

# Behavior and Effectiveness of Adult *Hippodamia convergens* (Coleoptera: Coccinellidae) as a Predator of *Acyrtosiphon pisum* (Homoptera: Aphididae) on a Wax Mutant of *Pisum sativum*

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**ABSTRACT** Adult females of the coccinellid predator *Hippodamia convergens* (Say) spent more time walking and less time grooming on a line of peas, *Pisum sativum* L., that has reduced waxbloom on all parts of the plant (due to the mutation *wel*) compared with a near-isogenic sister line with normal waxbloom. *H. convergens* walking was distributed over all parts of the low-wax plants, whereas on normal-wax plants walking occurred mostly on stems and the edges of leaves and stipules. The beetles were able to generate 30 times the adhesive traction force on leaf surfaces of low-wax plants compared with normal-wax plants. In cage studies, *H. convergens* (4 adults per plant) were more effective at reducing population growth of pea aphid, *Acyrtosiphon pisum* (Harris), on low-wax plants than on normal-wax plants, but only at initial aphid densities of 10 aphids per plant. At higher initial densities (20 and 40 aphids per plant), differential impact of *H. convergens* was not observed or disappeared after 4–5 d. The results indicate that reduced waxbloom in peas could improve the effectiveness of *H. convergens* on peas at low prey densities.

**KEY WORDS** *Acyrtosiphon pisum*, pea aphid, ladybird beetles, plant waxes, predator behavior, tritrophic interactions

WAXBLOOMS ON PLANT SURFACES can interfere with insect adhesion (Stork 1980, Juniper 1995) and as a result, can provide protection against insect herbivory (Edwards 1982, Edwards and Wanjura 1990, Stoner 1990, Bodnaryk 1992). However, it is more common that plants with reduced waxbloom are reported resistant to insects, especially when evaluated in the field (Eigenbrode and Espelie 1995, Eigenbrode 1996). The mechanisms of insect resistance in reduced waxbloom or so-called glossy or low-wax crop varieties are poorly understood, but antixenotic effects of associated changes in wax chemistry (Eigenbrode et al. 1991a, b) or pleiotropic effects of the reduction in waxbloom on internal defenses (Cole and Riggall 1992) have been implicated. Alternatively, low-wax plants may appear resistant in the field because predatory insects achieve better adhesion and as a result forage more effectively on these plants. Evidence for this has been found in low-wax *Brassica oleracea* L., on which 3 species of generalist predator are more mobile and more effective at reducing artificial infestations of the diamond-back moth, *Plutella xylostella* L., than on a normal-wax genotype (Eigenbrode et al. 1995, Eigenbrode 1996). Although low-wax varieties of other crops might similarly enhance predator effectiveness, the possibility has only been examined in *B. oleracea*.

Several mutations that reduce the abundance and crystallization of epicuticular wax have been described in peas, *Pisum sativum* L. (Marx 1969, Macey and Barber 1970, Holloway et al. 1997, Kovalenko and Ezhova 1992). Recent experiments show that in the field, low-wax peas have partial resistance to pea aphid, *Acyrtosiphon pisum* (Harris) (Eigenbrode et al. 1997). The current study examines the effects of a specific low-wax mutation in peas on the behavior and mobility of *Hippodamia convergens* (Say), an abundant generalist predator in the fauna associated with peas in the Pacific Northwest of the United States, and on the ability of this predator to suppress populations of pea aphid on these plants.

## Materials and Methods

The low-wax mutation *wel*, first reported by Marx (1969), is unique among wax mutations in peas in that it strongly reduces waxbloom over all aerial surfaces of the plant and throughout plant development. For this reason, it was selected for tests with insects. Segregants of accession W6-15368 (Marx 406) in the G. A. Marx Pea Genetic Stock Collection at the USDA-ARS Western Regional Plant Introduction Station in Pullman, were used to generate 2 near-isogenic lines, low-wax 406G (*wel/wel*) and normal-wax 406N (*Wel/Wel*). Both lines also are fixed for the mutation *tl* (acacia leaf), which converts all tendrils to leaflets. This was done deliberately to eliminate the confounding effects of tendrils, which enhance attachment to peas by coccinellids (Kareiva and Sahakian 1990).

