Effect of Host-plant Genotype and Neighboring Plants on Strawberry Aphid Movement in the Greenhouse and Field

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ABSTRACT.—Herbivore movement behavior is a key mediator of how host-plant populations affect herbivore populations. We examined the effects of host-plant genotype and variance among host-plant genotypes on movement rates of apterous strawberry aphids, *Chaetosiphon fragaefolii* (Cockerell) (Homoptera: Aphididae), on *Fragaria chiloensis* (L.) P. Mill. In the field we estimated aphid movement rates over several years on experimental populations of five different plant genotypes. In the greenhouse, we followed the movement of individual aphids in plant arrays of a single genotype or three different genotypes. In both cases, aphid apterae movement differed among host plant genotypes, with more movement on higher quality genotypes. Movement rate in the field was also influenced by aphid population size. In the greenhouse, aphids showed no taxis toward particular plant genotypes but left different plant genotypes at different rates. Aphids also tended to move more often among plants in three genotype arrays (with a variety of plant genotypes) than predicted by their movement in single genotype arrays. Our results suggest that dispersal among plants by strawberry aphid apterae is affected by plant characteristics associated with genotype and quality of the host plant for the herbivore.

INTRODUCTION

Populations of insect herbivores often inhabit populations of host plants that are heterogeneous in quality as food (Denno and McClure, 1983). In natural systems, plant species or individuals may differ genetically in quality (Fritz and Simms, 1992), and in both natural systems and agricultural monocultures, plants may differ phenotypically in quality as a result of microhabitat, developmental stage or inducible resistance (*see, e.g.,* Lewis, 1984; Rossi and Strong, 1991; Karban and Baldwin, 1997). When hosts vary in quality, herbivore movement becomes an important aspect of the interaction between plant and herbivore populations. The amount and selectivity of herbivore movement will determine how herbivores sample plants and, therefore, how the plants affect herbivore population growth (Underwood, 2004). When herbivores move, they may also suffer performance costs due to energy expended, lost feeding time (Schultz, 1983), variation in their diet (Stockhoff, 1993) or increased vulnerability to predators (Bergelson and Lawton, 1988). Understanding how

herbivores move in heterogeneous environments is thus crucial to understanding how host plants affect herbivore populations and vice versa. As part of a larger study of how genetic variation in host quality influences the population dynamics of a specialist aphid [*Chaetosiphon fragaefolii* (Cockerell), strawberry aphid], we examined the effect of host [wild strawberry, *Fragaria chiloensis* (L.) P. Mill.] genotype on among plant movement of aphids in field and greenhouse experiments. In this study, all aphids were apterous, so all movement occurred by walking (or possibly wind transport) rather than flying.

Herbivores may change their movement rates in response to two levels of host-plant variation. First, they can respond behaviorally to the characteristics of individual plants, either through taxis toward preferred or (more commonly) movement away from less-preferred plants (Bernays and Chapman, 1994). Although studies have documented behavioral responses of many herbivorous insects to individual plant characteristics (Barker *et al.*, 1995; Hannunen and Ekbom, 2002), apterous aphids have sometimes been assumed not to be important dispersers (Jepson, 1983; Honek *et al.*, 1998), and relatively few studies have examined their movement responses to plant characteristics. Apterous aphids are, however, known to move among plants (*see, e.g.,* Tamaki *et al.*, 1970; Edson, 1985; Antolin and Addicott, 1991) and to respond to differences in quality both within plants (Jepson, 1983; Harrington and Taylor, 1990) and among plants (Schotzko and Smith, 1991; Honek *et al.*, 1998). In addition, herbivore movement rate can be affected by the amount of variation among neighboring host plants (Bernays, 1999). A substantial body of work addresses the effects of variation among plants on herbivore numbers (Andow, 1991), but fewer studies have explicitly considered effects of the level of variance among hosts on herbivore behavior (but *see* Tahvanainen and Root, 1972; Cantelo and Sanford, 1984; Wetzler and Risch, 1984; Bernays, 1999). The one study of this kind that we know of in aphids (Power, 1991) found that aphids move more in plant populations with more variance in quality.

To understand how insect populations are affected by the plant population they inhabit, we need to know whether herbivore movement is affected by plant identity (species or genotype) and/or by the variety of plant types present. In the present study, we addressed both these issues for movement of a specialist aphid. In both the field and the greenhouse, we asked whether movement rates of strawberry aphid apterae vary among plant genotypes (question 1). In the greenhouse, we asked two additional questions: (2) Is aphid host preference expressed as taxis toward plants or as the rate at which plants are left? (3) Is aphid movement influenced by variation among host plants in the population?

