

Interactive Effects of Different Types of Herbivore Damage: *Trirhabda* beetle Larvae and *Philaenus* spittlebugs on Goldenrod (*Solidago altissima*)

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ABSTRACT.—For pairwise coevolution to occur between a plant and one of its insect herbivores, the effects on plant fitness of that herbivore must be independent of other herbivore species. Here we present an experiment designed to test whether the effects of herbivory by *Trirhabda* beetle larvae and *Philaenus* spittlebugs are additive or whether the presence of one herbivore alters the impact of the other. We found that beetles and spittlebugs feeding together on tall goldenrod (*Solidago altissima*) reduce the mass of the apical bud and the foliage more than would be expected from either insect feeding alone. Reductions in stem, lateral shoot and root mass were also greater than expected, but these differences were not statistically significant. A multivariate analysis to examine effects on all components of the plant revealed greater reductions in plant biomass when beetles and spittlebugs fed together than when either fed alone. This suggests that the effects of herbivory by these two insects are not independent and that neither is likely to develop a simple pairwise coevolutionary relationship with the tall goldenrod. However, because damage to goldenrods is increased when the beetles and spittlebugs feed together, these insects may select more for increased plant resistance to herbivory when feeding together than feeding separately.

INTRODUCTION

Associations of herbivorous insects with their host plants have often been the focus of research on coevolution, or reciprocal change in interacting species (Ehlich and Raven, 1964). However, relatively few examples of simple pairwise coevolution in plant-insect systems have emerged (*e.g.*, Thompson, 1994; Rausher, 1996). Janzen's (1980; also *see* Fox, 1981; Futuyma and Slatkin, 1983) distinction between diffuse coevolutionary interactions among multiple species and strict pairwise coevolution brought to the fore the fact that most plant species are fed upon by multiple herbivorous insects (*e.g.*, Root and Cappuccino, 1992; Thompson, 1998, 1999). There are now explicit criteria to distinguish between diffuse and pairwise coevolution in plant-insect systems (Simms and Rausher, 1993; Hougen-Eitzman and Rausher, 1994; Rausher, 1996; Iwao and Rausher, 1997). Coevolution can be pairwise only if three conditions are met:

Criterion 1. There are no significant genetic correlations among plant resistance traits to different herbivores.

Criterion 2. Feeding by one insect species does not make plants more or less susceptible or attractive to other insect species.

Criterion 3. The effects on plant fitness of one species are not altered by the presence of other species (*i.e.*, the impacts of multiple parasites on plant fitness are additive).

Tests of these criteria are accumulating. Genetic correlations among plant traits that confer resistance to herbivory have been documented in some systems (*e.g.*, Maddox and Root, 1990), but appear to be absent from others (*e.g.*, Simms and Rausher, 1989; Roche

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and Fritz, 1997). With regards to the second criterion, there are many examples of interactions among herbivorous insect species that lead the presence of one herbivore species to either increase (facilitation) or decrease (competition, induced resistance) the abundance of other species (Faeth, 1986; Harrison and Karban, 1986; Gange and Brown, 1989; Moran and Whitham, 1990; Strauss, 1991; Pilson, 1992; Masters *et al.*, 1993; Denno *et al.*, 1995; Agrawal, 1999, 2000).

At least five studies exploring the third criterion have found significant non-additive effects on plant performance of feeding by multiple herbivorous insect species (Strauss, 1991; Karban and Strauss, 1993; Pilson, 1996; Wise and Sacchi, 1996; Juenger and Bergelson, 1998), whereas two studies (Hougan-Eitzman and Rausher, 1994; Maron, 1998) found the effects of different herbivores to be additive. Of the five studies that report significant nonadditive effects, Strauss (1991) and Wise and Sacchi (1996) found evidence that the effects of herbivory by two species were greater than expected from data on either feeding alone. The other three studies report a reduced impact of herbivory when plants were subjected to multiple herbivores relative to that expected from data on the herbivores feeding separately. Increased effects of multiple herbivores such as found by Strauss (1991) could occur if feeding by one herbivore makes a plant more susceptible to other herbivores or if different types of herbivory are physiologically more stressful on the plant than one type of damage. Decreased effects of multiple herbivores could be due to competition between the herbivores or induced resistance.

