect a known number of larvae and eliminate the need for direct handling. This method was repeated until 30 larvae were randomly placed on each apple plant. In total, 7,200 neonate larvae were applied to the 240 apple plants used in this experiment. Before placement in the field, inoculated plants were retained in a closed laboratory (at approximately 20°C, RH 65%, photoperiod 16:8 L:D) for 3–4 days to allow the larvae to naturally disperse and settle on the apple plants.

Experimental design

Four treatments of alyssum were used, each with variable floral abundance (full flower, one- and two-thirds flower and a non-flowering control). In the first treatment, the 'full flowering' alyssum was left untouched. In treatment two (one-third flower), all flowers were removed by hand from 80 randomly selected plants/plot. In treatment three (two-thirds flower), all the flowers were removed from 40 randomly selected plants/plot. In the control, all flowers were removed from all alyssum plants. The control plants in both trials were re-visited 24 h after initial flower removal and then again on day 4 in order to remove any newly emerged flowers. The study was temporally separated into two trials. The first commenced on 28 January 2003 and ran for 7 days. The second trial commenced 25 March 2003, when plants were also in the field for 7 days. In the second trial, the treatments were modified slightly. Treatment three, plants with two-thirds flower, was replaced by a procedural control. This second control, which excluded alyssum entirely, only contained the six inoculated apple plants. Despite regular flower removal from the control alyssum, new flowers were observed to emerge during the first trial. The procedural control was

an attempt to mitigate a possible confounding influence that might have been introduced with the original control treatment.

Twenty experimental plots ($\sim 2 \times 3$ m) were placed within the 300×300 m vineyard. Each plot was split to encompass two adjacent vine rows. Each of the four treatments were represented only once in replicate rows, which were parallel to the boundary separating the stone fruit orchard and the vineyard. To minimise potential edge effects, a 15 m buffer zone was established in from the four sides of the study site. The four treatments were positioned 87 m apart along each replicate row, with each replicate separated by approximately 68 m. This design resulted in one replicate of each treatment being present at 30, 98, 165, 233, and 300 m from the orchard. The replicates were arranged in a modified Latin square design; modified due to the presence of a fifth replicate of the four treatments. One hundred and twenty alyssum (sixty potting bags) were apportioned equally to the design, with plants placed on the herbicide strip under the vines. Similarly, six apple plants inoculated with neonate *E. postvittana* were apportioned equally among the design, two at each end and two in the middle. The apple plants were placed in green 10-L plastic buckets, which were tied to a vine wire. A hole ~ 50 mm from the base of the bucket provided a small reservoir of water while also allowing for overflow. All plants were watered at a rate of 25 L plot⁻¹ when first positioned in the field and again after 4 days. Berndt (2002) noted that the numbers of *E. postvittana* found between 4 and 11 days declined by $\sim 40\%$ as exposure to external factors increased. It was decided that an intermediate timeframe of 7 days would maximise larval recovery while allowing sufficient time for exposure to parasitoid attack.

Placement and retrieval of plants

Inoculated apple plants were transported to the study site and later taken back to the laboratory by carefully placing them in a high-sided trailer covered with a tarpaulin thereby reducing airflow around the plants and minimising the potential for larval displacement during movement. Inoculated apple plants were positioned in the field by mid morning. At the conclusion of both trials, the apple plants were uplifted, also by mid-morning, and returned to the laboratory (an approximate 30-min trip). While there was potential for larvae to have moved between plants during this trip, the likelihood of such an event occurring was considered minimal due to the vast majority of larvae at this stage being within webbing of leafrolls. We sought to reduce the potential for off-site parasitism by minimising the interval between plant removal from the laboratory and placement in the field and again when plants were uplifted 1 week later. Between each trial, the alyssum were removed from the vineyard and returned to the laboratory for watering and maintenance.

Once in the laboratory, the apple plants were separated to avoid any larval movement between them. Plants were systematically checked for live larvae using a magnification lamp. Using a fine paintbrush, leafroller larvae were removed from the plants and placed in individual labelled tubes containing a general-purpose diet (Singh 1983), which was stopped with a cotton-wool plug. Reared in an incubator (20°C, 65% RH, photoperiod 16:8 L:D), larvae were monitored regularly and replacement diet tubes provided if necessary. The fate of each larva was recorded until they (i) pupated, (ii) produced a parasitoid or (iii) died. Dead larvae were not dissected to determine parasitism and were therefore excluded from subsequent

analysis. Parasitism of larva by a gregarious species was counted as one cocoon. The identity of these insects was determined using keys such as Wharton et al. (1997) and by comparison with known specimens from the New Zealand Arthropod Collection (Auckland, New Zealand). The Braconids *Dolichogenidea* and *Glyptapanteles* identified in this study were mostly *D. tasmanica* and *Glyptapanteles demeter*, respectively, but also included some unidentified species in each genus. We thus refer to these parasitoids as *Dolichogenidea* spp. and *Glyptapanteles* spp.

