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Aphid-ant interaction reduces chrysomelid herbivory in a cottonwood hybrid zone

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In a cottonwood (*Populus*) hybrid zone, *Chaitophorus* aphids attract aphid-tending ants which subsequently reduce herbivory by the leaf-feeding beetle, *Chrysomela confluens*. Observations and experimental manipulations of aphids and beetle larvae on immature cottonwood trees demonstrated that: 1) via their recruitment of ants, aphids reduced numbers of beetle eggs and larvae on the host; 2) these interactions occurred within a few days of the host being colonized by aphids; and 3) although aphid colonies were ephemeral, their presence resulted in a 2-fold reduction in beetle herbivory. The aphid-ant interaction is most important in the hybrid zone where 93% of the beetle population is concentrated (for reasons unrelated to aphids and ants). Because beetle defoliation of immature trees is high (ca. 25%), the indirect effect of aphids in reducing herbivory is likely more beneficial to trees in the hybrid zone than in adjacent pure zones where beetle herbivory is virtually absent. Tree genotype likely affects the impact of the aphid-ant interaction on trees within the hybrid zone, since levels of herbivory differ between sympatric Fremont and hybrid cottonwoods.

Key words: Plant defense · Mutualism
Ant-aphid interaction · *Populus* · Indirect effects

Introduction

Mutualisms between homopterans and ants are a widely-recognized interaction that may be important as a plant defense. Homopterans that excrete sugars provide

ants with a rich source of nutrition. In return, ants protect these homopterans from parasites and predators. Further, by removing other phytophagous species, ants may protect the homopteran's food source by reducing overall herbivory on the host plant (see references in Hölldobler and Wilson 1990, pp. 522–526).

Plant hybrid zones are ideal sites for examining how host genotype affects the value of homopteran-ant interactions to plants. Plant quality may change homopteran-ant interactions from mutualistic to predation (Cushman and Addicott 1991; Cushman 1991) but the effect of plant genotype on these interactions in altering herbivory has been only rarely examined (e.g., Vrieling et al. 1991). Hybrid zones provide the opportunity to ask how homopteran-ant interactions affect herbivory across a range of pure and hybrid plant genotypes growing naturally at a common site.

Here we examine how the interaction between free-feeding aphids and ants affects the distribution of, and herbivory by, the beetle, *Chrysomela confluens* in a cottonwood hybrid zone. In this zone, the beetle is abundant and its herbivory is chronic (Floate et al. 1993); immature cottonwood trees can be completely defoliated year after year and may die as a result. Although the effects of homopteran-ant interactions on insect herbivores and herbivory have been previously reported (see references in Hölldobler and Wilson 1990, p. 526), our study differs in two respects. First, we manipulate homopterans to alter the distribution of other herbivore species. In contrast, previous studies have generally excluded ants to obtain this result. The significance of this is discussed later. Second, we begin to examine how plant genotype influences plant-aphid-ant-herbivore interactions and how these interactions might be most pronounced in a natural hybrid zone.

In this study, we ask "How does the initial presence of free-feeding aphids subsequently affect the abundance of ants and beetles, and the extent of beetle herbivory on cottonwood?". To address this question, we: 1) surveyed trees naturally colonized by aphids to examine the relationship between aphids, ants and beetles, 2) manipulat-

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ed aphids and beetle larvae to determine the effect of aphids on beetle distribution and herbivory, and 3) documented levels of herbivory on hybrid and pure trees to assess the importance of the aphid-ant interaction to different plant genotypes.

Study system

Our study was conducted in mid-April of 1992, in a cottonwood hybrid zone along the Weber River in northern Utah, where cottonwoods are a major component of the riparian community. Here, trees may be Fremont cottonwood (*Populus fremontii*), narrowleaf cottonwood (*P. angustifolia*), or hybrids of these two species (Whitham 1989; Keim et al. 1989; Paige et al. 1990). The boundaries of the hybrid zone, as defined for this study, are those used by Whitham (1989), which were based on the presence of Fremont, narrowleaf, and intermediate types. According to DNA analyses, pure narrowleaf cottonwood is rare in this zone (Keim et al. 1989), thus the study was limited to Fremont and hybrid trees. These two tree categories can be easily distinguished by differences in leaf phenology (i.e., hybrids flush leaves 3–4 wks before adjacent Fremont trees – Floate et al. 1993), leaf shape, and patterns of branching.

