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Size-Dependent Selective Leaf Damage by Insects and Some Methodological Implications of This Phenomenon

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Abstract—The area of leaves on birch (*Betula pubescens* ssp. *tortuosa*) auxiblasts and brachyblasts and the degree of their damage by the complex of leaf-gnawing and leaf-mining insects were studied in a light birch forest. The results showed that phyllophagous insects, primarily snout beetles, prefer young leaves on the apices of auxiblasts. Thus, selective damage is inflicted on smaller leaves, both on the auxiblasts and in the entire sample. This phenomenon is widespread and may manifest itself in different ways, depending on the pattern of leaf area distribution along the extended shoot and the feeding preferences of the insects. Thus, it is necessary to reconsider research methods and approaches based on the assumption that insects damage leaves non-selectively, irrespective of their size.

Key words: birch, auxiblasts, brachyblasts, leaf area, damage by phyllophages, research methods.

In studies dealing with leaf area, specialists use methodological approaches based on the a priori assumption that the initial sizes of damaged and undamaged leaves in the sample are equal. However, investigations performed in the 1980s and 1990s demonstrated that insects choose relatively large or small leaves more often than leaves of medium size (Nielsen, 1978; Whitham, 1978, 1983; Fuentes and Etchegaray, 1983; Bultman and Faeth, 1986; Auerbach and Simberloff, 1989; Faeth, 1989; Higashiura and Kikuzawa, 1990; Hiroaki, 1991; Bogacheva, 1994). This finding applies to both individual species and the entire complex of phyllophagous insects. Specialists explained this selectiveness by specific morphological and anatomical features or chemical composition of leaves having a certain size of even by preference for leaf size proper.

In the previous work (Bogacheva, 1994), I analyzed the samples in which the phenomenon of “leaf size selection by insects” was manifested. The results showed that this selection is determined by the insect preference for feeding on young leaves and by a certain pattern of leaf area distribution over a long shoot. Thus, the insects actually choose leaves of a certain age (this fact has been known to entomologists for a long time), and the effect of their preference for relatively large or small leaves in a randomized sample is only due to the relationship between leaf size and age, of which entomologists are apparently informed to a far lesser extent. Unfortunately, this work and the discussion about the aforementioned phenomenon appear to have escaped the attention of Russian researchers. Hence, I decided to demonstrate once again that insects choose leaves of a certain size, to consider the origin of this phenomene-

non, and to specially discuss methodological approaches based on the assumption that the sizes of intact leaves and leaves damaged by insects are equal.

MATERIAL AND METHODS

In early August 2000, a sample of branches was taken from birch trees (*Betula pubescens* ssp. *tortuosa*) growing in a narrow strip of a light birch forest (approximately 500 m long) near the city of Labytnangi, in the forest-tundra zone of the lower Ob region. In the late 1970s and 1980s, regular observations on the composition of the phyllophagous insect complex and the degree of damage to birch trees were performed at this site, designated plot 2 (Bogacheva, 1990, 1997). Birch trees reaching 5–6 m in height rarely had a single trunk; in most cases, these were tall bushes often consisting of many ramets. Branches were randomly taken from different sides of tree crown, in its lower part (below 2 m). Samples from the undergrowth were not taken.

It was planned to estimate the leaf area from linear dimensions (by multiplying leaf length and width) or weight (through the weights of a leaf and a 1-cm² fragment of leaf blade). Hence, each leaf (leaf blade) in the sample was measured with a ruler to an accuracy of 1 mm and weighed using a torsion balance to an accuracy of 1 mg. For calculating leaf area from these data, it was necessary to use a special calibration scale (see below). The data were recorded so as to indicate the type of shoot (long or short) from which the leaf was taken and, in the case of long shoots, the location of the leaf on shoot axis. The leaves were numbered beginning from the base of a shoot. As some leaves were lost together with petioles, each long shoot was carefully

examined using a magnifier to reveal the possible traces of such leaves. This was necessary for determining the correct ordinal number of leaves on the shoot. For each damaged leaf in the sample, the degree of damage in grades (Bogacheva, 1979) and the group of phyllophages responsible for it (Bogacheva, 1990) were recorded.

To make a calibration scale, branches of the same size were taken from ten trees growing in the plot. In this case, only undamaged leaves were used. They were weighed and outlined on graph paper to obtain data on the length, width, and area of each leaf. The types of shoots were not recorded. This sample (220 leaves) was used for determining the ratios of leaf linear dimensions to area and of area to weight.

