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The role of plant genotype, environment and gender in resistance to a specialist chrysomelid herbivore

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Summary. Patchiness in herbivore attack is a well-documented phenomenon. When neighboring plants suffer vastly different levels of attack, then one suspects genotypic differences among plants to be the underlying mechanism. In this study, I use common garden experiments in two natural, but divergent, habitats at the Cedar Creek Natural History Area in central Minnesota to determine the role of plant genotype, environment and gender in plant resistance to a specialist herbivore. Resistance was measured by larval survivorship and weight. Eight clones of *Rhus glabra* were selected and 12 equal-aged ramets were dug up and planted in two gardens (each garden received 6 ramets per clone). First instar *Blepharida rhois* (Coleoptera: Chrysomelidae) larvae of known parentage were transferred to ramets and censused every other day. At the end of the experiment, larvae were collected and weighed. Analysis of variance was used to determine the importance of plant genotype, environment and gender on larval mortality and weight. The experiment was repeated in its entirety one month later. Both plant genotype and environment significantly affected larval survivorship in the first run of the experiment. No interactions were significant. Results from the second run indicated marginally significant genotype and environment main effects, and a genotype by environment interaction in larval survivorship. There was a significant genotype by environment interaction in larval weight on the same run. In neither run did clone gender have significant affects on resistance.

Key words: *Rhus* – *Blepharida* – g-e interaction – Resistance

The patchiness of herbivore attack in nature may reflect any number of phenomena: the dispersal or host-locating abilities of the herbivore, microhabitat or larger environmental differences, the heterogeneous distribution of parasites or predators, and variation in genotypically-based plant defense. In several systems involving diverse herbivores, plants growing adjacent to one another in the field suffer very different levels of herbivore attack (e.g. Edmunds and Alstad 1979; Whitham and Mopper 1985; Stiling and Simberloff 1990). Differential attack levels on adjacent plants make less parsimonious the alternative hypotheses that herbivore dispersal abilities or environmetal differences are responsible for non-uniform herbivory. For this reason, there has been a recent focus on the role of plant genotype in resistance to herbivores (Service 1984; Maddox and Root 1987; Karban 1988; Fritz et al. 1986).

Several hypotheses propose mechanisms that could maintain genetic variability in plant populations in light of what appears to be strong, directional selective pressure by herbivores. Two of these, frequency-dependent selection and diversifying selection, have received much attention of late. Frequency-dependent selection by herbivores may maintain genetic diversity in the plant population by always selecting against more common plant genotypes (Haldane 1949; Edmunds and Alstad 1978). Diversifying selection relies on the presence of genotype-environment interactions to maintain plant variability; certain genotypically-based defenses may confer high fitness to individuals in some environments but not in others (Halkka et al. 1975; Hedrick 1986; for review).

In this study, I examine the relative importance of plant environment, genotype and gender in plant resistance to a specialist beetle herbivore. Because it is unclear which attributes of sumac are responsible for resistance to this herbivore, I have used a bioassay of beetle survivorship and larval weight to quantify resistance. I use common garden experiments in the field to determine whether plant resistance has a genetic component, and if so, to what extent genotypically based resistance is influenced by local environment.

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Methods

Natural history

The host plant, *Rhus glabra* (Linn.) or smooth sumac, is a clonal, dioecious species that grows in old fields, along forest edges and in oak savannah at the Cedar Creek Natural History Area in East Bethel, Minnesota, USA. Although typically associated with disturbed habitats such as old fields, smooth sumac has been present in the Cedar Creek area for at least 9000 years, based on pollen records from sediment cores taken in neighboring Washington County (Cushing pers. comm.). Sumac native habitats were probably similar to the oak savannah areas of Cedar Creek; these areas have experienced little or no human disturbance for the past 5000 years, and currently support populations of sumac.

The herbivore, *Blepharida rhois* (Foerster), is a specialist chrysomelid flea beetle that feeds almost exclusively on smooth sumac at Cedar Creek (pers. obs.). Overwintering adults emerge early in the spring and begin ovipositing almost immediately on sumac stems (Riley 1874; Frost 1973, pers. obs.). Adults hop from plant to plant and are relatively sedentary when food is plentiful. Because females are fecund, long-lived and oviposit over many weeks (unpubl. data), it is difficult to ascertain the number of generations at the site; no more than two generations occur per summer. In Minnesota, larvae hatch from eggs approximately 14 days after oviposition; they crawl to the top of the plant, where they feed on the young leaves and flower heads (pers. obs.). Larvae cover themselves in excrement and I have never witnessed any vertebrate predation, despite high densities of insectivorous birds in the area. When the weather gets hot in early and mid-July, adults, and perhaps larvae, aestivate and reappear with cooler weather in August–October. Densities of first-instar larvae are greatest early in the spring at the time of leaf expansion; they continue to be present in numbers until the hot period of mid-late July, when some may aestivate. Much smaller numbers of adults and larvae can be found in September and October feeding on the senescing foliage.

