FOREST INSECT GUILDS:
PATTERNS OF INTERACTION WITH HOST TREES

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REPEATED DAMAGE OF LEAVES
BY PHYLLOPHAGOUS INSECTS:
IS IT INFLUENCED BY RAPID INDUCIBLE RESISTANCE?

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INTRODUCTION

It was discovered more than 10 years ago that toxic and repelling substances may increase in plant tissue in response to damage by phyllophages. Such rapidly inducible chemical changes may appear a few hours after leaf injury and then disappear in a few weeks or months (Walker-Simmons and Ryan 1977, Baldwin and Schultz 1983, Van Hoven 1974, Wratten et al. 1984). This phenomenon has been investigated in detail on mountain birch, *Betula pubescens tortuosa*, in Finland (Haukioja and Niemelä 1977, 1979, Niemelä et al. 1979, Haukioja 1982, Neuvonen and Haukioja 1991). Research there has demonstrated that consumption of leaves from damaged shoots has detrimental effects on the development, fecundity, and sometimes the survival of several species of insects. The same adverse effects were found for insects feeding on damaged willow (Raupp and Denno 1984), larch (Niemelä et al. 1980), and other trees and shrubs. Although these effects may easily be demonstrated in laboratory and field tests, it is not clear what role they play in phyllophage population dynamics (Fowler and Lawton 1985). Are they a real defense against herbivores? If there are damage inducible defenses in plant leaves, it is reasonable to suppose that phyllophagous insects may have evolved mechanisms for coping with or rejecting damaged leaves. For example, laboratory trials have clearly shown that polyphagous lepidopteran larvae prefer to feed on intact birch leaves (Wratten et al. 1984). Arguments for the benefits of rapid inducible resistance (RIR) in plants are not so convincing. They emphasize the increased dispersion of insect injuries within a tree crown and the subsequent increase in mortality of the insects (Edwards and Wratten 1983, Silkstone 1987). However, this effect has been shown to be weak, and in many cases was not found at all (Silkstone 1987). Moreover, some laboratory experiments have shown that phyllophages are not capable of distinguishing damaged leaves and hence of avoiding them (Raupp and Denno 1984, Hartley and Lawton 1987).

I have investigated the effects of RIR on leaf choice by folivorous insects in Subarctic and southern taiga forests. In the Subarctic, different species of folivorous insects co-occurred on birch leaves more often than would have been expected according to the Poisson (random) distribution (unpubl. data). Initially, feeding wounds by chewing and sucking insects were distributed independently among leaves, but subsequently damaged leaves were more frequently and intensively attacked by insects than intact leaves. However, parallel observations made the same year in the southern taiga zone of the Urals gave quite different results. Co-occurrence of folivorous and sucking insects was more rare than expected according to the Poisson distribution, and some folivorous insects avoided certain leaf damage patterns (Bogacheva 1989). What is the reason for such a discrepancy between two different geographic regions? Why did we fail to demonstrate an over-dispersion of subsequent insect damage in

the Subarctic? What are the main factors in leaf preference by phyllophagous insects: qualitative changes in damaged leaves or ecological conditions of leaf environment? In this paper I address these questions both in the field and in the laboratory (food choice experiments).

EXPERIMENTAL METHODS

Field Experiments

Experiments similar to those by Silkstone (1987) were done in 1988 at two sites: in forest tundra (66° 40'N) at the Labytnangi field station in the Low Ob' region, and in southern taiga (56° 50'N) near the city of Sverdlovsk in the Middle Urals. Around Labytnangi we worked with the *Betula pubescens* ssp. *tortuosa* growing in the small groves. Near Sverdlovsk we worked with *Betula pubescens*, the most common tree species in this region. I defoliated growing leaves using a 0.5 cm cork borer. One leaf from each intact dwarf shoot was so damaged, amounting to 3 to 4 percent of the mean leaf area on dwarf shoots. This was equal to the mean value of natural leaf consumption in the Subarctic, but in Sverdlovsk the mean consumption level averages 2 to 3 times higher.

