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The effects of floral understoreys on parasitism of leafrollers (Lepidoptera: Tortricidae) on apples in New Zealand

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Abstract

1 Field and laboratory experiments on the conservation biocontrol of lepidopteran leafroller pests were carried out in apples at Lincoln, New Zealand.

2 Apple understoreys were planted with replicated treatments of alyssum (*Lobularia maritima*), phacelia (*Phacelia tanacetifolia*) and buckwheat (*Fagopyrum esculentum*).

3 Rates of parasitism of experimentally released larvae of the light-brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), by *Dolichogenidea tasmanica* (Cameron) (Hymenoptera: Braconidae) were significantly lower in phacelia and control treatments, and leafroller pupae were significantly more abundant in controls than in buckwheat and alyssum treatments.

4 Naturally occurring leafroller damage was up to 29% lower above all the floral understorey treatments compared with controls and there were more than twice as many *D. tasmanica* cocoons in the alyssum and buckwheat treatments than in controls.

5 Suction sampling of the understoreys gave *D. tasmanica* adult densities that were significantly more abundant in alyssum compared with other treatments. Numbers of *Anacharis zealandica* (Hymenoptera: Figitidae) (a parasitoid of larvae of the predatory brown lacewing) did not differ between treatments.

6 In the laboratory, flowering buckwheat and alyssum enhanced *D. tasmanica* longevity by up to 78% compared with the control, and buckwheat also enhanced potential fecundity by 62%.

7 In choice experiments, leafroller larvae in the laboratory consumed more than three-fold more apple leaf material than they did of the three understorey species, although alyssum increased leafroller fecundity and longevity.

8 The use of floral understoreys for conservation biocontrol of apple pests is discussed, along with the potential negative effects of some flowering species on pest populations and orchard agronomic practices.

Keywords Alyssum, buckwheat, conservation biocontrol, *Dolichogenidea*, fecundity, leafroller, longevity, phacelia, Tortricidae, understorey management.

Introduction

Leafrollers (Lepidoptera: Tortricidae) have a high pest status in New Zealand apple production, mainly because of zero tolerance in export crops and the requirement for blemish-free fruit (Lo *et al.*, 1997; Walker *et al.*, 1997). Intensive insecticide use has led to leafroller resistance (Suckling *et al.*, 1984; Wearing, 1995; Lo *et al.*, 1997), and consumers are increasingly questioning the negative

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effects of pesticides and demanding lower pesticide residues, or pesticide-free fruit (Wilson-Salt, 1993; , 2003). Furthermore, the range of pesticides available is diminishing, pesticide registration costs are rising, and permissible spray residue levels continue to be reduced (Wearing *et al.*, 1993). These trends are also occurring in Europe (Doubleday *et al.*, 1993) and other countries (Cooley & Manning, 1995).

The New Zealand pipfruit industry has moved towards a more sustainable management approach, called integrated fruit production. This programme requires growers to use monitoring procedures and action thresholds to determine when pesticide application is essential and strongly favours the use of insect growth regulators, such as tebufenozide (Mimic®, Dow AgroSciences, New plymouth, New Zealand) and reduced use of broad-spectrum insecticides (Batchelor *et al.*, 1997). Tebufenozide selectively targets Lepidoptera, and has little direct effect on natural enemies (Walker *et al.*, 1991). It could therefore allow an opportunity for utilizing beneficial arthropods such as *Dolichogenidea tasmanica* (Cameron) (Hymenoptera: Braconidae) for the biocontrol of leafrollers. *Dolichogenidea tasmanica* is one of the most important parasitoids of the lightbrown apple moth (LBAM) in New Zealand and Australia (Dumbleton, 1935; MacLellan, 1973; Collyer & van Geldermalsen, 1975). This would be even more desirable because leafroller resistance to tebufenozide has already occurred in New Zealand (Wearing, 1998), and a more integrated approach may have longer-term benefit.

One way of enhancing the efficacy of parasitoids of leafrollers may be via 'conservation biocontrol' (Barbosa, 1998; Pickett & Bugg, 1998; Gurr *et al.*, 2000; Landis *et al.*, 2000; Gurr *et al.*, 2004). Buckwheat *Fagopyrum esculentum* Moench (Polygonaceae) and phacelia *Phacelia tanacetifolia* Benth. (Hydrophyllaceae) enhance predator and parasitoid populations (Berndt *et al.*, 2002), which can lead to lower pest numbers (Hickman & Wratten, 1996; Baggen & Gurr, 1998; Stephens *et al.*, 1998; Irvin *et al.*, 2000; Tylianakis *et al.*, 2004). However, the sowing of annual plants may represent too high a labour cost; thus, research into a perennial plant for natural enemy enhancement in perennial crops, such as apples, is necessary. One candidate may be alyssum *Lobularia maritima* (L.) Desv. (Brassicaceae), which is perennial and seeds readily under lowland Canterbury, New Zealand conditions. Twenty-two flowering plant species, including phacelia, buckwheat, coriander *Coriandrum sativum* L. and alyssum, were recently ranked for their potential use as in-field 'insectary plants' in lettuce crops in California (Chaney, 1998). Alyssum showed the greatest potential because no other plant flowered as quickly when sown from seed or attracted as many beneficial insect species. Alyssum also attracted high numbers of hover flies (Diptera: Syrphidae) in recent comparisons of candidate 'insectary' plants in the U.S.A. (Colley & Luna, 2000). The present study therefore aimed to compare the potential value of alyssum, phacelia and buckwheat for enhancing populations of the leafroller parasitoid *D. tasmanica* and leafroller parasitism rates, and to explore the mechanisms (and potential negative effects) involved.