The above studies suggest that coevolution between plants and herbivorous insects will often be diffuse rather than pairwise. However, little is known about the characteristics of systems in which coevolutionary interactions tend to be diffuse or what conditions facilitate pairwise coevolution. Further examples from different types of systems are necessary before such patterns can be discerned.

Here we report on an experiment designed to test for nonadditive effects (Criterion 3) on the performance of the tall goldenrod (*Solidago altissima* L.: Asteraceae) of feeding by two herbivores, a leaf-chewing beetle (*Trirhabda* LeConte: Chrysomelidae) and a xylem-tapping spittlebug (*Philaenus spumarius* L.: Cercopidae). Previous research in this system (Meyer and Whitlow, 1992; Meyer, 1993; Meyer and Root, 1993) has shown that the beetle and the spittlebug are both detrimental to tall goldenrod performance, but that they affect plant growth and physiology in different ways. We follow up on those studies by examining whether these different types of damage are more injurious to the plants when they occur simultaneously, as is often found in the field. To this end, we subjected goldenrods to one or both insects at a range of densities and examined the relationship between plant biomass and herbivore load.

MATERIALS AND METHODS

The study system.—*Solidago altissima* is a self-incompatible, herbaceous perennial with a clonal growth form (Werner *et al.*, 1980; Melville and Morton, 1983). At least 101 insects feed on *S. altissima* in central New York (Root and Cappuccino, 1992). The impact of these herbivores is extremely variable, ranging from negligible effects to substantial decreases in leaf, stem, root, bud and inflorescence mass (Meyer, 1993; Root, 1996). Herbivory can also alter competitive interactions of *S. altissima* with other plants (Carson and Root, 1999). *Trirhabda* beetles and *Philaenus spumarius* spittlebugs are known to affect *S. altissima* performance (Meyer and Whitlow, 1992; Meyer, 1993). Feeding by *Trirhabda* beetle larvae and *Philaenus* spittlebug nymphs can reduce leaf area, leaf mass, bud and seed head mass, root mass and relative growth rate of goldenrods, with spittlebugs causing greater reductions than the beetles (Meyer and Whitlow, 1992; Meyer, 1993; Meyer and Root, 1993). Feeding

by spittlebugs reduces photosynthetic rates in goldenrods, while no significant effects of beetles on photosynthetic rates are apparent (Meyer and Whitlow, 1992).

There are two species of *Trirhabda* that cannot be distinguished in the larval stage. *Trirhabda virgata* LeConte emerges earlier and is more common than *T. borealis* Blake (Messina and Root, 1980), and is most likely the species used in this study. *T. virgata* is one of the most abundant insect species on *S. altissima* in central New York (Root and Cappuccino, 1992), and can reach densities that cause defoliation of entire fields of goldenrod (Messina, 1981). *Philaenus spumarius* is also abundant on *S. altissima*, though it never attains densities as high as those reached by *T. virgata* (Root and Cappuccino, 1992).

There is genetic variation in *Solidago altissima* in resistance to herbivory by *Trirhabda* and *Philaenus* (Maddox and Root, 1987), but resistance to these insects is uncorrelated (Maddox and Root, 1990). Thus, one of the criteria (criterion 1 above) necessary for pairwise evolution is met. However it is not known whether these insects affect each others' distributions (criterion 2) or whether their effects on plant biomass are additive or if the impact of one depends upon the presence of the other (criterion 3, the focus of this paper).

Experimental design.—To explore whether the impacts on plant size of feeding by *Trirhabda* beetle larvae and *Philaenus* spittlebugs (hereafter beetles and spittlebugs) are additive or if the presence of one alters the effects of the other, we manipulated their densities on experimental plants. There were three treatments: beetles alone, spittlebugs alone and beetles and spittlebugs feeding together. These treatments were imposed at a range of insect densities following the methods of Meyer (1993) (*see below*) to estimate the relationship between herbivore load and plant size. Immature insects were placed on potted plants using camel hair paint brushes and feather-weight forceps. The insects began feeding within an hour. They were left on the plants for 18 d, approximately the duration of their development to adulthood. Just before the insects matured, they were removed and the plants were harvested.

