E-Article

A Meta-Analysis of Genetic Correlations between Plant Resistances to Multiple Enemies

Roosa Leimu[1,*] and Julia Koricheva[2,†]

1. Section of Ecology, Department of Biology, University of Turku, FIN-20014 Turku, Finland;
2. School of Biological Sciences, Royal Holloway, University of London, Egham, Surrey TW20 0EX, United Kingdom

Submitted October 31, 2005; Accepted February 27, 2006; Electronically published June 20, 2006

abstract: Genetic correlations between plant resistances to multiple natural enemies are important because they have the potential to determine the mode of selection that natural enemies impose on a host plant, the structure of herbivore and pathogen communities, and the success of plant breeding for resistance to multiple diseases and pests. We conducted a meta-analysis of 29 published studies of 16 different plant species reporting a total of 467 genetic correlations between resistances to multiple herbivores or pathogens. In general, genetic associations between resistances to multiple natural enemies tended to be positive regardless of the breeding design, type of attacker, and type of host plant. Positive genetic correlations between resistances were stronger when both attackers were pathogens or generalist herbivores and when resistance to different enemies was tested independently, suggesting that generalists may be affected by the same plant resistance traits and that interactions among natural enemies are common. Although the mean associations between resistances were positive, indicating the prevalence of diffuse selection and generalized defenses against multiple enemies, the large variation in both the strength and the direction of the associations suggests a continuum between pairwise and diffuse selection.

Keywords: meta-analysis, plant resistance, multiple enemies, generalized defense, diffuse coevolution, community genetics.

Plants in natural populations are often attacked by multiple enemies, including various herbivores and pathogens, and usually display at least some degree of resistance to the majority of these enemies (e.g., Karban 1989; Marquis 1990, 1992). A fundamental question is whether plant resistances to different enemies are independent of each other or show positive or negative associations. A lack of genetic correlation between resistances indicates the absence of common genetic control for resistance to multiple enemies (Fritz 1992) and suggests that the selective effect of each enemy species on a plant is independent of the other enemy species. However, genetic correlations may also not be detected because of low statistical power or the selection of a trait irrelevant to plant defense (Strauss et al. 2005). If resistances to multiple natural enemies are not genetically correlated, selection is likely to be pairwise, leading to evolution of specific defensive mechanisms against individual enemy species (Hougen-Eitzman and Rausher 1994; Iwao and Rausher 1997; Strauss et al. 2005). Alternatively, significant negative or positive correlations between resistances are indicative of diffuse (multispecies) selection (Gould 1988; Strauss et al. 2005). A positive genetic correlation between resistances may occur if the same genes confer resistance to different enemies (positive pleiotropy) and thus the same resistance trait affects different enemies and acts as a generalized defense (Krischik et al. 1991). In this case, several natural enemies may collectively exert selection for greater resistance, even though each of the natural enemies alone may be too rare to cause significant selection (Futuyma 2000). The presence of positive correlations between resistances to different enemies facilitates plant breeding for multiple resistances to pests and pathogens because selection for increased resistance to one enemy will result in enhanced cross-resistance to another enemy species. Finally, negative genetic correlations suggest a trade-off between resistances to different enemies and are regarded as one type of ecological cost of resistance (Strauss et al. 2002). These correlations may arise as a result of negative pleiotropy or linkage disequilibrium between resistance loci (Falconer 1981) and indicate that natural enemies have opposite responses to (and thus exert conflicting selection on) the same defensive trait. As a result, negative genetic correlations maintain variation in the level of resistance and are likely to con-

* Corresponding author. Present address: Institute for Biochemistry and Biology, University of Potsdam, Maulbeerallee 1, D-14469 Potsdam, Germany; e-mail: roosa.leimu@utu.fi.

† E-mail: julia.koricheva@rhul.ac.uk.

Am. Nat. 2006. Vol. 168, pp. E15–E37.

strain evolution of plant phenotypes with optimal levels of resistance to different enemies.

Overall, genetic associations between plant resistances to multiple attackers have the potential to determine the mode of selection that natural enemies impose on a host plant (Rausher 1992, 1996), the structure of herbivore and pathogen communities, by affecting patterns of species co-occurrence on host plants (Fritz 1992), and the success of plant breeding for multiple disease and pest resistances (Mitchell-Olds et al. 1995). Uncovering the prevailing patterns of association between plant resistances to different enemies is therefore of great interest to ecologists, evolutionary biologists, plant breeders, and geneticists and is of considerable scientific and practical importance.

The existing studies examining genetic correlations between resistances to different herbivores and/or pathogens have found significantly positive relationships (e.g., Mitchell-Olds et al. 1995), significantly negative relationships (e.g., Juenger and Bergelson 1998; Stinchcombe and Rausher 2001), or no genetic correlations at all (e.g., Tiffin and Rausher 1999). The observed variation in the strength and direction of associations between plant resistances to multiple enemies could be caused by a number of factors. For instance, the degree of taxonomic and ecological relatedness between the natural enemies and the degree of their feeding specialization have been predicted to affect such genetic correlations (Maddox and Root 1990). While some plant secondary metabolites have been shown to affect both herbivores and pathogens (Krischik et al. 1991; Biere et al. 2004), herbivores and pathogens are assumed to induce different defensive responses in host plants (Felton and Korth 2000; Paul et al. 2000), and thus, positive genetic correlations may be less likely between plant resistances to herbivores and pathogens than between resistances to two herbivore or two pathogen species. Likewise, two herbivore species that utilize a host plant in a similar manner are more likely to be affected by the same plant characteristics and to impose similar selection pressures on the evolution of resistance mechanisms. Therefore, one might expect to find stronger positive correlations between plant resistances to herbivores belonging to the same feeding guild than between resistances to herbivores from different feeding guilds (Linhart 1991; Fritz 1992).

Plant resistance mechanisms to generalist and specialist herbivores are likely to be more different than those to two generalist herbivores, and thus one might expect to find weaker genetic correlations between plant resistances to generalist and specialist herbivores, as compared to resistances to two generalist species. Moreover, if plant resistance evolves in response to selection by generalist enemies while some herbivores adapt to this resistance factor, become specialized, and respond positively to it, resistances to specialist and generalist enemies should be negatively correlated (Beck and Schoonhoven 1980; Fritz 1992).

The evolutionary responses of plants to natural enemies may also vary depending on the life span and the apparency (Feeny 1976) of the host plants. Annual plants have short generation times that are comparable to the generation times of herbivores, and therefore they may be able to respond faster to selection from natural enemies than perennial plants. In addition, small and short-lived plants have been shown to host fewer herbivore and pathogen species than large and long-lived plants, and likewise, herbs appear to support fewer enemy species than trees (Linhart 1991). As a result, perennial and more apparent plants like trees and shrubs might be more likely to evolve generalized quantitative defenses that are not readily prone to counteradaptation and thus are effective against multiple enemies (Feeny 1976). In contrast, annual and less apparent plants, such as herbs, produce qualitative defenses that are effective against nonadapted enemies and might be more likely to evolve in a pairwise manner with the attacking enemies (Feeny 1976). We might thus expect positive genetic correlations between resistances of perennial apparent plants to different enemies and weaker or negative correlations between annual herb resistances to multiple enemies.

Genetic correlations between resistances may be confounded by ecological interactions between natural enemies. For instance, natural enemies may avoid attacking plants already colonized by other enemies and will thus be restricted to different plant genotypes (Maddox and Root 1990). Moreover, induced responses caused by one natural enemy can modify interactions between other enemies and the host plant and may influence the selective effect of the plant on other enemies (e.g., Agrawal 2000). As a result, the sign and the magnitude of detected genetic correlations between resistances may vary depending on whether resistances to different natural enemies are tested independently or different natural enemies are allowed to attack the plants simultaneously.

Previous reviews of studies examining genetic correlations between plant resistances to multiple enemies (Fritz 1992; Rausher 1992, 1996) have concluded that correlations are usually nonsignificant or positive and only rarely negative, suggesting potential for either pairwise selection or multiple resistance strategies. However, because of their qualitative or narrative nature, the above-cited reviews were unable to assess the average magnitude of the observed correlations, to distinguish between cases where nonsignificant correlations represented a true absence of genetic correlations or simply the low statistical power of the studies (Rausher 1992), or to reveal the sources of variation in the magnitude and direction of genetic correlations.

Here we review the results of published studies examining genetic correlations between plant resistances to multiple herbivores or pathogens by means of meta-analysis. Meta-analysis is a statistical method that enables us to combine the results from independent studies addressing the same research question, in order to estimate the mean effect size and to identify the factors that influence the magnitude and direction of the effect (Gurevitch and Hedges 2001). Meta-analysis assesses the magnitude rather than the statistical significance of the effect and weights the magnitude of the effect size by study variance. Meta-analysis is therefore especially useful in situations where the magnitude of the effect is relatively weak and many individual studies fail to detect a significant effect because of a low number of replicates, as is the case in the studies of genetic correlations between plant resistances to multiple enemies. In our analysis we address the following questions: Are resistances to different natural enemies genetically correlated? Does the sign or strength of these correlations depend on characteristics of natural enemies (herbivore vs. pathogen, feeding guilds and feeding specialization of herbivores), host plant characteristics (longevity and life form), or methodology (plant breeding design, whether resistances for different enemies are assessed independently of other enemies or whether the enemies are allowed to attack/infect the plants simultaneously, and whether resistance is measured as 1 − damage or 1 − herbivore abundance)?

Methods

We conducted keyword searches in the Web of Science (ISI) electronic bibliographic database to find studies that had examined genetic correlations between resistances to different herbivore or pathogen species. We used different combinations of the keywords "diffuse selection," "diffuse coevolution," "pairwise coevolution," "multiple herbivor*," "resistance," and "genetic correlation." In addition, previous reviews on the topic (Fritz 1992; Rausher 1996) were used to find additional studies. The final data set consisted of 467 genetic correlations from 29 studies published during 1975–2005 (appendix). Genetic correlations between resistances to different herbivore species were examined in 24 of the studies, with a total of 449 genetic correlations (appendix). Two studies with 13 correlations examined genetic correlations between resistances to different pathogen species, and three studies with six genetic correlations examined resistance to a herbivore and a pathogen. The studies were conducted on 16 plant species. Following Rausher (1992), we have restricted our analysis to wild plant species because in agricultural studies, the data are often obtained by crossing lines of unknown geographically distant origins, and hence the reported correlations reflect between-population differences. Furthermore, in these studies, the reported correlations are likely to reflect chance associations of resistance genes affecting different enemies instead of pleiotropic effects of the same set of genes (Rausher 1983).

Estimates of genetic correlations may be biased because of dominance or maternal effects, particularly if these correlations are based on clone or maternal family means (Falconer 1981; Simms and Rausher 1992). Hence, we tested whether the magnitude and direction of the correlations between resistances to multiple enemies differed depending on whether clones, full-sib families, or half-sib families were used.

We used the Pearson product-moment correlation coefficient *r* as a measure of effect size in our analysis, since most studies reported the association between resistances to pairs of natural enemies as correlation coefficients. If correlation coefficients were not reported in a study, we calculated them from the values given in tables or figures. When data were presented in figures, the plots were enlarged and digitized manually. If regression analysis was used to assess the relationship between resistances to different herbivores or pathogens, we took the square root of the coefficient of determination (R^2).

In most studies, several different herbivore or pathogen species were examined, and genetic correlations between resistances to all possible combinations of two species were presented, resulting in an average of 17 genetic correlations per study. Inclusion of multiple correlations reported within a single study, which represent statistically nonindependent observations, may violate the assumptions of independence of statistical tests, but averaging or selecting single correlations within a study would result in a dramatic loss of information. As a compromise approach, whenever possible, we conducted analyses at both study and individual correlation levels and compared the results. In addition, we assessed the relationship between the magnitude of the reported correlation and the number of natural enemies examined per study.