Free-feeding aphids, *Chaitophorus populicola*, and their tending ants are common on cottonwood in early April. These aphids form colonies of up to several hundred individuals located on the previous year's growth. They remain on their hosts until early May, when most trees have flushed leaves. Ants, particularly those of the genus *Formica*, frequently tend these aphids (K.D. Floate and T.G. Whitham, *personal observation*) as occurs for *Chaitophorus* aphids elsewhere (Edinger 1985; Degen et al. 1986). Although not tested, the association between aphids and ants on cottonwood is likely mutualistic. Ants gather honeydew directly from aphids and presumably protect aphids from predators and parasites, as indicated by the extreme aggression of ants towards other insects or researchers that intruded the aphid colony.

The beetle, *C. confluens*, is the major defoliator of immature cottonwood in the hybrid zone (K.D. Floate and T.G. Whitham, *personal observation*). Overwintering adults emerge in early April to feed and oviposit until late June, primarily on immature trees of both cottonwood species and their hybrids (Kearsley and Whitham 1989; Floate et al. 1993). Eggs hatch in about 7–10 d, whereupon larvae selectively consume young, expanding leaves. Pupation occurs on the host and new adults emerge from late May until early July. We restricted our study to immature trees, on which adult beetles preferentially feed and where their densities can be 400-fold higher than on mature trees (Kearsley and Whitham 1989).

Methods

Survey

To determine the strength and nature of the relationship between aphids and ants, we surveyed these insects on haphazardly selected trees in early April. Numbers of ants and aphid colonies on each tree were estimated using timed-censuses of duration determined by tree size. To account for differences in tree size and to reduce variation in insect counts, we standardized counts to 1 min. and normalized them as $\log(x+1)$. We then calculated Pearson's correlation between the number of aphid colonies and the number of ants.

We included counts of adult beetles in the early April census to examine the level of co-occurrence of aphids and beetles. In addition, beetle eggs were recorded because they represented a major source of future herbivory. Egg numbers were estimated by multiplying the number of egg clutches by the average number of eggs per clutch (mean \pm 1 SE = 35.5 ± 0.5 eggs/clutch, $n = 60$ clutches). Beetle larvae were not present at this time.

To examine whether aphids initiated interactions between ants and beetles, trees were categorized as "non-aphid" or "aphid" trees. We then compared numbers of beetle adults, beetle eggs, and ants between non-aphid and aphid trees using chi-square tests. Because the presence of different insect groups cannot be assumed to be independent (e.g., the abundance of beetle eggs and adults are likely correlated), critical p-values of 0.05 were adjusted using sequential Bonferroni tests (Rice 1989).

Because these observations were strictly correlational, the following experiments were necessary to separate cause and effect. For example, the results of this survey would not indicate whether the presence of beetles precluded the occurrence of ants or vice versa.

Experiments

We paired trees for site, size and genotype to reduce extraneous sources of variation. Trees in each pair ($n = 20$ pairs of trees) were within 2 m of each other and 1–2 m in height. Genotype was defined in this study as either Fremont or hybrid. To standardize for genetic differences in the timing of spring leaf flush (Floate et al. 1993), Fremont trees were paired with other Fremont trees, and hybrid trees were paired with other hybrid trees. Differences in leaf phenology within each genotype were further reduced by pairing trees with the same degree of flushed leaves.

Study trees did not originally have aphids and were carefully censused for all other insects which were then removed. We randomly designated one member of each pair as the treatment tree and the other member as the control. Since there were no pretreatment differences in insect numbers between control and treatment trees (ants, $p = 0.892$; beetle adults, $p = 0.359$; beetle eggs, $p = 0.490$; Wilcoxon signed-rank tests), we attributed subsequent responses to our aphid manipulations.

To examine their effect on herbivory and on the distribution of ants and beetles, we transferred *Chaitophorus* aphids (ca. 40 individuals) onto a branch of each treatment tree in mid-April by attaching an aphid-colonized twig from a common donor tree. Within hours, aphids moved from the twigs to settle and feed on treatment trees. To encourage high levels of herbivory, we placed 20 adult beetles (10 of each sex) at the base of each control and treatment tree immediately after aphid transfers. Aphid transfers were the only manipulations done to encourage ants to colonize trees.

One week after aphid transfer, we compared the number of aphids, ants, and all beetle life stages on control and treatment groups, which comprised over 90% of the insects seen on cottonwoods at this time. Aphids were included in these comparisons to gauge the success of aphid transfers.

