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THE ECOLOGY AND EVOLUTION OF GALL-FORMING INSECTS

Edited by
PETER W. PRICE
WILLIAM J. MATTSON
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Krasnoyarsk, Siberia
August 9-13, 1993

ABOUT THE COVER

On the cover are examples of three insect-stimulated plant galls, and one galling insect, a cecidomyiid fly. None are drawn to scale. In the foreground is a round goldenrod (*Solidago*) gall by the gall fly, *Eurosta solidaginsis*. Behind it, on the arrow-shaped willow (*Salix*) leaf are several galls by the willow redgall sawfly, *Pontania proxima*. In the background is a gall by the spruce gall aphid, *Adleges abietis*, on white spruce (*Picea glauca*). The fly is a representative member of the family Cecidomyiidae, one of the largest groups of insect gallmakers. Kristine A. Kirkeby is the artist.

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THE ECOLOGY AND EVOLUTION OF GALL-FORMING INSECTS

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PREFACE

This proceedings is the result of a symposium that was held August 9-13, 1993 in Krasnoyarsk, Siberia. It was organized under the guidelines of the International Union of Forestry Research Organizations (IUFRO) by the V.N. Sukachev Institute of Forest and Wood, Siberian Branch of the Russian Academy of Sciences, Northern Arizona University, Department of Biological Sciences, and two IUFRO working parties, S2.07-08, Forest gall midges, and S2.05-08, Mechanisms and genetics of woody plant resistance against insects.

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COMPARATIVE POPULATION DYNAMICS OF THE GALLING SAWFLIES

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Abstract. Three genera of galling sawflies *Euura*, *Pontania* and *Phyllocolpa*, which attack members of the plant family Salicaceae are considered. The characteristics of ecological importance in *Euura*, the stem, bud, petiole and midrib gallers, are strong preference/performance linkage between ovipositing females and survival of larvae, highly predictable populations, weak top-down effects from carnivores in the third trophic level, and resource regulation. Population dynamics is dominated by shortage of resources in the form of juvenile rapidly growing shoots. However, on shrubby willows such shoots are produced from the base of clones over many years, and this coupled with the pruning effects of resource regulation keeps resources and populations relatively stable. On willows that grow to be trees *Euura* populations are predictable, because colonization occurs on young trees, but aging effects of trees are very strong and populations crash to local extinction within a few years. In all *Euura* species studied the role of carnivores is weak and pattern in population change in time and space is dictated from the bottom up.

In general *Pontania* and *Phyllocolpa* populations are less constrained by plant resources, and natural enemies become much more important mortality factors. Dynamics are dictated more by an interaction between bottom-up and top-down forces, making the relative role of each more difficult to understand. Both these genera attack leaves exclusively, resources which appear to be less restricting than stems and buds, selecting for weaker responses to variable leaf size. Gall structure also appears to make members of these genera more accessible to parasitoids so that top-down forces become stronger.

INTRODUCTION

There are probably almost 200 species of galling sawflies in the world, all originally in northern latitudes, in the genera *Euura*, *Pontania* and *Phyllocolpa* (Hymenoptera: Tenthredinidae: Nematinae: Nematini). All attack members of the woody plant family Salicaceae containing the willows (*Salix*) and poplars (*Populus*). Many of the plant species are important as browse for herbivorous mammals, in soil conservation, in biomass and bioenergy plantations, in pulp and paper production, chip board manufacture, and perhaps most importantly in the making of cricket bats. Each genus of sawflies contains species with a circumscribed set of microhabitats on the plant used for gall initiation. *Euura* species gall stems, petioles, leaf midribs and buds. *Pontania* species form leaf galls, and *Phyllocolpa* cause leaves to fold or curl (Price and Roininen 1993).

The population dynamics of all *Euura* species studied are remarkably predictable, and are dominated by bottom-up effects through the plant hosts, with generally weak top-down effects from carnivores like parasitoid wasps, ants, and insectivorous birds. Population dynamics of *Pontania* gallers are less well understood, but in some species they are certainly less predictable, and with a much stronger role likely for top-down effects from carnivores. However, a few species may be *Euura*-like in their dynamics. The genus *Phyllocolpa* is even less well studied than *Pontania* in terms of population dynamics.

This paper attempts to develop a comparative approach to the understanding of the population dynamics in the three genera of galling sawflies. We admit that many questions remain unanswered, especially in the genera *Pontania* and *Phyllocolpa*, but we hope our approach will clarify the need for more studies and stimulate more comparative research on these genera. We will start with *Euura* sawflies which we have studied the most, and then move on in a more tentative way to *Pontania* and then *Phyllocolpa*. Generalizations are presented whenever the evidence permits, and concentration will be on studies in our research groups based in Arizona, USA, and North Karelia, Finland. More comprehensive treatments of the literature are provided in Clancy (1993) and Price and Roininen (1993).

CHARACTERISTICS OF EUURA SAWFLIES

In my research group we have studied *E. lasiolepis* in considerable detail. Collaboration in Finland on *E. mucronata* and *E. amerinae* has demonstrated how similar these are to *E. lasiolepis*. Studies on other *Euura* species indicate that all have a very similar set of characteristics which dictate their population dynamics. The characteristics can be summarized as four properties central to the ecology of *Euura* species, which are discussed next.

Strong Preference/Performance Linkage

In all galling sawflies the female places eggs and initiates gall formation exactly where the larva will live while feeding, or die in the attempt. In *Euura* sawflies there is a general and strong link between where the female prefers to oviposit and the performance of progeny in terms of larval survival. Preference is for the most rapidly growing shoots on young plants which, when growth in a season stops, prove to be the longest shoots on a plant, and on the plants with the longest shoots (Craig *et al.* 1986, 1989). If a full range of shoot length classes is sampled in a willow population, we invariably find a positive correlation between shoot length class and probability of attack by *Euura* sawflies (Table 1). Conversely, because mean shoot length in willows declines with age, there is a negative relationship between willow age and probability of attack. Note that in Table 1 all regression equations have a positive slope and the intercept is usually low (relative to a maximum probability of 1) and often negative. This results from lack of attack on the lowest shoot length classes. All the plant parts and host plant growth form utilized in the genus *Euura* are represented in the table.

Table 1.—Relationships between willow shoot length classes and probability of attack by *Euura* sawfly species

Euura species	Salix species and form	Gall type	Locality[a]	Regression equation[b]	R^2	P
amerinae	pentandra, tree	stem	J, F	$Y = -0.07 + (2.25E - 3)X$	0.92	0.01
atra	alba, tree	stem	J, F	$Y = -0.17 + (1.30E - 3)X$	0.91	0.01
exiguae	exigua, shrub	stem	U, U	$Y = 0.25 + (3.58E - 4)X$	0.51	0.05
lappo	lapponum, shrub	bud	K, F	$Y = 0.25 + (3.38E - 3)X$	0.62	0.05
lasiolepis	lasiolepis, shrub	stem	A, U	$Y = 0.06 + (4.78E - 3)X$	0.92	0.01
mucronata	cinerea, shrub	bud	J, F	$Y = -0.21 + (4.46E - 3)X$	0.95	0.01
unknown	lasiolepis, shrub	petiole	A, U	$Y = 0.33 + (3.65E - 3)X$	0.63	0.01
new sp.	exigua, shrub	midrib	A, U	$Y = -0.05 + (1.51E - 3)X$	0.76	0.01
new sp.	interior, shrub	stem	I, U	$Y = -0.04 + (8.48E - 4)X$	0.73	0.01

[a] Localities are indicated by a letter for a locality followed by a letter for the country: J, Joensuu; K, Kevo; F, Finland; A, Arizona; U, Utah; I, Illinois; U, USA.

[b] Regression equations: X = shoot length class; Y = probability of attack; E = exponent, for example (2.25E-3) = 0.00225. Low slopes result from high values for shoot length classes and probabilities of attack with a maximum of 1.

The longest shoot length classes which are preferred for attack usually occur very patchily in a landscape, resulting from disturbance such as land clearance, followed by regeneration, and serious damage to plants caused by heavy pruning, herbivore attack, or drought which kills older ramets (in Arizona). As willow stands age, mean shoot lengths decline and *Euura* sawflies become rarer. In fact, over a landscape, some *Euura* species may be viewed as rare insects because regeneration or damage is rare and aging effects of tree species are rapid (e.g. *E. amerinae* on the tree, *S. pentandra*). In contrast, some may be very common because their host species is common and shrubby growth retains some long shoots because of clonal growth and the production of juvenile shoots from basal dormant buds (e.g. *E. mucronata* on the shrub, *S. cinerea*). Abundance of these sawflies is dictated largely by the growth form of the host plant and the frequency of disturbance, coupled with the high preference/performance linkage between adult females and their progeny.

Highly Predictable Populations

Euura populations on shrubby willows are generally very predictable and stable because vigorous, juvenile shoots are produced as the shrub develops. Most *Euura* species utilize willows with a shrubby growth form. On willows with the stature of a tree, like *S. alba* and *S. pentandra*, plant aging has a stronger effect, and only juvenile trees or heavily damaged or pruned trees with rapid regrowth can be utilized by sawflies. In the latter case, *Euura* populations are predictable, but not stable. These two types of population dynamics will be illustrated by *E. lasiolepis* on the shrub *S. lasiolepis* in Arizona, and *E. amerinae* on the tree, *S. pentandra*, in Finland.

In its population dynamics, the arroyo willow stem-galling sawfly, *E. lasiolepis*, may illustrate one of the most predictable and stable species of insect herbivore ever described. Over a 10-year period in northern Arizona on a set of 15 willow clones, populations have changed more or less in unison with low amplitude per clone, but with large differences among clones. Clones in constantly wet environments have constantly high populations of stem gallers, and low populations are found in drier sites on old clones. Populations on these 15 willow clones, 10 years apart in 1983 and 1992, were highly correlated ($Y = 1.38X - 89.74$, $R^2 = 0.87$, $p < .01$). Populations in 1983 (X) accounted for 87 percent of the variance in populations 10 years later (Y). Correlations were not as strong in every comparison but they were always positive and usually significant (Table 2).

Table 2.—Correlations between years in populations of *E. lasiolepis* stem gallers on 15 clones in Flagstaff, Arizona[a]

Year	1983	1984	1985	1986	1987	1988	1989	1990	1991
1984	0.91**								
1985	0.99**	0.90**							
1986	0.89**	0.93**	0.89**						
1987	0.75**	0.94**	0.77**	0.89**					
1988	0.55**	0.80**	0.56**	0.76**	0.93**				
1989	0.66**	0.89**	0.66**	0.79**	0.96**	0.94**			
1990	0.85**	0.61**	0.84**	0.60**	0.40*	0.21	0.30* [b]		
1991	0.91**	0.70**	0.91**	0.72**	0.50**	0.30*	0.38*	0.98**	
1992	0.87*	0.64**	0.86**	0.63**	0.44**	0.25	0.33*	0.99**	0.98**

[a] Values of R^2 are given indicating the percent of variance accounted for. All values of R were positive. Significant correlations are indicated by * for $p < .05$ and ** for $p < .01$.

[b] The block of correlations accounting for less than 51% of the variance ($R^2 < .51$) is indicated by a dashed rectangle. A general drought during these three years, 1987-1989, resulted in weaker correlations with subsequent years, 1990-1992, because of interacting factors of willow dieback and other herbivores.

To test the effects of resource regulation on population size we increased the number of females on each of the 15 clones by caging females on branches. On all clones with low densities of galls, the number of galls increased dramatically compared to unaugmented population levels, but on the three clones with the highest populations of over 200 galls per four branches the female-supplemented populations hardly increased at all (Fig. 1). This result suggests that galling sites are close to being saturated in high populations but are much below carrying capacity on low-density clones. However, performance of larvae at the supplemented low-density sites was very poor, and sawfly emergence was correlated in control and treatment branches (Fig. 1). In general larvae performed less well in the supplemented populations presumably because females were forced to select sites that would have been rejected by free-ranging females.

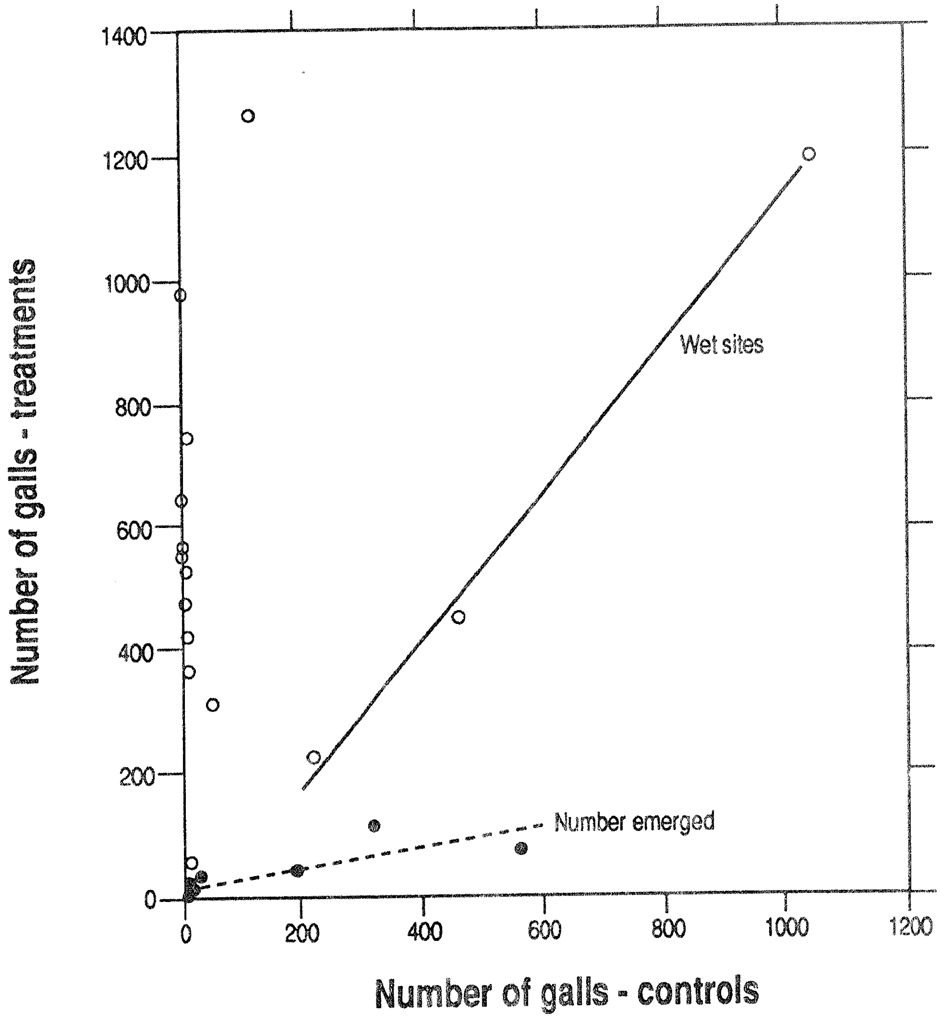

Figure 1.—The relationship between number of galls on natural branches and on branches supplemented with sawfly females of *Euura lasiolepis* - open circles for 15 clones. For the three clones with the highest sawfly populations, number of galls produced increased very little in treatments compared to the controls. The solid regression line for the three wet sites is $Y = 1.19X - 62.26$, $n = 3$, $R^2 = 0.99$, $p < .05$. The relationship between number of adults that emerged on treatment and control branches in the supplemented female experiment is indicated with solid circles and the dashed regression line $Y = 10.73 + 0.17X$, $n = 15$, $R^2 = 0.67$, $p < .01$. Most of the 15 data points are clustered close to the origin and are not shown individually. Note that although gall production in treatments was very high, production of adults was very low.

The population supplement experiment confirms the reasons for predictable and stable populations per clone. Suitable oviposition sites where larvae can perform well are limiting, and this sets a bottom-up limit on each clone on the carrying capacity for that clone. Competition for oviposition sites becomes limiting even at low populations (Craig *et al.* 1988, 1990a), and rapid negative feedback from competition between ovipositing females results in rapid population responses to change in clone quality after damage, or with soil moisture changes from year to year (Price and Clancy 1986a, Price 1992).

The bottom-up effects of the tree, *S. pentandra*, on *E. amerinae* are even stronger than for the example just described. This is because with a single trunk aging effects are stronger, being unmodified by the frequent production of vigorous juvenile shoots from dormant buds near the ground. This difference in plant architecture changes the nature of the sawfly population dynamics in a predictable way. Only very young trees can be colonized successfully, but they remain susceptible to attack for only a few years, and performance of larvae declines rapidly well before local extinction (Roininen et al. 1993) (Fig. 2). Population dynamics is predictable, but not stable, except perhaps at a landscape level of metapopulations.

Euura sawflies we have studied on other shrubby willows appear to have predictable and stable populations: *E. exiguae* (Price 1989), *E. mucronata* (Price *et al.* 1987a,b), and an undescribed midrib galler in Arizona (unpublished data). However, we have not censused populations for these species over the long term in order to establish this point with certainty.

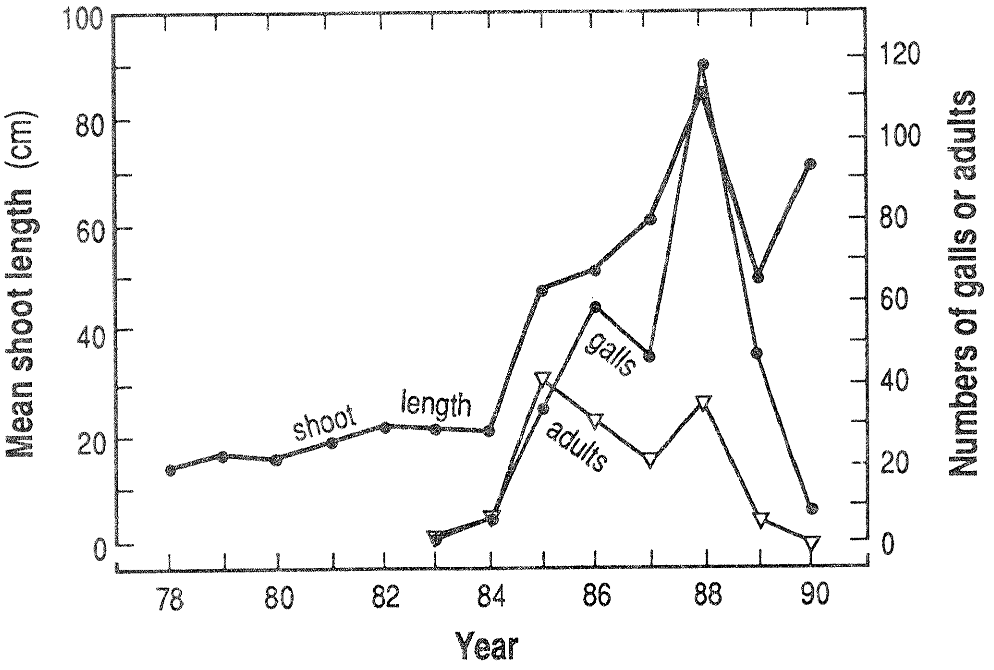

Figure 2.—The flush-crash population dynamics of *Euura amerinae* studied by Roininen *et al.* (1993). Note that although gall numbers increase in the population from 1982 to 1988, productivity of adults per gall decreases over this period from 2 per gall to 0.3 per gall, while growth of young trees was rapid. The year 1978 was the approximate time of establishment of the *S. pentandra* population in a newly disturbed site. In 1983 one gall was established by natural colonization and the population went extinct in the 1990 generation. Data are presented as results for the year a generation was started, so both number of galls and number of adults emerged are plotted in the same year, even though adults emerged in the spring of the year following gall initiation.

Weak Top-Down Effects

Effects from carnivores have been studied for *E. amerinae*, *E. exiguae*, *E. lasiolepis*, *E. mucronata* and the midrib galler. In no case do the carnivores account for the pattern of sawfly attack or survival, or the major features of population dynamics. In experiments with parasitoids present and absent for three generations *E. lasiolepis* populations remained the same (Woodman 1990, Price 1990).

For *E. lasiolepis* the reasons for weak top-down effects are well understood. For small parasitoids large galls provide a refuge for sawfly larvae from attack (Price and Clancy 1986b, Price 1988), and for larger parasitoids gall toughness is limiting (Craig *et al.* 1990b). In fact, the parasitoid community is dictated in subtle ways from the bottom up (Craig 1993). Each willow clone defines in its own way mean gall size, rate of gall growth and toughening, such that even clones side by side differ in the parasitoid species present in the community and their impact on the sawfly population (Craig 1993). Studies on the other *Euura* species have not been conducted in the same detail, but similar effects are probably involved.

In general, these three-trophic-level systems of willows, *Euura* sawfly gallers and parasitoids are driven from below, via plant quality as influenced principally by plant age, moisture supply in drier areas like Arizona, plant architecture, and other characters defining gall growth rate, size and toughness. In a sense, there are ramifying effects up the path of energy flow from plants to herbivores to carnivores, with very little passing downwards.

Resource Regulation

One effect that does pass down in the trophic system is from the herbivores to the plants. *Euura* species that gall stems and buds in fact perform the equivalent of pruning their host plants, resulting in stronger growth more favorable to sawflies. Craig *et al.* (1986) called this "resource regulation" because the sawfly population on favorable clones kept the clones in a more juvenile state than if the sawflies were absent.

Salix lasiolepis responds to heavy galling by *E. lasiolepis* by resprouting proximally to the clone base relative to the gall, because gall tissue is invaded rapidly by fungi causing necrosis and death (Craig *et al.* 1986). New proximate shoots may grow from branches several years nearer to the root stock than those that would have grown if unattacked by sawflies, and hence they grow more vigorously. *Euura mucronata* kills buds on *S. cinerea* reducing competition among new shoots for parental resources, such that the remaining shoots grow more strongly and are more heavily attacked by sawflies (Roininen *et al.* 1988). Such resource regulation contributes to the stability of populations in favorable sites, because clonal age effects, and water availability effects are mitigated by sawfly-induced pruning.

CHARACTERISTICS OF *PONTANIA* SAWFLIES

A major distinction between *Pontania* and *Euura* sawflies is that *Pontania* species gall leaves exclusively. Leaves seem to provide a substantially different resource when compared to stems, petioles and buds, most commonly utilized by *Euura* species. This shift in the resource base appears to change the ecology of the leaf gallers substantially, relative to *Euura* species.

Ten or more *Pontania* galls can develop on a leaf, whereas at a node only one *Euura* gall would be formed, be it on the internode of the stem, the bud, petiole, or midrib. Hence, the resource base is much higher for *Pontania* than for *Euura*. In addition, female *Pontania* near *pacifica* sawflies were not selective for larger leaves in a willow clone, although they did lay more eggs per leaf on leaves that would become larger (Clancy *et al.* 1993). Large galls can develop on small leaves, and only a weak correlation between leaf size and gall size was found by Clancy et al. (1993). *Pontania* can become abundant on clones with ramets too old for high *Euura* populations, and early in the attack a positive correlation between shoot length and probability of attack may be found (Table 3). These three characteristics of the multiple galls per leaf, the weaker preference of females, and the utilization of older and larger clones indicate that the resource base for *Pontania* is much higher than for *Euura*. This is likely to result in a weaker bottom-up influence from the plant host, and probably less predictable populations because other factors are likely to become important.

Table 3.—Relationships between willow shoot length classes and probability of attack by *Pontania* and *Phyllocolpa* species

Species	Species and form	Gall type	Locality[a]	Regression equation[b]	R^2	P
Pontania nr pacifica	S. lasiolepis, shrub	leaf gall	A, U	Y = -0.07 + 0.01X	0.90	0.01
Pontania pustulata	S. phylicifolia, shrub	leaf gall	J, F	Y = 0.04 + (2.98E - 3)X	0.78	0.01
Phyllocolpa coriacea	S. cinerea, shrub	leaf fold	J, F	Y = -0.06 + (1.56E - 3)X	0.86	0.01
Phyllocolpa excavata	S. pentandra, tree	leaf fold	J, F	Y = 0.19 + (1.05E - 3)X	0.51	0.01
Phyllocolpa sp.	S. lasiolepis, shrub	leaf fold	A, U	Y = 0.07 + 0.01X	0.87	0.01
Phyllocolpa sp.	P. tremuloides, tree	leaf fold	A, U	Y = 0.04 + (2.18E - 3)X	0.70	0.01

[a] Localities are designated as in Table 1.
[b] Regression equations are in the form explained in Table 1.

Indeed, most studies on *Pontania* species have described heavy mortality by natural enemies including parasitoids and inquilines that kill the galler (Clancy 1993). Clancy and Price (1989) found that natural enemies caused two times more death of larvae than plant resistance factors and over six times more death than intraspecific competition. In the Flagstaff area, mortality caused by natural enemies on early cohorts of larvae in the season was so high that it was hypothesized that sawfly phenology was delayed in this area relative to others where enemies had weaker effects (Clancy and Price 1986).

Mortality from natural enemies on *Pontania* near *pacifica* was overall not strongly selective in relation to leaf area on which attacked galls were situated (Clancy *et al.* 1993). However, galls that developed rapidly and grew to a larger size were increasingly liable to attack by parasitoids, up to 100 percent in the largest gall diameter classes (Clancy and Price 1987). Such selective attack must tend to stabilize gall size below the optimum for sawfly development, and perhaps reduce the advantage to females of any preference that results in higher larval performance.

The potential for natural enemies to play important roles in the local evolution of *Pontania* is high, but whether they play an important role in population dynamics has yet to be determined. Ants can practically eradicate *Pontania* near *pacifica* in very local sites defined by constant water supply from springs (Woodman and Price 1992) but these sites are too infrequent in Arizona to be of general importance.

In general, the three-trophic-level interactions for *Pontania* appear to be more complex than for *Euura*. The gall of *Pontania* provides less of a refuge from attack by carnivores than the *Euura* gall. The *Pontania* gall is relatively thin walled with little woody tissue, while the *Euura* stem gall includes considerable xylem, and the rest is solid parenchyma through which the larva bores. Thus, *Pontania* appears to be under the influence of much weaker bottom-up effects from the plants, than for *Euura*, and much stronger top-down effects from natural enemies.

In Flagstaff, *Pontania* near *pacifica* populations have cycled, with strong density changes over the last 15 years. Populations were very high in 1979 to 1981 and then declined until they were hard to find by 1987, and since then they have been increasing steadily. Unfortunately, we have not censused populations through these 15 years, but it is clear that populations are more variable than *Euura* in the same localities.

The situation we have described for *Pontania* near *pacifica* may represent the more general case in the genus. However, there are *Pontania* species, such as *P. pustulata*, which associate strongly with young plants after disturbance. Their ecology may well have a strong bottom-up component, but unfortunately no three-trophic-level studies have been published on these kinds of species.

CHARACTERISTICS OF *PHYLLOCOLPA* SAWFLIES

Phyllocolpa sawflies all cause folding of leaf edges or curling of leaves and the larva feeds within the fold or curl. They are usually grouped with the galling sawflies because of their close taxonomic affinity and slight differential swelling of the leaf results in the fold. Leaf length defines the length of the fold and the amount of food available to the larva, so short leaves are not attacked frequently. Understandably, longer shoots with larger leaves have a higher probability of attack than shorter shoots in the four species we have studied (Table 3). Fritz and Noble (1989) found the same relationship. The leaf curling or rolling species, such as *P. nudipectus* on *S. phylicifolia*, seem to need more vigorous growth than the folders, although no detailed studies have been completed.

Fritz and Noble (1990) found very variable survival of a *Phyllocolpa* species over 3 years, principally because of increasingly strong effects by predators and parasitoids, with mean survival shifting from 34 percent in 1984 to 1.5 percent in 1985, and 1.1 percent in 1986. Such heavy and variable mortality from carnivores suggests that natural enemies may play an important part in the population dynamics of *Phyllocolpa* species. In addition, many small herbivorous insects use folds and rolls as feeding sites, and incidentally cause the death of the sawfly larva. Thysanopterans, aphids and small heteropterans can be found in high frequencies in leaf folds in some populations, apparently with heavy impact on sawfly survival.

DISCUSSION

Euura species appear to be very different from the other genera of galling sawflies in their three-trophic-level interactions and population dynamics. Strongly dominated by bottom-up effects through plant quality variation, these species have been relatively easy to study and understand. Response to variation in plant architecture and plant age is very strong in the form of strong preference/performance linkage. Coupled with resource regulation, the effect on population dynamics is very stabilizing. Top-down effects are weak from carnivores, and these systems become simple as a result.

The proximate, mechanistic explanation for the need in *Euura* species for rapidly growing, vigorous, juvenile plants is not understood yet. Studies are needed. In all species the larva is closely associated with plant parenchyma in the gall when it hatches from the egg because the larvae must tunnel through solid parenchyma tissue in the gall. This stage is the determining phase in larval survival. Very high mortality can occur just as the larva emerges from the egg in plants with depressed vigor (Preszler and Price 1988, Price 1992). Our suspicion is that water balance between gall tissue and the newly hatched larva is critical.

The nature of the gall in these genera may be a crucial difference in their ecologies. *Pontania* larvae emerge from the egg into a cavity in the gall and do not tunnel through parenchyma cells. *Phyllocolpa* larvae hatch into a leaf fold and feed from the external surface of the leaf, even though enfolded. This reduced intimacy between plant tissue and hatchling larvae may have ramifications on the evolution of preference/performance linkage, and vulnerability to natural enemies, and be the defining characteristic resulting ultimately in differences in population dynamics.

Just how *Euura* has evolved into such relatively effective enemy-free space is not clear in all cases. Craig (1993) made a convincing argument for the stem galler, *E. lasiolepis*, that gall size and toughness are very limiting on parasitoid attack. This case pertains to the other stem gallers, no doubt. But bud, petiole and midrib galls are smaller and less woody, and larvae could be expected reasonably to be as vulnerable as *Pontania* larvae. However, mortality caused by parasitoids remains relatively low (Price and Pschorn-Walcher 1988).

The case of the *Euura* gallers raises the interesting question of what characteristics in a woody plant are changing with age. Two processes were distinguished by Kearsley and Whitham (1989): irreversible, genetically defined, ontogenetic aging, and reversible physiological aging. Practically, these are hard to separate, but in the case of *E. amerinae*, plant age effects became so strong, before growth rate declined noticeably, that ontogenetic aging was suspected by Roininen *et al.* (1993). Hence, the precise physiological mechanisms remain a mystery at present. These are of considerable interest as resistance factors in woody plants.

A certain kind of "ecological freedom" seems to have been attained by galling leaves, in the genera *Pontania* and *Phyllocolpa*. Leaves, as resources, appear to be less limiting than stems and buds. However, freedom from bottom-up control has its liabilities because top-down effects become much stronger. The balance between plant effects and enemy effects becomes harder to understand, so we have not made as much progress with the genera other than *Euura*.

However, obtaining a clear understanding of *Euura* sawfly ecology, apparently so uniform across all members of the genus, does provide a basic and perhaps extreme case of a bottom-up system, from which a comparative ecology can develop. We wish to understand the other galling genera better, and to use the comparative approach also to study the free-feeding tenthredinid sawflies on plants in the family Salicaceae.

Interesting differences in population size and stability are notable among the *Euura* species. *Euura mucronat* on the shrub *Salix cinerea* may be one of the most common herbivorous insects in Finland. In the same geographic a *Euura amerinae* on the tree *Salix pentandra* is a rare insect. Members of the genus in Arizona are uncommon in gen and lie between the two extremes noted in Finland. We predict that host plant ecology and architecture are critical in explaining these differences. *Salix cinerea* is very common in moist sites in Finland, and its strongly clonal, shrubby habits keep a supply of vigorous ramets available to *E. mucronata* over a long period of time, perhaps for decades. *Salix pentandra* is a less common willow, and its tree form limits availability to *E. amerinae* to a brief residence time of less than a decade in any one population. In Arizona, the relatively dry climate restricts willows usually to narrow riparian belts or springs, and even here some streams are ephemeral and leave many willows in a population too dry for vigorous growth when older and for sustained attack by *E. lasiolepis* and the *Euura* petiole galler. *Salix lasiolepis* is less strongly clonal than *S. cinerea*, resulting in a less abundant supply of vigorous ramets. This prediction will have to be tested on a landscape level so that the relative abundance and distribution of the different host plant species and sawflies can be compared directly. For each plant species the density of modules like shoots, petioles or buds suitable for attack would have to be estimated also.

Another prediction we can make is that population variation in the genera *Pontania* and *Phyllocolpa* will be greater than in *Euura* on the same shrubby willow species. This is for the reasons explained above. An extension of this prediction is that *Phyllocolpa* will generally remain closer than *Pontania* in its population dynamics to *Euura* on the same host willow because large leaves develop on long stems, so the resources needed by *Phyllocolpa* and *Euura* are similar. For example, *Euura amerinae* and *Phyllocolpa excavata*, both utilizing the tree *Salix pentandra*, should be expected to have similar population dynamics in the absence of natural enemies and competitors. However, in natural populations *Phyllocolpa* would normally be less predictable than *Euura* because of carnivores and competitive inquilines.

We think that working from known ecologies to predictions on related species is an important aspect in the development of generalizations and factually based theory on plant-herbivore-carnivore interactions. Further collaborative and strongly comparative studies on the galling sawflies may permit such theory to emerge for this group encompassing about 200 species.

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DOES THE WILLOW BUD GALLER, EUURA MUCRONATA, BENEFIT FROM HARE BROWSING ON ITS HOST PLANT?

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Abstract. We tested the impact of winter browsing by mountain hares *Lepus timidus* on the food resources and performance of the bud galler, Euura mucronata, on *Salix cinerea.* We demonstrated an indirect effect of hare feeding on an unpruned ramet when surrounding ramets were pruned, and a direct effect after pruning the same ramet. In the field, browsed ramets had the same or fewer number of total buds, and the same or a higher number of attacked buds as unbrowsed ramets. However, the survival of larvae was always the same on browsed and unbrowsed ramets. In experiment I, when all other ramets in a clone except one were pruned, the unpruned ramet had a higher number of buds, and a higher number of attacked buds. When pruned ramets were growing with unpruned ones, they provided a low amount of resources. Pruned ramets growing with other pruned ramets, and unpruned ramets growing with other unpruned ramets had similar amounts of resources and produced similar numbers of sawfly larvae. In experiment II, when the leading shoots of ramets were pruned, there was no pruning effect in the 25% and 50% shoot removal treatments, but there was a slight negative effect on resources and *E. mucronata* when 75% of leading shoots were removed. In general, hare browsing had a positive or neglible effect on resources and performance of *E. mucronata.* Our results also indicate that indirect effects of hare browsing may be more important than direct effects.

INTRODUCTION

Browsing by hares (Bryant 1981; Bryant *et al.* 1992) and moose (Danell and Huss-Danell 1985; Bergström and Danell 1987) has been shown to induce a growth reaction in many deciduous trees and shrubs. New shoots induced by feeding damage are longer (Danell and Bergström 1989) and are extremely unpalatable to hares (Bryant 1981). Danell and Huss-Danell (1985) found that many insects were more abundant on browsed than unbrowsed birch, but Neuvonen and Danell (1987) did not observe any differences in performance of *Epirrita autumnata* between browsed and unbrowsed birch.

Stem and bud galling sawflies of the genus *Euura* (Hymenoptera: Tenthredinidae) attack young, vigorous willow (*Salix* spp.) plants and long, fast-growing shoots (Craig *et al.* 1986, 1989; Price *et al.* 1987 a,b; Roininen *et al.* 1988; Price 1989; Price and Roininen 1993). Attack by these sawflies often stimulates the growth of their host plants and thus maintains or increases the high quality of food for subsequent generations. Survival of *Euura* larvae is better on long, fast-growing shoots of willows (Craig *et al.* 1986, 1989; Price *et al.* 1987b; Roininen *et al.* 1988).

In the boreal forests of Scandinavia, willows are winter food for the mountain hare, *Lepus timidus*, (Pulliainen 1972; Helminen *et al.* 1984; Tahvanainen *et al.* 1985). Some willow species, e.g. *S. caprea, S. cinerea* and *S. phylicifolia*, are often extensively browsed year after year. Consequently the juvenile, fast-growing, shrub-like growth form can be maintained by hares for 5 or more years. The growth reaction of willows stimulated by hare browsing is similar to that induced by sawfly attack. Attack by sawflies and hares is equivalent to pruning, well known to increase plant vigor and juvenility of shoots. Therefore, it is possible that there is an asymmetrical positive interaction between these two ecologically and taxonomically very different herbivorous animals.

We posed the following questions: (1) How do *Salix cinerea* ramets react to browsing by mountain hares? (2) Does browsing by hares increase the quality or quantity of food resources for the bud galling sawfly, *E. mucronata*? (3) Do ovipositing *E. mucronata* adults prefer new shoots on browsed branches compared to those on unbrowsed branches? To answer these questions we studied three populations of *S. cinerea* ramets which were partly browsed by mountain hares. We also conducted two experiments in which we studied direct and indirect effects of browsing separately.

MATERIALS AND METHODS

Life History

E. mucronata is a very common herbivore on *S. cinerea* in S.E. Finland (Price *et al.* 1987a, b). Females oviposit on young growing shoots, piercing through petiole bases into axillary buds, and causing galls to form in the bud (Price and Roininen 1993). The larvae live through the summer in the galled buds and in late autumn they leave the galls and overwinter in the soil. The galls and emergence holes in them can be recognized easily after the growing season.

Field Studies

In 1988, we studied three populations of *S. cinerea* ramets, which had extensive hare browsing during the preceding winter of 1986/87. All three study sites, situated in Eastern Finland, were typical habitats of *E. mucronata.* The three *S. cinerea* populations were located in Linnunlahti, a district within the town of Joensuu, in Savonranta about 70 km southwest of Joensuu, and in Kelvä about 50 km north of Joensuu. The Linnunlahti site was typical boreal forest where *S. cinerea* is found as sparse stands in the shrub layer under open scots pine forest. The Savonranta and the Kelvä sites were small bogs, where *S. cinerea* grows on the edges.

At each site 22-33, branches of hare-browsed and unbrowsed ramets were taken randomly from the upper parts of *S. cinerea* clones. Browsed and unbrowsed branches were always taken from the same clones and they were not significantly different in age (Mann-Whitney U-test, $P>0.05$). At Linnunlahti, branches were sampled from 22 clones, at Savonranta from eight clones and at Kelvä from four clones. The ramets at Linnunlahti and Kelvä were 12-17 years-old, but those at Savonranta were just 2-years-old.

In this study we defined the branch as a unit containing the shoots formed in two previous years; the unbrowsed or browsed 2-year-old shoot with current year shoots. Browsed branches were always consumed during the previous winter and unbrowsed branches had been untouched at least for two winters.

We took samples late in the autumn after the fully developed *Euura* larvae had emerged from the galled buds. The following measurements were made on the branches: mean length of all shoots, number of shoots, number of buds, number of abscised shoots during the current growing season, number of attacked buds per branch, number of emerged larvae per branch, percent of buds attacked and survival of larvae. The emergence holes in the galled buds indicated successful development of larvae through the completed feeding period.

In Linnunlahti forest and the Kelvä site, the intensity of hare browsing was estimated by measuring the amount of browsing on the main stem of ramets within the last five years: the length of the remaining stubs and unbrowsed shoots of the previous growing season. Hares had always browsed less than 100% of the growth of the preceding year.

Experimental Studies

We did two experiments to estimate effects of hare browsing on the ramets of host plants and on the quantity and quality of resources for *E. mucronata.* In Experiment I we studied the indirect effects of browsing. We used 2-year-old clones growing under pines at Linnunlahti. These clones had from 5 to 12 separate ramets growing from the same root stock. We had two browsing-intensity levels: in the low-intensity-browsing treatment we pruned one ramet per clone and left others untouched, and in the high-density-browsing treatment we pruned all except one ramet (Fig. 1). Pruning involved removal of 75% from the length of individual shoots. Our pruning method mimics real hare browsing well because hares sharply cut shoots with their incisors, as did our pruning shears. On browsed ramets all current year shoots were pruned. Pruning was done in March, 1989, when willows are inactive and hares use them as a normal part of their winter diet.

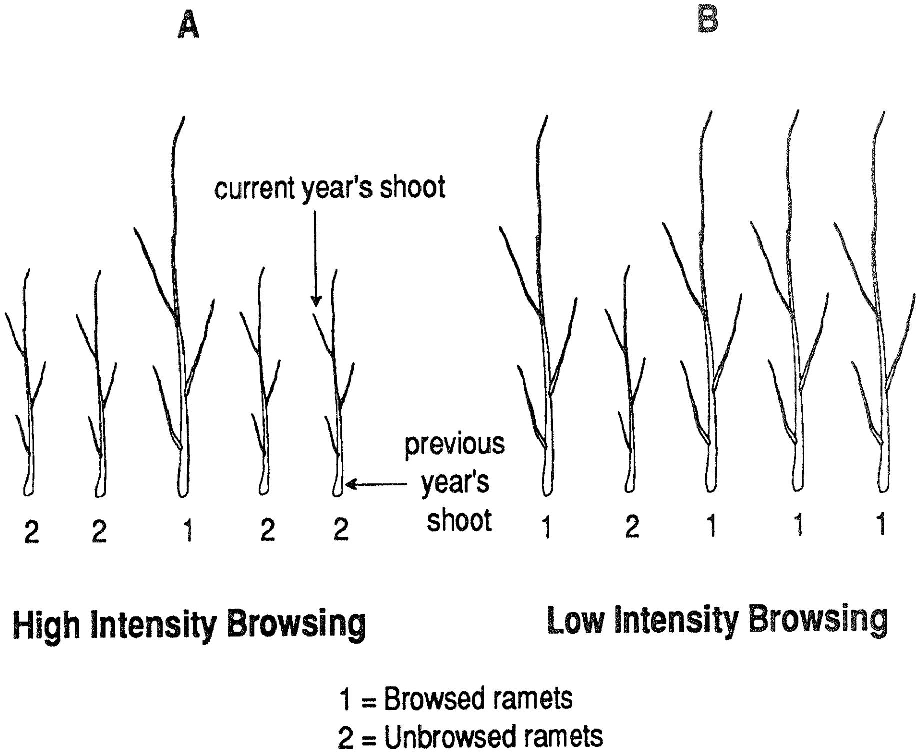

Figure 1.—Illustration showing high (A) and low (B) intensity pruning treatments in Experiment I.

After one growing season when *E. mucronata* had finished development on the new shoots formed after pruning, we measured the following variables: total buds, attacked buds, number of emerged larvae, mean shoot length, number of new shoots and number of abscised shoots. All measurements were per experimental unit, i.e. branch (defined above). Data were collected from the tops of ramets so that results were fully comparable to field results and the second experiment.

In Experiment II we used from 12- to 17-year-old ramets. In the browsed treatment we pruned only the leading shoot of the ramet and left others untouched. Four treatments (25%, 50%, 75% of leading shoot of ramets removed and control) in different ramets of the same clone were established, and replicated in 22 clones. By this experimental design (genets of willows as blocks) we were able to eliminate clonal variation when differences between treatments were analyzed. This design was necessary because earlier studies emphasized the importance of genetic or environmental among-clone variation (Fritz *et al.* 1986; 1987; Fritz and Price 1988; Fritz 1990; Fritz and Nobel 1990). All the same measurements were taken on these treatments as in Experiment I.

Statistical Analyses

For the observational study we used oneway ANOVA separately for each study site. The Mann-Whitney U test was used if the distribution of variables was not normal. Individual branches of willow clones were replicates in our study, and values or mean values for each branch represented independent observations in the statistical analyses (cf. Hurlbert 1984). For the data from Experiment I we used two-way ANOVA with fixed factors of hare browsing (yes and no) and intensity of browsing (high and low). In Experiment II we used a randomized block design where willow clones were blocks having all treatments within one block (clone) (Sokal and Rohlf 1981). When the ANOVA indicated differences between treatments, we employed Tukey tests for multiple comparison. Multiple comparisons were considered significantly different when P was ≤ 0.05.

RESULTS

Responses of Branches to Browsing in the Field

Mean shoot length was significantly longer on the browsed than unbrowsed branches in all populations of *S. cinerea* (Fig. 2a, Linnunlahti; ANOVA, $F_{1,53}=24.19$, $P<0.001$, Savonranta; ANOVA, $F_{1,60}=45.99$, $P<0.001$, Kelvä; ANOVA, $F_{1,57}=43.84$, $P<0.001$). There were significantly more shoots on the browsed branches in Linnunlahti (Mann-Whitney U test, $P<0.05$) and Savonranta (Mann-Whitney U test, $P<0.001$) sites (Fig. 2b). The number of buds per branch was significantly different on unbrowsed and browsed branches only at the Kelvä site (Fig. 2d, ANOVA; $F_{1,57}=9.75$, $P<0.01$). Numbers of abscised shoots were significantly higher on the unbrowsed than on the browsed branches (Fig. 2b, Mann-Whitney U test, $P<0.05$ in all sites). The shoots which were abscised during the summer grew from the base of the last year's shoots and were very short. However, they started to grow synchronously with other shoots (Roininen *et al.* 1988).

Responses of *E. mucronata* to Browsing in the Field

Numbers of attacked buds and emerged larvae were significantly higher on the browsed branches at the Kelvä site, but at Linnunlahti and Savonranta there were no differences between the treatments (Fig. 3a,b, Kelvä; ANOVA for attacked buds, $F_{1,57}=10.05$, $P<0.01$ and Mann-Whitney U test for emerged larvae, $P<0.01$). The percentage of attacked buds was significantly higher on browsed branches in two study sites (Fig. 3c, Savonranta; $F_{1,60}=3.84$, $P=0.055$, and Kelvä; ANOVA, $F_{1,57}=11.51$, $P<0.01$). The survival of larvae was slightly higher on browsed branches at all three sites, but differences were not significant (Fig. 3d, ANOVA separately for each site, $P>0.05$).

Intensity of Hare Browsing

Long term browsing intensity was measured at the Linnunlahti and Kelvä sites. The proportion of ramets which had not been browsed at all within the last 5 years was 56 and 12% in Linnunlahti and Kelvä, respectively (Table 1). In Linnunlahti the proportion of repeatedly browsed ramets was relatively low (Table 1). In Kelvä 17% of ramets were browsed in all 5 successive years. The proportion of annually browsed ramets varied from 13 to 42 and from 56 to 60 at Linnunlahti and Kelvä, respectively (Table 2).

Indirect Effects of Browsing (Experiment I)

There were large differences in measured variables of ramets which may be important for *E. mucronata* at the individual and population levels. Mean length of shoots was longer in browsed ramets than in unbrowsed ramets (Fig. 4a; ANOVA, $F_{1,28}=3.897$, $P=0.058$), but there were no differences in high and low intensity browsing (Fig. 4a; ANOVA, $F_{1,28}=2.228$, $P>0.10$). The numbers of buds on unbrowsed branches was higher than on browsed ones (Fig. 4b; ANOVA, $F_{1,28}=42.077$, $P<0.001$), but in the low intensity browsing both ramets, browsed and unbrowsed, had lower numbers of buds (Fig. 4b; ANOVA, $F_{1,28}=15.905$, $P<0.001$). There were higher numbers of shoots in unbrowsed ramets (Fig. 4c; ANOVA, $F_{1,28}=41.089$, $P<0.000$) and the number of shoots was differently affected in high and low intensity browsing (Fig. 4c: interaction between browsing and intensity of browsing, ANOVA, $F_{1,28}=6.422$, $P<0.05$). Browsing reduced strongly the numbers of abscised shoots per branch (Fig. 4d; ANOVA, $F_{1,28}=11.689$, $P=0.002$).

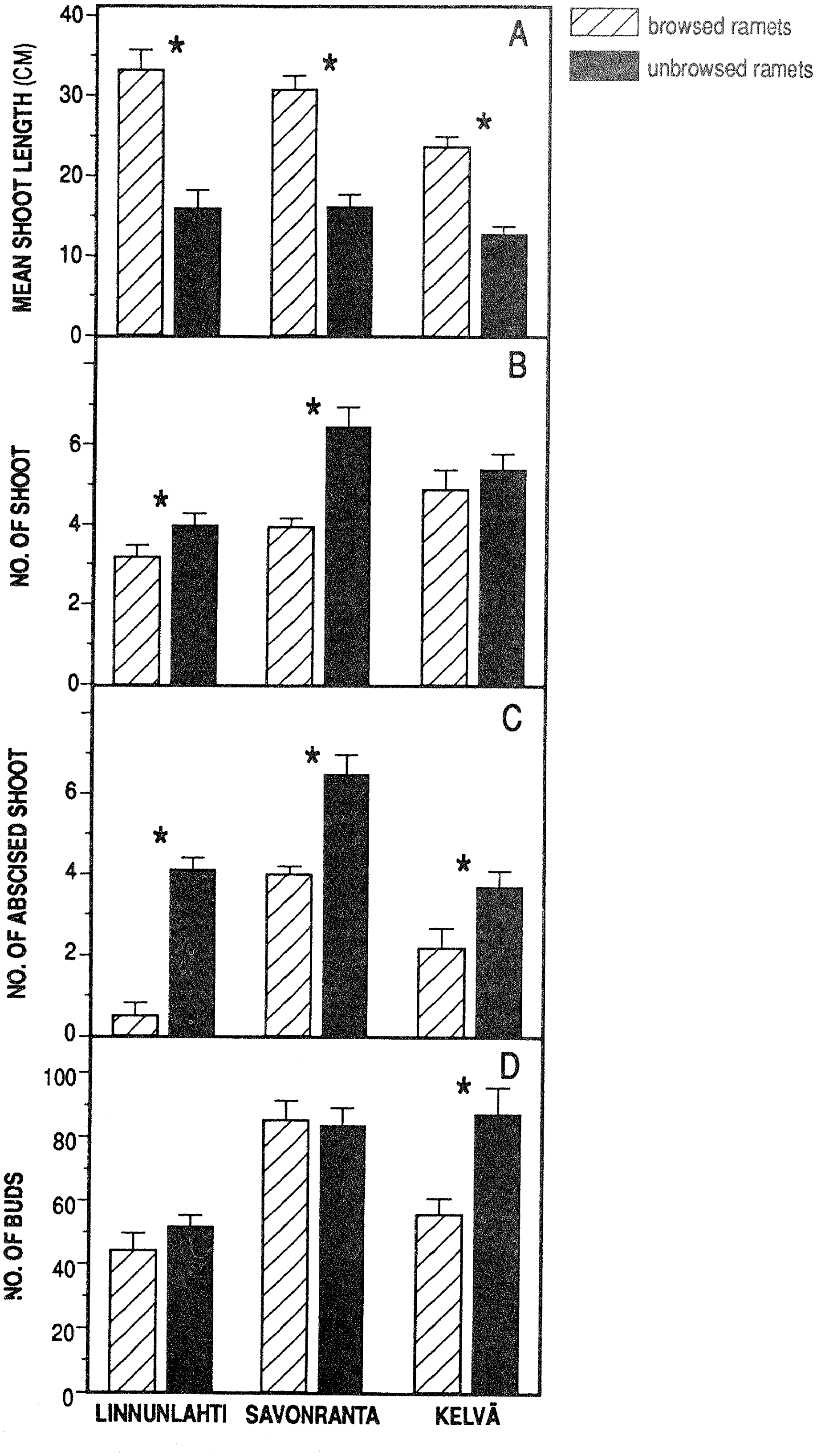

Figure 2.—The mean length of shoots (A), number of shoots (B), number of the abscised shoots (C) and number of buds (D) on browsed and unbrowsed branches of *Salix cinerea* in Linnunlahti, Savonranta and Kelvä sites. The thin black lines represent 1 SE. *=P<0.05.

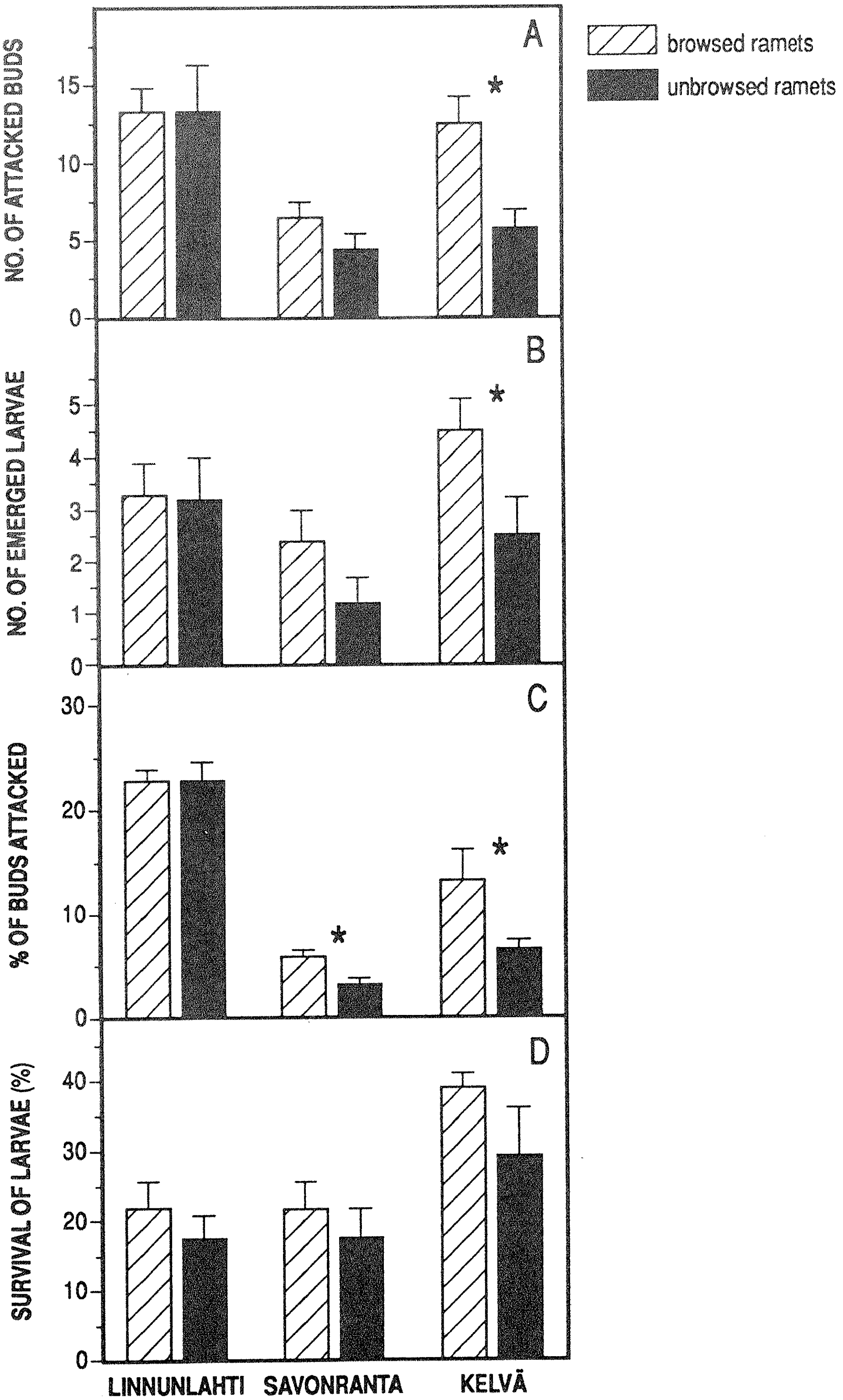

Figure 3.—Numbers of attacked buds (A), numbers of emerged larvae (B), percent of buds attacked (C) and survival of larvae (D) on browsed and unbrowsed branches of *Salix cinerea* in Linnunlahti, Savonranta and Kelvä sites. The thin black lines represent 1 SE. *=P<0.05.

Table 1.—The number of times ramets have been browsed by hares in the last 5 years in Linnunlahti and Kelvä based on 119 and 113 samples of ramets, respectively

Number of times browsed in 5 years	Percent of ramets browsed	
	Linnunlahti	Kelvä
1	16	18
2	14	23
3	6	18
4	3	12
5	0	17

Table 2.—Annually browsed ramets during 5- year period in Linnunlahti and Kelvä based on 119 and 113 samples of ramets, respectively

Browsing year	Percent of annually browsed ramets	
	Linnunlahti	Kelvä
1987	42	57
1986	31	56
1985	19	60
1984	15	57
1983	13	58

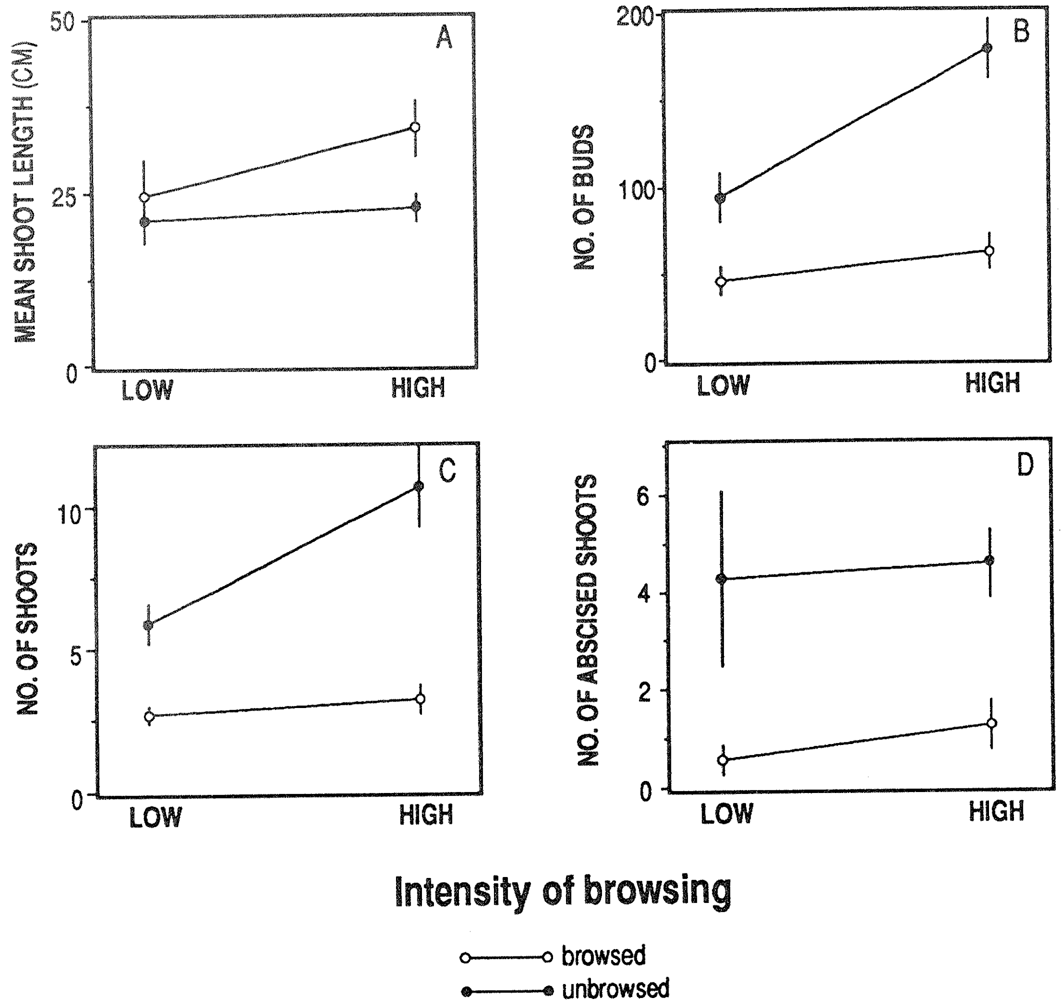

Figure 4.—The effect of browsing treatment (browsed, unbrowsed) and intensity of browsing (high and low) on mean length of shoots (A), total number of buds (B), number of shoots (C) and number of abscised shoots (D) in the branches of ramets. The vertical black lines represent 1 SE.

Browsing also affected the total and relative attack and performance of *E. mucronata*. The total number of attacked buds on ramets was affected by the presence and intensity of browsing (Fig. 5a; ANOVA, $F_{1,28}$=16.894, P<0.001 and $F_{1,28}$=10.805, P<0.01, respectively). Unbrowsed ramets in the high intensity browsing environment had about a 3-fold higher rate of attack than browsed ramets, but there were no differences between browsed in high intensity browsing and unbrowsed in low intensity browsing (Fig. 5a). Intensity of browsing significantly affected the percentage of buds attacked (Fig. 5b; ANOVA, $F_{1,28}$=4.881, P<0.05) but browsing had no effect (Fig. 5b; ANOVA, $F_{1,28}$=0.440, P>0.10). Both unbrowsed and browsed ramets had a higher probability of attack in the high intensity browsing environment (Fig. 5b).

Numbers of emerged full grown larvae were affected also by browsing and browsing intensity (Fig. 5c; ANOVA, $F_{1,28}$=10.063, P<0.05 and $F_{1,28}$=4.004, P<0.05). The highest numbers of emerged larvae were produced on unbrowsed ramets in the high intensity browsing environment but there were no differences between other treatments (Fig. 5c). There was high variability in survival, so the higher means in the high intensity browsing are not statistically significant (Fig. 5d).

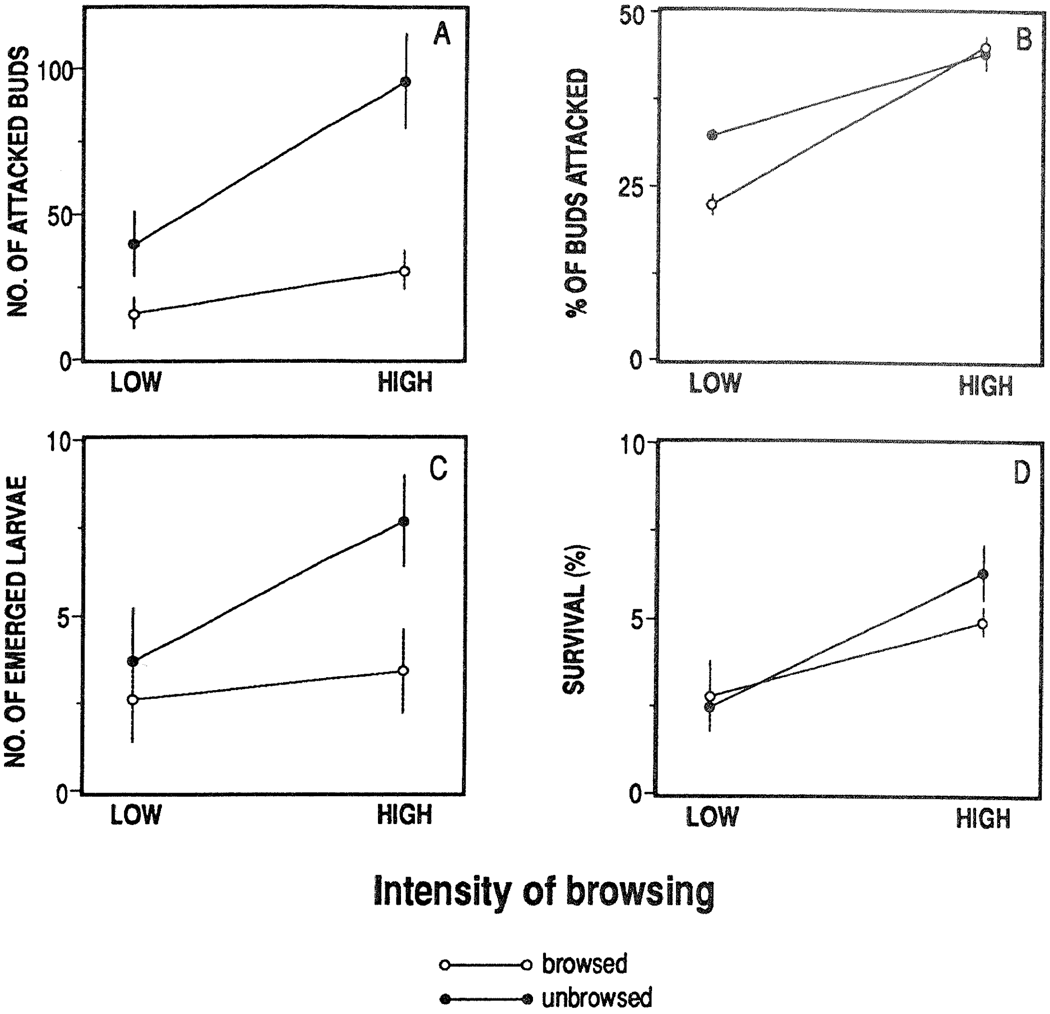

Figure 5.—The effect of browsing treatments (browsed, unbrowsed) and intensity of browsing treatments (high and low) on number of attacked buds (A), percentage of buds attacked (B), number of emerged larvae (C) and percent of larval survival (D) in the branches of ramets. The vertical black lines represent 1 SE.

Browsing Effects Within Clones (Experiment II)

Clonal variation was significant and explained a relatively high proportion of the variance in the following characteristics of branches; mean shoot lengths, total numbers of buds, numbers of abscised shoots, numbers of attacked buds, but not in numbers of shoots produced (Table 3). All measured performance characteristics of *E. mucronata* also showed significant clonal effects (Table 3).

In Experiment II mean shoot lengths were slightly but only significantly affected by browsing treatments (Fig. 6a; $F_{3,62}$=4.153, P<0.05). Highest numbers of buds were produced in the control, and the number of buds decreased with increased browsing (Fig. 6b; ANOVA, $F_{3,63}$=22.014, P<0.001). Number of shoots and number of abscised shoots followed the same pattern having the highest numbers on control ramets (Fig. 6c,d; ANOVA, $F_{3,62}$=17.389, P<0.001 and $F_{3,62}$=23.687, P<0.000, respectively).

The total number of attacked buds was similar in the control and slightly (25%) browsed ramets, but was lower on heavily browsed ramets (Fig. 7a; ANOVA, $F_{3,62}$=4.676, P<0.01). Buds in the control treatment had the lowest probability of attack, and attack rates were similar in all browsed treatments (Fig. 7b, ANOVA, $F_{3,62}$=7.966, P<0.001). Number of emerged larvae and larval survival were not significantly different in control and browsing treatments (Fig. 7c,d; ANOVA, $F_{3,62}$=2.309, P=0.085 and $F_{3,62}$=0.005, P>0.10, respectively).

Table 3.—Explained variances (R^2) and p-values of clone effect on measured characteristics of branches and performance of *E. mucronata*. Explained variance for number of abscised shoots was tested after logaritmic transformation (LN(X+1)).

Variable	R^2	P-value
In willow branches		
Mean shoot length	0.41	0.003
Number of buds	0.40	0.001
Number of shoots	0.14	0.586
Number of abscised shoots	0.35	0.007
In performance of *E. mucronata*		
Number of attacked buds	0.43	0.001
Percent of attacked buds	0.49	0.001
Number of emerged larvae	0.65	0.001
Survival	0.58	0.001

DISCUSSION

Winter browsing by the mountain hare and the pruning induced a growth reaction in the damaged branches characterized by an increase in mean length of shoots and decrease in numbers of abscised shoots and in the number of shoots produced (Figs. 1, 3 and 5). The total number of buds produced was similar on browsed and unbrowsed branches in the field. In the browsing experiment, only the heavily (75% of shoot length removed) pruned treatment had a significantly lower number of buds (Fig. 6b). In addition, browsed branches in the high intensity browsing treatment had the same number of buds as unbrowsed branches in the low intensity browsing (Fig. 4b). Thus it seems that hare browsing on the ramets of *S. cinerea* does not increase the total amount of resources for *E. mucronata*, but it may increase the quality of resources because the mean length of shoots was longer on browsed branches. Long, fast-growing shoots have been shown to be more preferred for oviposition by *Euura* species (Craig *et al.* 1986; Price *et al.* 1987b; Price 1988; Kolehmainen *et al.* manuscript in prep.). Several other studies have shown that plants overcompensate for biomass loss following herbivory when compared with unbrowsed plants (see references in Whitham *et al.* 1991, Belsky *et al.* 1993 and Hjältén *et al.* 1993). But there are no studies showing how this increase in biomass correlates with quantity and quality of resources of any insect herbivores.

We found that the intensity of browsing had strong indirect effects; unbrowsed ramets when growing in the high intensity browsing environment were the superior resource for *E. mucronata*. They had the highest number of attacked buds and emerged larvae. Browsed ramets in the low intensity browsing environment provided lower quality and quantity of resources (Fig. 5a,b). Thus the intensity of hare browsing had strong indirect effects on unbrowsed ramets. Unbrowsed ramets growing with browsed ones in the same clone, grew in good light conditions and may be sinks for nutrients from other ramets which are not growing as vigorously. On the other hand, browsed ramets in the low browsing environment may be shadowed and outcompeted by numerous other unbrowsed ramets in the same clone. Because we studied extreme ends of the continuum in feeding intensities we cannot compare directly our results from the field and from the browsing-intensity experiment. However the different browsing effects found in the field study and in the experiment emphasize that the relationships between browsing intensities and performance of *E. mucronata* are not linear on browsed and unbrowsed ramets.

Browsed branches were more heavily attacked in two of three sites in the field (Fig. 3a,b) and the browsing experiment (Fig. 7b). Although the total number of attacked buds were almost the same on the unbrowsed and browsed

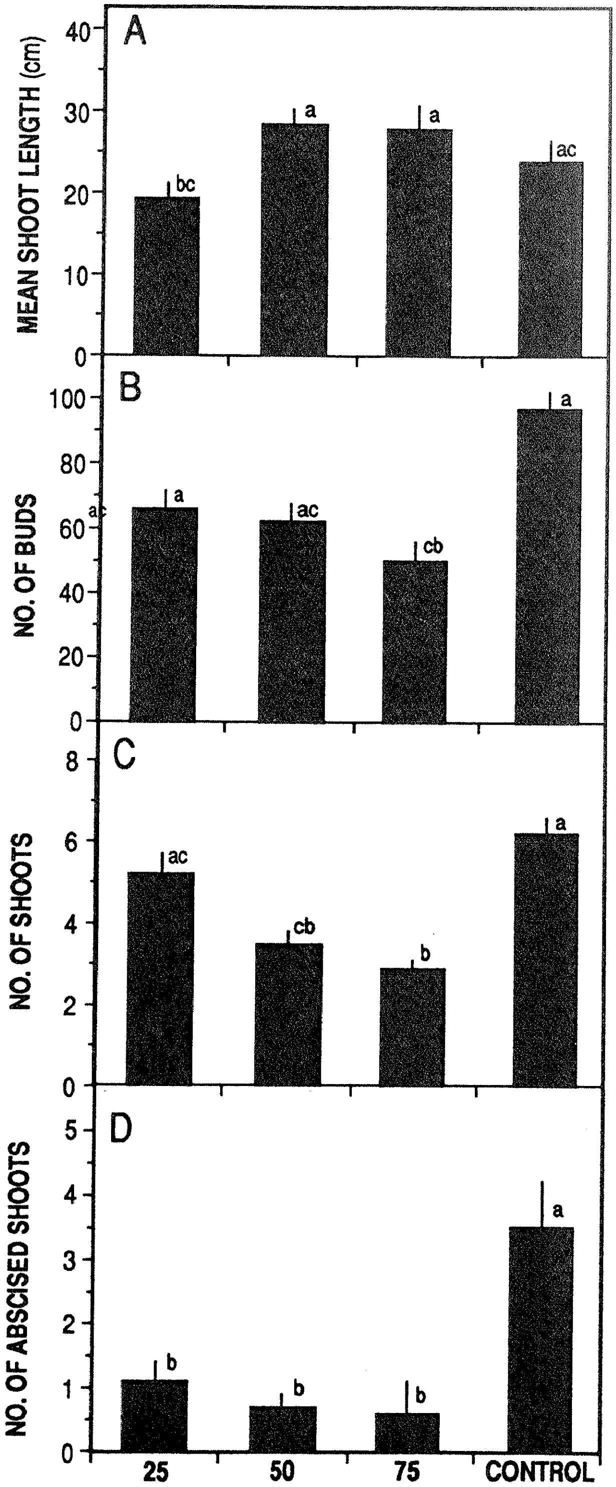

Figure 6.—The effect of browsing treatments (control, 25, 50 or 75% of leading shoots removed) on mean length of shoots (A), number of buds (B), number of new shoots (C) and number of abscised shoots (D) in the branches of ramets. The thin black lines represent 1 SE; different letters above bars indicate differences between treatments at P≤0.05.

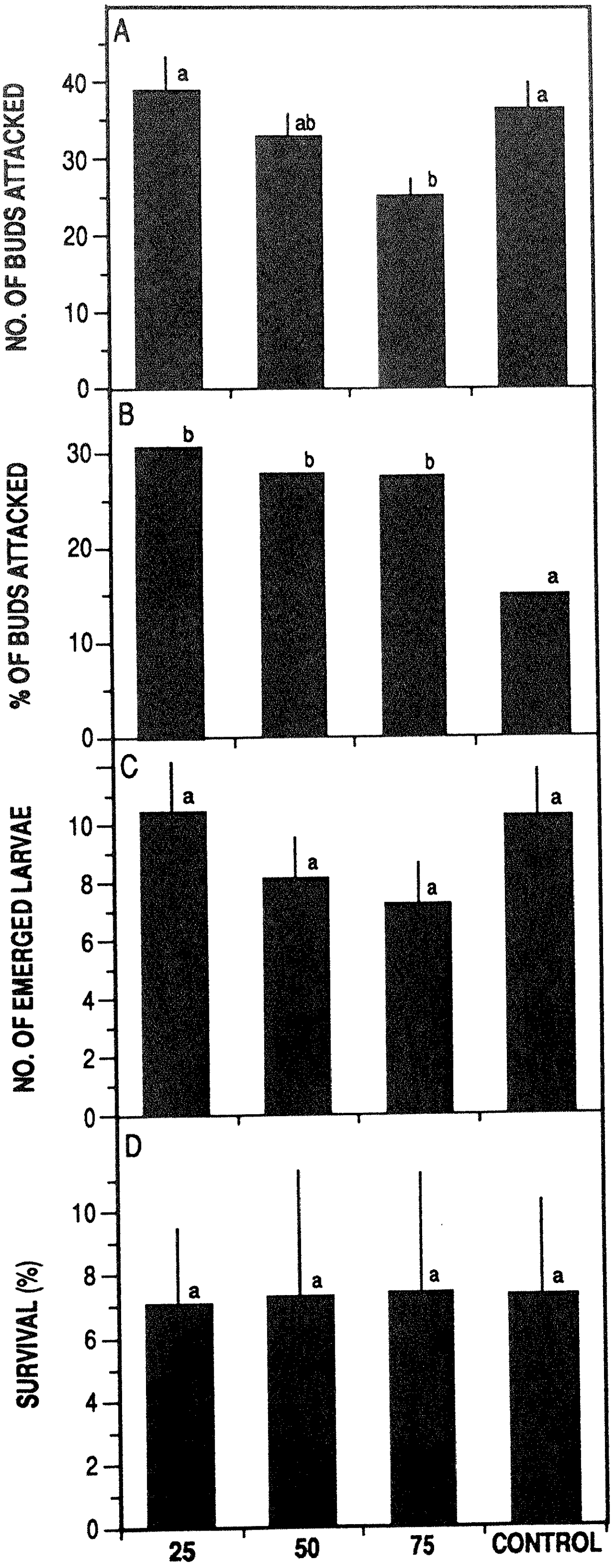

Figure 7.—The effect of browsing treatments (control, 25, 50 or 75% of leading shoots removed) on number of attacked buds (A), percent of buds attacked (B), number of emerged larvae (C) and percent of larval survival (D) in the branches of ramets. The thin black lines represent 1 SE; different letters above bars indicate differences between treatments at P≤0.05.

branches, the buds on browsed ones had higher probability of attack. Thus we provide here correlative and experimental evidence that juvenile shoots induced by hare browsing are preferred or equally attacked when compared with unbrowsed shoots. In earlier studies, leaves on damage-induced shoots were preferred by insects over those on undamaged shoots (Danell and Huss-Danell 1985). But the snowshoe hare avoids feeding on newly sprouted shoots stimulated by earlier feeding damage (Bryant 1981).

There were no differences in survival of *E. mucronata* larvae on the browsed and unbrowsed ramets (Figs. 2, 4 and 6). Although *E. mucronata* preferred hare-browsed branches, survival was not significantly higher on these branches. Several authors have observed that establishment and survival of larvae of gall-forming sawflies are better in or on long shoots (Craig *et al.* 1986; Price 1987a, b; Roininen *et al.* 1988; Price 1989). Better survival on long shoots has been suggested to be the ultimate reason why *E. mucronata* (Price *et al.* 1987a) and *E. lasiolepis* (Craig *et al.* 1986, 1989) oviposit on them. The mean length of shoots in our study was almost 2-fold longer than in the study of Price *et al.* (1987a), and all shoots were in the length range resulting in high survivorship of *E. mucronata* in the studies by Price *et al.* 1987a,b. Therefore, the lack of short shoots in the current study accounts for the absence of differences in survival of larvae.

Clones explained significant amounts of variance in all variables measured on the performance of *E. mucronata*. Clone explained 58 and 65% of the variation in survival of larvae and number of emerged larvae, respectively. Variation among individual plants has been shown to be important for many herbivorous insects, e.g. for pemphigus aphids (Whitham 1978), for diprionid sawflies (Mopper and Whitham 1992), for pine tip moth (Whitham and Mopper 1985) and for tenthredinid sawflies (Fritz and Price 1988). It is interesting that clone still explains a high proportion of the variance, although the ramets within clones had such different growth reactions in the different treatments.

Although hare browsing seems to have little or no direct effect on population levels of *E. mucronata*, our data indicate that browsing is continuously high and therefore indirect effects can be an important factor in the population dynamics of *E. mucronata* (Table 1). Because continuous browsing may keep ramets at a young, juvenile stage, they are relatively susceptible to *E. mucronata* attack if compared with naturally aging ramets (Price *et al.* 1987a).

We propose that host plant relationships of these two very different kinds of herbivores are diverse. The growth reaction of willows is expected to be a defensive mechanism against hare browsing (Bryant 1981; Tahvanainen *et al.* 1985a) due to increased concentrations of phenolic glycosides. On the other hand, phenolic glycosides have been shown to govern the food selection of many willow-feeding insects and can facilitate the feeding or oviposition of adapted herbivores (Tahvanainen *et al.* 1985b; Kelly and Curry 1991). Moreover, the long, fast-growing shoots are favorable or even superior for development of *E. mucronata* (Price *et al.* 1987a, b; Roininen *et al.* 1988).

The buds on shoots that abscised during the growing season were present when *E. mucronata* laid eggs, but larval development was not possible in these shoots and eggs were laid very rarely on such shoots. For the female *E. mucronata* it is probably easier to find suitable buds for larval establishment and development on browsed branches on which only a smaller proportion of potentially lethal shoots are formed and which are expected to drop off during the growing season (Figs. 1, 3 and 5).

There was little or no direct effects of browsing on population levels of *E. mucronata* (Fig. 7). Numbers of emerged larvae and survival of larvae were similar on browsed and unbrowsed ramets (Figs. 2 and 6). In the high intensity browsing environment, browsed branches produced the same number of larvae as untouched branches in the environment of low browsing (Fig. 5c). Because unbrowsed branches in the environment of high browsing produced the highest number of larva, the highly browsed environments may support higher populations of *E. mucronata* than unbrowsed or slightly browsed environments. Thus the answer to our question "Can hare browsing benefit the bud galler" is yes, although the reason for this effect is not the direct result of browsing in the same ramet. Instead, the spatial distribution of browsing and browsing rate among ramets most probably affects *E. mucronata*. One could certainly find an optimal distribution and rate for browsing which maximizes the number of produced larvae and perhaps survival as well. More research is needed to estimate the ideal level of browsing for sawflies.

Browsing mammals often feed on the tops of trees or shrubs and induce lateral branching (Owen 1980) or compensatory growth (McNaughton 1983). Herbivore damage involves changes in physiology, development and a modification of the environment (McNaughton 1983). All these kinds of changes, higher concentration of nutrients and phenolic glycosides (eg. Bryant 1981, Tahvanainen *et al.* 1985a), juvenile reactions (e.g. Craig *et al.* 1986, Roininen *et al.* 1988) and number of shoots per branch, modify host plants and make them more favorable for *E. mucronata*. We suspect that bud and stem galling sawflies have adapted to benefit from damage-induced growth reactions of their host plants, which is a general and ancient adaptation to diverse, non-specific selective pressures such as mammal browsing, frost kill, fire, snow, and ice damage (Roininen *et al.* 1988; see Whitham *et al.* and Belsky *et al.* 1993).

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CAN LARVAL GREGARIOUSNESS INCREASE FITNESS OF THE PINE NEEDLE GALL MIDGE (DIPTERA: CECIDOMYIIDAE)?

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Abstract. I examined the effects of the gregariousness of larvae of the pine needle gall midge, *Thecodiplosis japonensis* Uchida et Inouye (Diptera: Cecidomyiidae), on the mortality, the number of eggs, and the reproductive success of the midge by field observations and laboratory experiments. Competition among larvae in galls was not strong enough to cause the death of larvae, but it decreased their size, which resulted in the increased mortalities of larvae and pupae in the soil, and decreased fecundity. Females developing from medium size larvae deposited many more eggs than those from either large or small larvae. The number of eggs deposited per gall increased as the number of larvae per gall increased up to six.

Key words: gall midge, gregariousness of larvae, intraspecific competition, reproductive success.

INTRODUCTION

The gregariousness of individuals can lead to intraspecific competition for food and space which affects not only survival (Varley 1947, Kowalsky and Benson 1978, Sunose 1983), but also reproduction (Holmes 1982). Larvae of the pine needle gall midge, *Thecodiplosis japonensis* Uchida et Inouye (Diptera: Cecidomyiidae), spend three instars in galls before they fall to the ground for hibernation (Sone 1980). In a gall, two or more larvae usually live together (Sone 1980, 1985, 1986, 1987). Intraspecific competition among larvae is not strong enough to cause the death of larvae in a gall, but it reduces their size and their fecundity (the number of ovarian eggs) (Sone 1985). On the other hand, gregariousness may permit the larvae in galls to use the resources more efficiently. Therefore, gregariousness probably confers significant advantages on the reproductive success of the midge.

Sone (1985) pointed out that galls with more larvae seem to yield more ovarian eggs per gall. However, he could not examine the relationship between the number of larvae per gall and the realized fecundity (the number of deposited eggs) per gall and the effects of the gregariousness on the reproductive success of the midge because he did not relate the size of larvae to the reproduction of females. Therefore, in 1991 and 1992 I conducted similar experiments as Sone (1984, 1985) to examine this relationship and furthermore to determine the effects of gregariousness and the oviposition pattern of the midge on the reproductive success.

