DIRECT, INDIRECT, AND CUMULATIVE EFFECTS OF THREE NATIVE HERBIVORES ON A SHARED HOST PLANT

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Abstract. The effects of three herbivores on growth, survivorship, and fruit production of smooth sumac (Rhus glabra) were measured over the 1984–1986 growing seasons. The herbivores, a specialist chrysomelid beetle (Blepharida rhois), a specialist cerambycid beetle (Oberea ocellata), and whitetail deer (Odocoileus virginianus), feed on different plant parts and are active during different times of the year. My goals were to determine (1) the effects on ramets of each herbivore separately and in combination over several years, (2) whether herbivore effects were consistent from year to year, (3) whether the history of attack affects subsequent herbivory, both within and between seasons, (4) whether herbivores interact directly, and/or indirectly, through changes in the host plant, and (5) whether any herbivores emerge as particularly prominent selective agents on the plant, considering both their direct and indirect effects.

Selective exclosures were used to manipulate herbivory histories of ramets. All manipulations were done in the field under natural densities of all herbivores. Herbivory treatments were cumulative over 3 yr, so that by 1986, each treatment comprised a history of 3 yr of absence/presence of browsing and beetle attack. Differing combinations of attack allowed me to detect how herbivory in one year affected ramet growth in following years.

The effects of deer, chrysomelids, and cerambycids on sumac differed not only in their magnitude and direction, but also in their effects in combination. Chrysomelid herbivory (randomly assigned, using natural densities of beetles) over 3 yr was always injurious to sumac ramets. Damage in 1984 was especially injurious, and was still detectable 2–3 yr later in ramet growth, despite the absence of any subsequent herbivory. Cumulative effects of chrysomelid damage were also found, i.e., the more years a ramet was exposed to chrysomelid herbivory, the more likely it was to die.

In contrast to chrysomelid damage, deer browsing was generally associated with increased ramet growth and/or reproduction. These effects were weaker and had no detectable long-term effects. The positive effects associated with browsing may reflect selectivity on the part of deer rather than positive effects of browsing, since browsing was not randomly assigned (Strauss 1988a).

I found nonadditive effects of damage by different herbivores on ramet growth or mortality. For example, there was no effect of browsing on the magnitude of chrysomelid effects on ramet growth; however, browse effects on ramet growth disappeared on chrysomelid-attacked ramets, but were still apparent on ramets protected from chrysomelid herbivory.

Many interactions between herbivores were found. Each pair of herbivore species, despite very different feeding habits, exhibited at least one interaction. Most interactions resulted from temporally separated herbivory events and were thus mediated by the host plant. In no cases were interactions symmetrical.

From 3 yr of observations, chrysomelids were always the most injurious herbivore, deer were never injurious (and were potentially beneficial), and cerambycids, although injurious alone, were even more so in conjunction with the chrysomelid. Although the strengths of selection exerted by each herbivore varied from year to year, their relative effects on the plant did not change. From this result, I argue that selective effects of herbivores on sumac at Cedar Creek are not diffuse, but are consistent from year to year.

Key words: Blepharida rhois; diffuse coevolution; herbivore–herbivore interactions; long-term effects; nonadditive effects; Oberea ocellata; Rhus glabra.

INTRODUCTION

Plants are consumed by a diverse array of herbivores, pathogens, and fungi. The cumulative selective effects of this community on a plant are often difficult to judge. The result may be a diffuse selective pressure on the host plant favoring generalized defenses (Fox 1981), or subsets of an herbivore community may act as strong selective agents, either consistently or in episodic bouts, thus favoring specific defenses aimed at these organisms. In this paper, I examine the effects of three herbivores on a shared host plant, smooth sumac...
(Rhus glabra, Anacardiaceae) and on each other. Two of these herbivores are specialist beetles that rely almost exclusively on this host plant species at the study site. The third is a vertebrate generalist, whitetail deer. Two years of observations before the study showed that these herbivores were responsible for the greatest amounts of sumac biomass removal. They feed on different plant parts and use plants at different times of the year. By using selective exclosures, I was able to separate the effects of two of these herbivores and to examine their impact both together and separately. For the third herbivore, I was able to describe and to manipulate some aspects of its impact on the plant. Because I collected data over several years, I can address both the consistency and the longevity of herbivore effects.

My goal was to determine: (1) the effects of each herbivore separately on sumac, (2) whether these effects change when more than one herbivore feeds on the plant within a season, (3) whether the history of attack affects subsequent herbivory, both within and between seasons, (4) whether the effects of each herbivore are consistent from year to year, and (5) whether any herbivore(s) emerge as particularly prominent selective agents on the plant.

In determining the effects of an herbivore, I consider not only direct effects on ramet growth, reproduction, and survivorship, but also indirect effects, such as how a plant's response to damage from one herbivore may affect others. Plant response to herbivory includes slight to major phenological shifts (Sholes 1981, Louda 1984, Marquis 1985), reduction in biomass produced (Morrow and LaMarche 1978, Lamb 1984, Louda 1984), reduction in flower or fruit production (Kraft and Denno 1982, Marquis 1985, Whitham and Mopper 1985, Crawley and Pattarasudhi 1988), changes in architecture (Oppenheimer and Lang 1969, Simberloff et al. 1978, Whitham and Mopper 1985), and changes in plant chemistry (Haukiola and Niemela 1977, Edwards and Wratten 1983, Neuvonen and Haukiola 1985, Bergelson et al. 1986, Faeth 1986). Although these resulting changes may persist for > 1 yr (e.g., Myers 1981, Sholes 1981, Marquis 1985), few researchers have attempted to document their effects on herbivore communities over periods longer than a single season. As Crawley and Pattarasudhi (1988) have argued, many interactions among herbivores resulting from plant biomass removal may go unnoticed simply because they haven't been addressed experimentally.

Plant responses to damage may not necessarily inhibit subsequently colonizing species. Facilitation can be found in herbivore/herbivore systems (Shearer 1976, Schultz and Allen 1977, Lewis 1979, Kidd et al. 1985). In general, the relationships documented among herbivores have been asymmetric (Seifert and Seifert 1976, Stiling 1980, Lawton and Hassell 1981, Stamp 1984, Karban 1986), usually with one species benefiting or suffering while the other remains relatively unaffected.

Ultimately, I hope to show that, for this system, herbivore effects on the plant are relatively consistent, though they may vary in magnitude and in longevity among species. Effects of herbivores are also altered in combination such that the community as a whole may exert different selective pressures than each species separately. In addition, I find that indirect effects through herbivore–herbivore interactions affect both the plant and the populations of other herbivores. Finally, if the nature of selection exerted by the herbivore community is indeed relatively consistent from year to year, then, rather than finding generalized defenses against a suite of herbivores, one might expect to find specific defenses aimed at herbivores that are consistently the most injurious (as measured by both direct and indirect effects).

