

Variation in the outcome of competition between two aphid species on pecan: plants matter more than predators

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The relative importance of resource-mediated competition versus apparent competition was studied in two native aphids, *Monellia caryella*, and *Melanocallis caryaefoliae*, on pecan, *Carya illinoensis*. We compared reproduction and body size of the two aphid species when they were caged on pecan leaves as single or mixed species, and when green lacewing larvae (*Chrysoperla comanche* or *Chrysopa nigricornis*) were present or absent. The experiment was repeated two times on mature compound leaves in the field in the autumn of 1997 and summer of 1998 and once in a greenhouse, on young seedlings with simple leaves.

Our results suggest that interspecific competition was variable and asymmetric; in both the Summer 98 experiment and the greenhouse experiment, reproduction of *M. caryaefoliae* was significantly reduced in the mixed species treatments relative to the single species treatment, while *M. caryella* reproduction was significantly reduced only in the Summer 98 experiment. No evidence of an effect of competition on reproduction was found in the Autumn 97 experiment. *M. caryella* body size was reduced in one of the mixed species treatments in the Autumn 97 experiment. Body size of both aphid species was reduced in the mixed species treatments of the greenhouse experiment.

The introduction of green lacewing larvae reduced the reproduction of aphids in two of the three experiments in comparison to controls. However, a significant interaction between aphid and predator treatment (*M. caryella* in the greenhouse experiment) was found in only one experiment. Variation in the outcome of competition was more likely to be due to aspects of plant quality, including leaf age and previous aphid feeding.

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The importance of interspecific competition among phytophagous insects has been the subject of lively debate for the last few decades (e.g. Hairston et al. 1960, Schoener 1983, Denno et al. 1995). Denno et al. (1995) presented abundant evidence for the importance of competition in its impacts on the persistence, abundance, or fitness of herbivore populations and has marked the start of a renewed appreciation for the role of competition in structuring communities. Especially relevant to this study, Denno et al. (1995) found that there was more evidence for competition in sessile

insects, especially in the sap-feeding Homoptera, and that competition was more intense among closely related taxa (Miller 1967), and in managed as opposed to natural systems. Other studies have found less support for the importance of interspecific competition in herbivore dynamics (e.g., Lawton and Hassell 1984, Strong et al. 1984, Cornell et al. 1998).

Many possible biotic influences on the outcome of competition have been recognized, and can be categorized as ‘top-down’ and ‘bottom-up’ effects (Hunter and Price 1992, Power 1992). ‘Top-down’ attacks from

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natural enemies may change the relative abundance of co-occurring herbivores. This has been called 'apparent competition' (Holt 1977), in which independent interactions of herbivores with their shared natural enemies may lead to patterns similar to those expected by direct resource-based competition. Apparent competition may operate by several different mechanisms. An example is if the natural enemies exhibit preference for one of the herbivore species (Settle and Wilson 1990, Karban et al. 1994) or if no preference is exhibited but density thresholds for predator aggregation are more likely to be exceeded in two-species patches leading to suppression of the slower growing species (Müller and Godfray 1997). Over a longer period, the prey species with a greater reproductive rate will better be able to withstand non-selective predation and will prevail over the slower-growing species (Holt and Lawton 1993, Bonsall and Hassell 1997). Over a shorter period, the reverse situation can also occur; predator satiation in two-species patches may lead to a short-term 'apparent mutualism' of the predator with the slower-growing population (Edson 1985, Bergeson and Messina 1997).

An emerging area of study is the potential influence of the 'bottom-up', host-plant quality effects on competitive outcome (Karbon and Myers 1989, Hunter and Price 1992, Power 1992, Masters et al. 1993, Inbar et al. 1995, Karban and Baldwin 1997, Inbar et al. 1999, Fisher et al. 2000). Clearly, these effects are likely to be complex, with variation in plant nutrition, constitutive plant defense, and local and systemic induced responses all having the potential to differentially affect one of a pair of herbivores sharing the same plant resource. These types of indirect interactions are likely to be relatively common, and are interesting because like other 'interaction modifications' (Wootton 1994), changes in the intermediary species (here the host plant) alters not only the relative abundance of the competing species, but also the quality of the interaction between the herbivores. The extent to which plant quality explains spatial and temporal variation in the intensity of herbivore competition is still not well known (Denno et al. 1995).

Identification of the relative potential importance of 'top-down' and 'bottom-up' forces in mediating interspecific competition within particular communities is likely to provide a clearer understanding of community dynamics (Denno et al. 1995). In this study, we examined interactions between two closely related aphid species on pecan in the field at two times in the tree phenology as well as on pecan seedlings in the greenhouse. We asked whether competition could occur, whether competition could be mediated by lacewing predators, and whether the outcome of the interaction was influenced by variation in foliage age and quality.

Study system

Pecans (*Carya illinoensis* (Wang.) K. Koch) are native to the southeastern and south central United States and were recently introduced to the western US as a horticultural crop. Only two of its native herbivorous insects are abundant and reach pest status in Arizona orchards: the blackmargined pecan aphid, *Monellia caryella* (Fitch), and the black pecan aphid, *Melanocallis caryaefoliae* (Davis) (both Sternorrhyncha: Aphididae: Drepanosiphinae: Phyllaphidini). Both aphid species feed on the compound leaves, and co-occur throughout most of the year, although their populations often peak at different times (Teddars 1978, Petersen unpubl.). Early in the season there appears to be some resource partitioning between the two aphid species; *M. caryella* is more abundant in the outer parts of the canopy and *M. caryaefoliae* is more abundant in the central parts (e.g., Teddars 1978). The aphids also differ slightly in where they feed on the leaf. While both species appear to prefer to feed on the underside of the leaf, *M. caryaefoliae* is also found on the upper surface (Teddars 1978). Further, *M. caryella* tends to feed on primary leaf veins, while *M. caryaefoliae* prefers tertiary and quaternary veins (Teddars 1978, Kaakeh and Dutcher 1994).

Both *M. caryella* and *M. caryaefoliae* overwinter as eggs under the bark or in crevices on pecan trees. In the spring, fundatrices hatch from the eggs and initiate several generations of parthenogenetic females during the spring and summer. All adults have wings. In the autumn, sexual individuals develop and co-occur with parthenogenetic females. Oviparous females mate and then lay the overwintering eggs (Bissell 1978, Teddars 1978). The aphids can survive on the pecan leaves until leaf fall at the time of the first frost (November or December in southern Arizona).

