THE SOVIET JOURNAL OF

ECOLOGY

ЭКОЛОГИЯ/ÉKOLOGIYA

TRANSLATED FROM RUSSIAN

POSSIBILITY OF REPEATED FOOD RESOURCE UTILIZATION BY PHYLLOPHAGIC
INSECTS: ZONAL ASPECT

I. A. Bogacheva
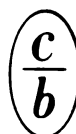
The hypothesis that damage to leaves protects them (and the entire plant once a definite exploitation level is reached) against further damage has been veri- fied. Our research was conducted on birches in the forested tundra (lower Ob Valley) and southern taiga (Sverdlovsk). It was shown that, in the southern taiga, chewing phyllophages avoid leaves that have been chewed (repellence), while sucking insects avoid leaves damaged by chewing and sucking; however, the changes in phyllophage distribution are minor, and no resistance develops at the tree level. In the forested tundra, on the other hand, injured leaves are subsequently damaged more often and to a greater extent. Methodological ap- proaches to study of this problem are discussed.

It was established more than a decade ago that the content in plant tissues of substances with a toxic or repellent action can increase in response to phyllophage feeding. The type of reaction in which chemical changes occur in leaf tissues over a period of several hours or days after part of the leaf has been removed and then disappear quite rapidly has been con- vincingly demonstrated for many plants (Walker-Simmons and Ryan, 1977; Baldwin and Schultz, 1983; VanHoven, 1984; Raupp and Denno, 1984; Wratten et al., 1984). This phenomenon has been studied in particular detail for crooked birch (Betula pubescens ssp. tortuosa). Finnish researchers have shown phenol content to increase in a damaged leaf and leaves adjoining it. Experiments in which larvae of birch phyllophages were fed various diets showed that leaves from damaged twigs inhibited their growth and led to a reduction in imago weight (and hence fertility: Haukioja and Niemela, 1977; Niemela et al., 1979; Haukioja, 1982); a statistically reliable increase in mortality was also reported for one species (Haukioja and Niemela, 1979). The same pattern was later demonstrated for phyllophages of willow (Raupp and Denno, 1984), larch (Niemela et al., 1980), and other trees.

Since feeding on damaged leaves is clearly detrimental, it might be hypothesized that a mechanism for avoidance of such leaves exists in phyllophages; a laboratory experiment actually showed that lepidopteran caterpillars prefer to feed on undamaged birch leaves (Wratten et all., 1984). Such a reaction would be beneficial for both the phyllophages and the tree, since it would result in redistribution of damage within the crown (Edwards and Wratten, 1983; Silkstone, 1987), so as to preserve its extension units, i.e., twigs. Another possible benefit to the plant is culling of some phyllophages as they move about, through falls and predation (Edwards and Wratten, 1983). Some researchers also believe that a defi- nite level of leaf exploitation by resident pests (60-70%) causes "buildup of overall resis- tance" (Rafes, 1980; Rafes and Sokolov, 1984), so that the remaining 30-40% of the leaves remain unaffected. The main objective of the present study was to demonstrate the existence of a reaction whereby phyllophages avoid already damaged leaves.

Our analysis was based on the fact that phyllophages can be said to avoid already dam- aged leaves when the number of multiple injuries is reliably less than would be observed with a random phyllophage distribution over the leaves. Other researchers have utilized this criterion (Putman, 1984; Faeth, 1985; Silkstone, 1987). One cannot limit oneself to "visual" estimates of the "few multiple injuries" sort (Rafes and Sokolov, 1984) not supported by such a comparison.

We made such an analysis in 1986 for crooked birch, utilizing data collected in 1983- 1984 along the lower reaches of the Ob River (in the vicinity of Labytnangi) and in the Polar Urals. Multiple injury to leaves by different phyllophages had not previously been studied
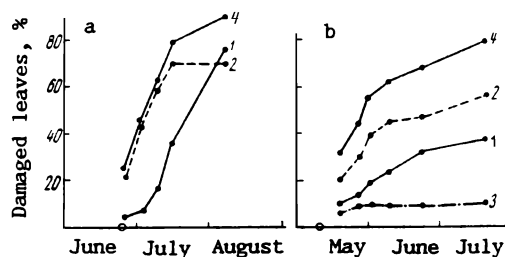
Fig. 1. Change in extent of damage to birch leaves by different groups of phyllophages over observation period. a) Labytnangi; b) Sverdlovsk. 1) chewing; 2) sucking; 3) mining phyllophages; 4) total damage; circle on abscissa denotes point at which leaves opened.

