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Interactions among convergent lady beetle (*Hippodamia* convergens) releases, aphid populations, and rose cultivar

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Abstract

Release of adult convergent lady beetles, *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae), provided inundative control of aphids (Homoptera: Aphididae) infesting *Rosa hybrida* outdoors in nursery containers and in the landscape. In potted roses, a single release of 100 lady beetles per 19 liter plant provided 66-88% aphid control during 1994 and 1995. In the landscape, a single release of about 175 or 350 lady beetles per 0.5-1 m tall shrub during 1994, 1995, and 2002 failed to reduce aphid density. However, each of one or two subsequent releases of about 1400–1750 *H. convergens* per shrub reduced aphid densities in the landscape to near zero (93–100% control). Releasing 10–20 beetles per flower bud controlled aphids on shoots caged to prevent insect dispersal. On uncaged rose shoots, 100 or more *H. convergens* per bud were required to control aphids. The effective rate for inundative release in landscape roses was about 2300 beetles/m² (210/ft²) of shrub-covered surface, or two orders of magnitude greater than the 11-22 beetles/m² ($1-2/ft^2$) commonly recommended by beetle sellers. Based on three lady beetle releases during April–May when aphids are abundant on rose in California's Central Valley, lady beetle costs are about the same as one soil drench of the systemic insecticide imidacloprid. Rose cultivar affected aphid density, but cultivar did not affect augmentative predation. Cultivar selection and high-rate predator release are complimentary strategies for aphid management on rose.

Keywords: Convergent lady beetle; Hippodamia convergens; Augmentative release; Aphid control; Macrosiphum rosae; Rosa hybrida; Rose

1. Introduction

The convergent lady beetle, *Hippodamia convergens* Guérin-Méneville, is a common aphid predator that naturally occurs throughout much of North and South America. It also is released for aphid control in part because large aggregations overwintering in California's Sierra Nevada allow beetles to be readily collected and profitably sold. Coccinellids are the most widely used predators for biological control (Obrycki and Kring, 1998) and, although no data are available, we believe that *H. convergens* is the most widely released predaceous insect, in part because it is often the only predator

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available at retail garden stores and nurseries. Apparently several billion convergent lady beetles are collected in California and sold each year, based on information from our supplier.

The University of California has historically recommended against releasing aggregation-collected *H. con*vergens (Hagen, 1982; Moore and Koehler, 1981) because of observations that *H. convergens* fly away soon after release and reports from early workers that release does not control aphids. For example, Davidson (1919, 1924) released marked beetles in barley (*Hordeum* vulgare L.) and wheat (*Triticum* sp.) and found $\approx 10\%$ of beetles remained after 1 week. Most *H. convergens* dispersed soon after release in aphid-infested sugar cane (*Saccharum officinarum* L.) (Eddy, 1939) and alfalfa (*Medicago sativa* L.) (Ingram et al., 1939; Packard and

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Campbell, 1926). Cooke (1963) credited *H. convergens* release for some aphid reduction in alfalfa, but like Fenton and Dahms (1951) and Hatch and Tanasse (1948), Cooke concluded that releases would not be economical in comparison with insecticides. Starks et al. (1975) found that 72% of *H. convergens* dispersed immediately after release in sorghum (*Sorghum vulgare* Persoon) and that releases did not significantly reduce aphid densities.

Except for Starks et al. (1975), none of these workers report aphid densities before or after releases, none report using nonrelease control plots in their experimental designs, and the release rate per crop area cannot be determined from most publications. These were observational studies of inoculative control, and at least some workers did not consider it possible that released beetles could provide inundative control. For example, Packard and Campbell (1926) observed a decrease in pea aphids, *Acyrthosiphon pisum* (Harris), but did not credit this to their release because "it was too soon after liberation for progeny of the introduced beetles to have become effective."

Subsequent studies identify physiological reasons why aggregation-collected H. convergens disperse soon after release and why few aggregating beetles will oviposit before dispersing. Beetles from spring aggregations have immature ovaries (Hagen, 1962, 1987). Females must consume protein and fat for a week or longer before ovaries mature and oviposition can begin (Davis and Kirkland, 1982). After feeding, juvenile hormone (JH) production increases and this JH stimulates ovary maturation. Juvenile hormone also strongly induces long-distance migratory flight behavior in H. convergens (Davis and Kirkland, 1982; Rankin and Rankin, 1980a,b). Because "Juvenile hormone is necessary for ovarian development" and JH also "stimulates long-duration flight behavior in both sexes" (Rankin, 1991), it appears physiologically obligatory that "dispersal flight of the lady beetles alternates with feeding behavior until the ovaries are mature" (Davis and Kirkland, 1982) and beetles from aggregations will disperse soon after release even where aphids are abundant.