Plants.—Goldenrod seeds were collected from mature flower heads in old fields close to Ithaca, New York late in the fall of 1993. To reduce variability in plant response due to genotype and maternal effects, seeds from two maternal parents were used. Because *Solidago altissima* is an obligate outcrosser (Melville and Morton, 1982), seeds from the same maternal parent are half- or full-sibs. Following the methods of Meyer (1993), seeds were sown in the greenhouse in mid-March in 240 ml paper cups filled with fritted clay with two tablespoons of potting soil on top. Fritted clay is a granular material made by firing coarsely-milled, dry clay in a rotary kiln (van Bavel *et al.*, 1978). It is commonly used in plant physiological ecology (*e.g.*, Emerman and Dawson, 1996; Geber and Dawson, 1997). We used fritted clay here because it is easy to wash off of roots. We started plants early so that they would be comparable in size to new stems sprouting from rhizomes in the field at the start of the experiment (about 10 cm tall). Three wk after sowing, the seedlings were thinned to one per cup and hardened off. We transplanted the hardened-off seedlings into large pots (21 cm in diameter by 22 cm deep) filled with fritted clay on the roof of Corson Hall, Cornell University. The roof of Corson Hall provided an environment with high light levels and reduced colonization by unwanted herbivores. We fertilized plants every other day with 3.5 g Miracle Grow® per liter of water (15%N, 30%P₂O₅, 15%K₂O plus trace minerals). Plants varied somewhat in size at the start of the experiment so were separated into three size classes. Plants initially grew as a single stem. Part way through the experiments lateral stems sprouted from the base of the main stem. Because insects were initially placed on the main stem, most damage occurred there.

Insects.—We collected first instar beetle larvae and spittlebug nymphs from a local old field at the end of May and transferred them to the experimental plants. Insects were placed

on plants for each treatment at a range of densities: 2, 4, 8 or 10 insects per plant. These densities are well within the range of densities found in natural populations (Root, 1996). For the beetle plus spittlebug treatment, each level consisted of half beetles and half spittlebugs (*i.e.*, 1 beetle and 1 spittlebug, 2 beetles and 2 spittlebugs, etc.). There were 11 to 13 replicates of each treatment and density combination, plus 46 control plants with no insects for a total of 184 plants. Plants in different size classes were assigned evenly across the treatments and ranges of densities. The experimental insects were counted 1 d after being transferred. Most of the approximately 860 insects were accounted for and were observed feeding actively. Roughly 40 missing insects (5%) were replaced at that initial counting. All insects were counted and removed from the plants 18 d later, just before molting to adulthood. The density of insects on the treatment plants at final count ranged from 1 to 12 (suggesting some insects thought to have been missing were simply not found at the initial count).

Harvest.—We harvested the plants 5 d after removing the insects by dividing each plant into 5 samples: the main stem, the bud on the main stem, the leaves on the main stem, the lateral shoots (stems, buds and leaves combined) and the roots. After drying to constant mass at 70 C, the plant samples were weighed.

Analysis.—We analyzed the data with a multivariate general linear model (JMP Version 3.2, SAS Institute, Inc., 1997) with five response variables: the masses of the bud, leaves, stem, lateral shoots and roots. All response variables were log transformed to fit assumptions of normality. The model examined the effects on plant biomass of the number of insects removed from the plant in each of the three treatments (beetles, spittlebugs or both). Thus, rather than examining an overall treatment effect, this model estimates the relationship between plant biomass and herbivore load for each treatment separately. Parent plant and the initial size class of the plants were included in the model. Preplanned contrasts were performed to compare the parameter estimates (analogous to slopes of regression lines for univariate models) for the three insect treatments. The parameter estimates for the effect of both insects feeding together were compared with the averages of the estimates for beetles and spittlebugs feeding alone. These contrasts test the null hypothesis that both insects feeding together have the same effect on plant mass as the average effect of the beetles and spittlebugs feeding alone (the additive model). A rejection of this null hypothesis indicates that the effects of both insects feeding together are nonadditive and either have a greater or lesser than expected effect on plant biomass. The contrasts were performed on the multivariate model described above and on each response variable separately to examine how the different plant parts responded to herbivory.

