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Using selective food plants to maximize biological control of vineyard pests

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Summary

1. Habitat manipulation is important for enhancing biological control of arthropod pests, but identification of selective food plants that benefit only natural enemies is required in order to avoid inadvertently exacerbating pest damage.
2. Greenhouse experiments were conducted to identify potential ground-cover plant species that would improve performance of the egg parasitoid *Trichogramma carverae* when mass released in vineyards to control the leafroller pest *Epiphyas postvittana.* Further experiments determined which plants increased immature survival and adult longevity of *E. postvittana* and a field experiment investigated field enhancement of biological control.
3. Greenhouse survival of *T. carverae* was greater in the presence of flowering shoots of *Lobularia maritima* than with flowering shoots of either *Brassica juncea* or *Coriandrum sativum*, or with shoots of any species from which flowers had been removed or a control with no shoots. Similar experiments with *Fagopyrum esculentum* and *Borage officinalis* showed survival was higher in the presence of shoots with flowers than in without-flower and control treatments.
4. Daily fecundity of *T. carverae* was greater in the presence of flowering shoots of *L. maritima* than *F. esculentum* and with treatments without flowers. There was no significant enhancement of fecundity with *Brassica juncea* and *Borage officinalis* flowers.
5. Adult longevity of male and female *E. postvittana* was as long in the presence of *Borage officinalis* and *F. esculentum* flowers as when fed a honey-based artificial diet but longevity was significantly lower than in the artificial diet treatment when caged with *C. sativum* and *L. maritima*, irrespective of whether flowers were present or not.
6. Larval development of *E. postvittana* on intact potted plants was lower on *C. sativum* and *L. maritima* than on *Brassica juncea*, *Borage officinalis*, *F. esculentum* and *Trifolium repens* (a known host of *E. postvittana*).
7. In the first and second 48-h periods after release of *T. carverae* in a field experiment, parasitism was significantly higher in pooled treatments with flowers (*C. sativum*, *F. esculentum* and *L. maritima*) than in pooled treatments without flowers (conventional ground-cover or bare earth).
8. *Lobularia maritima* provided clear benefit to *T. carverae* but was not used by adult and larval *E. postvittana.*
9. *Synthesis and applications. Lobularia maritima* is recommended as the selective food plant best suited to this system and its use beneath vines offers the additional advantage of suppressing weeds, so avoiding the need for herbicide applications and mechanical control.

Key-words: conservation biological control, *Epiphyas postvittana*, fecundity, longevity, nectar, parasitoid, *Trichogramma carverae*

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Introduction

Research in a variety of agro-ecosystems has shown that many adult parasitoids use nectar and/or pollen as a food and this is an important consideration for biological control (Landis, Wratten & Gurr 2000; Lee & Heimpel 2004; Heimpel & Jervis 2005). Carbohydrate-rich nectar is a source of energy, whereas pollen is a nutrient source for egg production in some parasitoids, and such adult food increases the longevity and fecundity of parasitoids (Jervis, Lee & Heimpel 2004; Lee, Heimpel & Leibee 2004). Availability of floral resources is often poor in modern agricultural systems and this has focused attention on ways in which habitat manipulation can provide resource subsidies for natural enemies (Gurr, Wratten & Altieri 2004). For example, coriander *Coriandrum sativum* L., buckwheat *Fagopyrum esculentum* Moench and borage *Borago officinalis* L. increased the parasitism rate of the potato moth *Phthorimaea operculella* (Zeller) by *Copidosoma koehleri* Blanchard (Baggen & Gurr 1998; Baggen, Gurr & Meats 1999). Importantly, however, only borage was not fed upon by the pest and this demonstrated the importance of identifying 'selective food plants' for use in habitat manipulation.

The lightbrown apple moth *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) is a serious insect pest of Australian and New Zealand grapevines (Glenn & Hoffmann 1997). In Australia, the endemic parasitoid *Trichogramma carverae* Oatman and Pinto (Hymenoptera: Trichogrammatidae) is inundatively released to augment natural populations in vineyards (Glenn & Hoffmann 1997) but this is expensive and the short longevity of the adults demands precise monitoring of the host population to ensure that releases coincide with the peak in host-egg availability.

Provision of appropriate adult food offers scope to increase the impact of a given release of *T. carverae* on *E. postvittana* through maximizing fecundity and longevity. Gurr & Nicol (2000) demonstrated that adult survival was increased in the laboratory by a honey diet, while more recent laboratory work with a range of plant species has demonstrated that nectar benefited *T. carverae* (Begum *et al*. 2004a,b). The highly polyphagous nature of *E. postvittana* larvae (Danthanarayana 1975; Suckling *et al*. 1998), however, demands an extension of the Baggen & Gurr (1998) notion of screening to identify selective food plants. Feeding by *E. postvittana* larvae on foliage as well as adult feeding on nectar may render a plant species unsuitable for enhancement of *T. carverae*. Many adult Lepidoptera feed on floral nectar (Kevan & Baker 1984) and *E. postvittana* is known to benefit from honey (Gu & Danthanarayana 1990).