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Wax morphology of the 2 pea lines was characterized with scanning electron microscopy of the upper and lower leaf surfaces. For microscopy, leaf samples were frozen in liquid nitrogen and lyophilized. Leaf fragments were coated with gold for 10 or 20 s at 10 mA and examined at 15 KV and 5,000 $\times$  with a Hitachi S-500 scanning electron microscope (Hitachi, Tokyo, Japan). Three fields were examined on each of 4 leaves of each type and densities of crystal types quantified. Representative images were selected for presentation. The method is similar to that used by Eigenbrode et al. (1991b) and produces images of the crystals free of artifacts.

*Acyrtosiphon pisum* were from a clonal, virus-free colony maintained at the University of Idaho. *H. convergens* beetles were obtained commercially (Nature's Control, Medford, OR). Only female beetles were used and they were fed on pea aphids for several days and then starved except for water for 24 h prior to all experiments.

Behavior of 40 individual beetles was recorded on 5-node low-wax and normal-wax peas free of aphids. Each observation lasted 5 min, or until the beetle left the plant. The proportions of insects falling, flying from, or remaining on the plant were recorded. The location and activity of the insects remaining on the plant for 2 min were continuously recorded using The Observer (Noldus Technology, Wageningen, The Netherlands). Activities recorded were walking, grooming, resting, or other (undefined), and the locations were leaf and stipule upper and lower surfaces and edges, stem, and other locations (petiole and petiolule, flower bud). The proportions falling, flying from, or remaining on the 2 plant types were compared with chi-square. Multivariate analysis of variance (MANOVA) (Harris 1985) was used to compare simultaneously the times in all behavioral categories at each location on the 2 wax types. For the MANOVA, each combination (activity  $\times$  location) was treated as a single category. Data (proportion of time in each category) were transformed to the arcsine  $\sqrt{x}$  to stabilize variances. After the MANOVA confirmed differences between the 2 lines in overall behavioral pattern, Student's *t*-tests were used to compare proportion of time spent in the most influential behavioral categories (based on vector assignments in MANOVA) on low-wax and normal-wax plants. For these *t*-tests, if the assumption of equal variance was rejected, the approximate *t* and adjusted degrees of freedom were used (Cochran and Cox 1950).

The adhesive traction obtained by beetles on upper surfaces of low-wax and normal-wax peas was measured with a force tenaxometer approximately following the methods of Edwards and Wanjura (1990). Insects were induced to walk across a horizontally oriented leaf surface until they reached the end of a nylon monofilament tether fastened to the elytra with a drop of ski wax (Swix 'blue' 1-5°C). The other end of the tether was attached to a force transducer (Harvard Apparatus, South Natick, MA) that produces a voltage proportional to force applied. As the beetle pulled against the tether, the resulting output was

plotted on a strip chart recorder for 2 min and calibrated to grams by using standard weights. The 2-min record for each beetle was divided into twelve 10-s intervals and the maximum force (in grams) generated in each interval was recorded and averaged for the observation. Twelve beetles (4 adults on 1 leaflet from each of 3 plants) were tested on each pea line.

The effect of the predators on *A. pisum* was compared on the 2 pea lines by introducing 4 adult female *H. convergens* onto individually caged low-wax and normal-wax pea plants infested with pea aphids and measuring aphid population growth on these plants and on an equal number of control plants without beetles. Two experiments were conducted. In experiment 1, five replicate plants per treatment were infested with 40 aphids and aphid populations were assessed at 5 and 10 d after infestation. In experiment 2, three replicate plants were infested at each of 3 initial aphid densities (10, 20, and 40 aphids per plant), and aphid populations were determined at 2, 4, and 8 d after infestation for each density. Experiment 1 was conducted in a greenhouse at the USDA Plant Introduction Station in Pullman, WA, during March 1996, and greenhouse temperatures were 24:15°C (day:night). Experiment 2 was conducted in a greenhouse at University of Idaho during November 1996, and greenhouse temperatures were 27:18°C (day:night). Both experiments used 10-week-old 18-node plants in 4-liter pots, with greenhouse potting mix. Plants received a standard fertilizer (Osmocote) and were drip irrigated daily. Supplemental lighting ( $\approx 400 \mu\text{moles}/\text{m}^2/\text{s}$ ) maintained a photoperiod of 16:8 (L:D) h. In both experiments aphids initially were placed on the upper surface of leaves of the 12th node of each plant. After 3 d, aphid numbers were reduced to desired numbers in an  $\approx 3:1$  nymph:adult ratio. On the same day, 4 *H. convergens* adults were introduced into the predator treatment cages and the experiment was started. Aphid populations were monitored 5 and 10 d after starting the 1st experiment, and 2, 4, and 8 d after starting the 2nd experiment. On each sample date, aphid densities on each plant were recorded by stage (nymphs, adults), location (stem, upper surface leaf or stipule, lower surface leaf or stipule, and off the plant in experiment 1), and by node.