The meta-analysis was carried out by using the Meta Win 2.0 statistical program (Rosenberg et al. 2000). Individual correlation coefficients were *z*-transformed and weighted by their sample size. The transformed coefficients were combined across studies using the mixed-effects model, which assumes that differences among studies within a class are due to both sampling error and random variation. In ecological data synthesis, the assumptions of mixed models are more likely to be met than those of fixed-effects models, and the former are thus preferred (Gurevitch and Hedges 2001). We used bias-corrected 95% bootstrap confidence intervals generated from 4,999 iterations (Adams et al. 1997) to define the significance of the relationship between resistances to different natural enemies. A relationship was considered significant if the

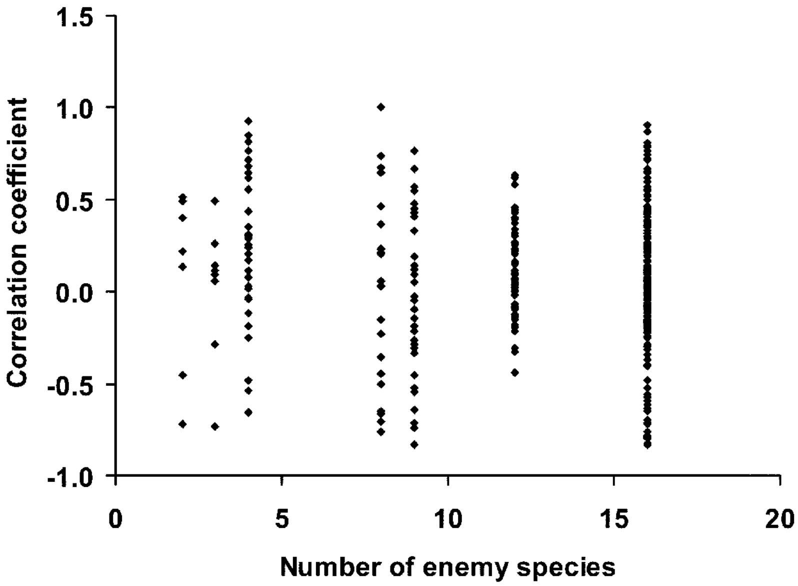

Figure 1: Individual genetic correlations between plant resistances to pairs of natural enemies in relation to the number of natural enemy species examined per study.

confidence interval did not include 0. At the end of the analysis, the mean *z* values and their 95% confidence intervals were back-transformed to the Pearson correlation coefficients for ease of interpretation.

To test the importance of different sources of variation in determining the sign and magnitude of the correlation between multiple resistances, we subdivided studies in terms of various study characteristics and examined between-group heterogeneity, using a χ^2 test statistic, Q_b. The following sources of variation were examined: type of enemy (herbivore or pathogen), host specialization of the enemy (specialist or generalist), feeding guild of the herbivores (correlations between and within guilds), plant longevity (annual or perennial), plant growth form (herb, shrub, or tree), breeding design (half-sib, full-sib, clones), and the measure of resistance used (1 − damage or 1 − abundance). We defined specialists as those herbivores or pathogens that feed on or infest only one plant species or genus. The feeding guilds of the herbivores included in the analysis were chewers, miners, browsers, suckers, gallers, and folders. In 23 of the studies, herbivores and pathogens were allowed to attack the plants simultaneously in a common garden or an experimental field, while in six studies, resistances to different enemies were examined independently. We therefore also tested differences between the two types of experiments.

We used a funnel-plot (Light and Pillemer 1984; Palmer 1999) approach to examine the range and distribution of the correlations presented in individual studies. We also plotted the number of variables in a study (i.e., the number of herbivore and/or pathogen species) against the individual correlation coefficients in order to examine whether the number of variables in a study (i.e., the number of herbivore and/or pathogen species) influences the magnitude of the correlation.

Results

Range of Individual Genetic Correlations and Overall Mean Correlations

Individual genetic correlations between resistances to pairs of natural enemies varied in strength and direction both between and within studies and ranged from −0.833 to +1 (fig. 1; appendix). However, examination of frequency distributions of effect sizes revealed that the majority of correlations were positive and that for each group examined there was a single peak in frequency distribution of correlations that roughly corresponded to the mean correlation for the group (fig. 2). Therefore, we concluded that despite variation in strength and direction of individual correlations, means reflected the magnitude and the direction of the majority of correlations within the group. The overall genetic correlations between resistances to pairs of natural enemies, correlations between resistances to pairs of different herbivores, and resistances to various pathogens were significantly positive both at the level of study and at the level of individual correlations (table 1).

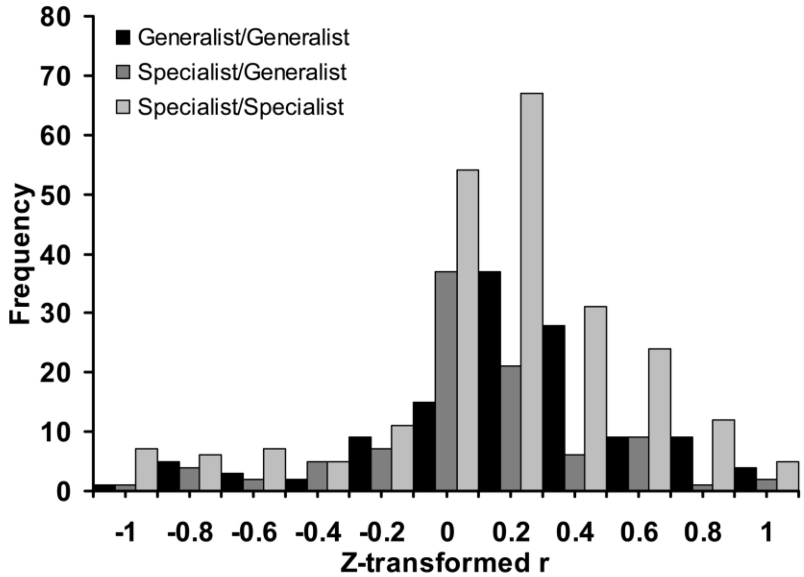

Figure 2: Frequency distribution of effect sizes (*z*-transformed *r*) of the associations between resistances to specialist and/or generalist natural enemies.

For pairs of herbivores, the correlations were significant at the level of individual correlations but not at the level of study (table 1).

Characteristics of Natural Enemies

We found marginally significant differences between the pairwise combinations of the different types of natural enemies (herbivore-herbivore, pathogen-pathogen, herbivore-pathogen; $Q_b = 8.426$, $df = 2$, $P = .0714$). The positive correlations tended to be stronger between pathogens, although these correlations were based on only a few studies.

We found significant differences among genetic correlations between resistances depending on the feeding specialization of the enemies, that is, whether the compared enemies were both generalists, both specialists, or one generalist and one specialist ($Q_b = 12.20$, $df = 2$, $P = .0034$). A positive genetic correlation between the resistances was found when both of the compared species were generalists (table 2) and when both of the compared species were specialists (table 2), although in the latter case the relationship was very weak. No significant genetic correlation was found between resistances to a generalist and a specialist (table 2). Similar results were found when only herbivores were included in the analysis (results not shown).

Significant positive genetic correlations were found between resistances to herbivores both within and between feeding guilds (table 2), and the difference between these two classes was not significant ($Q_b = 0.1685$, $df = 1$, $P = .7082$). However, feeding guild of herbivores affected the magnitude and sign of correlations within guilds ($Q_b = 12.823$, $df = 5$, $P = .0540$) and between guilds ($Q_b = 35.22$, $df = 10$, $P = .0002$). Within guilds, significant positive correlations were found between resistances to pairs of herbivores belonging to miners, browsers, and leaf folders (table 2). Between guilds, a significant negative genetic correlation was found between resistances to miners and browsers and to browsers and suckers (table 2), whereas positive genetic correlations were found between resistances to miners and gallers, to miners and folders, and to gallers and folders (table 2).

Plant Characteristics

A positive genetic correlation between resistances to different natural enemies was found for perennial plants, whereas no significant genetic correlation was found for annual plants (table 3). The difference between these two plant types was, however, nonsignificant ($Q_b = 0.1789$, $df = 1$, $P = .7140$). A significant positive correlation between resistances was found in herbs but not in shrubs or trees (table 3), but the difference between the groups was nonsignificant ($Q_b = 0.5031$, $df = 2$, $P = .8004$).

Table 1: Mean genetic correlations (r_+) between resistances to natural enemies

Category of studies/level of analysis	N	r_+	Bias-corrected bootstrap 95% CI
Overall mean across studies	29	**.1470**	.0143 to .2630
Overall mean of individual correlations	467	**.0920**	.0589 to .1255
Between herbivores:			
Study level	24	.1442	−.0013 to .2672
Individual correlations	448	**.0760**	.0425 to .1063
Between pathogens:			
Study level	2	**.8926**	.1577 to 1.2070
Individual correlations	13	**.7305**	.3225 to .9988
Between pathogen and herbivore:			
Study level	4	**.2698**	.0412 to .5111
Individual correlations	6	**.1967**	.0899 to .3865

Note: CI = confidence interval. Correlations that differ significantly from 0 are shown in boldface.

Methodological Issues

The magnitude of correlations between resistances to multiple enemies was not significantly different among studies using clone, half-sib, or full-sib design ($Q_b = 2.2599$, df = 2, $P = .4090$), although only the first two types of correlations were significantly different from 0 (table 4). We found marginally significant differences in the relationships between resistances to different enemies depending on whether resistances were measured independently or after the enemies were allowed to attack the plants simultaneously ($Q_b = 4.358$, df = 1, $P = .0712$). A significant positive correlation was found between resistances to different enemies when these were measured independently ($r_+ = 0.3811$, bias-corrected bootstrap 95% confidence interval [CI] = 0.2400–0.5196, $N = 6$), whereas no significant relationship between resistances was found when the enemies were allowed to attack the plants simultaneously ($r_+ = 0.0950$, bias-corrected bootstrap 95% CI = −0.0406 to 0.2252, $N = 23$). Furthermore, a marginally significant difference in the relationship between resistances to two herbivores was found, depending on whether resistance was measured as 1 − damage or as 1 − herbivore abundance ($Q_b = 3.318$, df = 1, $P = .07$). The relationship was positive and significant only when resistance was measured as 1 − damage ($r = 0.124$, $N = 234$, 95% CI = 0.0646–0.1755). Funnel plots revealed no relationship between effect size and sample size ($r = -0.044$, $P = .3424$, $N = 468$), but the magnitude of individual correlations correlated weakly negatively with the number of enemy species in individual studies ($r = -0.1007$, $P = .030$, $N = 465$; fig. 1).

Discussion

The large variation observed in the strength and direction of the genetic associations between resistances suggests that rather than being strictly pairwise or diffuse, selection imposed by a community of natural enemies is likely to form a continuum from purely pairwise to purely diffuse selection, with most cases falling between these two extremes. However, although individual genetic correlations reported between pairs of natural enemies varied from strongly negative to strongly positive, the majority of individual correlations, as well as the mean correlations calculated at either study or correlation level, were positive (table 1). The sources of variation examined (type and feeding specializations of attackers, longevity and life form of the host plant, type of breeding design) affected the magnitude and statistical significance of these correlations but not their sign (tables 1, 3, 4). The prevalence of positive associations between resistances indicates that generalized defenses against multiple enemies are common and that diffuse selection is likely to be more common than pairwise selection. The observed positive genetic mean correlations were, on the other hand, often relatively weak, suggesting potential for pairwise selection between some natural enemies and/or under some conditions.

Only a few significant negative mean correlations were detected (between resistances to miners and browsers and to browsers and suckers), and all of these correlations were based on very low sample sizes ($N = 4$). Although strong negative individual correlations have been reported (figs. 1, 2), they were clearly less frequent than positive correlations (fig. 2). The relative rarity of negative genetic correlations between plant resistances to different enemies suggests that evolving resistance against one type of enemy is not likely to constrain the evolution of resistance to another enemy attacking the same host plant. If the same pattern holds for crops as well, this would facilitate plant breeding for multiple resistances to pests and pathogens. In general, the results of our analysis, together with those of the previously conducted meta-analyses on trade-offs between plant defense and fitness (Koricheva 2002), be-

Table 2: Effects of feeding specialization and herbivore feeding guild on the mean genetic correlations (r_+) between resistances to natural enemies

Category of studies	N	r_+	Bias-corrected bootstrap 95% CI
Generalist vs. generalist	129	**.157**	.0812 to .2335
Specialist vs. specialist	101	**.063**	.0227 to .1007
Generalist vs. specialist	96	.015	−.0308 to .0872
Between herbivores from the same feeding guild	93	**.0784**	.0159 to .1417
Chewers	24	.0669	−.0163 to .1475
Miners	6	**.1858**	.1092 to .2925
Browsers	3	**.6737**	.5586 to 1.0007
Suckers	16	−.0095	−.2157 to .1452
Gallers	40	.0610	−.0811 to .1632
Folders	4	**.4400**	.1924 to .7761
Between herbivores from different feeding guilds	213	**.0517**	.0153 to .0846
Chewer and miner	23	.1005	−.0093 to .1904
Chewer and browser	15	.1631	−.2196 to .4425
Chewer and sucker	33	.0087	−.0541 to .0837
Chewer and galler	19	−.0329	−.0753 to .0148
Miner and browser	4	**−.9140**	−1.0726 to −.6852
Miner and sucker	23	.0321	−.0958 to .1166
Miner and galler	26	**.0833**	.0234 to .1435
Miner and folder	8	**.3283**	.1864 to .5005
Browser and sucker	4	**−.3939**	−.7388 to −.0490
Sucker and galler	28	.0248	−.0178 to .0677
Galler and folder	30	**.1290**	.0149 to .2482

Note: CI = confidence interval. Correlations that differ significantly from 0 are shown in boldface.

tween plant antiherbivore defenses (Koricheva et al. 2004), and between plant tolerance and resistance (Leimu and Koricheva 2006), suggest that negative genetic correlations between different types of plant defenses against various attackers occur under a much more restrictive set of conditions than has been previously assumed.