Methods

Field experiments

Parasitism rate of released leafroller larvae: experimental design and pest control practices. Three replicates of each of four treatments (alyssum, phacelia, buckwheat and a herbicide-treated control) were set up in a randomized complete block design in 4-year-old apple trees (cv. Braeburn) at the Lincoln University Horticultural Research Area. Treatments were sown as 25 m × 25 m plots. The apple trees were mulched with bark *Pinus* sp. and the inter-row sward consisted of ryegrass *Lolium perenne* L. that was mown frequently. No conventional control practices for lepidopteran pests were used during the experimental period (from November 1998 to April 1999); however, one application of mineral oil (2%) and two of lime sulphur (15%) were applied in September, 1998 for control of scale insects, mites, aphids, blackspot (*Venturia inaequalis* Cke. Wint.) and powdery mildew, *Sphaerotheca fuliginea* (Schlecht.) Poll. Three later applications, each of a mixture of copper hydroxide at 250 g/L (Kocide®DF 400 g/kg, Du Pont Agricultural Products, Auckland, New Zealand) at 5 L/ha and lime 1.6 kg/100 L were made in October, 1998 with a fourth application in November that year.

Agronomy of the understorey plants. To prepare the understorey for sowing, the north-east side of the tree line was sprayed with glyphosate (Roundup®XTRA 480 g/L) at 4 L/ha in 400 L and with glyfosinate-ammonium (Buster® 200 g/L) at 6 L/ha in 400 L water in September, 1998. In October, 1998 alyssum (cv. Carpet of Snow), phacelia (cv. Balo) (both commercially coated to standardize the seed size for the seed drill) and buckwheat (cv. Shinano Natsu) were drilled in six rows below the outer tree canopy at rates of 20 kg/ha, 20 kg/ha and 100 kg/ha, respectively. These cultivars were used throughout the subsequent field and laboratory experiments.

The alyssum seeds did not germinate; thus, these plots were sprayed with glyfosinate-ammonium at 4 L/ha in 400 L water in November, 1998, and flowering alyssum plants were planted approximately 30 cm apart in one row in December 1998. Also, a row of alyssum seed was sown 1 cm deep beside the alyssum transplants, and raked over, in December 1998. In November 1998, three of the six rows of buckwheat and phacelia were removed to allow room for another sowing of these species. The soil thereby exposed was sprayed with glyfosinate-ammonium at 3 L/ha in 300 L water in December 1998 and was redrilled 4 days later. This staggered plant development and prolonged the flowering period. In January 1999, the upper two thirds of the plants in the first drilling of phacelia and buckwheat were removed to encourage lateral growth and to prolong flowering.

Experimental release of leafroller larvae. By mid-January 1999, the first drillings of buckwheat and phacelia were flowering and leafroller release began. Batches of approximately 150 laboratory-produced LBAM *Epiphyas postvittana* (Walker) eggs, laid on sheets of paper, were placed on a randomly selected apple branch using the middle three trees in each plot on 15 January, 29 January, 12 February, 26 February and 15 March. LBAM is considered to be the most common leafroller species in the south island of New Zealand (Scott, 1984). Nylon mesh closed-ended sleeves (60 × 20 cm) were placed over the release branch to allow the hatched larvae to settle and to protect the eggs from predation and egg parasitoids. The sleeves were removed after 4–8 days, exposing the larvae to natural enemies. Two egg releases were conducted on each date in each treatment; for one of these, larvae were collected after 2 weeks and the other after 4 weeks. All leaves from the release branch were removed and inspected for larvae. The latter were removed and placed individually into tubes of diet (Singh, 1983). The larvae were reared to adult moths or parasitoids at 16.5 ± 2 °C, and the numbers of leafroller pupae, parasitoid cocoons and the sex of the emerging parasitoids were recorded.

Data analysis. Parasitism rate was expressed as: (the number of cocoons/number of larvae collected) × 100. The percentage of leafrollers reaching pupation was expressed as: (the number of pupae/number of larvae collected) × 100 and both metrics were log-transformed $[\log_e(x + 1)]$ prior to analysis to stabilize the variance and normalize the distribution. The percentage of female parasitoids emerging from the diet tubes was also calculated. Parasitism rate, percentage leafroller pupae and percentage females were compared between treatments and collection dates using repeated measures analysis of variance (ANOVA) and significant results were further explored using Fisher's least significant difference test.

Abundance of D. tasmanica, *leafroller larvae and a lacewing parasitoid.* A suction sampler (Arnold, 1994) was used in February 1999 on the north-east side of each row of all three replicates of each of the alyssum, phacelia, buckwheat and control plots. One sample consisted of walking down the entire row length at a constant rate of 2 m/s, sampling the flowering part of the plant with the nozzle of the sampler within 10 cm of the flowers. The sampler (0.02 m^2 catching area) delivered the catch into a 350-mL cup. The contents were later placed into 70% ethanol to await sorting under a binocular microscope (× 50 magnification) in the laboratory. The numbers of *D. tasmanica* adults, *Anacharis zealandica* Ashmead (Hymenoptera: Figitidae), a parasitoid of the brown lacewing *Micromus tasmaniae* Walker (Neuroptera: Hemerobiidae) (Stephens *et al.*, 1998) and leafroller larvae were recorded. Data were log-transformed $[\log_e(x + 1)]$ and differences between treatments were compared using the above analysis.

