Oecologia (2000) 123:82–89

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Positive interactions between leafrollers and other arthropods enhance biodiversity on hybrid cottonwoods

Received: 19 April 1999 / Accepted: 8 November 1999

Abstract We examined the potential of a common herbivore to indirectly influence other diverse community members by providing habitat. Larvae of the leafroller *Anacampsis niveopulvella* commonly construct shelters by rolling leaves of cottonwood trees. These leaf rolls are later colonized by other arthropods. We first documented 4 times greater species richness and 7 times greater abundance on cottonwood shoots that contained a rolled leaf compared to adjacent shoots without leaf rolls. Second, with both removal and addition experiments, we showed that leaf rolls are responsible for these differences in arthropod assemblages. Leaf roll removal caused a 5-fold decline in richness and a 7-fold decline in abundance; leaf roll addition resulted in a 2.5-fold increase in richness and a 6-fold increase in abundance. Third, to determine whether rolled leaves are colonized for food or for shelter, we compared colonization of natural and artificial leaf rolls. Both richness and abundance were approximately 2-fold greater in artificial leaf rolls, indicating that leaf rolls are colonized primarily for shelter. Fourth, in a natural hybrid zone we found that leafroller densities were 2-fold greater on backcross hybrids than on F_1 hybrids. These differences are likely associated with genetically-based differences in leaf morphology and/or leaf chemistry. Ultimately, plant genotype affects positive indirect interactions that have the potential to affect community structure. This study and others demonstrate that shelter builders (i.e., leafrollers and gall formers) enhance biodiversity, while free-feeders are more likely to negatively affect biodiversity.

Key words Positive interactions · Indirect effects · Hybridization · Leafrollers · Herbivory

Introduction

Ecological research during the 1980s was dominated by studies of the direct interactions between two species (e.g., predation, herbivory, competition). This led to increased scientific rigor because these relatively simple systems are more amenable to experimental manipulation. However, the resulting view of species interactions is probably oversimplified if we fail to consider potential indirect interactions between the diverse organisms that make up the community (Strauss 1991; Wootton 1994). While indirect interactions have only recently received serious study, they may be as important as direct interactions in structuring communities.

Since Hairston et al. (1960), interactions among species of herbivorous insects (especially competition) have often been considered unimportant (but see Denno et al. 1995). Instead of documenting relationships within trophic levels, most subsequent research has focused on interactions between herbivores and their host plants, or herbivores and their natural enemies (Hunter 1992; Damman 1993).

Interactions within trophic levels in herbivore communities are likely to be subtle and indirect. Damman (1993) considers three types of such indirect interactions: (1) resource-mediated interactions, where feeding by one insect species causes changes in host plant quality that affects other species; (2) enemy-mediated interactions, where one herbivore species influences another through changes in the population dynamics or foraging behavior of shared natural enemies; and (3) the provision of shelters by one species for another, which affects both resources and natural enemies.

Enemy-mediated interactions between herbivore species are most commonly negative (Damman 1993). Resource-mediated interactions can be negative, positive, or neutral (Faeth 1986; Hunter 1992). Shelter building is

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a positive interaction, as it almost always benefits the species that acquires the shelter. For example, Cappuccino and Martin (1994) showed that removal of early-season shelter-builders reduced the abundance of later-season species, and this indirect effect extended to the following year. Although the late-season species were capable of making their own shelters, they tended to colonize preformed shelters. Such positive interactions are now recognized as being important components of community structure (Kareiva and Bertness 1997).

Many lepidopteran larvae build shelters by rolling, folding, or tying leaves together with silk. Shelters built by early-season Lepidoptera on oak and birch are frequently colonized by late-season species (Carroll and Kearby 1978; Cappuccino 1993) or by later generations of the same species (Carroll et al. 1979; Damman 1987). Other insects, including both herbivores and predators, have also been found in these shelters on oaks (Carroll and Kearby 1978; Carroll et al. 1979). Because they modify habitats (albeit at a small scale), shelter builders fit the recently proposed definition of “ecosystem engineers” (Jones et al. 1997). Even these small-scale effects are likely to be far-reaching, both at the population and community levels, and both within and among trophic levels.