The cage experiments were analyzed as a completely randomized split-plot design, with time as the split factor, approximating a univariate repeated measures design. Predator (*H. convergens* present and absent) and wax type (low-wax and normal) were main effects in the 2-way ANOVA, with aphids per plant the response variable. Planned contrasts also tested the effects of predators on aphid densities within each wax type on each sample day. Degrees of freedom limitations prevented explicitly testing the effects of starting density in experiment 2, so each starting density (10, 20, and 40 aphids per plant) was analyzed separately. The effects of predator and wax type on the proportion of aphids in 2 developmental stages, on different locations within the plant, and on different nodes within a plant by the end of each experiment were examined with ANOVA.

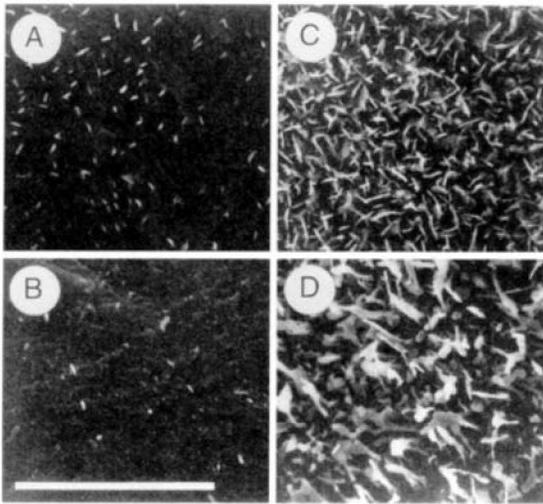


Fig. 1. Scanning electron micrographs of the upper and lower leaf surfaces of low-wax and normal-wax peas. Low-wax (A, B; upper, lower). Normal-wax (C, D; upper, lower). Scale bar = 10  $\mu\text{m}$ .

### Results

Leaf surfaces of *wel* low-wax peas had greatly reduced densities of larger wax crystals on all surfaces of the plants (Fig. 1). The prominent crystals on the upper surface of normal-wax plants are plates with a mean density of 248 plates per 100  $\mu\text{m}^2$  and the dominant crystals on the lower surface of normal-wax plants were crenate ribbons at a density of 55 ribbons per 100  $\mu\text{m}^2$ . On low-wax plants, only minute crystals ( $\leq 1 \mu\text{m}$ ) were present on either surface. Including these minute crystals, total crystal densities were significantly greater on normal-wax than on low-wax upper leaf surfaces (267 versus 78 crystals per 100  $\mu\text{m}^2$ ,  $t$ -test:  $df = 8$ ,  $P = 0.0001$ ) but not on lower surfaces (103 versus 90/100  $\mu\text{m}^2$ ,  $t$ -test:  $df = 8$ ,  $P = 0.6151$ ) leaf surfaces. Reductions in crystal density occur on stipules and stems of *wel* plants, but the greatest differences occur on leaves (Eigenbrode et al. 1998). Plants expressing *wel* also have less wax (reduced by 75%) and altered wax composition (mainly decreased proportions of alkanes and alcohols) compared with normal-wax controls (Eigenbrode et al. 1998).

Behavior of *H. convergens* adults differed on low-wax and normal-wax peas. The insects fell more frequently from normal-wax plants and as a result fewer remained on the plants for the duration of the observation ( $\chi^2 = 14.51$ ,  $df = 2$ ,  $P < 0.001$ ) (Fig. 2). Beetles falling from low-wax plants fell only from stipule edges and stems and did so equally frequently from these 2 plant parts. Beetles falling from normal-wax plants fell mostly from leaf and stipule edges (79%) and the rest fell from other parts of the plants. Among those insects remaining on the plant for 2 min (15 on normal and 24 on low-wax) times allocated to behavioral categories differed significantly (Fig. 3) (MANOVA:  $F = 10.08$ ;  $df = 10, 26$ ;  $P \leq 0.0001$ ). The most influential vectors in the MANOVA were for walking on leaf or stipule