I administered three kinds of treatments: 1) making one hole on one side of the leaf lamina, leaving the leaf margin undamaged (hereafter referred to as "middle hole"); 2) making two holes on one side of a leaf, but along the leaf margin, their total area and perimeter similar to those of the "middle hole" (this damage pattern hereafter referred to as "marginal holes"); and 3) keeping intact leaves as a control. All three leaves formed one replicate; they were similar both in size and in their position on a branch. Leaves were marked with dots of type-correction fluid. We used 20 replicates per tree, and there were 25 study trees at Labytnangi, 26 at Sverdlovsk. Unfortunately, some leaves were lost during the course of the experiments, 3 weeks at Labytnangi (6/30/88 - 7/24/88) and over 3 months at Sverdlovsk (5/27/88 - 9/12/88), i.e. until leaf fall. At the end of the experiments, mines and holes made in the leaves by insects were classified according to the list of 15 types of feeding damage earlier described (Bogacheva 1984). Amount of injury was measured using graph paper. Frequency distribution patterns of the damage size classes for each different damage type were compared using Chi-square tests. Galls found on leaves were recorded, but were rare; feeding injury by sucking insects was not recorded.

Laboratory Tests

We conducted laboratory tests at the Labytnangi field station in 1988 using the geometrid, *Epirrita autumnata* Bkh., and the weevil, *Phyllobius maculatus* Tourn. These two experimental insects were reared in the laboratory at room temperature (17 to 25°C) and natural photoperiod. Solitary insects were kept in Petri dishes on a damp filter paper. Two damaged and two intact leaves were placed in each dish daily. Each pair of leaves was similar in size and position within the tree crown, and all of the leaves used for each experimental series were collected from one birch tree. Only intact leaves from intact dwarf shoots were used. We artificially damaged one leaf in each pair 1 to 3 days before the experiments by creating the "middle hole" of the above-mentioned size. The food was changed every 24 hours and the amount of leaf lamina eaten was measured using graph paper. For weevils, the total number of feeding holes and their position within a leaf were also registered. Only last instar larvae were used in trials. *Epirrita autumnata* were very abundant in 1988, so they were changed every day or every two days during the experiments in order to rule out possible influence of individual induced preference. Weevils, on the other hand, were not abundant and thus were changed only in case of death or feeding refusal. In total, 53 specimens of geometrid larvae and 18 specimens of beetles were used; leaves for them were collected from 6 and 4 different birch trees, respectively.

RESULTS

Field Experiments

Only four birch leaves were lost in the field experiment at Labytnangi. Since incomplete replicates were excluded from the calculations, we had a total of 496 rather than 500 replicates (Table 1).

At Sverdlovsk a large number of leaves was lost and many replicates became incomplete so the calculations were carried out in two ways: 1) only on complete replicates, of which there were 347, and 2) on all the leaves of each treatment, including those of incomplete replications. Owing to the larger sample size (Table 2), more data appeared to differ significantly when the second method was used. However, the mean value of the data did not change considerably.

There were no differences among treatments at Labytnangi (Table 1). At Sverdlovsk, on the other hand, there were significant differences among treatments (Table 2). The data suggest that insect responses to the two patterns of artificial damage were not equal: insects apparently avoided leaves with marginal holes, preferring leaves with middle holes. Although these two damage patterns differed significantly from one another, neither differed significantly from the control (Table 2).

