

The effects of natural enemies, competition, and host plant water availability on an aphid population

William F. Morris*

Department of Zoology, NJ-15, University of Washington, Seattle, WA 98195, USA

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Summary. I used a factorial experiment repeated in two years to assess the relative effects of natural enemy attack, interspecific competition, and water availability to the host plant, and of interactions among these factors, on the population dynamics of the aphid *Aphis varians* feeding on fireweed (*Epilobium angustifolium*). The impact of a suite of coccinellid and syrphid predators emerged as the predominant factor affecting the success of aphid colonies: colonies protected from natural enemies grew in size at a rate of ten percent per day, were only one tenth as likely to go extinct, and produced over ten times more dispersing alates. In contrast, I found only minor effects of removing flea beetles, the most abundant herbivore with which *A. varians* colonies cohabit fireweed stems, and of supplementing water availability to fireweed host plants, in spite of a significant effect of watering frequency on aphid growth in the greenhouse. There was no evidence of significant two- or three-way interactions among factors. Hence, despite the potential complexity of the food web in which it is embedded, the dynamics of *A. varians* appears to be driven predominantly by a single factor, i.e. interactions with natural enemies.

Key words: *Aphis varians* – Three trophic level interactions – Population dynamics – Higher-order interactions – Insect herbivores

Occupying an intermediate position in most terrestrial food webs, populations of insect herbivores are vulnerable to assault on three fronts: they may be limited by the availability or suitability of their host plants; they may compete with other herbivores; and they may fall prey to natural enemies. This observation raises two interrelated questions that have long occupied the attention of community ecologists. First, can we identify

which of these 3 factors has the greatest effect on the density or dynamics of a given herbivore population or of herbivores in general? Better understanding of the relative effects of natural enemies, competitors, and host plants would allow us to determine the degree to which herbivore characteristics such as host plant range are dictated by host plant chemistry vs. generalist predators (see Bernays and Graham 1988 and accompanying papers), and how often interspecific competition plays a significant role in the ecology of insect herbivores (Hirston et al. 1960; Lawton and Strong 1981; Strong et al. 1984; Karban 1986; Harrison and Karban 1986). Second, do biotic factors operating at different trophic levels have interactive effects on herbivore populations? (Lawton and McNeill 1979; Price et al. 1980; Faeth 1987). For example, do host plant features alter the susceptibility of herbivores to natural enemy attack? (Smiley et al. 1985; Price and Clancy 1988). We need to examine the extent of such interactive effects if we are to understand the complexity of the links joining insect herbivores to other species in the community, and consequently the level of complexity we need to build into our models of community dynamics (Murdoch and Walde 1989).

Despite the long history of debate surrounding these questions, few experimental studies have simultaneously manipulated biotic factors on the three trophic levels that impinge directly on insect herbivores (but see Karban 1989). Here I report the results of a study focused on the fireweed aphid *Aphis varians* in which I altered the availability of water to host plants, the density of a potential competitor, and natural enemy attack in a full factorial experiment. While factorial experiments have long been used to study multiway interactions in freshwater communities (Wilbur 1972, 1987; Morin 1986; Van Buskirk 1988; Wilbur and Fauth 1990; Huang and Sih 1991), they have been less commonly used to study interactions involving insect herbivores. Using analysis of variance, I evaluate the relative effects of natural enemies, competitors and host plant suitability on aphid performance, and I test for interactions among these factors.

* Present address and address for offprint requests: Center for Population Biology, University of California, Davis, CA 95616, USA

Methods

Natural history of the field system and rationale for experimental manipulations

Parthenogenetic generations of the aphid *Aphis varians* Patch feed exclusively on the upper stems and developing flower buds of fireweed (*Epilobium angustifolium* L.) at the study site located at 900 m in elevation within the Mount St. Helens National Volcanic Monument, Washington State, USA. Fireweed dominates the zone in which trees were blown down by the 1980 eruption of Mount St. Helens, and is currently growing in discrete clumps of stems, most of which probably represent individual fireweed clones. Below I describe the biotic factors whose effects on the performance of *A. varians* colonies were examined.