in the Subarctic, although appearance of phenols in leaves in response to damage had been observed in this zone for the birch species in question. In 1985, we analyzed the joint occurence of different types of damage inflicted on leaves by chewing and mining phyllophages (a total of 15 types; Bogacheva, 1984); we also assessed the incidence of damage to adjacent leaves on clipped shoots. These techniques did not make it possible to establish whether phyllophages avoided previously a damaged leaf (or leaves adjacent to it, where protective compounds also accumulated).

Judging from the data in the literature, conclusive proof that phyllophages avoid damaged leaves has not been obtained for the mid-lattitude zone, although the phenomenon itself has been quite extensively investigated. Some authors denote it by the term "antibiosis," others by "competition," and still others by "repellence." Since the first two terms cover a quite broad range of phenomena, we will utilize "repellence," as most precisely reflecting the actuality.

We made parallel observations in 1987 in the forested tundra zone (Labytnangi, experiment station grounds, sparse birch forest) and in the southern taiga (Sverdlovsk, forest reserve, pine and birch forest). Our research subjects were crooked birch in the forested tundra and white birch (Betula pendula) and common birch (B. pubescens) in the southern taiga; both species exhibit the "fast responses" phenomenon and evoke the same phyllophage reaction (Edwards et al., 1984; Silkstone, 1987).

Analysis of the incidence of multiple injuries was carried out once at the beginning of the growing season, when the "fast response" is clearest (Haukioja and Niemela 1979). One model branch was chosen in the lower portion of the crown for each tree (10 trees at Sverdlovsk and 12 trees at Labytnangi). The branch was marked, and the locations of the twigs and leaves were plotted. The records were made in a definite format, noting the presence of insects and wounds on the leaves; the number of wounds per leaf and their approximate size on a point scale (Bogacheva, 1979) were also recorded for chewing insects and miners. The first observations were made shortly after the leaves emerged, with three repetitions at one-week intervals; two additional sets of observations were made at Sverdlovsk and one at Labytnangi. We thus tracked the fate of each leaf in the field observations and had quite accurate information on the time at which all wounds were inflicted, together with their source.

Most phyllophage groups were common to our observation sites, which were separated by a considerable distance. During the first few weeks of the season, leaves were chewed by geometrids (Oporinia autumnata Bkh. at Labytnangi and two unidentified species at Sverdlovsk). Isolated sawflies of the family Tenthredinidae appeared later, also inflicting similar wounds (type 1 damage). Two additional sawfly species inflicted damage of other types: skeletonization of small leaf areas, usually from the underside (type 2), and patterned chewed areas in the leaf blade, which did not reach the leaf margin or cross major veins (type 3). There were numerous small bites taken from the leaf margin by weevils of the genus Polydrusus (type 4). A very early leafroller species was also encountered at Sverdlovsk, taking numerous bites from the entire leaf surface (type 5) during the first week after leaf emergence. The characteristic "packets" of sawflies of the species Pamphilius sp. (type 6) were rarely encountered at Labytnangi and not observed at Sverdlovsk. The sucking phyllophages were dominated by aphids (Euceraphis punctipennis Zett. in the north), with considerably fewer cicadas and true bugs of the families Miridae and Acanthosomatidae. There were few mines in the leaves. A total of six mines was detected at Labytnangi (in August), belonging to

TABLE 1. Number of Birch Leaves Jointly Damaged by Different
Groups of Phyllophages

Study site	Date	Total number of leaves	Chewing + sucking				Chewing + mining		
			expected from theory		actual	r	expected from theory		actual
			with uniform distribution	true			with uniform distribution	true	
Labytnangi	26.06	734	6,8	12,8	8	+0,68	—	—	—
	03.07	766	23,0	37,5	35	+0,66	—	—	—
	10.07	768	73,6	89,0	85	+0,58	—	—	—
	16.07	767	202,3	206,6	208	+0,32	—	—	—
	08.08	766	409,0	413,5	425	+0,19	—	—	—
Sverdlovsk	18,05	450	9,0	12,6	5 *	+0,45	2,5	2,7	6
	26,05	402	17,0	22,5	14 *	+0,56	5,0	5,2	8
	01,06	410	30,2	37,9	29	+0,68	7,5	8,0	9
	09,06	424	44,6	50,9	39	+0,59	9,3	10,6	10
	23,06	459	69,5	73,3	57 *	+0,30	13,8	13,6	13
	20,07	453	93,3	94,2	76 *	+0,08	17,3	18,7	19

*Reliable differences: $p < 0.05$.

