INDIRECT INTERACTIONS MEDIATED BY CHANGING PLANT CHEMISTRY: BEAVER BROWSING BENEFITS BEETLES

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Abstract. We documented an indirect interaction between beavers (*Castor canadensis*) and leaf beetles (*Chrysomela confluens*), mediated by changing plant chemistry of their cottonwood hosts (*Populus fremontii* × *P. angustifolia*). Resprout growth arising from the stumps and roots of beaver-cut trees contained twice the level of defensive chemicals as normal juvenile growth. However, rather than being repelled by these defenses, leaf beetles were attracted to resprout growth, resulting in a strong positive association between beavers and beetles. Why? Cottonwoods contain phenolic glycosides, chemicals that are defensive against mammalian herbivores, but are sequestered and used by the beetles for their own defense. Experiments showed that beetles fed resprout growth were better defended against their predators than those fed nonresprout growth. There also may have been a nutritional benefit, because the conversion of the plant's defense, salicin and other phenolic glycosides, to salicylaldehyde releases glucose. Also, resprout growth contained more total nitrogen than did nonresprout growth. Transfer experiments showed that, in apparent response to these increased nutritional benefits, beetles fed resprout growth developed faster and weighed more at maturity.

Although indirect interactions are much less studied than direct interactions, our work suggests that the indirect interactions resulting from beaver cutting of cottonwoods have important consequences for other organisms and could represent an important component of community structure. The habitat mosaics created by beaver herbivory increase arthropod biodiversity and may benefit other organisms such as birds and mammals. Furthermore, by stimulating the production of resprout growth, beavers may play an important role in the regeneration of a habitat type that is rapidly vanishing in the West.

Key words: beavers; cottonwoods; defensive chemistry; indirect interactions; leaf beetles; phenolic glycosides; sequestration.

INTRODUCTION

Through its feeding and dam-building activities, the beaver, *Castor canadensis,* acts as a keystone species and has disproportionate impacts on the community (Naiman et al. 1986, Johnston and Naiman 1990, Jones et al. 1994, Naiman et al. 1994). Once a major herbivore of riparian habitats, beavers were heavily trapped and extirpated from most of North America by the turn of the century (Jenkins and Busher 1979). In recent years, however, they have returned to much of their former range. The removal of dominant herbivores such as beavers can have profound impacts on the landscape. For example, the near-elimination of beavers from Yellowstone National Park in the 1800s is thought to have resulted in the conversion of beaver ponds and riparian habitat to dry grasslands (Chadde and Kay 1991). Here, we examine how beaver feeding impacts an abundant insect herbivore and affects a habitat type that is designated as threatened due to human activity (Noss et al. 1995).

Few studies have examined indirect interactions be-

tween distantly related taxa. More common are studies of distant relatives that interact directly, and these interactions are often negative, e.g., competition (Brown and Davidson 1977, Hay and Taylor 1985) and predation (Paine 1966, Estes and Palmisano 1974). However, indirect interactions in which one organism benefits from the actions of another may be common; such interactions are not well documented because they are probably more difficult to detect. For example, in the short term, desert ants, birds, and mammals compete for seeds (Brown et al. 1986), but in the long term, rodents facilitate both ants (Davidson et al. 1984) and birds (Thompson et al. 1991).

Many studies have shown that herbivores affect plants and plant communities (reviewed by Huntley 1991), but few have examined the effects of one herbivore on other herbivore species. Mammalian herbivores are notable because they impact plant communities in two major ways. First, their browsing impacts vegetation and can change competitive interactions among dominant species (McNaughton 1976, Cantor and Whitham 1989, McInnes et al. 1992). Second, the disturbances they create greatly alter landscapes, e.g., beaver dams (Naiman et al. 1986), mima mounds

(Mielke 1977), and other soil disturbances created by fossorial mammals (Platt 1975, Reichman and Smith 1985, Huntley and Inouye 1988, Whicker and Detling 1988, Martinsen et al. 1990). Beavers are especially important because they radically alter communities in both ways. The changes in plant communities that beavers create almost certainly affect other herbivores and other trophic levels.

At the individual plant level, it is well known that herbivory can induce changes in defensive chemistry (e.g., Tallamy and Raupp 1991). Such changes are likely when beavers cut down cottonwoods (*Populus* sp.), removing nearly all aboveground biomass. When felled by beavers, these trees often vigorously resprout from their stumps and sucker from their roots. We predicted that resprout growth resulting from beaver herbivory would contain higher levels of defensive chemicals (Basey et al. 1990). Phenolic glycosides are a group of defensive chemicals found in many members of the Salicaceae (Palo 1984). Although higher levels of phenolic glycosides in resprout growth could repel generalist herbivores, here we specifically examine how these plant defenses might attract a specialist insect herbivore, the leaf beetle *Chrysomela confluens,* which is known to sequester them for its own defense (Kearsley and Whitham 1992). If beaver herbivory causes an increase in plant defensive chemicals, then leaf beetles benefit.