Whether releasing sufficient numbers of aggregationcollected H. convergens can provide inundative control prior to beetle dispersal was not answered by the studies cited above. More recent controlled studies found that aphids were not controlled in cotton (Minzenmayer and Fuchs, 1994) or wheat (Randolph et al., 2002) by releasing 1–2 adult H. convergens/ m^2 . Conversely, small-scale studies using higher rates found that about 12 H. convergens adults/m² controlled Aphis spiraecola Patch on caged Pyracantha lelandii (Raupp et al., 1994). On uncaged plants, release of 400 or more H. convergens/m² controlled a woolly aphid (Eriosoma sp.) infesting landscape *Elaeagnus pungens* (Raupp et al., 1994) and melon aphid, Aphis gossypii Glover, on potted Dendranthema grandiflora in a nursery (Dreistadt and Flint, 1996; Flint et al., 1995).

Thirty-one species of aphids are reported from *Rosa* species (Blackman and Eastop, 1984). We did not identify aphids to species during sampling and at least sometimes a mixture of species was present. Rose aphid, *Macrosiphum rosae*; potato aphid, *Macrosiphum euphorbiae* (Thomas); and *Wahlgreniella nervata* (Gillette) comprised 86, 12, and 2%, respectively, of aphids from our landscape rose buds identified by the USDA-ARS Systematic Entomology Laboratory, and *Macrosiphum* spp. and *W. nervata* infested our potted rose.

This study evaluated whether inundative releases of H. convergens can control aphids infesting rose in the nursery and landscape. We also determined whether rose cultivar affected predator augmentation. Finally, we compared the cost of effective lady beetle releases to the cost of commonly used pesticides.

2. Materials and methods

2.1. Nursery study site and plants

We conducted potted-plant experiments outdoors at a Davis Arboretum nursery on the University of California, Davis campus. The study area was an outside 130×80 m gravel surface free of plants, except for those in our studies. Plants were *Rosa hybrida* 'Tropicana' (Jackson and Perkins Bear Creek Gardens, Somis, CA) in 19 liter pots that in 1993 were 2 years old and about 0.5 m tall.

2.2. Landscape study site and plants

Our second site we call "landscape" was an outdoor public rose garden at 3rd and B Streets, Davis, California. It was a 6×11 m block of roses with trunks spaced about 1 m from adjacent roses, containing 43 roses during 1994 and 1995, and 35 roses during 2002 (because some died). Shrubs were about 0.5–1 m tall, and were planted in 1991. Roses were not planted in a randomized layout; plants were clumped by cultivar to group plants with the same blossom color, a typical design strategy in large rose gardens. We sampled up to 26 of these plants each year in our studies of predator augmentation and cultivar effect as summarized in Table 1.

2.3. Beetles and release methods in the nursery

Adult *H. convergens* were provided by A-1 Unique Insect Control (Citrus Heights, CA). Beetles were collected about late February each year from aggregations at about 600 m altitude in Placer County, California, and were stored by the supplier and later by us at 4– 10 °C until we released them outdoors in the landscape or nursery.

Table 1 Summary of landscape beetle release experimental methods

Number, and dates of trials	Number of plants and cultivars	Design	Analyses
2, April 1994, April 1995	6 Tropicana	Each shrub with four branch cages (two cages each with and without beetles) plus beetles released beneath uncaged foliage	Aphid densities with and without beetles compared before and after releases to assess predator release efficacy
2, April 2002, May 2002	4 each Brandy, Oregold, Tropicana	As above	As above, plus assessment of cultivar effect on predation
2, April 1994, April 1995	4 each Angel Face, Brandy, Oregold, Sheer Elegance, Sun Flare	Beetles released beneath each uncaged shrub	Rank order of relative aphid density among plants compared before and after releases to assess cultivar effect on predation

All trials were conducted in a 6×11 m block of roses, non-randomly planted with trunks spaced at intervals of ca. 1 m, outdoors in a public park rose garden. In every trial, beetles were released twice at an interval of about 1 week, except the May 2002 trial used 1 release. See Table 3 for release numbers.

