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DAMAGE TO TWISTED-BIRCH LEAVES BY INSECTS IN PERIPHERAL AND INNER PARTS OF THE CROWN

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According to their position on the branch and with respect to quality (density of the leaf, content of dry matter), the leaves of brachyblasts on the distal part of a branch can be considered as lighted; and leaves near the base of the branch, as shaded. Leaves from the distal part of the branch of twisted birch Betula pubescens *ssp.* tortuosa *in the Subarctic are more heavily damaged than leaves at the base of the branch by phyllophages of one species (weevils* Polydrusus ruficornis*), as well as by whole community of phyllophages. However, in laboratory tests, three common species of insect phyllophages do not show a preference for distal birch leaves; consequently, their greater degree of damage observed in nature is not due to the quality of the leaves themselves, but to their position on the branch. Insects have a tendency to feed on sunlit leaves; the use of solar radiation to raise their body temperature is typical of insects of the Subarctic.*

In investigating damage by insects to various leaves within the crown of a tree, the categories of so-called "lighted" and "shaded" leaves are discussed comparatively often. They mean the leaves in illuminated and shaded parts of the tree's crown, most often in the peripheral and inner parts, or in the shaded lower part of the crown and on the illuminated top of the tree.

Different degrees of damage by insects to lighted and shaded leaves can be considered from the point of view of the forage plant's chemism. In fact, it has been shown that leaves in the illuminated part of the crown differ from shaded ones in a number of morphological, anatomic, and biochemical parameters. Of these, the most significant for insect phyllophages are the thickness of the lamina (Duba and Carpenter, 1978; Claridge, 1986; Hagen and Chabot, 1986), the rigidity of the leaves (Schultz, 1983; Claridge, 1986; Hagen and Chabot, 1986), and the contents of carbohydrates (Claridge, 1986), nitrogen (Claridge, 1986; Moore et al., 1988; Jensen, 1988), protective phenolic compounds (Schultz, 1983; Claridge, 1986; Larsson et al., 1986), and water (Duba and Carpenter, 1978; Schultz, 1983; Claridge, 1986; Larsson et al., 1986; Moore et al., 1988). As the degree of illumination of leaves increases, their water content decreases, while all of the other indices, on the contrary, rise.

Of course, we must keep in mind that for insects a plant is not only a food object, but also a habitat, and they can choose suitable food, as well as the microclimatic conditions most suitable for them. Since microclimatic factors simultaneously affect the insects themselves and the plant's leaves, it is rather hard to separate the direct and indirect action of microclimate on the insects.

In studying the intracrown variability of damage to leaves of twisted birch *Betula pubescens* ssp. *tortuosa* in the Subarctic, we evaluated differences in the degree of damage to leaves on the terminal part of axial branches (peripheral part of the crown) and basal parts of branches (inner part of the crown) (Bogacheva, 1989) and tried to establish the reason for these differences.

The work was performed in the lower reaches of the Ob, in the forest-tundra zone, at the Salekhard scientific research field station of the Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences, in Labytnangi (66°40' north latitude, 66°15' east longitude). Its territory includes an area of birch open forest, which has been under observation since 1977. Many of the trees here reach a height of 7-8 m. A more detailed description of the vegetation has been published previously (Bogacheva, 1980).

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Qualitative Differences in the Leaves. We only determined the content of dry matter and the density of apical and basal leaves from branches about 40 cm long chosen at random in the lower part of a birch tree's crown, at a height up to 2 m. The whole investigation was performed just on the leaves of brachyblasts, since auxiblasts continue to produce young foliage in the summer, which differs in food qualities from the foliage of brachyblasts and is frequently preferred by forest phyllophages (Bogacheva, 1986). Different ratios of auxiblasts and brachyblasts in different parts of an axial branch could therefore affect the results. Thus, in 1990, in the distal part of a branch (10 cm segment) the ratio of auxiblasts and brachyblasts was approximately 1:1; closer to the trunk, in the next 10 cm, 1:3; then, 1:6; and still closer to the trunk, in the last 10 cm of the 40-centimeter branch, 1:15. In order to avoid the effect of such a potent factor as foliage of different ages, we conducted the work only on leaves of one age, i.e., taken from brachyblasts.

The investigation was performed on July 8 and 9, 1988. To determine the content of dry matter, we took one distal and one basal leaf each from a branch of 25 birch trees. The leaves were weighed with accuracy to within 1 mg; after drying to a constant weight they were reweighed. To determine the density of the lamina, excisions with an area of 0.5 cm^2 were made from 20 distal and 20 basal leaves and weighed immediately. According to the results, we calculated the wet weight of 1 cm^2 of lamina.

Evaluation of Damage to Leaves in Nature. For this purpose, we cut off 40-centimeter branches from the trees (one per tree), and on each selected branch we took leaves from three brachyblasts at the tip and from three at the base of the branch. The total sample volume in different years is indicated in Table 1. The area that had been removed was evaluated by the point method (Bogacheva, 1979). For each leaf, we simultaneously recorded the types of damage (Bogacheva, 1984).