Accordingly, the primary objective of this study was to investigate the effect of candidate ground-cover plant species on activity of adult *T. carverae* to identify the plants that maximize its impact as a biological control agent. The secondary objective of this study was to investigate whether these ground-cover plant species would provide any benefit to adults or larvae of *E. postvittana*, in order to identify selective food plants for use in habitat manipulation of vineyards. A field experiment was then conducted to measure the effect of ground-cover plant species on parasitism of *E. postvittana*.

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Methods

LONGEVITY OF *T. CARVERAE*

Plants of alyssum *Lobularia maritima* L. (Cruciferae; cv. Small White Flower), borage *Borago officinalis* L. (Borginaceae; cv. Borage), buckwheat *Fagopyrum esculentum* Moench (Polygonaceae; cv. Ikeda), coriander *Coriandrum sativum* L. (Umbelliferae; cv. Macrocarpum) and mustard *Brassica juncea* (L.) Czernj. (Brassicaceae; cv. Peacock Tail) were grown from seed in a greenhouse. All have agronomic compatibility with vineyard conditions. *Trichogramma carverae* was obtained from a commercial supplier as produced capsules containing paper substrate bearing *Sitotroga cerealella* Oliver eggs parasitized by *T. carverae* (Bugs for Bugs, Bio Resources Pty Ltd, Mundubbera, Australia).

Because plants did not bloom synchronously, three experiments were conducted. In the first, a randomized block design with five replicates and seven treatments was used. The first three treatments comprised flowering shoots of *Brassica juncea*, *C. sativum* and *L. maritima.* Each flowering shoot had several buds to ensure continuous flowering throughout the experimental period. A further three treatments consisted of the above plant species from which flowers and flower buds were removed. A final control treatment with no plant material was used. The second experiment used an identical design with *F. esculentum* (with and without flowers) and a plant-free control. A third experiment used *Borage officinalis* (with and without flowers), water alone and a plant-free control.

In these experiments, plastic vials ($5{\cdot}5 \times 4{\cdot}5$ cm) contained insect and plant material. In the bottom of each vial there was a small circular hole (1 cm diameter) through which the cut end of three shoots of the designated type were passed into water contained in a second vial ($11 \times 2{\cdot}5$ cm) beneath the first. Shoots were sealed into the holes with a non-setting adhesive (Blue-Tack, Bastik Findley Australia Pty., Thomas-Town, Australia). The top of the upper vial was then sealed with a sheet of tissue paper held in place with a rubber band. Ten unsexed, adult *T. carverae* (< 24 h after eclosion) were released in each vial. All experiments were conducted on a greenhouse bench top with a 16-h light:8-h dark photoperiod, 20 °C light/16 °C dark temperature at an average relative humidity of 67% in the first experiment, 59% in the second and 47% in the third experiment. The number of live *T. carverae* in each cage was recorded every 24 h until all had died.

Data for the proportion of live insects on each day were angular transformed. Exponential curves of the form $y = A + BR^x$ (where y = number of live insects, x =

number of days, A and B = linear parameters, R = survival rate) were fitted to the data to compare the differences in position (A), slope (B) and curvature (R) for each treatment. GenStat release 6.1 (GenStat Committee 2002) was used for all data analyses.

DAILY FECUNDITY OF *T. CARVERAE*

Plants and *T. carverae* were prepared as described above. The host insect, *E. postvittana*, was reared in the laboratory on an artificial diet modified from Shorey & Hale (1965; 180 mL honey, 1800 mL water, 10·8 g (0·6%) ascorbic acid, 1·8 g (0·1%) sorbic acid, 1·8 g (0·1%) paraben and 10 mL 70% ethanol), using procedures based on Glenn & Hoffmann (1997).

Asynchronous flowering of plant species necessitated separate experiments. In the first, *F. esculentum* and *L. maritima* were tested. Two treatments used flowering shoots (as above), two treatments consisted of the above plant species from which flowers and flower buds were removed and a final control treatment used no plant materials. Treatments were replicated 10 times in a randomized block design. The second experiment used equivalent treatments for the plant species *Brassica juncea* and *Borage officinalis*.

