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The influence of floral resource subsidies on parasitism rates of leafrollers (Lepidoptera: Tortricidae) in New Zealand vineyards

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Abstract

Biological control of pests in agroecosystems may be enhanced by the use of habitat manipulation techniques to provide floral and other 'resource subsidies' for natural enemies. This was examined in vineyards by adding flowering buckwheat (*Fagopyrum esculentum* Moench) and assessing the effect of this on the parasitism rate of leafroller (Lepidoptera: Tortricidae) larvae. Leafroller larvae were collected from vines in plots with and without buckwheat flowers at two commercial vineyards in Marlborough, New Zealand. At one vineyard, the parasitism of these pests was increased by more than 50% when buckwheat flowers were present. At the other, buckwheat had no effect, however leafroller populations were lower and insecticides had been used in part of the experiment. The presence of buckwheat did not reduce leafroller abundance during the two months of the study. These results show that habitat manipulation, by providing floral resource subsidies for parasitoids, can enhance parasitism rate. However, the value of this technique for reducing damage done by leafrollers in the vineyard system studied remains to be determined.

Keywords: Braconidae; Conservation biological control; *Dolichogenidea tasmanica*; *Epiphyas postvittana*; *Fagopyrum esculentum*; Floral resources; Habitat manipulation; Parasitism; Resource subsidies; Tortricidae

1. Introduction

Many adult parasitoids require non-host food, which can be obtained from flowers, extra-floral nectaries, and honeydew-producing Homoptera (Landis et al., 2000). By planting flowers in an agroecosystem, growers can provide 'resource subsidies' for parasitoids, potentially improving biological control of insect pests (Gurr et al., 2004; Kean et al., 2003; Tylianakis et al., 2004). Langellotto and Denno (2004) demonstrated through meta-analysis that when habitat structure is increased, this leads to an increase in natural enemy abundance, supporting the top-down theory that the provision of floral resource subsidies can increase parasitoid abundance through the provision of pollen and/or nectar. Showing an effect of flowers on the efficiency of a parasitoid at reducing a pest's population is a critical step in demonstrating the value of providing floral resources in this way (Wratten et al., 2000). The ratio of parasitized hosts to the total number of hosts available (parasitism rate) is often used as a measure of the efficiency of the parasitoid (e.g., Cappuccino et al., 1998; Haseeb et al., 2000). Parasitism rate may at times be a poor indicator of the impact a parasitoid has on its host, because of the effect of host and parasitoid phenology (van Driesche, 1983). However, because of the difficulties of overcoming these effects it remains the only useful measure of parasitoid efficiency (van Driesche, 1983; van Driesche and Hoddle, 2000).

The presence of flowers can increase the parasitism rate of many pests. For example, in a chickpea crop with a border of coriander flowers, parasitism of the gram pod borer was four times greater than that in chickpeas without a border (Pimbert and Srivastava, 1989). Baggen and Gurr (1998) showed that the parasitism rate of the potato moth was greater on potatoes opposite a strip of borage flowers

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than in control plots. In a New York vineyard, English-Loeb et al. (2003) showed that parasitism rate of *Erythroneura* leafhoppers (Homoptera: Cicadellidae) was increased by 20% when flowering buckwheat (*Fagopyrum esculentum* (Moench)) was present between vine rows.

Leafrollers (Lepidoptera: Tortricidae) are an important pest of fruit crops in many parts of the world. In New Zealand, the viticulture industry has identified them as a key insect pest. On grape vines, leafroller larvae feed on leaves but cause the most significant damage to flowers and fruit (Lo and Murrell, 2000). In the Marlborough region of New Zealand, where the current study was conducted, leafrollers are most abundant close to harvest. At this time, feeding scars on ripe berries can lead to infection by the fungus *Botrytis cinerea* Pers. Fr. (Lo and Murrell, 2000). Crop losses due to leafroller damage have been estimated as NZ$60–NZ$360/ha in a dry year, with a significant increase in losses in wetter years (Lo and Murrell, 2000).

The pest leafroller complex in New Zealand consists of five native species (*Ctenopseustis obliquana* (Walker), *C. herana* Dugdale, *Planotortrix excessana* (Walker), *P. octo* Dugdale, and *Cnephasia jactatana* (Walker)) and one exotic species (*Epiphyas postvittana* (Walker)) (Suckling et al., 1998). They all have apparently similar biology (Baker et al., 1994) and vary in species combinations and proportions with crop type and location (Foster, 1990). Leafrollers are multivoltine, with the number of generations per year varying from four in the North of the country to two in the South (Wearing et al., 1991). At least 22 native and introduced parasitoid species attack these leafrollers, but the most abundant is the exotic larval endoparasitoid *Dolichogenidea tasmanica* (Cameron) (Hymenoptera: Braconidae) (Charles et al., 1996; Suckling et al., 1998).