Parasitism of naturally occurring leafrollers. In February 1999, four trees in each of the alyssum, phacelia, buckwheat and control treatments were sampled randomly by tree and row numbers, excluding trees that had been used for leafroller release. A 3-min search of apple foliage was conducted at a height of 1–2 m, in a band around the tree. The number of leafroller larvae and pupae, *D. tasmanica* cocoons and of leaves showing probable leafroller feeding damage were recorded. Data were log-transformed $[\log_e(x + 1)]$ to normalize distributions and treatments were compared using the above analysis.

Laboratory experiments

The effect of floral resources on parasitoid longevity. Seven replicates, each of seven treatments (water, 50 : 50 honey/water solution, buckwheat with flowers, buckwheat without flowers, flowering alyssum and buckwheat and alyssum combined) were set up in a randomized complete block design under an LD 16 : 8 h photoperiod at 16.5 ± 2 °C. Phacelia was not included in this investigation because it was not available, but is included later (see below). A 'buckwheat without flowers' treatment was included to determine whether any increase in longevity was a result of an increase in humidity from transpiring leaves or of the flowers themselves. Buckwheat and alyssum were combined as one treatment to investigate whether a potentially wider range of nutrients in the nectar, and probable different temporal patterns of nectar production, increased longevity.

The water and honey/water treatments were contained in 4 cm × 1.5 cm vials sealed with a cotton-wool plug. A water-filled vial was also placed in each treatment to prevent dehydration. Plant treatments consisted of a 5 cm length of a flowering stem placed in a vial and sealed as above. Vials were replenished with water or honey/water solution as necessary and plant material was replaced every 6 days.

A pair of newly emerged adult *D. tasmanica* was placed in each vial and these were covered with a cylindrical acetate sheet (30 × 150 mm) with netting at one end. Parasitoids were obtained from adults emerging from the diet tubes containing larvae that had been collected from the field. Parasitoid longevity (days) for both sexes was checked daily, or occasionally every second day. Dead males were not replaced. Survival rates were compared between treatments using a log-rank test, and Kaplan–Meier estimates of mean survival were calculated (Kaplan & Meier, 1958).

The effect of pollen and nectar on parasitoid longevity, egg load and pollen content. Five replicates of each of five treatments (water, flowering buckwheat, buckwheat with anthers removed, water/pollen and phacelia) were set up in a randomized complete block design under the same conditions described above. Anthers and unopened flowers were removed from the buckwheat stems using a pair of 8-cm spring-type micro scissors when the stem was inverted, to avoid pollen falling into the nectar, and the surface of the remaining flowers was airbrushed. The cut anthers were placed on a microscope slide and used for the water/pollen treatment. Water was replaced as necessary and plant material was replaced every 9 days.

One male and three female newly emerged adult *D. tasmanica* were placed in each replicate. Parasitoid longevity was checked daily or, occasionally every second day. Males were not replaced once dead. After 5 and 10 days, one female parasitoid was removed and placed in alcohol for dissection using the methods of Wratten *et al.* (1995). The number of eggs and pollen grains were counted using up to × 400 magnification.

A Kruskal–Wallis nonparametric ANOVA was used to compare parasitoid longevity and the number of eggs and

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pollen grains they contained after 5 and 10 days. Where there were significant effects, these were further explored using Mann–Whitney *U*-tests. The Wilcoxon signed rank test was used to compare differences between the sexes over all treatments.

Leafroller larval 'preference' for understorey plant species. Forty Petri dishes were each lined with two sheets of damp filter paper. A piece of leaf (approximately 2 cm^2) of each of the four plant species [buckwheat, alyssum, phacelia and apple (cv. Braeburn)] was cut out and the area measured with a Licor Model 3100 area metre (LI-COR Biosciences, Lincoln, NE). The weight of each disc was also recorded. Leaf pieces from each of the four plant species were placed in a random sequence in a square arrangement on the filter paper. Half the replicates were used as a control to determine loss of water, leaf area and weight. One third-instar LBAM larvae (see above) were placed in the middle of each dish and the lid was labelled. Petri dishes were placed in a controlled-temperature room as described above and, after 48 h, the area and weight of each leaf disc were recorded again. Data were corrected for natural loss in leaf area and weight and were compared between treatments using repeated measures ANOVA. Significant effects were further explored using Fisher's least significant difference test.

Effect of floral resources on adult leafroller longevity and fecundity. Seven replicates of four treatments (water, 50 : 50 honey/water solution, flowering alyssum and no food or water) were set up in a randomized block design as described earlier. Water and honey/water solutions were added as necessary and plant material was replaced every 6 days. Vials were covered with a cylindrical acetate sheet (see above). Inside each sheet was another, scored with lines 1 cm apart, to enhance leafroller oviposition (King, 1972).