Plastic vials (as above) held plant material and one adult *T. carverae* of each sex (< 12 h from eclosion). To measure fecundity, sentinel cards were prepared bearing *E. postvittana* eggs: 23·11 (range 6–76; half bearing 15–28) eggs in experiment 1 and 26·22 (range 6–62; half bearing 15–35) eggs in experiment 2. Sentinel cards were replaced every 24 h. In each cage, live adults were recorded every 24 h until both individuals were dead. Egg masses were subsequently incubated at 23 °C until parasitized eggs became black. They were then counted. Both experiments were established under similar greenhouse conditions to above. Humidity averaged 54% in the first experiment and 71% in the second experiment.

The number of eggs parasitized was calculated per live female. A square-root transformation $v(x + 0{\cdot}5)$ was used and exponential curves were fitted for experiment 1 but not in experiment 2 as all *T. carverae* died by the third day. Exponential curves of the form $Y = A + BR^x$ were fitted as previously described.

LONGEVITY OF ADULT *E. POSTVITTANA*

Plant materials and *E. postvittana* were sourced and established for experiments as above. A randomized block design with 10 replicates and nine treatments was used. The first four treatments used flowering shoots of *L. maritima*, *Borage officinalis*, *F. esculentum* and *C. sativum*. A further four treatments consisted of the above plant species from which flowers and flower buds were removed. A positive control comprised the previously described adult *E. postvittana* diet. Cotton wool balls were moistened with this solution and placed in each replicate and remoistened every second day using a hypodermic syringe. Plant material, and cotton wool in the control treatment, was replaced once per week. One male and one female (< 24 h after eclosion) adult *E. postvittana* were placed in each vial. The number of live individuals was recorded at 24-h intervals until all had died. The experiment took place in a greenhouse under previously described conditions and an average relative humidity of 54%.

Once flowering plants of *Brassica juncea* were available a separate experiment was conducted using *Brassica juncea* with and without flowers, the previously described artificial adult food and water alone. This experiment was conducted under the same greenhouse conditions with an average relative humidity of 60%.

Data recorded days until death for each vial and were analysed separately for each sex using a randomized block ANOVA. If the treatment F-test was significant, treatments were compared using a least significant difference (LSD) test. Data from the *Brassica juncea* experiment were analysed separately from the first experiment.

DEVELOPMENT OF LARVAL *E. POSTVITTANA*

A randomized block experimental design was used with five replicates. Each replicate consisted of a potted plant of *Brassica juncea*, *Borage officinalis*, *C. sativum*, *F. esculentum*, *L. maritima* and *Trifolium repens.* Pots were 850 mL and the plants were covered with fine nylon mesh supported by a single bamboo cane and secured around the pot's rim with rubber bands. Twenty neonate (< 24-h old) larvae of *E. postvittana* were introduced into each cage. Replicates were checked every week after the first 6 weeks and all pupae present on each occasion were collected. The experiment was conducted in a greenhouse, as above.

The numbers of pupae collected from each replicate by the end of the experiment were subject to angular transformation then analysed using ANOVA. The numbers of pupae present on each collection date were angular transformed. Exponential curves were fitted to the cumu-lative pupation data and compared as described above.

FIELD EXPERIMENT

An experiment was conducted in a cv. Chardonnay vineyard at Canowindra, New South Wales, Australia, managed under an organic system. The experiment used a randomized block design with five treatments replicated five times. Rows 5, 10, 15, 20 and 25 of the 55 in the vineyard were designated as blocks. Plots were 1·5 m long and 0·6 m wide, located beneath two vines, and each plot was separated by 20 m along the vine row.

Brassica juncea, *Borage officinalis*, *C. sativum*, *F. esculentum* and *L. maritima* seeds were sown sequentially on 9 September and 7 October 2003 beneath vine rows. In a further effort to maximize the flowering period, flowering *L. maritima* plants were transplanted into appropriate plots on 11 December 2003. *Brassica juncea* and *Borage officinalis* failed to flower during the experiment so these treatments were disregarded. Additional treatments were (i) the existing weedy vegetation without flowers and (ii) a cultivated bare earth control. A motorized brush cutter was used to remove weed flowers and unopened buds from the weeds on either side of plots and for a distance of approximately 10 m along the row from either end of each plot.

Before release of *T. carverae*, the activity of naturally occurring egg parasitoids was surveyed using three sentinel cards per plot, each bearing an *E. postvittana* egg mass. Cards were placed on 15 December 2003 and recovered after 24 h. One card was stapled to the vine leaves 1 m above the soil at each end of the plot. An additional card was stapled to a central vine leaf 1·5 m above the soil. The mean number of eggs per card was 49·68 (range 18–86; half bearing 38–57). Recovered egg cards were kept in individual sealed plastic bags in an incubator at 23 °C to check for parasitism.

