

Mika Sipura

Tritrophic interactions: willows, herbivorous insects and insectivorous birds

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Abstract Insectivorous birds can increase plant growth by consuming herbivorous insects and reducing insect damage. However, plant traits such as the level of chemical defense may affect the quantity and quality of insects, and alter the foraging behavior of birds. Therefore, I predicted that plant traits can also modify the effect of birds on leaf damage and plant growth. This study compared the effect of insectivorous birds on the herbivory and growth of two chemically different willow species, weakly defended *Salix phylicifolia* and strongly defended *S. myrsinifolia* under two fertilization levels. Half of the willows were protected from birds using a translucent gill-net, which did not limit access by insects. The effect of birds on the densities of leaf-chewing insects and leaf damage was considerable on unfertilized *S. phylicifolia* but less obvious on fertilized ones. The effect of bird predation was negligible on *S. myrsinifolia*, which had very low insect densities in all treatments. Birds increased the growth of the experimental willows, but the effect was clear only in unfertilized *S. phylicifolia*. I suggest that birds avoided foraging on willows with low populations of insects and little visible damage. The study shows that bird predation can alter the patterns of insect densities we see on willows, emphasizing the importance of considering multitrophic effects when studying plant-insect interactions.

Key words Willows · Herbivory · Insectivorous birds · Predation · Multitrophic interactions

Introduction

Several studies have demonstrated that insectivorous birds can reduce remarkably the number of their insect prey (e.g., Holmes et al. 1979; Kroll and Fleet 1979;

Loyn et al. 1983) and leaf damage to plants from consumption by leaf-chewing insects (Atlegrim 1989; Marquis and Whelan 1994). Although the use of birds in biocontrol was attempted much earlier than that of invertebrate predators or parasitoids (Otvos 1979), the study by Marquis and Whelan (1994) was the first to show that birds can increase plant growth by consuming herbivorous insects. In their experiment, exclusion of birds from white oaks (*Quercus alba* L.) increased the number of leaf-chewing insects and leaf damage. Since insect damage retarded the growth of the white oaks, bird exclusion led to considerable decrease in leaf size and biomass production of these trees.

Overall, the existing evidence suggests that birds may potentially benefit plants (see Marquis and Whelan 1994 for references). However, this may not always occur even if both birds and herbivorous insects are abundant (see Mattson 1974 for example). Firstly, plants may tolerate moderate levels of insect damage (Owen and Wiegert 1976; Paige and Whitham 1987; Strauss and Agrawal 1999), which is likely to obscure the indirect effect of birds on plant growth. Secondly, birds attack both phytophagous and entomophagous prey, and may prefer parasitised or otherwise predation-prone insects (Betts 1955; Tscharnke 1997). Birds that consume relatively large amounts of predatory invertebrates may therefore even increase the numbers of herbivorous insects (Kristin 1991; Tscharnke 1997). Thirdly, birds may prefer some plants as foraging sites because of the expected quantity of insect prey and discard less profitable or unpredictable feeding sites. Since plants differ in their acceptability to herbivorous insects (e.g., Fritz and Simms 1992), different amounts of prey can obviously be obtained on different plants. Fourthly, plants may affect the detectability of insect prey. For example increased movements (Bergelson and Lawton 1988) or active feeding (Bernays 1997) by insects may affect their vulnerability to their natural enemies. Plants may also differ in architecture and foliar structure, which may either facilitate or constrain the way birds detect or capture their prey (Holmes 1990). Finally, herbivorous insects may use the

M. Sipura
Department of Biology, University of Joensuu, P.O. Box 111,
FIN-80101 Joensuu, Finland
e-mail: Mika.Sipura@joensuu.fi
Fax: +358-13-251-3590

defensive compounds of plants for their own defense (Smiley et al. 1985; Pasteels et al. 1988; Pasteels and Rowell-Rahier 1991), and hence be lower-quality food for predators if growing on strongly defended plants. As a result, genetically and environmentally determined traits of plants may modify the degree to which birds can benefit them.

This study examined the impact of avian predators on insect herbivore densities, leaf damage, and growth of two willow species at two fertilization levels. The two willow species used in this study, the tea-leaved willow (*Salix phylicifolia* L.) and the dark-leaved willow (*S. myrsinifolia* Salisb.) are among the most widespread willow species in northern Europe, and can be found abundantly along streams, lakesides and other open habitats including cultivated fields (Hämet-Ahti et al. 1998). The willow species are morphologically similar but show remarkable differences in the secondary chemistry of their leaves. Generally about 50-fold differences in concentrations of phenolic glycosides (including salicin and salicortin) have been found between bitter tasting *S. myrsinifolia* and mild *S. phylicifolia* (Tahvanainen et al. 1985; Julkunen-Tiitto 1986; Rank et al. 1998). Phenolic glycosides have been shown to repel generalist herbivores (e.g., Tahvanainen et al. 1985; Dodge et al. 1990), whereas some specialists may use them as stimulants for feeding or oviposition (Tahvanainen et al. 1985; Soatens and Pasteels 1994; Kolehmainen et al. 1995). On the other hand, considerable amounts of a flavonoid, ampelopsin, have been found in the leaves of *S. phylicifolia* but not in *S. myrsinifolia* (Rank et al. 1998). However, this compound has been observed to be rather inert to some generalist insects (M. Sipura and A. Ikonen, unpublished work). Therefore I predict that when generalist herbivores predominate, *S. phylicifolia* should suffer more severely from insect damage than *S. myrsinifolia*.