MATERIALS AND METHODS

STUDY ORGANISMS

Wild strawberry and the strawberry aphid are native to the Pacific coast of the Americas, and plants and aphids are active year round in coastal dune populations in northern California, where this research was conducted. *Fragaria chiloensis* occurs near the coast in Chile, the Hawaiian Islands and from California to Alaska (Hancock and Luby, 1993). In California, it grows both in sandy sites such as dunes and bluffs and in coastal grasslands (Alpert *et al.*, 1993; Alpert, 1999, pers. obs.). California populations are typically dioecious (Alpert *et al.*, 1993; Hancock and Luby, 1993), and genets are easily cloned from asexual runners. Clones vary in their resistance to disease and herbivores, including strawberry aphids (Hancock and Luby, 1993). Apterous strawberry aphids are diminutive (0.9–1.3 mm in length, Rondon and Cantliffe, 2004) specialists on the genus *Fragaria* and do not alternate hosts. Although they may reach high densities on irrigated strawberry crops (*Fragaria x ananassa*, Shanks and Finnigan, 1972), typical densities were fewer than five

aphids/plant on *F. chiloensis* near our field site, and aphids are dispersed over the plant rather than forming dense colonies. Parasitism occurs very rarely in these aphids (Oatman and Platner, 1972; Shanks and Finnigan, 1972), and was never observed in 3 y of censuses in our field populations. Generalist predators have been suggested to influence populations of *Chaetosiphon fragaeflii* on strawberry crops (Shanks and Finnigan, 1972), but generalist aphid predators were also rare in our field site.

Plant clones for our experiments were collected in the field (Sonoma County, California, clones 'Wrights 2' and 'Doran 3') or obtained from the USDA National Clonal Germplasm Repository (Corvallis, Oregon, clones '34', '46', '55' and '361'). All plants used in these experiments resulted from several "generations" of asexual reproduction in a common greenhouse environment. Likewise, we collected *Chaetosiphon fragaefolii* for these experiments from multiple populations in the field (Sonoma County, California) and reared them for several generations in the greenhouse. We reared aphids on a shifting mixture of strawberry genotypes not used in these experiments. Because colonies experienced a variety of plant genotypes whose identities changed through time, it is unlikely that they underwent conditioning that could lead to a feeding bias within the aphid populations.

We used wild strawberry rather than cultivated strawberry varieties for these experiments because this work is part of a larger study of how genetic variation within a host-plant population influences insect herbivore population dynamics (Underwood, 2009); thus we were concerned with estimating responses to naturally occurring genotypes rather than cultivated varieties.

ESTIMATING MOVEMENT IN THE FIELD

The field experiment was conducted at the University of California Bodega Marine Reserve (Sonoma County, California, USA). We estimated aphid movement on five different plant genotypes using three years of census data from *Fragaria chiloensis* populations in the field that were part of an experiment examining long term aphid population dynamics (Underwood, 2009). A full description of the experimental design is in Underwood (2009). Briefly, each experimental plant population used for these analyses consisted of six plants of a single clone (a monoculture—*see* Fig. 1 in Underwood, 2009; there were monocultures of each of the five different genotypes). Aphid populations were initiated by placing one adult aphid from the laboratory colony on each plant in each population, and aphids were reintroduced at the same density when aphid populations went extinct. No natural aphid populations occur in the area where the experiment was conducted. Migration of aphids from outside the experimental area or between populations within the experiment is highly unlikely because in preliminary experiments (data not shown), plants more than 1 m from a plant with aphids were never colonized over several weeks of observation. Over 3 y, we counted the aphids on each plant in each population every 10 to 20 d during the peak season for aphids (~May–Jul.; new aphid populations were initiated for each field season). Under the experimental conditions, generation times for these aphids are approximately 2 wk. Although strawberry aphids have five instars, we could reliably distinguish only three size classes in the field: large (adult), medium and small. The experiment included 22, 12 and 13 populations in 2000 [n = 4 (genotypes 55, 361, D3) or n = 5 (genotypes 34, W2)], 2002 [n = 4 (genotype 34) or n = 2 (all others)], and 2003 [n = 3 (genotypes 34, D3, W2) or n = 2 (genotypes 55, 361)], respectively, and we censused populations 6 to 9 times per year.

