Lara Lee Dickson · Thomas G. Whitham

Genetically-based plant resistance traits affect arthropods, fungi, and birds

Abstract We examine how the distribution of a leaf-galling aphid (*Pemphigus betae*) affects other species associated with natural stands of hybrid cottonwoods (*Populus angustifolia* × *P. fremontii*). Aphid transfers on common-garden clones and RFLP analysis show that resistance to aphids in cottonwoods is affected by plant genotype. Because susceptible trees typically support thousands of galls, while adjacent resistant trees have few or none, plant resistance traits that affect the distribution of this abundant herbivore may directly and/or indirectly affect other species. We found that the arthropod community of aphid-susceptible trees had 31% greater species richness and 26% greater relative abundance than aphid-resistant trees. To examine direct and indirect effects of plant resistance traits on other organisms, we experimentally excluded aphids and found that abundances and/or foraging behavior of arthropods, fungi, and birds were altered. First, exclusion of gall aphids on susceptible trees resulted in a 24% decrease in species richness and a 28% decrease in relative abundance of the arthropod community. Second, exclusion of aphids also caused a 2- to 3-fold decrease in foraging and/or presence of three taxa of aphid enemies: birds, fungi, and insects. Lastly, aphid-exclusion resulted in a 2-fold increase in inquilines (animals who live in abodes properly belonging to another). We also found that fungi and birds responded to variation in gall density at the branch level. We conclude plant resistance traits affect diverse species from three trophic levels supporting a "bottom-up" influence of plants on community structure.

Key words Aphids · Indirect effects · Plant resistance · Community structure

L. L. Dickson · T. G. Whitham (✉)
Northern Arizona University, Flagstaff, AZ 86011-5640, USA
Fax 520-523-7500 E-mail tgw@nauvax.ucc.nau.edu

Introduction

Several studies have examined how plant resistance traits affect herbivores (e.g., Maddox and Root 1987; Fritz and Price 1988; Moran and Whitham 1990; Paige et al. 1990; Boecklen and Price 1991; Mopper et al. 1991; Fritz and Simms 1992). However, less is known about the indirect effects of plant resistance traits on diverse taxa from different trophic levels (but see Weis and Abrahamson 1986; Ruberson et al. 1989; Gehring and Whitham 1991; Hare 1992; Christensen and Whitham 1993). Here we examine how the resistance traits of natural stands of hybrid cottonwood trees (*Populus angustifolia* × *P. fremontii*) influence the distribution of a common herbivore, the leaf-galling aphid *Pemphigus betae* (Whitham 1989), which in turn affects the distribution of arthropods, fungi, and birds.

Plant genetics represents a bottom-up influence on community structure (Price et al. 1980; Fritz and Simms 1992; Matson and Hunter 1992). Bottom-up regulation refers to direct or indirect dependence of community structure on variation in lower trophic levels or in their resources, and includes abiotic factors (Dunson and Travis 1991), nutrient availability (Neill and Peacock 1980), plant quality (Rhoades and Cates 1976) and quantity (Feeny 1976). In contrast, top-down regulation refers to situations where the structure of lower trophic levels depends directly or indirectly on the activities of higher trophic levels, e.g., predation (Paine 1966; Brown and Heske 1990; Kerbes et al. 1990).

Two cottonwood species (*Populus angustifolia* and *P. fremontii*) hybridize to produce F1 hybrids. Genetic introgression in this system is unidirectional; F1 hybrids cross with *P. angustifolia*, but not *P. fremontii*, to produce a series of backcrosses resulting in a hybrid swarm (Keim et al. 1989). These naturally occurring complex backcross hybrids vary greatly in their resistance to *P. betae*; survival of colonizing aphids ranges from 0 to 90% (Whitham 1989; this paper).

Aphid-resistant trees support few to no galls while aphid-susceptible trees support up to 50 000 galls (Whitham 1983). Natural cottonwood hybrid zones are found commonly throughout the United States and Canada (Eckenwalder 1984). The hybrid zone we studied paralleled the Weber River and measured 13 km in length (Keim et al. 1989). The genetic basis of resistance to *P. betae* is supported by two lines of evidence:

1. Common garden experiments show that clones maintain the same aphid resistance traits as the parental trees from which they were derived (Whitham 1989).
2. Molecular genetic studies using RFLP analyses show that F1 hybrids are highly resistant to *P. betae*, whereas complex backcross hybrids are often highly susceptible (Paige et al. 1990; Paige and Capman 1993).