In addition to species-specific differences, there are environmental factors like soil fertility that may affect both insect herbivores and their enemies (e.g., Strauss 1987; Haartvigsen et al. 1995). In *S. myrsinifolia* nitrogen fertilization has been observed to increase the nitrogen content in the leaves, and to cause a slight decrease in the concentration of phenolic glycosides (Hakulinen et al. 1995). Basically, fertilization could affect insect densities, and also change the foliar architecture of willows. These changes may affect foraging by insectivorous birds.

Here I will concentrate on four questions relevant to tritrophic interactions among willows, willow feeding insects and insectivorous birds. First, do the two willow species have different herbivore loads and do they suffer from different amounts of herbivore damage? Second, how does fertilization alter insect densities on these willows? Third, do insectivorous birds reduce insect densities and leaf damage on the two willow species and does bird predation on herbivorous insects indirectly affect willow growth? And fourth, how does the effect of birds on herbivory and growth differ between the two willow species and how do birds respond to fertilization of willows?

Materials and methods

Study site and experimental design

The study was conducted in Parikkala, southeast Finland (61°33'N, 29°33'E). The experimental willows were growing on the shore of a highly eutrophicated lake on a narrow embankment constructed to prevent flooding of the fields surrounding the lake. There was a belt of larger trees growing on both sides of the embankment, and younger (<10 years) *S. phylicifolia* and *S. myrsinifolia* on the top of the embankment.

The bird community in the area was censused using a standard mapping method (Enemar 1959). The study area was long but very narrow (about 1600×4 m), and it was not possible to determine the actual bird densities. However, the commonest bird species in the area were sedge warbler (*Acrocephalus schoenobaenus* L.) with seven pairs, pied flycatcher (*Ficedula hypoleuca* Pallas) with six pairs, willow warbler (*Phylloscopus trochilus* L.) with four pairs and reed bunting (*Emberiza schoeniclus* L.) with four pairs. Altogether, individuals from 16 species of insectivorous birds were observed to forage regularly in the study area.

Just before budbreak in spring 1998, I selected 12 blocks with four *S. phylicifolia* and four *S. myrsinifolia* individuals in each and randomly divided the willows into fertilization and bird exclusion treatments. The ages of the willows (determined from annual rings) varied from 4 to 9 years. Willows in the fertilization treatment received 100 g m⁻² of complete fertilizer (N:P:K 8:4:14; Puutarhan yleislannos, Kemira Agro Oy, Finland), and unfertilized willows served as controls. The cages for excluding birds were made of four wooden side poles (diameter 3–5 cm) erected on the ground. The sides of the cages varied between 0.8 to 2.5 m, depending on the size of the willow. A completely translucent monofilament gill-net (Pietarinkerko, Kivikangas Oy, Finland) with 22-mm-diameter holes and 0.2-mm thread was stretched upon the side poles. Although the hole size is rather small for the largest insects, some butterflies with a wingspan of 40 mm were seen to fly through the net. Also, caterpillars of the largest insects found on willows, *Smerinthus ocellatus* L. and *Cerura vinula* L., were observed both on caged and control willows. Because the erection of the side poles for the net may cause root damage to the experimental willows, I also pierced four holes in the ground next to the control willows. At the end of the growing season some shoots (less than 3% of the estimated shoot biomass) of three fertilized willows of both species had grown out of the cages. However, I observed that birds avoided foraging near the cages, and assume this error to be negligible.

Insect censuses

Insect populations were censused by counting all herbivorous insects on the experimental willows five times during the growing season 1998 (see Fig. 1. for census dates). Because it was not possible to open the cages, some of the smallest insects, such as thrips and smallest aphid nymphs, had to be omitted from the censuses. I avoided disturbing insects, and counted the constructions of concealed insects rather than individuals.

I determined insect densities per leaf area by counting the number of shoots and measuring the length of 20 randomly selected shoots from each willow at each census time. At each time I also collected a sample of 40 shoots from both species from adjacent willows. After measuring the lengths of these sampled shoots I dried the leaves under a moderate pressure, took a photocopy of each leaf and measured the leaf surface area of each shoot with a planimeter. The shoot length significantly explained 76–94% of the variation in the total leaf area in regression models. Therefore, on the basis of the number of shoots and the mean shoot length I was able to obtain a good estimate of leaf area of each experimental willow at each census time. I calculated all insect densities for 1 m² of leaf surface area.

