



Increasing floral diversity for selective enhancement of biological control agents: A double-edged sword?

Blas Lavandero I.^{a,*}, Steve D. Wratten^a, Raphael K. Didham^b, Geoff Gurr^c

^aNational Centre for Advanced Bio-Protection Technologies, Lincoln University, Canterbury, New Zealand

^bSchool of Biological Sciences, University of Canterbury, Christchurch, New Zealand

^cCharles Sturt University, Orange, NSW, Australia

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Summary

Floral resource subsidies can have differential effects on insect herbivores compared with the herbivores' natural enemies. While the nectar of many plant species enhances parasitoid fitness, it may also increase damage by herbivores. This may occur as a result of enhanced herbivore fitness or by enhancing fourth-trophic-level processes, possibly disrupting a trophic cascade as a result. The responses of different arthropod guilds to different floral resource subsidies were compared using *Plutella xylostella* (Hyponomeutidae), its parasitoid *Diadegma semiclausum* (Ichneumonidae) and data from two other published herbivore–parasitoid systems. These were *Dolichogenidea tasmanica* (Braconidae) and its host *Epiphyas postvittana*, and *Copidosoma koehleri* (Encyrtidae) and its host *Phthorimaea operculella*. The parasitoids and hosts in the three systems exhibited differential responses to the nectar sources. The differential response was not explained by morphology, demonstrating that physical access to nectaries alone does not determine the potential of flowers as a food source. For some flowering plants, enhancement of herbivore and parasitoid fitness occurred. Other flowering plants, such as buckwheat and phacelia, conferred a selective enhancement on parasitoids by increasing only their fitness. More effective conservation biocontrol may be achieved by the provision of selective floral resources. Attempts to 'engineer' agroecosystems to enhance biological control require an extensive knowledge of the ecology of the herbivore, its enemies and their interactions with potential resource subsidies.

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*Corresponding author. Instituto de Biología Vegetal y Biotecnología, Universidad de Talca, 2 Norte 685, Casilla 747, Talca, Chile. Tel.: +56 71 200277; fax: +56 71 200276.

E-mail address: blavandero@utalca.cl (B. Lavandero I.).

Zusammenfassung

Die Unterstützung durch Blütenressourcen kann andere Auswirkungen auf Insektenherbivore im Vergleich zu den natürlichen Feinden der Herbivoren haben. Während der Nektar vieler Pflanzenarten die Parasitoidenfitness fördert, könnte er ebenso den Schaden durch Herbivore erhöhen. Dies kann als Ergebnis einer verbesserten Herbivorenfitness auftreten oder durch die Förderung eines Prozesses auf vier trophischen Ebenen, der möglicherweise im Ergebnis eine trophische Kaskade unterbricht. Die Reaktionen verschiedener Arthropodengilden auf unterschiedliche **Blütenressourcen** wurden bei *Plutella xylostella* (Hyponomeutidae) und ihrem Parasitoiden *Diadegma semiclausum* (Ichneumonidae) sowie anhand von Daten zu zwei anderen publizierten Herbivor-Parasitoid-Systemen verglichen. Diese waren *Dolichogenidea tasmanica* (Braconidae) und ihr Wirt *Epiphyas postvittana* und *Copidosoma koehleri* (Encyrtidae) und ihr Wirt *Phthorimaea operculella*. Die Parasitoide und Wirte der drei Systeme zeigten unterschiedliche Reaktionen auf die Nektarquellen. Die unterschiedlichen Reaktionen wurden nicht durch die Morphologie erklärt und demonstrierten dadurch, dass der physische Zugang zu den Nektarien allein nicht das Potenzial der Blüten als Nahrungsquelle bestimmt. Bei einigen Blütenpflanzen fand eine Förderung der Herbivoren- und Parasitoidenfitness statt. Andere blühende Pflanzen wie *Phacelia* und Buchweizen verursachten eine selektive Förderung der Parasitoiden, indem nur ihre Fitness erhöht wurde. Eine effektivere biologische Kontrolle könnte erreicht werden, indem selektiv Blütenressourcen zur Verfügung gestellt werden. Die Versuche, Agrarökosysteme zu „bauen“ um die biologische Kontrolle zu fördern, benötigen ein umfangreiches Wissen über die Ökologie der Herbivoren, ihre Feinde und ihre Interaktionen mit potenziellen Ressourcen.