At Mount St. Helens, aphid colonies are attacked by a wide variety of natural enemies, the most common of which are the adults and larvae of ladybird beetles (*Hippodamia convergens*, *Coccinella transversoguttata*, and *Scymnus* sp.) and the larvae of syrphid flies (*Scaeva pyrastris*, *Epistrophe* sp.). Lacewing larvae (Neuroptera: Chrysopidae) and braconid wasps (*Aphidius* sp.) are less commonly encountered. The experiments described below were designed to quantify the impact of this ensemble of natural enemies on aphid colony performance.

The population of *A. varians* I studied shares fireweed stems with > 12 other species of insect herbivores (personal observation). I examined whether *A. varians* colonies compete with the flea beetle *Altica tombacina* Mann. (Coleoptera: Chrysomelidae), which was the most abundant fireweed herbivore encountered at the site (flea beetle density averaged 5.7, 49.3, and 2.1 larvae per stem in 1987–1989 (Morris et al. 1992)). Flea beetle adults chew holes in the upper leaves of fireweed stems in late spring, and the larvae strip the underside of leaves throughout the summer, often causing extensive damage (see Table 5 below).

Host plant water status has often been shown to affect aphid performance (Wearing 1967; Wearing and van Embden 1987; Service and Lenski 1982; Michels and Undersander 1986; Sumner et al. 1986). To determine if *A. varians* is sensitive to fireweed water status, I conducted a greenhouse experiment in which I grew aphid colonies on potted fireweed plants subjected to a range of watering frequencies. Since I found a significant effect of fireweed water status on *A. varians* growth in the greenhouse (see Results), I incorporated a watering treatment into the field experiment described below.

At other locations throughout western USA, *A. varians* colonies are tended by ants, which can significantly reduce the impact of natural enemies on colony persistence and growth (Addicott 1978b, 1979; Cushman and Addicott 1989). However, the study site was dominated by an old growth douglas fir forest prior to the eruption of Mount St. Helens, where the density of ants is typically low (Sugg 1989). Substantial ant recolonization had not occurred at the time of the experiments reported here (< 5% of the experimental aphid colonies were tended by ants (personal observation)).

Greenhouse watering experiment

To assess the sensitivity of *A. varians* growth to host plant water status, I varied the frequency of watering of potted fireweed plants on which I established aphid colonies. Thirty six fireweed plants initiated from seeds collected at Mount St. Helens were grown in a standard potting soil mixture in 3000 cm³ pots in a greenhouse on the University of Washington campus. When plants began to produce flower buds, I randomly assigned them to one of three watering frequency treatments (the soil within the pots was soaked either daily, every other day, or every fourth day). Twelve days after initiating the watering treatment, I established a single *A. varians* colony on each stem and enclosed the colonies in bags constructed from spun-bonded polyester, the same material used to construct cages for the factorial experiment described below. I counted the

number of aphids in each colony at the end of seven days. I then performed a Kruskal-Wallis non-parametric analysis of variance to test for effects of watering frequency on the ratio of final to initial number of aphids.

Three-way factorial experiment

Experimental design. In a field experiment repeated in two years, I manipulated host plant water availability, the density of a potentially competing herbivore, and the intensity of natural enemy attack, and then quantified their effects on aphid performance. At the initiation of fireweed shoots in May, 1988, I chose 32 discrete fireweed clones and thinned them to 5 stems per clone. Each clone was then randomly assigned to one of two natural enemy treatments (enemies present or absent), one of two competitor treatments (flea beetles present or removed), and one of two host plant treatments (control or watered). Treatments are described in detail below. The host plant, competition, and natural enemy treatments were crossed in a full factorial design, yielding eight treatment combinations, each replicated four times (Table 1).