Measuring insect damage and willow growth

I measured the leaf damage caused by leaf-chewing insects in two ways. Because willows tend to abscise badly damaged leaves early in the growing season, I determined the proportion of early-abscised leaves at the fourth census by counting the leaves and leaf scars from 20 randomly selected shoots per willow. At the last census I collected all remaining leaves from 50 randomly selected shoots per willow, and stored them in a freezer. I determined the total leaf area and damaged or missing leaf area from 50 randomly selected leaves per willow using transparent scale paper. I used a sample size of 50 leaves, since primary observations showed that fluctuations of means diminished sharply after 40 leaves. In the analyses I used the mean proportion of early abscission and the mean proportion of damaged leaf area as variables.

At the end of the growing season I measured the lengths of 50 randomly selected shoots from each willow and used mean shoot length as a growth variable. Also, I cut down all the experimental willows, and took a piece from the basal stem at height of 2 cm to determine the annual radial growth. I measured the thickness of previous and current-year growth rings under a stereomicroscope and used a relative radial growth (current year growth/previous year growth) as a second growth variable.

Data analysis

The experiment was originally planned as a completely randomized block design with three factors. I tested the block effects prior to final analyses. Because no significant effects were found, I omitted blocks from the analysis to save the degrees of freedom. I analyzed all insect densities using a three-factor repeated-measures GLM ANOVA, with censuses as the within-subject measures and willow species, fertilization treatment and predation treatment as fixed factors. First, I analyzed the total sum of insect densities of all herbivorous insects, and then divided them into three functional groups as follows:

1. *Concealed feeders* like galling insects, leaf-folders and leaf-tiers, which may be safe from predatory birds
2. *Sap suckers* like aphids and leaf hoppers, which are probably vulnerable to bird predation, but do not leave feeding marks to leaves
3. *Leaf chewers* such as larvae of moths, sawflies and chrysomelid beetles, which are vulnerable to bird predation, and whose effect can be estimated later as damaged leaf area

I analyzed leaf damage and growth variables using three-way GLM MANOVA with willow species, fertilization treatment and predation treatment as fixed factors. I use eta-squared values (η^2) as estimates of effect sizes: η^2 is the squared ratio of the between-groups sum of squares and the total sum of squares (Keppel 1982), and can be interpreted as R^2 -values. Most variables were log ($x+1$) or arcsin-square-root transformed to meet the criteria of the analysis of variance.

Results

Insect densities

There was no significant difference in total herbivore density between *S. phylicifolia* and *S. myrsinifolia* ($F_{1,88}=0.48$, $P=0.49$). Concealed-feeding and leaf-chewing insects were, however, more abundant on *S. phylicifolia* whereas sap-sucking insects were more abundant on *S. myrsinifolia* (Fig. 1, Table 1). An aphid, *Pterocomma salicis* L., that made up 89.9% of the sap-sucking guild, was clearly more abundant on *S. myrsinifolia*