Three weeks after aphid transfer, we compared levels of herbivory of control and treatment trees. We measured herbivory as

the percent of leaves attacked per shoot ($n=10$ shoots, ca. 5–11 leaves/shoot) for each tree. Many of the leaves attacked were completely consumed, and partially consumed leaves prematurely abscised within a few weeks.

Because data was not normally distributed, we used Wilcoxon signed-ranks tests to compare insect taxa between control and treatment trees. Critical p -values of 0.05 were adjusted with sequential Bonferroni adjustments due to the likely non-dependence of taxa (Rice 1989). Levels of beetle herbivory were normally distributed, so comparisons of defoliation between treatment and control trees were made using paired t -tests.

To test whether the presence of aphids excluded beetle larvae, we transferred a clutch of larvae onto each of 15 shoots colonized with aphids. For the control, we placed a clutch of larvae on each of 15 shoots on the same tree without aphids. The presence or absence of ants was not considered in shoot selection. Each clutch contained an average of 28 1st-instar larvae. The number of larvae in each clutch was recorded at hourly intervals until virtually no larvae remained on branches with aphids.

General herbivory

To assess the importance of aphid-ant interactions in plant defense, we visually estimated folivory at the study site in early May, by which time beetle adults and larvae had been feeding for about 5 wk. Genotype (Fremont or hybrid) and extent of herbivory was recorded for trees in a 200 m \times 20 m quadrat. Trees were placed in one of six categories based on the extent of defoliation; (0%, 1–25%, 26–50%, 51–75%, 76–99% and 100%). Although more accurate estimates of defoliation are available (e.g., Bray 1961; Morrow and Fox 1989), visual estimates of defoliation are commonly used (Barbosa and Wagner 1989 – p. 408) and allowed us to quickly survey a large number of trees. Trees surveyed for herbivory were primarily 2–4 yr in age and 1–2 m in height.

In estimating average tree herbivory, the minimum level of defoliation was used for each category. For example, each tree in the 26–50% defoliation category was assumed to be 26% defoliated. Average tree herbivory was calculated as the sum of individual tree defoliation divided by the total number of trees surveyed. For comparing levels of herbivory of Fremont and hybrid trees, trees were ranked (1 [0% defoliation] to 6 [100% defoliation]) and data analyzed using a Mann-Whitney U test.

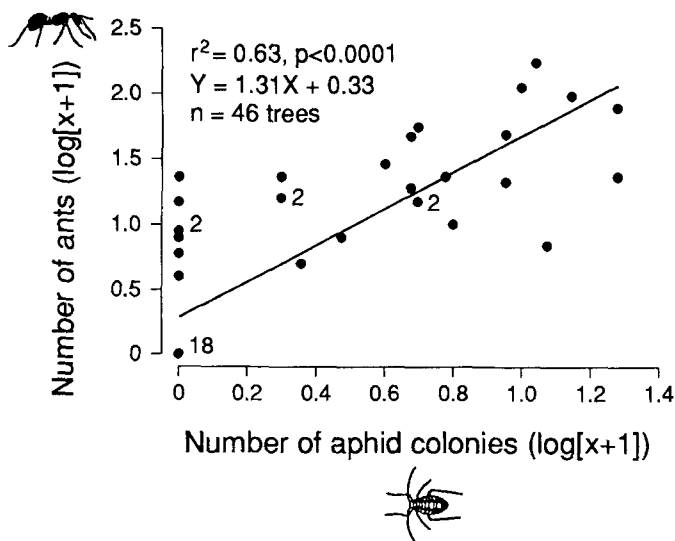


Fig. 1 *Chaitophorus* aphids are positively correlated with ants which indicates that this association is a predictable interaction on immature cottonwood trees. (Note: In this survey, 18 trees had neither aphids nor ants)

Results

Survey

Our survey showed a non-random occurrence of aphids and ants on cottonwoods. First, there was a significant ($p < 0.0001$), positive correlation between the abundance of ants and aphids on a given tree (Fig. 1). Second, although ants were found in the absence of aphids (of 28 trees on which ants occurred, 7 trees did not have aphids), aphids were never seen without tending ants (of 21 trees on which aphids occurred, all had ants). Eighteen trees had neither aphids nor ants.