To exclude natural enemies, I enclosed fireweed clones in 1.75 × 1.75 × 1.75 m cages constructed from spun-bonded polyester (Reemay™) supported by four wooden poles and buried at the ground surface. Throughout the experiment, any natural enemies found within the cages were removed. In addition to excluding natural enemies, cages may exert other effects on aphid performance (e.g. by altering environmental conditions). I used 2 procedures to control for the indirect effects of cages. First, aphid colonies to which natural enemies were allowed access were enclosed in half cages of the same design as the full cages but which, while creating similar shading and wind reduction effects, were open on their east and west faces to allow natural enemies access to the fireweed stems within. Second, I corrected the measures of aphid colony growth using an estimate of indirect cage effects obtained from the literature. Turchin and Kareiva (1989) compared the growth rate of *A. varians* colonies enclosed in Reemay bags to that of colonies from which all natural enemies were removed by hand. The growth rate of colonies in the hand removal treatment was 92% that of bagged colonies. I corrected for indirect cage effects by multiplying the estimates of growth rate (see “Data Analysis” below) for colonies in full cages by 0.92 prior to analysis. This correction had no effect on the outcome of the analysis; consequently the unadjusted growth rates are reported below.

On fireweed clones assigned to the flea beetle removal treatment, all flea beetle eggs, larvae, and adults were removed by hand at weekly intervals. On the remaining clones, flea beetles were left at ambient densities.

Table 1. Design of 3-way factorial experiment to determine effects of natural enemies, competitors, and host plant water stress on aphid performance

Natural Enemy Treatment ^a	Competition Treatment ^b	Host Plant Water Stress Treatment ^c	Number of Replicate Cages
P	P	W	4
		C	4
		W	4
	A	C	4
A	P	W	4
		C	4
		W	4
	A	C	4

^aP = natural enemies present (open cages); A = natural enemies absent (closed cages)

^bP = flea beetles present; A = flea beetles removed

^cW = supplemental watering; C = control

The ground surrounding fireweed clones assigned to the watering treatment was soaked twice weekly throughout the summer with 15 L of water collected from a stream bordering the experiment, while control cages were not watered.

On each of the five stems within a cage, I established a colony of *A. varians* by temporarily attaching a section of fireweed inflorescence infested with aphids to the experimental stem and allowing the aphids to transfer. Each new aphid colony was then thinned to 10 individuals. I censused all colonies at weekly intervals, recording the number of winged and wingless aphids (hereafter referred to as alatae and apterae, respectively). Each week, extinct colonies were replaced with new ones as described above. Censuses were discontinued in September at the end of the fireweed flowering period, at which point the aphids had completed approximately 8 asexual generations.

I repeated the experiment in 1989 with 2 modifications. First, since natural flea beetle densities were extremely low in 1989 (Morris et al. 1992), I supplemented the high flea beetle density treatment by placing fireweed leaves infested with approximately 50 flea beetle larvae into the appropriate cages, while continuing to remove beetles from flea beetle removal cages. The resulting larval density was within the range of natural densities observed at the site (Morris et al. 1992). Second, due to above-average rainfall in 1989, fireweed clones assigned to the watering treatment were watered only once per week. Hence the difference in water availability between watering treatments was greater in 1988 than in 1989.

Data analysis. To quantify the effects of water availability, competition, and natural enemy attack on the success of *A. varians* colonies, I measured three indices of aphid performance. First, I calculated the average daily rate of colony extinction within each experimental cage by dividing the total number of colony extinctions by the duration of the experiment, measured in days. Since I replaced extinct colonies at each weekly census, I was able to record continuous extinction rates throughout the season.