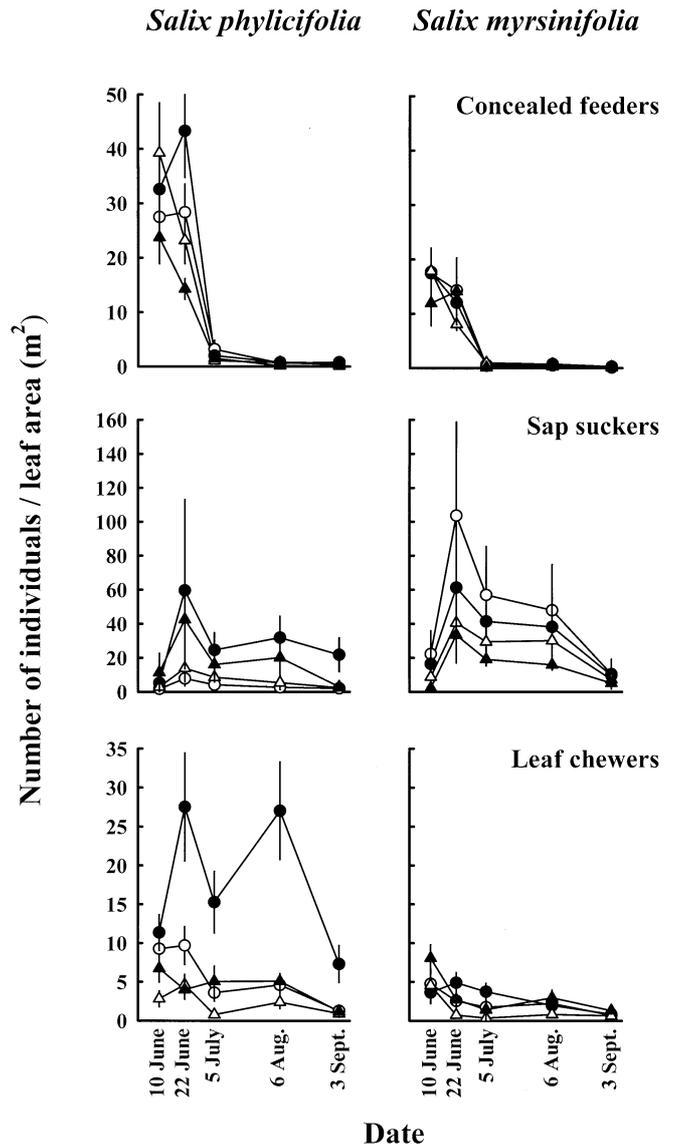


Fig. 1 Densities of concealed-feeding, sap-sucking and leaf-chewing insects on the experimental willows (mean \pm 1 SE; $n=12$ for each treatment combination, \circ unfertilized control, \bullet unfertilized cage, \blacktriangle fertilized cage)

($F_{1,88}=16.9$, $P<0.001$, $\eta^2=0.16$), whereas there was no difference in densities for the rest of the insects in this guild ($F_{1,88}=0.27$, $P=0.61$).

Fertilization caused a significant reduction in overall insect density per leaf area ($F_{1,88}=7.45$, $P=0.008$) on the willows studied, but explained only 7.8% of the variance. The difference disappeared when mean leaf area was used as a covariate ($F_{1,88}=0.91$, $P=0.76$), suggesting that the difference in overall insect densities resulted mainly from the increased leaf area in fertilized willows. The reduction in densities due to fertilization was significant in concealed feeders and leaf chewers but not in sap suckers (Fig. 1, Table 1). There was also a significant willow species \times fertilization -interaction in leaf chewer densities (Fig. 1, Table 1), showing that fertilization caused strong-

Table 1 Between-subject effects of the repeated-measures analysis of variance on the effects of willow species (W), fertilisation treatment (F) and bird predation treatment (P) on the insect densities of experimental willows

Source of variation	df	Concealed feeders ^a				Sap suckers ^a				Leaf chewers ^a			
		MS	F	P	η^2	MS	F	P	η^2	MS	F	P	η^2
Willow species	1	3.49	32.81	<0.001	0.27	19.64	17.94	<0.001	0.17	10.60	63.06	<0.001	0.42
Fertilisation treatment	1	0.51	4.78	0.031	0.05	1.40	1.28	0.26	0.01	4.40	26.17	<0.001	0.23
Predation treatment	1	0.35	3.30	0.073	0.04	2.70	2.46	0.12	0.03	6.26	37.22	<0.001	0.30
W×F	1	0.0457	0.43	0.51	0.005	0.406	0.37	0.54	0.004	3.94	23.45	<0.001	0.21
W×P	1	0.0283	0.27	0.61	0.003	1.012	0.92	0.34	0.01	1.012	6.02	0.016	0.06
F×P	1	0.242	2.27	0.14	0.03	1.60	1.47	0.23	0.02	0.118	0.70	0.40	0.008
W×F×P	1	0.0511	0.48	0.49	0.005	0.115	0.105	0.75	0.001	0.99	5.91	0.017	0.06
Error	88	0.106				1.095				0.168			

^aData were log (x+1) transformed before the analyses

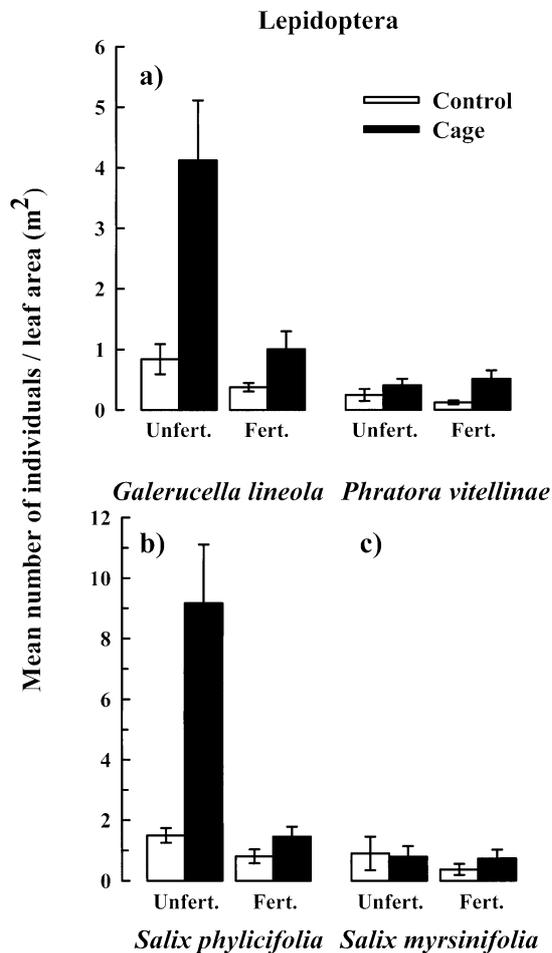


Fig. 2. Mean densities (mean±1 SE; $n=12$ for each bar) of **a** lepidopteran larvae, and larvae of the leaf beetles **b** *Galerucella lineola* and **c** *Phratora vitellinae* on the experimental willows. The larvae of the leaf beetles were not present at the first census and the mean is calculated from the last four censuses

er reduction in the densities of leaf-chewing insects on *S. phylicifolia* than on *S. myrsinifolia*.