METHODS

Current shoots with galled needles were collected in a young stand of *Pinus thunbergii* x *P. massoniana* F1 hybrids at the Kamigamo Experiment Station of the Kyoto University Forest, Kyoto, in November, 1991. Galls were dissected and the number of third-stage larvae was counted for each gall. Body length was measured and mortality due to parasitism or other factors was examined for each larva. After excluding parasitized larvae, larvae were divided into three groups based on their body length as in the experiments by Sone (1985); large (2.5 mm-:group L), medium (2.0-2.5 mm: group M), and small (1.5-2.0 mm: group S). Then, 500-1200 larvae of each group were reared in 17 cm diameter clay pots containing forest soil and litter of pine needles with sufficient moisture. Before planting larvae, the soil and litter were heated and dried at 80 C for 48 hours in a oven with a ventilator to kill predators. The following spring, the adults that emerged from each pot were captured. Mated females were placed into a nylon net cage containing one current shoot with 100-300 pairs of needles of 1.5-3.0 cm long, on which surfaces females were allowed to oviposit. After all females were dead, they were collected to measure the sizes (width x length) of a mesonotum and a wing and to count the number of eggs remaining in the ovaries for each female. One possible factor which affects flight of females is the load of eggs. Then, the load of eggs to wing (load index) was calculated by (the volume of an egg) x(the number of eggs in ovaries)/(the size of a wing) for each female. The number of eggs deposited on the surfaces of each pair of needles was counted. The experiments were repeated 6, 9, and 7 times for adult females that emerged from larval groups S, M, and L, respectively, from 22 May to 16 June, 1992. A total of 18, 125, and 129 females from groups S, M, and L were allowed to oviposit. Some females were killed just after emergence and then measured and counted as described to serve as a comparison.

RESULTS

Size of Larvae in Galls

Table 1 shows the relative abundances of larvae of groups S, M, and L and the mean body length of the third-stage larvae in galls with different numbers of larvae. The relative abundance of large larvae (group L) decreased with the number of larvae per gall, while small larvae (group S) became more abundant with the number of larvae. Medium larvae (group M) become less abundant in galls with 10 or more larvae. Mean body length of the third-stage larvae gradually decreased about 20¡% as the number of larvae per gall increased from one to 18.

Table 1.—Frequencies of the larval groups and mean body length of the third-stage larvae in galls with various numbers of larvae

No. of larva per gall	Body length (mm) Group S (1.5mm-)	Group M (2.0mm-)	Group L (2.5mm-)	Mean	S.D.	N
1	0.10	0.76	0.14	2.25	0.22	51
2	0.17	0.64	0.19	2.22	0.23	120
3	0.16	0.74	0.10	2.21	0.21	115
4	0.16	0.76	0.08	2.19	0.21	181
5		0.64	0.36	2.17	0.20	176
6	0.23	0.68	0.09	2.15	0.23	177
7	0.33	0.65	0.02	2.09	0.22	147
8	0.19	0.77	0.04	2.14	0.23	94
9	0.32	0.67	0.01	2.09	0.19	97
10	0.49	0.50	0.01	1.94	0.21	82
11	0.63	0.37		1.95	0.23	65
12	0.71	0.28	0.01	1.89	0.20	81
13	0.77	0.23		1.82	0.25	52
14	0.63	0.37		1.91	0.16	68
15	0.46	0.54		1.97	0.15	13
16	0.75	0.25		1.79	0.20	15
17	0.65	0.35		1.91	0.27	17
18	0.87	0.13		1.81	0.15	15

Mortality of Larvae in Galls

Mortality of third-stage larvae in galls due to resinosis, disease, and desiccation was very low. About 20-30% of the third-stage larvae were parasitized by two species of wasps, *Platygaster matsutama* and *Inostemma seoulis*, and percent parasitism showed neither consistent increase nor decrease with the number of larvae per gall (Fig. 1).

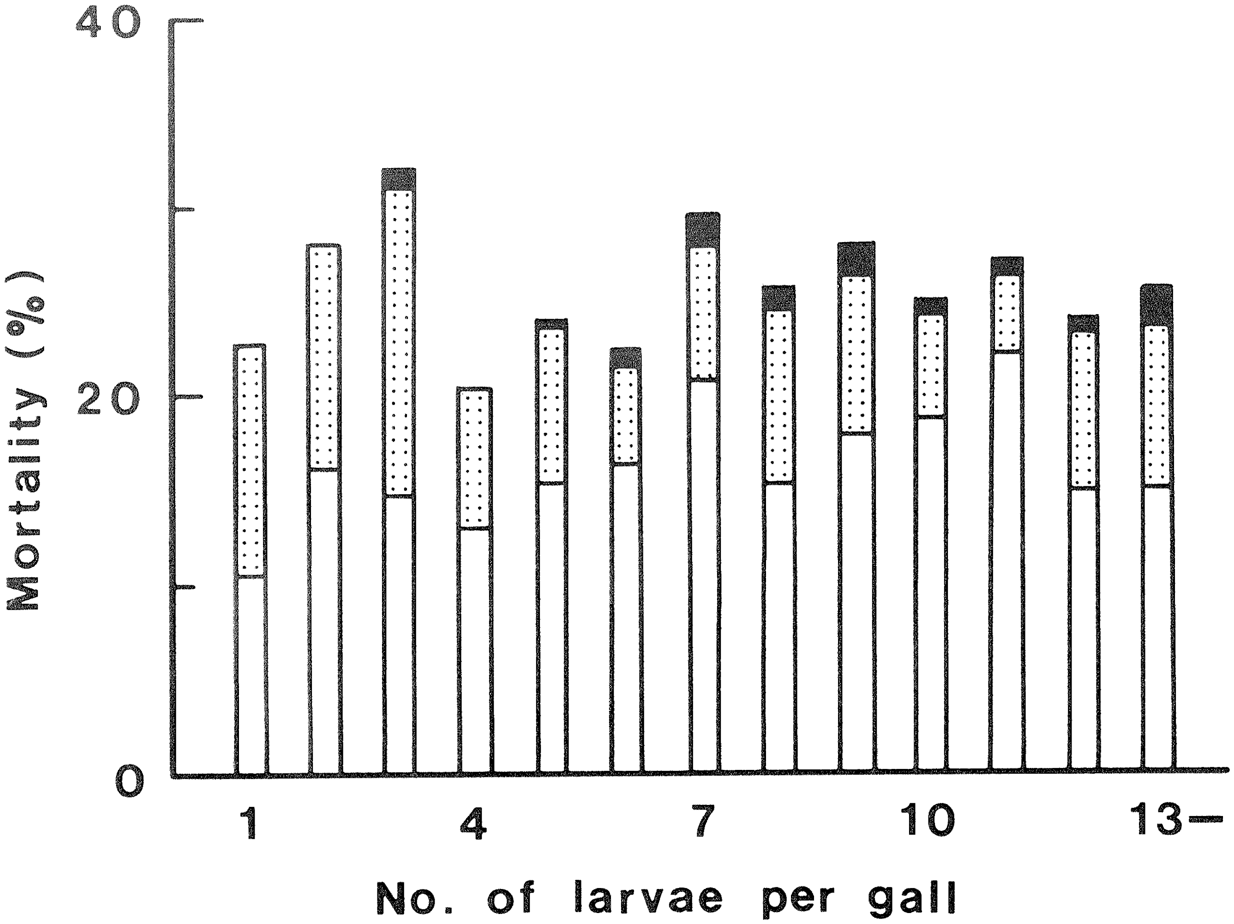

Figure 1.—Mortality of larvae in galls with different numbers of larvae: White: parasitism by *Platygaster matsutama*, Stippled: parasitism by *Inostemma seoulis*, Black: mortality due to other factors.

Mortality of Larvae and Pupae in Soil

All emerged adults were not collected because some did not fly up to the tubular cage of the emergence trap. Therefore, overwintering mortalities of each larval group could not be estimated accurately.

Size of Adult Females

The size of each adult female was expressed by the size of her mesonotum because a mesonotum is hard and its size does not change after death. The size of a mesonotum was largest for adult females emerging from group L, followed by those from groups M and S. The differences in the mean mesonotum size among the groups were examined by the GT2-method (Sokal and Rohlf 1981) and the differences among the groups were significant (Table 2).

Fecundity and Egg Loading to Wing Size

Mean fecundity was highest for adults from group L and lowest for those from group S (Table 2). The differences in the mean fecundity among groups were significant. The mean volume of eggs did not differ significantly among the groups. The mean egg loading index was largest for females from group L and lowest for those from group S. The differences among the groups were significant (Table 2). The fecundity per female correlated positively with mesonotum size (Fig. 2) and the ratio of mesonotum size to wing size correlated positively with the loading index (Fig. 3). Therefore, the ratio could be an indicator of a loading index of each female.

Table 2.—Size of mesonotum, size and number of eggs in ovaries (fecundity), and the load of ovarian eggs to a wing in relation to larval size.

	Group S			Group M			Group L		
Trait	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N
Mesonotum size (mm^2)	0.57a	0.11	7	0.70b	0.10	47	0.85c	0.09	50
Fecundity	75.4a	20.9	7	116.5b	27.6	47	157.0c	25.5	47
Egg size (mm^3/8000)	116.6	5.5	7	121.0	6.5	46	121.0	4.8	44
Load of eggs (index)	4.44a	1.05	7	5.62b	1.25	46	6.81c	1.16	46

Means followed by the same letter are not significantly different at the level of P=0.05.

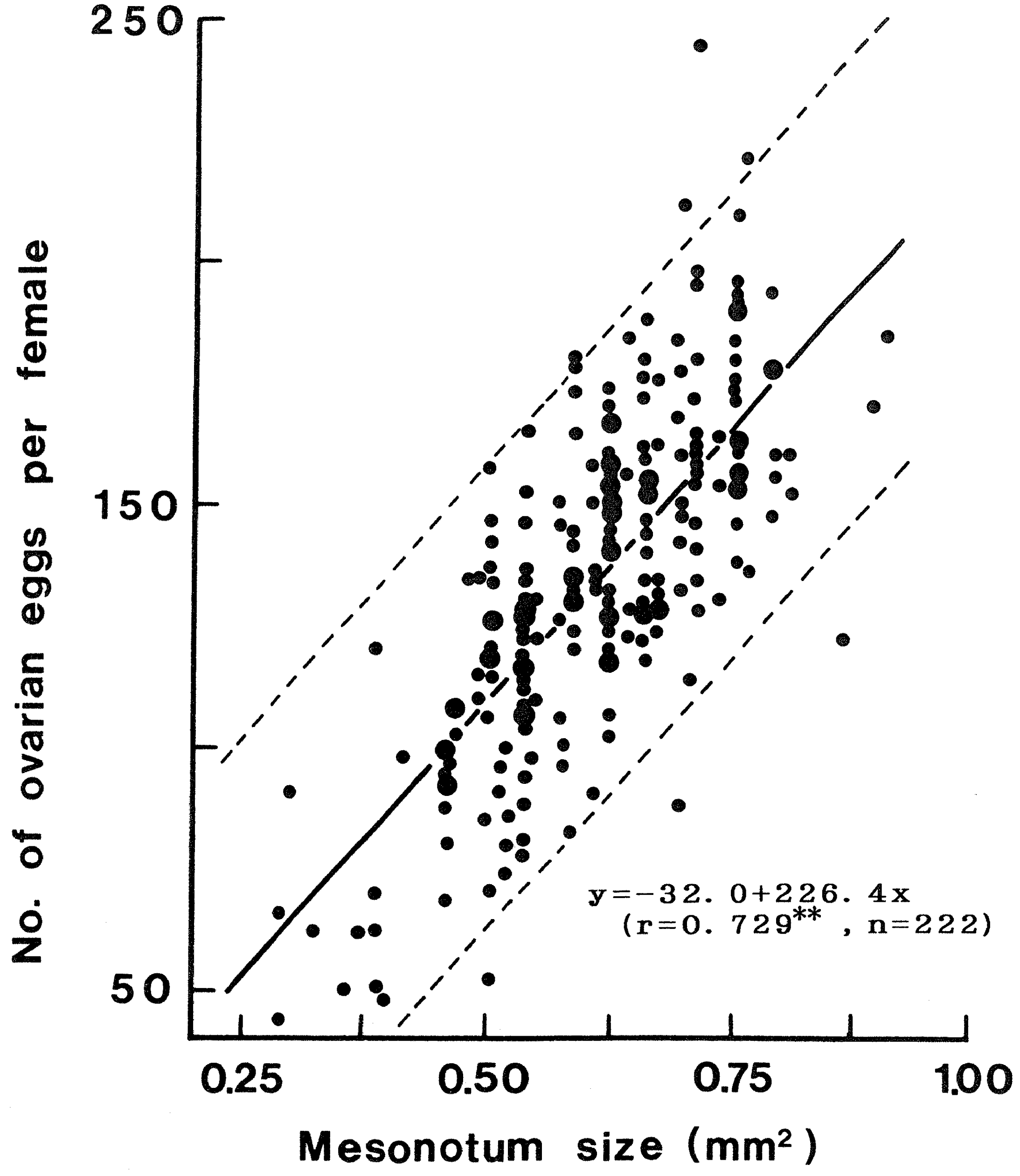

Figure 2.—Relationship between the number of ovarian eggs (fecundity) per female and the size of her mesonotum. Dotted lines show the 95% reliance limits of the estimated regression line.

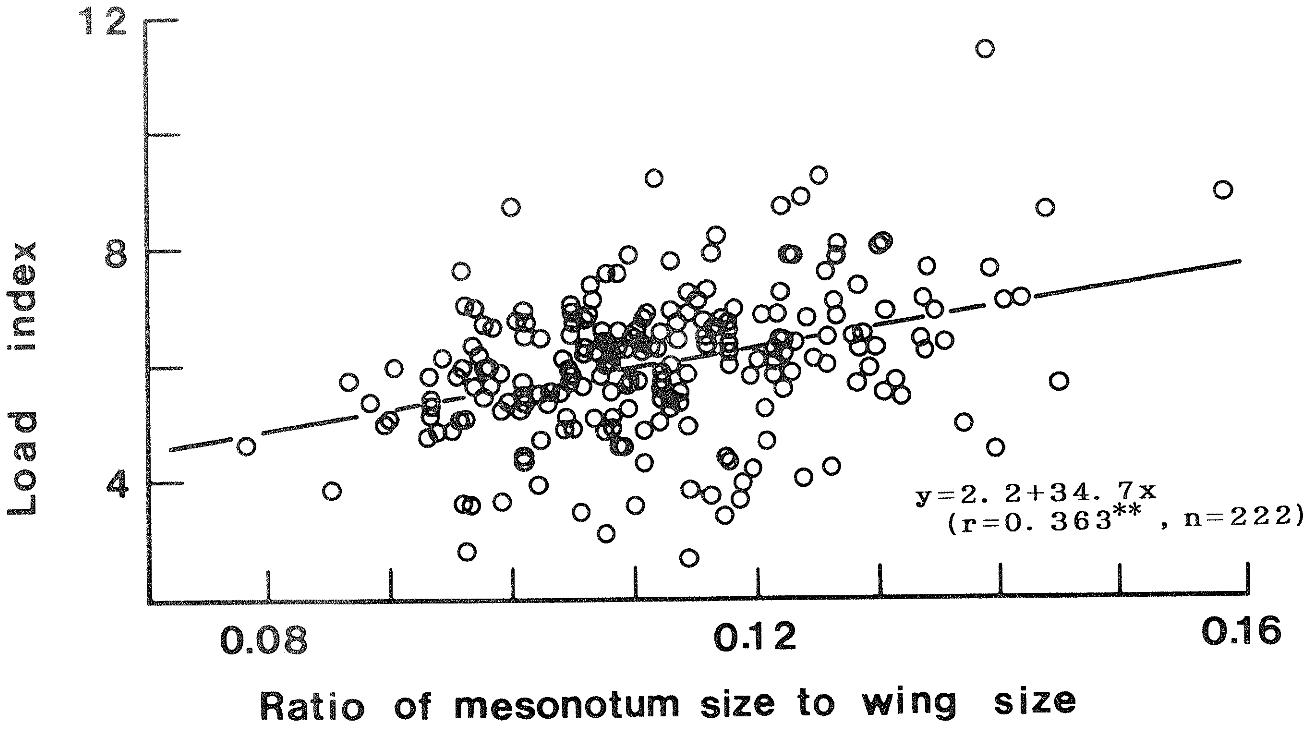

Figure 3.—Relationship between the ratio of mesonotum size to wing size and load index.

Realized Fecundity per Female

The number of eggs that remained in ovaries varied greatly from 0 to 194 among females as Sone (1984) reported. In most cases, two or more females were allowed to deposit their eggs on a single shoot. Therefore, both fecundity and realized fecundity could not be estimated for each female. The mean number of eggs deposited per female and its ratio to that of eggs in ovaries (percent realized fecundity) were highest for females from group M larvae and lowest for those from group S larvae (Table 3). The number of eggs that remained in ovaries was compared with estimated fecundity by relating mesonotum size and fecundity. Females were considered to deposit their most ovarian eggs if the number of eggs remaining in ovaries was less than 15% of the estimated fecundity and they were considered to deposit no or few eggs if the number of eggs remaining in ovaries did not differ significantly from the expected fecundity at $\underline{P}=0.70$ level.

Table 3.—Mean numbers of ovarian eggs and deposited eggs per female and the percent realized fecundity in relation to larval size.

Trait	Group S	Group M	Group L
Ovarian eggs	76.6	107.5	133.5
Deposited eggs	5.9	28.9	16.3
% realized fecundity	7.7	26.9	12.2
No. of females	18	125	129

In group M, about 15% of individuals were considered to deposit most of their eggs in ovaries and about 45% individuals were considered to deposit no or few eggs. While, in groups S and L, only about 5% of individuals were considered to deposit most ovarian eggs and about 85 and 60% of individuals were considered to deposit no or few eggs, respectively (Table 4). Both in groups L and M, females that deposited most of their ovarian eggs had lower ratio of mesonotum size to wing size, load of eggs, than those that deposited no or few eggs (Table 5).

Table 4.—Relative abundances of females which seemed to deposit almost of all or few ovarian eggs.

Trait	Group S	Group M	Group L
Females (%) which seemed to deposit:			
almost all ovarian eggs	5	15	6
none or few ovarian eggs	85	45	59

Table 5.—Comparisons of the ratio of mesonotum size to wing size between females with a high realized fecundity and those with a low realized fecundity.

Ratio of mesonotum size to wing size	No. of females which seemed to deposit	
	No or few eggs	Almost all eggs
Group M		
>0.100	26	5
<0.100	22	13
Fisher's exact probability	P=0.0490	
Group L		
>0.110	28	0
<0.110	58	8
Fisher's exact probability	P=0.0516	

Realized Fecundity per Gall

The realized fecundity per gall with various numbers of larvae was calculated as follows; (the number of larvae per gall)x(sex ratio=0.5)x(the survival rate in galls)x(the survival rate in soil) x(the mean number of eggs actually de-posited per female). The survival rate in soil was assumed to be the same as reported by Sone (1985) because it was not estimated correctly the rate in this study. The survival ratios and the mean number of eggs per female were obtained by weighting these values of each group with the relative abundance of each group of larvae in galls (Table 1). Realized fecundity increased with the number of larvae for galls with less than six larvae but did not show a significant increase for galls with more than 6 larvae (Fig. 4).

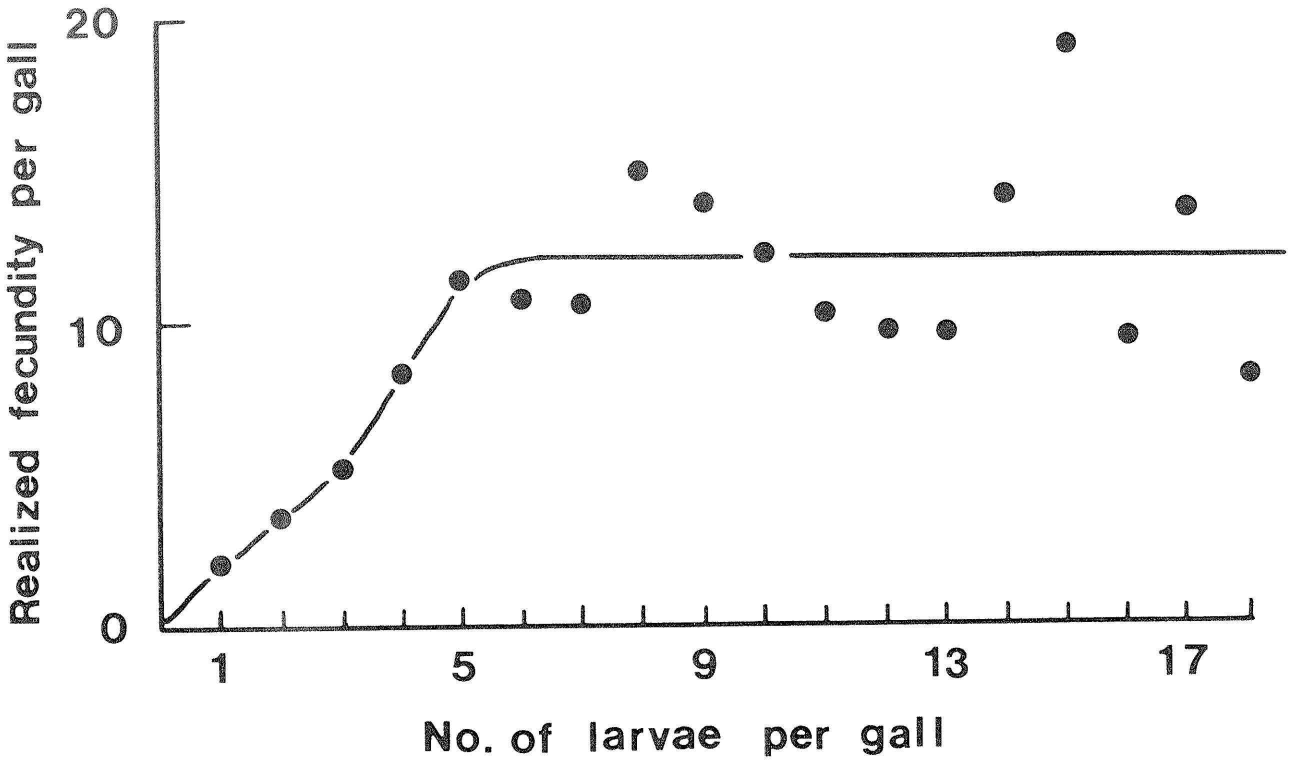

Figure 4.—Relationship of the number of larvae per gall to the expected values of the realized fecundity per gall.

DISCUSSION

The pine needle gall midge deposits eggs in clusters, and two or more larvae usually live together in a gall (Miura 1962, Sone 1980, 1985, 1986, 1987). The gregariousness of larvae is expected to have some impacts on the reproductive success and population dynamics of the midge.

Gregariousness may attract their natural enemies. Mortalities of eggs and larvae due to predation are usually very low (Sone 1987, Sone and Takeda 1983). The larvae were attacked by two species of parasitic wasps, *Platygaster matsutama* and *Inostemma seoulis*, which deposit their eggs in eggs or newly hatched larvae of the midge before gall formation (Miura 1962, Ko 1966, Yoshida and Hirashima 1979). Number of larvae per gall did not affect the percent parasitism by these wasps.

Gregariousness also induces intra-specific competition which can sometimes cause severe mortality in midges (Varley 1947, Kowalsky and Benson 1978, Redfern and Cameron 1978). However, intraspecific competition among larvae of the gall midge was not strong enough to cause death of larvae in galls but it did cause a reduction in the size of larvae as reported by Sone (1985). The low mortality of larvae in galls suggests that the midges can utilize its resources more effectively by being gregariousness.

The reduced size of larvae induced decreases in the survival of larvae and pupae in soil (Sone 1985) and the fecundity per female. The decrease in the larval size did not simply decrease the realized fecundity per female. Realized fecundity per female was largest for females from medium sized larvae. Most females from groups S and L could not deposit their ovarian eggs. Less active flight was often observed in the oviposition behavior of large and small females. A small egg loading index seemed to be necessary for active oviposition. Females from group L larvae had a larger load than those from group M larvae. Therefore, a larger load of ovarian eggs could restrict large females from active oviposition. Small females might not have enough vigor to attain a high realized fecundity.

These results suggest that the reproductive success of the midge can be largely determined by the relative intensities of positive and negative effects of the gregariousness of larvae; the increase in the number of larvae in a gall and the decreased survival and fecundity per female. Galls with a single larvae will produce a large female which deposits only a few eggs. Thus, the realized fecundity will not be high for these galls. As the number of larvae per gall increases, the relative abundance of large and small larvae decreases and increases, respectively, but that of medium larvae does not change appreciably. Therefore, realized fecundity per gall will first increase with the number of larvae per gall. However, a further increase in the number of larvae per gall will produce more small females whose realized fecundity is very low. Therefore, there should be an optimum number of larvae per gall above which the realized fecundity per gall does not increase with the number of larvae per gall.

The realized fecundity calculated per gall increased with the number of larvae per gall up to 6, but not thereafter. These results suggest that the midge can increase fitness by increasing the number of larvae per gall from 1 to 5, but can not gain any extra benefits by increasing the number of larvae in a gall to more than 6. In the field, the mean number of larvae per gall was 3.5-5.0 (Sone 1985, 1987). Therefore, the midge might use its resources most effectively and realize maximum realized fecundity per gall by gregariousness.

The reproductive success of a female depends not only on the realized fecundity per gall but also on its oviposition pattern. The longevity of females is about one day. Therefore, they should deposit their eggs within 24 hours of emergence (Sone 1986). Two extreme ovi-position patterns are possible; One is to deposit only one egg on as many needles as possible and the alternative one is to deposit as many eggs as possible on only one pair of needles. Females fly from needle to needle to deposit their eggs but are unable to fly toward the wind when wind velocity exceeds 2.8 m/sec. They stop flying when wind velocity exceeds 6.1 m/sec (Ko and Lee 1975). The most critical period during oviposition is the time when the midges are flying.

If the midges adopt the former strategy, they must fly frequently and the possibility that the midges could deposit all ovarian eggs would be extremely low. Furthermore, galls with one larva usually produce a single large offspring whose realized fecundity is low. The midges which adopt the latter strategy also have poor reproductive success because the gregariousness of more than six larvae reduces body size of adults and their realized fecundity. Therefore, the optimal oviposition pattern should be lie somewhere between these strategies.

If a midge could deposit all of its ovarian eggs without incurring any mortality during its flight from needle to needle, then maximum reproduction would be realized by the strategy of depositing only one egg on each pair of needles and the number of adults produced would decrease monotonically with the number of eggs deposited per cluster. But if mortality of females does occur during flight, there would be a unimodal pattern between the number of adults produced in the next generation and the number of deposited eggs per cluster. The number of eggs per cluster which would yield the maximum number of adults, would increase with the adult mortality rate. However, the number of eggs deposited by the daughters showed a peak when the mothers deposited about 10 eggs on each pair of needles irrespective to the mortality of adults during flight (Fig. 5). In the field, the mean number of deposited eggs per cluster was 7-8 (Sone 1980, 1986). Egg clusters of 7 or 8 eggs were the most frequent classes, and those ranging from 5-10 eggs made up 73-81% of the total eggs laid.

In conclusion, larval gregariousness can increase reproductive success only up to a point because too many larvae decreases it. The oviposition pattern and the gregariousness of larvae in a gall observed in the field should reflect optimal strategies for the midge to maximize its reproduction.

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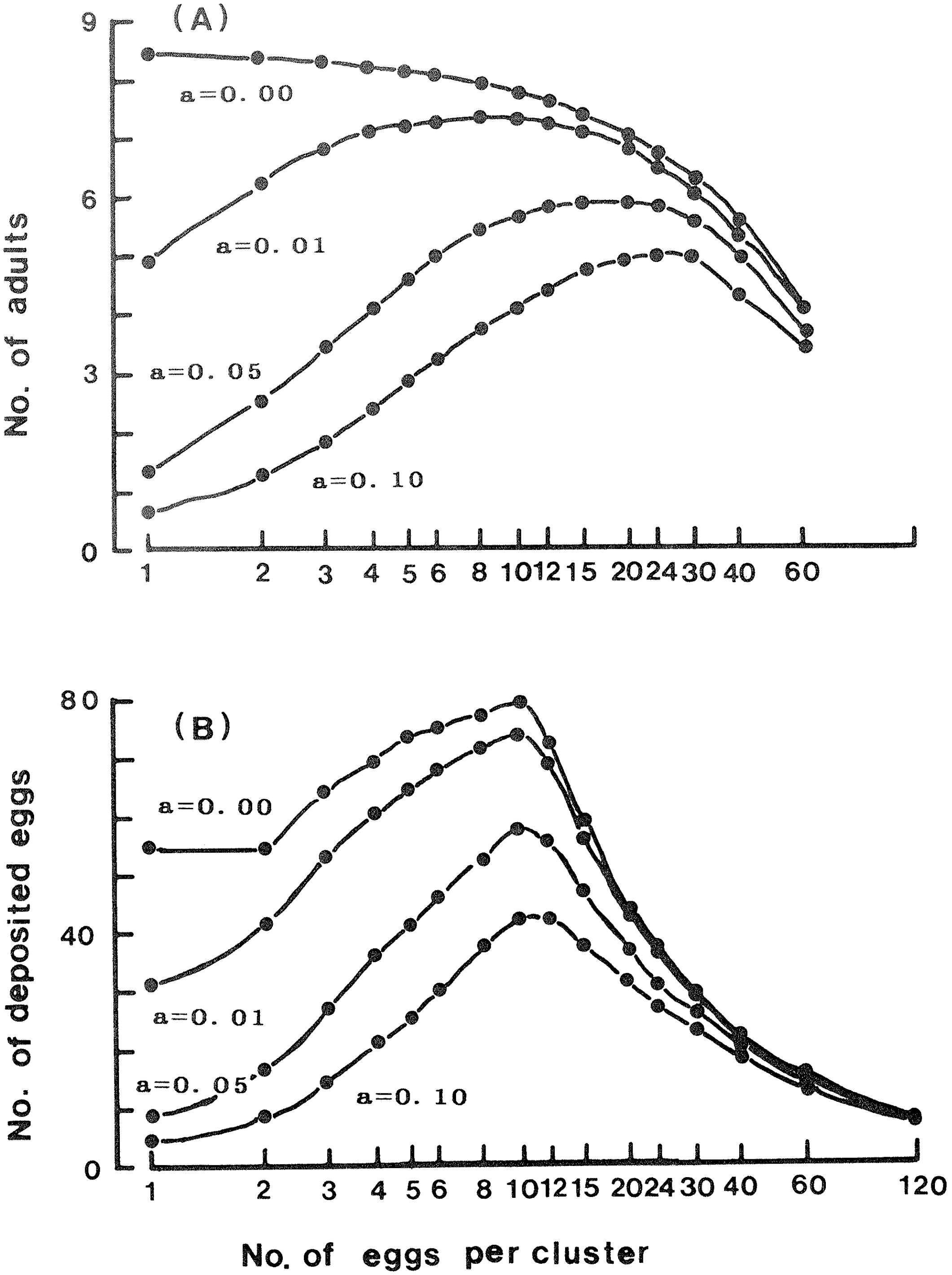

Figure 5.—Relationship of the number of deposited eggs per cluster to the expected numbers of emerged adults (A) and deposited eggs (B) in the next generation. The numbers of adults and eggs were calculated under the following assumptions. A female has 120 eggs in her ovaries and deposits clusters of fixed number of eggs with some mortality during flight (a). Larvae of 60% of egg clusters will form galls and 50% of these larvae will be dead before fall formation. These mortality rates of egg clusters and hatched larvae are the mean values of the six generations of the natural population at Kamigamo.

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STATUS OF THE PINE NEEDLE GALL MIDGE IN KOREA

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Abstract. The pine needle gall midge, *Thecodiplosis japonensis*, is the most injurious pest of *Pinus densiflora* and *Pinus thunbergiana* forests which occupy almost half of the total forests in Korea. An outbreak of this pest was first recorded in Korea in 1929. By 1992, the forest area damaged by the midge was 212 thousand hectares. Severe damage occurs in the frontal zone of spread. This paper describes outbreak history, present status and ecology of the pine needle gall midge.

Key words: Thecodiplosis japonensis, Outbreaks history, Population fluctuation, Pinus densiflora, Pinus thunbergiana.

INTRODUCTION

Korea has more than 6.5 million hectares of forest, covering 66% of its surface area. More than half of the forests are coniferous, principally *Pinus densiflora* and *Pinus thunbergiana.* The pine gall midge infests both species. The fact that pure pine forests, which are highly susceptible to insect damage, comprise almost half of the total forest land in Korea accounts for the severity and extent of damage by the pine needle gall midge. Since its arrival in Korea, the midge has been continually expanding its range. Observations on the progress of the gall midge infestations in several areas have shown that the percent foliage infested peaks 6 to 7 years after initial attack and subsequently declines (Fig. 1). After 12 years, the percentage of foliage infested stabilizes at a low level and the surviving trees to recover. In recent years, serious gall midge damage has been confined to the frontal zone of range advancement. It, however, remains to be seen whether the outbreaks will cyclically recur in areas where populations have now subsided to endemic level. Outbreaks history, present status and ecology of the pine needle gall midge are briefly described in this paper.

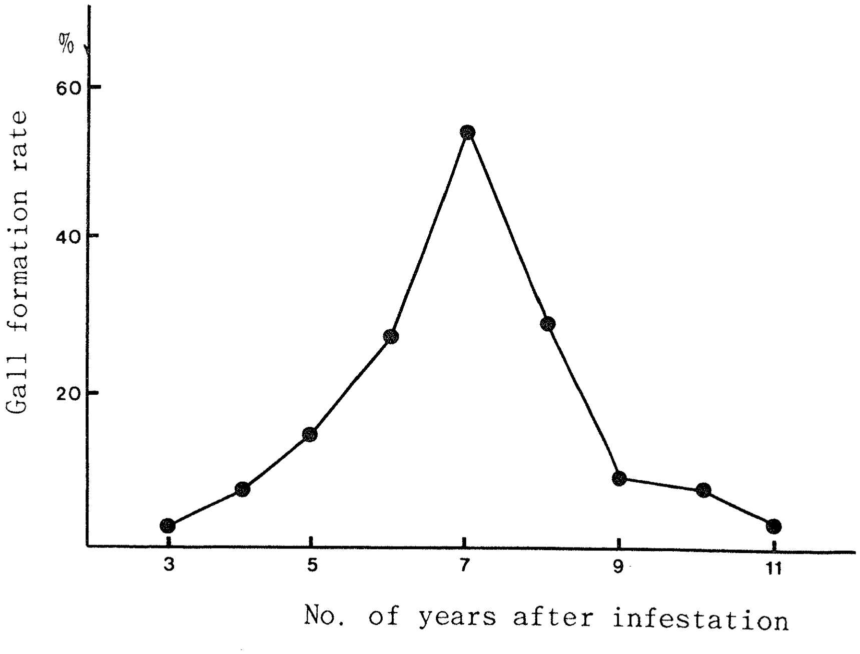

Figure 1.—Changes in the pine needle gall midge population (Park and Hyun 1983).

OUTBREAK HISTORY

The first infestation of the pine needle gall midge in Korea was reported in 1929 at Seoul and Mokpo (Takagi 1929), and was discovered subsequently in Pusan in 1930. Expansion of the midge infestation was mainly initiated from above mentioned three areas (Kim 1955). There is no record concerning the expansion of the infestation during the 1940-1960 period, but extensive damage at the beginning of the 1960s again triggered public interest. In 1964, a new outbreak was found in Tanyang, Chungchongbuk-do, a place remote from the earliest infested areas. By the early 1970s, the insect had spread northward from the locus of the earliest infestation in Pusan city. From Seoul, the midge has spread across the north branch of Han River into the Chunchon area, Gangwondo (Park *et al.* 1985). In 1982, the insect was found in a natural red pine stand at Mt. Seolak, which is located in northeast of Korea. In 1990, a new outbreak was found on Jeju island.

Surveys of the outbreak areas have been carried out every year since 1960. The pine needle gall midge now occurs in nearly all parts of Korea (Fig. 2). Figure 3 shows that the areal extent of the outbreak peaked in 1961, when approximately 410,000 ha of red pines and black pines were infested. The extent of the area with severe damage diminished afterward, supposedly as a result of the large-scale sanitation salvage harvests. In the 1970s, cutting of infested trees was discouraged because trees can recover. Thereafter, the total area with appreciable damage has remained more or less static (Park *et al.* 1985).

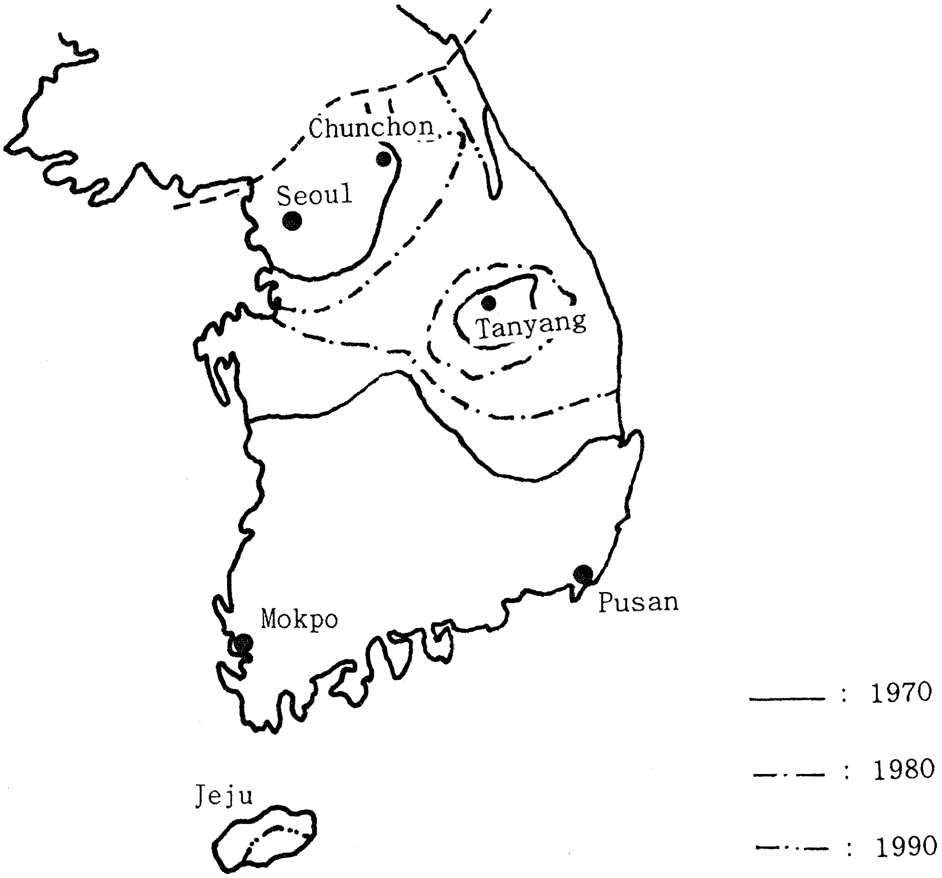

Figure 2.—Expansion of the pine needle gall midge in Korea.

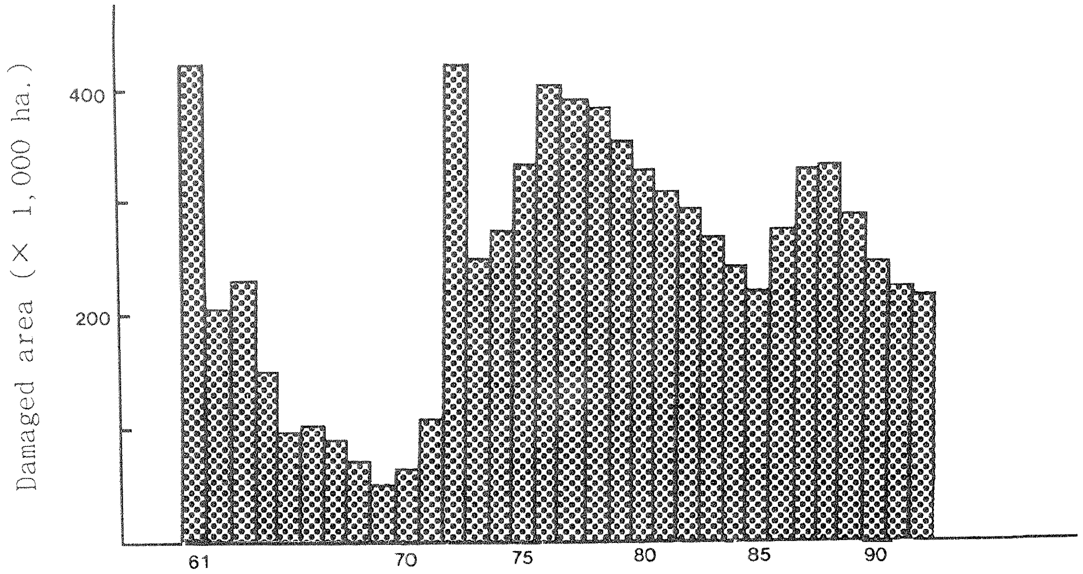

Figure 3.—Damaged area by the pine needle gall midge in Korea.

POPULATION FLUCTUATION

The yearly changes in gall formation by the pine needle gall midge were investigated for four years in four Korean red pine forests having different outbreak histories located in Chungchongnam-do province where the midge appeared recently. At the starting year of investigation, two sites (A and B in Fig. 4 and Table 1) had increasing but another (C and D in Fig. 4 and Table 1) had decreasing populations.

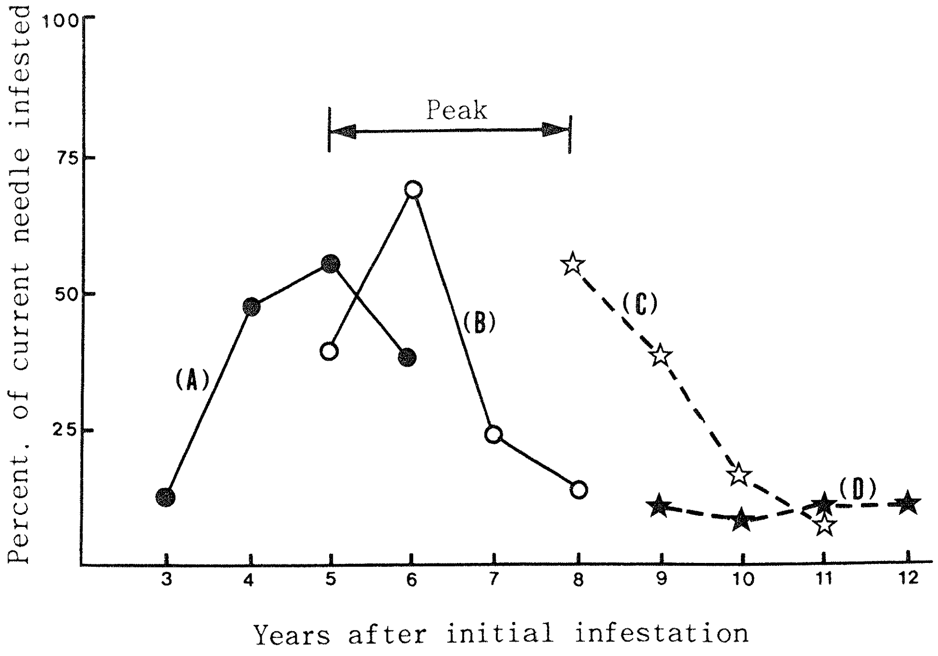

Figure 4.—Annual changes in the percentage of infested needle pairs on the progress of the midge infestation. The midge was first detected in 1981 (site A), 1979(site B), 1976(site C) and 1975(site D).

As shown in Figure 4, observations on the progress of the gall midge infestation have shown that the percent gall formation peaks at 5 to 8 years after initial attack and decreases rapidly thereafter. The damage eventually stabilizes at a low level more than 8 to 10 years after initial infestation, and the surviving trees begin to recover. A similar pattern was reported by Park and Hyun (1983).

Years After Initial Infestation

The frontal zone of the midge expansion is typically comprised of separate, small spot infestations. Populations increase rapidly in those spots with ample soil litter, but later they spread into the interjacent areas irrespective of their habitat conditions.

Table 1.—Yearly changes in the midge population after initial infestation

Site	Initial infestation	Year of peak damage year	No. of adults per 100 m^2		
			'84	'85	'86
A	1981	1985	36.2	132.7	20.5
B	1979	1984	97.6	74.0	4.5
C	1976	1983	52.7	11.7	2.5
D	1975	before 1982	16.1	8.3	14.4

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THE GEOGRAPHY OF GALLING INSECTS AND THE MECHANISMS THAT RESULT IN PATTERNS

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Abstract. Insect galls are tremendously diverse and common in all biogeographical realms. In spite of many studies on the natural history and host relations between galling insects and their food plants, there are few biogeographical and evolutionary studies that account for the patterns in their distribution. We review the literature on the biogeography of gall-forming insects and show the existence of a clear and global pattern in their distribution. Galling insect richness increases with decreasing elevation in xeric renvirnonments in all biogeographical regions. This increased richness is best explained by increasing environmental harshness at lower elevations because gall richness does not change with decreasing elevation in paired mesic habitats.

Field data indicated that gallers have higher population densities on plants in xeric habitats than in mesic habitats. The major mechanisms producing this strong differential distribution are the increased mortality in mesic habitats caused by plant resistance and natural enemies. To test field patterns in mortality and survivorship, we studied the galls of *Aciurina trixa* (Diptera: Tephritidae) on *Chrysothamnus nauseosus hololeucus* (Asteraceae) in the southwestern US. Within a habitat, control and stressed plants mimicked xeric conditions, while watered and fertilized plants mimicked mesic conditions. *Aciurina trixa* that colonized watered and fertilized plants suffered higher mortality than those that colonized control and stressed plants. These results support the hypothesis that the gall richness patterns are the result of differential mortality among habitats. We postulate that lower mortality caused by natural enemies and plant resistance in xeric habitats reinforce the galling habit, fostering speciation and radiation in harsh environments.

GALLING ORGANISMS AND THEIR GALLS

Galls result from increases in plant cell volume (hypertrophy) and/or number (hyperplasy) caused by foreign organisms (Mani 1964, Meyer 1987). As in many animal tumors, the exact mechanisms of plant gall induction are as yet unknown. Many animal and plant taxa induce galls on plants (Mani 1964, Meyer 1987), but we focus only on the galls formed by insects. From an evolutionary point of view, galls can be seen as adaptations that allowed some insect taxa to feed on high quality plant tissues and to successfully colonize dry habitats (Price *et al.* 1986, 1987, Fernandes and Price 1988, 1991).

Galling insects are useful in ecological studies due to the sessile habits of their larvae, as well as the conspicuousness of the galls. Galls are also very diverse and abundant, making them easier to census than unconcealed herbivores. Survivorship curves and sources of mortality can usually be evaluated by dissecting galls at the end of each generation, thus facilitating mechanistic studies. Furthermore, plant responses to environmentally induced stresses may be more readily sensed by gallers which generally have the most intimate relationships with their food plants (Fernandes and Price 1992).

DIVERSITY AND DISTRIBUTION OF GALL-FORMING INSECTS

Approximately 13,000 insect galls have been recorded worldwide (Buhr 1965). Many more species have been described since then, but to our knowledge, a complete list of the described insect galls is not available. The most common gall-forming insects belong to the six orders Diptera, Homoptera, Lepidoptera, Thysanoptera, Hemiptera, and Coleoptera (Dreger-Jauffret and Shorthouse 1992). Amongst all gallers, the most diverse are the Cecidomyiidae (Diptera) (Mani 1964, Gagné 1989).

The world distribution of major taxa of gall-forming insects has been the subject of several reviews (e.g., Mani 1964, Gagné 1984, Skuravá *et al.* 1984). Despite the paucity of studies in the tropics, it has been established that gall-forming thysanopterans are most common in the Eastern Hemisphere (Raman and Ananthakrishnan 1984), gall-forming scales are most common in the tropics (Beardsley 1984), psyllids in Australia (Hodkinson 1984), and cynipid wasps in the Holartic region (Askew 1984), while cecidomyiids are well represented in all biogeographical regions (Gagné 1984). The distribution of gallers has also been correlated with the break up and movement of the continents (Gagné 1984), but we will further address the diversity of gall-forming insects in relation to biogeographical regions nor to highlight the differences in faunal compositions. Rather, we will show here the existence of global consistent patterns in the distribution of galling insects within regions.

GLOBAL PATTERNS IN GALL DISTRIBUTION

A global pattern for galling species richness is emerging and becoming clearer with the development of several studies in different biogeographical regions. The uniqueness of these studies relies on the fact that a global catalogue of species or compendiums is still unavailable (Price 1991). A common method of data collection was used, censusing galls on 45 trees, 100 shrubs, and 1000 herbs or by a one hour census (see Fernandes 1987, Price 1991). Even when reanalysing data collected 90 years ago (Docters van Leeuwen-Reijnvaan and Docters van Leeuwen 1926) , the same pattern emerges, strongly suggesting the existence of a global pattern in galling insect distribution.

Temperate Patterns

We collected galls in temperate areas, from the lower Sonoran Desert at sea level (Bahía Kino, Mexico) to the top of the San Francisco Peaks (3843m) in the United States (Fernandes 1987). Both xeric and mesic habitats were sampled at single elevations to eliminate the effect of altitude on comparisons. Xeric habitats are distant from water courses, while mesic habitats are in riparian vegetation. The altitudinal gradient was comprised of six different vegetation types: desert, chaparral, pinyon-juniper woodland, ponderosa pine forest, spruce-fir forest, and alpine-tundra. Approximately 69,000 plants were surveyed for insect galls (Fernandes 1987).

Species richness of temperate gallers was strongly influenced by variations in altitude in xeric habitats (Fernandes and Price 1988). The richness of galling insects increased with decreasing elevation ($r^2 = 0.78$, $p < 0.0001$, Fig. 1). In contrast, species richness was not influenced by variations in altitude in mesic habitats ($r^2 = 0.03$, $p > 0.05$). Therefore, the effect of altitude was best explained by increasing hygrothermal stress in xeric habitats at lower elevations. The pattern was also apparent within host plant family, genus or species, such as *Asteraceae, Quercus, Juniperus*, and *Larrea tridentata.* In otherwords, the distribution of galling insects is linked to habitat harshness. Corroborating these findings, we observed that species richness of galling insects was significantly higher in species in xeric habitats than mesic habitats at any elevation, and that species richness of free-feeding insects had opposite distribution patterns (Fernandes and Price 1991). Waring and Price (1990) demonstrated the same pattern of increasing gall richness on *Larrea tridentata* with increasing environmental harshness.

Neotropical Patterns

Galls were collected from Lagoa Santa at 800 meters above sea level to the top of Serra do Cipó at 1500 meters in southeastern Brazil. Habitats and plants were surveyed following the same methods used in temperate regions. The sample sites comprised eight different altitudes at 100 meter intervals and four different vegetation types: cerradão, cerrado, campo rupestre (rocky heaths), and high altitude moorland. Approximately 45,000 plants were surveyed for galls (Lara and Fernandes, in prep.).

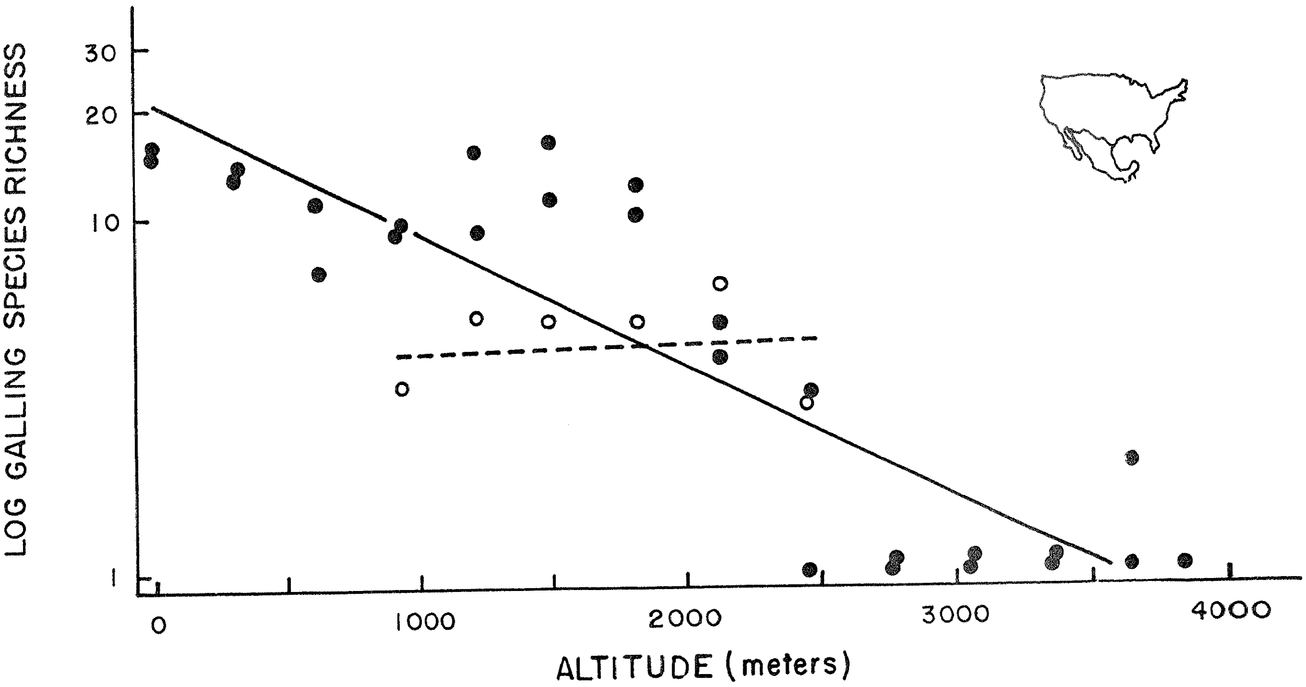

Figure 1.—Gall-forming species richness in xeric and mesic habitats along altitudinal gradients in temperate areas of North America. Species richness in xeric habitats (solid line and solid circles) increased with decreasing elevation (r^2= 0.78, n= 27, y= 1.32 - 0.00037x, p< 0.0001). In mesic habitats (dashed line and open circles) species richness was not influenced by variations in altitude (r^2= 0.03, n= 19, y= 0.59388 + 0.00002x, p> 0.05).

In xeric habitats, galling species richness was strongly influenced by altitudinal variations, increasing with decreasing elevation (r^2= 0.83, p< 0.0001, Fig. 2). No pattern was observed however, in the mesic habitats (r^2= 0.11, p > 0.05). As in the temperate areas, the effect of altitude in xeric habitats can be explained by higher hygrothermal stress at lower elevations. Galling insects were also more species rich in xeric habitats compared to mesic habitats at equivalent altitudes, and had distributional patterns opposite those of free-feeding herbivores (Fernandes and Price 1991).

Old World Tropical Patterns

For the Old World Tropics, we analyzed data from the Indonesian Islands which was extracted from the work of Docters van Leeuwen-Reijnvaan and Docters van Leeuwen (1926) (see Fernandes 1992, Fernandes and Lara 1993 for details). The data were well suited for our purpose, because records of altitude from sea level to 3400m were kept for the registered galls.

Just as for the other two biogeographical regions, galling species diversity was strongly inversely correlated with altitude (r^2= 0.76, p< 0.0001, Fig. 3). These data clearly corroborate our findings that there is a strong correlation between environmental harshness and gall species richness, as hygrothermal stress also appears to increase at lower elevations (see Docters van Leeuwen-Reijnvaan and Docters van Leeuwen 1926).

MECHANISMS THAT RESULT IN PATTERNS

The differences between galling species richness in xeric and mesic habitats must be evaluated in detail, as the galling habit appears to be associated with increased harshness of environmental conditions (Fernandes and Price 1988, 1991, Waring and Price 1990). To address this question, studies were performed in both tropical and temperate regions

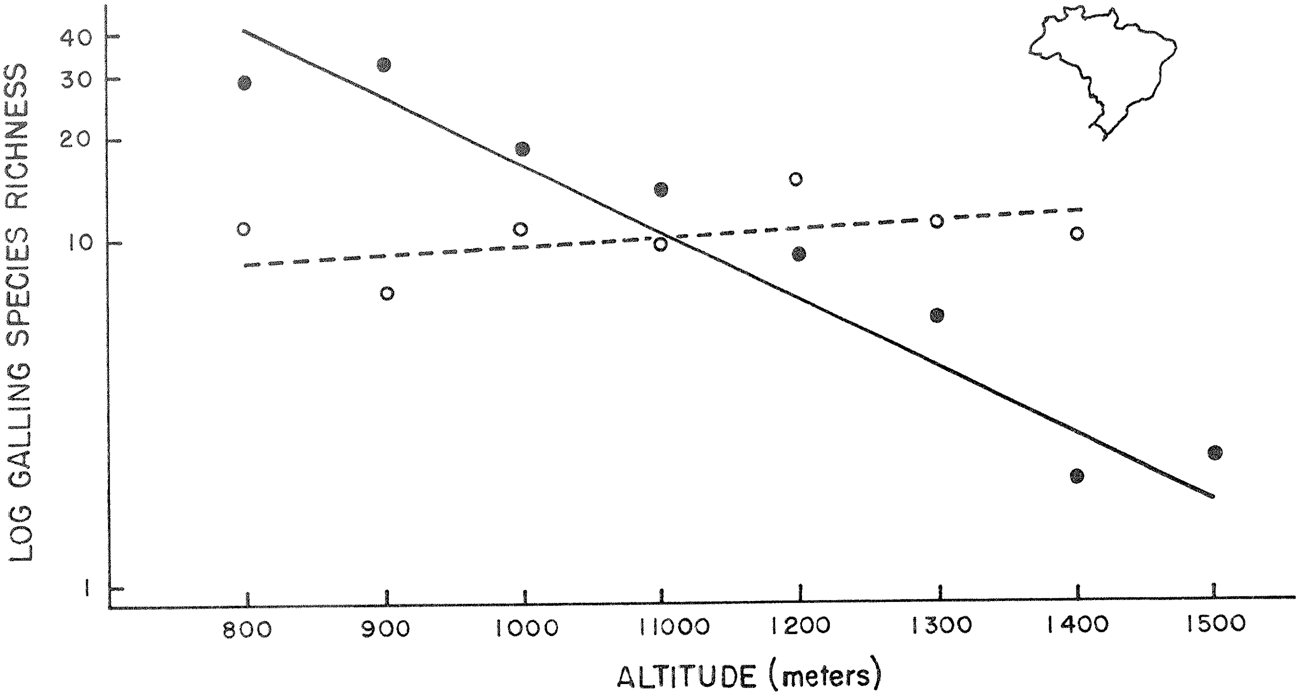

Figure 2.—Gall-forming species richness in xeric and mesic habitats along altitudinal gradients in the New World Tropics (Brazil). Species richness in xeric habitats (solid line and solid circles) increased with decreasing elevation (r^2= 0.83, n= 24, y= 3.219 - 0.002x, $p < 0.0001$). In mesic habitats (dashed line and open circles) species richness was not influenced by variations in altitude (r^2= 0.11, n= 20, y= 0.7637 + 0.0002x, $p > 0.05$).

focusing on mechanisms. Survivorship data were obtained for eight different galling species to test the "differential habitat mortality hypothesis", which predicts that gallers generally have lower mortality rates in xeric than in mesic habitats (see Fernandes and Price 1992).

Populations of tropical and temperate gallers were higher in xeric than in mesic habitats (Fernandes and Price 1992). In addition to higher gall densities per plant, there were more larvae per gall in xeric than in mesic habitats. Furthermore, gallers suffered lower mortality, and consequently experienced higher success in xeric than in mesic habitats (Fernandes and Price 1992). Mortality was caused primarily by natural enemies (disease, parasitism and predation) and plant resistance to the galling larvae.

Despite these strong trends, the data are circumstantial and correlative. In order to provide an experimental test, we studied the response of the galling fly, *Aciurina trixa* (Diptera: Tephritidae), on *Chrysothamnus nauseosus hololeucus* (Asteraceae) to changes in water and nutrient availability in Arizona (see Fernandes 1992). Plants were randonmly assigned into four treatments: control, stressed (which had their roots trenched), watered (which received 38 l of water weekly), and fertilized (which were watered [38 l of water/week] and fertilized with 13 g of NPK [20:20:20] at every other week). Control and stressed plants should simulate, within a habitat, the effects of xeric conditions, whereas watered and fertilized plants should simulate, within a habitat, the effects of mesic conditions. Most of the mortality of *A. trixa* was caused by natural enemies (predation and disease) and plant resistance. The experimental survivorship correlated the above mentioned field observations found for *A. trixa* and several other galling taxa. Also, three other species of gallers on *C. n. hololeucus* also showed a similar response, indicating some generality (Fernandes and Price, in preparation). The challenge now is to test these patterns and mechanisms until they become established, and to examine the extent to which the conclusions can be extended to other insect herbivores.

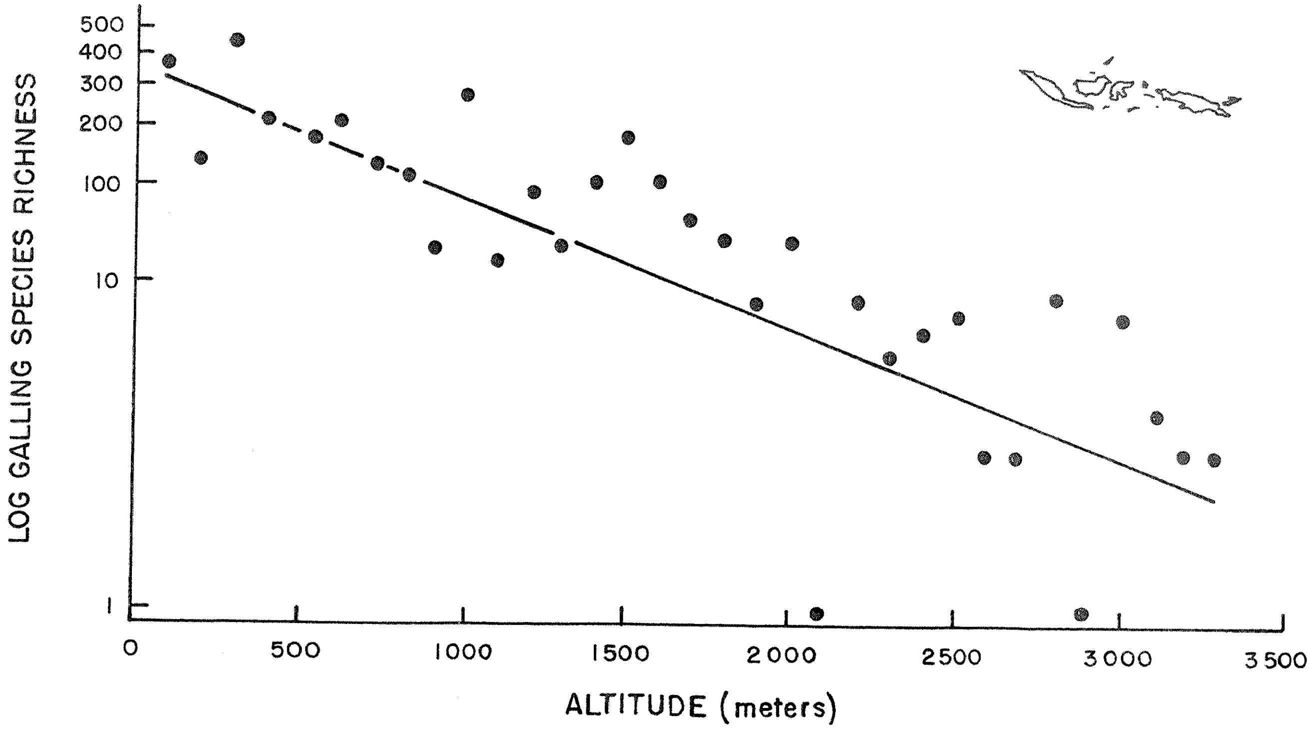

Figure 3.—Gall-forming species richness along altitudinal gradients in the Old World Tropics (Indonesia). Species richness increased with decreasing elevation (r^2= 0.76, n= 33, y= 2.6332 - 0.0007x, P< 0.0001).

Evolution of Gallers in Harsh Environments

The mechanisms producing the differential abundance of gall-forming insects in xeric and mesic habitats are differential mortality and survivorship. These findings are supported by several different studies, such as those of Carroll (1988) on the needle galling *Contarinia* sp. on pines, and of Tscharntke (1988) on the galling midge, *Giraudiella inclusa* on *Phragmites australis* in dry and wet habitats.

It is possible that galling insects have speciated and radiated in harsh environments. Galls are commonly associated with sclerophyllous plants (Fernandes and Price 1991, Price 1991) having long-lived leaves, reduced probability of leaf abscission, low-nutrient status, resource stability and predictability, and high chemical defense. These plant traits may all be part of a syndrome favoring galling species (Fernandes and Price 1991).

The lower mortality caused by natural enemies and plant resistance in xeric sites appears to reinforce galling in those habitats, promoting speciation and radiation in harsh environments. Plant pathogens are less active in drier environments (Preece and Dickinson 1971). In addition, in xeric sites, gallers occupy a niche with a relatively reduced incidence of enemies. Thus, gall-forming insects have a higher probability of surviving in drier habitats. Selection pressures exerted by some plant resistance mechanisms such as plant hypersensitive reactions, may be naturally lower in hygrothermally stressed habitats (Fernandes 1990). Elicitation of the plant hypersensitive reaction may be prevented by warm environments (see Tingey and Singh 1980). On the other hand, warm temperatures may increase the general phenolic content in plant tissues which increases resistance to pathogens (Fernandes 1990). The inter-play of selection pressures operating between and within habitats shape the distribution and richness of gall-forming insects.

In summary, mortality imposed by plant resistance and natural enemies may select against gall insect colonization in mesic habitats. Female preference and increased larval performance on chronically stressed hosts may have reinforced galler success in xeric habitats. Thus, this study supports the harsh environment, and the plant stress hypotheses (White 1984, Price *et al.* 1987, Fernandes and Price 1988, 1991). However, more work is needed to test the present findings for other gallers. Future studies of tropical and temperate systems will address these questions in order to bridge the gaps in our knowledge of the mechanisms and processes shaping the evolution of gallers in harsh environments.

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INSECT INDUCED GALLS ON AUSTRALIAN VEGETATION

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Abstract. Literature and museum records suggest that the gall insect fauna of Australia is dominated by chalcid wasps and coccoid scales. However, galls induced by psyllids and thrips are relatively common. Only a few species of beetles, moths, and cynipid wasps are known to stimulate gall formation. No native aphid or sawfly gallers are known.

Field comparison of the gall-forming insect species assemblages on vegetation of infertile and fertile soils showed a much higher diversity of gall-forming insect species on infertile soils. In addition, the galls on plants of infertile soils were more complex than those on plants of fertile soil. Galling by insects is concentrated in the Myrtaceae (especially the genus *Eucalyptus*) and is not apparent in many other lineages.

Key words: Australia; gall-forming insects; infertile soil; Eucalyptus.

INTRODUCTION

The Australian environment is characterised by widespread soil infertility (especially low phosphorus), aridity, and frequent fire. These factors have played a major role in the evolution of the modern flora which is comprised mainly of sclerophyllous species (having leathery, hard, spiny or reduced leaves in response to low soil fertility). The dominant canopy taxon is the genus *Eucalyptus*. The vegetation is of the dry sclerophyll type except for small areas of broad-leafed rainforest and the wet sclerophyll forests in highland parts of south-eastern Australia and southern Western Australia (White 1986).

Australian Gall Insects and Their Host Plants

Information from the literature and museum specimens indicates that the major galling taxon is the chalcid wasps (Chalcidoidea) of which there are at least 200 species of gall-associated chalcids in 13 genera (Boucek 1988, Naumann 1991). However, a wide range of plant genera have galls made by chalcids. Many galls are on the leaves, stems or flower buds of *Eucalyptus* and *Acacia* (Noble 1941). Wasps of the chalcid subfamily, Agaoninae, gall the female florets of *Ficus* species (Boucek 1988). The number of actual gall-forming chalcid wasp species may be smaller than these figures indicate as the literature does not always distinguish between species that are true gall-formers and those that are gall inquilines or parasitoids.

Another group of Australian gall insects, the coccoid scales (Coccoidea), has been thoroughly researched. There are 130 known species of gall-forming coccoids in 15 genera (Gullan 1983, Beardsley 1984). Many seem to be associated with more than one species of a host plant genus and some occur on several plant genera (Gullan 1984a). Numerous host plant families are attacked by coccoid gallers but most are found on Myrtaceae, especially the genus *Eucalyptus*, where they gall stems, leaves, and flower buds (Beardsley 1984).

Twenty-one genera (at least 43 species) of the family Phlaeothripidae are reported by Ananthakrishnan and Raman (1989) to be associated with galls in Australia. It is not known how many of these are true gall inducers. Several species can occur in the same gall, making it difficult to separate the primary galler from species which merely modify the existing gall or are inquilines. Thrips galls are mainly found on leaves or phyllodes (expanded petioles which function as leaves) and, like those in India, tend to be more complex than thrips galls in most other countries (Dreger-Jauffret and Shorthouse 1992). The plant genera known to be associated with the most species of gall-forming thrips are *Acacia* and *Geijera*. There are no thrips galls recorded from *Eucalyptus* (Bagnall 1929, Mound 1971a, b).

There are at least 25 gall-forming species in 6 genera in the family Psyllidae. Australian psyllids are generally found on a single host plant species or a closely related group of species (Carver *et al.* 1991). Most reported host plants belong to the genus *Eucalyptus* (Taylor 1984). Psyllid galls are predominantly on leaves (Hodkinson 1974).

Dipteran gall-formers belong to the families Cecidomyiidae, Tephritidae, Agromyzidae, and Fergusoniidae. The taxonomy and biology of most species (especially the Cecidomyiidae) has received so little study that no reliable estimates of total numbers of galling species can be made. About 10 genera are known to have species which cause galls. These are mainly on stems, leaves or flower buds. Host plant genera are numerous and include members of the families Asteraceae, Myrtaceae, Mimosaceae and Pittosporaceae (Skuse 1888, Tillyard 1926, Currie 1937, Hering 1962, Colless and McAlpine 1991).

Few Australian beetles (Coleoptera) are reported to be gallers. Froggatt (1923) describes a buprestid beetle which causes round swellings on the branchlets of *Allocasuarina distyla.* Another buprestid species is known to produce large round stem galls on *Pultenaea stipularis* and two buprestids gall the roots of *Dillwynia ericifolia* (Froggatt 1893). A weevil is reported to live gregariously in galls on eucalypts but it may not be the gall initiator (Lawrence and Britton 1991).

Records of moths (Lepidoptera) causing galls are rare and unclear. One unnamed species of the Alucitidae forms large elliptical stem galls on *Canthium sp.* and some Cosmopterigidae may be gallers (Nielsen and Common 1991). The paucity of gallers in the orders Coleoptera and Lepidoptera is universal (Dreger-Jauffret and Shorthouse 1992).

Unlike other parts of the world where cynipid wasps (Cynipidae), aphids (Aphididae) and sawflies (Symphyta) are major gallers (Dreger-Jauffret and Shorthouse 1992), it appears that Australia has only few cynipid and no sawflies, and no native aphids which induce galls (Naumann 1991, Carver *et al.* 1991).

A disproportionate number of gall species seem to occur on eucalypts. Rough estimates derived from the above sources indicate that about 400 species of insect are associated with galls on vascular plants in Australia. Approximately half these insect species are recorded from *Eucalyptus* (the genus comprises about 700 species (Brooker and Kleinig 1990)). The rest of the known gall insect species are distributed unevenly among the remaining plant genera (comprising about 16,600 species (Hnatiuk 1990)). Many plant genera are not attacked by gall insects.

Comparison of Gall Insect Diversity on Infertile and Fertile Soils

The apparent size and importance of the gall insect groups and their host plant species, suggested by the information collected to date, may simply reflect the uneven attention given to the various groups rather than indicating the real situation. In contrast, the field work described below was the starting point in a series of studies designed to identify basic patterns in gall insect diversity. It demonstrates how a broad comparative approach can be used to provide answers to questions about galling, even when taxonomic and life history data are limited.

Casual observation had suggested that the species richness of gall-forming insects was higher at infertile soil sites than at fertile ones. I carried out a field comparison of gall insect diversity on infertile and fertile soil vegetation to test this observation.

METHODS

Four infertile and four fertile woodland sites in national parks or state forests near Sydney were chosen for the study. At each site a 50x20m quadrat was marked out. The total soil phosphorus (mg/kg) in the quadrats was known from previous studies (Westoby *et al.* 1990, French and Westoby 1992) or was measured during this study by taking five (20cm x 20cm) random samples of the top 10cm of soil, bulking the samples, and analysing them for total soil phosphorus by standard methods (Lambert 1983). Within each quadrat, 200 plants <50cm high and 100 plants 50-200cm high were chosen randomly and examined for insect-induced galls. The sites were visited three times between May 1991 and April 1992. During each visit representatives of each gall morphospecies and its host plant were collected for identification.

Identification of galls to species level (and even to family or order) was often not possible. Many gall species had not been formally described; some galls never contained the galling insect; some galls only ever contained very immature insects which could not be reared to the adult stage; and the original galling insect species could not always be distinguished from inquiline or parasitoid species. For these reasons morphospecies (based on the external and internal morphology of the gall and the insects in it) was used in conjunction with species to estimate gall insect diversity. Studies by Cornell (1985) have also employed morphospecies and Taper and Case (1987) found that using numbers of morphospecies gave virtually the same results in their analyses as using numbers of taxonomically correct species.

Gall species were also grouped into two categories according to whether they had a simple or complex form. Those classified as simple galls were deformations like leaf masses, rolls, or pits in which the insect was only partly surrounded by the gall. Galls in the complex category were more enclosed, often woody, and without an exit hole (or with a hole that was very small or blocked). Lists of all the plant species sampled in the quadrats were compiled from surveys made during each visit and checked with lists made during previous studies (where these were available) (Westoby *et al.* 1990, French and Westoby 1992).

RESULTS

Total soil phosphorus concentrations in the quadrats were in the range 65-110 mg/kg at infertile soil sites and 216-961 mg/kg at fertile soil sites (Table 1). The mean number of gall insect species at infertile soil sites (23.0 gall species/quadrat) was significantly higher than the mean number (7.5 gall species/quadrat) at fertile soil sites (Table 1) (t=5.8, df=6, P<0.005).

Table 1.—Soil fertility (mg/kg total phosphorus) and gall distribution at infertile and fertile sites

Site Properties	Fertile sites				Infertile sites			
	1	2	3	4	5	6	7	8
Total soil P (mg/kg)	650	216	786	961	110	103	65	100
Total gall species	8	7	10	5	17	23	29	23
Gall species on Myrtaceae	0	0	10	0	10	21	18	13
Myrtaceous plant species present	1	0	2	0	8	7	6	7
Gall species on eucalypts	0	0	0	0	9	19	7	11

At both infertile soil and fertile soil sites, only a minority of plant species had any galls (Fig. 1). The proportion of plant species with associated gall species was significantly higher at infertile soil sites than at fertile soil sites ($G^2=9$, df=1, P=0.0028). The plant families occurring at infertile soil sites were substantially different from those at fertile soil sites. This is important because a large proportion of gall species occurred on Myrtaceae (Table 1). Individual Myrtaceous plant species, especially eucalypts, often had much higher numbers of associated gall species than members

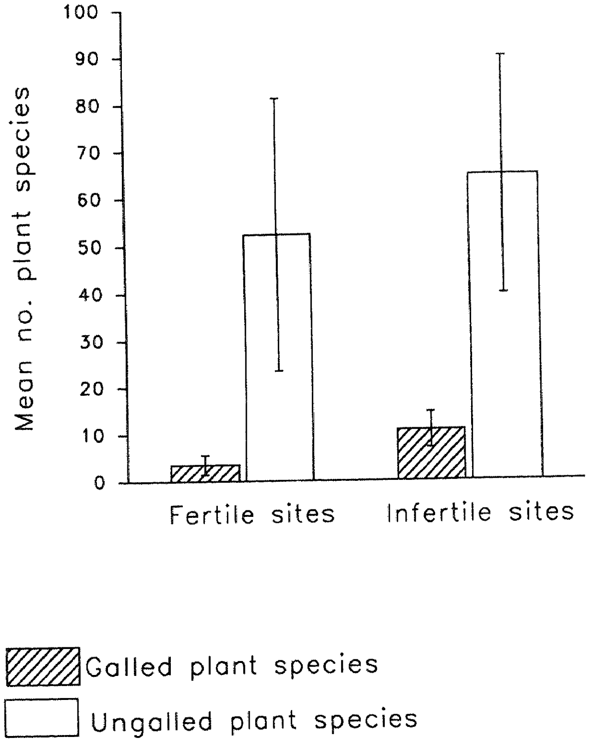

Figure 1.—Galled and ungalled plant species at fertile and infertile sites (mean±SD).

of any other plant family (up to 13 different gall species on a single Myrtaceous species at a site). The family Myrtaceae was absent or poorly represented at fertile soil sites (Table 1). When only gall species on non-Myrtaceous plant species were considered the mean number of gall species at infertile soil sites (7.5 gall species/quadrat) was not significantly different from the mean number of gall species (5.0 gall species/quadrat) at fertile soil sites.

At the infertile soil sites there were far more complex gall species relative to the simple kind of gall species that were at fertile soil sites ($G^2 = 8.3$, df=1, P=0.0039). In fact the larger number of gall species on infertile soils consisted almost entirely of those with complex galls (Fig. 2).

DISCUSSION

The results support the original observation that vegetation on infertile soils has more gall species than vegetation on fertile soils. One explanation of this result could involve longevity of plant parts. Plants growing on infertile soils retain their parts longer (Coley *et al.* 1985, Escudero *et al.* 1992,) (and perhaps abscise damaged parts less readily) than plants growing on fertile soils. This is because the cost of replacing parts is higher on infertile than fertile soils. As most gall-forming insects are unable to move successfully to new plant sites once gall initiation has commenced, it seems reasonable that plant species with long-lived parts would be more favorable hosts for such insects and so would acquire and retain, over evolutionary time scales, a greater diversity of galling species.

The higher proportion of complex kind of gall on infertile soil vegetation gives further support to this idea. Noble (1940, 1941) found that the larvae of two species of chalcid wasp which cause complex galls on *Acacia* spend 9-10 months in the gall before pupating. During this time the gall continues to grow and mature. There is also evidence to suggest that some gall-forming coccoids inhabit their complex galls for at least two years (Gullan 1984b). No information is available on the duration of life cycles of Australian insects which cause simple galls. It seems possible that complex galls require more time to reach maturity or are occupied longer by the gall insect than are simple galls. If so, the greater proportion of complex gall species on infertile soil vegetation may reflect the longer retention time of plant parts on infertile soils. However, it would be expected that increased gall species richness brought about predominantly

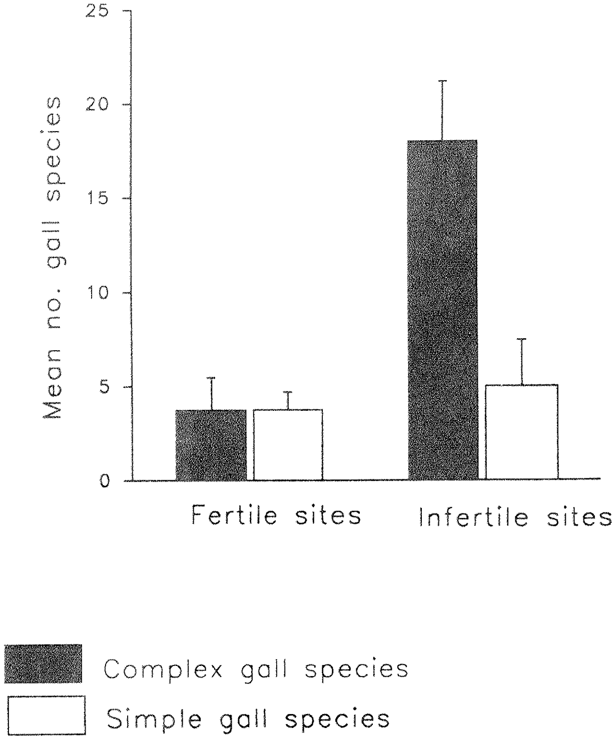

Figure 2.—Complex and simple gall species at fertile and infertile sites (mean±SD).

by longer retention of plant parts would be uniformly distributed across all infertile soil plant genera. This was not the case. Galling was concentrated in the Myrtaceae (especially in the genus *Eucalyptus*). The difference in the number of galled Myrtaceous species alone explains the difference in gall diversity between the two soil types.

Given the high susceptibility of *Eucalyptus* to galling, the next step in the investigation will involve a shift in emphasis from comparison of soil types to a study of galling within the genus *Eucalyptus*. Preliminary data (Blanche unpublished) suggest that galling is not uniform throughout the genus. Most eucalypt species have no galls; others have some, and only a few have many. Perhaps characteristics which promote galling are more pronounced in those eucalypt species with many associated gall species. Range size is variable within the genus *Eucalyptus* (Chippendale and Wolf 1981). Those species with broad distributions might be expected to have more associated gall species because they potentially encompass a greater diversity of environmental conditions (i.e. have a larger gall species pool to draw on), and extinction rates for associated gall insect species should be lower than those of more restricted eucalypt species. Data from the literature and museum specimens (Blanche unpublished) indicate that there is a significant (though weak) positive relationship between the number of gall insect species associated with a eucalypt species and the size of its range. Having a small range apparently limits the number of associated gall species, but a very broad range is not necessarily linked to having many gall insects.

Some eucalypts are known to continue assimilation under drought conditions either by having deep roots which can tap ground-water supplies or by tolerating high levels of desiccation (Grieve 1956). The resulting provision of a continuous food supply is likely to be advantageous to sedentary insects like gall-formers. Eucalypt species which provide a continuous food supply may, over evolutionary time scales, may favor greater gall species diversity than eucalypt species without this ability.

Many eucalypts resprout readily in response to defoliation (by fire, severe drought or herbivore impact). New shoots can be produced from axillary, accessory, and epicormic buds, and from lignotubers (Ohmart and Edwards 1991). Eucalypt species with available meristem at numerous sites could provide more, spatially separated niches for gall insect species to colonise than eucalypt species with limited resprouting ability offer. In addition, if gall-forming insects are also able to respond to defoliation events, then temporal separation of gall insect populations may occur and promote gall insect speciation.