Chrysomela confluens (Coleoptera Chrysomelidae) is a chemically defended leaf beetle that feeds predominately on juvenile cottonwood trees (Kearsley and Whitham 1989, Floate et al. 1993). We studied these beetles and their cottonwood hosts (*Populus fremontii, P. angustifolia,* and their hybrids) along the Weber River in northern Utah, USA. Adult beetles emerge in April, feed on developing leaves, mate, and lay eggs on the leaves. One female may produce several clutches of 10–40 eggs. The larvae skeletonize cottonwood leaves often completely defoliating small trees (Floate and Whitham 1994). As they feed on leaf tissue, larvae consume salicin and other phenolic glycosides that break down to salicin. Ingested salicin is transported to paired dorsal glands, where it is converted to salicylaldehyde (Pasteels et al. 1983). When a larva is threatened, it everts these glands, exposing the potential predator to the salicylaldehyde. All larval development is completed by mid-July. The new adults feed briefly before dropping to the ground, where they overwinter.

Beavers are locally abundant on the Weber River and are important cottonwood herbivores. They cut down trees ranging in size from seedlings to 1 m diameter mature trees. When cut down or otherwise disturbed, most of the cottonwoods at our study sites resprouted. Our initial observations showed that beetles appeared to be concentrated on resprout growth. We hypothesized that the resprout growth is better beetle habitat than comparably sized young cottonwoods for two rea-

sons: (1) resprout growth is likely to be better defended and to contain more phenolic glycosides, which are the basis of the beetles' defense; and (2) resprout growth is a better food resource, as it is more vigorous and probably higher in limiting nutrients such as nitrogen.

METHODS

Beaver/beetle association

In order to document the relationship between beavers and beetles, specifically, that beetles prefer cottonwood resprouts caused by beaver herbivory, we censused adult beetles on resprout (cottonwood ramets arising from a stump) and adjacent nonresprout (other juvenile cottonwood ramets) growth. These censuses were conducted on hybrid cottonwoods, and the ramets were matched for height. We performed a total of 22 paired counts, each 2 min long. The data were analyzed using a paired t test.

Where beavers are active, they commonly cut down several cottonwoods, creating patches of potential beetle habitat. To determine whether beetles respond positively to increased patch size, we set up circular plots 4 m in diameter and counted number of beaver-caused stumps, number of resprout ramets, and number of clutches of *Chrysomela confluens* larvae. We censused a total of 25 of these plots. The data were analyzed using regression analysis.

Assays of beetle performance

If resprout cottonwood caused by beaver herbivory contains more phenolic glycosides, then *C. confluens* larvae feeding on resprout foliage should be better defended than those feeding on nonresprout growth. To test this prediction, we collected larvae from >100 different ramets of both types of foliage and exposed them to thatching ant (*Formica propinqua*) predators. This bioassay is reasonable, because beetle larvae are commonly encountered by ants tending colonies of free-feeding aphids (*Chaetophorus* sp.) on juvenile cottonwood trees. In the field, there are as many as five ant–beetle encounters per minute (Kearsley and Whitham 1992, Floate and Whitham 1994). We placed pairs of larvae on ant mounds and recorded the time it took for the defenses of each larva to be overwhelmed, at which time they were dragged into the mound. The larvae were always paired for size. We replicated this experiment using six different ant mounds. The data were analyzed using paired t tests.

Cottonwoods are easily cloned, and we have established common gardens by vegetatively propagating known genotypes of cottonwoods and then planting several copies of each genotype at the same site. At the time of the study, these gardens were 10 years old and included clones of one Fremont cottonwood, three narrowleaf cottonwoods, and 15 hybrids. Because beavers have cut down several trees, our gardens contained pairs of resprout and nonresprout trees from the

same clone. We used these gardens to (1) conduct bioassays using *C. confluens* and (2) compare leaf chemistry of resprout and nonresprout cottonwoods, while holding both tree genotype and site constant.

To determine whether resprout cottonwood is a better food resource for leaf beetles, we experimentally transferred newly hatched first-instar larvae of *C. confluens* to the same clones of resprout and nonresprout cottonwoods. To control for genetic differences among beetles, we split two clutches of larvae: half of each clutch was transferred to resprout foliage and half to nonresprout foliage. Thus, we were able to compare the performance of beetles that were at least half siblings. We transferred 30–35 larvae onto each tree type and then placed cages over the shoots. The cages always included enough foliage to allow the larvae to complete their development. *Chrysomela confluens* passes through three larval instars and then pupates on or near the host plant (in this experiment, many of the pupae attached themselves to the inside of the cage). We collected the pupae, placed them in petri dishes, and waited for the new adults to emerge. We separated the beetles by sex and recorded: (1) time in days to adult emergence and (2) mass of the newly emerged adults. For each tree, we computed means for male and female development time and mass. These data (four measures of beetle performance for 18 pairs of resprout and nonresprout trees) were analyzed using a one-way MANOVA, with tree genotype as a blocking factor, followed by paired *t* tests with sequential Bonferroni adjustments (Rice 1989).

Leaf biochemistry

We collected leaves from pairs of resprout and nonresprout cottonwoods growing in our common gardens in June 1992. This was the time when densities of larval *C. confluens* on naturally occurring cottonwoods were highest. We collected only the phenologically youngest leaves. Because resprout leaves are much larger, we had to sample from more nonresprout shoots to obtain an equivalent amount of young leaf material. The leaves were immediately frozen using dry ice, transported to an ultracold ($-70°C$) freezer, and later freeze-dried in preparation for chemical analyses. Our experiments indicate that this is the best method for preventing interconversion of phenolic glycosides (E. M. Driebe, *unpublished data*).