■ Low-wax  $\chi^2 = 14.51$ ,  $df = 2$   
 □ Normal-wax  $P < 0.001$

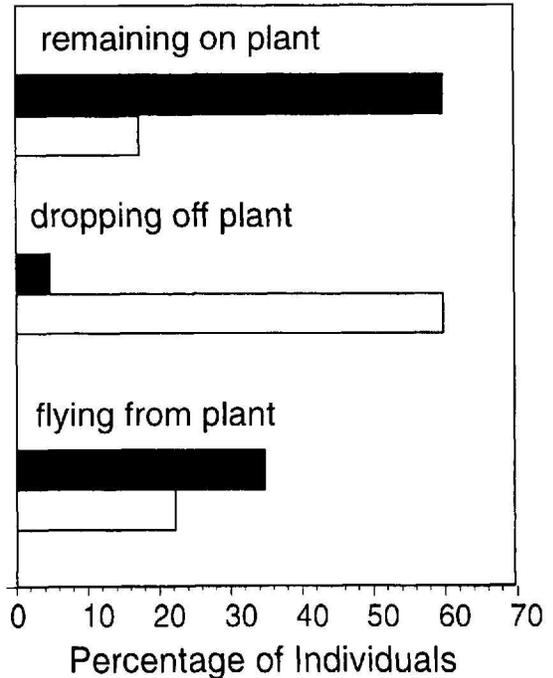


Fig. 2. Percentage of *H. convergens* adult females remaining on, dropping from, or flying from low-wax and normal-wax peas during a 5-min observation. For each plant type,  $n = 40$ .

surfaces and grooming. Walking and grooming together comprised more than 97.7% of the time on the 2 types of peas. *Hippodamia convergens* spent a significantly greater percentage of time walking on low-wax peas ( $97.7 \pm 1.3\%$ ) than on normal-wax peas ( $82.5 \pm 6\%$ ) ( $t = 2.57$ ,  $df = 17$ ,  $P \leq 0.019$ ). The percentage of time spent walking on leaf or stipule surfaces was much greater on low-wax peas ( $37.5 \pm 3\%$ ) than on normal-wax peas ( $2.2 \pm 3.5\%$ ) ( $t = 11.4$ ,  $df = 37$ ,  $P \leq 0.0001$ ). *Hippodamia convergens* spent a significantly smaller percentage of time grooming ( $t = 3.14$ ,  $df = 14.7$ ,  $P \leq 0.0069$ ) on low-wax as compared with normal-wax peas. Walking was distributed more evenly over all surfaces of low-wax peas compared with normal-wax peas (Fig. 3). On low-wax peas the beetles spent more than twice as much time walking on upper surfaces than on lower surfaces ( $t = 7.02$ ,  $df = 44$ ,  $P = 0.0001$ ), whereas on normal-wax peas walking time was allocated equally to upper and lower surfaces ( $t = 1.06$ ,  $df = 24$ ,  $P = 0.2972$ ). Traction adhesion generated by beetles was >30-fold greater on the upper leaf surface of low-wax peas than on the upper leaf surface of normal-wax peas (Fig. 4).

In both cage experiments, the effect of *H. convergens* on pea aphid densities was always significant ( $P \leq 0.0277$ ) and the effect of wax type was never significant (Table 1). The interaction between the predator

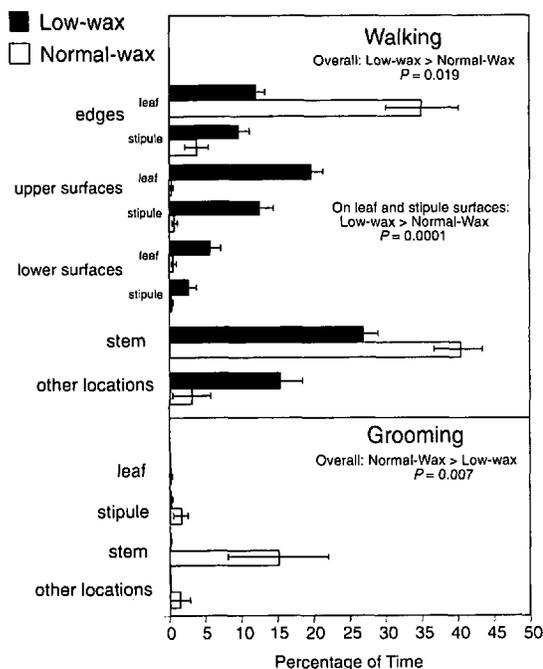


Fig. 3. Percentage of time *H. convergens* adult females spend walking and grooming on different parts of low-wax and normal-wax pea plants during a 5-min observation. MANOVA for effect of wax type (normal-wax versus low-wax) on all behavioral categories:  $F = 10.08$ ;  $df = 10, 26$ ;  $P \leq 0.0001$ .