A pair of LBAM pupae due to emerge within three days was placed in each vial. The number of days until death of each moth were recorded. Males were included to allow the performance of mated female leafrollers to be assessed, and male longevity data are not presented here. The acetate sheets were replaced every 3 days and the number of leafroller eggs laid on these and other surfaces was counted under a binocular microscope for each treatment. Eggs from the sheets were incubated at 20 °C with a 2 °C range and the proportion that hatched (fertility) was recorded.

Survival curves were compared between treatments using a log rank test and Kaplan–Meier estimates of mean survival were calculated as above. The total number of eggs, and of fertile eggs, were compared between treatments using ANOVA and significant effects were further explored using Fisher's least significant difference test. Data from females that died through drowning, or that escaped, were not included in the longevity and fecundity analyses.

Results

Field experiments

Parasitism rate of released leafroller larvae. There was a significant effect of treatment on leafroller parasitism rate ($F = 13.841$, d.f. = 3,6, $P < 0.01$; Table 1), with phacelia and the control showing significantly lower parasitism rates than all other treatments. There were between 90 and 84% fewer leafroller pupae in the buckwheat and alyssum treatments, respectively, compared with the controls ($F = 5.27$, d.f. = 3,6, $P < 0.05$; Table 1). The sex ratio of *D. tasmanica* that emerged from the diet tubes did not differ significantly between treatments or collection dates (treatment: $F = 3.82$, d.f. = 3,6, $P > 0.05$; date: $F = 0.49$, d.f. = 4,8, $P > 0.05$). There were no significant date/treatment interactions for any comparison.

Abundance of D. tasmanica, *leafroller larvae and a lacewing parasitoid.* There was a highly significant effect of treatment on *D. tasmanica* abundance in the understorey ($F = 60.16$, d.f. = 3,5, $P < 0.001$) because there were significantly greater numbers in alyssum than in all other treatments (13 *D. tasmanica* collected). The number of *D. tasmanica* captured in phacelia was significantly lower than in all other treatments (with only one *D. tasmanica* individual collected), compared with four in the buckwheat treatment and five in the control. There was no significant difference in *A. zealandica* abundance between treatments ($F = 0.83$, d.f. = 3,5, $P > 0.05$). However, *A. zealandica* occurred only in the control and alyssum treatments and three-fold as many were found in the controls compared with the latter. No leafroller larvae were found in any treatments.

Parasitism of naturally occurring leafroller populations. Leafroller damage and the number of leafroller larvae present were 20.3 and 29.3% lower in the flowering treatments compared with controls and there were over two-fold as many *D. tasmanica* cocoons in the alyssum and buckwheat treatments compared with controls. However, there was no significant difference in leafroller damage, or the number of leafroller larvae and parasitoid cocoons collected between the different treatments (leafroller

Table 1 Percentage of released leafroller larvae collected (a) that were parasitized by *Dolichogenidea tasmanica* and (b) that became leafroller pupae

	Treatment			
	Alyssum	Buckwheat	Phacelia	Control
% parasitized by *D. tasmanica*	77.53^{b} ($n = 152$)	72.21^{b} ($n = 159$)	52.16^{a} ($n = 155$)	50.24^{a} ($n = 171$)
% leafrollers collected that became leafroller pupae	0.74^{a}	0.43^{a}	1.31^{a,b}	4.5^{a}

n, number of leafroller larvae; different superscript letters indicate significant differences between treatments ($P < 0.05$).

damage: $F = 1.37$, d.f. = 3,42, $P > 0.05$; leafroller larvae: $F = 0.338$, d.f. = 3,42, $P > 0.05$; parasitoid cocoons: $F = 1.58$, d.f. = 3,42, $P > 0.05$).

Laboratory experiments

The effect of floral resources on parasitoid longevity. There was a highly significant effect of treatment on longevity for female and male *D. tasmanica* (male: $\chi^2 = 28.56$, d.f. = 5, $P < 0.001$; female: $\chi^2 = 31.04$, d.f. = 5, $P < 0.001$). For males, all floral treatments except 'buckwheat without flowers' resulted in a significantly greater longevity than for controls (Fig. 1). Buckwheat gave a significantly longer survival time than did the alyssum, buckwheat/alyssum and 'buckwheat without flowers' treatments ($P < 0.05$; Fig. 1). For female *D. tasmanica*, all floral treatments gave a significantly greater longevity than did water or 'buckwheat without flowers' (Fig. 1). There was no significant difference ($\chi^2 = 2.37$, d.f. = 1, $P > 0.05$) between the sexes for longevity over all treatments (mean longevity: male 23.6 days; female 29.0 days).

The effect of pollen and nectar on parasitoid longevity, egg load and pollen content. There was a significant effect of floral treatment on longevity of males ($U = 14.01$, $n = 5$, $P < 0.01$; Fig. 2), but not of females ($U = 7.57$, d.f. = 4, $P > 0.05$; Fig. 2). For males, buckwheat led to a significantly longer survival than did phacelia, water and water/pollen.

Buckwheat did not significantly enhance parasitoid survival compared with the 'buckwheat with anthers removed' treatment for either sex (Fig. 2). The 'buckwheat with anthers removed' treatment had no significant effect on longevity compared with the water/pollen or water-only treatments ($P > 0.05$). There was no significant difference in parasitoid survival between the sexes ($Z = 0.245$, $P > 0.05$).