**Natural History**

The host plant, *Rhus glabra × borealis* (Anacardiaceae) (Hardin and Phillips 1985), or smooth sumac, is a clonal perennial shrub that grows along forest edges and in old fields at the Cedar Creek Natural History Area in East Bethel, Minnesota, USA. Most of this work was carried out in an old field abandoned in 1956. *R. glabra* is dioecious; at Cedar Creek, the sex ratio of clones is extremely female biased, and the experimental clone and surveyed clones were all female. A separate experiment indicates that clone gender has no effect on herbivore attack (Strauss 1990). Each year, a branch on a ramet typically matures one or two shoots. These lignify over the fall and winter and new shoots are produced the next spring, usually from the second or third buds on the woody stem (S. Y. Strauss, personal observation). This growth form allows a reliable measure of ramet age (Gilbert 1966, Larch and Sakai 1983, D. Waller, personal communication).

In Minnesota, *R. glabra* produces new shoots relatively late in spring at the end of May. If buds are killed by frost or herbivore damage, the plant matures the next bud down on the woody stem. The previous year's woody stem has, on average, 20 buds that can serve as the source of a new shoot. If all buds on this stem are destroyed, either as a result of fire or herbivory, the ramet does one of three things: (1) matures a shoot from an older portion of the woody stem, (2) produces a shoot from a meristem just below the soil surface near the junction of the the woody ramet and the rhizome, or (3) dies or ceases shoot production. One of the first two scenarios is most likely.

I have placed shoots into three classes: (1) "woody" shoots, or those maturing from the previous year's growth (the normal growth form), (2) "low" shoots, or those maturing from buds on the woody stem, but below the last year's woody tissue, and (3) "basal" shoots, or those originating from below the soil surface, at the base of the ramet (Fig. 1). The distinctions between shoot types are important and play a key role in evaluating the effects of herbivores. Basal and low shoots are never capable of sexual reproduction in their 1st yr and 3 yr is the usual age of first reproduction.
Basal shoots are morphologically indistinguishable from 1st-yr shoots, but are recognizable because they are always located at the base of a woody ramet, rather than completely in the open. If a basal shoot is destroyed or damaged, plants can produce another, depending on the timing of damage and the ramet’s physiological state. Within a season, a ramet may produce anywhere from one to six basal shoots.

Whitetail deer, *Odocoileus virginianus*, browse woody sumac stems, usually in late fall or very early spring when snow levels are low but herbaceous shoots are not readily available (S. Y. Strauss, *personal observation*). Browsed stems are identifiable by the uneven appearance of the shoot tip and a shiny coating on the stem. Although deer occasionally remove developing flower heads or a single leaf from shoots during the spring and summer, the majority of biomass lost to deer is during the fall and winter.

In contrast, the two beetle herbivores use exclusively the green tissue of sumac. The more abundant is *Blapharididae rhois* (Forst.) (Coleoptera: Chrysomelidae), the sumac flea beetle. The association of the genera *Blapharididae* and *Rhus* is very old and is found primarily in the Old World (Africa and the Middle East, Furth and Young 1988). Although beetles are documented as *Rhus* generalists (Frost 1973), I have found them feeding almost exclusively on *R. glabra* at Cedar Creek, and only very occasionally and in low numbers on *R. typhina*. One can observe a range of beetle attack on sumac clones at Cedar Creek, including many sites with heavy attack. Heavy attack is not unique to this study site; Riley (1874) describes infestations of beetles in Colorado, Texas, and other states, and I have found attack in Wisconsin and Florida.

*B. rhois* overwinter as adults, often beneath the litter of the same clone where they fed in the previous summer (S. Y. Strauss, *personal observation* [mark-recapture data]). They emerge as the weather warms in early May and begin to feed on the pubescence and--tissue of expanding overwintering buds of *R. glabra*. Complete destruction of buds usually results in basal shoot production by an attacked ramet. After 1 wk, adults begin copulating and females start oviposition shortly thereafter. Eggs are laid in fecula, masses of ≈10 eggs covered by excrement, on sumac stems. Egg masses are often laid in large aggregations by multiple females, so that an individual sumac ramet may have well over 40 egg masses. Female beetles are extremely fecund and long lived, and laboratory and caged field individuals have produced from 300 to 600 (S. Y. Strauss, *personal observation*) to 900 eggs (Frost 1973) in 6 wk. Adults hop most of the time (hence the name flea beetle) and remain fairly localized. At times of food shortage, however, I have seen adults fly many metres.

*B. rhois* larvae emerge from fecula after 10–14 d and immediately crawl up the stems to the very youngest leaf tissue or flower buds, where they begin to feed. As they feed, they cover themselves in wet excrement. Larvae feed singly on young leaflets, but often line up in groups along the feeding edge of an older leaf. *B. rhois* larvae undergo four instars, usually molting in rolled leaves or near the base of older leaves. When ready to pupate, they drop to the ground, bury themselves in the sand and create a case from a mixture of sand and excrement.

The third herbivore, active during mid-June to August, is the sumac stem borer, *Oberea ocellata* (Coleoptera: Cerambycidae). This specialist beetle uses sumac stems and rhizomes as sites for oviposition and larval development. Like many cerambycids, adults cause plants to wilt or break at the time of oviposition. A male and female begin the process by chewing on most
of the older leaf petioles, causing leaves to curl. Then, the female moves onto the stem 10–20 cm from the ground where she begins to chew around the circumference of the green stem in three rings. Girdling patterns are always the same and are often used as characters for the species (Linsley 1961). Upon completion of the third girdle, the female lays a single egg beneath the girdle. In almost every case, girdled stems wilt and break at the topmost girdle. Occasionally, larger stems heal and girdling scars are incorporated into the woody tissue.

Females select primarily vegetative shoots as oviposition sites. Stems girdled more than once are found at times of very high cerambycid densities. In contrast to B. rhois adults, adult cerambycids are extremely good flyers and are highly dispersive. The cerambycid larva hatches within the stem and eats its way through the pith and into the center of the rhizome (Craighead 1923). Like other pith-feeding cerambycids, development time is long; it takes 2 yr for the larva to become an adult (Gosling 1984). Cerambycid beetles emerge in mid-June and are active through July (thus their activity coincides with part of the adult and larval B. rhois population in summer). For the rest of the paper, I refer to cerambycid beetles as "cerambycids." Other references to "beetles" refer to the chrysomelid (B. rhois).

This paper is divided into two main sections: the first examines the effects of herbivores on the plant, the second addresses interactions among herbivores. Each section has results from several years of data collection. Because treatments and experiments often hinge on the results of previous years, I present methods and results separately for each year in the second section.

I. Effects of Herbivores

Methods

Sumac ramets in an old field were selected in an area of beetle infestation. Clone identities were difficult to establish unequivocally, but based on clone morphology, clone gender, phenology and morphology of fruit trichomes, I surmised that all reproducing ramets belonged to a single clone. The advantage to using a single clone is that genotypic variation, barring somatic mutation, is eliminated. The disadvantage is that results are vulnerable to the idiosyncrasies of a particular genotype in that habitat. To redress this disadvantage partially, I have taken descriptive data on other clones in different areas to corroborate and generalize some of my experimental results.