treatment and wax type was significant ( $P = 0.0470$ ) in experiment 2, but only with a starting density of 10 aphids per plant. This reflects the significant suppression of aphid populations, starting with 10 aphids per plant, but not on normal-wax plants on each sample day (Fig. 5B). At higher initial densities in experiment 2 and in experiment 1, greater suppression of aphid population growth by beetles was only evident, when it did occur, during the first 4 or 5 d after initiation of the experiments (Fig. 5A and B) and the interaction between wax type and predator was not significant (Table 1). At an initial density of 20 aphids per plant in experiment 2, suppression of aphids by *H. convergens* was greater on low-wax plants at 4 d, but not at 8 d, by which time the beetles were equally effective on both wax types. A similar effect occurred in experiment 1, in which plants were infested with 40 aphids per plant and population growth rates of aphids on controls were lower than in experiment 2 (Fig. 5A). At an initial density of 40 aphids per plant and the higher aphid population growth rate in experiment 2, *H. convergens* did not suppress aphid population growth significantly on either pea type (Fig. 5B), although trends were similar to those observed in other treatments with 20 and 40 aphids.

At the end of the cage experiments, there were significant differences in the distribution of aphids among the parts of the pea plants (Table 2). The proportion of aphids was always lowest on leaf upper

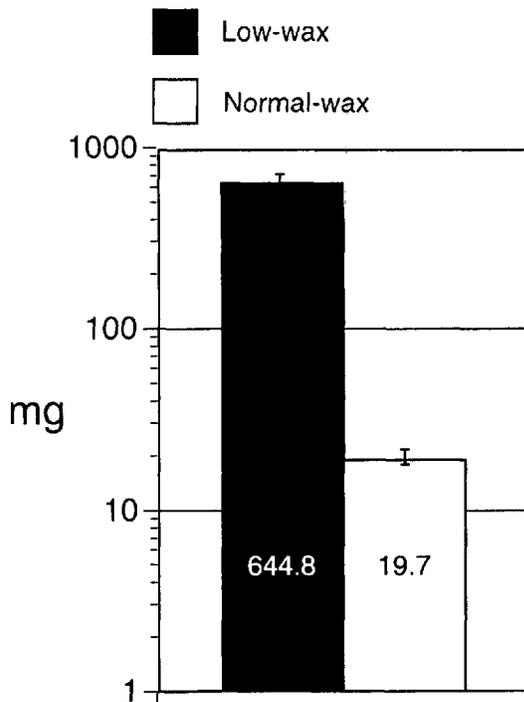


Fig. 4. Adhesive force produced by *H. convergens* adult females pulling against a tether while walking on the upper leaf surface of low-wax and normal-wax plants.

surfaces compared with lower surfaces and stems. The proportion on lower surfaces tended to be greater on low-wax plants than on normal-wax plants. The proportion of aphids on lower surfaces was often higher whereas the proportion on stems was lower on plants with *H. convergens* than on predator-free plants. This occurred in every case on low-wax peas, but only once

Table 1. ANOVA statistics for effects *H. convergens* (predator), low-wax and normal-wax peas (wax type), and their interaction on pea aphid population densities in 2 cage experiments

Aphids per plant at start		F	df	P
Experiment 1				
40	Model	8.62	23, 16	0.0001
	Predator	20.49	1, 1	0.0003
	Wax type	0.98	1, 1	0.3581
	Predator $\times$ wax type	0.05	1, 1	0.4982
Experiment 2				
10	Model	10.91	23, 16	0.0004
	Predator	27.01	1, 1	0.0001
	Wax type	0.02	1, 1	0.9019
	Predator $\times$ wax type	4.66	1, 1	0.0470
20	Model	5.48	23, 16	0.0057
	Predator	12.18	1, 1	0.0030
	Wax type	1.97	1, 1	0.1808
	Predator $\times$ wax type	0.70	1, 1	0.4144
40	Model	6.53	23, 16	0.0012
	Predator	6.15	1, 1	0.0277
	Wax type	0.31	1, 1	0.5889
	Predator $\times$ wax type	0.38	1, 1	0.5989