Here, we extend these previously documented patterns of the indirect effects of shelter builders on oak and birch to another common tree, cottonwood (*Populus*). By experimentally removing and creating leaf rolls, we show that shelter builders interact positively with both predators and other herbivores. Such experiments have not previously been conducted to study the community-wide effects of shelter building Lepidoptera. Furthermore, no previous studies have examined how plant genotype might indirectly affect biodiversity by affecting leaf roller abundance. We studied the arthropod fauna associated with leaf rolls made by *Anacampsis niveopulvella* (Chambers) (Gelechiidae). We studied *Anacampsis* in northern Utah, where larvae roll leaves of hybrid cottonwoods (*Populus angustifolia* × *P. fremontii*).

First, we documented higher species richness and abundance in leaf rolls compared to adjacent unrolled leaves. We then created leaf rolls that were later colonized more frequently than adjacent control leaves. Because many of the arthropods associated with rolled leaves were predators, we performed another experiment to determine whether leaf rolls were colonized for food or shelter. This experiment compared colonization of natural leaf rolls (containing an *A. niveopulvella* larva or pupa) and human-made (hereafter “artificial”) leaf rolls on adjacent shoots. Finally, to determine how host plant genotype might directly affect leafrollers and indirectly affect other community members, we compared the abundance of leafrollers on F_1 hybrids and trees that are backcrosses to *P. angustifolia* (narrowleaf cottonwood)

Methods

This research was conducted along the Weber River near Ogden, Utah. Here, the ranges of Fremont cottonwood (*P. fremontii*) and narrowleaf cottonwood (*P. angustifolia*) overlap and the two species freely hybridize (Eckenwalder 1984; Keim et al. 1989). Cottonwoods are the dominant riparian vegetation. The leafroller *Anacampsis* is common on *Populus*, especially aspen (*P. tremuloides*) and has a transcontinental distribution (Henson 1958a; Prentice 1965; Furniss and Carolin 1977). Larvae are present from early may to late july, with most occurring in June. Pupae are found from mid-May to early August, and adults are present from June to August.

Leafroller densities vary greatly among trees and across years. At high densities, up to 10% of a tree’s shoots (each shoot has 7–10 leaves) may contain a rolled leaf, and there are sometimes two leaf rolls per shoot. We have observed *Anacampsis* leaf rolls on all classes of hybrid cottonwoods, but initial observations indicated that densities were especially high on backcrosses to narrowleaf cottonwood. We chose to focus on hybrid trees because leafrollers are rarely found on Fremont cottonwood, and narrowleaf cottonwood is uncommon in the hybrid zone.

To examine the effect of leaf rolls on the cottonwood arthropod community, we censused insects and arachnids in mid-June, on shoots with and without leaf rolls. Initial observations indicated that there were more arthropods on shoots with rolled leaves than on shoots without rolls. Within a tree, shoots with leaf rolls were paired with adjacent shoots without leaf rolls (20 pairs of shoots per tree). Rolled leaves were opened and all organisms except *A. niveopulvella* counted. We surveyed 15 trees in this manner; statistical comparisons of species richness and total abundance were made on totals (20 paired shoots) for each tree. Because total abundance can be driven by one or a few common species, we also computed an index of standardized abundance. For each species, samples were standardized to equal maxima (SPM) such that the sample with the maximum for that species received a value of 1 and counts of that species in all other samples were proportional to the maximum. SPM values were then summed for each sample. Thus, samples with high values of this standardized abundance index were centers of abundance for most species, whereas, samples with values approaching 0 supported few or no individuals of each species (Faith et al. 1987).

To experimentally determine whether the presence of leaf rolls increased local arthropod species richness and abundance, we manipulated leaves of adjacent shoots. Five categories of shoots (20 shoots per category per tree) were used. Category 1 shoots contained a natural leaf roll that was subsequently removed to examine the effect of leaf roll removal on local arthropods. To control for the possible effect of plant wounding on category 1 shoots, an unrolled leaf was removed from category 2 shoots. Category 3 shoots examined the effect of an artificial leaf roll, made with a paper clip, on local arthropods. To control for the possible effect of the paper clip itself, we attached a paper clip to a leaf on category 4 shoots. Category 5 shoots were unmanipulated and served as overall controls.