We measured concentrations of phenolic glycosides in cottonwood leaves using high-performance liquid chromatography (HPLC). Our protocol was a modification of the one described by Lindroth and Pajutee (1987). Because other phenolic glycosides (e.g., salicortin, tremuloidin, tremulacin) can be converted to salicin (Lindroth and Pajutee 1987, Clausen et al. 1989), we also measured their concentrations in the resprout and nonresprout samples. Individual phenolic glycoside concentrations were quantified using stan-
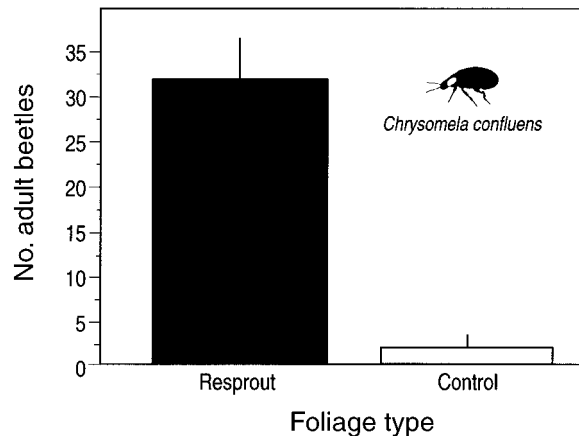

Fig. 1. Timed, 2-min censuses of adult *Chrysomela confluens* (mean $+$ 1 SE) on resprout and adjacent nonresprout cottonwood foliage show that beetles are 15 times more abundant on resprout growth ($n = 22$, paired $t = 7.28$, $P < 0.001$). Cottonwoods felled by beavers frequently resprout from the stumps and roots.

dards. These defensive chemistry data were analyzed with paired *t* tests.

The conversion of salicin to salicylaldehyde by chrysomelid larvae liberates a molecule of glucose, which is then available to the larva for nutrition (Pasteels et al. 1983, 1990). This sequestration may represent no metabolic cost, because the beetles derive both defense against predators and nutrition from the host plant defenses (Kearsley and Whitham 1992). It may even represent a net benefit to the beetle if the increased performance is a result of their ingesting more plant defenses. However, because many studies demonstrate a positive relationship between plant nitrogen concentration and insect performance (reviewed by Mattson 1980, Scriber and Slansky 1981), we also measured total nitrogen in our resprout and nonresprout leaves.

Total nitrogen and total carbon were measured using a LECO CNS-2000 (LECO, St. Josephs, Michigan, USA). Approximately 1 g of freeze-dried tissue was completely combusted at 1350°C. Carbon was measured using an infrared detector; the nitrogen detector measured thermal conductivity. Data were analyzed using paired *t* tests.

RESULTS

Beavers and beetle distribution

At two levels of examination, we found a close association between beavers and leaf beetles. First, the distribution of adult beetles is strongly associated with resprout cottonwood foliage arising from beaver herbivory. There were 15 times more adult beetles on resprout growth than on adjacent nonresprout growth (Fig. 1). Beetles are probably attracted to these vigorously growing plants because of both reduced leaf toughness and increased nutritional quality. An alter-
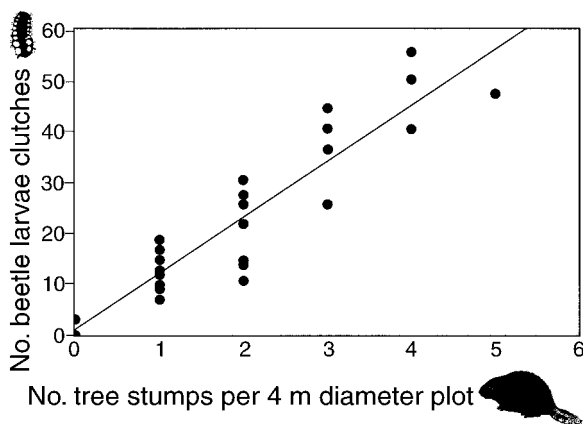
FIG. 2. The abundance of the leaf beetle *C. confluens* is strongly associated with the amount of resprout growth caused by beaver felling of cottonwoods ($y = 1.14 + 11.05x$, $r^2 = 0.84$, $P < 0.005$). Resprout ramets were highly correlated with stumps and were dropped from the multiple regression model. Censuses were conducted on 4 m diameter circular plots. Increased numbers of stumps generated more resprout cottonwood ramets and more beetle habitat.

native explanation is that beetle predators are more abundant on nonresprout growth and that resprout growth represents enemy-free space. However, this possibility seems unlikely; the arthropod and vertebrate predators examined at our study sites have been shown to forage in a density-dependent fashion (Dickson and Whitham 1996).

Second, increased beaver activity generates more resprout ramets for more beetles to feed upon. Not only are adult beetles more abundant on resprout growth, but they also respond positively to patch size, laying more clutches of eggs where stump density and resprout growth are greatest (Fig. 2). Eighty-four percent of the variation in egg/larval clutch number is explained by the number of stumps. There are also strong relationships between number of stumps and number of resprouts ($r^2 = 0.72$), and number of resprouts and clutches of beetle larvae ($r^2 = 0.63$). Because we censused clutches of young larvae or eggs prior to a build-up of predators, these results were little affected by predation. Thus, increased beetle densities are most likely due to their preference for large patches of resprout cottonwood resulting from beaver herbivory.