To estimate aphid movement from these data, we counted instances in which aphids clearly moved to a plant, which we called a 'gain.' We considered gains rather than movement away from plants ('losses') because we could not distinguish losses from
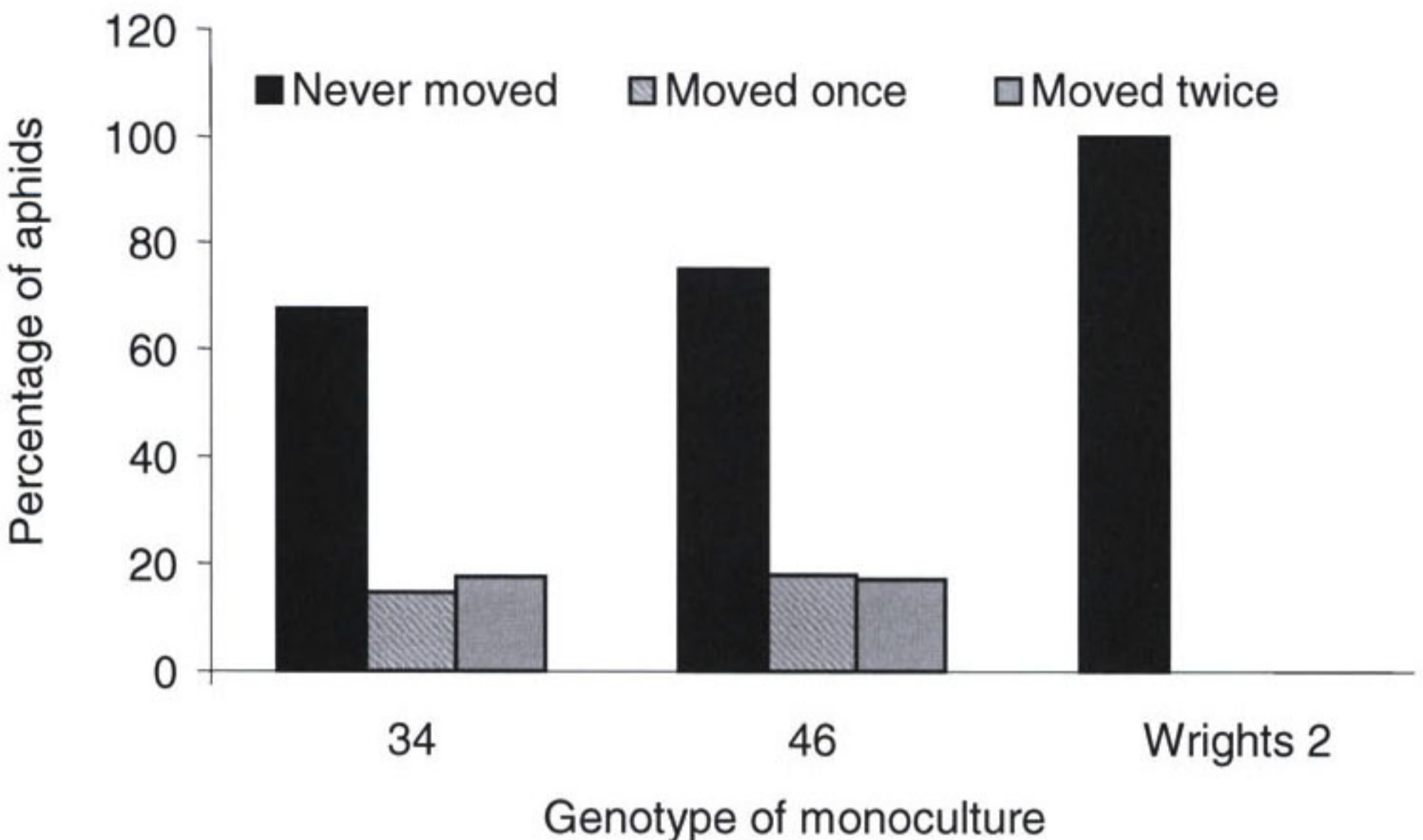
FIG. 1.—Effect of plant genotype in monocultures on aphid movement over four single-aphid movement trials in the greenhouse. Each aphid was observed twice at 24-h intervals and scored as having moved (from one plant to another) or not. Genotype significantly affected aphid movement rate (n between 28 and 34 for each genotype)

mortality. To avoid confounding reproduction with movement, we followed strict rules for coding increases in aphid numbers as gains. If any aphids were present on a plant in the previous census, the number of gains was the difference between the number of large aphids in the current census and the sum of all aphids in the previous census. This rule precluded incorrectly counting either offspring of resident aphids or aphids that had grown into larger size classes as gains from movement. If no aphids were present at the previous census, the number of gains for a plant was either the number of large aphids (excluding medium and small aphids for the same reason as before) or the sum of the numbers of medium and small aphids, if large ones were absent. These rules may lead to conservative estimates of gains. For example, a plant that had 3 small aphids in one census and 3 large and 10 small aphids in the next could have gained aphids from reproduction, movement of small aphids, or both, but we counted it as a gain of zero because we could not determine the source of the small aphids. When an entire population went extinct (*i.e.*, had zero aphids at a census), we excluded that data point from movement analyses because no movement could be observed in the absence of aphids.

To compare gains on different plant genotypes, we calculated total gains for all six plants in a population at each census and average gains per census for each year. We estimated gains per census because years differed in number of censuses. Because aphid population size might affect the probability of movement, or the probability of detecting a gain, we also calculated average aphid number for each population each year and used it as a covariate in analyses.

We tested for differences in movement among genotypes using a general linear model with three factors (PROC GLM in SAS). We confirmed that the error structure met the assumptions of the analysis. We compared gains per census for different plant genotypes

using a model including total number of aphids per census, year, genotype and all two-way interactions as predictors.

ESTIMATING MOVEMENT IN THE GREENHOUSE

Greenhouse experiments were conducted at the University of California, Davis. We rooted plants in 25.4-cm Cone-tainers (Stuewe & Sons, Corvallis, Oregon, USA) in UC Davis greenhouse potting mix, watered plants as needed and fertilized with Miracle-Gro (The Scotts Company, Marysville, Ohio, USA). Plants received supplemental light, and the greenhouse temperature was maintained between 25 and 27 C.