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LIFE HISTORY STRATEGIES OF THREE GALL-FORMING FLIES TIED TO NATURAL VARIATION IN GROWTH OF PHRAGMITES AUSTRALIS

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Abstract. Three flies of the genus *Lipara* (Diptera: Chloropidae) are strict monophagous parasites of the common reed, *Phragmites australis* (Poaceae) in Belgium. Females deposit their eggs on the surface of the reed shoot, into which the first instar larvae bore. Therein they feed upon the newly emerging leaves. Due to the larval presence, a species specific gall chamber is formed. When the gall is completed, the larvae of *L.lucens* and *L. rufitarsis* gnaw through the growing point and enter the gall chamber where they continue their life cycle. On the other hand, larvae of *L. pullitarsis* never pass through the growing point and live instead between the enwrapped leaves. The three *Lipara* species are not homogenously distributed in their common habitat. Each species' larval survival and populations are uniquely correlated with reed shoot diameter (a measure of plant vigor). The ovipositing females are able to discriminate between shoots of different quality.

Lipara species are attacked by a number of hymenopterous parasitoids and a vertebrate predator. Although some of these natural enemies may influence the habitat selection (shoot diameter) of the flies, our data indicate that the impact of natural enemies may be relatively minor compared to that due to host plant resistance. During the evolution of the genus *Lipara*, a trade-off between obtaining the necessary food supply and growth dependent host plant resistance has been a major force in structuring the life cycle strategies.

INTRODUCTION

Host plants can reduce the success of their herbivores in two different ways. First the plant can act directly through its defense systems (Coley *et al.* 1985, Karban and Myers 1989, Smith 1989, Stiling and Simberloff 1989, Gould 1991). Secondly, it can evolve certain traits which affect herbivore vulnerability to the herbivores' enemies (Price *et al.* 1980, Faeth 1985, Craig *et al.* 1988, Gross and Price 1988, Waring and Price 1989, Andow and Prokrym 1990). Insect induced plant galls are usually a result of complex structural and chemical changes of the original plant tissues (Bronner 1977, Rohfritsch 1992). They form a base for a complex community of parasitoids and predators (Price 1971, 1972, 1973; Force 1974, Weis 1982). The high variation in gall morphology observed in nature has raised the question on the adaptive nature of insect galls (Price *et al.* 1987a). In many cases, the gall contents can serve as an important food resource for gall-making insects. Sometimes, however, certain characteristics of gall morphology have no apparent relationship to its nutritional status. The latter is usually explained by the fact that galls surrounding the herbivore may protect it from parasitoids and predators.

Grasses possess a simple plant architecture, low protein concentration, and a low diversity of secondary compounds compared to more complex plants. This influences the insect community feeding on them (Bernays and Barbehenn 1987, Tscharntke 1988). Earlier studies have shown that grass habitats support low herbivore species richness (Strong and Levin 1979, Lawton 1983). The common reed, *Phragmites australis* (Cav.) Trin. ex Steud., occur all over the world in large natural monocultures. Several organisms use these reed beds as a source of food or to raise their offspring. Due to the developmental constraints of the host, reed beds harbor many specialised herbivore parasites (e.g. Skuhravy 1981; Vogel 1984; Tscharntke 1988, 1989). The flies of the genus *Lipara* Meigen (Diptera: Chloropidae) are strict monophagous parasites of the common reed, in which they induce characteristic cigar- or spike-like galls (Chvála *et al.* 1974).

Natural History

Phragmites australis is a perennial rhizomatous grass that produces fresh shoots every year in spring (April-May) (Björk 1967, Van der Toorn 1972). The erect culms (1.5-3m high) bear lanceolate leaves at each node. Above the growing point, only the newly formed, enwrapped leaves are present. The leaves are point upward in line with the shoot. Below the soil surface, the different shoots of a reed clone are connected via a rhizome. The vegetative phase lasts until the end of June, after which an ear is formed (start of the reproductive phase). In autumn, the shoots dry up and the above ground parts of the reed clone die.

In Belgium, three *Lipara* species are encountered frequently on the common reed, viz. *L. lucens* Meigen, *L. pullitarsis* Doskocil and Chvála and *L. rufitarsis* (Loew) (De Bruyn 1985). Adults emerge in spring from the end of May until early July. There is only one annual generation. The females deposit their eggs on the surface of the reed shoot. After hatching, the first instar larvae enter the shoot under the edge of a leafsheath and gnaw their way down through the enwrapped leaves until they reach the growing point. Here they feed on the enwrapped leaves above the growing point. Due to the larva, the newly formed internodes do not elongate any more and the species specific gall chamber forms (Chvála *et al.* 1974). Although the new internodes do not elongate any more, they still widen. The nodes do not produce a septum as do normal shoots. In contrast to normal internodes, where only a very faint layer of pith is present, the resulting gall chambers of *L. lucens* and *L. rufitarsis* are filled with a dense mass of a parenchymatous tissue (Wagner 1907, De Bruyn 1993a). After a few weeks, when gall formation is completed, the larvae of *L. lucens* and *L. rufitarsis* gnaw through the growing point and enter the gallchamber wherein they continue breeding. The larvae of *L. pullitarsis* never pass the growing point and live between the enwrapped leaves during their entire larval phase. At the end of August, the last instar larvae of all species stop feeding and go into diapause. Pupation takes place in the next spring. Only one *Lipara* larva can develop per shoot.

Lipara larvae are attacked by a number of hymenopterous parasitoids and a herbivore predator (Giraud 1863, Mook 1967, Chvála *et al.* 1974, Nartshuk 1977). During our study we encountered five hymenopterous parasitoids and one vertebrate predator (De Bruyn 1987a). *Polemochartus liparae* (Giraud) and *P. melas* (Giraud) (Hymenoptera; Braconidae) oviposit in the *Lipara* eggs while they are attached on the outside of the reed shoot (Mook, 1961). *Polemochartus* induces premature pupation of its host. When the galls are opened during the winter, a dark (almost black) pupal case of the *Lipara* species is found with a larva of the parasitoid. The *Polemochartus* parasitoids emerge from the gall by clearing a way through the enwrapped leaves at the top of the gall. *Stenomalina liparae* (Giraud) (Hymenoptera; Pteromalidae) is a parasitoid which infests the *Lipara* hosts after the larvae have entered the reed shoot, but before gall formation has completed. Therefore they have to insert the ovipositor through the reed shoot. During winter, only the shrivelled skin of the *Lipara* larva is left, in which the *S. liparae* larva overwinters. The adult wasps emerge by gnawing a little hole through the wall of the gall. *Tetrastichius legionarius* Giraud (Hymenoptera; EuMwphidae) are small, gregarious larval parasitoids. How the female wasps attack their hosts is unknown so far. During winter, one can find more than 40 *T. legionarius* specimens in one single *Lipara* larva. The adult parasitoids leave the gall through the enwrapped leaves of the gall. The parasitoid, *Scambus* sp. (Hymenoptera; Ichneumonidae) possesses a relative long free ovipositor. The biology of this parasitoid is largely unknown. During winter, only the hibernating larvae, accompanied with a few remnants of the larval skin of the host can be found in the gallchamber. The adult *Scambus* wasps emerge through the enwrapped leaves.

When *Lipara* galls are collected, one can regularly find a gall with a large hole, hewn out by a bird. The gallchamber is empty. According to Mook (1967) this bird predator is the Blue Tit, *Parus caeruleus* L., a species which also attacks other reed inhabiting herbivores (Tscharntke 1992). During winter, when there is a shortage of food, Blue Tits often forage in reed beds.

Plant-Herbivore Interaction and Habitat Quality

During several decennia, *Lipara* galls have attracted the attention of many naturalists (Giraud 1863, Blair 1932, Theowald 1961, Skuhravy 1980). Their studies indicated that the *Lipara* galls are not homogenously distributed in their habitat. *L. lucens* is usually found in reed beds in dry places, whereas *L. pullitarsis* commonly occurs in marshy to wet circumstances (Mook 1971, Pokorny 1971, Vogel 1984). Mook (1967) showed that the diameter of a reed shoot strongly influences the survival of *L. lucens*. In this part of the study we analyzed the direct interactions between the gall-makers and their hostplant, the common reed. Our attention was mainly focused on the habitat distribution (macro-habitat) and the resource exploitation patterns (micro-habitat) of the three *Lipara* species. To analyze the importance of these differences in gall formation, we carried out a structural and chemical analysis of the *Lipara* galls.

MATERIALS AND METHODS

To analyze the hostplant-herbivore interactions, we carried out two field tests and one laboratory test where habitat distribution and hostplant exploitation are studied. In the first (habitat distribution) experiment we collected galls at 45 reed beds in Belgium and the Netherlands (De Bruyn 1987b, 1993b). The different localities ranged from high quality habitats such as wet, nutrient rich soils (e.g. large, high density reed beds in marshlands) to low quality habitats with dry and/or nutrient poor soils (thin reed beds along roadsides or the edges of woods). For detailed information on the localities and sample dates, refer to De Bruyn (1989a). At each place, six random shoot samples (0.25 m^2) were taken. The basal shoot diameter (first above ground internode, with leafsheet removed) was measured with a calliper to the nearest 0.1 mm to assess the shoot diameter distribution. As a measure of habitat quality, soil moisture and nitrogen content were assessed according to the Ellenberg method (Ellenberg 1974, De Bruyn 1989a).

To investigate hostplant exploitation by the gall-maker, we measured the shoot diameter preference of ovipositing flies and larval survival up until gall formation (De Bruyn 1989b). In June, during the oviposition period, a muslin bag containing a single, mated female fly was pushed over the top of a reed shoot. The next day, the bag was removed and checked for eggs. Superfluous eggs were removed so that only one egg remained on the shoot. At the beginning of August, when the galls are easy to detect, the infested shoots were checked for galls. Female oviposition preference was assessed with a laboratory experiment. In a glass cage, single, mated female flies were offered 36 reed shoots (cut off from the top 50 cm of a shoot) arranged in six rows of six, each 5cm apart. Shoots were evenly spread over six diameter classes ranging from 3-4 mm to 8-9 mm. Position of the diameter classes in the experimental arena was randomised. Each day, new shoots were offered while the number of eggs oviposited and their location on the reed shoot cuttings were recorded.

The galls used for the structural and chemical analyses were collected in early August. At this time, gall formation is completed, but the larvae have not entered the gall chamber and are still feeding on the young enwrapped leaves. The tissues in the gallchamber are still intact. To assess differences in gall growth and final gall size, both shoot diameter (first internode under the gall) and gall diameter, were measured with a calliper to 0.1 m . The galls used for the chemical analysis were transported on ice to the laboratory where they were dissected. A portion of the enwrapped leaves and the parenchymatous tissue in the gall chamber were separated for analysis. Water content of the tissues was obtained by measuring fresh and oven-dry (temp: 70°C) weight on a microbalance. Tissues parts used for the chemical analysis were lyophilised immediately. Total protein and sugar content were measured (three replicates) by a modified Lowry method (Markwell *et al.* 1978) and the anthrone method (Snell *et al.* 1981) respectively.

RESULTS

The diameter of all reed shoots in the habitat distribution experiments ranged between 1.2 mm and 9.9 mm with a mean of 3.89 ±1.38 (median=3.60). The mean (±S.D.) shoot diameter of the 45 sampled habitats varied between 2.73 ±0.54 mm and 6.75 ±1.41 mm. Ninety-five percent of the inter-habitat shoot variation was explained by soil moisture and soil nitrogen (multiple linear regression: shoot diameter = 0.23 moisture + 0.41 nitrogen: $F_{2,43}=452.308$, $P<0.001$). Wet and nutrient rich habitats support significantly thicker shoots than dry and nutrient poor habitats.

L. lucens galls can be found on shoots from 1.4 mm to 6.6 mm. However, most galls appear on thinner shoots (mean=3.00 ±0.85 mm; median=2.80 mm). At a particular sample locality, the *L. lucens* gall density is dependent on mean shoot diameter (partial-r=0.34, $t_{42}=2.330$, $P<.025$) and shoot density (partial-r=-0.48, $t_{42}=-3.372$, $P<.001$) (multiple regression: $F_{2,43}=18.134$, $P<.001$, $r^2=0.44$). To eliminate the effect of shoot density, we recalculated *L. lucens* density as number of galls per 100 shoots. *L. lucens* densities (Fig. 1) are highest in habitats with on average thin shoots and decline significantly when the mean shoot diameter rises ($y= 1/(0.21x - 0.47)$; $F_{1,43}=27.236$, $P<0.001$, $r^2=0.39$).

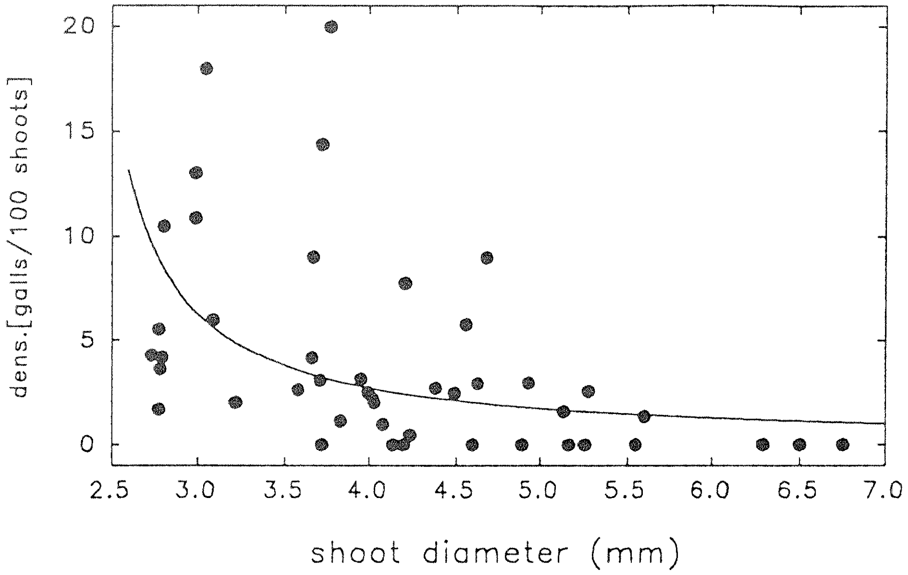

Figure 1.—The relationship between *Lipara lucens* gall density and mean shoot diameter of the reed beds.

In the larval survival experiments, 44% of the 205 infested shoots carried a gall. The highest proportion (77%) of galled shoots was found on shoots between 3 and 4 mm (Fig. 3a). When the diameter rises, the proportion of galled shoots declines. On shoots thicker than 7.6 mm, *L. lucens* failed to induce a gall. Thus, there is a greater possibility that a gall develop on thinner shoots (logistic regression: l_h=1.578 - 0.390x; Wald-Q=22.537; df=1; p<0.001). Only in the smallest diameter class (2-3 mm) we see a small deviation where the survival rate is lower. In the oviposition preference experiments, the *L. lucens* showed a clear peak preference for shoots of intermediate size (Fig. 4). Most eggs were found on shoots with a diameter between 5 and 6 mm. The 22 tested females on average oviposited 54.17 eggs with a maximum of 84. Before ovipositing the female fly wanders around on the shoot for some time. Mook demonstrated that searching time is shoot diameter dependent (Mook 1967). When the shoot is of appropriate size, she deposits an egg and leaves the shoot immediately to search for another shoot. Under field conditions, the eggs are almost always situated on the top 20cm of a reed shoot.

The results for *L. rufitarsis* are comparable to those found for *L. lucens*. Here again the population density of the galler is negatively correlated with the mean shoot diameter of the reed habitats (Fig. 2a: Y=1/(0.25 + 0.12x); $F_{1,43}$=11.79; p<0.001; r^2=0.22). In general, *L. rufitarsis* galls are found on shoots with a diameter from 1.5 mm to 5.2 mm (mean=2.87 ±0.76 mm; median=2.70 mm). Survival the *L. rufitarsis* larvae is highest on the thinnest shoots (Fig. 3b). Thicker shoots produce proportionally less galls (logistic regression: l_h= 4.147 - 1.132x; Wald-Q=27.286; df=1; p<0.001). The thickest shoot carrying a gall was 6.3 mm wide. Twenty-three females of *L. rufitarsis* were tested in the oviposition choice experiments (Fig. 4). The frequency distribution is shifted to the left and most eggs were deposited on shoots of the diameter class between 4 and 5 mm. The mean number of eggs oviposited by a single female was 28.86 with a maximum of 50 eggs.

In contrast to the two former species, *L. pullitarsis,* attains highest population densities in reed beds with on average thick reed shoots, and populations decline when mean shoot diameter decreases (Fig. 2b: Y=exp(0.64x -1.25); $F_{1,43}$=21.68; p<0.001; r^2=0.64). The overall shoot diameter range with galls of *L. pullitarsis* is also very broad and extends from 1.4 mm to 9.5 mm. Most galls are found on thicker shoots (mean=4.40 ±1.21 mm; median=4.4 mm). As expected from the habitat distribution data, survival is rather high (70% of the 222 shoots tested) for all diameter classes (Fig. 3b), although it may be less on the thinner shoots. For shoots with a width over 6 mm, survival rate is roughly even. The possibility for *L. pullitarsis* to successfully induce a gall increases when shoot diameter rises (logistic regression: l_h= -1.218 - 0.369x; Wald-Q=15.893; df=1; p<0.001).

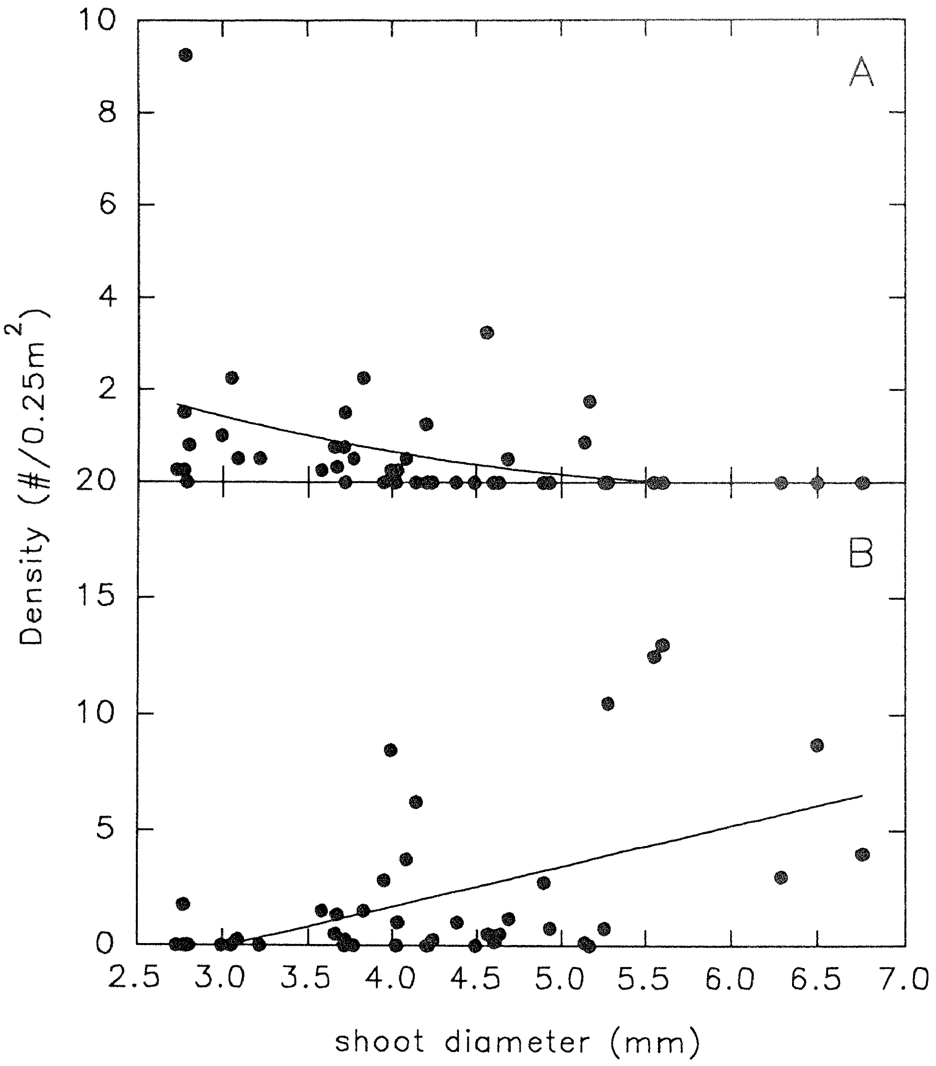

Figure 2.—The relationship between gall density and the mean shoot diameter of the reed beds (A: *L. rufitarsis;* B: *L. pullitarsis).*

L. pullitarsis (n=18) oviposited most eggs on thicker reed shoots (Fig. 4). However, shoots wider than 7 mm received slightly less eggs. On average, single female flies deposited 92 eggs with a maximum of 135. During oviposition, they display only a weak searching behavior. Usually the female oviposits an egg a few moments after landing on a reed shoot. In many cases she oviposits a second or more eggs before leaving the shoot. In nature on can find reed shoots with up to 32 eggs. These eggs are not grouped on top of the shoot as in *L. lucens* but they are spread all over from the soil up to the top, on the culm as well as on the leaves.

L. lucens and *L. rufitarsis* both produce a gall chamber filled with a dense mass of the parenchymatous pith tissue. The internodes are strongly widened in *L. lucens* (Fig. 5a: mean = 2.41 ±0.52 times the normal shoot diameter) resulting in a relatively large gall chamber. The size increase is particularly high on the thinner shoots and diminishes when shoot diameter rises. The galls of *L. rufitarsis* are clearly smaller than those of *L. lucens.* Fewer internodes are involved and moreover are less widened (Fig. 5b: mean=1.81 ±0.59 times the normal shoot diameter). The impact of the herbivore is highest on the thinner shoots although less pronounced as in *L. lucens.*

L. pullitarsis does not induce a gall chamber at all. The larva feeds upon the enwrapped leaves in a narrow, dark brown furrow. There is practically no widening of the shoot (Fig. 5c).

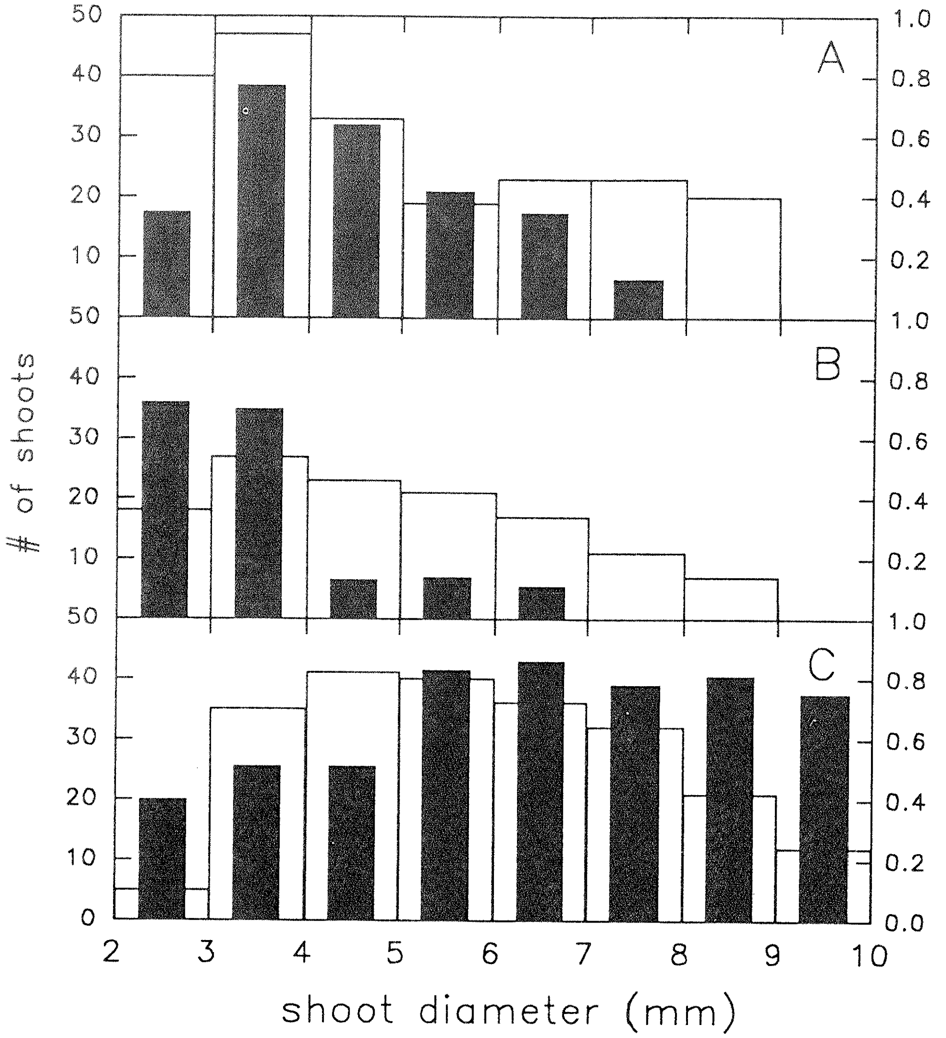

Figure 3.—Shoot diameter dependent larval mortality due to plant resistance. white bars = number of shoots tested; black bars = proportion galled. A) *L. lucens* B) *L. rufitarsis* C) *L. pullitarsis.*

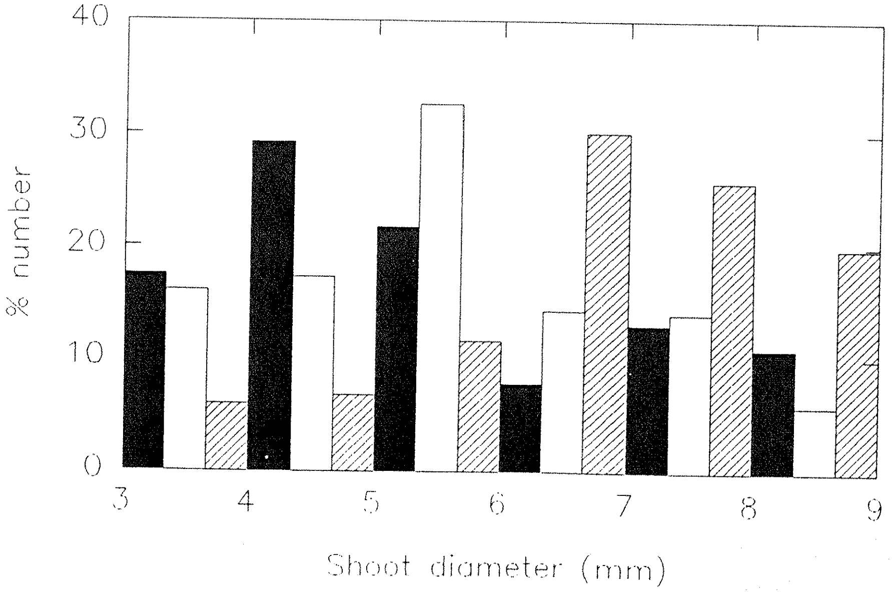

Figure 4.—Shoot diameter preference for ovipositing female flies. white = *L. lucens;* black = *L. rufitarsis* hatched = *L. pullitarsis.*

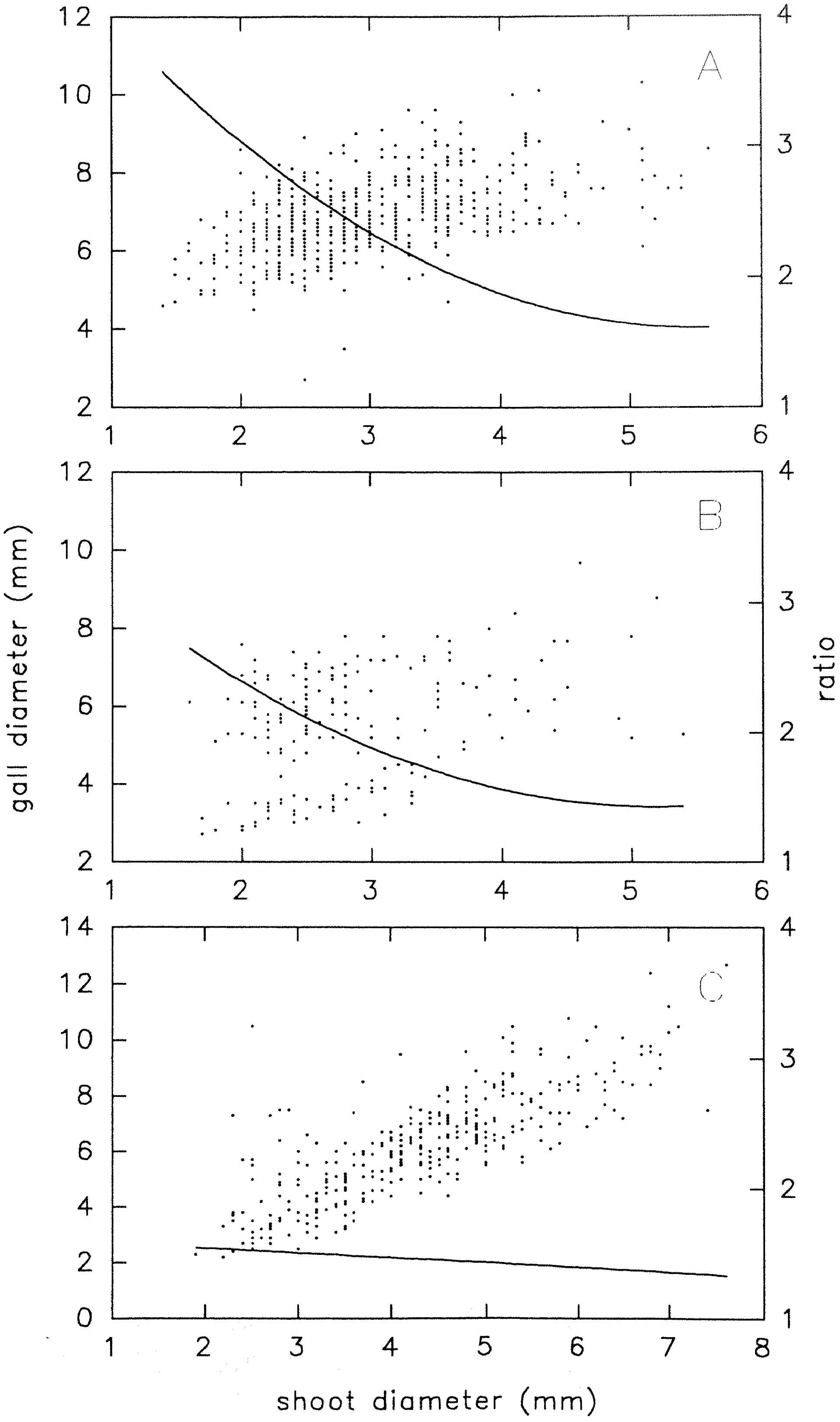

Figure 5.—Relationship between shoot diameter and gall diameter. Scatter diagram = shoot versus gall diameter; line = proportional size increase as a function of shoot diameter. A) *L. lucens* B) *L. rufitarsis* C) *L. pullitarsis.*

The chemical analyses revealed the parenchymatous tissues were higher in all three measured parameters than the enwrapped leaves (Table 1). This was particularly the case for protein (paired-t=5.92; df=23; $p<0.001$) and water (paired-t=5.54; df=78; $p<0.001$) content. The difference in carbohydrate content was less pronounced, but still significant (paired-t=2.07; df=23; $p=0.05$). Moreover, there is also a histological difference. The parenchymatic pith consists of relatively large, soft cells. The enwrapped leaves, on the otherhand, contain numerous parallel fibrous veins which increase toughness, and as such hamper or even prevent food uptake and digestion.

Table 1.—Water, protein and carbohydrate content of the different gall tissues (data are mean ±S.D.)

Tissue	Water	Protein	Carbohydrate
	(mg/g wet wt)	(mg/g dry wt)	(mg/g dry wt)
Enwrapped leaves	849.70 ±35.77	242.41 ±98.74	149.36 ±97.46
Parenchyma	886.02 ±57.85	407.36 ±166.22	190.06 ±79.61

DISCUSSION

The study has revealed that the diameter of a reed shoot plays a crucial role in the habitat selection and subsequent survival for all three species. Former studies on Cecidomyiid stem gallers (Diptera) and Lepidopteran shoot borers of the common reed also showed that shoot diameter may play a crucial role in the survival of these herbivores (Mook and van der Toorn 1985, Tscharntke 1988, 1990).

The diameter of a shoot is constant throughout the growing season. Previous studies have revealed that shoot diameter is positively correlated with growth rate, final shoot length, the probability to produce an ear, and as such is a measure of shoot vigor (Mook 1967; Haslam 1969, 1971; Van der Toorn 1972). Variation in shoot diameter is mainly due to variable water and nutrient supply: dry, nutrient-poor habitats yield thinner shoots than wet, rich habitats (Gorham and Pearsal 1956, Björk 1967, Haslam 1971, Van der Toorn 1972). Stressed reed shoots not only display a morphological weakness, but they also contain less minerals, water, nitrogen and silica (Tscharntke 1988, 1989, 1990).

L. pullitarsis showed a strong positive relationship between larval performance and shoot width. Larval survival was higher on thick, vigorous growing shoots (Fig. 3c), and up to 76 times more galls were found in wet, nutrient rich habitats than in dry, nutrient-poor habitats (Fig. 2b).

The two other species however, displayed an opposite response. Larval survival was clearly higher on thin (Fig. 3a and b), stressed shoots, and population densities were higher in dry, nutrient-poor habitats (Fig. 1: *L. lucens* up to 112 times; Fig. 2a: *L. rufitarsis* up to 37 times). These findings, contradict the hypothesis that gall forming insects should generally perform better on vigorous hostplants (Larsson, 1989 and Price, 1991). Gall inducing insects, as most other internally feeding herbivores, display an intimate relationship with their hostplant (Mattson *et al.* 1988, Preszler and Price 1988, Thompson 1988, Craig *et al.* 1989). The andophytic larvae have to develop at the site where the female has oviposited and strictly dependent on locally available food resources. According to the plant vigor hypothesis, galling insects should therefore be tightly linked to rapid growing modules within non-stressed plants.

As mentioned before, the three *Lipara* species produce strikingly different gall types. Both *L. lucens* and *L. rufitarsis* induce a gallchamber while *L. pullitarsis* does not. From our results we can conclude that *L. lucens* and *L. rufitarsis* have evolved the possibility to improve the quality of their hostplant by aggregating highly nutritious tissues in their galls. Reeds growing in habitats with reduced water and/or nutrient supply not only produce thinner shoots, but these shoots also contain a lower amount of nutrients (proteins, water, minerals) (Tscharntke 1988, 1989, 1990) and provide only a poor food resource for developing larvae. The capability to manipulate parts of its hostplant by inducing a large gall chamber, filled with a nutrient rich parenchymatous tissue, provides *L. lucens* a solution to this problem. *L. pullitarsis,* on the contrary, does not alter the growth and quality of its host in any conspicuous manner. As a consequence, it is dependent on the ambient level of nutrients offered by the hostplant. This explains why *L. pullitarsis* prefers and performs better on vigorous growing host plants.

If we compare the results obtained during the oviposition choice experiments with those from the survival experiments, we find a relatively close correspondence for all three species. *L. lucens* and *L. rufitarsis* females prefer thinner shoots for oviposition, where survival of the larvae is also highest. The slight shift for oviposition preference to thicker shoots for *L. lucens* (Fig. 4), can be explained by the fact that larval survival is slightly lower for very thin shoots (Fig. 3a). Moreover, earlier work (De Bruyn 1989b) revealed that thin reed shoots produce smaller females, which in turn results in a lower egg production of these females. Analogously, *L. pullitarsis* prefers mainly thicker shoots to deposit the eggs. Here also survival rate of the larvae up to gall formation is highest.

Our study demonstrated that female flies of all three species are able to discriminate between shoots of different quality. By carefully selecting the oviposition site, they increase the survival chance of their offspring.

NATURAL ENEMIES

According to early theory, parasitoids and predators should play an important role in regulating insect herbivore densities (Hairston *et al.* 1966, Slobodkin *et al.* 1967). However, field studies have revealed that this is not universally true (Stinner and Abrahamson 1979; Washburn and Cornell 1979, 1981; Abrahamson *et al.* 1983; Price 1985; Weis and Abrahamson 1985; see Price *et al.* this volume). Moreover, variation within and among host plants has been shown to have both direct effects on herbivore mortality and indirect effects through impacts on natural enemies. This variation may be due to environmentally induced phenotypic variation, as well as genotypic components (Price *et al.* 1987b, Collinge and Louda 1988, Fritz and Price 1988, Price 1989, Fritz and Nobel 1990, Alexander 1991, Smith and Rutz 1991). Here we analyzed the mortality factors acting on the three *Lipara* species. First we studied the direct influence of the reed shoots on the possibility of a larva to induce a gall. Secondly we assessed the impact of the natural enemies on the survival of the *Lipara* species. Special attention was paid to the impact of shoot diameter.

Materials and Methods

We analyzed the effects of the hymenopterous parasitoids and bird predators on the herbivore with a field experiment. During the winter, from November to April, *Lipara* galls were collected at several reed beds. At this time, all gall inhabitants are in diapause and easily identifiable. The galls were transported to the laboratory where they were dissected and the contents identified. The shoot diameter (leafsheets removed) was measured with a calliper to the nearest 0.1 mm to assess the shoot diameter distribution.

Results

The different members of the parasitoid guild attacking the three *Lipara* species all show a more or less specific host spectrum (Table 2 and De Bruyn 1987b). The mortality due to parasitoids and predators is highest for *L. rufitarsis* (28.2%) and *L. lucens* (29.5%). *S. liparae* (16.40%) and *P. liparae* (6.85%) are the two major parasitoids of *L. lucens*. The first parasitoid also attacks the two other *Lipara* species, although the mortality caused is much lower. *P. liparae* can occasionally also be found in the galls of *L. pullitarsis.* Highest mortality rates in *L. rufitarsis* are due to the *Scambus* species (13.08%) and *P. melas* (8.72%). The *Scambus* species is largely restricted to *L. rufitarsis,* although it also infests galls of *L. lucens.* The latter only occurred when *L. rufitarsis* was also present in the same reed bed. *P. melas* attacks all three *Lipara* species but is only occasionally found in *L. lucens* and *L. pullitarsis* galls.

Finally we can mention that *T. legionarius* was exclusively found in the galls of *L. lucens.* This species however, is rather rare and the mortality rate only attains 1.27%. The overall mortality rate in *L. pullitarsis* is very low and only attains 9.89%. Two thirds of the 66 dead *L. pullitarsis* larvae was due to bird predation. Birds primarily attacked galls of *L. pullitarsis.* Here however the impact of predation is practically negligeable.

Some of the *Lipara* galls were fully developed but contained no larvae or a dead one. These are grouped under the common name "unknown" factors in table 2. In some cases (*L. lucens* and *L. rufitarsis* galls), the gall chamber was fully developed and completely filled with the parenchymatous pith tissue. The shoot even may have resumed normal growth above the gall chamber. Here the larva died before penetrating the growing point. Most of these galls were found on thin shoots (De Bruyn 1993a). This may indicate that the larvae can induce a gall on the very thin shoots, but the induced food resources are insufficient to support its development. Gall formation was also less likely on the thinnest shoots (Fig. 3a) which supports this proposition.

Table 2.—Relative mortality rates due to parasitization and predation

	L. lucens		*L. rufitarsis*		*L. pullitarsis*	
# galls collected	1183		344		667	
# flies emerged	834	70.50 %	247	71.80 %	601	90.11 %
S. liparae	194	16.40 %	7	2.03 %	7	1.05 %
P. liparae	81	6.85 %	5	0.75 %		
P. melas	6	0.51 %	30	8.72 %	2	0.30 %
T. legionarius	15	1.27 %				
Scambus sp.	9	0.76 %	45	13.08 %		
Birds	3	0.25 %	8	2.33 %	44	6.59 %
unknown factors	41	3.46 %	7	2.03 %	8	1.20 %

Sometimes, completely deformed galls can be found. The leaves and leafsheets around and above the gall are blackish-brown and stuck together with a cancer-like tissue. This kind of deformation is triggerred by *Stenotarsonemus phragmitidis* (Von Schlechtendal) (Acari, Tarsonemidae) (Durska 1970). The leaves above the gall chamber are hardened and block the exit hole of the gall chamber, so that the adult flies cannot emerge.

The mortality due to parasitism and predation was not homogeneously distributed among the different shoot diameter classes (De Bruyn 1993a). Mortality for *L. lucens* was high on thin reed shoots and diminished when shootdiameter rose (Fig. 6a). There was a higher chance of survival (40%) on the thicker shoots where all galls carried fully developed larvae. The difference is mainly due to *S. liparae,* the major parasitoid of *L. lucens. S. liparae* attacks when the host is already inside the reed shoot, and to penetrate the shoot, the wasp uses a long ovipositor. This ovipositor however, is limited in length (mean=1.91 ±0.24 mm; n=7). When the wall of the shoot is too thick, the parasitoid can no longer reach the hosts larva. The second important parasitoid, *P. liparae,* attacks the eggs of the host while attached on the surface of the reed shoot, and so there are no physical barriers which prevent infestation on thicker shoots.

Comparable results were obtained for *L. rufitarsis* (Fig. 6b), although less pronounced. Even on the thickest shoots, 10% of the galls were infested. The mortality pattern for *L. rufitarsis* is caused by the *Scambus* species. How and when this species attacks its host is unknown. The fact that it possesses a long ovipositor may suggest the mechanism is as in *S. liparae.* In this case we can assume there exists an upper shoot diameter limit above which *Scambus* sp. is unable to reach its host.

No diameter dependent mortality due to parasitation or predation was found for *L. pullitarsis* (Fig. 6c). Survival rate was high for all diameter classes.

DISCUSSION

Three-Trophic-Level Interactions and Environmental Variation

We have seen that there are two major exploitation patterns used by the species of the genus *Lipara* where the diameter (vigour) of the reed shoots plays a major role. *L. lucens* and *L. rufitarsis* select thin, stressed shoots where larval survival is highest. *L. pullitarsis* selects and performs better on thicker, vigourous growing shoots. For *L. pullitarsis,* shoot selection is essentially defined by hostplant resistance. Mortality due to parasitation and predation is practically negligeable and imposes no shoot diameter dependent mortality. For the other two species the possibility to induce galls and mortality due to natural enemies are both shoot diameter dependent. Small shoot diameters make the flies more vulnerable to parasitic attack and exerts an upward pressure on the tri-trophic-level system. On the contrary, thicker shoots increase the difficulty of gall induction and exert a downward selective pressure in the opposite direction. However, the direction in which these interactions will evolve depends upon the relative importance of the selective pressures, and the existence of genetic variation in the species concerned for the selected trait.

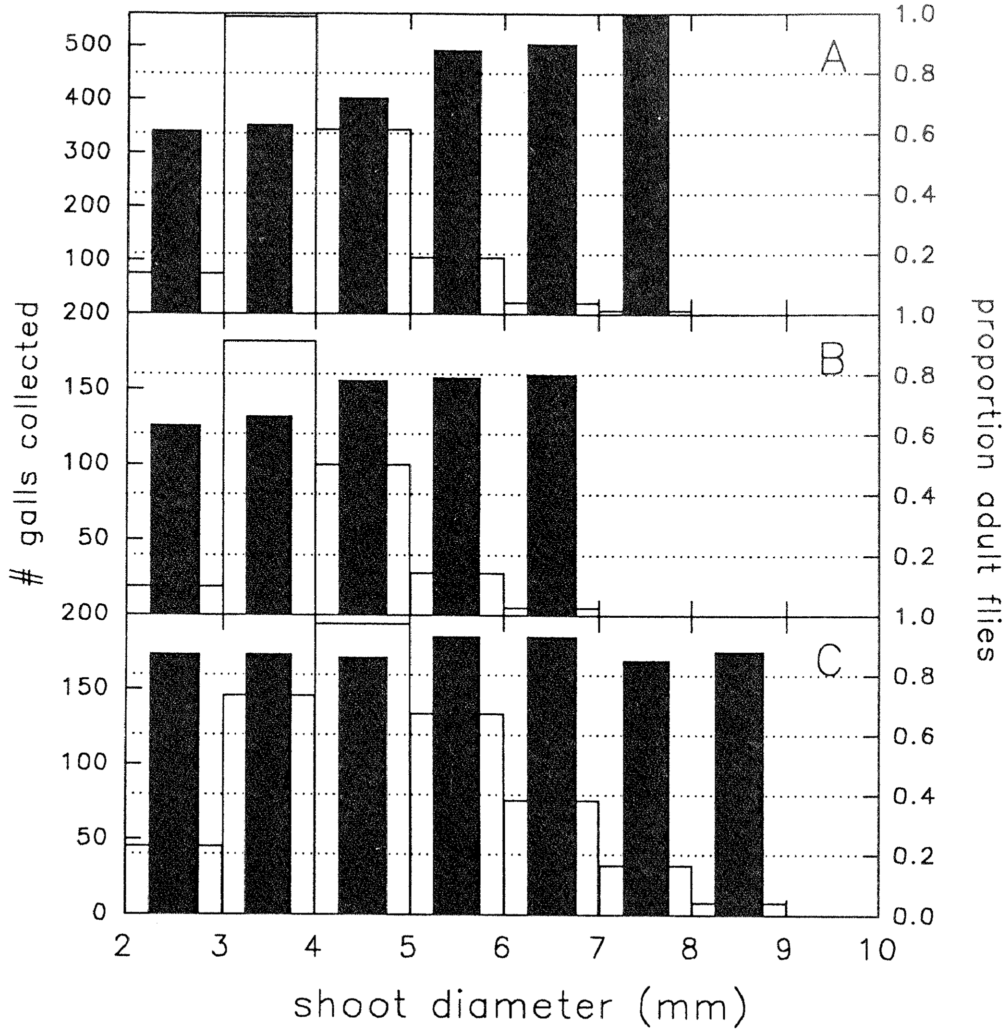

Figure 6.—Shoot diameter dependent mortality due to natural enemies. white bars = number of shoots tested; black bars = proportion surviving A) *L. lucens* B) *L. rufitarsis* C) *L. pullitarsis.*

Under natural conditions plant quality and natural enemy populations differ from site to site. In the habitat distribution experiments, the sampled reed beds showed a wide range in mean (±S.D.) shoot diameter, varying between 2.73 ±0.54 mm and 6.75 ±1.41 mm. If we consider a hypothetical optimal shoot diameter range based on the survival experiments (Fig. 3) for the habitat specialists *L. lucens* (3-7 mm) and *L. rufitarsis* (<4 mm) then, for the 45 reed beds, about 57% of the stems were suitable for *L. lucens* and 54% for *L. rufitarsis*. This percentage, however, depends on the field in question, and varies between 7% and 91% for *L. lucens*. For *L. rufitarsis* we found reed beds where 98% of the shoots were suitable, but also places where all shoots were too thick to induce a gall.

Similar variability is found for the impact of natural enemies. The mortality due to parasitoids is highest for *L. rufitarsis* and *L. lucens*. However, in many localities, the parasitoids are completely absent (*L. rufitarsis:* 53% of 57 localities; *L. lucens:* 43% of 79 localities; De Bruyn, unpublished data). For the remaining localities survival rate varies between 28.6% and 97.5% for *L. lucens* and between 96.4% and 0% for *L. rufitarsis*. *L. pullitarsis* is free of any parasitoid in 66% of the 61 localities visited. Predation by birds is also very variable, both in space and time. First, *P. caeruleus* is not a typical inhabitant of reed habitats but lives in woods, parks or gardens. The birds usually enter the reed beds during winter to forage when there is a shortage of food. So, the juxtaposition of the reed bed will probably play an important role. Secondly, during harsh winters, the predation pressure is much higher than in mild winters (Mook 1967). Finally, many galls are opened by the birds, but the *Lipara* larva escape, suggesting that the birds stopped searching when they found one of the inquilines which can co-occur in the *Lipara* galls in high numbers (De Bruyn, 1985).

To examine the relative impact of host plant resistance and natural enemies, we constructed a partial life table of three *L. lucens* populations (Table 3). Density was censused at three life stages. In each locality we counted the number of eggs deposited by the females in spring, the number of galls formed later during the season, and the number of galls producing unparasitized adult flies. The first two localities (Table 3: site A and B) were reed beds growing in a dry environment, with on average thin (mean=3.71 mm and 3.77 mm respectively) shoots. The third (site C) was a reed bed growing in a marshy area with on average thick reed shoots (mean=5.28 mm).

Table 3.—Comparison of the mortality due to host resistance and natural enemies for L. lucens at three different localities.

		Locality					
		A		B		C	
		reed density (#/m2)					
		95		65		78	
shoot diameter (mm)	mean ±S.D.	3.77 ±0.85		3.71 ±1.10		5.28 ±1.00	
	median	3.70		3.70		5.30	
	minimum	1.90		1.90		3.30	
	maximum	7.00		6.60		7.30	
	shoots with eggs	36.19		2.41		20.06	
			52%		17%		90%
density (#/m2)	galls	19.00		2.00		2.01	
			32%		0%		0%
	adults	13.00		2.00		2.01	

At the first locality (site A), initial egg density was very high (36.19 egg-bearing shoots/m^2). In spite of the rather high (52%) subsequent mortality due to plant resistance 19 galls/m^2 are induced. The flies of 13 galls (32%) were later killed by one of the parasitoids. At the second locality (site B) the initial number of eggs was much lower (2.41 egg-bearing shoots/m^2). Mortality was rather low, but due to the low initial density, only 2.0 galls/m^2 were initiated. None of these galls turned out to be parasitised. The absence of parasitoids can probably be explained by the low egg and gall density in comparison with site A. At site A, the galls were parasitised by *P. liparae* (attacks the eggs while outside the reed shoot) and *S. liparae* (attacks first instar larvae when they have entered the shoot). At site B (one egg per 26.97 shoots and one gall per 32.50 shoots) the population is more widely scattered then in site A (one egg per 2.62 shoots and one gall per 5 shoots) and therefore harder to find by the searching parasitoids. Finally, at the locality with on average thick reed shoots (site C), the initial egg density is intermediate (20.06 egg-bearing shoots/m^2). Mortality due to host plant resistance is however extremely high. 90% failed to induce a gall, resulting in a low gall density (2.01 galls/m^2). Just as in locality B, none of the galls were parasitised and produced adult flies. At site C, *L. pullitarsis* co-existed with *L. lucens*. *L. pullitarsis* galls were heavily attacked by *P. caeruleus* (45%), while none of the *L. lucens* galls were attacked. This can be explained in three ways. First, *L. lucens* gall density was much lower (1 gall per 39.0 shoots) in contrast with *L. pullitarsis* density (1 gall per 1.9 shoots). Secondly, because *L. pullitarsis* galls are formed on thicker shoots, the galls are much easier to detect. Finally, the walls of the galls of *L. pullitarsis* do not lignify as those of *L. lucens,* and are easier to open by the birds.

The results of this analysis suggests that population dynamics of *L. lucens* is largely determined by plant quality/resistance. Natural enemies are only successful when the *L. lucens* density is high enough. Furthermore there is a high spatial variation in selection pressures acting on the herbivores. In future research it will also be necessary to incorporate temporal variation. As a conclusion we can state that during the evolution of the genus *Lipara* the trade-off between obtaining the necessary food supply and growth dependent hostplant resistance has been a major force in structuring the lifecycle strategies.

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TRITROPHIC INTERACTIONS IN GALLMAKER COMMUNITIES ON PHRAGMITES AUSTRALIS: TESTING ECOLOGICAL HYPOTHESES

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Abstract. Hypotheses on ultimate and proximate reasons of gall induction were reviewed and tested using analyses of the species-rich herbivore-parasitoid communities on common reed *Phragmites australis* (Poaceae). Evolution of gall induction is accompanied by two great advantages but also two significant disadvantages. Firstly, finely tuned manipulations of plant growth improve nutrition and weaken plant defenses. Secondly, the humid microenvironment inside galls reduces hygrothermal stress, so cuticles can be thin reducing losses from moulting, and adding to the enhanced energy use and productivity due to the immobility of gall-inducing larvae. Accordingly, gall-forming holometabolous insects like gall wasps and gall midges show a perfect "division of labor": larval capabilities are reduced to an efficient food assimilation, whereas the short-lived adults only care for an adequate egg distribution.

These "nutrition" and "microenvironment" hypotheses on benefits for the gall maker can be contrasted with "plant defense" and "parasitism" hypotheses on benefits for the host plant. Availability of reactive host tissue, a specific demand of gallers, is temporally and spatially restricted, thereby increasing the gallers' susceptibility to plant defenses. Enhanced mortality of the young larvae inducing the galls and a great restriction of feeding to particular parts of the variable host plants appear to be the consequences. Large galls are often less parasitized than small galls of the same species, but in evolutionary time scales, the discoverability and heterogeneity of large and complex galls should be the reason why gallers have more parasitoid species than their non-galling relatives.

The galler/grazer dichotomy in herbivores is strikingly similar to the koinobiont/idiobiont dichotomy in parasitoids. Koinobionts as well as the immobile parasites inducing morphological or simply physiological galls depend on manipulations of host physiology, show interdependend growth and delayed feeding, whereas the individual growth of idiobionts or grazers allows feeding immediately after attack.

Results from the insect community on *Phragmites australis* showed that the 9 gall making species attacked on average significantly thinner shoots than the 8 non-galling stem borers. Thick shoots provide more biomass and a higher nutrient content (nitrogen, water, minerals) than thin shoots, but they are also better defended (silicate-richer). Obviously, gall makers can better accomodate a low nutrient content than high defense, because they stimulate the plant for a local increase of nutrients. Gall induction was an all-or-nothing reaction in the gall midge *Giraudiella inclusa* (Diptera: Cecidomyiidae): Successful gall induction on the well supplied thick panicle shoots resulted in particular large females with an enhanced egg load, but 92% of the young larvae failed to induce a gall, so gall abundance was low. *Giraudiella*'s host manipulation comprised five characteristics: formation of "rice-grain" galls, elongation of attacked internodes in dependence on gall number, biomass increase, nutrient enrichment and a 7% to 11% shoot elongation. Shoot elongation depended negatively on shoot diameter, i.e. success in manipulation was greatest in stressed shoots. Similarly, *Lipara lucens* (Diptera Chloropidae) induced an up to 20% increase in the number of internodes forming the larval chamber only on thin shoots.

Chloropidae and Cecidomyiidae on *P. australis* each comprised five species ranging from non-galling herbivores, gallers inducing only slightly altered tissue growth, to gall formers with conspicuous galls. Number of parasitoid species and percent parasitism significantly increased with the complexity of these ten galls, but were not related to host abundance or host size. Each of the four sibling species of the genus *Lipara* induced relatively larger galls on thin shoots than on thick shoots, but only the two species with the largest and most complex galls prefered thin shoots, while the two species with small and simple galls attacked all kinds of shoots. These results give evidence that susceptibility of shoot type plays a major role both in ecological and evolutionary time-scales. Accordingly, two *Lipara* spp. evolved an improved host exploitation via complex galls at the cost of (i) a restriction to the susceptible thin shoots and (ii) an increase in parasitoid pressure. The dichotomy between the two specialists (with complex galls) and the two opportunists (with simple galls) could not be confirmed by morphological or genetic distances, indicating that an evolutionary concept on gall evolution (from simple to complex galls) cannot simply rely on ecological gall features.

Key words: Cecidomyiidae, Chloropidae, evolutionary constraints, gall, grazer, herbivore community, parasite, parasitoid, Phragmites australis, plant-insect relationships, nutrition, stress, tritrophic interactions.

INTRODUCTION

Simple two-species interactions often fail to explain patterns of coexistence and abundance in communities, but experimental studies of multitrophic effects are mostly impractical. Plant galls and their inhabitans provide the opportunity to analyse plant-herbivore and herbivore-predator interactions simultaneously, since such mini-ecosystems or mini-food webs are quick to survey, can be characterized with easily measurable parameters, and experimental manipulations are simple (Zwölfer 1985; Tscharntke 1991, 1992b). Induction of plant galls is a major type of herbivory, so comparisons between characteristic features of gallers and non-gallers are of fundamental importance for both applied and general ecology. The conspicuous structures of galls have always fascinated naturalists, and a sea of informations on galls has been published, starting with Marcello Malphigi (1628-1694) who included a chapter "De Gallis" in his famous "Anatome plantarum" (Beiderbeck and Kowevoet 1979). During the last decade large numbers of papers on galls showed a revival of interest, in particular in ecology and evolution (see the reviews of Askew 1980, Meyer 1987, Price 1980, Cornell 1983, Ananthakrishnan 1984, Price *et al.* 1987, Shorthouse and Rohfritsch 1992).

The feeding niche of phytophagous insects affects mortality of the critical immature stages (Cornell 1990; Hawkins 1993, 1994). Ectophages, which feed externally on leaf tissue by chewing or scraping, can be distinguished from endophytic feeders, which include leaf miners, gallers, and borers. These feeding categories have been shown to influence the extent that hosts occupy refuges from parasitoid attack (Hawkins 1993, 1994) and overall survival (Price 1984, Cornell 1990). Differences in feeding niche include varying degrees of concealment. Gall formers differ from all the other endophages, in that they manipulate tissue growth of the host plant and thereby produce morphologically destinct, abnormal plant growth (Beiderbeck and Koevoet 1979, Redfern and Askew 1992). Gall induction is certainly the most complex and specialised type of herbivory and evidently improves nutrition and environmental protection of larvae. However, the great intimacy of the plant-insect relationship increases vulnerability to host defense, and the apparency of galls attracts enemies.

In this chapter, a short review of main ideas on both ultimate and proximate reasons of gall induction will be combined with a test of hypotheses using data from the stem-boring insect community on common reed, *Phragmites australis* (Poaceae). Variability in plant-galler-parasitoid-communities include changes in the relative importance of each interaction type, thereby shedding light on the adaptive nature and ecological significance of gall induction. Among the reed herbivores, Cecidomyiidae and Chloropidae (Diptera) each comprise five species ranging from non-galling herbivores, gall makers causing little alterations in tissue growth to gall makers forming conspicuous galls, so comparative analyses could be done (Fig. 1). Differences in the life-history strategy of these ten herbivore species can be easily judged, since they (i) are taxonomically closely related species, (ii) attack the same host plant species, and (iii) live in the same, well-defined habitat-type.

P. australis grows in large, pure stands in wetlands and forms late-successional ecosystems. The insect community living in its shoots is the most diverse among the Poaceae of middle and northern Europe (Tscharntke 1993). Nearly all of the about 100 insect species of *P. australis* are monophagous, i.e. their occurrence is restricted to *Phragmites* shoots, so all interactions among species were inside *Phragmites*-habitats. Accordingly, this insect assemblage is a true community food web of a clearly defined habitat-type or ecosystem (see Pimm *et al.* 1991). Several aspects of this insect community are studied by e.g. Chvala *et al.* (1974), Skuhrava and Skurahvy (1981), Skuhravy (1981), and Vogel (1984).

MATERIALS AND METHODS

Studies are based on about 13,000 dissected and accurately measured *Phragmites* shoots from 11 habitats in southern Germany near Karlsruhe (Upper Rhine Valley). Samples are from 1987 to 1989 and include 27 controls differing in site or year. The cut internode of the shoot base provided basal shoot diameter (without leaf sheath) and was counted as the first internode. Basal shoot diameter varied from 4.1 to 7.5mm (5.6±0.9, n= 27) and shoot density from 26 to 117 (57±22, n= 27). Altogether, 241±128 shoots with 475±224 attacked internodes from usually 8 plots (100cm x 60cm) per habitat were sampled and dissected (n= 27 controls). Evaluation of altered shoot growth due to gall maker attack was based on a comparison with unattacked panicle shoots of the same basal shoot diameter, so observed numbers could be related to expected numbers. For example, length of a galled shoot (%) is the ratio of the length of galled shoots (cm) to the length of panicle shoots (cm), multiplied by 100. Basal shoot diameter is constant during the season and is closely and positively correlated with other properties of the undamaged panicle shoot, such as shoot and flower

Figure 1.—Drawings of ten monophagous insects on reed (*Phragmites australis*): From left to right with decreasing gall complexity (for biological details see Table 2):

a) Chloropidae: *Lipara lucens* (in addition to the gall: adult, puparium, a defoliated and an opened larval chamber), *L. rufitarsis*, *L. pullitarsis* and *L. similis* form apical shoot galls; *Platycephala planifrons* damages the shoot top without gall induction.

b) Cecidomyiidae: *Giraudiella inclusa* (in addition to the gall: adult and puparium), *Lasioptera arundinis* (only on side shoots), *L. hungarica* and *L. flexuosa* live inside internodes; *Asynapta phragmitis* lives among wilted leaves.

length, shoot and rhizome biomass, growth rate, internode number, etc. (Mook 1967, Tscharntke 1988 and unpubl.). Mean shoot diameter of the 9 galler and 8 non-galler was calculated using the diameter of attacked main shoots and attacked side shoots. Most of my published studies were conducted in northern Germany near Hamburg (Elbe estuary).

RESULTS AND DISCUSSION

Induction of plant galls is the most specialised type of herbivory, and the complex response of the plant to the finely tuned manipulation of the parasite has been always fascinated researchers. Perfection of the complex gall and an idealized view of nature apparently promoted the idea that such extraordinary plant organs can only be the result of a cooperative plant-insect interaction with a mutual benefit. Gall induction is, at least in Germany, traditionally appreciated to be a mutualistic relationship or a compromise with advantages for both the insect and the plant encapsulating the gall former and thereby preventing recognizable damage (e.g. Zweigelt 1941; Buhr 1964,1965; Fröhlich 1960; Weidner 1961; Weber and Weidner 1974).

Indeed, in a few special cases of plant-galler interactions there are clear mutual benefits. In root-nodule bacteria attacking legumes, gall makers supply their host plants with nitrogen. One *Rhizobium* nodule can bind 100mg N/day (Beiderbeck and Koevoet 1979). Similarly, alder (*Alnus* spp.) and Elaegnaceae have nitrogen-binding symbionts. Gall induction by ecto-mykorrhiza also promotes plant growth. Another mutualistic adaptation is in fig wasps promoting reproduction in figs by pollination (Wiebes 1979).

An assessment of galling as one of many successful strategies of herbivores should rate the relative importance of the contrasting selecting pressures. Four hypotheses concerning the adaptive nature of galls include all possible explanations: 1.) Gall maker benefit hypotheses, 2.) plant benefit hypotheses, 3.) mutual benefit hypotheses, 4.) null benefit hypotheses. Only the gall maker benefit and the plant benefit hypotheses include plausible interpretations of some ecological and evolutionary importance addressing the main constraints on gall induction (Fig. 2). The parasitic nature of gall induction is widely accepted, so in general, nothing supports the null benefit or mutual benefit hypotheses (Price *et al.* 1987). This asymmetric relationship in plant-galler relationships may have been the reason why certain aspects of plant benefits have been underestimated in the past. In particular, needs for a finely tuned plant growth manipulation make the galling attacker greatly sensitive to plant defenses, and in addition, large or complex galls attract natural enemies and promote biocontrol of the attacker. These selection pressures on gall formers including both advantages and disadvantages will be considered more detailed in the following. Emphasis of my arguments lays on gall-inducing holometabolous insects, which include the vast majority of gall makers.

Main Constraints on Gall Induction

Gallmaker Benefits	**Plant Benefits**
* Nutrition	* Plant defence
* Microenvironment	* Predation

Figure 2.—Summary figure on the two types of hypotheses characterizing the adaptive nature of plant galls. For details see text.

The Nutrition Hypothesis

The nutrition hypothesis can be subdivided into a "nutrition hypothesis" in a narrow sense and a "weakening of plant defense" hypothesis. In general, induction of galls is an induction of a locally increased biomass. Further, gall makers usually concentrate nutritive compounds such as nitrogen, since galls work as a sink for assimilates and nutrients (Abrahamson and McCrea 1986, Weis and Kapelinski 1984). Contrary to free-living herbivores, gall makers do not search for nutritious food items but force the host plant to deliver nutrients and biomass to the site of attack, due to a partial block to the resource flow or a translocation of nutrients from other parts of the clone (Abrahamson and Weis 1987, Tscharntke 1989a).

Detailed analyses of host manipulations by gall induction were made with respect to the gall midge *Giraudiella inclusa* (Diptera: Cecidomyiidae) attacking *Phragmites australis* (Tscharntke 1989a). All the five features of host growth regulation are most likely adaptive, improving the outcome of midge survival:

1.) Growth changes were not restricted to induction of the characteristic and conspicuous "rice-grain" galls, which should provide nutritious tissues (and environmental protection).
2.) Attacked internodes were elongated, thereby increasing space for the gall clusters. The positive correlation of internode elongation and gall number per internode appeared to be the reason why intraspecific larval competition was absent (Tscharntke 1988, 1989a).
3.) Elongation was associated with a biomass accumulation within attacked internodes.
4.) Nutrient enrichment, particularly an increase in percent nitrogen, should add to these parasitic growth alterations.
5.) Finally, shoot elongation by 7% to 11% can be expected to prevent premature death or reduced productivity of attacked shoots, since light is a limiting factor of photosynthesis in dense *Phragmites* monocultures and shaded shoots die early (Van der Toorn and Mook 1982). Usually, herbivores are only known to reduce plant size, when they affect the linear growth at all (Belsky 1987).

Subtle manipulations of tissue growth by gallers include a weakening of plant defenses. Cytological and histochemical studies show reductions in cell walls, cuticles as well as lignin or phenol contents with regard to the nutritive tissues (Rohfritsch and Shorthouse 1982). Enzymes catabolize diverse phenols (Miles 1968) and in *Pontania-Salix* relationships tannins are oxidized by phenoloxidase systems (Nierenstein 1930). Enrichment of tannic polyphenols in oak galls is restricted to the tissue external to the nutritive zone (Cornell 1983). Nematodes stimulate zytokinins thereby reducing plant resistance (Pegg 1985). Therefore, both decreases of defensive chemicals and increases in nutrients characterize nutritive layers.

The Microenvironment Hypothesis

Inside galls, percent water content is high (e.g. Hawkins and Unruh 1988), so hygrothermal stress is diminished and larval survival in xeric sites is improved (Fernandes and Price 1991, 1992). Galls provide a thermal (direct sunlight) and mechanical (e.g. rain drops) buffer against a changing environment, so larval development is less disturbed and harsher regions should be colonized more easy.

Because larvae are encased in plant tissue and immobile, well-developed sense organs for detecting tissue quality or secondary compounds should be lacking (showed for leaf miners, Sehgal 1971). Sedentary, gall-inducing larvae do not need complicated behavioral attributes, do not expend energy by moving and are usually a morphologically little differentiated eating-stage. Protection from evaporation and immobility of larvae are evidently further reasons why weight of skin-losses due to moulding is minimized in gall-inducing larvae, but can be e.g. 14% of net production in free-living aphids (Llewellyn 1972). In gall-inducing Cecidomyiidae, larval skins are thin and can hardly be recognized (pers. observ.). A humid environment makes protection against water-losses superfluous. Immobility alone leads to an efficient energy use with a large ratio of assimilation to respiration (Stinner and Abrahamson 1979) or an increased ratio of body growth to energy consumed (Llewellyn 1972). Accordingly, gall-inducing holometabolic insects like gall wasps and gall midges show a perfect "division of labor": larval capabilities are reduced to an efficient food exploitation and energy assimilation, whereas the short-lived adults only care for an adequate egg distribution, thereby promoting gene flow (dispersion, migration) and often genetic variation (via copulation).

The Enemy Defense Hypothesis

Galls vary in size and many intraspecific comparisons show that small galls are less parasitized than large galls of the same species (e.g. Jones 1983, Weis *et al.* 1985, Price and Clancy 1986, Hemmerling 1987, Zwölfer and Arnold-Rinehart 1993), thereby supporting the hypothesis that concealment with large galls protect the inhabitants from parasitoid attack. Larger galls reduce access to parasitoids (at least in endoparasitoids), because ovipositors do not reach the host. Several authors collected evidence that gall morphology has most likely been driven by parasitoid attack (Askew 1961, 1980; Price 1980; Cornell 1983; Weis and Abrahamson 1985; Weis *et al.* 1985), and no alternative hypotheses explaining divergence of gall morphology on the same host plant seems to be viable (Price *et al.* 1987). But Price *et al.* (1987) argue that divergence of gall types can be also seen in gallers without parasitoids (e.g. eriophyd mites, aphid galls), so changes in gall morphology could not be linked with reduced parasitism.

Plant Benefit Hypotheses

The Protection by Encapsulation Hypothesis

Zweigelt (1941), Weidner (1961), Mani (1964) and others suggested that the plant benefits by encapsulating the gall former, thereby restricting the damage or even completely preventing disadvantages for the plant. The struggle between the attacking herbivore and the reacting host plant should result in an ideal compromise with advantages for both sides. However, damage by gall formers is not isolated, since gallers force host plants to divert assimilates and nutrients to the site of attack (see above for details on gallers' nutrition). Gall formation is due to the activity of the parasitic gall maker and first of all, the galler alone benefits from his manipulation of plant growth (Price *et al.* 1987, Tscharntke 1989a). The protection by encapsulation hypothesis ignores the parasitic nature of the plant-gall relationship (Palct 1972), the great number of gall-inducing pests (e.g. Fröhlich 1960, Mamaev 1968, Fernandes 1987, Dennill 1988), and the selection of gall makers for biocontrol of weeds (see Julien 1992). The main plant defense against gallers is nonreactivity: Resistant plant parts show no growth response, they refuse the manipulation attempts (Rohfritsch and Shorthouse 1982, Tscharntke 1988, Weis *et al.* 1988; see below, the susceptibility to plant defense hypothesis), or even show a hypersensitivity response with locally limited necrosis (Fernandes 1990). Further, if galling capability is a defensive trait of plants, galling should be as strongly linked to plant phylogenies as are chemical defenses such as mustard oils, cardiac glycosides and alkaloids, but that is not true (Price *et al.* 1987).

The Susceptibility to Plant Defense Hypothesis

Immobility of many endophages means that they cannot avoid nonnutritious, physically or chemically defended plant parts and that they cannot select the only slightly defended tissue. In addition to this feature of many endophages, gall formers have to manipulate tissue development. Subtle control of tissue growth characterizes the specialized and intimate plant-galler relationship, which should be generally correlated with (i) an enhanced dependence on the temporal and spatial availability of suitable plant parts, (ii) negative effects of host plant variability, and (iii) an increased susceptibility to permanent or induced plant defenses.

Most gall makers are not only monophagous, they need distinct plant parts and a fixed time within the season, otherwise a successful attack of meristematic active tissue fails (Weis *et al.* 1988). Polyphagy or opportunistic changes of host plant species are rare (e.g. Roskam 1985) and eggs laid on nonnutritious plant parts suffer great mortality (Ahman 1986, Tscharntke 1988). Gall-inducing larvae depend not only on a specific and reactive tissue, but also cannot compensate for mistakes of their mother's oviposition, since they are immobile (mid-stage larvae, at the latest). Local control of plant growth is also important in overcoming plant defenses (see above, the nutrition hypothesis). Accordingly, increases or only changes in plant defense should affect gallers more than non-gallers. In this paper, two consequences of the susceptibility to plant defense hypothesis will be tested more detailed:

1.) Ovipositing females should often fail to meet all the host plant variation, not totally considering the highly specific larval requirements, so mortality of the very young (mainly first instar) larvae can be expected to be greater in gallers than in non-gallers, and to be the key factor in population dynamics (Tscharntke 1989b).
2.) High specifity of gallers should restrict success of gall induction to only a small part of the plant clone (phenotypic

variability) or of the plant population (genotypic variability). Such reductions of galler populations and corresponding reductions in the gallers' herbivory have obvious advantages for the plant. Spatial and temporal differences in gall distribution can be expected to be closely resource-based, with the abundance of suitable host tissue allowing the best predictions of gall abundance.

Firstly, some evidence supports the hypothesis that the young larvae inducing galls suffer from a particular high mortality. In a comparison of leaf miners and gall formers, Cornell (1990) showed that the age-specific mortality of gallers tends to decrease with age (producing Type III survivorship). In contrast, leaf miner survivorship increased with age (Types I-II). Despite first impression, Cornell's comparison does not support my argument, because (i) the survivorship curves are mainly based on the mortality between larval and pupal stage, and (ii) divergence in survival between leaf miners and gallers is due to the mortality of mid-stage larvae. Cornell argues that this divergence should be attributable, at least in part, to differences in enemy success. This interpretation contradicts findings of Hawkins (1993, 1994) that leaf miners generally suffer a significantly higher percent parasitism than gallers. Cornell's data show also that gallers suffer from a higher mortality between the egg and young-larval stage than leaf miners (ca. 20-45%, n= 3 species, versus ca. 2-30%, n= 7). This remarkable contribution to a Type III survivorship curve should come from difficulties of establishment of the early gall-inducing larvae. In detail, survivorship of the stem-galling sawfly *Euura lasiolepis* (H Tenthredinidae, Price and Craig 1984, included in the analysis of Cornell 1990) shows a 39% mortality before the first instar larvae had established in the gall, whereas all other causes of mortality accounted for only 19%. Egg death can even reach 58% and 79% when host plants are stressed (Price and Craig 1984; see also Preszler and Price 1988). In contrast, mortality of lepidopterous leaf miners included in the analysis of Cornell (1990) show only a <10% mortality between the egg and larval stage.

Oviposition of *Diplolepis rosae* (H Cynipidae) occurs readily on both vigorous and weak *Rosa* plants, but no galls are induced on the former (Schröder 1967). Despite a remarkable fecundity (>700 eggs per female), *Diplolepis* galls are not very common in Europe. Females of the Cynipidae *Disholcaspis cinerosa* lay almost identical egg numbers on resistant and susceptible oak trees (Frankie and Morgan 1984). Ahman (1986) concluded from oviposition studies on six gall midge species that midge females often lay eggs on plants which cannot be successfully attacked by the gall-inducing larvae. Equally, the gall midge *Giraudiella inclusa* selected *Phragmites* shoots randomly with respect to shoot diameter. Clutch size increased with shoot diameter, but size of gall clusters increased only in the case of thick shoots damaged by stem-boring moths and not in the case of thick and undamaged shoots (Tscharntke 1988, 1989b). A 92% mortality of gall-inducing first instar larvae on thick panicle shoots (Tscharntke 1988) contrasted with a 69% mortality on thin panicle shoots (Tscharntke unpubl.). While in other oligophagous insects larval host range is commonly broader than that used by the females for oviposition (e.g. Wiklund 1982), the specific requirements of the gall-inducing larvae obviously cannot be completely considered by the short-lived adult midges. This appears to be due to the short time available for the distribution of large egg numbers, resulting in more frequent oviposition on unsuitable plants.

Secondly, gall abundance depends greatly on the availability of special plants or plant parts. The heritable differences among *Solidago* genotypes for resistance to stem-galling species were consistently (though not significantly) larger than to other insects (Maddox and Root 1987) supporting the view that great specialization is required of insects depending on finely tuned plant responses. According to Mattson *et al.* (1988), herbivores with intimate host associations tend to exhibit greater plant-to-plant differences in population levels than do free feeders. Galls of *Diplolepis rosae* are more numerous where roses are obviously under stress and occur only exceptionally on cultivated roses (Schröder 1967). Despite an average parasitism over 80%, rareness of *Diplolepis* galls appears to be due to the host plant's resistance or egg mortality respectively.

A main feature of *Phragmites* grass shoots that can be easily related to a general defense mechanism against herbivores is the basal shoot diameter. Mean shoot diameter is larger on wet and rich soils than on dry or poor soils, and susceptibility of thin shoots stressed by nutrient or water deficiency appeared to be greater than of thick, well supplied shoots. Three examples will illustrate significance of shoot diameter for herbivore attack:

(i) Abundance of the gall midge *Giraudiella inclusa* (Diptera: Cecidomyiidae) is higher on thin shoots than on thick shoots, and further increases with the number of side shoots, with these two variables explaining 92% of the variance (Tscharntke 1989b). Availability of side shoots completely depends on killing the apical meristem, mainly induced by stem-boring caterpillars (Tscharntke 1990). Accordingly, numbers of both the thin main shoots and the even thinner side shoots characterize the availability of nutritious food, which is the key factor of population dynamics (despite on average 56% parasitism and 70% bird predation, Tscharntke 1992b).

(ii) The gall midge *Lasioptera arundinis* (Diptera: Cecidomyiidae) attacks only side shoots and induces thickened and stouted internodes. Abundance of side shoots and midge abundance were closely related. Length of attacked side shoots was positively correlated with shoot diameter (x_1) and negatively with the number of attacked internodes (x_2) (percentage of expected side shoot length= $-1.23 + 0.364x_1 - 0.026x_2$, F= 5.9, r= 0.332, n= 98, p= 0.004). Accordingly, narrow side shoots could be better shortened than thick side shoots, so shoot diameter appeared to be also a stress indicator among the anyway narrow side shoots.

(iii) *Lipara lucens* (Diptera: Cecidomyiidae) induces a distinctive apical gall by compression of the shoot top. The cigar-like gall consists of ten stout apical internodes. Females select thin shoots for oviposition, and survival of the young larvae is also negatively correlated with shoot diameter (Mook 1967, 1971; Chvala *et al.* 1974, see Fig. 3). Abundance depended on the availability of thin shoots, so dry reed habitats supported more galls than wet reed habitats (Fig. 3c). Galls became thicker with diameter of attacked shoots (Fig. 3a), but the percent increase in thickness (the ratio of gall thickness to shoot diameter) decreased (Fig. 3b). Positive correlations between shoot width and size of these apical galls were not surprising, but the relative increases in gall size became smaller. These difficulties with the gall maker's manipulation of thick shoots could be underlined by a further data set. *Lipara lucens* induced an increase in the number of stouted internodes - a not yet reported form of growth manipulation. Figure 3d shows that the very thin and thereby very small shoots could be stimulated to have 20% more internodes. For example, induction of a gall on a 2.5mm shoot developing usually only 14 internodes resulted in a shoot with 17 internodes. The significance of this manipulation may even be greater, because expected internode numbers are based on the long flowering shoots, whereas shoots shortened by *Lipara lucens* had only 75% of panicle shoot length. On average (n= 195 galled shoots examined), shoots with galls had 111% of the expected internode number with 55% of the internodes forming the gall chamber (this are on average 10 stouted and lignified internodes).

These three examples cover only gall makers and in general, all the 9 species of gall makers attacking *Phragmites australis* prefered on average thinner shoots than the 8 non-galling herbivore species (Fig. 4). Alternative hypotheses that the dichotomy between gallers and non-gallers can be related to population abundance, population variability (coefficient of variation) or larval size could not be supported. Accordingly, gall makers avoided thick shoots, although thick shoots were the richest resource of primary plant substances (largest biomass with highest levels of nitrogen, water, minerals, Tscharntke 1990 and unpubl.). Thin shoots were less nutritious, but had also smaller percentages of silicate. Hardness of silicate-rich tissue is generally a main factor of grass defense (e.g. Moore 1984, McNaughton *et al.* 1985). Obviously, gall makers can better accomodate a low nutrient content than with enhanced plant resistance, because they manipulate plant growth and stimulate a local increase in nutrient content and biomass. This can be linked to the performance of the reed-attacking gall midge *Giraudiella inclusa* (Tscharntke 1988, 1989a): Females hatching from galls on thick shoots had 1.7 times more eggs than females from thin shoots (apparently due to the better nutritional value of thick shoots), but gall abundance was 3.6 times less (due to the enhanced mortality of the gall-inducing first instar larvae). When gall induction on thick shoots was successful, larvae achieved highest weights, but midge weight or fecundity differences were of secondary importance for reproduction or population dynamics (Tscharntke 1989b). Gall induction appears to be generally an all-or-nothing reaction. Furthermore, the gall maker's enrichment of the nutritive tissue inside galls is generally a way to compensate for a low nutrient status of the host plant. These data from *Phragmites australis* support the view that the gall makers' dependence on finely tuned host responses determines a strongly resource-based population abundance and distribution.

Fernandes and Price (1991, 1992) found that galls are more abundant in xeric than in mesic sites and conclude that this is because parasitism and fungal diseases are reduced in the xeric environment (the Harsh Environment Hypothesis). Hawkins (1994) also presents data showing holarctic gallers (but not ectophytic hosts) to be on average less attacked by parasitoids in colder regions with more fluctuating temperatures. However, the data on *Phragmites* herbivores support the plant stress hypothesis of White (1984) and Mattson and Haack (1987), and are in contrast to both the harsh environment and the plant vigor hypothesis discussed by Price (1991; e.g. based on willow gall makers). Gall makers' preferences of thin reed shoots did not include a general preference of dry reed habitats characterized by on average thinner shoots, but a preference of both thin shoots and narrow side shoots inside each habitat type (Tscharntke 1988, 1990). *Lasioptera*-galls and *Giraudiella*-galls were much more abundant in wet reed when the thick shoots were damaged by stem-boring moths, since these gall midges were greatly facilitated by the narrow side shoots produced after damage. Flush-crash cycles of the moth and corresponding high damage levels only occured in wet reed (Tscharntke 1990). *Lipara lucens* and *L. rufitarsis* only attacked thin shoots, but were abundant not only in dry reed habitat, but also on thin shoots growing near the edges of mesic "wet reed". Accordingly, reduced mortality of gall-inducing larvae due to a reduced defense of thin shoots appeared to be more important than a xeric environment.