Second, I calculated the rate at which aphid colonies grew in size through asexual reproduction. Asexual reproduction reduces the probability of clone extinction both by mitigating the effects of demographic stochasticity and by reducing the per capita risk of predation by a major predator of *A. varians* clones, the ladybird beetle *Hippodamia convergens* (Turchin and Kareiva 1989). In addition, asexual reproduction affects the number of dispersing alates produced, since the number of alates per colony is correlated with colony size (see Results). To quantify asexual reproduction, I calculated the daily per capita growth rate λ of each aphid colony, averaged over all census intervals, using the formula:

$$\lambda = (1/S) \sum_{i=2}^S (N_i/N_{i-1})^{1/\tau_i}$$

where N_i is the number of aphids at the i^{th} census (alatae plus apterae), τ_i is the number of days between the $i-1^{\text{th}}$ and the i^{th} censuses, and S is the number of censuses.

Thirdly, I quantified alate production directly by calculating the maximum number of alates observed per colony. Alate production is a crucial component of colony success, since alates serve to

colonize additional fireweed stems as well as the woody hosts (*Ribes* spp.) on which *A. varians* overwinters. The maximum number of alates was square root transformed prior to analysis.

I analyzed each index of performance using a fixed effects three-way analysis of variance model (using the SYSTAT MGLH Procedure, Wilkinson 1989) to test for main effects of the natural enemy, competition, and watering treatments, and for all two- and three-way interactions among these factors. Since the five aphid colonies within each cage cannot be treated as independent sample units, average values for each cage were used in the analysis.

Results

The effect of water availability: greenhouse experiment

A reduction in the frequency of watering resulted in a significant decline in the growth of aphid colonies in the greenhouse (Kruskal-Wallis test statistic = 6.97; $df = 2$; $p = 0.031$). When fireweed plants were watered only once every four days, aphid colonies declined in size (i.e. the ratio of final to initial numbers of aphids was less than one), while colonies on well-watered plants increased in size (Fig. 1).

The relative effects of water availability, competition, and natural enemies

The natural enemy treatment had a highly significant effect on the extinction rate of *A. varians* colonies in the

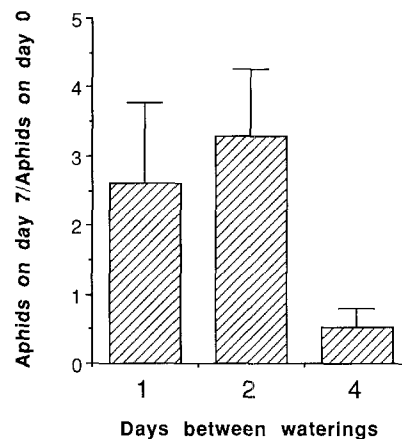


Fig. 1. The effect of watering frequency on the growth of aphid colonies on potted fireweed plants

Table 2. Analysis of variance results for the daily rate of colony extinction

Source	1988					1989				
	SS	df	F	p	% SS _T	SS	df	F	p	% SS _T
Watering	0.00004	1	0.301	0.59	0.2	0.00001	1	0.0607	0.81	0.04
Competition	0.00006	1	0.470	0.50	0.3	0.00068	1	6.48	0.018	3.0
Natural Enemies	0.0158	1	120.4	< 1 × 10 ⁻⁹	81.9	0.0188	1	179.1	< 1 × 10 ⁻⁹	4.1
W × Comp	0.00000	1	0.0188	0.89	0	0.00003	1	0.330	0.57	0
W × NE	0.00001	1	0.0752	0.79	0.05	0.00000	1	0.00674	0.94	0.7
Comp × NE	0.00012	1	0.922	0.35	0.6	0.00016	1	1.52	0.23	0.7
W × Comp × NE	0.00012	1	0.922	0.35	0.6	0.00016	1	1.52	0.23	0.7
Error	0.00315	24			16.3	0.00252	24			11.3