Both plant and beetle are native with largely coincident ranges; the beetle is recorded as feeding on several species of *Rhus* over its entire range (Frost 1973). Attack by *B. rhois* can result in extensive defoliation of some sumac clones. Heavy attack has been reported from locations in many states (Riley 1874) and is not unique to this study site. Even when defoliation is not catastrophic, beetle herbivory significantly reduces sumac growth, survivorship and reproduction (Strauss 1988). Attack is patchy. In many instances, sumac clones in close proximity to heavily infested ones suffer little or no damage. Because clones with varying attack levels are often only a few meters apart, factors other than the dispersal ability of beetles are likely to cause patchiness of beetle attack.

Because sumac clones are dioecious, I was able to examine the role of plant gender in resistance to herbivore attack. Plant gender has been shown to affect several attributes of plants, including susceptibility to herbivores, pathogens and frost (Bawa and Opler 1978; Danell et al. 1985; Agren 1987; Agren 1988); gender has also been linked to differences in sumac phenology (Gilbert 1961), which in turn, may affect herbivore attack.

Experimental design

To determine the role of plant genotype, environment and gender on sumac resistance to *B. rhois* attack, I created 2 common gardens in different habitats at Cedar Creek. There, sumac is abundant in fields abandoned for ca. 25 years as well as in oak savannah habitats. The first garden site was located in a field abandoned in 1957. The second garden was located in burr oak savannah approximately 500 m from the field site. I chose these garden sites because both are representative of areas in which sumac occurs, they are near one another and yet markedly different. In this design, environment is replicated (i.e. two gardens in different locations with the same plant genotypes). Because gardens are not replicated within habitats, I draw no conclusions about the specific attributes of savannah versus field habitats; I am solely concerned with general, broad environmental effects and their potential interaction with plant genotypic effects. Garden sites within habitats were selected such that naturally-occurring sumac clones were present within 15 m of both gardens. Gardens were at least 100 m from any beetle populations.

In spring 1986, eight sumac clones (5 female and 3 male) were selected from separate areas (some separated by several miles) within Cedar Creek. Clones were identified within areas by examining domed clone architecture (Gilbert 1961), determining clone gender and selecting clones that were relatively isolated from neighboring clones. Ramets selected for the experiment were of equal age (3 years) and grew close to one another within clones. Ramets can be accurately aged from branching patterns (Larch and Sakai 1983). From each clone, 12 ramets were dug up with approximately 25 cm of rhizome. Ramets were randomly assigned to the gardens (six ramets per clone per garden), and randomly assigned a position in each garden (a 6×8 grid with ramets separated from each other and the fence by 1 meter). Each ramet received a single watering with Rootone solution upon planting. Plants were allowed to grow for one year prior to experimentation. I assume that this period provided several benefits: 1) maternal effects could be minimized since two seasons' worth of foliage was produced in the new environment (including that of the experimental run) with minimal resources from the original clone, 2) recuperation time reduced or eliminated the effects of transplant shock and 3) two seasons' growth allowed greater opportunity for environmental effects to occur.

Only two ramets died during the 1986 growing season. But, 23% of the ramets died through the winter (mortality ranged from none to 2 ramets per clone). In both the first and second growing seasons, ramets in the two gardens differed in foliage color, suggesting that the different environments were affecting plants.

In early May 1987, I collected 20 gravid female beetles from several locations at Cedar Creek; none were sites from which clones were taken. I used beetles from new sites to avoid any effects of local differentiation by beetle populations onto individual experimental sumac clones. Females were brought into the lab, numbered and supplied with sumac leaves in Aquapics and a woody sumac stem for oviposition. Female *B. rhois* are extremely fecund and can lay several hundred eggs. Every other day, I removed sticks with egg masses and placed them in petri dishes labelled with maternal identity. Because I wished to reduce variation arising from larval genotypes in the experiment, I sorted first-instar larvae into groups of 12 such that each group had the same number of larvae from the same maternal genotypes. I used between 1 and 3 larvae from 7 females; every ramet received exactly the same number of larvae from all maternal genotypes. As a result of these groups, all experimental ramets received larvae of similar genetic stock (barring the fact that I could not control whether larvae from the same mother were full- or half-sibs).