Initially, shoots with lepidopteran-formed leaf rolls (i.e., category 1) were located and randomly assigned a number (1–5). This number determined which four additional shoots were used in the experiment. For example, if the number was 4, then the leaf-rolled shoot would be the fourth of five adjacent shoots counting towards the branch apex (distally). Once identified, these four shoots were randomly assigned numbers 2–5, corresponding to the remaining categories.

We censused shoots to determine the pattern of arthropod distributions before the experiment. All arthropods were then removed and manipulations performed as described above. Two weeks later, we re-censused the shoots to determine the effect of our manipulations on the local arthropod assemblages that had subsequently developed. This experiment was done on each of five trees in late June.

Because many of the organisms found in rolled leaves were predators (e.g., spiders, coccinellids, pentatomids), we conducted

Table 1 Partial list of taxa found inside *Anacampsis niveopulvella* leaf rolls (*OTU* operational taxonomic unit)

Order	Family	Species or OTU
Acarina	Trombiculidae	1 species
Araneae	Araneidae	4 species
	Salticidae	3 species
Dermaptera	Forficulidae	1 species
Hemiptera	Pentatomidae	*Apateticus* sp.
	Anthocoridae	*Anthocoris* sp.
	Miridae	1 species
Homoptera	Cicadellidae	Cicadellinae(2 species) Idiocerinae(1 species)
	Cixiidae	1 species
	Aphidida	*Chaitophorus populocola* Chaitophorinae(1 species)
	Diaspididae	1 species
Neuroptera	Chrysopidae	*Chrysopa* sp.
Coleoptera	Coccinellidae	*Adalia bipunctata*
	Curculionidae	Otiorhynchinae(1 species)
Lepidoptera	Tortricidae	1 species
	Geometridae	*Alsophila pometaria*
Hymenoptera	Formicidae	Dolichoderinae(1 species) *Formica propinqua*

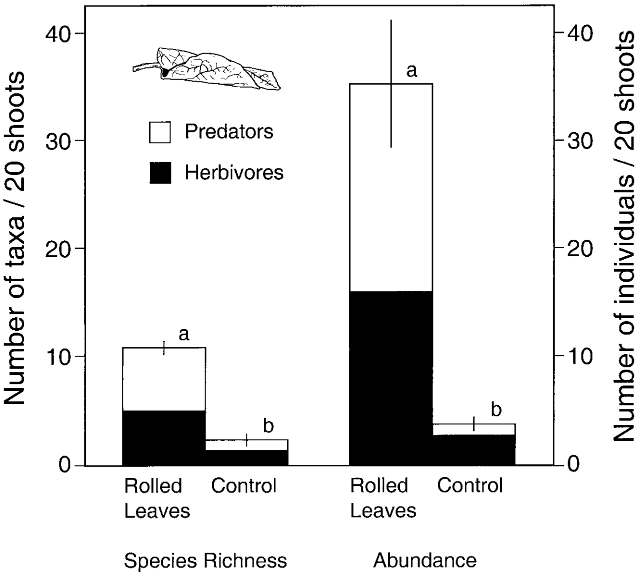


Fig. 1 Both species richness and abundance were greater on shoots containing a leaf roll than on adjacent shoots without a leaf roll (richness: t=10.31, P<0.001; abundance: t=4.79, P<0.001; n=15 trees, total of 20 pairs of shoots per tree). *Vertical lines* represent ±1 SE and different *letters* indicate significant differences. Overall means are broken down into herbivores and predators. Also shown is a simplified drawing of *typical leaf roll* formed by *Anacampsis niveopulvella*

another experiment in late June of the following year to determine if leaf rolls are colonized for food (e.g., the lepidopteran pupa within the roll) or simply for shelter. We found a shoot with a natural leaf roll and then, using a paper clip, created an artificial leaf roll on a shoot of the closest adjacent branch. Because leafroller densities were lower that year, this experiment used ten pairs of shoots per tree on ten different trees. After two weeks, arthropods were censused in both types of leaf rolls and analyses performed on total arthropods per ten shoots (n=10 trees).

For these observational and experimental data, statistical analyses were performed on measures of species richness and total abundance using paired t-tests. A list of taxa found in leaf rolls is provided in Table 1.