On 16 December 2003, after 1 day of incubation at 26 °C, *T. carverae* were starting to emerge in an 'indicator vial' prepared by the supplier such that adult eclosion occurred approximately 24 h before the adults in the rest of the consignment. All capsules were then taken out of the incubator and kept for 3 h at room temperature in preparation for placement in the field. Four capsules were placed in each plot. Two were mounted with wire on a bamboo cane pushed into the soil in the middle of the plot so that capsules were 0·3 m above the soil surface. Two additional capsules were stapled on to the vine leaves 1·5 m above the soil. A single, additional capsule was positioned in row 15, enclosed in a ventilated glass vial, so that timing of adult emergence from the other capsules could be assessed.

Sentinel cards (as described above) were stapled on the upper surface of the vine leaves in each plot on 16 December 2003. The mean number of eggs per card was 34·39 (range 13–85; with half bearing 25–41 eggs). After 48 h, sentinel cards were recovered from the field and remaining eggs counted under a binocular dissecting microscope (10×) to determine predation rates. Each card was then placed in a small, sealed plastic bag in an incubator at 23 °C until parasitized eggs became black, and were then counted. On 18 December, a fresh batch of sentinel egg card was placed in the field. These cards were replaced on 20 December, giving three successive 48-h monitoring periods. Recovered cards were handled as above.

A rain gauge and temperature logger (GLM, Version 2.8, Gemini Data Loggers, Chichester, UK) were placed in the field to record meteorological data. To monitor the activity of wild *E. postvittana*, a single-sex pheromone trap was placed in the vineyard, 20 m from the nearest point of the experiment.

The numbers of eggs parasitized and predated were calculated per plot. The number of eggs per plot was used as a covariate and found to be non-significant and then excluded. Predation and parasitism data were analysed using randomized block ANOVA. The treatment effect was partitioned, with one degree of freedom allocated to the difference between treatments with flowers and treatments without flowers and three degrees of freedom allocated to differences within these two groups.

Results

LONGEVITY OF *T. CARVERAE*

In the first experiment fitted exponential curves for treatments differed significantly in curvature ($F = 115{\cdot}10$, d.f. = 6, 133, $P < 0{\cdot}001$) (Fig. 1a). The daily survival rate (± SE) of *T. carverae* on intact flowers was *Brassica juncea*, 0·547 ± 0·0224, *C. sativum*, 0·592 ± 0·0203, *L. maritima*, 0·922 ± 0·0105. In treatments that used shoots only, equivalent values were 0·233 ± 0·0319, 0·247 ± 0·0317 and 0·391 ± 0·0275, respectively, and in the control treatment 0·099 ± 0·0337.

In the second experiment fitted exponential curves for treatments also differed significantly in curvature ($F = 76{\cdot}78$, d.f. = 2, 45, $P < 0{\cdot}001$) (Fig. 1b). The survival rate of *T. carverae* was significantly higher when caged with *F. esculentum* flowers (0·921 ± 0·0175) than without flowers (0·582 ± 0·0277) or in the control (0·477 ± 0·0329).

Fitted exponential curves for treatments differed significantly in curvature in the third experiment ($F = 7{\cdot}24$, d.f. = 3, 28, $P < 0{\cdot}001$) (Fig. 1c). The survival rate of *T. carverae* for the *Borage officinalis* with-flower treatment was 0·744 ± 0·0450, without-flower 0·589 ± 0·0427, water treatment 0·483 ± 0·0456 and control 0·430 ± 0·0481.

DAILY FECUNDITY OF *T. CARVERAE*

Fitted exponential curves for treatments differed significantly in position ($F = 21{\cdot}28$, d.f. = 4, 60, $P < 0{\cdot}001$) and slope ($F = 18{\cdot}97$, d.f. = 4, 60, $P < 0{\cdot}001$), indicating far greater and more sustained oviposition in the *L. maritima* treatment. Rate of change in the number of parasitized eggs differed between *L. maritima* and *F. esculentum* with- and without-flower treatments, although differences in overall curvature were non-significant ($F = 1{\cdot}41$, d.f. = 4, 60, $P = 0{\cdot}241$) (Fig. 2).

In the second experiment, which included *Brassica juncea* and *Borage officinalis*, low rates of parasitism were observed in all treatments and no parasitism was observed after day 6.