Prior to placing larvae on ramets, I removed all insects on the ramets and placed a 3-inch band of Tanglefoot on the woody portion of the stem. Larval predators are restricted to other arthropods (pers. obs.); carabid beetles were prevented from preying on larvae by the Tanglefoot. Winged hemipteran predators were not present until later in the season. First-instar larvae were transferred in their groups to ramets in the experimental gardens at the time of leaf expansion. I used twelve larvae per ramet to reflect the average number of eggs in an egg mass. By placing the same number of larvae on each ramet, I avoided complications associated with edge effects and non-uniform colonization by herbivores. The field garden experiment was started 8 days later than the savannah garden owing to the limited availability of first instar larvae (23 May and 31 May, respectively). Larvae were counted every other day after initiation of the experiment, and the experiment was terminated on the first date when a ramet within that garden had no remaining larvae (the duration the experimental run was 10 days). Surviving larvae were collected, placed on ice and weighed within 12 h of collection.

The experiment was repeated several weeks later at both savannah and field sites (8 June and 19 June 1987, respectively) when sumac was flowering and when most leaves were fully expanded. Several conditions and methods differed between the first and second run aside from plant flowering. First, densities of young larvae were generally lower than earlier in the season. Second, there were seasonal differences in ambient temperature and leaf maturation; third, the female clone with the smallest sample size was not used because of a shortage of larvae; fourth, fewer larvae (10) were used and larval maternal genotypes differed between the runs; and fifth, larvae were protected from predators by net bags. Finally, since the same ramets were used in both the first and second runs, any induced changes in ramets as a result of previous damage were necessarily incorporated into the second run.

Statistical analysis

Analysis of variance was used to determine the importance of each attribute to larval survivorship. The mixed model included gender and environment as fixed factors and clone genotype as a random factor. Clone genotype was nested within gender; all interactions were included in the model. I used Type IV analysis of variance because of unequal sample sizes (Via 1984). Analyses were done on unweighted means, but weighted and unweighted means differed by less than 5% for all clones, and by less than 2% in most cases.

The response variable, number of larvae surviving of 12 (or of 10 in the second run), needed no transformation. All larvae on one ramet disappeared without trace after the first 4 h of the first experiment. Thus, this outlier was dropped from the analysis on the first run. This ramet was, however, included in the analysis of the second run, since larvae did not disappear. SPSS MANOVA program was used to calculate Type IV ANOVA (unique sums of squares). I used rank correlation to examine the relationship between larval survival and larval weight on a per clone basis. For each experimental run, mean clone values were averaged over environment, ranked and correlated.

I also wished to determine whether there were microhabitat differences associated with individual ramets within clones that may have made some ramets more or less favorable. To remove clone effects from ramet effects, I standardized ramet effects by subtracting the clone mean from the observation for each individual ramet (within gardens). This subtraction resulted in a set of deviations from the clone mean for each ramet based on 1) number of larvae surviving and 2) larval weight. For larval weight, I subtracted the mean weight of larvae on a ramet from the mean weight of larvae on that clone (again, within gardens). Significant correlation between deviations of weight and survivorship could indicate microhabitat effects that were not genetically based.

Finally, to examine how suitable individual clones were as host plants for larvae, I examined how mean larval survivorship on individual clones was correlated within each environment between the two experimental runs, and also, between the two environments within each experiment.

Results

Run 1

The mean number of larvae surviving per clone ranged from 5.17 to 9.40 in the savannah garden, and from 2.00 to 7.00 in the field garden (Fig. 1). Using analysis of variance, I found significant clone and environment main effects, and no effect of plant gender on larval survivorship (Table 1). No interactions were significant. Since it is not possible to obtain independent estimates of the sums of squares explained by each factor using a non-orthogonal analysis, I also did an ANOVA using orthogonal sums of squares. With this model, almost half or 46.9% of the variance in larval mortality is explained. The amount of total variation accounted for by clone (plant genotype) was 13.4% while that accounted for by environment was 20%. The environment effect reflected greater overall larval survivorship in the savannah garden. To show genotypic differences in the context of environment, I used dashed lines to connect clone means in the two environments; no environmental continuum is implied. These lines are statistically indistinguishable from parallel, indicating that plant clones behave similarly in the two environments with respect to resistance (as measured by larval performance).