Characteristics of Natural Enemies

While we have found a considerable number of studies examining genetic correlations between plant resistances to various herbivores, only a couple of studies so far have estimated genetic correlations between wild plant resistances to various pathogens (Hill and Leath 1975; Mitchell-Olds et al. 1995) or between resistances to pathogens and herbivores (Simms and Rausher 1993; Biere et al. 2004; Valkama et al. 2005). This is surprising, given the intensity of current research on the crosstalk and trade-offs between signal-response pathways inducing plant resistance to herbivores and pathogens (e.g., Felton et al. 1999; Thaler et al. 1999; Paul et al. 2000). Our analysis suggests that resistances to pathogens are more strongly correlated than resistances to herbivores. This is a potentially very interesting pattern, but more studies are required in order to adequately understand it. We also found significant positive correlations between plant resistances to herbivores and pathogens. This indicates the absence of genetic trade-offs between plant resistances to herbivores and/or pathogens. These results contradict those of studies on the crosstalk and trade-offs between signal-response pathways inducing plant resistance to herbivores and pathogens (e.g., Felton et al. 1999; Thaler et al. 1999), but they support the idea of considerable overlap in plant responses to herbivores and pathogens at the whole-organism level in plants (Paul et al. 2000). Our conclusions regarding the sign and the significance of genetic correlations between plant resistances to herbivores and pathogens should be considered only as tentative until more empirical studies in this field become available.

Generalist herbivores are usually negatively affected by host plant defenses, whereas specialists, because of the long coevolutionary history with their host plants (Ehrlich and Raven 1964; Rausher 1996), may be able to tolerate or detoxify plant defensive compounds (Rhoades 1979; Berenbaum and Zangerl 1998) and thus are usually unaffected by them or even prefer higher levels of certain chemicals (e.g., Bowers 1984; Bowers and Puttick 1988; Van Zandt and Agrawal 2004). Hence, specialist and generalist enemies can cause opposing selection pressures on plant defenses, which could result in a negative genetic correlation between resistances to specialists and generalists. In addition, host specialization has been suggested to increase

Table 3: Effects of plant growth form and longevity on the mean correlations (r_+) between resistances to natural enemies

Category of studies	N	r_+	Bias-corrected bootstrap 95% CI
Perennials	19	**.2253**	.0870 to .3556
Annuals	10	.1675	−.0978 to .4379
Herbs	18	**.2155**	.0232 to .3978
Shrubs	5	.0697	−.0324 to .3215
Trees	7	.2189	−.1465 to .4562

Note: CI = confidence interval. Correlations that differ significantly from 0 are shown in boldface.

the potential for pairwise coevolution (Fox 1988). Because specialists often interact in a pairwise manner with their hosts, selection by these enemies is also more likely to be pairwise than diffuse.

We found no significant genetic correlation between plant resistances to a generalist and a specialist enemy, which suggests that resistances to generalists and specialists might evolve independently or that generalists and specialists are not deterred by the same defenses. Our results, however, do not support the idea that resistances to generalist and specialist enemies should, in general, show negative genetic correlations (Beck and Schoonhoven 1980). On the other hand, we found significant positive genetic correlations between resistances to pairs of generalists, as well as to pairs of specialist natural enemies. This suggests that pairs of generalists and pairs of specialists may be influenced by the same plant defensive compounds or traits, and it supports the hypothesis of generalized defenses against multiple enemies.

It has been suggested that responses to herbivores of the same feeding guild are likely to correlate positively because the physiologies and reactions of such herbivores (e.g., against defenses) are likely to be similar and because resistances should affect herbivores of the same guild similarly (Linhart 1991; Fritz 1992). In contrast, negative correlations (trade-offs) are assumed to be common between resistances to very different types of feeders, such as mammalian and insect herbivores (e.g., Stinchcombe and Rausher 2001). In contrast to the first prediction, we found that mean genetic correlations between resistances were significantly positive, although weak, regardless of whether herbivores belonged to the same feeding guild. This suggests that generalized defenses may also evolve when a plant is attacked by multiple herbivores from different guilds. However, we also found that the sign and the magnitude of the correlations depended on the guilds of the compared herbivores. As predicted, resistances to very different types of feeders, such as browsers and miners or browsers and suckers, tended to be negatively correlated. Genetic correlations between resistances to members of different guilds could be used to predict patterns of natural-enemy community structure (Fritz 1992). For instance, our data (table 3) suggest that various species of miners, folders, and gallers are likely to co-occur on the same plant genotypes, while miners and suckers or miners and browsers are likely to prefer different plant genotypes. These patterns could be due either to differing responses of the above groups to the same resistance traits (Fritz 1992) or to induced changes in plant quality (Danell and Huss-Danell 1985; Johnson et al. 2002).

Plant Characteristics

The evolutionary responses of plants to natural enemies may be very different, depending on the life span of the plant species. We predicted stronger positive correlations between resistances to multiple natural enemies in perennial plants and in trees. In accordance with the first prediction, we found that resistances were positively correlated in perennial plants but not in annual plants. However, contrary to the second prediction, correlations between resistances to multiple enemies were significant only in herbs but not in trees or shrubs. The latter pattern could be due to the lower number of studies on woody plants. Thus, although perennial plants might be more likely to express generalized defenses to natural enemies than annual plants and diffuse selection for resistances may be common, further studies are required to understand the effects of life span and plant life form on evolutionary responses to natural enemies.

Methodological Issues

Correlations between plant resistances to different natural enemies may be due to true genetic associations between the genes encoding resistance traits and/or to ecological interactions between enemies (i.e., induced resistance or behavioral avoidance of plant genotypes colonized by other enemies). Our analysis hints that both mechanisms may affect the magnitude of genetic correlations between plant resistances to multiple enemies. Significant positive genetic correlations among resistances were found in studies where resistance to each enemy species was assessed

Table 4: Effects of genetic background (clone, full-sib family, or half-sib family) on the mean genetic correlations (r_+) between resistances to natural enemies

Category of studies	N	r_+	Bias-corrected bootstrap 95% CI
Clone	9	**.2240**	.0562 to .4379
Full-sib	10	.0733	−.2029 to .2614
Half-sib	10	**.2995**	.0664 to .5760

Note: CI = confidence interval. Correlations that differ significantly from 0 are shown in boldface.

independently, indicating true positive genetic correlations between resistances to different enemies. In contrast, in studies where resistances were assessed in the presence of other natural enemies, overall genetic correlation between resistances was not significant. This implies that interactions between different enemies in the field are predominantly negative, tend to reduce the magnitude of genetic correlations, and may alter response to selection. However, the difference between the two types of studies was only marginally significant, and effects of interactions between multiple enemies on plant fitness have not been measured in most of the studies. It would be useful to address these points experimentally in future studies by comparing single and multiple natural enemy species treatments (Strauss et al. 2005).

We found no significant effect of the breeding design (clones, full sibs, half sibs) on the magnitude of genetic correlations between resistances to natural enemies. This is reassuring because full-sib design and clonal analysis are prone to bias because of dominance and maternal effects, which may inflate the estimates of genetic correlations (Falconer 1981; Simms and Rausher 1992). The highest positive correlations were observed for studies using half sibs, which is the most reliable method for estimating genetic correlations. This indicates that the magnitude of the correlations is not overestimated in our study because of the differences in the genetic backgrounds of the plant material used.

Our analysis suggests that the outcome of studies that examined genetic correlations between resistances to multiple enemies may vary depending on the way resistance is measured. When resistance to both herbivores examined was measured as $1 - $ damage, a significant positive genetic correlation was found between the resistances, indicating that the herbivores in question are potentially influenced by the same defensive traits or compounds and that these herbivores are likely to cause diffuse selection. On the other hand, when resistance was measured as the inverse of herbivore abundance, the resistances were uncorrelated, indicating the potential for pairwise selection and suggesting that the compared herbivores are not influenced by the same defensive traits. The difference between the two categories of studies was, however, only marginally significant. Herbivore damage can be considered to be more indicative of plant defensive compounds or traits than herbivore abundance because damage levels are more likely to be directly influenced by these plant traits. Yet, measuring resistance as either $1 - $ damage or $1 - $ herbivore abundance does not allow us to determine whether the same defensive traits or compounds affect the compared herbivores (generalized defenses) or whether resistance is caused by different traits or compounds. Therefore, a more trait-oriented approach to assessing plant resistance to herbivores in coevolutionary studies should be advocated (Strauss et al. 2005).

Conclusions

Results of meta-analysis of genetic correlations between resistances to multiple enemies suggest that diffuse selection and generalized defenses against multiple enemies are likely to be common. However, since many of the observed correlations were relatively weak, especially those among herbivores, this does not exclude the possibility of pairwise selection between some pairs of plants and natural enemies. Moreover, the large variation observed in the strength and direction of associations between resistances to multiple enemies suggests that instead of a strict dichotomy between pairwise and diffuse selection, there is a continuum between the two selection types.

In addition, our results indicate that the presence of one enemy may influence plant resistance to other enemy species and that the evolution of plant resistances is also likely to affect the community patterns of natural enemies. Since most of the reviewed studies have been conducted in the field with naturally co-occurring herbivores, the magnitude of true genetic correlations between resistances to different natural enemies is likely to be underestimated. In addition, studies where genetic associations were estimated among many species of attackers tended to report somewhat weaker correlations than studies examining correlations among just a few herbivore or pathogen species. However, it could be argued that to assess the potential for natural selection by herbivores and pathogens on resistance traits in plants, the effects of herbivore and pathogen communities should be examined under natural conditions, including the natural interactions between species (Roche and Fritz 1997). Our results highlight the importance of considering the community of interacting species in order to understand how individual species and traits evolve. Moreover, although our review was limited to wild plant species, our results can have implications for plant breeding. General knowledge of the degree of linkage between plant resistances to multiple enemies and of factors that affect it is useful for planning plant breeding. If the prevalence of positive correlations between plant resistances to multiple enemies holds true for crops as well, crop breeding for multiple resistance against natural enemies could be facilitated.

Acknowledgments

We thank A. Agrawal and three anonymous reviewers for valuable comments on previous versions of the manuscript. The study was supported financially by the Academy of Finland.

APPENDIX

Table A1: Data on genetic correlations between plant resistances to multiple enemies