It is not clear why these two damage patterns are of different attractiveness for phyllophages despite the fact that the areas and perimeters of the holes are similar in both cases. One likely explanation is the differential detection of damaged leaves by insects using leaf blade shape outlines. Thus different positions of grazings on leaf blade surfaces appeared to cause different insect reactions. As for insect reactions to damaged leaves, they were found to be different at Labytnangi and Sverdlovsk, but, again, the reasons are not clear. Feeding damage of type 2 (large holes on leaves) is caused by insects of several families (many lepidopterans, some species of Tenthredinidae and Curculionidae species). At Labytnangi feeding injuries of this type are caused mainly by spring species of *Epirrita autumnata*, while at Sverdlovsk they are caused mainly by summer species of lepidoptera and Tenthredinidae. Feeding injuries of type 4 (small skeletonized spots on the underside of leaves) were caused by one summer tenthredinid species at Labytnangi and mainly by one late summer species of the Coleophoridae family at Sverdlovsk. Finally, feeding marks of type 7 (the tortuous grazings at leaf edge) were caused by Polydrusus weevils at both sites, though clearly by different species.

In summary, there were no differences in insects' responses to damaged and intact leaves at Labytnangi, but such differences did occur at Sverdlovsk, where insects were apparently attracted to leaves with middle holes and repelled by those with marginal damage. The latter damage pattern predominates in nature and our results thus run contrary to current theory, which predicts avoidance of all damaged leaves. Contrary to our results, on the other hand, Silkstone (1987) reported that middle lamina injuries decreased further insect damage. The reasons for this discrepancy will be discussed later.

Laboratory Tests

Under the conditions of our experiment, *Epirrita autumnata* larvae fed equally on both damaged and intact birch leaves (Table 3), while Phyllobius beetles preferred damaged leaves (Table 4). This suggests that different phyllophagous species may have different reactions to damaged leaves.

Table 1. Percent leaf damage and area of insect consumption per damaged leaf (mm^2) on *Betula pubescens* ssp. *tortuosa* trees in the field experiment at Labytnangi

Types of damage[a]	Leaf damage (%) and consumption (mm^2)	Treatment of leaves		
		Middle hole A	Marginal holes B	Control C
General	Damage (%)	52.5	46.9	46.9
	Consumption	17.3	13.3	15.2
Type 2	Damage (%)	7.3	5.1	3.8
	Consumption	74.9	59.9	100.8
Type 4	Damage (%)	1.2	5.3	3.2
Type 7	Damage (%)	44.4	41.8	43.2
	Consumption	7.3	7.0	6.8
Total leaves		496	496	496

[a]Type 2 — large holes; type 4 — small skeletonized spots; type 7 — tortuous grazings at leaf edge (for details see Bogacheva 1984, and discussion in text).

Why should different species have different responses? First, taxonomically different species may have different chemoreceptors. Second, moths feed on leaves during the larval stage whereas weevils feed at the adult stage, and in that sense they are ontogenetically different. Third, rapidly induced responses may have different effects depending on the ecological peculiarities of insects (Edwards and Wratten 1983, Wratten et al. 1984). Both species involved here are considered generalists. In the Low Ob' region, I found *Epirrita* caterpillars feeding on mountain birch, *Betula nana*, *Alnus fruticosa*, *Salix*, *Populus tremula*, *Rosa acicularis*, and *Lonicera coerulea*. In the same region, I found *Phyllobius maculatus* on mountain birch and alder only, so, at that site at least it appears to be oligophagous. Finally, food choice may depend on insect mobility (Schultz 1983, Neuvonen and Haukioja 1991). The mobility of the two test species is also different: in 24 hours the weevils usually "travel" throughout an entire birch crown, *Epirrita* larvae only within a single branch, as a rule. This difference in mobility has been observed in experiments as well: *Epirrita* caterpillars damaged only two (1.81 ± 0.09) of four leaves available in Petri dishes, as a rule, inflicting four ($\bar{x} = 4.18 \pm 0.40$) holes. *Phyllobius* specimens often damaged all four leaves available ($\bar{x} = 3.21 \pm 0.09$), inflicting about nine ($\bar{x} = 9.88 \pm 0.47$ holes).