Using the calibration scale, it was found that deviations from the actual leaf area in calculations based on leaf length and width were approximately two times smaller, on average, than those in calculations based on the total leaf weight and the weight of 1-cm² leaf fragment (error of mean was 4.19% in the first case and 8.39% in the second). Moreover, as the weight–area relation is nonlinear, the second method overestimated the area of large leaves and underestimated the area of small leaves. One more advantage of the first method was that the area of not only intact, but also of damaged leaves could be determined from their length and width without additional corrections. Multiplying the length of each leaf by its width in the calibration scale and calculating the ratio of the product to leaf area, the following linear function was obtained: $S = 0.657ld - 2.187$, where S is leaf area, l is leaf length, and d is leaf width. This method for determining leaf area has been used by other researchers (e.g., Vuorisalo *et al.*, 1989).

In some damaged leaves (72 in the sample), either length or width was impossible to measure, and this dimension was calculated using the formula of linear dependence of leaf width on length: $d = 0.925l + 0.578$ (derived from the calibration scale). Then, both dimensions were used for calculating leaf area (see above).

Finally, 27 leaves in the sample were damaged to such an extent that neither their length nor width were possible to measure. Most these leaves (25) were from long shoots. Their approximate area was estimated using the average dimensions of leaves consecutively located on long shoots (Fig. 1). The area of two leaves located on brachyblasts was taken as average for the brachyblasts of a given branch.

Thus, the area of each leaf in the sample was calculated (for damaged leaves, including the fragment that was lost by the moment of sampling), and all data were prepared for subsequent treatment.

RESULTS

Leaf distribution by size in the sample. The average leaf size was 761.3 mm² (see the table). However, the sample included branches with leaves considerably dif-

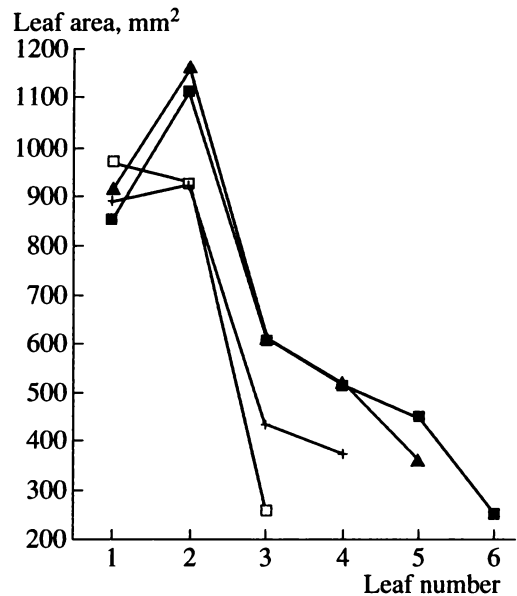


Fig. 1. Leaf size on auxiblasts with different numbers of leaves (leaves are numbered beginning from the base of shoot).

fering in this parameter, which ranged from 450.6 ± 17.1 ($n = 59$) to 1111.2 ± 48.4 mm² ($n = 53$). To some extent, this was accounted for by within-crown variation. As the crown was represented in the sample by only one branch, this component of total variation was impossible to characterize quantitatively. Previous data show, however, that this component is minor (Bogacheva, 1994). The main role belonged to individual variation. The trees with large and small leaves visually identified in the plot remained so from year to year. This was indeed individual variation (rather than microbiotopic), because the plants with large and small leaves often grew close to one another. The correlation between leaf size and tree age was apparently insignificant, as both old and young trees could be large- or small-leaved.

