

## 6. The Chrysomelidae: a useful group for investigating herbivore-herbivore interactions

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### 1. INTRODUCTION

The Chrysomelidae comprise one of the most abundant and diverse families of herbivorous insects. A large proportion of chrysomelid species are monophagous or oligophagous, and the group has long been used to investigate the evolution of host specificity in phytophagous insects (Mitchell 1981, Smiley 1982, Crowson 1981, p. 589, Jolivet 1986). Of 139 chrysomelid genera in North America, 46.8% use only one genus of host plant, and an additional 46.7% use between two and five genera (Mitchell 1981). For 298 native N. American species, the average number of host plants used is approximately 1.5 plant species per species of chrysomelid (data tabulated by J. Kochmer from Wilcox 1979). In many chrysomelids, both adults and larvae feed on the same host resource (Raupp and Denno 1983), a fact that may have a large influence on patterns of host use in the Chrysomelidae. Although several other insect orders contain monophagous species, adult and larval resources are often different (Mitchell 1981, Price 1975). For example, in monophagous Lepidoptera, adult butterflies require nectar or pollen for their metabolic maintenance. Adult flight and alighting behaviors are commonly phasic, and flight paths can be alternately affected by densities of flowering plants (adult nectar resources) and larval resources (Stanton 1983, Gilbert and Singer 1973). The different needs of the two life stages may influence the dispersion of eggs in particular habitats (Murphy 1983, Gilbert and Singer 1973).

In contrast, for many chrysomelids, mating, oviposition, and adult and larval feeding all take place on the same plant species. Data on the dispersal behavior of several species of chrysomelids indicate that adults often do not move far over the course of their lifespan (Mason and Lawson 1980, Smith and Whittaker 1980, DeRoe and Pasteels 1982, Suzuki 1985), and larvae may complete development on plants only meters away from those that supported their parents' own development (Carne 1966). Lower dispersal rates are associated, in general, with more specialized phytophagous species (Stinner et al. 1983). Female chrysomelid beetles often lose their ability to disperse once

the short period of ovarian development has been completed (Messina 1982, DeRoe and Pasteels 1982, Suzuki 1985). As a result, some chrysomelid populations may remain fairly localized and could potentially specialize on plant resources in the immediate area. A study of two closely related carabid species differing in vagility has shown that the brachypterous species exhibits genetic differentiation more closely related to local environmental conditions (Liebherr 1986). Differentiation between demes or populations of chrysomelids has been documented by Virrki and Zambrana (1979), Mikheev et al. (1984), Hsiao (1978, 1982) and Hare and Kennedy (1986) with regard to host plant use. I propose that differentiation in some species may result, in part, from the shared resources of adults and larvae and low propensity of adults to disperse. Life history characteristics such as monophagy, shared adult and larval resources and the potential for low dispersal rates all strengthen the bond between insect and host plant.

Given the intimacy that many chrysomelids have with their host plants, the group may be unusually useful to investigators of herbivore-herbivore interactions. Not only may chrysomelids inflict heavy damage on their hosts and thus influence the behavior of co-occurring herbivores, but they themselves may be very responsive to the actions of other herbivores. Chrysomelid damage can occur consistently at moderate to heavy levels (Morrow 1979, Louda 1981) as well as during irregular outbreaks (Felt 1907, Young and Hall 1986, Young 1979, Sholes 1981, Strauss, unpubl. data). In either case, their damage may influence other co-occurring herbivores.

In this chapter, I discuss studies that document, or fail to document, interactions between herbivores, concentrating primarily on studies of the Chrysomelidae, but supporting some of my statements with results from studies of other chewing herbivores. First, I outline the various ways in which herbivores may influence each other's behavior, including use of a host resource. Then I review what evidence we have to date for these types of interactions. Finally, I discuss the types of evidence that may best allow us to detect whether such interactions are indeed occurring.

The mechanisms through which herbivores may interact are various. It is important to bear in mind that not all interactions are of an antagonistic nature. Herbivores may facilitate the use of a host plant as well as impede usage by other species. The following is a partial list of mechanisms through which one herbivore may affect the host usage of other herbivores.

(1) One herbivore may directly interfere with another's use of a host plant through aggressive encounters.

(2) One herbivore may exploit plant tissue such that other species sharing the same host are limited in the amount of resources available to them.

(3) An herbivore may alter the acceptability of a host through changes in plant chemistry as a result of feeding; these changes may repel or may attract additional herbivores.