Table 2. Percent leaf damage and area of insect consumption per damaged leaf (mm^2) on *Betula pubescens* trees in the field experiment at Sverdlovsk

Types of damage	Leaf damage (%) and consumption (mm^2)	Treatment of leaves					
		A-1	B-1	C-1	A-2	B-2	C-2
General	Damage (%)	42.7	36.0	41.2	45.0	35.2	41.6
	Consumption	53.0	30.2	39.4	51.4a	29.8b	41.4
Type 2	Damage (%)	10.1	9.5	8.7	9.5	8.6	8.6
	Consumption	184.3a	73.2b	127.8	200.5b	72.8a	133.6
Type 4	Damage (%)	18.7	15.0	21.3	20.8	14.7c	22.7b
	Consumption	6.5	7.6	7.3	5.9a	7.7b	7.0b
Type 7	Damage (%)	18.7	13.5	14.1	17.3	13.9	12.8
	Consumption	8.8	7.1	7.4	8.6	7.1	7.6
Total leaves		347	347	347	400	397	406

a, b, and c indicate different treatments (see Table 1); 1 and 2 indicate different methods of calculation. Consumption data with different letter indexes differ significantly ($p \leq 0.05$).

Table 3. Consumption (mm^2) of damaged and intact *Betula* leaves by *Epirrita* larvae

Tree number	Replicates	Days after treatment	Damaged leaves (mm^2)	Intact leaves (mm^2)	Statistical significance
1	8	1	195.62	165.62	n.s.
2	10	2	179.30	104.00	n.s.
3	10	3	151.40	191.90	n.s.
4	10	2	284.80	298.80	n.s.
5	20	2-3	161.20	146.00	n.s.
6	9	2	131.67	296.67	n.s.
Total for all experiments	67	1-3	180.85	191.97	n.s.

Table 4. Consumption (mm^2) of damaged and intact *Betula* leaves by Phyllobius weevils

Tree number	Replicates	Days after treatment	Damaged leaves (mm^2)	Intact leaves (mm^2)	Statistical significance
7	20	1-2	50.65	33.95	n.s.
8	10	1	126.50	43.30	$p \leq 0.01$
9	20	1-2	60.70	60.10	n.s.
10	30	1-3	64.17	40.80	$p \leq 0.05$
Total for all experiments	80	1-3	68.34	44.22	$p \leq 0.001$

Furthermore, the experimental data suggest that different plants elicit different insect responses to leaf damage. Weevils showed a clear preference for damaged leaves from trees 8 and 10, but could not distinguish between damaged and intact leaves from tree 9 (Table 4). Heterogeneity of plants is an important source of variation (Fowler and Lawton 1985, Neuvonen and Haukioja 1985, Neuvonen and Haukioja 1991). When observing food selection by weevils, I learned that they prefer to begin eating at the artificial hole. The number of their feeding marks within 1 cm of the marginal hole was 4 to 5 times greater than that within 1 cm of the undamaged leaf edge (weevils' grazings were strictly marginal). The presence of the cork borer hole itself seems to account for the attractiveness of damaged leaves to weevils. It alone seems to facilitate grazing, although follow-up investigations are necessary to confirm this (Gibberd et al. 1988).

DISCUSSION

Two phyllophagous insects common in the Low Ob' subarctic region did not reject damaged leaves in the laboratory tests. Birch insect guilds are represented by dozens of species, but most of them are rare. Because I failed to find rejection of damaged leaves in two mobile, spring phyllophagous species, I would not expect to find it in summer or in less mobile species. It was not surprising that avoidance of damaged leaves was not detected in the field experiments for *Polydrusus ruficornis* Bonsd. (Curculionidae), the most abundant summer species in those sites (Table 1, type 7). When analyzing the course of natural leaf damage, I found already damaged leaves more likely to be damaged subsequently than the controls. Furthermore, subsequent insect grazing on the damaged leaves was more intensive (Bogacheva 1989).