In commercial pecan orchards, pecan aphids are considered serious pests. Feeding by *M. caryaefoliae* may cause defoliation if the population outbreak is severe. The honeydew produced by *M. caryella* is ten times higher in glucose-equivalents than that produced by *M. caryaefoliae* (Wood et al. 1987) and reduces photosynthesis and serves as substrate for sooty mold, a secondary fungus (Teddars 1978, Wood et al. 1985, 1987). Other studies have suggested that the two aphid species may be differentially affected by natural enemies because *M. caryella* produces copious amounts of honeydew. It has been suggested that the honeydew of *M. caryella* may attract or arrest natural enemies to a greater extent than the honeydew of *M. caryaefoliae* (Bumroongsook and Harris 1992, Harris and Li 1996). Green lacewings are among the most abundant natural enemies in pecans (Liao et al. 1985). In southern Arizona the species *Chrysoperla comanche* (Banks) and *Chrysopa nigricornis* Burmeister were most abundant (Petersen unpubl.).

Differences in morphology and behavior of the aphids may also influence their interactions with natural enemies. *M. caryaefoliae* is olive-green to black, appears to be more sclerotized and bears a number of tubercles on the thorax and abdomen, while *M. caryella* is pale yellow and relatively smooth-bodied (Teddars 1978). Both aphids are disturbed easily (Teddars and Thompson 1981) but our casual observations suggest their response to disturbance is different; *M. caryaefoliae* is more likely to jump and *M. caryella* to walk or fly.

The two pecan aphid species also have different interactions with the host plant. Feeding by *M. caryaefoliae* causes chlorotic and necrotic damage to the leaf tissue as well as an increase in free amino acids in the phloem. In contrast, *M. caryella* often leaves no macroscopic evidence of damage and the levels of free amino acids in the phloem of fed-upon leaves is similar to control leaves (Petersen and Sandström unpubl.). The large amount of honeydew produced by *M. caryella* is likely to be a consequence of this aphid's inability to increase the phloem amino acid content. Feeding by *M. caryella* causes microscopic damage to sieve elements (Teddars and Thompson 1981, Wood et al. 1985), which appears to reduce the ability of later-feeding *M. caryaefoliae* to manipulate the phloem amino acid content, thus reducing its reproductive performance (Petersen and Sandström unpubl.).

Methods and materials

Insect cultures

Pecan aphids and green lacewings were collected in the orchard block that was the location of the field study (see below). The two pecan aphid species were reared in the greenhouse on pecan seedlings germinated from nuts of 'Wichita' variety trees intercropped with 'Western Schley' variety pollinator trees. The green lacewing species *C. comanche* and *C. nigricornis* were reared on a mixture of bird cherry oat aphids (*Rhopalosiphum padi* L.) and greenbugs (*Schizaphis graminum* Rondani). These aphids were reared on barley seedlings. All cultures were kept in cages at 20–27°C and lighting was provided to extend the day length to 15 h.

Field experiments

Field experiments were carried out during October 1997 and June 1998 (here called 'Autumn 97' and 'Summer 98'). Experiments were performed in the central part of an unsprayed pecan orchard block (10 ha) on trees that were approximately 30 yr old in Sahuarita, Arizona (31° 57' N, 111° 00' W). The experimental unit consisted of a single compound leaf enclosed in a sleeve

cage (56 cm long and 17 cm wide) made of nylon organdy and supported by a circular wire frame near the top of the cage. The top of the cage was closed around the petiole with a wire twist tie tightened around a block of foam rubber. The bottom of the cage was closed similarly. Each leaf was washed on both sides with a moistened sponge before being caged. One week after the cages were placed over the leaves, pecan aphids were introduced. Adult aphid females that were less than 24 h old were aspirated into glass tubes and kept cold in an ice chest during transport to the field.

Four different aphid treatments were performed; (1) 10 *M. caryaefoliae*, (2) 10 *M. caryella*, (3) a mixture of 5 *M. caryaefoliae* + 5 *M. caryella* or (4) a double density mixture of 10 *M. caryaefoliae* + 10 *M. caryella*. These four aphid treatments were randomly set up on the four fully developed terminal leaves on each branch used. In the 'Autumn 97' experiment, two branches were used on both the north and the south facing section of three trees for a total of 12 replications per treatment. In the Summer 98 experiment three different branches on both the east and the west facing sections of six trees were used for a total of 36 replications per treatment.

In the Autumn 97 experiment, a predator treatment was randomly assigned to each of the aphid treatments 19 d after the infestation with aphids. The predator treatment was either (1) no predator ('control') or (2) two newly hatched first instar *C. comanche* larvae. Each treatment combination (aphid × predator) was replicated six times. The experiment was terminated five days after introduction of the lacewing larvae; caged leaves were cut off and brought back to the laboratory where the number of *C. comanche* larvae and aphids (adults and nymphs of each species) were counted. In this experiment as well as in the other two, aphids in the mixed species treatments were intermixed on the leaves at the time of counting; there was no evidence of spatial partitioning of the leaf surface with respect to aphid species. Dry weight was measured after freeze killing of adult aphids from predator 'control' treatments and of lacewing larvae that were alive at the end of the experiment. Aphids were dried for 24 h and lacewing larvae for 48 h, both at 60°C. Weights were measured on a CAHN C31 Electro balance.

In the Summer 98 experiment, the number of adults and nymphs of each aphid species was counted 15 d after introduction of aphids. A predator treatment was then randomly assigned to each of the aphid treatments. The predator treatments were (1) no predator ('control'), (2) one second instar *C. comanche* larva or (3) one second instar *C. nigricornis* larva. Each treatment combination (aphid × predator) was replicated 12 times. Two days after the introduction of the predators, the number of adults and nymphs of each aphid species were counted again. The lacewing larvae were killed and the dry weight determined after 48 h at 60°C.

Hourly readings of the air temperature (2 m above the soil surface) during both field experiments were obtained from the Arizona Meteorological Network (AZMET) Campbell farm station (Tucson, AZ) which has the most similar climatic conditions to the field site (P. Brown, AZMET, pers. comm.). Estimation of the cumulative physiological time accrued in the three experiments was made using an estimated temperature threshold of $T_0 = 5^\circ\text{C}$. This value was obtained from another tree-living aphid species belonging to the genus *Myzocallis* Passerini (Sternorrhyncha: Aphididae: Drepanosiphinae: Phyllaphidini) (P. Kindlmann pers. comm.).