Our initial observations indicated that leafrollers were more concentrated on hybrid cottonwoods than on either parental tree species. Hence, genetic differences among closely related host plants appeared to affect this leafroller's distribution. To further document a plant genetic effect on *A. niveopulvella* abundance, we compared leafroller densities on two distinct hybrid classes: F_1 hybrids and backcross hybrids, using a t-test.

Results

Observed patterns of biodiversity

Arthropod diversity on shoots that contained a rolled leaf was much greater than on adjacent shoots without a leaf roll (Fig. 1). Rolled shoots contained an average of 4 times as many species and 7 times as many individual organisms as unrolled shoots. Both species richness and total abundance were significantly greater on shoots with a leaf roll (richness: t=10.31, P<0.001; abundance: t=4.79, P<0.001). These differences are a result of the leaf roll, because over 90% of the organisms on shoots with a leaf roll were found in the roll itself.

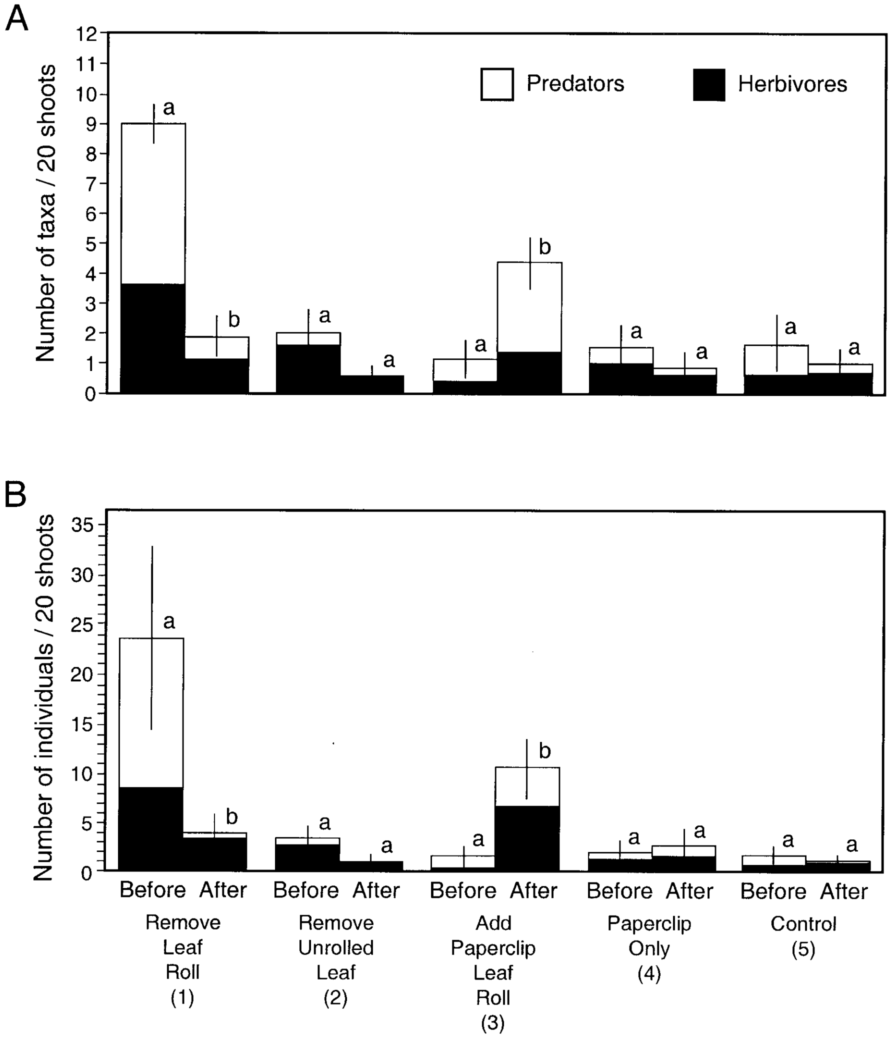
The increase in total abundance on shoots with leaf rolls is not due to just a few very common species, but reflects a community-wide response. Increases in total abundance could be caused by a few very common species or could represent a community-wide response in which most species show increased abundance on shoots with leaf rolls. To separate these two alternative interpretations of total abundance, we standardized abundance, so that each species contributed equally to the overall abundance. With standardized abundance, we found the same pattern: shoots with leaf rolls supported significantly greater abundance than shoots without leaf rolls (t=7.89, P<0.001; leaf roll mean=5.35, SE=0.57; unrolled shoot mean=0.79, SE=0.23). Thus, the observed pattern of abundance reflects a community-wide pattern, not a pattern driven by a few common species.