Experiments on food preference were conducted in 1988. In the crown of a birch tree we selected a branch at random and took two leaves from it, a distal one and a basal one. Just one pair of leaves was taken from a tree; we used only leaves from undamaged brachyblasts.

Two pairs of leaves (i.e., leaves from two trees) were put into Petri dishes lined with moistened filter paper. In order to distinguish the leaves at the end of the test, we marked them with small squares (lower leaves) or triangles (distal leaves) of leucoplaster. In three different variants of the test, one caterpillar of *Epirrita autumnata* Bkh. (Geometridae), or one weevil *Phyllobius maculatus* Tourn., or four *Polydrusus ruficornis* Bonsd. (Curculionidae) were put into one Petri dish. The insects in the enclosures were changed if they died or refused to eat; the *Epirrita* caterpillars were changed more often, in order to avoid the possible effect of individual food preference (which, however, was not revealed in the course of the tests). In all, we used 44 caterpillars of *E. autumnata*, 14 *Ph. maculatus* weevils, and 50 *P. ruficornis* weevils in the tests. The test was conducted daily for each species in 8-12 replications; the total number of replications is indicated in Table 3. The food in the enclosures was changed daily. The leaf area consumed by the insect was measured according to graph paper with 1 mm squares, and the result was expressed as the percent of the area of basal leaves consumed in relation to all consumed food, which was taken as 100%. Thus, the 50% level means the absence of food preference for a particular category of leaves.

Determination of the content of dry matter showed that the percent of it is higher in distal leaves than in basal ones (29.90 ± 0.37 as opposed to $27.43 \pm 0.29\%$, $p < 0.001$). The density of the lamina was also higher in distal leaves (18.6 as opposed to 16.6 mg/cm^2, $p < 0.05$).

The total removal of area of an average leaf taken from the distal end of a branch exceeded the removal of area of a leaf at the base of the branch by 1.5-2.5 times (Table 1). The degree of damage to the leaves changed in the same direction: this index of the intensity of insects' feeding proved to be just as informative as removal of the leaves' area, and we preferred it on account of its simplicity.

Use of the degree of damage to leaves and removal of their area to characterize the intensity of insects' feeding meets the reasonable objection that the peripheral and central parts of the crown may be inhabited by different species of insects (perhaps with different population density or different body size). However, we have precisely identified to which insects certain types of damage belong (Bogacheva, 1984). When we analyzed damage of the most common type, which belongs to the weevil *P. ruficornis*, an important consumer of birch leaves in the vicinity of Labytnangi, we discovered the same trend of change in degree of damage and removal as that found for the whole community of leaf-eating insects (Table 2).

The species used in the tests on food preference are common consumers of birch leaves at the field station (Bogacheva, 1980). However, none of the species displayed selective feeding on distal leaves of the birch branch in the tests. On the contrary, all of the species demonstrated a tendency to select lower leaves of the branch, although it was not statistically reliable. If the data for all species are combined (the correctness of such a procedure could be questioned, it is true), then the preference for the lower leaves becomes reliable (Table 3).

TABLE 1. Use of Distal (above the line) and Basal (below the line) Leaves on a Branch of Twisted Birch by a Set of Insect Phyllophages

Year	Number of leaves	Degree of damage, %	Reliability	Removal, %	Reliability
1983	$\frac{176}{179}$	$\frac{65{,}34}{38{,}55}$	$p<0{,}001$	$\frac{3{,}12}{1{,}55}$	$p<0{,}001$
1984	$\frac{144}{160}$	$\frac{82{,}64}{61{,}88}$	$p<0{,}001$	$\frac{3{,}84}{1{,}34}$	$p<0{,}01$
1987	$\frac{585}{652}$	$\frac{67{,}86}{53{,}68}$	$p<0{,}001$	$\frac{3{,}24}{1{,}96}$	$p<0{,}05$
1989	$\frac{255}{289}$	$\frac{38{,}82}{31{,}84}$	Unreliable	$\frac{1{,}98}{1{,}11}$	Unreliable

TABLE 2. Use of Distal (above the line) and Basal (below the line) Leaves on a Twisted-Birch Branch by Weevils *P. ruficornis*

Year	Degree of damage, %	Reliability	Removal, %	Reliability
1983	$\frac{51{,}70}{31{,}28}$	$p<0{,}001$	$\frac{1{,}45}{0{,}80}$	$p<0{,}01$
1984	$\frac{72{,}92}{53{,}12}$	$p<0{,}001$	$\frac{1{,}18}{0{,}65}$	$p<0{,}001$
1987	$\frac{56{,}92}{40{,}49}$	$p<0{,}001$	$\frac{1{,}28}{0{,}42}$	$p<0{,}001$
1989	$\frac{13{,}33}{9{,}69}$	Unreliable	$\frac{0{,}42}{0{,}13}$	$p<0{,}05$

Leaves from the distal and basal sections of the birch branch cannot rightly be considered as true lighted and shaded leaves, especially because the crowns of birch trees are not dense in the Subarctic; nonetheless, in the peripheral part of the crown the leaves are in conditions of better illumination than in the central part. The direction of differences in density of the lamina and content of dry matter between them is the same as between true lighted and shaded leaves (Duba and Carpenter, 1978). The amount of the differences is less than between true lighted and shaded leaves (Schultz, 1983), but, in any case, it is much greater than between leaves on the south and north sides of the tree's crown, which are sometimes (Moore et al., 1988) considered as lighted and shaded.