Experimental ramets were not severed at the rhizome; this study is thus open to the criticism that ramet responses to treatments may not be independent. In almost all cases to date, however, ramets suffering defoliation have received additional nutrients from neighboring ramets (e.g., Schmid et al. 1988, Jonsdottir and Callaghan 1989). If damaged sumac ramets receive nutrients from undamaged neighbors, then results would be biased against detecting differences in growth between ramets in different treatments. Furthermore, Jonsdottir and Callaghan (1989) show with repeated defoliation of Carex that nutrient supply from intact neighboring ramets to the damaged ramet cases. Finally, sumac ramets are woody and aboveground parts persist for ≈15 yr; it is unclear how much nutrient exchange actually takes place between older ramets, as opposed to between herbaceous ramets that die back year after year (e.g., Solidago, Carex). To date, no such documentation of belowground ramet exchange has been done for sumac.

In early spring, sumac ramets were identified as having been browsed the previous winter by inspection of the stem tip. These ramets were then randomly assigned to two groups: either protected from beetles or left exposed to beetles. This assignment was done in a fully crossed design with respect to deer browsing and chrysomelid beetle attack.

Beetle exclosures were constructed around each plant using coarse "hobby netting" stapled to wooden lath. These exclosures were not "beetle proof," but rather "beetle resistant" and required some regular chrysomelid beetle removal. Netting holes were ≈5 mm in diameter. Because netting was coarse, slender cerambycids and other herbivores could enter and leave plants with netting. Measurements with an integrating light meter indicated that netting reduced light by 8% at ground level, and by only 4% at 10 cm below the netting, where sumac canopies were located. The effects of netting were determined in 1986 by selecting equal-sized and -aged ramets in a clone without beetles and comparing the growth of ramets inside and outside netting. There were no effects of netting on ramet growth, as measured by total shoot width produced (difference between netted and control plants = 0.152 ± 0.574 cm [Y ± sd]; n = 15 pairs; paired t test, t = 1.07, 14 df; P = .32). Shoot width in all experiments was measured with calipers as the basal diameter of each shoot at the end of the growing season. Fruit production was too low in both treatments to use for meaningful comparison between treatments.

I used several types of response variables to estimate the effects of herbivores: total ramet growth measured as either total shoot length (1984) or total shoot width produced per ramet (1985, 1986), shoot type produced per ramet, fruit production, and ramet mortality.

In spring 1985, I added new ramets that had been attacked by beetles in the previous year to the design. At this time, I was using all living woody ramets in the experimental clone. Because I was interested in cumulative effects of herbivores, experimental treatments incorporated both past herbivory as well as the current year's treatment. For example, of stems that
had been browsed and protected from chrysomelids in 1984, only a portion may have been browsed again in 1985. Thus stems that were all in the same treatment in 1984 (“deer, no beetles”) now became split between two treatments in 1985 (“deer, no beetles 1984/deer, no beetles 1985” was one treatment, and “deer, no beetles 1984/no deer, no beetles 1985” was the other). Ramets that were protected from chrysomelids in 1984 remained protected in 1985. Of ramets that were added in 1985, some were randomly assigned protection from chrysomelids while the others remained exposed to herbivory. In 1986, ramet treatments reflect 3 yr of herbivore history. Because I incorporated past history of ramets into treatments, I was able to detect, in many cases, how past herbivory by a species affected current ramet growth.

For cerambycids, I measured the average amount of plant tissue removed by girdling. In addition, I examined oviposition preference with respect to shoot width by comparing stems that were girdled to those left intact. I also determined use of different shoot types through a survey of 13 sumac clones by comparing girdling rates on ramets of different reproductive status, age, and shoot type.

**Statistical analysis**

Analysis of variance on total shoot length produced per ramet (log-transformed) in 1984 was used to determine the effects of chrysomelid beetles, deer browse, and any interaction. No ramets produced fruit in 1984. It should be noted that ramets receiving deer browse were selected by deer and not at random, unlike those ramets receiving beetle attack. I eliminated any ramets with cerambycid attack to determine just the effects of chrysomelid beetles and deer. I used a fixed-effect model. In examining total plant growth, I eliminated three plants from the analysis because their “zero” growth resulted in heteroscedasticity among treatments. Since these values were all located in the treatment with the smallest mean (plants receiving beetle herbivory but no browsing) their elimination makes detecting differences between this treatment and others more difficult, and therefore makes the statistical tests conservative. Because sample sizes are unequal between treatments (due to mortality, availability, etc.), sums of squares attributable to each factor in the ANOVA are non-orthogonal. In the tables, I present the sums of squares from the full model. In the text I also report the maximum relative effect of each factor (obtained by fitting models other than the full model and placing the maximum sums of squares for each factor over the error term of the full model).

Comparisons to evaluate beetle effects in 1985 and 1986 refer to comparisons of plants protected from vs. exposed to chrysomelid herbivory (those inside vs. outside of netting). Ramets with cerambycid attack are included in the analysis (in contrast to 1984). The response variable shoot width, used in 1985 and 1986 analyses, minimizes the effects of cerambycids, since girdling removes stem length but occurs after the majority of shoot elongation, when shoot width is close to its maximum size.

Owing to missing treatment combinations, an ANOVA approach was no longer appropriate for data analysis in 1985 and 1986. I resorted instead to a limited number of pairwise treatment comparisons that allowed me to detect effects of past and current herbivory. Nonparametric Mann-Whitney U tests were used to accommodate nonnormal data. I also used contingency tables to examine the incidence of fruit production, mortality, and shoot types between some treatments.

To analyze the combined effects of cerambycids and chrysomelids, I examined mortality rates of ramets with damage from both beetles to those with just chrysomelid damage using chi-square contingency tables. The effects of deer browsing and chrysomelid and cerambycid attack on ramet mortality were estimated using a log-linear model.

**RESULTS I—EFFECTS OF HERBIVORES ON THE PLANT**

In 1984, deer browsing and chrysomelid herbivory both significantly affected total ramet growth (Table 1,
TABLE 2. Shoot types produced by smooth sumac exposed to herbivory treatments. “Beetle” here refers to *Blepharida rhois*.

<table>
<thead>
<tr>
<th>No browse</th>
<th>Browse</th>
</tr>
</thead>
<tbody>
<tr>
<td>WOODY SHOOT</td>
<td></td>
</tr>
<tr>
<td>No beetles</td>
<td>Beetles</td>
</tr>
<tr>
<td>20</td>
<td>13</td>
</tr>
<tr>
<td>LOW SHOOT</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>10</td>
</tr>
<tr>
<td>BASAL SHOOT</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>8</td>
</tr>
</tbody>
</table>

\[ G^2 = 1.09, 2 \text{ df}, P = .58 \]
Best model: shoot type + beetle attack + (shoot type × beetle attack)

Fig. 2, but in different directions. Browed stems grew more than unbrowed ones, and stems suffering beetle herbivory grew significantly less than did those protected from beetles, *Blepharida rhois* and deer herbivory explain a maximum of 37.6 and 11.7%, respectively, of the variation in plant growth. A marginally significant interaction between effects of deer and beetle damage (Table 1, Fig. 2) suggests that in the presence of chrysomelid attack, the positive effects of deer browse on ramet growth are lost.

As described earlier (Natural history), shoot types (woody, low, or basal) produced by a ramet can affect the potential for fruit production. Low and basal shoots usually do not become reproductive until the 3rd yr. Shoot types were highly significantly different between treatments (Table 2). Deer browsing had no effect on shoot type; in the absence of chrysomelid attack, shoots produced were always woody (i.e., from last year's woody growth). In contrast, more than half the plants exposed to beetle attack produced either basal or low shoots, a result of bud destruction.