Plant species (longevity, life form), type of comparison[a]	Natural enemy 1	Natural enemy 2	Specialization[b] Enemy 1	Specialization[b] Enemy 2	Feeding guild[c] Enemy 1	Feeding guild[c] Enemy 2	Resistance measures[d] 1	Resistance measures[d] 2	Correlation coefficient	Sample size	Reference
Asclepias syriaca (P, H):											
H/H	*Tetraopes tetraophthalmus*	*Liriomyza asclepiadis*	S	S	Chewer	Miner	INVD	INVD	.360	26	Agrawal 2004
H/H	*Rhyssomatus lineaticollis*	*T. tetraophthalmus*	S	S	Chewer	Chewer	INVD	INVAB	.4620	23	Agrawal 2005
H/H	*R. lineaticollis*	*Lygaeus kalmii*	S	S	Chewer	Sucker	INVD	INVAB	.1770	23	Agrawal 2005
H/H	*R. lineaticollis*	*L. asclepiadis*	S	S	Chewer	Miner	INVD	INVAB	.2920	23	Agrawal 2005
H/H	*T. tetraophthalmus*	*L. kalmii*	S	S	Chewer	Sucker	INVAB	INVAB	.4810	23	Agrawal 2005
H/H	*T. tetraophthalmus*	*L. asclepiadis*	S	S	Chewer	Miner	INVAB	INVAB	.3570	23	Agrawal 2005
H/H	*L. kalmii*	*L. asclepiadis*	S	S	Miner	Sucker	INVAB	INVAB	.0540	23	Agrawal 2005
Betula pendula (P, T):											
H/H	*Epirrita autumnata*	*Lepus timidus*	G	G	Chewer	Browser	INVP		.110	15	Mutikainen et al. 2002
H/H	*E. autumnata*	*Microtus agrestis*	G	G	Chewer	Browser	INVP		.090	15	Mutikainen et al. 2002
H/H	*L. timidus*	*M. agrestis*	G	G	Browser	Browser			.495	15	Mutikainen et al. 2002
H/H	*M. agrestis*	Chewer	G	G	Browser	Chewer	INVP	INVP	.490	20	Pusenius et al. 2002
H/H	*L. timidus*	*M. agrestis*	G	G	Browser	Browser	INVD	INVD	.556	8	Rousi et al. 1997
H/H	*L. timidus*	*Polydrosus* sp.	G	S	Browser	Chewer	INVD	INVD	.811	8	Rousi et al. 1997
H/H	*L. timidus*	*Polydrosus* sp.	G	G	Browser	Chewer	INVD	INVD	.558	8	Rousi et al. 1997
H/H	*M. agrestis*	*Polydrosus* sp.	G	S	Browser	Chewer	INVD	INVD	.173	8	Rousi et al. 1997
H/H	*M. agrestis*	*Phyllobius* sp.	G	G	Browser	Chewer	INVD	INVD	.012	8	Rousi et al. 1997
H/H	*Polydrosus* sp.	*Phyllobius* sp.	S	G	Chewer	Chewer	INVD	INVD	.679	8	Rousi et al. 1997
H/H	*Phyllobius argentatus*	*Eriocrania* coll.	G	S	Chewer	Miner	INVD	INVAB	−.643	8	Tikkanen et al. 2003
H/H	*P. argentatus*	*Polydrosus mollis*	G	G	Chewer	Chewer	INVD	INVD	.548	8	Tikkanen et al. 2003
H/H	*P. argentatus*	*Operophtera brumata*	G	G	Chewer	Chewer	INVD	INVP	.429	8	Tikkanen et al. 2003
H/H	*P. argentatus*	*Microtus argentatus*	G	G	Chewer	Browser	INVD	INVD	.333	8	Tikkanen et al. 2003
H/H	*P. argentatus*	*Phytobia betulae*	G	S	Chewer	Miner	INVD	INVAB	−.286	8	Tikkanen et al. 2003
H/H	*P. argentatus*	*Symydobius oblongus*	G	S	Chewer	Sucker	INVD	INVAB	.667	8	Tikkanen et al. 2003
H/H	*P. argentatus*	*L. timidus*	G	G	Chewer	Browser	INVD	INVD	.571	8	Tikkanen et al. 2003
H/H	*P. argentatus*	*Euceraphis betulae*	G	S	Chewer	Sucker	INVD	INVAB	−.262	8	Tikkanen et al. 2003
H/H	*Eriocrania* coll.	*P. mollis*	S	G	Miner	Chewer	INVAB	INVD	−.333	8	Tikkanen et al. 2003
H/H	*Eriocrania* coll.	*O. brumata*	S	G	Miner	Chewer	INVAB	INVP	−.452	8	Tikkanen et al. 2003
H/H	*Eriocrania* coll.	*M. argentatus*	S	G	Miner	Browser	INVAB	INVD	−.714	8	Tikkanen et al. 2003
H/H	*Eriocrania* coll.	*P. betulae*	S	S	Miner	Miner	INVAB	INVAB	.429	8	Tikkanen et al. 2003
H/H	*Eriocrania* coll.	*S. oblongus*	S	S	Miner	Sucker	INVAB	INVAB	−.310	8	Tikkanen et al. 2003
H/H	*Eriocrania* coll.	*L. timidus*	S	G	Miner	Browser	INVAB	INVD	−.833	8	Tikkanen et al. 2003
H/H	*Eriocrania* coll.	*E. betulae*	S	S	Miner	Sucker	INVAB	INVAB	.476	8	Tikkanen et al. 2003
H/H	*P. mollis*	*O. brumata*	G	G	Chewer	Chewer	INVD	INVP	.452	8	Tikkanen et al. 2003
H/H	*P. mollis*	*M. argentatus*	G	G	Chewer	Browser	INVD	INVD	.143	8	Tikkanen et al. 2003
H/H	*P. mollis*	*P. betulae*	G	S	Chewer	Miner	INVD	INVAB	−.190	8	Tikkanen et al. 2003
H/H	*P. mollis*	*S. oblongus*	G	S	Chewer	Sucker	INVD	INVAB	.190	8	Tikkanen et al. 2003
H/H	*P. mollis*	*L. timidus*	G	G	Chewer	Browser	INVD	INVD	.095	8	Tikkanen et al. 2003

H/H	*P. mollis*	*E. betulae*	G	S	Chewer	Sucker	INVD	INVAB	−.143	8	Tikkanen et al. 2003
H/H	*O. brumata*	*M. argentatus*	G	G	Chewer	Browser	INVP	INVD	.571	8	Tikkanen et al. 2003
H/H	*O. brumata*	*P. betulae*	G	S	Chewer	Miner	INVP	INVAB	−.095	8	Tikkanen et al. 2003
H/H	*O. brumata*	*S. oblongus*	G	S	Chewer	Sucker	INVP	INVAB	−.310	8	Tikkanen et al. 2003
H/H	*O. brumata*	*L. timidus*	G	G	Chewer	Browser	INVP	INVD	.405	8	Tikkanen et al. 2003
H/H	*O. brumata*	*E. betulae*	G	S	Chewer	Sucker	INVP	INVAB	−.024	8	Tikkanen et al. 2003
H/H	*M. argentatus*	*P. betulae*	G	S	Browser	Miner	INVD	INVAB	−.548	8	Tikkanen et al. 2003
H/H	*M. argentatus*	*S. oblongus*	G	S	Browser	Sucker	INVD	INVAB	−.214	8	Tikkanen et al. 2003
H/H	*M. argentatus*	*L. timidus*	G	G	Browser	Browser	INVD	INVD	.762	8	Tikkanen et al. 2003
H/H	*M. argentatus*	*E. betulae*	G	S	Browser	Sucker	INVD	INVAB	−.714	8	Tikkanen et al. 2003
H/H	*P. betulae*	*S. oblongus*	S	S	Miner	Sucker	INVAB	INVAB	.048	8	Tikkanen et al. 2003
H/H	*P. betulae*	*L. timidus*	S	G	Miner	Browser	INVAB	INVD	−.738	8	Tikkanen et al. 2003
H/H	*P. betulae*	*E. betulae*	S	S	Miner	Sucker	INVAB	INVAB	.476	8	Tikkanen et al. 2003
H/H	*S. oblongus*	*L. timidus*	G	G	Sucker	Browser	INVAB	INVD	.119	8	Tikkanen et al. 2003
H/H	*S. oblongus*	*E. betulae*	G	S	Sucker	Sucker	INVAB	INVAB	−.048	8	Tikkanen et al. 2003
H/H	*L. timidus*	*E. betulae*	G	S	Browser	Sucker	INVD	INVAB	−.524	8	Tikkanen et al. 2003
P/H	*E. autumnata*	*Melampsoridium betulinum*	G	S	Chewer				.401	10	Valkama et al. 2005
Betula pubescens ssp. *czerepanovii* (P, T):											
P/H	*E. autumnata*	*M. betulinum*	G	S	Chewer				.401	10	Valkama et al. 2005
Brassica rapa (A, H):											
H/H	*Phyllotreta cruciferae*	*Ceutorhynchus assimilis*	G	G	Chewer	Seed pr.			.140	40	Pilson 2000
P/P	*Albugo candida*	*Peronospora parasitica*	G	G					.846	20	Mitchell-Olds et al. 1995
P/P	*A. candida*	*Leptosphaeria maculans*	G	G					.833	20	Mitchell-Olds et al. 1995
P/P	*P. parasitica*	*L. maculans*	G	G					.829	20	Mitchell-Olds et al. 1995
H/H	*P. cruciferae*	*C. assimilis*	G	G	Chewer	Seed pr.	INVD	INVD	.260	40	Pilson 2000
Datura stramonium (A, H):											
H/H	*Epitrix* sp.	Generalist herbivores	S	G			INVD	INVD	.398	100	Shonle and Bergelson 2000
Ipomoea hederaceae (A, H):											
H/H	Grasshoppers, fleahoppers, lepidopteran larvae	Browser	G	G	Chewer	Browser	INVD	INVD	−.720	18	Stinchcombe and Rausher 2001
Ipomoea purpurea (A, H):											
H/H	Grasshoppers, fleahoppers, lepidopteran larvae	Fleahoppers	G	G	Chewer	Chewer	INVD	INVD	−.733	10	Fineblum and Rausher 1995
H/H	Grasshoppers, fleahoppers, lepidopteran larvae	Insects damaging apical meristem	G	G	Chewer	Ap. dam.	INVD	INVD	.055	10	Fineblum and Rausher 1995
H/H	Fleahoppers	Fleahoppers	G	G	Chewer	Ap. dam.	INVD	INVD	−.285	10	Fineblum and Rausher 1995
H/H	*Chaetocnema confinis*	*Deloyala guttata*	S	S	Chewer	Chewer	INVD	INVD	−.041	140	Rausher and Simms 1989
H/H	*C. confinis*	Generalist insects	S	G	Chewer	Chewer	INVD	INVD	−.185	140	Rausher and Simms 1989
H/H	*D. guttata*	*Heliothis zea*	S	G	Chewer	Chewer	INVD	INVD	.080	140	Rausher and Simms 1989
H/H	*D. guttata*	Generalist insects	S	G	Chewer	Chewer	INVD	INVD	.204	140	Rausher and Simms 1989
H/H	*H. zea*	Generalist insects	G	G	Chewer	Chewer	INVD	INVD	.294	140	Rausher and Simms 1989

Table A1 (*Continued*)

Plant species (longevity, life form), type of comparison[a]	Natural enemy 1	Natural enemy 2	Specialization[b] Enemy 1	Specialization[b] Enemy 2	Feeding guild[c] Enemy 1	Feeding guild[c] Enemy 2	Resistance measures[d] 1	Resistance measures[d] 2	Correlation coefficient	Sample size	Reference
H/H	*C. confinis*	*D. guttata*	S	S	Chewer	Chewer	INVD	INVD	.004	140	Simms and Rausher 1989
H/H	*C. confinis*	*H. zea*	S	G	Chewer	Chewer	INVD	INVD	−.156	140	Simms and Rausher 1989
H/H	*C. confinis*	Generalist insects	S	G	Chewer	Chewer	INVD	INVD	−.085	140	Simms and Rausher 1989
H/H	*D. guttata*	*H. zea*	S	G	Chewer	Chewer	INVD	INVD	.077	140	Simms and Rausher 1989
H/H	*D. guttata*	Generalist insects	S	G	Chewer	Chewer	INVD	INVD	.122	140	Simms and Rausher 1989
H/H	*H. zea*	Generalist insects	G	G	Chewer	Chewer	INVD	INVD	.197	140	Simms and Rausher 1989
P/H	*Colletotrichum dematium*	*H. zea*	G	G		Chewer			.070	142	Simms and Rausher 1993
P/H	*C. dematium*	Flea beetle	G	S		Chewer			.070	142	Simms and Rausher 1993
P/H	*C. dematium*	Generalist folivores	G	G		Chewer			.250	142	Simms and Rausher 1993
H/H	Beetles, grasshoppers, lepidopteran larvae	Leaf-feeding beetle	G	S	Chewer	Chewer	INVD	INVD	.510	35	Tiffin and Rausher 1999
Medicago sativa (P, H):											
P/P	*Uromyces striatus*	*Stemphylium botryosum*							−.192	5	Hill and Leath 1975
P/P	*U. striatus*	*Pseudopeziza medicaginis*							.129	5	Hill and Leath 1975
P/P	*U. striatus*	*Phoma herbarum*							−.185	5	Hill and Leath 1975
P/P	*U. striatus*	*Leptosphaerulina briosiana*							.477	5	Hill and Leath 1975
P/P	*S. botryosum*	*P. medicaginis*							.437	5	Hill and Leath 1975
P/P	*S. botryosum*	*P. herbarum*							−.008	5	Hill and Leath 1975
P/P	*S. botryosum*	*L. briosiana*							−.023	5	Hill and Leath 1975
P/P	*P. medicaginis*	*P. herbarum*							.374	5	Hill and Leath 1975
P/P	*P. medicaginis*	*L. briosiana*							.358	5	Hill and Leath 1975
P/P	*P. herbarum*	*L. briosiana*							.104	5	Hill and Leath 1975
Piper arieianum (P, S):											
H/H	*Ambates* sp.	*Anacrucis piriforana*					INVD	INVD	−.301	8	Marquis 1990
H/H	*Ambates* sp.	*Anacrucis stapiana*					INVD	INVD	.031	8	Marquis 1990
H/H	*Ambates* sp.	*Atta cephalotes*					INVD	INVD	−.791	8	Marquis 1990
H/H	*Ambates* sp.	Dipteran leaf miner sp. 1					INVD	INVD	−.370	8	Marquis 1990
H/H	*Ambates* sp.	Dipteran leaf miner sp. 2					INVD	INVD	.143	8	Marquis 1990
H/H	*Ambates* sp.	*Eois* sp. 1					INVD	INVD	.333	8	Marquis 1990
H/H	*Ambates* sp.	*Homeomastox robertsi*					INVD	INVD	−.313	8	Marquis 1990
H/H	*Ambates* sp.	*Peridinetus* spp. (3, 9, 10)					INVD	INVD	−.167	8	Marquis 1990
H/H	*Ambates* sp.	*Peridinetus* spp. (5, 6)					INVD	INVD	.558	8	Marquis 1990
H/H	*Ambates* sp.	*Peridinetus* sp. (8)					INVD	INVD	−.786	8	Marquis 1990
H/H	*Ambates* sp.	Phasmidae		G			INVD	INVD	−.714	8	Marquis 1990
H/H	*Ambates* sp.	*Qadrus evans*					INVD	INVD	−.791	8	Marquis 1990
H/H	*Ambates* sp.	Tettigoniidae		G			INVD	INVD	−.524	8	Marquis 1990
H/H	*Ambates* sp.	*Gephyra costinotata*					INVD	INVD	−.571	8	Marquis 1990
H/H	*Ambates* sp.	Unknown		G			INVD	INVD	−.833	8	Marquis 1990
H/H	*A. piriforana*	*A. stapiana*					INVD	INVD	−.592	8	Marquis 1990
H/H	*A. piriforana*	*A. cephalotes*					INVD	INVD	−.097	8	Marquis 1990
H/H	*A. piriforana*	Dipteran leaf miner sp. 1					INVD	INVD	−.252	8	Marquis 1990