Greenhouse experiment

A greenhouse experiment was carried out during October 1998. The experimental unit was a pecan seedling with 5–7 simple leaves. Each plant was grown in a pot (17 cm high with a diameter of 15 cm – 3.8 l) with Premier® Pro Mix soil. Plants were watered regularly with tap water. The aphid treatments were the same as used in the field experiments (see above) and were blocked in time with a total of 18 replicates. After introduction of adult aphids, each plant was covered with a fabric bag made of nylon organdy (57 cm high and 35 cm wide) secured with rubber bands around the pot below the rim. After 17 d incubation in the greenhouse at 15 h light per day the number of aphids (adults and nymphs of each species) was counted. Thereafter, a predator treatment was assigned to each pot and the bag was replaced over the plant. The two predator treatments were (1) no predator ('control') or (2) one newly molted second instar *C. nigricornis* larva. The treatments were blocked in time and each treatment combination (aphid \times predator) was replicated 9 times in a complete randomized block design. Five days after initiation of the predator treatment, the experiment was terminated. The number of aphids (adults and nymphs) was counted. The dry weight of the lacewing larvae and dry weight of adult aphid specimens from the 'control' predator treatment was measured (see above). Temperature in the greenhouse was measured every 30 min by a temperature logger mounted on a (non-experimental) pecan seedling.

Statistical analysis

In all three experiments, an analysis of variance using aphid species as a main factor was used to analyze the number of aphids in the single and high density mixed species treatments. An overall test of the results on interspecific competition from the three experiments was done by a simple meta-analysis combining probabilities from each of the experiments ($-2\sum \ln P$, with

a χ^2 distribution with $2k$ degrees of freedom, where k is the number of separate tests) (Sokal and Rohlf 1995). A paired t -test was used to compare aphid numbers in the two mixed species aphid treatments (high and low density). The dry weights of aphids in the single and mixed species treatments, and the proportional abundance of the aphid species in the two species mixture treatments were both tested by analysis of variance using aphid treatment as a main factor. In the analysis of aphid weights, leaf area and the number of aphids were used as co-variates. The per capita rate of increase for each aphid species was calculated using the equation $N_t = N_0 \lambda^t$, where N_0 is the initial density and N_t the number of aphids after t days. A value of $\lambda > 1$ indicates a population increase and a value $\lambda < 1$ indicates a population decrease. A comparison of the per capita rate of increase was performed by analysis of variance with aphid treatment and predator treatment as main factors. A significant interaction of aphid and predator treatments would provide evidence of apparent competition in our experiments. For all three experiments, leaf area was used as a co-variate. A test of lacewing larval performance as measured by final dry weight was performed using analysis of variance with aphid treatment as a main factor and the number of aphids at the time of predator introduction as a co-variate (the latter only the Summer 98 and the greenhouse experiments).

Results

Population growth of aphids in single species treatments

Population growth of the two pecan aphids in single species treatments was not significantly different in any of the three experiments (Fig. 1). Populations reached a mean number of 104 or less when they were developing on single compound leaves in the field; both in the Autumn 97 and the Summer 98 experiment (Fig. 1A, B). The two species also reached similar mean numbers when in single species treatments on pecan seedlings in the greenhouse, but while the leaf area of pecan seedlings was generally about twice the leaf area of a single compound leaf in the field, the mean number of aphids was 7–12 times greater on pecan seedlings in the greenhouse than on compound leaves in the field. Differences in physiological time accrued in the three experiments are unlikely to explain this difference in reproductive rate. In the Autumn 97 experiment, populations were censused after 312°D (24 d) while in the Summer 98 experiment the aphid census occurred after 320°D (15 d). In the greenhouse experiment, aphids were censused at 306°D (17 d).

The outcome of competition: mixed species treatments

The outcome of competition was variable in the three experiments. While in the Autumn 97 experiment, the mean numbers of each aphid species were almost exactly equal in the two mixed treatments (Table 1), in

the Summer 98 experiment, *M. caryella* comprised a mean proportion of 0.82 of the aphids present in the low density species mixture and 0.75 in the high density mixture (Table 2). Leaves in the two field experiments differed not only in age, but also in histories of aphid infestation. In 1997 the mean number of *M. caryella* reached a peak of 129 per leaf in June, higher than the

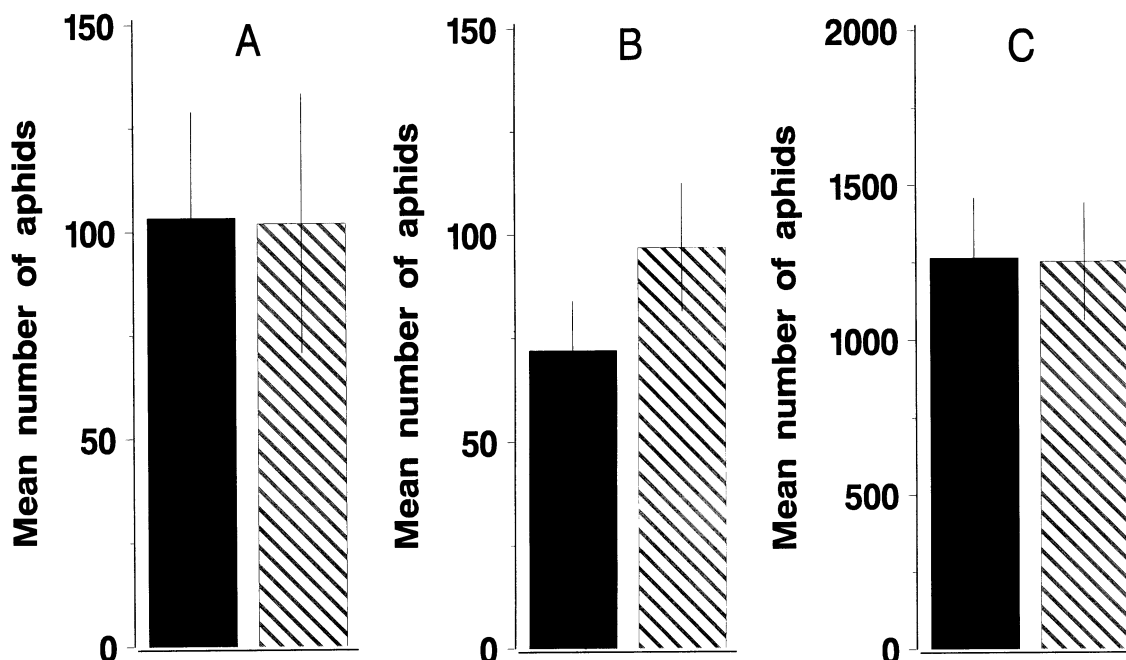


Fig. 1. Mean number \pm SE of pecan aphids in the single species treatments. (Black bars) *Melanocallis caryaefoliae* and (dashed bars) *Monellia caryella*. Initial density was 10 < 24-h-old adults in each cage. (A) Field experiment on single compound leaves in sleeve cages, Autumn 1997. $N = 6$ at day 24. $F_{1,11} = 0.06$, $P = 0.81$. (B) Field experiment on single compound leaves in sleeve cages, Summer 1998. $N = 36$ at day 15. $F_{1,67} = 1.04$, $P = 0.31$. (C) Greenhouse experiment on pecan seedlings. $N = 18$ at day 17. $F_{1,33} = 0.00$, $P = 0.97$.