Phytochemistry

Consistent with the hypothesis that beetles are attracted to greater amounts of defensive chemicals in resprout foliage, we found that leaves of resprout cottonwood ramets had twofold higher phenolic glycoside levels than those of nonresprout ramets (Fig. 3). For all comparisons, both site and tree genotype were held constant; in most cases, these were the same trees that were used in the performance experiments previously described. Salicortin, not salicin, was by far the most abundant phenolic glycoside. However, salicortin, tre-

muloidin, and tremulacin are labile compounds, and their hydrolytic degradation produces salicin (Lindroth and Pajutee 1987). In fact, crushing of leaf tissue, designed to mimic the effects of chewing insects, resulted in the complete conversion of salicortin to salicin (Clausen et al. 1989). Chrysomelid beetles then use the salicin for both defense (salicylaldehyde) and nutrition (glucose). Thus, higher levels of phenolic glycosides in resprout cottonwood benefit these beetles in two important ways.

Although there were no differences in total carbon between leaves of resprout and nonresprout ramets from the same clone, levels of total nitrogen were almost 20% higher in resprout leaves (Fig. 4). This increased plant nitrogen probably provided an additional nutritional benefit to the developing beetle larvae (see the following section).

Beetle performance

Not only do beetles show a strong association with resprout cottonwood (Figs. 1 and 2), but also their performance on resprout foliage is better than on nonresprout growth. Development times on resprout growth are significantly faster (10%, on average), and adult mass is significantly (16–20%) greater (Fig. 5). Growth rate, the combination of development time and adult mass, on resprout foliage was 30–35% greater than on nonresprout foliage. These data support the hypothesis that resprout cottonwood is a better food resource. As mentioned previously, both high levels of phenolic glycosides and high levels of nitrogen in cottonwood leaves could provide a nutritional benefit to the beetles.
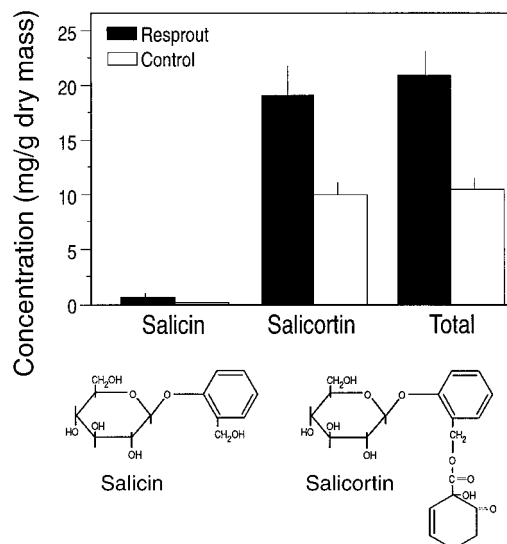

FIG. 3. Resprout cottonwood leaves contain, on average, twice the concentration (mean + 1 SE) of phenolic glycosides as nonresprout leaves ($n = 15$, paired $t = 3.31$, $P < 0.05$). The total includes salicin, salicortin, tremulacin, and tremuloidin. Salicortin is by far the most common phenolic glycoside. Larval beetles sequester these plant defensive chemicals and use them for both nutrition and their own defense.
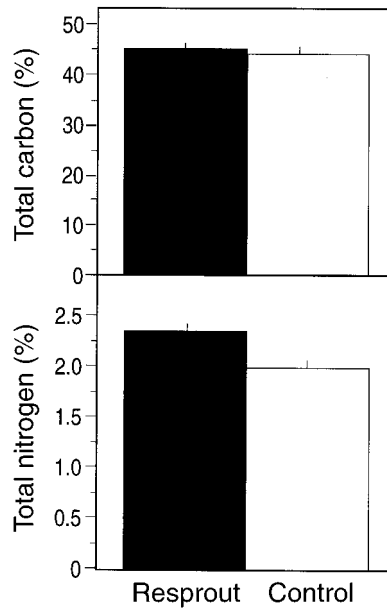
FIG. 4. Resprout and nonresprout leaves contain equal percentages (mean + 1 SE) of total carbon ($n = 15$, paired $t = 1.63$, $P > 0.05$). However, resprout leaves are almost 20% higher in total nitrogen ($n = 15$, paired $t = 4.12$, $P < 0.001$), which is potentially very important to beetle nutrition.

Consistent with the hypothesis that beetles are attracted to highly defended resprout growth, where they increase their own levels of defensive chemicals, we found that larvae that feed on resprout cottonwood foliage survive an average of 28% longer when attacked by ants than do larvae fed nonresprout leaves. This relationship is statistically significant ($P < 0.05$) in five of six sets of experimental trials (Fig. 6). These results strongly suggest that beetle larvae feeding on resprout cottonwood acquire more phenolic glycosides from their host plant. Ants are a major predator of chrysomelid beetle larvae (Floate and Whitham 1994), and thus represent a realistic bioassay of the effectiveness of larval defenses against predation.

DISCUSSION

Defensive chemistry of phenolic glycosides

Phenolic glycosides are effective against mammalian herbivores (Markham 1971, Edwards 1978, Tahvanainen et al. 1985a, Reichardt et al. 1990). Concentrations of these compounds can vary within a plant; in particular, they are highest in juvenile tissues that are most subject to browsing. Hares (*Lepus* spp.) prefer to feed on mature salicaceous trees, avoiding juvenile trees; within trees, they avoid juvenile shoots such as those generated by previous herbivory (Bryant 1981, Bryant et al. 1983, Tahvanainen et al. 1985a, Reichardt et al. 1990). Basey et al. (1990) found similar preferences for beavers feeding on quaking aspen (*Populus tremuloides*). Many of these studies have also shown differences in defensive phytochemistry between ju-

venile and mature shoots. The concentrations of two chemicals that are breakdown products of phenolic glycosides were highest in juvenile *Populus balsamifera* (Reichardt et al. 1990). Additionally, Tahvanainen et al. (1985a) found much higher concentrations of phenolic glycosides in juvenile twigs than in mature twigs of several willows (*Salix* sp.)