Floral treatment significantly affected the number of pollen grains and eggs in dissected female *D. tasmanica* after 5 days (pollen: $U = 14.62$, $n = 5$, $P < 0.01$; eggs: $U = 12.77$, $n = 5$, $P < 0.05$; Fig. 3). Buckwheat significantly enhanced egg load compared with all other treatments (Fig. 3). There were significantly more pollen grains in the gut of parasitoids in the phacelia treatment compared with buckwheat ($P < 0.05$); however, phacelia did not significantly increase parasitoid fecundity compared with buckwheat. There was no difference in the number of pollen grains per parasitoid in the buckwheat and water/pollen treatments (Fig. 3).

Leafroller larval 'preference' for understorey plant species. There was no significant difference in the leaf area eaten from each plant species ($F = 0.575$, d.f. = 3,57, $P > 0.05$; Table 2); however, there was a highly significant difference between treatments in weight eaten ($F = 10.64$, d.f. = 3,57, $P < 0.001$). Leafroller larvae consumed over three-fold more apple than the other three plants and significantly more phacelia than buckwheat (Table 2).

Effect of floral resources on adult leafroller longevity and fecundity. The type of resource provided significantly affected leafroller longevity ($\chi^2 = 21.73$, d.f. = 3, $P < 0.001$). Alyssum and honey/water led to a significantly longer survival than did water and no food (Fig. 4). There was no significant difference in longevity between sexes ($\chi^2 = 0.429$, d.f. = 1, $P > 0.05$) over all treatments (mean longevity: male 13.4 days; female 15.3 days).

There was a highly significant effect of floral treatment on the total number of eggs ($F = 21.91$, d.f. = 3,14, $P < 0.001$). Alyssum led to a significantly higher total per female than did honey/water, water and no food (Fig. 5). Honey/water did not significantly increase egg number compared with no food but this treatment led to a significantly lower number of eggs than did water. The number of fertile eggs differed significantly between floral treatments ($F = 6.52$, d.f. = 3,13, $P < 0.01$). Alyssum gave a significantly greater number of fertile eggs than did no food and

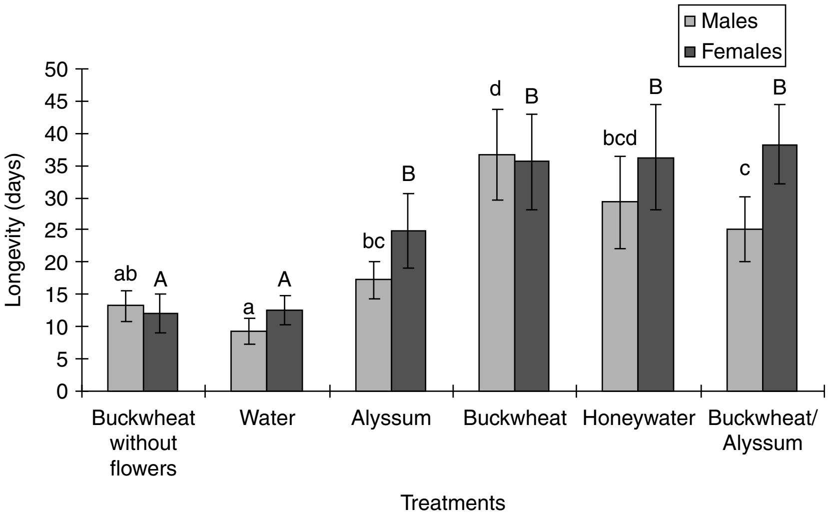

Figure 1 Mean longevity (days) of male and female *Dolichogenidea tasmanica* provided with different food sources in the laboratory at 16.5 °C. Different letters indicate a significant difference between treatments ($P < 0.05$).

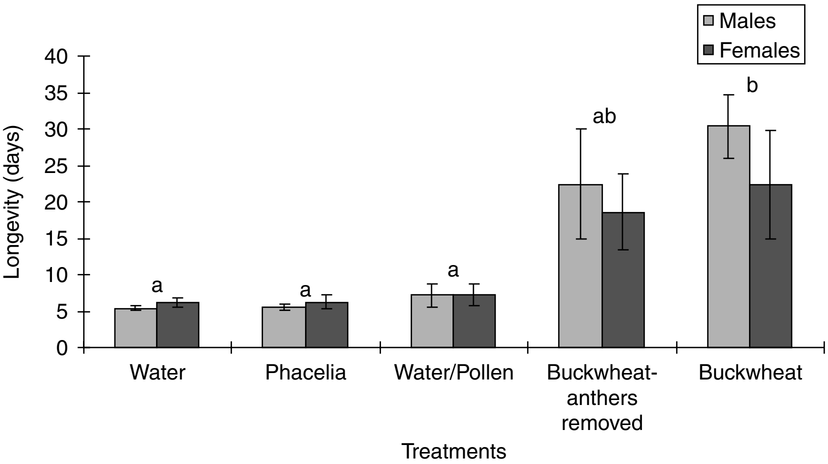

Figure 2 The influence of buckwheat pollen and nectar, and phacelia flowers on the mean longevity (days) of male and female *Dolichogenidea tasmanica* in the laboratory at 16.5 °C. Different letters indicate significant differences between treatments ($P < 0.05$).

honey/water but did not significantly enhance the number of fertile eggs produced compared with water.