Table 1. Field experiment, Autumn 97. Mean number \pm SE of *M. caryella* and *M. caryaefoliae* and proportion of *M. caryaefoliae* (mean \pm SE) of the total number of aphids in treatments where both species were introduced with a density of either 5 or 10 of each species. The number of aphids of each species was compared within treatment by a paired *t*-test. The number of aphids of one species was compared between the two aphid treatments by a *t*-test. $N = 6$.

	Low (5+5)	High (10+10)	Statistics
<i>M. caryella</i>	68 \pm 22	75 \pm 8	$t = 0.75$ NS
<i>M. caryaefoliae</i>	78 \pm 34	96 \pm 28	$t = 0.68$ NS
Paired <i>t</i> -test	$t = -0.20$ NS	$t = -0.87$ NS	
Proportion of <i>M. caryaefoliae</i> of the total number of aphids	0.50 \pm 0.16	0.51 \pm 0.09	$F_{1,9} = 0.05$ NS

Table 2. Field experiment, Summer 98. Mean number \pm SE of *M. caryella* and *M. caryaefoliae* and proportion of *M. caryaefoliae* (mean \pm SE) of the total number of aphids in treatments where both species were introduced with a density of either 5 or 10 of each species. The number of aphids of each species was compared within each aphid treatment by a paired *t*-test. The number of aphids of one species was compared between the two aphid treatments by an *F*-test. $N = 36$.

	Low (5+5)	High (10+10)	Statistics
<i>M. caryella</i>	96 \pm 11	52 \pm 8	$F_{1,65} = 11.30$, $P < 0.01$
<i>M. caryaefoliae</i>	21 \pm 5	13 \pm 3	$F_{1,65} = 1.38$ NS
Paired <i>t</i> -test	$t = 4.52$, $P < 0.001$	$t = 3.83$, $P < 0.001$	
Proportion of <i>M. caryaefoliae</i> of the total number of aphids	0.18 \pm 0.04	0.25 \pm 0.04	$F_{1,64} = 1.33$ NS

Table 3. Greenhouse experiment. Mean number \pm SE of *M. caryella* and *M. caryaefoliae* and proportion of *M. caryaefoliae* (mean \pm SE) of the total number of aphids in treatments where both species were introduced with a density of either 5 or 10 of each species. The number of aphids of each species was compared within each aphid treatment by a paired *t*-test. The number of aphids of one species was compared between the two aphid treatments by an *F*-test. *N* = 18.

	Low (5+5)	High (10+10)	Statistics
<i>M. caryella</i>	775 \pm 162	1216 \pm 207	$F_{1,34} = 1.65$ NS
<i>M. caryaefoliae</i>	602 \pm 157	723 \pm 154	$F_{1,34} = 0.00$ NS
Paired <i>t</i> -test	$t = 0.71$ NS	$t = 1.84$ NS	
Proportion of <i>M. caryaefoliae</i> of the total number of aphids	0.45 \pm 0.06	0.40 \pm 0.06	$F_{1,33} = 0.33$ NS

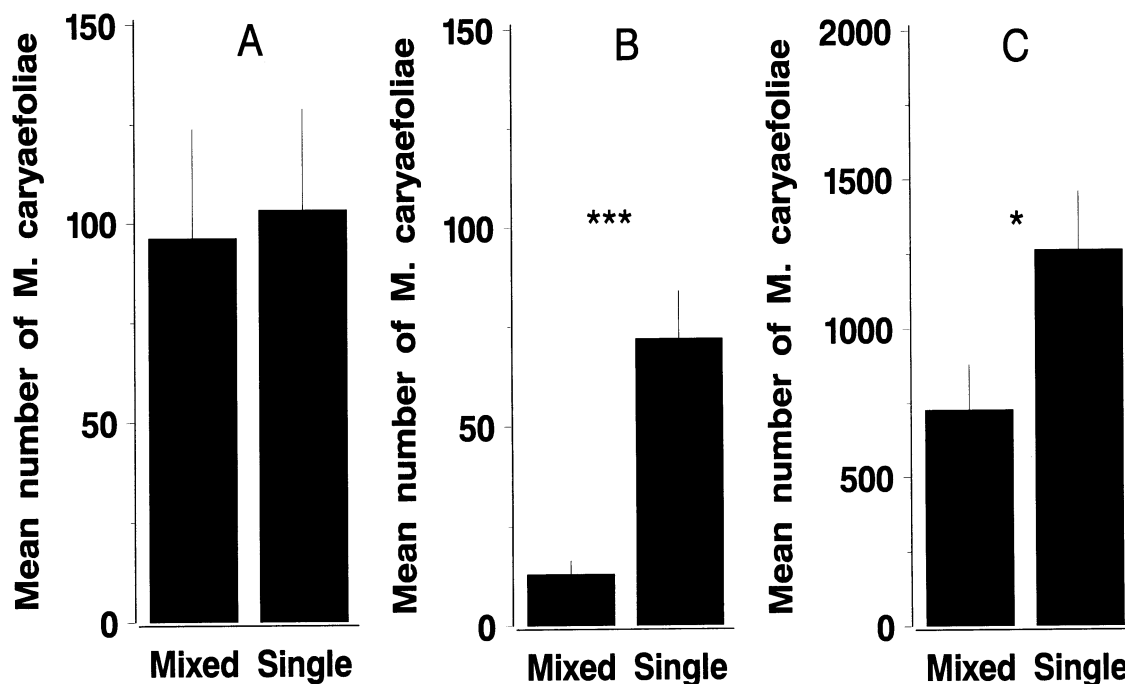


Fig. 2. Mean number \pm SE of *M. caryaefoliae* in single species treatments and in species mixture with *M. caryella*. Initial density was 10 < 24-h-old adults in each cage in the single species treatment and 10 < 24-h-old adults of each species in the mixed species treatment. (A) Field experiment, Autumn 1997. *N* = 6 at day 24. $F_{1,10} = 0.04$, $P = 0.85$. (B) Field experiment, Summer 1998. *N* = 36 at day 15. $F_{1,67} = 22.68$, $P < 0.001$. (C) Greenhouse experiment. *N* = 18 at day 17. $F_{1,34} = 4.72$, $P < 0.05$.

densities observed in our experimental cages. In 1998, only very low densities (<1 per compound leaf) of both species of aphid had been observed before the experiment. In the greenhouse experiment where no aphids were present on the plants before the experiment, the mean number of the two species was not significantly different, but here *M. caryella* also tended to be more abundant than *M. caryaefoliae* (Table 3) as in the Summer 98 experiment.