The presence of leaf rolls has a positive effect on both predators and other herbivores. Shoots with leaf rolls contained 7 times as many predator species and 17 times as many predators as adjacent shoots without leaf rolls (Fig. 1). Similarly, leaf rolled shoots contained 4 times as many herbivore species and 7 times as many herbivores as shoots without leaf rolls (Fig. 1). The response of predators to potential prey was not unexpected, but the fact that leafrollers have such strong effects on other herbivores was impressive.

Experimental confirmation

To determine whether the leaf roll had a positive effect on arthropod diversity as our observations suggested, in the first experiment we both removed a natural leaf roll

Fig. 2A,B Results of the experiment comparing removal of lepidopteran-formed leaf rolls and addition of artificial leaf rolls made with paper clips. **A** Species richness, **B** total abundance (*n*=5 trees, total of 20 leaves per treatment per tree). *Vertical lines* represent ±1 SE and different *letters* indicate significant differences



and added an artificial leaf roll. We found that leaf roll removal caused a dramatic decline in both richness (from an average of 11 to 2 species; t=10.69, P<0.001) and abundance (from an average of 29 to 4 organisms; t=6.55, P<0.001) (Fig. 2). This result was solely due to the removal of the leaf roll, because removal of an unrolled leaf had no effect (richness: t=2.15, P>0.05; abundance: t=2.3, P>0.05).

Conversely, the addition of an artificial leaf roll made with a paper clip increased both richness (from an average of 2 to 5 species; t=2.37, P<0.05) and abundance (from an average of 2 to 12 organisms; t=2.44, P<0.05). Again, the leaf roll itself was responsible, because addition of a paper clip alone had no effect. Also, there was no change in arthropod species richness or abundance on the leaves that served as overall controls.

Both predators and herbivores responded to the removal and addition experiments, a result consistent with the observational data. Leaf roll removal caused a 3-fold decline in herbivore species richness, an 8-fold decline in predator species richness, a 2.5-fold decline in herbivore abundance, and a 25-fold decine in predator abundance (Fig. 2). Conversely, leaf roll addition led to a 3.5-fold increase in both herbivore and predator species richness, a 17-fold increase in herbivore abundance, and a 3-fold increase in predator abundance.

Mechanisms

Another experiment supported the hypothesis that increased diversity in leaf rolls results primarily from the shelter they provide rather than arthropods being attracted to them for the prey found within (Fig. 3). To determine whether leaf rolls are colonized for food or shelter, we selected a natural leaf roll and added an artificial leaf roll on the nearest branch. We found that artificial leaf rolls did not differ from natural leaf rolls in the number of taxa they supported (t=2.24, P>0.05), but they did support significantly greater abundances of arthropods (t=2.69, P<0.05). The fact that artificial leaf rolls are as good as or better than natural leaf rolls argues that arthropods are attracted to leaf rolls for shelter rather than the prey they contain.

Shelter could be important to both herbivores and predators, but our data indicate that herbivores show a dis-

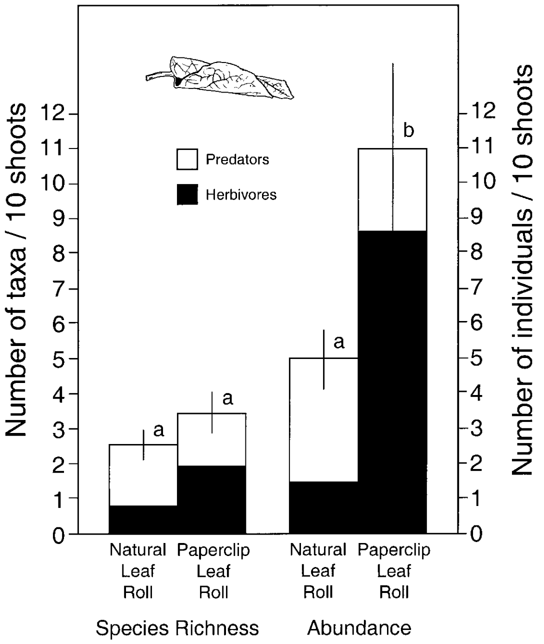


Fig. 3 At least as many arthropods colonized our artificial leaf rolls as colonized naturally occurring leaf rolls (richness: t=2.24, P<0.10; abundance: t=2.69, P<0.05; n=10 trees, total of 10 paired shoots per tree). *Vertical lines* represent ±1 SE and different *letters* indicate significant differences