Discussion

Field experiments

Parasitism rate of released leafroller larvae. Leafroller parasitism was significantly higher in the alyssum and buckwheat treatments compared with controls. This supports previous studies showing that buckwheat enhanced parasitism rates of leafrollers (Stephens *et al*., 1998; Irvin *et al*., 2000) and indicates that alyssum may have potential as a semiperennial understorey plant for apple orchards. Grossman & Quarles (1990) also showed an increase in parasitism of the green peach aphid *Myzus persicae* Sulz (Hemiptera: Aphididae) by the wasp *Diaeretiella rapae* (McIntoch) (Hymenoptera: Aphidiidae) when lettuce fields were interplanted with alyssum. In the present study, there were 90 and 84% fewer leafroller pupae in the buckwheat and alyssum treatments, respectively, compared with controls. This strongly suggests that the effect of flowering plants in the understorey on increasing leafroller parasitism can lead to a decrease in pest abundance.

Although phacelia is potentially a good source of nectar (Crane *et al*., 1984), the flowers have deep corollae, probably making the nectar inaccessible to short-tongued parasitoids (Holland *et al*., 1994). The results from this study indicate that, unlike some other braconids, *D. tasmanica* may not have elongated mouthparts to feed on flowers that have deep corollae (Jervis *et al*., 1996) and that this species may not crawl down the corolla tubes of phacelia flowers to exploit nectar. The results from laboratory trials support this hypothesis.

Providing floral resources in the understorey did not appear to have any effect on the sex ratio of *D. tasmanica* in the field. Like most Hymenoptera and most *Apanteles* spp. (Allen & Smith, 1958), *D. tasmanica* (formerly *Apanteles tasmanica*) has arrhenotokous ovaries, in that haploid eggs develop into males if not fertilized, and into females if fertilized. Therefore, the sex ratio of progeny from *D. tasmanica* may be more strongly determined by female mating, than by food supply. By contrast, Berndt *et al*. (2002) found an effect of buckwheat understoreys on *D. tasmanica* sex ratio in vineyards. In that study, male *D. tasmanica* were more abundant in the presence of buckwheat, and mating opportunities were more readily available for females in the vicinity of buckwheat. This provided females with more opportunities to fertilize eggs and subsequently led to a female-biased sex ratio. Furthermore, because males often emerge before females, the availability of floral resources, which increase male longevity, may lead to a greater likelihood of mating, again resulting in more

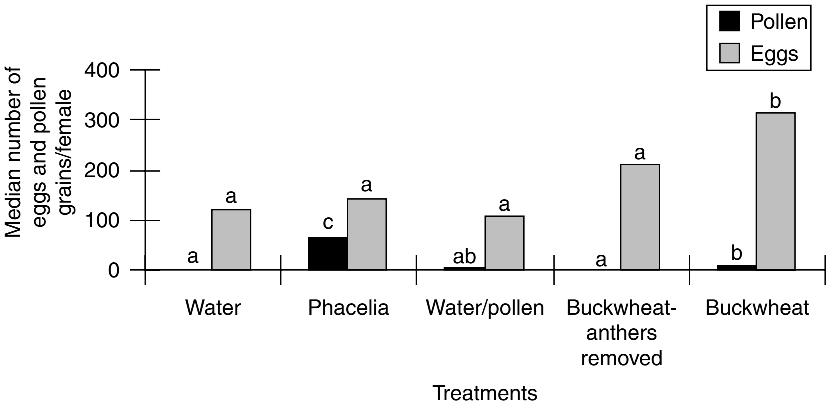

Figure 3 The influence of buckwheat pollen and nectar, and phacelia on the number of eggs and pollen grains in dissected female *Dolichogenidea tasmanica* after 5 days. Different letters indicate significant differences between treatments ($P < 0.05$).

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Table 2 The mean leaf area (mm^2) and weight (mg) of four plant species consumed by *Epiphyas postvittana* larvae after 48 h

	Treatment			
	Alyssum	Buckwheat	Phacelia	Control
Leaf area consumed (mm^2)	1.22	0.19	0	0
Weight consumed (mg)	2.85^a	0^c	0.71^b	0^c

Superscript letters indicate significant differences in weight consumed between treatments ($P < 0.05$); leaf area consumed did not significantly differ between treatments ($P > 0.05$).

opportunities for females to fertilize their eggs (Godfray, 1994).

Abundance of D. tasmanica, *leafroller larvae and* A. zealandica. *Dolichogenidea tasmanica* abundance was more than two-fold higher in the alyssum treatment compared with buckwheat, phacelia and control, indicating that alyssum is very attractive to this parasitoid. These trends are similar to those for parasitism rate; however, buckwheat also enhanced leafroller parasitism compared with phacelia and control, whereas it apparently did not enhance *D. tasmanica* abundance. This may have been a result of difficulty in suction sampling buckwheat and phacelia, which were taller than controls, because previous studies have shown an increase in *D.* tasmanica captured on yellow sticky traps in buckwheat plots compared with controls (Stephens *et al.*, 1998; Irvin *et al.*, 2000).

Although not discussed in the results, alyssum had the potential benefit of harbouring significantly fewer aphids than did buckwheat and control plots. However, the key species of aphid pests in New Zealand orchards do not attack the Brassicaceae (Scott, 1984). If apple was not a host of the aphid species found, they may have been beneficial by providing alternative prey, hosts and honeydew for natural enemies.