Exclusion of birds caused a significant increase in overall herbivore insect density ($F_{1,88}=7.85$, $P=0.006$), but the treatment explained only 8.2% of the variance. Con-

cealed feeders were slightly but not significantly (Fig. 1, Table 1) more abundant on control bushes, whereas bird exclusion treatment increased significantly the densities of free-living leaf chewers (Table 1). In leaf chewers there is a significant willow species×predation treatment interaction (Table 1). Caged *S. phylicifolia* had far higher insect densities than caged *S. myrsinifolia* (Fig. 1). It can also be seen that bird exclusion had a strong effect on unfertilized *S. phylicifolia*, but only a slight effect on fertilized ones. A slight effect of predation treatment occurred in fertilized *S. myrsinifolia*, whereas no effects could be seen in unfertilized ones (Fig. 1). Therefore, there is also a significant three-way interaction between willow species, fertilization treatment, and predation treatment (Table 1).

To clarify the effect of birds on herbivore densities, three abundant subgroups of leaf chewers were chosen for closer examination. Generalist lepidopteran caterpillars made up 14% of leaf-chewing individuals on *S. phylicifolia* and 21% on *S. myrsinifolia*, and because of their large size, they may cause considerable leaf damage on willows. As can be seen in Fig. 2a the caterpillars were significantly more abundant on *S. phylicifolia* ($F_{1,88}=56.60$, $P<0.001$, $\eta^2=0.39$). Although the main effect of birds was clear ($F_{1,88}=36.75$, $P<0.001$, $\eta^2=0.30$), it was significantly more pronounced on *S. phylicifolia* (willow species×predation treatment-interaction: $F_{1,88}=10.22$, $P=0.002$, $\eta^2=0.10$). There is also a significant willow species×fertilization-interaction ($F_{1,88}=11.57$, $P=0.002$, $\eta^2=0.10$), and a significant three-way interaction between all three factors ($F_{1,88}=7.72$, $P=0.007$, $\eta^2=0.08$).

Larvae of the leaf beetle *Galerucella lineola* F. made up 34% of leaf chewers on *S. phylicifolia*, but this beetle never occurred on *S. myrsinifolia*. Another common leaf beetle, *Phratora vitellinae* L. consisted 22% of leaf chewers on *S. myrsinifolia* but only few individuals were observed on *S. phylicifolia*. Fertilization affected negatively on the densities of *G. lineola* ($F_{1,44}=9.18$, $P=0.004$, $\eta^2=0.17$). The predator exclusion treatment caused a dramatic increase in the densities of *G. lineola* on unfertilized *S. phylicifolia*, whereas the effect was negligible on fertilized bushes (main effect: $F_{1,44}=13.83$, $P=0.001$, $\eta^2=0.24$; Fig. 2b). However, the fertilization×bird predation -interaction was not significant ($F_{1,44}=2.84$, $P=0.099$). On the

Table 2 Analysis of variance on the effects of willow species (W), fertilisation treatment (F) and predation treatment (P) on early leaf abscission and leaf damages on experimental willows

	df	%Early abscission ^a				%Leaf area damaged ^a			
		MS	F	P	η^2	MS	F	P	η^2
Willow species	1	0.156	7.70	0.007	0.08	0.524	185.34	<0.001	0.68
Fertilisation treatment	1	0.131	6.49	0.013	0.07	0.013	4.55	0.035	0.05
Predation treatment	1	0.145	7.14	0.009	0.08	0.048	17.15	<0.001	0.16
W×F	1	0.406	20.04	<0.001	0.19	0.040	14.03	<0.001	0.14
W×P	1	0.021	1.05	0.31	0.01	0.027	9.60	0.003	0.10
F×P	1	0.030	1.46	0.23	0.02	<0.001	0.001	0.98	<0.001
W×F×P	1	0.076	3.74	0.056	0.04	0.011	3.96	0.05	0.04
Error	88	0.020				0.003			