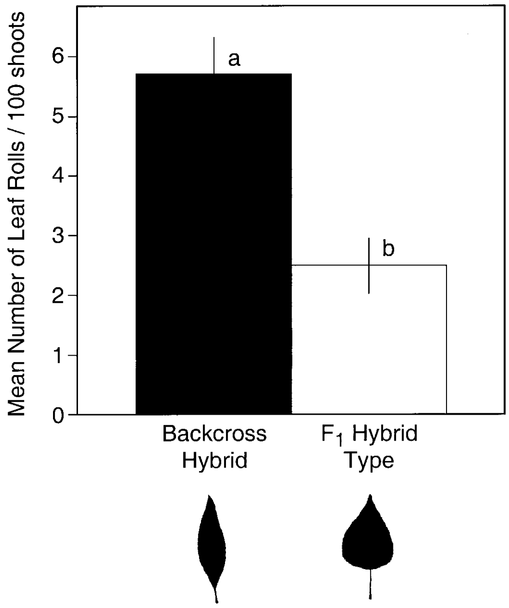


Fig. 4 The abundance of rolled leaves was significantly greater on backcross hybrids than on F_1 type hybrid cottonwoods (t=3.53, P<0.005, n=27, 29 trees). Six censuses were conducted on each tree. *Vertical lines* represent ±1 SE and different *letters* indicate significant differences. *Leaf silhouettes* show the different morphologies of the hybrid types

proportionate response to artificial leaf rolls. Herbivore abundance was 5-fold higher on artificial leaf rolls than on natural leaf rolls, while predator abundance was actually lower on artificial leaf rolls. Arthropods may prefer artificial leaf rolls because of their clear openings; natural leaf rolls often have webbed openings created by the leafroller or by predators such as spiders that have colonized them. Also, our artificial leaf rolls were newer and thus made of fresher leaf material than the adjacent natural leaf rolls. Nevertheless, these experiments demonstrate that the leaf roll results in a positive indirect effect that affects a diverse arthropod community. These results also show that the leaf rolls we made with paper clips are an effective mimic of lepidopteran-formed rolls.

Hybrid plants

Leaf rolls created by *A. niveopulvella* occur on all classes of hybrid cottonwoods, but densities are more than 2-fold greater on backcrosses to narrowleaf cottonwood than on F_1 hybrids (Fig. 4). The smaller backcross leaves are probably easier to roll (see leaf silhouettes in Fig. 4), but there are other important genetically based differences between the tree types. For example, backcross hybrid leaves contain more condensed tannins but less phenolic glycosides (the major groups of cottonwood defensive chemicals) than F_1 leaves (L. Mota-Bravo and T.G. Whitham, unpublished work). Regardless of the proximate mechanism, the differences in leafroller densities are likely genetically based, as other studies of hybrids and parental species of cottonwoods in the wild and in our common gardens have demonstrated pronounced clonal effects on insect performance and survival (Whitham 1989; Floate et al. 1993).

Discussion

Why live in a shelter?

There is a diverse arthropod fauna associated with leaf rolls made by larval *A. niveopulvella*. The organisms inhabiting rolled leaves range from other herbivores such as leafhoppers and aphids to predators such as spiders and pentatomid bugs. Although these leaf roll associates are found on unrolled cottonwood leaves, they are far more abundant within leaf rolls.

The potential advantages of living within a leaf roll include a more favorable microclimate, better food quality, and predator avoidance. Organisms inside a leaf roll are better able to avoid desiccation (Henson 1958a; Hunter and Willmer 1989) and maintain body temperature higher than the ambient temperature (Henson 1958b). The leaf roll may reduce leaf toughness and lower levels of plant defensive chemicals, and hence provide more easily eaten food (Lewis 1979; Sagers 1992). Some tortricids feed on St. Johns wort (*Hypericum perforatum*) by rolling leaves to avoid direct sunlight that would activate plant defenses (Sandberg and Berenbaum 1989). Finally, leaf rolls may be important as refuges from predators (Damman 1987; Altegrim 1992).