Recent evidence suggests that the breakdown products of phenolic glycosides, not the glycosides themselves, are defensive toward insect and mammalian herbivores (Clausen et al. 1989, Reichardt et al. 1990). Salicortin, the most abundant phenolic glycoside in our cottonwoods, is converted to salicin and 6-hydroxy-2-cyclohexenone (6-HCH). Clausen et al. (1989) showed that 6-HCH is an electrophile, capable of reacting with biological nucleophiles such as proteins and nucleic acids. Under basic conditions (e.g., insect gut), 6-HCH converts to catechol, a substance toxic to insects (Todd et al. 1971, Reese and Beck 1976, Clausen et al. 1989). Under acidic conditions, as are found in the mammalian gut, 6-HCH converts to phenol, which is highly toxic
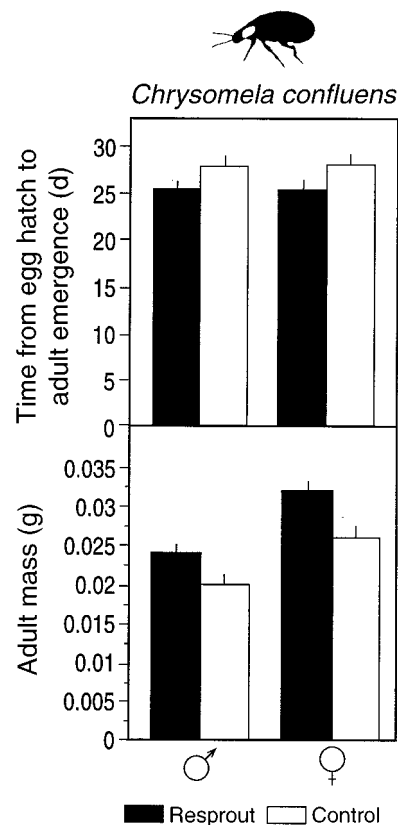

FIG. 5. *Chrysomela confluens* larvae develop 10% faster and grow 20% larger when feeding on resprout cottonwood foliage, based on a sample of 30–40 larvae that were transferred onto 18 pairs of resprout and nonresprout cottonwoods. Data shown are means + 1 SE, and all differences are statistically significant ($P < 0.05$). The data are analyzed separately by sex, because female beetles are 25–30% larger than males.

FIG. 6. Results of paired trials comparing survival of *C. confluens* larvae from resprout and nonresprout foliage when placed on ant mounds show that larvae are better defended when fed resprout growth. Each trial consisted of ~20 pairs of larvae placed on an ant mound, one pair at a time. Survival times are the time (mean + 1 SE) it took for larvae to be dragged into the ant mound. Asterisks denote significant differences ($P < 0.05$) using paired *t* tests.
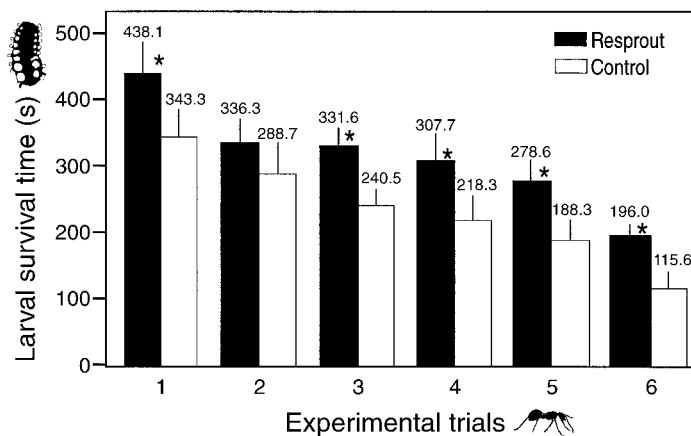
to mammals (Sax and Lewis 1989). For example, as little as 1 g of phenol can kill a human (Budavari 1989).

Sequestration of an induced defense

Chrysomelids that are specialized to feed on willows and cottonwoods (Salicaceae) incorporate salicin from the host plant and convert it to salicylaldehyde, which is an effective defense against arthropod predators such as ants (Pasteels et al. 1983, Kearsley and Whitham 1992). Salicin and related phenolic glycosides are not effective defenses against these specialist insects; in fact, the beetles benefit from ingesting salicin, which they convert to salicylaldehyde and glucose. However, it is not known how beetle larvae are able to deal with the other breakdown products of salicortin, 6-HCH and catechol, which are toxic.