We examined aphid movement in two types of three plant arrays: monocultures of each of three different clones ('46,' 'Wrights 2' and '34') and a mixture of all three clones (the triculture). To imitate the natural sand dune habitat of the plants, we placed each three-plant array in sand in a 2 gal bucket (sinking the Cone-tainer for each plant into the sand). To avoid disturbing aphids, plants were watered (as needed) by hand at the soil surface with a watering can. Plants were evenly spaced near the perimeter of the bucket, approximately 14 cm apart. We placed a wooden toothpick in the center of the array, 7 cm from each plant. The toothpick was about as tall as the plants and provided a neutral point from which aphids could be released into the array. To prevent aphid movement into or out of the buckets, we entirely covered each bucket with a light mesh net bag (Fibe-Air Sleeve, Kleen Test Products, Milwaukee, Wisconsin, USA). The experiment included seven replicate arrays (buckets) of each treatment type for a total of 28 arrays; buckets were arranged randomly on greenhouse benches.

Each movement trial began with placement of an adult aphid on the top of the toothpick. Trials started in the evening, and we recorded the aphid's location (plant clone) every 24 h for 72 h. (In preliminary trials, we did not detect additional movement with more frequent observations.) At each census, we also recorded the number, size and location of any offspring, and offspring were removed at each census. If the adult aphid could not be located, we ended the trial and started a new aphid trial in the same array. No aphids were ever found on the toothpick after release, so they either moved to a plant or were lost and not included in analyses. Individual aphids were used only once in the experiment, and up to 16 aphids were run in each array. Trials were conducted in four temporal rounds, starting in Feb. and ending in Apr. of 2004.

We calculated two measures of aphid movement from these data. For each trial we determined the aphid's initial location (first plant on which it was found) and its movement rate among plants. To calculate movement rate, we assigned a score of zero to each instance in which the aphid did not move between observations (was found on the same plant at two successive observations) and a score of one to each instance in which the aphid had moved between plants. We averaged the observations for each aphid to produce a single movement rate score for that aphid. Array (individual bucket) was never a significant factor in any analysis and was dropped from analyses presented here. For all analyses, therefore, each datum consists of the average movements of a single aphid during a single trial. Because movement scores could take one of only three values, we used nonparametric statistics for these analyses. We compared movement rates on the three monocultures to each other using a Kruskal-Wallis test.

We also compared fecundity of aphids in monocultures of the three different genotypes. We measured fecundity as the number of daughters produced per adult aphid per observation. We tested for differences in aphid fecundity among plant clones using ANOVA. Fecundity was square-root transformed for analysis to produce residuals that showed no significant deviation from a normal distribution.

TABLE 1.—Sources of variation in aphid movement rates (measured as population gains per census) in monocultures in the field. The tests used Type III sums of squares, and gains were square-root transformed before analysis. n = 47. P values indicating significant effects ($\alpha = 0.05$) indicated in bold

Source	df	SS	F	P
Total aphid number (per census)	1	0.56	11.1	**0.003**
Year	2	0.37	3.65	**0.041**
Total aphid number × year	2	0.01	0.07	0.930
Genotype	4	0.65	3.20	**0.030**
Total aphid number × genotype	4	0.73	3.59	**0.019**
Year × genotype	8	0.24	0.59	0.777
Residual	25	1.26		

TAXIS AND EFFECTS OF HETEROGENEITY ON MOVEMENT IN THE GREENHOUSE

We addressed questions 2 and 3 using data from the arrays in the greenhouse. To determine whether aphids showed taxis toward particular plant clones, we compared the distributions of initial locations among the three clones in the mixed arrays using a G-test. To test for an effect of plant heterogeneity on aphid movement we compared movement in the heterogeneous environment to the average movement rate in the homogeneous environments by comparing the mixed arrays to the pooled monocultures using a Wilcoxon two-sample test. Using the pooled monocultures tests whether movement rates in the mixed arrays is greater than the average of movement in the monocultures. Finally, we asked whether aphid movement away from each particular clone depended on the plant context in which the clone was growing. To do so, we compared movement rates of aphids in monocultures of a particular clone (*e.g.*, Wrights 2) to those of aphids observed on that same clone in mixed arrays using a Kruskal-Wallis test. An alpha-level of P = 0.05 was used in interpretation of all statistical tests.

RESULTS

MOVEMENT RATES AMONG GENOTYPES OF DIFFERENT QUALITY

We detected movement of aphid apterae in both environments. In the greenhouse, aphid movement rate ranged from an average of 0.21 moves/census (round one) to an average of 0.12 moves/census (round 4). In the field, we identified at least one gain in 43% of the population-census combinations. We observed 0 to 14 gains per population in individual censuses (mean = 0.88, median = 0) and 0 to 23 gains per population per year (mean = 6.6, median = 6).

Movement rates of aphids varied significantly in these experiments. Plant genotype affected overall aphid movement rates in the greenhouse ($\chi^2_{df = 2} = 11.3$, $P_{two-tailed} = 0.0035$) and the field (P = 0.03, Table 1). In the greenhouse, aphids moved most often in monocultures of clone 34 and least often in monocultures of clone Wrights 2 (Fig. 1). In the field, post-hoc tests of the genotype main effect on gains indicate that genotype 55 had fewer gains than all other genotypes (all P < 0.02) but that gains for the other four genotypes were not statistically distinguishable (all P > 0.76).