Data analysis

Difference in the proportion of larvae parasitised between trials was examined using the Pearson's Chi-squared test (R Development Core Team 2005). We used a binary generalised linear model with a logit-link function to examine the probability of the *E. postvittana* larvae being parasitised (R Development Core Team 2005). The analysis is based on a row-column (a modified Latin square) design, as we had four treatments but five replicates of each treatment. Factors included in the model were treatment (addition of alyssum flowers), distance from the nearby orchard which we considered a refuge for parasitoids (a row-effect), and the transect line coming from the orchard (the line-effect). Normality was examined via examination of residuals. Hourly weather data for rainfall and temperature was recorded for the duration of both trials at Twyford, northwest of Hastings. At a distance of 7.5 km, Twyford was the nearest permanent weather station to Dry Creek Vineyard.

Results

During the course of this experiment, 13.5% of the total leafroller larvae inoculated onto the apple plants were recovered. The number of recovered larvae in March (641) was almost twice that of January (333) (Table I). A similar percentage of larvae in both trials pupated (46 and 47%). The overall percentage of parasitised larvae in January (25%) was significantly lower than that observed in March (35%) ($\chi^2 = 9.16$, $df = 1$, $P = 0.002$). During both trials, the mean hourly temperature (19.0°C in January, 18.3°C in March – range 7.1–31.9°C) and total rainfall (0.0 mm in January; 0.05 mm in March) was similar. In total, over 300 parasitoids emerged from recovered larvae in January and March (Table I). *Dolichogenidea* spp. was the most abundant parasitoid, representing 94.0 and 98.3% from the apple plants in January and March, respectively. The only other parasitoid recorded, *Glyptapanteles* spp., was observed from five larvae in each trial.

The effects of the alyssum treatment were not significant in January ($P = 0.277$), but significant differences were observed in the March trial ($P = 0.04$) (Table II). However, in the March trial the results were not consistent with higher amounts of alyssum treatments having higher percentage parasitism rate. The significant result was instead related to the 33% alyssum treatment, which had a consistently higher rate of parasitism throughout the distances examined in the trial, compared to other treatments (Table II; Figures 1 and 2). Distance from the orchard was highly significant in both the trials ($P \leq 0.003$), perhaps indicating that the orchard was a major source of parasitoids. In the January trial, a significant treatment \times distance interaction was observed ($P = 0.010$), as the parasitism rate in the control treatment appeared to increase with distance from the orchard, while parasitism rates in all the

Table I. The outcome of recovered *E. postvittana* larvae (and proportion of recovered larvae) from both vineyard trials, Hawke's Bay, New Zealand.

Placement date and treatment	No. of larvae recovered	No. of larvae pupated	No. of larvae parasitised	No. of dead larvae*
<i>28 January 2003</i>				
Full flower	76	33	18	25
One-third flower	101	53	26	22
Two-thirds flower	82	39	17	26
No flowers (control)	74	27	22	25
Total	333 (0.09 [§])	152 (0.46)	83 (0.25)	98 (0.29)
<i>25 March 2003</i>				
Full flower	148	80	47	21
One-third flower	174	63	70	41
No alyssum control	195	101	64	30
No flowers (control)	124	57	41	26
Total	641 (0.18 [§])	301 (0.47)	222 (0.35)	118 (0.18)

[§]Proportion of total inoculated larvae recovered per trial ($n=3,600$). *Larvae excluded from subsequent analysis.

other treatments decreased (Figure 2). The apparent increase in parasitism rates in the control treatment with increasing distance from the orchard is likely a result of low sample size of larvae in the 300-m treatment ($n=10$), of which 70% were parasitised. This outlier in the extreme end of the regression line is having an unduly high influence on the slope of the regression line. There was also a significant line effect in the March trial ($P=0.002$), indicating parasitism rates differed significantly between the transect lines coming from the orchard, which was on the western side of the experimental block. An examination of the parasitism rates on the four transects lines showed that parasitism rates increased in a south–north direction (mean parasitism rates from most southern to northern lines, respectively: 33.1, 36.0, 49.6, 50.8%).