^aData were arcsin-square-root transformed before the analyses

Table 3 Analysis of variance on the effects of willow species (W), fertilisation treatment (F) and predation treatment (P) on shoot length and relative radial growth of the experimental willows

	df	Shoot length ^a				Relative radial growth ^a			
		MS	F	P	η^2	MS	F	P	η^2
Willow species	1	0.058	3.64	0.06	0.04	0.014	0.99	0.32	0.01
Fertilisation treatment	1	1.70	106.88	<0.001	0.55	0.28	19.70	<0.001	0.18
Predation treatment	1	0.031	1.96	0.165	0.02	0.163	11.43	0.001	0.12
W×F	1	0.0012	0.077	0.78	0.001	0.0124	0.87	0.35	0.01
W×P	1	0.068	4.27	0.042	0.05	0.0184	1.29	0.26	0.01
F×P	1	0.0172	1.085	0.30	0.01	0.0003	0.002	0.96	<0.001
W×F×P	1	0.0195	1.23	0.27	0.01	0.023	1.62	0.21	0.02
Error	88	0.0158				0.0142			

^aData were log (x+1) transformed before the analyses

other hand, fertilization and predation treatments did not have any effects on the densities of *P. vitellinae* on *S. myrsinifolia* ($P>0.43$ in every case; Fig. 2c).

Ants (*Myrmica rubra* L.) and spiders formed 97% of the individuals of invertebrate predators observed on experimental willows. Although cages may have provided additional substrates for web-building spiders, the bird predation treatment did not affect spider densities ($F_{1,88}=0.42$, $P=0.52$), nor was there any interaction between willow species and predation treatment ($F_{1,88}=0.10$, $P=0.75$). Likewise, birds did not affect densities of ants ($F_{1,88}=0.48$, $P=0.49$) and plant species did not interact with predation treatment ($F_{1,88}=1.71$, $P=0.20$). Ants were, however, significantly more abundant on *S. myrsinifolia* than on *S. phylicifolia* ($F_{1,88}=7.67$, $P=0.007$, $\eta^2=0.08$). In a data pooled over experimental treatments there were on average 32.32 ± 6.03 (SE) ants on *S. myrsinifolia* and 13.78 ± 3.11 on *S. phylicifolia*.

Leaf damage

Leaves of caged willows abscised prematurely significantly more than leaves of control willows (Table 2, Fig. 3.). In *S. phylicifolia* leaves from unfertilized bushes abscised prematurely more than leaves from fertilized bushes, whereas the reverse was true in *S. myrsinifolia* (Table 2, Fig. 3.). This may have been caused by *Melampsora* rust that mostly attacked fertilized *S. myrsinifolia*. In data pooled over willow species and experimental treatments the percentage of early abscission was significantly correlated with the mean density of leaf chewers during first three censuses ($r_s=0.53$, $P<0.001$, Spear-

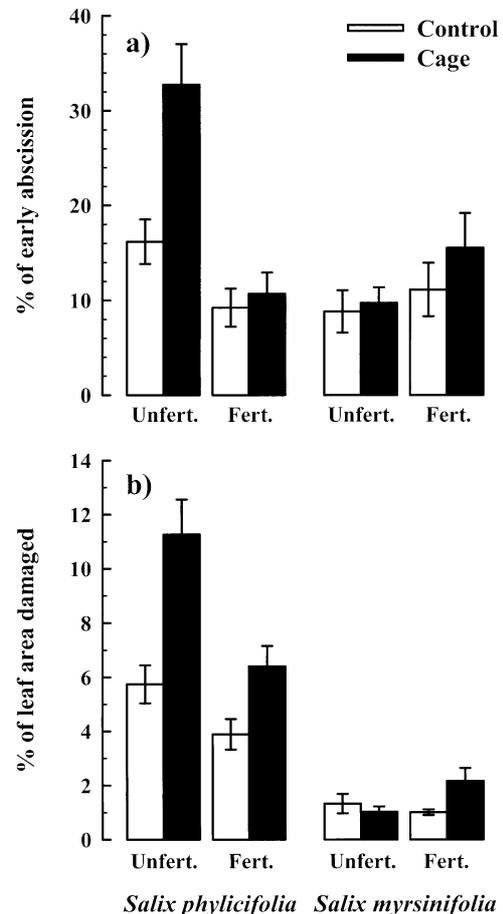


Fig. 3. a Percentage (mean \pm 1SE; $n=12$ for each bar) of early leaf abscission and b percentage of leaf area damaged on the experimental willows