Lyonetiidae. Most of the mines at Sverdlovsk appeared early and belonged to Coleophora; iso-
lated mines of Agromyzidae were observed in mid-summer (Gusev and Rimskii-Korsakov, 1951).
The change in leaf damage level over the observation period is shown in Fig. 1. There were
very few gall-forming insects at either locations, and the galls were not counted.

The simplest analysis method is comparison of the actual and theoretically anticipated
numbers of multiple injuries per leaf (Table 1); however, one should be cautioned against
the sample randomization usually recommended for such studies (Putman, 1984). In computing
the theoretically anticipated number of multiple injuries for such an averaged sample, we
proceeded on the assumption that phyllophages are more or less uniformly encountered every-
where. However, this is rarely the case in nature; quite the contrary, insects usually do
selective damage to individual trees and to different sections of an individual crown. If
the ecological requirements of two species (or groups) under investigation differ, there may
be a negative correlation between the incidence levels for the injuries they produce on model
branches (Rafes and Sokolov, 1976); in other words, insects disperse to different branches
(or trees) for reasons having nothing to do with repellence, and multiple injuries may there-
fore be less frequently encountered than would be expected for a uniform phyllophage distri-
bution. If species' ecological requirements are identical and the incidence correlation is
positive (see Table 1), then multiple injuries are encountered more frequently than for a
uniform phyllophage distribution. The data must therefore be analyzed for individual twigs
and, if a sample contains many twigs, the level expected from theory for the sample has to
be computed by summing the results for individual twigs rather than by averaging over the
entire sample. The resultant difference can be quite substantial, as shown in Table 1 for
chewing and sucking insects, and affect the conclusions. A randomized sample is therefore
unsuitable for analysis, since correct conclusions regarding the problem at hand cannot be
drawn from such data.

It can be seen from Table 1 that neither chewing nor sucking insects avoided leaves
damaged by miners. Mutual avoidance was exhibited only by chewing and sucking phyllophages
in the southern taiga. No such pattern was observed in the north.

We tracked the subsequent fate of damage leaves, establishing how phyllophages of each
group behaved with respect to them, in order to identify the active factor in mutual avoidance
for chewing and sucking phyllophages. Only our conclusions will be presented, since the
corresponding tables are quite cumbersome. Neither sucking nor chewing phyllophages avoided
leaves damaged by insects of the other group in the north; quite the contrary, damage by
insects of the same group was subsequently encountered even more frequently than for undamaged
leaves (the differences were reliable for sucking insects, $p < 0.01$). The insects evidently
preferred to feed on the same leaves.

Chewing phyllophages in the mid-latitude belt also exhibited no avoidance of leaves
previously damaged by sucking insects, but the latter clearly avoided feeding on chewed

TABLE 2. Number of Leaves Jointly Damaged by Different Species of Chewing Phyllophages

| Damaged types | Labytnangi | | | Damaged types | Sverdlovsk | | |
| | expected from theory | | real | | expected from theory | | real |
	with uniform distribution	true			with uniform distribution	true	
1+2	25,0	14,3	20	1+2	4,8	6,7	6
1+4	84,4	83,9	81	1+3	0,5	0,6	0
1+6	0,5	0,4	1	1+4	3,8	4,3	1
2+4	98,2	99,0	99	1+5	8,4	9,2	0 *
2+6	0,6	0,3	0	2+3	0,1	0,0	0
4+6	2,6	1,7	1	2+4	0,6	0,8	1
				2+5	1,4	2,0	2
				3+4	0,1	0,0	0
				3+5	0,1	0,0	0
				4+5	1,1	1,4	1

*Differences reliable: p < 0.01.