In the nursery we made one release of *H. convergens* during May 1994 and in May 1995. One day before each release, we sampled aphids and divided 32 roses into eight plots each of four roses so there were no significant differences in mean aphid densities among plots. We used a randomized block of 2×4 plots, four plots each randomly assigned to release or nonrelease treatments. Each container was about 0.5 m from the nearest other pots in that plot, and the edge of each plot was 4–5 m from the nearest adjacent plot.

Beetles were removed from cold storage, sprayed with sugar water as recommended by suppliers, and confined outdoors in shade for ca. 8 h prior to release. Around sunset, 100 beetles were released onto the potted soil beneath each plant. This rate equaled 500 beetles/m² or 25 (in 1994) or 31 (1995) beetles per bud.

We sampled aphids at 2.5 days after beetle release and 7.5 days (during 1994) or 5.5 days (1995) after release, and counted the *H. convergens* on plants (beetle counts not presented).

2.4. Release methods for predator exclusion-enclosure in landscape

We conducted predator exclusion-enclosure studies using cages on six 'Tropicana' rose plants during 1994 and 1995 and on four each 'Brandy,' 'Oregold,' and 'Tropicana' (12 plants total) during 2002 in the landscape. Aphid densities were compared, before and after lady beetle release, on rose buds receiving three treatments: aphids caged with no predators (the nonrelease controls), aphids caged with beetles, and aphids with beetle releases without cages.

We conducted one trial each during April 1994, 1995, and 2002, releasing lady beetles on two dates each year. During 2002, aphid populations rebounded after the second release, so we made a third release during May. By design, this third release comprises a separate trial because we removed all cages after the first two releases, then 3 weeks later repeated the sampling and treatment grouping procedures before the third release.

We placed four cages per shrub on aphid-infested terminals and released adult *H. convergens* into one-half of the cages. Cages were 0.5 m long organdy tubes held open in their center with a 20 cm diameter wire hoop, tied closed at their distal end, and sealed proximally around each branch. We removed all predators from cages then added lady beetles to two cages per shrub at a rate of 10 beetles per bud, or 20 beetles per bud in cages with only one bud. We regularly inspected and maintained cages, removed any non-*Hippodamia* predators we observed inside, and deleted from analyses the few cages where we failed to maintain bag integrity. We counted and removed beetles in bags immediately prior to any subsequent release.

We also released beetles on the open ground beneath all the roses in our study block at about 7 p.m. The same numbers were released on each plant, ranging from 175 to 1750 *H. convergens* per plant depending on the trial as listed in Table 3. We compared insects on foliage in cages with and without beetles, and on uncaged foliage, in part to assess whether preventing dispersal improved aphid control and because some studies have found that cages themselves can have a treatment effect (Luck et al., 1988).

2.5. Aphid count sampling

Our sample unit was a terminal rose bud in stages one through five as classified and illustrated by Maelzer (1976). These are the only bud stages suitable for infestation by all stages of M. rosae (Maelzer, 1977). We counted (or estimated as below) all aphids from the tip of the flower bud (or leaf tip for bud stage one) to the base of the bud petiole. We stopped counting aphids at the point where the base of the petiole of the first leaf (cluster of up to five leaflets) was clearly separated from the flower bud petiole.

Table 2

Aphids per rose bud 1 day before and at intervals (days) after one release of convergent lady beetles on 'Tropicana' rose in an outdoor nursery on 3 May 1994 and 10 May 1995

Year	Time	Aphid density	Percent control ^b		
		Without beetles Mean (SE)	With beetles ^a Mean (SE)	Mean (SE)	
1994	Before 2.5 days 7.5 days	129.9 (9) a 89.4 (18) abc 72.5 (14) c	128.2 (10) ab 77.2 (12) bc 16.5 (8) d	25 (14) NS ^c 87 (9)	
1995	Before 2.5 days 5.5 days	115.9 (17) a 101.5 (22) a 76.4 (13) ab	113.8 (17) a 19.9 (5) bc 5.7 (3) c	66 (12) 88 (7)	

^a Within years, means followed by a same letter are not significantly different according to Tukey's test for all paired comparisons (P > 0.05).

^b Percent control according Abbott (1925) method.