Mortality rates of shoots were examined with respect to treatment. Ramets exposed to chrysomelid attack in 1984 were much more likely to have died by the spring of 1985 than those protected from attack (Table 3). Stem mortality was not affected by prior browsing.

Cerambycid beetles attacked primarily basal or low shoots. In a survey of 13 clones in 1985, females had girdled 1.9% of reproductive, woody shoots (age 3 yr), 16% of 2-yr-old vegetative woody shoots at 37 and 40% of 1st-yr and basal shoots, respectively (Table 4). Cerambycids used vegetative over reproductive shoots and used more basal and 1st-yr shoots than woody shoots. Since basal shoots are more likely to be girdled than woody shoots, ramets in the experimental clone that were exposed to chrysomelid beetle attack were more likely to be girdled than those protected from beetles (Table 5). In 1985, this pattern was only marginally significant (Table 5b) because a late frost killed many of the basal and 1st-yr shoots and only woody shoots remained. The combined probability for all 3 yr indicates that the relationship is highly statistically significant overall (Table 5).

Ovipositing females did not accept all basal shoots. Based on a field survey of freshly girdled and intact shoots, I found the mean (±sd) diameter of girdled shoots (0.50 ± 0.08 cm, n = 25) to be greater than that of shoots left ungirdled (0.35 ± 0.06 cm, n = 25; t = 2.88, 48 df, P < .05). Girdling causes the loss of an average of 9.4 ± 3.4 cm of green stem above the girdle, based on measurements of wilted shoots still attached to the topmost girdle (n = 13).

For 1984 data, I used a log-linear model to examine the relationship between girdling, browsing, and ramet mortality when all ramets had *B. rhois* attack. The only model that fit the data included all main effects and a two-way interaction between mortality and girdling. In other words, ramet mortality was independent of prior browsing but, as shown before, ramets with attack from both beetles were more likely to die than those with just *B. rhois* attack (Table 6).

To summarize, in 1984 browsed plants grew significantly more than intact plants in 1984. This effect may result from (1) positive effects of deer browsing on plant growth, (2) nonrandom selection by deer of more vigorous shoots, or both (Strauss 1988a). Beetle herbivory (1) significantly reduced stem growth, (2) resulted in a shift from woody shoot production to basal and low shoot production in more than half the ramets, and (3) led to increased mortality of attacked stems. For all 3 yr of the study, especially in 1984 and 1986, cerambycid girdling occurred primarily on ramets that were attacked by chrysomelid beetles, probably because more basal shoots were produced by chrysomelid-attacked stems. Ramets experiencing attack from both beetle species in a single season were more likely to die than those with just chrysomelid attack; browsing in conjunction with beetle attack had no effect on mortality rates.

**Effects of herbivores in 1983 and cumulative effects of herbivory**

Total shoot length produced in 1985 for ramets in all treatments is depicted in box and whisker plots (Fig. 3). Because 1985 treatments include both past and present herbivory, I was able to examine how herbivory in 1984 affected ramet growth in 1985, as well as the effects of current herbivory. First I discuss the ef-

**TABLE 3. Mortality of stems in spring 1985 with respect to 1984 herbivory.**

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Alive in 1985</th>
<th>Dead in 1985</th>
</tr>
</thead>
<tbody>
<tr>
<td>No browse/no <em>B. rhois</em></td>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td>No browse/<em>B. rhois</em></td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td>Browse/no <em>B. rhois</em></td>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td>Browse/<em>B. rhois</em></td>
<td>20</td>
<td>11</td>
</tr>
</tbody>
</table>

\[ G^2 = 2.57, 2 \text{ df}, P = .306 \]
Best model: mortality + beetle attack + mortality × beetle attack
Table 4. Cerambycid girdling with respect to ramet age and stage from 13 *K. glabra* clones.

<table>
<thead>
<tr>
<th>Woody, reproductive shoots (age ≥ 3 yr)</th>
<th>Woody, vegetative shoots (age = 2 yr)</th>
<th>1st-yr shoots</th>
<th>Basal shoots</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. girdled</td>
<td>7</td>
<td>16</td>
<td>40</td>
</tr>
<tr>
<td>No. intact</td>
<td>375</td>
<td>99</td>
<td>106</td>
</tr>
<tr>
<td>% girdled</td>
<td>1.9</td>
<td>16.2</td>
<td>37.7</td>
</tr>
<tr>
<td>$\chi^2 = 109.1$, 3 df, $P &lt; .001$</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Effects of past and present beetle herbivory in a variety of contexts, then, the effects of deer browsing. Because treatments and comparisons are complex, I have referenced each comparison with treatment letters at the left of the data field in Fig. 3. Treatments differ significantly when $P \leq .006$, based on eight comparisons at $\alpha = .05$.

Stems with chrysomelid attack in 1984 still had significantly less growth in 1985 when compared with ramets protected from beetle attack for 2 yr ($U = 199.5$, $P < .001$; treatments C vs. F in Fig. 3). The same negative effect of 1984 chrysomelid attack can also be detected in conjunction with browsing effects (ramets that received deer browsing in both years) ($U = 160$, $P = .003$; treatments A vs. D in Fig. 3).

Owing to missing treatment combinations, I cannot examine effects of beetles in 1985 in the absence of any other herbivory. Plants with beetle attack in both years did not fare significantly worse than those with attack just in 1984 ($U = 129.5$, $P = .36$; treatments F vs. E in Fig. 3).

One can make the final, somewhat trivial, comparison of stems exposed to beetles in both years with those protected for 2 yr and find that, not surprisingly, ramets receiving protection from beetles for 2 yr grew more than those exposed to beetle attack ($U = 260.5$, $P = .002$; treatments C vs. E in Fig. 3).

Another effect of beetle attack on ramets was an increase in stem mortality. From a survey of all stems early the following spring, I found that ramet mortality increased with increasing years of prior beetle attack (Table 7), although stems experiencing attack in both 1984 and 1985 had only marginally significantly greater mortality than those with attack in 1984 only.

Deer browsing in 1984 did not affect stem growth in 1985 in the absence of beetle attack ($U = 67$, $P = .90$; treatments B vs. C in Fig. 3). In the presence of 2 yr of beetle herbivory, there was still no significant effect of browsing in 1984 on ramet growth in 1985 ($U = 37.5$, $P = .12$; treatments G vs. E in Fig. 3). For stems browsed in 1984, there was no additional effect of subsequent browsing in 1985 ($U = 51$, $P = .47$; treatments A vs. B in Fig. 3). Since browsed plants in 1984 grew more than nonbrowsed plants (Fig. 1), these results may indicate either no effect of browsing in 1985, or no additional effects over benefits accrued in 1984. In the absence of beetle attack, growth of stems browsed for 2 yr vs. those unbrowsed in both years was also not significantly different ($U = 36$, $P = .21$; treatments A vs. C in Fig. 3), although stems browsed for 2 yr were more likely to produce fruit than were unbrowsed plants (47 vs. 17%; $x^2 = 3.75$; 1 df, $P = .053$, $n = 35$).