(4) Similarly, one herbivore may change the plant architecture in ways that affect subsequent host use by other herbivores.

(5) Some herbivores may themselves have associations with other species that indirectly affect co-occurring herbivores.

## 2. INTERFERENCE COMPETITION

Interference competition is usually associated with agonistic encounters between two species over a shared resource. However, a more subtle mechanism of interference competition available to chrysomelids, as a group, is the use of chemical secretions. Most chrysomelid beetle larvae have eversible glands that emit chemical repugnants often derived at least in part from the host plant (Rowell-Rahier and Pasteels 1982). Although generally considered a defensive adaptation (see Pasteels et al. 1983 for review), the role of these chemicals in deterring other herbivores has been recently documented. Willow leaf beetle larvae (*Plagioderia versicolora*) were able to deter effectively the lepidopteran larvae of *Nymphalis antiopa* from feeding on stems of a shared willow host (Raupp et al. 1986). Chemical secretions used in this way must be considered a means through which chrysomelid herbivores actively prevent feeding by co-occurring herbivores. Since many chrysomelid larvae possess these defensive glands (Crowson 1981, p. 592), interference competition through this mechanism may be common, though still relatively undocumented.

Historically, interactions between herbivores have been considered in light of competition theory, and the experimental evidence sought to document interactions has been tailored to this theory. In a series of studies by Strong (1977, 1981, 1982) and Seifert and Seifert (1976, 1979a, 1979b), several communities of herbivores feeding on *Heliconia* host plants were examined for the presence of interspecific competition. Seifert and Seifert's work examined a community of insects with varying feeding habits ranging from folivory to nectivory and detritus feeding. Based on distributional data, they found few interactions between co-occurring herbivores with diverse feeding habits, and those they did find were primarily mutualistic interactions between detritivores (Seifert and Seifert 1979a). However, in a more experimental study of two folivorous hispine beetles on *Heliconia* in Venezuela, Seifert and Seifert (1979b), do document higher emigration rates by one beetle larva from bracts containing natural densities of larvae from a second species. In addition, they show that these two species occupy slightly different locations on plants in the field, a phenomenon attributed to interspecific competition (based on data from laboratory feeding experiments). Strong (1982) examines communities of phytophagous hispine chrysomelids using a variety of *Heliconia* hosts from several different sites. He uses the degree of leaf co-occupancy by adult hispine beetles to examine competition among chrysomelid species. Hyperdispersion of species among plants could indicate the presence of interference competition between species. Strong found virtually no evidence for competition

between adults based on pairwise comparisons of their distributions. In addition, experiments using three species of hispines at different densities on *H. imbricata* showed no effect of the presence of these species on subsequent immigration or emigration by co-occurring species. Strong (1982) also was unable to observe aggressive interactions between species of hispines in Petri plates.

A preliminary study by Bach (1977) suggested that what initially appeared to be different food plant preferences by the chrysomelids *Acalymma vittata* and *Diabrotica virgifera* on cucurbits, actually may have reflected competitive interactions between the two species. Food preference tests and field distributions indicated that one cucurbit species, *Cucumis maxima*, was most attractive to *Acalymma*, in the absence of *Diabrotica*. In the field, this species was the one in which *Diabrotica* was most common, and accounted for less than half the plant usage by *Acalymma*. From choice tests, Bach felt that *Diabrotica* beetles were preventing *Acalymma* from using their preferred host. The conclusive manipulations in which *Diabrotica* beetles were excluded from this host were not performed, so the results remain somewhat speculative.

Other studies have examined different communities of herbivores for similar patterns (Rathcke 1976, Stiling and Strong 1983). Stiling and Strong (1983) considered a taxonomically diverse community of stem-boring insects comprising two beetles in the Mordellidae and Languriidae, as well as dipteran and lepidopteran herbivores. Distributional data were used to infer competition. In six of seven species pairs where sample sizes were great enough to detect competition, there was significantly more species segregation than expected. To complement dispersion data, laboratory trials showed that all species attacked one another when they encountered other larvae in the stem. Rathcke (1976) was also able to document competition between a mordellid beetle and another stem borer, although interference interactions were documented only in 2 of 13 species. Other stem-boring communities of lepidoptera show a very small incidence of interference competition (see Strong et al. 1984 for review). One might expect interference competition to be most detectable in systems where the physical environment is constraining, as within stems. Solid- versus hollow-pithed plant species may also affect the incidence of interference competition between herbivores in the same stem (P. Stiling, pers. comm.).