^c Non-significant difference.

We sampled only stage two through four buds from throughout each shrub on shoots growing from the trunk above its graft with the rootstock. We sampled buds in stage one and five only if less than 10 buds of stage two to four were available for sampling on that shrub. Aphids reported here are the number of live apterous (nymphs plus wingless adults) and alate aphids of all species combined, excluding mummified (obviously parasitized) aphids. Sample frequency and dates are shown in Figs. 2 and 3 and Tables 2 and 3.

2.6. Aphid estimate sampling

For all buds, we counted all aphid alates. In the nursery and during 2002 in the landscape, we also counted all apterous aphids. We also used this "count sampling" in the landscape on five dates during 1994 and seven dates in 1995. We used "estimate sampling" on an additional 10 dates in 1994 (6 April–10 May) and four dates during 1995 (11, 18, 25 April, and 2 May) if there were 16 or more apterous aphids in a sample.

2.6.1. Estimate sampling of continuous aphid colonies

If a continuous colony of adjacent aphids was present, we estimated the aphids/mm of bud. Because aphids/mm of bud increases with aphid density (Maelzer, 1977), we used different estimates of apterous aphids/mm. We categorized each colony into population density range intervals (RI): <16 aphids per bud, all of which we counted (RI = A); 16–75 aphids per bud (RI = B); 76–200 (RI = C); or over 200 aphids per bud (RI = D). To estimate apterous aphids per sample (Aph_E), we pooled count samples (Aph_C) from the same population range intervals on dates that year when we counted all aphids and measured their colony length (Ln_C). For each estimate sample with a continuous colony of measurable length (Ln_E), we used mean Aph_C/ Ln_C values to estimate apterous aphid numbers (Aph_E):

Table 3

Percent control (Abbott, 1925) of aphids from release of adult *H. convergens* outdoors in the landscape on caged or uncaged rose

Release date	No. of beetles released			Percent control	
	Per plant	Per bud	Per m ²	Days ^{a,b}	Mean (SE)
Caged					
1994					
11 April	c	11	430	4 ^a	83 (10)
				8 ^a	100 (0.01)
21 April	c	12	430	6 ^b	100 (0.1)
1995					
15 April	c	18	430	5 ^a	85 (7)
20 April	c	19	300	4 ^b	97 (1)
2002 Trial 1					
13 April	c	16	440	3 ^a	80 (6)
				6 ^a	81 (9)
19 April	c	16	440	3 ^b	97 (2)
				7 ^b	99 (0.1)
				12 ^b	100 (0.04)
				19 ^b	100 (0.01)
2002 T : 1 2					
2002 Trial 2	с	1.6	500	28	00 (1)
10 May		16	580	3 ^a	99 (1)
				7 ^a	100 (0.01)
				14 ^a	100 (0.02)
Not caged					
1994					
11 April	350	49	580	4 ^a	28 (12) NS
1				8 ^a	32 (17) NS
21 April	1400	205	2330	6 ^b	100 (0.2)
1995 Trial					
15 April	175	24	290	5 ^a	NS ^d
20 April	1050	93	1750	4 ^b	85 (11)
-	1000		1,00	·	00 (11)
2002 Trial 1		4.0		• 2	
13 April	350	19	580	3 ^a	7 (11) NS
				6 ^a	NS ^d
19 April	1750	147	2920	3 ^b	93 (4)
				7 ^b	64 (24)
				12 ^b	NSd
				19 ^b	NS ^d
2002 Trial 2					
10 May	1400	311	2330	3 ^a	100 (0.1)
				7 ^a	98 (1)
				14 ^a	98 (1)

NS, No significant difference (P > 0.05) in aphid density on these beetle-treated rose buds in comparison with predator-free buds according to ANOVA and Tukey's tests on data as presented in Figs. 1 and 2.

^a Days after the first of 1 or 2 releases.

^b Days after a second release.

^c Per plant category does not apply as beetles were released into field cages enclosing only a portion of each plant.

^d Abbott (1925) values were negative, non-significant numbers.

$$Aph_{E} = Ln_{E} \times (Aph_{C}/Ln_{C}).$$

2.6.2. Estimate sampling of discontinuous aphid colonies

If aphids were not in an adjacent group of measurable colony length, we let Aph_E equal the mean of Aph_C samples that lacked a Ln_C value (we used the mean densities of discontinuous aphid colonies from count samples). We used separate means for Aph_C for each RI (B–D) for each year. This method was used for relatively few estimate samples. During 1994 and 1995, 89% (1549 of 1701) of landscape count samples with 16 or more aphids had a measurable colony length.