This system is well-suited to examine the effects of plant resistance traits on other members of the community. First, resistant and susceptible backcross hybrids grow side by side and are locally abundant. Second, cottonwoods sucker from the roots and form natural clones allowing us to use one ramet as a treatment and another ramet of the same clone as a control, thereby eliminating plant genotype as a factor in paired comparisons. Third, cottonwoods are dominant species in riparian habitats and provide essential habitat for a variety of species (e.g., Finch and Ruggiero 1993).

To determine how host plant resistance to aphids might directly or indirectly affect other community members, we addressed the following questions:

1. Do the arthropod communities of aphid-resistant and -susceptible backcross hybrids differ?
2. Using aphid exclusion experiments on susceptible trees we asked, how might the presence of aphids affect: (a) the arthropod community; (b) aphid enemies; and (c) inquilines?

Because experimental results showed that aphid enemies selectively foraged or were more abundant on susceptible trees with high aphid densities, we addressed two additional questions:
3. How do fungi respond when honeydew (a sugary aphid excretion) is experimentally increased?
4. Because avian predators selectively forage on aphid-susceptible trees where prey are abundant, do they also discriminate among branches within a tree?

Materials and methods

All studies were conducted on complex backcross hybrids of *Populus angustifolia* × *P. fremontii* along the Weber River in northern Utah, USA during the spring and summer of 1993.

Observational arthropod community censuses

To begin examining the effects of genetically-based plant resistance traits on community structure, we censused the arthropod community on backcross hybrid trees that were either highly resistant ($n = 20$) or highly susceptible ($n = 14$) to the gall aphid, *P. betae*. Censusing was conducted the first 2 weeks of June. Aphid-resistant trees had 0–48 successful galls per 100 attempts ($x = 18.4$, $n = 12$) and aphid-susceptible trees had 69–90 successful galls per 100 attempts ($x = 80.3$, $n = 12$). We identified at least 42 taxa (herbivores, their predators, and generalist taxa attracted to aphid honeydew) from at least 35 families representing 14 orders. Our reference collection was compared to Utah State University's insect collection. This analysis specifically excluded *P. betae* and those taxa found inside the galls such as insect predators. Because *P. betae* is more abundant and has greater survival on mature trees than on juvenile trees (Kearsley and Whitham 1989), and mature and juvenile trees support different arthropod communities (Martin and Whitham, unpublished data), arthropods were censused only on mature foliage (i.e., foliage producing flowers). All censusing was done on a per shoot basis; a shoot was defined as the current year's growth originating from one bud. Counts were standardized to number of arthropods per 1000 shoots.

To determine an overall community response, we compared species richness and relative abundance between aphid-susceptible and -resistant trees. Species richness was expressed by summing the total number of species per 1000 shoots on each tree. Relative abundance values were calculated by log-transforming the counts per 1000 shoots, and then standardizing those counts for each taxon to have a standard deviation of 1 and a mean of 0.5. The standardized values were then summed. This standardization prevented common species from swamping the abundances of rarer species. Both species richness and relative abundance data were analyzed with t-tests.

Aphid exclusion experiment

To examine indirect effects of plant resistance to aphids on other organisms, we performed an aphid exclusion experiment. Aphids were excluded from 12 susceptible ramets to match aphid densities found on aphid-resistant trees, and paired with 12 control ramets from the same susceptible clones.

Aphids were excluded by placing a sticky barrier (Tanglefoot) on tape that was then wrapped around tree trunks to prevent colonizing aphids (fundatrices) from crawling from overwintering sites at the bases of trees to developing leaves. Since colonization is highly synchronized with bud-break and lasts only a few days (Whitham 1978), removal of the sticky barrier at the end of the brief colonization period minimized impact on other arthropod species. Because these aphids are one of the first species to become active on cottonwood when late season snowfall is common, the sticky barrier had no effect on later arriving species we surveyed 1 month later. This aphid exclusion technique was supplemented on some trees by removing colonizing aphids by hand with a fine (000) brush.