### 3. EXPLOITATIVE COMPETITION

Evidence for exploitative competition between herbivores is difficult to gather. Documenting competition requires showing a difference in population numbers of one herbivore species in the presence, versus absence, of a second species. Few investigators have taken the time to selectively exclude one species and watch the changes in another (but see Zwolfer 1977, as cited in

Zwolfer 1979, Karban 1986). Comparisons between sites of coexistence and absence of one species require replication in order to avoid confounding site effects with herbivore effects. Unfortunately, even with replication, site effects may be important if there is a correlation between factors responsible for the absence of the first species and the population numbers of the second.

Although exploitative competition has been documented in other herbivore systems (Zwolfer 1979, Karban 1986, Stamp 1984), few studies have addressed chrysomelid communities. Recent articles by Suzuki (1985, 1986) discuss the coexistence between three species of chrysomelids using *Rumex* in disturbed habitats of Japan. Suzuki was able to document that at times when all three species co-occurred, in multiple habitats, most of the available plant resource was consumed. Food limitation resulted in the death of many larvae (Suzuki 1986). Resources were also reduced in most sites with just two co-occurring species. One species, *Galerucella vittaticollis*, appeared to show temporal displacement in population peaks when it occurred with high densities of either of the other species. Over two years, two sites exhibited this shift. The author proposes a reasonable mechanism to explain the shift and presents laboratory data to support his claim. Female *Galerucella* require 15 mg dry weight of plant tissue before they are able to mature eggs. If food is not available in sufficient quantity, females return to the litter. In addition, if ovipositing females were starved, they ceased ovipositing and also returned to the litter. Evidence of shifting peaks of beetle abundances, coupled with documented low resource availability suggests that exploitative competition could be occurring, and a forthcoming paper promises to discuss this possibility in more detail (Suzuki 1986).

Other studies of communities of chrysomelids find no evidence for competition. For example, hispine beetles on *Heliconia* in Costa Rica were found not to be limited by leaf availability (Strong 1983). Many other studies document the coexistence of species through their partitioning of host plant species growing in the same habitats, or of host plant parts or seasonal separation of species abundances (Wapshere 1982, Hicks and Tahvanainen 1974, Suzuki 1985). However, even in these studies, anecdotal tidbits often refer to the possibility of interactions between herbivores. For example, Hicks and Tahvanainen (1974) document perfect niche differentiation between six species of crucifer-feeding chrysomelid beetles, of which 3 are native, and the rest introduced. Differentiation occurred through shade and sun habitat preferences and species of host plant used. In the discussion, however, they mention that prior to the introduction in the 1920's of *Phyllotreta cruciferae*, the native beetle, *P. bipustulata*, was documented as feeding on a much larger range of host species – many of these host species are now utilized almost solely by the introduced beetle. In addition, another introduced species, *Psylliodes napi*, uses a variety of host plants in Europe, several of which are present in the U.S., but the beetle uses only one host species, *Barbarea oleracea*, at the study site. None of the other five beetle species use this host. Such narrative suggests that

interactions have occurred between these herbivores. Without experimental evidence, these reports are difficult to assess. Some would question the value of documenting interactions between non-native species at all, since their behaviors evolved in an ecological context different from the one in which their interactions take place.

Exploitation competition has been documented in artificial systems, often with introduced beetles on crops or introduced weeds. For example, introduced *Chrysolina quadrigemina* outcompeted introduced *C. hyperici* through its highly effective control of Klamath weed in California (Huffaker and Kennett 1969). The success of *C. quadrigemina* appeared to be related to its ability to break diapause earlier than *C. hyperici* and to defoliate large areas of host plant completely. In collard crops planted at three different densities, interspecific competition between two introduced flea beetles and an introduced butterfly occurred at the highest density of collards (Kareiva 1982).