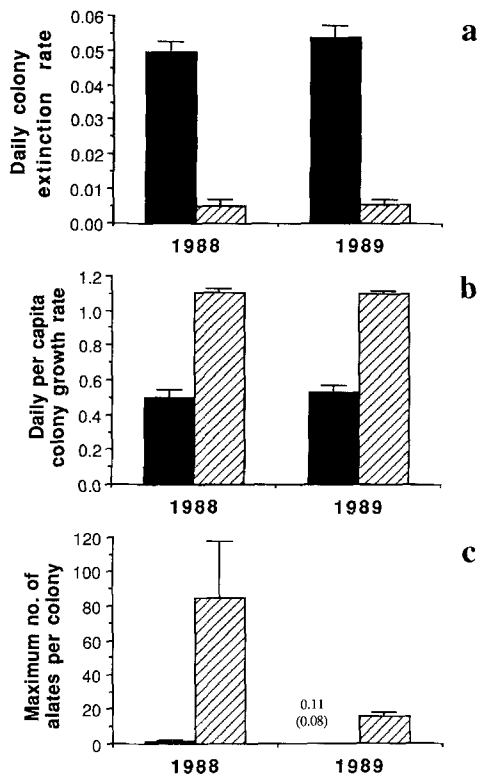


Fig. 2. Three measures of aphid performance in the presence (open cages = ■) and absence (closed cages = ▨) of natural enemies. a) extinction rate; b) rate of asexual reproduction; c) maximum number of alates per colony

field in both years (Table 2). When protected from attack by natural enemies, the rate of colony extinction declined to one tenth the rate in the open cages (Fig. 2a). Similarly, the removal of natural enemies strongly affected both the rate of asexual reproduction and the number of alates produced in both 1988 and 1989 (Tables 3 and 4). In closed cages, colonies grew at a rate of approximately 10% per day (Fig. 2b). In contrast, the average growth rate of colonies exposed to predation was substantially less than 1, indicating that, while some colonies managed to grow in spite of predation pressure, most declined in size. Colonies that grew large produced more alates (Fig. 3). Consequently, the maximum number of alates observed on colonies protected from natural enemies was more than ten times greater than on colonies in open cages (Fig. 2c).

In contrast with the natural enemy removal treatment, the effects of the competitor removal and watering treatments were relatively small and inconsistent between years. In 1989, the removal of flea beetles led to a slight but significant decline in the probability of colony extinction (Table 2, Fig. 4a) and a marginally significant increase in the rate of colony growth (Table 2, Fig. 4b). However, these effects were not significant in 1988, despite the fact that beetle removal resulted in a more pronounced difference in the amount of flea beetle damage in 1988 than in 1989 (Table 5). Surprisingly, there was no evidence of a decline in growth rate even on fireweed clones which were completely defoliated by flea beetles in 1988 (Fig. 5).

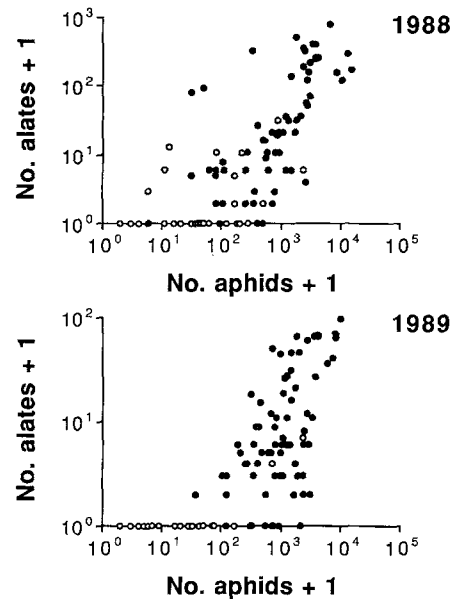


Fig. 3. The relationship between maximum colony size and the maximum number of alates observed. Open dots – open cages; closed dots – closed cages