H/H	*A. piriforana*	Dipteran leaf miner sp. 2		INVD	INVD	−.723	8	Marquis 1990
H/H	*A. piriforana*	*Eois* sp. 1		INVD	INVD	.048	8	Marquis 1990
H/H	*A. piriforana*	*H. robertsi*		INVD	INVD	−.613	8	Marquis 1990
H/H	*A. piriforana*	*Peridinetus* spp. (3, 9, 10)		INVD	INVD	−.482	8	Marquis 1990
H/H	*A. piriforana*	*Peridinetus* spp. (5, 6)		INVD	INVD	.264	8	Marquis 1990
H/H	*A. piriforana*	*Peridinetus* sp. (8)		INVD	INVD	.012	8	Marquis 1990
H/H	*A. piriforana*	Phasmidae	G	INVD	INVD	.036	8	Marquis 1990
H/H	*A. piriforana*	*Q. evans*		INVD	INVD	.166	8	Marquis 1990
H/H	*A. piriforana*	Tettigoniidae	G	INVD	INVD	−.193	8	Marquis 1990
H/H	*A. piriforana*	*G. costinotata*		INVD	INVD	−.205	8	Marquis 1990
H/H	*A. piriforana*	Unknown	G	INVD	INVD	.434	8	Marquis 1990
H/H	*A. stapiana*	*A. cephalotes*		INVD	INVD	.375	8	Marquis 1990
H/H	*A. stapiana*	Dipteran leaf miner sp. 1		INVD	INVD	.067	8	Marquis 1990
H/H	*A. stapiana*	Dipteran leaf miner sp. 2		INVD	INVD	.436	8	Marquis 1990
H/H	*A. stapiana*	*Eois* sp. 1		INVD	INVD	−.343	8	Marquis 1990
H/H	*A. stapiana*	*H. robertsi*		INVD	INVD	.245	8	Marquis 1990
H/H	*A. stapiana*	*Peridinetus* spp. (3, 9, 10)		INVD	INVD	.047	8	Marquis 1990
H/H	*A. stapiana*	*Peridinetus* spp. (5, 6)		INVD	INVD	−.241	8	Marquis 1990
H/H	*A. stapiana*	*Peridinetus* sp. (8)		INVD	INVD	−.031	8	Marquis 1990
H/H	*A. stapiana*	Phasmidae	G	INVD	INVD	−.171	8	Marquis 1990
H/H	*A. stapiana*	*Q. evans*		INVD	INVD	.054	8	Marquis 1990
H/H	*A. stapiana*	Tettigoniidae	G	INVD	INVD	−.171	8	Marquis 1990
H/H	*A. stapiana*	*G. costinotata*		INVD	INVD	.047	8	Marquis 1990
H/H	*A. stapiana*	Unknown	G	INVD	INVD	.047	8	Marquis 1990
H/H	*A. cephalotes*	Dipteran leaf miner sp. 1		INVD	INVD	.234	8	Marquis 1990
H/H	*A. cephalotes*	Dipteran leaf miner sp. 2		INVD	INVD	.355	8	Marquis 1990
H/H	*A. cephalotes*	*Eois* sp. 1		INVD	INVD	−.191	8	Marquis 1990
H/H	*A. cephalotes*	*H. robertsi*		INVD	INVD	.525	8	Marquis 1990
H/H	*A. cephalotes*	*Peridinetus* spp. (3, 9, 10)		INVD	INVD	.546	8	Marquis 1990
H/H	*A. cephalotes*	*Peridinetus* spp. (5, 6)		INVD	INVD	−.697	8	Marquis 1990
H/H	*A. cephalotes*	*Peridinetus* sp. (8)		INVD	INVD	.464	8	Marquis 1990
H/H	*A. cephalotes*	Phasmidae	G	INVD	INVD	.791	8	Marquis 1990
H/H	*A. cephalotes*	*Q. evans*		INVD	INVD	.906	8	Marquis 1990
H/H	*A. cephalotes*	Tettigoniidae	G	INVD	INVD	.518	8	Marquis 1990
H/H	*A. cephalotes*	*G. costinotata*		INVD	INVD	.791	8	Marquis 1990
H/H	*A. cephalotes*	Unknown	G	INVD	INVD	.791	8	Marquis 1990
H/H	Dipteran leaf miner sp. 1	Dipteran leaf miner sp. 2		INVD	INVD	−.089	8	Marquis 1990
H/H	Dipteran leaf miner sp. 1	*Eois* sp. 1		INVD	INVD	−.179	8	Marquis 1990
H/H	Dipteran leaf miner sp. 1	*H. robertsi*		INVD	INVD	.717	8	Marquis 1990
H/H	Dipteran leaf miner sp. 1	*Peridinetus* spp. (3, 9, 10)		INVD	INVD	.294	8	Marquis 1990
H/H	Dipteran leaf miner sp. 1	*Peridinetus* spp. (5, 6)		INVD	INVD	−.633	8	Marquis 1990
H/H	Dipteran leaf miner sp. 1	*Peridinetus* sp. (8)		INVD	INVD	.792	8	Marquis 1990
H/H	Dipteran leaf miner sp. 1	Phasmidae	G	INVD	INVD	.383	8	Marquis 1990
H/H	Dipteran leaf miner sp. 1	*Q. evans*		INVD	INVD	.117	8	Marquis 1990
H/H	Dipteran leaf miner sp. 1	Tettigoniidae	G	INVD	INVD	.664	8	Marquis 1990
H/H	Dipteran leaf miner sp. 1	*G. costinotata*		INVD	INVD	.255	8	Marquis 1990
H/H	Dipteran leaf miner sp. 1	Unknown		INVD	INVD	.089	8	Marquis 1990
H/H	Dipteran leaf miner sp. 2	*Eois* sp. 1		INVD	INVD	.452	8	Marquis 1990

Table A1 (*Continued*)

Plant species (longevity, life form), type of comparison[a]	Natural enemy 1	Natural enemy 2	Specialization[b] Enemy 1	Specialization[b] Enemy 2	Feeding guild[c] Enemy 1	Feeding guild[c] Enemy 2	Resistance measures[d] 1	Resistance measures[d] 2	Correlation coefficient	Sample size	Reference
H/H	Dipteran leaf miner sp. 2	*H. robertsi*					INVD	INVD	.386	8	Marquis 1990
H/H	Dipteran leaf miner sp. 2	*Peridinetus* spp. (3, 9, 10)					INVD	INVD	.643	8	Marquis 1990
H/H	Dipteran leaf miner sp. 2	*Peridinetus* spp. (5, 6)					INVD	INVD	−.076	8	Marquis 1990
H/H	Dipteran leaf miner sp. 2	*Peridinetus* sp. (8)					INVD	INVD	−.214	8	Marquis 1990
H/H	Dipteran leaf miner sp. 2	Phasmidae		G			INVD	INVD	.238	8	Marquis 1990
H/H	Dipteran leaf miner sp. 2	*Q. evans*					INVD	INVD	.109	8	Marquis 1990
H/H	Dipteran leaf miner sp. 2	Tettigoniidae		G			INVD	INVD	.190	8	Marquis 1990
H/H	Dipteran leaf miner sp. 2	*G. costinotata*					INVD	INVD	.333	8	Marquis 1990
H/H	Dipteran leaf miner sp. 2	Unknown		G			INVD	INVD	−.190	8	Marquis 1990
H/H	*Eois* sp. 1	*H. robertsi*					INVD	INVD	−.193	8	Marquis 1990
H/H	*Eois* sp. 1	*Peridinetus* spp. (3, 9, 10)					INVD	INVD	.286	8	Marquis 1990
H/H	*Eois* sp. 1	*Peridinetus* spp. (5, 6)					INVD	INVD	.381	8	Marquis 1990
H/H	*Eois* sp. 1	*Peridinetus* sp. (8)					INVD	INVD	−.405	8	Marquis 1990
H/H	*Eois* sp. 1	Phasmidae		G			INVD	INVD	.071	8	Marquis 1990
H/H	*Eois* sp. 1	*Q. evans*					INVD	INVD	−.218	8	Marquis 1990
H/H	*Eois* sp. 1	Tettigoniidae		G			INVD	INVD	.095	8	Marquis 1990
H/H	*Eois* sp. 1	*G. costinotata*					INVD	INVD	−.167	8	Marquis 1990
H/H	*Eois* sp. 1	Unknown		G			INVD	INVD	−.286	8	Marquis 1990
H/H	*H. robertsi*	*Peridinetus* spp. (3, 9, 10)					INVD	INVD	.783	8	Marquis 1990
H/H	*H. robertsi*	*Peridinetus* spp. (5, 6)					INVD	INVD	−.822	8	Marquis 1990
H/H	*H. robertsi*	*Peridinetus* sp. (8)					INVD	INVD	.530	8	Marquis 1990
H/H	*H. robertsi*	Phasmidae		G			INVD	INVD	.651	8	Marquis 1990
H/H	*H. robertsi*	*Q. evans*					INVD	INVD	.442	8	Marquis 1990
H/H	*H. robertsi*	Tettigoniidae		G			INVD	INVD	.723	8	Marquis 1990
H/H	*H. robertsi*	*G. costinotata*					INVD	INVD	.747	8	Marquis 1990
H/H	*H. robertsi*	Unknown		G			INVD	INVD	.133	8	Marquis 1990
H/H	*Peridinetus* spp. (3, 9, 10)	*Peridinetus* spp. (5, 6)					INVD	INVD	−.647	8	Marquis 1990
H/H	*Peridinetus* spp. (3, 9, 10)	*Peridinetus* sp. (8)					INVD	INVD	.095	8	Marquis 1990
H/H	*Peridinetus* spp. (3, 9, 10)	Phasmidae		G			INVD	INVD	.762	8	Marquis 1990
H/H	*Peridinetus* spp. (3, 9, 10)	*Q. evans*					INVD	INVD	.546	8	Marquis 1990
H/H	*Peridinetus* spp. (3, 9, 10)	Tettigoniidae		G			INVD	INVD	.714	8	Marquis 1990
H/H	*Peridinetus* spp. (3, 9, 10)	*G. costinotata*					INVD	INVD	.810	8	Marquis 1990
H/H	*Peridinetus* spp. (3, 9, 10)	Unknown		G			INVD	INVD	.190	8	Marquis 1990
H/H	*Peridinetus* spp. (5, 6)	*Peridinetus* sp. (8)					INVD	INVD	−.558	8	Marquis 1990
H/H	*Peridinetus* spp. (5, 6)	Phasmidae		G			INVD	INVD	−.710	8	Marquis 1990
H/H	*Peridinetus* spp. (5, 6)	*Q. evans*					INVD	INVD	−.697	8	Marquis 1990
H/H	*Peridinetus* spp. (5, 6)	Tettigoniidae		G			INVD	INVD	−.786	8	Marquis 1990
H/H	*Peridinetus* spp. (5, 6)	*G. costinotata*					INVD	INVD	−.761	8	Marquis 1990
H/H	*Peridinetus* spp. (5, 6)	Unknown		G			INVD	INVD	−.596	8	Marquis 1990
H/H	*Peridinetus* sp. (8)	Phasmidae		G			INVD	INVD	.500	8	Marquis 1990
H/H	*Peridinetus* sp. (8)	*Q. evans*					INVD	INVD	.382	8	Marquis 1990
H/H	*Peridinetus* sp. (8)	Tettigoniidae		G			INVD	INVD	.595	8	Marquis 1990