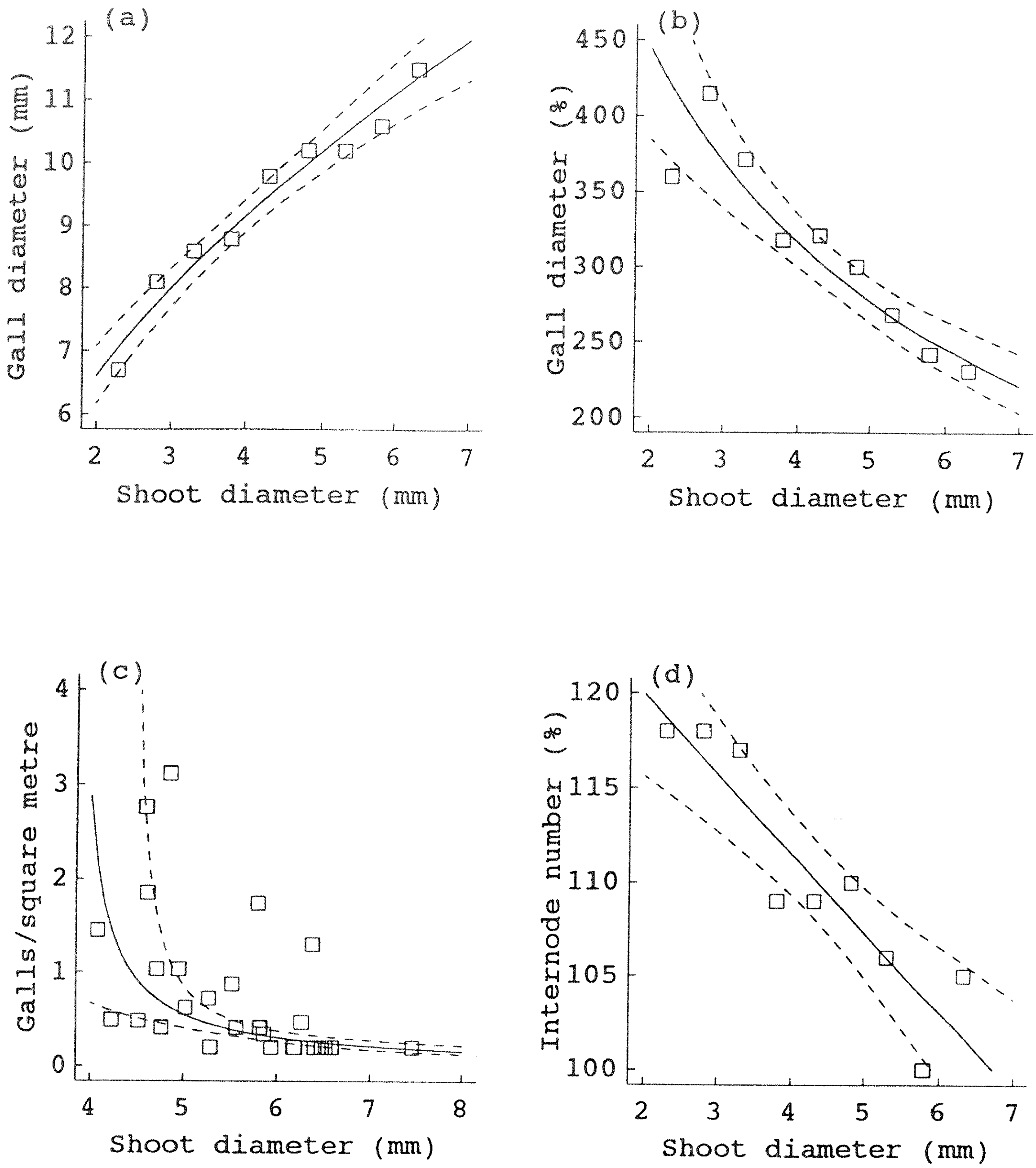

Figure 3.—Performance of *Lipara lucens* (Diptera: Chloropidae) on *Phragmites* shoots. Figure 3 a, b, d are based on 195 galled shoots put in 9 classes according to shoot diameter (class interval: 0.5 mm), Figure 3 c on 27 samples differing in habitat or year.

a) Gall diameter (mm) versus basal shoot diameter (mm).
Ln y= 1.56 +0.474 ln x, F= 164, r= 0.979, n= 9, p< 0.001.

b) Gall diameter (%) versus basal shoot diameter (mm).
Gall diameter (%)= ratio of diameter of the gall to diameter of the internode below the gall.
1/y= 0.0013 +0.00045x, F= 65.7, r= 0.951, n= 9, p< 0.001.

c) Galls/m^2 versus mean basal shoot diameter (mm) per habitat or year.
1/y= -13.7 +3.28x, F= 22.5, r= 0.688, n= 27, p< 0.001.

d) Number of internodes (%) versus basal shoot diameter (mm).
Internode number (%)= Ratio of observed internode number to the internode number expected from undamaged panicle shoots of the same diameter.
Y= 128 -4.23x, F= 37.1, r= -0.917, p< 0.001.

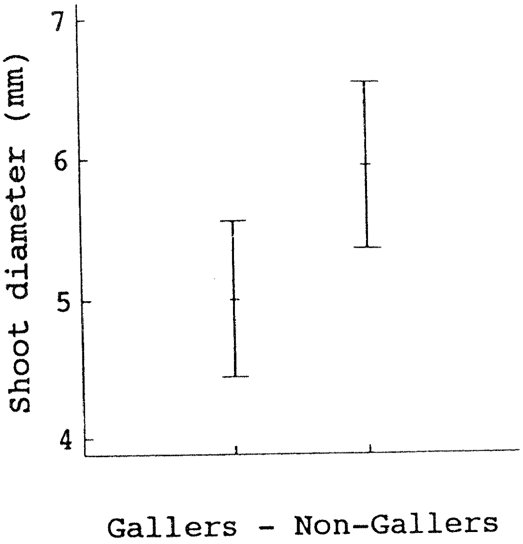

Figure 4.—Habitat use of 9 gallers and 8 non-gallers stem-boring in *Phragmites*-shoots: Differences in the attacked basal shoot diameter (mm). $F_{1,15}$= 6.2, p= 0.025.

The Predation Hypothesis

Despite the plausible and wide-spread assumption that protection by gall tissue should reduce impact of natural enemies, gallers are attacked by far more parasitoids than their non-galling relatives (Hawkins 1988, 1990). These interspecific comparisons of species richness of parasitoid complexes show that host concealment does not provide an enemy-free space compared with similarly concealed, non-galling hosts (stem, wood, fruit or seed borers). Many parasitoid species concentrate on galls, which represent highly visible and heterogeneous resources. Accordingly, host plants should benefit from the production of large galls by facilitating enemy numbers and biocontrol of their pests. Contrasting results to this general pattern come from studies on Tortricidae (Mills 1993) and Tenthredinidae (Price and Pschorn-Walcher 1988).

Differences of parasitoid impact between galling and non-galling species were analyzed using *Phragmites*-herbivores. Three hypotheses with respect to the number of parasitoid species per host were tested using five gallmidges and five chloropid flies, each group with distinctly galling, slightly galling and non-galling representatives: (i) Larger larvae should support more parasitoid species, since they offer a larger amount of food, (ii) abundance and parasitoid number should be correlated, since abundant hosts can be found more easily, (iii) larger or more complex galls should carry more parasitoids. Gall complexity is characterized by the features presented in Table 1 (see also Fig. 1). Ranking of the analyzed Diptera is from non-galling, but sedentary species (*Platycephala planifrons, Asynapta phragmites*), gall formers with hardly visible alterations of host plant growth (*Lipara similis, Lasioptera hungarica, Lasioptera flexuosa*), herbivores with morphologically distinct but simple galls (*Lipara pullitarsis, Lasioptera arundinis*), to complex gall formers (*Lipara rufitarsis, Lipara lucens, Giraudiella inclusa*). Results on parasitoid species richness, percent parasitism, abundance and larval size provides Table 2.

In stepwise multiple regression, gall complexity was significantly correlated both with species number of parasitoids (r_s= 0.818, n= 10, p= 0.01) and percent parasitism (r_s= 0.741, n= 10, p= 0.03; see Fig. 5). Abundance and larval size were not related to parasitism. Parasitoid species number depended also on gall complexity when Chloropidae (r_s= 0.894, n=5, p= 0.07) and Cecidomyiidae (r_s= 0.975, n=5, p= 0.05) were analyzed separately. These results support the predictions of Askew and Shaw (1986), Hawkins (1988) and Hawkins and Gagne (1989) that larvae of gall formers support more parasitoids, because they are highly visible, apparent, and therefore easily detectable. But enhanced species richness of distinct galls may not only be due to visible cues for parasitoids. An additional or alternative hypothesis is that the greater complexity or heterogeneity of a galler's microhabitat will enables more specialisations of parasitism (enhancing speciation), compared with the simple, homogeneous microhabitat of little differentiated galls or even non-galling borers (Tscharntke 1992a).

Table 1.—Features of gall complexity of Chloropidae and Cecidomyiidae from *Phragmites australis*

Features	Ranking of gall complexity				
	0	1	2	3	4
Chloropidae:	*P.plan.*	*L.simi.*	*L.pull.*	*L.rufi.*	*L.luce.*
Stouted internodes (%)(n)	0 (0)	19 (3.1)	38 (5.3)	32 (4.6)	57 (10.2)
Shoot length (%) (cm)	61 (108)	97 (186)	77 (149)	83 (137)	75 (128)
Gall diameter (%)(mm)	160 (5.5)	140 (3.8)	180 (7)	200 (4.7)	310 (9.3)
Larval chamber	--	--	--	++	++
Lignification	--	--	--	--	++
Internode augmentation	--	--	--	--	++
Cecidomyiidae:	*A.phra.*	*L.flex.*	*L.hung.*	*L.arun.*	*G.incl.*
Internode growth affected	--	?	?	++	++
Kokon	--	--	--	++	++
Symbiotic fungi	--	--	++	++	--
One larva/gall	--	--	--	--	++
Larval chamber	--	--	--	--	++

Ranking no. and species abbreviations correspond to the species given in Table 2 and Figure 1; arithmetic means are given; % length or internodes= percentage of unattacked panicle shoots; % gall diameter= diameter of gall/diameter of internode beneath the gall.

Table 2. Tritrophic interactions in the Chloropidae and Cecidomyiidae of *Phragmites australis*.

Species	Gall complexity	Parasitoid spp.	Parasitism (%)*	Abundance (n/m^2)*	Larval size (mm)*,**
Chloropidae:					
Platycephala planifrons	0	1	1	3.1	7.6
Lipara similis	1	1	22	1.7	8.1
Lipara pullitarsis	2	1	2	1.8	7.2
Lipara rufitarsis	3	3	19	0.4	6.6
Lipara lucens	4	4	36	0.6	9.4
Cecidomyiidae:					
Asynapta phragmitis	0	2	1	13.1	2
Lasioptera flexuosa	1	2	14	61	3.2
Lasioptera hungarica	2	3	3	558	4.1
Lasioptera arundinis	3	4	5	52	3.9
Giraudiella inclusa	4	16	56	179	4.3

* Arithmetic means, ** mean size of last instar larvae

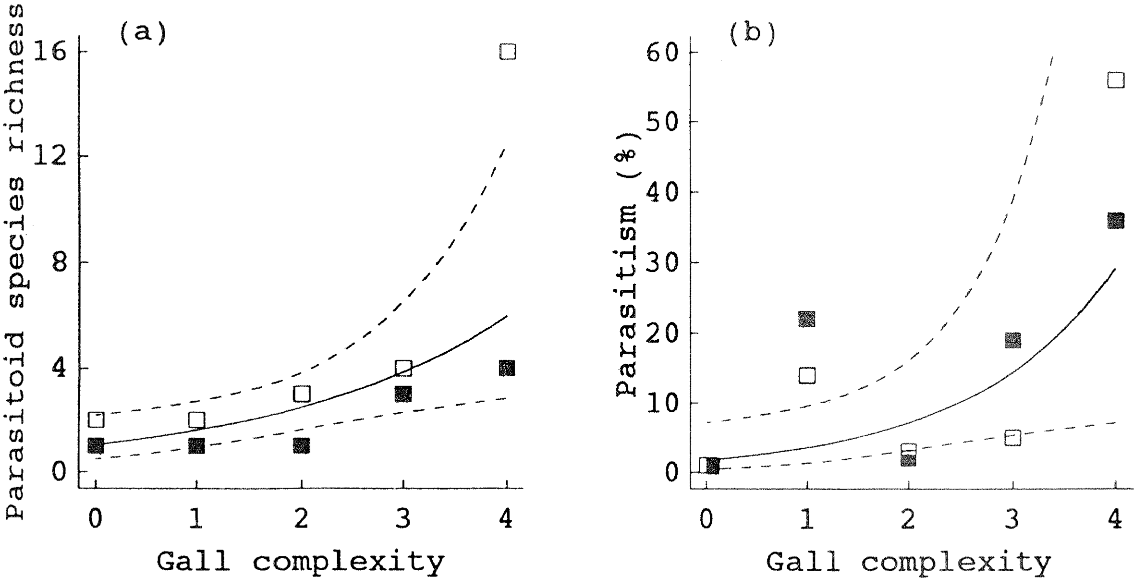

Figure 5.—Gall complexity and a) number of parasitoid species and b) percent parasitism. For the ranking of gall complexity see Table 1 and 2; open squares: Cecidomyiidae, filled squares: Chloropidae.
a) Ln y= 0.04 +0.44x (F= 11, r= 0.761, n= 10, p= 0.01),
b) Ln y= 0.56 +0.70x (F= 8, r= 0.706, n= 10, p= 0.02).

Benefits of Transitional Stages Between Non-Galling and Gall-Inducing Herbivores

Morphological and physiological galls

Which feeding habits can be supposed to be "transitional stages" and which selection pressures are involved? During the evolution of the galling habit two pathways may have been followed, one via mobile feeding and one via sedentary feeding (Price *et al.* 1987). Leaf miners, plant miners and leaf folders are protected by plant tissue in a simple way. Larvae are mobile and usually do not alter the local tissue growth. Production of callous tissue, which can fill the mine but which is not eaten by the leaf miner, cannot be regarded as a gall induction. In several species within e.g. the Agromyzidae and Nepticulidae however, the induced callous tissue is fed upon by the larvae and thereby resembles a simple gall (see Hering 1951, Redfern and Askew 1992). Further, leaf miners may produce "green islands" by larval secretions, i.e. a local preservation of chlorophyll on old, already discolored leaves (Hering 1951), which is a slight and probably adaptive tissue change, looking similar to some stimuli of gall formers.

Sedentary endophages and many plant-sucking ectophages like aphids, leafhoppers, bugs, or plant mites continuously feed on the same site, induce a change in tissue growth, and wait for the induced improvement of their feeding site (Kloft 1960, Miles 1968, Hori 1976, Packham 1982). Accordingly, first of all the gall grows and only afterwards larval growth can start. Waiting for the induced tissue changes by the immobile larvae can be expected to be a time-consuming feeding-type. According to Lalonde and Shorthouse (1988), once the gall of *Urophora cardui* (Diptera Tephritidae) on *Cirsium arvense* enters the maturation phase, the larvae grow quickly, attaining over 98% of their final weight during this last phase of gall development.

The presumed transition from immobile borers to gallers can be examplified in gall midges (Diptera: Cecidomyiidae) and phytophagous chalcid wasps of the genus *Tetramesa* (Hymenoptera Eurytomidae), since gallers have non-galling sibling species. Larvae of the non-galling stem-borers are as sedentary as the larvae of gallers, and their continuous tissue sucking leads often to hardly visible larval chambers. A sedentary life-strategy can be expected to be the most important prerequisite of local changes in tissue growth and so the most probable starting point for the evolution of a gall-induction, whereas leaf-mining appears to be mainly an alternative way of a mobile living. Tissue changes and nutrient enrichment induced by sucking, non-galling, more or less sedentary larvae can be coined a physiological gall (see Kloft 1960).

Gall induction developed independently in many groups, so evolutionary prerequisites differed greatly. E.g., gallers among Cynipidae and Eurytomidae are considered to be secondary phytophagous descending from zoophagous parasitoids (Malyshev 1968), whereas gall-inducing Cecidomyiinae have phytophagous ancestors that are not concealed by plant tissue (Roskam 1985). Nethertheless, both types of presumed ancestors have a sedentary or immobile "parasitic" life-strategy.

The galler/grazer and idiobiont/koinobiont dichotomy

Herbivores can be classified as parasites or grazers (Begon *et al.* 1990, see Price 1984). Parasites, here presented by gallers, concentrate on a part of one host and are intimately associated whith it, whereas grazers, represented by mobile caterpillars or large vertebrates like sheep and cattle, are less selectively when removing parts of large numbers of prey. Attack by physiological or morphological gallers permits the host plant to grow beyond the stage attacked, and the galler benefits from this continued life, whereas grazers consume the host plants in the state when they are attacked and do not depend on further plant development. Gall formers manipulate plant growth in favor of the parasite and feeding of larvae is delayed, grazers often arrest host growth and immediately consume host tissue causing compensatory plant growth in favor of the host plant. Divergent gall morphologies on the same host plant due to the stimuli of different gall-inducing species contrasts with a general compensatory response like side-shoot induction due to many kinds of mechanical damage breaking apical dominance (e.g., Tscharntke 1990, Carroll and Quiring 1993).

Feeding types of gallers and grazers are strikingly similar to feeding types of koinobionts and idiobionts (Tscharntke 1991, see Table 3), a dichotomy refering to concepts in parasitoids (Askew and Shaw 1986, Hawkins 1994). Gall formers resemble koinobionts in that they permit the host to grow beyond the stage attacked, influence intimately host physiology, manipulate host growth, depend on further host development, delay the beginning of feeding, and in addition, their host ranges are limited by their need to interact with the living host. Grazers like mobile caterpillars or vertebrate herbivores are similar to parasitoid idiobionts in that they often arrest host tissue growth in the stage it is when attacked, do not manipulate host physiology, are independent on further host development, start feeding immediately after host attack, and in addition, their nutritional requirements and their host ranges are basically broad. Idiobionts and grazers can be said to be generalists, koinobionts and parasites are specialists. Obvious consequences include that host damage is more conspicuous in grazers and idiobionts, but does not necessarily have a stronger effect on hosts (see e.g. Mamaev 1968, Dennill 1988). Parasites (and koinobionts) have a great diversity of specific and small species, whereas grazers (and idiobionts) have a low diversity of little specific and large species.

Table 3. Feeding types of herbivores compared with parasitoids

Gallers and Koinobionts	Grazers and Idiobionts
1.) Immobile parasites inducing physiological or morphological galls: Intimate host associations.	1.) Mobile grazers like caterpillars or large vertebrate herbivores: Little selective host use.
2.) Dependence on manipulations of host physiology; interdependend growth and delayed feeding.	2.) Independence on host physiology; individual growth and feeding immediately after attack.
3.) Host damage inconspicuous, but not necessarily weak.	3.) Host damage conspicuous.
4.) Narrow host ranges due to the need to physiologically interact with the living host.	4.) Basically broad host ranges due to less physiological constraints.
5.) Great diversity of specific species.	5.) Low diversity of little specific species.

Koinobionts are more specialised than idiobionts because they evade host defenses by regulation of the host's physiology (Hawkins 1994), and also in parasitic herbivores, physiological constraints can be expected to cause a greater selection pressure for monophagy than adaptations in behavior or morphology. Further characteristic features of parasites are discussed in Price (1980, 1984).

Tritrophic interactions and evolutionary versus ecological time scales

Comparisons among the *Lipara* spp. may allow some conclusions on the pattern of gall evolution in a context of tritrophic interactions (see Table 2). Each of the four sibling species induced relatively larger galls on thin shoots than on thick shoots (examplified for *L. lucens*, Fig. 3b), since thin shoots were generally less resistant against herbivore manipulations than thick shoots. *Lipara lucens* and *L. rufitarsis* had not only significantly larger and more complex galls than *L. pullitarsis* and *L. similis*, and could only be found on thin shoots, whereas the latter two species (with their small and simple galls) attacked all kinds of shoots. Accordingly, susceptibility to shoot type appeared to play a major role in both ecological and evolutionary time-scales. Ability to form complex galls means a great success in host manipulation, but is at the expense of (i) a restriction to a small part of the host plant population (thin shoots) and (ii) an enhanced discoverability causing a higher mortality by parasitism (Fig. 5a). As can be expected from life-history theory (e.g. Price 1984), the two specialist species were on average less abundant than the two opportunists (Table 2). This specialist/opportunist dichotomy did not correspond with taxonomic differences: Morphological and genetic distances grouped *L. lucens* with *L. similis* and *L. rufitarsis* with *L. pullitarsis* (Kuhnhenne, Brandl and Tscharntke, in prep.). Accordingly, stepwise increase in gall complexity from *L. similis* to *L. lucens* does not imply that the evolutionary differentiation worked also this way. Similarities in a biological or ecological feature like gall induction may suggest relationships which contrast to the kinship based on evolutionary or taxonomical characters.

These and other results show that effects of plant defense on gall formers are a paradox. On the one hand, evolution of gall induction increases specifity, so nutritious plant parts become spatially and temporally restricted and the gallers become prone to host plant variability. On the other hand, comparisons between plant-herbivore associations support the hypothesis that endophage-ectophage ratios increase on more heavily defended plants (Cornell 1989), because endophages like gall formers are more facile at feeding selectively and can manipulate tissue development to avoid physical and chemical defenses, whereas ectophages can be considered to be mainly unselective feeders. This paradox can be solved with the differentiation between ecological and evolutionary effects. Ecological specifity is an ideal prerequisite for rapid speciation (Mayr 1963), and Price (1980) showed that chemical diversity of potential hosts apparently forced adaptive specialisations of the parasites resulting in great species diversity (examplified in the adaptive radiation of Agromyzidae on Umbelliferae). Accordingly, plants with diverse defenses reduce attack possibilities of each of the specialised gallers greatly, but in the long run, these complex defenses will be overcome by a large number of stepwise evolving specialist species.

Similarly, effects of gall induction for parasitism can be considered a paradox. On the one hand, small galls are less parasitized than large galls of the same species, because a larger gall diameter protects the inhabitants from attack. On the other hand, species with large galls suffer from more parasitism than their relatives with small galls or even without galls. This paradox can be solved, when ecological and evolutionary time scales are separated. Parasitoids may have forced gall formers to produce larger or more complex galls, which in turn provided new starting points for the evolution of a stepwise parasitoid specialization, resulting in increased species richness by coevolution (Tscharntke 1992a). Complex or large galls are highly visible, apparent targets and provide a great heterogeneity of microhabitats or ecological niches, thereby promoting evolutionary differentiations in parasitoid attack.

In addition to the effects of parasitism, predation may often play a significant role in shaping tritrophic interactions in gall maker communities. Large and thereby highly visible galls are a preferred prey of birds (e.g. Weis and Abrahamson 1985), and gall spines (e.g. the spiked form of *Diplolepis nervosa*) may be actual or anachronistic defenses to herbivory of mammals prefering such protein-rich food items (see Janzen 1979 for a discussion of anachronism in evolution). Elevated tannin-concentrations in oak galls should also deter predators as well as fungi and microorganisms (Cornell 1983). Little is known about the relative importance of selection pressures exerted by gall predation on the plant-herbivore-parasitoid food chain (but see Abrahamson *et al.* 1989, Tscharntke 1992b). Washburn (1984) showed that extrafloral nectaries on galls attract ants that suppress parasitism on the galler from 48% in their absence to 25% in their presence. Possibly, such ant attraction may not only help the gall maker, but also the plant to decrease density of free-living herbivores like caterpillars, beetle larvae, etc.

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EUROPEAN GALL MIDGES (DIPTERA: CECIDOMYIIDAE): THEIR HOST PLANTS AND ENVIRONMENT

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INTRODUCTION

The family Cecidomyiidae is one of the largest families of Diptera in the world, comprising 4,600 species. There are known 2,200 species in 300 genera in the Palaearctic Region (Skuhrava 1986), 1200 species in 125 genera in the Nearctic Region (Foote 1965), 360 species in 130 genera in the Neotropic Region (Gagne 1968), 332 species in 92 genera in the Indomalayan Region (Gagne 1973), 156 species in 75 genera in the Afrotropic Region (Harris 1980) and 210 species in 47 genera in the Australasian Region (Gagne 1992). New gall midge species are discovered and described all the time and all over the world, in all zoogeographical regions. The total number of gall midges in the world will probably eventually reach 8,000 species.

The Euro-Siberian Subregion with 1,324 species is the best explored territory of the Palaearctic Region. From that large territory the best explored area of the world is the western part of Europe beginning from France up to Bulgaria and from Finland up to Italy. The following numbers of gall midge species are known in various European countries: Norway 65, Great Britain 603, France 547, Switzerland 81, Portugal 137, Sweden 261, Netherlands 295, Germany West 580, Germany East 406, Liechtenstein 0, Spain 111, Finland 135, Belgium 89, Denmark 160, Poland 360, Austria 370, Czech Republic 496, slovak Republic 350, Hungary 240, Romania 320, Bulgaria 240, Italy 330, Slovenia 222, Albania 11, Greece 19. The differences in the occurence of gall midge species in various countries of western part of the Euro-Siberian Subregion are influenced by several factors, above all by the intensity of scientific research gall midges, further by the diversity of plants and plant communities, and by the geographical position and elevation (above sea level).

THE DEPTH OF KNOWLEDGE OF GALL MIDGES

According to the level of scientific exploration, European countries may be divided into three groups:
a) countries in which the gall midge fauna is well known: Norway, Sweden, Finland, Great Britain, Denmark, the Netherlands, Belgium, France, Germany, Czech Republic, Slovak Republic, Poland, Hungary, Romania, Slovenia and Austria; b) countries in which gall midge fauna are poorly known: Spain, Switzerland, Italy and Bulgaria; and
c) countries in which knowledge of gall midge fauna is practically neglible: Liechtenstein, Albania, Greece and Turkey.

Diversity of Plant Species

If we evaluate the plant diversity in the western half of the Euro-Siberian Subregion from the north to the south, then in the north there occur coniferous forests with species-poor plant communities: to that area there belong northern parts of Norway, Sweden and Finland. These parts change into plant communities of middle-European, i.e. deciduous forests with much richer diversity of plant species and plant communities. This type covers the territory from Great Britain and France up to Poland and Bulgaria. In these deciduous forests of various types, there grow many species of trees, shrubs and abundant herbivory flora. The high diversity of plant species there provides hosts for many gall midge species.

The deciduous forests change gradually up to Mediterranean sclerophyll type with various shrub formations, sometimes with evergreen shrubs and with various Artemisia-species in the Sub-Mediterranean area and, above all, in the Mediterranean Sub-Region.

These southern-central biogeographical provinces are grounds for high diversity of gall midges. In contrast, only a small number of gall midge species occurs in the North-European countries. The number of gall midge species peaks in the south, and in the middle part of Europe and, in the contrary, the number of species decreases in the direction to the south, to the territory of southern Europe and also to the territory of North Africa which belongs to the Palaearctic Region.

Geographical Position and Elevation

Long-term investigations of gall midge fauna carried out in several European countries in localities lying in different elevations above sea level showed that the number of plant species and the number of gall midge species decreases rapidly with increasing elevation (Skuhrava 1987). See, for example, the altitudinal gradients in species richness in the territory of Czech Republic (Skuhrava 1994) and Slovak Republic (Skuhrava 1991) (Table 1).

Table 1.—The declining average number of gall midge species per one locality with increasing elevation in two middle-European countries

Elevation (m)	Average number of gall midge species	
above sea level	Czech Republic	Slovak Republic
1900-2000	-	1
1800-1900	-	-
1700-1800	-	1
1600-1700	-	3
1500-1600	-	1,5
1400-1500	1	2
1300-1400	3	3
1200-1300	3	6
1100-1200	3	-
1000-1100	11	10
900-1000	11	13
800- 900	16	17
700- 800	17	15
600- 700	23	20
500- 600	27	19
400- 500	27	22
300- 400	32	25
200- 300	30	25
100- 200	30	19

Similar changes in numbers of gall midge species may be observed with respect to geographical position: the number of species decreases to both north and south of middle Europe where richness is the highest. In northern Europe it seems that the more abundant the gall midges develop in galls on leaves of various trees (above all the species of the genus *Dasineura*) whereas in the southern territories, that is in the southern part of Europe and in northern Africa, there are gall midges developing in flower and leaf bud galls and in fruits of various herbaceous host plant species, above all the species of the genera *Asphondylia* and *Contarinia*. For example, more than 50 species of the genus *Asphondylia* are known to be in the Palaearctic Region. But no species of this genus is known to occur in Norway, only 1 in Finland, 3 in Denmark, 4 in Sweden, 6 in Netherlands, 12 in Great Britain, 16 in Germany and in Bulgaria, 18 in France, Czech Republic, Slovak Republic and even 24 in Italy.

The areas where a particular genus of gall midges has its highest diversity may be designated its center of origin as it is presumed with plant genera. It seems that the center of the origin of the genus *Asphondylia* isin the southern part of Europe - in the Mediterranean subregion. The genus *Lasioptera Meigen*, 1818 comprises 47 species in the Palaearctic Region. The highest number including 16 species occurs in Germany, nine species occur in Czech Republic, seven in Slovak Republic, eight are known in France. Lasioptera seems to have its centre of origin in the Middle Europe. The genus *Stephaniola Kieffer*, 1913 includes 62 species in the Palaearctic Region the most of which occur in the Middle Asian territory which seems to be the center of origin of this genus. The genus *Dasineura Rondani*, 1840 comprises 320 species of gall midges in the Palaearctic Region. It is the genus with the highest number of species in the world and seems to have the center of its origin in middle Europe. The genus *Contarinia Rondani*, 1860 includes 190 species in the Palaearctic Region. The highest number of species occur in middle Europe which seems therefore to be its center of origin. The genus *Halodiplosis Kieffer*, 1912 has 36 species which occur scattered in the Middle-Asian Subregion of the Palaearctic Region which seems to be its center of origin.

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COMPARING THE OAK GALLING CYNIPID FAUNA OF TRANSCARPATHIA WITH THAT OF NORTHERN HUNGARY AND THE REST OF THE UKRAINE

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Abstract. A comparative analysis of the oak galling cynipids (Hymenoptera: Cynipidae, Cynipinae) of the Transcarpathia, the rest of the Ukraine, and Northern Hungary is given. Variations in species numbers in different parts of the Ukraine and Northern Hungary are analysed.

INTRODUCTION

The Transcarpathian region is located in the western end of the Ukraine on the border with Romania, Hungary, Slovakia and Poland. Its lowland part, the Prytyssanska Lowland, is a continuation of the large Pannonian lowland and separated from Hungary only by the Tysa river. The border with Romania and Slovakia consists of mountains covered with beech forests.

An analysis of the literature and our own studies have shown that the oak galling cynipid fauna (Hymenoptera: Cynipidae) of West and Central Europe behind the Carpathian mountain ridge is richer than that of the rest of the Ukraine and the whole European part of the former USSR beyond the Carpathians. The richest fauna can be found in Hungary (about 100 species according to Ambrus, 1974; 97 species and 123 forms are known now—G. Csoka); 56 species are known from Poland (Kierych 1979); 82 from Romania (Ionescu 1973); 45 from the European part of the former USSR (Zerova *et al.* 1988), particularly 29 from Moldova (Plugaru 1963, 1965, 1969, 1975), and less than 20 from the Crimea (Djakontshuk 1987).

Further to east and north through the European part of the former USSR, the oak cynipid fauna becomes increasingly poor. Some species of *Cynips* and *Neuroterus* can be found even in the Mordva Republic, Kalinin (now Tver), and in the Leningrad region of Russia in the north (Shevchenko 1955). These species are penetrating from the west through the Carpathian mountain ridge. If we analyze the oak galling cynipids of the Caucasus and Transcaucasus Republics (Azerbajdzhan: 15 species, (Majsuradze 1961; Belizin and Majsuradze 1965); Georgia: 22 species, (Supatashvili and Kharazashvili 1964)) and their species composition, we can see that there are some species which are associated with the evergreen species oaks (the genera *Plagiotrochus, Andricus, Dryocosmus*, etc., Mediterranian cynipid elements). In the territory of the former USSR, these evergreen oaks grow naturally only in the territory of the Transcaucasus Republics. In Iran 36 species of oak galling cynipids are known (Chodjai 1980), from which 29 can be found in Central Europe and the Ukraine as well. The literature about oak galling cynipids of the Russian regions beyond Caucasus (Stavropol, Krasnodar, Rostov regions) have shown that the species composition is much poorer than that of the Ukraine and Transcaucasus, and does not include Transcaucasus elements. This proves that the Caucasus mountain ridge is a substantial barrier for cynipids penetration into the northern regions (Shevchenko 1955, Zakharov and Levkovich 1951, Strokov 1952, Nikolskaya 1950, Pomerancev 1949). In the lowland oak forests, which mainly consist of *Q. robur*, and in the foothills of Transcarpathia, we have found 52 species with 75 forms (agamic and bisexual generations) of galling cynipids, associated with *Quercus robur, Q. petraea* mainly, and also with *Q. cerris, Q. daleshampii, Q. pubescens*.

In order to understand why the fauna becomes more and more poor by moving to east and north-east beyond the Carpathian mountains, we must have some information on the oak forests over the remaining territory of the Ukraine and Transcarpathia in particular. Oak forests in the territory of the Ukraine exist only in the form of small insular populations: mixtures of *Q. robur* with hornbeam, or *Q. robur* with lime-tree. The greatest number of these "islands" are situated on the right bank of the Dnieper river. It must be pointed out that *Q. petraea* forests are very rare in the Ukraine. They can be found only in Transcarpathian foothills and the lower forest beech belt. Some "islands" of them are situated along the border with Moldova and in the mountainous Crimea. *Quercus pubescens* grows only sporadically in Transcasrpathia and in Crimea. As to *Quercus cerris*, natural populations of this species occur only in Transcarpathia. Over the rest of the Ukraine, this species is absent (S. Stojka, personal communication). Even in Transcarpathia there exist only 3 sites where *Q. cerris* grows: Chorna Hora, Julian Mountains, and in the environs of Vary village, which strongly influences the invasion of heteroecous oak galling cynipids to this geographical site. There is a great gap between the Transcarpathians oak forests and that of the remaining territory of the Ukraine beyond the Carpathians. The first oak forests beyond the Carpathians can be found only in the valley of the Dniester river.

DISTRIBUTION OF GALL FORMING CYNIPIDS

The comparison of the oak galling cynipids of Transcarpathia and that of Northern Hungary is of particular interest. It depends on spreading of oak galling cynipids up into the mountainous country of Transcarpathia, and into the foothills and the lower forest zone in which beech is dominant with admixtures of *Q. petraea* and sometimes with a few specimens of *Q. robur*. It is well known that the oak cynipid fauna of Hungary is the richest in Europe (97 species with 123 forms are known yet—G. Csoka). It must be noted that this high richness depends first of all on a great number of species associated with *Q. cerris*. The latter is wide spread throughout Hungary, and coexists very easily with other *Quercus* species. But this is only one explanation. It must also be noted that in Hungary, 6 *Quercus* species grow naturally: *Q. robur, Q. petraea, Q. pubescens, Q. cerris, Q. farnetto, and Q. virgiliana.* If we divide *Q. petraea* and *Q. daleshampii* into separate species it would be more than that. There is a great diversity at the subspecies level of oak trees (morphology, phenology, etc.). We believe that this large subspecies diversity has also influenced the cynipid species and intraspecific diversity.

Another very important fact is the high level of mixing of different *Quercus* species. Their coexistence in different mixtures (species diversity and different abundancy of each oak species) in the same territories also positively influence the oak cynipid species diversity. This is especially true for the admixtures of *Q. cerris*. This is very important, because until we know how many cynipid species have their bisexual generations on *Q. cerris*, we believe that a number of monophagous species which develop on *Q. cerris* are bisexual generations of well-known species (but now are registered under different names) that develop on other oaks in their agamic generations.

In the Northern part of Hungary, which borders with Transcarpathia, only 75 species and 106 forms (agamic and bisexual generations) are known. Under "North Hungary" we include the territories to the east and north from Budapest, what is the Eszaki Kozephegyseg mountains and this territory belong to the basin of the Tysa river. In Transcarpathia we have found only 52 species with 75 forms (agamic and bisexual generations) (Table 1.). The Tysa river is not a barrier for cynipid penetration into the Transcarpathian Lowland from Hungary. There exist other barriers for the heteroecous species: very few sites of *Q. cerris* and, perhaps, a more severe climate.

Table 1.—The oak gall-maker cynipid fauna of Transcarpathia and North Hungary (a comparative analysis)

Cynipid species	Generation	Site of col.		Host plant			
		a	b	1	2	3	4
Andricus aestivalis Gir.	only bisex.	+	-	—	-	—	+
A.ambiguus Trotter	only agamic	+	+!!	++	+	+	-
A.*amblycerus* Gir.	only agamic	+r	-	+	+	+	-
A.*amenti* Gir.	only agamic	+	-	-	+	+	-
A.*aries* Gir.	only agamic	+	+!!	++	-	+r	-
A.*callidoma* Htg.	agamic	+	+!	+r	++	+r	-
	bisexual	+	+!	+r	++	?	-
A.*caputmedusae* Htg.	only agamic	+	-	+	+	+	-
A.*caliciformis* Gir.	only agamic	+	+r	+	+	+	-
A.*conificus* Htg.	only agamic	+	+r!!	++	+	+	-
A.*conglomeratus* Gir.	only agamic	+	+	+	+	+	-
A.*coriarius* Htg.	only agamic	+	+	+	+	+	-
A.*coronatus* Gir.	only agamic	+	+r!!	+r	++	+	-
A.*corruptrix* Schlcht.	agamic	+	+r!!	+	+	+	-
	bisexual	?	?	-	-	-	-?
A.*curvator* Htg.	agam.,bisex.	+	+	+	+	+	-
A.*cydoniae* Gir.	only bisex.	+	-	-	-	-	+
A.*fecundator* Htg.	agam.,bisex.	+	+	+	++	+	-
A.*galeatus* Gir.	only agamic	+	+!!	+	+	+	-
A.*gallaetinctoriae* Ol.	only agamic	+	+	++	+	+	-
A.*gemmea* Gir.	agamic	+	?	+	+	+	-
	bisexual	?	?	-	-	-	+?
A.*giraudianus* D.T.-Kffr.	only agamic	+r	-	+	+	+	-
A.*glutinosa* Gir.	only agamic	+	+	++	+	+	-
A.*hartigi* Marshal	only agamic	+r	+r	-	+	+	-
A.*hungaricus* Htg.	only agamic	+	+	+	-	-	-
A.*hystrix* Trotter	only agamic	+r	-	+	+	+	-
A.*inflator* Htg.	agam.,bisex.	+	+	++	+	+	-
A.*kollari* Htg.	agamic	+	+	+	++	-	-
	bisexual	+	?	-	-	-	+
A.*lignicola* Htg.	agamic	+	+	+	+	+	-
	bisexual	?	?	-	-	-	+?
A.*lucidus* Htg.	only agamic	+	+	+	+	+	-
A.*marginalis* Schlcht.	only agamic	+	+r!	+	+	-	-
A.*mayri* Wachtl	only agamic	+	+	+	+	-	-
A.*mitratus* Mayr	only agamic	+	+!	+	++	+r	-
A.*multiplicatus* Gir.	only sexual	+	-	-	-	-	+
A.*nudus* Adler	agam.,bisex	+	+!!	+	++	?	-
A.*ostreae* Htg.	agam.,bisex	+	+	+	+	+	-
A.*panteli* Kffr.	only agamic	+r	-	+	?	-	-
A.*paradoxus* Rados.	only agamic	+	+!	+	+	+	-
A.*quadrilineatus* Htg.	only agamic	+	+!	+	+	+	-
A.*quercuscalicis* Burgsd.	agamic	+	+	+	-	-	-
	bisexual	+	?	-	-	-	+
A.*quercuscorticis* Htg.	agamic	+	+r!	+	+	+	-
	bisexual	+	+	+	+	+	-
A.*quercusradicis* F.	agam.,bisex.	+	+	+	+	+	-
A.*quercusramuli* Htg.	agam.,bisex.	+	+	+	+	+	-
A.*quercustozae* Bosc.	only agamic	+	+	+	+	+	-

(table 1 continued on next page)

(table 1 continued)

Cynipid species	Generation	Site of col.		Host plant			
		a	b	1	2	3	4
A.rhyzomae Htg.	only agamic	+	+r!	+	+	-	-
A.seckendorfii Wachtl	only agamic	+	-	+	+	+	-
A.seminationis Gir.	only agamic	+	+r?	+	+?	-	-
A.serotinus Gir.	only agamic	+r	-	+	+	-	-
A.singulus Mayr	only agamic	+	-	-	-	-	+
A.solitarius Fonsc.	agam.,bisex.	+	+	+	++	+	-
A.superfetationis Gir.	only agamic	+	-	+	+	+	-
A.testaceipes Htg.	agam.,bisex.	+	+	+	+	+	-
A.tinctoriusnostrus Stf.	only agamic	+	-	+	+	+	-
A.truncicola Gir.	only agamic	+	+	+	+	+?	-
Aphelonyx cerricola Gir.	only agamic	+	-	-	-	-	+
Chilaspis nitida Gir.	agam.,bisex.	+	-	-	-	-	+
Synophrus politus Htg.	only bisex.	+	-	-	-	-	+
Biorhiza pallida Ol.	agam.,bisex.	+	+	+	+	+	-
Cynips agama Htg.	agamic	+	+	+	+	+	-
C.cornifex Htg.	only agamic	+r	-	-	-	+	-
C.disticha Htg.	agam.,bisex.	+	+	+	+	+	-
C.divisa Htg.	agam.,bisex.	+	+	+	+	+	-
C.longiventris Htg.	agamic	+	+	+	+	+	-
	bisexual	+	?	+	+	+?	-
C.quercus Fourcr.	agamic	+	+	+	+	+	-
	bisexual	+?	+?	+	+	+	-
C.quercusfolii L.	agam.,bisex.	+	+	+	+	+	-
Trigonaspis megaptera Htg.	agam.,bisex.	+	+	+	+	+	-
T.synaspis Htg.	agam.,bisex.	+	+	+	+	+	-
Callirhytis glandium Gir.	only agamic	+	+	+	+	+	+
Neuroterus fumipennis Htg.	agam.,bisex.	+	+!	+	+	+	-
N.laeviusculus Schenck	agam.,bisex.	+	+	+	+	+	-
N.numismalis Ol.	agam.,bisex.	+	+	+	+	+	-
N.macropterus Htg.	only agamic	+	-	-	-	-	+
N.minutulus Gir.	only agamic	+	-	-	-	-	+
N.petioliventris Htg.	agam.,bisex.	+	+r	+	+	+	-
N.obtectus Wachtl	only bisexua	+	-	-	-	-	+
N.quercusbaccarum L.	agam.,bisex.	+	+	+	+	+	-
N.saliens Koll.	agamic	+	+	-	-	-	+
	bisexual*	+	-	-	-	-	+

a - North Hungary; b - Transcarpathia; 1 - *Quercus robur*; 2 - *Q. petraea*; 3 - *Q.pubescens*; 4 - *Q.cerris*; r - rare species; !- species new for the cynipidofauna of Transcarpathian; !!- species, new for the fauna of the Ukraine and the whole territory of the European part of the former USSR; ? - there are some doubts as to what species the founded galls belong to; * - now it is known that *N.saliens* and *N.glandiformis* are different generations of the same species - now its valid name is *N.saliens* Koll.

The cynipid fauna of the Transcarpathian Lowland is the same as that of Northern Hungary, but may be poorer in species richness. Another thing is the cynipid fauna of foothills and lower mountain zone (up to 900-950 m a.s.l.). Of 52 lowland cynipid species, only 24 can be found in the upper zone of foothills and in the lower forest belt. It is interesting to note that all the 6 species of the genus Cynips (*C. agama* Htg., *C. divisa* Htg., *C. longiventris* Htg., *C. quercus* Fourcr., *C. quercusfolii* L., and *C. disticha* Htg.) can be found at altitudes of 850-900 m a.s.l. as well as the two species of genus *Neuroterus*: *N. numismalis* Ol., and *N. quercusbaccarum* L. Moreover, it is these species that reach the most eastern (Kalinin, Saratov regions of Russia) and northern (Leningrad region) parts of the cynipid distribution area (Shevchenko, 1955). The same picture can be seen while analyzing the vertical distribution of cynipid species in the territory of Norh Hungary: in the highest parts of the Bukk and Zemplin mountains the species diversity is also poorer than in the lowlands. The cynipid fauna of Transcarpathia is richer than that of the rest of the Ukraine and even the whole European territory of the former USSR beyond the Carpthian mountains. Even the cynipid fauna of Moldova number only 29 known species (Plugaru 1963). It is only half of that in Transcarpathia. During our investigations in Transcarpathia, we found 18 species new for the Transcarpathians, and 8 species new for the fauna of the whole European part of the former USSR and particularly for the Ukraine (Table 1).

Some features of some heteroecous species are of particular interest. These comprise the following species: *Andricus quercuscalicis* Burgsd., *A. kollari* Htg., and *A. lignicola* Htg. We never found the bisexual generations of these speies in Transcarpathia. Moreover, *A. kollari* and *A. lignicola* can be found on *Q. petraea* in the foothills and even in the lower forest beech zone at 650-900 m a.s.l. and they exist there in the form of isolated populations; the nearest sites of *Q. cerri* (the host plant of their bisexual generations) are at least 100-150 km far away from the lowland (Chorna Hora and Julian mountains in Vynohradovo district). These two species are abundant on the top of Plishka hill, where a plot of *Q. petraea* can be found. It is a task of great interest to investigate if they exist there in the form of only agamic generations for a longer period of time or the females of the bisexual generations are transferred by wind to such great distances from the lowland, where *Q. cerris* can be found. It is interesting to note that Ambrus (1974) wrote about the bisexual generation of *A. lignicola*, which is associated only with *Q. cerris*. But the bisexual generation has not been found in Hungary and Transcarpathia yet. Perhaps the cause of it is the gall form which is closely related to that of bisexual generation of *A. kollari* (they develop on *Q. cerris* also) and is very small in size and hardly visible. The same is true with the bisexual generation of *A. corruptrix*. We have never found it in Hungary and Transcarpathia, but P. Walker (personal communication) has found its galls on *Q. cerris*.

A. quercuscalicis, a common, and during some years an abundant species, is unknown beyond the Carpathian mountains. Such examples are very interesting from the zoogeographical point of view and need further investigation. During recent times, there have been plantings of *Q. cerris* in different places in the European part of the former USSR and accordingly we can expect the invasion of some heterogenous species to these sites.

According to L. Diakontshuk (personal communication) one more oak cynipid species can be found in Transcarpathia, *Neuroterus minutulus* Gir. We have not yet found this species. We think that in Transcarpathia, due to its geographical position, one can find 20-25 more species and 25-30 more galls of oak galling cynipids. They can easily penetrate from Hungary. The Tisa river is not an obstacle. Transcarpathian cynipid fauna is really a continuation of the Hungarian fauna. The Carpathian mountain ridge is a serious barrier for oak cynipid invasion to east. Transcarpathia is a natural boundary of distribution for a great number of oak cynipid species.

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A COMPILATION OF THE OAK GALLING CYNIPIDS (HYMENOPTERA: CYNIPIDAE) IN THE UKRAINE

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Abstract. The oak galling cynipid fauna of the Ukraine is represented by 54 species with 75 forms (agamic and bisexual generations), which are associated mainly with *Quercus robur* and *Q.petraea.* The list of oak cynipid gall inquilines from the genera *Synergus* Hartig and *Ceroptres* Hartig include 23 species (22 from the genus *Synergus* and 1 from *Ceroptres*). Their relationships with different oak cynipid galls are given.

The oak galling cynipid fauna of the Ukraine is represented by 54 species with 77 forms (agamic and bisexual generations). Of the 14 species of oaks found in the Ukraine, only 6 are infested by cynipids: (1) *Quercus robur* L., is distributed over the greatest part of the Ukrainian forests but is rare in the steppe and absent in the extreme south, but it appears in the northern part of the mountainous Crimea. In Transcarpathia, where the oak forests total 7%, *Q. robur* can be found in the lowland and in the foothills up to 500-700 m above see level. Two forms of this Quercus species are distinguished: an early and a late phenological type. The oak galling cynipids more strongly infest the latter. (2) *Quercus petraea* (Mattuschka) Liebl. can be found in Transcarpathia in the lowland and foothills up to 700-900 m a.s.l. In Polesje this oak species is very rare. In the mountainous Crimea, *Q. petraea* is distributed in the middle and higher vegetation belts. (3) *Quercus pubescens* Willd. can be found sporadically in southern parts of Transcarpathia, where this species is very rare. It also can be found in the mountainous Crimea, mainly in the lower belt. (4) *Quercus suber* L. and (5) *Q.ilex* can be found only in the parks and arboretums of the south coast of Crimea. (6) *Quercus macrocarpa* Michx. can occur in parks and arboretums all over the territory of the Ukraine.

Apart from the above mentioned oak species in Transcarpathia, two more *Quercus* species grow naturally. *Quercus polycarpa* Schur. is a very rare species and occurs only sporadically (Julian mountains, Chorna Horaand in Beregovo) (we did not investigate its cynipids), and *Quercus cerris* L. is a very important species from the point of view of cynipids. In Ukraine, the latter can be found only in the southern lowlands of Transcarpathia in 3 little plots: Chorna Hora, Julian Mountains and the environs of the Vary village. There exists also one artificial site of this oak species inthe Rafajlovo forest, Transcarpathia. According to botanists there exists one more oak species, *Quercus dalechampii* Ten. which can be found in Transcarpathia also. But different European botanists consider *Q. dalechampii* as a subspecies or variety of *Q. petraea.* Only 3 species of oaks can be singled out from the point of view of cynipid faunal richnes: *Q. robur* with 51 species of gall-makers, *Q. petraea* with 46 species, and *Q. pubescens* with 39 species (Table 1).

The most abundant and wide-spread cynipid species belong to the genera *Andricus*: *A. curvator*, *A. fecundator*; *Neuroterus*: *N. numismalis*, *N. quercusbaccarum*; *Cynips*: *C. quercusfolii*, Biorhiza pallida. Species of *Cynips*, *Neuroterus*, and *Biorhiza pallida* are wide-spread and abundant throughout the Ukraine, as well as to the north and east of the republic. The species of genus *Andricus* is mainly distributed in the western part of the country, especially in Transcarpathia. Such species as *A. kollari*, *A. conglomerata*, *A. hungaricus*, *A. gallaetinctoriae*, *A. lucidus*, *A. quercuscalicis*, *A. glutinos*, *A. lignicola*, *A. ambiguus*, *A. coriarius*, and some others, which are common and sometimes even abundant in Transcarpathia, are absent from the rest territory of the Ukraine (species which can be found only in Transcarpathia are marked with "!" in Table 1).

Table 1.—Oak galling cynipids (Hymenoptera: Cynipinae) of the Ukraine

Cynipid species	Generation	Host plant						
		1	2	3	4	5	6	7
A.ambiguus Trotter	! only agamic	++	+	+	-	-	-	-
A.aries Gir.	! only agamic	++	-	+r	-	-	-	-
A.callidoma Htg.	agamic	+r	++	+r	-	-	-	-
	bisexual	+r	++	?	-	-	-	-
A.caliciformis Gir.	only agamic	+	+	+	-	-	-	-
A.conificus Htg.	! only agamic	++	+	+	-	-	-	-
A.conglomeratus Gir.	only agamic	+	+	+	-	-	+	-
A.coriarius Htg.	! only agamic	+	+	+	-	-	-	-
A.coronatus Gir.	! only agamic	+r	++	+	-	-	-	-
A.corruptrix Schlcht.	! agamic	+	+	+	-	-	-	-
	bisexual -?	-	-	-	-?	-	-	-
A.curvator Htg.	agam.,bisex.	+	+	+	-	-	-	-
A.fecundator Htg.	agamic	+	++	+	-	+	+	+
	bisexual	+	+	+	-	-	-	-
A.galeatus Gir.	! only agamic	+	+	+	-	-	-	-
A.gallaetinctoriae Ol.	! only agamic	++	+	+	-	-	-	-
A.gallaeurnaeformis (Ol.)	only agamic	-	+	+	-	-	-	-
A.glutinosa Gir.	! only agamic	++	+	+	-	-	-	-
A.hartigi Marshal	! only agamic	-	+	+	-	-	-	-
A.hungaricus Htg.	! only agamic	+	-	-	-	-	-	-
A.inflator Htg.	agamic	++	+	+	-	+	+	-
	bisexual	+	+	+	-	-	-	-
A.kollari Htg.	agamic	+	++	-	-	+	+	-
	! bisexual	-	-	-	+	-	-	-
A.lignicola Htg.	! agamic	+	+	+	-	-	-	-
	bisexual -?	-	-	-	+?	-	-	-
A.lucidus Htg.	! only agamic	+	+	+	-	-	-	-
A.marginalis Schlcht.	only agamic	+	+	-	-	-	-	-
A.mayri Wachtl	only agamic	+	+	-	-	+	+	-
A.mitratus Mayr	only agamic	+	++	+r	-	-	-	-
A.nudus Adler	! agam.,bisex	+	++	?	-	-	-	-
A.ostreae Htg.	agamic	+	+	+	-	+	+	+
	bisexual	+	+	+	-	-	-	-
A.paradoxus Rados.	only agamic	+	+	+	-	-	-	-
A.polycerus Gir.	only agamic	+	-	-	-	-	-	-
A.quadrilineatus Htg.	! only agamic	+	+	+	-	-	-	-
A.quercuscalicis Burgsd.!	agamic	+	-	-	-	-	-	-
	bisexual	-	-	-	+	-	-	-
A.quercuscorticis Htg.	agamic	+	+	+	-	-	-	-
	bisexual	+	+	+	-	-	-	-
A.quercusradicis F.	agamic	+	+	+	-	+	+	-
	bisexual	+	+	+	-	-	-	-
A.quercusramuli Htg.	agam.,bisex.	+	+	+	-	-	-	-
A.quercustozae Bosc.	only agamic	+	+	+	-	-	-	-
A.rhyzomae Htg.	! only agamic	+	+	-	-	-	-	-
A.seminationis Gir.	only agamic	+	+?	-	-	-	-	-
A.solitarius Fonsc.	agamic	+	++	+	-	-	+	-
	bisexual - ?	+	+	-	-	-	-	-

(table 1 continued on next page)

(table 1 continued)

Cynipid species	Generation	Host plant						
		1	2	3	4	5	6	7
A.testaceipes Htg.	agam.,bisex.	+	+	+	-	-	+	-
A.truncicola Gir.	! only agamic	+	+	+?	-	-	-	-
Biorhiza pallida Ol.	agam.,bisex.	+	+	+	-	-	-	-
Cynips agama Htg.	agamic	+	+	+	-	-	-	+
C.disticha Htg.	agamic	+	+	+	-	+	+	-
	bisexual	+	+	+	-	-	-	-
C.divisa Htg.	agamic	+	+	+	-	-	-	+
	bisexual	+	+	+	-	-	-	-
C.longiventris Hart.	agamic	+	+	+	-	-	-	+
	bisexual	+	+	+?	-	-	-	-
C.quercus Fourcr.	agamic	+	+	+	-	-	+	-
	bisexual -?	+	+	+	-	-	-	-
C.quercusfolii L.	agamic	+	+	+	-	-	-	+
	bisexual	+	+	+	-	-	-	-
Callirhytis glandium Gir.	only agamic	+	+	+	+	-	-	-
Fiorella Marianii Kffr.	agamic	+	-	-	-	-	-	-
Neuroterus fumipennis Htg.	agam.,bisex.	+	+	+	-	-	-	-
N.laeviusculus Schenck	agam.,bisex.	+	+	+	-	-	+	-
N.numismalis Ol.	agam.,bisex.	+	+	+	-	-	-	+
N.petioliventris Htg.	agam.,bisex.	+	+	+	-	-	-	-
N.quercusbaccarum L.	agamic	+	+	+	-	-	-	+
	bisexual	+	+	+	-	-	-	-
N.saliens Koll.	agamic	-	-	-	+	-	-	-
Trigonaspis megaptera Htg.	agam.,bisex.	+	+	+	-	-	-	-
T.synaspis Htg.	! agam.,bisex.	+	+	+	-	-	-	-

1 - *Quercus robur*; 2 - *Q. petraea*; 3 - *Q. pubescens*; 4 - *Q. cerris*; 5 - *Q. suber*, 6 - *Q. ilex*, 7 - *Q. macranthera*; r - rare species; ! - species known only from Transcarpathian; ? - there are some doubts due to what species belong the found gall belong to.

So, the oak galling cynipids of the whole Ukraine number 54 species with 77 forms (agamic and bisexual generations). The richest fauna is in Transcarpathia, 52 species with 75 forms. Among them, 20 species in the Ukraine can be found only in Transcarpathia (see above). For comparison, the oak cynipids of Moldova numbers only 29 species. Among them only 2 species, *A. glandulae* Hart. and *A. beyerincki* Trott., have not been found in the Ukraine up to now. It is interesting to note the scarcity of the oak cynipids in the mountainous Crimea, only 16 species are registered for this region (Diakontshuk, 1987). But, we think that the Crimean cynipid fauna is far richer and needs further investigations.

From different oak cynipid galls we have reared 23 species of inquilines from the genera *Synergus* Hartig and *Ceroptres* Hartig (Table 2). We have found that the greatest number of inquilines occur in leaf galls, rather than the stem and bud galls. In the catkin galls the inquilines number is poorer. Perhaps it is explained by their small size or, maybe, by habitat peculiarities.

Table 2.—Trophic relationships of the inquilines in oak galls

Inquiline species	Oak cynipid hosts
Genus Ceroptres Hartig	
C.arator Hartig	*Andricus conglomerata*, agamic
	A.lignicola, agamic
	A.seminationis, agamic
	Neuroterus numismalis, agamic
Genus Synergus Hart.	
S.albipes Hart.	*Andricus callidoma*, agamic
	A.curvator, agamic
	A.kollari, agamic
	A.lignicola, agamic
	A.ostreae, agamic
	A.seminationis, agamic
	A.solitarius, agamic
	Cynips agama, agamic
	C.disticha, agamic
	C.divisa, agamic
	C.longiventris, agamic
	C.quercusfolii, agamic
	Neuroterus fumipennis, agamic
	N.numismalis, agamic
	N.quercusbaccarum, agamic
	Trigonaspis megaptera, agamic
S.apicalis Hart.	*Andricus conglomerata*, agamic
	A.fecundator, agamic
	A.inflator, agamic
	A.lignicola, agamic
	A.quercusradicis, bisexual
	A.testaceipes, agamic
	Neuroterus laeviusculus, agamic
	some galls of *Cynips* sp.,agamic
S.clandestinus Eady	from the acorns of *Q.robur*
S.crassicornis (Curtis)	*Andricus fecundator*, agamic
	A.inflator, agamic
	A.kollari, agamic
	A.mayri, agamic
S.gallaepomiformis Boyer de Fonsc.	*Andricus callidoma*, agamic
	A.curvator, agamic
	A.fecundator, agamic
	A.ostreae, agamic
	A.quadrilineatus, agamic
	A.quercusradicis, agamic
	A.quercusramuli, bisexual
	A.seminationis, agamic

(Table 2 continued on next page)

(Table 2 continued)

Inquiline species	Oak cynipid hosts
	A.solitarius, agamic *Cynips divisa*, agamic *C.longiventris*, agamic *C.quercusfolii*, agamic *Neuroterus fumipennis*, agamic *N.quercusbaccarum*, agamic *Trigonaspis megaptera*, bisexual *Biorhiza pallida*, bisexual
S.hayneanus Hart.	*Andricus conglomerata*, agamic *A.coriarius*, agamic *A.gallaetinctoriae*, agamic *A.kollari*, agamic *A.lignicola*, agamic *A.mayri*, agamic *A.quercuscalicis*, agamic
S.incrassatus Hart.	*A.coriarius*, agamic *A.curvator*, agamic *A.hungaricus*, agamic *A.quercuscalicis*, agamic *A.quercuscorticis*, agamic *A.quercusradicis*, agamic *A.seminationis*, agamic *Biorhiza pallida*, bisexual
S.nervosus Hart.	*Andricus callidoma*, agamic *A.curvator*, agamic and bisexual *A.inflator*, agamic *A.kollari*, agamic *A.ostreae*, agamic *A.quercusramuli*, bisexual *A.seminationis*, agamic *A.solitarius*, agamic *Cynips divisa*, agamic *C.longiventris*, agamic *C.quercusfolii*, agamic *Neuroterus fumipennis*, bisexual *N.quercusbaccarum*, agamic *Trigonaspis megaptera*, agamic
S.pallicornis Hart.	*Andricus conglomerata*, agamic *A.coriarius*, agamic *A.glutinosa*, agamic *A.hartigi*, agamic *A.kollari*, agamic *A.lignicola*, agamic *A.quercuscalicis*, agamic *Cynips agama*, agamic *C.disticha*, agamic *C.divisa*, agamic *C.longiventris*, agamic

(Table 2 continued on next page)

(Table 2 continued)

Inquiline species	Oak cynipid hosts
	C.quercus, agamic
	C.quercusfolii, agamic
	Neuroterus numismalis, agamic
	N.quercusbaccarum, agamic
S.pallidipennis Mayr	*Andricus coriarius*, agamic
	A.gallaetinctoriae, agamic
	A.kollari, agamic
	A.lignicola, agamic
S.radiatus Mayr	*Andricus coriarius*, agamic
	A.curvator, agamic
	A.ostreae, agamic
	A.paradoxus, agamic
	A.quercusramuli, agamic
	A.solitarius, agamic
	Cynips divisa, agamic
	Neuroterus fumipennis, agamic
	N.numismalis, agamic
	N.quercusbaccarum, agamic
	Trigonaspis megaptera, agamic
S.reinhardi Mayri	*Andricus caliciformis*, agamic
	A.gallaetinctoriae, agamic
	A.glutinosa, agamic
	A.hartigi, agamic
	A.kollari, agamic
	A.lignicola, agamic
	A.quercuscalicis, agamic
S.rotundiventris Mayr	*Andricus curvator*, agamic
	A.inflator, agamic
	A.kollari, agamic
	A.quercusradicis, bisexual
	Callirhytis sp., agamic
S.ruficornis Hart.	*Andricus curvator*, agamic
	A.fecundator, agamic
	A.inflator, agamic
	A.lignicola, agamic
	A.ostreae, agamic
S.thaumocerus (Dalman)	*Andricus ostreae*, agamic
	Neuroterus fumipennis, agamic,bisex.
	N.quercusbaccarum, agamic, bisexual
	Trigonaspis megaptera, agamic,bisex.
S.tristis Mayr	*Andricus gallaetinctoriae*, agamic
	A.ostreae, agamic
	Cynips quercusfolii, agamic

(Table 2 continued on next page)

(Table 2 continued)

Inquiline species	Oak cynipid hosts
S.tscheki Mayr	*Andricus curvator*, agamic
	A.ostreae, agamic
	A.seminationis, agamic
	Cynips disticha, agamic
	C.divisa, agamic
	C.longiventris, agamic
	C.quercusfolii, agamic
	Neuroterus fumipennis, agamic
	N.quercusbaccarum, agamic
S.umbraculus Ol.	*Andricus caliciformis*, agamic
	A.conglomerata, agamic
	A.coriarius, agamic
	A.fecundator, agamic
	A.gallaetinctoriae, agamic
	A.glutinosa, agamaic
	A.hungaricus, agamic
	A.kollari, agamic
	A.lignicola, agamic
	A.lucidus, agamic
	A.quercuscalicis, agamic

In Table 2 the Synergus species are given according to the taxonomical review on genus *Synergus* by one of the authors (Diakontschuk 1986, 1987). In this paper the author distinguished the following species of Synergus, Section II (Mayr 1872): *S. incrassatus*, *S. gallaepomiformis*, *S. nervosus*, *S. radiatus*, *S.pallicornis*, *S.tscheki* and *S.albipes*. These species have well marked, distinguishing morphological features. We know, that R.D. Eady (1952) synonimized Mayr's *radiatus* with *nervosus* Htg.; Mayr's *tristis* with *albipes* Htg.; Mayr's *tscheki* with *nervosus* Htg. also. It must be noted, that, really the "*tristis*", "*tscheki*", "*radiatus*", "*nervosus*", "*albipes*" are very closely related to one another in the morphological characteristics of their imago, but we can find differences between them. That is why it is very necessary to make a detailed modern review of this genus, using not only morphological features of adult insects for the species identification, but also the large data on their ecology and biology, host relationship.

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HOST PLANTS OF THE GALL-FORMING HYMENOPTERA IN THE EAST EUROPEAN PLAIN

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Abstract. In the East European Plain, gall-forming insects make up more than 800 species in 6 insect orders (Homoptera, Heteroptera, Coleoptera, Lepidoptera, Hymenoptera, Diptera). Their hosts include almost 700 species in the families Asteraceae, Fabaceae, Fagaceae, Poaceae, Rosaceae, and Salicaceae. Phytophagous gall wasps (Cynipoidea and Chalcidoidea) are represented by some relatively small groups such as the Cynipinae and a few genera in the families Eurytomidae and Torymidae among the chalcids. Among the Cynipinae, all larvae development takes place in galls, whereas among the chalcids only a small part of its life cycle occurs in galled vegetation. In both cynipids and chalcids, we consider phytophagy to be a secondary phenomenon originating independently from parasitic Hymenoptera groups. In many different families and genera of chalcids, phytophagy has independently arisen many times. Nevertherless, the biology of gall-forming cynipids and chalcids is characterized by many similar features. In the majority of cases gall development begins after larvae emerge. The larvae of all galling cynipids and chalcids develop latently in plant tissues.

As a whole, phytophagous Hymenoptera in the former USSR are represented by 315 species (185 cynipid and 130 chalcid species) on 17 plant families. Among chalcids, the seed feeders predominate (69 species), whereas among cynipids, it's the gallformers (159 species). There are also 30 species of gallformers among the chalcids.

Host plant family	Numbers of species of phytophagous Hymenoptera			
	Total	Gall-formers	Non-gallers	Seed feeders
		CYNIPOIDEA		
1. Fagaceae	75	75		
2. Aceraceae	1	1		
3. Rosaceae	32	37		
4. Papaveraceae	4	2	2	
5. Asteraceae	52	37	20	
6. Lamiaceae	16	14	2	
7. Scrophulariaceae	1	1		
8. Fabaceae	1	1		
9. Brassicaceae	1	1		
10. Apiaceae	2		2	
		CHALCIDOIDEA Eurytomidae		
1. Pinaceae	1			1
2. Rosaceae	5			5
3. Poaceae	70	29	41	
4. Fabaceae	24			24
5. Apiaceae	10			10
6. Lamiaceae	3			3
7. Euphorbiaceae	2			2
8. Scrophulariaceae	1			1
9. Brassicaceae	2			2
10. Anacardiaceae	1			1
11. Ephedraceae	2	1		1
		TORYMIDAE		
1. Anacardiaceae	1			1
2. Rosaceae	6			6
3. Cupressaceae	9			9

GALL-FORMING WASPS (HYMENOPTERA: CYNIPIDAE) IN AN OAK HYBRID ZONE: TESTING HYPOTHESES ABOUT HYBRID SUSCEPTIBILITY TO HERBIVORES

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Abstract. We examine patterns of gall densities for eight species of cynipid wasps in a *Quercus grisea* x *Q. gambelii* hybrid zone. We use the density data to test four competing hypotheses regarding patterns of herbivore loads in host plant hybrid zones. At the community level, cynipid densities are most consistent with the hypothesis of hybrid intermediacy; that is, cynipid densities exhibit a gradient from *Quercus grisea*, through the intermediate forms, to *Q. gambelii.* At the species level, all four hypotheses have empirical support. The null hypothesis of no differences among host taxa is supported by two species, the hypothesis of hybrid susceptibility by two species, the hypothesis of hybrid intermediacy by three species, and the hypothesis of hybrid resistance by one species. Total herbivore load supports the hypothesis of hybrid intermediacy. Cynipid densities exhibit significant patterns of covariation with host morphology within the contact zone.

Key words: cynipids; herbivory; hybrid zones; oaks; plant-insect interactions.

INTRODUCTION

There has been much recent interest among ecologists and evolutionary biologists in the effects of host plant hybridization on herbivore community structure and population dynamics (e.g. McClure 1985, Whitham 1989, Boecklen and Spellenberg 1990, Paige *et al.* 1990, Aguilar and Boecklen 1992, Floate and Whitham 1993, Paige and Chapman 1993). Hybrid zones are centers of genetic variation (Endler 1977, Harrison 1990), and so provide an ideal arena for testing evolutionary mechanisms thought to underlie plant-herbivore interactions, particularly those mechanisms concerned with host selection and plant defense. To date, investigations of plant hybrid zones have focused on describing patterns of herbivore loads on hybrid and parental hosts (e.g. Drake 1981, Whitham 1989, Boecklen and Spellenberg 1990, Floate and Whitham 1993), and on elucidating the functional form of the relationship between host hybrid status and susceptibility to herbivores (see Manley and Fowler 1969, Roskam and Van Uffelen 1981, Paige *et al.* 1990, Aguilar and Boecklen 1992, Paige and Chapman 1993).

Boecklen and Spellenberg (1990) presented three mutually exclusive hypotheses regarding patterns of herbivory in host hybrid zones that can be tested against the null hypothesis (H_0) of no differences among host taxa: H_1, hybrid hosts support higher densities of herbivores than do parental taxa; H_2, hybrid hosts support intermediate densities compared to parental taxa; and H_3, hybrid hosts support lower densities of herbivores than do parental hosts. This set of hypotheses is appropriate for investigations that treat hybrids as a single taxonomic category (e.g. Boecklen and Spellenberg 1990), or that subdivide hybrid forms into F1's and backcrosses (e.g. Aguilar and Boecklen 1992).

The number of case studies examining herbivory in plant hybrid zones is few, nevertheless all three alternative hypotheses have empirical support. For example, recent support for the hypothesis of greater hybrid susceptibility (H_1) comes from two host plant systems. Drake (1981) observed that hybrid hosts in a *Eucalyptus melanophloia* x *E. crebra* hybrid zones suffered higher rates of seed predation than did parental hosts. Similarly, Whitham (1989) reported that hybrid hosts in a *Populus angustifolia* x *P. fremontii* hybrid zone were more susceptible to the gall-forming aphid, *Pemphigus betae*, than were parental hosts. Subsequent work on the *P. angustifolia* x *P. fremontii* species complex both supports (Floate and Whitham 1993) and challenges (Paige and Capman 1993) the original description of hybrid susceptibility.

The hypothesis of hybrid intermediacy in herbivore loads (H_2) has recent support from three distinct host plant systems. Manley and Fowler (1969) reported that when compared to parental hosts, hybrids in a *Picea rubens* x *P. mariana* hybrid zone suffered intermediate rates of defoliation by spruce budworm. Drake (1981) observed intermediate rates of seed predation on hybrid hosts in a *Eucalyptus populmea* x *E. crebra* hybrid zone, while Aguilar and Boecklen (1992) documented that hybrids in the *Quercus grisea* x *Q. gambelii* species complex supported intermediate densities of leaf-mining moths and gall-forming wasps when compared to parental hosts.

Boecklen and Spellenberg (1990) presented evidence from two oak species complexes that was consistent with the hypothesis of hybrid resistance (H_3). Hybrid hosts in *Quercus depressipes* x *Q. rugosa* and *Q. coccolobifolia* x *Q. emoryi* hybrid zones supported lower densities of leaf-mining moths and gall-forming wasps than did corresponding parental hosts.

Here, we test the competing hypotheses regarding herbivory in hybrid zones with density data for gall-forming wasps (Hymenoptera: Cynipidae) in a *Quercus grisea* x *Q. gambelii* hybrid zone. We compare herbivore loads, both at a community level and at an individual species level, among five categories of host plants representing parental, F1, and backcrossed forms. We then examine patterns of covariation between cynipid densities and host morphology within the contact zone.

METHODS

Study Site and Organisms

We conducted this study in the San Mateo Mountains of west central New Mexico, USA. The region is classified as pine-oak woodland (Brown and Lowe 1980) and is dominated by pinyon pine (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*) at lower elevations; by gray oak (*Quercus grisea*), Gambel's oak (*Q. gambelii*), and ponderosa pine (*P. ponderosa*) at mid-elevations; and by quaking aspen (*Populus tremuloides*) and Douglas fir (*Pseudotsuga menziesii*) at high evelations.

We examined a hybrid zone between *Quercus grisea* Liebm. and *Q. gambelii* Nutt. on the north side of Mt. Withington at approximately 2500 m elevation. The hybrid zone contained large numbers of both parental species, as well as, hybrids (*Q. undulata*; Tucker 1961) and intergrades between the parental species and *Q. undulata*. Parental, hybrid, and intergrade taxa were intermixed in the contact zone.

The hybrid combination here examined is part of the *Quercus undulata* species complex (Tucker 1961). The complex is centered on *Q. gambelii*, which hybridizes throughout its geographic range with six other white oaks (subgenus Lepidobalanus), including *Q. grisea*. All F1 progeny in the complex are recognized as *Q. undulata* (Tucker 1961), and the hybrid nature of *Q. undulata* has been confirmed through experimental crosses (Cottam *et al.* 1981). At the Mt. Withington hybrid zone, *Q. gambelii* and *Q. grisea* are the only parental taxa of the species complex present.

Quercus grisea is common below the contact zone and is restricted to xeric sites with increasing elevation. The growth form of *Q. grisea* varies throughout its geographic range form a medium-sized tree (to 10 m) with a single trunk to a clonal shrub (to 2 m). It is evergreen or drought deciduous depending upon winter precipitation. At the Mt. Withington site, the tree form (to 3.5 m) is most common at lower elevations (approximately 2000 m), gradually giving way to the shrub form at the contact zone.

Quercus gambelii is common above the contact zone and is restricted to mesic sites with decreasing elevation. *Q. gambelii* is a small to medium-sized tree (1.5 to 15 m), often occurring in small clones. It is deciduous, losing its leaves in mid-October. Detailed descriptions of *Q. grisea*, *Q. gambelii*, hybrids, and intergrades are given elsewhere (Tucker 1961, Cottam *et al.* 1981, Aguilar and Boecklen 1992).

The *Quercus grisea* - *Q. gambelii* species complex supports a diverse community of phytophagous insects, including more than 30 species of cynipid wasps (Aguilar and Boecklen 1992). For the present study, we will restrict the analyses to the 8 most common cynipids. Owing to poor taxonomic coverage, most of these cynipids cannot be identified at the species level. We will instead refer to these species using operational names. Fortunately, gall morphologies are species-specific and quite distinct for these cynipids. The set of eight contains three species (*Neuroterus* spp.) that gall leaf midrib veins. The first of these (MRG1) forms a series of gall chambers inside the midrib, the second (MRG2) forms blister-shaped galls immediately adjacent to the midrib, and the third (MRG3) forms spherical galls with protruding white hairs. The stalk galler (STG; probably *Amphibolips* sp.) forms a spheroidal gall at the end of an approximately 10 mm stalk that originates from a leaf vein. The pellet galler (PLG; probably *Andricus pilularis*) forms pellet-shaped galls on the leaf blade. The red-spangle galler (RSG; *Andricus* sp.) forms red or yellow spangle-shaped galls on the leaf blade, while the leaf-splotch galler (LSG; probably *Neuroterus lamellae*) forms blister-shaped galls on the leaf blade. Finally, the petiole galler (PTG) forms spherical galls on the petiole.

Sampling Design and Statistical Analyses

We haphazardly sampled 93 trees from the hybrid zone and sorted them into 5 taxonomic categories based on micro- and macro-anatomical characters (see Aguilar and Boecklen 1992): *Q. grisea* (N=19), intergrades between *Q. grisea* and *Q. undulata* (N=19), *Q. undulata* (N=21), intergrades between *Q. undulata* and *Q. gambelii* (N=19), and *Q. gambelii* (N=15). From each tree, we haphazardly sampled 373 leaves, on average, and scored leaves for cynipid galls. We calculated densities (galls/100 leaves) and compared cynipid community structure on host taxa with a one factor multivariate analysis of variance (MANOVA). We also constructed contrasts that compared cynipid community structure on *Q. grisea* and *Q. gambelii* (Contrast 1), the parental taxa with *Q. undulata* and intergrades (Contrast 2), and the parental taxa with *Q. undulata* only (Contrast 3). We then partitioned the MANOVA and contrasts into univariate analyses of variance and contrasts to examine the responses of each herbivore individually, as well as, that of the total herbivore load (TOTAL = total galls/100 leaves).

We examined the relationship between cynipid densities and morphological variation of host plants within the hybrid zone as follows. We haphazardly sampled 10 leaves from each tree in the hybrid zone. From each leaf, we measured perimeter, area, length, width, petiole length, number of lobes, and depth of lobes. We also measured two categorical variables: length of mucro (1-3; where, 1= short, 2= medium, and 3= long) and leaf color (1-3; where, 1= grey, 2= intermediate, and 3= green). We then haphazardly subsampled 3 leaves and measured density of upper surface hairs, density of lower surface hairs, number of rays per upper-surface hair, number of rays per lower-surface hair, and angle of hairs (1-3; where, 1= upright, 2= intermediate, and 3= flat). We calculated means for each tree and transformed the means by natural logarithms. In order to quantify variation in leaf morphology within the hybrid zone, we used these $\log_e$-transformed means in a principal components analysis (PCA) based on the correlation matrix. We then tested for independence of gall densities and morphological variation of host plants by regressing $\log_e$-transformed gall densities against scores along the first two principal components.

RESULTS

Density Patterns Across Host Taxa

Multivariate analysis of variance indicated highly significant ($p < 0.001$) differences overall among host taxa in cynipid densities (Table 1). The contrasts suggested that most of this variation among host taxa was due to differences between the parental taxa (Contrast 1: $p < 0.001$). Hybrids as a group (*Q. undulata* and backcrosses) did not differ significantly from the parental taxa (Contrast 2: $p = 0.486$), but *Q. undulata* alone did so (Contrast 3: $p = 0.018$). These results are most consistent with a pattern of hybrid intermediacy (H_2) with cynipid densities exhibiting a gradient from *Q. grisea*, through the hybrids, to *Q. gambelii* (see below).

Univariate analyses of variance indicated that most of the multivariate differences among host taxa were due to variation in the densities of three species: MRG1, PLG, and RSG (Table 1). The midrib galler, MRG1, exhibited highly significant differences overall among host taxa ($p = 0.002$), between the parental taxa (Contrast 1), and between the parental taxa and *Q. undulata* (Contrast 3). Densities of MRG1 decreased from *Q. grisea* to *Q. undulata*, then increased

Table 1.—Comparison of cynipid densities among host taxa in a *Quercus grisea* x *Q. gambelii* hybrid zone. Contrast 1 compares parental hosts, Contrast 2 compares parental hosts versus all hybrids, and Contrast 3 compares parental hosts versus *Q. undulata*. Values for the univariate tests represent p-values.

Multivariate analysis of variance

Source	d.f.	F	p
Host taxa	32,300	2.19	<0.001
Contrast 1	8,810	4.25	<0.001
Contrast 2	8,810	0.94	0.486
Contrast 3	8,810	2.49	0.018

Univariate analyses of variance

Herbivore	Mean density (galls/100 lvs)	Host Taxa	Contrast 1	Contrast 2	Contrast 3
		p - values			
MRG1	5.79	0.002	0.008	0.122	0.027
STG	4.70	0.263	0.536	0.436	0.765
PLG	3.47	0.022	0.002	0.266	0.213
MRG2	1.97	0.730	0.771	0.948	0.394
LSG	1.89	0.146	0.388	0.590	0.051
RSG	1.66	0.020	0.049	0.842	0.229
MRG3	0.78	0.101	0.032	0.287	0.179
PTG	0.63	0.075	0.958	0.122	0.006
TOTAL	20.88	0.001	<0.001	0.413	0.449

to their highest values for *Q. gambelii* (Fig. 1). The pellet galler, PLG, also varied significantly among host taxa ($p = 0.022$), and differed significantly between the parental taxa (Contrast 1). It did not differ significantly with respect to Contrast 2 or Contrast 3. Densities of PLG described a gradient from *Q. grisea*, through the hybrids, to *Q. gambelii* (Fig. 1). Similarly, the red-spangle galler, RSG, differed significantly among host taxa ($p = 0.020$) and between the parental taxa (Contrast 1), but did not vary significantly with respect to the other contrasts. Densities of RSG largely exhibited a gradient from *Q. grisea* to *Q. gambelii*, although the highest densities were attained on the backcrosses to *Q. gambelii* (Fig. 1). There was no significant difference, however, between densities on these backcrosses and those on *Q. gambelii* ($F_{1,32} = 0.07$; $p = 0.797$).

The petiole galler, PTG, exhibited marginally significant ($p = 0.075$) differences among host taxa (Table 1). There were no significant differences between the parental taxa (Contrast 1) or between the parental taxa and the hybrids taken as a group (Contrast 2). There was, however, a significant difference between densities on the parental taxa with those on *Q. undulata* (Contrast 3). Densities of PTG described a triangular pattern across host taxa, increasing from *Q. grisea* to *Q. undulata*, then decreasing to *Q. gambelii* (Fig. 1).

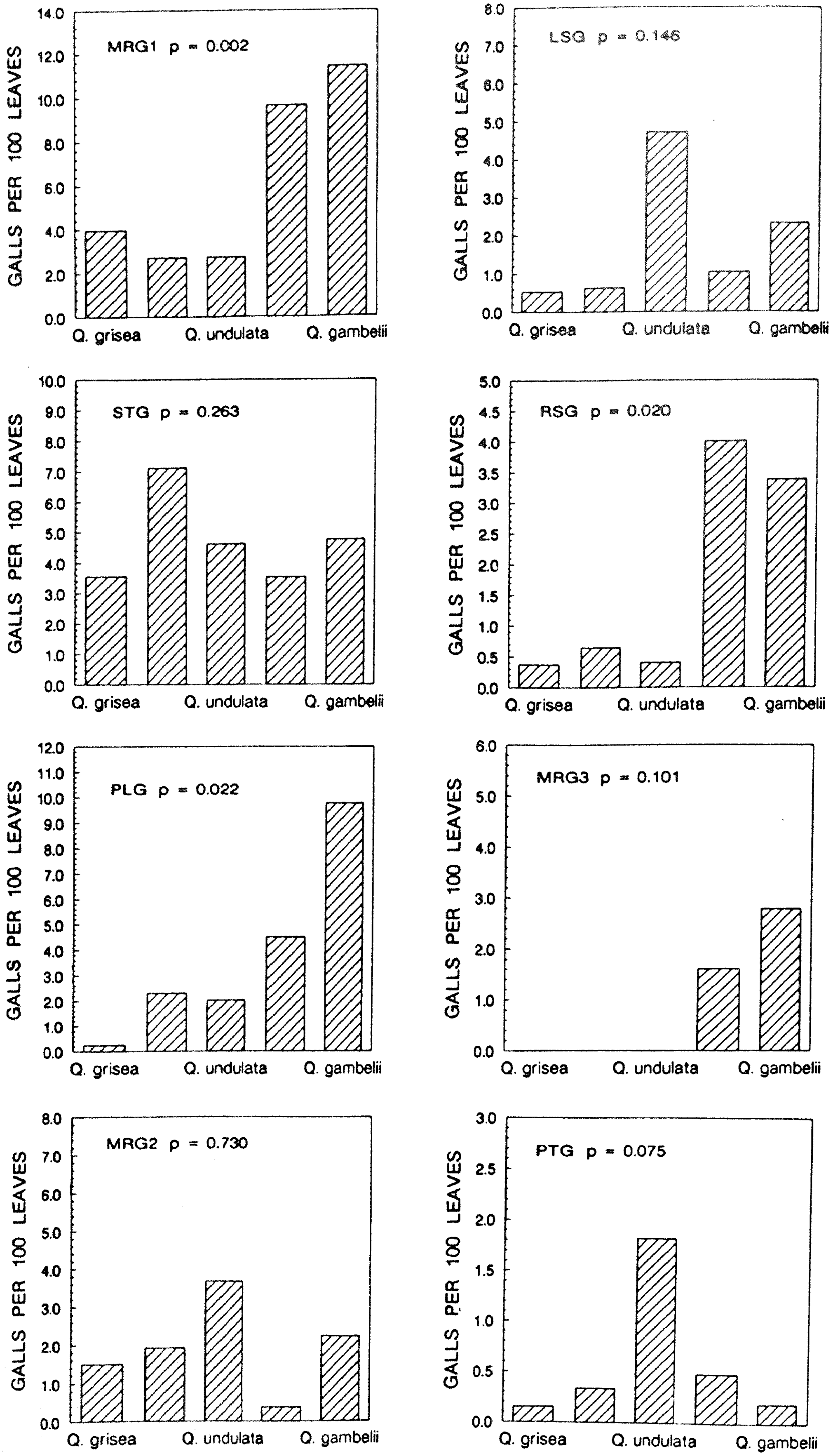


Figure 1.—Mean densities of cynipid gall wasps by host taxa in a *Quercus grisea* x *Q. gambelii* hybrid zone. P-values represent the results of tests for differences among host taxa as determined by analyses of variance.