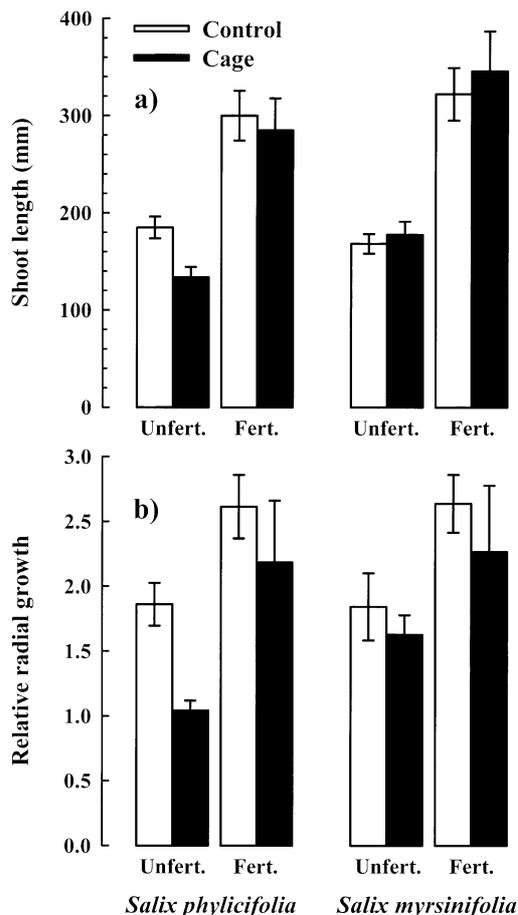


Fig. 4. a Shoot length and b relative radial growth of the experimental willows (mean \pm 1 SE; $n=12$ for each bar)

man correlation), but even more closely with the mean density of an abundant leaf-tying moth *Brachylochia viminalis* F. (Lepidoptera, Noctuidae) ($r_s=0.62$, $P<0.001$).

The percentage of early abscission and the percentage leaf area damaged were strongly correlated with the densities of leaf-chewing insects (Fig. 3, Table 2). There was significantly more damage on *S. phylicifolia* than on *S. myrsinifolia*. Fertilization decreased the level of damage in *S. phylicifolia* but not in *S. myrsinifolia*. Predator exclusion significantly increased the amount of leaf damage, and the effect was more pronounced in *S. phylicifolia*. The significant three-way interaction of all factors (Table 2) can be interpreted so that the more there were insect damage, the larger was the effect of bird predation (Fig. 3).

Willow growth

Predation treatment had a significant effect on willow growth (MANOVA for shoot length and relative radial growth, Wilks' $\lambda=0.89$, $F_{2,87}=5.61$, $P=0.005$, $\eta^2=0.12$). There was no significant willow species \times predation treatment interaction (Wilks' $\lambda=0.95$, $F_{2,87}=2.17$, $P=0.12$). Predation treatment had no significant effect on the length of shoots, but there was a significant willow spe-

cies \times bird predation treatment interaction (Table 3). When the relative radial growth is considered (Table 3), bird predation seems to have had a significant overall effect on willow growth, but the willow species \times predation treatment interaction was not significant. As seen in Fig. 4, the effect of birds on willow growth is most evident in unfertilized *S. phylicifolia*, which also had the largest herbivore load.

Discussion

The results show that birds decrease densities of leaf-chewing insects but have a negligible effect on concealed-feeding and sap-sucking insects. There are many studies that show that insectivorous birds can heavily attack insect galls, which may lead to remarkable consequences on the ecology and evolution of some gallers and coupled multitrophic systems (Tscharntke 1992, 1997; Abrahamson and Weis 1997). In these systems, however, the galls and gallmakers are usually larger than those of studied willows, and the action of birds takes place during fall or winter when alternative food is probably scarce. It is therefore possible that insects in galls and other shelters may escape birds when alternative and more profitable prey sources are available. On the other hand, the dominant sap-sucking insects on willows are either quick-moving (leafhoppers) or protected vigorously by ants (aphids).

The increase of leaf chewers due to bird exclusion was more pronounced on *S. phylicifolia* compared to *S. myrsinifolia*, which clearly had lower insect densities even when birds were excluded. The difference in insect densities can be reduced to leaf chemistry of the willows. Some of the chrysomelid beetle species [including *G. lineola* and *Lochmaea caprea* (L.)] observed on the experimental willows, have been shown to avoid feeding on salicylate-rich willows like *S. myrsinifolia* (Tahvanainen et al. 1985; Kolehmainen et al. 1995) and in some studies generalist herbivores were shown to perform worse on willows rich in phenolic glycosides (Roininen and Tahvanainen 1989; Denno et al. 1990; Matsuki and MacLean 1994). The specialist leaf beetle *Phratora vitellinae* that usually predominates in the leaf-chewing guild on *S. myrsinifolia* was rather scarce in this study area. In sites where *P. vitellinae* is abundant, *S. myrsinifolia* may have even more leaf damage than *S. phylicifolia* (M. Sipura, unpublished work).