Although beetles sequester plant defenses, the increased production of phenolic glycosides by resprout cottonwood ramets is probably an induced defense against mammalian herbivores such as beavers (Basey et al. 1990). Concentrations of these compounds can vary within a plant; in particular, they are highest in juvenile tissues such as those generated by previous herbivory (Tahvanainen et al. 1985*a*, Basey et al. 1990, Reichardt et al. 1990). Some authors argue that because mammalian herbivory causes a phase change from mature to juvenile growth, it is not an example of an induced response (Karban and Myers 1989, Bryant et al. 1991). However, because we found more defensive compounds in resprout growth than in other juvenile growth, induction is suggested. Another possibility is that the difference between resprout growth and unbrowsed juvenile trees is simply a consequence of the relaxation of juvenile-phase defenses in the unbrowsed trees, a process that occurs in as little as 2–3 years in *Populus* (Fox and Bryant 1984).

Chrysomela confluens both prefers resprout cottonwood foliage and performs better when fed resprout foliage. Several other studies have shown that chrysomelids feeding on salicaceous hosts prefer trees with high leaf phenolic glycoside concentrations (Rowell-Rahier 1984, Smiley et al. 1985, Tahvanainen et al. 1985*b*, Denno et al. 1990, Rank 1992, 1994). Smiley et al. (1985) documented lower levels of natural predation on beetles feeding on willows with high phenolic glycoside levels. Denno et al. (1990) showed mixed results: beetles fed willows rich in phenolic glycosides were better defended against coccinellid predators, but larval development time and pupal dry mass were not different for larvae reared on willows with high levels vs. low levels of glycosides. Rank (1994) found only a weak relationship between host plant chemistry and larval survival, probably because the specialist predators in his system were not affected by larval defensive secretions. In our field assays, beetle larvae feeding on leaves highest in phenolic glycosides (resprout growth) developed faster, were larger at maturity, and were better defended against generalist predators.

Indirect interactions

An indirect interaction occurs when the impact of one species on another requires the presence of a third species (Wootton 1994). Experimental ecological research has been dominated by studies of direct interactions (e.g., competition, predation, herbivory), and the potential importance of indirect interactions has only recently been appreciated (Carpenter 1988, Strauss 1991, Wootton 1994).

Many of the best illustrations of indirect interactions involve predators. For example, the classic studies of keystone species (Paine 1966, 1969) are of keystone predators. Indirect interactions are also better documented in aquatic systems than in terrestrial ones. One common type of indirect interaction, trophic cascades, in which the top-down effects of a predator suppress herbivores and benefit plants, are largely unknown in terrestrial systems (Strong 1992; but see Marquis and Whelan 1994 for an exception). In terrestrial systems, perhaps it is better to look for indirect interactions among herbivores, their host plants, and other herbivore species. Several examples include closely related

herbivore taxa (McNaughton 1976, Faeth 1986, Hunter 1987, 1992).

We have shown that beaver herbivory facilitates leaf beetle growth rates and defense by changing the chemistry of their cottonwood hosts. Positive indirect interactions between distantly related herbivores may be common, even in terrestrial systems, but they are difficult to detect. Granivorous desert rodents facilitate both ants (Davidson et al. 1984) and birds (Thompson et al. 1991), and winter browsing of birch by moose later benefits several species of insects (Dannell and Huss-Dannell 1985). Mammalian herbivores that can alter plant growth form, phytochemistry, and even species composition are likely to interact indirectly with a wide variety of organisms and ultimately impact community structure, in much the same way that top predators control some aquatic communities.

Beavers and riparian areas

Although cottonwood trees are one of the most productive and sensitive components of riparian ecosystems in western North America, this habitat type is vanishing rapidly: >100 000 ha are lost annually (Finch and Ruggiero 1993). Cottonwoods support many species, both invertebrates and vertebrates, especially birds (Carothers et al. 1974, Strong and Bock 1990). Beavers are thought to be important agents in the formation and preservation of riparian areas (Naiman et al. 1986, 1994, Chadde and Kay 1991), and beaver herbivory may be very important to the maintenance of cottonwood stands.

With the advent of dam building and the resultant decline in natural flooding, which is crucial for creating seed beds for cottonwood establishment (Rood and Mahoney 1990), cottonwoods that typically resprout after beaver cutting may ultimately be dependent on beavers for regeneration. Furthermore, species such as *Chrysomela confluens* that are restricted to juvenile cottonwoods may become increasingly dependent on the resprout growth caused by beavers.

Beaver herbivory creates a habitat mosaic of mature trees and juvenile resprout growth. These mixed-aged stands promote biodiversity, because juvenile and mature ramets of the same cottonwood clone support different arthropod communities (Waltz and Whitham 1997). Beaver herbivory probably also benefits vertebrates. For example, mixed-aged stands support greater avian biodiversity than even-aged stands (Derleth et al. 1989).

Beavers are considered keystone species that can literally alter the environment at the landscape level. Here, we have shown their diverse impacts on plant chemistry and on an insect that sequesters plant defenses for its own use. Because the sequestered chemicals may also be used for nutrition, this is an example of a no-cost defense. Beaver herbivory could be important in affecting the geographic distribution of the beetles and stimulating regeneration of cottonwoods, which are currently suffering widespread decline in the West.

LITERATURE CITED

Basey, J. M., S. H. Jenkins, and G. C. Miller. 1990. Food selection by beavers in relation to inducible defenses of *Populus tremuloides*. Oikos **59**:57–62.

Brown, J. H., and D. W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. Science **196**:880–882.

Brown, J. H., D. W. Davidson, J. C. Munger, and R. S. Inouye. 1986. Experimental community ecology: the desert granivore system. Pages 41–61 *in* J. L. Diamond and T. J. Case, editors. Community ecology. Harper and Row, New York, New York, USA.