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Introduction

Increasing biodiversity in agro-ecosystems can result in a hierarchy of benefits for pest management (Gurr, Wratten, & Luna, 2003). In particular, the provision of floral 'resource subsidies' for predators and parasitoids (Gurr, Wratten, Tylianakis, Kean, & Keller, 2005; Tylianakis, Didham, & Wratten, 2004) can enhance natural-enemy effectiveness through aggregation, sex-ratio changes, increases in longevity, fecundity, parasitism rates and ultimately reduced pest populations (Wratten et al., 2002). However, although a wide range of flowering plants has been used for this purpose in agro-ecosystems, there has been relatively little research into the selection of the most appropriate plant species to employ (Gurr, Wratten, & Altieri, 2004; Landis, Wratten, & Gurr, 2000). Different plant species can have different effects on herbivores compared with their natural enemies, and while many enhance parasitoid activity, they may also increase rates of herbivory. This may occur as a result of enhanced fitness of the herbivore, by enhancing fourth-trophic-level processes (Stephens, France, Wratten, & Frampton, 1998) or by 'masking of host-induced plant odors' (Tahvanianen & Root, 1972) acting on the parasitoids (Price, 1981). This is the masking of odours (that the

parasitoids use to find hosts) by associated plant odours (Price, 1981), such as those which may be produced by the added floral resources.

It follows that more effective enhancement of natural-enemy effectiveness in biocontrol programmes may be achieved by the provision of selective floral resources. These can enhance natural-enemy efficacy without increasing the density or activity of the herbivore (Baggen, Gurr, & Meats, 1999). For example, if flowering plant species enhance herbivore fitness, then any effect of floral subsidies on the natural-enemy population of the herbivore population could be masked or decreased (e.g. Baggen, Gurr, and Meats, 2000). Historically, plant species to be used as subsidies have been selected on the basis of their potential to improve the effectiveness of natural enemies (Baggen & Gurr, 1998; Hickman & Wratten, 1996; Jervis, Kidd, Fitton, Huddleston, & Dawah, 1993; Tooker & Hanks, 2000; Wratten, 1992). Usually, little account is taken of possible unintended enhancement of herbivore populations when floral resource subsidies are used inappropriately (Berndt, Wratten, & Hassan, 2002; Landis et al., 2000; White, Wratten, Berry, & Weigmann, 1995).

The success of 'classical' biological control of arthropods by arthropods has not improved for more than 100 years (Gurr, Wratten, & Barbosa,

2000), and the general lack of attention to ecological needs of the biological control agent is likely to have contributed to this low success rate. Understanding the role of resource subsidies in enhancing the fitness and efficacy of natural enemies can improve this situation, as well as testing a key element in conservation biological control (see Landis et al., 2000).

The responses to different floral resource subsidies of *Plutella xylostella* (L.) and its parasitoid *Diadegma semiclausum* (Helen) are tested experimentally here, and are compared with published data for *Dolichogenidea tasmanica* and *Copidosoma koehleri*.

The aim is to explore how selective floral subsidies can affect parasitoid species, without affecting the fitness of their hosts.

Materials and methods

Adults of *Plutella xylostella* were collected from fields around Christchurch, New Zealand, and 50 pairs were transferred to acrylic cages (70 × 70 × 70 cm), each with a nylon mesh door. Broccoli plants (*Brassica oleracea* L. var. *italica*) in 1.5 l pots were offered as hosts for egg laying and as food for the larvae. Cages were placed in a controlled environment room at 23 °C (± 2 °C) and a 16/8 h day/night cycle.

Diadegma semiclausum adult parasitoids were obtained from an existing culture and were kept in cages consisting of an acrylic cylinder (30 × 20 cm). Cages had side ventilation holes of 4 cm in diameter covered with fine mesh and a feeder containing 10% solution of honey and water. A total of 20–25 pairs of *Diadegma semiclausum* were placed in each cage. Undiluted honey was also provided as a food source on the inner roof of the cages, and was replaced weekly. Parasitized host larvae were reared until pupation and checked every 2–3 days to ensure that there was sufficient leaf material for the larvae. *Diadegma semiclausum* cocoons were collected 2 days after pupation, to ensure that they were robust enough for handling (G.M. Walker, pers. comm.).

Parasitoid longevity

The longevity of *Diadegma semiclausum* was assessed in the following five treatments: flowering plants of phacelia (*Phacelia tanacetifolia* Bentham (Hydrophyllaceae)), buckwheat (*Fagopyrum esculentum* Moench (Polygonaceae)), alyssum

(*Lobularia maritima* (L.) Desv. (Brassicaceae)), diluted honey (10% v/v) or water.