Table II. Results from the binary generalised linear model with a logit-link function, examining the probability of the *E. postvittana* larvae being parasitised.

Effect	d.f.	Deviance	Residual d.f.	Residual deviance	<i>P</i>
<i>28 January 2003</i>					
Treatment	3	3.86	231	296.22	0.277
Distance	4	16.30	224	273.59	0.003
Line	3	6.32	228	289.89	0.097
Treatment × Line	6	18.61	218	254.99	0.005
Treatment × Distance	3	11.45	215	243.54	0.010
<i>25 March 2003</i>					
Treatment	3	8.06	519	705.00	0.040
Distance	4	63.42	512	626.76	<0.001
Line	3	14.81	516	690.19	0.002
Treatment × Line	6	9.25	506	617.51	0.160
Treatment × Distance	3	2.49	503	615.02	0.480

The analysis is based on a row-column (a modified Latin square) design. Factors included in the model were treatment (addition of alyssum flowers), distance from the nearby orchard which we considered a refuge for parasitoids (a row-effect), and the transect line coming from the orchard (the line-effect). d.f., degrees of freedom. Separate analyses were performed for each month as treatments differed between months.

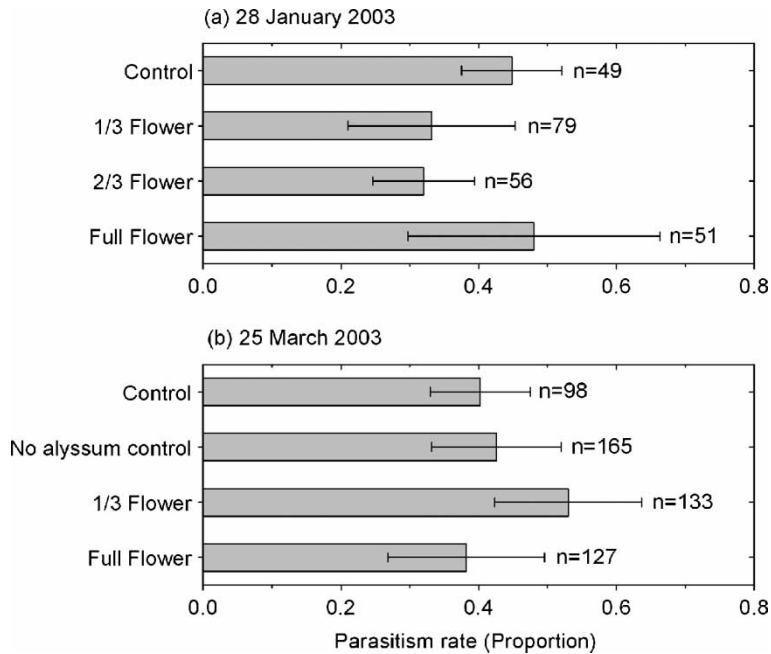


Figure 1. Mean proportion parasitism (± 1 SE) by treatment of *E. postvittana* in the Hawke's Bay vineyard, over the (a) January and (b) March trial dates. $N=5$ replicates. Numbers at end of each bar represent larvae recovered, less dead larvae.

A similar trend was observed in the January trial, with highest parasitism rate on the most northern line (range: 21.0–44.4%), though the line effect was not significant in this trial ($P=0.097$).

Finally, a significant treatment \times line effect was observed in the January trial ($P=0.005$), indicating the effect of percent alyssum on the parasitism rate was different on different transect lines. For example, the parasitism rate on line 2 was lowest in the 100% alyssum treatment (parasitism rate = 8%, $n=12$ larvae) and highest at in the control (parasitism rate = 50%, $n=8$ larvae). In contrast, on line 3 the parasitism rate was highest in the 100% alyssum treatment (parasitism rate = 100%, $n=6$ larvae) and lowest at in the control (parasitism rate = 33%, $n=12$ larvae). The low rate of larval recovery likely influenced these results, relative to the March trial wherein almost twice as many larvae were recovered and no significant treatment \times line effect was observed ($P=0.480$; Table II).