In addition, gains in the field generally increased as population sizes increased (main effect of total aphid number, Table 1), but plant genotypes differed in the relationship between population size and number of gains (genotype–by–total aphid number interaction, Table 1, Fig. 2). The effects of plant genotype on this relationship are driven
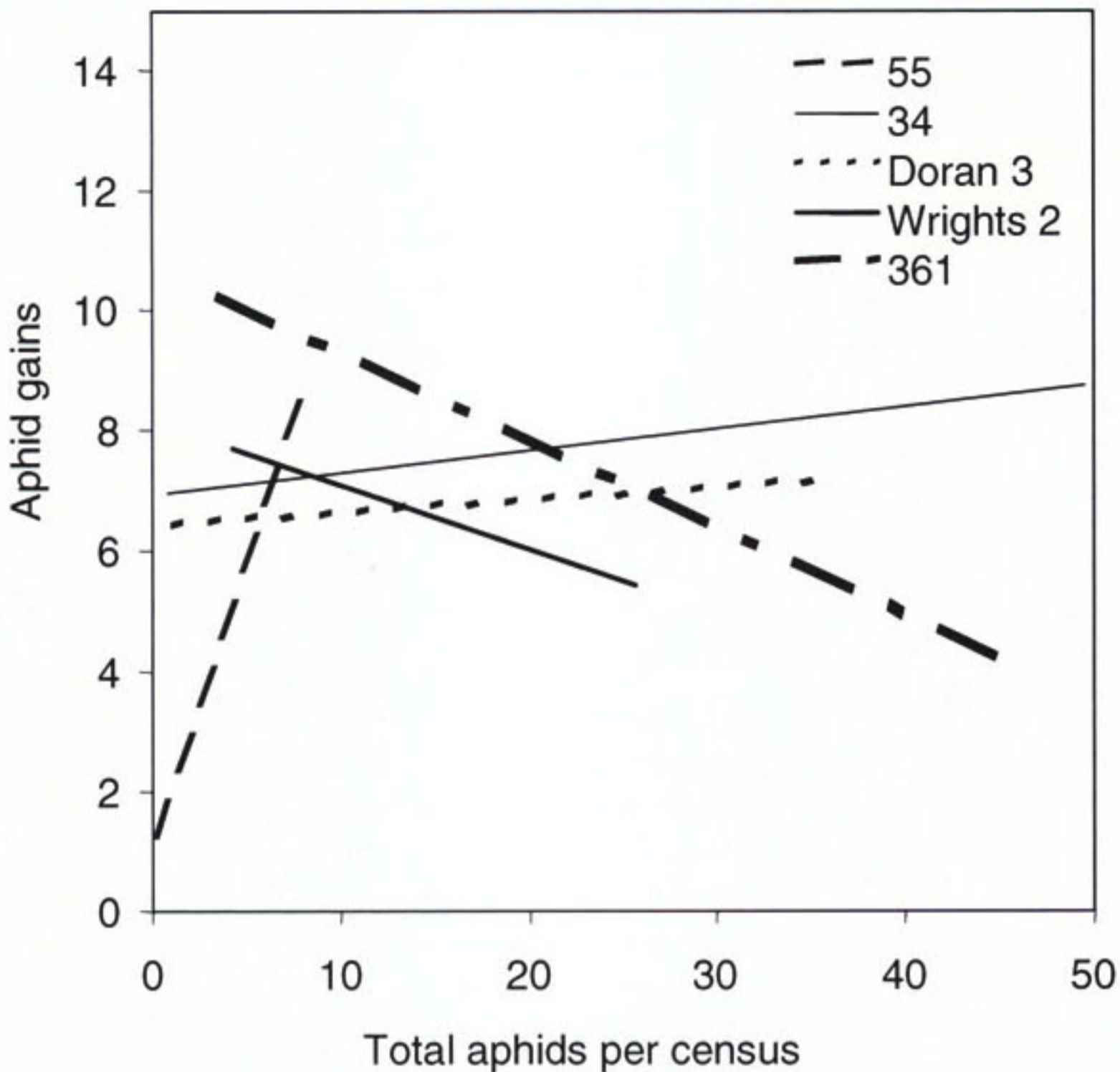
FIG. 2.—Effect of plant genotype on the relationship between aphid movement rate (measured as the number of aphids gained by individual plants between censuses) and overall aphid population size in monocultures of each plant genotype in the field. Lines are least-squares regressions

largely by genotype 55: higher aphid population sizes were strongly associated with higher gains for genotype 55 but had weaker effects for other genotypes. Slopes of the relationship between aphid population size and gains ranged from positive to negative. The slope of this relationship was significantly different from zero for genotype 55 (β = 0.20 ± 0.06, P = 0.003) and marginally significant for genotype 34 (β = 0.02 ± 0.01, P = 0.075).