The same was true for *Phyllobius maculatus* in laboratory tests at Labytnangi, but in nature this species is not the main consumer. One of the latter, *E. autumnata*, did not distinguish between damaged and intact leaves. Comparing my observations in nature with my experimental data, I conclude that insect preference for damaged leaves is caused not by leaf attractiveness (as a result of damage) but by some other property. All the comparisons were made between leaves from brachyblasts within one branch, i.e. with homogeneous plant material. Even within a single branch, however, some degree of heterogeneity does exist, including genetic fluctuations of defensive substances' content (Whitham 1981), uncertain variability in foliage feeding quality (Schultz 1983), and different light conditions in various twig parts can promote insect feeding on a certain leaves. Temperature (lighting of leaves) may be among the main factors determining insect food preference in the subarctic.

In the southern taiga zone at Sverdlovsk, the avoidance of damaged leaves by phyllophages was demonstrated in both laboratory and field experiments (Bogacheva 1989). The avoidance was rather weak, however, because the damaged and adjacent leaves were not free from subsequent insect damage. How can one explain the differences observed between the two sites? One possible explanation may be that in the subarctic forest, differences between damaged and intact leaves are not as important as some other factors, particularly ecological ones. In the south taiga, on the other hand, where the suppressing effects of low temperatures are eliminated, slight variations in leaf chemistry may be of greater importance. Nevertheless it is undeniably true that similar leaf damage patterns are caused at two sites by different insect species. However, even closely related species are known (Fowler 1984) to have different food preferences. The next step required to obtain an unambiguous explanation is experimentation with the same phyllophagous species at the two sites and/or chemical analysis of damage-induced leaf alterations.

With respect to the general significance of rapid inducible resistance against phyllophages, integrating my data and those of others, I believe that the pattern of responses by phyllophages to damaged-induced changes in leaves varies with many factors. The causes of these differences in phyllophages' responses can be classified into three large groups. 1) Given the inherent properties of a damaged plant, phyllophages' responses to injured leaves vary depending on (a) plant species (Edwards et al. 1986); (b) plant individual within the species (Fowler and Lawton 1985, Neuvonen and Haukioja 1985, Lawton 1986, Hartley and Lawton 1987, our observations); (c) site conditions (Baldwin 1988); (d) leaf age (Haukioja and Niemelä 1979, Edwards et al. 1986, Hartley and Lawton 1987); and (e) time span between damage and subsequent insect feeding (Fowler and Lawton 1985, Edwards et al. 1986, Hartley and Lawton 1987). Rapid induced response may be modified by the weather conditions during the growing season as well (Haukioja and Hanhimaki 1985); just as it may also modify the insects' responses. 2) Given the origin of the primary damage, phyllophages may respond differently if (a) primary damage is caused by insects of different ecological feeding modes (folivorous or sucking insects, miners, and so on) (Hartley and Lawton 1987); or (b) primary damage occurs within lamina position of grazing injury (e.g. middle or marginal wounds, etc.). Doubtless, these differences are realized for phyllophages through their host plant. 3) Different responses by phyllophages to similar leaf damage patterns are observed (a) in phyllophages of various ecological types, such as folivores, sucking insects, miners, and so on (Hartley and Lawton 1987, Neuvonen and Haukioja 1991); (b) in specialists and generalists (Edwards and Wratten 1983, Wratten et al. 1984, but see Fowler 1984); (c) in phyllophages of different mobility (Schultz 1983, Neuvonen and Haukioja 1991); and (d) at different developmental stages of a single phyllophage species which may be connected also with their mobility (Harrison and Karban 1986). Finally, in nature coexisting leaves can differ in food quality and ecological conditions, i.e. there are conditions both for food choice by insects and for repeated grazings on more favorable leaves (Baranchikov 1983, Bultman and Faeth 1985, Fritz et al. 1987, our observations).