We found at least one other species of lepidopteran larvae, a tortricid leaftier, in *A. niveopulvella* leaf rolls. Cappuccino (1993) reported several species in four different families using preformed leaf rolls and "leaf sandwiches" on paper birch. These shelters were almost always constructed by one early-season species of leaftier. Larvae that develop in a preformed leaf shelter do not have to spend time and energy building the shelter. Time spent building a shelter increases exposure to predators and is time that could otherwise be spent feeding.

Although the above studies argue that protection from predators is an advantage of leaf rolling, our results are less certain. Because of the high densities of arthropod predators in rolled leaves, we question the value of leaf rolls as refuges from predation. Damman (1987) found that leaf shelters reduced susceptibility of caterpillars to predators such as ants and spiders. In contrast, ants and spiders were some of the most common inhabitants of our leaf rolls. McNeil et al. (1978) found that 71% of the identifiable lepidopterans collected by ants were leafrollers and leaftiers. However, Fowler and MacGarvin (1985) showed that leaf-tiers were less affected by ant predation than were free-feeding caterpillars.

Leaf rolls may be an effective defense against bird predation (e.g., Altegrim 1992); however, there is also evidence that birds use rolled leaves as a visual search cue (Heinrich and Collins 1983; Gradwohl and Greenberg 1984; Greenberg 1987). The worm-eating warbler (*Helmitheros vermivorous*) forages on dead curled leaves in the winter, probably because arthropod biomass is tenfold greater on curled versus live leaves (Greenberg 1987).

Our data indicate that leaf rolls are colonized for shelter rather than for the food they contain. Regardless of the exact reason that the presence of leaf rolls promotes increased biodiversity, their positive effects are likely widespread. Leaf rolling behavior is common, particularly among the Lepidoptera, where it occurs in at least 17 families (Frost 1959). There is a family of leaf rolling weevils (Coleoptera: Attelabidae), there are leaf rolling sawflies (Hymenoptera: Pamphiliidae), and an unusual example in the Orthoptera, the leaf rolling grasshopper *Camptonotus carolinensis*. Leaf rolling occurs on a wide variety of plants, ranging from trees and shrubs to herbs and even ferns. In addition, studies of leaf rolls almost invariably report other arthropods using the preformed rolls. Thus, there is great potential to study both direct and indirect interactions in these shelter building systems.

Positive and negative effects of common herbivores on biodiversity

Our observations and experiments clearly show that leafrollers have a positive effect on arthropod diversity. With the removal of shelters produced by *A. niveopulvella* larvae, species richness declined 84% and abundance declined 86% relative to shoots with leafrollers. Similarly, at the same study site, Waltz and Whitham (1997) found that the presence of the leaf-galling aphid, *Pemphigus betae*, had a positive effect on other arthropods. Aphid removal decreased species richness and relative abundance by 32% and 55%, respectively. These galls provided shelter for other species, altered sink-source relationships that apparently facilitated the use of galled leaves by other herbivores, and attracted predators and parasites. Thus, in both studies, sessile insects that formed shelters (leaf rolls and galls) had a positive effect on biodiversity.

In contrast to the positive effects of these two species, two other insects that do not produce shelters have a negative effect on other arthropods. The leaf beetle *Chrysomela confluens* defoliates juvenile trees, thus reducing the resource base for other organisms. Waltz and Whitham (1997) found that when these beetles were removed, species richness and relative abundance increased by 120% and 75%, respectively. In another study, the free-feeding aphid *Chaitophorus populocoli* caused a similar decline in arthropod diversity. In this case, the aggressive behavior of the tending ant, *Formica propinqua*, was responsible for the decline (G.M. Wimp and T.G. Whitham, unpublished work).