2.7. Cultivar affects on predator augmentation

During 1994 and 1995, we sampled in the landscape four roses each of five cultivars: 'Angel Face,' 'Brandy,' 'Oregold,' 'Sheer Elegance,' and 'Sun Flare,' to assess cultivar effect on predation. We compared relative aphid density among these cultivars before and after releasing lady beetles on open ground beneath these uncaged plants and the surrounding roses. If the same cultivars (and the same plants) that hosted the most (or least) aphids before releases were also the most (or least) infested after releases, we concluded that predator augmentation was not affected by cultivar (Fig. 3).

During 2002, we investigated whether cultivar affected aphid control by conducting predator exclusionenclosure studies on three cultivars (Table 1). We used multiple analysis of variance tests (MANOVA) to investigate any sample date–cultivar interaction and any date–cultivar–treatment effect. Separately on each of 10 sample dates, and for all dates pooled for each of two trials, we used the MANOVA test and the Wilks' Lambda F statistic repeated measures ANOVA tests (SAS Institute, 1988). Fig. 2 data are for all three cultivars ('Brandy,' 'Oregold,' and 'Tropicana') pooled as there was no interaction between sample date and cultivar and there was no date–treatment–cultivar effect as discussed in Section 3.

2.8. Release economics

We consulted Suppliers of Beneficial Organisms in North America (Hunter, 1997) to identify mail order vendors, then searched the World Wide Web (Web) to identify the price of adult *H. convergens* (including shipping and tax) for vendors who sold beetles by the 0.5 liter (a pint, the most commonly sold unit according to Cranshaw et al., 1996) or 3.8 liter (the gallon unit we purchased).

We compared beetle prices to the material cost for two home garden use soil-applied systemic insecticides (disulfoton and imidacloprid). Disulfoton (Systemic Rose and Flower, 2.3 kg or 5 lb granules from Bayer Corporation, Birmingham, Alabama, and also from Bonide, Oriskany, NY) is sprinkled around the base of plants. Imidacloprid (Advanced Tree and Shrub Insect Control, 0.9 liter or 32 oz liquid, Bayer Corporation) is measured into a bucket, diluted with water, and then poured onto soil at the base of plants. We priced these products at several retail outlets in Davis, CA, and from mail-order vendors located using Google (www.google. com) on the Web. Separately we calculated the average mail order and retail costs, including any shipping and tax.

2.9. Statistical analyses

Our sample units (buds) were pooled by plant to generate means for comparison. On each date, about 4 (SE = 0.2) and 17 (SE = 1) buds per plant were sampled, respectively, in the nursery and landscape. Except when samples were pooled by cultivar as described below, plants were our replicate, so the statistical N for analyses equals the number of plants sampled (df + 1 presented in ANOVA statistics).

We used PROC GLM, an ANOVA for unbalanced data (SAS Institute, 1988) for regressions of aphid control on potted plants. Means were compared with Tukey's tests. Because the same shoots were resampled over time in the landscape, we used repeated measures ANOVA, PROC GLM REPEATED (SAS Institute, 1988), with sample date as the repeated (within-subjects) factor and lady beetle releases and cultivar (during 2002) as the between-subjects factors. Landscape plant means were log(x + 1) transformed before ANOVAs to provide statistically valid comparisons of means and errors that may not be normally distributed and independent (Sokal and Rohlf, 1973) due to resampling landscape shoots each date.

For *H. convergens*-release treatments, we compared mean aphid density before and after releases and calculated "percent control" of aphids (C) according to Abbott's (1925) method

 $C = \left[(N - R) / N \right] \times 100,$

where N is the percentage of aphids alive (postrelease density divided by prerelease density, multiplied by 100) on nonrelease plants and R is the percentage of aphids alive on release plants at each sample interval after release.

To assess cultivar effects in the landscape during 1994 and 1995, we ranked the 20 uncaged (non-'Tropicana') plants from least infested (ranked 1) to most infested. Because most lady beetles disperse from plants within 2 days after release even when aphids are abundant (Dreistadt and Flint, 1996; Flint et al., 1995), we compared aphid counts on the day before and within several days after each release.