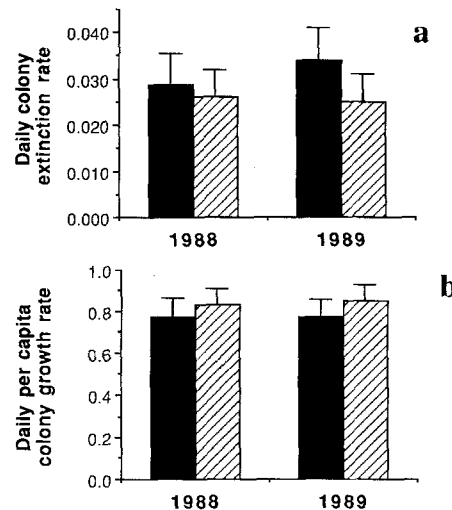


Fig. 4. The effect of flea beetle removal on a) extinction rate and b) rate of asexual reproduction (beetles present = ■, absent = ▨)

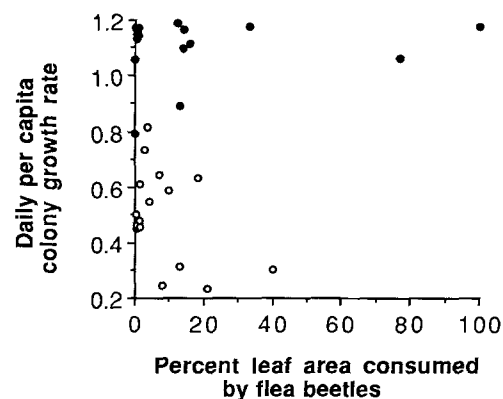


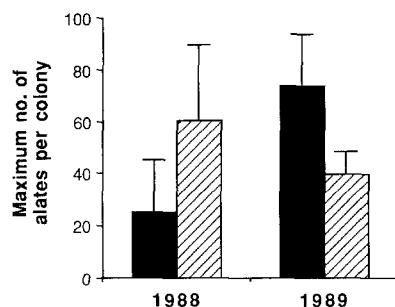
Fig. 5. The relationship between flea beetle damage and the rate of asexual reproduction of aphids on experimental clones in 1988. Open dots – open cages; closed dots – closed cages

Table 3. Analysis of variance results for the daily per capita rate of colony growth

Source	1988					1989				
	SS	df	F	p	% SS _T	SS	df	F	p	% SS _T
Watering	0.00000	1	0.000	1.0	0	0.00001	1	0.00038	0.99	0
Competition	0.0259	1	1.15	0.29	0.7	0.0514	1	3.73	0.065	1.7
Natural Enemies	2.887	1	128.1	$<1 \times 10^{-9}$	82.2	2.62	1	189.4	$<1 \times 10^{-9}$	86.8
W × Comp	0.00935	1	0.415	0.53	0.3	0.00295	1	0.213	0.65	0.1
W × NE	0.00158	1	0.0702	0.79	0.05	0.00394	1	0.285	0.60	0.1
Comp × NE	0.0389	1	1.72	0.20	1.1	0.00403	1	0.292	0.59	0.1
W × Comp × NE	0.00760	1	0.337	0.57	0.2	0.00581	1	0.420	0.52	0.2
Error	0.541	24			15.4	0.331	24			11.0

Table 4. Analysis of variance results for the maximum number of alates per colony (squareroot transformed)

Source	1988					1989				
	SS	df	F	p	% SS _T	SS	df	F	p	% SS _T
Watering	43.6	1	2.20	0.15	5.5	26.2	1	26.2	0.051	6.0
Competition	20.1	1	1.01	0.33	2.5	6.90	1	6.90	0.30	1.6
Natural Enemies	272.9	1	13.8	0.0013	34.5	240.0	1	240.0	$<1 \times 10^{-5}$	5.1
W × Comp	0.106	1	0.00535	0.94	0.01	2.05	1	2.05	0.57	0.5
W × NE	34.8	1	1.76	0.20	4.4	3.07	1	3.07	0.49	0.7
Comp × NE	3.30	1	0.167	0.69	0.4	4.70	1	4.70	0.39	1.1
W × Comp × NE	0.285	1	0.0144	0.91	0.04	3.10	1	0.497	0.49	0.7
Error	415.8	24			52.6	149.6	24			34.3