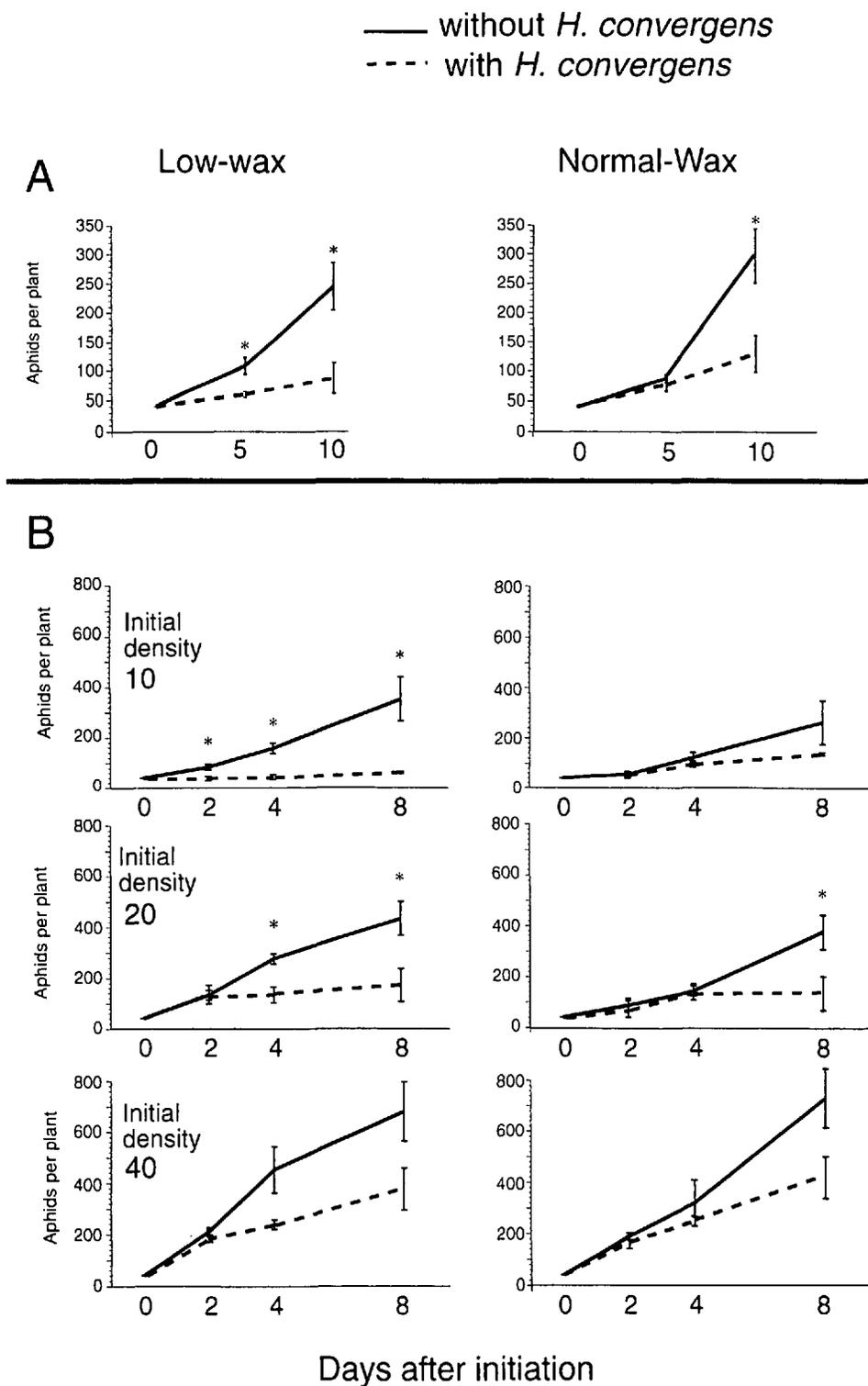


Fig. 5. Pea aphid populations on low-wax and normal-wax peas caged with 4 adult female *H. convergens* or without predators. (A) Experiment 1, starting aphid density 40 per plant. (B) Experiment 2, 3 starting aphid densities: 10, 20, and 40 per plant. \* Indicates aphid populations with and without predators differ (planned contrast;  $P \leq 0.05$ ). Results of analysis are in Table 1.