Because the above studies of four insect herbivores (two aphid species, one beetle and one lepidopteran) were conducted at the same study sites, and on the same host plants, it appears that a key factor in determining the community response was the presence or absence of shelters. Both species that produced shelters positively affected other arthropods, whereas both species that did not produce shelters negatively affected other arthropods. Also, plant susceptibility to an herbivore can lead to increased biodiversity in some cases and decreased biodiversity in others. Although we suspect that susceptibility is more often associated with greater arthropod diversity and trophic complexity than not, future studies need to examine this issue. Furthermore, it is important to avoid the assumption that the presence of a rich community on susceptible hybrids is somehow unstable and that these plants will be automatically be selected against. Recent reviews show that the fitness of hybrids cannot be characterized as generally inferior to their parental species (Arnold and Hodges 1995; Rieseberg 1995).

Direct and indirect effects of plant genetics

Natural hybrid zones are ideal sites to study species interactions and to examine the plant genetic components of arthropod community structure (see review by Whitham et al. 1999). Hybrid zones are generally ecotones where two or more species co-occur with F_1 hybrids and complex backcrosses. Plant hybrid zones generate extensive genetic variation that affects the distributions of many herbivores and pathogens (Whitham et al. 1994; Fritz 1999). Differences in insect abundances may result because some hybrid phenotypes exhibit increased susceptibility due to hybrid breakdown, while other phenotypes exhibit increased resistance due to heterosis. As a result, hybrid swarms may contain both the most resistant and most susceptible plants.

Because individual trees within the hybrid zone vary greatly in the numbers of leafrollers they support, our studies of the effects of rolled leaves on other organisms were performed on paired shoots of the same tree. This experimental design eliminated confounding plant genetic effects that could mask the effect of leafrollers on other community members. As a consequence, our findings are most accurate when applied to the scale of shoots and small branches with and without leafrollers. Can our results then be scaled up to the level of whole trees or stands of trees? We suspect so, for the following reason. Using trees growing side-by-side to eliminate or reduce site effects, Floate and Whitham (1995) found that arthropod communities on F1 hybrids were different from those on backcross hybrids, and both were different from Fremont cottonwoods. Although this study argued that plant genetic differences influence arthropod community structure, they did not examine potential mechanisms. Our study provides one of several potential mechanisms that might explain why different hybrid types support different arthropod communities.

Our results suggest that plant genetics directly affects leafrollers and, via leafrollers, indirectly affects many other community members. For example, backcross hybrids supported nearly 2.5 times more leafrollers than F_1 hybrids, and based upon the decline in other arthropods when leaf rollers were removed, we would predict that arthropod diversity on backcross hybrids is greater than on F_1 hybrids. Although we did not specifically examine the direct and indirect effects of plant genetics with leaf rollers, Dickson and Whitham (1996) addressed this issue with the gall aphid, *Pemphigus betae*. Some backcross hybrids are highly resistant to this aphid, while other backcross hybrids are highly susceptible (Whitham 1989). Although aphid-susceptible trees support greater species richness and abundance than aphid resistant trees, the effect of tree resistance on the rest of the community could have been direct (i.e., trees resistant to aphids are also resistant to other herbivores) or indirect (i.e., susceptible trees attract aphids which in turn make the host more suitable for other herbivores and their associated predators and parasites). Aphid removal experiments showed that the community effect was indirect. Thus, in this case, plant resistance traits affected the distribution of a common herbivore whose abundance then determined the presence and abundance of other diverse taxa including insects, birds and fungi.

These and other studies of direct and indirect effects suggest that the importance of indirect interactions may equal or exceed that of direct interactions (Power 1990; Wootton 1992), but as yet insufficient studies have been completed to make a critical assessment. Nevertheless, it is clear that some species greatly enhance biodiversity while others have the reverse effect. It is important to emphasize, however, that the overall mosaic created by both positive and negative interactions, and both direct and indirect interactions is likely to result in greater biodiversity than a community composed of one type of interaction alone.

Acknowledgements We thank K. Charters, N. Cobb, K. Gehring, J. Ganey, K. Haskins, P. Price, J. Ruel, and J. Schweitzer for comments on the manuscript. R. Hodges and J. Brown, Systematic Entomology Laboratory, Agricultural Research Service, USDA, identified the leafroller. This research was supported by N.S.F. grants DEB-9726648 and 9615313, and U.S.D.A. 95-37302-1801. Pacificorp furnished housing.

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