In the total sample, 925 out of 1500 leaves (61.67%) were located on 449 brachyblasts, and the rest, on 135 auxiblasts. The average leaf size on brachyblasts was significantly greater than on auxiblasts (by approximately 25%). Leaf sizes in both groups varied considerably, and the range of variation was approximately the same (table). On the same branch, a brachyblast with large leaves could be located near a brachyblast with much smaller leaves, and similar differences in leaf size (by a factor of 2–3) occurred in the same brachyblast. Variation in the average leaf size on auxiblasts of the same branch was much lower than on brachyblasts, but differences in leaf size within the same shoot, including the serial component, were higher (Bogacheva, 1994). The serial component concerns the constant pattern of change in leaf size along the shoot: the second leaf of an auxiblast is usually

Average leaf size in different categories of leaves in the sample, mm²

Shoot type	Category of leaves	Average leaf area, $M \pm m$	Number of leaves, n
Auxiblasts	Undamaged	838.6 \pm 22.8 (126–1801)	186
	Damaged	570.6 \pm 17.1 (116–1653)	389
	All leaves	657.6 \pm 14.7 (116–1801)	575
Brachyblasts	Undamaged	809.8 \pm 12.1 (163–1805)	659
	Damaged	865.6 \pm 20.4 (150–2166)	266
	All leaves	825.9 \pm 10.5 (150–2166)	925
Total sample	Undamaged	816.2 \pm 10.7 (126–1805)	845
	Damaged	690.4 \pm 14.3 (116–2166)	655
	All leaves	761.3 \pm 8.2 (116–2166)	1500

larger than the first (except for the shoots with three leaves), and the following leaves gradually decrease in size (Fig. 1). The smallest leaves are at the apex; therefore, these are the youngest leaves, which is of crucial importance for discussing the results.

Distribution of leaf injuries. The sample contained 655 damaged leaves (43.7% of the total size), and the proportion of leaf area removed by insects was 4.3%. These values correspond to the averages for this plot that were repeatedly determined in the 1970s–1990s (Bogacheva, 1990, 1997).

Most leaf injuries were of two types (Bogacheva, 1990): (1) bites of various sizes, which usually began at the leaf edge and were inflicted by either the cankerworm *Epirrita autumnata* Bkh. or some solitary sawflies (Tenthredinidae), and (2) small meandering bites at leaf edge inflicted by the snout beetle *Polydrusus ruficornis* Bonsd. They occurred in 16.8 and 30.0% of leaves, respectively. In addition, approximately 2% of leaves were damaged by the leaf beetle *Phratora polaris* Schneid., and five types of injuries (mainly leaf mines) occurred in single leaves. Thus, the composition of phyllophagous was also typical of the plot.

The distribution of these injuries over branches was nonuniform, with the proportion of damaged leaves per branch varying from 20.5 to 91.7%. In this case, microtopographic variation apparently prevailed (especially concerning snout beetles), but variation within the crown (depending on its side and level) certainly played a certain role.

Phyllophagous insects proved to prefer auxiblasts to brachyblasts: the respective proportions of damaged leaves were 67.6 and 28.8%. This preference, revealed for the insects of both basic groups, obviously resulted from their selective feeding on young leaves, because virtually all leaves on the apices of auxiblasts were damaged.

Relationship between the degree of damage and leaf size. In the total sample, selective leaf damage by insects depending on leaf size was obvious: the average size of a damaged leaf was markedly smaller than the

average leaf size in the sample (table). Let us consider the causes of this phenomenon.

As shown above, both leaf size and the degree of leaf damage varied from branch to branch. However, no relationship between these parameters was revealed: all the correlation coefficients, both for total leaf damage and for each of its two basic types, were very low. Therefore, the preference of insects for small leaves is not explained by their choice of small-leaved trees on the plot (such a choice could have been determined by some unknown parameters correlating with leaf size), and the factor responsible for this preference is within a tree.

We can reveal it by considering selective damage of leaves on brachyblasts and auxiblasts. Approximately the same range of variation in leaf size on brachyblasts and auxiblasts offers the insects equal opportunities to choose the leaves of their favorite size (if this size exists). However, all size classes of leaves on brachyblasts are damaged with approximately equal frequencies (Fig. 3), and the average size of a damaged leaf coincides with that of a leaf from brachyblast (table). In auxiblasts, by contrast, the proportion of damaged small leaves (compared to large) is much higher (Fig. 3), and an average damaged leaf is much smaller than an average leaf from auxiblast. Small leaves selectively damaged by insects are the leaves growing on the apices of auxiblasts (Fig. 2), i.e., young leaves. Thus, “selection in favor of small leaves by insects” is determined by their preference for young leaves, which is typical of many insect groups in nature. When leaf size is unrelated to leaf age (as on brachyblasts, whose leaves open simultaneously), no such selection is observed.