Each experimental unit consisted of a small cylindrical acetate container (20 × 9 cm) enclosing one flowering shoot of a potted plant. Containers were attached to the plant shoot using wooden rods fastened with elastic bands, and the rods were inserted into the soil of each plant pot. Containers had a mesh top and a foam plug at the bottom that had a 4 cm slit to introduce the plant shoots. A small hole, plugged with foam, was cut in the side of the container to allow introduction of insects. For the non-flower treatments, diluted honey (10% v/v) or water were provided using a 100 ml plastic vial with a cotton wick protruding through a 1 cm hole in the cap. The vials were filled with the honey solution or water and placed inside the same type of containers as with the flowers. Plants, water and diluted honey were changed every 3 days.

A newly emerged female and male of *Diadegma semiclausum* were introduced to each container with six replicates of each treatment in a controlled environment room (see above). Containers were checked daily for survival under the different treatments.

Parasitoid fecundity

To determine the effect of different food resources on the egg load of *Diadegma semiclausum*, newly emerged females were offered buckwheat, phacelia, diluted honey (10% v/v) or water inside containers (see above). Following these treatments, 60 females were dissected 6, 12, 24, 48 and 72 h after emergence to assess potential fecundity. Randomly selected females from the different treatments were anesthetized for easier manipulation. The ovipositor was pulled with fine forceps and the abdominal contents were spread over a microscope slide. Acetocarmine (0.5 g carmine boiled in 100 g of 45% acetic acid for 3 min) was used to stain the mature eggs, which were then counted under a compound microscope (40 ×).

Herbivore longevity and fecundity

Longevity and fecundity of *Plutella xylostella* were measured in response to the same treatments as above. Other methods were also similar, except that within containers, a broccoli leaf disc (4 cm diameter) was placed on top of moist cotton wool, and one male and one female *Plutella*

xylostella were placed inside. Every 2 days the number of eggs laid on the disc was counted under a binocular microscope ($40\times$) and the leaf disc was replaced. Water, diluted honey and flower shoots were replaced every 3 days. Longevity and lifetime fecundity were recorded with five replicates.

Statistical analysis

Survival analysis was used to compare the effect of the food resources on the longevity of parasitoid and herbivore. The Kaplan–Meier estimate of the survival function was determined and survival curves for treatments were compared using Cox’s Proportional Hazard Model (Afifi & Clark, 1990; Hosmer & Lemeshow, 1999). For potential fecundity, the data for egg number were analysed using a generalized linear model routine and the significances of the main effects and interactions determined. The mean total number of eggs laid by *Plutella xylostella* in different treatments was analysed with one-way ANOVA, after checking for normality and homogeneity of variances. All analyses were performed using SAS (version 6.11).

Results

Enhanced fitness of the parasitoids

Survival curves differed significantly between treatments (log-rank $p = 0.0001$; Wilcoxon $p = 0.0001$), but there was no statistical difference in longevity between the sexes of *Diadegma semiclausum* in response to different treatments (log-rank $p = 0.3007$; Wilcoxon $p = 0.2654$). The mean longevity of *Diadegma semiclausum* was highest when the parasitoid was provided with buckwheat flowers (28.0 ± 3.18 days) and with honey solution (20.6 ± 2.40) compared with only 1.9 ± 0.14 days with water (Fig. 1A). Paired comparisons between buckwheat and each of the other treatments using Cox’s Regression Model showed that only the honey treatment enhanced longevity of *Diadegma semiclausum* as much as did buckwheat. Nevertheless, longevity of individuals fed with phacelia was significantly greater than for those fed with water ($p = 0.001$) or those fed on alyssum ($p = 0.001$) (Fig. 1A).