TAXIS AND EFFECTS OF HETEROGENEITY ON MOVEMENT

Aphids did not show taxis toward particular plant clones within the mixed arrays (number of aphids initially found on Wrights 2 = 12, on 34 = 11 and on 46 = 13). The overall movement rate of aphids in mixed (heterogeneous) arrays was somewhat higher than that in monocultures (Fig. 3). The difference was marginally significant by a one-tailed test corresponding to our expectation, based on the results of previous studies (Power, 1991; Bernays, 1999) that movement would be more frequent in the more-heterogeneous triculture (Wilcoxon $P_{one-tailed}$ = 0.056). Moreover, when aphids were most active (in the first round of the experiment), the greater movement in the heterogeneous arrays was highly significant (Wilcoxon $P_{one-tailed}$ = 0.003). The trend toward higher movement in the mixed arrays was due to significantly greater movement of aphids away from Wrights 2 plants when those plants were in the mixed arrays than when they were in monoculture (pooled data, $\chi^2_{df = 1}$ = 11.8, $P_{two-tailed}$ = 0.0006, Fig. 4). For the other two clones, the monocultures and the triculture did not differ in movement rates.
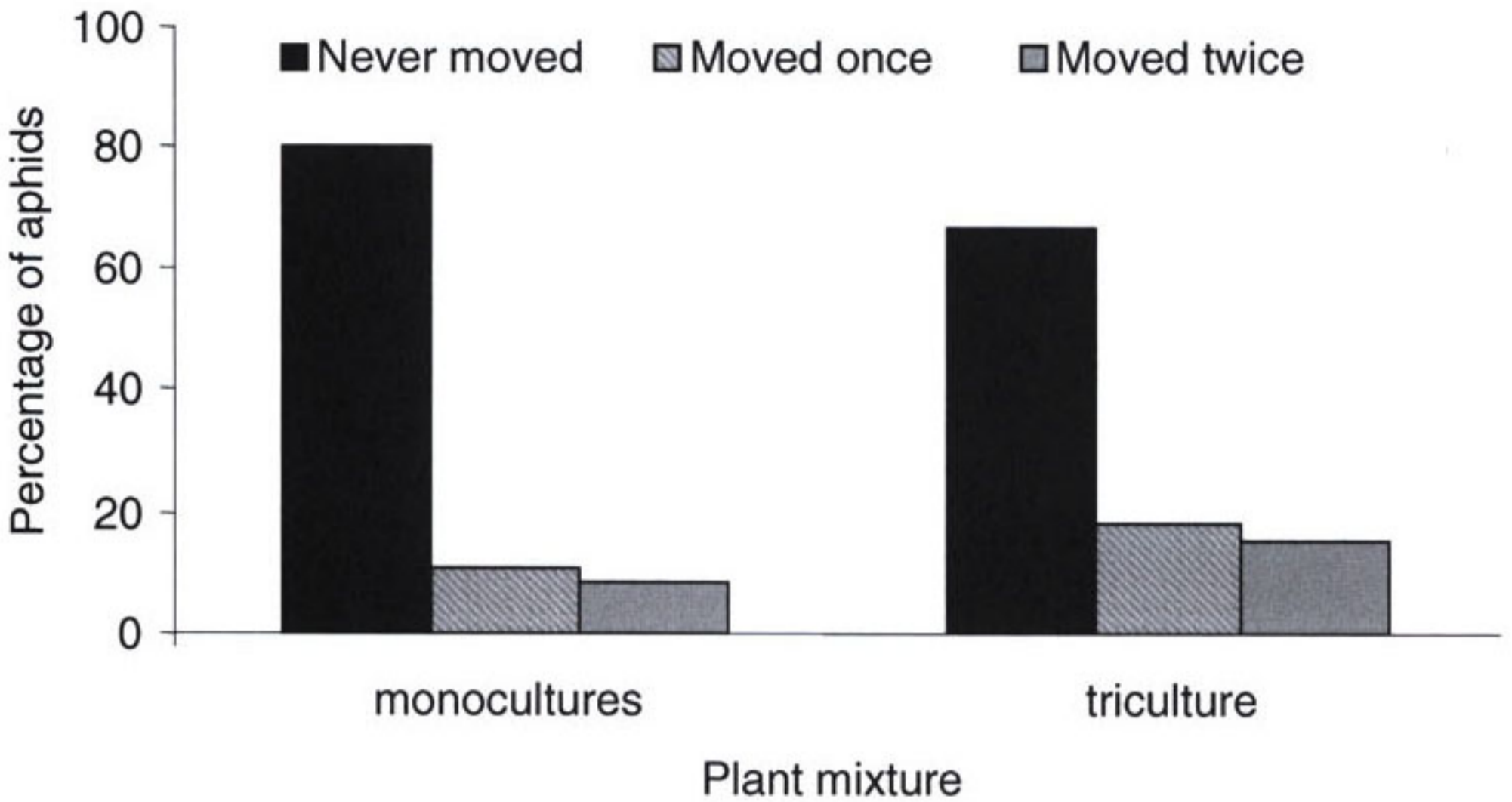
FIG. 3.—Effect of plant mixture type on aphid movement. Data from four movement trials in the greenhouse were pooled. Monocultures consisted of plants of a single genotype (three types of monocultures pooled); tricultures were a mixture of the three genotypes used in the monocultures. Aphids moved significantly more often in the triculture in the first trial, but this effect was only marginally significant in the pooled data because of lower overall movement in the later trials. n = 33 for the tricultures and 99 for the monocultures