H/H	*Peridinetus* sp. (8)	*G. costinotata*					INVD	INVD	.357	8	Marquis 1990
H/H	*Peridinetus* sp. (8)	Unknown		G			INVD	INVD	.405	8	Marquis 1990
H/H	*Phasmidae* sp.	*Q. evans*	G				INVD	INVD	.873	8	Marquis 1990
H/H	*Phasmidae* sp.	Tettigoniidae	G	G			INVD	INVD	.762	8	Marquis 1990
H/H	*Phasmidae* sp.	*G. costinotata*	G				INVD	INVD	.905	8	Marquis 1990
H/H	*Phasmidae* sp.	Unknown	G				INVD	INVD	.643	8	Marquis 1990
H/H	*Q. evans*	Tettigoniidae		G			INVD	INVD	.518	8	Marquis 1990
H/H	*Q. evans*	*G. costinotata*					INVD	INVD	.873	8	Marquis 1990
H/H	*Q. evans*	Unknown		G			INVD	INVD	.873	8	Marquis 1990
H/H	Tettigoniidae	*G. costinotata*	G				INVD	INVD	.619	8	Marquis 1990
H/H	Tettigoniidae	Unknown	G	G			INVD	INVD	.429	8	Marquis 1990
H/H	*G. costinotata*	Unknown		G			INVD	INVD	.548	8	Marquis 1990
Plantago lanceolata (P, H):											
P/H	*Diaporthe aucubin*	*Spodoptera exigua*	S	G		Chewer			.480	35	Biere et al. 2004
Pseudotsuga menziesii (P, T):											
H/H	*Contarinia oregonensis*	*Megastigmus spermotrophus*	S	S	Galler	Seed pr.	INVD	INVD	−.450	12	Schowalter and Haverty 1989
Raphanus raphanistrum (A, H):											
H/H	*Pieris rapae*	*L. timidus*	S	G	Chewer	Chewer	INVAB	INVD	.220	13	Agrawal and Sherriffs 2001
Salix lasiolepis (P, S):											
H/H	*Pontania* sp.	*Phyllocolpa* sp.	G	G	Galler	Folder			.289	9	Fritz and Price 1988
H/H	*Pontania* sp.	*Euura lasiolepis*	G	G	Galler	Galler			−.035	9	Fritz and Price 1988
H/H	*Pontania* sp.	*Euura* sp.	G	G	Galler	Galler			.251	9	Fritz and Price 1988
H/H	*Phyllocolpa* sp.	*E. lasiolepis*	G	G	Folder	Galler			.713	9	Fritz and Price 1988
H/H	*Phyllocolpa* sp.	*Euura* sp.	G	G	Folder	Galler			.927	9	Fritz and Price 1988
H/H	*E. lasiolepis*	*Euura* sp.	G	G	Galler	Galler			.765	9	Fritz and Price 1988
H/H	*Pontania* sp.	*Phyllocolpa* sp.	G	G	Galler	Folder			.111	6	Fritz 1990
H/H	*Pontania* sp.	*E. lasiolepis*	G		Galler	Galler			.620	6	Fritz 1990
H/H	*Pontania* sp.	*Euura* sp.	G		Galler	Galler			.643	6	Fritz 1990
H/H	*Phyllocolpa* sp.	*E. lasiolepis*	G		Folder	Galler			.355	6	Fritz 1990
H/H	*Phyllocolpa* sp.	*Euura* sp.	G		Folder	Galler			.242	6	Fritz 1990
H/H	*E. lasiolepis*	*Euura* sp.			Galler	Galler			.852	6	Fritz 1990
H/H	*Pontania* sp.	*Phyllocolpa* sp.	G	G	Galler	Folder	INVAB	INVAB	−.115	51	Fritz et al. 1987
H/H	*Pontania* sp.	*E. lasiolepis*	G	G	Galler	Galler	INVAB	INVAB	−.252	51	Fritz et al. 1987
H/H	*Pontania* sp.	*Euura* sp.	G	G	Galler	Galler	INVAB	INVAB	−.537	51	Fritz et al. 1987
H/H	*Phyllocolpa* sp.	*E. lasiolepis*	G	G	Folder	Galler	INVAB	INVAB	.205	51	Fritz et al. 1987
H/H	*Phyllocolpa* sp.	*Euura* sp.	G	G	Folder	Galler	INVAB	INVAB	.310	51	Fritz et al. 1987
H/H	*E. lasiolepis*	*Euura* sp.	G	G	Galler	Galler	INVAB	INVAB	.080	51	Fritz et al. 1987
Salix sericea (P, S):											
H/H	*Phyllocnystis* sp.	*Phyllocolpa nigrita*	G	G	Miner	Folder	INVAB	INVAB	.438	6	Orians and Fritz 1996
H/H	*Phyllocnystis* sp.	Skeletonizing damage	G	G	Miner	Chewer	INVAB	INVAB	−.659	8	Orians and Fritz 1996
H/H	*Phyllocnystis* sp.	Mites	G	G	Miner	Mite	INVAB	INVAB	.304	8	Orians and Fritz 1996
H/H	*P. nigrita*	Skeletonizing damage	G	G	Folder	Chewer	INVAB	INVAB	.029	6	Orians and Fritz 1996
H/H	*P. nigrita*	Mites	G	G	Folder	Mite	INVAB	INVAB	.717	6	Orians and Fritz 1996
H/H	Skeletonizing damage	Mites	G	G	Chewer	Mite	INVAB	INVAB	−.485	8	Orians and Fritz 1996
H/H	*Phyllonorycter salicifoliella*	*Phyllocolpa* spp.	G	G	Miner	Galler	INVD	INVD	.340	13	Roche and Fritz 1997

Table A1 (*Continued*)

Plant species (longevity, life form), type of comparison[a]	Natural enemy 1	Natural enemy 2	Specialization[b]		Feeding guild[c]		Resistance measures[d]		Correlation coefficient	Sample size	Reference
			Enemy 1	Enemy 2	Enemy 1	Enemy 2	1	2			
H/H	*P. salicifoliella*	*Phyllocolpa terminalis*	G	G	Miner	Galler	INVD	INVD	.270	13	Roche and Fritz 1997
H/H	*P. salicifoliella*	*Pontania* sp.	G	G	Miner	Galler	INVD	INVD	.205	13	Roche and Fritz 1997
H/H	*P. salicifoliella*	*Phyllocnistis* sp.	G	G	Miner	Miner	INVD	INVD	.260	13	Roche and Fritz 1997
H/H	*P. salicifoliella*	*Caloptila* sp.	G	G	Miner	Folder	INVD	INVD	.375	13	Roche and Fritz 1997
H/H	*P. salicifoliella*	LF-V (Lepidoptera)	G	G	Miner	Folder	INVD	INVD	.265	13	Roche and Fritz 1997
H/H	*P. salicifoliella*	LF (Lepidoptera)	G	G	Miner	Folder	INVD	INVD	.585	13	Roche and Fritz 1997
H/H	*P. salicifoliella*	*Rabdophaga rigidae*	G	G	Miner	Galler	INVD	INVD	−.195	13	Roche and Fritz 1997
H/H	*P. salicifoliella*	*Rabdophaga salicisbrassicoides*	G	G	Miner	Galler	INVD	INVD	−.020	13	Roche and Fritz 1997
H/H	*P. salicifoliella*	*Iteomyia salicifolia*	G	G	Miner	Galler	INVD	INVD	−.325	13	Roche and Fritz 1997
H/H	*P. salicifoliella*	*Aculops tetanothrix*	G	S	Miner	Galler	INVD	INVD	.430	13	Roche and Fritz 1997
H/H	*Phyllocolpa* spp.	*P. terminalis*	G	G	Galler	Galler	INVD	INVD	.620	13	Roche and Fritz 1997
H/H	*Phyllocolpa* spp.	*Pontania* sp.	G	G	Galler	Galler	INVD	INVD	.235	13	Roche and Fritz 1997
H/H	*Phyllocolpa* spp.	*Phyllocnistis* sp.	G	G	Galler	Miner	INVD	INVD	.070	13	Roche and Fritz 1997
H/H	*Phyllocolpa* spp.	*Caloptila* sp.	G	G	Galler	Folder	INVD	INVD	.000	13	Roche and Fritz 1997
H/H	*Phyllocolpa* spp.	LF-V (Lepidoptera)	G	G	Galler	Folder	INVD	INVD	.630	13	Roche and Fritz 1997
H/H	*Phyllocolpa* spp.	LF (Lepidoptera)	G	G	Galler	Folder	INVD	INVD	.205	13	Roche and Fritz 1997
H/H	*Phyllocolpa* spp.	*R. rigidae*	G	G	Galler	Galler	INVD	INVD	.395	13	Roche and Fritz 1997
H/H	*Phyllocolpa* spp.	*R. salicisbrassicoides*	G	G	Galler	Galler	INVD	INVD	.065	13	Roche and Fritz 1997
H/H	*Phyllocolpa* spp.	*I. salicifolia*	G	G	Galler	Galler	INVD	INVD	.095	13	Roche and Fritz 1997
H/H	*Phyllocolpa* spp.	*A. tetanothrix*	G	S	Galler	Galler	INVD	INVD	−.080	13	Roche and Fritz 1997
H/H	*P. terminalis*	*Pontania* sp.	G	G	Galler	Galler	INVD	INVD	.155	13	Roche and Fritz 1997
H/H	*P. terminalis*	*Phyllocnistis* sp.	G	G	Galler	Miner	INVD	INVD	.165	13	Roche and Fritz 1997
H/H	*P. terminalis*	*Caloptila* sp.	G	G	Galler	Folder	INVD	INVD	.165	13	Roche and Fritz 1997
H/H	*P. terminalis*	LF-V (Lepidoptera)	G	G	Galler	Folder	INVD	INVD	.460	13	Roche and Fritz 1997
H/H	*P. terminalis*	LF (Lepidoptera)	G	G	Galler	Folder	INVD	INVD	.110	13	Roche and Fritz 1997
H/H	*P. terminalis*	*R. rigidae*	G	G	Galler	Galler	INVD	INVD	.255	13	Roche and Fritz 1997
H/H	*P. terminalis*	*R. salicisbrassicoides*	G	G	Galler	Galler	INVD	INVD	.110	13	Roche and Fritz 1997
H/H	*P. terminalis*	*I. salicifolia*	G	G	Galler	Galler	INVD	INVD	.005	13	Roche and Fritz 1997
H/H	*P. terminalis*	*A. tetanothrix*	G	S	Galler	Galler	INVD	INVD	−.070	13	Roche and Fritz 1997
H/H	*Pontania* sp.	*Phyllocnistis* sp.	G	G	Galler	Miner	INVD	INVD	.050	13	Roche and Fritz 1997
H/H	*Pontania* sp.	*Caloptila* sp.	G	G	Galler	Folder	INVD	INVD	.020	13	Roche and Fritz 1997
H/H	*Pontania* sp.	LF-V (Lepidoptera)	G	G	Galler	Folder	INVD	INVD	.115	13	Roche and Fritz 1997
H/H	*Pontania* sp.	LF (Lepidoptera)	G	G	Galler	Folder	INVD	INVD	.150	13	Roche and Fritz 1997
H/H	*Pontania* sp.	*R. rigidae*	G	G	Galler	Galler	INVD	INVD	−.150	13	Roche and Fritz 1997
H/H	*Pontania* sp.	*R. salicisbrassicoides*	G	G	Galler	Galler	INVD	INVD	.090	13	Roche and Fritz 1997
H/H	*Pontania* sp.	*I. salicifolia*	G	G	Galler	Galler	INVD	INVD	−.310	13	Roche and Fritz 1997
H/H	*Pontania* sp.	*A. tetanothrix*	G	S	Galler	Galler	INVD	INVD	.110	13	Roche and Fritz 1997
H/H	*Phyllocnistis* sp.	*Caloptila* sp.	G	G	Miner	Folder	INVD	INVD	.155	13	Roche and Fritz 1997
H/H	*Phyllocnistis* sp.	LF-V (Lepidoptera)	G	G	Miner	Folder	INVD	INVD	.220	13	Roche and Fritz 1997
H/H	*Phyllocnistis* sp.	LF (Lepidoptera)	G	G	Miner	Folder	INVD	INVD	.040	13	Roche and Fritz 1997
H/H	*Phyllocnistis* sp.	*R. rigidae*	G	G	Miner	Galler	INVD	INVD	.070	13	Roche and Fritz 1997