There were highly significant effects of treatment (deviance = 349.9, $df = 4$, $p = 0.001$), time since emergence (deviance = 43.7, $df = 2$, $p = 0.001$) and their interaction (deviance = 38.7,

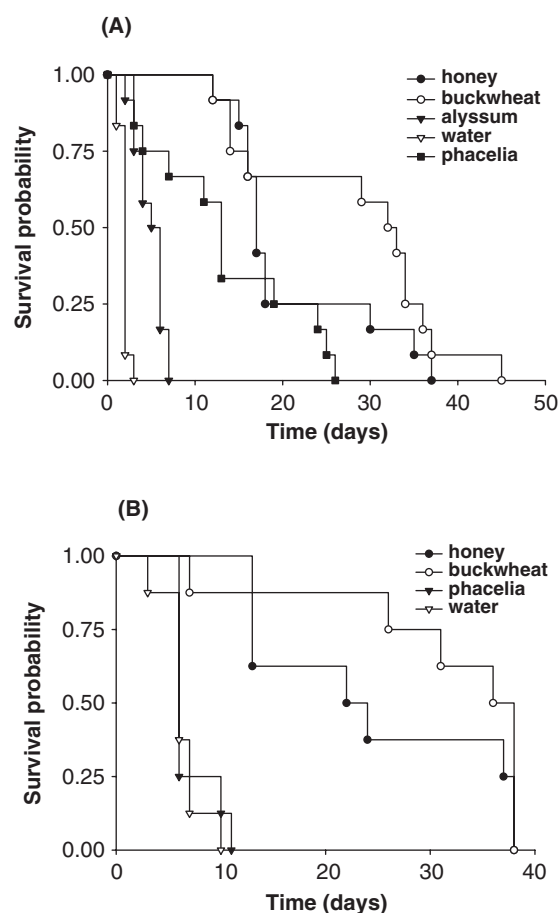


Figure 1. Kaplan–Meier estimates of the survivorship functions of *Diadegma semiclausum* (A) and *Plutella xylostella* (B) under different treatments.

$df = 8$, $p = 0.001$) on the number of eggs in *Diadegma semiclausum* females. There were significantly more mature eggs in the honey, buckwheat and phacelia treatments compared with water (Fig. 2A). The maximum number of mature eggs was significantly highest at 72 h after adult eclosion, for all treatments.

Enhanced fitness of the herbivores

Buckwheat significantly enhanced *Plutella xylostella* longevity ($p = 0.0009$) but phacelia did not (Fig. 1B). No floral treatment affected the fecundity of the moth ($df = 3$; $F = 1.3323$; $p = 0.3176$) (Fig. 2B). Since 90% of the eggs laid in all treatments had been laid after 4 days (Lavandero, unpublished data), an increased longevity caused by buckwheat would, compared to the parasitoid, benefit the herbivores populations less. Similar findings were reported by

Pivinick, Jarvis, Gillott, Slater, and Underhill (1990), although they found that adults continue laying eggs until day 10.

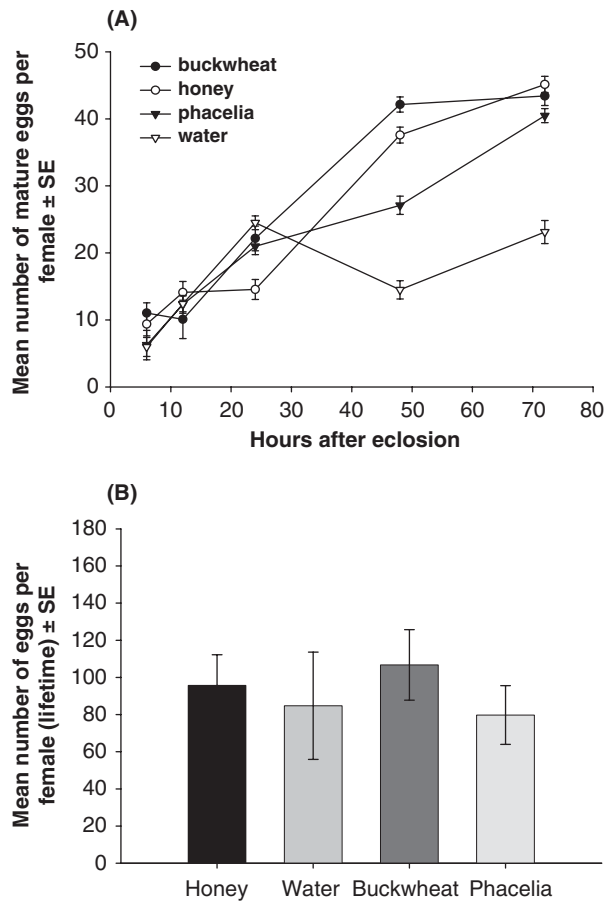


Figure 2. Mean number of mature eggs per female \pm SE of *Diadegma semiclausum* (A) and *Plutella xylostella* (B) under different treatments.