The ultimate number of aphids of each species in the two mixed treatments (high and low density) was not generally significantly different, in spite of the initial difference in density (Tables 1–3). In only the Summer 98 experiment was there a significant difference, and in that case, contrary to expectation, almost twice the number of *M. caryella* were produced in the low density mixture relative to the high density mixture.

The impact of competition: comparison of population growth in single and mixed species treatments

Evidence for significant impacts of competition was obtained by a comparison of the reproduction of the two aphid species in single vs the 'high density mixed' species treatments, in which the starting number of each species was the same, but the total number of aphids doubled (Figs 2, 3). The reproduction of *M. caryaefoliae* was significantly suppressed when developing together with *M. caryella* in a species mixture in both Summer 98 and greenhouse experiments (Fig. 2B, C). However, in the Autumn 97 experiment *M. caryaefoliae* was not suppressed when it co-occurred with *M. caryella* (Fig. 2A). Combining the probabilities from the three experiments lead us to conclude that *M. caryaefoliae* is significantly depressed when developing

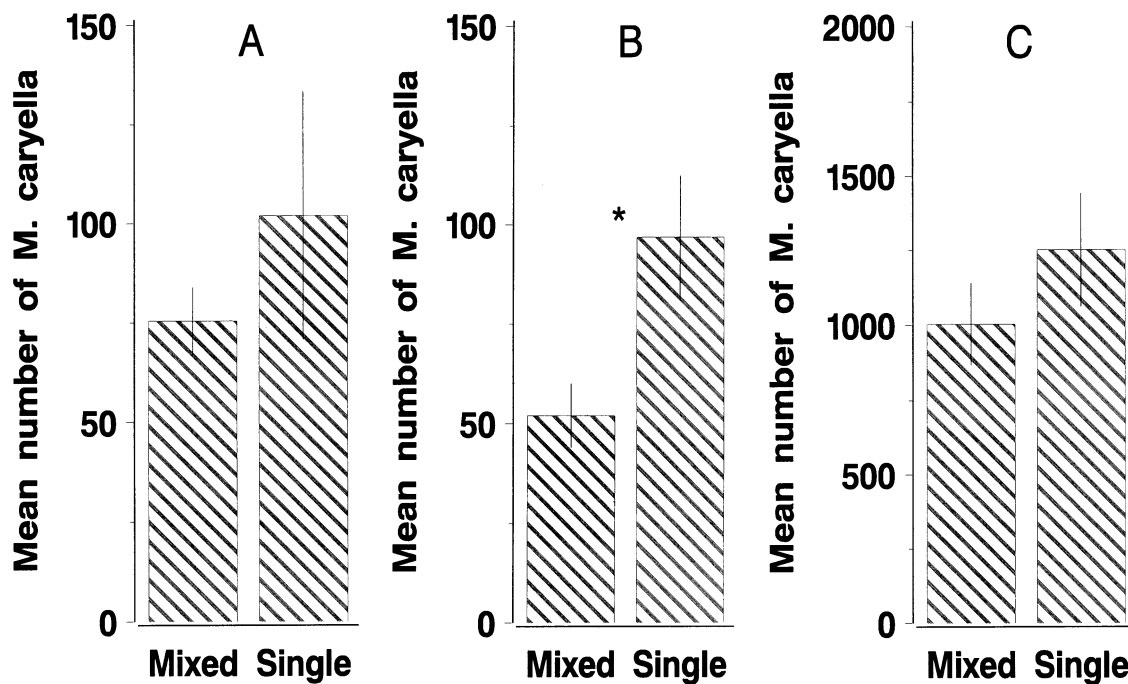


Fig. 3. Mean number \pm SE of *M. caryella* in single species treatments and in species mixture with *M. caryaefoliae*. Initial density was 10 < 24-h-old adults in each cage with the single species treatment and 10 < 24-h-old adults of each species in the mixed species treatment. (A) Field experiment, Autumn 1997. $N = 6$ at day 24. $F_{1,10} = 0.56$, $P = 0.47$. (B) Field experiment, Summer 1998. $N = 36$ at day 15. $F_{1,67} = 7.10$, $P < 0.01$. (C) Greenhouse experiment. $N = 18$ at day 17. $F_{1,34} = 1.14$, $P = 0.24$.

in a mixed culture with *M. caryella* compared to a single culture ($\chi^2_{[6]} = 20.7$, $P < 0.01$). *M. caryella* was also significantly influenced by competition with *M. caryaefoliae* ($\chi^2_{[6]} = 12.9$, $P < 0.05$), although marginally so, and in the individual experiments was only significantly affected in the Summer 98 experiment (Fig. 3B). In the other two experiments, there was a trend in the same direction, but there were no significant differences in the mean number of *M. caryella* produced in the single species treatments relative to the mixed species treatments (Fig. 3A–C).

Effects of competition on aphid size

The effect of competition on aphid size (dry weight) was variable in the two experiments in which it was measured, and did not entirely correspond to the effect of competition on aphid reproduction. In the Autumn 97 experiment, no effect of competition on reproduction was measured; however, the mean body size of *M. caryella* was significantly reduced in the high density mixed treatment relative to the single species treatment (Table 4). There was no significant reduction in the body size of *M. caryaefoliae* (Table 4) but the dry weight of this species was found to be significantly affected by the number of conspecifics (*M. caryaefoliae*: $F_{1,13} = 6.12$, $P < 0.05$; *M. caryella*: $F_{1,14} = 2.48$, $P = 0.15$). Variation in leaf area did not have a significant

influence on the body size of either aphid species (*M. caryella*: $F_{1,14} = 0.08$, $P = 0.78$; *M. caryaefoliae*: $F_{1,13} = 1.00$, $P = 0.34$).