The exclusion experiment was effective (x galls/1000 shoots ± 1 SE; aphid-resistant ramets 20.9 ± 3.92, $n = 20$; aphid-exclusion ramets = 33.8 ± 5.14, $n = 12$; control ramets = 220.0 ± 29.36, $n = 12$); gall density on exclusion ramets did not differ from resistant trees (Mann-Whitney test statistic = 168.00, $P > 0.05$). Thus, we held plant genotype constant and examined how the presence of aphids affected other community members.

On aphid-exclusion and control ramets three data sets were collected. We censused the arthropod community on shoots, whereas, for aphid enemies and inquilines we specifically examined galls and their contents.

Arthropod community

The arthropod community on exclusion and control ramets was censused the same time and analyzed in the same manner as our observational studies.

Aphid enemies

To examine how organisms intimately associated with galls were affected by the exclusion experiment, we compared the percentage of galls attacked by birds, fungi, and insects. This census occurred during 1 week in late June, when aphids were at high densities. Galls were haphazardly collected and immediately censused. On each of 12 control ramets, 100 galls were censused and an average of 33 galls (range 5–60; SE = 1.4) were censused on paired exclusion ramets. Comparisons were made with Wilcoxon signed-rank tests, followed by a sequential Bonferroni adjustment. Avian predators such as Black-capped Chickadees (*Parus atricapillus*) and insect predators representing five orders [e.g., Heteroptera (Anthocoridae) *Anthocoris* sp. and Diptera (Chamaemyiidae) *Leucopis* sp. larvae] fed on the hundreds of aphids that could be found in each gall (Whitham 1978). Fungi, particularly the mold, *Cladosporium cladosporioides* (Wilson 1995), fed on honeydew excreted by aphids, and also trapped the aphids with their extensive mycelia (Harper 1959; Grigarick and Lange 1968).

Inquilines

We also examined how inquilines (animals who live in abodes properly belonging to another) were affected by our exclusion experiment by comparing the percentage of galls inhabited by inquilines. As with aphid enemies, 100 galls were censused on each of 8 control ramets and an average of 22 galls (range 8–44; SE = 1.1) on paired exclusion ramets, and compared with a Wilcoxon signed-rank test. Censusing was conducted during the first week of August, after *P. betae* had emigrated. We identified seven taxa from seven orders of arthropods; the most common was free-feeding aphids [Hemiptera (Aphididae)].

Density-dependent responses of fungi and birds

Having shown that fungal infection of galls was disproportionately greater on control ramets with high aphid densities than on aphid-exclusion ramets, we experimentally examined the hypothesis that honeydew excreted by aphids attracted fungi. In an attempt to increase honeydew levels, on nine aphid-susceptible trees we sprayed one branch with sugar (sucrose) water and another branch of the same tree with water to serve as a control. After 2 weeks, 678 galls on treatment branches and 653 galls on control branches were censused and results were analyzed with a paired *t*-test.

Similarly, having demonstrated that birds disproportionately forage on aphid-susceptible trees with high aphid densities, we then addressed if birds also discriminate at a finer scale, i.e., among individual branches of the same tree. Using regression analysis, we compared avian predation rates by examining 575 galls distributed among 10 large branches of one tree.

Results

Observational censusing of arthropod community

We found that the arthropod community of aphid-susceptible trees had 31% greater species richness
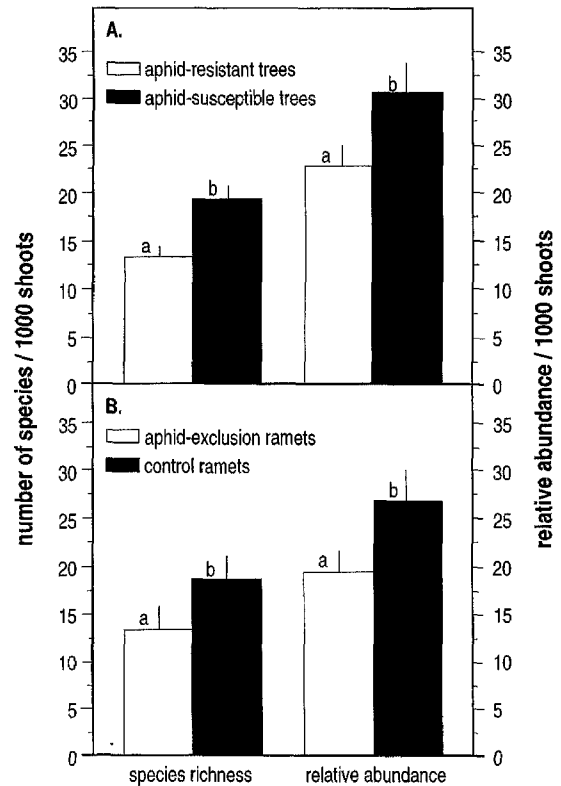