Discussion

Selective resource subsidies

The ability of parasitoids to utilize floral resource subsidies is dependent on a wide range of factors, including flower morphology, colour, odour, timing of nectar production, parasitoid mouthpart size and structure and the parasitoids' ability to locate flowers in the field (Heimpel & Jervis, in press). To meet the nutritional requirements of the parasitoid and ultimately have an impact on the herbivore population, careful selection of the flowering species for use in the field must be made. There can be negative impacts of poor management decisions in the field, such as herbivore population enhancement (Baggen & Gurr, 1998; Zhao, Ayers, Grafius, & Stehr, 1992) or fourth-trophic-level effects (Stephens et al., 1998), from the planting of inappropriate resource subsidies. In the present study, it is clear that different plants can have different impacts on the fitness of parasitoids and their host (see Table 1).

The parasitoids

The data presented here on *Diadegma semiclausum* suggest that buckwheat and phacelia could be potentially useful plants for enhancing fecundity (parasitism rates) of the parasitoid (Fig. 2A). Survival time can also play an important role, as this species is synovigenic (it matures eggs during its lifetime (see Jervis, Heimpel, Ferns, Harvey, & Kidd, 2001); so females that can live longer will mature more eggs. *Diadegma semiclausum* provided with diluted honey in the laboratory could parasitize 117 ± 10 *Plutella xylostella* larvae during its lifetime (24.7 ± 2.2 days) (Ooi, 1980; Yang, Chu,

Table 1. Effect of different floral nectar sources on parasitoid and host fitness

Flower	Parasitoid	Effect	Herbivore	Effect
Buckwheat	<i>D. semiclausum</i>	++	<i>P. xylostella</i>	0
Alyssum	<i>D. semiclausum</i>	0	<i>P. xylostella</i>	—
Phacelia*	<i>D. semiclausum</i>	+	<i>P. xylostella</i>	*
Buckwheat	<i>C. koehleri</i>	+*	<i>P. operculella</i>	++*
Alyssum	<i>C. koehleri</i>	—	<i>P. operculella</i>	—
Phacelia*	<i>C. koehleri</i>	+*	<i>P. operculella</i>	0*
Buckwheat	<i>Do. tasmanica</i>	++ [†]	<i>E. postvittana</i>	—
Alyssum	<i>Do. tasmanica</i>	+ [†]	<i>E. postvittana</i>	++ [†]
Phacelia	<i>Do. tasmanica</i>	0 [†]	<i>E. postvittana</i>	—

++: high; +: medium; *: low; 0: no effect, —: not tested.

*From Baggen and Gurr (1998).

[†]From Irvin et al. (unpublished).

& Talekar, 1993). Fecundity without any resource subsidies is markedly shorter, with a life span of only 1–3 days (Fig. 1A). As with *Diadegma semiclausum*, the longevity of *Dolichogenidea tasmanica* increased when it had fed on buckwheat but in contrast with the former, alyssum also enhanced its longevity (Irvin, Wratten, Frampton, Chapman, & Tylanakis, unpublished) (Table 1). *C. koehlerii* benefited from buckwheat and phacelia, compared with a control without flowers (Baggen et al., 1999) (Table 1).

The hosts

When presented to adult *Epiphyas postvittana*, a host of *Dolichogenidea tasmanica*, alyssum flowers enhanced fitness significantly compared with no flowers (Irvin et al., unpublished). In contrast, *Phthorimaea operculella*, a host of *C. koehlerii*, when provided with phacelia did not increase fitness, but buckwheat did (Baggen et al., 1999) (Table 1). Similarly, *Plutella xylostella* appeared not to be able to lay more eggs with food. Moreover, under natural conditions moths are likely to spend more time on energy costly behaviour as compared to laboratory conditions. This may considerably reduce lifespan and realized fecundity of food-deprived moths in the field. Therefore, any effects of these resource subsidies on longevity as found under the experimental conditions (see Figs. 1B and 2B) would have less impact on populations of this herbivore as compared to the benefits to the parasitoid. This is supported also in part by the fact that when buckwheat was deployed in the field, there was a marked effect on the parasitoids abundance and *Plutella xylostella* parasitism rates (Lavandero, Wratten, Shishebor, & Worner, 2005).