Until recently, leafroller management methods at many vineyards involved the use of broad-spectrum insecticides, applied on a calendar basis with little regard to pest abundance (Hocksbergen, 2000). In 1998, the New Zealand wine industry introduced a 'sustainable' management scheme, New Zealand Integrated Winegrape Production (NZIWP), for use in vineyards, and now the majority of New Zealand's vineyard area is managed under this scheme. NZIWP encourages the use of biological control methods, including the use of plant diversity to enhance natural enemies already present in the system (Crosse, 1998) although little information is given to growers on how to achieve this in practice. The presence of cover crops could benefit natural enemies in a number of ways: by providing shelter, as a source of alternative hosts or prey, or by providing non-host foods such as nectar and pollen (Landis et al., 2000; Langellotto and Denno, 2004). This study focuses on the latter of these benefits.

The present work is a continuation of that described by Berndt et al. (2002). In that study, the addition of flowers to a vineyard ecosystem increased parasitoid abundance, but had no effect on the parasitism rate of released 'sentinel' leafroller larvae. In this study, the effect of flowers on leafroller parasitism is examined using naturally occurring, rather than released larvae.

2. Materials and methods

Buckwheat (cv. Shinano Natsu) was chosen for use in this experiment because it has increased the abundance, longevity, and parasitism rate of *D. tasmanica* in previous studies (Irvin et al., 1999; Stephens et al., 1998). It also has a short sowing-to-flowering time, and can be managed to produce flowers over the entire grape growing season (Bowie et al., 1995). The seed is inexpensive and easy to sow and maintain, and the plant is killed by frost which mitigates against it becoming a weed. For these reasons buckwheat was chosen over other plant species, such as alyssum (*Lobularia maritima* (L.)), coriander (*Coriandrum sativa* L.), and phacelia (*Phacelia tanacetifolia* Bentham) which have also been found to benefit parasitoids (Baggen and Gurr, 1998; Irvin et al., 1999).

2.1. Site description and experimental layout

Experiments were conducted at Squire Estate and Kaituna Estate, two Montana Wines Ltd vineyards in Marlborough, New Zealand. Both vineyards are managed under the NZIWP sustainable management scheme (Jordan, 1997). In each vineyard, an area of Pinot Noir vines was chosen for the experiment, and five replicates each of buckwheat and control treatments were laid out in a randomized block design. The experimental area at Squire Estate was bordered by other vine cultivars to the east and west, with pasture to the south and a road and another vineyard to the north. At Kaituna Estate, vineyards and pasture bordered three sides of the experimental area, with a river and riparian vegetation on the fourth side to the north. Each replicate consisted of a strip of vegetation between one pair of vine rows, with the number of rows between treatments varying between vineyards (Table 1). Buckwheat was drilled into cultivated ground in the allocated replicates at 75 kg/ha in a

Table 1
Physical attributes of the experimental areas and the number of leaves and bunches sampled at Squire and Kaituna Estates

	Squire Estate	Kaituna Estate
Vine cultivar	Pinot noir	Pinot noir
Number of vine rows used	65	650
Vine row spacing (m)	2.4	2.4
Vine row length (m)	455	207–426 (mean 300)
Vine spacing along rows (m)	1.8	1.8
Minimum distance between treatments (m)	12	156
Total number of leaves and bunches sampled in December	15,870	19,583
Total number of leaves and bunches sampled in January	21,677	24,005

1.5-m wide strip on 13 October 2000, and began flowering around 28 November 2000. The standard ground cover for all three vineyards was a mown grass and clover sward with some adventive weed species, such as dove's-foot cranesbill (*Geranium molle* L.), hawksbeard (*Crepis capillaris* (L.) Wallr.), and large-flowered mallow (*Malva sylvestris* L.). This ground cover was used as the control treatment. Row and vine spacing, the size of the experimental area and the distance between treatments are given for each vineyard in Table 1. Vine rows were orientated approximately north–south, and the prevailing wind was from the north–west. At Squire Estate, buckwheat and control strips in each block were allocated respectively to one half of the row length to keep treatments as far apart as possible. This was not done at Kaituna Estate, where treatment strips ran the full-length of the vine rows (Table 1).

At Squire Estate, no insecticides had been applied to the experimental vines for at least 5 years, and none was used during the experiment. At Kaituna Estate, chlorpyrifos (Lorsban, 750 g/kg active ingredient, WP, applied at 1 kg/ha) was sprayed on two sections of six vine rows on 12 December 2000, incorporating one of the buckwheat plots and one of the control plots. At the same time, tebufenozide (Mimic, applied at 0.26 kg/ha, WP), a Lepidoptera-specific insecticide, was sprayed on two six-row sections near another buckwheat plot and another control plot, but not on any vines involved in sampling. These insecticides were applied with a Technoma sprayer unit with T-jet nozzles that delivered 12–15 L/min. These insecticide sprays were conducted by the grower and were not planned as part of the present experiment.