Fig. 1 Species richness and relative abundance of the arthropod community on **A** aphid-susceptible ($n = 14$) and aphid-resistant trees ($n = 20$), and **B** paired aphid-exclusion and control ramets ($n = 12$ pairs). *Bars* represent mean counts per 1000 shoots ± 1 SE. Means with different letters (a, b) are significant at the $P < 0.05$ (*t*-tests and paired *t*-tests, respectively)

($t = 3.251$, $P = 0.05$) and 26% greater relative abundance than aphid-resistant trees ($t = 1.976$, $P < 0.05$; Fig. 1A).

Aphid exclusion experiment

The arthropod community, aphid enemies, and inquilines all responded to the exclusion of aphids. These results demonstrate the indirect effects of plant resistance traits acting through aphids to affect other species.

Arthropod community

Exclusion of gall aphids on susceptible trees resulted in a 24% decrease in species richness ($t = 1.755$, $P < 0.05$) and a 28% decrease in relative abundance ($t = 2.073$, $P < 0.05$) of the arthropod community (Fig. 1B). The most abundant taxon of arthropods surveyed, leafhoppers (Cicadellidae), was significantly more abundant on control than on exclusion ramets (x leafhoppers per 1000 shoots ± 1 SE; $x = 40.1 \pm 12.10$ and $x = 20.9 \pm 6.92$, respectively; $Z = 2.703$, $P < 0.05$).

Fig. 2 A Percentage of galls attacked by birds, fungi, and insects on paired exclusion and control ramets (n = 12 pairs). **B** Percentage of galls with inquilines on paired exclusion and control ramets (n = 8 pairs). *Bars* represent means ± 1 SE. Means with different letters (*a, b*) are significant at the P < 0.05 using a sequential Bonferroni adjustment (Wilcoxon signed-rank tests)
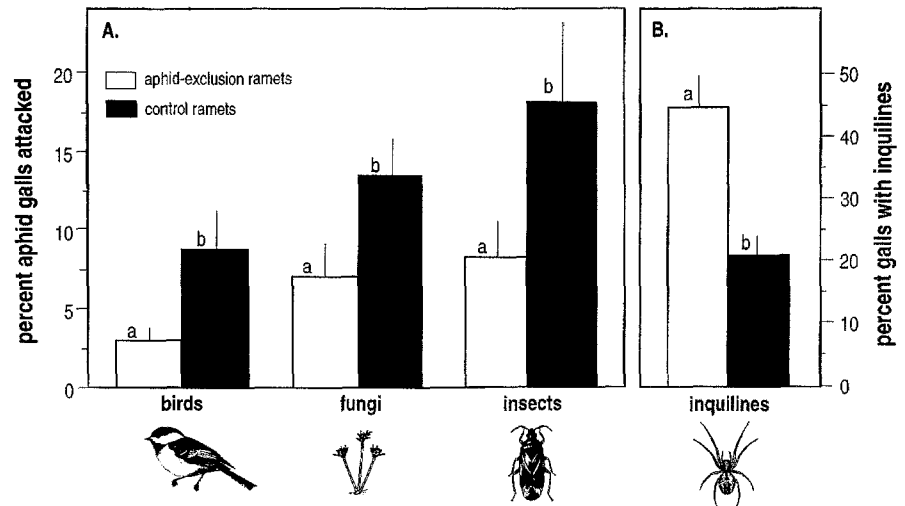
The fact that biodiversity declined even when plant genotype was held constant (i.e., paired ramets of the same susceptible clones used for both exclusion and control), suggests that these arthropods were affected the presence of *P. betae*. Furthermore, these results suggest that observed differences in species richness and relative abundance (Fig. 1A) were due to indirect effects rather than direct effects of plant resistance traits.