LONGEVITY OF ADULT *E. POSTVITTANA*

Female *E. postvittana* lived for between 16·4 and 18·5 days in the presence of an artificial diet and flowers of *F. esculentum* and *Borage officinalis* (Table 1). Longevity was significantly ($F = 4{\cdot}79$, d.f. = 8,72, $P < 0{\cdot}001$) lower in treatments with flowerless shoots of *F. esculentum*, *L. maritima* and *C. sativum* as well as the *C. sativum*

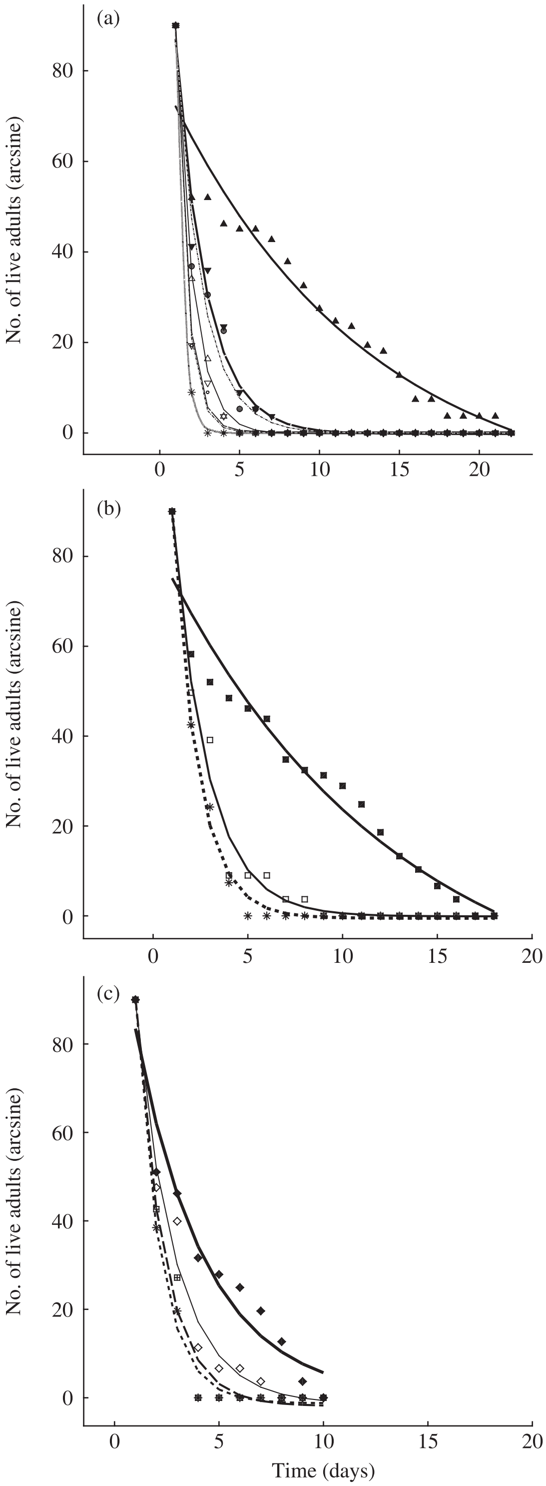

Fig. 1. Mean longevity of adult *T. carverae* when confined with (a) *Brassica juncea* with flowers (black circles), *Brassica juncea* without flowers (white circles), *C. sativum* with flowers (black inverted triangle), *C. sativum* without flowers (white inverted triangle), *L. maritima* with flowers (black triangle), *L. maritima* without flowers (white triangle) and a control treatment (star) (adjusted $R^2 = 98{\cdot}1\%$); (b) *Fagopyrum esculentum* with flowers (black squares), *F. esculentum* without flowers (white squares) and a control (star) (adjusted $R^2 = 97{\cdot}5\%$); (c) *Borago officinalis* with flowers (black diamonds), *Borage officinalis* without flowers (white diamonds), control water (square with cross) and control (star) adjusted ($R^2 = 97{\cdot}1\%$). Points denote treatment means, lines denote fitted relationships and R^2 values are for the model allowing separate parameters for each line.

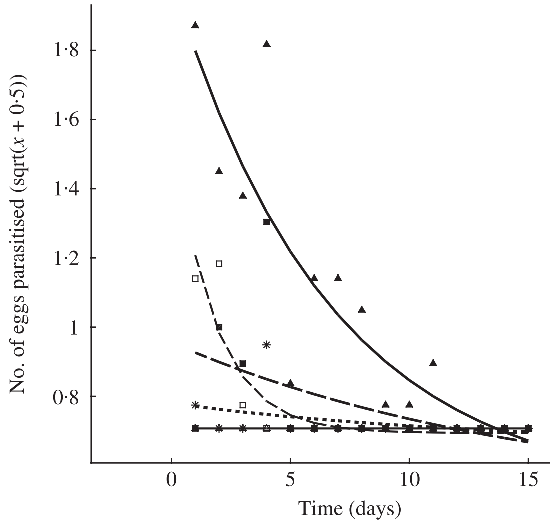

Fig. 2. Mean daily fecundity of *T. carverae* when confined with different ground-cover plant species: *F. esculentum* with flowers (black squares), *F. esculentum* without flowers (white squares), *L. maritima* with flowers (black triangles), *L. maritima* without flowers (white triangles) and a control (star) (adjusted $R^2 = 74{\cdot}5\%$). Points denote treatment means, lines denote fitted relationships and R^2 values are for the model allowing separate parameters for each line.