To summarize, beetle attack in 1984 reduced ramet growth in 1985 for both browsed and unbrowsed ramets. Beetle attack in 1985 was less detrimental to plant growth than attack in 1984; ramets attacked by beetles for 2 yr were marginally more likely to die than those with just 1984 damage. I could not test for the effect of beetle attack in 1985 in the absence of 1984 beetle herbivory and hence could not truly estimate the magnitude of these effects, though they appear to be less injurious than 1984 chrysomelid effects.

In contrast to beetle herbivory, the greater growth of browsed stems in 1984 was not reflected in ramet growth in 1985 in either beetle-attacked or protected ramets. Total shoot width produced by stems browsed for 2 yr vs. those intact was also not significantly different in 1985, but the number of stems producing fruit was greater for browsed ramets (in the absence of beetle attack). To sum up, the basic patterns of negative effects of beetle attack and positive effects of browsing held over both 1984 and 1985. The positive effects of browsing seemed to be more a result of the current season's browsing patterns (unlike beetle herbivory) and were expressed in terms of fruit production rather than stem growth in 1985. These positive effects disappeared in the presence of beetle attack.

Table 5. Patterns of cerambycid girdling in relation to *Blepharida rhois* attack.

<table>
<thead>
<tr>
<th>B. rhois attack?</th>
<th>Yes</th>
<th>No</th>
</tr>
</thead>
<tbody>
<tr>
<td>a. 1984</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. shoots girdled*</td>
<td>43</td>
<td>4</td>
</tr>
<tr>
<td>No. shoots intact</td>
<td>29</td>
<td>41</td>
</tr>
<tr>
<td>$x^2 = 37.63$, 1 df, $P &lt; .001$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b. 1985</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. shoots girdled*</td>
<td>42↑</td>
<td>44</td>
</tr>
<tr>
<td>No. shoots intact</td>
<td>29↑</td>
<td>51</td>
</tr>
<tr>
<td>$x^2 = 2.58$, 1 df, $P = .10$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>c. 1986</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. shoots girdled*</td>
<td>20</td>
<td>19</td>
</tr>
<tr>
<td>No. shoots intact</td>
<td>18</td>
<td>52</td>
</tr>
<tr>
<td>$x^2 = 7.21$, 1 df, $P = .007$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Combined probability: $x^2 = 28.34$, 6 df, $P &lt; .005$</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* For all years, number of shoots girdled may include multiple shoots from a single ramet.
† Ramets in simulated *B. rhois* treatment included in this category.
Table 6. Combined effects of three herbivores on stem mortality in 1985; all stems with *Blepharida rhois* attack.

<table>
<thead>
<tr>
<th></th>
<th>No. stems dead</th>
<th>No. stems alive</th>
</tr>
</thead>
<tbody>
<tr>
<td>Browsed</td>
<td>11</td>
<td>20</td>
</tr>
<tr>
<td>Intact</td>
<td>20</td>
<td>39</td>
</tr>
<tr>
<td>Girdled</td>
<td>19</td>
<td>17</td>
</tr>
<tr>
<td>Intact</td>
<td>10</td>
<td>44</td>
</tr>
</tbody>
</table>

\[ G^2 = 5.28, P = .17 \]
Model: browse + girdling + mortality + (mortality x girdling)

Long-term and cumulative effects of herbivory: data from 1986

Treatments in 1986 consisted of 3 yr of herbivore attack; total stem width per ramet for all treatments in 1986 are presented in box and whisker plots (Fig. 4): Small sample sizes generally preclude finding statistical significance at the level required to meet the experiment-wise error rate (\( P = .006 \) based on nine comparisons at \( \alpha = 0.05 \)). Despite this, I present comparisons with \( P \) values to show that herbivore effects were generally consistent with those in the previous 2 yr. To examine effects of browsing alone, I used only stems with at least 2 yr of protection from beetle damage. I found that stems browsed in all 3 yr grew significantly more than stems never browsed (\( U = 2, P = .002 \); treatments A vs. D, Fig. 4), and marginally significantly more than those browsed just in 1984 (\( U = 26, P = .045 \); treatments A vs. E, Fig. 4) or in both 1984 and 1985, but not in 1986 (\( U = 44, P = .062 \); treatments A vs. C, Fig. 4).

With respect to long-term effects, I found no difference in the 1986 growth of ramets browsed just in 1984 vs. those browsed in both 1984 and 1985 (\( U = 33, P = 1.0 \); treatments E vs. C, Fig. 4). Nor was there a difference between plants never browsed and those browsed only in 1984 and 1985 (\( U = 72, P = .43 \); treatments D vs. C, Fig. 4). Browsing, therefore, again appears to have few long-term effects, and seems most influential with respect to the previous winter's treatment.

In 1986, none of the browsing treatments differed in

---

Fig. 3. Box and whisker plots of total ramet growth in 1985 (using total shoot width) produced by ramets in different herbivore treatments. A single treatment includes herbivore histories for both the 1984 and 1985 season. Letters assigned to each treatment (at left of date field) are referred to in text to simplify discussion of analysis. The median value for each treatment is marked by the central vertical line; first and third quartiles form the ends of the box (hinges). Whiskers (fences) delimit the range of observations, barring asterisks and open circles. These symbols represent values >1.5 and >3.0 times the magnitude of the difference between the first and third quartiles beyond the whiskers, respectively (Wilkinson 1988: 188).
the likelihood or quantity of fruit produced, despite the fact that several treatments differed significantly in total ramet growth.

Total shoot width and fruit production in 1986 were significantly reduced in stems experiencing 3 yr of beetle herbivory vs. those protected from beetles for 3 yr ($P < .001, P = .002$, respectively; treatments D vs. H, Fig. 4). Ramets with chrysomelid herbivory in 1984 only grew marginally significantly more than those suffering attack in all 3 yr ($U = 101.5, P = .066$; treatments F vs. H, Fig. 4). Mortality patterns of stems are consistent with growth data. Ramets with 3 yr of beetle herbivory were more likely to die than those protected from beetles since 1984 ($52\%$ of beetle-attacked ramets had died by the spring of 1987 vs. $4\%$ of protected ramets, $P < .001$; $\chi^2 = 35.4, 1$ df; $n = 117$ ramets).

Unlike deer browsing, the effects of chrysomelid herbivory just in 1984 were still detectable at the end of 1986 in growth of unbrowsed stems ($U = 179, P = .005$; treatments F vs. D, Fig. 4). The same pattern was present for fruit production by these stems, though it is at best only marginally statistically significant ($U = 143, P = .016$). The effects of 1984 beetle herbivory may also be present (marginally) in the 1986 growth of browsed plants ($U = 28, P = .018$; treatments B vs. A in Fig. 4).

To summarize, despite small sample sizes, many of the patterns found in 1984 and 1985 held in 1986, though some were only marginally statistically significant. Browsing in 1986 was again associated with increased ramet growth, but had no detectable effects on fruit production. As before, no long-term effects of browsing were found. Beetle damage had a negative
II. INTERACTIONS AMONG HERBIVORES

Methods

There are two basic methods I used to examine interactions among herbivores. In 1985, I used an experimental approach to investigate the relationship between the two beetle species, since I had already shown that there was a positive correlation between girdling and prior chrysomelid attack. I also used contingency tables to examine how prior herbivory by one species affects subsequent use of stems by other species.