It was already mentioned above that lighted and shaded leaves differ not only in the density of the lamina and its water content, but in many other characteristics, which we did not study. In this case, it is important, however, that the different qualities of lighted and shaded leaves are preserved in the experiment, but do not result in the insects' preference for leaves from the distal part of the branch, which is observed for them in nature. Hence, in nature it is due to microclimatic factors acting directly on the insect phyllophages.

The results obtained enable us to make two important comments. First, the natural degree of damage to plants is sometimes judged on the basis of laboratory experiments on food preference. This is incorrect, since in nature the degree of damage may be determined not by the leaves' food qualities, but by some fairly potent abiotic factor. Secondly, the degree of damage observed in nature cannot be directly linked with the quality of leaves (including their chemism), even when such changes in the leaves' quality are discovered. Only simultaneous evaluation of the degree of damage to plants in nature and in laboratory experiments on food preference can help distinguish the direct action of ecological factors on insects and their indirect action through changes in food quality. This technique has been used previously for analogous purposes. Thus, for

TABLE 3. Preference of Insect Phyllophages for Lower Leaves of a Branch in an Experiment (50% level indicates the absence of preference)

Phyllophage species	Date of experiment	n	Degree of preference, %	Reliability
Epirrita autumnata	04—11.07	63	57,93	Unreliable
Polydrusus ruficornis	13—18.07	59	53,00	»
Phyllobius maculatus	14—20.07	54	54,34	»
All species	04—20.07	176	55,18	$p<0{,}05$

Typhlocybinae leaf hoppers, it was shown (Claridge et al., 1981) that in laboratory conditions they feed primarily on excisions from lighted leaves, on which they are also found more often in nature. In this case, we can suppose that the preference for lighted leaves in nature is explained precisely by their quality as a food resource. On the other hand, it happens that in tests (Maiorana, 1981) phyllophages prefer to feed on lighted leaves, but in nature they damage shaded ones more. In this case, the phyllophages' feeding in nature is not directly connected with the leaves' food qualities, but is explained by some other factors.

When it feeds on lighted leaves (in the peripheral part of the crown), an insect's microclimatic environment differs in many parameters from that which surrounds it in the inner part of the crown. The insect has the possibility of raising its body temperature on account of solar radiation; it is in conditions of reduced humidity, but may be subjected to the direct action of precipitation and strong wind with greater probability. This whole set of factors changes simultaneously with movement from the inner part of the crown to the outer part; therefore, it is interesting to discuss which of these factors is decisive in conditions of the Subarctic.

It is well known that solar radiation is an important factor for accelerating an insect's development in severe climatic condiitons, where its existence is limited by low temperatures of the vegetation season (Strel'nikov, 1940; Downes, 1965). The need for long heating for caterpillars of *Gynaephora groenlandica* is apparently an extreme example of this sort (Kukal and Dawson, 1989). For this species, long periods of heating alternate with brief feeding periods, but insects also try to feed on illuminated leaves. Therefore, they prefer to inhabit the southern part of the tree's crown (Bogacheva, 1984; Grossmueller and Lederhouse, 1985), sunlit trees (Lincoln and Mooney, 1984; Moore et al., 1988), and plants on south slopes (Stroganova, 1981). We think that the high level of consumption on the distal part of a twisted-birch branch (i.e., on the periphery of the crown), with its sunlit leaves, is yet another manifestation of the same pattern. Our hypothesis is supported by published data, according to which in the moderate zone insects express no preference for any particular part of an axial branch, as a rule (Baranchikov, 1983; Gurov and Petrenko, 1986; Nielsen and Ejlerson, 1977). In arid regions, on the other hand, the inner part of the crown is more intensively appropriated (Bultman and Faeth, 1986), and also plants in the shade (Maiorana, 1981).

Feeding of insects on sunlit leaves, branches, and trees in the forest-tundra zone, of course, is only a general tendency. The insects' behavior is fairly flexible; during hot times of the day or the vegetation season, they are seen to move to the lower surface of a leaf, or to shaded leaves, branches, or even trees (for example, winged aphids *Euceraphis punctipennis* Zett.) Since such behavior is most characteristic of small insects that do not have a dense cuticle, its main purpose is probably to avoid loss of moisture.

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