The same analysis on the wet weight of surviving larvae explained only 5% of the variation in larval weight, and no single factor was significant. Mean larval weight in the savannah and field gardens were 6.18 and 5.83×10^{-3} g respectively ($s = 4.44 \times 10^{-3}$ g; overall comparison based on mean of 8 clone means in each environment; each clone mean had a sample size of between 11 and 48 larvae).

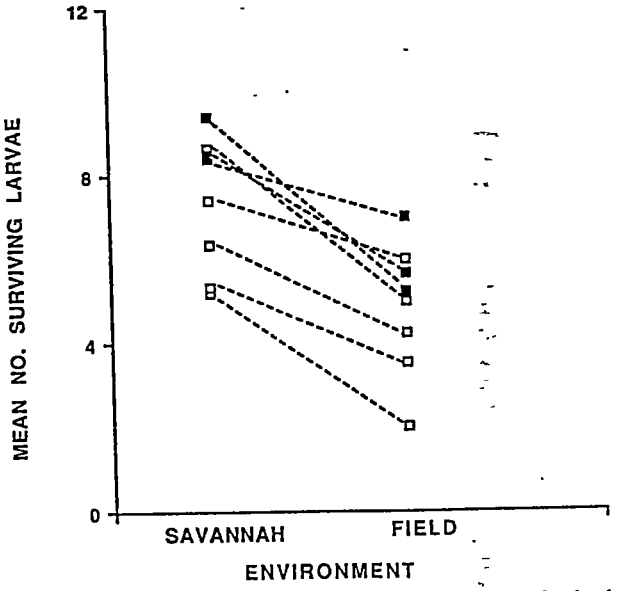

Fig. 1. Mean larval survivorship per clone is plotted for both gardens. Dashed lines connect values of the same clone in the two environments; no environmental continuum is implied. Blackened squares represent male clones, hollow squares, female clones. Results are from the first run of the experiment. Parallel lines illustrate the lack of genotype by environment interactions

Table 1. ANOVA on larval survivorship; Run 1

Source	SS	df	MS	F	p-value
Sex	5.45	1	5.45	0.42	ns
Clone w sex	78.26	6	13.04	2.32	0.044
Environment	73.13	1	73.13	27.39	<0.001
Sex by env	0.46	1	0.46	0.17	ns
Clone w sex by env	16.02	6	2.67	0.47	ns
Within cells	326.47	58	5.63		

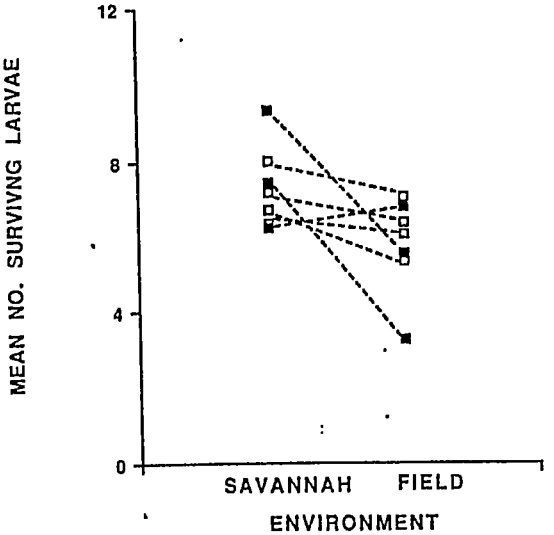

Fig. 2. Mean larval survivorship for each clone in both gardens; results are from the second run of the experiment. See legend in Fig. 1 for interpretation of lines and squares