I attempted to discriminate among several hypotheses that could explain the positive correlation between cerambycid girdling and chrysomelid beetle attack. These hypotheses are: (1) that cerambycids and chrysomelids are attracted to the same individual ramets, (2) that sumac architectural changes resulting from chrysomelid herbivory, i.e., the shift from woody shoot to basal shoot production, allows increased clone use by cerambycids, (3) that some aspect of *chrysomelid* wounding makes plants attractive to cerambycids, and (4) that wounding in general makes plants attractive to cerambycids.

To address these questions, I used both experimental and descriptive data. In one experiment, I randomly assigned ramets with the same herbivore history to receive either a simulated chrysomelid herbivory treatment or to be left open to chrysomelid attack. I simulated chrysomelid attack by removing buds with a knife as they matured sequentially. All shoots subsequently produced by ramets in this treatment were either basal shoots or low shoots. I then examined girdling rates on shoots produced by ramets in these treatments.

I collected a second set of data (1) to generalize the relationship between chrysomelid and cerambycid attack over a range of chrysomelid densities, sites, and sumac genotypes and (2) to determine whether cerambycid beetles oviposited disproportionately more in clones with high chrysomelid densities. To address these points, I used transect data taken from 13 clones with a range of early spring chrysomelid densities (0–0.82 beetles/ramet). Within each clone, I created a single transect that ran, in a haphazardly chosen direction, from the center of the clone near the oldest ramets in a straight line to the periphery of the clone, where young ramets are produced. I established the transects in May, when *B. rhois* adults were feeding and ovipositing. For all stems within 0.6 m of the transect line, I tabulated ramet age and the number of chrysomelid adults. I marked the ends of the transect with flags. I then returned at the end of the summer, when cerambycids had finished girdling stems. Using the same endpoints, I ran another transect line and tabulated shoot type (basal, vegetative woody, reproductive woody) and whether or not stems had been girdled. I then used rank correlations to examine the relationships between (1) spring chrysomelid density and number of basal shoots produced, (2) percent of the clone comprising basal shoots and spring chrysomelid density, (3) the number of shoots girdled in summer and density of chrysomelids in spring, and (4) the proportion of basal shoots girdled per clone and the actual number of basal shoots produced by that clone. The last comparison was to determine whether cerambycids were disproportionately attracted to clones with heavy chrysomelid attack. I also compared girdling rates on 1st-yr shoots to those on basal shoots. Basal shoots, which are morphologically indistinguishable from 1st-yr shoots, are the result of bud destruction on a woody ramet; 1st-yr shoots are part of the natural recruitment into the ramet population. If girdling rates differ between these shoot types, then the initial wounding responsible for basal shoot production may also affect subsequent use of these shoots by cerambycids.

In addition, I wished to investigate whether *O. ocellata* and *B. rhois* interacted during July when both beetles were using sumac stems simultaneously. A small portion of the chrysomelid beetle larval population is still feeding during cerambycid oviposition activities. At high chrysomelid densities, there is often no green tissue left on the woody stems for these late-emerging larvae. Larvae will then crawl down the stem where they feed on the young leaves of basal shoots. I examined the fate of chrysomelid larvae feeding on shoots that subsequently become girdled by *O. ocellata*. To do this, I selected 12 pairs of basal shoots of equal size. One was randomly selected to receive protection from *O. ocellata* (using netting enclosures), the second was left open to *O. ocellata* attack. Shoots were checked several times per day. As soon as a shoot was girdled, this stem was also placed within netting and 13 first-instar chrysomelid larvae were placed on the young tissue of both plants. Within 1 wk, all shoots assigned the “to-be-girdled” treatment were indeed girdled by *O. ocellata*. I then compared the number of surviving chrysomelid larvae after 1 wk and again at 12 d in both treatments (before larvae had time to pupate). I also measured leaf toughness of the first fully expanded leaf in both treatments using a leaf penetrometer.

RESULTS II—INTERACTIONS AMONG HERBIVORES

Relationship between chrysomelid and cerambycid beetles

The proportion of stems girdled on naturally attacked ramets and on those with simulated chrysomelid herbivory did not differ significantly (Table 8). These results indicate that, at least within a clone, there is no inherent ramet property mutually attractive to
both beetles that is responsible for joint beetle attack (since randomly selected ramets were as attractive as those selected by chrysomelids). In addition, since plants damaged by hand with a knife are as attractive as those chewed by chrysomelids, no chemicals or pathogens introduced through chrysomelid feeding per se are causing these patterns.

In the survey of 13 sumac clones, I documented the association of chrysomelid and cerambycid beetles over a range of chrysomelid densities (0–0.82 beetles/ramet). I found that the density of chrysomelid beetles was significantly and positively correlated with both the absolute number of basal shoots produced by a clone, as well as with the percent of the clone composed of basal shoots ($r_s = 0.62$ and 0.70, respectively; $P < .02$ and $P < .01$, 11 df; Fig. 5a, b). These results corroborate experimental findings that attack by chrysomelids is associated with increased basal shoot production. The number of girdled shoots in late July was also positively correlated with spring chrysomelid densities ($r_s = 0.69$, 11 df; $P < .01$; Fig. 5c). However, the percent basal shoots girdled in a clone was not related to the number of basal shoots ($r_s = 0.272$, 11 df; $P > .10$; Fig. 5d). This result indicates that clones with high densities of chrysomelids are not disproportionately more attractive to cerambycids than are clones with low densities (i.e., cerambycids do not forage in a density-dependent fashion).

Circumstantial evidence that supports the architectural basis of cerambycid facilitation by chrysomelids is that there was no difference in girdling rates between 1st-yr and basal shoots in the 13 clones surveyed (Table 4; $x^2 = 0.09$, 1 df, $P = .90$). The morphology and phenology of these shoots are identical. Since 1st-yr shoots are not a product of wounding, the fact that there is no preference between shoot types indicates that architectural change, and not damage, may be responsible for the increased use of chrysomelid-attacked sumac clones by cerambycids.

The whole picture that emerges from these results is that chrysomelid damage facilitates cerambycid attack and that this association is not simply an artifact of very high chrysomelid densities or of a particular clone genotype. Architectural changes are likely to be the mechanism behind increased girdling of chrysomelid-attacked clones.

The above interaction takes place between these species via changes in the plant and depends on the feeding patterns of chrysomelid beetles early in the season, prior to cerambycid emergence. Chrysomelids and cerambycids may also interact when they coexist on sumac stems, especially when both species occur in high densities.

Girdling of a stem upon which young chrysomelid larvae are feeding has a negative effect on chrysomelid larval survivorship (Table 9). This may be due to any number of factors. Although larvae in both treatments were under netting to prevent hemipteran predation, ground-dwelling carabid beetles probably had access to larvae on plants. Older leaves, the only ones remaining after girdling, are fully expanded, lower to the ground and may not offer as much protection from these predators as young, folded leaves on ungirdled stems. Even if some differential predation were occurring, other sources of mortality also contributed to differences between treatments. I frequently found the bodies of dead larvae, indicating perhaps an effect of plant quality.