**Table 2.** Distribution of pea aphids on upper and lower blade surfaces (leaf and petiole combined) or stems, of glossy and normal-wax pea plants caged with adult *H. convergens* (*H.c.*) and without adult *H. convergens* (*No H.c.*)

Initial Aphid Density	Location on plant	Reduced-wax No <i>H.c.</i>	Reduced-wax <i>H.c.</i>	Normal-wax No <i>H.c.</i>	Normal-wax <i>H.c.</i>	Effects <sup>a</sup>				
						Location	Wax × location	Predator × location	Predator × wax × location	
Experiment 1										
40	Upper surface	0.13 ± 0.04	0.09 ± 0.04	0.13 ± 0.05	0.26 ± 0.10					
40	Lower surface	0.35 ± 0.04	0.59 ± 0.04	0.63 ± 0.06	0.52 ± 0.10	0.0001	0.0297	0.0084	0.0751	
40	Stem	0.44 ± 0.09	0.15 ± 0.04	0.22 ± 0.04	0.14 ± 0.08					
40	Offplant	0.08 ± 0.04	0.17 ± 0.08	0.02 ± 0.01	0.08 ± 0.05					
Experiment 2										
10	Upper surface	0.00 ± 0.00	0.06 ± 0.05	0.06 ± 0.03	0.04 ± 0.03					
10	Lower surface	0.47 ± 0.05	0.75 ± 0.13	0.70 ± 0.11	0.67 ± 0.07	0.0001	0.9034	0.0255	0.0057	
10	Stem	0.53 ± 0.05	0.19 ± 0.11	0.24 ± 0.12	0.29 ± 0.09					
20	Upper surface	0.03 ± 0.01	0.05 ± 0.03	0.06 ± 0.03	0.03 ± 0.01					
20	Lower surface	0.31 ± 0.09	0.56 ± 0.24	0.56 ± 0.19	0.82 ± 0.06	0.0001	0.0544	0.0857	0.9330	
20	Stem	0.65 ± 0.10	0.32 ± 0.09	0.38 ± 0.17	0.15 ± 0.05					
40	Upper surface	0.05 ± 0.02	0.07 ± 0.05	0.09 ± 0.03	0.08 ± 0.02					
40	Lower surface	0.47 ± 0.02	0.73 ± 0.06	0.69 ± 0.07	0.58 ± 0.16	0.0001	0.4858	0.3775	0.0056	
40	Stem	0.49 ± 0.05	0.20 ± 0.01	0.22 ± 0.05	0.34 ± 0.14					

<sup>a</sup> ANOVA statistics: Experiment 1, 40 aphids,  $F = 8.63$ ;  $df = 15,64$ ;  $P \leq 0.0001$ , Experiment 2, 10 aphids,  $F = 9.36$ ;  $df = 11,24$ ;  $P \leq 0.0001$ , Experiment 2, 20 aphids,  $F = 4.42$ ,  $df = 11,24$ ;  $P \leq 0.0011$ , Experiment 2, 40 aphids,  $F = 12.90$ ,  $df = 11,24$ ;  $P \leq 0.0001$

on normal-wax peas, partly accounting for the significant wax type × predator × location interaction in 2 of the 4 tests (Table 2).

The proportion of aphids on different nodes of the pea plants always differed significantly ( $F = 9.13$ ;  $df = 10, 219$ ;  $P < 0.0001$ ), but there were no significant effects on this distribution by wax type, presence of predators, or their interaction (data not shown). Similarly, the adult:nymph ratio was not affected by predator, wax type, or their interaction.

## Discussion

*Hippodamia convergens* adult beetles are more mobile on low-wax peas than on normal-wax peas. That is, on low-wax peas, the insects spend more time walking and less time grooming and their walking is distributed more evenly over all parts of the plant. In contrast, on normal-wax plants the beetles walk less and their walking occurs mostly on stems and on leaf and stipule edges and rarely occurs on leaf and stipule surfaces. In addition, during 5-min observations, the insects fall about twice as frequently from normal-wax plants as they do from low-wax plants. All of these effects must arise from the ≈30-fold greater adhesive traction obtained by the beetles on low-wax versus normal-wax pea leaf surfaces (Fig. 4). Because the test lines are near-isogenic and differ in the expression of the *wel* wax mutation, these results confirm that waxblooms interfere with coccinellid mobility on peas, as has been suggested by other observations (Carter et al. 1984, Kareiva and Sahakian 1990). The finding is also consistent with evidence that similar waxblooms on *Brassica* interfere with predator mobility (Arzet 1973, Shah 1982, Grevstad and Klepetka 1992, Eigenbrode et al. 1995, 1996).