H/H	*Phyllocnistis* sp.	*R. salicisbrassicoides*	G	G	Miner	Galler	INVD	INVD	.035	13	Roche and Fritz 1997
H/H	*Phyllocnistis* sp.	*I. salicifolia*	G	G	Miner	Galler	INVD	INVD	−.095	13	Roche and Fritz 1997
H/H	*Phyllocnistis* sp.	*A. tetanothrix*	G	S	Miner	Galler	INVD	INVD	.400	13	Roche and Fritz 1997
H/H	*Caloptila* sp.	LF-V (Lepidoptera)	G	G	Folder	Folder	INVD	INVD	.145	13	Roche and Fritz 1997
H/H	*Caloptila* sp.	LF (Lepidoptera)	G	G	Folder	Folder	INVD	INVD	.445	13	Roche and Fritz 1997
H/H	*Caloptila* sp.	*R. rigidae*	G	G	Folder	Galler	INVD	INVD	−.180	13	Roche and Fritz 1997
H/H	*Caloptila* sp.	*R. salicisbrassicoides*	G	G	Folder	Galler	INVD	INVD	.265	13	Roche and Fritz 1997
H/H	*Caloptila* sp.	*I. salicifolia*	G	G	Folder	Galler	INVD	INVD	−.125	13	Roche and Fritz 1997
H/H	*Caloptila* sp.	*A. tetanothrix*	G	S	Folder	Galler	INVD	INVD	.370	13	Roche and Fritz 1997
H/H	LF-V (Lepidoptera)	LF (Lepidoptera)	G	G	Folder	Folder	INVD	INVD	.320	13	Roche and Fritz 1997
H/H	LF-V (Lepidoptera)	*R. rigidae*	G	G	Folder	Galler	INVD	INVD	−.325	13	Roche and Fritz 1997
H/H	LF-V (Lepidoptera)	*R. salicisbrassicoides*	G	G	Folder	Galler	INVD	INVD	.100	13	Roche and Fritz 1997
H/H	LF-V (Lepidoptera)	*I. salicifolia*	G	G	Folder	Galler	INVD	INVD	−.090	13	Roche and Fritz 1997
H/H	LF-V (Lepidoptera)	*A. tetanothrix*	G	S	Folder	Galler	INVD	INVD	−.140	13	Roche and Fritz 1997
H/H	LF (Lepidoptera)	*R. rigidae*	G	G	Folder	Galler	INVD	INVD	−.135	13	Roche and Fritz 1997
H/H	LF (Lepidoptera)	*R. salicisbrassicoides*	G	G	Folder	Galler	INVD	INVD	−.180	13	Roche and Fritz 1997
H/H	LF (Lepidoptera)	*I. salicifolia*	G	G	Folder	Galler	INVD	INVD	−.440	13	Roche and Fritz 1997
H/H	LF (Lepidoptera)	*A. tetanothrix*	G	S	Folder	Galler	INVD	INVD	−.080	13	Roche and Fritz 1997
H/H	*R. rigidae*	*R. salicisbrassicoides*	G	G	Galler	Galler	INVD	INVD	−.215	13	Roche and Fritz 1997
H/H	*R. rigidae*	*I. salicifolia*	G	G	Galler	Galler	INVD	INVD	.300	13	Roche and Fritz 1997
H/H	*R. rigidae*	*A. tetanothrix*	G	S	Galler	Galler	INVD	INVD	.320	13	Roche and Fritz 1997
H/H	*R. salicisbrassicoides*	*I. salicifolia*	G	G	Galler	Galler	INVD	INVD	−.020	13	Roche and Fritz 1997
H/H	*R. salicisbrassicoides*	*A. tetanothrix*	G	S	Galler	Galler	INVD	INVD	.020	13	Roche and Fritz 1997
H/H	*I. salicifolia*	*A. tetanothrix*		S	Galler	Galler	INVD	INVD	.100	13	Roche and Fritz 1997
Solidago altissima (P, H):											
H/H	*Lygus lineolaris*	*Slaterocoris* spp.	G	S	Sucker	Sucker			.010	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Corythuca marmorata*	G	G	Sucker	Sucker			−.150	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Philaenus spumarius*	G	G	Sucker	Sucker			.120	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Uroleucon caligatum*	G	S	Sucker	Sucker			−.220	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Uroleucon nigrotuberculatum*	G	S	Sucker	Sucker			−.130	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Exema canadensis*	G	S	Sucker	Chewer			−.060	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Microrhopala vittata*	G	S	Sucker	Miner			.000	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Ophraella conferta*	G	S	Sucker	Chewer			.010	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Trirhabda virgata*	G	S	Sucker	Chewer			.100	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Epiblema scudderiana*	G	S	Sucker	Galler			.030	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Epiblema* spp.	G	S	Sucker	Miner			.060	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Dichomeris* spp.	G	S	Sucker	Chewer			−.060	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Asteromyia carbinifera*	G	S	Sucker	Galler			−.090	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Rhopalomyia solidaginis*	G	S	Sucker	Galler			.040	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Eurosta solidaginis*	G	S	Sucker	Galler			−.140	18	Maddox and Root 1990
H/H	*L. lineolaris*	*Ophiomyia/Phytomyza*	G	S	Sucker	Miner			−.700	18	Maddox and Root 1990
H/H	*Slaterocoris* spp.	*C. marmorata*	S	G	Sucker	Sucker			.000	18	Maddox and Root 1990
H/H	*Slaterocoris* spp.	*P. spumarius*	S	G	Sucker	Sucker			−.060	18	Maddox and Root 1990
H/H	*Slaterocoris* spp.	*U. caligatum*	S	S	Sucker	Sucker			.020	18	Maddox and Root 1990
H/H	*Slaterocoris* spp.	*U. nigrotuberculatum*	S	S	Sucker	Sucker			−.800	18	Maddox and Root 1990
H/H	*Slaterocoris* spp.	*E. canadensis*	S	S	Sucker	Chewer			−.400	18	Maddox and Root 1990
H/H	*Slaterocoris* spp.	*M. vittata*	S	S	Sucker	Miner			.070	18	Maddox and Root 1990

Table A1 (*Continued*)

Plant species (longevity, life form), type of comparison[a]	Natural enemy 1	Natural enemy 2	Specialization[b]		Feeding guild[c]		Resistance measures[d]		Correlation coefficient	Sample size	Reference
			Enemy 1	Enemy 2	Enemy 1	Enemy 2	1	2			
H/H	*Slaterocoris* spp.	*O. conferta*	S	S	Sucker	Chewer			−.050	18	Maddox and Root 1990
H/H	*Slaterocoris* spp.	*T. virgata*	S	S	Sucker	Chewer			.050	18	Maddox and Root 1990
H/H	*Slaterocoris* spp.	*E. scudderiana*	S	S	Sucker	Galler			.020	18	Maddox and Root 1990
H/H	*Slaterocoris* spp.	*Epiblema* spp.	S	S	Sucker	Miner			.020	18	Maddox and Root 1990
H/H	*Slaterocoris* spp.	*Dichomeris* spp.	S	S	Sucker	Chewer			−.060	18	Maddox and Root 1990
H/H	*Slaterocoris* spp.	*A. carbinifera*	S	S	Sucker	Galler			.100	18	Maddox and Root 1990
H/H	*Slaterocoris* spp.	*R. solidaginis*	S	S	Sucker	Galler			.100	18	Maddox and Root 1990
H/H	*Slaterocoris* spp.	*E. solidaginis*	S	S	Sucker	Galler			−.060	18	Maddox and Root 1990
H/H	*Slaterocoris* spp.	*Ophiomyia*/*Phytomyza*	S	S	Sucker	Miner			.010	18	Maddox and Root 1990
H/H	*C. marmorata*	*P. spumarius*	G	G	Sucker	Sucker			−.040	18	Maddox and Root 1990
H/H	*C. marmorata*	*U. caligatum*	G	S	Sucker	Sucker			.570	18	Maddox and Root 1990
H/H	*C. marmorata*	*U. nigrotuberculatum*	G	S	Sucker	Sucker			.370	18	Maddox and Root 1990
H/H	*C. marmorata*	*E. canadensis*	G	S	Sucker	Chewer			−.050	18	Maddox and Root 1990
H/H	*C. marmorata*	*M. vittata*	G	S	Sucker	Miner			−.050	18	Maddox and Root 1990
H/H	*C. marmorata*	*O. conferta*	G	S	Sucker	Chewer			−.110	18	Maddox and Root 1990
H/H	*C. marmorata*	*T. virgata*	G	S	Sucker	Chewer			.090	18	Maddox and Root 1990
H/H	*C. marmorata*	*E. scudderiana*	G	S	Sucker	Galler			−.070	18	Maddox and Root 1990
H/H	*C. marmorata*	*Epiblema* spp.	G	S	Sucker	Miner			.030	18	Maddox and Root 1990
H/H	*C. marmorata*	*Dichomeris* spp.	G	S	Sucker	Chewer			.170	18	Maddox and Root 1990
H/H	*C. marmorata*	*A. carbinifera*	G	S	Sucker	Galler			−.070	18	Maddox and Root 1990
H/H	*C. marmorata*	*R. solidaginis*	G	S	Sucker	Galler			−.090	18	Maddox and Root 1990
H/H	*C. marmorata*	*E. solidaginis*	G	S	Sucker	Galler			−.160	18	Maddox and Root 1990
H/H	*C. marmorata*	*Ophiomyia*/*Phytomyza*	G	S	Sucker	Miner			.420	18	Maddox and Root 1990
H/H	*P. spumarius*	*U. caligatum*	G	S	Sucker	Sucker			−.030	18	Maddox and Root 1990
H/H	*P. spumarius*	*U. nigrotuberculatum*	G	S	Sucker	Sucker			.110	18	Maddox and Root 1990
H/H	*P. spumarius*	*E. canadensis*	G	S	Sucker	Chewer			−.040	18	Maddox and Root 1990
H/H	*P. spumarius*	*M. vittata*	G	S	Sucker	Miner			.000	18	Maddox and Root 1990
H/H	*P. spumarius*	*O. conferta*	G	S	Sucker	Chewer			−.050	18	Maddox and Root 1990
H/H	*P. spumarius*	*T. virgata*	G	S	Sucker	Chewer			−.130	18	Maddox and Root 1990
H/H	*P. spumarius*	*E. scudderiana*	G	S	Sucker	Galler			.080	18	Maddox and Root 1990
H/H	*P. spumarius*	*Epiblema* spp.	G	S	Sucker	Miner			−.070	18	Maddox and Root 1990
H/H	*P. spumarius*	*Dichomeris* spp.	G	S	Sucker	Chewer			−.120	18	Maddox and Root 1990
H/H	*P. spumarius*	*A. carbinifera*	G	S	Sucker	Galler			−.050	18	Maddox and Root 1990
H/H	*P. spumarius*	*R. solidaginis*	G	S	Sucker	Galler			.060	18	Maddox and Root 1990
H/H	*P. spumarius*	*E. solidaginis*	G	S	Sucker	Galler			.220	18	Maddox and Root 1990
H/H	*P. spumarius*	*Ophiomyia*/*Phytomyza*	G	S	Sucker	Miner			−.020	18	Maddox and Root 1990
H/H	*U. caligatum*	*U. nigrotuberculatum*	S	S	Sucker	Sucker			.300	18	Maddox and Root 1990
H/H	*U. caligatum*	*E. canadensis*	S	S	Sucker	Chewer			.020	18	Maddox and Root 1990
H/H	*U. caligatum*	*M. vittata*	S	S	Sucker	Miner			−.070	18	Maddox and Root 1990
H/H	*U. caligatum*	*O. conferta*	S	S	Sucker	Chewer			−.180	18	Maddox and Root 1990
H/H	*U. caligatum*	*T. virgata*	S	S	Sucker	Chewer			−.010	18	Maddox and Root 1990
H/H	*U. caligatum*	*E. scudderiana*	S	S	Sucker	Galler			−.020	18	Maddox and Root 1990