Young first- and second-instar larvae feeding on plants in the field are almost always found on the tender young leaves, in contrast to older third and fourth instars (95.3% of young larvae on young leaves as opposed to 41.3% of older larvae; $x^2 = 35$, $P < .001$, $n = 135$). Leaf toughness measurements were taken using a penetrometer calibrated in units of “grams of force.” Using the surface area of the spring-loaded rod ($5.009$ mm$^2$) and the conversion factor of 1 g/mm$^2 = 9.80665$ kPa, I converted the instrument units to kilopascals of pressure. Measurements from the first fully expanded leaf on basal shoots were significantly lower, than those taken from the first leaves of girdled shoots ($\bar{X} \pm SD = 44.3 \pm 15.4$ kPa, $n = 26$, vs. $79.3 \pm 19.9$ kPa, $n = 19$; $t = 6.38$, $P < .05$). These data suggest that toughness, or some correlate, could be a factor contributing to larval mortality on girdled stems.

**Table 8. Girdling of stems with simulated and natural herbivory.**

<table>
<thead>
<tr>
<th></th>
<th>Simulated herbivory</th>
<th>Natural <em>Blepharida rhais</em> herbivory</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. girdled</td>
<td>8</td>
<td>17</td>
</tr>
<tr>
<td>No. not girdled</td>
<td>9</td>
<td>11</td>
</tr>
<tr>
<td>$x^2 = 0.80$, 1 df; $P = .37$</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Interactions among herbivores as determined by patterns of plant use**

I used ramets with known herbivore histories to determine in more detail the effect of prior herbivory on the subsequent use of ramets by other herbivores. I found that while cerambycid girdled stems independently of prior winter browsing in 1983/1984 (30% of browsed stems vs. 36% of unbrowsed stems; $x^2 = 0.37$, 1 df, $P = .54$; $n = 117$), in the next winter, deer were much less likely to browse stems girdled the previous summer (5% of girdled vs. 41% ungirdled; $x^2 = 9.54$, 1 df, $P = .002$; $n = 87$). These results are consistent with the hypothesis that deer prefer to browse more vigorous shoots or, a variation, that beetle attack makes plants less palatable to deer.

I also wished to determine whether I could make stems that had been initially rejected by deer attractive to them simply by protecting them from chrysomelid attack. I used ramets in two treatments, all of which
Fig. 5. Rank correlations between chrysomelid densities and (a) the number of basal shoots produced in fall, (b) the percent clone comprising basal shoots, and (c) the number of shoots girdled in the fall. Plot (d) shows rank correlation between the number of basal shoots produced by a clone and the percent of these shoots girdled by cerambycids. Significant positive correlations were found in (a), (b), and (c). Correlation and probability values are presented in the text (Results II—interactions among herbivores: Relationship between chrysomelid and cerambycid beetles).

had been rejected by deer in the winters of 1983/1984 and 1984/1985, and manipulated subsequent chrysomelid history. Ramets had either (1) chrysomelid attack in 1984 only or (2) chrysomelid attack in 1984–1986. Stems were protected from browsing in the winter of 1985/1986 using individual poultry-netting caps placed over shoot tips. I then left all stems open to browsing over winter 1986/1987 and surveyed them in early spring 1987.

Significantly more plants protected from chrysomelid herbivory for 2 yr were browsed in spring 1987 than those attacked by beetles (60 vs. 11%; χ² = 7.7, 1 df, P = .005; n = 38).

I also compared browsing in winter 1986/1987 on ramets that had been browsed every year with those in my protected-from-browsing treatment (treatment 2 above); all of these stems had been protected from chrysomelid attack for at least 2 yr. I used this last comparison to examine whether unbrowsed stems were as attractive as those browsed for 3 yr in the absence of beetle attack.

There were no significant differences in browsing rates between stems that had been browsed every year and those that had never been browsed, in the absence of beetle attack (77 vs. 60%; χ² = 0.26, 1 df, P = .61; n = 29). These results together indicate that deer browsing is not independent of prior chrysomelid attack, but is independent of prior browsing. By protecting ramets from beetles, I was able to make initially unacceptable ramets acceptable to deer. In addition, no “benefits” solely attributable to deer browsing over 3 yr altered the relative attractiveness of browsed and unbrowsed stems in the absence of beetle herbivory.

**Discussion**

Results from this study bear on diverse aspects of plant–herbivore and herbivore–herbivore interactions. I have divided the discussion into three parts. First, I
Table 9. Comparison of Bilepharida rhei larval survivorship on girdled and intact stems. Initial sample = 13 larvae per shoot.

<table>
<thead>
<tr>
<th>Replicate</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Girdled</td>
<td>5</td>
<td>0</td>
<td>3</td>
<td>3</td>
<td>6</td>
<td>8</td>
<td>4</td>
<td>4</td>
<td>6</td>
<td>5</td>
<td>5</td>
<td>9</td>
<td>4.83</td>
</tr>
<tr>
<td>Control</td>
<td>9</td>
<td>9</td>
<td>12</td>
<td>12</td>
<td>10</td>
<td>11</td>
<td>11</td>
<td>8</td>
<td>7</td>
<td>5</td>
<td>11</td>
<td>9</td>
<td>9.33</td>
</tr>
<tr>
<td>Girdled</td>
<td>5</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>3</td>
<td>4</td>
<td>3</td>
<td>5</td>
<td>5</td>
<td>5</td>
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<td>3.83</td>
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<td>Control</td>
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<td>8</td>
<td>6</td>
<td>0</td>
<td>8</td>
<td>8</td>
<td>8.25</td>
</tr>
</tbody>
</table>

Sign test on differences between treatments: $P = .039$ (10 +'s, 2 −'s, counting the tie as a minus); $n = 12$ pairs of basal shoots.

discuss the nature of selective pressures exerted by herbivores separately and together on sumac, and the importance of considering herbivore effects in the context of the coexisting community of herbivores. Second, I discuss the frequency and impact of herbivore-herbivore interactions on both the plant and, where possible, on herbivore populations. Finally, I contend that the selective pressure exerted by the herbivore community as a whole on sumac is not diffuse, at least over the duration of this study. I address problems in estimating the impact of herbivores on the fitness of long-lived plant genotypes such as sumac, and conclude with a small section on predicting what defenses we might expect to find in sumac, given the prominence of the chrysomelid beetle as a selective agent.

Effects of herbivores and nonadditive effects

The effects of deer, chrysomelids, and cerambycids on sumac differed not only in their magnitude and direction, but also in their effects in combination. Chrysomelid herbivory (randomly assigned, using natural densities of beetles) over 3 yr was always injurious to sumac ramets. Damage in 1984 was especially injurious, and was still detectable 2–3 yr later in ramet growth, despite the absence of any subsequent herbivory. Since I was still able to detect effects of herbivory at the end of the experiment from the 1st yr of manipulations, “control” or protected ramets could also still retain effects from prior chrysomelid attack. Should this be the case, then the effects of chrysomelids as I have measured them would be underestimated. I attribute the particularly strong impact of 1984 herbivory to a late frost in the spring of 1985 (Strauss 1988b). Chrysomelid-attacked ramets were much more likely to receive frost damage than were their undamaged counterparts, a fact that will be discussed in more detail in a forthcoming paper. Cumulative effects of chrysomelid damage were also found, i.e., the more years a ramet was exposed to chrysomelid herbivory, the more likely it was to die.