Potential mechanisms of selectivity

Diadegma semiclausum was able to use nectar from phacelia whereas *Dolichogenidea tasmanica* could not (Irvin et al., unpublished). When the latter species has access only to water, it had a higher mean longevity (10.9 ± 1.51 days compared with 5.9 ± 0.50 days with phacelia), reflecting the fact that *Dolichogenidea tasmanica* could not feed on phacelia nectar. Similar to *Diadegma semiclausum*, *C. koehlerii* was able to use nectar from this plant, which enhanced its longevity significantly compared to a control without flowers (Baggen et al., 1999). Flowers of the Hydrophyllaceae, such as phacelia, have stamen appendages that limit access to the nectaries by some insects. In addition, the style has upward-projecting hairs that could also limit access by some larger insects, such as adult moths, despite their long probosces. Access to these nectaries for *Diadegma semiclausum*, *Dolichogenidea tasmanica* and *C. koehlerii* would also be limited by the size of the gaps between the appendages, which are smaller than the head widths of all three parasitoids (Table 2). *Diadegma semiclausum* and *C. koehlerii* do not have any special mouthparts for reaching floral nectaries, as some agathidine braconids do (Quicke, 1997). Then nectar probably becomes available to the parasitoids compared here by capillary action, most likely via grooves on the upper surface of the stamen appendages, an effect described for phacelia (Baggen et al., 1999) and for cardamom flowers (*Elettaria cardamomum*) (Belevadi, Venkateshalu, & Vivek, 1997). However, this would still not explain why *Dolichogenidea tasmanica* does not use the nectar of phacelia, given that this plant is considered to be an important source (Crane, Walker, & Day, 1984; Williams & Christian, 1991).

Table 2. Parasitoid ability to use floral resources in relation to their head width and floral corolla aperture

Species	Head width (mm)	Flower	Corolla aperture (mm)	Feeding occurrence (\pm)
<i>D. semiclausum</i>	0.92 ± 0.030	Buckwheat	$6.59 \pm 0.23^*$	+
		Alyssum	1.84 ± 0.08	—
		Phacelia*	$0.15 \pm 0.01^{*,\dagger}$	+
<i>C. koehlerii</i>	$0.43 \pm 0.004^*$	Buckwheat	$6.59 \pm 0.23^*$	+*
		Alyssum	1.84 ± 0.08	Not tested
		Phacelia*	$0.15 \pm 0.01^{*,\dagger}$	+*
<i>Do. tasmanica</i>	0.65 ± 0.020	Buckwheat	$6.59 \pm 0.23^*$	+‡
		Alyssum	1.84 ± 0.08	+‡
		Phacelia	$0.15 \pm 0.01^{*,\dagger}$	—‡

*From Baggen and Gurr (1998).

†Diameter of gaps between phacelia stamen appendages.

‡From Irvin et al. (unpublished).

Other aspects of flowers such as colour, pattern and odour could attract or repel different species (Mahmuda, Gurr, Wratten, & Nicol, 2004; Wäckers, 2004; Waser & Price, 1981) or interfere with attractive chemicals used by the parasitoids to find hosts (Price, 1981). It seems surprising, though, that *Dolichogenidea tasmanica* would starve to death because it is not attracted to phacelia, even though it could have access to nectar by capillary action. There is some evidence that a parasitoid could be repelled by a plant's chemistry, a phenomenon that has been observed for some plant species when presented to parasitoid wasps in choice experiments (Wäckers, 2004). This demonstrates that physical access to nectaries alone does not determine the potential of flowers as a food source.

Prospects for selectivity in practice

For *Diadegma semiclausum* the best choice would be buckwheat, because it can enhance the parasitoids' longevity and fecundity, with no effect on the herbivore's fitness. Certainly the literature shows both local (Tylianakis et al., 2004) and landscape enhancement of insect fitness (Westphal, Steffan-Dewenter, & Tschardtke, 2003) following provision of flowers, but the present work is laboratory-based, so field work is needed to test this idea further.

The fact that adult herbivores also benefit from flowers has frequently been demonstrated. For example, Irvin et al. (unpublished) showed that *E. postvittana* had increased longevity and egg production in the presence of alyssum (Table 1). A similar enhancement of the herbivore was recorded by Baggen and Gurr (1998) when *Phthorimaea operculella* fed on coriander (*Coriander sativum*) and broad bean (*Vicia faba*), highlighting the need for experiments such as those in the present study to identify plant species that strongly favour natural enemies rather than their hosts.