A dramatic reduction in the body size of *M. caryaefoliae* was seen in the greenhouse experiment; the mean weight of an adult in the high density mixed treatment was about a fourth the weight of an adult in the single species treatment (Table 5). In this experiment, competition influenced both reproduction and body size of *M. caryaefoliae*. Similarly to the Autumn 97 experiment, the leaf area of the pecan seedlings in the greenhouse experiment did not contribute significantly to the difference in dry weight of either species, although it was very close to significant in its effects on *M. caryella* (*M. caryella*: $F_{1,25} = 4.00$, $P = 0.06$; *M. caryaefoliae*: $F_{1,21} = 1.82$, $P = 0.20$). The number of conspecifics significantly influenced the size of *M. caryella* (*M. caryella*: $F_{1,25} =$

Table 4. Mean dry weight \pm SE of *M. caryella* and *M. caryaefoliae* after 24 d population growth in control cages in the field, autumn 1997. Comparisons of mean dry weight between the aphid treatments are made for each species by a *t*-test, $\alpha = 0.05$. Only values with different letters are significantly different. $N = 6$ for each aphid species and aphid treatment.

	<i>M. caryella</i>	<i>M. caryaefoliae</i>
Single	0.073 \pm 0.002 a	0.068 \pm 0.005 a
Low (5+5)	0.067 \pm 0.003 ab	0.072 \pm 0.007 a
High (10+10)	0.065 \pm 0.002 b	0.062 \pm 0.007 a

Table 5. Mean dry weight \pm SE (mg) of *M. caryella* and *M. caryaefoliae* after 22 d population growth on control plants in greenhouse, winter 1998. Comparisons of mean dry weight between the aphid treatments are made for each species by a *t*-test, $\alpha = 0.05$. Only values with different letters are significantly different. $N = 9$.

	<i>M. caryella</i>	<i>M. caryaefoliae</i>
Single	0.051 \pm 0.004 ab	0.095 \pm 0.013 a
Low (5+5)	0.057 \pm 0.004 a	0.038 \pm 0.011 b
High (10+10)	0.042 \pm 0.004 b	0.022 \pm 0.011 b

5.42, $P < 0.05$; *M. caryaefoliae*: $F_{1,21} = 3.34$, $P = 0.09$). In neither of the two experiments was aphid body size affected by the total number of aphids on a leaf. That conspecific density had a greater effect on dry weights than total aphid density suggests that body size of both species may be more strongly affected by intraspecific competition than by interspecific competition.

Effect of introduction of a generalist predator

In the Summer 98 and the greenhouse experiments, the per capita rate of increase of *M. caryaefoliae* and *M. caryella* was reduced in cages in which a green lacewing larva was introduced in comparison with the 'no predator' treatments (Table 6) (*M. caryella*: Summer 98: $F_{2,52} = 4.5$, $P < 0.001$, Greenhouse: $F_{1,49} = 30.8$, $F < 0.001$; *M. caryaefoliae*: Summer 98: $F_{2,32} = 5.89$, $P < 0.01$, Greenhouse: $F_{1,47} = 14.4$, $P < 0.001$). Interestingly, no such reduction was found when two first instar lacewing larvae were released in the Autumn 97 experiment (*M. caryella*: $F_{1,33} = 0.72$, $P = 0.40$; *M. caryaefoliae*: $F_{1,31} = 0.03$, $P = 0.86$). This may reflect the fact that this experiment was carried out in the cooler part of the season when the lower temperature development threshold for aphids would have favored aphid reproduction over lacewing development. Thus, the rate of aphid consumption by the first instar lacewing larvae would have been lower than the aphid population's rate of increase (Petersen unpubl.).

Table 6. Per capita rate of increase (λ) of *M. caryella* and *M. caryaefoliae* on pecan foliage in the absence or presence of green lacewing larvae (mixed aphid treatments pooled). Aphids were developing on single compound leaves in the field 1997 and 1998 or on pecan seedlings in a greenhouse experiment 1998. Comparisons of λ between the predator treatments are performed for each aphid species by a *t*-test, $\alpha = 0.05$. Only values with different letters are significantly different.

	Predator treatment		
	Control	<i>C. comanche</i>	<i>C. nigricornis</i>
Field 1997 (19+5 d)			
<i>M. caryella</i>	1.10 \pm 0.009 a	1.11 \pm 0.009 a	–
<i>M. caryaefoliae</i>	1.10 \pm 0.009 a	1.10 \pm 0.011 a	–
Field 1998 (2 d)			
<i>M. caryella</i>	0.73 \pm 0.03 a	0.48 \pm 0.05 b	0.29 \pm 0.07 c
<i>M. caryaefoliae</i>	0.97 \pm 0.08 a	0.50 \pm 0.11 b	0.62 \pm 0.16 b
Greenhouse (5 d)			
<i>M. caryella</i>	1.02 \pm 0.02 a	–	0.83 \pm 0.02 b
<i>M. caryaefoliae</i>	1.02 \pm 0.03 a	–	0.87 \pm 0.03 b

Only in one of the two experiments in which predators had a significant effect was the interaction between aphid treatment and predator treatment statistically significant (*M. caryella*: Summer 98: $F_{2,52} = 0.91$, $P = 0.41$, Greenhouse: $F_{1,49} = 5.08$, $P < 0.05$; *M. caryaefoliae*: Summer 98: $F_{2,32} = 0.62$, $P = 0.54$, Greenhouse: $F_{1,47} = 2.08$, $P = 0.16$) and thus indicating apparent competition (Table 6). In the greenhouse experiment, the rate of increase of *M. caryella* was significantly enhanced when a predator was present in the mixed species treatment ($\lambda = 0.90$) relative to the single species treatment ($\lambda = 0.76$), while when the predator was absent, the rate of increase of this species was equal in the mixed species ($\lambda = 1.01$) and the single species ($\lambda = 1.02$). The introduction of a generalist predator did not change the proportion of the two aphid species when they occurred in species mixtures (Fig. 4). This pattern suggests that the lacewing predators did not preferentially consume one species over the other. Further, the results suggest that no indirect effects of predator foraging, for example differential susceptibility to disruption of the two aphid species, occurred in any of the experiments.