The leaf splotch galler, LSG, did not differ significantly among host taxa (Table 1), between the parental taxa (Contrast 1), or between the parental taxa and hybrids taken as a group (Contrast 2). There was a marginally significant (p = 0.051) difference between densities on the parental taxa and those on *Q. undulata* (Contrast 3). Densities of LSG across host taxa approximated the triangular pattern exhibited by the petiole galler; densities increased from *Q. grisea* to *Q. undulata*, then generally decreased to *Q. gambelii* (Fig. 1).

The midrib galler, MRG3, did not vary significantly overall among host taxa (Table 1), but it did exhibit a significant difference between the parental taxa (Contrast 1). In fact, MRG3 was absent from *Q. grisea*, backcrosses to *Q. grisea*, and *Q. undulata* (Fig. 1). It attained the highest densities on *Q. gambelii*.

The stalk galler, STG, and the midrib galler, MRG2, did not differ significantly among host taxa, nor were any of the contrasts for these species significant (Table 1). Densities of STG and MRG2 showed no obvious patterns with respect to host taxa (Fig. 1).

Total herbivore load (TOTAL) varied significantly among host taxa (p = 0.001), and exhibited highly significant (p < 0.001) differences between the parental taxa (Table 1). Total herbivore load did not vary significantly with respect to Contrast 2 or Contrast 3. Total gall densities exhibited a gradient from *Q. grisea*, through the hybrids, to *Q. gambelii* (Fig. 2).

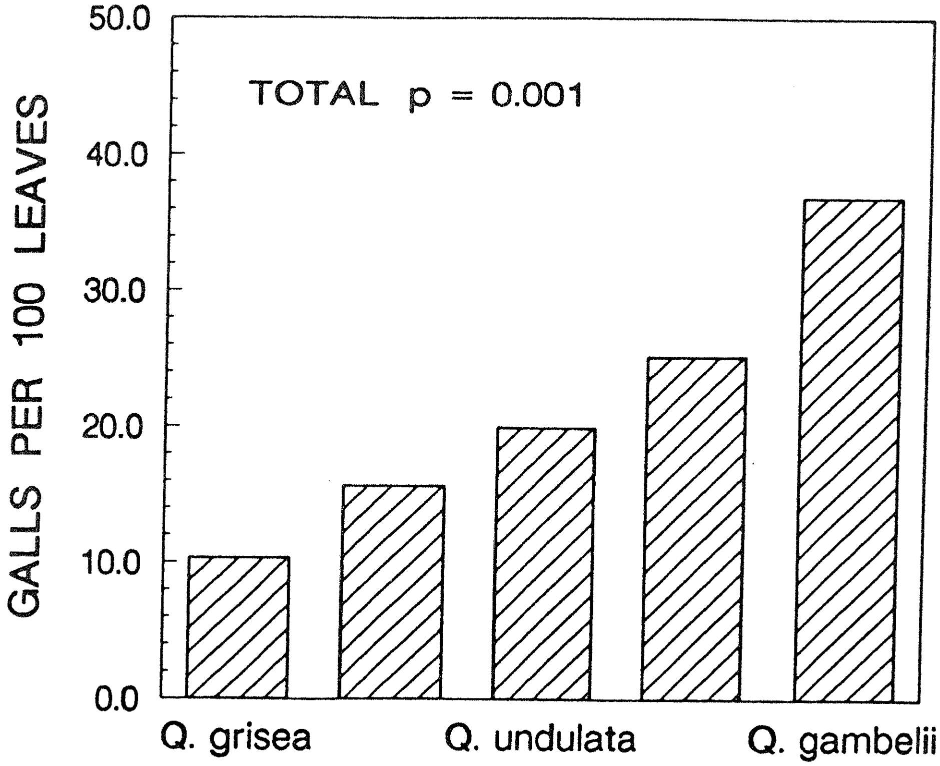


Figure 2.—Mean herbivore loads by host taxa in a *Quercus grisea* x *Q. gambelii* hybrid zone. The p-value corresponds to a test of overall differences among host taxa as determined by analysys of variance.

Covariation of Host Morphology and Gall Densities

Principal components analysis of host morphology produced two axes relevant to examining patterns of herbivory in the *Quercus grisea* x *Q. gambelii* hybrid zone. Collectively, the two axes explained approximately 73% of the variation in host morphology. The first axis explained approximately 63% of the variation and chiefly represented increasing leaf size and decreasing numbers of rays per leaf hair (Table 2). The axis roughly ordinated the trees from *Q.*

Table 2.—Principal components analysis of leaf characteristics in a *Quercus grisea* x *Q. gambelii* hybrid zone. Values associated with variables are factor coefficients. Upper-surface characters are designated by (us), lower-surface characters by (ls).

Variable	PC1	PC2
Perimeter	0.964	-0.064
Lobe Depth	0.942	0.161
Area	0.928	-0.047
Width	0.922	0.007
Rays/Hair (us)	-0.892	0.181
Color	0.849	-0.157
Rays/Hair (ls)	-0.844	0.148
Hair Angle	-0.814	0.170
Length	0.772	-0.085
Number of Lobes	0.728	0.515
Petiole Length	0.726	-0.278
Hair Density (ls)	0.618	0.422
Hair Density (us)	0.519	0.590
Mucro Length	-0.263	0.638
Eigenvalue	8.79	1.42
Variance Explained (%)	62.79	10.18

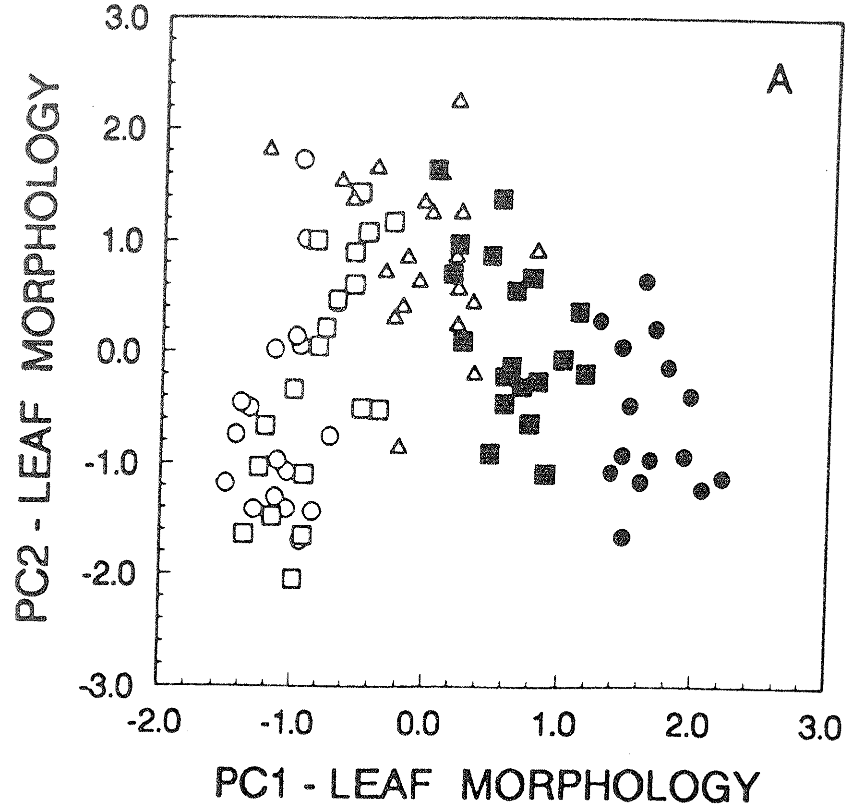
grisea, through the hybrids, to *Q. gambelii* (Fig. 3A). The second axis accounted for approximately 10% of the variation in host morphology, and primarily corresponded to increasing mucro length, hair density, and numbers of lobes. The axis largely represented a gradient from the parental taxa (low scores), through the backcrosses, to *Q. undulata* (high scores).

There was significant positive covariation between cynipid densities at the community level (represented by the first principal component based on $\log_e$-transformed densities) and host morphology as represented by the first principal component described above (Fig. 3b). Cynipid densities significantly covaried with the gradient of host morphologies - lowest on *Q. grisea*, intermediate on hybrids, and highest on *Q. gambelii.*

At the species level, four species (MRG1, PLG, RSG, and MRG3) exhibited significant positive linear relationships with the first principal component of host morphology (Table 3). Only two species, MRG1 and PTG, were significantly related to the second principal component of host morphology, which largely represented a gradient from the parental hosts to *Q. undulata.* The midrib galler, MRG1, was related inversely to the second principal component, while the petiole galler, PTG, exhibited a positive linear relationship. Densities of the remaining three species (STG, MRG2, and LSG) were statistically independent of host morphology as represented by the first two principal components.

DISCUSSION

Patterns of cynipid densities at the community level are most consistent with the hypothesis of hybrid intermediacy (H_2). There is significant positive covariation between the set of cynipid densities and the first principal component of host morphology. This first principal component largely represents a gradient of host morphologies from *Quercus grisea*, through the intermediate forms, to *Q. gambelii*. In addition, total herbivore load (TOTAL) differs significantly among host taxa and exhibits an obvious gradient from *Q. grisea* to *Q. gambelii.* These results are consistent with those reported by Aguilar and Boecklen (1992) for leaf-mining moths and gall-forming wasps in a distinct *Q. grisea* x *Q. gambelii* hybrid zone.



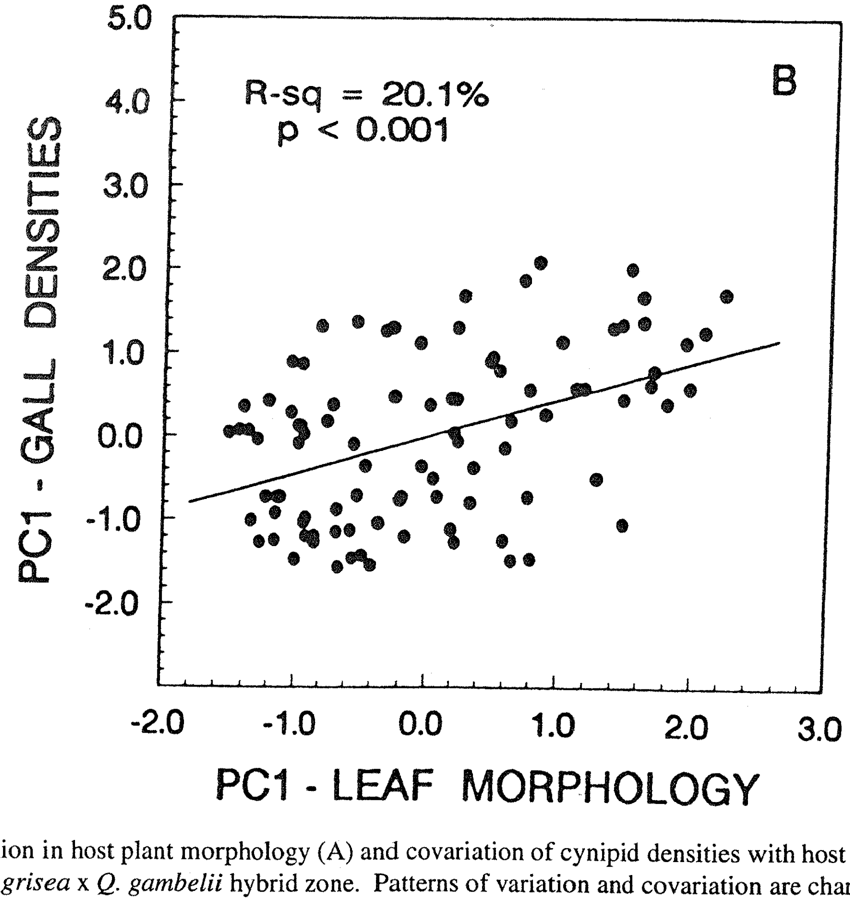


Figure 3.—Variation in host plant morphology (A) and covariation of cynipid densities with host plant morphology (B) in a *Quercus grisea* x *Q. gambelii* hybrid zone. Patterns of variation and covariation are characterized by principal components analysis. For (A), open circles represent *Q. grisea*, open squares backcrosses to *Q. grisea*, triangles *Q. undulata*, closed squares backcrosses to *Q. gambelii*, and closed circles *Q. gambelii*.

Table 3.—Relationship between cynipid densities and host morphology in a *Quercus grisea* x *Q. gambelii* hybrid zone. Host morphology is represented by the first two principal components based on the correlation matrix of 16 macro- and micro-anatomical characters (see text for details). The contribution of each principal component (PC1 and PC2) is given by the significance of a partial F test in multiple linear regression analysis. Analysis is based on $\log_e$-transformed cynipid densities.

Taxa	PC1	PC2	R^2 (%)
MRG1	<0.001	0.027	22.1
STG	0.353	0.116	3.6
PLG	0.001	0.392	11.7
MRG2	0.973	0.467	0.6
LSG	0.466	0.314	1.7
RSG	0.049	0.855	4.3
MRG3	0.001	0.198	12.8
PTG	0.844	0.037	4.8

At the species level, all four hypotheses have empirical support (Table 4). Densities of the stalk galler, STG, and the midrib galler, MRG2, support the null hypothesis (H_0) as they exhibit no significant pattern with respect to host taxa. The hypothesis of hybrid susceptibility (H_1) is supported by densities patterns of the petiole galler, PTG, and is supported weakly by those of the leaf splotch galler, LSG. The critical evidence that argues for hypotheses H_1 for these species are the significant differences for Contrast 3, and in the case of PTG, the significant positive relationship with the second principal component of host morphology. Densities of the pellet galler (PLG), red-spangle galler (RSG), and midrib galler (MRG3) are most consistent with a hypothesis of hybrid intermediacy (H_2). All three species exhibit a gradient of densities across host taxa and their densities covary positively (and significantly) with the first principal component of host morphology. Finally, the hypothesis of hybrid resistance (H_3) is supported by the density pattern of the midrib galler, MRG1. The critical evidence here is the significant effect for Contrast 3 and the significant inverse relationship with the second principal component of host morphology.

Table 4.—Hypotheses supported by the density patterns of cynipid wasps in a *Quercus grisea* x *Q. gambelii* hybrid zone. The category Total represents total herbivore load.

Taxa	Hypothesis supported
MRG1	H_3: Hybrids Resistant
STG	H_0: No Differences
PLG	H_2: Hybrids Intermediate
MRG2	H_0: No Differences
LSG	H_1: Hybrids Susceptible
RSG	H_2: Hybrids Intermediate
MRG3	H_2: Hybrids Intermediate
PTG	H_1: Hybrids Susceptible
Total	H_2: Hybrids Intermediate

These results strongly suggest that there is no universal pattern regarding patterns of herbivory in host plant hybrid zones and that earlier attempts at generalization (i.e. Whitham 1989) may be premature. Not only do case studies on distinct host plant systems yield mixed results (see above), but as demonstrated in this study, herbivores within the same hybrid zone can respond quite differently across host taxa (see also Roskam and Van Uffelen 1981). Floate and Whitham (1993) have attempted to discount studies that have failed to conform to a general pattern, claiming that in such studies "...different categories of hybrids are not usually distinguished even though their susceptibilities to herbivores may be very different." This claim is simply erroneous as there are several studies that have considered hybrids as multiple categories (e.g. Aguilar and Boecklen 1992, Paige and Capman 1993) or have considered hybrids as a continuum (Manley and Fowler 1969, Roskam and Van Uffelen 1981, Aguilar and Boecklen 1992). Of course, it is hard to argue against fine-level analyses in studies of plant-herbivore interactions in host hybrid zones given that Whitham's (1989) original description of hybrid susceptibility in a cottonwood contact zone was largely contradicted following detailed genetic analysis (see Paige and Capman 1993).

Patterns of parasite distributions in hybrid zones involving other host-parasite systems have also yielded mixed results. For example, Dupont and Crivelli (1988) reported higher densities of gill parasites in a hybrid cyprinid when compared to parental taxa, while Le Brun *et al.* (1992) observed a pattern of hybrid intermediacy in a *Barbus barbus* x *B. meridionalis* species complex. Sage *et al.* (1986) reported that densities of intestinal parasites in hybrid mice were higher than those in the parental taxa (see also Moulia *et al.* 1991). In contrast, Heaney and Timm (1985) observed that hybrid pocket gophers (*Geomys bursarius* x *G. lutescens*) had significantly fewer parasitic lice than did parental hosts.

The development of a general theory on the effects of host hybridization on the susceptibility to parasites awaits the resolution of two major questions. The first is, "Which of the competing hypotheses is the most prevalent in nature?" The second is, "What are the factors that determine which pattern is likely to obtain for a given host hybrid zone?" Boecklen and Spellenberg (1990) outline several factors that may be important in understanding patterns of parasite loads in host hybrid zones. These include the structure of the hybrid zone itself, taxonomic relationships of the parental hosts, morphological relationships of the parental hosts, the relative of importance of host defense versus parasite ovipostional cues, and the autecologies of the parasites. Clearly, the development of a general theory will require a larger compendium of case studies than now exists. We hope that the results reported here will contribute to that end.

ACKNOWLEDGMENTS

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GALL-FORMING INSECTS CONCENTRATE ON HYBRID PHENOTYPES OF EUCALYPTUS

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Abstract. We examined distributions of 33 gall forming insect species on parent species and three hybrid phenotypes in two *Eucalyptus* hybrid zones in Australia. Variation in insect abundance among hybrid classes was greater than variation between species suggesting that hybrid zones are sites of dynamic interactions between plants and herbivores. For instance, of 25 galling species in Victoria, 52% showed significant differences in abundance among hybrid classes, whereas only 24% differed between pure host species. While some components of hybrid use were very predictable, others were not. Based on galler use of pure species, we could accurately predict which hybrid phenotype would be most used. Our data show that most gall species concentrate on the hybrid class that is most similar to the parent species on which it is most abundant. However, species related taxonomically or by feeding guild did not exhibit consistent responses to hybrid and parent hosts. Thus pooling either hybrid classes or insect species for statistical analysis may mask underlying patterns. Overall, galler responses to three hybrid phenotypes are consistent with the hypothesis that plant hybrid zones and especially backcross hybrids are centers of insect species richness and abundance. Furthermore, galler response to hybrid plants suggests that the narrow host specificity characteristic of gallers may be less strongly influenced by plant developmental processes than generally thought.

Our observations support the hypothesis that genetic differences among host plants in hybrid zones underly patterns of insect host use. They also suggest that other mechanisms might be involved. Hybrid zone studies may have much to tell us about the ecology and evolution of plant-herbivore interactions.

Key words: plant hybrid zones, galls, Eucalyptus, plant stress, hybrid breakdown, phenotypic affinity hypothesis, host specificity hypothesis.

INTRODUCTION

The genetic variation present in natural plant hybrid swarms and its implications for the associated insect community has been an active area of research since Whitham (1989) reported extraordinarily high densities of a gall-aphid on hybrids of two species of *Populus* (Paige *et al.* 1990, Boecklen and Spellenberg 1990, Aguilar and Boecklen 1992, Floate *et al.* 1993, Paige and Capman 1993, Floate and Whitham 1993, Whitham *et al.* 1991, Fritz *et al.* 1994, Erickson *et al.* 1993, Martinsen and Whitham 1994).

Whitham (1989) proposed that hybrids may be less resistant to phytophages than parents because co-adapted gene complexes for resistance in the parent species can be disrupted in hybrids. The presence of highly susceptible individuals could have important implications for understanding the ecology and evolution of plant-insect interactions. For example, relaxed selection on susceptible hosts may act as ecological and/or evolutionary traps for phytophages that could be important in pest management (Whitham 1989). Conversely, for non-pest species they could provide important habitats for insect conservation (Whitham *et al.* 1991). Furthermore, the presence of hybrid intermediates could affect race formation in insects (Moran and Whitham 1988) and/or facilitate the evolution of host shifts between plant species (Floate and Whitham 1993). So few studies have examined plant-herbivore interactions in diverse hybridizing systems that general patterns, if they exist, are not yet known.

We examined the generality of Whitham's results by determining host-use patterns of gall-forming insects in hybrid zones of *Eucalyptus* (Myrtaceae), the species-rich (>500) genus of evergreen trees that dominates Australian forests (Pryor and Johnson 1971). Because eucalypts hybridize readily (Griffith *et al.* 1988), support a rich insect fauna (Morrow 1977, CSIRO 1990), and have an evolutionary history very different from northern hemisphere systems (White 1986), they provide an ideal contrast to the few other systems that have been studied. This study supports the hypothesis that hybrid zones are centers of insect abundance. The communities of gall-forming species on hybrids were significantly richer in species, and population densities were significantly higher, than on co-occurring pure parent species.

We also addressed several other hypotheses that try to probe underlying patterns and account for the greater abundance of phytophages on *Eucalyptus* hybrids. First, we examined the phenotypic affinity hypothesis which states that phytophages, especially host specialists, will be concentrated on the hybrid phenotype most similar to the preferred" parent species (Whitham *et al.* 1994). Although our studies do not experimentally address host choice or suvivorship, our observations of the distributions of 33 gall forming insects are consistent with this hypothesis. Thus, it appears that knowledge of an insect's abundance on pure species allows one to predict the hybrid phenotype on which it will be most abundant.

We discuss the implications of high gall densities and species numbers in hybrid zones for the two major hypotheses that propose an explanation for these results. Our data largely support the genetic hypothesis which posits that differences in host use are responses to genetic differences between parent and hybrid genotypes. The stress hypothesis argues that increased host use occurs because hybrid zones experience greater environmental stress which makes trees more susceptible to phytophages.

Finally, we examine the hypothesis that the extreme host specialization characteristic of gall-forming insects (e.g. Craig *et al.* 1993, Dodson 1991, Abrahamson *et al.* 1989) is imposed by the complex manipulations required for gall formation. Gallers must orchestrate plant morphogenesis to produce an abnormal plant growth of precise size, shape and tissue organization (e.g. Wool 1984, Shorthouse and Rohfritsch 1992, Weis *et al.* 1988) and control the within-plant movement of assimilates (Dreger-Jauffret and Shorthouse 1992, Larson and Whitham 1991). Failure of the plant to react results in death of the galler (e.g. Price *et al.* 1987).

This specificity hypothesis predicts that gallers should be unable to induce viable galls on plants that differ even slightly from their host species, which should include hybrids. In contrast to this prediction, gallers were most abundant on hybrids. This suggests that control of gall growth and differentiation does not by itself impose constraints as narrow as studies of host race development in galling insects have suggested.

METHODS

Plant and Insect Classification

We examined the gall-forming insect fauna associated with natural hybrid swarms of *Eucalyptus* in Victoria (*E. obliqua x E. baxteri*) and in New South Wales (*E. caliginosa x E. stellulata*), Australia. At each site, the parent species had distinctive morphological traits that facilitated their identification and the subjective division of hybrids into three phenotypic classes, one intermediate between the parent phenotypes (H), and two backcross hybrid phenotypes each intermediate between H and one of the parent phenotypes. Although morphology is not a foolproof estimator of genotype (Paige and Capman 1993), it is likely to be reasonably accurate (Fritz *et al.* 1994). Moreover, if morphology is not a good indicator of genotype, then if would bias against finding differences among hybrid classes since multiple genotypes might have the same phenotype. The method is consequently a conservative one.

In Victoria, we traversed the hybrid zone several times, assigning trees with accessible canopies to one of the five phenotypic classes on the basis of leaf and seed capsule characteristics. Up to 15 trees per class were located throughout the hybrid zone. Our subjective field classification was refined (several trees were reclassified) and the continuous nature of the variation in the hybrid zone was quantified by calculating a hybrid index score for each tree sampled. The hybrid index is a discriminant function calculated to differentiate pure stand samples of each parent species. The analysis was based on seven morphological traits of the seed capsules: peduncle length, pedicel length, capsule maximum width, capsule length/width ratio, capsule disc width/fruit width ratio, capsule shape, angle of disc. The scores on this discriminant function were then calculated for the hybrid zone trees and the discriminant function rescaled so that the pure parent stand samples had mean scores of 0 or 1 (procedure detailed in Potts and Reid 1985).

At the New South Wales site, trees were assigned to phenotypic classes based on prior studies of the zones (J. B. Williams, unpublished). A hybrid index was not calculated for these trees.

At both sites, we censused galls induced by insects in the orders Homoptera, Diptera and Hymenoptera. The insect that induced the gall could not be identified to species in many cases because the insect was immature, the insect had emerged or a taxonomic study of the group has not been made. However, taxonomists confirmed that the structures were likely to have been caused by different species.

Field Sites

Point Addis: South of Melbourne, Victoria, we examined the gall fauna in a natural hybrid swarm of *E. obliqua* L'Herit. and *E. baxteri* (Benth.) Maiden et Blakely and nearby pure stands of each parent species. The narrow, 1 km long hybrid zone parallels a road running along a flat ridge to Point Addis. All five phenotypes occur throughout the hybrid zone, but individuals of the *E. obliqua* backcross phenotype (OH) are concentrated in the seaward half of the zone while trees of the *E. baxteri* backcross phenotype (BH) are concentrated in the inland two thirds. The pure *E. baxteri* and *E. obliqua* stands are near the inland edge of the hybrid zone.

In each of the pure parental stands we censused 15 trees. In the hybrid zone we censused 66 trees - 17 *E. baxteri* (B), 16 *E. obliqua* (O), 4 intermediate phenotypes (H), 13 backcross phenotypes resembling *E. baxteri* (BH) and 16 resembling *E. obliqua* (OH). The H phenotype was uncommon.

We censused galls at all canopy heights using ladders. In the hybrid zone, we censused 22 species by collecting all galled leaves that could be found during a 12-minute collection period. These leaves were later sorted in the laboratory. The three most abundant gall species in the hybrid and pure stands were individually censused by counting all galls that could be seen during a two-minute period by two observers. These three gall species were censused in both the hybrid zone and pure parent stands.

Census data were standardized into counts per minute and log-transformed to normalize the data. Analyses of variance followed by least squares significant differences (if the former was significant at $P<0.05$) were employed to examine potential population differences between the five phenotypic classes. We also calculated the relative abundance values for each tree by standardizing the log-transformed counts per minute for each taxa to have a total standard deviation of 1 and a mean value of 0.5 across the 25 taxa censused. We then summed these standardized values for each tree. This standardization prevented common species from swamping the abundances of rare species, thereby allowing us to examine community-wide patterns.

To examine potential for galler variation in use of specific hybrid classes, for each gall species, we noted which parent species had greater gall densities. We then determined which hybrid phenotype was used most and analyzed with a X^2 test for homogeneity to determine if the distribution on a pure parent species predicted the most used hybrid class. Because F_1 hybrid phenotypes were rare, they were not used in this analysis. We also censused seed capsules on the 96 trees in both pure and hybrid zone stands by counting all capsules seen in a two-minute period. The number of seed capsules was used as an indicator of plant fitness.

Guyra: In rolling hills northeast of Armidale, New South Wales, we studied a hybrid swarm in mature woodland. *E. caliginosa* Blakely et McKie occupies the drier, less fertile soils of the middle and upper slopes while *E. stellulata* Sieb. ex DC. is found in the vales and lower slopes where soils are deeper, moister and more fertile. Both sites have an altitudinal range of <100 meters. The hybrid swarm, comprised of parents and hybrids, occupies a 30 meter wide altitudinal band between pure stands of the parent species.

In the hybrid zone we sampled 8 species of stem gallers by cutting a single 1 - 2 cm diameter branch from the canopy of each tree using a 6 meter pole pruner. The branch was bagged and later examined in the laboratory. Because both species were at different stages of abscising their leaves, we could not rely on the accuracy of leaf gall analyses and we restricted our study to stem galling species. Data were standardized to galls per twig by dividing counts for each species by the number of previous season twigs on the branch. The number of twigs varied from 15 to 93 (47±20 s.d.). Data were analyzed as described for Point Addis.

We sampled 75 trees in the hybrid zone, 15 *E. caliginosa* phenotypes (C), 20 *E. stellulata* phenotypes (S), 14 trees intermediate between parent phenotypes (H), 20 hybrids with a stronger resemblance to *E. caliginosa* (CH) and 6 hybrids with a stronger resemblance to *E. stellulata* (SH). The *E. stellulata* backcross (SH) phenotype was uncommon. We did not analyze gall distribution among parent and hybrid phenotype because of the small sample size of galling species.

RESULTS

Identification of Phenotypes and Plant Performance

Point Addis: Hybrid indices based on 7 capsule characteristics show no overlap between *E. obliqua* and *E. baxteri* growing in pure stands (Fig. 1). But in the hybrid zone the hybrid indices show trees indistinguishable from the pure parent phenotypes as well as a full range of intermediate phenotypes (Fig. 1).

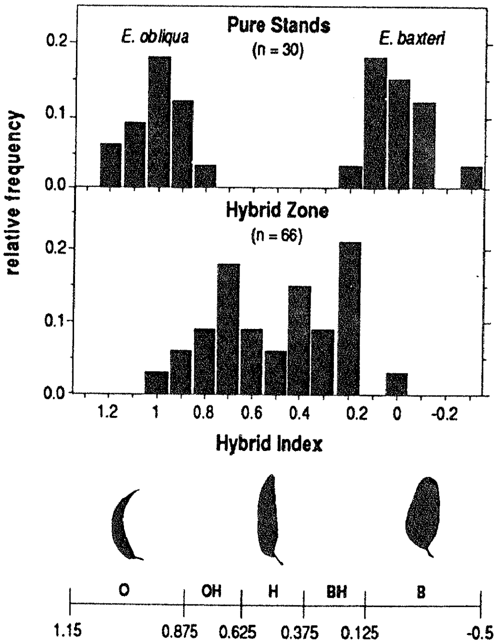

Figure 1.—Hybrid indices for trees in pure *E. obliqua* and pure *E. baxteri* stands (top panel) exhibit no overlap in morphological traits while trees in the hybrid zone (bottom panel) exhibit a continuum of intermediate and pure traits. Bottom line marks the boundaries of phenotypic classes used in our analyses (pure *E. obliqua* phenotype = O; *E. obliqua* backcross phenotype = OH; F_1 intermediate phenotype = H; *E. baxteri* backcross phenotype = BH; pure *E. baxteri* phenotype = B). Hybrid indices are based on 7 capsule characters (see text); however, leaf silhouettes are used here to show differences in phenotypic classes because differences in capsule characteristics are difficult to illustrate.

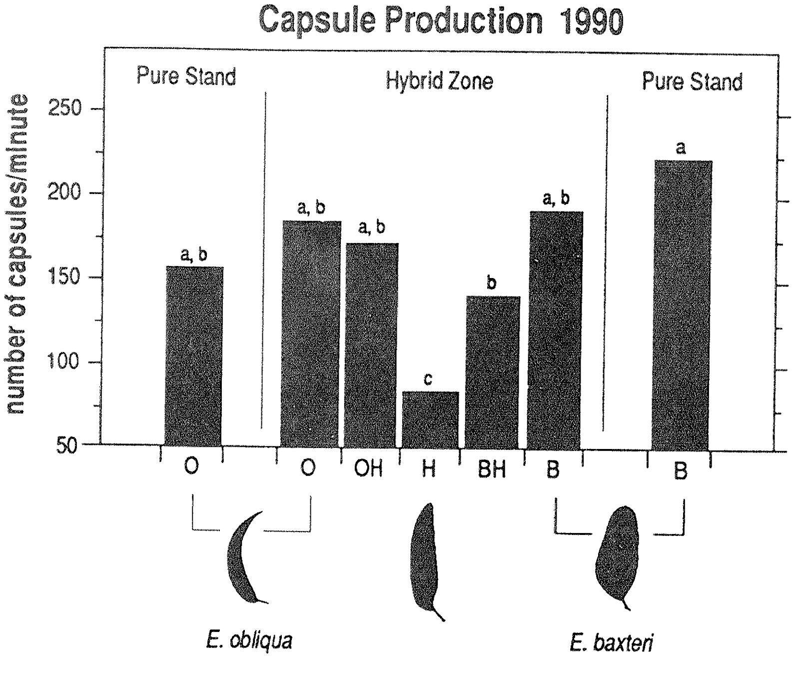

Figure 2.—Average number of seed capsules are shown for each of three hybrid and two parent phenotypes in the *E. obliqua* x *E. baxteri* hybrid zone, and for the parent species in pure stands. Analyses show that the F_1 phenotype (H) produces significantly fewer capsules than other phenotypes. O, OH, H, BH, and B as in Figure 1. Changes in letters at the top of each bar indicate significant differences determined by least significant differences ($P<0.05$). Figures 2-6 employ the same statistical methodology to make multiple comparisons.

Capsule counts show that the F_1 hybrid phenotype (H) produced significantly ($P<0.05$) fewer capsules than the other phenotypes in the hybrid zone (Fig. 2). Nevertheless, the continuum of intermediate forms (Fig. 1) argues that the F_1's, despite possibly suffering reduced fitness, are capable of backcrossing with parental species.

Guyna: *E. caliginosa* (C) is readily distinguished from *E. stellulata* (S) by its thick fibrous bark and the prominent midvein and oblique base of its broadly lanceolate adult leaves. In contrast, the bark of *E. stellulata* is smooth and its ovate adult leaves have "lateral" veins parallel to the midvein. Lateral veins of the F_1 hybrid phenotypes (H) have broader angles and a more pronounced midvein than *E. stellulata* (illustrated in Fig. 6) and fibrous bark extends to small branches and thereafter is smooth. The backcross phenotypes are intermediate between H and the relevant parent phenotype.

Patterns of Parent and Hybrid Use By Individual Galling Species

Point Addis: Two general patterns of phenotype use were found among the 25 gall-forming species. 1) Concentrations on *E. obliqua* and *E. obliqua* backcrosses: The range of variation in this pattern is illustrated by two examples. An unidentified wasp (Hymenoptera) forms smooth reddish spherical leaf galls about 5 mm in diameter (Fig. 3A). This galler was restricted to *E. obliqua* (O) and its backcross phenotype (OH) and was about 50% more abundant on the backcrosses (OH). A pocket gall formed on leaves by the psyllid *Glycaspis ?cameloides* (Homoptera: Psylloidea) was found on all phenotypes but was twice as abundant on the backcross *E. obliqua* phenotype (OH) (Fig. 3B). Other species with this pattern of distribution were found in the Hymenoptera, Diptera and Homoptera and included both stem and leaf gallers. 2) Concentrations on *E. baxteri* (B) and *E. baxteri* backcrosses: *Schedotrioza serrata* sp. n. (Homoptera:

Psylloidea) forms a distinctive large green gall spotted with brown, scale-like, dry woody tissue. It was not uncommon to see >60 of these galls in a two-minute census. *S. serrata* was equally common on *E. baxteri* (B) and its backcrosses (BH) (Fig. 4A). An unidentified stem galler was present on all phenotypes but the *E. baxteri* backcross (BH) had about twice as many galls as *E. baxteri* (B) in the pure stand and about four times as many galls as *E. obliqua* (O) in the pure stand (Fig. 4B). As with the first pattern, species from three orders and leaf and stem gallers displayed this distribution pattern.

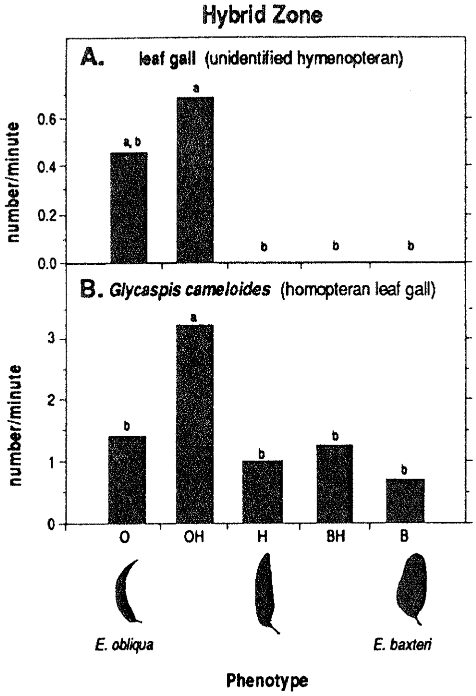

Figure 3.—Two examples illustrate gall species that are concentrated on *E. obliqua* and its closest hybrid phenotype. (A) shows the abundances of an unidentified wasp (Hymenoptera) restricted to *E. obliqua* (O) and its backcross phenotype (OH). (B) shows the distribution of *Glycaspis?cameloides* (Homoptera: Psylloidea) which is present on all phenotypes but significantly concentrated on the *E. obliqua* backcross phenotype (OH). O, OH, H, BH, and B as in Figure 1.

Species clustered by taxonomy, feeding guild, tissue galled, or morphological complexity of gall structure did not have similar patterns of host use.

Overall, the most common pattern of host use was for species to use all phenotypes but to be most abundant on one of the backcross phenotypes (Figs. 3B, 4B). It was less common for a species to use only one of the parent species, but when they did, their densities were similar on that parent and its backcross (Figs. 3A, 4A). No gall species was restricted to or significantly more abundant on a parent species (O or B) than on its backcross phenotype (OH or BH) and no species were concentrated on the intermediate phenotype (H).

Guyna: Gall species in the *E. caliginosa-E. stellulata* hybrid zone used all phenotypic classes and all species were four to eight times more common on hybrids. Species varied in the hybrid class most used; several were most abundant on the F_1 phenotype (H), others on the *E. caliginosa* backcrosses (CH), others on the *E. stellulata* backcrosses (SH).

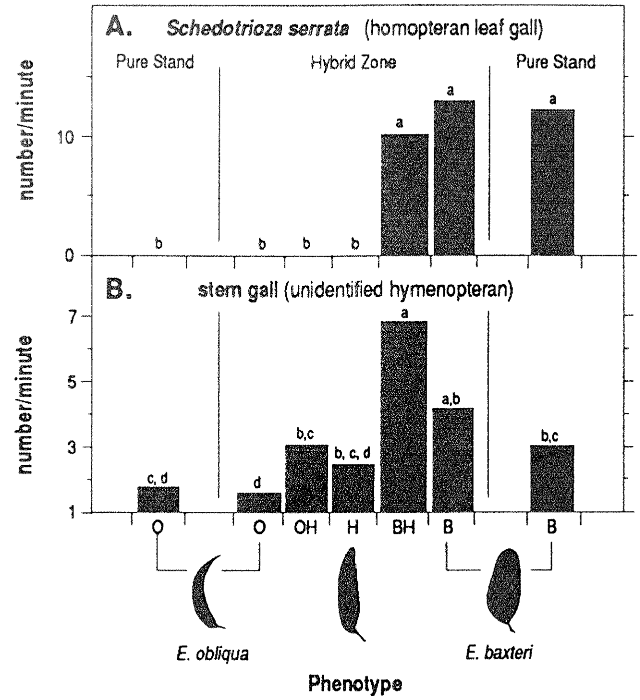

Figure 4.—Two examples illustrate gall species that are concentrated *E. baxteri* and its closest hybrid phenotype. (A) shows the abundances of *Schedotrioza serrata* (Homoptera: Psyllidae), a leaf galler restricted to *E. baxteri* (B) and its backcross phenotype (BH). (B) shows the distribution of an unidentified stem galler (Hymenoptera) present on all phenotypes but concentrated on the *E. baxteri* backcross phenotype (BH). O, OH, H, BH, and B as in Figure 1.

Community Responses of the Gall-Forming Fauna

Point Addis: Both species richness and relative abundance show that gall species concentrate on backcross phenotypes. In the hybrid zone, the number of gall-forming species on the average pure parent tree did not differ significantly between *E. obliqua* (O, $\bar{x} = 9.8 \pm 0.5$ s.e.) and *E. baxteri* (B, $\bar{x} = 9.0 \pm 0.5$). Neither parent supported as many species as *E. obliqua* backcrosses (OH, $\bar{x} = 11.7 \pm 0.5$) or *E. baxteri* backcrosses (BH, $\bar{x} = 10.7 \pm 0.6$) (Fig. 5A, Table 1). In addition to supporting more species, the average relative abundance of galls on trees of both *E. obliqua* backcrosses (OH, $\bar{x} = 17.3 \pm 1.2$) and *E. baxteri* backcrosses (BH, $\bar{x} = 15.7 \pm 1.3$) were significantly greater ($p < 0.01$) than on trees of pure *E. obliqua* (O, $\bar{x} = 10.5 \pm 1.2$), pure *E. baxteri* (B, $\bar{x} = 9.8 \pm 1.1$) and intermediate F_1 phenotypes (H, $\bar{x} = 6.9 \pm 2.4$) (Fig. 5B). For the three gall species censused in both pure and hybrid stands, the average relative abundance of the three gall species was not different for *E. obliqua* in pure and hybrid zones. But abundance on *E. baxteri* was significantly higher ($\bar{x} = 5.2 \pm 0.3$) in the hybrid zone than in the pure stand ($x = 3.5 \pm 0.3$).

Guyna: The same general patterns were observed at Guyna as at Point Addis, except there was marked asymmetry in the response with a bias toward phenotypes tending toward *E. caliginosa* in the hybrid zone. The average *E. caliginosa* backcross tree (CH) in the hybrid zone supported significantly more species ($\bar{x} = 4.0 \pm 0.3$) than any category except the F_1 phenotype (H, $\bar{x} = 3.6 \pm 0.3$) (Fig. 6A, Table 1). The relative abundance of galls was significantly higher on the hybrid phenotypes, particularly on *E. caliginosa* backcrosses (CH, $\bar{x} = 7.2 \pm 0.7$; H, $\bar{x} = 5.0 \pm 0.8$; SH, $\bar{x} = 3.5 \pm 1.3$) than on the pure *E. caliginosa* (C, $\bar{x} = 2.6 \pm 0.7$) or pure *E. stellulata* (S, $\bar{x} = 1.78 \pm 0.7$) (Fig. 6B).

Relationship Between Densities on Parent Species and Hybrid Phenotypes

Densities of gall forming species differed among hybrid classes significantly more often than they differed between the pure parent species. At Point Addis, 13 (52%) of the 25 species were significantly more abundant on one of

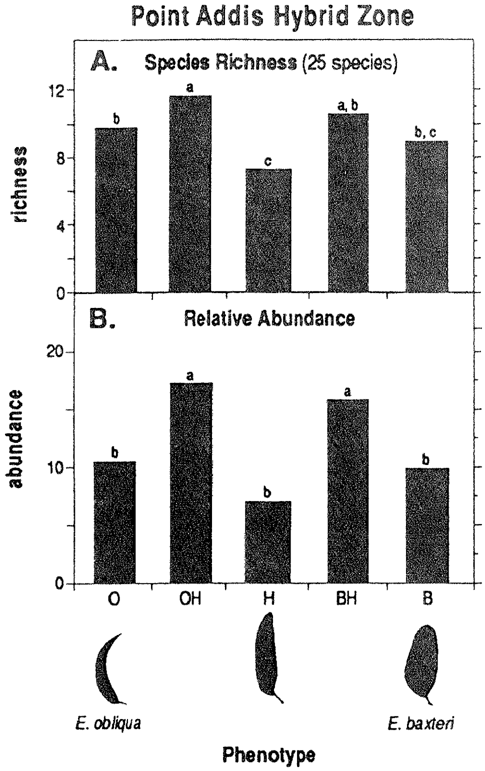

Figure 5.—Both species richness (A) and relative abundances (B) of 25 gall-forming species are greatest on backcross hybrids (OH and BH) in the *E. obliqua* x *E. baxteri* hybrid zone at Point Addis, Victoria. O, OH, H, BH, and B as in Figure 1.

Table 1.—ANOVA's for species richness and standardized abundances on two parent and three hybrid phenotypes in the community of gall-forming insect species at Point Addis and Guyna

POINT ADDIS

Species Richness:

Source	df	Mean Square	F Value	Pr > F
Phenotype	4	24.81	5.83	0.0005
Error	61	4.25		

Relative Abundance:

Source	df	Mean Square	F Value	Pr > F
Phenotype	4	203.93	9.12	0.0001
Error	61	22.37		

GUYNA

Species Richness:

Source	df	Mean Square	F Value	Pr > F
Phenotype	4	9.03	5.66	0.0005
Error	75	1.60		

Relative Abundance:

Source	df	Mean Square	F Value	Pr > F
Phenotype	4	95.36	9.91	0.0001
Error	75	9.62		

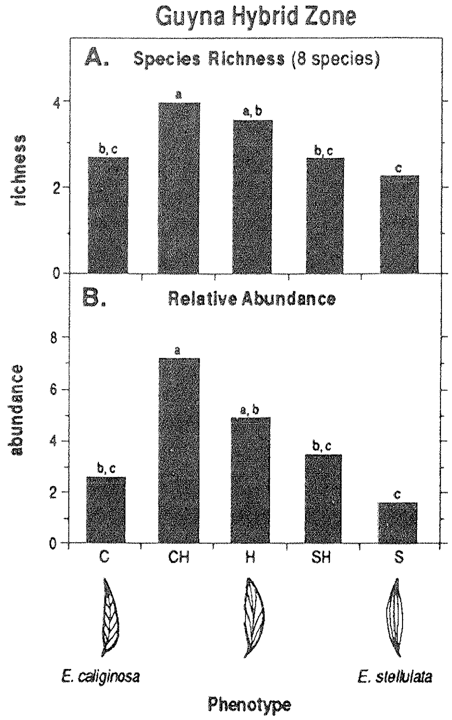

Figure 6.—Both species richness (A) and relative abundances (B) of 8 gall-forming species are greatest on the *E. caliginosa* backcross hybrids (CH) in the *E. caliginosa* x *E. stellulata* hybrid zone at Guyna, N.S.W. (pure *E. caliginosa* phenotype = C; *E. caliginosa* backcross phenotype = CH; F_1 intermediate phenotype = H; *E. stellulata* backcross phenotype = SH; pure *E. stellulata* backcross phenotype = S).

the hybrid classes than other hybrid classes, whereas only 6 (24%) of the 25 species were significantly more abundant on one of the pure parent species than the other (X^2=5.333, df=1, $P<0.05$). At Guyna, four of eight taxa were significantly more abundant on one of the three hybrid phenotypes while none were significantly more abundant on one parent than on the other.

According to the "phenotypic affinity hypothesis", densities of a gall species should be highest on the backcross class most similar to the parent species with the highest density of that gall. Thus at Point Addis the density of a galler should be higher on the *E. obliqua* backcross phenotype (OH) when its density is higher on the pure *E. obliqua* (O) than on pure *E. baxteri* (B). Similarly, a galler's density should be higher on the backcross phenotype to *E. baxteri* (BH) when it is more abundant on pure *E. baxteri* (B) than on pure *E. obliqua* (O). Our data confirm this prediction; 20 of the 25 gallers (80%) were more abundant on the backcross phenotype most closely resembling the phenotype of the pure parent on which they were most abundant (X^2=9.000, df=1, $P<0.01$).

At Guyna, the density of a gall species should be higher on the *E. caliginosa* backcross (CH) phenotype when its density is higher on pure *E. caliginosa* (C) and higher on the *E. stellulata* backcross (SH) phenotype when it is most abundant on pure *E. stellulata* (S). This prediction was true for six of the gallers (75%). Although X^2 analyses were not performed due to the small number of species, the trend is as predicted. Thus, regardless of which parent species a gall species used most, we could accurately predict which hybrid phenotype would support the greatest gall densities.

DISCUSSION

Gall-forming species responded as individuals to the phenotype of their *Eucalyptus* hosts; closely related species and members of the same feeding guild were no more likely to have similar responses than were species in different orders or guilds. The same has been found in other hybrid zone studies where responses of individual phytophagous species are reported, namely, *E. amygdalina x E. risdonii* (Whitham *et al.* 1991, 1994), *Eucalyptus* *melanophloia x E. crebra, E. populnea x E. crebra* (Drake 1981), *Populus angustifolia x P. fremontii* (Whitham 1989, Floate and Whitham 1993, Floate *et al.* 1993), *Salix sericea x S. eriociphala* (Fritz *et al.* 1994). Taxa in these studies include stem, leaf and bud gallers, leaf tiers and miners, stem borers, leaf chewers, mites and fungi.

Although responses differed among species, overall, gall-formers at Point Addis and Guyna were more abundant on a hybrid phenotype than on either parent species. This was also the case for insects censused in the *Populus* hybrid zone and the *E. amygdalina x E. risdonii* studies cited above. In contrast to the above studies, in two hybrid zones of *Quercus*, herbivore richness and total insect abundance was lower on hybrids than parents (Boecklen and Spellenberg 1990, Aguilar and Boecklen 1992). They, however, give data only for feeding guilds, and the first study did not discriminate among different types of hybrids. Based on the findings of the present study and Whitham *et al.* (1994), combining species on the assumption that similarity of feeding mode will predict responses to host phenotype could potentially obscure dynamic differences.

These results argue, first, that the term "hybrid" is too vague to portray accurately the diversity of herbivore-plant interactions in hybrid zones; there are at least several hybrid classes to which herbivores may response. Second, they suggest that the genetic variation among hybrid phenotypes is as great if not greater than the variation between parent species. Third, they show that species responses to hybrid classes should be examined individually. The guild concept, whereby species are grouped if they exploit the same class of resources in a similar way (Root 1967), has been a powerful tool for generalizing about nature; but in hybrid zone studies it may mask patterns.

Mechanistic Explanations For Host Use Patterns

Two primary mechanisms may explain the high densities of phytophages on hybrids. The genetics hypothesis argues that plant resistance has a strong genetic basis. There is strong evidence for the existence of both simple and multigenic variation in resistance of plants (Kennedy and Barbour 1992, Fritz and Simms 1992); simple resistance traits may be lost or gained and multigenic resistance may be disrupted by hybridization (Grant 1981).

Three lines of evidence support a genetic explanation for variation in the density of galls among phenotypes. First, in a common habitat, the hybrid zone, gall species have significantly different distributions on parent species and hybrids (14 of 25 taxa at Point Addis, 5 of 8 at Guyna). Second, hybrid phenotypes are not used equally by the phytophagous community; half of the species examined at both sites were significantly more abundant on one hybrid phenotype than another (13 of 25 taxa at Point Addis, 4 of 8 taxa at Guyna).

Third, based upon knowledge of herbivore use of the parent species, we were able to predict which hybrid phenotype would be most used. Gallers were predictably more abundant on the hybrid phenotype most resembling the parent on which they were most abundant, regardless of which parent this was. At both sites, ≥ 75% of the gallers examined exhibited this pattern which we conclude strongly supports the "phenotypic affinity hypothesis" (Whitham *et al.* 1994). Because all pure and hybrid phenotypes were growing in close proximity within the hybrid zone, site effects were minimal. Thus, we argue that in these two systems, galler selection of species and hybrid phenotypes is largely genetically based.

Additional support for the genetics hypothesis comes from the similarity of phytophage distributions in two very different hybrid systems, those of *Eucalyptus* and *Populus*. For instance, many *Eucalyptus* species have narrow geographic ranges associated with the distributions of particular microhabitat and edaphic conditions (Pryor 1976, Morrow 1977) whereas the geographic ranges of *Populus* species are very large (Eckenwalder 1984). Similarly, the hybrid zones of *Eucalyptus* tend to be frequent, small and interspersed in the forest mosaic while those of *Populus* can be very large (e.g. 13 km; Keim *et al.* 1989) and linear in shape due to the riparian habitat frequented by this genus. Even the patterns of introgression are different; the *Eucalyptus* in our studies appear to have bidirectional introgressions (i.e. F_1's backcross to both parents) while the *Populus* species studied to date have a unidirectional pattern of introgression (Keim *et al.* 1989).

The stress hypothesis predicts that abiotic stress increases plant quality and the performance of phytophages (White 1976; Mattson and Haack 1987a,b; Louda and Collinge 1992; reviewed in Waring and Cobb 1992). If the margins of species' geographical ranges coincide with their physiological limits, then hybrid zones, which occur at range margins, may experience more frequent or greater levels of stress than pure parent stands and should consequently support higher gall densities. Experimental and observational tests of the stress hypothesis give variable results (Larsson 1989, Waring and Cobb 1992). Galling species have been shown to perform best on hosts in arid, presumably stressful, habitats (Fernandes and Price 1991, Waring and Price 1990). Conversely, gall species often prefer and perform best on vigorous, presumably unstressed, hosts (Price *et al.* 1990, Price 1991, Rohfritsch and Shorthouse 1992).

Thus while our observations strongly support the genetics hypothesis, we can say little about the role played by stress. Common garden experiments in sites with different levels of stress are required to critically address both hypotheses. Additional hypotheses to explain variation in phytophage densities in hybrid zones are explored in Whitham (1994), Aguilar and Boecklen (1992), Paige and Capman (1993) and Fritz *et al.* (1994). It would be naive to assume that only one factor is involved in the production of this variation.

Galler Host Specificity

Plant resistance can be divided into factors that interfere with host discovery and recognition and post-discovery defenses that reduce feeding after discovery. There is no reason to assume that the effects of changes in discovery and recognition cues would differ in their effects on gall-forming vs. other phytophagous insects (Weis *et al.* 1988). But postdiscovery effects should differ between gallers and other plant consumers. Gallers must redirect the host's developmental processes to produce precise structures that will feed, shelter and later allow the insect to leave (Rohfritsch and Shorthouse 1982). The precision required for this manipulation is assumed to contribute substantially to the very narrow host ranges typical of gall-forming insects (e.g. Ananthakrishnan 1984, Weis and Abrahamson 1986, Weis *et al.* 1988, Anderson *et al.* 1989).

Changes in morphological attributes of hybrids (e.g. leaf thickness, cuticle surface, timing of shoot initiation), result from altered development patterns. It can be argued that such alterations would pose problems for gall induction if gall-formers are as closely adapted to their hosts as the available studies suggest (Anderson *et al.* 1989, Abrahamson *et al.* 1989, Craig *et al.* 1994, Dodson 1991). The best defense a plant can have against gallers is to fail to form a gall and this is the usual response when gallers oviposit on non-host species or races (Price *et al.* 1987).

Changes in plant development patterns should make it more difficult for a galler to manipulate the plant into forming a gall, be it simple or complex. It is consequently puzzling that responses of gall-forming species in this study have similar responses to hybrids as those reported for phytophagous insects that only consume their host, i.e. leaf miners, tiers and other chewers (Whitham *et al.* 1994). The increase in mean relative abundance on hybrid phenotypes at Point Addis and Guyna was not due to gallers being exceptionally successful on a few trees—they induced galls on an equal or larger proportion of trees in their "preferred" hybrid class than in their "preferred" parent species. The increased use of hybrids by gall species suggests that host location and recognition cues may signal a host even though a considerable portion of the hybrid genome is of a genome foreign to the insect. This further suggests that plant development pathways, or the insect stimulus manipulating them, are not as constraining as assumed.

It is clear from our studies that gall forming insects exhibit a strong response to hybridizing eucalypts. Because hybrids exhibit extreme genetic variability and produce unique genotypes not present in the pure species, these plant may provide the natural genetic experiments that allow us to understand both host selection and the elusive mechanisms responsible for gall development.

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VARIATION IN THE SUSCEPTIBILITY OF NORTH AMERICAN WHITE SPRUCE POPULATIONS TO THE GALL-FORMING ADELGID, ADELGES ABIETIS (HOMOPTERA: ADELGIDAE)

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Abstract. The eastern spruce gall adelgid, *Adelges abietis*, infested two white spruce, *Picea glauca*, range-wide provenance plantations in Michigan and Minnesota for more than 20 years. These chronic infestations permitted an assessment of the variation in adelgid susceptibility of 28 different spruce populations. Generally, the least susceptible populations came from Alaska, Manitoba, Minnesota, Montana, and western Ontario. On the other hand, the most susceptible populations came from eastern North America (i.e. east of 83° w. longitude), the Great Plains (South Dakota, Saskatchewan), and British Columbia. The most susceptible populations had both a higher percentage of attacked individuals and higher gall counts per infested plant. Spruce populations from Wisconsin, Michigan, and the Yukon were intermediate. *Pineus similis*, the ragged spruce gall adelgid, which occurred in abundance only at the Minnesota study site, showed a remarkably similar pattern of infestation. Data from three widely separated North American plantations showed that patterns of adelgid infestation among spruce populations were consistent, suggesting that the patterns are indeed real, and that there is no genotype by environment interaction effect on the expression of the innate plant/insect relationship.

Key words: host plant resistance, provenance variation, competition, introduced insect, Pineus similis.

INTRODUCTION

The eastern spruce gall adelgid, *Adelges abietis*, is one of the most common adelgids on spruce, *Picea* spp (Pinaceae), throughout the north temperate and boreal forests of the world. The insect is native to the Palaearctic, but was apparently introduced to North America sometime during the early 19th century (Wilford 1937, Plumb 1953). Since its introduction, it has spread over the continent and can be found on several species of American and introduced spruces. White spruce, *Picea glauca*, is its most common North American host, although it also occurs on Engelmann spruce, *P. engelmannii*, and Sitka spruce, *P. sitchensis*, in the west. In Europe, its most common host is *P. abies* and its close relatives.

The insect causes distinctive, spherical to pineapple-shaped galls to develop on its hosts, always at the base of a newly elongating shoot. The size and shape of the gall varies in relationship to the species of host, the individual tree, and the vigor of the attacked shoot. On white spruce, the galls are more or less spherical with a diameter of about 1.5 cm. Nearly fully formed needles emerge from the surface of the gall giving it a spiny appearance (Rose and Lindquist 1977). Because the galls are relatively small and woody, they can persist on the branches for many years, thereby making it possible to measure the long-term susceptibility of trees to the adelgid.

There is great variation among trees in their susceptibility to the adelgids: some having no galls at all, and others having hundreds. Susceptible and putative resistant trees are commonly found growing immediately adjacent to one another with no apparent changes in their susceptibility status over tens of years (Friend and Wilford 1933,Wilford 1937). Highly infested trees often have a brown, ragged appearance because of the negative impact of the adelgids on the development of the tree canopy and the death of needles on the attacked shoots. On most trees the injuries appear to be cosmetic and of little consequence to fitness, although there are occasional trees so badly infested that they cannot compete with their more resistant neighbors owing to their diminished canopy of actively photosynthesizing needles. To our knowledge, no one has measured the impact of gall adelgid infestations on tree growth and competitive ability, although Wilford (1937) reported that severely galled trees are usually smaller than their competitors.

The purpose of this study was to assess variation in susceptibility to adelgids among 28 widely separated populations of white spruce which spanned the entire transcontinental distribution of white spruce, from Labrador in the east to Alaska in the far west. Seeds were collected from these populations in the late 1950's by forest geneticists, and the seedlings from same were planted in more than fourteen replicate plantations across North America in the early 1960's. Canavera and DiGennaro (1979) were the first to study variation in adelgid susceptibility among these spruce populations in one of the replicate plantations on the Penobscot Experimental Forest in Maine. The study reported herein tested the generality of Canavera's and DiGennaro's conclusions that populations from eastern North America were most susceptible and those from the Great Lake States region and far western Canada were least susceptible.

METHODS

In 1987, we selected two widely separated (Isabella, Minnesota, and Wellston, Michigan) provenance plantations which had identical ages (29 years) and high survival rates. The plantation in Minnesota consisted of 10 complete blocks of the 28 populations, where each source was represented by a total of 40 trees, 4 per block. The plantation in Michigan consisted of 4 complete blocks, where each seed source was represented by a total of 196 trees, 48 per block.

Owing to differences in the density and height of the plantation trees, we used slightly different methods for measuring gall adelgid infestations. At the Minnesota site, there were large numbers of old galls on the trees (formed during the first 15 years of tree growth) hanging on the largely dead lower crown branches. In 1988, we measured the adelgid infestation on all trees by counting as many galls as possible during a timed (30 second) count: two observers standing on the ground on opposite sides of the tree—counting all galls from ground level upward as high as one could see, about 2.5-3.5 m, because crown closure was so dense at that point that it prevented one from seeing the tops of the trees. In 1990, we revisited the plot and counted all the galls visible during a timed 30 second count from 3.5 m in height to the top of each tree on 5 of the 10 blocks. As before there were two observers, each on opposite sides of the tree, standing on orchard ladders to make the counts. Essentially the counts between ground level and 3.5 m high measured the cumulative infestations during roughly the first 12-15 years of tree life, whereas the measurements from 3.5 m to the top measured cumulative infestations during the most recent 10-15 years of tree life.

In Michigan, on the other hand, the tree's live crowns went largely to the ground, probably because initial spacing in this stand was not so dense as in Minnesota, and it was not possible to measure the cumulative galling on the trees during their early years. Thus we used a different measurement. We counted all of the newly formed galls in one year (current 1987 growth) on the live branches occurring from the top to the bottom of each sample tree. Two observers, each standing on an orchard ladder on opposite sides of the tree, counted galls for 60 seconds to arrive at the total for a tree. On very large trees, 60 seconds was not sufficient to count all of the galls,but on small to medium trees, 60 seconds was more than enough to do a complete census. In any case, the time allowed for the development of an accurate index of a tree's relative susceptibility to *A. abietis*. Remeasuring the galls on selected trees showed that our second estimates were invariably within 10-15% of the first ones. We randomly selected 20 trees per seed source in blocks one and four. In some cases there were not 20 surviving trees in a block, so we measured all that were available. If there were fewer than five survivors per block we then went into the remaining two blocks to attempt to find more trees to make a reliable estimate of that seed source's susceptibility to *A. abietis.* This was necessary for only 4 populations, 3 from Alaska, and one from Montana—all of which had very low survival at this particular site.

We also measured the diameters of all sampled trees in both plantations for the purpose of assessing any relationship between tree growth rates and susceptibility to adelgid infestations.

To test for differences among spruce populations, the data for each study area were subjected to separate analyses of variance (completely randomized block design) after transformation of the raw counts to stabilize variance. Percentage infestation values were transformed to their arcsin square root counterparts, whereas the gall counts were transformed to their log (X + 1.0) counterparts. Seed source (i.e. population) means were ranked and separated using the Waller-Duncan technique. Diameters were converted to basal areas ($(D/2)^2$ x pi) and used in regressions and ANOVAs to test for relationships with gall counts and population infestation levels.

RESULTS

Percentage of Population Infested

For the Michigan data set, analysis of variance clearly showed that there were significant differences ($p < .0001$) among populations in the percentage of their individuals that were successfully attacked (i.e. a gall formed) by *A. abietis* in 1987. A population x block interaction effect was also significant, indicating that the overall ranking of infestation severity for populations varied by block, although blocks themselves were not significantly different. In any case, the highest rate of infestation per population in 1987 was 50.4%, the lowest 0.0%, and the grand mean was 25.8% (Table 1).

Table 1.—Ranking 28 white spruce populations in the Michigan and Minnesota plantations according to the percentage of individuals in each population that were infested with *Adelges abietis* galls. Gall counts are the mean number per infested plant.

Michigan Provenance Plantation				Minnesota Provenance Plantation			
Source population	Percent attacked[1]		Galls/ plant	Source population	Percent attacked[2]		Galls/ plant
Ak.(c)[3]	0	g[4]	0.0	Ak.(c)	24.0	m[4]	4.3
Ak.(n)	0	g	0.0	Mont.	31.6	ml	10.6
Man.(s)	7.5	gf	13	Man.(n)	42.5	mlk	5.3
Ont.(w)	7.5	gf	11.3	Man.(c)	47.2	jlk	11.9
Man.(n)	9.1	gf	4.0	Ak.(n)	51.6	jik	3.6
Labr.	10.0	gf	14.5	Sask.(n)	54.1	jhik	11.4
Minn.	10.0	gf	21.5	Minn.	59.0	jhig	12.1
Mont.	10.3	edgf	3.0	Ont.(w)	62.9	fhig	11.2
Man.(c)	12.5	edgcf	6.0	Mich.	65.8	fhig	11.0
Minn.	15.0	edgcf	44.8	Yukon	67.6	fheg	2.4
Wis.	17.5	ebdcf	20.0	Ak.(s)	73.7	fdeg	5.9
Ont.(e)	17.5	ebdcf	16.7	Man.(s)	76.3	fdec	21.0
Ont.(e)	24.4	ebdacf	24.2	Minn.	82.1	bdec	12.5
Yukon	25.0	ebdacf	13.0	Ont.(e)	87.2	bdac	25.4
Ont.(e)	27.5	ebdacf	9.3	Lab.	90.0	bac	17.4
Labr.	30.0	ebdac	20.9	Ont.(e)	90.0	bac	14.8
Mich.	30.0	bdac	30.0	Ont.(e)	90.0	bac	24.8
N.B.	32.5	bac	32.8	B.C.	90.9	bac	12.3
Que.	32.5	bac	6.0	Wis.	91.7	bac	15.5
Maine	35.0	ba	36.9	Sask.(s)	94.6	bac	13.3
N.York	35.0	ba	26.9	N.H.	94.9	ba	24.1
Que.	35.0	ba	10.9	N.York	95.0	ba	24.2
Ak.(s)	36.1	ba	36.0	Maine	97.1	ba	19.5
Sask.(s)	37.5	ba	33.2	N.B.	97.4	ba	28.7
S.Dak.	37.5	ba	57.3	Lab.	97.4	ba	12.7
N.H.	37.5	ba	22.5	S.Dak.	97.4	ba	20.4
B.C.	42.5	a	69.1	Que.	97.4	ba	24.2
Sask.(n)	50.4	a	30.0	Que.	100	a	25.7

[1] N=30 on average, ranging from 12-41, [2] N=34 on average, ranging from 20-40, [3] c, e, n, s indicate central, eastern, northern, and southern populations from the province or state in question, [4] values with the same letter within a column are not significantly different from one another ($p \leq 0.05$).

For the Minnesota data set, analysis of variance likewise showed highly significant ($p < .0001$) differences among populations in the percentage of individuals successfully attacked by *A. abietis* during roughly the first 15 years of their growth. Block effects and population x block interactions were not significant. The highest and lowest infestation rates per population were 100% and 24.0%; and the grand mean was 80.0 % (Table 1). An individual tree was classified as "infested" if it had at least one gall/tree.

Because the time periods (single vs multiple years) used for assessing susceptibility to adelgids were not the same, it's not appropriate to directly compare the Michigan and Minnesota infestation values. However, it is appropriate to compare relative ranking of various populations. To do so, we plotted percentage infestation per population for both the Michigan and Minnesota data sets against the degrees longitude of origin of each population, thereby arraying the data for a visual impression of the pattern of each relative to one another (Fig. 1, Table 1.). Wilkinson *et al.* (1971) showed that the cortical monoterpene composition of white spruce was related to the longitude of its population origin, thereby suggesting that white spruce populations may be differentiated geographically into at least two major subgroups (eastern and western) and probably several others owing to their separation into several, isolated glacial refugia during the Pleistocene (Gordon 1985). Hence, we expected that insect infestations might likewise vary in relation to the longitude and the evolutionary history of each population.

After trying several mathematical functions to describe the relationship between a population's tendency to be infested and its longitude, we selected the 4th degree polynomial because it fit well ($r^2 = 0.48$ and 0.30 for Minnesota and Michigan, respectively) and likewise conformed to our interpretation of the data, i.e. a multimodal frequency distribution of the proportion of populations infested relative to longitude. For example, infestations appeared universally high among the far eastern populations (i.e. those east of 83° w : Maine, New Brunswick, New Hampshire, New York, Quebec, and eastern Ontario). Going westward toward midcontinent (between 83° and 110°), populations in the Great Lakes and Western Central Canada, as a rule, tended to be less susceptible except for those at the southern edge of the spruce distribution in the great plains (e.g. southern Manitoba, and Saskatchewan, and South Dakota). One population from Montana was only very lightly infested. Going further westward, susceptibility seemed to clearly rise for the one population from north central British Columbia, but then fell again in the far western (> 130° w) populations of Yukon and Alaska. The susceptibility of the 3 populations from Alaska is not yet clearly resolved because these trees were more frequently damaged by late spring frosts than all others owing to their propensity to flush and grow before other trees. Thus any nymphal adelgids on these plants were very likely to be killed because all young, developing galls would likewise have been killed. The same may be true for the single Montana population which was also among the earliest to flush in the spring (Blum 1988).

Surprisingly, the 4th degree polynomial function fit nearly identically, though separated by a constant amount) to both Michigan and Minnesota data sets, even though their infestation data represent different periods of time in plant ontogeny. The high degree of correspondence between the two widely separated replicate plantations (500 km distance), suggests that there is, in fact, a real and consistent difference among spruce populations in their overall susceptibility to *A. abietis.* This trait is consistently expressed even in different environments with perhaps even different populations of adelgids.

Quantity of Galls per Plant

Analyses of variance for both the Michigan and Minnesota data sets showed once again that populations were significantly different ($p < .0001$). Blocks effects were significant but population x block effects were not in both locations. In the case of Michigan, the highest and lowest average gall count per infested tree per population were 69.1, and 0.0. For Minnesota the corresponding data were 28.7, and 2.4, respectively (Table 1).

Next we plotted mean numbers of galls per infested plant per population against the degrees longitude of population origin (Fig. 1). We used galls per infested plant rather than counts averaged over all plants because we wished to eliminate from consideration those individuals which were not successfully attacked. We fit a fourth degree polynomial to both Michigan ($r^2 = 0.12$) and Minnesota ($r^2 = 0.62$) data sets which showed weak and good resemblance, respectively, to the aforementioned pattern for the proportion of individuals infested: high gall loading per plant in populations from the eastern one third of North America, with a decline in loading toward midcontinent, and then a rise again toward the west (British Columbia), but ultimately low galling per tree in the far west, i.e. the Yukon and Alaska populations.

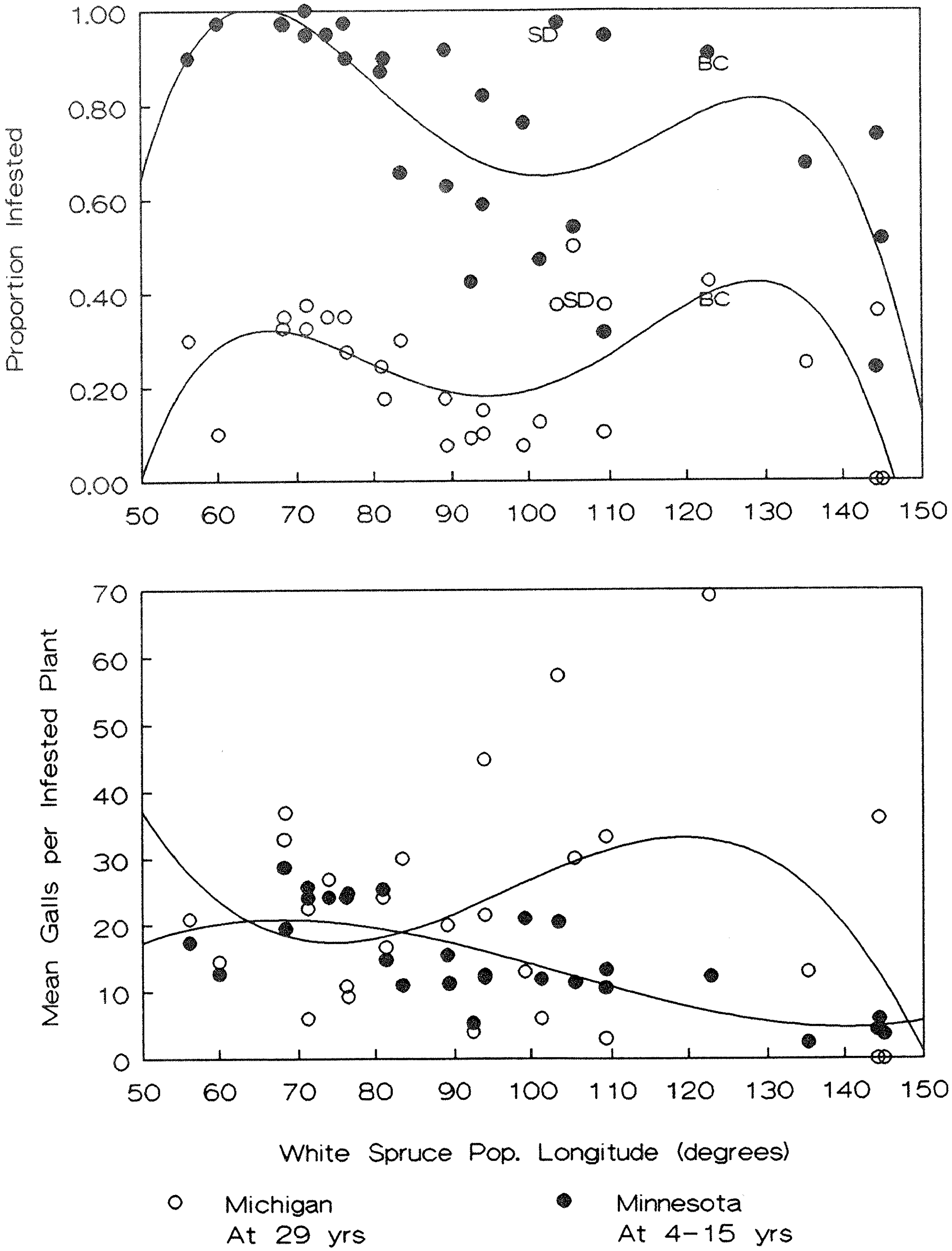

Figure 1.—Testing whether longitude of a white spruce population explains any of the variation in susceptibility to *Adelges abietis*. (Upper panel): Plotting the proportion of individuals infested in 28 spruce populations against the degrees longitude of each population. (Lower panel): Plotting the mean number of *A. abietis* galls per infested tree in different spruce populations against the degrees longitude of each population. Black and white circles represent data derived from the Minnesota (cumulative galling over about 11 years) and Michigan (galling in one year) study sites, respectively. The curved lines represent a 4th degree polynomial fit to each data set, showing the multimodal nature of the data. Each data point is based on an N of roughly 30-40. BC and SD indicate British Columbia and South Dakota populations, respectively, for reference.

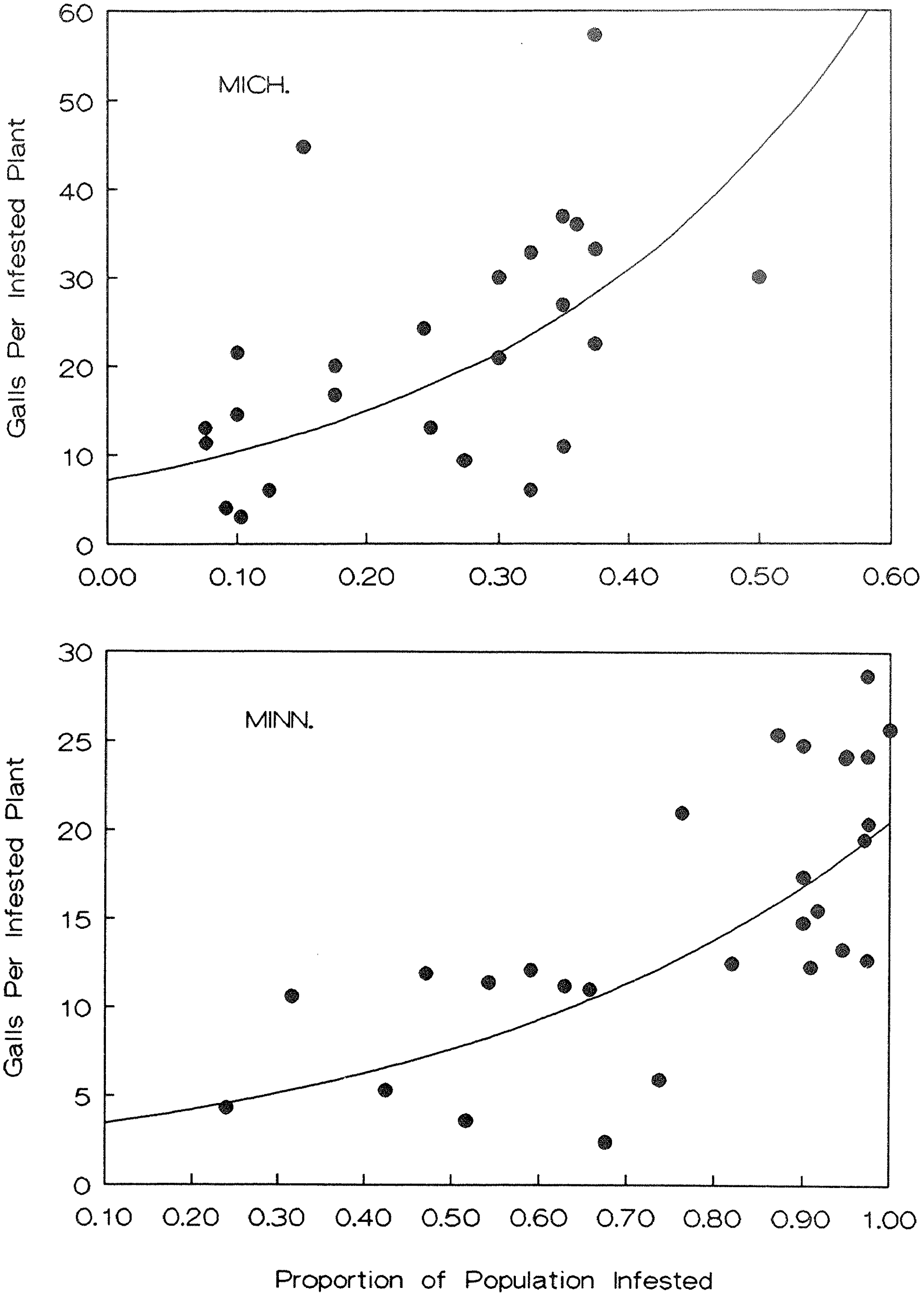

Figure 2.—Testing whether galling intensity per tree is linked to the overall tendency of a population to be infested by *Adelges abietis*. Plotting the mean numbers of galls per infested tree against the proportion of infested individuals in 28 spruce populations against the degrees longitude of each population, at the Michigan (Upper panel) and Minnesota (Lower panel) study sites. Each data point is based on an N of roughly 30-40.

The trend for concordant high population infestation, and high gall loading per tree, at least in eastern North American populations, implies that gall loading per infested tree and the proportion of infested individuals per population must be related. Hence, we regressed number of galls per infested plant against the proportion of trees infested per population for both Michigan and Minnesota data sets (Fig. 2). In both cases there was a significant, nonlinear increase in galls per infested plant with the proportion of individuals infested per population. Hence, weakly infested populations tend to have only few galls per infested plant, whereas highly infested populations tend to have large numbers of galls per infested plant. We do not believe that this is a simple cause and effect relationship. In other words, high gall loading per plant is not merely an inevitable, mathematical consequence of large numbers of individuals in the population having been attacked. In addition, we suspect that weakly susceptible spruce populations have low gall counts per tree because there only few adelgids out of the many attempting to colonize which can successfully establish on such trees (i.e. cause galls to form), whereas the opposite is true for highly susceptible spruce populations (Rohfritsch 1988). Moreover, weakly susceptible trees generally produce smaller galls with fewer progeny per colonizing stem mother (personal observations).

Declining Susceptibility to *Adelges Abietis* over Time: Minnesota Site

The Minnesota plantation afforded a unique opportunity to examine changes in tree susceptibility over time because the galls formed during the first 15 or so years of tree life were still hanging on the nearly completely dead lower crown branches. Hence, for each population we plotted the proportion of trees infested in their upper crowns (i.e. the most recent 15 years or so) against the proportion infested in their lower crowns (Fig. 3). Recent infestation levels showed a weakly rising, nonlinear relationship with past infestation levels per population. For example, populations having had 50% of their individuals attacked in the early years now had only 5% infestations. Populations having between 90 and 100% of their individuals attacked in the early years had less than 50% of the same individuals infested in more recent years.

However, plotting mean cumulative gall loading per tree in the recent years against loading in the early years revealed no apparent correlation (Fig. 3). In general gall counts in the most recent 15 years were much lower than in the first 15 years of the plantation's life. But, there were some exceptional individuals, mostly within 4 populations, which sustained higher adelgid attack rates. In these, gall loading propensity had for some reason remained relatively high, about half what it was in the earlier years. These four were from British Columbia (BC), South Dakota (SD), Wisconsin, and Quebec, all of which had been in the medium or highly susceptible population classes in earlier years. BC and SD were, in fact, the populations with the first and second highest gall loadings per infested tree in the Michigan plantation in 1987. Thus, both study sites confirm that at least some individuals have remained in the medium to highly susceptible class throughout their first 32 years of life, whereas most others have declined precipitously in susceptibility as shown in the Minnesota plantation.

Variation in White Spruce Susceptibility to the Ragged Spruce Gall Adelgid

Another species of adelgid, the ragged spruce gall adelgid, *Pineus similis*, had also heavily colonized the provenance plantation in Minnesota at about the same time as *A. abietis*. It was, on the contrary, very scarce in the Michigan plantation. We therefore measured its abundant old galls in the lower crowns of the Minnesota trees in the same manner as for the former species, and plotted the proportion of individuals in each spruce population that were infested against the degrees longitude of the source population (Fig. 4). Using a 4th degree polynomial to describe the relationship between the tendency of a population to be infested and its longitude of origin, there was a very good fit ($r^2 = 0.48$ and 0.67 for *Adelges* and *Pineus*, respectively. Just as for A. *abietis*, there was a clear tendency for the central region (Long. 83-110° w.) and far western (>130°) populations to be less infested than the eastern (< 85°) and British Columbia populations. Fitting a 4th degree polynomial to ragged gall loading per infested tree and longitude revealed a weaker ($r^2 = 0.62$ and 0.31 for *Adelges* and *Pineus*, respectively) but similar pattern (Fig. 4), except for one population from Manitoba. It had a low infestation rate but the few attacked trees were heavily loaded, averaging more than 100 galls/tree. In summary, there was strong concordance in the patterns of infestation by both species of galling adelgids among the 28 spruce populations.