In addition to this main analysis, we performed simple analyses of variance to examine whether the number of insects removed from the plants and the percent of insects missing was influenced by the initial density or the treatment to determine whether there is evidence of density dependent intra- or interspecific competition (JMP Version 3.2, SAS Institute, Inc., 1997).

RESULTS

Feeding damage by the beetles and the spittlebugs, both separately and together, significantly reduced overall plant biomass (Table 1, MANOVA column). For the spittlebugs feeding alone and for both insects feeding together, feeding reduced each of the separate components of biomass (Table 1). However, feeding by the beetle larvae alone did not have a significant effect on the mass of the bud or the lateral shoots, but it did reduce the mass of the leaves, the stem and the roots (Table 1). The more of each insect present on the plants, the greater the reduction in biomass (Table 2, negative parameter estimates).

TABLE 1.—Wilk's Lambda F-tests and significance for each response variable and the full MANOVA. All response variables were log transformed for analysis to decrease heteroscedasticity. Other MANOVA tests (Pillai's Trace, Hotelling-Lawley, Roy's Max Root) showed the same patterns. R² values from univariate tests are given for each response variable

Source	Bud		Leaves		Stem		Lateral shoots		Roots		MANOVA	
	F _{df1,df2}	P	F _{df1,df2}	P	F _{df1,df2}	P	F _{df1,df2}	P	F _{df1,df2}	P	F _{df1,df2}	P
Intercept	873.0 _{1,177}	***	2653.5 _{1,177}	***	404.0 _{1,177}	***	4029.0 _{1,177}	***	4029.0 _{1,177}	***	1151.7 _{30,173}	***
Plant sibship	1.8 _{1,177}	NS	74.1 _{1,177}	***	4.7 _{1,177}	*	172.5 _{1,177}	***	172.5 _{1,177}	***	47.8 _{5,173}	***
Plant size class	3.1 _{2,177}	*	14.8 _{2,177}	***	13.9 _{2,177}	***	23.6 _{2,177}	***	23.6 _{2,177}	***	6.1 _{1,0346}	***
Beetles	2.2 _{1,177}	NS	4.1 _{1,177}	*	8.6 _{1,177}	**	22.4 _{1,177}	***	22.4 _{1,177}	NS	5.2 _{5,173}	**
Spittlebugs	13.8 _{1,177}	**	57.5 _{1,177}	***	12.8 _{1,177}	**	12.8 _{1,177}	***	12.8 _{1,177}	**	19.1 _{5,173}	***
Both	25.9 _{1,177}	***	43.5 _{1,177}	***	10.5 _{1,177}	**	10.5 _{1,177}	***	10.5 _{1,177}	**	18.0 _{5,173}	***
Univariate R ²		0.18		0.47		0.21		0.34		0.62		

* P < 0.05, ** P < 0.01, *** P < 0.0001, NS > 0.1

TABLE 2.—Parameter estimates from the MANOVA which describe the relationships between the number of insects removed from each plant and the mass of each plant part. The linear contrasts test the null hypothesis that the effects of both species feeding together are additive, *i.e.*, that the parameter estimates for both species feeding together are not significantly different from the average of the parameter estimates for beetles or spittlebugs feeding separately

Source	Parameter estimate					MANOVA
	Main Bud	Leaves	Stem	Lateral shoots	Roots	
Beetles	-0.0011	-0.0051	-0.0067	-0.0071	-0.0091	
Spittlebugs	-0.0025	-0.0180	-0.0077	-0.0129	-0.0153	*
Both	-0.0037	-0.0167	-0.0075	-0.0113	-0.0157	
Contrast F	6.78	4.15	0.02	0.09	3.28	2.71
df1, df2	1, 177	1, 177	1, 777	1, 177	1, 177	5, 173
P-value	0.0100	0.0433	0.8998	0.7605	0.072	0.0220

* Parameters are not estimated for the full MANOVA, however, the linear contrast for the full model can still be performed to test the null hypothesis