**Fig. 6.** The effect of the watering treatment on the maximum number of alates per colony (control = ■, watered = ▨)

In contrast to the greenhouse experiment, the watering treatment had little effect on aphid performance in the field. There was a marginally significant decline in the maximum number of alates per colony due to the watering treatment in 1989 (Table 4 and Fig. 6). An opposite effect of watering, though not significant (Table 4), was observed in the dryer summer of 1988 (Fig. 6), suggesting that the effect of watering is unpredictable from year to year.

A simple way to assess the relative effects of natural enemy attack, competition, and water availability on aphid performance is to examine the percentage of the total sum of squares in the analysis of variance that is attributable to each factor (cf. Morin et al. 1988, Wilbur and Fauth 1990). Note that it is appropriate to make such a comparison in this case since the sum of squares assigned to each term in the ANOVA (both main effects and interactions) has the same number of degrees of freedom (Tables 2–4). The presence or absence of natural

enemies clearly emerges as the dominant factor dictating aphid performance. More than 80% of the variance in the rates of extinction and asexual reproduction was due to the natural enemy treatment in both years, while the variance attributable to competition and watering treatments was comparatively negligible (Tables 2 and 3). Although the maximum number of alates per colony had more unassigned variance (note the large Error terms in Table 4), the natural enemy treatment still explained a much higher percentage of the total variance than did the competition or watering treatments.

Interactions among natural enemy, competition, and watering treatments

Although all three treatments had significant main effects on at least some aspects of aphid performance in at least one year, there was no evidence of interactions among water availability, competition, and natural enemy attack in either year of the study (Tables 2–4). None of the

Table 5. The effect of the flea beetle removal treatment on the percentage of leaf area damaged by flea beetles in experimental cages

	Percent leaf area damaged (mean ± SE)		
	Beetles present	Beetles removed	Probability ^a
1988	25.03 ± 6.69	0.90 ± 0.25	<0.001
1989	5.00 ± 0.65	0.34 ± 0.14	<0.001

^a Based on Mann-Whitney U Test with 1 df

two or three way interactions accounted for more than 5% of the variance in aphid performance among experimental cages (Tables 2–4).

Discussion

The factorial experiments reported here demonstrate that natural enemy attack is the predominant biotic factor dictating the success of *Aphis varians* colonies feeding on fireweed at Mount St. Helens. When protected from natural enemies, aphid colonies were only one tenth as likely to go extinct; they grew in size at a rate of 10% per day while control colonies tended to decline; and they consequently produced over ten times more dispersing alates. The magnitude of the natural enemy effect was remarkably consistent between years (Fig. 2). In contrast, the effects of competitor removal and watering were both minor and variable: there was weak evidence for an effect of competitors on aphid colony survival and growth, and of watering on production of alates, in 1989 but not in 1988.

The absence of strong competitive effects of flea beetles, even when they caused massive damage to fireweed foliage, may be due to the fact that *A. varians* and flea beetles feed on different portions of fireweed stems. Apparently, flea beetle damage to leaves has little effect on the nutritional quality of the phloem at aphid feeding sites on developing flower buds. Most studies that have detected significant competition between insect species sharing the same host plant have focused on herbivores feeding on the same plant tissues (McClure and Price 1975; Seifert and Seifert 1976; Stiling 1980; Gibson and Visser 1982; Stiling and Strong 1983, 1984; Karban and Carey 1984; Karban 1986; Harrison and Karban 1986; Stamp 1984; but see Strauss 1991a). In fact, Addicott (1978a) found that *A. varians* nymphs grew significantly smaller on greenhouse cuttings of fireweed that they shared with the aphid *Macrosiphum valerianae*, which feeds on phloem just below *A. varians* on fireweed inflorescences (Addicott 1978a). A fruitful avenue for future research would be to extend the experiments presented here to other fireweed herbivores that, while less abundant than flea beetles, may exert stronger competitive effects on *A. varians*.