APHID FECUNDITY

In the greenhouse, plant clones differed significantly in aphid fecundity in the three monocultures ($F_{2,86}$ = 9.17, P = 0.0002). Fecundity was highest on genotype 34 and lowest on genotype Wrights 2.
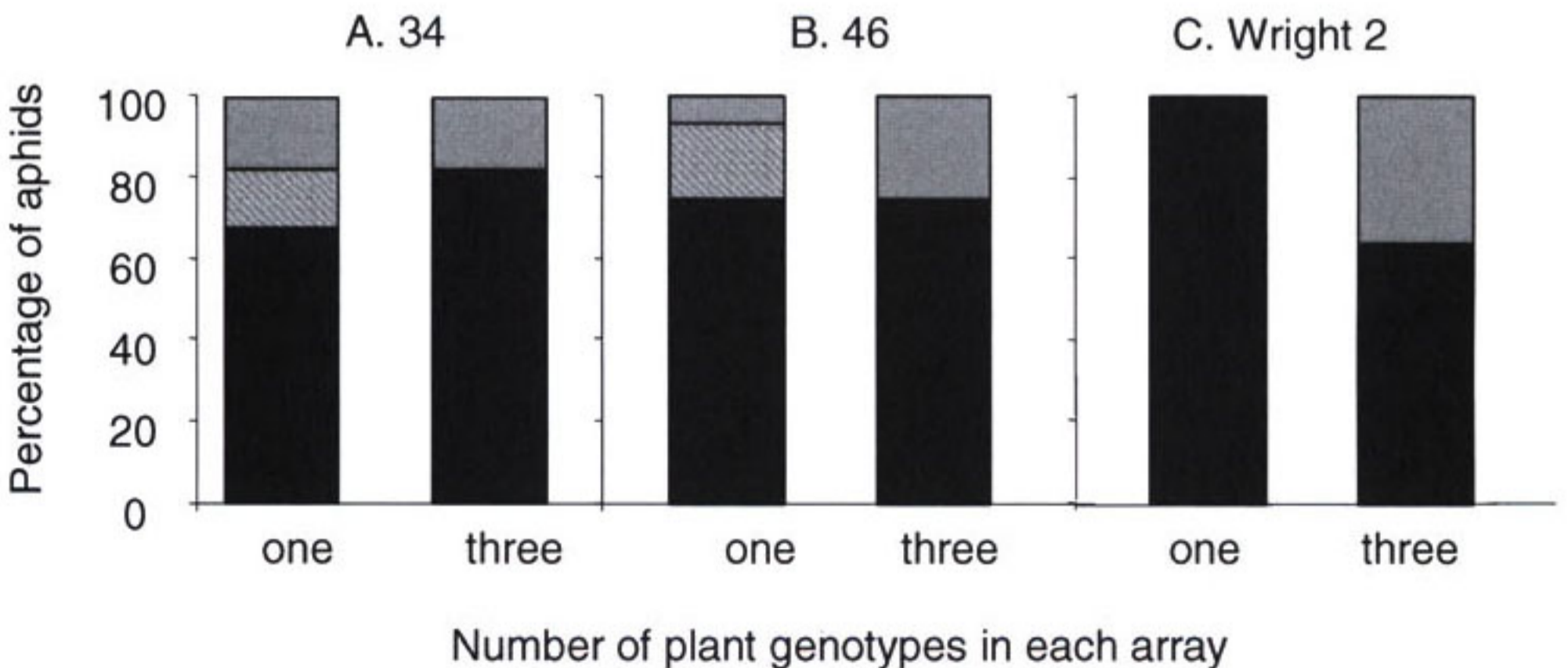

FIG. 4.—Effect of plant mixture type on aphid movement away from genotype 34 (A), genotype 46 (B) and genotype Wrights 2 (C). Data from four movement trials in the greenhouse were pooled. Aphid movement rate from Wrights 2 in the triculture differed significantly from that in the monoculture. n = 33 for each monoculture and triculture. Bar patterns as in Figure 1

DISCUSSION

Our observations suggest that intrapopulation movement among plants by *Chaetosiphon fragaefolii* at our sites is likely to be dominated by walking. In Sonoma County, California, where the field portion of this research was done, alates of this aphid are quite rare (Underwood, pers. obs.). In both the greenhouse and the field, we found that apterous strawberry aphids moved among plants. Movement of aphids away from plants in the greenhouse, in the absence of predators or abiotic disturbances such as wind or rain, suggests that they left the plants voluntarily, rather than as a result of being disturbed or dislodged. Once these aphids have left plants, they are able to travel across sand for an observed minimum of 14 cm in the greenhouse and 25 cm in the field, even under hot and dry conditions (Underwood, pers. obs.).

MOVEMENT DIFFERS AMONG HOST PLANT GENOTYPES

Our experiments indicate that the genotype of the host plant affects walking movement by *Chaetosiphon fragaefolii* (question 1). When apterous aphids can respond to differences among plants by moving, then they can contribute to host choice (*e.g.*, Caillaud, 1999). Although most host-plant choice in aphids is assumed to be exercised by alates (Blackman, 1990), in this system alates are rare. If most dispersal within populations is attributable to apterae, then apterous aphids should be able to exercise some host choice.

To qualitatively assess the relationship between host plant quality and aphid movement, we estimated host plant quality for genotypes in the two experiments. In the greenhouse, we compared host plant quality using aphid fecundity. We chose this measure of host plant quality because aphid densities were very low in this study; fecundity at low densities is related to the intrinsic rate of increase, which is also measured at low densities and can vary among genotypes in the greenhouse (Underwood, 2007). In the field, where aphid populations were much greater, we used published estimates of the equilibrium population size of aphids on different genotypes to rank host plant quality; the ranking (K) was 361 (24.5) $\geq$ Doran 3 (14.3) > Wrights 2 (8.2) $\geq$ 34 (6.6) $\geq$ 55 (0.2) (Underwood, 2009).