Most work concerning the application of resource subsidies to biological control has not considered the importance of parasitoid/host selectivity. Also, apart from Stephens et al. (1998), no study has determined the effect of selected plants on the fourth trophic level (hyperparasitoids or predators of predators and parasitoids). More effective conservation biocontrol may be achieved by the provision of selective floral resources, and will help the understanding of the ecological processes involved in increasing biodiversity at the field level (Thies & Tschardtke, 1999; Tylianakis et al. 2004; Westphal et al., 2003).

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References

- Affi, A. A., & Clark, V. (1990). *Computer-aided multivariate analysis* (2nd ed.). New York, London: Chapman & Hall.
- Baggen, L. R., & Gurr, G. M. (1998). The influence of food on *Copidosoma koehleri* (Hymenoptera: Encyrtidae), and the use of flowering plants as a habitat management tool to enhance biological control of potato moth, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). *Biological Control*, 11, 9–17.
- Baggen, L. R., Gurr, G. M., & Meats, A. (1999). Flowers in tri-trophic systems: Mechanisms allowing selective exploitation by insect natural enemies for conservation biological control. *Entomologia Experimentalis et Applicata*, 91, 155–161.
- Baggen, L. R., Gurr, G. M., & Meats, A. (2000). Field observations on selective food plants in habitat manipulation for biological control of potato moth by *Copidosoma koehleri* Blanchard (Hymenoptera: Encyrtidae). In A. D. Austin, & M. Dowton (Eds.), *Hymenoptera: Evolution, biodiversity and biological control* (pp. 388–395). CSIRO.
- Belevadi, V., Venkateshalu, V., & Vivek, H. R. (1997). Significance of style in cardamom corolla tubes for honey bees. *Current Science*, 73, 287–290.
- Berndt, L. A., Wratten, S. D., & Hassan, P. G. (2002). Effects of buckwheat flowers on leafroller (Lepidoptera: Tortricidae) parasitoids in a New Zealand vineyard. *Agricultural and Forest Entomology*, 4, 39–45.
- Crane, E., Walker, P., & Day, R. (1984). *Directory of important world honey sources*. Gerard Cross, UK: International Bee Research Association.
- Gurr, G., Wratten, S. D., & Barbosa, P. (2000). Success in conservation biological control of arthropods. In G. Gurr, & S. D. Wratten (Eds.), *Biological control: Measures of success* (pp. 105–132). Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Gurr, G. M., Wratten, S. D., & Altieri, M. A. (2004). *Ecological engineering for pest management: Advances in habitat manipulation for arthropods*. Australia: CSIRO Publishing.
- Gurr, G. M., Wratten, S. D., & Luna, J. M. (2003). Multi-function agricultural biodiversity: Pest management and other benefits. *Basic and Applied Ecology*, 4, 107–116.
- Gurr, G. M., Wratten, S. D., Tylianakis, J., Kean, J., & Keller, M. (2005). Providing plant foods for insect