Discussion

In this study, we used alyssum in a Hawke's Bay vineyard to measure the influence of this plant on leafroller parasitism rates. Despite a relatively large study site (9 ha) with minimal understory heterogeneity, increasing the amount of flower resources available for parasitoids did not increase the parasitism rate of *E. postvittana*. We did, however, observe a strong negative correlation between distance from the nearby orchard and leafroller parasitism among the various replicate rows.

In New Zealand, two studies have previously sought to gauge the usefulness of alyssum to increase the fitness of parasitoids and to enhance leafroller parasitism rates

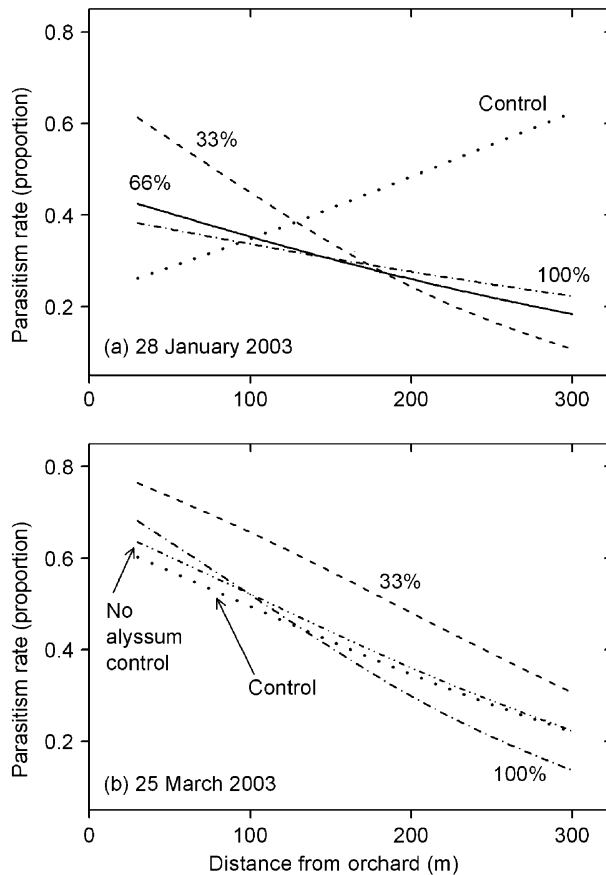


Figure 2. The predicted proportion of *E. postvittana* parasitism, as a function of distance from a nearby orchard and alyssum treatment, from the binary generalised linear model with a logit-link function. Results from the trials in January (a) and in March (b) are shown. The treatment names are shown associated with each line: 33–100% treatments indicates the percentage of alyssum flowers left on the plants; 'control', all alyssum flowers removed; 'no alyssum control', no alyssum plants in the plots (only in the second date).

(Irvin 1999; Berndt 2002). In laboratory trials, longevity and fecundity of adult *D. tasmanica* was significantly higher in the presence of alyssum flowers compared to a no-flower treatment (Berndt 2002), and to water only (Irvin 1999). In field trials in a Canterbury apple orchard, Irvin (1999) observed significantly higher abundance of *D. tasmanica* and leafroller parasitism by the same species in alyssum plots compared to control plots. In contrast, flowering alyssum had no observed effect on *D. tasmanica* parasitism of leafroller in a Canterbury vineyard (Berndt 2002). While these results suggest the fitness of *D. tasmanica* can be enhanced by alyssum, the contribution of this plant to leafroller biological control remains unclear.

Only one New Zealand study observed a significant increase in parasitism rates as a result of adding alyssum (Irvin 1999). Irvin's (1999) methodology relied on the simultaneous use of phacelia (*Phacelia tanacetifolia* Benth), buckwheat (*Fagopyrum esculentum* Moench), alyssum and a herbicide control, each in adjacent 25-m² replicated plots. Irvin (1999) found a significant increase in leafroller parasitism in plots containing buckwheat and alyssum. It is unclear to us if this result reflected the

suitability of the floral resources of buckwheat or alyssum or some combination of the two for *D. tasmanica*. We suggest that the close proximity of these plots may have provided a complementary effect as others have observed a significant effect of buckwheat on leafroller parasitism rates by the same parasitoid (Stephens et al. 1998).