For each plant, we calculated the differences between ranks, and separately for each year we used Wilcoxon's signed-ranks tests (Sokal and Rohlf, 1973) to compare which plants had the most (and least) aphids: (1) before the first release in comparison with after the first release, (2) before the second release in comparison with after the second release, and (3) before the first release versus after the second release (N = 20 plants for each of three

comparisons per year). Separately for each year we also pooled samples by cultivar then used Wilcoxon's signed-ranks tests to make these same three comparisons (numbered 1–3 above), so that N = 15 (5 cultivars per year × 3 pairs of comparison dates for each year).

3. Results

3.1. Beetle releases

To assess whether inundative predator release controlled aphids, we conducted several outdoor trials in a nursery and the landscape (Table 1). A single augmentative release of adult *H. convergens* controlled aphids infesting *R. hybrida* 'Tropicana' in pots outdoors in a nursery. In comparison with prerelease densities, aphid numbers were significantly reduced at 2.5 days and about 1 week after a single release of 100 lady beetles per 19 liter potted rose during May 1994 and 1995 (Table 2). Lady beetle release provided 66–88% aphid control (Table 2). ANOVA statistics were: 1994 (F = 15.4; df = 5, 74; P < 0.0001), 1995 (F = 11.4; df = 5, 90; P < 0.0001).

Aphids on rose buds caged in the landscape were reduced significantly after the first release of 10–20 beetles per bud (Figs. 1 and 2), and almost all aphids were con-

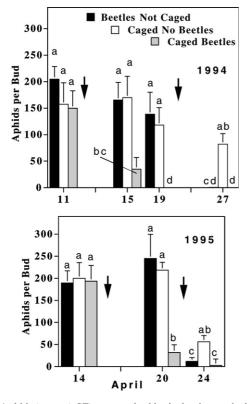


Fig. 1. Aphids (mean + SE) per rose bud in the landscape during April 1994 and 1995. Within years, bars topped by a same letter are not significantly different according to Tukey's tests for all paired comparisons (P > 0.05). See Table 3 for beetle release methods, numbers, and dates.

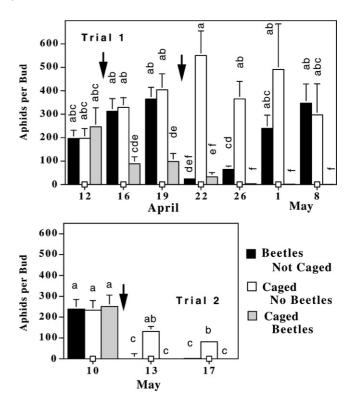


Fig. 2. Aphids (mean + SE) per rose bud in the landscape during 2002. Separately for each trial, bars topped by a same letter are not significantly different (P > 0.05) according to Tukey's tests for all paired comparisons. See Table 3 for beetle release methods, numbers, and dates.

sumed after a second release into cages during 1994, 1995, and 2002. Aphid densities were not reduced on uncaged buds after an initial release outdoors of about 20–50 *H. convergens* per bud during 1994, 1995, or 2002. A second release in the landscape of about 150–200 beetles per uncaged bud reduced aphids to near zero (Figs. 1 and 2). Aphids rebounded during 2002, and aphids were controlled by releasing about 300 beetles per bud 3 weeks after the second release (Fig. 2). Repeated measures ANOVA statistics for Fig. 1 are: 1994 (F = 15.0; df = 2, 15; P < 0.0001), 1995 (F = 6.7; df = 2, 15; P < 0.0001). Repeated measures ANOVA statistics for Fig. 2 are: first trial (F = 16.1; df = 2, 27; P < 0.0001), second trial (F = 118.5; df = 2, 24; P < 0.0001).

With release of sufficient numbers, lady beetles provided 93-100% aphid control on uncaged rose foliage (Table 3). The effective (aphid-controlling) rates in the nursery, or on caged buds in the landscape, were approximately 300-400 beetles/m² of foliage-covered ground area (Tables 2 and 3). On uncaged rose in the landscape, the effective rates were about 2300-2900 beetles/m².