Such a diversity of factors influencing responses by insects to damaged-induced leaf change enables us to say that the damaged leaf protects itself and adjacent leaves against subsequent injuries by only some herbivores. Damaged leaf rejection may be inherent in certain phyllophages species feeding on certain host plants. Though it may be possible to find damaged leaf avoidance among an entire insect guild on a certain plant, because the guild consists usually of few species, there is no justification for extending this response pattern to all plants and all consumers. I propose that the avoidance of injured leaves by insects does not exist as a general phenomenon. One can still ask, however, whether this effect, when it occurs, is beneficial for a plant. We have already mentioned that owing to the adverse effect of damaged leaves on insect performance, damaged leaf avoidance seems to be more necessary for insects than for plants. However, it is disputable even for insects. Is it more profitable for herbivores to continue feeding on damaged leaves, which retards their development (increased mortality due to carnivores and parasites) and decreases their fecundity, or to search for an intact leaf, thereby wasting energy (loss of body weight and fecundity) and increasing their chances of being detected by their natural enemies? Obviously, we are not ready to answer such a question.

Hartley and Lawton (1987) have studied the adaptive value of insect rejection of damaged leaves from the point of view of individual variability in plant chemistry. They found that foliar phenol content was so variable that it was sometimes higher in undamaged leaves than in damaged ones. "Hence, avoidance of damage is certainly no guarantee of better foliage quality" (Hartley and Lawton 1987). It is not surprising, then, that avoidance does not occur in all cases. When we state that a damaged leaf protects itself against subsequent damage, we consider the situation in terms of a leaf, though it is not the leaf but the plant that is the system to be protected. Let us consider rapid inducible defense in those terms. Increased dispersion of insect grazing throughout the tree crown and heightened mortality of phyllophages during their "traveling" in the canopy should not be considered a real benefit to plants because they also cause damage to previously intact leaves and may increase the fitness of the phyllophages. One can hardly characterize such consequences as a plant defense. I hypothesize that the alternate strategy, forcing insects to feed on damaged leaves, protecting the intact ones, and thus effecting deterioration of phyllophages' fitness, would be more beneficial to plants. Indeed, it requires that damaged leaves be attractive instead of repellent. When discussing rapid inducible resistance as a defense against subsequent, more serious damage to the whole plant, Rafes (1980, 1981) proposed that after the overall damage level attained a 60 to 70 percent threshold, there should follow a significant elevation in general resistance, such that the remaining 30 to 40 percent of the leaves would go undamaged. This phenomenon might be really profitable to a plant if it did indeed occur. One must consider, however, what would happen if insect feeding were not yet completed and the threshold damage level of 60 to 70 percent had been reached. The insect is not likely to die because mortality increases rather insignificantly in insects that feed on damaged leaves (Haukioja and Niemelä 1979). Many phyllophagous species are not readily able to change their host tree and will thus simply continue to feed. Foliage damage of 80 to 90 percent has often been recorded (Dmitrienko 1976, Petrenko and Petrenko 1981, Bogacheva 1989), even at low levels of leaf area consumption, to say nothing of the situation during insect outbreaks. Hence it appears that the existence of a threshold value of damaged leaves triggering resistance to inhibit subsequent damage is not supported by evidence.

SUMMARY

It was established earlier that in the Low Ob' region (forest tundra zone), damaged leaves of mountain birch received more frequent and more intensive subsequent phyllophages damage than intact ones, whereas in the Middle Urals the opposite trend was found. To obviate the factors of ecological heterogeneity and inherent leaf variability, field and laboratory experiments were carried out. Field studies in the forest tundra zone did not reveal different insect responses to damaged and intact leaves. On the other hand, in the south taiga, insects avoided leaves with marginal holes and were attracted to those with middle holes. In food choice experiments, neither of two phyllophagous species avoided injured leaves; in fact one insect, *Phyllobius maculatus*, preferred them. Although it is correct to view damaged leaf avoidance as a plant defense, one cannot consider it a general phenomenon.

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