Despite the lack of evidence and controlled experiments in native systems, the potential for exploitation competition may exist for many species of chrysomelids. For example, several studies have documented the tremendous damage inflicted by chrysomelid populations in both native and introduced systems. Often, damage is extensive enough to result in complete defoliation of the host or prevents plants from reproducing sexually (Felt 1907, Young 1979, Hopkins and Whittaker 1980, Sholes 1981, Brunsting 1982, Kraft and Denno 1982, Young and Hall 1986, Strauss, unpubl. data). In addition, plants defoliated early in the season may be defoliated a second time, as the second flush of new leaves is, in general, more attractive to chrysomelids than older tissue of unattacked neighbors (Felt 1907, Luck and Scriven 1979, Rockwood 1974, Young 1979). Patterns of chrysomelid damage also may make leaf tissue unavailable to other herbivores. Taylor and Bardner (1968) found that leaf area injured by moth larvae was linearly related to the weight consumed. In contrast, larvae of the chrysomelid, *Phaedon cochleariae*, fed such that a much larger area of the leaf was injured relative to the amount consumed. In all of these systems, one would expect other herbivores using the same hosts to experience a food shortage; unfortunately, there have been few studies to explicitly document the responses of other herbivores to outbreaks of a single species.

I have found that high levels of chrysomelid attack on sumac clones result in significantly lower levels of deer browse on these clones over the following winter (Strauss in prep). I attribute this to significantly lesser growth by chrysomelid-attacked ramets, as well as generally reduced ramet vigor. However, decreased acceptability to deer of attacked ramets may also reflect long-term changes in plant chemistry as a response to attack. Whatever the ultimate mechanism, this system illustrates how temporally separated herbivores may still influence the availability of plant tissue for other herbivores.

Less experimental studies also indicate that exploitation competition may be occurring in other systems with native chrysomelids. Hopkins and Whittak-

er (1980) investigated interactions between two stem-boring weevil herbivores of *Rumex obtusifolius*. Although they were not able to document interactions between the two weevils, they did state that extensive damage of *Rumex* by the chrysomelid, *Gastrophysa viridula*, resulted in reduced plant biomass and was likely to affect the success of co-occurring *Apion* weevils. In the same vein, the herbivore community of *Baccharis*, an abundant composite in California, contains folivorous *Trirhabda* beetles as well as several species of flower- and fruit-feeding heteropteran herbivores, among others (Kraft and Denno 1982). At one of two sites, damage from *Trirhabda* was so great that few of the stems flowered. Since the main thrust of this study was not an investigation of the structure of the herbivore community, the densities of heteropterans at both sites were not assessed. It is not unreasonable to believe, however, that the lack of flowers and fruit at the heavily damaged site may influence the numbers of flower and fruit feeding herbivores.

One need not rely on sporadic incidents of heavy herbivory to create the opportunity for herbivore-herbivore interactions. Louda (1984) has shown that even low levels of herbivory by native flea beetles on hosts can have a large effect on plant growth, phenology, reproduction and leaf area. Similar effects have been documented in crop systems as a result of chrysomelid herbivory (Lamb 1984). Substantial alteration of phenology, or the reduction of plant biomass, reproduction or survivorship are all potential sources of limitation to other herbivorous species.

#### 4. CHANGES IN PLANT CHEMISTRY

The previous two sections have dealt with ways in which herbivores may interfere with one another as they share a common host. However, herbivore damage may also facilitate the use of host plants by other herbivores. Chemical changes in leaf composition as a response to damage have been well documented and are not solely defensive (McIntyre 1980, Rhoades 1983 for review).

In the chrysomelid literature, Carroll and Hoffman (1980) have shown that damage to squash leaves is an attractant for the specialist chrysomelid, *Acalymma vittata*, and a deterrent to the generalist coccinellid, *Epilachna tredecimnotata*. Green and Ryan (1972) report that Colorado potato beetle damage to tomato or potato leaves leads to an increase in the levels of proteinase inhibitors and suggest that this increase may reduce subsequent herbivore attack. This reduction was not documented. As defoliators, chrysomelids may increase the susceptibility of hosts to secondary attack by boring insects and pathogens, as has been documented in other defoliator systems (Rhoades 1983).

A growing body of literature documents plant-mediated interactions in other groups of herbivores. Harrison and Karban (1986) have shown damage by an early-season moth reduces oviposition and larval growth rates of a later

season moth both in the laboratory and in the field. Similarly, plume moth damage on *Erigeron* reduces the success of spittlebugs feeding on those plants (Karban 1986). In contrast, damage to leaves by other herbivores, including cerambycid beetles and lepidoptera, has been shown to increase plant acceptability to *Melanoplus* grasshoppers (Lewis 1979). In addition, fall webworm larvae raised on foliage from trees damaged previously by tent caterpillars grew faster and attained heavier pupal weights than did those fed foliage from unattacked trees (Williams and Myer 1984). Since many species of chrysomelids overwinter as adults, adult beetle damage is often inflicted early in the spring (Rockwood 1974). If the presence or absence of damage influences the succession of subsequent herbivores on plants, chrysomelids may again prove to be an influential group on the fates of subsequent herbivores and the host.