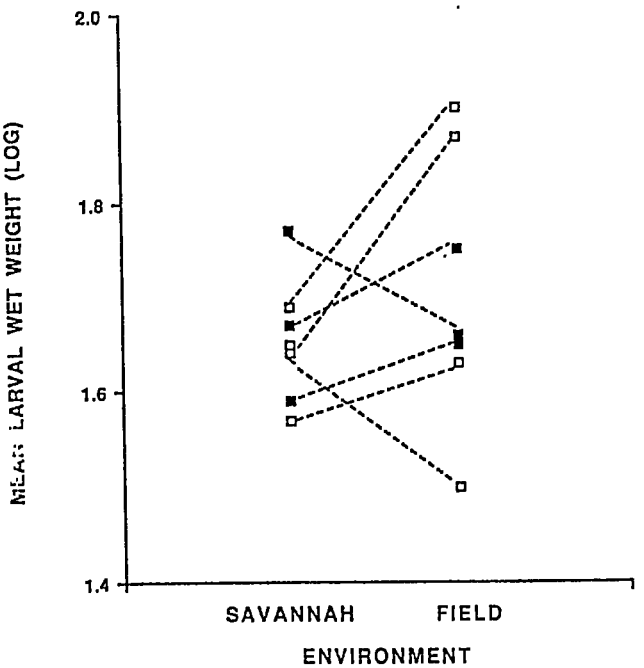

Fig. 3. Mean larval weight (in 10^{-4} g, log transformed) for each clone; data from the second run of the experiment. Lines connect mean larval weight on the same clone in the two environments. Non-parallel lines indicate a significant genotype by environment interaction. See legend in Fig. 1 for full explanation of lines and squares

Table 2. ANOVA on larval survivorship; Run 2

Source	SS	df	MS	F	p-value
Sex	7.78	1	7.78	1.19	ns
Clone w sex	32.67	5	6.53	1.97	0.10
Environment	48.28	1	48.28	7.58	0.09
Sex x env	12.16	1	12.16	1.91	ns
Clone w sex x env	31.87	5	6.37	1.93	0.10
Within cells	178.58	54	3.30		

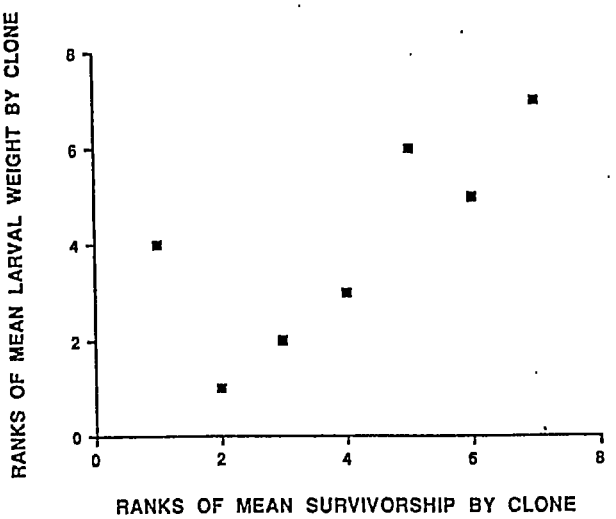

Fig. 4. Rank correlation between mean larval survivorship and mean larval weight for each clone ($r=0.75$, $P<0.05$)

Run 2

No gender effects on larval survivorship were observed, as in the early run. In this run, however, plant genotype and environment had only marginally significant effects ($P=0.09$ and 0.10, respectively), and there was also a marginal clone genotype by environment interaction ($P=0.10$) (Table 2). Despite the lack of significance of any one term, the model as a whole explained 25.5% of variance in larval mortality (using orthogonal sums of squares). Plots of mean larval survivorship on clones in the two environments are in Fig. 3.

For variation in larval weight, the model explained only a small portion of the variance (7.2%); however, the same factors that were important in larval survivorship were significant in determining larval weight. The effect of clone was highly significant ($P<0.001$) and there was also a significant clone by environment interaction ($P=0.038$).

Rank correlation of mean larval survivorship versus mean larval weight on a per clone basis was positive and significant ($r=0.75$, $P<0.05$) (Fig. 4), indicating that clones supporting greater larval survivorship also supported better larval growth. In contrast, larval survivorship and weight on a per ramet basis (standardized for clone effects) was not correlated ($r=0.07$), indicating that this relationship is probably not due to micro-environmental effects at the level of individual ramets.

Larval survivorship on individual clones compared between environments was significantly and positively correlated in the first run ($r=0.79$, $P<0.05$), a result consistent with significant genotype effects. Larval survivorship on individual clones was not correlated between environments in the second run ($r=-0.09$), consistent with genotype by environment interactions. I found no correlation between runs 1 and 2 in individual clone suitability (based on mean larval survivorship) for the savannah garden ($r=0.033$); however, in the field garden,

Table 3. ANOVA of larval weight, Run 2 (after log-transformation)

Source	SS	df	MS	F	p-value
Sex	0.08	1	0.08	0.15	ns
Clone w sex	2.74	5	0.55	4.57	<0.001
Environment	0.11	1	0.11	0.39	ns
Sex x env	0.47	1	0.47	1.68	ns
Clone w sex x env	1.42	5	0.28	2.38	0.038
Within cells	50.46	421	0.12		

there was a significant negative correlation in larval performance on individual clones between runs ($r = -0.76$; $P = 0.05$).