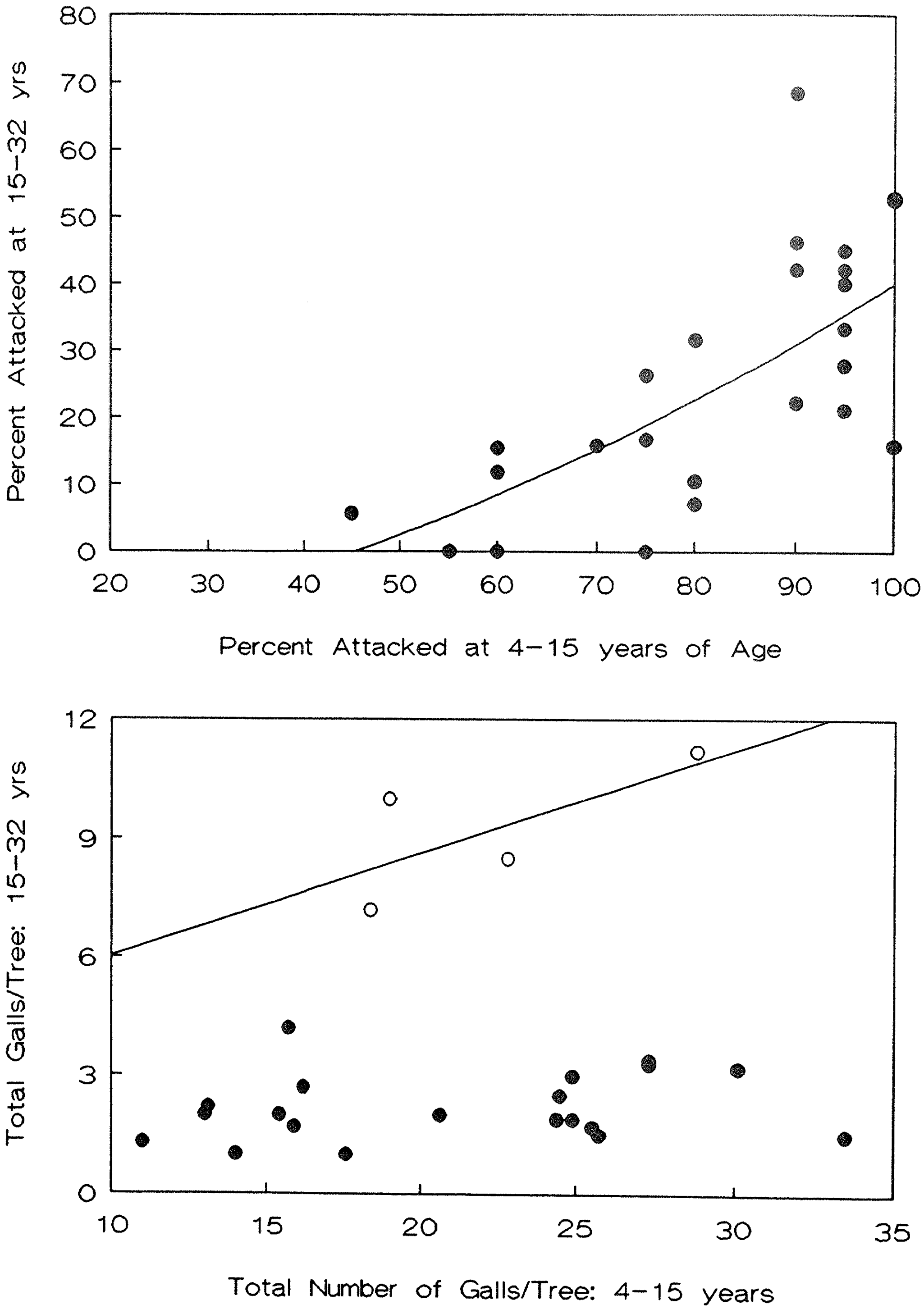

Figure 3.—Testing the stability of *Adelges abietis* infestations over time in different spruce populations. (Upper panel): Plotting the percentage of attacked individuals in each population during their most recent 15 or so years of life (at ages 18-32 years) against the proportion attacked during their first 15 years of life at the Minnesota study site. (Lower Panel): Plotting the mean number of galls per tree during their most recent 15 years of life (at ages 18-32 years) aginst the mean number of galls forming in their first 15 years of life at the Minnesota study site. White circles represent four populations that appeared to be more susceptible to *Adelges abietis* than the others during ages 15-32 years. Each data point is based on a N of about 20. based on a N of about 20.

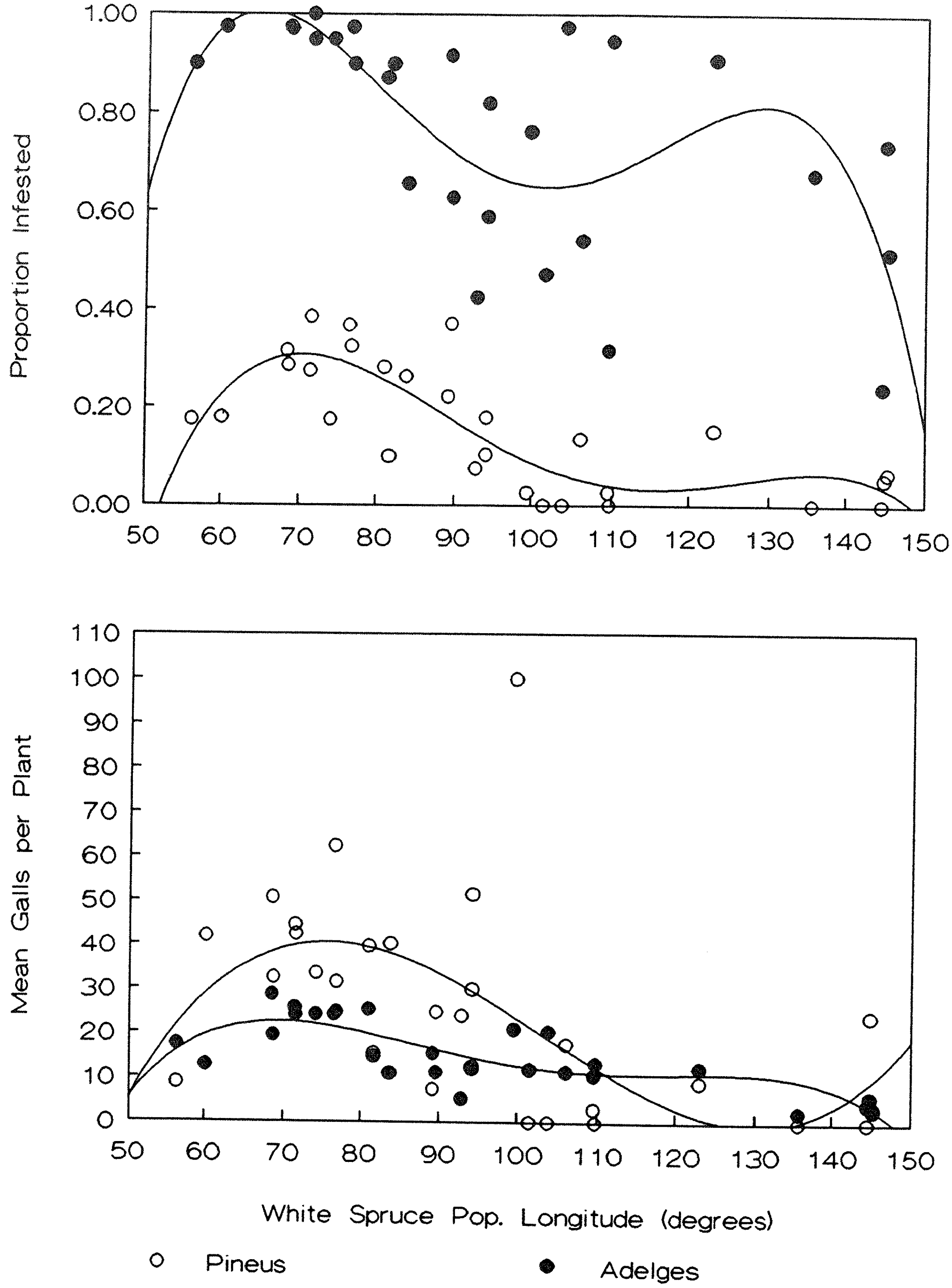

Figure 4.—Testing the tendency of white spruce populations in the Minnesota plantation to be attacked by both the ragged spruce gall adelgid and the eastern spruce gall adelgid. (Upper panel): Comparing the proportion of individuals infested by both *Pineus similis* (white circles) and *Adelges abietis* (black circles) in each spruce populations against the degrees longitude of its origin. (Lower panel): Comparing the number of galls per infested tree by the two adelgids in relation to the degrees longitude of the populations. The curved lines represent a 4th degree polynomial fit to each data set, showing the multimodal nature of the data. Each data point is based on an N of roughly 30-40.

Galling Propensity in Relation to Tree Size

It was apparent during gall sampling that smaller trees tended to have fewer galls than did larger trees. To formally test this hypothesis, we did an ANOVA of tree basal area (at breast height) after trees were stratified into three adelgid infestation classes: zero, 1-5 , and ≥ 6 galls/tree. There were significant differences in tree basal area among these three infestation classes at the Minnesota, but not at the Michigan site. In Michigan, the zero infestation class averaged 85.1 cm^2 basal area, and both the light and heavy classes both averaged 99 cm^2. In Minnesota, the average basal area of the trees increased with infestation level: the zero (46.0 cm^2) and light (57.0 cm^2) classes having basal areas that were 42% and 52%, respectively, of the highest (109.8 cm^2) class. However, there was a significant population x infestation class interaction due to the following: in 2 populations the light infestation class had an average basal area exceeding that of the highest, and in four populations the zero class was higher than the light class. In no case, however, did the zero class have a larger mean basal area than the highest infestation class.

Next, we plotted number of galls per tree in relation to tree basal area (cm^2) at breast height. Pooling all trees regardless of seed source, the relationship was linear for Minnesota ($NGalls_{lcrown} = 0.423 + 0.169\ BA_{cm2}$, $r^2 = 0.37$), but insignificant for Michigan. To sort out individual seed source effects, we regressed the data for each population separately, paying attention to their slopes, i.e. the relationship of gall loading propensity to tree size (Table 2). None of the individual population regressions was signficant at the Michigan site. But, the opposite was true for Minnesota where two-thirds of the populations had significant gall loading (lower crown) vs basal area regressions. Slopes varied roughly two-fold accross the various North American populations, from 0.13 to 0.31 galls per unit basal area. In other words, the populations with the highest propensity to support adelgids had about twice as many galls per crown as the less susceptible populations, after correcting for tree size effects. There was no obvious trend by longitude, except for the fact that the populations with insignificant regressions were primarily from midcontinent, 85-110° longitude, and 46-50° latitude. The spruce populations within this rectangle lie almost entirely within the states of Michigan, Wisconsin, and Minnesota, and western Ontario. These data essentially endorse the earlier analyses showing that populations from this western Great Lakes region are among the least susceptible to *A. abietis*.

Finally, to test the relationship between population susceptibility to infestation and its growth rate, we plotted the proportion of infested individuals in each population at roughly 15 years of age against population mean basal area at age 30 (Fig. 5). The tendency of a population to be infested increased with the log of population basal area ($r^2 = 0.56$).

DISCUSSION

Although there are differences in susceptibility to adelgids, we have no information about the actual defense mechanisms that may cause this variation. We speculate that there is probably only a single mechanism such as that described by Rohfritsch (1988), or at most very few mechanisms, and that the variation in apparent susceptibility is in part a consequence of the variation in the frequency of the resistant gene(s) among populations. Because *Adelges abietis* is an introduced adelgid, it is likely that the resistance mechanism(s) against it in white spruce may be of a general nature (e.g. hypersensitive reaction) that evolved to defend against one or more native adelgids such as *Pineus similis* or *Adelges cooleyi*. Variation in the frequency of resistance genes among populations may be strictly stochastic, owing to historical accidents such as the particular glacial refugium from whence a population was derived. Or it may be dependent on the historical importance of adelgids as agents of natural selection in the various North American ecoregions in which white spruce has evolved.

Variation in susceptibility among populations may be also due to inherent differences in their growth rates. The most susceptible populations are among the fastest growing, and by contrast the least susceptible are among the slowest growing (Fig. 5). Eidmann and Erikkson (1978) found that the same was true for *Picea abies* in Sweden. Population susceptibility could be linked to the average number of active growing points per plant because each bud offers the potential for adelgid colonization. Faster growing, taller trees not only have more buds for adelgids, they also present more target area for intercepting flying females. Hence over the long run, they may accrue more units of damage per tree than slower growing, shorter trees. So, the apparent population differences may be partly explained by or at least confounded with tree growth rates.

However, this does not satisfactorily explain the high variation among individuals because it is very common to find two fast or two slow growing trees immediately next to one another, but with vastly different gall counts. Clearly

Table 2.—Parameter values of a linear regression of galls per tree on the basal area of trees for 28 spruce populations, identified by their coordinates of latitude and longitude (degrees and minutes)

Population coordinates		Regression parameters			
Longitude	Latitude	Intercept	Slope	r^2	Prob. level[1]
Eastern N. American					
56.26	52.36	-4.82	.3022	.46	***
60.05	53.46	0.05	.1491	.30	**
68.21	47.50	5.47	.1931	.20	**
68.38	44.50	15.53	.0331	.02	ns
71.22	48.18	9.24	.1291	.16	**
71.26	44.51	-1.34	.2475	.30	**
74.6	44.23	-12.48	.2913	.54	***
76.30	46.32	-2.05	.2126	.40	***
76.51	45.44	-3.98	.1944	.38	***
81.00	48.00	2.81	.1767	.25	**
81.40	52.15	-1.43	.1895	.28	***
Great Lakes and Great Plains					
83.45	44.30	-8.99	.1724	.59	***
89.30	48.30	10.79	.0122	.01	ns
89.7	45.41	-5.05	.2171	.43	***
94.09	47.33	4.75	.0662	.05	ns
94.80	47.33	6.21	.0789	.01	ns
99.30	49.51	18.04	.0251	.01	ns
103.55	44.10	-2.44	.3108	.52	***
109.31	46.48	10.04	.0198	.01	ns
109.40	49.40	4.24	.1463	.21	**
Western Central Canada					
92.51	56.56	1.50	.1303	.37	**
101.36	54.39	-6.66	.2738	.23	**
105.59	59.19	0.16	.2391	.71	***
123.00	54.00	-4.94	.2565	.37	***
Far Western					
135.35	60.49	1.09	.1348	.29	*
144.30	65.21	2.34	.1477	.25	ns
144.53	63.45	0.42	.2071	.52	***
145.11	66.35	2.88	.0569	.09	ns

[1] ns= nonsignificant ($p > 0.05$), * = 0.05, **= 0.01, and ***= 0.001 significance levels

there are resistant individuals, and their frequency within a population depends on the frequency of the genes conferring resistance/susceptibility within the population gene pool.

Canavera and DiGenaro (1979) measured A. *abietis* infestations in one replicate plantation of this range-wide provenance study, 16 years after it had been planted in Maine. Their data agree well with our interpretations of variation in spruce population susceptibility. For example, they found that the 8 most highly infested (58.0-76.5%) populations all

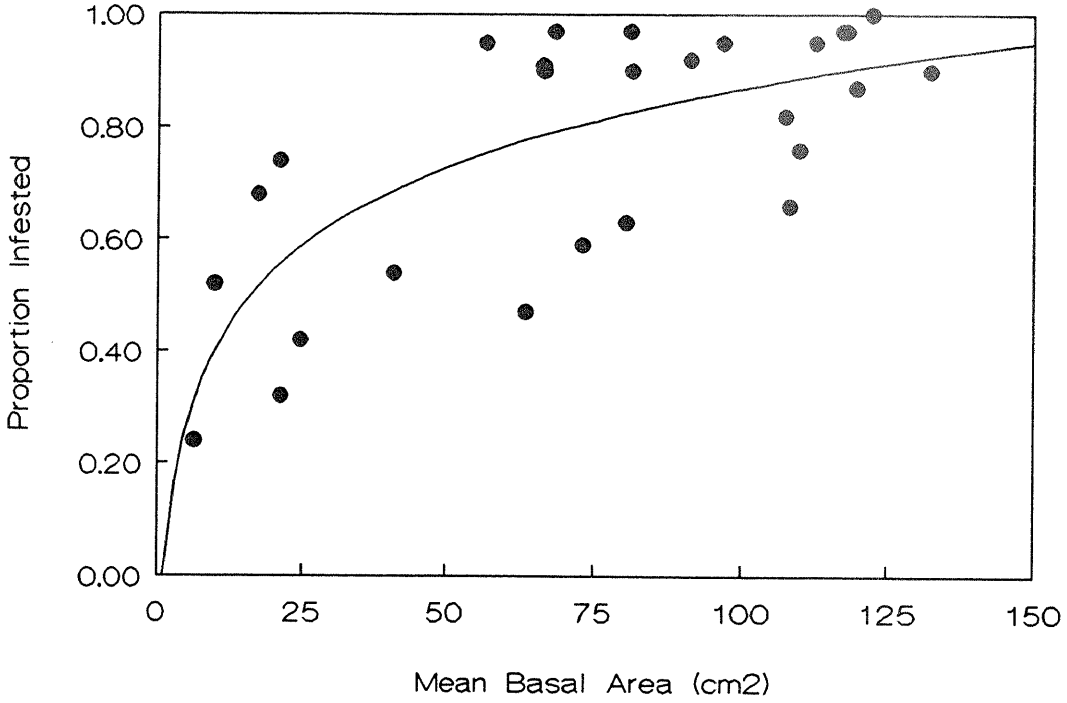

Figure 5.—Examining the relationship between the tendency of a population to be infested by *Adelges abietis* and the mean growth rate of the trees in the population. Plotting the proportion of individuals infested at roughly 15 years of age in 28 spruce populations against the mean basal area of the trees at 30 yrs of age.

came from the far eastern part of white spruce's geographic range, except for one from South Dakota. Likewise, the 8 least infested (10.0-34.0%) populations came from the central part of the geographic range (Minnesota, Montana, Western Ontario, Wisconsin, Michigan, and Saskatchewan). A single population from Labrador was, as we found in our Lakes States provenance plantations, in the midrange of susceptibility, somewhat different from the rest of the eastern populations. The British Columbia population in the Maine study was in the center of their relative rankings, not among the top third as we have found at two different study sites in the Lake States. We conclude, therefore, that there is no apparent environment by genotype (population) effect on the basic expression of plant resistance to the adelgid because the same infestation pattern was consistent in all three, widely separated study sites.

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VARIATION IN QUERCUS ROBUR SUSCEPTIBILITY TO GALLING WASPS (HYMENOPTERA:CYNIPIDAE) LINKED TO TREE PHENOLOGY

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Abstract. Variation in the abundance of 17 bud-galling and 1 acorn-galling cynipid species (Hymenoptera: Cynipidae) was examined for 20 individuals of *Quercus robur* in a stand at the Gödöllô Arboretum, 30 km east of Budapest, Hungary in 1990 through 1992. The hypothesis was that the abundance of each gall species was correlated with the time of host budburst. Gall abundance correlated with host phenology for only three cynipids. Of the bud-galling species, *Andricus hungaricus* was more abundant on late budbursting trees, while *Neuroterus petioliventris* sexual galls were more abundant on early budbursting trees. The acorn-galling *Andricus quercuscalicis*, was more abundant on early trees. The possible causes of these correlations are discussed with reference to differences in life cycles between species.

Key words: Quercus robur, gall wasps, budburst phenology, Andricus hungaricus, Andricus quercuscalicis, Neuroterus petioliventris.

INTRODUCTION

The architecture and nutritional quality of plants change markedly through phenological time. For phytophagous insects, the timing of these changes may be crucial to successful growth and reproduction. This is particularly true for species attacking ephemeral structures on the tree, such as flowers or fruits. Exploitation of these resources requires an insect phenology which is closely coupled to that of the host plant. There is also evidence for intraspecific variability in the strength of the host plant's defense against herbivores (Haukioja and Niemela 1976; Haukioja *et al.* 1978; Wainhouse *et al.* 1988, 1990). Both of these factors combine to generate high intraspecific variability in the susceptibility of trees to insect herbivores. Patterns generated from this interaction between herbivores and their plant hosts have long been a subject of particular interest for ecologists (Satchell 1962; Bale 1984; Leather 1985; Crawley and Aktheruzzaman 1988; Hunter 1990, 1992; Watt and McFarlane 1991).

One group of insects for which phenological variation in the host plant should be critical are the gall wasps of the family Cynipidae (Hymenoptera: Cynipidae). To date few studies of intraspecific variation in levels of herbivore attack on oaks have focused on cynipid wasps. Hails and Crawley (1991) found high tree-to-tree variation in the galling rate of both sexual and agamic generations of the cynipid, *Andricus quercuscalicis*, which were consistent from year to year. Ambrus (1974) mentions for several cynipid species that galls were consistently found in large numbers on particular trees but were absent from others. Hartley and Lawton (1992) also mention consistent tree-to-tree variation in galling rates by the spangle gall, *Neuroterus quercusbaccarum*, from year to year. Only a few studies have attempted to relate these patterns in galling rates to characteristics of the individual trees such as the timing of budburst. Askew (1962) examined the between- and within-tree variation in abundance and distribution of spangle galls. Galls of *Neuroterus numismalis* and *N. quercusbaccarum* were shown to occur in larger number on early-flushing trees. Crawley and Aktheruzzaman (1988) showed that *Neuroterus numismalis* and *N. quercusbaccarum* were more abundant on late budburst trees. This study describes (for 17 bud and 1 acorn galler species) the first results from a long term examination of this question, and tests whether the patterns associated with oak phenology are a common phenomenon in all Cynipids or might be restricted to just the *Neuroterus* species.

SITE AND METHOD

The work was done at the Gödöllô Arboretum of the Hungarian Forest Research Institute, which is located 30 km east of Budapest, Hungary (Latitude: N 47-37, Longitude: E 37-03, Altitude: 200-220 m above the Baltic Sea, yearly average temperature: 9.1° C, yearly average precipitation: 595 mm). Five species of oaks (*Quercus robur*, *Q. petraea*, *Q.*

cerris, *Q. pubescens* and *Q. rubra*) are numberous and occur in stands, and 6 more species are reprsented by a few single trees. There are 74 gall types of 64 species of cynipid gall wasp on the oaks in this arboretum (Csóka 1991). This is approximately 60% of all the gall types, or 65% of all the Cynipid species, recorded in Hungary (Ambrus, 1974).

Two scoring methods for the cynipid fauna were used in the experimental plot which was an 18-year old (in 1990) pure pedunculate oak stand. The average height of the trees is 12 m, with an average diameter 1 m above ground of 14 cm. 1) 20 individual trees were selected randomly in early spring 1990 on the edge of this stand. Twice in each of the three sample years all bud galls on each tree were counted. One census was done in mid-April to score the spring galls of the sexual generation of *Neuroterus petioliventris* HTG. (this is the earliest spring gall which must be censused 3-4 weeks before any other spring galls). The second census was done in October to score the other bud galls. The spring census required approximately 20 minutes per tree and the autumn check, 30. All bud galls were counted and classified into four abundance-categories as follows: 0= no gall; 1= 1-5 galls; 2= 6-20 galls; 3= 21-50 galls; and 4= more than 50 galls. 2) For *Andricus quercuscalicis* only, fifteen 70 cm long branches on each of the same sample trees were selected at random at a height of between 1 and 3 m above the ground. All galls and acorns were counted, and these abundances used in statistical analyses.

Two methods were used to assign oaks to phenological classes: 1) The 20 sample trees were classified into 4 groups according to their budburst phenology using the method of Mátyás (1962) for all three years (1990-1992). The categories are: 1- very early budburst (the five earliest trees from the 20); 2) early budburst (the second five trees from the 20); 3- late budburst (the third five trees from the 20); and 4- very late budburst (the last five trees from the 20). (2) In the 1992 season only a phenological rank of the 20 trees was also made using the method of Crawley and Aktheruzzaman (1988).

Correlations between budburst and bud gall abundance was tested using chi-squared values from contingency tables. The proportion of acorns galled by *A. quercuscalicis* were analyzed with a linear regression model with binomial errors and a logit link function corrected for overdispersion.

RESULTS

The list of budgalls found on the 20 sample trees between 1990 and 1992 is given in Table 1 and 2. Only two budgalling species showed a significant correlation between abundance and phenological category. (A) The agamic generation of *Andricus hungaricus* HTG. was found at higher frequency on late budburst trees. It has never been observed on the trees belonging to the earliest budburst category, and was found at very high abundance on trees of the 3rd and 4th budburst categories. While this pattern was similar for all three years, the correlation was significant only in 1992 (chi-squared=33.3, 17d.f., $p< .025$). (B) The sexual gall of *Neuroterus petioliventris* HTG. was generally most abundant on early budburst trees and was never recorded from the late budburst trees. This pattern was similar in the all three years and was significant in 1991 (chi-squared=33.8, 17d.f., $p< .01$) and 1992 (chi-squared=34.7, 17d.f., $p< .01$).

There was also a significant negative correlation between budburst rank and the proportion of acorns galled by *A. quercuscalicis* ($F(1,15)=7.08$). This is particularly interesting because the galls occur only by the end of July on the tree. No significant correlation was found between the budburst rank and the gall species richness of the individual trees.

DISCUSSION

In 1992 trees showing later budburst had significantly higher abundance of *Andricus hungaricus* galls. This pattern is difficult to explain. According to Ambrus (1974), the adults emerge from the galls in February-March and should therefore have all phenological categories in the experimental stand available to attack. Little is known about the physical or physiological state of particular plant organs required for oviposition by gall wasps. The results presented here might suggest that even as early as February the buds on individual trees may be different enough for the ovipositing female to discriminate between early or late budburst trees. Alternatively it is conceivable that some defense mechanism in the plant may be linked to the time of budburst. Finally, it is also possible that the females which emerge in February do not start ovipositing immediately. Tests on the agamic females of *A. quercuscalicis* showed that they can survive, when fed, for about 3 weeks on average, with a maximum of 4 weeks (Personal communication K. Schönrogge). A similar life span might provide agamic *A. hungaricus* females with the time to find later buds in the right state. All three hypotheses could produce a pattern in the distribution of bud galls described here.

Table 1.—The total number of trees in each phenology class and sample year on which each bud-gall species was found. The maximum value in any phenological class is 5.

Year and phenology class	1990				1991				1992			
	1	2	3	4	1	2	3	4	1	2	3	4
Andricus ambiguus TROTTER agamic	0	0	0	0	1	0	0	0	2	2	0	1
Andricus aries GIR. agamic	2	2	1	2	1	1	2	1	1	0	1	0
Andricus caliciformis GIR. agamic	0	0	0	0	0	0	0	0	0	0	0	1
Andricus caputmedusae HTG. agamic	0	0	1	0	0	0	0	0	0	0	0	0
Andricus corruptrix SCHDL. agamic	0	2	1	1	0	2	2	1	2	1	1	1
Andricus fecundatrix HTG. sexual	1	3	3	1	3	4	1	1	2	3	1	1
Andricus gallaetinctoriae OL. agamic	0	2	0	1	0	0	0	0	0	0	0	0
Andricus glutinosus GIR. agamic	0	1	0	0	0	0	0	0	0	0	0	0
Andricus hungaricus HTG. agamic	0	2	1	3	0	4	1	3	0	5	2	3
Andricus inflator HTG. sexual	5	4	3	1	5	4	3	2	5	4	4	2
Andricus kollari HTG. agamic	3	2	4	4	2	2	2	3	1	1	4	2
Andricus lignicola HTG. agamic	5	4	4	5	3	4	5	5	3	2	4	5
Andricus lucidus HTG. agamic	4	4	1	5	2	3	2	5	2	3	3	5
Andricus mitratus MAYR. agamic	0	1	0	1	0	0	0	0	0	0	0	0
Andricus solitarius FONSC. agamic	2	0	1	2	0	1	2	0	0	0	1	0
Andricus truncicola GIR. agamic	0	0	0	0	0	0	0	0	1	0	0	0
Neuroterus petioliventris HTG. sexual	4	3	0	0	5	3	0	0	5	3	0	0

Table 2.—The total abundance scores for each cynipid species summed over all 5 trees in each phenology class for each year. Values in each phenology class are obtained by adding the abundance scores for all 5 trees in the class.

Year and phenology class	1990				1991				1992			
	1	2	3	4	1	2	3	4	1	2	3	4
Andricus ambiguus TROTTER agamic	0	0	0	0	2	0	0	0	3	2	0	1
Andricus aries GIR. agamic	2	3	1	2	2	1	2	1	2	0	1	0
Andricus caliciformis GIR. agamic	0	0	0	0	0	0	0	0	0	0	0	1
Andricus caputmedusae HTG. agamic	0	0	1	0	0	0	0	0	0	0	0	0
Andricus corruptrix SCHDL. agamic	0	2	2	1	0	3	2	1	4	3	1	1
Andricus fecundatrix HTG. sexual	1	5	4	1	3	4	2	2	2	4	1	1
Andricus gallaetinctoriae OL. agamic	0	2	0	1	0	0	0	0	0	0	0	0
Andricus glutinosus GIR. agamic	0	1	0	0	0	0	0	0	0	0	0	0
Andricus hungaricus HTG. agamic	0	2	3	6	0	5	4	9	0	8	8	1
Andricus inflator HTG. sexual	9	7	4	2	8	9	5	3	8	8	6	4
Andricus kollari HTG. agamic	3	2	7	7	2	2	3	3	1	1	4	2
Andricus lignicola HTG. agamic	12	7	13	11	6	5	13	9	8	4	11	9
Andricus lucidus HTG. agamic	7	6	1	8	4	6	5	8	3	6	4	8
Andricus mitratus MAYR. agamic	0	1	0	1	0	0	0	0	0	0	0	0
Andricus solitarius FONSC. agamic	2	0	1	2	0	1	2	0	0	0	1	0
Andricus truncicola GIR. agamic	0	0	0	0	0	0	0	0	1	0	0	0
Neuroterus petioliventris HTG. sexual	10	7	0	0	14	7	0	0	16	9	0	0

Because of differences in life cycle between cynipids, some species may require buds in different developmental states than others. *N. petioliventris* has 2 generations a year. The bud gall of its sexual generation develops very fast during the budburst period. Full development (from the first visible sign of the gall) to adult emergence takes no longer than 8-10 days. The agamic generation develops in small catkin galls, which are available only for a short period immediately after budburst. The sexual females have to find flushing flower buds in which to oviposit. If the sexual generation were to develop in late budburst trees they would miss the flushing flower buds essential for their agamic generation. Development of the sexual generation in early budburst trees suggests that the preceding agamic generation may be able to somehow recognize these trees. Agamic females laying eggs in later budburst trees would produce a sexual generation unable to find oviposition sites for the next agamic generation. If selection of early budburst trees by agamic females has a genetic basis, such late-favouring agamic lines would soon become extinct.

That the patterns observed for *A. hungaricus* and *N. petioliventris* were significant in only one and two years out of three suggests that the strength of these correlations varies between years. It is worth noting that the years which produced the significant results for both species were those in which these galls were most abundant (see Table 2).

The agamic galls of *Andricus quercuscalicis* were most abundant on early budburst trees. This distribution may be explained by the lifecycle of this species, which involves two generations each year and two host oak species. The sexual generation develops on the catkins of Turkey oak, *Q. cerris*, and the agamic generation develops on the acorns of Pedunculate oak, *Q. robur*. The adults of the sexual generation emerge in early May, at which time the early budburst individuals of *Q. robur* have a higher proportion of their female flowers at a suitable stage for galling. The female flower initials of the late budburst trees are in partially or entirely closed buds and may be relatively better protected from ovipositing females. There has, however, been no experimental analysis of egg-laying preferences by sexual females.

That no correlation between tree phenology and cynipid species richness could be found might be due to the low resolution of the scoring method. Unquantified observations suggest that there is a pattern to be found.

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COMPARING RESISTANCE TO THE PINE GALL MIDGE AMONG SEEDLINGS PRODUCED FROM CONTROLLED POLLINATION AND GRAFTING

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Abstract. Control-pollinated seedlings from putative resistant *P. thunbergii* parents showed 36.6% resistance to the pine gall midge, compared to 22.1% among open-pollinated seedlings. Grafted seedlings of Chungbuk-3 (CB-3) and Kyungbuk-27, -30, and -38 (KB-27, -30, and -38) showed lowered oviposition rate and parasitism rate. The hybrid *P. densiflora* CB-3 x *P. thunbergii* BR-23 showed better resistance than *P. densiflora* x *P. thunbergii* BR-23. There is a potential to breed for resistance to the pine gall midge.

INTRODUCTION

The pine gall midge *Thecodiplosis japonensis* Uchida et Inouye is one of the most dangerous insects damaging Korean red pine, *Pinus densiflora S.* et Z., and black pine, *Pinus thunbergii* Parl., in Korea. The galls its larvae cause are formed at the needle base, although eggs are oviposited on upper parts of the needles. The galled needles do not grow as much as normal ones and are subject to an early death. This insect was first discovered in both Seoul and Mokpo areas in 1929. Today, 250,000 ha. of pine forests are damaged by this pest (Forestry Administration 1992). Various methods of control for this insect have been proposed (Ko 1966, Hyun 1967, Park 1967, Hong *et al.* 1983). Among them, research on breeding resistant pines has been underway since 1974 through selection and crossing of phenotypically resistant individuals. More than 500 trees of *P. thunbergii* and *P. densiflora* were selected as phenotypically resistant, throughout the country (Hong *et al.* 1983).

Resistant *P. thunbergii* or *P. densiflora* and *P. rigida* have different anatomies than susceptible trees (Lee 1970, Lee *et al.* 1981). In resistant trees, several layers of tissue first surround the larvae, and then secrete a resin-like substance and die. The aim of this study was to test resistance to the pine gall midge among the 10-year-old seedlings produced from artificial- or open-pollination and grafting after they were planted at three locations.

MATERIALS AND METHODS

In April, 1980, 2-year-old seedlings produced from control- or open-pollination and grafting were planted at Buyo, Anmyon island and Ongjingun areas where there were populations of this insect. A randomized block design with three replications (10 trees per replicate) was used for laying out the plantations in 5m x 5m spacing. In September, 1990, three trees per replicate were sampled to measure oviposition, needle scarring and gall formation. The crowns of each sample tree were divided into the upper, middle and low parts, from which nine new shoots were collected. After examining all of the needles in the shoots, the number of needles with eggs was calculated by adding number of scarred needles and numbers of galled needles, and oviposition rate was estimated by dividing the number of needles with eggs by the total number of needles, and the parasitism rate by dividing the number of galled needles by the number of needles with eggs.

Table 1.—Open-pollinated progenies of *P. thunbergii* tested for resistance to pine gall midge at Buyo

Clone number	Gall formation rate (%)	Scar rate (%)	Resistant progeny (%)
75-SO-T- 3*	29.2	3.1	1.9
4	34.7	6.7	16.2
5	29.7	11.2	28.2
6	28.5	6.5	31.5
9	26.7	11.7	36.3
10	36.7	10.0	23.2
11	32.0	3.1	4.5
12	32.7	10.2	25.9
13	36.7	3.6	15.0
14	37.9	4.5	12.4
15	20.2	10.0	48.8
17	24.4	10.5	20.1
Mean	28.2	7.6	22.1

*75-SO-T-3 refers to: 75; years of selection, SO; location of selection, T; *Pinus thunbergii*, 3; selection number

RESULTS AND DISCUSSION

Resistance Between the Control- and Open-Pollinated Seedlings of *P.thunbergii*

Open-pollinated progenies showed a 28.2% rate of gall formation, a 7.6% scarring rate, and 22.1% resistance (Table 1). The progeny of clone 75-SO-T-15 had the best resistance (48.8%). Their control-pollinated progenies had a higher proportion of resistant progeny than open-pollinated ones (Tables 1, 2), which indicates a potential of breeding for resistance to this insect. Clone 75-SO-T-12 showed higher resistance than others, whether it was used as mother or pollen tree. The result that control-pollinated progenies had higher resistance than open-pollinated ones, was also reported by Hong *et al.* (1983).

Resistance Among the Clones of Plus Trees in *Pinus densiflora*

The mean percentage of needles attacked on 422 clones of plus trees was 39.8% (Table 3). Among them, Chungnam-1, Chungbuk-3 and Kyungbuk-38 showed the lowest rates, 18, 27 and 33%, respectively. However, the mean percentage of needles having galls for all the clones was 92%. Chungbuk-3, Kyungbuk-27, -30 and -39 showed 79.0, 75.3, 70.0 and 74.6%, respectively. Thus, Chungbuk-3, and Kyungbuk-27, -30 and -38 may be choices for use in resistance breeding.

Table 2.—Control-pollinated progenies of *P. thunbergii* tested for resistance to pine gall midge at Buyo

Cross combination		Gall formation rate (%)	Scar rate (%)	Resistant progeny (%)
75-SO-T- 3 x	75-SO-T-12	20.2	19.4	47.2
4 x	12	36.6	12.3	37.4
4 x	17	27.9	17.5	55.0
5 x	17	27.0	11.1	35.4
8 x	12	41.3	18.6	32.1
9 x	9	35.6	2.2	10.1
9 x	17	29.9	9.2	24.9
10 x	12	32.0	15.0	42.9
12 x	9	35.3	12.9	33.8
12 x	12	35.3	13.4	47.9
13 x	1	34.7	12.3	37.5
17 x	9	29.9	11.3	34.8
Mean		31.9	12.9	36.6

Table 3.—Number of normal, scarred, and galled needles, oviposition rate and parasitic rate for grafted clones of plus trees in *P. densiflora* at Anmyon island

Number of needles		Percent needles				Percent needles
Clone		Normal	Scarred	Galled	Attacked	forming galls
Kangwon	44	819	9	125	14.0	93.3
	124	774	63	187	24.6	75.0
Chungbuk	1	551	4	105	16.6	96.0
	3	920	25	92	10.6	79.0
Chungnam	1	918	6	66	7.0	91.6
Kyungbuk	4	681	15	97	13.6	85.6
	8	767	57	180	24.0	76.6
	10	582	35	114	20.3	78.3
	27	664	34	100	17.3	75.3
	30	632	37	91	18.0	70.0
	38	975	32	112	13.3	78.3
	39	814	59	169	22.3	74.6
Mean					39.8	92.0

The seedlings produced from crosses between selected or plus trees of *P. densiflora* and *P. thunbergii* showed differences in resistance to this insect (Table 4). The hybrid between *P. densiflora* CB-3 and *P. thunbergii* BR-23 showed higher resistance (78%) than susceptible *P. densiflora* x *P. thunbergii* BR-23 (86 or 87%). Clones BR-23 and JH-12 have a potential as breeding materials for resistance to this insect.

We conclude that there is a potential to breed for resistance to the pine gall midge.

Table 4.—Number of normal, scarred and galled needles, oviposition rate and parasitic rate for cross combinations between *P. densiflora* and *P. thunbergii* at Ongjingun

Cross combination			Number of needles			Oviposition rate (%)	Parasitism rate (%)
			Normal	Scarred	Galled		
Chungbuk(CB) 2(DP)	x	Boryung(BR)23(TR)*	1,127	47	293	23	86
CB 3(DP)	x	BR 23(TR)	1,362	91	316	23	78
Kyungbuk(KB) 1(DP)	x	BR 23(TR)	1,519	53	356	21	87
Chonnam (CN) 37(TP)	x	Kangwon(KW)29(DP)	1,255	39	310	22	89
CN 37(TP)	x	KW 29(DP)	1,303	25	358	23	93
Chungnam(CM) 4(TP)	x	KW 29(DP)	1,352	60	522	30	90
Jinhae (JH) 12(TP)	x	JH 12(TR)	1,471	171	309	25	64
JH 8(TR)	x	JH 12(TR)	1,236	111	260	23	70

* DP, TR and TP indicate plus tree of *P. densiflora*, *P. thunbergii* selected for resistance and plus tree of *P. thunbergii*, respectively

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WHAT CAN GALLMAKERS TELL US ABOUT NATURAL SELECTION ON THE COMPONENTS OF PLANT DEFENSE?

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Abstract. As in all enemy-victim species interactions, gallmakers must complete a sequence of tasks to successfully attack their host plants. There is then the opportunity for natural selection to favor evolution of plant characters that can interfere with the gallmaker at each step of the sequence; these characters are defined as resistance traits. After an attack is completed, plant characters that minimize the fitness loss caused by damage can also be favored; these characters are defined as tolerance traits. Since plant defense components affect fitness in a sequential hierarchy, their individual contributions to fitness are non-additive. This paper highlights the elements of the defense hierarchy shown by tall goldenrod (*Solidago altissima* L.; Asteraceae) to the gallmaker *Eurosta solidaginis* Fitch (Diptera; Tephritidae). It then uses a developmental-genetic model to show how the selective value of individual defense components in a sequential hierarchy varies with gallmaker population density.

INTRODUCTION

Gallmakers and their host plants are a subset of the large variety of enemy-victim interactions. In virtually all such interactions the victim species show characters that can be interpreted as defenses. Here I argue that the evolutionary pressures in all such interactions share basic similarities, and therefore parallels in defense across a broad array of systems should be expected. The actual defense mechanisms themselves may be highly diverse and specific, but the basic strategies may be general. One of the most basic of these strategies is 'defense in depth', that is, a series of characters that are employed in a specific sequence. Bacteria, for instance, have surface proteins that prohibit invasion by most viruses. Should a virus succeed in attaching to one of these proteins and invade the cell, restriction enzymes can allow the bacterium to excise the viral DNA. Two levels of defense are also seen in zebras. The pattern of vertical stripes makes it difficult for predators to identify the outline of individual zebras in a herd. But confusing the predator is insufficient as a defense and hence zebras also have long legs and hooves which allow them to out-run their enemies. These parallels of hierarchial defense stem from the hierarchial arrangement of characters needed by the enemy to successfully attack its victim. Studies of defense have contributed greatly to our understanding of natural selection. In a review of 164 selection studies by Endler (1986), 30% concerned defense traits. From the 1930's several important studies have explored both ecological and genetic components of defense evolution in natural populations (see Ford 1975, Weis and Abrahamson 1986, Fritz and Simms 1992). What is missing from our accumulated knowledge of defense is a clear picture of how natural selection acts on the individual defense components when they are employed in a sequential hierarchy.

THE STRUCTURE OF ATTACK AND THE OPPORTUNITY FOR PLANT DEFENSE

The characters involved in defense can be roughly divided into two types—those that influence the likelihood of being attacked by an enemy and those that mediate the consequences of an attack (Thompson 1988, Weis and Campbell 1992). From a plant's perspective these are called resistance (the propensity to incur damage) and tolerance (the ability to minimize reproductive loss after attack) respectively. The 'in-depth' structure of defense corresponds to the sequence of actions that enemies must take to successfully attack—steps required even when the victim is not defended. This point was elaborated by Kogan (1975) who presented insect attack on plants as a process with a five step sequence: (1) host-habitat finding, (2) host finding, (3) host recognition, (4) host acceptance, and (5) host suitability. Of course the latter could be subdivided, as the former, into another sequence of steps. In regard to gallmakers, each of the first four steps must be followed before the gall-induction process begins. Host-habitat finding is the array of behaviors that lead the insect to a location where the host plant occurs, and consists of responses to very general stimuli, such as light intensity, humidity and temperature. Host finding consists of the response to sensory stimuli that cause a foraging herbivore to inspect a plant. Some of the cues that trigger closer inspection of a plant can be general and widely distributed, such as leaf color or 'green leaf' volatile compounds. More specific cues are involved in host recognition. When the proper stimuli are presented, gallmakers may then beginning probing the plant for suitable gall-induction sites. Host acceptance is evidenced by oviposition in the case of most gallmakers, or by continued feeding at the induction site in the case of gall-inducing aphids and thrips. The cues which elicit acceptance may be chemical or physical. Host suitability, the final step in Kogan's scheme, is determined by factors influencing performance of the gallmaker after the encounter is under way. These may include successful gall induction and maturation, survivorship to the adult stage, and growth performance culminating in adult fertility and fecundity.

The final four steps (host finding through host suitability) that determine success from the insect's perspective are behavioral and physiological responses to corresponding plant traits. The physical and chemical characteristics of an individual host plant can influence the probability that an encounter will end in a successful attack. Other plant characteristics, particularly those involved in developmental and physiological regulation, will determine what the fitness consequences of an attack will be for the plant.

Consequences of a Defense Hierarchy for Natural Selection

The course of natural selection on traits involved in plant defense against herbivores is complicated by the sequential contribution of the putative defense traits to fitness. For instance, the contribution of the plant resistance factors to fitness is not independent from the contribution made by tolerance. Suppose, for example, that a plant population is fixed for a gene that discouraged gallmaker attack to the degree that the galling rate never exceeded 30% of the ramets per genet. If a new gene that prevented the galling rate from exceeding 10% entered the population would it spread when rare? That depends on the level of tolerance. If every plant could endure a 35% galling rate without loss of fitness, the new gene would be neutral since the lower galling rate would yield the same fitness as the higher one. Similarly, a new gene that allowed the plant to endure an increased galling rate of 45% would be neutral since no more than 30% galling occurs. Thus the contributions of the various defense components to fitness are non-additive. A similar phenomenon is seen in selection on individual enzymes in a metabolic pathway. A new conformation of an enzyme that doubles the flux of material through one metabolic step will not double the flux through the entire pathway if a different enzyme at another stem is rate limiting (Dykheizen 1988).

The Sequential Hierarchy of Attack and Defense Characters In the Eurosta-Solidago System

Over the past 15 years, a number of studies by W. G. Abrahamson and his associates have generated a great deal of insight on how sequentially interacting traits may influence fitness in both plant and gallmaker as they interact. The system they have studied involves *Eurosta solidaginis*, which induces galls on the stems of tall goldenrod, *Solidago altissima*. The host plant is a perennial, clonal herb. Each goldenrod genet consists of one to several hundred ramets, each consisting of a single upright stem, which eventually produces a terminal branched inflorescence. In the middle of spring the adult *Eurosta* emerge and mate, and the females then search out goldenrods for oviposition. When a plant is found, the female *Eurosta* probes the terminal vegetative bud with its ovipositor, leaving a conspicuous puncture scar. Often a female will leave after several probes without ovipositing. However, when a suitable plant is encountered, females typically lay a single egg in the bud (Uhler 1951). After the larva hatches, it burrows through the bud and into the stem just below the apical meristem. It then induces the poorly differentiated stem tissue to form a spheroid, unilocular gall. Galls grow to their mature size within three weeks of initiation while larval growth continues into the early fall. The fully grown larva then overwinters in the gall, and pupates the following spring. After flowering at the end of the season, the ramet stem dies back to the ground, while the rhizome survives the winter beneath the soil surface.

Under field conditions, galled goldenrod ramets allocate fewer resources to reproduction than do ungalled ramets growing nearby (Hartnett and Abrahamson 1979, McCrea and Abrahamson 1986). This suggests that the gallmaker can act as an agent of selection on defense characters. However, it is difficult to project these ramet-level effects on growth across the entire genet, and across the two decades that the genet lives. Therefore, when we consider the putative mechanisms of plant resistance to *Eurosta*, it is possible that the plant's tolerance of the gallmaker reduces selection intensity on these defenses to trivial levels.

One of the striking features of this interaction is the marked variation in the infestation rates of goldenrod genets. In a field survey of 117 genets, McCrea and Abrahamson (1987) found nearly half of them had no galls, while about one fifth of them had galls on 30% or more of their ramets (Fig. 1a). Variation in infestation was not due to the fly's failure to discover the ungalled genets, since 95% of the genets had at least one of their ramets punctured (Fig. 1b); however, galls formed on less than half of the punctured stems (Fig. 1c). This variation in host quality sets up a selection regime on the gallmaker that will favor increased ability to find the plants most suitable for gall induction and for improved ability to develop on plants that are poor substrates for gall induction. At the same time, the presence of variability in the plant population suggests there may be selection pressures exerted by the gallmaker that will favor plants which resist attack and that manage to maintain their level of growth and reproductive output should attack occurs. A series of experiments and surveys with the *Eurosta-Solidago* interaction were undertaken by Abrahamson and his associates to determine how the various characters in the attack sequence contributed to the observed variation in infestation levels seen in the field. These studies can provide some insight on the structure of the selective regimes on plant defense.

Foraging *Eurosta* females must first find the proper host plant species. While the cues involved in host plant finding are not yet well known, it is clear that females preferentially land on tall plants, perhaps in part because they extend above the surrounding canopy (Walton *et al.* 1990). They can distinguish *Solidago altissima* from its congeners based on cues from the unfolded leaves on the terminal bud, as shown by Abrahamson *et al.* (1989). These experimenters presented buds of non-host species of *Solidago* to the fly, but these failed to elicit an oviposition response. However, the flies readily probed these non-host buds if they were wrapped with *S. altissima* leaves. This suggests that contact cues on the leaf surface are responsible for initial host recognition. Although wrapped leaves were probed, the probing bouts were very short and never ended in oviposition, which suggests that additional host plant recognition cues are detected by sensory receptors on the ovipositor tip.

When the proper host species is located, they will probe the bud with their ovipositor, with as many as five probes per bud being common. But since not every probed plant forms a gall, some host plants may be rejected (eggs not laid), others may fail to respond positively to the inducing stimulus, and some plants may be frequently rejected and also fail to respond when accepted. Anderson *et al.* (1989) performed a survey to asses the relative importance of these post-probing events on 38 of the plant genets, including some of those studied by McCrea and Abrahamson (1987). First they counted the proportion of punctured buds on each genet. Then they dissected 20 punctured buds from each genet to determine what proportion had received eggs. Finally they marked 40 punctured buds to determine what proportion of them went on to form galls. Field observations suggested that the between-genet variability in puncture rate, oviposition rate and infestation rate were greater than expected by random, which suggested genetic variation in resistance. Common garden experiments using cloned replicates of these genets confirmed this. The likelihood that a plant will be punctured correlates with several plant characters, including bud diameter, bud water content, and specific leaf mass (Horner and Abrahamson 1992). Bud diameter was in this experiment correlated with stem growth rate. Further experiments have confirmed that *Eurosta* preferentially oviposits on the fastest growing plants (J.D. Horner, personal communications), as observed in other gallmakers (Price *et al.* 1987, Craig *et al.* 1989). Only one plant character seems to predict when a punctured plant will go on to produce a gall, and that is the ratio of bud diameter to length (Horner and Abrahamson 1992). This suggests that it may be easier in a short but stout bud to inject the egg into a position from which the resulting larva will be able to find the meristem.

The question arises, is the final infestation level more dependent on the number of ramets that are punctured or on the number of punctured ramets that receive eggs? Anderson *et al.* (1989) fit their field data to a path model that examined the contributions of these two factors to the proportion of galled ramets per genet (Fig. 2). The direct influence of the proportion of ramets punctured accounted for 44% of the variance in the proportion of stems galled. Only 4% of the variance in proportion galled is directly explained by the proportion of punctured ramets to receive eggs. But, variance in the proportion punctured explains 20% of the variance in proportion to receive eggs, i.e. the two are correlated. This could arise if some of the cues which stimulate probing also stimulate oviposition. However, the cues exert most of their effect on infestation level through stimulation of probing behavior.

Some S. *altissima* genets may have perennially low infestations because of resistance factors that act after oviposition. Anderson *et al.* (1989) found evidence of a hypersensitive response (*sensu* Rohfritsch 1981) to *Eurosta* in the two genets with the perennially lowest infestation levels. Only 11 of the 41 larvae observed to reach the gall induction site just below the apical meristem survived. Those that were dead were surrounded by necrotic plant tissue. By contrast, 51 of the 53 larvae observed in the two most infested genets survived.

The available data suggest that the attractiveness of a genet for oviposition is not highly correlated with its reactivity. Apparently some of the plants which escape oviposition are nonetheless suitable hosts. In a greenhouse

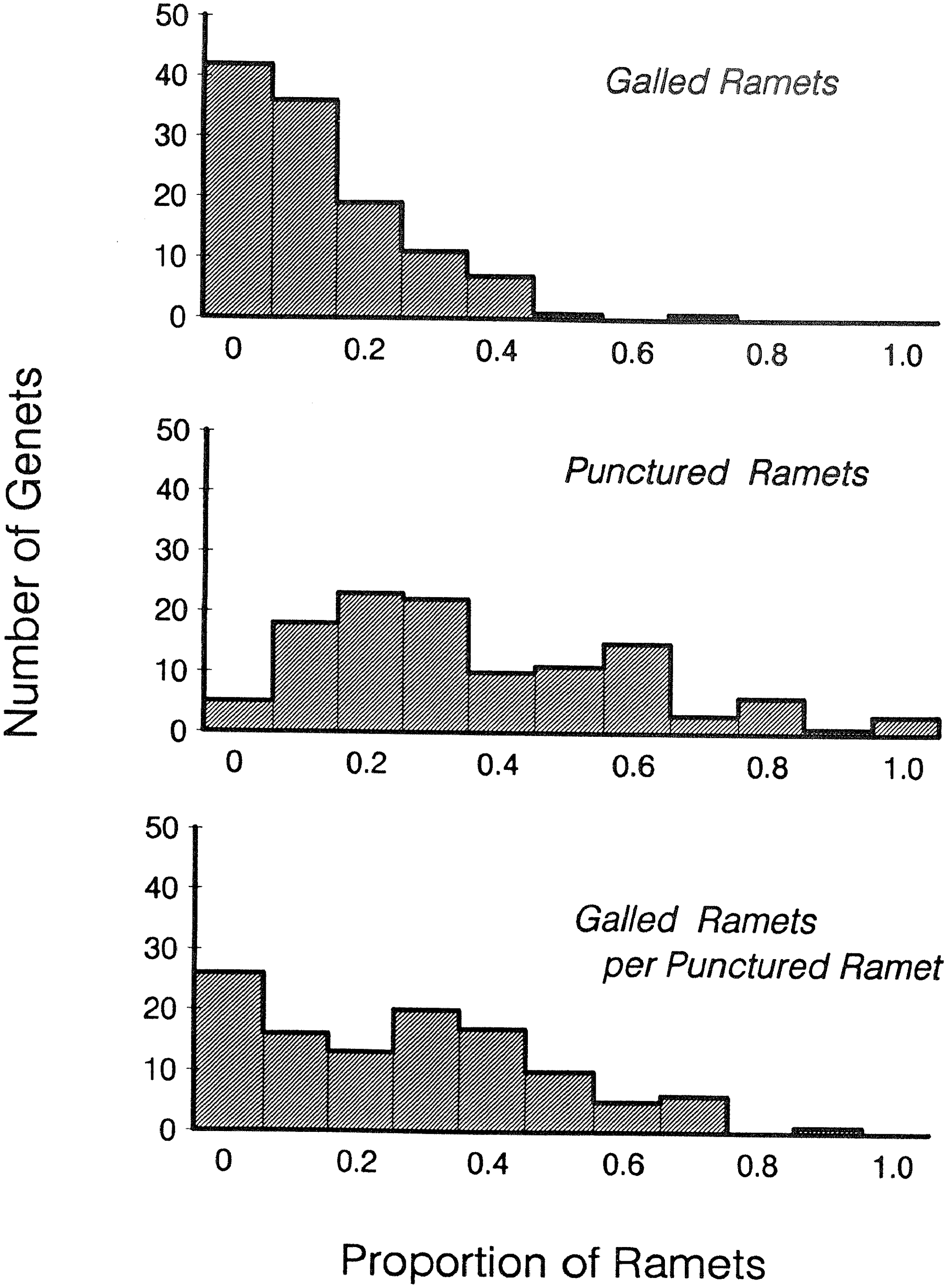

Figure 1.—Among-genet variation in susceptibility of Solidago altissima to attack by Eurosta solidaginis. The histograms show the frequency distributions of the proportion of galled ramets, proportion of ovipunctured ramets, and the proportion of punctured ramets to be galled. A total of 117 genets were examined under field conditions. After McCrea and Abrahamson (1985).

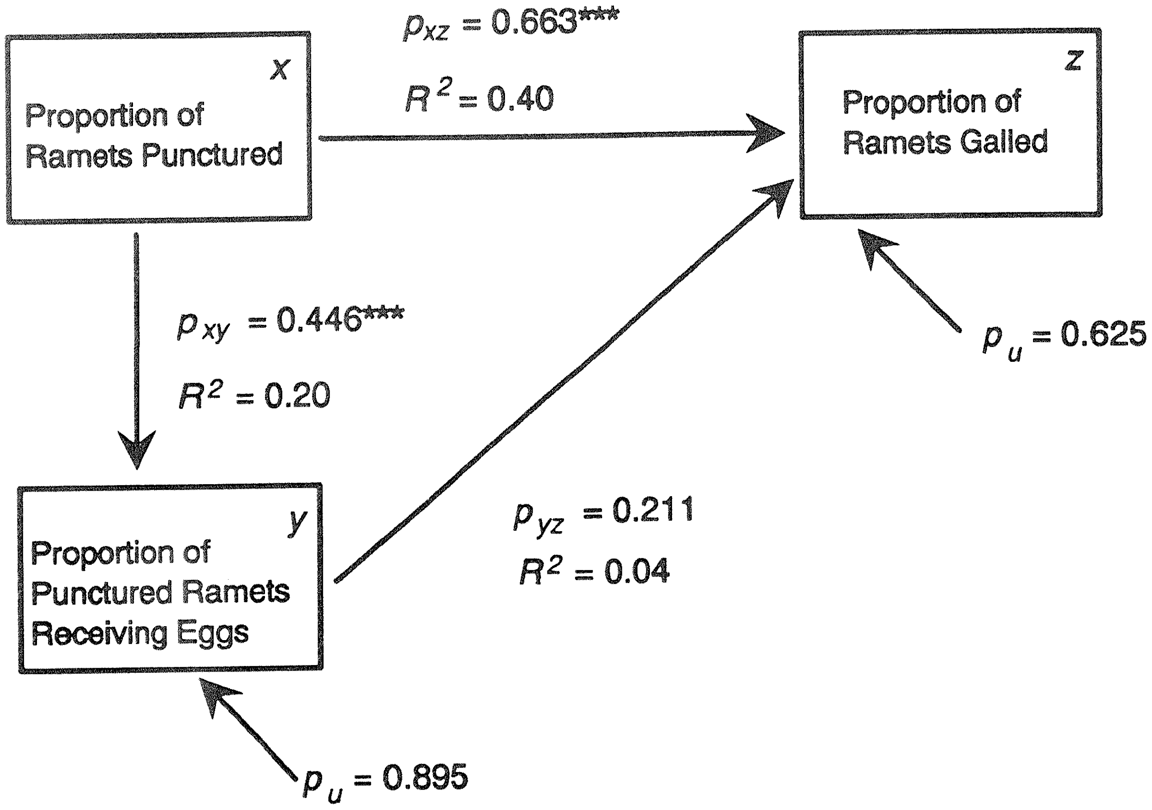

Figure 2.—Path model that decomposes the variance in the proportion of galled ramets per genet into components due the variance in proportion of ramets punctured, and proportion of punctured ramets to receive eggs. Path coefficients and partial coefficients of determination are displayed. Path coefficients marked by asterisks are significant beyond the $P = 0.005$ level. After Anderson *et al.* (1989).

experiment Horner and Abrahamson (1992) cloned four of the field genets and exposed them to fly oviposition. Two of these genotypes were taken from clones that were seldom galled ("resistant") in the field and two from clones that were usually heavily galled ("susceptible"). In the experiment, where the flies had a very limited choice of plants, one of the genotypes that was "resistant" in the field was punctured at a rate comparable to the "susceptible" genotypes. In addition, the "resistant" genotype also formed galls at a rate almost as high as the "resistant" genotypes. Thus, there does not appear to be a necessarily strong correlation between a plants attractiveness to *Eurosta* and its reactivity to the gall induction stimulus. This raises the possibility that a female fly with very selective oviposition preferences may bypass suitable plants.

Once a gall is induced, the next opportunity for the plant to limit its fitness losses is to limit gall growth. Experiments using ^{14}C labeling have shown that a disproportionately greater amount of energy is intercepted by large galls than small ones (McCrea *et al.* 1985). Greenhouse experiments have shown that gall size varies with plant genotype (Weis and Abrahamson 1986, Weis and Gorman 1989). But, greenhouse experiments have also failed to show any decrease in growth or reproductive output in plants producing large galls (McCrea and Abrahamson 1985, A.E. Weis unpublished data); experiments under realistic field conditions have yet to be completed.

To consider the gallmaker's perspective, larvae are under strong selection to induce large galls (Weis and Abrahamson 1986, Weis *et al.* 1992). Larvae occupying small galls (<18 mm) are very vulnerable to attack by the parasitoid *Eurytoma gignatea* Walsh (Hymenoptera: Eurytomidae). Larvae in large galls (>22 mm) are almost never attacked because they are protected by a gall wall too thick for the parasitoid's ovipositor to penetrate (Weis *et al.* 1985). Although bigger is better for *Eurosta's* protection from parasitoids, biggest is not always best. Insectivorous birds, predominantly the Downy Woodpecker (*Picoides pubesences*), often prey upon the gallmaker during winter months. Larger galls are more frequently attacked (Weis *et al.* 1992). Parasitoid attack is more frequent than bird attack, so on balance, larger galls are safer than small ones.

By reviewing the sequence of events in the *Eurosta-Solidago* interaction it becomes apparent that the host-plant species has the opportunity to evolve defense in depth if needed. Evolutionary modification or loss of plant traits that the gallmaker uses as cues for host finding would render the plant resistant to puncturing. Similar modifications of cues within the bud could confer resistance by causing breakdown in host plant recognition and acceptance. These are evolutionary modifications that would greatly decrease the likelihood that an encounter between the plant and a gallmaker leads to an attack. Likewise, antibiotic defenses such as a hypersensitive response would terminate attacks before appreciable damage was done. Defense at any of these points can be considered resistance because they prevent the gallmaker from putting a drain on plant fitness. Low plant reactivity to the gall-inducing stimulus, such that only small galls are produced, offers another avenue for resistance that in this case is not realized. It is important to note in passing that potential defensive advantage of low reactivity would not stem from the increased mortality of gallmakers in small galls. Parasitoid and bird attack occur after the gall has reached full size (Weis *et al.* 1985) and therefore the gallmaker is not killed until after the damage has been done. (This illustrates the paradox that plant characters which reduce herbivore fitness do not necessarily enhance plant fitness [Price *et al.* 1981]). Rather, any potential advantage to low reactivity could come about only by reducing the energy drain on plant reproduction.

After the damage is done, there may be the opportunity for an additional plant defense. This opportunity is compensatory growth to overcome, in part or in full, the resources lost to the gallmaker (see Trumble *et al.* 1993). Galled ramets still flower, although at reduced levels (Hartnett and Abrahamson 1979, McCrea and Abrahamson 1986). However, experimental results from the greenhouse indicate that when the entire genet is considered, plants with galls grow and reproduce as much as ungalled plants (McCrea and Abrahamson 1985). Although the definitive field experiments have yet to be done, the preliminary data suggest that *S. altissima* may be very tolerant of gallmakers. In the next section I will present a model that demonstrates the necessity of measuring plant tolerance in order to accurately asses the fitness contributions made by resistance.

AN ECOLOGICAL GENETIC APPROACH TO ANALYZING SELECTION ON DEFENSE TRAITS

The discussion of the sequential hierarchy of defense given above has illustrated how a series of defensive characters can work in sequence to modify the likelihood of a completed attack, and then to mediate the consequences. But what are the consequences for natural selection on the individual defense components when they are part of a hierarchy? When the contributions one character makes to fitness depends on the contribution of others, special effort is required to determine the relative strength of selection on each. Laboratory and greenhouse experiments which explore the mechanisms by which defense traits operate and interact are key to understanding what there is for selection to act upon, but they will usually be inadequate to determine the relative strength of selection on these components. This is because the selection strength will often vary with environment (Wade and Kalisz 1990), and so accurate measurements can only be made in realistic environments.

There are many environmental factors that could modify the impact that herbivores make on their host plants, which will then alter the selective value of a defensive factor. For instance, when plants are supplied with unusual levels of water, mineral nutrients and light, plant nutritional quality and defensive chemistry could change, and thus alter herbivore consumption (Mattson 1980, Bryant *et al.* 1987). Further, changes in these resources could alter the capacity for compensatory growth following herbivory (see Machinski and Whitham 1989, Trumble *et al.* 1993). The importance of resource availability in the ecology and evolution of plant defenses has been the focus of much recent research, stimulated by Coley *et al.* (1985). As essential as resource availability may be, I will discuss another feature of population ecology that alters the strength of selection on defense traits. This is the density of herbivores available for attack. Herbivore density is key to understanding selection on defense hierarchies because herbivores are ultimately the agents of selection defense.

Herbivore Density and Variable Selection: A Developmental-Genetic Model

In this section I present a simple graphic model that illustrates how the wax and wane of herbivore population density can alter the intensity of selection on defense. This is a fuller exposition of ideas first present by Weis and Campbell (1992). The model is not predictive in the sense that it is trying to determine optimal allocation to defense or equilibrium genetic variance in defense. Rather, it is a descriptive tool to show the ways that genetic variation in a series of sequentially acting defenses can lead to a variety of selective results. It is a developmental-genetic model in form because it shows how input of genetic and environmental effects interact to yield phenotypes; in this case the ultimate phenotype to be predicted is plant fitness.

To simplify the discussion, the model will make the following assumptions. First, the plant species reproduces asexually. Second, the plant is attacked by a single species of gallmaker. Third, there are two alternative genotypes for each defensive trait; these traits are assumed to be polygenic. And fourth, the plant population inhabits a uniform and invariant environment except for the population size of its gallmaker. Because of its developmental-genetic structure, the model assesses the relative fitness of the genotypes based on their defense reaction norms. The term reaction norm refers to the expected relationship of phenotype to some environmental factor for a given genotype.

To understand what reaction norms are, consider how they would be measured in an experiment to determine the effect of dietary nitrogen on pupal weight. Suppose two inbred strains of a single lepidopteran species were used in the experiment. Several caterpillars from each strain could be reared on a low N diet, several each on a number of intermediate N levels, and finally several each on high N diets. At pupation, one could then graph the pupal weight achieved at each N level for each genetic strain. Two curves could then be drawn—one for each strain. These curves could differ in shape or position, and thereby show how the two strains reacted differently to N in the diet. Therefore, these curves show the reaction norm of size to dietary nitrogen for these two genetic strains. For a continuous variable like weight, the reaction norms can be quantified as algebraic functions, which can be estimated by regression (Weis and Gorman 1989, Gavrilets and Scheiner 1993).

The developmental-genetic model is shown in Figure 3, which illustrates the interactions of genes and environment which determine plant fitness. When gallmakers are absent, plant fitness will be determined by a series of genes regulating growth and development and by environmental inputs such as light, mineral nutrients, and water. These sets of factors interact to determine a basic plant fitness reaction norm. However, as mentioned above, this discussion assumes such environmental factors are constant, and so basic fitness will be determined by genes alone.

The hypothetical plant species has genes coding for defense. Some of these code for a resistance factor, such as a secondary metabolite that deters the gallmaker. The alternate resistance genotypes, *a* and *b*, code for two different tissue concentrations of the chemical and so they will experience different levels of damage, which can be measured in terms such as biomass devoted to galls and gallmakers (damage is not measured as fitness loss at this point). But, how much damage will plants of each genotype receive? This will depend on the density of adult gallmakers that forage through the habitat. When none are present, neither genotype suffers any damage. But if gallmakers are abundant, the genotype producing more of the deterrent (*a*) will suffer less damage than the one with lower deterrent levels (*b*). The amount of damage incurred will increase with gallmaker density for both *a* and *b*. It could thus be possible to determine the algebraic relationship between gallmaker density and damage for the two genotypes (Fig. 4a); these are the resistance reaction norms. At zero density the two genotypes are identical because there is no damage, but at high gallmaker densities the two genotypes diverge. A pattern similar to this has been observed for basket willow (*Salix verminalis* L.) when attacked by the gall midge *Dasynura marginemtorquens* Bremi. Strong *et al.* (1993) found that, during outbreaks, some willow strains were almost untouched by the midge while others were heavily galled. As the outbreak subsided in subsequent midge generations, infestation levels became more equitable among the strains. The resistance reaction norms depicted in Figure 4a are accelerating functions, but as will be discussed below, other shapes could be expected.

By themselves, the resistance reaction norms do not indicate which of the resistance genotypes will confer higher fitness. To determine this, one must also consider tolerance to damage. This too can be depicted as a reaction norm, where the expected reproductive output is measured as a function of damage (Fig. 4b). When no damage occurs, we will assume that both genotypes reproduce at the same maximum level of 1.0. However, when damaged, reproductive output will be less. In this example, genotype *y* suffers heavily with increasing levels of damage. However, genotype *x* is able to undergo partial compensatory growth, and hence suffers less. Tolerance reaction norms also can have a variety of shapes, depending on the degree of compensation (including overcompensation [Trumble *et al.* 1993]).

Although the tolerance reaction norm shows the expected fitness given the level of damage, it does not predict the level of fitness expected at any particular gallmaker density. This fitness is determined by the combined effects of the resistance and tolerance reaction norms, which can be called the defense reaction norm. When the algebraic function for resistance (damage versus gallmaker density) is substituted into the damage term for the tolerance function (fitness versus damage) a new expression results that depicts fitness as a function of gallmaker density (Fig. 4c). This defense reaction norm can be used to evaluate the relative contributions of the resistance and the tolerance genes to fitness, and how they change with the gallmaker population density.

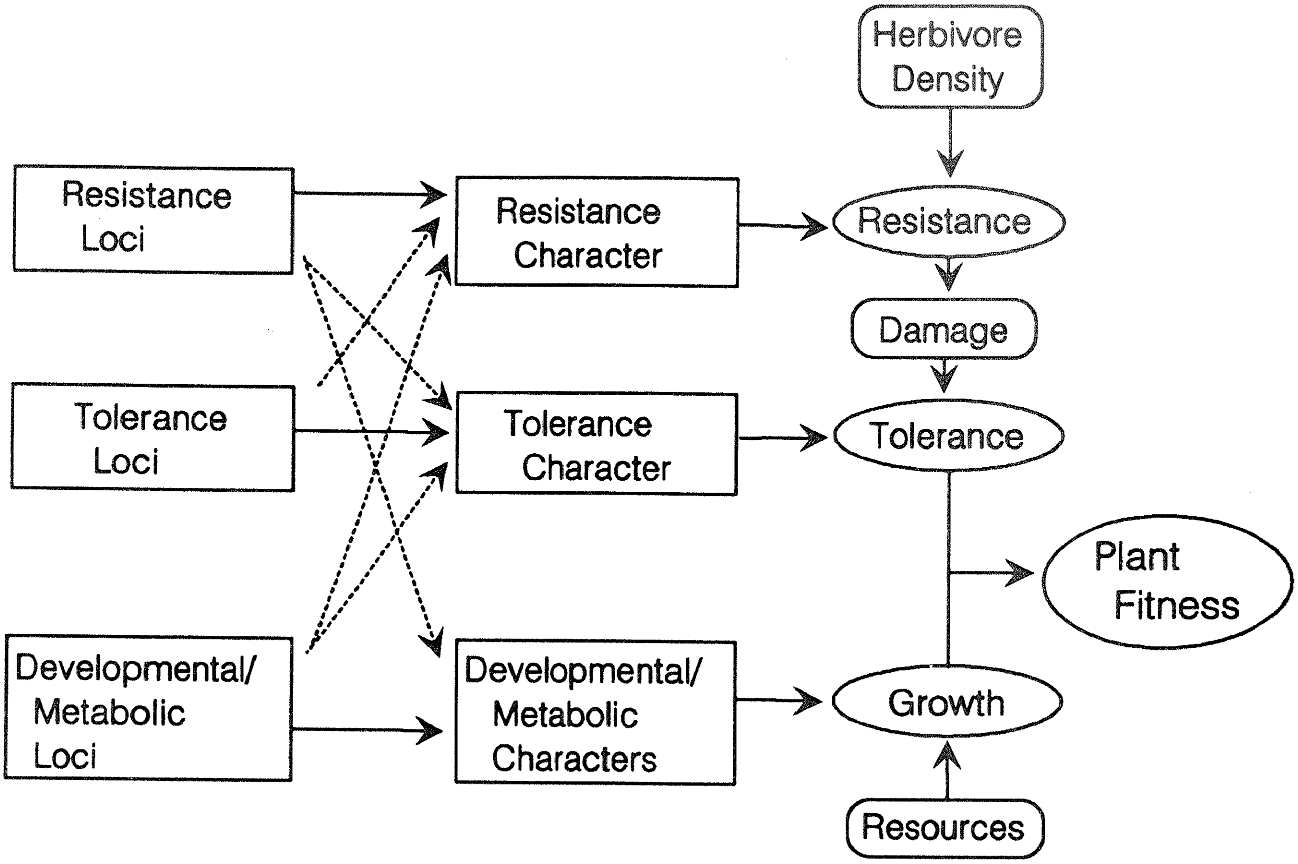

Figure 3.—A developmental-genetic model for contributions of plant defense components to plant fitness. Rectangles represent genetic loci and the traits they encode. Rounded rectangles represent environmental factors. Ellipses represent reaction norms, that is, phenotypic responses to environmental variation. The model reflects the fact that resistance and tolerance are expressed as part of a sequential hierarchy of defense. The intensity of selection on resistance to fitness will depend on the level of tolerance, and the intensity of selection on tolerance will depend on the level of resistance.

An examination of Figure 4c shows a few possible relationships between resistance and tolerance. The four genotypes represented are the four possible combinations of the two genotypes for each defense component. Genotypes *ax* and *ay* have high fitness across the range of gallmaker densities, and diverge only when gallmakers are very abundant. Although these two have different levels of tolerance, this difference makes almost no impact on fitness differences. This occurs because neither of the genotypes suffer much damage, thanks to the high resistance levels; although *ax* is potentially better at compensatory growth at high damage levels than *ay*, that potentiality does not come into play because not enough gallmakers attack to inflict that much damage. By contrast, *bx* and *by* have lower fitness across the spectrum of densities, and the two diverge from one another when gallmakers are abundant. Increased tolerance is an asset to *bx* because it is likely to suffer heavy damage, whereas low tolerance puts *by* at a disadvantage for the same reason.

The result from the particular set of circumstance laid out in this hypothetical example is that genes that increase resistance conferred a greater selective advantage than those which improved tolerance. Although this may be a common outcome in natural populations, it is not inevitable. Differences in the level of genetic variance in resistance and tolerance is one factor that could alter this outcome. Other important factors that could alter the relative selective advantages of improved resistance and tolerance includes costs to defenses.

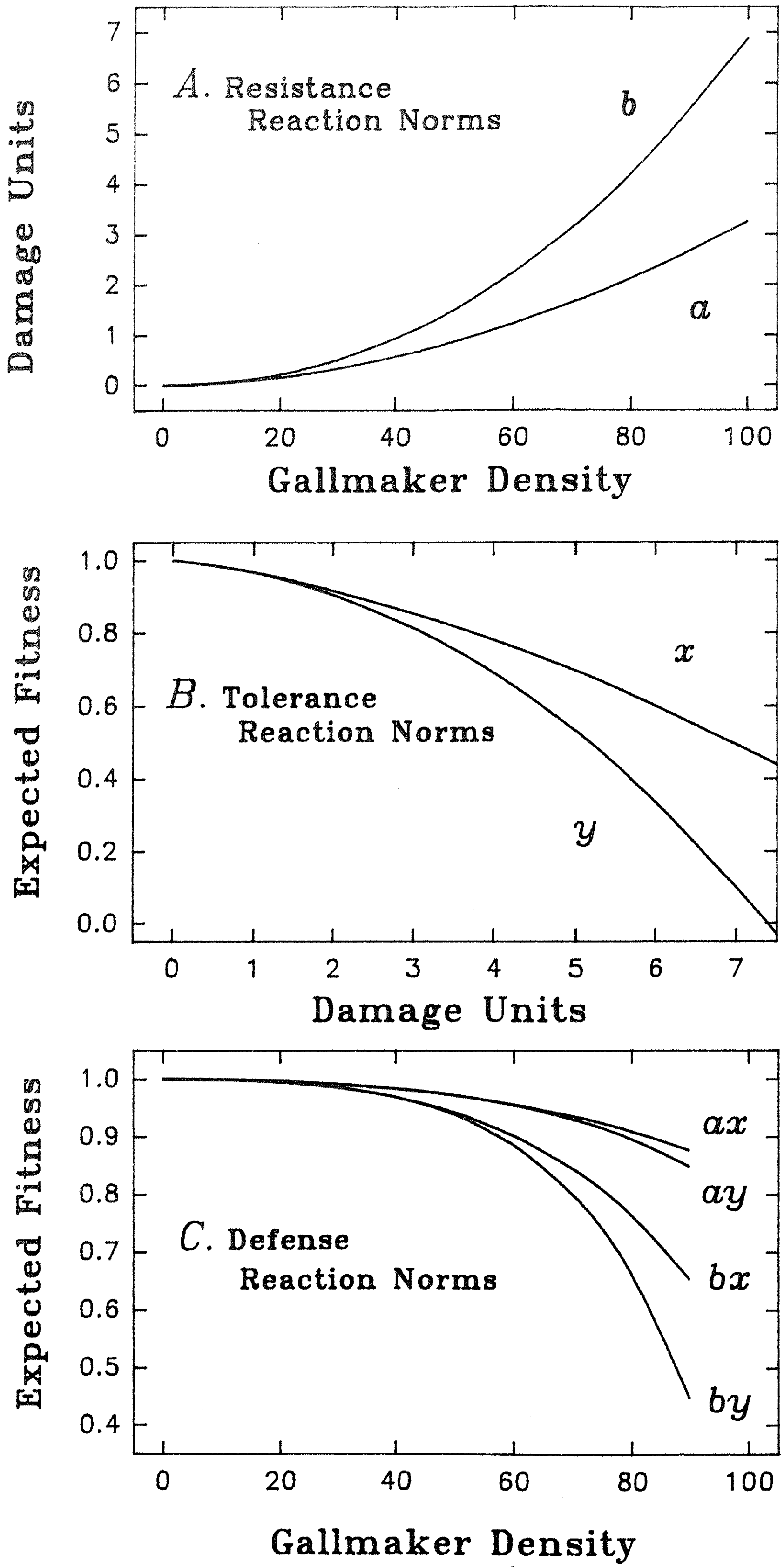

Figure 4.—Hypothetical reaction norms for defense components. (A) Two resistance genotypes differ in the amount of damage they incur with increases in gallmaker population density. (B) Two tolerance genotypes differ in the amount of fitness lost with increasing levels of damage. (C) the total damage reaction norms are the product of the two component reaction norms. In this case selection is stronger on resistance than on tolerance.

Herbivore Density and the Costs of Defense

The production of a defense could impose metabolic or developmental costs on a plant. Much thought and work has been devoted to the costs of resistance, although many empirical studies have failed to demonstrate a cost (see review by Simms 1992). Some difficulty arises since nearly all studies of natural systems to date integrate the impacts of resistance and tolerance on fitness. Since the developmental-genetic model outlined above disentangles resistance and tolerance, it can serve as a vehicle to better understand to selective consequences to defense costs.

In the typical scenario for a cost to resistance, the allocation of resources to factors which deter herbivores causes reduced allocation to reproduction. When resistant and non-resistant plants are grown in a herbivore-free environment, the defended plants are expected to achieve lower fitness than the undefended ones since they pay the cost but receive no benefit. Relative fitnesses are reversed when insects are present, however, because the defended plant receives less damage and hence realizes a benefit for the cost paid. The undefended plant pays no cost but suffers the consequence. This scenario can be depicted by defense reaction norms, as illustrated in Figure 5. As above, the a resistance genotype deters gallmakers better than *b* (Fig. 5a). However, some of the resistance loci at the same time influence the level of tolerance since they alter the resource base available for reproduction. For simplicity, assume the two tolerance genotypes are identical at all other loci except for those that also contribute to resistance. The result is that tolerance genotype *x* is always associated with resistance genotype *b* and tolerance genotype *y* is always associated with resistance genotype *a*. Note that tolerance genotype *y* has 10% lower expected fitness across all damage levels (Fig. 5b); this reflects the cost associated with resistance factor a. When the resistance and tolerance reaction norms are combined, the typical scenario for a cost to resistance is seen (Fig. 5c). When gallmakers are absent genotype *bx* (low resistance) confers greater fitness, but when they are abundant the fitness of genotype *ay* (high resistance) is the greater; at an intermediate level fitnesses are equal. The implication of these results is that the strength of selection on the two defense components can change with the wax and wane of herbivore population density.

Most thought on the cost of resistance has focused on production of plant structures or compounds that will deter herbivores. It is probably true that things such as mustard oils and dense mats of trichomes will keep most insects off a plant. But resistance factors like these are frequently overcome by specialists, and in fact some characters, such as volatile secondary metabolites, are important recognition cues for specialist insect herbivores. When choosing among hosts within a population, specialists may not be avoiding the most noxious plants, but rather searching for the healthiest—these may be the plants that offer the greatest nutritional rewards. This is likely to be true with gallmakers, since it has been shown in a number of cases that the most rapidly growing plants and plant parts are preferred for gall induction (e.g. Whitham 1979, Craig *et al.* 1989, Horner and Abrahamson 1992). This would indicate a uncompensated cost to resistance (Weis *et al.* 1989). This scenario can also be depicted as a set of reaction norms (Fig. 6). As in the typical 'cost of resistance' scenario, the genetic loci that influence resistance level also influence tolerance. Plants of genotype *b* grow rapidly and so are attractive to gallmakers (Fig. 6a). When many gallmakers are present, this genotype is more heavily galled. Plants of genotype *a* grow slower and are less heavily galled. But because of *b*'s superior growth characteristics, it is also able to tolerate a greater level of damage. The tolerance reaction norm *x* shows that the attractive genotype not only has a higher reproductive potential in the undamaged condition, but loses less of that potential when attacked, as compared to reaction norm *y* for the unattractive genotype (Fig. 6b). As a result, the defense reaction norm for genotype *bx* is superior to *ax* at every gallmaker density (Fig. 6c); although resistant to attack, this genotype never achieves greater fitness. The later genotype would eventually disappear from the population unless it is sometimes favored by other variable environmental conditions.

Other Population and Community Phenomena which can Alter Selection on Defense Components

A long list of ecological variables may alter the value of a resistance mechanism, and so alter the contribution that resistance makes to fitness relative to that made by tolerance. Only a few of these factors can be briefly mentioned here. All of them deserve further theoretical and empirical investigation.

Intraspecific competition among gallmakers could alter the rate at which plants accumulate damage as gallmaker populations increase. Competition for galling sites could be manifest in several ways. Oviposition-deterring pheromones could deter ovipositing females from otherwise suitable and attractive plants; so could direct agonistic interactions (see Whitham 1979). This would cause the resistance reaction norms to reach a plateau. At very high insect densities, all plants could suffer similar oviposition rates and so post-oviposition defenses would be the more strongly selected.