Aphid enemies

All three taxa of aphid enemies showed disproportionate responses to gall density on aphid-exclusion and control ramets. On aphid-exclusion ramets bird predation was 3 times less (Z = 2.119, P < 0.05), fungal infection 2 times less (Z = 2.002, P < 0.05), and insect predation 2 times less (Z = 2.490, P < 0.05) when compared to control ramets (Fig. 2A). Hence, aphid enemies selectively foraged or were more abundant on trees where gall densities were highest.

Inquilines

In contrast to aphid enemies, inquilines exhibited a negative response to gall density. The percentage of galls with inquilines was 2 times greater on aphid-exclusion ramets compared to controls (Z = 2.100, P < 0.05; Fig. 2B). Note that inquilines moved into galls after the aphids emigrated and thus did not directly interact with the aphids.

Density-dependent responses of fungi and birds

Proportionately more galls contained fungi on branches treated with sugar water (x = 31.1 ± 2.43, n = 678 galls) than those sprayed with water alone (x = 23.1 ± 3.39, n = 653 galls; t = 4.47, P < 0.05, n = 9
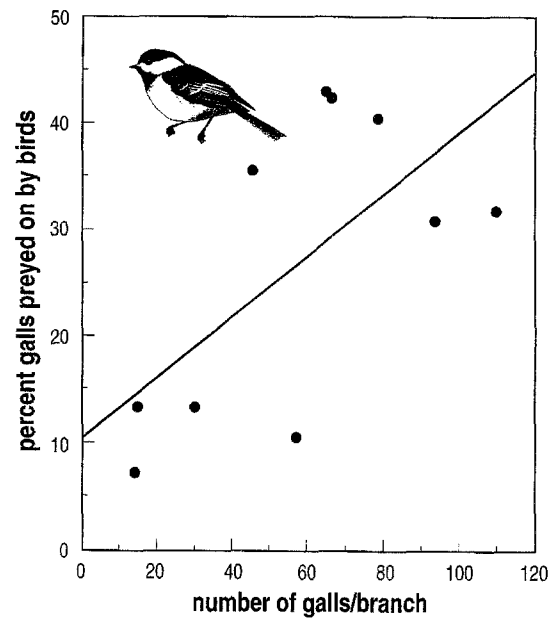

Fig. 3 Percentage of galls preyed on by birds as a function of gall density per branch (n = 575 galls, n = 10 branches, r^2 = 0.42, P < 0.05)

paired branches). These results suggest that fungi increase in abundance when more honeydew was available, and also suggest a mechanism whereby galls on aphid-susceptible trees have a higher probability of becoming infected with fungi than galls on aphid-resistant trees.

As gall density on individual branches increased, the proportion of galls preyed upon by birds also increased. A linear regression showed that gall density explained 42% of the variation of bird predation (P < 0.05, n = 10 branches; Fig. 3). There was a marked increase in bird predation when gall density exceeds approximately 50 galls/branch, suggesting a threshold effect. Not only did avian predators selectively forage on aphid-susceptible trees, they also foraged at a finer scale by discriminating among different branches of the same tree.

Discussion

Indirect effects of plant resistance traits

Plant resistance traits and/or genotype may affect aphid distribution and performance (e.g., Campbell and Eikenbary 1990). Aphids, in turn, may affect other species in several major ways. First, they can significantly impact host plant growth and reproduction, thereby facilitating or reducing host attractiveness to other species. In this system, *P. betae* is known to affect the sink-source translocation patterns of cottonwoods (Larson 1989; Larson and Whitham 1991). Aphid galls function as mobilizing sinks, and on susceptible trees aphids are able to import photosynthate from other leaves of the same shoot. However, on resistant trees, aphids utilize only carbon produced by the leaf they occupy. This altered sink-source relationship may facilitate host use by other herbivore species. For example, phloem-feeding leafhoppers, often observed on the galls themselves, probably take advantage of the increased photosynthate of susceptible trees.