Both insects feeding together reduced the biomass of the bud and the leaves significantly more than would be expected from either insect feeding separately (Table 2, contrasts; Figs. 1a, b). However, the effect on stem and lateral shoot mass of both insects feeding together was not significantly different from the additive model (Table 2, Figs. 1c, d), while there was a marginally nonsignificant effect of both insects feeding together on the root biomass (Table 2, Fig. 1e). Overall, both insects feeding together caused a greater reduction in plant biomass than expected from the effects of either insect feeding alone (Table 2, MANOVA contrast). Thus, the null hypothesis of additive effects of herbivory by the beetles and spittlebugs is rejected.

As expected, the number of insects placed on the plants strongly predicted the numbers removed after 18 d of feeding ($F_1 = 2181$, $P < 0.0001$). The insects did not appear to compete with each other, as the slope of the relationship between the number put on and the number removed was not significantly different from 1 (95% CI = 0.94–1.02). Neither the treatment (beetles, spittlebugs or both) nor the number of insects initially placed on the plants significantly effected the percent of insects missing at the end of 18 d ($F_2 = 2.1$, $P = 0.13$), suggesting no significant differences in density dependent competition among the insects at these densities whether feeding separately or together.

DISCUSSION

The effects on the tall goldenrod of feeding by *Trirhabda* beetle larvae and *Philaenus* spittlebug nymphs were not additive overall. Damage by both herbivores decreased plant biomass more than damage by either insect feeding alone. The two different types of herbivory, leaf chewing and xylem tapping, cause more damage to the plant when occurring together than when occurring separately. Interactions between the types of damage could be mediated by a number of different physiological mechanisms. For example, the reduction in photosynthetic rates of goldenrods associated with spittlebug damage (Meyer and Whitlow, 1992) may be greater in the presence of leaf-chewing damage. It is interesting that an interactive effect was observed on the biomass of leaves on the main stem. The beetle larvae fed directly on those leaves, but the spittlebugs did not. This suggests that whole-plant physiology mediated the plant growth response, and that it was not limited to directly damaged tissues.