Although the association between aphids and ants was positive, these taxa were negatively associated with beetles. Ants were 15-fold more common on aphid trees ($n=21$), than on non-aphid trees ($n=25$). In contrast,

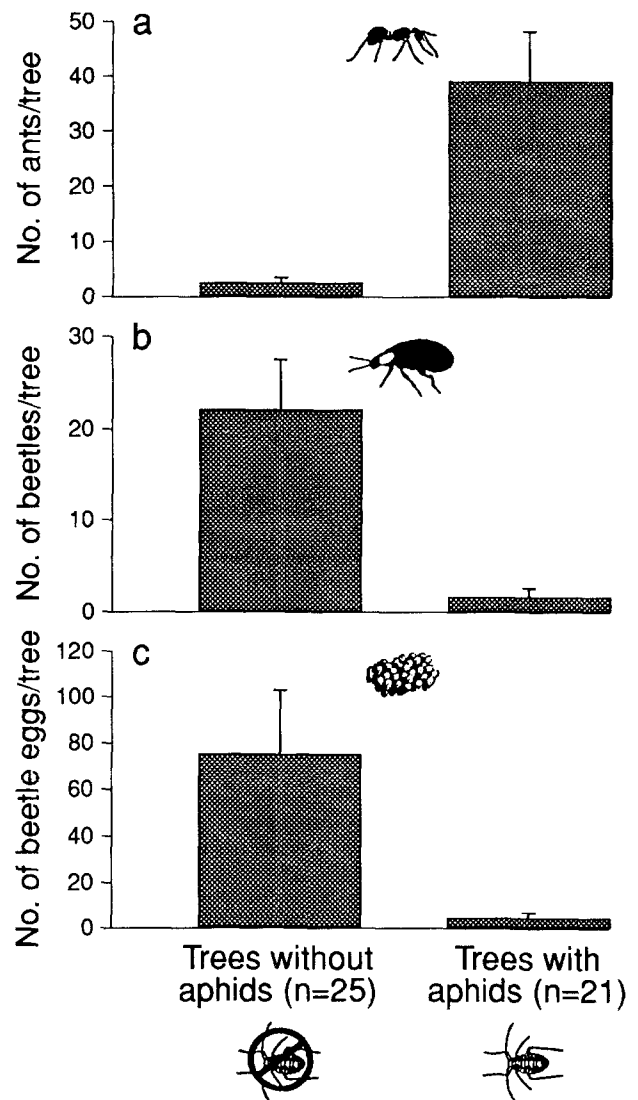


Fig. 2a–c Trees without aphids have different patterns of insect distributions compared to trees with aphids, which suggests that aphids influence the insect fauna of their host plants. Bars denote ± 1 SE