3.2. Cultivar affects on predator augmentation

Aphid densities differed significantly among rose cultivars. However, there was no apparent affect of cultivar

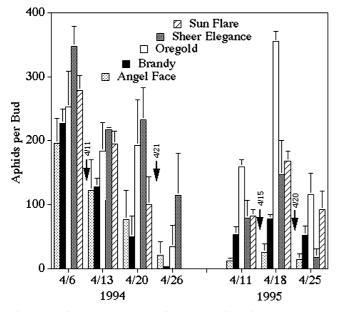


Fig. 3. Aphids (mean + SE) on five rose cultivars in the landscape before and after convergent lady beetle releases on open ground beneath uncaged plants during 1994 and 1995. Predation was not affected by cultivar, according to Wilcoxon's signed-ranks tests. The 1994 mean for 'Sun Flare' on 4/26 is zero.

on predation by *H. convergens* based on eight separate Wilcoxon's signed-ranks tests (Sokal and Rohlf, 1973) of the relative density of aphids among cultivars and plants before predator releases in comparison with after releases (Fig. 3).

During both 1994 and 1995, there were no significant differences (P > 0.05) among cultivars or plants in terms of which hosted the most or least aphids before the first release in comparison with after the first release, before the second release in comparison with after the second release, or before the first release in comparison with after the second release (Fig. 3). 'Angel Face' and 'Brandy' had the lowest aphid densities both before and after lady beetle releases. 'Oregold,' 'Sun Flare,' and 'Sheer Elegance' had the highest aphid densities.

During 2002 when *H. convergens* release-exclusion trials were conducted on three cultivars, there was no significant interaction between sample date and cultivar during all dates pooled for the first (12 April–8 May) trial (F = 2.0; df = 12, 32; P > 0.03) or the second (10–17 May) trial (F = 3.0; df = 4, 34; P > 0.03). There was no date-treatment-cultivar effect during the first (F = 1.4; df = 24, 58; P > 0.13) or second (F = 3.0; df = 8, 34; P > 0.04) trials. Individually by sample date, there was no significant (P > 0.05) date-cultivar interaction on 9 of 10 dates, and no date-treatment-cultivar effect during 8 of 10 dates.

The few comparisons indicating a cultivar effect may be because roses can differ among cultivars in their seasonal abundance and time of flowering, and flower bud development stage highly influences susceptibility to aphids (Maelzer, 1977). Also, statistically we would expect at least one Type 1 error when assessing cultivar effects using 24 regression analyses, each with a 0.05 significance level.

3.3. Release economics

Each 3.8 liter (1 gal) unit we purchased contained approximately 60,000 beetles, or an estimated range of 14,700–21,000 per liter (56,000–80,000 beetles/gal) (Cranshaw et al., 1996; Dreistadt and Flint, 1996). Our commercial supplier (A-1 Unique Insect Control, Citrus Heights, CA) reports selling \approx 19,000 liter (5000 gal) of convergent lady beetles each year, and estimates these sales are \approx 10% of the California market. Apparently several billion convergent lady beetles are collected and sold each year.

Hippodamia convergens is relatively inexpensive when purchased in bulk from a primary supplier. The 3.8 liter unit could be mail-ordered from a primary supplier during 2003 at a cost of about \$60 per gallon (3.8 liter), which included shipping within California. Out-of-state shipping from our supplier was about \$3 extra. H. convergens are also frequently sold by the 0.5 liter (1 pint) containing about 9000 beetles (Cranshaw et al., 1996). Assuming that beetles are healthy and plants are similar to ours, this 0.5 liter would temporarily control aphids on 90 relatively large potted (19-liter) roses or about six landscape rose shrubs (0.5-1 m tall) heavily infested with aphids. If beetles were purchased by the gallon (3.8 liter), this amount would be sufficient for one effective application to about 720 large potted roses or 51 landscape roses.

Depending on the supplier and unit size purchased, material cost for a single beetle-release is about \$0.10 to 0.50 per potted rose and \$1.30 to 7.20 per landscape rose. This compares with material costs of \$0.20 to \$9.40 per shrub for a homeowner application of systemic insecticide to soil. In comparison with one systemic insecticide application to soil, the lady beetles for three releases cost about the same, somewhat less, or much more than a soil-applied insecticide, depending on the number of beetles purchased, choice of insecticide (disulfoton versus imidacloprid), and where materials are purchased.