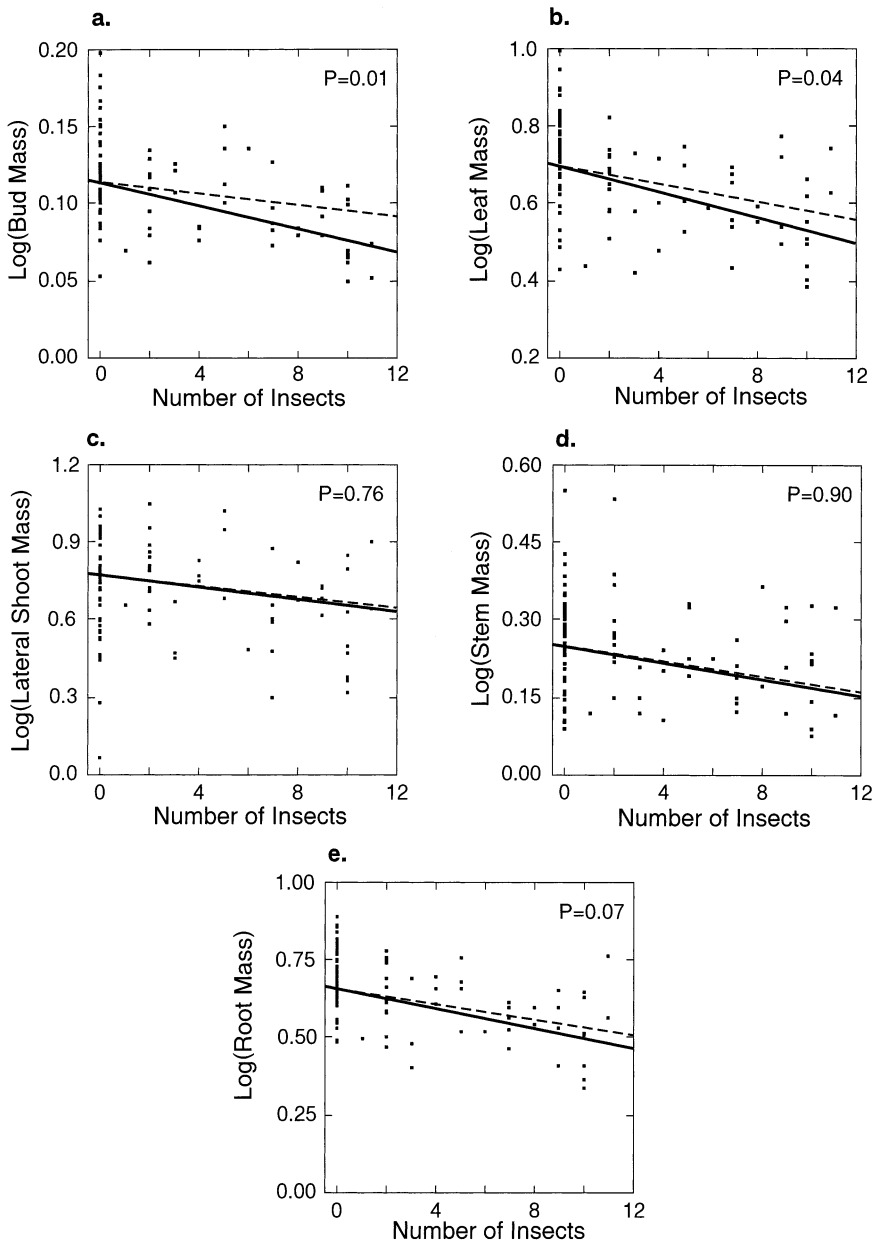


FIG. 1.—Relationship between the number of insects removed from experimental plants in the treatment with both beetles and spittlebugs feeding together and the logarithm of the mass of different components of the experimental plants. The slopes of the solid lines are the parameter estimates describing the relationship between insect number and plant mass from the statistical analysis and represent the negative effects of both insects feeding together. The dashed lines represent the null hypothesis of additive effects on plant biomass and are the average of the parameter estimates for beetles and spittlebugs feeding separately. P-values refer to contrasts testing for differences between the solid and dashed lines from Table 2

The main implication of the nonadditive effects of damage by *Trirhabda* and *Philaenus* is that selection for increased plant resistance may be greater when they are both present than when only one or the other is present. Thus, coevolutionary interactions between goldenrods and these herbivores are diffuse rather than pairwise. The specific nature of this diffuse interaction increases selection for plant resistance rather than decreasing it.

These results should be interpreted with caution for several reasons. First, although the null hypothesis of additivity was rejected by the MANOVA, the univariate analyses showed that the biomass of different components of the plant did not all respond similarly: the effect on the mass of the stem and lateral shoots of both insects feeding together was not significantly different than additive. Second, we did not measure plant fitness directly. However, our measure of bud mass is likely to be correlated with maternal and paternal components of fitness (ovaries and pollen), and root mass is likely to be correlated with clonal reproduction by rhizomes (Gross *et al.*, 1983; Abrahamson and McCrea, 1986). Third, we measured plant performance shortly after the herbivores fed, and do not know to what degree the plants may have been able to compensate for the damage over time (*e.g.*, Sacchi and Connor, 1999). However, in a similar experiment, Meyer and Root (1993) found that three weeks of early season feeding damage by *Trirhabda* beetles and *Philaenus* spittlebugs (feeding separately) delayed flowering and reduced total seed production of the tall goldenrod at the end of the season. Thus, the tall goldenrod may not be able to completely compensate for early season herbivory such as that imposed here.

Our data add to the growing number of studies that test explicitly whether the effects on plant performance of one herbivore depend upon the presence of others. As more studies documenting such nonadditive effects of herbivores on plants accumulate, eventually it may be possible to make inferences about whether interactions among herbivores tend to decrease (*e.g.*, Karban and Strauss, 1993; Pilson, 1996; Juenger and Bergelson, 1998) or increase (*e.g.*, Strauss, 1991; Wise and Sacchi, 1996; this study) the effects of herbivory on plant performance, and whether there are classes of herbivores or plants that are associated with either decreased or increased effects on plant fitness.