The first experimental planting of buckwheat finished flowering in late January. In an attempt to have a second flowering of buckwheat, this planting was cultivated and new seeds were sown around 29 January. Due to a severe drought (Agnew, 2001), these seeds failed to germinate. Irrigation of the seeds was not possible, and the drip irrigation for the vines did not provide sufficient water for the buckwheat. Due to this lack of flowers, the experiment was finished in January, rather than continuing as planned until grapes were harvested in April.

2.2. Sampling methods

During each sampling period (4–5 December 2000 and 15–16 January 2001), 10 vines were sampled in vine rows adjacent to each treatment plot. Random numbers were used to select vines, and no vines were sampled more than once. A 25-vine buffer of unsampled vines was left at either end of each plot to minimize edge effects. On each vine, only the side facing the treatment plot was sampled. The vine was divided into three sections, or feeding sites: grape bunches (BU, approximately 0.90 m above ground), lower canopy leaves (LC, up to approximately 1.2 m), and upper canopy leaves (UC, above 1.2 m). All leaves and bunches in each section were examined and the numbers of each sampled were recorded (Table 1). For each section of the vine, the number of leafroller eggs, larvae, and pupae, and of parasitoid cocoons were recorded. Any live leafrollers or parasitoid cocoons were collected and reared. Emerging adult leafrollers and parasitoids were identified. These specimens have been deposited with the Entomology Research Museum, Lincoln University, New Zealand.

2.3. Analysis

The proportion of leafrollers parasitized was analyzed using a generalized linear model with binomial error distribution and logit link function (Genstat, 2003, seventh ed.). Statistical analysis was conducted on Squire Estate data only, due to very low leafroller abundance at Kaituna Estate. All bunches and leaves on selected vines were examined and the number of leafrollers was obtained as the total of live leafroller larvae, pupae or parasitized cocoons collected from the selected vines. Parasitized cocoons were included in the total because a cocoon of a larval parasitoid, such as *D. tasmanica*, represents a host that was part of the same cohort as an unparasitized late-instar leafroller larvae and leafroller pupae. Empty pupae and empty parasitoid cocoons were not taken into account because these may persist in the environment and so can accumulate over the season. The number of leafrollers was analyzed using a generalized linear model with Poisson error distribution and log link function. To adjust the leafroller counts for the number of bunches and leaves examined, the log of the number examined was included in the model as an offset variable. Results for leafroller abundance are presented as the mean number of leafroller per 100 leaves or bunches.

Parasitism rate was calculated using the following formula:

$$\text{Parasitism rate} = \frac{\text{number of live parasitoid cocoons collected or reared}^{*}}{\text{total number of live leafroller larvae, pupae, and parasitoid cocoons collected}} \times 100$$

(* gregarious parasitoid cocoons from one host were counted as one cocoon.)

3. Results

Epiphyas postvittana was the most common leafroller species, constituting 89 and 76% of identified leafrollers collected from Squire and Kaituna Estates, respectively (Table 2). *Ctenopseustis* spp. and *Planotortrix* spp. made up the remainder of leafrollers collected (Table 2). Leafroller abundance was very low, especially at Kaituna Estate where numbers were insufficient for statistical analysis (Table 2). In December, *D. tasmanica* was the only parasitoid species found. In January, *Glyptapanteles demeter* (Wilkinson) (Hymenoptera: Braconidae) and *Glabridorsum stokesii* (Cameron) (Hymenoptera: Ichneumonidae) also emerged from collected leafrollers, although these two species were rare (Table 2). In December, all leafrollers collected were larvae, but in January some pupae and

Table 2
Outcome of rearing leafrollers and parasitoid cocoons collected in December 2000 and January 2001 at two vineyards in Marlborough, with treatments combined

	Squire		Kaituna	
	December	January	December	January
Leafroller species				
Epiphyas postvittana	5	20	0	13
Ctenopseustis spp.	0	2	2	0
Planotortrix spp.	0	1	0	2
Unidentified leafrollers	0	6	1	4
Parasitoid species				
Dolichogenidea tasmanica	1	11	0	4
Glyptapanteles demeter	0	1	0	0
Glabridorsum stokesii	0	1	0	0
Total number of leafrollers and parasitoids collected	6	42	3	23

Unidentified leafrollers died of unknown causes before reaching adulthood. Leafrollers that died due to parasitism are recorded as the parasitoid species that emerged.

parasitoid cocoons were found. No leafroller eggs were found on either date.

The parasitism rate of leafrollers in buckwheat at Squire Estate was 48 ± 13.2% ($n = 22$), significantly higher than the 17 ± 7.3% ($n = 26$) found in control plots (χ^2 probability = 0.036). The same trend was observed at Kaituna Estate (observed parasitism rate: control = 0% ($n = 9$); buckwheat = 25% ($n = 17$)), although statistical analyses could not be conducted. There was no significant difference in parasitism rate between feeding sites on vines at Squire Estate.