Anacharis zealandica abundance was three-fold lower in alyssum plots compared with controls. *Anacharis zealandica* is a parasitoid of the Tasmanian lacewing, which is a general insect and mite predator (Leathwick, 1989). This result is similar to that obtained by Irvin *et al.* (2000) who showed that buckwheat in the orchard understorey did not enhance numbers of *A. zealandica*. However, it is in contrast to the results of Stephens *et al.* (1998) who found that there were up to 10-fold more *A. zealandica* trapped in buckwheat plots compared with in the controls. Very few *A. zealandica* were captured in the current study, which is in contrast to the high numbers captured with suction sampling and yellow sticky traps in Stephens *et al.* (1998) and Irvin *et al.* (2000), respectively. This may be an artefact of the different sampling methods used.

Parasitism of naturally occurring leafrollers. No conclusions could be drawn from sampled natural leafroller populations, possibly due to the small number of replicates and the low leafroller population present. This justifies the leafroller releases to increase the leafroller population and makes it easier to detect significant differences in parasitism rates between treatments. Parasitoid cocoons were at least two-fold more abundant in the alyssum and buckwheat treatments compared with controls. Leafroller damage was also 20.3% lower in the flowering treatments compared with the control, indicating that increasing leafroller parasitism rate can lead to pest suppression and a decrease in damage to apple foliage. The number of larvae found in the flowering treatments was 29.3% lower than controls, providing further supporting evidence. However, it is not known how many of these larvae were parasitized by *D. tasmanica*.

Laboratory experiments

The influence of floral resources on parasitoid fitness. The 'buckwheat without flowers' treatment reduced parasitoid longevity compared with buckwheat with flowers for both

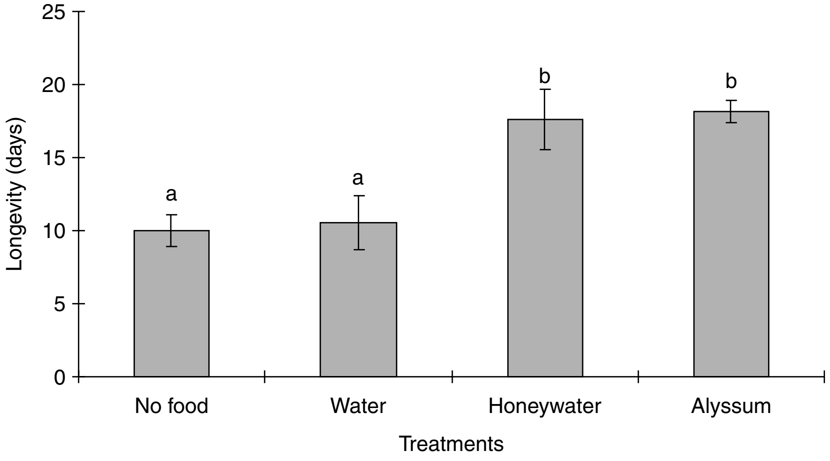

Figure 4 The mean longevity (days) of female adult *Epiphyas postvittana* provided with different food sources in the laboratory at 16.5 °C. Different letters indicate significant differences between treatments ($P < 0.05$).

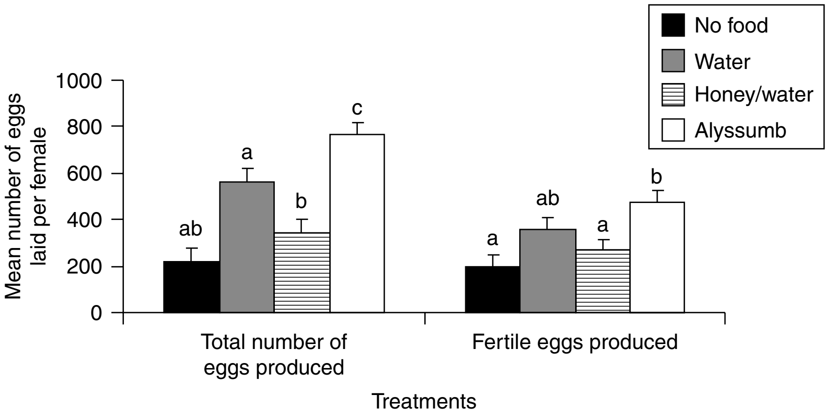

Figure 5 The mean number of total and fertile eggs produced by female *Epiphyas postvittana* provided with different food sources in the laboratory at 16.5 °C. Different letters indicate significant differences between treatments ($P < 0.05$).

sexes. This supports Irvin *et al.* (2000) who showed that it is the flower that enhances parasitoid longevity, and not the shelter or aphid honeydew that the plant may also provide.

Alyssum did not perform as well as buckwheat in enhancing parasitoid survival. For male *D. tasmanica*, buckwheat also gave a higher longevity than buckwheat/alyssum combined. This is in contrast to the work of Irvin *et al.* (1999) who showed that, for male *D. tasmanica*, a combination of buckwheat and coriander gave a significantly greater longevity than either species on their own, possibly by providing a wider range of amino acids, sugars and proteins required by the parasitoid. The results from the present study suggest that the addition of alyssum to the buckwheat treatment reduced parasitoid survival compared with buckwheat alone. Nectar from some plants may contain metabolically harmful substances, such as melezitose (Harborne, 1988) that may depress longevity (Avidov *et al.*, 1970). However, alyssum significantly enhanced parasitoid survival compared with water for both sexes, and fieldwork showed a higher parasitism rate and parasitoid abundance in alyssum treatments compared with controls. However, this experiment was limited by the use of cut stems placed in water, which are unlikely to produce as much nectar as a flowering stem on an actively growing plant.