Bryant, J. P. 1981. Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees. Science **313**:889–890.

Bryant, J. P., F. S. Chapin III, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos **40**:357–368.

Bryant, J. P., K. Danell, F. Provenza, P. B. Reichardt, T. A. Clausen, and R. A. Werner. 1991. Effects of mammal browsing on the chemistry of deciduous woody plants. Pages 135–155 *in* D. W. Tallamy and M. J. Raupp, editors. Phytochemical induction by herbivores. John Wiley, New York, New York, USA.

Budavari, S., editor. 1989. The Merck Index. Merck, Rahway, New Jersey, USA.

Cantor, L. F., and T. G. Whitham. 1989. Importance of belowground herbivory: pocket gophers may limit aspen to rock outcrop refugia. Ecology **70**:962–970.

Carothers, S. W., R. R. Johnson, and S. W. Aitchison. 1974. Population and social organization of southwestern riparian birds. American Zoologist **14**:97–108.

Carpenter, S. C., editor. 1988. Complex interactions in lake communities. Springer-Verlag, New York, New York, USA.

Chadde, S. W., and C. E. Kay. 1991. Tall willow communities on Yellowstone's northern range: a test of the "natural regulation" paradigm. Pages 231–262 *in* R. B. Keiter and M. S. Boyce, editors. The Greater Yellowstone ecosystem. Yale University Press, New Haven, Connecticut, USA.

Clausen, T. P., P. B. Reichardt, J. P. Bryant, R. A. Werner, K. Post, and K. Frisby. 1989. Chemical model for short-term induction in quaking aspen (*Populus tremuloides*) foliage against herbivores. Journal of Chemical Ecology **15**:2335–2346.

Dannell, K., and K. Huss-Dannell. 1985. Feeding by insects and hares on birches earlier affected by moose browsing. Oikos **44**:75–81.

Davidson, D. W., R. S. Inouye, and J. H. Brown. 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. Ecology **65**:1780–1786.

Denno, R. F., S. Larsson, and K. L. Olmstead. 1990. Role of enemy-free space and plant quality in host plant selection by willow leaf beetles. Ecology **71**:124–137.

Derleth, E. L., D. J. McAuley, and T. J. Dwyer. 1989. Avian

community response to small-scale habitat disturbance in Maine. Canadian Journal of Zoology **67**:385–390.

Dickson, L. L., and T. G. Whitham. 1996. Genetically based plant resistance traits affect arthropods, fungi, and birds. Oecologia **106**:400–406.

Edwards, W. R. N. 1978. Effect of salicin content on palatibility of *Populus* foliage to opossum (*Trichosurus vulpecula*). New Zealand Journal of Science **21**:103–106.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science **185**:1058–1060.

Faeth, S. H. 1986. Indirect interactions between temporally separated herbivores mediated by the host plant. Ecology **67**:479–494.

Finch, D. M., and L. F. Ruggiero. 1993. Wildlife habitats and biological diversity in the Rocky Mountains and northern Great Plains. Natural Areas Journal **13**:191–203.

Floate, K. D., M. J. C. Kearsley, and T. G. Whitham. 1993. Elevated herbivory in plant hybrid zones: *Chrysomela confluens, Populus,* and phenological sinks. Ecology **74**:2056–2065.

Floate, K. D., and T. G. Whitham. 1994. Aphid–ant interaction reduces chrysomelid herbivory in a cottonwood hybrid zone. Oecologia **97**:215–221.

Fox, J. F., and J. P. Bryant. 1984. Instability of the snowshoe hare and woody plant interaction. Oecologia **63**:128–135.

Hay, M. E., and P. R. Taylor. 1985. Competition between herbivorous fishes and urchins on Caribbean reefs. Oecologia **65**:591–598.

Hunter, M. D. 1987. Opposing effects of spring defoliation on late-season oak caterpillars. Ecological Entomology **12**:373–382.

———. 1992. Interactions within herbivore communities mediated by the host plant: the keystone herbivore concept. Pages 287–325 *in* M. D. Hunter, P. W. Price, and T. Ohgushi, editors. Effects of resource distribution on animal–plant interactions. Academic Press, San Diego, California, USA.

Huntley, N. 1991. Herbivores and the dynamics of communities and ecosystems. Annual Review of Ecology and Systematics **22**:477–503.

Huntley, N., and R. Inouye. 1988. Pocket gophers in ecosystems: patterns and mechanisms. BioScience **38**:786–793.

Jenkins, S. H., and P. E. Busher. 1979. *Castor canadensis*. Mammalian Species **120**:1–8.

Johnston, C. A., and R. J. Naiman. 1990. Browse selection by beaver: effects on forest composition. Canadian Journal of Forest Research **20**:1036–1043.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos **69**:373–386.

Karban, R., and J. H. Myers. 1989. Induced plant responses to herbivory. Annual Review of Ecology and Systematics **20**:331–348.

Kearsley, M. J. C., and T. G. Whitham. 1989. Developmental changes in resistance to herbivory: implications for individuals and populations. Ecology **70**:422–434.

Kearsley, M. J. C., and T. G. Whitham. 1992. Guns and butter: a no-cost defense against predation. Oecologia **92**:556–562.

Lindroth, R. L., and M. S. Pajutee. 1987. Chemical analysis of phenolic glycosides: art, facts, and artifacts. Oecologia **74**:144–148.