DISCUSSION

The phenomenon of the preference for leaves of a certain size in insects was observed by many researchers and widely discussed in the late 1970s to early 1990s. As observations on selective damage of large leaves were more frequent, it was suggested that this

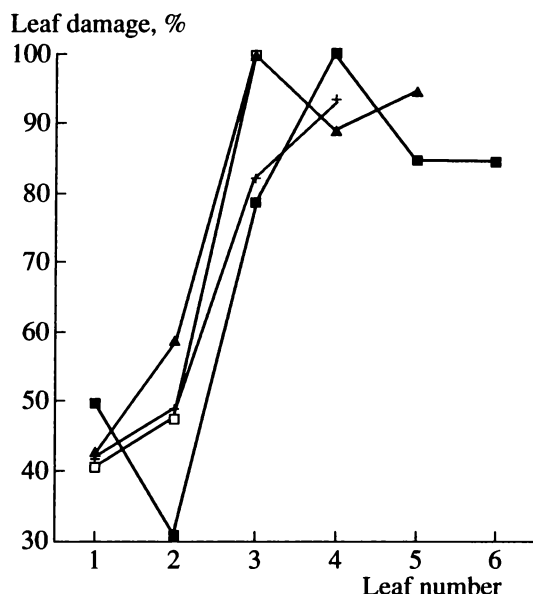


Fig. 2. Leaf damage on auxiblasts with different numbers of leaves.

selection was primarily determined by leaf size per se, especially in the case of insects using the same leaf throughout life, such as leaf-rolling beetles, leaf miners, or gall midges (Auerbach and Simberloff, 1989; Faeth, 1989; Higashiura and Kikuzawa, 1990; Hiroaki, 1991). Another hypothesis was that large leaves are of high quality and especially useful for insects (Whitham, 1978, 1983; Zucker, 1982; Bultman and Faeth, 1986). These concepts led to contradictions in cases when the opposite trends in preference for leaf size were revealed in the groups of ecologically similar species (Bultman and Faeth, 1986). Attempts to discuss the relationship of leaf size and age (Rhomberg, 1984; Higashiura and Kikuzawa, 1990) did not receive due attention, and specialists usually dealt with the so-called randomized samples in which the connection between a leaf and the type of shoot was lost. My previous study (Bogacheva, 1994) showed that insect preference for leaves of a certain age in a randomized sample produces the effect that many researchers interpret as “leaf size selection,” and that the same factor may induce the choice of either small or large leaves.

In the present work, selective damage of smaller leaves in *B. pubescens* ssp. *tortuosa* was demonstrated using the sample taken from the concrete plot. For this and other plots in the lower reaches of the Ob, where *P. ruficornis* snout beetles dominate among birch leaf-eating insects, this direction of selectiveness is constant, being slightly modified by weather conditions in a given year. In the years when the proportion of these beetles decreases and other phyllophages prevailing in the region gain dominance (Bogacheva, 1997), this effect may level off, because these phyllophages (*E. autumnata* and sawflies) usually show no preference

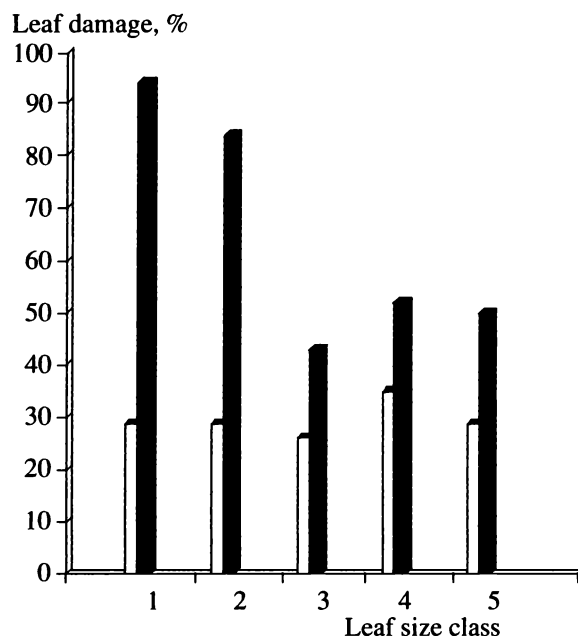


Fig. 3. Relationship between leaf damage and the size of leaves on auxiblasts (solid bars) and brachyblasts. Leaf size classes, mm²: (1) < 300, (2) 301–600, (3) 601–900, (4) 901–1200, and (5) > 1200.

for young leaves. Hence, “selection in favor of small leaves” in the plots free from snout beetles could be expected only in certain years. In the dry growing season of 2000, for example, sawflies also manifested a preference for young leaves.