Table 1. Mean longevity of *Epiphyas postvittana* when enclosed with shoots of different ground-cover plants species (+, shoots with flowers; –, shoots without flowers) and a control treatment (artificial adult food)

Treatment	Male longevity (days)	Female longevity (days)
Borago officinalis (+)	13·0e	16·4bc
Borago officinalis (–)	6·8ab	11·8ab
C. sativum (+)	6·0a	10·0a
C. sativum (–)	6·9abc	9·3a
F. esculentum (+)	9·8bcde	18·2c
F. esculentum (–)	7·3abc	10·1a
L. maritima (+)	7·8abc	12·9ab
L. maritima (–)	8·4abcd	9·7a
Control	11·6de	18·5c
LSD ($P = 0{\cdot}05$)	3·43	4·83

Means followed by the same letter do not differ significantly ($P = 0{\cdot}05$).

and *L. maritima* shoots with flowers. Longevity was intermediate in other treatments. Male longevity tended to be lower with less marked treatment differences, although the artificial diet and *Borage officinalis* with-flower treatment means were significantly ($F = 3{\cdot}81$, d.f. = 8,72, $P < 0{\cdot}001$) higher than in treatments with flowerless shoots of *Borage officinalis*, *C. sativum* and *F. esculentum* and the with-flower treatments of *C. sativum* and *L. maritima*. Other treatments were intermediate.

In the experiment with *Brassica juncea*, longevity ranged between 9·3 and 11·1 days for females and 8·9 and 13·2 days for males but treatments did not differ significantly ($F = 0{\cdot}34$, d.f. = 3, 27, $P = 0{\cdot}795$; $F = 2{\cdot}31$, d.f. = 3, 27, $P = 0{\cdot}099$ for females and males, respectively).

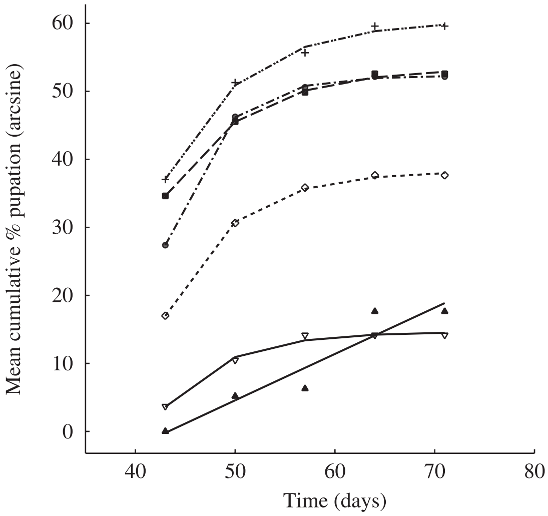

Fig. 3. Mean cumulative pupation of *E. postvittana* when caged with potted plants of *Brassica juncea* (black circles), *Borage officinalis* (white diamonds), *C. sativum* (white inverted triangles), *F. esculentum* (black squares), *L. maritima* (black triangles) and *T. repens* (positive control; plus sign). Adjusted R^2 = 99·4%. Points denote treatment means, lines denote fitted relationships and R^2 values are for the model allowing separate parameters for each line.

Table 2. Effect of ground-cover treatments on *E. postvittana* egg parasitism in the field

Treatment	Mean no. of eggs parasitized Days 1–2	Days 3–4	Days 5–6
Treatments with flowers			
C. sativum	10·4	10·2	6·8
F. esculentum	11·4	18·4	2·4
L. maritima	10·8	7·6	0·0
Treatments without flowers			
Bare earth	0·8	0·8	0·0
Vegetation without flowers	1·6	2·4	1·6
P (treatment comparisons)	0·29	0·15	0·22
Pooled data			
Mean of with-flower treatments	10·9	12·1	3·1
Mean of without-flower treatments	1·2	1·6	0·8
P (pooled mean comparison)	0·03	0·04	0·28

DEVELOPMENT OF LARVAL *E. POSTVITTANA*

Fitted exponential curves for pupation differed significantly in curvature (F = 5·20, d.f. = 5, 12, P = 0·009; Fig. 3). The daily pupation rates (± SE) were *Brassica juncea* 0·818 ± 0·0359, *Borage officinalis* 0·861 ± 0·0326, *C. sativum* 0·856 ± 0·0647, *F. esculentum* 0·884 ± 0·0330, *L. maritima* 0·100 ± 0·0240 and *T. repens* 0·880 ± 0·0271.