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LITERATURE CITED

- ABRAHAMSON, W. G. AND K. D. MCCREA. 1986. Nutrient and biomass allocation in *Solidago altissima*: effects of two stem gallmakers, fertilization, and ramet isolation. *Oecologia*, **68**:174–180.
- AGRAWAL, A. A. 1999. Induced responses to herbivory in wild radish: effects on several herbivores and plant fitness. *Ecology*, **80**:1713–1723.
- . 2000. Specificity of induced resistance in wild radish: causes and consequences for two specialist and two generalist caterpillars. *Oikos*, **89**:493–500.
- CARSON, W. P. AND R. B. ROOT. 1999. Top-down effects of insect herbivores during early succession: influence on biomass and plant dominance. *Oecologia*, **121**:260–272.
- DENNO, R. F., M. S. MCCLURE AND J. R. OTT. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Ann. Rev. Entomol.*, **40**:297–331.
- EMERMAN, S. H. AND T. E. DAWSON. 1996. The role of macropores in the cultivation of bell pepper in salinized soil. *Plant and Soil*, **181**:241–249.

- ERHLICH, P. R. AND P. H. RAVEN. 1964. Butterflies and plants: a study in coevolution. *Evolution*, **18**:586–608.
- FAETH, S. H. 1986. Indirect interactions between temporally separated herbivores mediated by the host plant. *Ecology*, **67**:479–494.
- FOX, L. R. 1981. Defense and dynamics in plant-herbivore systems. *Am. Zool.*, **21**:853–864.
- FUTUYMA, D. J. AND M. SLATKIN. 1983. Coevolution. Sinauer, Sunderland, Massachusetts, USA. 555 p.
- GANGE, A. C. AND V. K. BROWN. 1989. Effects of root herbivory by an insect on a foliar-feeding species, mediated through changes in the host plant. *Oecologia*, **81**:38–42.
- GEBER, M. A. AND T. E. DAWSON. 1997. Genetic variation in stomatal and biochemical limitations to photosynthesis in the annual plant *Polygonum arenastrum*. *Oecologia*, **109**:535–546.
- GROSS, K. L., T. BERNER, E. MARSCHALL AND C. TOMOMCKO. 1983. Patterns of resource allocation among five herbaceous perennials. *Bul. Torrey Bot. Club*, **110**:345–352.
- HARRISON, S. AND R. KARBAN. 1986. Effects of an early-season folivorous moth on the success of a later-season species, mediated by a change in the quality of the shared host, *Lupinus arboreus* Sims. *Oecologia*, **69**:354–359.
- HOUGEN-EITZMAN, D. AND M. D. RAUSHER. 1994. Interactions between herbivorous insects and plant-insect coevolution. *Am. Nat.*, **143**:677–697.
- IWAO, K. AND M. D. RAUSHER. 1997. Evolution of plant resistance to multiple herbivores: quantifying diffuse coevolution. *Am. Nat.*, **149**:316–335.
- JANZEN, D. H. 1980. When is it coevolution? *Evolution*, **34**:611–612.
- JUENGER, T. AND J. BERGELSON. 1998. Pairwise versus diffuse natural selection and the multiple herbivores of scarlet gilia, *Ipomopsis aggregata*. *Evolution*, **52**:1583–1592.
- KARBAN, R. AND S. Y. STRAUSS. 1993. Effects of herbivores on growth and reproduction of their perennial host, *Erigeron glaucus*. *Ecology*, **74**:39–46.
- MADDOX, G. D. AND R. B. ROOT. 1987. Resistance to 16 diverse species of herbivorous insects within a population of goldenrod, *Solidago altissima*: genetic variation and heritability. *Oecologia*, **72**:8–14.
- AND ———. 1990. Structure of the encounter between goldenrod (*Solidago altissima*) and its diverse insect fauna. *Ecology*, **71**:2115–2124.
- MARON, J. L. 1998. Insect herbivory above- and belowground: individual and joint effects on plant fitness. *Ecology*, **79**:1281–1293.
- MASTERS, G. J., V. K. BROWN AND A. C. GANGE. 1993. Plant-mediated interactions between above- and below-ground insect herbivores. *Oikos*, **66**:148–151.
- MELVILLE, M. R. AND J. K. MORTON. 1982. A biosystematic study of the *Solidago canadensis* (Compositae) complex. I. The Ontario populations. *Canad. J. Bot.*, **60**:976–997.
- MESSINA, F. J. 1981. Plant protection as a consequence of an ant-membracid mutualism: interactions on goldenrod (*Solidago* sp.). *Ecology*, **62**:1433–1440.
- AND R. B. ROOT. 1980. Association between leaf beetles and meadow goldenrods (*Solidago* spp.) in central New York. *Ann. Entomol. Soc. Am.*, **73**:641–646.
- MEYER, G. A. 1993. A comparison of the impacts of leaf- and sap-feeding insects on growth and allocation of goldenrod. *Ecology*, **74**:1101–1116.
- AND R. B. ROOT. 1993. Effects of herbivorous insects and soil fertility on reproduction of goldenrod. *Ecology*, **74**:1117–1128.
- AND T. H. WHITLOW. 1992. Effects of leaf and sap feeding insects on photosynthetic rates of goldenrod. *Oecologia*, **92**:480–489.
- MORAN, N. A. AND T. G. WHITHAM. 1990. Interspecific competition between root-feeding and leaf-galling aphids mediated by host-plant resistance. *Ecology*, **71**:1050–1058.
- PILSON, D. 1992. Aphid distribution and the evolution of goldenrod resistance. *Evolution*, **46**:1358–1372.
- . 1996. Two herbivores and constraints on selection for resistance in *Brassica rapa*. *Evolution*, **50**:1492–1500.
- RAUSHER, M. D. 1996. Genetic analysis of coevolution between plants and their natural enemies. *Trends in Genetics*, **12**:212–217.