leaves. Both groups also inflicted less subsequent damage on leaves already damaged by phyllophages of the same group; however, the differences were unreliable. It is scarcely possible to speak of repellence here, since the insects of both groups were found to prefer feeding on undamaged leaves of exploited twigs (p < 0.05). Since protective compounds accumulate both in damaged leaves and in those adjoining them (Haukioja, 1980; Haukioja and Niemela, 1977; Niemela et. al., 1979; Wratten et al., 1984), one would expect selective phyllophage feeding on undamaged twigs if a repellent effect were to occur. The pattern observed was different: as the twigs elongated, the phyllophages moved onto newly opened leaves, remaining on the twig selected.

Joint occurence of different types of damage, i.e., injuries inflicted by different species (or groups of species) of chewing phyllophages, could also be analyzed with our data. We did not find any species of chewing phyllophages to avoid others on birches in the forested tundra zone (Table 2). At Sverdlovsk, leaves injured by the leafroller at the beginning of the season (type 5) were not later damaged by lepidopterans or sawflies (type 1).

The data in Table 2 again show the need to take the spatial heterogeneity of the data into account. There was a strong negative correlation between the incidence levels for damage of types 1 and 2 on the model branches (Labytnangi), and the true theoretically anticipated number of multiple injuries was smaller then would be expected with a uniform distribution. It also follows from Tables 1 and 2 that the presence of a negative correlation for the incidences of different phyllophage groups on individual branches cannot be used as proof of repellence, as is sometimes done (Rafes and Sokolov, 1976).

How do phyllophages recognize that a leaf has previously been damaged? Tactile, olfactory, and especially gustatory stimuli are assumed to participate in this process (Silkstone, 1987). However, if the latter predominate, it is possible that repellence can be more correctly assessed not from presence or absence of damage but from its extent: repellence might be operative if a phyllophage began to feed but quickly stopped. Such an analysis is possible for chewing phyllophages, although the method we employed to evaluate the area eaten for this purpose might not have been sufficiently accurate. It was found that an additional 3.6% of leaf area was eaten in cases where there was previous damage by chewing phyllophages, while the corresponding figures for leaves damaged by sucking insects and undamaged leaves were 3.2 and 2.1% (the differences were reliable). The figures at Sverdlovsk were 4.3, 10.5 and 11.8% respectively (the differences were unreliable, because of the small number of data). Thus, leaves already injured by chewing phyllophages in the north not only were subsequently damaged more frequently than intact leaves but had a larger proportion of their area eaten; the trends at Sverdlovsk were just the opposite.

Thus, phyllophagic insects of the chewing and sucking groups exhibit a definite tendency to avoid already damaged leaves on birches in the mid-latitude zone. Sucking insects avoid all previously damaged leaves, while chewing insects are indifferent to damage by sucking insects but do less damage to chewed leaves; moreover, they eat a smaller proportion of the leaf surface in this case. The same pattern has been observed for chewing phyllophages in a field experiment in England (Silkstone, 1987).

It must be noted, however, that repellence is not as significant as was previously thought (Rafes, 1980), even at middle latitudes. Damaged leaves are not always avoided by other groups of pests. Thus, chewing and sucking phyllophages damage leaves already injured by early miners (Coleophora) at the same rate as undamaged leaves; neither are chewing phyllophages found to avoid leaves damaged by sucking. Elimination of competition among species within a single group (chewing phyllophages) is not a general rule. Changes in insect distribution resulting from repellence are also minor; researchers concerned with this problem have not always been able to detect them (Silkstone, 1987). These changes can scarcely be of major significance even for insect redistribution within the crown of a tree. "Buildup of resistance," assuring cessation of further leaf damage and retention of 30-40% intact leaves on a tree, was not observed: 71-95% of the leaves on the model branches were damaged midway through the growing season.

No tendency toward avoidance of damaged leaves was detected in the north. On the contrary, there was a tendency toward repeated utilization of the same leaves, those that were most suitable for phyllophages on the basis of particular properties. Leaf illumination level and a location in the crown providing favorable temperature conditions for insect feeding may be considerably more important in the north than the deterioration of leaf nutrient qualities resulting from damage, although the occurrence of such deterioration and its unfavorable effects on phyllophages have been conclusively proved in the laboratory.