Overall pupation rate on *T. repens* (a known host plant) was 74·39% and was not significantly lower on *F. esculentum* and *Brassica juncea*. Overall pupation was significantly (F = 7·88, d.f. = 5, 20, P < 0·001) lower in *C. sativum* and *L. maritima* than in other treatments.

FIELD EXPERIMENT

No parasitism was recorded from surveying naturally occurring egg parasitoids. The field experiment showed a significant effect of flower treatment on parasitism by *T. carverae* of *E. postvittana* eggs in the first (F = 5·42, d.f. = 1,16, P = 0·033) and second 48-h period (F = 5·25, d.f. = 1, 16, P = 0·036) when with-flower (*C. sativum*, *F. esculentum* and *L. maritima*) treatments were pooled and compared with the pooled without-flower (vegetation without flowers and control) treatments (Table 2). There were no significant differences between treatments within either of the two groups (with and without flowers). There was no significant treatment effect on day 5. Numbers of eggs predated from sentinel cards ranged from 3·6 to 29·0 and were numerically greater than parasitism values on all but one of the treatment–date combinations (results not presented) but no treatment effects were significant.

During the period of surveying naturally occurring egg parasitoids and 8-day period of monitoring *T. carverae* activity with sentinel cards, the average daily temperature was 25 °C (maximum 44 °C, minimum 13 °C), daily rainfall was 1·25 mm and an average of 11·25 *E. postvittana* adults was caught in the sex-pheromone trap.

Discussion

The success of biological control is determined largely by the longevity and reproductive success of agents such as parasitoids. The present greenhouse study found that *L. maritima*-fed *T. carverae* survived longer than those fed on *Brassica juncea*, *C. sativum* or no plant material. Although the experiments used excised shoots and we cannot rule out the possibility that this may have affected nectar secretion in some or all species, findings are consistent with previous *T. carverae* work using whole plants (Begum *et al*. 2004b) and the increased survival in the presence of adult food is in general agreement with previous research on *T. carverae* (Gurr & Nicol 2000; Begum *et al*. 2004a). The second and third greenhouse experiments suggest that access to *F. esculentum* and *Borage officinalis* flowers increased survival of *T. carverae* compared with shoots without flowers or control treatments. Similarly, benefits to other parasitoids have been reported for *F. esculentum* (Stephens *et al*. 1998; Irvin *et al*. 1999; Lee & Heimpel 2004; Lee, Heimpel & Leibee 2004) and *Borage officinalis* (Baggen & Gurr 1998). The effects of plant species on *T. carverae* could not be evaluated in a single experiment because of asynchronous flowering, so direct comparisons between the plants tested in different experiments could not be made. It is clear, however, that several plant species significantly increase survival of *T. carverae*, most dramatically *L. maritima.*

The present study found that *T. carverae* parasitized a greater number of *E. postvittana* eggs when fed *L. maritima* flowers compared with *Brassica juncea*, *Borage officinalis*, *C. sativum* and *F. esculentum* flowers. Bennett (2002) found that *T. carverae* was intermediate between proovigenic and synovigenic with the first 24 h of egg laying, representing only 20–25% of the reproductive capacity of a *T. carverae* female, which survives for 6 days with continuous access to host eggs. The longevity of *T. carverae* is less than 7 days when no food source is available (Gurr & Nicol 2000) but the present daily fecundity results demonstrate that *T. carverae* females need to survive longer than 7 days in order to deposit all their eggs.

Feeding from flowers of *L. maritima* in the present study not only increased the period of time over which this agent was parasitizing pest eggs, these animals also produced more eggs whilst young. Therefore, female *T. carverae* with access to flowers, especially of *L. maritima*, survive longer and are more likely to reach their full reproductive potential.