- natural enemies in farming systems: Balancing practicalities and theory. In F. L. Wackers, P. van Rijn, & J. Bruin (Eds.), *Plant-derived food and plant–carnivore mutualism* (pp. 326–347). Cambridge: Cambridge University Press.
- Heimpel, G. H., & Jervis, M. A. (in press). An evaluation of the hypothesis that floral nectar improves biological control by parasitoids. In F. Wackers, P. van Rijn, & J. Bruin (Eds.), *Plant-provided food and plant–carnivore mutualism*. Cambridge: Cambridge University Press.
- Hickman, J. M., & Wratten, S. D. (1996). Use of *Phacelia tanacetifolia* flower strips to enhance biological control of aphids by hoverfly larvae in cereal fields. *Journal of Economic Entomology*, *89*, 832–840.
- Hosmer, D. W., & Lemeshow, S. (1999). *Applied survival analysis: Regression modeling of time to event data*. New York: Wiley.
- Irvin, N. A., Wratten, S. D., Frampton, C. M., Chapman, R. B., & Tyljanakis, J. M. (unpublished). The effects of floral understoreys on parasitism of leafrollers (Tortricidae: Lepidoptera) on apples in New Zealand. *Agricultural and Forest Entomology*.
- Jervis, M. A., Heimpel, G. E., Ferns, P. N., Harvey, J. A., & Kidd, N. A. (2001). Life-history strategies in parasitoid wasps: A comparative analysis of “ovogeny”. *Journal of Animal Ecology*, *70*, 442–458.
- Jervis, M. A., Kidd, N. A. C., Fitton, M. G., Huddleston, T., & Dawah, H. A. (1993). Flower-visiting by hymenopteran parasitoids. *Journal of Natural History*, *27*, 67–105.
- Landis, D. A., Wratten, S. D., & Gurr, G. M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, *45*, 175–201.
- Lavandero, B., Wratten, S., Shishehbor, P., & Worner, S. (2005). Enhancing the effectiveness of the parasitoid *Diadegma semiclausum* (Helen): Movement after use of nectar in the field. *Biological Control*, *34*, 152–158.
- Mahmuda, B., Gurr, G. M., Wratten, S. D., & Nicol, H. I. (2004). Flower color affects tri-trophic-level biocontrol interactions. *Biological Control*, *30*, 584–590.
- Ooi, P. A. C. (1980). Laboratory studies of *Diadegma cerophagus* (Hym: Ichneumonidae), a parasite introduced to control *Plutella xylostella* (Lep: Hyponomeutidae) in Malaysia. *Entomophaga*, *25*, 249–259.
- Pivinick, K., Jarvis, B., Gillott, C., Slater, G., & Underhill, E. (1990). Daily patterns of reproductive activity and the influence of adult density and exposure to host plants on reproduction in the diamondback moth (Lepidoptera: Plutellidae). *Environmental Entomology*, *19*, 587–593.
- Price, P. W. (1981). Semiochemicals in evolutionary time. In D. A. Nordlund, R. L. Jones, & W. J. Lewis (Eds.), *Semiochemicals: Their role in pest control* (pp. 251–279). New York, USA: Wiley.
- Quicke, D. L. J. (1997). *Parasitic wasps*. New York, London: Chapman & Hall.
- Stephens, M. J., France, C. M., Wratten, S. D., & Frampton, C. M. (1998). Enhancing biological control of leafrollers (Lepidoptera: Tortricidae) by sowing buckwheat (*Fagopyrum esculentum*) in an orchard. *Biocontrol Science and Technology*, *8*, 547–558.
- Tahvanianen, J. O., & Root, R. B. (1972). The influence of vegetational diversity on the population ecology of the specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia*, *10*, 321–346.
- Thies, C., & Tschardtke, T. (1999). Landscape structure and biological control in agroecosystems. *Science*, *285*, 893–895.
- Tooker, J. F., & Hanks, L. M. (2000). Flowering plant hosts of adult Hymenopteran parasitoids of central Illinois. *Annals of the Entomological Society of America*, *93*, 550–588.
- Tyljanakis, J. M., Didham, R. K., & Wratten, S. D. (2004). Improved fitness of aphid parasitoids receiving resource subsidies. *Ecology*, *85*, 658–666.
- Wäckers, F. (2004). Assessing the suitability of flowering herbs as parasitoid food sources: Flower attractiveness and nectar accessibility. *Biological Control*, *29*, 307–314.
- Waser, N. M., & Price, M. V. (1981). Pollinator choice and stabilizing selection for flower color in *Delphinium nelsonii*. *Evolution*, *35*, 376–390.
- Westphal, C., Steffan-Dewenter, I., & Tschardtke, T. (2003). Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, *6*, 961–965.
- White, A. J., Wratten, S. D., Berry, N. A., & Weigmann, U. (1995). Habitat manipulation to enhance biological control of *Brassica* pests by hover flies (Diptera: Syrphidae). *Journal of Economic Entomology*, *88*, 1171–1176.
- Williams, I. H., & Christian, D. G. (1991). Observations on *Phacelia tanacetifolia* Benth (Hydrophyllaceae) as a food plant for honey bees and bumble bees. *Journal of Apicultural Research*, *30*, 3–12.
- Wratten, S. D. (1992). Weeding out the cereal killers. *New Scientist*, *1835*, 31–35.
- Wratten, S. D., Berndt, L., Gurr, G., Tyljanakis, J., Fernando, P., & Didham, R. (2002). Adding floral diversity to enhance parasitoid fitness and efficacy. In Proceedings of the first international symposium on biological control of arthropods, Honolulu, Hawaii.
- Yang, J., Chu, Y., & Talekar, N. S. (1993). Biological studies of *Diadegma semiclausum* (Hym: Ichneumonidae), a parasite of diamondback moth. *Entomophaga*, *38*, 579–586.
- Zhao, J. Z., Ayers, G. S., Grafius, E. J., & Stehr, W. (1992). Effects of neighboring nectar-producing plants on populations of pest Lepidoptera and their parasitoids in broccoli plantings. *The Great Lakes Entomologist*, *25*, 253–258.