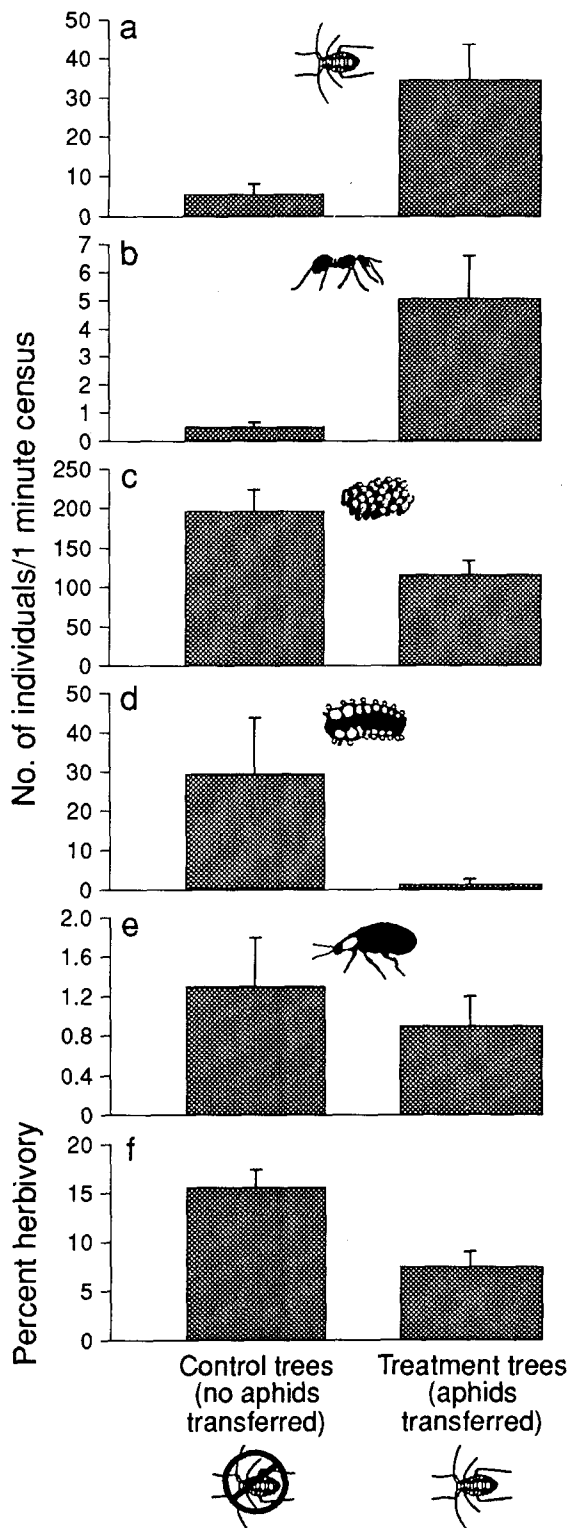


Fig. 3a–f Insect distributions on immature cottonwood trees were experimentally altered by one application of aphids to treatment trees paired with control trees for age, height, genotype and site ($n = 20$ pairs). Initially, neither treatment nor control trees had any insects, but 1 wk after aphid transfers, aphids (a) and ants (b) were more common on treatment trees than on controls. Beetle eggs (c) and larvae (d) were less common on treatment trees relative to control trees, and beetle adults (e), were equally abundant on treatment and control trees. Three weeks after aphid transfers, defoliation of treatment trees was half the level of defoliation of paired, control trees (f). Bars denote ± 1 SE

beetle adults and eggs were, respectively, 13- and 15-fold less abundant on aphid trees than on non-aphid trees (Fig. 2). All differences were significant at $p < 0.001$.

Experiments

The presence of aphids on trees increased ant numbers and, via ants, reduced beetle numbers and beetle herbivory (Fig. 3). Although there were no differences between treatment and control trees prior to the experiment, 1 wk after transferring aphids onto treatment trees, there were significantly more aphids ($p = 0.002$) and ants ($p = 0.003$) on these trees than on control trees. Conversely, beetle eggs and larvae were significantly less abundant on treatment trees ($p = 0.011$ and $p = 0.012$, respectively) than on control trees. There was no significant difference in adult beetle numbers ($p = 0.633$) between treatment and control trees. These results show that beetle eggs and larvae are most sensitive to foraging ants while adult beetles may be little affected. Because beetle larvae forage gregariously and they outnumber adults, they have greater potential for defoliating trees. The observed difference in larval abundances is likely responsible for the decrease in defoliation when aphids are present; 3 wk after aphid transfers, defoliation of treatment trees was half that of control trees ($p < 0.001$).

Ants respond quickly to the presence of larvae and begin removing them within minutes of larvae being experimentally transferred to shoots supporting aphids (Fig. 4). Within 6 hr, repeated attacks by ants reduced larval clutch size by 99.7% (a loss of 421 larvae out of 422 larvae transferred) on aphid-colonized shoots. In contrast, larval clutch size on control shoots declined only 19.7% over the same period (a loss of 73 larvae out of 410 larvae transferred). Transfer shoots with aphids initially had a mean (± 1 SE) of 8.5 ± 1.6 ants, but virtu-

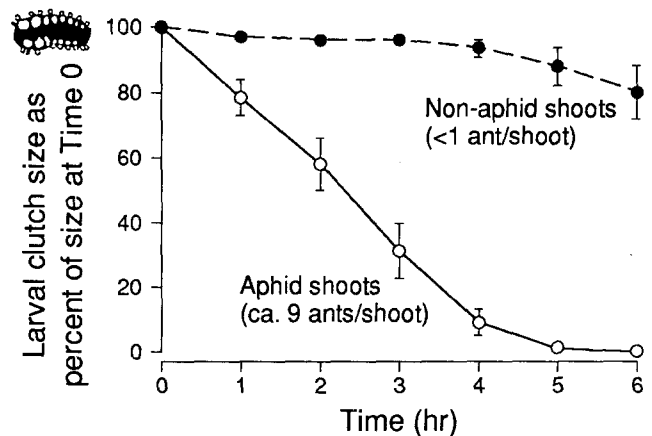


Fig. 4 Aphids reduce numbers of beetle larvae on cottonwood trees via the aggressive actions of aphid-tending ants. During a 6-hr period, ants caused the virtual extinction of beetle clutches (initially about 28 1st-instar larvae/clutch) on shoots with aphids whereas clutches on shoots without aphids were relatively unaffected. (Note: Values are based on means from 15 clutches [1 clutch/shoot]). Bars denote ± 1 SE

ally no ants were on control shoots which lacked aphids. The reduction on control shoots was mainly the result of two clutches being encountered, and then attacked, by foraging ants. This shows that although ants are most effective in removing larvae on shoots occupied by aphids, ants also remove beetle larvae from nearby, non-aphid shoots. We observed similar attacks where ants removed 2nd- and 3rd-instar larvae and adult beetles from trees.