A risk associated with the use of nectar-producing plants in conservation biological control is increasing the fitness of pests. Gu & Danthanarayana (1990) showed that honey increases longevity of *E. postvittana*. In the present study, the relatively low longevity of female *E. postvittana* in the treatments without flowers compared with the artificial diet treatment suggests that *E. postvittana* was food deprived. Depressed longevity in *C. sativum* and *L. maritima* with-flower treatments indicates that these flowers do not provide a suitable food for adult *E. postvittana*. This result contradicts the findings of Irvin *et al*. (1999), who found that when this lepidopteran had access to *L. maritima* flowers or honey both longevity and fecundity were significantly increased compared with water. Male *E. postvittana* benefited from *Borage officinalis* and *F. esculentum* flowers, while female longevity was increased in the presence of flowers of the latter. In the second experiment neither male nor female longevity was improved by access to honey-based adult diet compared with the water-only diet. This lack of effect is unexplained and its anomalous nature means that the effect of *Brassica juncea* flowers remain to be elucidated.

Epiphyas postvittana adults obtain both water and nutrients when feeding upon nectar and the experimental design used in the first experiment did not include a water-only control to indicate the relative importance of each dietary component. It is clear, however, that provision of *Borage officinalis* and *F. esculentum* as floral resources for natural enemies in a vineyard may increase the longevity of *E. postvittana.* In the absence of evidence to the contrary, *Brassica juncea* also must be considered as a possible food source for this pest.

Epiphyas postvittana larvae may benefit from ground-cover plant species. Suckling *et al*. (1998) reported that larvae feed on weeds commonly found in or near vineyards. In the present study, the larval developmental period of *E. postvittana* was extended on *C. sativum* and *L. maritima* compared with other plant species. Pupation rate was lower on these plants, suggesting overall that they are poor hosts of *E. postvittana.* In contrast, *Brassica juncea*, *Borage officinalis*, *F. esculentum* and *T. repens* are suitable hosts.

Baggen & Gurr (1998) suggested the value of 'selective food plant' species that increased the fitness of the hymenopteran parasitoid *C. koehleri* whilst denying benefit to adults of its pestiferous host, the solanaceae-specific *P. operculella*. The present study is the first equivalent work on a *T. carverae*–*E. postvittana* habitat manipulation system but extends the Baggen & Gurr (1998) concept by considering the polyphagous larval as well as adult feeding. This represents a significant methodological advance in the development of conservation biological control towards targeted approaches and away from shotgun approaches (Gurr *et al*. 2005). The value of this approach is evident in the identification of *C. sativum* and *L. maritima* as vineyard ground-cover species that do not benefit the key pest *E. postvittana*. Of these two plant species, however, only *L. maritima* exhibited clear and consistent benefits to the important natural enemy, *T. carverae*.

The field survey showed that, at least at the time of sampling, the activity of *E. postvittana* parasitoids was undetectably low and illustrates the potential value of inundative releases of agents such as *T. carverae* in this system. Although predation of *E. postvittana* eggs from sentinel cards was not significantly affected by treatment, rates were above 10% for all treatment–date combinations and generally exceeded parasitism levels. It is important that future work aims to identify the predator taxa active in this system. This may allow adjustment of the current form of habitat manipulation to increase its impact or for complementary approaches, such as revised crop management (Thorbek & Bilde 2004) and alterations to nearby non-crop vegetation (Schmidt *et al*. 2005), to be developed for predator enhancement, thereby providing control of pests other than *E. postvittana.*

The observed levels of egg predation may have led to the removal of parasitized eggs from sentinel cards and may explain the lack of statistically significant treatment effects on parasitism. This lack of significance made valid a comparison between pooled flowering treatments and pooled without-flower treatments that revealed effects consistent with *T. carverae* benefiting from flower nectar, as shown in the previous greenhouse experiments and in earlier work (Begum *et al*. 2004a,b). The mean numbers of eggs parasitized per sentinel card were highest, 18·4 out of 34·4, in the *F. esculentum* treatment on the second release date; for all other date–treatment combinations parasitism was less than 50%.

Although work of the type reported here cannot control for differences in biomass between plant treatments, overall results suggest that availability of nectar is important and that *L. maritima*, *C. sativum*, *Brassica juncea*, *Borage officinalis* and *F. esculentum* increased the longevity and fecundity of *T. carverae* to varying degrees. The utility of *Borage officinalis*, *Brassica juncea* and *F. esculentum* is clearly constrained by their apparent use by adults and larvae of *E. postvittana.* The value of

C. sativum to *T. carverae* appeared slight but the other 'selective food plant', *L. maritima*, markedly increased the survival and fecundity of the parasitoid, so is recommended for use as a below-vine ground-cover to enhance biological control of *E. postvittana* in vineyards. *Lobularia maritima* is a readily available, hardy perennial that flowers virtually year-round. Its prostrate habit means that it will not interfere with the air flow in the vineyard, which is critical for prevention of frost and fungal diseases. The use of *L. maritima* for enhancement of biological control is feasible because it offers the additional advantage of suppressing weed growth below vines, avoiding the need for herbicide applications and mechanical control.

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