LITERATURE CITED

Baldwin, T. J. and Schultz, J. C., "Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants," Science, 221, No. 4607, 277-279 (1983).

Bogacheva, I. A., "Simplified method for determining proportion of leaf surface eaten by chewing insects," in: Use of Quantitative Methods in Ecology [in Russian], Sverdlovsk (1979), pp. 110-116.

Bogacheva, I. A., "Distribution of phyllophagic insects in crown of crooked birch at northern treeline," Ékologiya, No. 3, 60-66 (1984).

Edwards, P. J. and Wratten, S. D., "Wound induced defences in plants and their consequences for pattern of insect grazing," Oecologia (Berl.), 59, No. 1, 88-93 (1983).

Faeth, S. H., "Host leaf selection by leaf miners: interactions among three trophic levels," Ecology, 66, No. 3, 870-875 (1985).

Gusev, V. I. and Rimskii-Korsakov, M. N., Key to Damage to Forest and Ornamental Trees and Shrubs in European USSR [in Russian], Goslebumizdat, Moscow—Leningrad (1951).

Haukioja, E., "Influences of winter temperatures on reproductive upsurges in Oporinia autumnata (Lepidoptera, Geometridae)," in: Animal Adaptation to Winter Conditions [in Russian], Moscow (1980), pp. 126-132.

Haukioja, E., "Inducible defences of white birch to a geometrid defoliator, Epirrita autumnata," Proc. 5th Symp. Insect–Plant Relationships, Wageningen (1982), pp. 199–203.

Haukioja, E. and Niemela, P., "Retarded growth of a geometric larva after mechanical damage to leaves of its host tree," Ann. Zool. Fenn. 14, No. 1, 48-52 (1977).

Haukioja, E. and Niemela, P., "Birch leaves as a resource for herbivores: seasonal occurrence of increased resistance in foliage after mechanical damage of adjacent leaves," Oecologia (Berl.), 39, No. 2, 151-160 (1979).

Niemela, P., Aro, E. M., and Haukioja, E., "Birch leaves as a resource for herbivores: damage-induced increase in leaf phenols with trypsin-inhibiting effects," Rep. Kevo Subartic Res. Stat., 15, 37-40 (1979).

Niemela, P., Ojala, H., Ojala, M.-L., and Haukioja, E., "Retarded growth of lepidopteran larvae after mechanical damage to leaves of tamarack and dwarf birch near Schefferville, central Quebec-Labrador peninsula," McGill Sub-Arct. Res. Rep., 30, 52-56 (1980).

Putman, R. J., "Detection of inter- and intra-specific competition in the insect communities of British trees: a practical exercise in community ecology," J. Biol. Educ., 18, No. 4, 313-315 (1984).

Rafes, P. M., Biocenological Studies on Phytophagic Forest Insects [in Russian], Nauka, Moscow (1980).

Rafes, P. M. and Sokolov, V. K., "Interaction of resident leaf pests and food trees," Dokl. Akad. Nauk SSSR, 228, No. 1, 246-247 (1976).

Rafes, P. M. and Sokolov, V. K., "Interacton of resident leaf pests with food tree," in: Biocenoses of Transural Forested Steppe (With Troitskii Forested Steppe Reserve as Model) [in Russian], Sverdlovsk (1984), pp. 85-89.

Raupp, M. J. and Denno, R. F., "The suitability of damaged willow leaves as food for the leaf beetle, _Plagiodera versicola_," Ecol. Entomol., 9, No. 4, 443-448 (1984).

Silkstone, B. E., "The consequences of leaf damage for subsequent insect grazing on birch (Betula ssp.): a field experiment," Oecologia (Berl.), 74, No. 1, 149-152 (1987).

VanHoven, W., "Trees' secret warning system against browsers," Custos, 13, No. 5, 14-16 (1984).

Walker-Simmons, M. and Ryan, C., "Wound-induced accumulation of trypsin-inhibitor activities in plant leaves," Plant Physiol., 59, No. 3, 437-439 (1977).

Wratten, S. D., Edwards, P. J., and Dunn. J., "Wound-induced changes in the palatability of _Betula pubescens_ and _B. pendula_," Oecologia (Berl.), 61, No. 3, 372-375 (1984).