General herbivory

Folivory at our study site was high, and was greater on hybrid trees than on Fremont trees. We estimated that the average immature cottonwood suffered 25% defoliation (based on 270 trees). We estimated defoliation of hybrid ($n = 135$) and Fremont ($n = 135$) trees, respectively, at about 33% and 16.5%. These differences were significant (U test statistic = 6069.5, $p < 0.001$).

Discussion

Rapid effect of aphids on ants and beetles

Transfers of aphids onto trees resulted, within 1 wk, in a 10-fold increase in ant numbers and a 23-fold decrease in the density of beetle larvae, relative to control trees. Beetle eggs, representing a major source of future herbivory, were also significantly less abundant on aphid-transfer trees (Fig. 3). This response was particularly impressive given that about 40 aphids were transferred onto each treatment tree whereas naturally colonized trees had an average of about 400 aphids per tree ($n = 21$ trees). A similar pattern of beetle and ant distributions was seen between trees naturally colonized by aphids and trees without aphids (Fig. 2).

Manipulations of 1st-instar beetle larvae demonstrated the speed with which aphids indirectly reduced beetle numbers. Larvae placed on shoots with aphids were removed by tending ants in a matter of hours, whereas larvae on paired, control shoots were relatively unaffected (Fig. 4). Because ants frequently encounter beetle adults and larvae on aphidcolonized shoots (e.g., 2.5–4.9 encounters per minute; Kearsley and Whitham 1993), the speed with which ants remove beetles from a tree might be expected. However, larvae sequester host-based salicylaldehyde which is an effective defense against ants (Kearsley and Whitham 1993). This chemical defense first must be exhausted by repeated attacks until ants succeed in removing the larva.

Similar studies have produced conflicting results. *Formica* ants tending membracids on goldenrod, reduced numbers of adult chrysomelid beetles (*Trirhabda* sp.) on the host, but did not exclude beetle larvae (Messina 1981). In our study, ants tending aphids on cottonwood excluded *C. confluens* larvae, but did not significantly reduce adult beetle numbers. In contrast, *Formica*

ants tending membracids on black locust, increased numbers of chrysomelid, *Odontota dorsalis*, larvae by excluding larval predators (Fritz 1983). Clearly, interactions in similar systems (i.e., chrysomelid beetles, *Formica* ants, and ant-tended homopterans) cannot be assumed to have the same outcome.

Herbivory reduced when aphids present

Aphids reduced beetle herbivory on immature cottonwoods, via the actions of their tending ants (Fig. 3f). However, the benefit of this reduced herbivory to the plant may have been negated by the feeding activity of the aphids. For example, the hairy wood ant *Formica lubugris* reduced most herbivore species of birch, but benefits to the plant may have been offset by a 3000-fold increase in numbers of the ant-tended aphid, *Symydobius oblongus* (Fowler and MacGarvin 1985). However, there were only 34 aphids per treatment tree at the end of the first week in our experiment (Fig. 3a), and these were gone by the third week. Given that these aphid numbers significantly reduced spring herbivory on our experimental trees from 16% to 7%, we contend that aphids caused a net reduction in herbivory.

Aphids reduce beetle herbivory in the spring, when such protection is of greatest benefit to the plant. *Chrysomela confluens* preferentially feeds on leaves that are young and still-expanding (Kearsley and Whitham 1989). Hence, in the spring all of the leaves on a tree are at risk from beetle herbivory. *Chaitophorus* aphids are present only from early April to early May, but the protection they provide during this period can be important to all leaves on the tree. Beetles continue to feed until late June, but since most leaves on a tree are mature by this time, only a small fraction of a tree's total foliage is at risk from herbivory.