In both the greenhouse and the field, the lowest quality genotypes had the lowest average movement rates, and vice versa. The trend toward a positive relationship between plant quality and aphid movement is somewhat puzzling, although it has also been observed in other sucking insects (Hannunen and Ekbom, 2002). We might expect aphids to move less on high quality plants (in order to stay there), especially because our greenhouse results suggest that strawberry aphid movement does not include taxis toward particular plant genotypes. One explanation for the positive correlation between quality and movement would be a tendency for adults to move after reproducing, perhaps to reduce competition between nymphs. If higher quality plants allow faster reproduction, the result would be higher movement rates on high quality plants. In natural populations in Sonoma County, first-instar aphids are commonly seen alone on plants (Underwood, pers. obs.), as they would be if adults moved after reproduction.

In addition to overall lower movement rates on lower quality plants, the data from the field suggest that *Chaetosiphon fragaefolii* movement is influenced by population size, although this effect depends on plant quality (Fig. 2). For plant clones that hosted large aphid populations on average, increasing population size had little effect on the tendency to move. In contrast, for the plant clone that hosted the smallest aphid populations (genotype 55), the number of moves observed increased as population size increased. This pattern could arise if aphids are less tolerant of increasing density on low quality than on high quality plants. Alternatively, observing movement might be easier initially in small, growing

populations but more difficult to perceive as populations become large because plants are already occupied. This latter process is unlikely to be driving the observed pattern for two reasons. First, plant clones differ in the slope of the relationship between population size and movement as measured by numbers of aphid gains, even over ranges of aphid population sizes at which all the clones overlap in population size (Fig. 2). Second, adding aphid population size as a quadratic term to the ANOVA of effects of plant clone on gains (providing an initially increasing and then decreasing relationship between population size and gains, as would be expected if detection of movement changed with aphid density) did not improve the model significantly ($P = 0.2146$).

TAXIS AND HETEROGENEITY

Our greenhouse results show that aphid movement does not include taxis toward particular plants but rather consists of moving away from certain plants (question 2). This pattern also occurs in host races of both alate and apterous pea aphids, *Acyrthosiphon pisum* (Harris), which do not preferentially settle on their preferred host plant species but do rapidly leave the alternative host before feeding (Caillaud, 1999; Caillaud and Via, 2000). These results suggest that strawberry aphids (like pea aphids) cannot compare plants from a distance but must interact closely with them to detect cues, such as plant chemistry, that they use to evaluate quality and to determine whether to remain on the plant.

In comparison with some other studies (*e.g.*, Caillaud and Via, 2000), *Chaetosiphon fragaefolii* appear to move away from plants relatively slowly (*i.e.*, in days rather than minutes). Because we observed aphids more frequently in preliminary trials for the greenhouse study (N. Underwood, pers. obs.), we know that these aphids do stay put for long periods of time on individual leaves. The extremely small size of *C. fragaefolii* may contribute to their generally slow movement rates. It's also possible that characteristics of the plant and habitat affect how quickly *C. fragaefolii* move. For example, the ventral leaf surface where these aphids feed are extremely hirsute, which may hinder movement or increase the time required for aphids to insert stylets into cells that provide chemical information about the plant.

The greenhouse results suggest that movement of *Chaetosiphon fragaefolii* may also be affected by the context in which the current plant occurs (question 3). Aphids in the greenhouse tended to move more in the triculture than would be predicted from their average movement in monocultures of the clones included in the triculture (Fig. 3). In particular, aphids were more likely to leave strawberry clone Wrights 2 in the triculture than in the monoculture. These data suggest that surrounding plants might influence aphid movement. Several other studies have found greater movement of insect herbivores in mixtures than in monocultures in the lab (Bernays, 1999) and field (Power, 1991). More data are clearly needed before we can clarify the extent to which host-plant variation affects strawberry aphid movement.

When they occur, changes in movement with variation among plants can affect both herbivore population dynamics (Underwood, 2004) and disease spread through plant populations (Power, 1991). In particular, host plant variation can influence herbivore population sizes when herbivores move among plants, and in theory the influence of variation should increase as movement increases (Underwood, 2004). Variation among host plants can directly influence strawberry aphid population size (Underwood, 2009). If strawberry aphid movement also increases with variation among plants, the effect of variation in plant quality on aphid populations could be magnified.

CONCLUSION

We conclude that strawberry aphid apterae voluntarily move among plants and can respond behaviorally to the genotype of the plant on which they occur. Although alates are sometimes assumed to be primarily responsible for host-plant choice (Blackman, 1990), apterous aphids can also respond behaviorally to their hosts, can be important dispersers (Hardie, 1980), and may choose among plant genotypes that differ in quality. Our evidence from the greenhouse also suggests that they might respond to the level of variation among plants in a population, although this pattern clearly bears further investigation. Thus, even a diminutive herbivore that might be expected to move relatively little can respond actively to its host plant environment.

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