Predator performance

The performance of lacewing larvae, measured as dry weight at the end of the experiments was not significantly different among treatments within experiments, and was independent of the aphid species (single or mixed) they were fed within each experiment. *C. comanche* introduced in the Autumn 97 experiment had molted into second instar larvae by the end of the experiment and had a mean dry weight of 0.13 \pm 0.03 mg (\pm SE). In the Summer 98 experiment, *C. comanche* larvae that were introduced as second instar larvae had developed into third instar larvae by the end of the experiment, with a final dry weight of 1.14 \pm 0.10 mg (\pm SE), which was independent of the number of

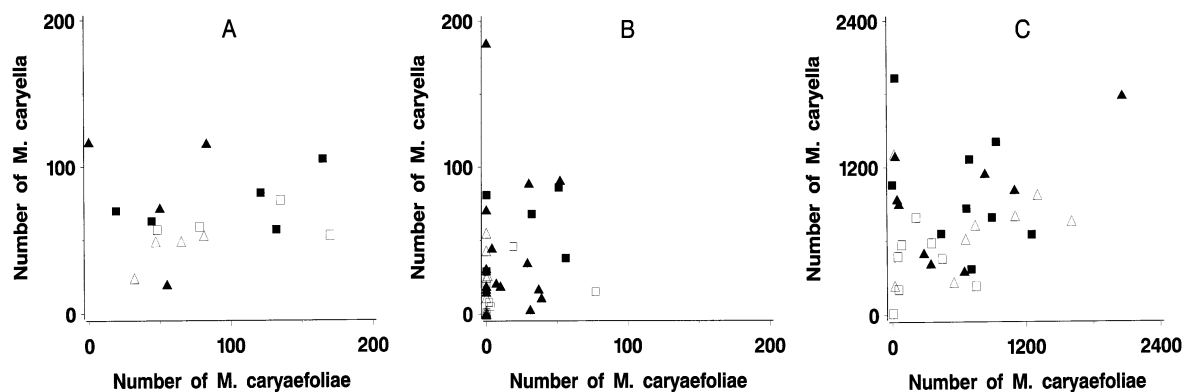


Fig. 4. Mean number of *M. caryella* plotted against the mean number of *M. caryaefoliae* in the two mixed species treatments. Initial aphid density was either five of each species (triangles) or 10 of each species (squares). (A) Field experiment, Autumn 1997. Solid symbols are control treatments (no predator) and open symbols were treatments that received two first instar *C. comanche* larvae. (B) Field experiment, Summer 1998. Solid symbols are control treatments (no predator), and open symbols are treatments that received a second instar *C. comanche* larva or a second instar *C. nigricornis* larva. (C) Greenhouse experiment. Solid symbols are control treatments (no predator) and open symbols are treatments that received a second instar *C. nigricornis* larva.

aphids at the time of its release. In the same experiment *C. nigricornis* had also matured from second instar into third instar larvae with a mean dry weight of 1.69 ± 0.20 mg (\pm SE). Unlike *C. comanche*, the dry weight of *C. nigricornis* was significantly affected by the number of aphids at the time of the release (*C. nigricornis*: $F_{1,27} = 20.0$, $P < 0.001$; *C. comanche*: $F_{1,18} = 0.57$, $P = 0.46$). In the greenhouse experiment, *C. nigricornis* larvae were about to make a cocoon when the experiment was terminated. The larvae had a dry weight of 7.86 ± 0.28 mg (\pm SE), a weight independent of the number of aphids at the time of its release.

Discussion

Effects of competition on aphid reproduction

The results of our study showed that competition between the pecan aphids can occur and is asymmetric, a common observation in studies of competition in herbivores (Crawley 1983, Schoener 1983, Denno et al. 1995). *M. caryella* was more likely to dominate the competition with *M. caryaefoliae* when the two aphid species were released at the same time and in an equal number (summarized in Table 7). The dominance of *M. caryella* was not due to intrinsically higher population growth rates of this aphid; the two aphid species had similar growth rates in the single species treatments. *M. caryaefoliae* also had a negative influence on *M. caryella*, but in only one of the three experiments (Table 7).

The three experiments were not consistent in their results with regard to competitive outcome (Table 7), even though the experimental design of the aphid com-

petition treatments was identical, and ran for approximately equivalent amounts of physiological time. In two of the three experiments (Autumn 97 and the greenhouse experiment), *M. caryella* was not significantly greater in density than *M. caryaefoliae* when censused, and in the Summer 98 experiment, the effect of competition was reciprocal; both aphids caused a reduction in the numbers of the other (Figs 2B, 3B). Abiotic factors such as rain or temperature differentially affecting the aphids (e.g., Dixon 1979, Tedders et al. 1992) cannot explain the variation because one would then expect differences in growth rates in the single species treatments.

The most likely explanation for variation in competitive outcome is differences in leaf quality. The experiments differed dramatically in the condition of the experimental units (compound leaves or seedlings). Greenhouse seedlings bore young, simple, juvenile leaves that had not had any previous aphid feeding. Leaves in the Summer 98 experiment were mature compound leaves of medium age, and exposure to aphid feeding was low. Leaves in the Autumn 97 experiment were older, mature compound leaves that had experienced an outbreak of *M. caryella* earlier in the season. Three aspects of plant quality may be especially relevant here. Whether leaves are physiologically juvenile or mature may have a large effect on the insects that feed on them (Waltz and Whitham 1997). Waltz and Whitham (1997) report large differences in insect communities between juvenile and mature leaf tissues on the same plant. Secondly, leaves were of different chronological age. Many studies show leaf chemistry changes markedly over the life of a leaf, with variable consequences for herbivore feeding (Wellings and Dixon 1987, Kaakeh and Dutcher 1992). Thirdly, the

Table 7. Summary of the outcome of competition.

Experiment	Numerical dominance of one species?	Reproduction in single species treatments > Reproduction in mixed species treatments*	Reduction in body size	Apparent competition
Autumn 97 (field)	No	Neither species	<i>M. caryella</i>	No
Summer 98 (field)	<i>M. caryella</i>	<i>M. caryella</i> <i>M. caryaefoliae</i>	–	No
Greenhouse	No	<i>M. caryaefoliae</i>	<i>M. caryaefoliae</i>	<i>M. caryella</i>

*In at least one of the mixed species treatments.

differences in the history of aphid feeding on the experimental leaves are likely to have influenced the results (e.g., Bumroongsook and Harris 1992). Phloem feeding insects may facilitate conspecific or heterospecific feeding by altering the flow of photosynthate or the amino acid composition in a way that increases the body size or reproduction of others (Shearer 1976, Kidd et al. 1985, Heard and Buchanan 1998). Conversely, feeding may inhibit reproduction by conspecifics or heterospecifics (Tamaki and Allen 1969, Moran and Whitham 1990, Heard and Buchanan 1998).