The aphid-ant interaction should most benefit trees in the hybrid zone. The interaction between *Chaitophorus* aphids and ants occurs in both the hybrid zone and in adjacent pure zones of Fremont and narrowleaf cottonwood. However, *C. confluens* may completely defoliate immature cottonwood trees in the hybrid zone, where 93% of its population is concentrated (Floate et al. 1993). Of the 270 trees we surveyed in early May, 11% were completely defoliated and 26% were considered more than 50% defoliated. In adjacent pure zones of Fremont and narrowleaf cottonwood, beetles are uncommon, and folivory is rare (K.D. Floate, *personal observation*). Because aphids are the major herbivores on trees in the pure zones, their feeding activity likely has an overall negative impact on the host. The high density of *C. confluens* in the hybrid zone is due its extended period of leaf flush, relative to that of adjacent pure zones. The hypothesis that beetles attain greatest fitness on hybrid trees was specifically tested and rejected (Floate et al. 1993).

Host genotype effects on homopteran-ant interactions

Higher levels of herbivory on hybrid trees, relative to sympatric Fremont trees, suggest that host genotype affects the impact of the homopteran-ant interaction on the host plant. In mid-April, adult *C. confluens* are concentrated on hybrid trees which have begun to flush leaves. By mid-May, most of the foliage on hybrid trees has matured and the majority of adult beetles occur on Fremont trees which have only recently flushed leaves (Floate et al. 1993). As a result of this seasonal distribution, hybrid trees suffer an average of 33% defoliation by early May, compared to 16.5% defoliation for Fremont cottonwoods. Consequently, hybrid trees stand to benefit more from the protective services of aphid-tending ants during the spring, than will Fremont trees. Because there is a large genetic component to the timing of leaf phenology (Floate et al. 1993), hybrid trees will continue to benefit most from aphid-ant interactions year after year.

Variation in host genotype may alter the outcome of homopteran-ant interactions (see Cushman 1991), but few studies have examined this experimentally. In one study (Vrieling et al. 1991), genetically-based differences in plant chemistry explained differential herbivory on the plant *Senecio jacobaea*. Aphids occurred mainly on plants with high pyrrolizidine alkaloid concentrations, relative to plants without aphids. Aphid-tending ants excluded larvae of the moth *Tyria jacobaeae*, which reduced herbivory on the host plant. Further work of this nature will increase awareness of the complex interactions between plants, homopterans, their tending ants, and other insect species.

Aphids or ants – which to manipulate?

In this study, we chose to manipulate aphids, rather than ants, as the more realistic approach to understanding how aphid-ant interactions affect their host plants. First, the initial presence of aphids was the main factor accounting for the subsequent presence of aphid-tending ants on plants – not vice versa. We suspect this is true for most homopteran-ant mutualisms. Second, complete exclusions of ants in nature are rare (Cushman 1991, Cushman and Whitham 1991) and were not observed in our cottonwood system.

Previous studies have generally used ant exclusions to examine the effects of homopteran-ant mutualisms on plant herbivory and other insects (e.g., Banks and Macauley 1967; Room 1972; Bradley 1973; Samways 1983; Whittaker and Warrington 1985; Compton and Robertson 1988; Cushman and Whitham 1989; Tedders et al. 1990; Ito and Higashi 1991). Although ants may be important, or even essential, for maintaining or increasing homopteran numbers on plants (see references in Hölldobler and Wilson 1990, pp. 525–528), homopteran manipulations can lead to new insights on the occur-

rence and duration of homopteran-ant interactions. For example, if the primary factors affecting the initial colonization of plants by homopterans can be identified, researchers may be able to predict when and where these interactions will occur. By altering these factors, researchers may then be able to selectively protect plants via homopteran-tending ants.