Markham, K. R. 1971. A chemotaxonomic approach to the selection of opossum-resistant willows and poplars for use in soil conservation. New Zealand Journal of Science **14**:179–186.

Marquis, R. J., and C. J. Whelan. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology **75**:2007–2014.

Martinsen, G. D., J. H. Cushman, and T. G. Whitham. 1990.

Impact of pocket gopher disturbance on a shortgrass prairie community. Oecologia **83**:132–138.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics **11**:119–161.

McInnes, P. F., R. J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology **73**:2059–2075.

McNaughton, S. J. 1976. Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science **191**:92–94.

Mielke, H. W. 1977. Mound building by pocket gophers (Geomyidae): their impact on soils and vegetation in North America. Journal of Biogeography **4**:171–180.

Naiman, R. J., J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology **67**:1254–1269.

Naiman, R. J., G. Pinay, C. A. Johnston, and J. Pastor. 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology **75**:905–921.

Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Biological Report 28. U.S. Department of the Interior, National Biological Service, Washington, D.C., USA.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65–75.

———. 1969. A note on trophic complexity and community stability. American Naturalist **103**:91–93.

Palo, R. T. 1984. Distribution of birch (*Betula* spp.), willow (*Salix* spp.), and poplar (*Populus* spp.) secondary metabolites and their potential role as chemical defense against herbivores. Journal of Chemical Ecology **10**:499–520.

Pasteels, J. M., S. Duffey, and M. Rowell-Rahier. 1990. Toxins in chrysomelid beetles. Possible evolutionary sequence from de novo synthesis to derivation from food plant chemicals. Journal of Chemical Ecology **16**:211–222.

Pasteels, J. M., M. Rowell-Rahier, J. C. Braekman, and A. Dupont. 1983. Salicin from host plant as precursor of salicylaldehyde in defensive secretion of chrysomeline larvae. Physiological Entomology **8**:307–314.

Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tallgrass prairie. Ecological Monographs **45**:285–305.

Rank, N. E. 1992. Host plant preference based on salicylate chemistry in a willow leaf beetle (*Chrysomela aeneicollis*). Oecologia **90**:95–101.

———. 1994. Host plant effects on larval survival of a salicin-using leaf beetle *Chrysomela aeneicollis* Schaeffer (Coleoptera: Chrysomelidae). Oecologia **97**:342–353.

Reese, J. C., and S. D. Beck. 1976. Effects of allelochemics on the black cutworm: effects of catechol, *L*-dopa, dopamine, and chlorogenic acid on larval growth, development, and utilization of food. Annals of the Entomological Society of America **69**:68–72.

Reichardt, P. B., J. P. Bryant, B. R. Mattes, T. P. Clausen, F. S. Chapin, III, and M. Meyer. 1990. Winter chemical defense of Alaskan balsam poplar against snowshoe hares. Journal of Chemical Ecology **16**:1941–1959.

Reichman, O. J., and C. S. Smith. 1985. Impact of pocket gopher burrows on underlying vegetation. Journal of Mammalogy **66**:720–725.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution **43**:223–225.

Rood, S. B., and J. M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. Environmental Management **14**:451–464.

Rowell-Rahier, M. 1984. The food plant preferences of *Phra-*

tora vitellinae (Coleoptera: Chrysomelidae). A. Field observations. Oecologia **64**:369–374.

Sax, N. I., and R. J. Lewis, Sr. 1989. Dangerous properties of industrial materials. Seventh edition. Van Nostrand, Reinhold, New York, New York, USA.

Scriber, J. M., and F. Slansky, Jr. 1981. The nutritional ecology of immature insects. Annual Review of Entomology **26**:183–211.

Smiley, J. T., J. M. Horn, and N. E. Rank. 1985. Ecological effects of salicin at three trophic levels: new problems from old adaptations. Science **229**:649–651.

Strauss, S. Y. 1991. Indirect effects in community ecology: their definition, study, and importance. Trends in Ecology and Evolution **6**:206–210.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor control in speciose ecosystems. Ecology **73**:747–754.

Strong, T. R., and C. E. Bock. 1990. Bird species distribution patterns in riparian habitats in southeastern Arizona. Condor **92**:866–885.

Tahvanainen, J., E. Helle, R. Julkunen-Tiitto, and A. Lavola. 1985*a*. Phenolic compounds of willow bark as deterrents against feeding by mountain hare. Oecologia **65**:319–323.

Tahvanainen, J., R. Julkenen-Tiitto, and J. Kettunen 1985*b*. Phenolic glycosides govern the food selection pattern of willow feeding leaf beetles. Oecologia **67**:52–56.

Tallamy, D. W., and M. J. Raupp, editors. 1991. Phytochemical induction by herbivores. John Wiley, New York, New York, USA.

Thompson, D. B., J. H. Brown, and W. D. Spencer. 1991. Indirect facilitation of granivorous birds by desert rodents: experimental evidence from foraging patterns. Ecology **72**: 852–863.

Todd, G. W., A. Getahun, and D. C. Cress. 1971. Resistance in barley to the greenbug, *Schizaphis graminum*. I. Toxicity of phenolic and flavinoid compounds and related substances. Annals of the Entomological Society of America **64**:718–722.

Waltz, A. M., and T. G. Whitham. 1997. Plant development affects arthropod community structure: opposing impacts of species removal. Ecology **78,** *in press*.

Whicker, A. D., and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. BioScience **38**:778–785.

Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology and Systematics **25**:443–466.