Second, great abundance of aphids may attract generalist predators, and third, their excretion of copious amounts of honeydew may attract arthropods and decomposers (Llewellyn 1972; Fedde 1973; Dixon 1985). Furthermore, Grier and Vogt (1990) found that aphid honeydew reaching the soil caused a reduction in available nitrogen, nitrogen mineralization rates, above-ground net primary production, and nitrogen uptake by trees. Lastly, by forming galls, aphids create habitat that other species may inhabit.

In our study, indirect effects occurred through an interaction chain (Strauss 1991; Wootton 1994): plant resistance influenced the distribution of a common leaf-galling aphid, *P. betae*, which in turn influenced other community members. A richer arthropod community on trees with high aphid densities relative to those with low aphid densities may be a function of: (1) other herbivores responding to host plant quality, which may be modified by the aphids; (2) predators responding to more abundant prey; or (3) both.

A separate analysis of aphid enemies (birds, fungi, and insect predators) showed that aphid exclusion caused a 2- to 3-fold decrease in enemy foraging and/or presence. Predictably, aphid enemies responded to gall density.

In contrast to aphid enemies, inquilines were more abundant per gall on aphid-exclusion ramets compared to controls. Because inquilines did not respond to gall density, this result is more difficult to interpret. One explanation is that the few galls on exclusion ramets represent a limiting resource and are thus used at a higher rate than the more numerous galls on control ramets.

Bottom-up effects

Our study supports a bottom-up influence on community structure and suggests that the distribution of many organisms may map onto the underlying genetics of the plant population. The effects of plant resistance traits may extend beyond herbivores to foraging behaviors and habitat selection of diverse taxa representing multiple trophic levels (e.g., herbivores, vertebrate and insect predators, and decomposers). Our findings are conservative because our studies did not include the parental tree species and their F1 hybrids, which cumulatively possess greater variation in morphology and resistance to aphids, and support different arthropod communities than the backcross hybrids we studied (Paige et al. 1990; Floate and Whitham 1993, 1995; Martin and Whitham, unpublished data). Further support of the effects of plant genetics on community structure is the observation that within the hybrid swarm, bird nest densities were significantly greater on F1 hybrids than on either parental cottonwood species (Martinsen and Whitham 1994).

We know of only one other system that has demonstrated the effects of plant resistance traits on community structure. Allozyme studies by Mopper et al. (1991) found that pinyon pines, *Pinus edulis*, growing in stressful, volcanically derived cinder soils exhibited genetic variation in resistance to the stem- and cone-boring moth, *Dioryctria albovittella*. This insect reduced the tree's ability to support mycorrhizae, and when insects were removed from susceptible trees, ectomycorrhizae rebounded to levels found on resistant trees (Gehring and Whitham 1991). Furthermore, due to the negative impacts of insect herbivory on cone production, avian seed dispersers and mammalian seed predators selectively foraged where cone crops were greatest (Christensen and Whitham 1991, 1993).

Top-down effects

The impacts of enemies on aphids demonstrate a top-down influence. Aphid galls on high density trees (control ramets) were 2–3 times more likely to be attacked by bird or insect predators or be infected by fungi than galls on low density trees (aphid-exclusion ramets). Price et al. (1980) argue that enemies of herbivores may be considered plant defenses. Other studies have also shown that birds may benefit plants by preying on herbivorous insects (Atlegrim 1989; Marquis and Whelan 1994).

Not only did aphid enemies respond to between-ramet variation in aphid density, they also responded to within-ramet variation. Experimental addition of sugar water to simulate increased honeydew production by aphids demonstrated that the fungus *Cladosporium cladosporioides* responded in a positive density-dependent fashion to aphids at the branch level.

Similarly, we found that bird predation rates on aphids were dependent upon gall densities of individual branches within a tree. Furthermore, fungi and birds respond to different cues. Fungi are attracted to honeydew, the sugary excretion of aphids, while birds are most likely visually discerning gall density.

In summary, we have shown genetically-based plant resistance traits directly affect a common herbivore, whose distribution then affects community structure. The presence of aphid galls on susceptible trees increases biodiversity by influencing diverse taxa (arthropods, birds, and fungi) from three trophic levels (other herbivores, predators, and decomposers). Lastly, excluding aphids resulted in community changes that nearly equaled the differences observed between aphid-susceptible and -resistant trees, therefore we conclude that indirect effects of plant resistance traits on community structure may be as important as direct effects.

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