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References

- Banks CJ, Macauley EDM (1967) Effects of *Aphis fabae* Scop. and of its attendant ants and insect predators on yields of field beans (*Vicia faba* L.). *Ann appl Biol* 60:445–453
- Barbosa P, Wagner MR (1989) Introduction to Forest and Shade Tree Insects. Academic Press, New York, 639 pp
- Bradley GA (1973) Effect of *Formica obscuripes* (Hymenoptera: Formicidae) on the predator-prey relationship between *Hyporaspis congressis* (Coleoptera: Coccinellidae) and *Toumeyella numismaticum* (Homoptera: Coccidae). *Can Entomol* 105:1113–1118
- Bray JR (1961) Measurement of leaf utilization as an index of minimum level of primary consumption. *Oikos* 12:70–74
- Compton SG, Robertson HG (1988) Complex interactions between mutualisms: Ants tending homopterans protect fig seeds and pollinators. *Ecology* 69:1302–1305
- Cushman JH (1991) Host-plant mediation of insect mutualisms: variable outcomes in herbivore-ant interactions. *Oikos* 61:138–144
- Cushman JH, Addicott JF (1991) Conditional interactions in ant-plant-herbivore mutualisms. In: Huxley CR, Cutler DF (eds) *Ant-Plant Interactions*. Oxford University Press, New York, pp. 92–103
- Cushman JH, Whitham TG (1989) Conditional mutualism in a membracid-ant association: Temporal, age-specific, and density-dependent effects. *Ecology* 70:1040–1047
- Degen AA, Gersani M, Avivi Y, Weisbrot N (1986) Honeydew intake of the weaver ant *Polyrhachis simplex* (Hymenoptera: Formicidae) attending the aphid *Chaitophorous populialbae* (Homoptera: Aphididae). *Insectes Soc* 33:211–215
- Edinger BB (1985) Conditional mutualism in three aphid-tending ants. *Bull Ecol Soc Am* 66:168
- Floate KD, Kearsley MJC, Whitham TG (1993) Elevated herbivory in plant hybrid zones: *Chrysomela confluens*, *Populus* and phenological sinks. *Ecology* 74:2056–2065
- Fowler SV, MacGarvin M (1985) The impact of hairy wood ants, *Formica lugubris*, on the guild structure of herbivorous insects on birch, *Betula pubescens*. *J Anim Ecol* 54:847–855
- Fritz RS (1983) Ant protection of a host plant's defoliator: consequence of an ant-membracid mutualism. *Ecology* 64:789–797
- Hölldobler B, Wilson EO (1990) *The ants*. The Belknap Press of Harvard University Press, Cambridge, 732 pp
- Ito F, Higashi S (1991) An indirect mutualism between oaks and wood ants via aphids. *J Anim Ecol* 60:463–470
- Kearsley MJC, Whitham TG (1989) Developmental changes in resistance to herbivory: Implications for individuals and populations. *Ecology* 70:422–434
- Kearsley MJC, Whitham TG (1993) Guns and butter: A no cost defense against predation for *Chrysomela confluens*. *Oecologia* 92:556–562

- Keim P, Paige KN, Whitham TG, Lark KG (1989) Genetic analysis of an interspecific hybrid swarm of *Populus*: Occurrence of unidirectional introgression. *Genetics* 123:557–565
- Messina FJ (1981) Plant protection as a consequence of an ant-membracid mutualism: interactions on goldenrod (*Solidago* sp.). *Ecology* 62:1433–1440
- Morrow PA, Fox LR (1989) Estimates of pre-settlement insect damage in Australian and North American forests. *Ecology* 70:1055–1060
- Paige KN, Keim P, Whitham TG, Lark KG (1990) The use of restriction fragment length polymorphisms to study the ecology and evolutionary biology of aphid-plant interactions. In: Campbell RK, Eikenbary RD (eds) *Aphid-Plant Interactions*. Elsevier, Amsterdam, pp. 69–87
- Rice WR (1989) Analyzing tables of statistical tests. *Evolution* 43:223–225
- Room PM (1972) The fauna of the mistletoe *Tapinanthus bangwensis* (Engl. & Krause) growing on cocoa in Ghana: Relationships between fauna and mistletoe. *J Anim Ecol* 41:611–621
- Samways MJ (1983) Interrelationship between an entomogenous fungus and two ant-homopteran (Hymenoptera: Formicidae – Hemiptera: Pseudococcidae & Aphididae) mutualisms on guava trees. *Bull ent Res* 73:321–331
- Tedders WL, Reilly CC, Wood BW, Morrison RK, Lofgren CS (1990) Behavior of *Solenopsis invicta* (Hymenoptera: Formicidae) in pecan orchards. *Environ Entomol* 19:44–53
- Vrieling K, Smit W, Van der Meijden E (1991) Tritrophic interactions between aphids (*Aphis jacobaeae* Schrank), ant species, *Tyria jacobaeae* L., and *Senecio jacobaea* L. lead to maintenance of genetic variation in pyrrolizidine alkaloid concentration. *Oecologia* 86:177–182
- Whitham TG (1989) Plant hybrid zones as sinks for pests. *Science* 244:1490–1493
- Whittaker JB, Warrington S (1985) An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*). III. Effects on tree growth. *J Appl Ecol* 22:797–811