H/H	*U. caligatum*	*Epiblema* spp.	S	S	Sucker	Miner	.070	18	Maddox and Root 1990
H/H	*U. caligatum*	*Dichomeris* spp.	S	S	Sucker	Chewer	.170	18	Maddox and Root 1990
H/H	*U. caligatum*	*A. carbinifera*	S	S	Sucker	Galler	.120	18	Maddox and Root 1990
H/H	*U. caligatum*	*R. solidaginis*	S	S	Sucker	Galler	.030	18	Maddox and Root 1990
H/H	*U. caligatum*	*E. solidaginis*	S	S	Sucker	Galler	.070	18	Maddox and Root 1990
H/H	*U. caligatum*	*Ophiomyia/Phytomyza*	S	S	Sucker	Miner	.330	18	Maddox and Root 1990
H/H	*U. nigrotuberculatum*	*E. canadensis*	S	S	Sucker	Chewer	.080	18	Maddox and Root 1990
H/H	*U. nigrotuberculatum*	*M. vittata*	S	S	Sucker	Miner	.110	18	Maddox and Root 1990
H/H	*U. nigrotuberculatum*	*O. conferta*	S	S	Sucker	Chewer	−.020	18	Maddox and Root 1990
H/H	*U. nigrotuberculatum*	*T. virgata*	S	S	Sucker	Chewer	−.020	18	Maddox and Root 1990
H/H	*U. nigrotuberculatum*	*E. scudderiana*	S	S	Sucker	Galler	.130	18	Maddox and Root 1990
H/H	*U. nigrotuberculatum*	*Epiblema* spp.	S	S	Sucker	Miner	.050	18	Maddox and Root 1990
H/H	*U. nigrotuberculatum*	*Dichomeris* spp.	S	S	Sucker	Chewer	.000	18	Maddox and Root 1990
H/H	*U. nigrotuberculatum*	*A. carbinifera*	S	S	Sucker	Galler	−.005	18	Maddox and Root 1990
H/H	*U. nigrotuberculatum*	*R. solidaginis*	S	S	Sucker	Galler	.060	18	Maddox and Root 1990
H/H	*U. nigrotuberculatum*	*E. solidaginis*	S	S	Sucker	Galler	.240	18	Maddox and Root 1990
H/H	*U. nigrotuberculatum*	*Ophiomyia/Phytomyza*	S	S	Sucker	Miner	.200	18	Maddox and Root 1990
H/H	*E. canadensis*	*M. vittata*	S	S	Chewer	Miner	.220	18	Maddox and Root 1990
H/H	*E. canadensis*	*O. conferta*	S	S	Chewer	Chewer	−.010	18	Maddox and Root 1990
H/H	*E. canadensis*	*T. virgata*	S	S	Chewer	Chewer	−.020	18	Maddox and Root 1990
H/H	*E. canadensis*	*E. scudderiana*	S	S	Chewer	Galler	−.050	18	Maddox and Root 1990
H/H	*E. canadensis*	*Epiblema* spp.	S	S	Chewer	Miner	.030	18	Maddox and Root 1990
H/H	*E. canadensis*	*Dichomeris* spp.	S	S	Chewer	Chewer	−.020	18	Maddox and Root 1990
H/H	*E. canadensis*	*A. carbinifera*	S	S	Chewer	Galler	.120	18	Maddox and Root 1990
H/H	*E. canadensis*	*R. solidaginis*	S	S	Chewer	Galler	.080	18	Maddox and Root 1990
H/H	*E. canadensis*	*E. solidaginis*	S	S	Chewer	Galler	.100	18	Maddox and Root 1990
H/H	*E. canadensis*	*Ophiomyia/Phytomyza*	S	S	Chewer	Miner	−.040	18	Maddox and Root 1990
H/H	*M. vittata*	*O. conferta*	S	S	Miner	Chewer	.010	18	Maddox and Root 1990
H/H	*M. vittata*	*T. virgata*	S	S	Miner	Chewer	−.030	18	Maddox and Root 1990
H/H	*M. vittata*	*E. scudderiana*	S	S	Miner	Galler	.090	18	Maddox and Root 1990
H/H	*M. vittata*	*Epiblema* spp.	S	S	Miner	Miner	.090	18	Maddox and Root 1990
H/H	*M. vittata*	*Dichomeris* spp.	S	S	Miner	Chewer	.050	18	Maddox and Root 1990
H/H	*M. vittata*	*A. carbinifera*	S	S	Miner	Galler	.170	18	Maddox and Root 1990
H/H	*M. vittata*	*R. solidaginis*	S	S	Miner	Galler	.160	18	Maddox and Root 1990
H/H	*M. vittata*	*E. solidaginis*	S	S	Miner	Galler	.270	18	Maddox and Root 1990
H/H	*M. vittata*	*Ophiomyia/Phytomyza*	S	S	Miner	Miner	.060	18	Maddox and Root 1990
H/H	*O. conferta*	*T. virgata*	S	S	Chewer	Chewer	−.070	18	Maddox and Root 1990
H/H	*O. conferta*	*E. scudderiana*	S	S	Chewer	Galler	−.100	18	Maddox and Root 1990
H/H	*O. conferta*	*Epiblema* spp.	S	S	Chewer	Miner	.320	18	Maddox and Root 1990
H/H	*O. conferta*	*Dichomeris* spp.	S	S	Chewer	Chewer	−.070	18	Maddox and Root 1990
H/H	*O. conferta*	*A. carbinifera*	S	S	Chewer	Galler	−.010	18	Maddox and Root 1990
H/H	*O. conferta*	*R. solidaginis*	S	S	Chewer	Galler	−.100	18	Maddox and Root 1990
H/H	*O. conferta*	*E. solidaginis*	S	S	Chewer	Galler	−.190	18	Maddox and Root 1990
H/H	*O. conferta*	*Ophiomyia/Phytomyza*	S	S	Chewer	Miner	.140	18	Maddox and Root 1990
H/H	*T. virgata*	*E. scudderiana*	S	S	Chewer	Galler	−.100	18	Maddox and Root 1990
H/H	*T. virgata*	*Epiblema* spp.	S	S	Chewer	Miner	.320	18	Maddox and Root 1990
H/H	*T. virgata*	*Dichomeris* spp.	S	S	Chewer	Chewer	.380	18	Maddox and Root 1990
H/H	*T. virgata*	*A. carbinifera*	S	S	Chewer	Galler	−.010	18	Maddox and Root 1990

Table A1 (*Continued*)

Plant species (longevity, life form), type of comparison[a]	Natural enemy 1	Natural enemy 2	Specialization[b]		Feeding guild[c]		Resistance measures[d]		Correlation coefficient	Sample size	Reference
			Enemy 1	Enemy 2	Enemy 1	Enemy 2	1	2			
H/H	*T. virgata*	*R. solidaginis*	S	S	Chewer	Galler			−.100	18	Maddox and Root 1990
H/H	*T. virgata*	*E. solidaginis*	S	S	Chewer	Galler			−.190	18	Maddox and Root 1990
H/H	*T. virgata*	*Ophiomyia*/*Phytomyza*	S	S	Chewer	Miner			.140	18	Maddox and Root 1990
H/H	*E. scudderiana*	*Epiblema* spp.	S	S	Galler	Miner			.000	18	Maddox and Root 1990
H/H	*E. scudderiana*	*Dichomeris* spp.	S	S	Galler	Chewer			−.060	18	Maddox and Root 1990
H/H	*E. scudderiana*	*A. carbinifera*	S	S	Galler	Galler			.060	18	Maddox and Root 1990
H/H	*E. scudderiana*	*R. solidaginis*	S	S	Galler	Galler			.360	18	Maddox and Root 1990
H/H	*E. scudderiana*	*E. solidaginis*	S	S	Galler	Galler			.230	18	Maddox and Root 1990
H/H	*E. scudderiana*	*Ophiomyia*/*Phytomyza*	S	S	Galler	Miner			−.020	18	Maddox and Root 1990
H/H	*Epiblema* spp.	*Dichomeris* spp.	S	S	Miner	Chewer			.130	18	Maddox and Root 1990
H/H	*Epiblema* spp.	*A. carbinifera*	S	S	Miner	Galler			.050	18	Maddox and Root 1990
H/H	*Epiblema* spp.	*R. solidaginis*	S	S	Miner	Galler			.130	18	Maddox and Root 1990
H/H	*Epiblema* spp.	*E. solidaginis*	S	S	Miner	Galler			.070	18	Maddox and Root 1990
H/H	*Epiblema* spp.	*Ophiomyia*/*Phytomyza*	S	S	Miner	Miner			.190	18	Maddox and Root 1990
H/H	*Dichomeris* spp.	*A. carbinifera*	S	S	Chewer	Galler			.000	18	Maddox and Root 1990
H/H	*Dichomeris* spp.	*R. solidaginis*	S	S	Chewer	Galler			−.080	18	Maddox and Root 1990
H/H	*Dichomeris* spp.	*E. solidaginis*	S	S	Chewer	Galler			−.010	18	Maddox and Root 1990
H/H	*Dichomeris* spp.	*Ophiomyia*/*Phytomyza*	S	S	Chewer	Miner			.260	18	Maddox and Root 1990
H/H	*A. carbinifera*	*R. solidaginis*	S	S	Galler	Galler			.110	18	Maddox and Root 1990
H/H	*A. carbinifera*	*E. solidaginis*	S	S	Galler	Galler			.080	18	Maddox and Root 1990
H/H	*A. carbinifera*	*Ophiomyia*/*Phytomyza*	S	S	Galler	Miner			−.020	18	Maddox and Root 1990
H/H	*R. solidaginis*	*E. solidaginis*	S	S	Galler	Galler			.210	18	Maddox and Root 1990
H/H	*R. solidaginis*	*Ophiomyia*/*Phytomyza*	S	S	Galler	Miner			−.050	18	Maddox and Root 1990
H/H	*E. solidaginis*	*Ophiomyia*/*Phytomyza*	S	S	Galler	Miner			−.060	18	Maddox and Root 1990
H/H	*Uroleucon tissoti*	*R. solidaginis*	S	G	Sucker	Galler	INVAB	INVAB	−.447	5	Pilson 1992
H/H	*U. tissoti*	Tephritidae sp.	S	G	Sucker	Galler	INVAB	INVAB	.462	5	Pilson 1992
H/H	*U. tissoti*	Cecidomyiidae sp.	S	G	Sucker	Galler	INVAB	INVAB	−.500	5	Pilson 1992
H/H	*U. tissoti*	*Gnorimoschema gallaesolidaginis*	S	G	Sucker	Galler	INVAB	INVAB	.738	5	Pilson 1992
H/H	*U. tissoti*	Noctuidae sp.	S	G	Sucker	Chewer	INVAB	INVAB	−.500	5	Pilson 1992
H/H	*U. tissoti*	Droop beetle	S	G	Sucker	Borer	INVAB	INVAB	−.359	5	Pilson 1992
H/H	*U. tissoti*	Bud scars	S	G	Sucker	Bud scars	INVAB	INVAB	−.154	5	Pilson 1992
H/H	*R. solidaginis*	Tephritidae sp.	G	G	Galler	Galler	INVAB	INVAB	.229	5	Pilson 1992
H/H	*R. solidaginis*	Cecidomyiidae sp.	G	G	Galler	Galler	INVAB	INVAB	.671	5	Pilson 1992
H/H	*R. solidaginis*	*G. gallaesolidaginis*	G	G	Galler	Galler	INVAB	INVAB	.059	5	Pilson 1992
H/H	*R. solidaginis*	Noctuidae sp.	G	G	Galler	Chewer	INVAB	INVAB	.671	5	Pilson 1992
H/H	*R. solidaginis*	Droop beetle	G	G	Galler	Borer	INVAB	INVAB	.057	5	Pilson 1992
H/H	*R. solidaginis*	Bud scars	G	G	Galler	Bud scars	INVAB	INVAB	−.229	5	Pilson 1992
H/H	Tephritidae sp.	Cecidomyiidae sp.	G	G	Galler	Galler	INVAB	INVAB	.205	5	Pilson 1992
H/H	Tephritidae sp.	*G. gallaesolidaginis*	G	G	Galler	Galler	INVAB	INVAB	.649	5	Pilson 1992
H/H	Tephritidae sp.	Noctuidae sp.	G	G	Galler	Chewer	INVAB	INVAB	.205	5	Pilson 1992
H/H	Tephritidae sp.	Droop beetle	G	G	Galler	Borer	INVAB	INVAB	.026	5	Pilson 1992

H/H	Tephritidae sp.	Bud scars	G	G	Galler	Bud scars	INVAB	INVAB	−.763	5	Pilson 1992
H/H	Cecidomyiidae sp.	*G. gallaesolidaginis*	G	G	Galler	Galler	INVAB	INVAB	.211	5	Pilson 1992
H/H	Cecidomyiidae sp.	Noctuidae sp.	G	G	Galler	Chewer	INVAB	INVAB	1.000	5	Pilson 1992
H/H	Cecidomyiidae sp.	Droop beetle	G	G	Galler	Borer	INVAB	INVAB	−.359	5	Pilson 1992
H/H	Cecidomyiidae sp.	Bud scars	G	G	Galler	Bud scars	INVAB	INVAB	−.667	5	Pilson 1992
H/H	*G. gallaesolidaginis*	Noctuidae sp.	G	G	Galler	Chewer	INVAB	INVAB	.211	5	Pilson 1992
H/H	*G. gallaesolidaginis*	Droop beetle	G	G	Galler	Borer	INVAB	INVAB	−.703	5	Pilson 1992
H/H	*G. gallaesolidaginis*	Bud scars	G	G	Galler	Bud scars	INVAB	INVAB	−.649	5	Pilson 1992
H/H	Noctuidae sp.	Droop beetle	G	G	Chewer	Chewer	INVAB	INVAB	−.359	5	Pilson 1992
H/H	Noctuidae sp.	Bud scars	G	G	Chewer	Borer	INVAB	INVAB	−.667	5	Pilson 1992
H/H	Droop beetle	Bud scars	G	G	Borer	Bud scars	INVAB	INVAB	.368	5	Pilson 1992
Urtica dioica (P, H):											
H/H	*Arianta arbustorum*	Mammalian herbivory	G	G	Chewer		INVP		.137	19	Puustinen et al. 2004

[a] Longevity: P = perennial; A = annual. Life form: H = herb; T = tree; S = shrub. Type of comparison: H/H = correlation between resistances to two herbivores; P/H = correlation between resistances to a pathogen and a herbivore; P/P = correlation between resistances to two pathogens.

[b] G = generalist; S = specialist.

[c] Seed pr. = seed predation; Ap. dam. = apical damage.

[d] INVD = inverse of damage; INVAB = inverse of herbivore abundance; INVP = inverse of herbivore performance.

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