We assumed three lady beetle releases during April– May because this is when aphids are abundant on rose in California's Central Valley. Other natural enemies were rare on our nursery plants and relatively uncommon on landscape roses when we released beetles early in the growing season. Aphids gradually decline then largely disappear by late May or early June (data not presented), at least partly in response to warmer temperatures (Maelzer, 1977; Miles, 1985) and coincident with an increase in native natural enemies. Disulfoton application is much less expensive than releasing lady beetles. However, this broad-spectrum, "highly toxic" (EXTOXNET, 1996) organophosphate is not recommended by the University of California for rose aphid control (Flint, 2000; Flint and Karlik, 1999; Robb et al., 2001). On the other hand, one soil drench with imidacloprid costs about the same, to somewhat more or less, in comparison with the cost of lady beetles needed for three applications. Imidacloprid is a somewhat selective, newer class of insecticides (chloronicotinyls) of moderate acute toxicity (EXTOXNET, 1998) that is recommended by the University of California (Flint, 2000; Robb et al., 2001).

4. Discussion and conclusions

Our studies show that inundative release of commercially available convergent lady beetles can control high aphid densities in a limited area, such as a nursery or rose garden, when beetles are applied to each plant. About 2300 beetles/m² (210/ft²) were required to control high aphid densities on uncaged landscape rose. This effective release rate was two orders of magnitude greater than the 11-22 beetles/m² ($1-2/ft^2$) commonly recommended by beetle sellers (A-1 Unique Insect Control, 1998; Cranshaw et al., 1996; Rincon Vitova, 2002). Releases of 500 beetles/ m^2 controlled aphids when cages prevented beetle dispersal. About 400-500 beetles/m² were effective in an outdoor nursery, perhaps because our potted roses had lower aphid densities and less plant biomass/m² in comparison with landscape roses.

High rates are required because beetles leave plants on average 1–2 days after release even when aphids are present (Dreistadt and Flint, 1996; Flint et al., 1995). High rates can be effective because each *H. convergens* will eat about 100 aphids per day before dispersing (Dreistadt and Flint, 1996). Preconditioning beetles, such as allowing them to fly and feed prior to release, sometimes causes statistically significant differences in dispersal rates, but any impact of preconditioning on dispersal is modest (Dreistadt and Flint, 1996).

Roses differ by cultivar in characteristics such as blossom color and size (Witt et al., 2002), and we found that aphid population levels varied greatly among rose varieties. However, although plant cultivars of the same species sometimes differently affect natural enemies (Bottrell et al., 1998), there was no effect of cultivar on *H. convergens* release efficacy in our experiments. Cultivar selection and high-rate predator release are complimentary strategies for aphid management on rose.

Inoculative release of relatively low numbers of *H. convergens* from aggregations will not control aphids. In this study, during three years of releases in both the nursery and the landscape, we found no coccinellid

egg masses on our potted roses, and coccinellid eggs in only one landscape cage with released beetles (2002). As reviewed in our introduction, inoculative release of *H. convergens* from aggregations is likely to be ineffective because, even when aphids are abundant, beetle physiology induces adults to soon disperse. Furthermore, beetles rarely oviposit before dispersing. We also observed that few dispersing beetles move on to close by plants (Dreistadt and Flint, 1996). Thus, it is likely that beetles released at one part of a garden or outdoor nursery will provide little if any aphid control on adjacent plants.

We found that the cost and labor of releasing *H. con*vergens purchased from wholesale suppliers was similar to a soil application of the systemic insecticide imidacloprid. If purchased in bulk directly from a primary supplier, H. convergens are relatively inexpensive and (in our experience) of good quality. However, consumers should be cautioned when considering over-the-counter purchase of *H. convergens*. Retail units contain relatively few beetles, are relatively expensive per beetle, and retail beetles can be of poor quality (Cranshaw et al., 1996; O'Neil et al., 1998). Some advise strongly against any release of convergent lady beetles (Obrycki and Kring, 1998). The potential ecological or nontarget impacts of large-scale harvesting of beetles from aggregations and relocating them from natural dispersal sites have not been investigated. There are quarantine considerations regarding the shipment of field-collected insects, which may harbor microorganisms, parasites, or other invertebrates. Adverse effects of release might be subtle and easily overlooked, such as compromising locally adapted H. convergens genotypes through mating with introduced specimens (Obrycki et al., 2001). On the other hand, concerns regarding pesticide hazards make lady beetle releases attractive for aphid control for gardens, greenhouses, and small nurseries, especially those seeking organic certification.

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