While contrasting results on rates of leafroller parasitism suggest the efficacy of added alyssum is unclear, other differences between the New Zealand studies suggest direct comparisons between them are difficult. For example, spatial variation in the experimental design between studies may have influenced the observed outcomes. Alyssum in Irvin's (1999) experimental design comprised 1% of the entire study site, which contrasts the present study and that of Berndt (2002) where alyssum in both comprised 0.1%. It is possible that at the extremely low density of alyssum resources used here, it was too low to show a significant effect in this study, perhaps indicating that densities much greater than 0.1% would be necessary to enhance biological control. Alyssum at higher densities and in the absence of the nearby orchard resources may have given a different result. Further, Berndt (2002) separated alyssum and control plots by up to 49 m. Such spatial separation aligned more closely with the distances between replicates in the present study but contrasted the much smaller design used by Irvin (1999), wherein small plots were adjacent to each other.

Parasitoid mobility

In his review of Root's (1973) enemies hypothesis, Russell (1989) argued that the scale of an experimental design is crucial when considering the benefits of vegetational diversity to natural enemies such as parasitoids. Enemies will perceive the spatial distribution of treatment plots at different scales based, in part, on their propensity for movement and dispersal. With relatively little known about the dispersal of free-living parasitoids (Antolin & Strong 1987; Godfray 1994; Corbett 1998; van Nouhuys & Hanski 2002), a quantitative assessment of the degree of mobility exhibited by the parasitoid(s) of interest should ideally be undertaken.

During the interval between the two vineyard trials, a study in a separate Hawke's Bay site monitored parasitoid dispersal in a 1 ha grazed pasture that was adjacent to an organic apple orchard (Bell 2004). Over three weeks in late February/early March 2003 (the peak of the New Zealand summer), *Dolichogenidea* spp. was found foraging for leafroller hosts to a distance of at least 100 m from the orchard, the maximum distance tested. Although parasitism at 100 m (25%) was half that of the orchard controls (49%), this result suggests *Dolichogenidea* spp. is capable of widespread movement in an environment with few resources. In the current study, it was therefore possible that *Dolichogenidea* spp. experienced the vineyard and its surroundings as a single polyculture, moving freely between the orchard and the vineyard treatments and replicate rows. The presence of the stonefruit orchard appeared to be influencing parasitism rates up to 300 m distant (though studies involving individual marking of parasitoids will be needed to confirm such results). Additionally, we observed a significant line effect, which probably indicated that the area to the north of our experimental block also may have contained a refuge for *Dolichogenidea* spp. Thus, at this site it seems dispersing individuals foraged for hosts and/or floral resources at distances that probably exceeded the experimental design of this study. In other words, parasitoid dispersal over a period of only 1 week may have been of sufficient scale to moderate any actual or perceived benefits of alyssum in the vineyard. Such an

outcome may mask potential treatment effects, highlighting the importance of spatial scale in experimental design.

Other researchers have found varying dispersal rates for parasitoids. In isolated bush vetch (*Vicia sepium* L.) plots, weevil parasitism decreased substantially at distances greater than 100 m (Kruess & Tscharrntke 2000). Other studies have shown some parasitoids disperse more than a kilometre, which influences herbivore densities (Antolin & Strong 1987; van Nouhuys & Hanski 2002). The decreasing parasitism rate with increasing distance from the orchard that we observed, likely due to decreasing immigration from this refuge, is in accordance with these studies. A dispersal distance encompassing hundreds of meters could be of substantial benefit for conservation biological control practitioners as it would mean that refuges for *Dolichogenidea* spp. could be relatively widely spaced.

Conclusion

In this study, no significant effect of alyssum on the leafroller parasitism rate was observed. This result suggests that adding alyssum, at the densities used in our study, may be of limited value for the biological control of leafrollers. Our study does not rule-out alyssum from being a useful species to enhance CBC, rather, it appears that densities much greater than 0.1% may be required if it is to be functional. Further, while it is unlikely that parasitoid mobility alone contributed to the conflicting outcomes of leafroller parasitism as found by Irvin (1999), Berndt (2002) and the present study, our work demonstrates that there is now evidence that the dispersal of *Dolichogenidea* spp. may be widespread and therefore of greater importance than previously thought. If so, parasitoid dispersal has implications for the design of CBC experiments, which should in future seek to control for such an influence. In the absence of data that quantifies the dispersal of *Dolichogenidea* spp. or any other parasitoid, an argument put forward by Russell (1989) is perpetuated: similarities in herbivore mortality might suggest a lack of evidence for the enemies hypothesis, or it might mean the treatments were too close together.

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