The effect of pollen and nectar on parasitoid fitness. The increased longevity of male *D. tasmanica* in the buckwheat treatment compared with water and water/pollen treatments reinforced the conclusion that nectar is essential for parasitoid survival and supports previous results (Hagley & Barber, 1992; Wäckers & Swaans, 1993; Idris & Grafius, 1995; Baggen & Gurr, 1998; Irvin *et al.*, 1999).

Buckwheat did not significantly enhance parasitoid survival compared with buckwheat with anthers removed, suggesting that pollen is not essential for enhanced longevity of this parasitoid species. This supports the finding by Hodgson *et al.* (1993) of no effect of pollen on longevity of *Microctonus hyperodae* Loan (Hymenoptera: Bracondiae). Similarly, fecundity of females in phacelia and water/pollen treatments did not differ significantly from those with water or buckwheat with anthers removed. Only buckwheat plants with flowers resulted in increased fecundity, which was likely to be the result of nectar rather than pollen availability. The higher number of *Phacelia* pollen grains in parasitoid guts compared with the buckwheat treatment may have been because the parasitoids were compensating for a lack of nectar in the phacelia treatment, or that phacelia pollen was a more frequent nectar contaminant than that of the other species (Jervis, 1998).

Leafroller larval 'preference' for understorey plant species. LBAM showed a distinct 'preference' for apple foliage over the understorey candidate plants offered, possibly because the latter were of lower nutritional value or, despite this species being highly polyphagous (Danthanarayana, 1975), contained antifeedants that caused the larvae to stop feeding and move to a more 'preferred' plant species (Russel & Lane, 1993; Schoonhoven *et al.*, 1998). Given the extreme abundance of favourable leafroller hosts in the orchard, including apple, these understorey plants are unlikely to contribute to the leafroller population.

Effect of floral resources on adult leafroller fitness. The results obtained in the present study were similar to those obtained by Gu & Danthanarayana (1990) in that honey/water enhanced adult leafroller female longevity compared with no food. The early mortality of female adults not given food or water is probably due to dehydration rather than exhaustion of their metabolic resources (Gu & Danthanarayana, 1990). Honey/water increased longevity compared with water, also supporting the results obtained by Gu & Danthanarayana (1990), and alyssum enhanced longevity compared with no food and water, suggesting that this lepidopteran can access the nectar of alyssum.

Female adults were able to lay eggs when given no water or floral resources. This supports the results obtained by Gu & Danthanarayana (1990) who showed that, because LBAM is able to lay fertile eggs without the ingestion of food or water, by their definition, it is an 'autonomous' insect. However, in the present study, egg production was more than two-fold higher when water was provided.

Not only did alyssum enhance female leafroller survival compared with water and no food, but it also enhanced total egg production compared with all other treatments. However, the number of fertile eggs did not significantly differ between alyssum and water. This suggests that, even though survival is increased and the number of eggs laid is increased, overall fertility is not increased. This may be because eggs laid later in the life of a female leafroller are less fertile (Howell, 1981). Although the production of fertile eggs after alyssum feeding is equivalent to that of water, they are produced over a longer period of time because survival is enhanced, allowing the moth a greater potential for dispersal.

In conclusion, buckwheat and alyssum show good agronomic performance for incorporation into integrated pest management programmes. Buckwheat germinates easily, has a short sowing to flowering time and, if sown in August in Canterbury, New Zealand, it flowers from November for up to 3 months (Bowie *et al*., 1995). Its seed is inexpensive and easily accessible in New Zealand and elsewhere (Wratten *et al*., 1995). Alyssum flowers almost all year round in the New Zealand climate and, because it is often used as an ornamental or bedding plant in household gardens, its seed is also inexpensive and readily available.

The present study demonstrates the increased aggregation of natural enemies around floral resources and increases in life-history parameters such as longevity and fecundity in flower-feeding natural enemies (Gurr *et al*., 2000; Landis *et al*., 2000; Gurr *et al*., 2004). However, enhancement of pest fitness via the same mechanisms as natural enemies is potentially inimical to conservation biocontrol. Leafrollers had increased longevity and egg production in the presence of alyssum. A similar enhancement of pests fitness was recorded by Baggen & Gurr (1998) when the potato tuber moth, *Phthorimaea operculella* (Zeller) fed on coriander and broad bean, *Vicia faba* L., highlighting the need for experiments such as those conducted in the present study to identify plant species that strongly favour natural enemies (Lavandero *et al*., 2005).

Although data are still lacking concerning the effects of understorey plants on the ability of this technique to contribute to the reduction of leafroller populations below economic thresholds, the cost of seed is very low and the potential of the approaches outlined here is high. Therefore, understorey management using floral resources may be an added strategy for pest control if incorporated into integrated fruit production programmes and organic (Anonymous, 2001) apple production.

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