Discussion

I found that both clone genotype and environment (in a broad sense) had significant effects on larval survivorship (Tables 1, 2). In neither case was the gender of a clone related to larval performance. For both runs, the ANOVA model explained a much greater portion of the variance in larval survivorship than larval weight. Since the density of young larvae is greatest early in the season, factors contributing to resistance in the first run may be generally more important. However, substantial numbers of larvae still emerge later in the season and these may be exposed to factors such as seasonal and/or induced changes in the plant that could mediate or alter the nature of genotype and enviroment effects as shown in the second experimental run. Between runs, there was no correlation between larval survivorship on individual clones in the savannah garden; however, larval survivorship on individual clones was negatively correlated between runs in the field garden. These results are difficult to interpret and may reflect variable seasonal or induced changes in the suitability of different plant genotypes within an environment for larvae.

Significant environment effects indicate that, regardless of clone genotype, sumac clones growing in some habitats may be more susceptible to beetles than clones growing in other areas, in the absence of other factors that modify beetle densities. Significant clone effects on larval survivorship indicate that some plant genotypes are more resistant to beetles than are others. For frequency dependent selection to maintain genetic variation in plant resistance traits, there must be a genetic component to resistance to beetles. Results from both experimental runs indicate that genetically-based variation in resistance occurs. Genetic factors were as important as environment effects in explaining larval mortality. For diversifying selection to maintain variation in the plant population, genotype-environment interactions must occur (Hedrick 1986). Genotype-environment interactions occurred in this study only in the second run and were weak effects.

I have shown previously that in the field sumac ramets suffering from beetle attack have reduced survivorship, growth and fruit set when compared to protected ramets (Strauss 1988). Since female beetles will oviposit on most clones including even those of staghorn sumac (*R. typhina*), which is a much less suitable host plant (Strauss, unpubl. data), plant attributes that affect the mortality of young larvae may offer strong selective advantages to sumac clones. I have observed that clones infested by beetles may remain infested for many years (Strauss 1988). Adult beetles marked the previous fall have been recaptured the following spring ovipositing on the same clone (Strauss, unpubl. data). Consistency in differing numbers of herbivores and/or level of attack on individual plants has been documented in several other systems as well (Strauss and Morrow 1988, Karban 1988, Crawley 1985). The benefits of lowered beetle population densities are likely to be felt at the individual clone responsible for this decline.

The underlying mechanism of resistance to beetle attack may be plant secondary chemistry. Sumac, a member of the Anacardiaceae, contains a diverse array of secondary chemicals including many flavonoid compounds, tannins and terpenes (Young 1979; Furth and Young 1988). The flavonoid chemistry of *Rhus* species affects interspecific host plant choice by several *Blepharida* species (Furth and Young 1988), and flavonoid compounds can influence host plant use by other phytophagous insects, acting as toxins, feeding deterrents or feeding stimulants (Harborne 1979). The relationship between the genera *Blepharida* and *Rhus* spans several biogeographic regions (Furth 1982; Furth 1985).

Intraspecific variation in secondary chemistry may also play a role in the feeding ecology of *Blepharida* on *Rhus*. Flavonoid chemistry differed among populations within species for all three species of *Rhus* in which several populations were sampled (Furth and Young 1988). Such intraspecific variation in secondary chemistry may partially explain patchiness of beetle attack within species, and could be important evolutionarily if chemical profiles of individual plants are heritable and affect both insect and plant fitness.

In summary, when sumac clones are attacked by beetles, they often experience years of fitness-reducing chronic herbivory (Strauss 1988), and potential death. The facts that not all clones are heavily attacked, that adjacent clones can suffer widely different levels of herbivory and that these common garden experiments show significant clone genotype effects, support the hypothesis that genotypic factors play a large role in the resistance of sumac to beetle herbivores. The environment in which clones are growing may mediate the success of individual genotypes in resting beetle attack and, in general, significantly affects larval performance. Although both plant genotype and environment had effects on resistance to beetles, there was only weak support for the existence of genotype by environment interactions. The maintenance of variability with respect to beetle resistance within this sumac population is better explained by evolutionary mechanisms requiring genotypically-based plant resistance, such as frequency-dependent selection, than by those requiring plant genotype-environment interactions, such as diversifying selection.

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