There was no significant effect of treatment on leafroller abundance at Squire Estate. Leafrollers were significantly more abundant in bunches than on leaves (χ^2 probability < 0.001). The maximum abundance found was in bunches in control plots at Squire Estate in January, of which 1.2% were infested. Leafroller abundance increased significantly from December to January at Squire Estate (χ^2 probability < 0.001), and the same trend was observed at Kaituna Estate.

4. Discussion

Adding flowers to a vineyard ecosystem can increase the impact of parasitoids on pest Lepidoptera, as demonstrated by the increase in parasitism rate of leafrollers in this study. This result adds to growing evidence that conservation biological control techniques, such as the provision of resource subsidies, have much to contribute to the development of sustainable agriculture (Landis et al., 2000; Tylianakis et al., 2004).

The availability of nectar can be an important limiting factor for parasitoids. Without access to carbohydrate foods, many parasitoids live for only a short time and produce few offspring (Irvin et al., 1999; Johanowicz and Mitchell, 2000; Leatemia et al., 1995). *D. tasmanica*, the most abundant parasitoid found attacking leafrollers in this study, is no exception. Laboratory studies of this species have shown that nectar can increase female longevity sixfold, with an eightfold increase in lifetime fecundity compared with the provision of water only (Berndt and Wratten, 2005). If suitable flowers are rare or not available in a field situation, parasitoids will need to expend more energy to find carbohydrates, or go without. Either way, the energy they have available to find and attack hosts will be reduced, limiting their potential to reduce pest numbers. By making suitable flowers freely available in an agricultural environment the potential of the parasitoid can be maximized.

In a previous study (Berndt et al., 2002), buckwheat flowers planted in a vineyard increased parasitoid abundance, but did not alter the parasitism rate of ‘sentinel’ (released) leafroller larvae. The present study examined the effect of these floral resource subsidies on the parasitism of naturally occurring leafrollers, finding an increase in parasitism rate at both vineyards studied. The next step in demonstrating success in conservation biological control is to show a reduction in the pest population (Wratten et al., 2000). This was not achieved in this study, possibly due to a drought ending the experiment early, before any population effects could be observed.

Although these results demonstrate the positive benefits of adding floral resource subsidies to agricultural systems, they should be interpreted in the context of leafroller management. Key issues are whether the parasitoids are capable of sufficiently reducing the leafroller population and whether the observed parasitism rate is sufficient to reduce the impact of leafrollers on the crop. Parasitism rate can be used as a measure of parasitoid efficiency, but this is best done with reference to host life table data (van Driesche, 1983). Life tables have been constructed for *E. postvittana* in Victoria, Australia, where parasitoids were found to be unimportant in determining population abundance, particularly for larval instars two to five (Danthanarayana, 1983). In that study, population fluctuations were related to the influence of climate, predation, and food quality and availability. These factors acted on egg production and the mortality of eggs and first-instar larvae. Danthanarayana (1983) found that egg production was greatest under cooler conditions, with periods of high temperature and drought having the potential to cause leafroller populations to crash. Little has been published on the population ecology of leafrollers in New Zealand, although an unpublished study was conducted on *E. postvittana*, *C. obliquana*, and *P. excessana* in an apple orchard (Green, 1984). As was found in Australia, mortality of first-instar larvae during the dispersal phase was an important factor affecting leafroller population density in that study, although predation and parasitism of other larval instars were also considered to be major factors. Another unpublished study cited weather and parasitism as important factors affecting leafroller abundance in a Canterbury apple orchard, but life tables were not constructed and the effect of predators on early instars was not examined (Tomkins, 1984). Tomkins (1984) also found that parasitism rate of 45% in the apple orchard in January did not prevent damage to fruit, possibly because the main parasitoid (*D. tasmanica*) does not prevent host larvae feeding until the fourth or fifth instar. The role that various mortality factors play in regulating leafroller populations in New Zealand vineyards needs to be investigated further.

Clearly, the addition of resource subsidies to an agroecosystem can benefit parasitoids and impact pest populations (this study; Baggen and Gurr, 1998; English-Loeb et al., 2003; Pimbert and Srivastava, 1989). The next step is to use this tool appropriately, alongside other integrated pest management techniques, to successfully manage pests. This requires in-depth knowledge of the ecology of the pest and its predators and parasitoids. Modeling techniques, such as that described by Kean et al. (2003), could be used to predict which systems might benefit from the addition of resource subsidies. For the leafroller-parasitoid system described in this study, the addition of buckwheat to the system did lead to greater parasitoid activity, but further research is required to determine if can translate into reduced leafroller damage in the crop.

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