There are at least three possible reasons why birds prefer foraging on weakly defended *S. phylicifolia* over strongly defended *S. myrsinifolia*. First, aphid tending ants that were more abundant on *S. myrsinifolia* may interfere foraging birds. Haemig (1996) have shown that great tits (*Parus major* L.) avoided foraging on artificial trees with *Formica* ants, which may lead to increased survival of insects from bird predation. In this study, however, using mean ant density as a covariate in the analyses of leaf chewer densities or leaf damage did not cause any notable changes to the results of ANOVA, suggesting that

the effect of ants on bird predation was insignificant in this case. Second, insects on *S. myrsinifolia* may be less palatable to birds because they use plant secondary chemicals for their own defense. It is well-known that larvae of *S. myrsinifolia*-feeding *P. vitellinae* convert salicylates from their host into salicylaldehyde, which has been shown to repel many natural enemies including one bird species, blackcap (*Sylvia atricapilla* L.) (Topp and Bell 1992). It has also been suggested that generalist herbivores may be either actively or passively defended just by having plant chemicals in their hemolymph or gut (Brower 1984; Bowers 1993). There are, however, no studies showing the effect of plant-derived chemicals on defense of generalist herbivores, and even the role of larval secretions of specialist herbivores is still controversial (Rank et al. 1996, 1998). The third possibility is that birds respond to herbivore densities in a density-dependent way (Dickson and Whitham 1996) by staying for longer in profitable bushes or flying more often to bushes with higher expected prey densities. Birds may use leaf damage as a cue for profitable foraging sites and therefore prefer foraging on willows with high damage levels. Heinrich and Collins (1983) have shown that black-capped chickadees (*Parus atricapillus* L.), learn to use trees with damaged leaves as foraging sites, and may even recognize the tree species where they have previously found food. To what extent birds use leaf damage as a cue in the field is not known (Heinrich 1993; but see Greenberg and Gradwohl 1980), but the hypothesis provides a promising explanation for the results reported here.

The results of this study contradict the hypothesis suggesting that predation on herbivores is higher on sub-optimal host plants (Feeny 1976; Clancy and Price 1987; Häggström and Larsson 1995). As shown earlier, the presence of phenolic glycosides has been found to have a negative effect on the growth of generalist herbivores. Prolonged development time, increased time devoted to foraging, and increased movements on poor-quality host plants may lead to increased exposure to natural enemies (Feeny 1976; Price et al. 1980; Bergelson and Lawton 1988; Häggström and Larsson 1994; Bernays 1997). However, here generalist lepidopteran caterpillars escaped bird predation better on *S. myrsinifolia* where their densities were lower.

The negative effect of fertilization on insect densities on *S. phylicifolia* is rather surprising. In their review Waring and Cobb (1992) report that 67% of the studies have found herbivores to perform better on fertilized plants. These results can be explained by increased nitrogen contents and decreased concentrations of carbon based secondary compounds in plants after fertilization (Hartley and Jones 1997). So far, no studies are available to show the effect of fertilization on the food choice or insect performance on *S. phylicifolia*. So, it is not clear whether the observed decrease in the densities of leaf chewers after fertilization is due to lowered food quality, altered composition of feeding or oviposition stimulants, or external factors. Because fertilization affected only leaf-chewing insects, it may be that insects responded to

the physical changes rather than the nutritional alteration of host plants after fertilization. It is possible that fertilization changed the structure of leaves, which made them less edible for herbivores. Because of the vigorous shoot growth it is also possible that fertilization changed abiotic conditions, thus making the willows less suitable substrates for exposed leaf-chewing insects.

The differences between willow species and the effect of fertilization on the bird predation leads me to suggest that the low insect densities and low level of leaf damage make *S. myrsinifolia* and fertilized *S. phylicifolia* less attractive to foraging birds. It may therefore be that density-dependent predation provides partial refuges for herbivorous insects on strongly-defended plants. The study of Haartvigsen et al. (1995) demonstrated that as predatory mites responded to prey increase on *Populus deltoides* Marsh., they masked the positive effect of fertilization to herbivorous mites. A similar indirect effect of fertilization was found by Strauss (1987). In her study the number of predatory ants increased in fertilized plots of *Artemisia ludoviciana* Nutt., leading to increased mortality of chrysomelid beetles and decreased leaf damage in fertilized plots. In this study birds appeared to have the strongest effect on unfertilized *S. phylicifolia*, thus masking the negative effect of fertilization on insect densities. The effects of fertilization on bird predation may be affected by architectural changes of the bushes or altered levels of foraging cues for birds. Because fertilized *S. phylicifolia* produced more and larger leaves, and had fewer leaf-chewing insects per leaf area, the level of visible insect damage was clearly lower on fertilized willows. In *S. myrsinifolia* the leaves were somewhat more damaged on fertilized bushes, which may explain the difference in the response of birds to fertilization of these willow species.

This study emphasizes the necessity of considering multitrophic interactions when trying to understand relationships between plants and insects. The species-specific and fertilization-induced differences in willow resistance to herbivores would have looked totally different if the effect of insectivorous birds had not been included. It is generally agreed that both the evolution of insect-plant interactions (Bernays and Graham 1988; Strong 1988; Schultz 1992) and control of herbivore populations (Lawton and McNeill 1979; Hunter and Price 1992; Karban 1997) result from a combination of bottom-up and top-down forces (Hartley and Jones 1997). This study evidently shows the dual control of the herbivore densities on willows: the effect of predatory birds was unimportant on chemically strongly defended *S. myrsinifolia* but substantial on milder *S. phylicifolia* which is favored by generalist herbivores.

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