In some plants, such as the willow, leaf size is smaller at the base of a shoot and increases toward its apex. When phyllophages preferring young leaves (i.e., the leaves growing at shoot apices) prevail in the corresponding area, “selection in favor of large leaves” is observed. This phenomenon was demonstrated in the study on *Salix phylicifolia* performed under the same conditions of the Ob forest-tundra (Bogacheva, 1994).

Thus, size-dependent selective leaf damage by phyllophagous insects may vary in different plant species and in the same species in different areas or years, because the composition of leaf-eating insect complexes is variable. The same complex may include species displaying the opposite trends in “leaf size selection” determined by the ecology of feeding, which may interfere with the establishment of a general trend for the entire species complex. Nevertheless, the existence of such a trend has been reported in many publications (Nielsen, 1978; Fuentes and Etchegaray, 1983; Bogacheva, 1994), and this makes us reconsider some methods used for different purposes by botanists and zoologists.

Some specialists (Rafes *et al.*, 1972; Haukioja and Koponen, 1975; Mauffette and Oechel, 1989) estimate the leaf area removed by insects by simply subtracting the weight of a damaged leaf from the weight of an

undamaged leaf, assuming that the leaves before damage were of equal average size. This assumption is erroneous. If the insects feed mainly on smaller leaves (as in our case), the difference between damaged and undamaged leaves includes not only the weight of the removed fragment, but also the initial difference in leaf size (weight). The proportion of removed material calculated in this way for our sample averages 11.5%, whereas the actual proportion is slightly above 4%. If the insects select leaves of a large average size, the difference between the damaged and undamaged leaves may be smaller than the weight of the removed fragment. Finally, if the initial difference in size is greater than the removed leaf area, the damaged leaf remains larger than the undamaged leaf, and the aforementioned method is inapplicable.

Cases when damaged leaves in the sample are similar in size to undamaged leaves or even larger are interpreted by some researchers as evidence for the compensatory growth of damaged leaves (Nosova and Fomicheva, 1979; Rafes, 1980). In view of the possible insect preference for leaves of a larger size, it is apparent that this evidence is invalid. As an example, consider my data on *S. phlycifolia* (Bogacheva, 1994): on average, the initial size of damaged leaves in the sample exceeded that of undamaged leaves by 32%, whereas the proportion of removed material was only 18%; therefore, an average damaged leaf remained larger than an undamaged leaf.

Finally, botanists commonly use undamaged leaves in comparative studies. For example, this concerns the comparison of average leaf sizes on brachyblasts and auxiblasts (Ermolova *et al.*, 2000). This approach is apparently based on the assumption that undamaged leaves are adequate for determining the average leaf size on a shoot. As follows from data discussed above, the existence of preference for a certain leaf size in insects disproves this assumption: indeed, an undamaged leaf on a brachyblast does not differ from the average leaf; on an auxiblast, however, mainly larger leaves at the base of the shoot remain undamaged (Figs. 1, 2). Having compared only undamaged leaves from brachyblasts and auxiblasts in our sample, we would have concluded that these shoots did not differ in leaf size, whereas the average leaf size on auxiblasts was significantly smaller (table).

For the same reason, undamaged leaves alone do not adequately characterize the average leaf size in the total sample and, hence, cannot be used for comparing leaf sizes in different plant species or in the same species in different areas or in different years, because changes in the composition of leaf-eating insect complexes may entail changes in their preferences for leaves of a certain size. All these comparisons should be made using both damaged and undamaged leaves in their natural proportions. In some cases, leaf damage by insects may be nonselective, thus allowing comparisons based on undamaged leaves alone. In the first place, however, it

is necessary to confirm the absence of leaf size selection, and this procedure involves the analysis of both intact and damaged leaves. The second method producing correct results is to compare only even-aged leaves (this is possible, for example, in studies on the spatial and temporal variation of leaf size in one species). In the species such as birch, the leaves of brachyblasts are convenient to use for this purpose.

On the basis of data discussed above, I conclude that the established fact of size-dependent selective leaf damage by insects makes it necessary to revise some research methods, even if they have already become conventional.

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