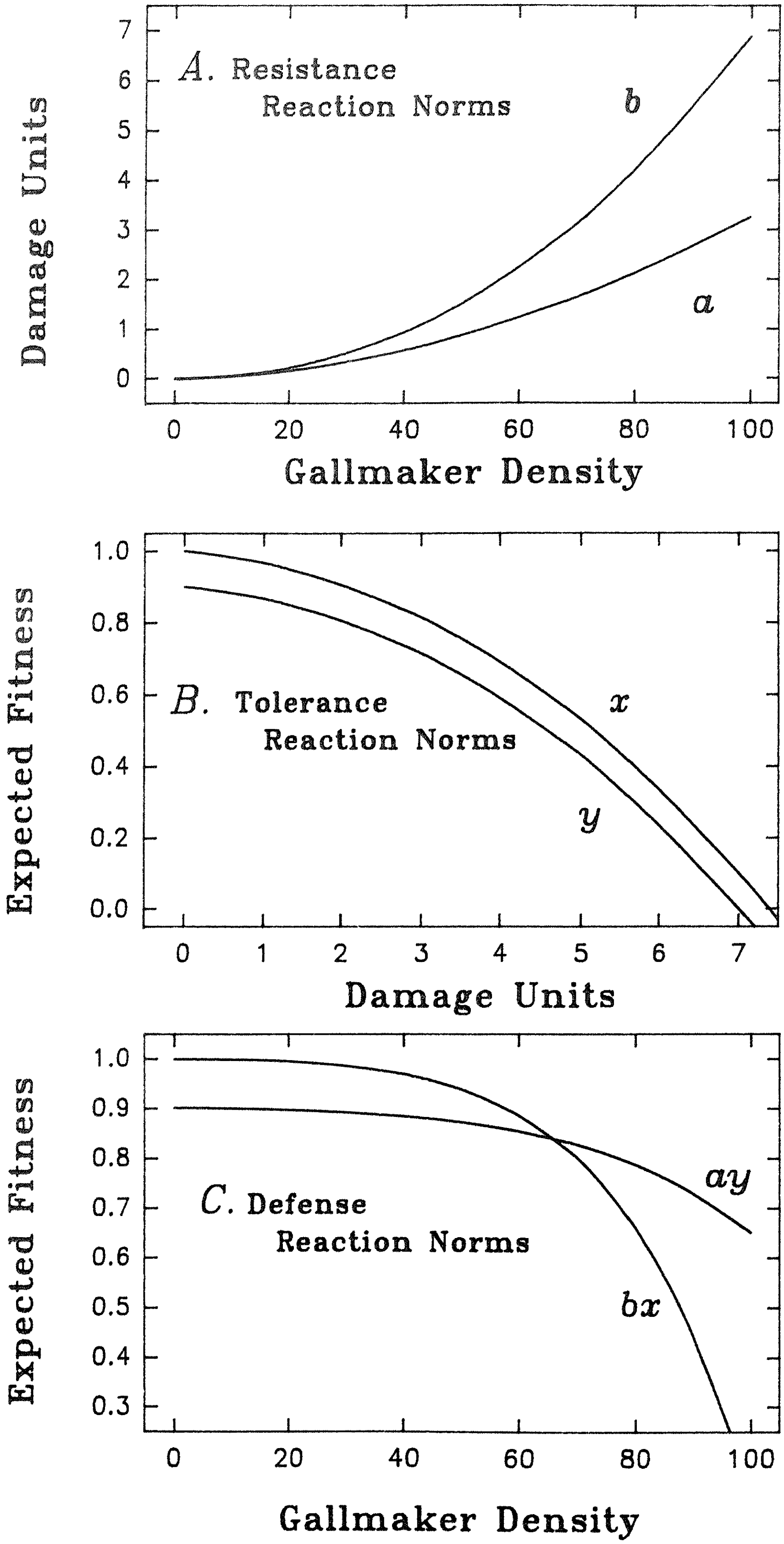

Figure 5.—Hypothetical reaction norms for defense components illustrating the example where resistance exerts a cost. (A) Same as Figure 4. (B) Tolerance reaction norm *y* is always associated with resistance reaction norm *a*, and similarly *x* with *b*. Since the resistance factor exerts a metabolic cost, the expected fitness of *y* is always lower than *x* which produces no resistance and hence pays no cost. (C) When gallmakers are scarce, *ay* pays the cost but receives no benefit. When gallmakers are abundant, *ay* does gain an advantge over *bx* because it has more protection.

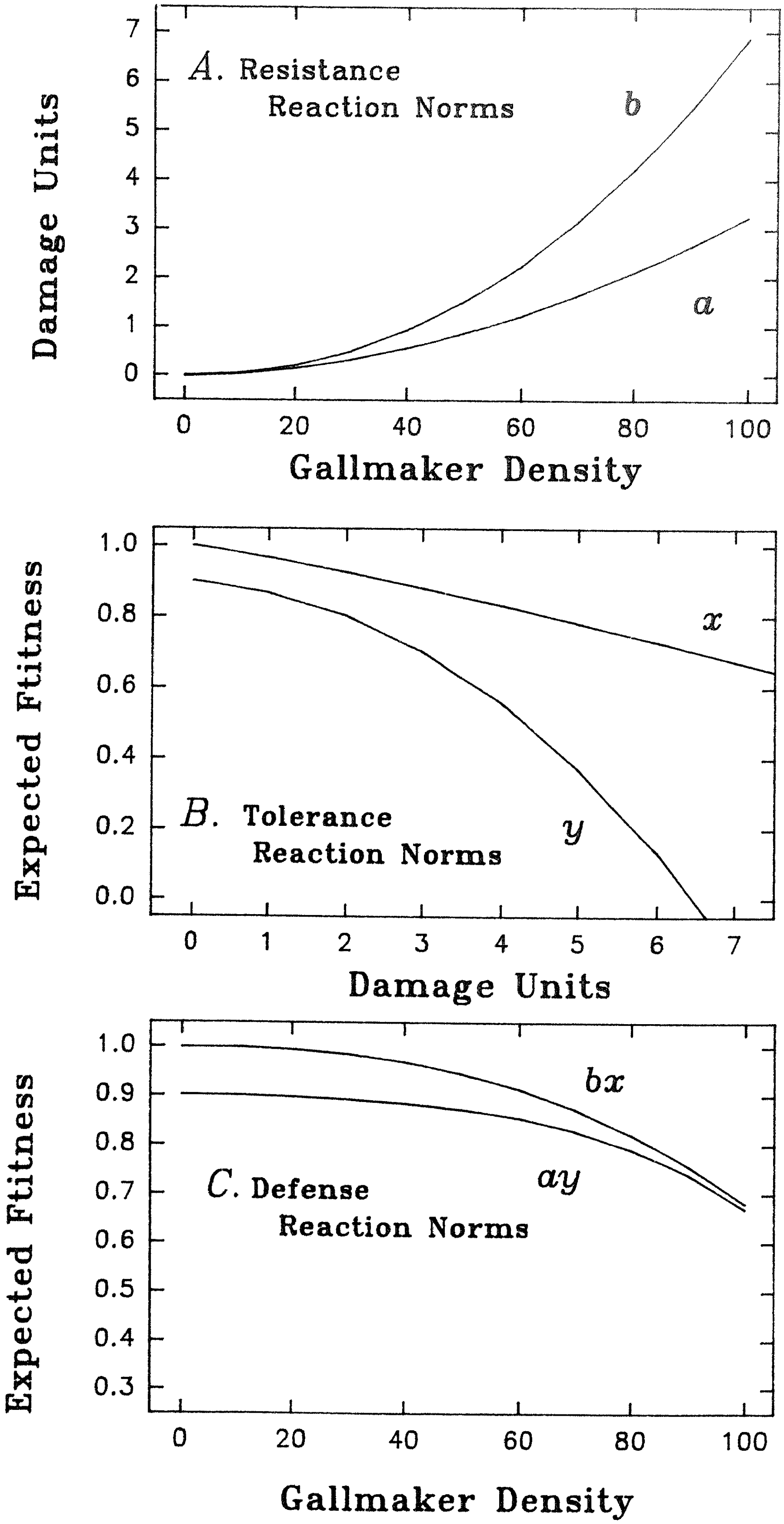

Figure 6.—Hypothetical reaction norms when gallmakers preferentially attach the more vigorous genotype. (A) Same as Figure 4. (B) Tolerance reaction norm *x* as always associated with resistance reaction norm *b*. The *bx* genotype is preferred by the gallmaker because it produces more vigorous plants. Because it is more vigorous, it also is better able to tolerate damage than *ay*. (C) Although *bx* has greater damage levels, it is sufficiently vigorous to maintain superior fitness under all levels of gallmaker density.

The resistance exhibited by a plant genotype may vary with its frequency in the population. An plant genotype that is intrinsically resistant may nonetheless get damaged if it is in the midst of conspecifics that are highly attractive. This could occur if a large aggregation of insects is drawn in by the attractive plants; part of this aggregation could then spill over onto the resistant plants. The fitness differential between the resistant and attractive genotypes could thus be less when resistance genes are at low frequency than when they are more common. Similarly, the disadvantage of having a susceptible genotype could be diminished when surrounded by r esistant individuals, since most foraging insects would first encounter resistant plants upon entering the habitat and leave. The details of the frequency and dispersion of resistance genotypes in the plant population can be a key component that determines the hierarchy of plant resistance (Horner and Abrahamson 1992).

Finally, most plant species are attacked by more than one insect species. Any particular plant defense mechanism might be effective against more than one of these, and so attack rates by two or more insect species can be correlated. A character that deters one herbivore may attract another and thus cause negatively correlated resistance. Selection intensity will fluctuate with the wax and wane with whole suites of herbivores; some of the consequences of correlated resistance are discussed by Maddox and Root (1990) and Fritz (1992). One interesting situation yet to be explored concerns correlations in tolerance to two or more herbivores. For instance, it is possible that the genes which would allow a plant to recover from defoliation would also decrease the ability to recover from gallmaker attack.

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BIOSYSTEMATICS OF HACKBERRY PSYLLIDS (PACHYPSYLLA) AND THE EVOLUTION OF GALL AND LERP FORMATION IN PSYLLIDS (HOMOPTERA: PSYLLOIDEA): A PRELIMINARY REPORT

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Abstract. Psyllids or jumping plant-lice are a group of more than 2000 species of phloem-feeding sternorrhynchous homopterans. Most psyllid species are monophagous or narrowly oligophagous on angiosperms. Many psyllids are free-living. However, two types of concealment, lerps and galls, have evolved. Both these forms of concealment or shelter construction reflect widespread evolutionary tendencies in Sternorrhyncha, raising several questions. How evolutionarily conserved are these features? What are the evolutionary origins of different types of concealment, and do they arise in a predictable phylogenetic sequence? What is the adaptive significance of these features? How might adoption of the galling lifestyle affect subsequent rates of character change and speciation? Our approach to these questions has included both detailed examination of the relationship between gall formation and speciation in the genus Pachypsylla, and broad comparative studies.

Among North American psyllids, Pachypsylla is perhaps the most complicated group of gall makers. They produce a variety of gall types on the leaves, petioles, buds and twigs of several species of Celtis subgenus Euceltis (Ulmaceae). The great variation in gall morphology has led to widely differing views on the systematics of Pachypsylla. Our life history and allozyme studies so far suggest the following: (1) The petiole gall maker, bud gall maker and twig gall maker are distinct species from the leaf gallers. (2) The leaf gall makers form a monophyletic group. (3) The leaf gall makers are very little diverged in allozymes or morphology; however, there are at least three species in the leaf gall maker complex and the different gall shapes might all be different species. (4) Collections of a single gall morph (blister gall) from two sympatric host species showed no evidence of allozyme divergence. (5) Center cell and side cell nymphs within the same individual nipple gall probably represent different species. (6) Side cell individuals are also distinct from other gall types, and probably represent an early stage in the evolution of inquilinism. (7) The phylogeny of Pachypsylla suggests that leaf galling is ancestral, and other gall positions derived. It seems possible that this evolutionary progression is driven by competition.

Pachypsylla forms completely enclosed galls, but its nearest relatives form lerps, partial (pit) galls, or both. This observation has suggested that, in psyllids, lerp formation and pit gall formation could be evolutionary precursors to fully developed galls. As a step toward testing for such long-term trends of galling evolution, we have mapped literature records of psyllid shelter formation onto the psyllid cladogram of White and Hodkinson (1985). Using a randomization approach, we find significant phylogenetic conservatism in the distribution of both galling and lerp formation, suggesting that the potential for large-scale trends exists.

INTRODUCTION

In recent decades, numerous aspects of insect galling have received intensive study, including gall morphology and development, physiology and biochemistry of gall tissues, life history, behavior, host specificity, and nutritional physiology of gall makers, and trophic relationships of the complex assemblages of organisms associated with galls (review in Mani 1992). However, there is still relatively little understanding of the evolutionary origin, adaptive significance and ecological and evolutionary consequences of gall formation (Price 1992, Price *et. al.* 1987). To investigate these questions further, we have undertaken a long-term study of the phylogeny and evolutionary biology of gall formation in the Psylloidea, with particular focus on North American hackberry gallers in the genus Pachypsylla.

The Psylloidea (Homoptera: Sternorrhyncha) comprise about 2000 species (Hodkinson 1984). They feed on a wide range of dicots, with a few species on monocots. They are usually narrowly host specific, and species that initially appear to feed on more than one plant family are likely to represent complexes of host specific sibling species (Hodkinson 1986, Klimaszewski 1964, Yang *et al.* 1986). As suggested by the common name "jumping plant lice," psyllids are sucking insects, feeding primarily on the soluble contents of phloem, though some species attack mesophyll tissues (Woodburn and Lewis 1973; Hodkinson 1973, 1984; White 1970). In Roskam's view (1992), feeding on plant sap offers homopterans extensive opportunities for manipulating host plants, accounting for the repeated evolution of gall formers in this group.

Gall-forming psyllids are broadly distributed across plant taxa and geographical regions. There are at least 350 gall-inducing species (Mani 1964, Hodkinson 1984, Dreger-Jauffret and Shorthouse 1992), constituting more than 15% of all psyllid species. Psyllid galls range from simple distortion of plants, such as leaf curling and leaf pit galls, to highly complex structures (Ashmead 1881, Crawford 1914, Morgan 1984), and are usually site-specific on their host plant. The complexity and specificity of ecological relationships in galling psyllids are exemplified by the North American genus Pachypsylla, commonly known as hackberry psyllids. Species in this genus produce a variety of gall types on the leaves, petioles, buds and twigs of their hosts (Fig. 1), four species of Celtis subgenus Euceltis (Ulmaceae), whose geographic distributions are partially overlapping (Fig. 2). The homogeneity of adult morphology in Pachypsylla, contrasted to the great variation in gall morphology and phenology, has led to much difficulty in delimiting species. Over two dozen specific entities have been named, but the status of most of these is unclear.

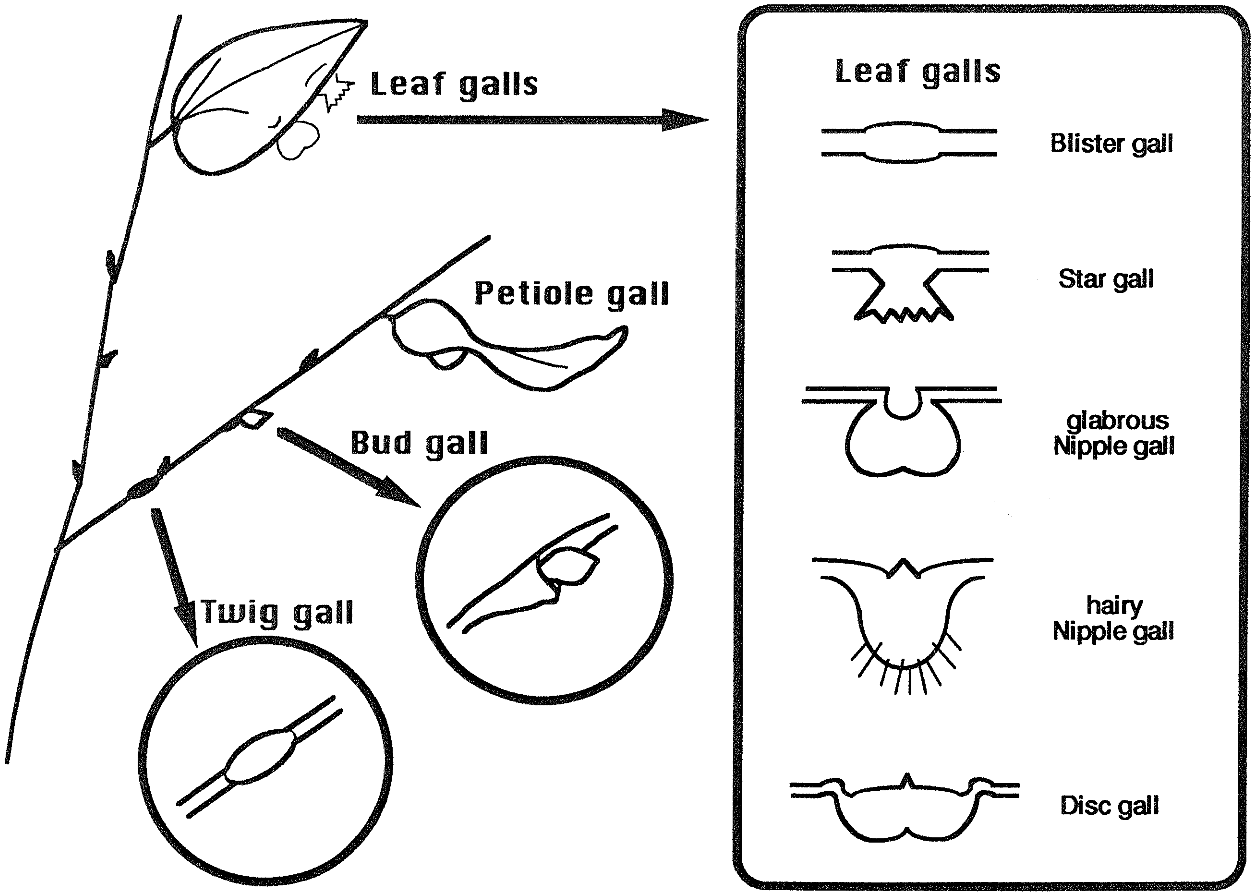
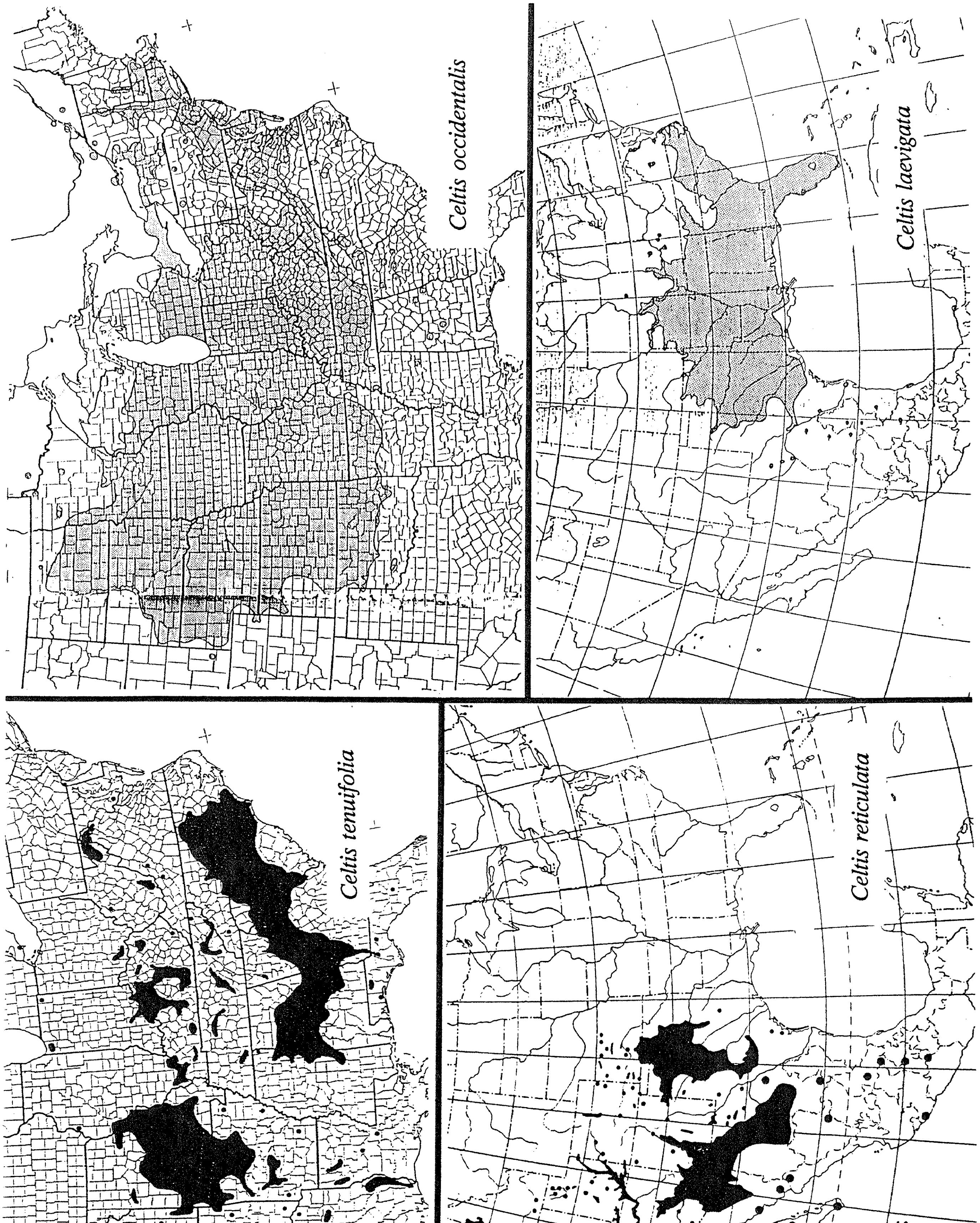


Figure 1.—Diagrammatic profiles of gall types in *Pachypsylla*.



Celtis occidentalis

Celtis laevigata

Celtis tenuifolia

Celtis reticulata

Figure 2.—Distribution of hosts of the hackberry psyllids, *Pachypsylla* (after Little 1977).

Our work on psyllids has had two main goals. The first has been to combine electrophoretic, morphological and life history data to determine species limits and phylogenetic relationships in Pachypsylla, as a basis for understanding speciation and the evolution of host use and gall formation in this group. The second is a phylogenetic, comparative analysis of galling and related habits in psyllids as a whole, asking whether several evolutionary patterns suggested by Pachypsylla reflect broader trends. In this paper we review progress toward these objectives. Our studies seek to address several broad questions about the nature of evolution in gall formers, derived in large part from writings by Price (1980) on the evolution of parasites. More than perhaps any other phytophages, gallers fit the broad definition of "parasites" that Price advanced. Price argued that parasitic lineages should show unusually high rates of diversification. One reason for this derives from the extreme ecological specialization often associated with parasitism. Parasites, such as galling insects, typically live within, and are specialized and intimately dependent for survival on, specific tissues of only one or a few host species. They should thus be especially subject to diversifying selection arising from host heterogeneity. Reproductive isolation could result from such selection either directly, e.g. through adaptive divergence in phenology (Wood *et al.* 1990, Prokopy *et al.* 1988), or indirectly, through pleiotropy (e.g. Rice 1984, 1985, 1987). Other mechanisms by which ecological specialization could promote diversification include reduction of competition between incipient species (Mayr 1976). The postulated association between diversification rate and narrow ecological niche has a considerable history (review in Futuyma and Moreno 1988), and will be termed here the "specialization-diversification hypothesis," following Wiegmann *et al.* (in press).

If galling insects are especially prone to the "specialization-diversification" effect, one expectation is that related species or incipient species should differ most prominently in host species, or in plant part attacked, or in phenology with respect to that of the host, or some other host-related niche dimension. If instead related species largely overlap in such features, then we might doubt the importance to speciation of narrow adaptation to the host. Thus, documentation of the degree and kinds of differences in host use between close relatives, a goal of our study of species limits in Pachypsylla, is a necessary first step in assessing the importance of host adaptation for the speciation of gallers. On a phylogenetic scale, the specialization-diversification hypothesis predicts that ecological specialists should be consistently more diverse than eurytopic clades of the same age, the ideal comparison being between sister groups (Wiegmann *et al.* in press). Previous study (Mitter *et al.* 1988) has shown that phytophagous insects diversify more rapidly on average than predators or saprophages (although this is not true of carnivorous parasitic insects Wiegmann *et al.* in press). If this trend results in part from relative ecological specificity in phytophages, a majority of which have been argued to fit the broad definition of "parasite" (Price 1980), we might expect that exceptionally specialized groups of phytophages, such as gallers, would diversify still faster than other plant feeders. Elevated diversity of gallers would also be expected under the hypothesis that galling is a relatively recent "key innovation" opening a new "adaptive zone" of increased nutrition and/or protection from physical stress and natural enemies (Zwölfer 1978). For example, galling might often be an adaptation to xeric habitats (Fernandes and Price 1992); this adaptation might have permitted radiation of gall formers as the extent of xeric regions increased during the Tertiary.

These predictions contrast sharply with an older view of narrow ecological specialization as an evolutionary "dead end", limiting the potential for subsequent character change and diversification (reviews in Moran 1988, Futuyma and Moreno 1988). The "dead end" hypothesis predicts that gall formers should be *less* diverse than their non-galling sister groups. The "dead end" hypothesis suggests as well a number of potential constraints on the evolution of galling habits themselves. For example, under this hypothesis we might expect evolutionary reversion from galling to free living to be rare, more so than the reverse. We might also expect gall formers to shift among host taxa less freely than related free-living forms. Evolutionary transitions among different types of galling habit, e.g. attack of different host tissues, might be limited to small steps, i.e. those requiring the least genetic change. Such constraint may be manifest from the sequence of habits on a phylogeny. For example, it could be predicted that in Pachypsylla, leaf blade galling should represent the ancestral gall position, as leaf feeding is typical of psyllids as a whole; attack of the petiole, bud and twig may represent successively more different and evolutionarily more recent habits. On a still broader scale, it has been hypothesized that true gall formation itself may arise by a predictable sequence from other forms of concealed feeding. Thus, construction of a lerp (a cover constructed from hardened honeydew; see below) and of partial galls by species in related genera have been suggested by Hodkinson (1984) as precursors to the enclosed galls formed by Pachypsylla.

Phylogenetic study across the psyllids should eventually permit statistical testing for these hypotheses concerning the evolution of gall formation, as galling habits have probably arisen multiple times. In this paper we report preliminary findings on phylogenetic conservatism of galling and related habits in *Pachypsylla* and other psyllids.

SPECIES LIMITS AS RELATED TO GALL FORM AND HOST SPECIFICITY IN HACKBERRY PSYLLIDS, PACHYPSYLLA

Background

Pachypsylla Riley can be divided into three groups based on nymphal and adult morphology and the position of the galls on the hackberry tree. These are the petiole gall maker, leaf blade gall makers, and the bud/twig gall makers. It is generally accepted that there is only one species of petiole gall maker. Several species of bud and twig gall makers have been named, but most of these are based on little information. There is probably only one species of twig galler, *P. celtisinteneris* Mally. The status of the glabrous and pubescent types of bud gall (*P. celtidisgemma* Riley and *P. pallida* Patch, respectively) is uncertain. They may represent one or two distinct species.

The taxonomic situation is most confusing in the leaf gall making complex, within which at least twelve names have been proposed. Riley named many new species based largely on the gall in his series of publications (1876-1890) on hackberry galls. His descriptions of the morphology of leaf, petiole and bud gall makers are contained in a key, in which leaf gall makers were not subdivided because they could only be distinguished by gall shape (Riley 1890). He provided a second key to Pachypsylla, using gall shape only, which distinguished 7 species and one variety among leaf gall makers. The eight types of leaf galls in his key fall roughly into four groups (Fig.1). The blister gall (*P. celtidisvesicula* Riley) is a small, inconspicuous gall which is frequently abundant on *C. occidentalis*. One may easily find more than a hundred blister galls on a single leaf. The star-shaped or flower-shaped gall (*P. celtidisasterisca* Riley) has an extended "corolla" on the underside of the leaf, while a third category is disc-shaped (*P. celtidisumbilicus* Riley). Many names have been attached to the fourth type, the nipple galls. Nipple galls may be glabrous or pubescent, relatively small or large (3-10 mm), and show much variation in shape. Riley named four species (*P. celtidismamma* Riley, *P. celtidispubescens* Riley, *P. celtidisglobulus* Riley and *P. celtidiscucurbita* Riley) and a variety (*P. celtidiscurcurbita* var.? Riley) among nipple gall makers. In our study, we sampled two of the less confused and more common nipple gall types, the hairy and glabrous nipple galls, as well as all the previous types of leaf galls.

Other authors (e.g. Mally 1894, Crawford 1914) questioned these distinctions, in large part because adult morphology is so homogeneous; the putative species differ primarily (if at all) in size. Crawford (1914) and Tuthill (1943), for example, considered all leaf gallers except the blister gall maker (P. *celtidisvesicula* Riley) to represent *P. celtidismamma* Riley. An added complication is the possibility that more than one species may be associated with a single leaf gall shape. Usually there is only one individual inside a gall, but sometimes there can be multiple individuals, each enclosed in a separate cell. The proportion of multiple-cell galls and the number of cells within one gall vary between gall types and localities. Within multiple-cell galls one can generally distinguish between a center cell, presumably the individual that initiated the gall, and one or more "side cells." Two different interpretations of these side cell individuals have been offered. Moser (1965) observed multiple cells in hairy nipple galls in New York State. He called the side cell a "marginal gall" and considered the side cell nymph equivalent to blister gall nymphs, the only other leaf gall that occurs in that area. Riemann (1961), in his unpublished dissertation, named a new species from side cells in many different gall types in Texas. He considered the side cell nymphs, across different gall types, to be the same species. He reported that the side cell species did not have the ability to induce a gall. He considered it an inquiline that became incorporated into the gall by feeding next to the gall maker during gall initiation in the spring, and reported that it could sometimes kill the gall maker by expanding its own cell too much.

A final uncertainty concerning species limits in the leaf gallers is the status of populations on different host species. Some species defined by gall shape use several hosts, and are widely distributed over the range of subgenus *Euceltis* in the United States, e.g. *P. venusta* and *P. celtidisinterneris*. Others are largely restricted to particular species of Celtis (Table 1). For example, in the northeastern United States, the hairy nipple gall (*P. celtidismamma*) and the blister gall (*P. celtidisvesicula*) are commonly associated with *C. occidentalis*, while the glabrous nipple gall (probably *P. celtidisglobulus*) and the star gall (*P. celtidisasterisca*) are usually on *C. tenuifolia*. Riemann (1961) postulated strict host specificity within two of the leaf blade gall making groups, the nipple gall group and blister gall group. He named two new species, separating the blister gall makers feeding on *Celtis laevigata* from those feeding on *C. reticulata*, and restricted the name *P. celtidisvesicula* to blister gallers on *C. occidentalis*. Similarly, he restricted *P. celtidismamma* to the *C. occidentalis* nipple gallmaker, applying a new name to nipple gallmakers on *C. reticulata*, and *P.* sp. (probably *P. celtidiscucurbita* var. ? Riley) to those on *C. laevigata*. Members of the nipple gall group were distinguished by host and gall shape differences as well as slight dissimilarities of male genitalia. The blister gallers were distinguished by host

Table 1.—Synopsis of hackberry psyllid gall types, their distribution and association with host species.

GALL TYPES	ASSOCIATED SPECIES NAMES	DISTRIBUTION	ASSOCIATED HOST PLANT
PETIOLE GALL	*P. venusta* (Osten-Saken 1861) *P. tridentata* Patch 1912 *P. celtidisgrandis* Riley 1876	All over the hosts range, northeast to CT, southwest to AZ, UT, southeast to Georgia, northwest to ID.	C. occidentalis C. tenuifolia C. laevigata C. reticulata
GLABROUS BUD GALL	*P. celtidisgemma* Riley 1885	Central and eastern U.S.	C. occidentalis C. tenuifolia C. laevigata
HAIRY BUD GALL	*P. pallida* Patch 1912	AZ, NM, OK	C. reticulata
TWIG GALL	*P. celtidisinterneris* Mally 1894 *P. ungulata* Caldwell 1938	Reported from central and eastern U.S.	C. occidentalis C. tenuifolia C. laevigata C. reticulata
REGULAR BLISTER GALL without upper central spine	*P. celtidisvesicula* Riley 1884	Northeastern U.S., as for C. occidentalis	C. occidentalis
	new sp. 1 Riemann 1961**	TX	C. laevigata
	new sp. 2 Riemann 1961**	TX, NM, AZ, OK	C. reticulata
BLISTER GALL with upper central spine	?	LA VA	C. laevigata C. tenuifolia*
ROUGH BLISTER GALL without upper central spine	new sp. 3 Riemann 1961**	TX	C. reticulata C. laevigata*
DISC GALL	*P. celtidisumbilicus* Riley 1890	MD, VA, AR, MO, IA, MS	C. occidentalis
HAIRY NIPPLE GALL	*P. celtidismamma* (Riley 1876)	Widely distributed in eastern North America, north to Ontario, south to NC, east to CT, NY, west to NE, KS, OK.	C. occidentalis
	P. rohweri Cockerell 1910	CO, TX, OK	C. reticulata
	P. celtidispubescens Riley 1890	Southwestern U. S., e.g. TX, OK, CO, MS.	C. reticulata
GLABROUS NIPPLE GALL	*P. celtidisglobulus* Riley 1890 *P. celtidiscucurbita* Riley 1890	Northeastern U. S., e.g. MD, VA, MO, MS.	C. tenuifolia
	P. sp. Riemann 1961** (probably= *P. celtidiscucurbita* var. ? Riley 1890)	Southern U.S., e.g. MO, TX, LA.	C. laevigata
STAR GALL with upper central spine	*P. celtidisasterisca* Riley 1890	Southern U.S., e.g. TX, MO, LA.	C. laevigata C. reticulata
STAR GALL without upper central spine	*P. celtidisasterisca* Riley 1890 e.g. MD, VA.	Northeastern U.S., C. occidentalis*	C. tenuifolia
UNKNOWN	*P. tropicala* Caldwell 1944	Mexico	unknown
INQUILINE	new sp. 4 Riemann 1961**	in TX and may be widespread in all gall types except occidentalis blister gall.	C. laevigata C. reticulata C. occidentalis C. tenuifolia

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* occasional observation.

** Unpublished dissertation. Proposed species here numbered arbitrarily.

differences and slight differences in the male genitalia, mainly the head/shaft ratio of the terminal segment of the aedeagus. Riemann attributed some exceptions to host specificity to hybridization among *Celtis* species. Hybridization and introgression among the hosts does seem plausible. The species of the subgenus *Euceltis* are very similar to each other, and there has been difficulty in defining species limits (Elias 1970, Wagner 1974).

Findings to Date

Species Status of Galls on Different Plant Tissues.

Collections of adults from sixteen localities across the United States, representing all four gall types defined by position on the plant, were obtained in 1991. Analysis of 14 allozyme loci in these samples, using cellulose acetate electrophoresis, confirmed that the psyllids that make petiole and bud galls are clearly separate species, from each other and from leaf gallers (Yang *et al.* in prep.). There were multiple fixed or nearly fixed allelic differences among sympatric or nearby populations of all these classes of gall types, in Maryland and Virginia and in other regions as well. (Owing to its rarity in these samples, the twig galler was not analyzed. However, preliminary analysis of subsequent nymphal samples shows clearly that it too is a distinct species.) These findings support the conclusions of previous authors (e.g. Riley 1883, Crawford 1914, Tuthill 1943).

Specific Distinctness Among Multiple Individuals Within the Same Leaf Gall.

The null hypothesis is that no single gall morph represents more than a single species. Moser's (1965) hypothesis predicts that in the multiple cell nipple gall, side cells are "marginal galls" that contain individuals of the co-occurring blister gall maker which have become incorporated into the nipple galls. Riemann's (1961) hypothesis predicts that the side cell individuals in various gall types represent a separate species that does not have the ability to form its own gall. To test these hypotheses, we examined nymphs from the hairy nipple gall and glabrous nipple gall from three populations in Maryland in 1992, plus two other types of galls that commonly co-occur with these (Yang and Mitter in prep. a). These were the blister gall, which never has multiple cells and often co-occurs with the hairy nipple gall, and the star gall, which often occurs with the glabrous nipple gall. We dissected each gall and separated the side cell nymphs from the center cell nymph for both types of nipple galls, and collected the nymphs from mono-cell galls for all four gall types as well.

We found consistent color differences, in general body color and especially in wing pad color, between nymphs from center cells and side cells within nipple galls. The bodies of center cell nymphs were green, with either brown or red maculation, while those of the side cell nymphs were are green with yellow maculation. The center cell nymph always had a darker wing pad, which was usually brown, whereas the side cell nymph always had a light wing pad, which was usually yellow. The mono-cell nymphs also exhibited the same two body color morphs as the center cell nymphs. Subsequent field observations and lab rearing also supported an association between first-instar nymph and adult coloration and cell position, at least in the glabrous nipple gall and the star gall in Maryland. Side cell nymphs in the first instar are white, usually with dark maculation. The adult females have a green abdomen. Center cell individuals have yellow first instar nymphs, and the adult female has a dark abdomen.

Allozyme frequencies in center cell nymphs versus nymphs from mono-cell galls in the same population were not significantly different, nor were the two populations of glabrous nipple gall makers. Within both the glabrous and the hairy nipple gall samples, however, there are strong frequency differences between side cell nymphs and center cell plus mono-cell nymphs. The most pronounced differences are at the malic enzyme locus. Moreover, some (though not all) tree-building methods, such as a distance Wagner tree based on Rogers' distance, group together side cell nymphs from different gall types and localities. Taken together, these observations support the idea that, at least within nipple galls, side cell individuals represent a different species from central cell and mono-cell nymphs. Furthermore, the side cell individuals are not likely to be conspecific with some other gall type, such as the blister gall, because they are markedly different in frequencies from sympatric mono-cell galls of both the blister and star type. Therefore, Moser's marginal gall hypothesis can be rejected. Initial experiments in which individual families of center and side cell forms were reared separately further supported Riemann's hypothesis that the side cell form is an inquiline incapable of starting its own gall.

Species Status of Different Leaf Blade Gall Types

The null hypothesis is that all the leaf blade gall makers, despite making different gall types, form a single species. Under the "two species hypothesis" of Crawford (1914) and Tuthill (1943), only the blister galler (*P. celtidisvesicula*) is distinct from all other gallers (*P. celtidismamma*). Under the "multiple species hypothesis" of Riley (1876-1890) and Riemann (1961), there are multiple species of leaf gall makers (up to seven) distinguished by gall shape and host species.

Our initial evidence on this question (Yang *et al.* in prep.) comes from the electrophoretic analysis of adults collected in 1991, as described earlier. The data suggest that species limits will be harder to determine within the leaf gallers than between these and other gall positions. The leaf gall types appear to be very recently diverged. There are no fixed or nearly fixed differences, and it seemed possible at first that all the leaf gall makers might form a single species. However, there are almost always significant frequency differences between different gall types from a single locality. For example, at Great Falls, Virginia, there are five co-occurring leaf gall types on *Celtis occidentalis*. Three of these types were collected from the same individual tree. At this site, nine out of the 10 pairwise comparisons between leaf gall types showed significant differences.

This finding strongly suggests that the leaf gall makers do not form a single randomly mating population. However, the hypothesis that they are separate species would be stronger if one could show consistent frequency differences of particular alleles, in comparisons from different locations. The best evidence so far for such consistent differences comes in contrasts between the blister gall maker and other gall makers. In particular, there is a consistently much higher frequency of the C allele and lower frequency of the E allele at the IDH-1 locus in the blister gall than in other sympatric gall types, in collections at three widely separated localities from the same host. Similar trends were also seen at the PGM and 6PGDH loci. These results suggest that the blister gall maker, at least, is a distinct species from other gall makers, as recognized by Crawford (1914) and Tuthill (1943). Further evidence consistent with species distinctness of gall form comes from the phenology of gall initiation. Detailed observations were made on glabrous nipple gallers and star gallers, the gall types co-occurring on a single tree at Beltsville, Maryland. The glabrous nipple galls were formed predominantly in early to late April, while the star galls were mostly initiated in late April and May. Progenies of individual females reared at the same time in the laboratory produced either nipple or star galls, but not both, further suggesting that the gall shape difference does not represent intra-population variation.

A difficulty with the allozyme data cited above was that in the adult samples, center-, mono- and side-cell individuals were combined. The inclusion of side cell individuals, which appear to represent a distinct species, could either decrease our ability to detect frequency differences between gall types, or produce apparent differences where none exist, depending on the relative frequency of side cells among different gall types. Thus, definitive resolution of species limits awaits analysis of nymphal samples excluding side cells. However, when we removed individuals carrying the malic enzyme allele most diagnostic of the side cell nymphs, there was no effect on the previous conclusions. This result suggests that the frequency differences or similarities among gall types are not due to "contamination" by the side cell form.

Species Status of Similar Gall Types on Different Host Species.

Riemann (1961) regarded populations of both nipple and blister gall makers on *Celtis laevigata* and *C. reticulata* in the southwestern U.S. as separate species. To test his hypothesis as applied to the blister gall maker, collections were made at three sites in Texas, including Riemann's original localities, in 1992. In each locality, samples of nymphs were dissected from galls collected from two or three sets of paired trees of *C. laevigata* and *C. reticulata*, located within ten meters of each other with no barriers in between.

Allozyme allele frequencies did not differ either between samples from different localities on the same host species or between the pooled collections from the two host species. Thus, these data provide no evidence that sympatric blister gall makers from the two different host species are different species (Yang *et al.* in prep.). Re-examination is needed of the morphological differences reported among blister gall makers from *C. laevigata*, *C. reticulata* and *C. occidentalis* by Riemann.

PHYLOGENETIC TRENDS IN PSYLLID GALLING HABITS

Background

Earlier we laid out a series of hypotheses on possible evolutionary trends among galling psyllid lineages. To test these hypotheses we need both a compilation of psyllid life histories, and a phylogeny. In this section we summarize the still fragmentary state of these comparative data, and present a preliminary search for phylogenetic pattern in psyllid concealment.

Our continuing literature compilation (Yang and Mitter in prep. b) has so far yielded information on galling habits, or lack thereof, for 110 genera, spread across all the families and subfamilies and a majority of tribes. The majority of psyllids are to some extent free-living, and mobile. However, at least two types of shelter construction by the nymphal stages are also widespread, lerp formation and gall induction. Even "free-living" species often exhibit some form of partial concealment, such as secretion of a waxy covering or hiding under bark. These habits illustrate a widespread evolutionary tendency in Sternorrhyncha, the repeated origin of a concealed, immobile way of life from more or less free-living forms.

A lerp is a case constructed from a carbohydrate secretion from the anus of psyllid nymphs (honeydew) which hardens upon exposure to the air (White 1972). These cases are usually found on leaf blades, and each is inhabited and constructed by a single nymph. The structure of the lerp is constant within species (Morgan 1984). Most lerps look rather like bivalve shells. Some look like oyster scale insects, and some form a horizontal tube. Lerps have generally been accorded a protective function, as a barrier against predator and parasite attack, a reflective shield against radiation, or a means of avoiding desiccation (White 1970). Most of the known lerp formers occur in dry regions of Australia, feeding on Eucalyptus, consistent with a moisture-conserving function.

Most psyllid galls are formed by the feeding of the nymphs. Partial galls, such as pit galls or rolled leaf galls, can be distinguished from complete, enclosed galls, exemplified by Pachypsylla. These broad categories may represent different degrees of evolutionary advancement.

Higher classification in psyllids has long been in confusion, with many poorly defined taxa. The most ambitious attempt at a modern phylogenetic arrangement is that of White and Hodkinson (1985). These authors provided a cladogram, based on nymphal and adult morphology, for representatives of 97 genera, about 40 percent of the total, and an opinion on tribal placement for most of the rest. Like most modern psyllid workers, they treat psyllids as a superfamily, with the traditional subfamilies (Psyllinae, Triozinae, Spondyliaspidinae and others) elevated to family rank (Vondracek 1957). In White and Hodkinson's (1985) scheme, *Pachypsylla*, *Celtisaspis* and *Tetragonocephala* constitute the apparently monophyletic subfamily Pachypsyllinae within the Spondyliaspididae. All three genera feed on *Celtis* subgenus *Euceltis*, and all are concealed feeders in the nymphal stages. *Tetragonocephala* contains only the lerp-forming *T. flava* Crawford, known from the southwestern U.S. and from Mexico. *Celtisaspis* species are known from Japan, China, and Korea. Some form lerps only, while others form both partial galls and lerps (Miyatake 1968, 1980; Yang and Li 1982). Pachypsyllinae are the only North Temperate spondyliaspidids, the great majority of which are restricted to Australia, where they feed predominantly on Myrtaceae. The construction of lerps in Tetragonocephala and Celtisaspis may represent retention of an ancestral spondyliaspidid trait, as lerp-forming is otherwise almost unknown in Holarctic psyllids.

Findings to Date

The first question to be addressed in these studies concerns the evolutionary lability of psyllid concealment forms. The hypotheses about evolutionary tendencies in galling clades sketched earlier all presume that galling and related habits arise infrequently enough, and persist long enough, that clades can in fact be characterized by their presence or absence. If instead these features reflect rapid and variable adaptation to local environmental conditions, they might appear and disappear with little phylogenetic pattern, and thus be unlikely to show long-term evolutionary consequences.

To address this question, we mapped the available information on concealment types onto the phylogeny of White and Hodkinson (1985). Each taxon (species or genus) was assigned to one of four concealment categories: free-living (F), lerp former (L), partial gall former (P), and enclosed gall former (G). These designations are certainly oversimplified; the various types of galls may not be homologous to each other, let alone to the lerp, for which the formative mechanism is entirely separate; indeed, a few species seem to form both. (These were coded as galling only.) These categories are meant as strictly heuristic, to permit a first assay for phylogenetic pattern. Two further limitations of this analysis reinforce its preliminary nature. Genera, the terminal taxa in White and Hodkinson's phylogeny, are sometimes variable in concealment type; such cases were scored as having the numerically predominant type. Second, the number of free-living genera is surely underestimated, as the only taxa so scored are those for which the free-living habit is explicitly reported.

To determine whether, despite these potential sources of error, there is detectable phylogenetic conservation of concealment types, we asked whether the minimum required number of origins of concealment types (treated as unordered character states) is smaller than would be expected if the distribution of types were entirely independent of phylogeny, following the random permutation approach of Faith and Cranston (1991). The first finding was that there have been many independent origins of at least some concealment types: the total number of origins is 25, whereas only 3 would be required if each condition arose just once (Yang and Mitter in prep. b). While this might suggest complete lability of these habits, random reassignment of concealment categories nearly always yields still more origins (P= 0.005 in 500 replications), strongly suggesting a phylogenetic component to their distribution. Similar results hold when lerps and gall are each considered separately. Inspection of the phylogeny confirms this impression: many large clades appear to be characterized, though not perfectly, by particular concealment types. Most Triozidae, for example, form pit galls, and the nymphs are flattened so as to conform to the gall shape.

The phylogeny requires only two origins of lerp formation, implying that comparative study alone may provide few degrees of freedom in identifying the adaptive value and evolutionary consequences of lerps. Lerp formation characterizes a large clade in Spondyliaspididae, which are mostly Australian Eucalyptus feeders, except for the north temperate Pachypsyllinae. The second origin also occurs in Eucalyptus-feeding Australian species of *Rhinocola* (*Aphalaridae: Rhinocolinae*); the other known Rhinocola species is South African, feeds on Anacardiaceae and forms no lerp. In contrast to lerps, enclosed galls have arisen at least 9 times, potentially providing a larger statistical base for the study of evolutionary trends.

The Pachypsyllinae appear to show striking conservation of concealment types over time and geography. It is therefore of interest to ask whether the most pronounced gall differences within Pachypsylla, those in plant part attacked, show another form of possible "constraint," namely, a phylogenetic progression suggesting that galling habits change only by small steps. For an analogous complex of galling tenthredinid sawflies, an evolutionary progression has been postulated leading from free feeding, to leaf folding, to leaf galling to petiole and bud galling, to shoot galling (Smith, 1970; Price 1988, 1992), suggesting that each stage originates from the most similar previous habit. A first test of this hypothesis in Pachypsylla comes from preliminary analysis of allozymes in the adult samples of 1991 (Yang and Mitter in prep. c). A distance Wagner tree was calculated on Rogers' genetic distance, and rooted by inclusion of Celtisaspis beijingana, collected in Shenyang, China. On this tree, the leaf blade gallers are closely related among themselves and form a monophyletic group. The petiole and bud galling samples each form clear groups, which are in turn each other's closest relatives. (The same relationships hold in a UPGMA tree on Rogers' genetic distance.) Leaf blade galling appears to be the ancestral condition from which other gall positions are derived, given that the outgroups are concealed feeder on Celtis leaves. The hypothesis predicts that the species forming galls most distant from the leaves, namely the twig galler, not yet analyzed, will be the sister species to the bud galler.

DISCUSSION AND CONCLUSIONS

The evidence to date is at least consistent with a role for narrow host adaptation in the speciation of Pachypsylla gallers, as expected under the "specialization-diversification" hypothesis. The most clear-cut species boundaries are among gallers of different plant parts—leaf blade, petiole, bud and twig. There is only one or two species of petiole, twig and bud gallers each and they have wide host ranges while there are probably lots of leaf gallers and they have narrower host ranges. Within the leaf galling complex, allozyme frequency differences strongly imply restriction, if not absence, of gene flow between sympatric gall morphs. The differences in gall morphology (most probably reflecting change in some aspect of the insect-plant relationship), coupled with the differential distribution of gall morphs over host species, imply that differences in host adaptation could also have figured in differentiation of these apparently incipient species.

The evidence so far points to a marked difference in proclivity to differentiation and speciation, between the leaf gallers and their apparent sister clade containing the remaining species. The allozyme data suggest that in some localities, there could be as many as six or seven sympatric leaf-galling entities. Non-leaf-galling species are fewer in number than leaf galling species. At least in any one locality, there is probably rarely, if ever, more than one species of non-leaf gallers attacking a given plant part. In addition, the non-leaf gallers are much more distinct from each other, in both allozymes and morphology, than any pair of leaf galling types; presumably their divergences are considerably older. They also differ in having broader, largely overlapping host ranges, as does the leaf gall inquiline (Table 1). The leaf gall morphs, in contrast, tend to be restricted to a single host species, at least in any one locality. It might be that the rigors of gall induction on a rapidly-developing leaf enforce especially narrow niche specificity, raising the potential for disruptive selection leading to population differences.

Much more study of the leaf gallers is needed, including extensive geographic sampling and the application of additional genetic markers, to gain a clear picture of the total number of species, their degree of current reproductive isolation and its causes, and the probable sequence and geography of their origin. The host species should be studied simultaneously, since relatively recent vicariance and secondary contact of both subgenus Euceltis and psyllid species is a plausible explanation for the current patterns.

The range of plant parts attacked is greater in Pachypsylla than in any other psyllid genus. It seems possible, though difficult to test, that the "stepwise" evolution from leaf to petiole, bud and twig galling here postulated has been driven in part by competition. The leaf and petiole gallers are frequently extraordinarily abundant, with casual observation suggesting that petiole galls may make the leaf significantly less habitable for the leaf gallers: the leaf blade frequently turns dry when there is a petiole gall on the same leaf.

Our confirmation that the leaf galling complex includes an inquiline species exemplifies another way in which origin of the galling habit promotes diversification, namely by creating new niches. The apparently recent origin of the inquiline—it is substantially less differentiated in allele frequencies from the other leaf dwellers than the non-leaf gallers are from each other—may offer the opportunity to study the early stages in the evolution of inquilinism. One hypothesis to test is that the inquiline gains the advantage of bypassing high mortality in the settling and gall initiation stage as a consequence of its habit. Much additional study of psyllid phylogeny and life history is needed before definitive tests of the macroevolutionary origins and consequences of galling can be carried out. However, the detection of a strong phylogenetic component to the distribution of concealment habits, despite the coarseness of the current evidence, indicates that the possibility of large-scale patterns in the evolution of psyllid galling is worth investigating.

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SEED-FEEDING URODONTIDAE WEEVILS AND THE EVOLUTION OF THE GALLING HABIT

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Abstract. Urodontidae weevils have been recorded from an extensive range of plants in the Afrotropical and Palaearctic biogeographical regions. However, of all these plants only Iridaceae, Colchicaceae, Resedaceae and Aizoaceae are known to be utilized as reproductive hosts, presumably because they meet the crucial requirements necessary for these weevils to successfully complete their life-cycles. The most common reproductive trait of urodontid weevils is to utilize the sturdy seed-capsules and nutritional seeds of their hosts. The exception is, however, encountered in southern Africa where the life-cycle of certain urodontid species is completed in galls incited on the stems of woody Aizoaceae. With a reconstruction of the phylogeny of urodontid genera serving as a basis, it is hypothezised that this unusual galling trait was triggered by the degree in which the reproductive hosts were exploited during urodontid evolutionary development.

Key words: Urodontidae weevils; Afrotropical and Palaearctic regions; reproductive traits; evolution of galling; phylogeny.

INTRODUCTION

Insect induced plant galls are not numerous in Coleoptera. The majority of cecidogenous Coleoptera belong to the weevil families Curculionidae and Brentidae, whilst cases are also known from the Buprestidae and Cerambycidae (Meyer 1987). With the exception of a single instance in South America where a weevil is reported to cause root galls on a monocotyledon (Houard 1933), all the other beetles attack dicotyledons.

In southern Africa two of the 31 known species of the phytophagous weevil family Urodontidae induce galls on their host plants (Louw 1993). Since these weevils form a biologically close-knit group, this atypical phenomenon of selective galling is unexpected. The aim of this paper is to address this event by debating the possible evolutionary route along which cecidogeny developed in Urodontidae. This is done by comparing reproductive strategies of the Urodontidae as a whole and correlating this information with a phylogenetic development scenario of the group resulting from the analysis of morphological and distributional data.

SYSTEMATIC BACKGROUND

The Urodontidae are relatively small (total body length: 1.0-6.0 mm) phytophagous weevils showing both anthribid and nemonychid morphological affinities. Extant species have a fairly restricted continental Afrotropical and southern Palaearctic distribution (Fig. 1). Six genera, namely Ur*odoplatus* Motschoulsky (with 1 species), ***Breviurodon*** Strejcek (with 2 species), *Urodontidius* Louw *in litt.*(with 1 species), *Urodomorphus* Louw *in litt.* (with 1 species), *Urodontus* Louw *in litt.* (with 21 species of which 2 are cecidogeneous) and *Urodontellus* Louw *in litt.* (with 6 species), are known from Africa south of the Sahara (Louw 1991a, 1993). Two additional genera, namely *Bruchela* Dejean and *Cercomorphus* Perris, which both await revision on the species level, occur in the Mediterranean, southern European and southern Siberian Palaearctic. It is postulated that southern Africa is the center of origin of the group, as well as one of the centers of speciation, with the southern European region forming a second center of speciation (Louw 1993).

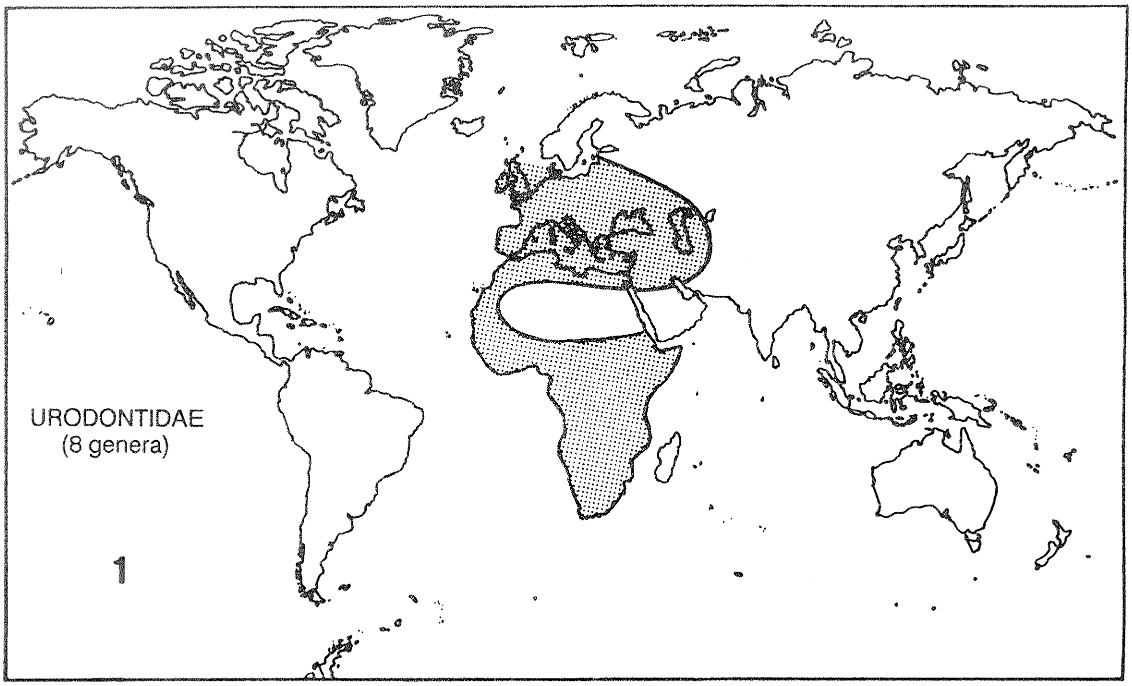


Figure 1.—Known world distribution of Urodontidae (stippled areas).

FEEDING AND REPRODUCTIVE STRATEGIES IN URODONTIDAE

An abundance of hosts has been recorded for urodontid weevils which at first seem to present an ill-defined picture regarding the degree of specialization in urodontid—host plant interaction. However, ongoing field and laboratory studies have revealed that this seemingly disorderly potpourrie of plant associations can actually be separated into two categories, namely primary (or reproductive hosts) and secondary (or feeding hosts) (Table 1). As far as feeding hosts are concerned the criterion is pollen, a feeding niche that lends itself to a high degree of opportunism, hence the wide range of plants that are utilized. The basic criterion for meeting the requirements of a reproductive host, on the other hand, apparently depends on the architecture of the seed capsules of the plant whereby the seeds provide adequate nutrition for immature development and the tough outer capsules provide the fragile immatures with the necessary protection. Reproductive host plants have also been identified where the reproductive requirements of certain urodontids in terms of nutrition and protection deviate noticably from the afore-mentioned more common situation. In such cases open seed-pods and galls are utilized.

The plant groups exploited by urodontids for reproductive purposes are Iridaceae, Colchicaceae and Aizoaceae in the Afrotropical part of their range, and Resedaceae in the Palaearctic part of the range (Table 1). The different reproductive strategies exhibited on these plants are presented in more detail below.

Development on Iridaceae and Colchicaceae

Seed-pods of these plants are slender and elongate and of the typical three-chambered monocotyledonous type (Fig. 2). Urodontids deposit eggs inside all chambers of young developing pods by inserting the ovipositor directly into the soft plant tissue. Complete beetle development occurs inside infested seed pods with larval instars feeding on seeds and pupae forming and eclosing inside pods. Although these host plants are annuals, adults remain inside the dead, dry pods until environmental conditions favour eclosion. Hatching adults chew holes through the outer wall of pods, thereby inflicting characteristic scars.

Table 1.—Known host-plants for all genera of Urodontidae weevils. Asterisks denote field or literature recorded reproductive hosts.

Genus CERCOMORPHUS			(Palaearctic)
	Leguminosae:	*Genista*	
	Frankeniaceae:	*Frankenia*	
Genus BRUCHELA			(Palaearctic)
	Resedaceae:	*Reseda* *	
	Brassicaceae		
Genus BREVIURODON			(Afrotropical)
	No data		
Genus URODONTIDIUS			(Southern African)
	Aizoaceae:	*Eberlanzia*	
Genus URODOPLATUS			(Southern African)
	Aizoaceae		
Genus URODOMORPHUS			(Southern African)
	No data		
Genus URODONTUS			(Afrotropical)
	Aizoaceae:	*Spalmanthus*	
		Mesembryanthemum *	
		Lampranthus	
		Psilocaulon	
		cf *Polymita*	
		Drosanthemum	
		Carpobrotus *	
		Rhuschia	
		Glottiphylum	
		Tetragonia	
		Galenia *	
	Iridaceae:	*Anapalina* *	
		Gladiolus *	
	Colchicaceae:	*Ornithoglossum* *	
	Zygophyllaceae:	*Zygophyllum*	
	Poaceae:	*Chaetobromus*	
	Asteraceae:	*Gazania*	
Genus URODONTELLUS			(Afrotropical)
	Iridaceae:	*Homeria* *	
		Moraea *	
		Watsonia *	
		Bobartia	
		Dietes	
	Asphodelaceae:	*Kniphofia* *	
	Aizoaceae:	*Carpobrotus*	
	Poaceae:	*Chaetobromus*	
	Fabaceae:	*Acacia*	

Development on succulent Aizoaceae

Seed-pods of succulent Aizoaceae are round and inflated and of the five-chambered dicotyledonous type (Fig. 3). Weevil oviposition, development and eclosion are identical to that found on Iridacaeae and Colchicaceae above.

Development on Resedaceae

Resedaceae are dicotyledonous herbs with single-chambered seed-pods which are open on top (Fig. 4). Urodontids oviposit inside young pods and larval development takes place inside infested pods. As pods mature and start opening up on top, exposed larvae compensate by spinning a web to close the openings. Fully developed larvae evacuate pods and pupate in pupal chambers in the soil. Adult eclosion occurs when environmental conditions become favorable.

Development on Galenia (Aizoaceae)

Galen*ia* is a dicotyledonous woody shrub 1.0 m or less in height which predominantly occurs in harsh environments (Fig. 5). Urodontid egg-laying takes place on soft growth tips of Ga*lenia* stems apparently by inserting the ovipositor directly into stem tissue. This action incites gall formation at the oviposition site inside which entire weevil development occurs. Adults possess unique strong-muscled, elongate mandibles which they use for chewing through the tough, thick sides of the galls when eclosing. Empty galls are characterized by distinct circular eclosion holes (Fig. 6).

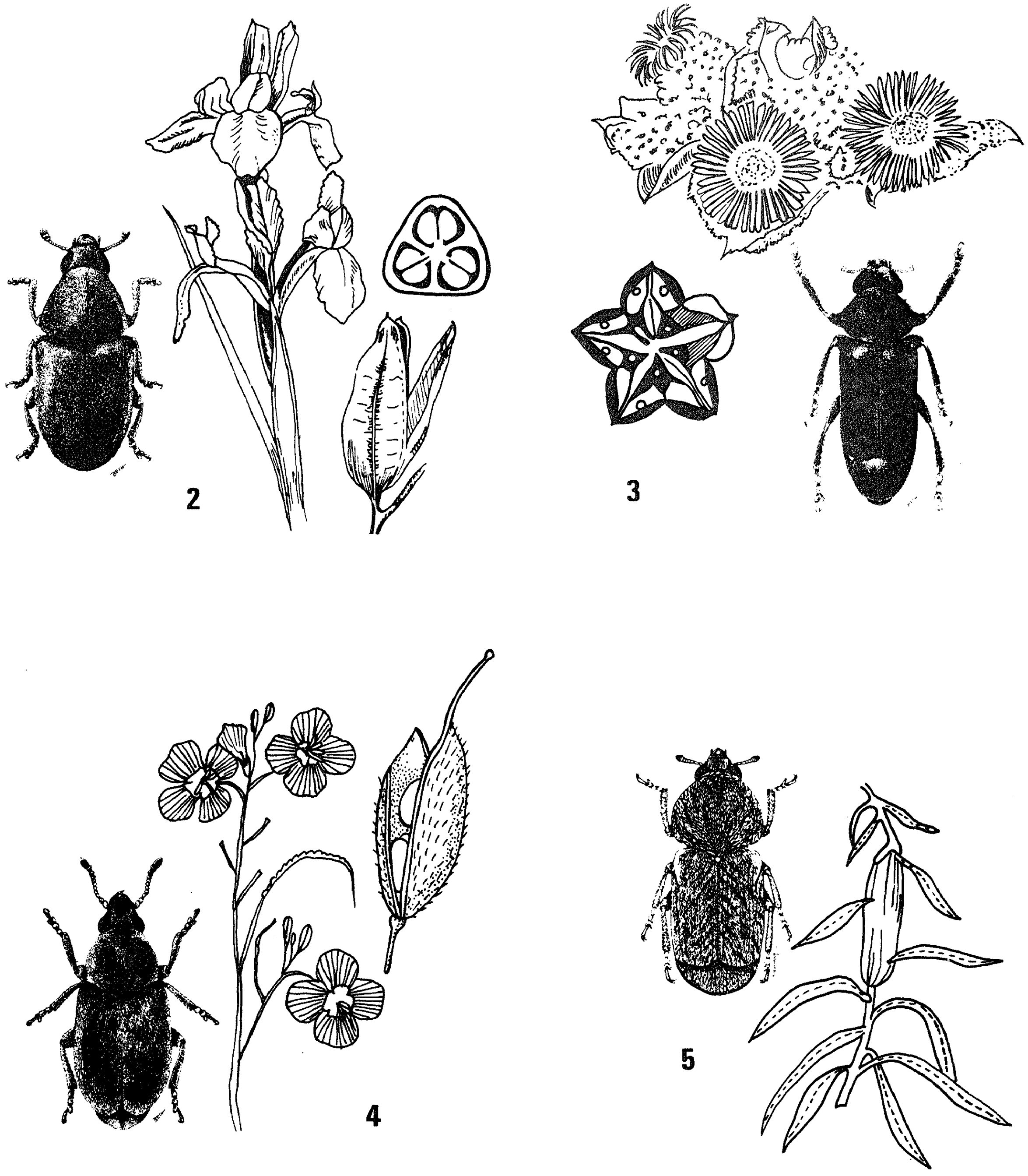
DISCUSSION

Analyses of tranformations of several morphological character suites have resulted in a phylogentic reconstruction of the Urodontidae (Louw 1993). Comparison of these morphological routes of evolutionary development with distributional ranges of extant urodontid genera, reflect a southern African origin for the group with subsequent radiation in a northernly direction prior to formation of the Sahara desert. When this route was eventually blocked by the Sahelian sandmasses, northern and southern speciation centers became established. Especially the more plesiotypic southern urodontid stock underwent further diversification which is identified as definite apotypic branch lineages of the main stock. Thus both the most plesiotypic and the most apotypic representatives of the group occur together in southern Africa.

During their life-cycle the all-important, sensitive immatures of phytophagous insects have to rely on some form of concealment to ensure their survival and ultimate success (Cornell 1990). In urodontid weevils the immature stages are concealed in three ways, v*iz*. inside closed seed pods, inside open seed pods and inside galls. This divergent manner of concealment is unexpected for a group which otherwise forms a biologically close-knit unit. An explanation for such lack of uniformity in immature concealment was therefore sought along the avenue of the previously postulated phylogenetic scenario which is briefly outlined above.

It is assumed that ancestral Urodontidae (with more or less *Urodontellus* affinities) originated on monocotyledonous Iridaceae in an early Tertiary thorn scrub—succulent woodland biome in central and southern Africa. In time the successful utilization of a rapidly expanding succulent flora was experienced when dicotyledonous Aizoaceae plants were colonized and exploited. Dense species packing by U*rodontus* on succulents in present-day Namaqualand in western South Africa bear testimony to continued optimal conditions within this biome which gave rise to intense speciation.

The ability of urodontids to shift between host-plants, which probably arose on account of eco-evolutionary pressure due to more than one species over-exploiting the same reproductive host (Louw 1991b, 1993), supposedly occurred along the main south-north dispersal route ultimately leading to the successful invasion of the Palaearctic. When the Palaearctic *Bruchela* stock became isolated due to the formation of the Sahara Desert, the colonization of Resedaceae (and possibly Brassicaceae) with their open seed-pods became a fixed trait. Successful exploitation of these hosts was achieved through apotypic adaptations; the larvae achieving protection within the seed-pods by spinning a web to close the openings and the pupae resting in the soil.



Figures 2-5. 2. Urodontellus species develop in closed three-chambered seed pods on Iridaceae hosts. 3. Majority of *Urondontus* species develop in closed five-chambered seed pods on succulent Aizoaceae hosts. 4. *Bruchela* species develop in open single-chambered seed pods on Brassicaceae hosts. 5. Certain *Urodontus* species develop in stem galls on woody Aizoaceae hosts.

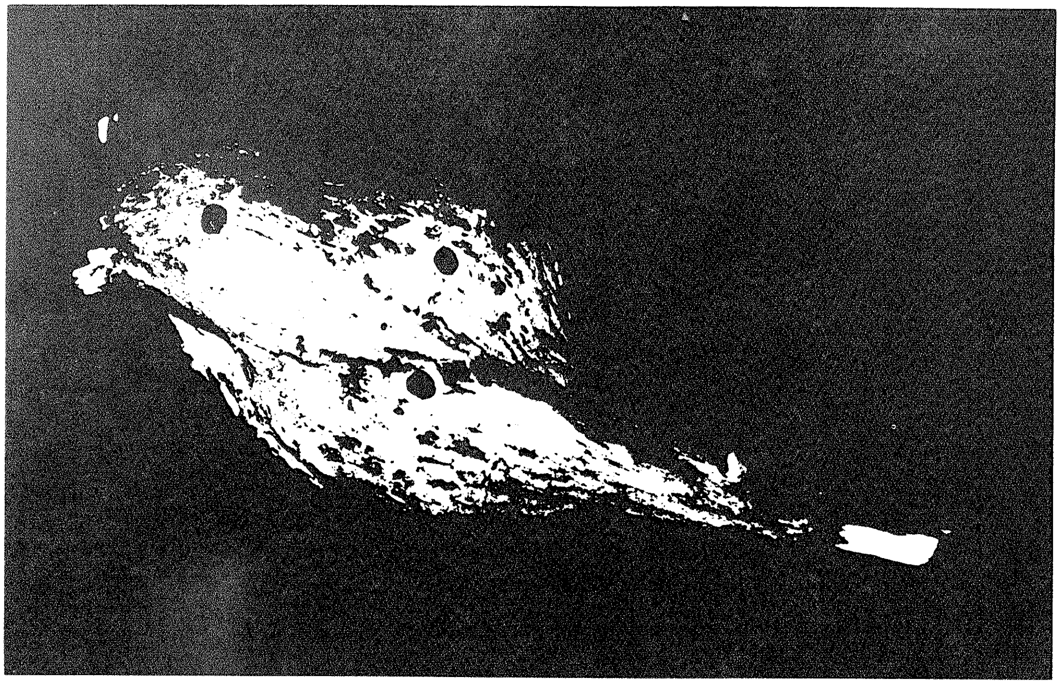


Figure 6.—*Galenia* gall with characteristic circular openings after weevil eclosion. (Note weevil emerging from left upper opening.)

In southern Africa the most advanced, specialized urodontid host shift occurred within the genus *Urodontus* where intense speciation on succulent Aizoaceae presumably caused varying ecological pressures to develop amongst the different species, two of which eventually shifted from succulents to successfully colonize the structurally different Aizoaceae genus *Galenia. Galenia* plants, which possess tough woody above-ground parts, are utilized by these weevils in that stem galls are incited inside which the complete development from egg through to adult occurs.

This scenario, which concerns the main lineages of evolutionary development in the Urodontidae viewed in terms of life history requirements, corroborates well with independant scenarios based on morphology and distribution and is summarized in Figure 7. Weis *et al.* (1988 mention that the phenologies of gall-makers and their hosts have to coincide in certain aspects for gall-makers to be able to reproduce successfully and that because of this there is a strong tendancy among gall-making insects towards a univoltine life history. In urodontid weevils this prerequisite would also appear to be the case in the gall-making species. Moreover, for all the urodontid reproductive traits to succeed a high level of synchrony between the life history of the weevil and the phenology of its host would have to exist. Weevil oviposition, whether it be inside seed-pods or on *Galenia* stems, to induce galls, would have to take place during a relatively brief period when plant growth meets the requirements of the weevils.

The adaptive significance of the galling habit in Urodontidae and its evolution appear to fit the microenvironment and nutrition hypotheses (Price *et al.* 1986, 1987). The hypotheses, however, become slightly more refined in this case in that ecological pressure on one host-plant triggered selective galling on another host-plant with the galling habit here serving as advanced survival and speciation strategies.

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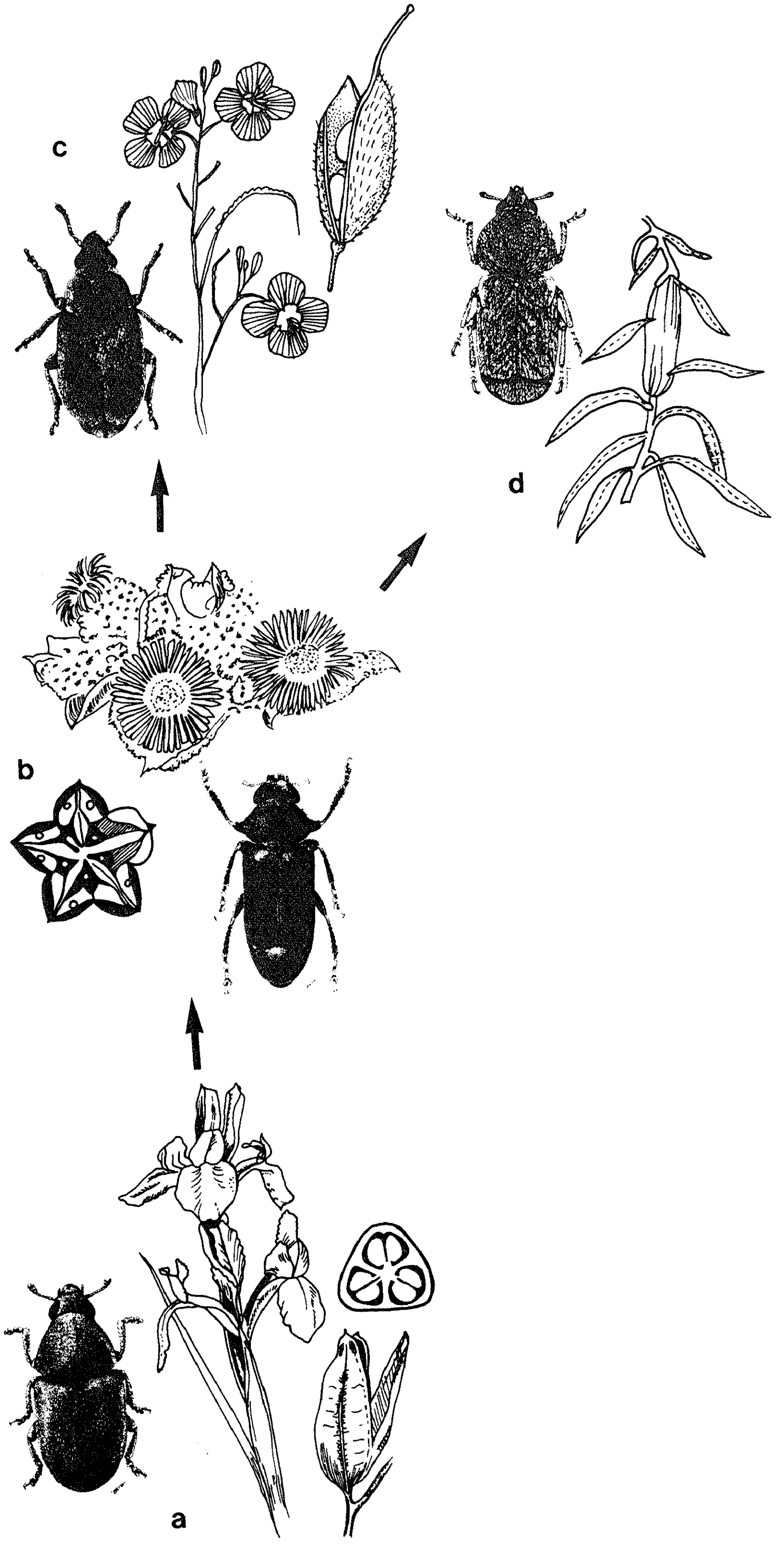

Figure 7.—Evolutionary development of reproductive strategies in Urodontidae. Development ranges from plesiotypic condition on monocotyledonous Iridaceae hosts (a) through to least apotypic condition on dicotyledonous succulent Aizoaceae hosts (b) from which development diverges to more apotypic condition on dicotyledonous Resedaceae -Brassicaceae hosts (c) and most apotypic condition on dicotyledenous woody Aizoaceae hosts (d).

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HOST SHIFTS AND SPECIATION IN GALL-FORMING INSECTS

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Abstract. The phylogenetic constraint of gall-forming results in an adaptive syndrome that has emergent properties that determine which modes of speciation are possible. Gall-forming is an adaptive syndrome that entails endophagy and resource manipulation. This adaptive syndrome leads to a high degree of inter- and intra-specific host specialization by the gall-former. Because of this syndrome the herbivore acquires host-plant characteristics that influence its ecological interactions. We consider how this adaptive syndrome influences emergent properties that could influence the probability of speciation in a host shift. The probability of speciation in herbivorous insects depends both upon the probability of a population of herbivores colonizing a new host and upon the probability that the colonists will become reproductively isolated. We conclude that the adaptive syndrome of gall-formers has the following emergent properties that increase the probability of colonization of a new host plant: they may form polymorphisms in response to intraspecific host-plant variation that may preadapt them for host shifts, and they may be subject to frequency-dependent selection so that individuals in a low-density colonizing population may have relatively high fitness. Gall-formers probably lack the ability to shift hosts on a non-genetic basis, such as experience, that would further facilitate host shifts. The adaptive syndrome of gall-formers has several emergent properties that would facilitate rapid reproductive isolation of populations once a host shift was initiated. 1) There is likely to be a negative correlation of performance traits (survival, reproduction and mating success) required to survive on any pair of host plants. 2) Gall-formers have a genetically based host preference, that is not easily altered by experience. 3) Mating occurs on the host plant. 4) Gall-formers are under strong selection to adapt to the phenology of the host plant on which they oviposit. A key determinant of both the probability of a host shift and of subsequent reproductive isolation is the number of genes involved in shifting host preference and the ability to survive on a new host. This has not been determined for any gall-forming species. An examination of the assumptions of sympatric and allopatric models of speciation shows that gall-formers are more likely to speciate sympatrically.

Key words: allopatric speciation, Eurosta solidaginis, gall-former, host race, host shift, Solidago altissima, Solidago gigantea, sympatric speciation.

INTRODUCTION

Gall-formers and Speciation

The basic processes of speciation in herbivorous insects are poorly understood, despite long debate (Bush 1982, Bush and Howard 1986, Tauber and Tauber 1989). The rate at which speciation proceeds, the genetic changes involved in speciation, the ecological conditions promoting speciation, and the degree of geographic separation between populations necessary for speciation are all poorly known. Specifically, the process of speciation in gall-forming insects has not been extensively explored.

In this chapter we review the evidence for how speciation proceeds in gall-forming insects. We believe that the phylogenetic constraints of gall-forming produce an adaptive syndrome with emergent properties that are crucial in determining the avenues by which speciation can occur. Our usage of the terms, phylogenetic constraint, adaptive syndrome and emergent properites follows that of Price *et al.* 1990). An adaptive syndrome has been defined by Eckardt (1979) as "the coordinated set of characteristics associated with an adaptation or adaptations of overriding importance, e.g. the manner of resource utilization, predator defense etc." Price *et al.* (1990) defined emergent properties as those insect traits (ecological, genetic, and/or behavioral) that inevitably arise as a result of the adaptive syndrome. This use of emergent properties is commonly used in behavioral discussions and should not be confused with Salt's (1979) usage: "an emergent property of an ecological unit is one which is wholly unpredictable from observation of the components of the unit". Our thesis is that the phylogenetic constraints of the gall-former life history strategy leads to an adaptive syndrome that in turn influences the means by which speciation can proceed in gall-formers. We will first discuss speciation models as they apply to herbivorous insects. We will then discuss the pertinent properties of gall-forming insects as they apply to the assumptions of speciation models. Finally, we will review the characteristics of *Eurosta solidaginis*, a stem-galling tephritid fly that forms galls on two *Solidago* species to determine how speciation may be proceeding in this gall-former.

Species Concept

Species concepts are notoriously controversial and it is difficult to find a concept that fits all groups of organisms. We cannot resolve the controversy here. For the gall-formers we are discussing in this chapter, we find it most useful to use the biological species concept of Mayr (1963): "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups." We are herein concerned with understanding how a single gene pool can evolve into two gene pools that are recognizably distinct from each other, and this concept is useful in understanding this process.

Models of Speciation

The possible modes of speciation have long been a source of controversy. Mayr (1947, 1963) has maintained that all speciation occurs through processes involving geographic separation of populations and that it is unnecessary and theoretically implausible to invoke models not involving geographic separation. However theoretical studies have indicated that sympatric speciation is feasible under certain conditions (e.g. Bush 1975a,b; Diehl and Bush 1984; Rice 1984). The resulting controversy has centered on the plausibility and the evidence for sympatric speciation. The degree of geographic isolation is just one aspect of the speciation process, and focus on this controversy may have impeded investigation of other important questions about the process of speciation (Bush 1982, Bush and Howard 1986, Futuyma 1987). Both allopatric and sympatric models of speciation make many assumptions about the behavior, genetics and the degree of spatial isolation that are necessary for speciation to occur. Progress towards understanding speciation requires that all of the assumptions of the speciation models be examined. Whether or not the assumptions are true will depend on the adaptive syndrome of the organism.

A common pattern in gall-formers is to find monophagous sibling species or host races on different species of plants (Ananthakrishnan 1984). We will examine in this paper how such patterns could originate. Because of the intimate association of gall-formers and their host plants, any speciation event will involve changes in the relationships with the host plant or plants. We hypothesize two processes could produce new monophagous species: host shift and host losses. In a host shift a population of monophagous gall-formers colonizes a new host plant, speciation could then result if this population becomes reproductively isolated on this new host resulting in two monophagous species: the ancestral and the derived species. In a host loss, a polyphagous species is divided into two populations at least one of which loses the ability to utilize one of the hosts, this is followed by reproductive isolation and the formation of a new monophagous species.

Speciation and Host Shifts

Models have been developed that demonstrate that speciation is feasible during a host shift in herbivorous insects (Maynard Smith 1966; Bush 1975 a, b; Diehl and Bush 1984, 1989; Rice 1984, 1987). Speciation by a herbivore during a host shift requires two processes. First, there must be mechanisms by which a host shift can be initiated. If it is too difficult for a species to colonize a new host plant, then it is unlikely that a population of an incipient species can be established on a new host. Second, once the shift has been initiated then there must be mechanisms by which reproductive isolation can become established between the new and ancestral populations.