## 5. CHANGES IN PLANT ARCHITECTURE

Damage by herbivores can also alter the architecture of a plant. For example, through the destruction of terminal buds herbivores may increase the degree of branching of a plant. Although cases such as these are rare in the literature, when they occur, they are often dramatic. *Cebus* monkeys eating growing tips of *Gustavia* trees cause increased branching (Oppenheimer 1969). A more branched and stunted growth form of pinyon pines is the result of damage by a moth specialist (Whitham and Mopper 1985). Increased architectural complexity through branching may also increase the numbers of other herbivores on pinyon pine (Whitham and Mopper 1985, Lawton 1983). Isopod and other boring insects increase the degree of root branching in mangroves (Simberloff et al. 1978). In general, changes in architecture affect the relative abundances of specific plant parts and, in turn, may influence the herbivores specializing on these parts. One caveat, however, is that architectural changes as a result of damage may also be accompanied by chemical responses to damage, and these effects may be confounded.

With regard to chrysomelids, in my own research I have found that high densities of the chrysomelid flea beetle, *Blepharida rhois*, on smooth sumac results in the production of sucker-like basal shoots owing to the destruction of all growing buds on a woody stem. Bud primordia under the litter are protected from beetles and initiate shoots after all above-ground primordia have been destroyed. These basal shoots resemble first year ramets of sumac clones. In unattacked sumac clones, first and second year shoots are the oviposition sites of the cerambycid specialist, *Oberea ocellata*. Clones attacked by chrysomelids produce significantly more shoots acceptable for cerambycid oviposition. Thus clones with high densities of chrysomelids also experience greater incidence of cerambycid oviposition. Simulation of chrysomelid damage on shoots resulted in the same changes in architecture, as well as the same increased incidence of cerambycid attack. Since cerambycids preferred basal



shoots to chrysomelid-damaged shoots on woody stems, I infer that damage alone is not sufficient to increase cerambycid attack rates, and that architectural changes resulting in an increase of herbaceous basal shoots are responsible for increased cerambycid oviposition. Architectural changes in the host plant as a result of chrysomelid damage facilitate the use of sumac by a cerambycid specialist.

## 6. HERBIVORE ASSOCIATIONS

Interactions among herbivores may be mediated by insect associations. A well-documented example is the effect of phloem-feeding insects on other herbivorous larvae via the actions of associated ants. High mortality rates of ectophagous larvae have been attributed to removal by ants that tend honeydew producing insects. Ant-caused mortality has been documented for chrysomelids with *Trirhabda* on goldenrod (Messina 1981) and indirectly for *Ophraella* larvae on *Artemisia* (Strauss 1987). Ants were also found to be responsible for restricting the distribution of the chrysomelid, *Physanota alutacea*, introduced to control black sage in Mauritius (Simmonds 1958, as cited in Gouden and Louda 1976). In contrast, ants tending membracids on black locusts have benefitted the endophagous chrysomelid larvae of *Odontata dorsalis* by excluding hemipteran predators (Fritz 1983). Adult beetles, however, were attacked by ants and were therefore discouraged from ovipositing in locust leaves. Although significantly fewer eggs were laid on ant-tended branches, net larval survivorship was significantly higher in two consecutive years on these branches owing to the exclusion by ants of larval predators (Fritz 1983). Depending on predation pressure and the feeding habits of chrysomelid larvae, the presence of phloem-feeding insects on the same-host plant may either increase or decrease chrysomelid fitness.

There are other ways in which the actions of one herbivore may influence another. For example, endophagous feeders or the eggs of other herbivores may be consumed by folivorous herbivores. Adult willow leaf beetles lay their eggs on leaves less likely to be consumed by co-occurring folivores of willow even though these leaves support inferior larval growth (Raupp and Denno 1983). Although consumption of one herbivore by another must happen, there is little documentation of how often or how important such events are to endophagous insects.

I have not discussed effects of the third trophic level for the purposes of this paper, but herbivore species that act as alternate hosts for parasitoids or predators of a second herbivore can provide another means of indirect interaction between herbivores. These interactions are, in general, more removed from the relationship between insect and plant and are therefore not included here. An exception occurs when plant volatiles, released from leaf tissue as a result of damage by one herbivore, attracts a variety of predators or parasites to the host (see Price et al. 1980).