In contrast to chrysomelid damage, deer browsing was generally associated with increased ramet growth and/or reproduction. These effects were weaker, not as consistent (ranging from no to positive effects) as chrys-
omelid herbivory, and had no detectable long-term effects. The positive effects associated with browsing may reflect selectivity on the part of deer rather than positive effects of browsing, since browsing was not randomly assigned (Strauss 1988a).

I found that the effects of certain types of damage on ramet growth or mortality were altered in the presence of other herbivory. For example, while there was no effect of browsing on the presence or absence of chrysomelid effects on ramet growth, the reverse was not true. In 1984, there was a marginally significant trend for chrysomelid damage to negate the positive effects of browsing on ramet growth. In 1985, this trend was significant; browsing effects on ramet growth did indeed disappear on chrysomelid-attacked ramets, but were still apparent on ramets protected from chrysomelid herbivory. As another example of the effects of herbivores in combination, stem mortality in 1985 was unaffected by browsing alone or by browsing in the presence of chrysomelid attack. In contrast, stem mortality was affected by chrysomelid attack alone, and significantly increased with combined attack by both beetle species. Because, in many cases, the effects of herbivores were not additive, my results emphasize the importance of determining herbivore effects on host plants in the context of the coexisting herbivore community, rather than in isolation.

Interactions among herbivores

Many interactions among herbivores were found and are summarized in Table 10. Every pair of herbivore species, despite very different feeding habits, exhibited at least one interaction. Most interactions resulted from temporally separated herbivory events and were mediated by the host plant. In no cases were interactions symmetrical. Both chrysomelid and cerambycid damage independently decreased the likelihood that ramets would be browsed by deer in the following season. In contrast, however, deer browsing had no effect on the subsequent use of ramets by girdling cerambycids. The most striking interaction was the facilitation of cerambycid oviposition by prior chrysomelid damage. Although herbivore-herbivore interactions have traditionally been considered in light of their effects on
Table 10. Interactions among herbivores with respect to host use.

<table>
<thead>
<tr>
<th>Species causing damage</th>
<th>Species’ response to damage with respect to plant use</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deer</td>
<td>Chrysomelids</td>
</tr>
<tr>
<td>Deer</td>
<td>?</td>
</tr>
<tr>
<td>Chrysomelids</td>
<td>–</td>
</tr>
<tr>
<td>Cerambycids</td>
<td>–</td>
</tr>
</tbody>
</table>

* Interaction shown to affect either egg or larval population densities.

Herbivore populations, my results indicate that indirect effects of an herbivore on subsequent host plant use may also have substantial fitness implications for the plant (see also Straus 1987). Such indirect effects should be included with direct effects in assessing the impact of an herbivore on the host plant.

How herbivore–herbivore interactions that alter host plant use affect population densities of herbivores is difficult to assess. I observed a marked increase in adult cerambycid densities over the course of the experiment and attributed this change to increased oviposition facilitated by chrysomelid attack. Unfortunately, I neglected to collect data on cerambycid oviposition at the beginning of the study; this is critical information (owing to the long development time of cerambycids) for determining the correlation between present adult cerambycid densities and past levels of oviposition. From all indications, however, chrysomelid damage appears to have a strong, positive effect on cerambycid population densities and cerambycid fitness. Ironically, the other interaction that directly affected herbivore population size was the negative effect of cerambycid girdling on chrysomelid larvae concurrently using girdled stems; however, this interaction may affect only the small subpopulation of young, late-emerging chrysomelid larvae and probably has little overall impact on chrysomelid densities.

The nature of herbivore–herbivore interactions may be as dynamic as the host plant. I have shown that combined cerambycid/chrysomelid attack leads to increased stem mortality. When sumac clone health declines in the face of repeated years of joint herbivory, it is likely that chrysomelids and cerambycids may ultimately compete indirectly for remaining plant resources. Attack by both beetles decreases the number of living stems available in the following season for spring-feeding chrysomelids. When chrysomelid populations become limited by the number of living stems, as I have witnessed in the cases where sumac clones actually die from herbivore attack, the effects of cerambycid damage on the chrysomelid population may increase in magnitude. In general, although I can show that many interactions among herbivores occur, much more work needs to be done to quantify how or whether such interactions affect population sizes of herbivores and herbivore fitness, and how these interactions may change with altered plant health.

Selective force exerted by the community as a whole on sumac

Fox (1981) proposed that because persistent plants are attacked by an array of herbivores, selection might favor defenses with generalized actions to counteract variable, if not conflicting, selective pressures exerted by that community. From 3 yr of observations, the nature of the selective effect of these herbivores together on sumac is probably more consistent than envisioned by the diffuse coevolution model. Chrysomelids were always the most injurious, deer were never injurious (and were potentially beneficial), and cerambycids, although injurious alone, were even more so in conjunction with the chrysomelid (both in terms of number of stems girdled and the cumulative effects of joint damage). Although the strengths of selection exerted by each herbivore varied from year to year, if one were to rank herbivores from most to least injurious on a yearly basis, the rankings of each species would not change. In addition, the indirect effects of herbivores through their interactions also remained consistent from year to year. As an example, facilitation by chrysomelids of cerambycid attack was present in all 3 yr of this study.

On the basis of both direct and indirect effects, and the longevity of these effects, chrysomelid beetles were the most detrimental herbivore to sumac. It is difficult to judge how strong, but potentially episodic, damage such as that of the chrysomelid beetle affects the lifetime fitness of a long-lived plant genotype such as sumac. Sumac ramets live \( \approx 15 \) yr at Cedar Creek, but rhizomes can persist for at least decades (Larch and Sakai 1983). I show that effects of damage from chrysomelids can be detected for a minimum of 2–3 yr and perhaps even longer, depending on how much the growth of control plants was influenced by prior herbivory. Even if chrysomelid herbivory resulted in a minimum of 6 yr of reduction in growth and reproduction of a sumac clone, we still have no idea how important this is to sumac fitness, were that genotype to survive. However, I have witnessed the death of at least four clones (i.e., genotypes) in the field as a result of repeated years of heavy chrysomelid/cerambycid attack; in these cases, chrysomelid herbivory is unmistakably having an effect on plant fitness.

Given that the actions of these herbivores were relatively consistent, the data taken in toto suggest that if sumac were to have specific defenses against an herbivore, at least at Cedar Creek, these defenses should be directed toward the chrysomelid beetle *B. rhois*. Since both plant and herbivore are native (with completely overlapping ranges), and sumac has been present in Minnesota for at least 9000 yr (E. J. Cushing,
personal communication), there has likely been opportunity for evolution or adaptation by these species. The facts that one can find a range of chrysomelid densities on clones and that some clones are partially invaded by chrysomelid beetles but not annihilated indicate that there may be sumac individuals capable of defending themselves from beetle attack. Subsequent experimental work using common gardens has allowed me to determine that there are both genetic and environmental components involved in sumac resistance to chrysomelid attack (Strauss 1990).

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LITERATURE CITED


———. 1988b. Interactions among three herbivores and their effects on a shared host plant. Dissertation. Florida State University, Tallahassee, Florida, USA.