Studies of pecan aphids suggest that previous feeding by *M. caryella* reduces the performance of *M. caryaefoliae* (Petersen and Sandström unpubl.) and another aphid species, the yellow pecan aphid, *Monelliopsis pecanis* Bissel (Bumroongsook and Harris 1992). It is yet unclear whether this inhibition of later feeding aphids is due to the physical damage to the sieve elements that this aphid causes (Teddors and Thompson 1981) or to other, as yet unexplored factors involved with the induction of host plant resistance (Gianoli and Niemeyer 1996, Karban et al. 1997, Agrawal 1998).

Not only was variation in competitive outcome found in the different experiments, but there were large differences in the maximum number of aphids produced in the field and greenhouse experiments, even when the difference in leaf area is accounted for. In all of the experiments, the number of aphids appeared to have reached a maximum at the time of census; aphid numbers in the 'low density mixed' treatment, started with ten aphids, were not significantly lower than those in the 'high density mixed' treatment, initiated with 20 aphids. In the greenhouse experiment, aphid densities were about an order of magnitude higher on seedlings that had only approximately twice the leaf area as compound leaves. The differences between the greenhouse and field experiments are also most likely attributable to differences in leaf quality.

Effects of competition on body size

Competition also affected aphid body size, but there was not a consistent correspondence between a reduction in the reproduction of one species and a reduction

in mean size (Table 7). Aphid body size has long been known to be influenced by crowding (Tamaki and Allen 1969) and leaf age, with aphids reared on younger leaves attaining a greater adult weight (Wellings and Dixon 1987). Clearly there is likely to be an interaction between these two factors, and indeed in our experiments, the smallest aphids produced were in the greenhouse experiment with the youngest leaves, but the highest density of aphids (Table 5).

The lack of correspondence between effects of competition on body size and reproduction are likely to be due to different competitive mechanisms influencing these life history parameters. One might predict that both interference and exploitative competition may cause mortality and a direct reduction of aphid reproduction, while exploitative competition would be more likely to result in decreased body size. Our data provide some support for this hypothesis. In the Summer 98 and in the greenhouse experiment, the census of the mixed species treatments revealed extinction or near extinction of *M. caryaefoliae* in between 1/4 to 1/2 of the replicates while in other replicates, both aphids produced similar numbers of offspring (Fig. 4B, C). One likely explanation for this pattern is that settling of the *M. caryaefoliae* occurred at a lower probability in the presence of heterospecifics. Another study suggests that feeding by *M. caryella* damages the leaf in a way that inhibits the ability of *M. caryaefoliae* to manipulate the amino acid composition of the leaf (Petersen and Sandström unpubl.); thus feeding by *M. caryella* may also reduce the probability of *M. caryaefoliae* establishing a feeding site.

In contrast, body size reduction is likely to occur at densities that approach or exceed the carrying capacity of the experimental unit (McGeoch and Chown 1997). Both experiments in which body size was measured showed a reduction in body size of at least one aphid species in the 'high density mixed' treatment. In the greenhouse experiment, the contribution of leaf area to aphid size of *M. caryella* was nearly significant, suggesting that aphids reached maturity at a smaller size as a result of sharing a diminished or degraded resource. For both aphids, conspecific density was generally more important a determinant of body size than total aphid density, suggesting a greater influence of intraspecific

competition than interspecific competition on this fitness trait.

Apparent competition

Several recent studies suggest that at least short term apparent competition can influence the interaction between phytophagous insects (Settle and Wilson 1990, Karban et al. 1994, Bergeson and Messina 1997, Müller and Godfray 1997) and may be important in structuring communities (Crawley 1983, Holt et al. 1994, Wootton 1994, Bonsall and Hassell 1997). Bergeson & Messina (1997) compared the influence of resource-based vs apparent competition on the population dynamics of two aphids, *Diuraphis noxia* (Mordvilko) and *R. padi* on wheat. In contrast to the results of this study, the results of their experiments suggested little influence of plant-mediated interspecific interactions on population growth, but *D. noxia* benefited by the presence of *R. padi* when lacewing larvae were present, probably because of the greater reproductive rate of the latter species, leading to greater dilution of *D. noxia* when mixed with heterospecifics.

In our study, evidence for apparent competition was found in only one of six possible interactions. In the greenhouse experiment, *M. caryella* appeared to derive some benefit from being in mixed species cages when a predator was present. The reason for this result is unclear; a dilution effect as observed by Bergeson and Messina (1997) is not a possible explanation, because *M. caryella* tended to be more abundant than *M. caryaefoliae* (Table 3). Further, if lacewing larvae exhibited preference for *M. caryaefoliae*, one might expect to see a significant interaction in the other two experiments.

We suggest that apparent competition may not be very important at the spatial scale examined in this investigation. The data presented here suggest that lacewing larvae do not exhibit preference for one of the two aphid species. Other experiments suggest that the adult females of both lacewing species do not prefer to oviposit in patches of one of the aphids, nor does the performance of larvae reared on the two aphids differ (Petersen and Hunter unpubl.). Preference is not necessary for the expression of short-term apparent competition, but in the absence of preference, different levels of conspicuousness leading to differences in rates of encounter, or different population growth rates may be required to produce changes in per capita mortality rates as a result of predator feeding in mixed patches (e.g. Bergeson and Messina 1997, Bonsall and Hassell 1997, Müller and Godfray 1997). In general, the examples of apparent competition that have been reported from the field suggest this phenomenon may often be transient in nature (Settle and Wilson 1990, Karban et al. 1994, Müller and Godfray 1997). A caveat is that at

a larger spatial scale it is possible that the difference in honeydew production of the two aphid species may cause differential long range attraction of lacewings; this possibility should be investigated.

The results of our work suggest that 'bottom-up', host plant quality effects are likely to be much more important than apparent competition in their potential influence on the interaction of these pecan aphid species. Further, the results of the experiments conducted on plants of variable age and foliage quality varied in the total number of aphids supported by leaves of a given size, the effects of density and competition on aphid body size, and in the strength and symmetry of competition. Aspects of leaf quality such as leaf age, physiological state, nutrition level, and feeding damage or defense induction are all likely to affect aphid fitness and interspecific competitive ability in ways that need to be systematically investigated.

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