## 7. EVIDENCE FOR HERBIVORE-HERBIVORE INTERACTIONS

I have discussed five classes of interactions that may be important to herbivores that share a common host. Only recently has experimental evidence been gathered to document these sorts of interactions. However, it is becoming clearer that herbivore-herbivore interactions may not conform to the types of symmetric models we have used in other systems (Lawton and Hassell 1981, Karban 1986). In almost every case where interactions are documented, we see one species affecting another without the reciprocal relationship. This one-sidedness is true for cases showing facilitation as well as competition, and implies that selection may be acting on only one species. For this reason, the relationships or interactions between herbivores within the same community may not be strictly coevolutionary.

In the past, distributional evidence has been used to infer the presence or absence of competition. There are however, potential problems with that approach. For example, preference for different plant parts, habitats or species may result in the hyperdispersion of herbivores that is not the result of competition. It has long been agreed that the causal mechanisms leading to patterns of resource partitioning are almost impossible to distinguish (Connell 1980).

Direct manipulation of herbivore populations seems the best way to assess potential interactions. Such manipulation entails removal or exclusion of one or more species and then examination of the host plant response to herbivore removal as well as the subsequent host use by other herbivores. However, even this seemingly straightforward approach is rife with hazards. For example, different life-stages of an herbivore may exhibit different patterns of interactions with other species. This is particularly a concern in groups where both adults and larvae are phytophagous. An example from the literature leaves us puzzled as to the relationship between two species of hispines on *Heliconia*. The same two species that exhibited competition between their larvae in Venezuela (Seifert and Seifert 1979b) were not detected as competing based on adult distributions in Costa Rica (Strong 1982). Do these species compete? The studies differed in species of host, life-stages of herbivores and site as well as in the conclusions drawn. How do we evaluate the relationship between these species?

In addition to site, host species and life-stage effects, other subtle effects may obscure relationships between herbivores. The effects of one herbivore on another may not be evident in the same year or the same season. My research on flea beetle damage has shown that folivory in the spring and summer by beetles affects future herbivory by deer in the winter. Temporally isolated herbivory events are not independent if they involve the same host individual – and some would argue that even undamaged neighboring plants respond to nearby herbivory (Rhoades 1983, Schultz and Baldwin 1982, but see Fowler and Lawton 1985). Residual effects of herbivore removal or

damage may persist for short time periods or as much as one year (Wallner and Walton 1979, Haukioja 1983, Strauss, unpubl. data) or more. To what extent does the documented partitioning of plant parts among species reflect previous damage to specific plant parts by an early-season herbivore? (Classically, this partitioning has been thought to reflect historical interactions/competition between herbivores that are no longer operative). The nature of many plants as long-lived resources results in carry-over effects from herbivory events that may influence the subsequent behavior of herbivorous communities.

One final property of insect-plant systems that may obscure the relationship between co-existing species lies in the dynamic nature of insect-plant interactions. Host plant health has been shown to influence the population dynamics of herbivores (White 1976, McIntyre 1980, Gershenson 1984). Herbivorous species feeding on a healthy plant may have different types of interactions than when they feed on a senescent, drought-stressed or diseased plant. Plant stress induced by herbivory itself may also change the relationships of all species involved. Herbivores facilitating each other's use of a healthy plant may end up competing as plant health degenerates.

A growing body of evidence suggests that herbivores do interact. Evolution or coevolution in any system can take place only in response to consistent selective pressure. It is possible that the recently documented interactions between herbivores reflect quirks in an otherwise unrelated existence of species and that these sporadic interactions do not constitute a strong enough selective pressure to result in any lasting evolutionary trends. This statement can be addressed only through further experimental research. Without the removal of specific herbivores and the thorough examination of responses by coexisting herbivores, we cannot ascertain the strength of herbivore-herbivore interactions. Two criteria met by natural systems could enhance the possibility of detecting these interactions – low dispersal by an herbivore once it is on a host and an intimate dependence by the insects upon the host plant (Karban 1986). There are many species in the family Chrysomelidae that meet these criteria. Because adult and larval stages often feed on the same plant species, the relationship between insect and plant in this group can be particularly close. For these reasons, natural systems in which chrysomelids are one member of the suite of herbivores sharing a host plant may be the most fruitful for examining the strength and consistency of herbivore-herbivore interactions.

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