Reduced walking by *H. convergens* on normal-wax peas should reduce prey encounter rates and the effectiveness of the predators at reducing aphid populations on normal-wax compared with low-wax peas. In cage experiments, a difference in the impact of *H. convergens* on aphid populations on low-wax and normal-wax peas was detected, but only at relatively low aphid densities. The effect persisted over the 8 d of the experiment on plants initially infested with 10 aphids. On plants with higher initial aphid densities, evidence of differential predation was absent or disappeared after 4–5 d. This was mostly due to increasing impact by the beetles on normal-wax plants as the tests progressed. There are several testable explanations for this pattern. Greater mobility on low-wax plants might provide an advantage to *H. convergens* only when aphid densities are low, requiring the beetles to effectively explore the plant. When aphids are abundant and accessible on all parts of the plant, the beetles should locate them equally well on both wax types. Additionally, if foraging success is initially low on normal-wax plants, foraging effort might increase with hunger and compensate for reduced mobility of the beetles on these plants. With experience, beetles might forage more on plant parts where aphids are accessible, and increase their success on normal-wax plants over time. The beetles also might modify their locomotory behavior to improve adhesion to waxy plants. As an illustration of this potential, during the adhesion bioassay, 1 beetle was observed to bite the normal-wax leaf surface apparently to augment tarsal adhesion.

The effects of waxbloom on *H. convergens* predation also might arise partly from differences in aphid population growth or behavior on low-wax and normal-wax peas. Although aphid densities on predator-free

controls were similar on the 2 types by the end of the experiments, in the 1st days after infestation aphid population growth was slower on normal-wax plants (Fig. 3 and 4). Lower aphid abundance may have contributed to reduced encounter rates and foraging on normal-wax plants. On control plants a smaller proportion of aphids was on lower surfaces and a greater proportion on stems of low-wax plants versus normal-wax plants (the wax  $\times$  location effect was significant twice; Table 2). Experiments by K. Schotzko (personal communication) indicate that mature apterous *A. pisum* mobility and apparent preference between upper and lower leaf surfaces is similar on *wel* low-wax and normal-wax peas during the 1st 24 h after contact. However, it is possible that in the presence of predators aphids behave differently on low-wax and normal-wax peas. *A. pisum* is known to respond to disturbance by predators by dropping off of plants (Roitberg and Myers 1979), and this response may be affected by surface waxes. In the first experiment, the proportion of aphids off of plants was recorded and it was higher on low-wax than on normal-wax plants (Table 2).

Predation by *H. convergens* tended to increase the proportion of aphids on lower surfaces, primarily on low-wax plants (Table 2). Although the effect was only significant in half of the comparisons, the trend may indicate that lower leaf and stipule surfaces provide a partial refuge from coccinellid predation on low-wax peas, as a result of the beetles foraging more on upper versus lower surfaces of these plants (Fig. 2).

More walking on stems and leaf and stipule edges of normal-wax peas suggests these structures provide additional opportunities for adhesion that offset the disruption of adhesion by the waxbloom. For apparently the same reason, some chrysomelid species walk and feed mostly on leaf edges of *Eucalyptus* and *Brassica* with prominent waxblooms (Superak 1976, Edwards and Wanjura 1990, Bodnaryk 1992). In peas, the mutation *af*, which converts all leaves to tendrils, improves mobility and attachment of coccinellids to the plants (Kareiva 1990; Kareiva and Sahakian 1990). By design, the pea lines used in the current study had no tendrils, due to the *tl* mutation, to eliminate this means of compensating for poor traction on leaf surfaces. Predator effectiveness must depend on the combined influences of plant architecture (Carter et al. 1984, Frazer et al. 1994, Kareiva and Sahakian 1990) and surface wax attributes.

Our study shows that mobility and adhesion of *H. convergens* can be impaired by plant-surface waxbloom on *Pisum*, and that a reduction in the waxbloom can result in greater aphid predation by this species under some conditions. In the field, the low-wax pea used in the current study develops lower populations of pea aphid than does the normal-wax sister line (Eigenbrode et al. 1998), which could result in part from increased predation by *H. convergens* on the low-wax type. These patterns illustrate the potential of reduced waxbloom crop varieties to improve the effectiveness of coccinellid predators.

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