The minor effects of manipulating water availability in the field, in contrast with watering experiments conducted in the greenhouse, probably indicates that fireweed plants that did not receive supplemental water rarely experienced sufficient water stress to affect the performance of aphid colonies they harbored. The alternative hypothesis, that both watering treatment and control plants were equivalently drought stressed, seems unlikely given that summer rains were frequent at Mount St. Helens, especially in 1989, and that none of the experimental plants exhibited obvious visual signs of drought stress (personal observation). Physiological measurements of fireweed water status during the aphid growing season would be valuable, as would further experiments that manipulate additional host plant characteristics (e.g. plant genotype, Karban 1989) that might influence aphid success.

Despite the potential for complexity in this mul-

tiespecies system, the absence of significant interactions among natural enemy attack, competition, and water availability indicates that the dominant influence of natural enemies on *A. varians* dynamics is not altered by the interspecific competitors or host plant characteristics I examined. These results parallel those of the only other published study of insect herbivores that simultaneously manipulated host plants, competitors, and natural enemies. Karban (1989) found that plume moths (*Platypilia williamsii*) feeding on *Erigeron glaucus* were limited only by predation, while spittle bugs (*Philaenus spumarius*) were limited only by competition with plume moths. In the 3 years of Karban's study, only one of 24 possible two- and three-way interactions among host plant genotype, competition, and predation were significant.

Since the insect community on fireweed was at an early successional stage at the time of this study, the system offers a unique opportunity to examine whether the complexity of interactions affecting *A. varians* populations will change as more species, particularly ants, invade the community. In addition to the potentially advantageous effect of removing honeydew, ants are known to indirectly benefit *A. varians* colonies by protecting them from natural enemy attack (Addicott 1978b, 1979; Cushman and Addicott 1989). Ants may also have indirect effects on the interaction between *A. varians* and its competitors, in two different ways. First, ant tending may directly increase the density of other aphid species that feed on fireweed to the detriment of *A. varians*. By reducing predation pressure, ant tending may thus lead to the emergence of a competitive interaction between *A. varians* and other fireweed aphids (cf. Edson 1985). Second, *A. varians* colonies have been shown to engage in both intra- and interspecific competition for the attention of ant mutualists (Addicott 1978b; Cushman and Addicott 1989). This raises the possibility that, as ants invade the study site, the relative impact of predation and competition on *A. varians* success may shift as ants reduce the intensity of natural enemy attack and become a limiting resource for which *A. varians* colonies must compete. These questions could be addressed by conducting 3-way factorial experiments akin to those reported here that manipulate ant, aphid, and natural enemy densities.

The predominant effect of a single factor and the absence of higher order interactions, both in this study and in that of Karban (1989), lend credence to the view that it may be possible to capture the dynamics of some multispecies associations by utilizing simplified models that incorporate only the dominant interactions among species (Murdoch and Walde 1989). Nevertheless, significant higher order interactions have been amply documented both for insect herbivores (Starks et al. 1972; Price and Clancy 1986; Faeth 1985, 1986; Weis and Abrahamson 1986; Kareiva and Sahakian 1990) and in aquatic communities (Wilbur 1972, 1987; Morin 1986; Morin et al. 1988; Wilbur and Fauth 1990; Huang and Sih 1991), where factorial experiments have a venerable history. The question ecologists must now address is how often higher order interactions play a significant role in community dynamics (Strauss 1991b). Only through repeated use of factorial experiments and other approaches

(for a review see Wilbur and Fauth 1990 and Strauss 1991b) will we gather the information needed to build such generalizations.

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