- ROCHE, B. M. AND R. S. FRITZ. 1997. Genetics of resistance of *Salix sericea* to a diverse community of herbivores. *Evolution*, **51**:1490–1498.
- ROOT, R. B. 1996. Herbivore pressure on goldenrods (*Solidago altissima*): its variation and cumulative effects. *Ecology*, **77**:1074–1087.
- AND N. CAPPUCCINO. 1992. Patterns in population change and the organization of the insect community associated with goldenrod. *Ecol. Monogr.*, **62**:393–420.
- SACCHI, C. F. AND E. F. CONNOR. 1999. Changes in reproduction and architecture in flowering dogwood, *Cornus florida*, after attack by the dogwood club gall, *Resseliella clavula*. *Oikos*, **86**:138–146.
- SAS INSTITUTE, INC. 1997. JMP Version 3.2. SAS Institute, Inc. Cary, NC.
- SIMMS, E. L. AND M. D. RAUSHER. 1989. The evolution of resistance to herbivory in *Ipomoea purpurea* 2. Natural selection by insects and costs of resistance. *Evolution*, **43**:573–585.
- AND ———. 1993. Patterns of selection on phytophage resistance in *Ipomoea purpurea*. *Evolution*, **47**:970–976.
- STRAUSS, S. Y. 1991. Direct, indirect, and cumulative effects of three native herbivores on a shared host plant. *Ecology*, **72**:543–558.
- THOMPSON, J. N. 1994. *The Coevolutionary Process*. University of Chicago Press, Chicago.
- . 1998. Coping with multiple enemies: 10 years of attack on *Lomatium dissectum* plants. *Ecology*, **79**:2550–2554.
- . 1999. The raw material for coevolution. *Oikos*, **84**:5–16.
- VAN BAVEL, C. H. M., R. LASCANO AND D. R. WILSON. 1978. Water relations of fritted clay. *Soil Sci. Soc. Am. J.*, **42**:657–659.
- WERNER, P. A., I. K. BRADBURY AND R. S. GROSS. 1980. The biology of Canadian weeds. 45. *Solidago canadensis* L. *Canad. J. Plant Sci.*, **60**:1393–1409.
- WISE, M. J. AND C. F. SACCHI. 1996. Impact of two specialist insect herbivores on reproduction of horse nettle, *Solanum carolinense*. *Oecologia*, **108**:328–337.