When a host shift is initiated a range of outcomes is possible (Fig. 1). The species can become a single polyphagous species, it can split into two species, or it may exist more-or-less indefinitely in two populations that are only partially reproductively isolated which are often termed "host races". The outcome will depend on the balance of forces favoring utilization of both hosts and those favoring reproductive isolation of the two populations. If the balance lies so that there is some degree of reproductive isolation between the populations once a host shift is made, yet the ecological, and or genetic conditions remain such that a "back shift" is possible, two partially reproductively isolated populations may be maintained indefinitely (Fig. 1b). If the two populations are so reproductively isolated once a shift is made that there is little possibility of additional shifts or "back shifts" then either selection and/or drift would proceed fairly rapidly to the formation of two species, and host races would be a transient situation (Fig. 1c).

Finally, there is the situation where reproductive isolating factors once a shift was made are very strong but where the probability of making a shift is so unlikely that it is an unimportant possibility (Fig. 1d). Below we discuss the factors favoring a host shift and those which favor reproductive isolation.

Factors Promoting a Host Shift

The following traits of herbivorous insects may facilitate the acquisition of a new host plant under some conditions:

1) Adaptation to one host plant may preadapt an herbivorous insect to utilization of a new host, which could facilitate a host shift. Closely related host plants may differ only slightly with respect to the herbivore's requirements (Bush 1975 a, b). Some insects have the ability to be able to survive on host plants that they do not recognize as hosts (Futuyma *et al.* 1984, Rausher 1984b, Via 1984, Hare and Kennedy 1986, Butlin 1987, Futuyma and Phillipi 1987) indicating that a new host could be acquired by a change in host preference alone. Variation found within the ancestral host-plant species may maintain variation in herbivore emergence times and different adaptations required to utilize a range of host genotypes in a population. Herbivores adapted to utilize extreme host genotypes may be preadapted to utilize extreme genotypes of another closely related plant species. If a mutation arose for a change in host preference, some individuals could survive immediately on the new host.

2) If herbivores preferentially oviposit or mate on hosts that they have previously experienced (whether as larvae or adults), the potential for host shifts without the need for genetic changes in preference will be increased (Maynard Smith 1966; Bush 1975 a, b; Futuyma 1983; Diehl and Bush 1989). While the evidence for "larval conditioning" is controversial (Wasserman 1981, Mitter and Futuyma 1983), good evidence exists for adult experience influencing oviposition choice (Prokopy *et al.* 1982, Papaj and Prokopy 1988).

3) If few genetic changes are necessary to enable a gall-former to be able to recognize and utilize a new host plant, then a shift would be facilitated. If many mutations are required, then the probability is small that the mutations would be brought together through recombination in a single individual capable of colonizing a new host.

4) Frequency-dependent selection can favor the establishment of a herbivore population on a new host. One obstacle to sympatric speciation is the maintenance of mutations for shifts in host preference in the interim preceding further mutations for host utilization (if needed). Individuals ovipositing on a novel host as a result of mutations in genes for host selection will have low fitness until mutations for maximizing performance on the new host arise. Therefore, variants ovipositing on plants other than the optimal host will tend to be eliminated by selection. However, models demonstrate that frequency-dependent selection can preserve variation in habitat selection during colonization of an empty niche, such as a novel host plant, if competition for resources is intense. Initially, poorly adapted morphs can persist because fitness obtained from feeding on an abundant, unexploited host where fecundity is low, can be as high as on the normal host where competition for resources is intense (Rosenzweig 1978; Pimm 1979 a, b; Rausher 1984a; Wilson and Turelli 1986).

5) The lower the degree of geographic isolation between host plants, the greater the probability of a gall-former colonizing a new host plant. If a combination of new mutations are necessary for colonizing a new host, the greater the number of colonization attempts there are, the greater the probability that a successful combination will be found.

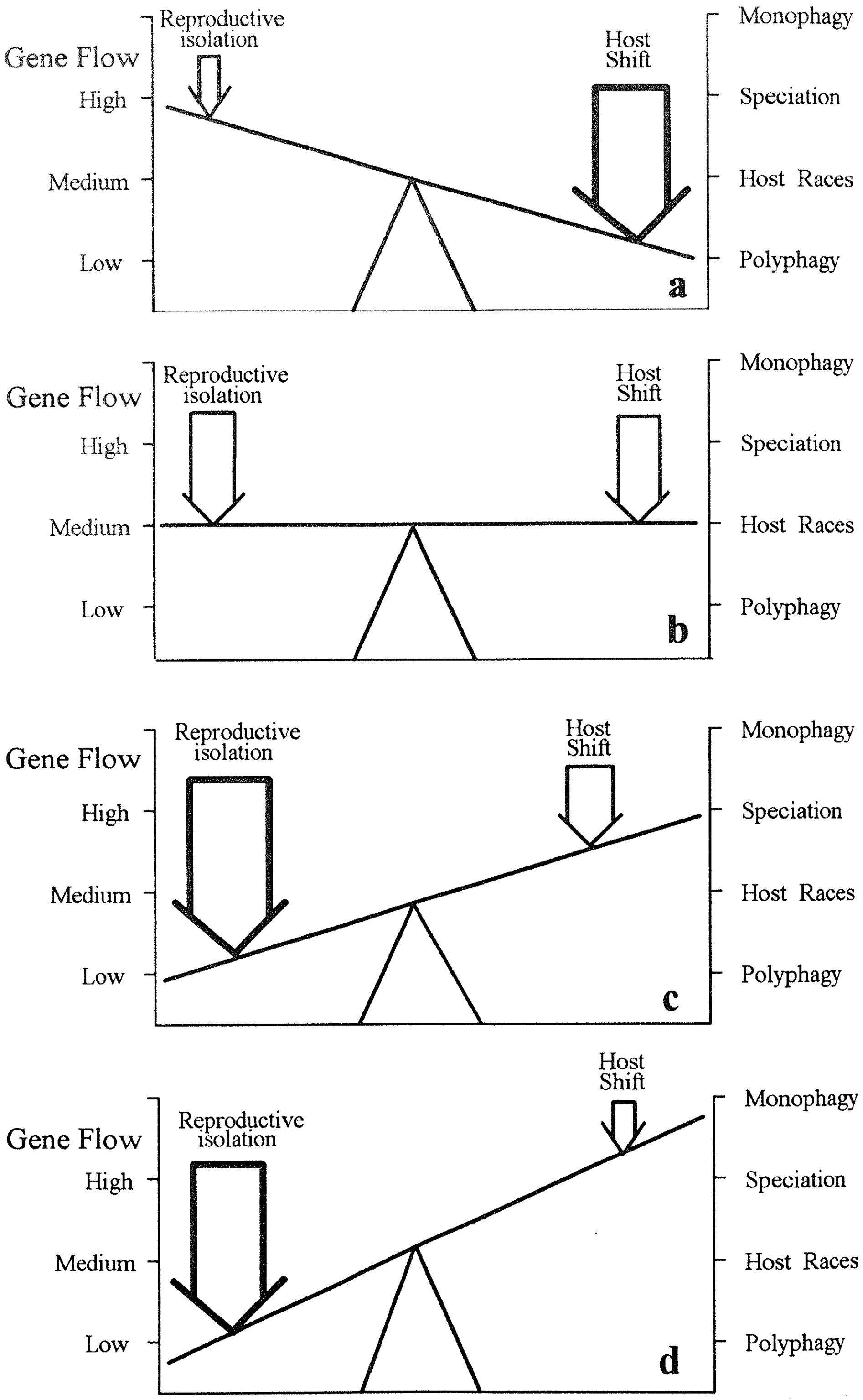

Figure 1.—A representation of how the balance between the forces favoring a host shift and the forces favoring reproductive isolation of populations will determine whether there will be: a) a polyphagous population b) host races c) sympatric speciation d) monphagy.

Factors Favoring Reproductive Isolation

The following factors can promote reproductive isolation in herbivorous insects:

1) Mating on the host plant. The requirements for sympatric speciation can be relaxed if mate choice is coupled with host selection (Bush 1975a, b; Diehl and Bush 1984, 1989; Rice 1984, 1987). This is biologically realistic, since many herbivores mate on their host plant (Price 1980, Diehl and Bush 1984). Assortative mating can arise as a correlated character of host selection (Rice 1984, 1987; Rice and Salt 1988). This coupling removes the selection-recombination antagonism, because the same genes are selected for in both host selection and assortative mating, eliminating the need for linkage between these loci (Rice 1984, 1987; Diehl and Bush 1989). If mate selection is coupled with habitat selection, significant disequilibrium can arise in the alleles for assortative mating/habitat selection and in loci for adaptation (Diehl and Bush 1989). The disequilibrium should be strongest when selection is intense and migration is low. If mating occurs on the host plant then the same genes may be selected for oviposition preference and assortative mating speeding the development of reproductive isolation (Bush 1975a, b; Diehl and Bush 1984, 1989; Rice 1984, 1987).

2) Selection against hybrids. If two host plants require negatively correlated herbivore traits for survival, growth and reproduction on the two plants, then there will be selection against the production of hybrids, leading to selection for premating isolating characteristics (Bush 1975a, b).

3) Genetic basis for host preference. If there is a genetic basis for host preference, with high penetrance then no alteration of host preference can be made by environmental conditions, decreasing the probability for oviposition and/ or mating on an alternate host plant, which can lead to gene flow between populations. A mutation would be required to change host preference leading to strong isolation of monophagous herbivores.

4) Host preference and performance requires few gene changes. If few genes are involved in determining the ability to recognize and utilize a host then the establishment of reproductive isolation by a colonizing population is more likely. Models have consistently shown (i.e. Diehl and Bush 1989) that if many loci are involved then recombination can rapidly break-up favorable genetic combinations for recognizing and utilizing a new host plants unless linkage is extremely tight.

5) Differences in adaptation to host-plant phenology could lead to divergence of populations. Reproductive isolation on new hosts can be rapid and selection for adaptations to use a new host plant can be strong if herbivore emergence is dependent on host-plant phenology (Wood 1980, Wood and Guttman 1983, Wood and Keese 1990, Wood *et al.* 1990). Since emergence times of many herbivores are cued to host-plant phenology, oviposition on a new host could shift emergence times, resulting in reproductive isolation. Once the initial reproductive isolation becomes established, intense selection to adapt to the chemistry and nutritional regime of the new host would take place.

6) Geographic isolation. Any degree of geographic isolation will decrease the probability of gene flow during the period when adaptations to a new host plant are being perfected. This will decrease the probability non-assortative mating and the break-up of genetic combinations necessary to utilize a new host plant.

Speciation and Host Loss

Host loss models require that a population of a previously polyphagous species, through selection and/or drift lose the ability to recognize and/or utilize a host, and form a new reproductively isolated monophagous species. Such a process would seem to require a period of geographic isolation of the population, if a species had previously been selected to utilize two species it seems improbable that a new selective force would arise that would lead to the evolution of reproductive isolation in sympatry. Two populations could be separated by a geographical barrier and on each side of the barrier the ability to utilize the alternate host plant would be lost. Each population would become adapted to recognizing and utilizing only the remaining host on its side of the barrier. It is questionable if selection for host adaptation would result in reproductive isolation. If the host plants had been similar enough to have been previously utilized by one herbivore species then it seems unlikely that there would be strongly divergent selection. During a long separation genetic drift could also lead to an accumulation of differences between populations, and could be the more important factor leading to reproductive isolation. Upon being reunited these populations might have become so differentiated that there is reproductive isolation when the populations are reunited.

In contrast to the host shift models, there is no need to identify factors that allow a host shift or colonization of a new host in the host loss models. Establishment and maintenance of reproductive isolation between the populations would be problematic. Why would populations that had been previously been polyphagous not coalesce when then were reunited? The following factors are the same ones identified in the discussion of host shifts that could contribute to reproductive isolation, but the strength of these factors are lost if the herbivore had previously been polyphagous.

1) Mating on the host plant. The populations could have reciprocally lost the ability to recognize the alternate host plant through drift. However, it is difficult to identify selective pressures that would lead to selection not to recognize the alternate host plant. If a population had the ability to discriminate against mating and ovipositing on all but two host plants, then it presumably would not be under further selection to improve it discrimination in the absence of the other host.

2) Selection against hybrids. The two host plants could not have required strongly negatively correlated traits for survival if the species was previously polyphagous. As a result during the period of geographic isolation selection to refine adaptations would not be likely to produce traits that would greatly reduce fitness on the other host plant. There would be little selection to avoid utilizing the other host plant and/ or to avoid hybridization upon a subsequent reuniting of the populations.

3) Genetic basis for host preference. It is difficult to identify selective pressures leading to a genetic divergence in host preference: why should a genetic preference for avoiding a plant that isn't present evolve? Presumably an insect that utilized two hosts, had already evolved the ability to differentiate between these plants and all other plants. There would only be selection to avoid the other host plant once the populations were reunited if the plants required different survival traits, which we have argued above is unlikely. Genetic drift could account for differences in host preference given a sufficient time period.

4) Differences in adaptation to host-plant phenology could lead to divergence of populations. Again, it is difficult to identify a reason why populations that had previously been able to utilize both host phenologies would not coalesce when they were reunited.

The Adaptive Syndrome of Gall-formers

The adaptive syndrome of gall-formers will influence the modes of speciation that are possible (Fig. 2). All gall-formers are endophages and resource manipulators. Craig *et al.* (1988) defined resource manipulation as "the active improvement of the herbivores environment initiated by the herbivore". Gall-formers have the ability to control and manipulate the growth of a plant. The degree to which gallers manipulate growth varies widely from simply inducing continued cell proliferation, to the production of complex structures not normally produced by the plants (Rohfritsch 1992). We hypothesize that resource manipulation and endophagy work together to produce two important characteristics: extreme specialization and the acquisition of plant characteristics by the gall-formers (Fig. 2).

Gall-formers are among the most specialized herbivores: most gall-formers feed on a single host species, they feed on a particular part of the plant, and they have preferences for the most rapidly growing plant parts. Gall-formers from a wide range of insect orders are reported to be highly host specific or monophagous (see references in Ananthakrishnan 1984), based on morphological identification of gall-formers. When host preference tests and/or genetic analysis of populations are actually conducted host specificity is almost always found (Koach and Wool 1977, Berube 1978, Craig *et al.* 1993). It is possible that the few reports of a single gall-former species attacking several plants will be identified as sibling species, or host races with closer examination. The causes of the extreme specialization of gall-formers are not clear. We hypothesize that the extremely intimate interaction of gall-formers and their host plants will select for specialization. We argue that it is very difficult for an insect that completes its life inside a host plant, while manipulating it to provide all the resources it requires, to be a generalist. Every shift to a new host plant will require unique adaptations. Endophagous insects in general are more intimately associated with their host plants than free feeders and as a result will be more specialized. Endophagy imposes selective forces that shape the evolutionary potential of gall-formers (Fig. 2). Most gall-former larvae develop from eggs laid inside host tissue, their fitness is completely dependent on the choice of oviposition site by the female. The larvae cannot move to different plants and must be adapted to the particular species and individual where they are developing. As a result inter- and intra-specific host plant variation has a strong potential to influence larval fitness. Internal feeding means that the interaction with both

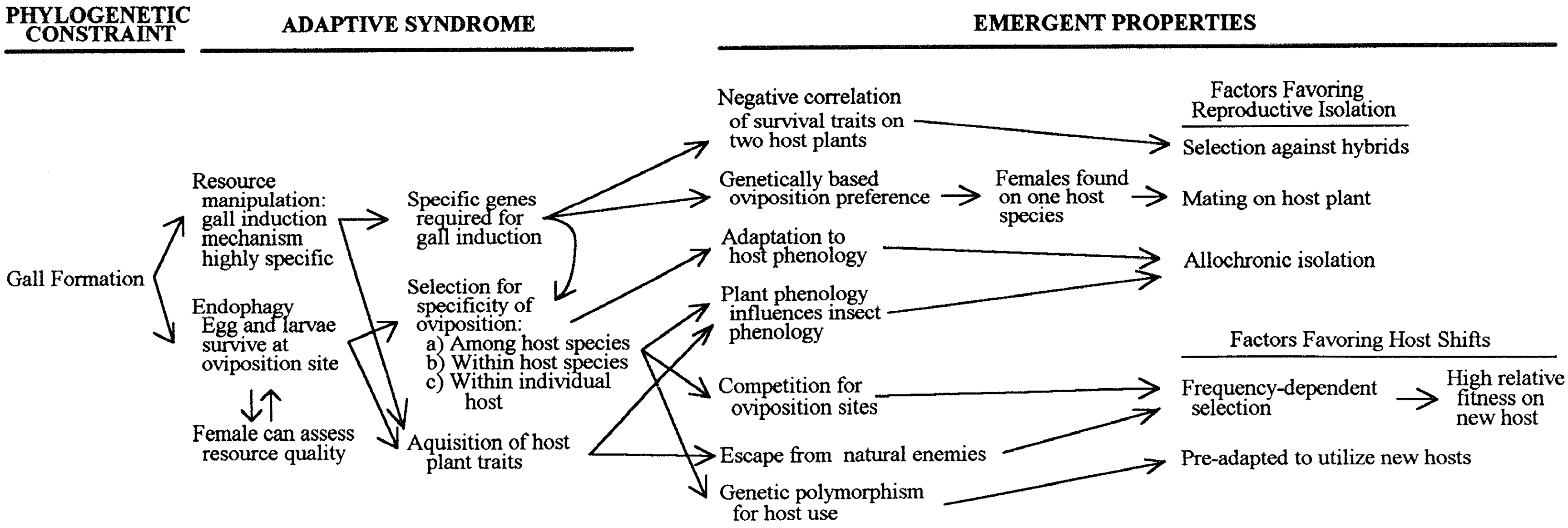

Figure 2.—Phylogenetic constraint, adaptive syndrome, and emergent properties of gall-forming insects that influence the mode of speciation.

the environment and higher trophic levels is mediated by the plant. As a result gall-formers will evolve to be highly responsive to host-plant variation, and the oviposition choices of the female will be highly responsive to host-plant variation.

Resource manipulation, which consists of gall induction for gall-formers, will select for specialization in host use. Gall-formers may utilize a wide range of mechanisms to induce gall growth including behavioral, mechanical, chemical, or genetic manipulation of the host plant to produce gall structures (Hori 1992). The specific manner in which gall growth is induced and maintained is almost completely unknown. Whatever the mechanism of gall induction, there is a strong indication that there must be a match between the genetics of the ability to induce galls by the insect and the susceptibility to gall formation in the plant. As a result, it is hypothesized that an insect species can induce galls only on a single plant species or a very limited number of closely related plant species. If an ovipositing female chooses the wrong plant or site for oviposition, a gall cannot be induced. This will again select for high specificity in oviposition choice (Fig. 2).

Gall-formers are host specific and if host specificity is adaptive, specialization will lead to several emergent properties critical to speciation. First, it should select for inflexible, genetically based, oviposition preferences among species. It is unlikely that individuals can improve their fitness by modifying their oviposition preference among species. Rather, ovipositing on any but the normal host will lead to reduced fitness. Genes for oviposition preference should have high penetrance. If females have fixed host preferences, then males can gain the greatest mating success by searching for them on the host plant. This in turn will lead to mating on the host plant which is a key assumption of speciation models. The high specificity required to utilize hosts could also lead to the development of genetic polymorphisms within a gall-former species. There is often large intraspecific variation in the suitability of host plants within a species for gall formation. This could select for variation within the insect population for utilization of different host plants. This could maintain a pool of genetic variation that might preadapt some individuals of species for utilization of a new host plant. The high specificity for attacking a particular host plant at the time when it has rapidly growing undifferentiated tissue will select for a tight match between insect and plant phenology. Any difference in host phenology will then select for a divergence in emergence times and allochronic isolation among herbivore populations using different hosts.

Implicit in the assumption of selection for high host specificity is the assumption that there is a negative correlation of traits leading to high fitness on two hosts. While this assumption has not been uniformly supported in studies of monophagous herbivores with other adaptive syndromes, the extreme nature of specialization in gall-formers may make this assumption true for gall-formers. If there is a negative correlation between the characteristics that allow survival on two hosts, then hybrids would have low fitness and there would be strong selection for reproductive isolation. High specificity of preference for oviposition sites can also contribute to selection favoring a host shift. Gall-formers prefer rapidly growing plant parts, and these sites are frequently rare, leading to competition for oviposition sites (Price *et al.* 1990). If part of a population shifted to a new host this sub-population could have increased fitness due to escape from competition, even if it suffered decreased fitness from poor adaptation to the host plant.

Acquisition of Host-Plant Characters

A second important feature of a gall-former's adaptive syndrome is the acquisition of host-plant characters. By this we mean that characters of the host plant influence the selective pressures on the gall-former, as well as characteristics of the insect. All endophages acquire some host-plant characters. For example, the susceptibility to natural enemies of all endophages is potentially strongly influenced by the host plant, because natural enemies frequently utilize host plant cues in locating victims (Vinson 1984). Herbivore phenology can be strongly affected by the host plant as demonstrated by the work of Wood and colleagues (Wood 1980, Wood *et al.* 1990), which can be important in establishing reproductive isolation.

Resource manipulators have an even stronger potential for having their evolution influenced by their host plant. A gall is plant tissue and represents an interaction of the insect and plant genotypes with the environment (Weis and Abrahamson 1986). Since the gall is plant tissue, gall characteristics may be influenced by plant characters. The potentials for color, size, shape, and toughness of a gall may be determined by the host plant (Weis and Abrahamson 1986, Craig *et al.* 1990, Craig 1994). These plant characters may determine insect phenology, susceptibility to natural enemies and other characters. A host shift resulting from a single change in a gene for host preference may lead to changes in all of these characters influencing selection on the insect, without any additional genetic changes. These changes may lead to increased fitness on a new host due to frequency-dependent selection, facilitating a host shift.

Number of Genes Involved in Host Shifts and Host Losses

A key assumption of speciation models for herbivorous insects is the number of genes involved in a host shift. The number of genes in a potential host shift is not determined, as are many of the other characters, by the adaptive syndrome of gall-forming. However, the adaptive syndrome indicates that the number of genes involved in reproductive isolation could be relatively small. Reproductive isolation could result from a change in one or a limited number of genes for host preference, and it would not require a massive reorganization of the genome. The number of genes involved in adapting to a new host shift will depend on the nature of host specificity in gall-formers, and the relatedness of the plant species attacked. To our knowledge, the number of genes involved in a host shift has not been determined for any gall-former.

Speciation and *Eurosta solidaginis*

Eurosta solidaginis is a tephritid fly that induces galls on two species of goldenrod, *Solidago altissima* and *S. gigantea*. We have embarked on a long-term study of the behavioral, ecological and genetic characteristics of *E. solidaginis* to determine how speciation may be proceeding in this gall-former, some of the data is reported in this volume. On the basis of genetic and behavioral evidence we have concluded that the populations are partially reproductively isolated from each other on the basis of host-plant preference, or they are host races by the definition of Diehl and Bush (1984). Our studies, and those of others, allow us to examine whether *E. solidaginis* has the emergent properties of the hypothesized adaptive syndrome of gall-formers. The results are briefly summarized below.

1) There is strong selection against hybrids between the host races. Hybrids between the host races have lower survival due to low rates of gall induction following oviposition, and high parasitism rates. Surviving F1's and back crosses are viable and fertile (Craig, Itami, and Horner unpublished data).

2) The host races are highly host specific, it is very difficult to induce them to oviposit on the other plant (Craig *et al.* 1993). Studies currently underway indicate that neither adult or larval conditioning influences mating or oviposition site choice (Horner, Itami, and Craig unpublished data). All data to date strongly implicate inflexible genetic control of oviposition- and mating-site choice.

3) There is intraspecific oviposition preference. There is a preference for rapidly growing ramets (Anderson *et al.* 1989; Horner and Abrahamson 1992; Craig, Schantz, Itami, and Abrahamson unpublished data).

4) A high proportion of mating takes place on the host species from which the fly emerges, leading to a very low rate of mating between the host races (Craig *et al.* 1993).

5) The Gigantea fly host race emerges a mean of 4-12 days earlier than the Altissima fly host race, this is enough of a difference to create partial allochronic isolation between host races (Itami *et al.* unpublished data). Results reported in this volume by Abrahamson *et al.* do not support the hypothesis that a character acquired from the host plant (gall color) alters insect phenology.

6) There is strong larval competition. Studies of the fly population on *S. altissima* show that there is no avoidance of buds that have been previously attacked (Craig, Schantz, Itami, and Abrahamson unpublished data) and there is strong competition among larvae sharing a gall (Hess 1993). Because buds in the field frequently have a large number of ovipunctures it is possible that there is often intense larval competition. As a result, a shift to a new host could have resulted in frequency-dependent selection leading to relatively high fitness on the new host.

7) *Eurosta solidaginis* may have escaped from some of its natural enemies during a host shift (see the discussion by Abrahamson *et al.* in this volume).

8) The genetics of preference and performance are not yet completely understood. We have determined that each host race has a very low survival rate on the host on which it does not normally oviposit (Craig, Itami, and Horner unpublished data), strongly suggesting that genes are required for survival on the two hosts.

Host-race Formation in *Eurosta solidaginis*

It is impossible to definitively reconstruct the past history of speciation or host-race formation. However, we can draw inferences from phylogentic reconstruction, and we can examine characteristics of currently existing populations to determine which speciation models they fit best. We believe the data supports a model where speciation involves a host shift, is rapid, requires few genetic changes, and does not require a period of geographical isolation.

Models have shown that a period of geographic isolation is not required for host-race formation and/or speciation. Sympatric speciation has been shown to be theoretically possible under a restricted set of conditions. Building on the models of Levene (1953), Maynard Smith (1966) showed that a stable polymorphism at a single locus for habitat selection (e.g. preference) could evolve if (1) density-dependent population regulation operates separately in the two habitats and (2) the selection is strong. However, when assortative mating and habitat preference are controlled by different loci, their mutual inheritance would have to be ensured by linkage in order for sympatric speciation to be possible. This linkage can be broken up faster by recombination than it is built up by selection unless selection is very strong and/or migration is very low. This requirement for tight linkage of a number of loci is a stringent condition for producing sympatric speciation and has been used to argue that sympatric speciation is unlikely (Futuyma and Peterson 1985, Futuyma 1986). However, the requirements for sympatric speciation can be relaxed if mate choice is coupled with host selection, (Bush 1975; Diehl and Bush 1984, 1989; Rice 1984, 1987). This coupling removes the selection-recombination antagonism, because the same genes are selected for both host selection and assortative mating, eliminating the need for linkage between these loci (Rice 1984, 1987; Diehl and Bush 1989). If mate selection is coupled with habitat selection, significant disequilibrium can arise in the alleles for assortative mating/habitat selection and in loci for host adaptation (Diehl and Bush 1989). This disequilibrium should be strongest when selection is intense and migration is low (Diehl and Bush 1989).

Our research to date indicates that characteristics of *E. solidaginis* host races meet the assumptions of these models. First, there is assortative mating primarily due to host plant preference. Second, we have found very low rates of migration: it is very rare for individuals from one host race to mate and/or oviposit on the alternate host plant. Third, selection against ovipositing on the wrong host plant is intense since survivorship is extremely low when flies oviposit on the alternate host. There is also strong selection against mating on the wrong host plant since hybrids between host races have very low viability. All of these characteristics are emergent properties resulting from the adaptive syndrome of gall-forming. This combination of characteristics makes geographic isolation unnecessary for speciation to occur, although it is not incompatible with the data.

Few genetic changes appear to be required for speciation in gall-formers. Only those genetic changes related to host use would need to be altered for speciation to take place, there would be no need for any other characteristics to change. The requirement for only a few genetic changes coupled with the strong selection operating on host choice means that speciation could be very rapid in gall-formers. The divergence of these populations through host loss seems a less parsimonious explanation but it cannot be ruled out. First, as discussed previously, if the species had been polyphagous then there would be forces leading to the recoalesence of the species. We have discussed above reasons why it would be difficult to prevent populations of a previously polyphagous species from being reunified once the geographic barrier had been removed, unless there had been a long period of separation. Requiring a long period of isolation is an additional assumption not needed for a host shift model. It would also require a specific pattern of distribution of host plants which is also not required in the host shift models. If the polyphagous ancestor had survived in even part of the range it would be a powerful force for gene flow that would cause the reunification of populations. While there are currently areas where one or other of the host races or host plants are lacking (How *et al.* 1993), the current broad overlap of the host plants makes the assumption that the distributions of host plants were once totally isolated questionable. A long period of allopatric isolation with the accumulation of many differences is not indicated by characteristics of the fly populations. Finally, it would require a polyphagous galling ancestor, such polyphagous gall-formers are rare and presumably were rare in the past.

CONCLUSION

We conclude that the adaptive syndrome of gall-formers produce emergent properties that facilitate speciation during a host shift. We have explored the adaptive syndrome of *Eurosta solidaginis* and concluded that it has emergent properties that would facilitate host-race formation and speciation as the result of a host shift. The most restrictive assumption of sympatric models is that there must be strong selection for intrinsic barriers to gene flow. Strong selection for host specialization is produced by endophagy and resource manipulation. Specialization selects for strong genetically based preferences for mating and ovipositing on a single host plant species. Mating on the host plant provides a mechanism for a strong intrinsic barrier to gene flow. The traits for survival on the two host plants are apparently negatively correlated and produce strong selection against the production of hybrids. While the patterns we observe could arise in allopatry, such an allopatric model would involve additional assumptions not necessary with a sympatric model. A plethora of other gall-formers with the same phylogenetic constraints share the adaptive syndrome we have outlined for *E. solidaginis,* and the adaptive radiation in many gall-formers may have occurred via sympatric speciation.

We realize that we have not fully documented all of the emergent properties of *E. solidaginis* we hypothesize to be important in speciation, but we hope our approach to the study of speciation has heuristic value. Determination of whether sympatric speciation is widespread among gall-formers depends on a detailed analysis of the adaptive syndrome and emergent properties of other gall-formers. However, the pattern seen in *E. solidaginis* is common: adaptive radiations of host races or sibling species on closely related host plants (i.e. Price and Roininen 1993). Clear conclusions about how speciation proceeds in gall-formers cannot be made until we know more about the genetics of preference and performance. This in turn may rely on an understanding of the mechanisms of gall induction. Because of the rich possibilities for manipulative experimentation in gall-former systems, these systems offer excellent model systems in which to study the genetics and ecology of speciation.

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GALLMAKER SPECIATION: AN ASSESSMENT OF THE ROLES OF HOST-PLANT CHARACTERS, PHENOLOGY, GALLMAKER COMPETITION, AND NATURAL ENEMIES

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Abstract. Gallmakers offer model systems to examine the details of host shifts and subsequent herbivore speciation. Here we explore three factors that may facilitate the acquisition of new host plants by *Eurosta solidaginis* (Diptera: Tephritidae) and promote speciation. These include (1) the host-plant traits of phenology, stem color, and bud chemistry, (2) the competitive interactions of gallmaker larvae for host resources, and (3) the potential for escape from natural enemies via a host shift. Host-associated populations of *E. solidaginis* in northern regions of the USA have genetically differentiated along host-plant lines and represent host races based on differences in adult emergence times, strong assortative mating, and oviposition preferences. *Solidago altissima* and *S. gigantea* occurring in both Minnesota (where both host species are infested) and Pennsylvania (where only *S. altissima* is attacked) were monitored for phenology. Minnesota hosts had similar growth traits and greater intraspecific variation than the same species in Pennsylvania. Although Minnesota *Eurosta* strongly preferred Minnesota *S. gigantea*, Pennsylvania *S. gigantea* did support gall formation. These results suggest a higher probability of a host shift occurring in sites where host plants are similar than in sites like Pennsylvania where host species differ phenologically. Adult emergence occurred earlier from experimentally treated galls of *S. gigantea* than from *S. altissima*, males from both host races emerged prior to females, and development rates were enhanced in a sun rather than a shade treatment. Although the stems and consequently the galls of the two host species differ in color, we found no relationship between host-plant species and gall reflectance or internal gall temperatures. *Eurosta* respond to chemical cues from their hosts, and the response is dependent on the relative concentrations of stimulant and deterrent compounds. Ovipositional stimulants for *S. altissima*-attacking *Eurosta* were masked by deterrents from *S. gigantea*. Differential acceptance of hosts by host races may result from variations in the absolute amount or ratio of stimulatory and deterrent chemicals. Similarities in host chemistry coupled with like host phenologies might facilitate host shifts in gallmakers if the extremes of the amounts or ratios of stimulant and repellent chemicals within similar hosts overlap. Larval competition on the ancestral host may create frequency-dependent selection favoring the establishment of a new host race. Poor adaptation for host utilization on the novel plant may be offset by reduced competition to result in similar or higher fitnesses on the novel host. Strong competition was detected among early instar *Eurosta* larvae which shared single buds. Finally, oviposition on *S. gigantea* has resulted in increased gall size relative to *S. altissima* galls and in differences in the natural-enemy guilds of the two host races. Where the wasp parasitoid *Eurytoma obtusiventris* was common, it attacked *S. altissima* galls and only rarely *S. gigantea* galls. Although *Eurosta* have higher survival on *S. altissima* host plants in the absence of parasitoids, the presence of *E. obtusiventris* can give *Eurosta* on *S. gigantea* hosts a survival advantage over those on *S. altissima*. Each trophic level—the host plant, gallmaker, and natural enemies—can play a role in facilitating a host shift and influencing the rates and mechanisms of speciation. Although individually subtle, the combined effects of similar host-plant phenology, intense larval competition, and differential natural-enemy attack on alternate host plants could create conditions promoting a host shift and subsequent speciation.

Key words: Eurosta solidaginis, Eurytoma obtusiventris, Eurytoma gigantea, gallmaker larval competition, gallmaker phenology, herbivore speciation, host shift, host-plant phenology, Mordellistena unicolor, natural-enemy attack, oviposition chemical cues, Solidago altissima, Solidago gigantea.

INTRODUCTION

Phytophagous insects and parasites have often been suggested as model systems to examine the details of speciation (Bush 1975a, b). Yet, the basic speciation processes of herbivorous insects are often difficult to study and hence are generally poorly understood (Bush 1982, Bush and Howard 1986, Tauber and Tauber 1989). This difficulty occurs in part because speciation is an inherently historical process. Although studies of contemporary behavioral, ecological, and genetic characteristics of recently speciated or speciating taxa can only suggest the most parsimonious explanation of how speciation has proceeded (Wood and Keese 1990), they can provide crucial insights into the processes of speciation. Many of the characteristics that brought about speciation should still exist in such taxa.

Additional difficulties in understanding the processes of herbivore speciation likely stem from the variety of associations that phytophagous feeding guilds have with their host plants. Borers, miners, and free feeders, for instance, each have distinct constraints placed on them by their hosts and, because of unique lines of descent, have differing adaptive potentials for exploitation of their host plants. The consequence is that modes of speciation have likely varied among herbivore guilds and lines of descent. However, by careful examination of the processes of speciation in herbivores which have an intimate and specific association with their host, we should be able to understand the conditions that promote or inhibit speciation. Gallmaker systems potentially offer excellent models for such exploration of speciation processes (see Craig *et al.* this volume, Weis this volume).

Gallmakers typically have a narrow host range, and their intimate association with host-plant tissue can create strong selection pressures for adaptation to their host. Furthermore, since gall characteristics are influenced by both the insect's and the host-plant's genotype (Weis and Abrahamson 1986), gall characters which affect the emergence times of a gallmaker might be altered simply by ovipositing on a different host (Craig *et al.* in press). Such an alteration of adult emergence, mating, or oviposition times could markedly reduce gene flow between populations associated with different hosts and would promote speciation, possibly under sympatric conditions.

As a consequence of the interactions of host-plant and gallmaker genotypes in the production of the gall phenotype, gallmakers that oviposit on a closely related but novel host may develop in a gall of different size and/or morphology. Such modifications of a gall's phenotype could alter adult emergence times, thus facilitating reproductive isolation, or change the susceptibility of the gallmaker to its natural enemies. The latter could markedly enhance gallmaker survival since gallmakers are well known for supporting diverse communities of parasitoids, inquilines, and predators (Mani 1964, Askew 1975, Abrahamson *et al.* 1989b, Weis *et al.* 1992). Galls are typically apparent, predictable resources for their natural enemies (Price *et al.* 1980, Abrahamson *et al.* 1983, Abrahamson and Weis 1987). There are any number of features of gall phenotypes that may influence natural-enemy attack including gall rigidity, size, or the presence of allelochemicals (e.g. Washburn and Cornell 1979, Weis 1982, Weis and Abrahamson 1985, Abrahamson *et al.* 1991, Jones and Lawton 1991, Hartley 1992).

The objective of this paper is to examine some of the factors that may facilitate the acquisition of new hosts by gallmakers and promote speciation. We report results from studies of the fly *Eurosta solidaginis* (Diptera: Tephritidae) which commonly attacks two species of the genus *Solidago* (Compositae) throughout much of North America. This gallmaker, like most others, is attacked by several natural enemies. Specifically, we examine if and how factors such as (1) traits of the host plant (e.g. host-plant phenology, stem color, and chemistry), (2) competitive interactions of gallmaker larvae for host resources, and (3) the susceptibility of the gallmaker to natural enemies in different hosts, influence the potential for host shift and subsequent speciation.

NATURAL HISTORY

The univoltine gallmaker E*urosta solidaginis* is a narrowly oligophagous herbivore that infests *Solidago altissima* throughout its range (Abrahamson *et al.* 1989a) but also attacks the frequently sympatric congener *S. gigantea* in the northern and western portions of its distribution (Waring *et al.* 1990, Lichter *et al.* 1990). Two subspecies of *E.*

solidaginis have been recognized by Ming (1989). However, all of the results reported here are from Ming's eastern subspecies, *E. solidaginis* subsp. *solidaginis.*

Adult emergence, mating, and oviposition occur in mid to late May in central Pennsylvania. The gall appears about 3 wk after oviposition and reaches full size in another 3 to 4 wk (Weis and Abrahamson 1985). The larva enters diapause in late September to overwinter and pupates within the gall during the following March or April (Uhler 1951).

Eurosta has five primary natural enemies (Uhler 1951; Abrahamson *et al.* 1983, 1989b; Weis *et al.* 1992): the parasitoid wasps *Eurytoma obtusiventris* and *E. gigantea* (Hymenoptera: Eurytomidae), the inquiline beetle *Mordellistena unicolor* (Coleoptera: Mordellidae), black-capped chickadees (*Parus atricapillus),* and downy woodpeckers (*Dendrocopus pubescens*). *Eurytoma obtusiventris* attacks *Eurosta* earliest, after gallmaker oviposition but prior to gall appearance and thus infests galls of all sizes (Weis and Abrahamson 1985). *Eurytoma gigantea* parasitizes *Eurosta* later; in central Pennsylvania attack occurs after maximum gall diameter has been reached (Weis and Abrahamson 1985, Weis *et al.* 1985). Females of this parasitoid probe galls of all sizes but can successfully parasitize only the smaller galls of any *Eurosta* population due to ovipositor length limitations (Weis *et al.* 1985). *Mordellistena unicolor* larvae initially feed on plant tissues by chewing tunnels through stem and gall tissues (Abrahamson *et al.* 1989b, Cappuccino 1992). However, *Eurosta* are consumed in the majority of galls containing *Mordellistena* as the predatory beetles tunnel into the gall's central cavity in late summer (Abrahamson *et al.* 1983, 1989b; Sumerford and Abrahamson submitted). Birds, particularly downy woodpeckers, preferentially prey upon *Eurosta* in the larger galls in any population during late autumn and winter (Confer and Paicos 1985, Weis and Abrahamson 1985, Abrahamson *et al.* 1989b, Weis *et al.* 1992)

GENETIC AND BEHAVIORAL BACKGROUND FOR A *EUROSTA* HOST SHIFT

Genetic studies have demonstrated that the gallmaker populations attacking *S. altissima* and *S. gigantea* from Minnesota to New England are distinct. Waring *et al.* (1990) used horizontal starch-gel electrophoresis of enzymes to determine that sympatric and allopatric *Eurosta* populations infesting these two host-plants had genetically diverged. Populations over a wide geographic area exhibited conspicuous allele frequency differences. An unweighted pair group (UPGMA) clustering of Nei's unbiased genetic distance (D) clearly separated *E. solidaginis* populations from *S. altissima* and *S. gigantea* on different branches. These results, coupled with the finding of significantly higher genetic heterozygosity in *S. altissima* populations, suggested that the initial host shift was from *S. altissima* onto *S. gigantea* and that the shift took place in a single geographic area (Waring *et al.* 1990). Current work in our laboratory using DNA-sequence variation in the cytochrome oxidase II gene of the mitochrondrial genome is consistent with the suggestion that all *S. gigantea*-associated *Eurosta* populations studied to date have been derived from a single shift from *S. altissima* (Brown and Abrahamson in progress). Studies of host-specific genetic differentiation in natural populations are limited, (but see Feder and Bush 1989, 1991; Feder *et al.* 1988, 1990) and thus our data represent important evidence for the potential role of host shifts in genetic differentiation and speciation (Waring *et al.* 1990).

Behavioral studies (Craig *et al.* this volume) show that the host-associated, genetically divergent populations of E. solidag*inis* are host races. Emergence times differ for the two host races with the *S. gigantea*-associated populations typically emerging over a week earlier than *S. altissima*-associated populations (Craig *et al.* in press; J. Brown, R. Packer, and W. Abrahamson unpublished). This does not mean, however, that sympatric host races are completely reproductively isolated. Flies have frequently lived 10 to 14 d under experimental conditions (Craig *et al.* in press; M. Hess and W. Abrahamson unpublished) and can live for several weeks in cool, moist environmental chambers (Abrahamson personal observation). Thus, in spite of marked differences in emergence times, the life spans of the host races overlap, making mating between races possible (Craig *et al.* in press). However, our experiments showed that each host race demonstrated strong assortative mating based on host-plant preference but only very weak assortative mating in the absence of host plants. Furthermore, females of both host races strongly preferred to oviposit into the buds of their own host-plant species. Such behavioral preferences for mating and oviposition are critical to reduce gene flow and promote partial reproductive isolation between host-associated populations (Bierbaum and Bush 1990). While the differences in *Eurosta* host-race emergence phenologies are insufficient to create complete reproductive isolation, there appears to be sufficient allochrony between host races to maintain genetic divergence (Craig *et al.* in press).

RESULTS AND DISCUSSION

The Role of Host-Plant Phenology

We examined *E. solidaginis*' host shift from *S. altissima* to *S. gigantea* by comparing the phenologies of host-plant populations in Minnesota, where both goldenrod species are infested, with populations of the same *Solidago* species in Pennsylvania, where only *S. altissima* is attacked but both species are present (How *et al.* 1993). Even though daily host-plant growth rates varied according to factors such as temperature, ramets of *S. altissima* were taller, grew faster, and were more uniform in size than *S. gigantea* in Pennsylvania, particularly during the oviposition period. However, in Minnesota there were no differences in growth characteristics (Fig. 1). Thus, the growth traits of *S. altissima* and *S. gigantea* converge in Minnesota (making a host shift more possible) but these same traits diverge in Pennsylvania (How *et al.* 1993).

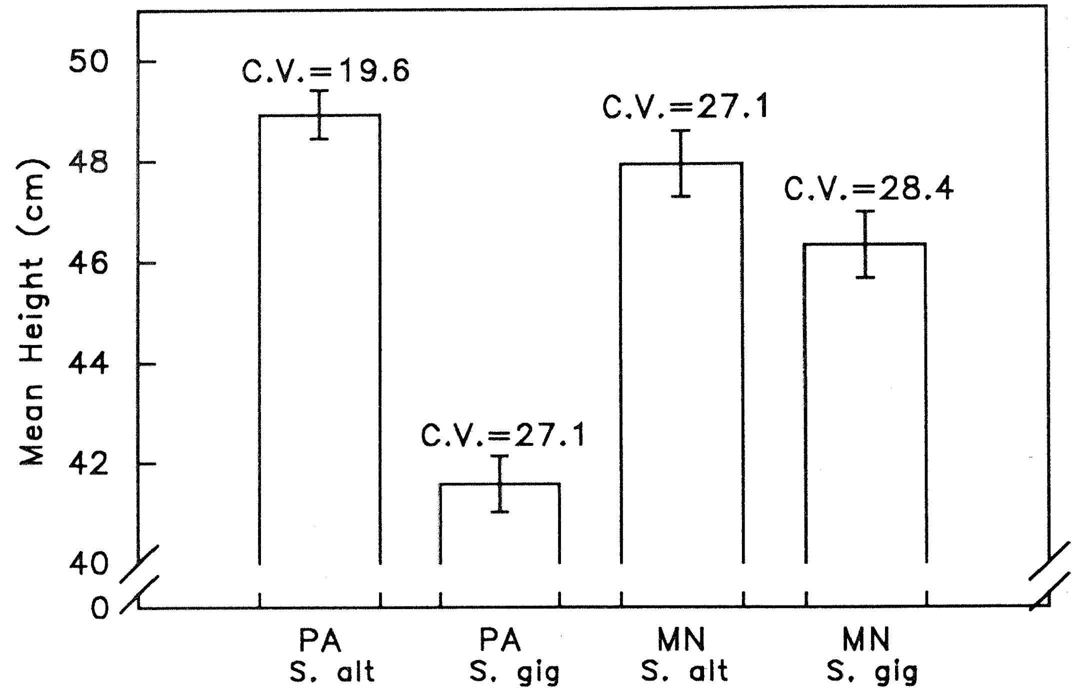

Figure 1.—Mean height (cm) ± standard error and coefficient of variation (C.V.) for goldenrod populations of the two host species in Pennsylvania and Minnesota fields during their respective *E. solidaginis* oviposition period. S. alt., *Solidago altissima*; S. gig., *S. gigantea* (modified from How *et al.* 1993).

How *et al.* (1993) also monitored the growth of both plant species from both locations in a Pennsylvania common garden. *Solidago altissima* from both locations had a longer growth period and consequently a broader timespan of reactivity to *Eurosta* than *S. gigantea.* The ramet growth of *S. gigantea* peaked earlier and more rapidly declined than that of *S. altissima.* The same study also examined oviposition preference of adult *S. gigantea*-infesting flies from Minnesota and the galling susceptibilities of *S. gigantea* plants from both Pennsylvania and Minnesota (How *et al.* 1993). These flies showed a strong oviposition preference for Minnesota rather than Pennsylvania *S. gigantea* ramets. This preference was likely related to the fact that Minnesota ramets were taller and faster growing than Pennsylvania ramets at the time of oviposition. Other *Eurosta* studies (Anderson *et al.* 1989, Horner and Abrahamson 1992) have also indicated a relationship between host size and vigor, and oviposition preference. But importantly, this study found that Pennsylvania ramets of *S. gigantea* supported gall formation under greenhouse conditions. Furthermore, Pennsylvania *S. gigantea* galls did contain a living *Eurosta* larva at the time of ramet senescence (How *et al.* 1993). However, Minnesota *S. gigantea* galls had larger gall diameters, greater gall fresh and dry masses, and higher peak larval dry masses than Pennsylvania galls. These findings may result from the adaptation of Minnesota *Eurosta* to Minnesota *S. gigantea* or from greater host vigor.

Such host-species differences in phenology and vigor, in addition to distinctions in reactivity to gallmakers, may create obstacles to host adoption. Such obstacles would likely make host shifts relatively rare events that occur only under optimal conditions. Jaenike (1990) has suggested that variation in host-plant abundance could lead to geographical differences in host use. In areas where top-ranking hosts are predominant, thresholds for host acceptance may remain high. The net effect would be to exclude lower-ranking hosts. However, where preferred hosts are rare or unapparent because of closely related, similar species, thresholds for host acceptance may fall and encourage the use of alternate hosts. *Solidago altissima* becomes less abundant in northern portions of its range (e.g. Minnesota and New England) where S. *gigantea* populations are more common (Brown and Abrahamson personal observation).

The Role of Host-Plant Stem Color

Galls have been considered to be an "extended phenotype" of the gallmaker's genome (Dawkins 1982). Weis and Abrahamson (1986), for example, showed that although a gall is plant tissue, the development of the gall phenotype is influenced by both the gallmaker's genotype, which produces the stimulus to the plant, and the host-plant's genotype, which is coded for growth and accordingly for a response to the insect's stimulus. While the gallmaker does exert considerable control over gall development, the host plant also has a strong influence over the gall's phenotype (Weis and Abrahamson 1986). The consequence is that once individuals of a gallmaker have shifted their host use to a novel plant species, they immediately acquire a new gall phenotype. If this acquired phenotype varies in characters that influence adult emergence time, reproductive isolation from the ancestral population may occur quickly and without genetic modification.

The external color of the gall may be an important phenotypic trait for a gallmaker like *E. solidaginis* which overwinters in its gall to pupate and emerge the following spring. Host-plant stems, and as a result the galls, range from green to purple during the growing season (Abrahamson personal observation). Growing-season galls of *S. altissima* generally are on the green end while *S. gigantea* galls are on the purple end of the continuum. Galls of some *S. gigantea* ramets are also covered with a white, waxy layer over the pigmented gall tissue. The outcome is that overwintering galls range in color from off-white to deep purple. Dark-colored galls may, by absorbing more heat energy during late winter and spring, have higher internal temperatures and hence their larvae may develop faster due to warmer internal temperatures than larvae in lighter-colored galls.

We have recently examined the relationships among gall color, gall heating, and emergence times for both host races of *E. solidaginis*. Galls of both host races were collected from a single location in Minnesota and were stored there under out-of-doors conditions. Galls were examined in March and May, two points during the diapausing larva's (March) or pupa's (May) development period (Uhler 1951). The May collection occurred within 2 wk of emergence time. The reflectance of galls was determined by irradiating the nearest point on the gall's equator with a 0.63 mm diameter beam of 633 nm light from a helium-neon laser and measuring the light reflected at 45° with a photocell connected to a voltmeter. The internal temperatures of galls were recorded for March and May collections with hypodermic thermister probes by placing the galls on a white surface in full sunlight and inserting a probe to the gall's center. Four galls and their thermister probes were allowed to equilibriate in full sunlight prior to measurement, and ambient temperatures were recorded before and after the assessment of each block of four galls. Ambient incoming energy levels were monitored after each block using a pyranometer.

The galls of *S. gigantea* were found to be larger in diameter than *S. altissima* galls for both samples (March: *S. gigantea* 25.2 ±2.8 (SD) mm; *S. altissima* 20.2 ±2.4 mm; F=179.33; df=1,195; p<.001; May: *S. gigantea* 22.9 ±2.8 mm; *S. altissima* 16.9 ±3.1 mm; F=195.81; df=1,186; p<.001). An analysis of covariance using gall diameter as the covariate showed that *S. gigantea* galls reflected significantly more red light than *S. altissima* galls in March (covariate: F=54.78; df=1,185; p<.001; species effect: F=11.63; df=1,185; p=.001). Near emergence time (May), an analysis of variance confirmed that *S. gigantea* galls reflected more red light than *S. altissima* (F=9.52; df=1,210; p=.002), however, the difference in reflectance by species disappeared (F=2.15; df=1,209; p=.14) when diameter was added as a covariate (F=8.29; df=1,209; p=.004). Notwithstanding, reflectance from galls is not simply a diameter effect since a regression of reflectance on gall diameter within each species resulted in non-significant relationships (*S. altissima*: r^2=0.03, p=.06, n=112; *S. gigantea*: r^2<0.01, p=.91, n=100). The enhanced red reflectance of *S. gigantea* galls is likely due to both their more reddish color and the white, waxy covering of their gall's epidermis.

More important, we found no significant differences between host races for either gall internal temperature or the difference between internal gall temperature and ambient temperature (delta temperature) in either the March and May samples. Instead, internal gall temperatures were strongly related to solar radiation ($r=0.65$, $p<.001$, $n=197$) in March, and to block (a measure of time of day) and solar radiation (multiple $r=0.36$, $p<.001$, $n=212$) in May. The May sample showed that as the internal gall temperature increased so did the delta temperature ($r=0.96$, $p<.001$). However, delta temperatures were scarcely related to ambient temperatures ($r=-0.13$, $p=.055$). Thus, the amount of heating within galls is primarily a function of solar radiation since, in these experiments, block includes the intensity of solar radiation.

To test if the differences between host-race emergence times could be affected by environmental variance, we collected galls of *S. altissima* and *S. gigantea* from 25 locations in New England (where both host plants are attacked). Galls of each *Eurosta* host race were randomly assigned to either a shade treatment (where galls were at out-of-doors air temperatures but received no direct solar radiation) or to a sun treatment (where galls received up to 7 h of direct solar radiation daily). The time from overwintering diapause to adult emergence for *S. altissima*-attacking *Eurosta* is approximately 21 d when galls are incubated at a constant 20C (Uhler 1951). Galls were removed from cold storage and placed into their assigned treatment for 2 wk, after which time they were moved to an air-conditioned laboratory, enclosed in individual emergence cups, and monitored every 12 h for emergence. All three main effects: host species ($F=1250.7$, $df=1,795$, $p<.001$), fly sex ($F=67.6$, $df=1,795$, $p<.001$), and sun or shade treatment ($F=42.5$, $df=1,795$, $p<.001$) were significant according to an analysis of variance on day of emergence. Flies from *S. gigantea* emerged earlier than flies on *S. altissima* (20.6 ±0.06 (SD) vs 24.6 ±0.09 d), males emerged prior to females (22.2 ±0.08 vs 23.0 ±0.07 d), and flies from sun-treated galls emerged before those from shaded galls (22.3 ±0.05 vs 22.9 ±0.09 d). The interaction of host species and light treatment was also significant such that emergence time of flies from *S. gigantea* was 0.4 d faster and that of flies on *S. altissima* 0.9 d more rapid under the sun treatment. These results do not support the hypothesis that emergence-time variances are at present principally due to host-plant traits. If host-plant traits affected emergence time, sun-treated *S. gigantea* galls should have had enhanced emergence times relative to sun-treated *S. altissima* galls.

The Role of Host-Plant Chemical Cues

Many studies (e.g. Shelley *et al.* 1987, Feeny *et al.* 1989, Mitter *et al.* 1991) have documented the important role of host-plant chemical cues to host selection and herbivore diversification in free-feeding herbivores but little research has examined the function of plant chemistry to gallmaker host choice. Yet, gallmakers are noted for their specificity to host-plant species. Such specificity suggests that gallmakers including *Eurosta* require particular physical and chemical conditions to promote acceptance and induce galling (Abrahamson and Weis 1987; Abrahamson *et al.* 1989a, 1991; Anderson *et al.* 1989). Craig *et al.* (in press) have shown that *S. altissima* and *S. gigantea* are not equally acceptable to the two host races of *E. solidaginis*. By ovipositing on their natal host-plant species, *Eurosta* females may increase the chances that their offspring will be successful. While our oviposition studies with *Eurosta* have documented the importance of physical cues such as bud shape and size (Horner and Abrahamson 1992), our work has also suggested the significance of chemical cues (Abrahamson *et al.* 1989a). *Eurosta* females presented with buds of *S. altissima* and *S. rugosa* externally wrapped with bud leaves of *S. altissima*, probed the external wrap leaf with equal frequency but accepted only the *S. altissima* buds for oviposition. Females were able to identify the correct host using information gained by probing with their ovipositors. Using artificial buds (a strip of sponge ≈0.5 x 1 x 6 cm wrapped with polyester/rayon gauze) painted with plant extracts, we found that *Eurosta*'s oviposition responses may be regulated by the chemistry (primarily terpenoids) of their host plants (S. Roth, J. Horner, and W. Abrahamson unpublished).

We used extracts or stems from greenhouse-grown *S. altissima* and *S. gigantea* to test if Pennsylvania *S. altissima-Eurosta* (1) could distinguish between real and artificial buds, (2) would accept artificial buds containing a crude methanolic-extract of *S. altissima*, and (3) could distinguish between artificial buds containing *S. altissima* extracts, *S. gigantea* extracts, or a combination of both extracts. *Eurosta* ovipositional behavior includes initial exploration of a bud, followed by abdomen arching and insertion of the ovipositor into the bud (Uhler 1951). For the purposes of our experiments, abdomen arching constituted acceptance of the bud.

Eurosta can discriminate between real and artificial buds. The 8 females that initially rejected distilled-water-treated artificial buds accepted real buds in every case and all 11 females that initially accepted real buds never accepted distilled-water-treated artificial buds ($X^2=19$, $p<.001$, testing the hypothesis that females equally accept the two bud types). However, when we applied a crude methanolic extract of *S. altissima* (10 ml of 50% methanol homogenized with each g of fresh bud mass, centrifuged at 3000 rpm for 5 min) containing such potential chemical cues as flavonoids, terpenoids, and simple phenolics (compounds that often serve as feeding or ovipositional deterrents or stimulants for herbivores, Harborne 1988) to an artificial bud (standard amount being 25% of the total amount of extract per bud), 11 of 36 (31%) flies tested accepted an artificial bud. Thus, *Eurosta* females will respond to chemical cues in crude extracts of *S. altissima* even though physical cues may be altered.

However, another experiment found that the relative concentrations of these chemical cues were critical. Although 45% of the 11 *S. altissima* flies tested responded by accepting artificial buds with low concentrations (15% of the total amount of extract per bud) of *S. altissima* extract, 100% accepted buds when the concentration was raised to the standard amount (Table 1). As expected, all 11 *S. altissima* flies tested did not accept artificial buds painted with standard amounts of *S. gigantea* extracts. Although the rejection rate decreased when the concentration of *S. gigantea* was lowered, the decline was not significant.

Table 1.—Acceptance and rejection of artificial buds treated with *S. altissima* and *S. gigantea* extracts in low (15% of the total extract per bud) and standard concentrations (25% of total extract per bud) by Pennsylvania *Eurosta* infesting *S. altissima*. Chi-square goodness of fit tests were performed to test the hypothesis that females would accept artificial buds equally, regardless of extract concentration (from S. Roth, J. Horner, and W. Abrahamson unpublished data).

Extract Type	Number Accepting		Number Rejecting
S. altissima only			
[low]	5		6
[standard]	11		0
		(X^2=8.26; $p<.01$)	
S. gigantea only			
[low]	3		8
[standard]	0		11
		(X^2= 3.47; $p<.10$)	
S. altissima [standard] with *S. gigantea*			
[low]	2		7
[standard]	0		9
		(X^2=2.25; $p<.20$)	
S. gigantea [standard] with *S. altissima*			
[low]	0		9
[standard]	5		4
		(X^2=6.92; $p<.01$)	

Another series of experiments was conducted to examine whether the addition of extracts of *S. gigantea* would function as a deterrent to oviposition by Pennsylvania *E. solidaginis*. Of nine flies that originally accepted an artificial bud treated with *S. altissima* extract, none would do so once a standard concentration of *S. gigantea* was added (Table 1). This rejection rate did decrease, although not significantly, if a low concentration of *S. gigantea* extract was used. We did find that adding *S. altissima* extracts at standard concentrations to artificial *S. gigantea* buds with standard extract levels lowered the rejection rate. The highest acceptance rate of buds initially treated with *S. gigantea* extracts resulted from an original low application, painted with a standard concentration of *S. altissima* extract (X^2=5.1, $p<.025$ compared to buds treated with an extract of *S. gigantea* only).

These experiments indicate that not only is the presence of chemical cues important to ovipositing females, but the absolute amount or the ratio of stimulant to deterrent compounds may be critical as well. Ovipositional stimulants were effectively masked by deterrents and vice versa. Our findings suggest that host choice is based on a complex interaction of stimulatory to deterrent cues.

Although we have only examined ovipositional chemical cues with Pennsylvania *S. altissima* flies, we suspect that both *Eurosta* host races selectively evaluate such cues. Differential acceptance of hosts by the host races may result from variations in the amount or ratio of stimulatory and deterrent chemicals. Indeed, such variation may have been critical to the host shift, particularly if the extremes of the amounts or ratios of stimulant and deterrent chemicals within similar hosts nearly overlap and if host phenologies are similar. Under such conditions, a host shift could be encouraged if *Eurosta* colonizing a new host lost some of its sensitivity to host-specific deterrent compounds. How *et al.* (1993) have shown that the phenology of *S. gigantea* could make it a suitable host in some regions but it would only serve as a host if individuals of *Eurosta* have altered their acceptability of stimulant and repellant cues. Our genetic and behavioral findings (Waring *et al.* 1990, Craig *et al.* in press) suggest that only one host shift has occurred from *S. altissima* to *S. gigantea*. This implies that the opportunities for *Eurosta* to lose sensitivity to deterrents in *S. gigantea* may be limited.

The Role of Gallmaker Larval Competition

The establishment of a gallmaker population on a new host could be also favored by selection caused by competition among larvae on the ancestral host. Intense competition among larvae could result in lower fitnesses on the ancestral host than for individuals ovipositing on a novel host. The potential for strong intraspecific competition among *Eurosta* larvae was suggested by field studies which showed that buds of some highly acceptable host-plant genotypes are both frequently (up to 100% of the ramets) and heavily punctured (up to 42 punctures/bud) by ovipositing *Eurosta,* but that galls contain only one larva (Anderson *et al.* 1989, M. Hess and W. Abrahamson unpublished). Furthermore, a laboratory study determined that *E. solidaginis* females were not deterred from ovipositing eggs into the buds of ramets that already contained multiple punctures or eggs (T. Craig, C. Shantz, J. Itami, and W. Abrahamson unpublished). Less well-adapted herbivores may persist on new hosts because fitness levels obtained from feeding on an abundant but underexploited host plant, where survival and fecundity are low, can be as high as on the ancestral host where competition for resources is intense (Rosenzweig 1978, Pimm 1979, Rausher 1984, Wilson and Turelli 1986). Gallmaker survival might be as high or higher on a novel, closely related host where larval competition is nonexistent or low in spite of poor physiological adaptation. To explore whether or not larval competition may have contributed to *Eurosta*'s host shift, we conducted a greenhouse study in which we manipulated *Eurosta* larvae density (M. Hess and W. Abrahamson unpublished).

Individual ramets of one susceptible clone of *S. altissima,* grown from rhizomes, were caged with Pennsylvania *Eurosta*. By manipulating the level of ovipuncturing, we created a low-attack (5-9 ovipunctures/bud) and a high-attack (>15 ovipunctures/bud) treatment. Buds were sampled and dissected to determine the number of eggs or larvae immediately after oviposition and at 3 wk post oviposition. Larval survivorship was determined by allowing a subset of the *Eurosta* larvae in punctured ramets from both treatments to fully develop, overwinter, and emerge.

Oviposition of eggs increased with the number of ovipunctures (Fig. 2), and some buds contained as many as 10 or 11 Eu*rosta* eggs as a consequence of up to 40 ovipunctures/bud (M. Hess and W. Abrahamson unpublished). Although *E. solidaginis* accepted previously ovipunctured buds, a t-test for comparing the homogeneity of the slopes of ovipunctures versus eggs for the two treatment levels indicated that flies more frequently injected an egg when ovipuncturing buds with fewer punctures. Extensive probing of some buds without proportionate egg injection may be a consequence of searches for suitable oviposition sites due to bud damage. Most consequential relative to larval competition was the finding that low and high ovipunctured treatments had similar numbers of larvae/bud just prior to gall appearance (Fig. 2). These results suggest that rapid, intense larval competition and its result, larval death, accompany higher puncture rates/bud. The occurrence of a necrotic, hypersensitive plant response (Fernandes 1990) causing early larval death increased with ovipuncture rate (accounting for 8% of the larval death in the low-attack treatment but 34% in the high-attack treatment). First reported in resistant S. *altissima* genotypes (Anderson *et al.* 1989), this hypersensitive response in the susceptible genotype used in this experiment suggests that there is an advantage to *Eurosta* which oviposit eggs into buds with fewer punctures of any host genotype (M. Hess and W. Abrahamson unpublished).

The occurrence of high puncture levels on the buds of high-ranked host genotypes in the field coupled with high larval mortality in heavily attacked buds would reduce the availability of high-quality buds for ovipositing *Eurosta.* Indeed, *Eurosta* females found buds which already contained high ovipuncture levels less acceptable than unattacked buds. Such patterns of host usage could cause the breakdown of acceptance thresholds for preferred, high-ranked hosts (Jaenike 1990). A breakdown of acceptance thresholds could initiate oviposition into low-ranked genotypes or novel host species, and hence encourage a host shift. Field data examining two susceptible (high-ranked) and two resistant (low-ranked) *S. altissima* clones showed that the rate of puncturing was initially higher on susceptible clones (Anderson *et al.* 1989). However, as susceptible clones were exploited the rate of puncturing of susceptible clones fell until it was similar to that of resistant clones.

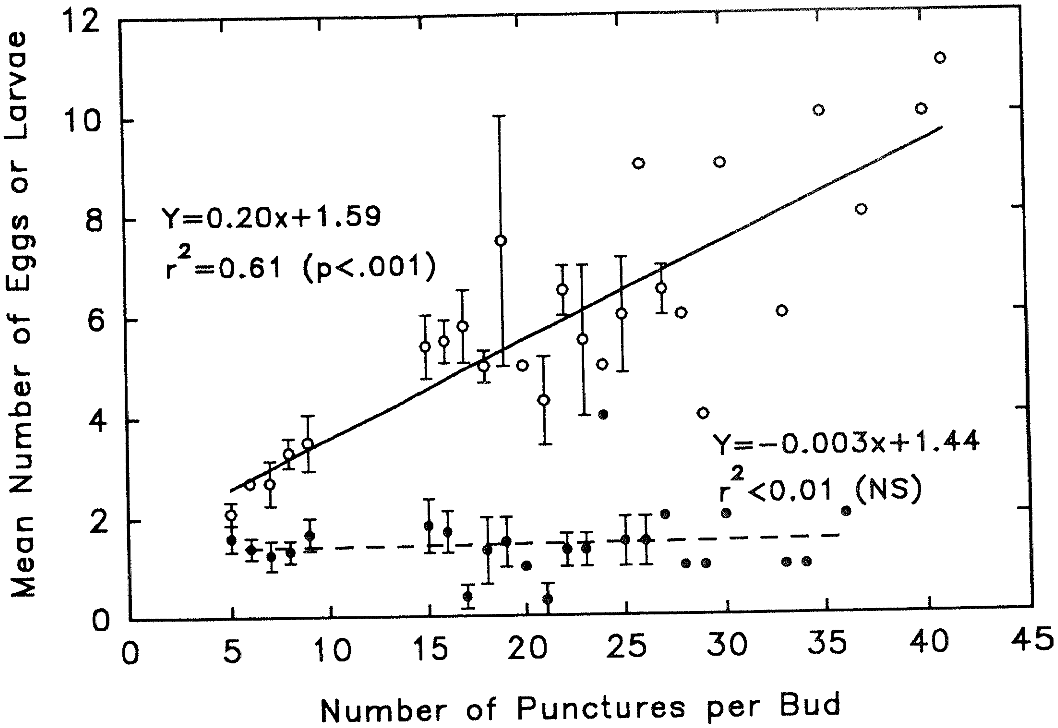

Figure 2.—The mean number ± standard error of eggs (open circles) or of larvae (filled circles) as a function of the number of ovipunctures for ramets attacked by Pennsylvania *Eurosta solidaginis* in a low-attack treatment (5-9 ovipunctures/bud) or high-attack treatment (>15 ovipunctures/bud). Regression analyses were performed on the number of eggs or larvae for each individual bud, not on the illustrated means (from M. Hess and W. Abrahamson unpublished data).

The Role of Escape From Natural Enemies

Oviposition on a novel host plant can result in a different gall size or morphology and could alter the cues available to natural enemies which use host-plant cues. One consequence of acquiring a new gall phenotype is the potential to reduce the susceptibility of the gallmaker to its natural enemies (i.e. move into enemy-reduced space). Earlier studies documented that *Eurosta* survivorship was dependent on gall size because the parasitoid wasp *Eurytoma gigantea* preferentially attacks smaller galls, and birds such as downy woodpeckers attack larger-sized galls (Weis and Abrahamson 1985, Abrahamson *et al.* 1989b, Weis *et al.* 1992). Several studies have found that *Eurosta* develop larger galls on *S. gigantea* than on *S. altissima* (Lichter *et al.* 1990; Sumerford and Abrahamson submitted; J. Brown, R. Packer, and W. Abrahamson unpublished).

In an attempt to determine if the *Eurosta* host shift may have been encouraged by natural-enemy attack, we compared the causes of gallmaker mortality for both *Eurosta* host races at allopatric and sympatric sites over a wide geographic area in 2 years (northcentral to the northeastern USA 1989 and 1991; Sumerford and Abrahamson submitted; J. Brown, R. Packer, and W. Abrahamson unpublished). With the exception of the 50-IA site, both studies confirmed that *S. gigantea* galls were larger than those of *S. altissima* at sympatric sites. Furthermore, both the 1989 and 1991 studies found that the parasitoid *E. gigantea* attacked larger *S. gigantea* galls than *S. altissima* galls and thus there was no escape from *E. gigantea* parasitism for *Eurosta* occupying *S. gigantea* galls (Fig. 3). This was unexpected since *E. gigantea* that attack *S. altissima* galls in Pennsylvania have been shown to attack after maximum gall size is reached (Weis *et al.* 1985). As a consequence, this parasitoid was expected to only attack small galls because of limitations due to ovipositor length and allow *Eurosta* in the larger *S. gigantea* galls to escape this parasitoid's attack.

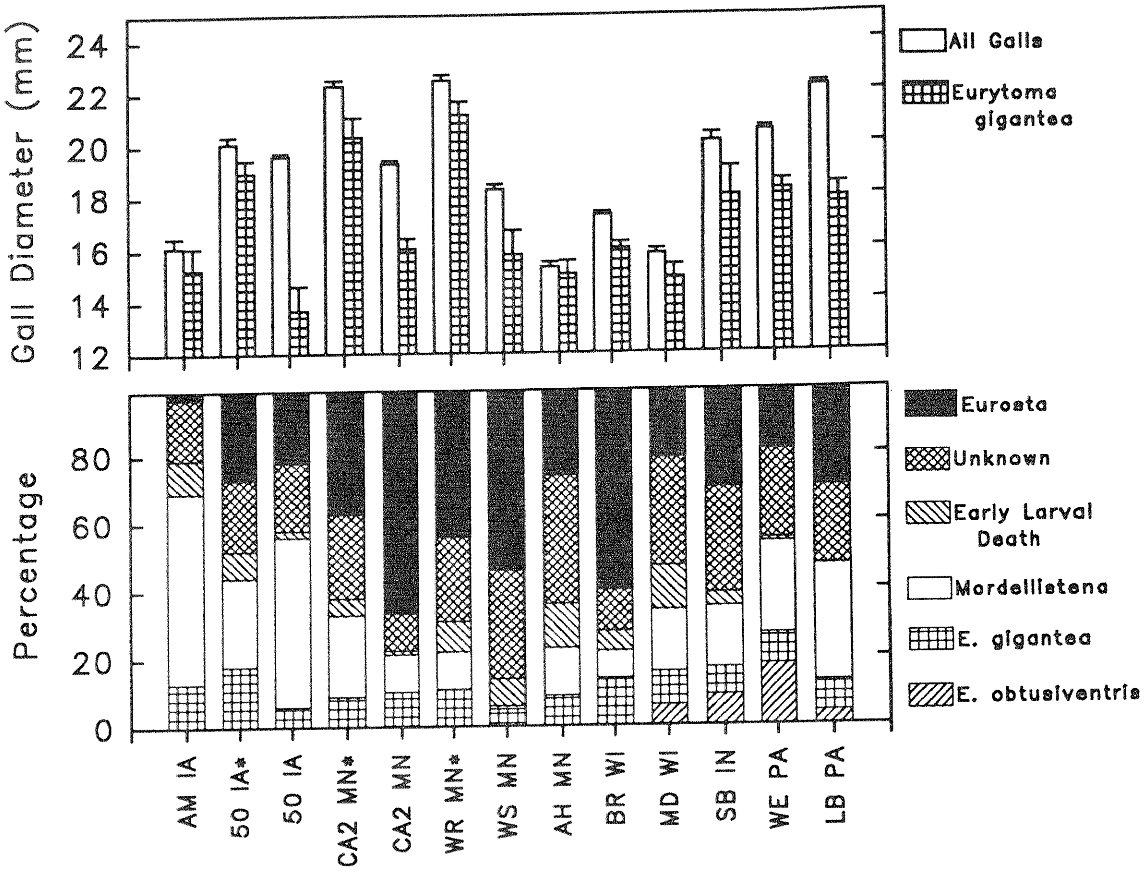

Figure 3.—(Upper) Mean gall diameter (mm ± standard errors) for all galls and galls parasitized by *Eurytoma gigantea*. (Lower) The percentage occurrence of *Eurosta* and its natural enemies by site. *Solidago gigantea* populations are denoted by asterisk (*) next to site names (see legend of Figure 4) (from Sumerford and Abrahamson submitted).

However, *E. gigantea* was able to attack the larger *S. gigantea* galls because of the significantly longer ovipositors of wasps emerging from this host compared to *S. altissima* (J. Brown, R. Packer, and W. Abrahamson unpublished). There was a significant relationship between this parasitoid's ovipositor length and the size of the gall from which it emerged. Since ovipositor length is a function of natal gall size, *E. gigantea* that shifted to attack *Eurosta* on *S. gigantea* likely experienced an immediate increase in mean ovipositor length as an effect of phenotypic plasticity in body size in response to natal gall size (Weis *et al.* 1989). The shifted parasitoid population could have consisted, within a generation or two, of females large enough to inflict similar parasitism rates on *S. gigantea* galls as were inflicted by the ancestral population on *S. altissima* galls (Sumerford and Abrahamson submitted).

The second parasitoid wasp (*E. obtusiventris*) should parasitize galls of all sizes and use host-plant cues since it attacks *Eurosta* prior to gall formation. This parasitoid, occurring in as high as 40% of the galls in eastern USA populations, was rare in northcentral USA populations (Sumerford and Abrahamson submitted; J. Brown, R. Packer, and W. Abrahamson unpublished). Both our 1989 and 1991 studies indicated that where this parasitoid did appear in appreciable numbers, it attacked *S. altissima* galls and only very rarely *S. gigantea* galls (Figs. 3 and 4; Sumerford and Abrahamson submitted; J. Brown, R. Packer, and W. Abrahamson unpublished). Our findings are consistent with those of Lichter *et al.* (1990) who did not observe *E. obtusiventris* parasitism at their sympatric site in Illinois. Furthermore, we know that the occurrence of *E. obtusiventris* is highly variable from year to year within a site (Weis *et al.* 1992). The net result of these distribution patterns is that *Eurosta* has higher survival on *S. altissima* host plants in the absence of parasitoids (due to elevated early larval death rates on *S. gigantea*). However, the presence of *E. obtusiventris* parasitoids gave *Eurosta* on *S. gigantea* hosts a survival advantage over those on *S. altissima* (J. Brown, R. Packer, and W. Abrahamson unpublished). *Eurosta* mortalities among New England collections of both host races indicate that *Eurosta*

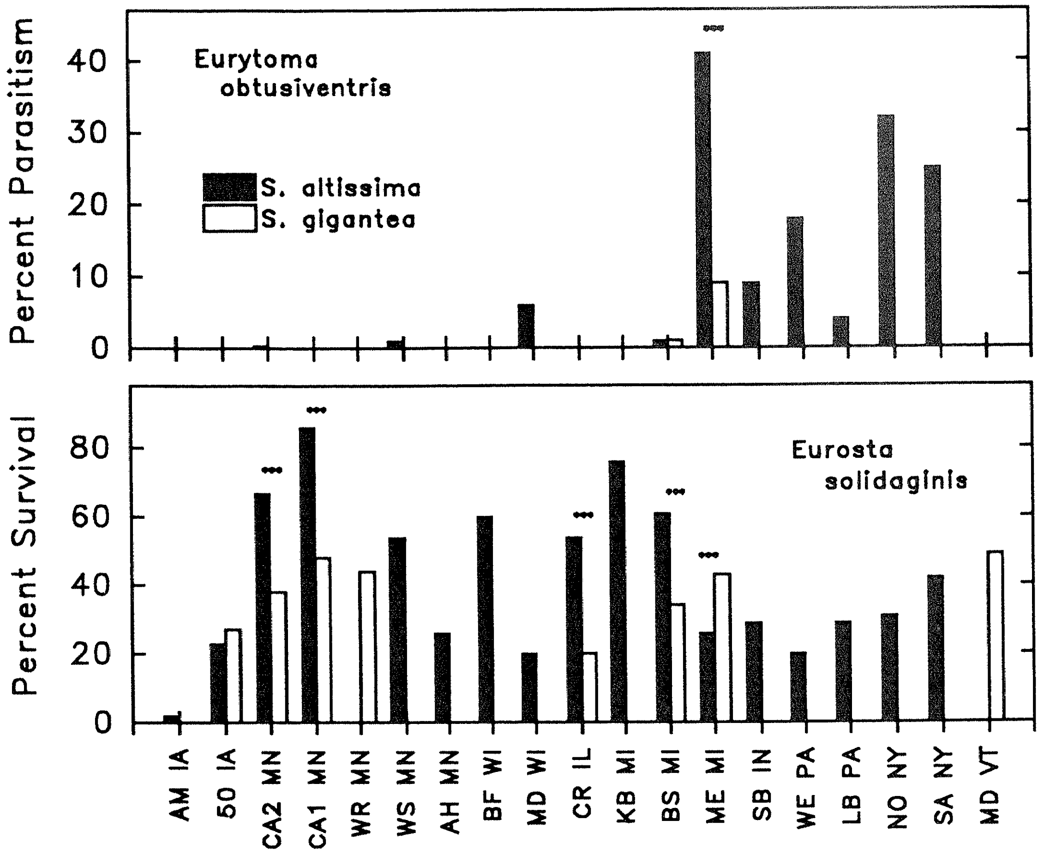

Figure. 4.—(Upper) Rates of parasitism on *Eurosta solidaginis* by *Eurytoma obtusiventris* and (Lower) survival of *Eurosta solidaginis* on *Solidago altissima* (filled bars) and *S. gigantea* (open bars) for 19 sites from Vermont to Iowa. All sites harboring the *S. gigantea* host race (indicated in the lower panel) do not necessarily have *E. obtusiventris* parasitism (upper panel). Site acronymns as follows: AM IA=Ames, IA (n=141); 50 IA=Route 50 near Ames, IA (n=107 *S. altissima*, n=155 *S. gigantea*); CA2 MN=Carlos Avery 1989, MN (n=460 *S. altissima*, n=269 *S. gigantea*); CA1 MN=Carlos Avery 1991, MN (n=1579 *S. altissima*, n=542 *S. gigantea*); WR MN=Wright County, MN (n=195); WS MN=Washington County, MN (n=158); AH MN=Arden Hills, MN (n=238); BF WI=Black River Falls, WI (n=512); MD WI=Madison, WI (n=296); CR IL=Castle Rock, IL (n=319 *S. altissima*, n=230 *S. gigantea*); KB MI=Kellogg Biological Station Hickory Corners, MI (n=392); BS MI=University of Michigan Biological Station Pellston, MI (n=340 *S. altissima*, n=375 *S. gigantea*); ME MI=Menominee, MI (n=659 *S altissima*, n=489 *S. gigantea*); SB IN=South Bend, IN (n=96); WE PA=Western PA (n=374); LB PA=Lewisburg, PA (n=363); NO NY=North Petersburg, NY (n=260); SA NY=Salem, NY (n=377); and MD=Mad River, VT (n=280). An asterisk indicates a significant difference at least at the p<.05 level (from Sumerford and Abrahamson submitted; J. Brown, R. Packer, and W. Abrahamson unpublished data).

from *S. altissima* galls suffer appreciably more mortality due to natural-enemy attack than *S. gigantea* galls (J. Brown, R. Packer, and W. Abrahamson unpublished). Such mortality would enhance the fitness of *Eurosta* on *S. gigantea* relative to *S. altissima* populations and could encourage a host shift to *S. gigantea* (Fig. 4).

While the 1991 study did not record appreciable populations of the predatory inquiline *Mordellistena unicolor*, some of the 1989 sites sampled exhibited high levels of predation by this predator (Fig. 3, Sumerford and Abrahamson submitted). *Mordellistena unicolor* produced the only significant relationship when we regressed the overall *Eurosta* mortality on the relative contributions of all natural enemies (r^2=0.95, p<.001), but its predation was as variable between *Solidago* hosts at sympatric sites as well as among all sites sampled (Sumerford and Abrahamson submitted). The consequence is that *M. unicolor* is not likely a driving force that would facilitate a host shift.

The Facilitation of a Host Shift

Individuals of a gallmaking species may be able to shift to a new host plant if the adaptations to the ancestral host preadapt the herbivore to utilize the novel host. Closely related (and chemically similar) hosts may differ only slightly in traits that affect herbivore survival, and as a result, there would be no need for a "genetic revolution" of adaptations for host-plant use (Bush 1975a,b; Craig *et al.* in press). This would be particularly true if the ancestral population displayed considerable variation in host use. Gallmakers adapted to extreme individuals of the ancestral host may perform reasonably well on some extreme individuals of the novel host. But in order for a host shift to occur in the first place, the phenologies of extreme individuals of both the ancestral and new host must at least overlap. Yet once the host shift has occurred, slight differences in host-plant phenologies between the ancestral and new host-plant species can be crucial to the reproductive isolation of the gallmakers on the novel host (Butlin 1990). Reproductive isolation on new hosts could be rapid (with strong selection for adaptation) when herbivore emergence is cued by host-plant phenology (Wood 1980, 1986; Wood *et al.* 1990; Keese and Wood 1991). Factors such as larval competition and natural-enemy attack could promote the initial host shift if they cause higher mortality to populations infesting the ancestral host plant than to populations on the novel host species.

The findings we present here, in combination with previously published results, provide evidence that each trophic level—the host plant, gallmaker, and natural enemies—could potentially play a role in facilitating a host shift and influencing the rates and mechanisms of speciation. Furthermore, the results reported by Craig *et al.* (this volume) indicate that gallmaking insects may be particularly conducive to host-race formation and subsequent sympatric speciation. Although individually subtle, the effects of factors such as host-plant phenology, competition among gallmaker larvae, and differential attack on gallmaker larvae by their natural enemies could have a strong collective influence on host shifts and speciation in gallmakers. While it is impossible to know which particular agent was responsible for the single host shift from S. *altissima* to *S. gigantea*, our results suggest that any one or probably a combination of such factors may contribute to a host shift.

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This international proceedings focuses on the biology, ecology, and evolution of gall-forming insects and their uniquely specialized relationships with their host plants. The individual contributions range in scope from detailed descriptive to profoundly theoretical, synthetic studies. One underlying theme of the proceedings is the important contribution of knowledge about gall-forming insects and their hosts to the development of robust, general principles about the ecology and evolution of plant-herbivore relationships.

KEY WORDS: Host plant resistance, tritrophic interactions, speciation, interspecies hybrids, plant stress, population dynamics, plant phenology, life history strategies, competition.