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# Leaf size selection by insects: a phenomenon created by random sampling

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Using random sampling as a simple method to collect leaves in a tree crown we have found in weewil *Polydrusus ruficornis* feeding on *Betula pubescens* ssp. *tortuosa* a clear preference for small leaves. The leaf beetle *Gonioctena pallidus* feeding on *Salix phylicifolia* was shown to prefer large leaves. Both these species tend to feed on young tip leaves of long shoots but leaf size in birch decreases from shoot base to its tip while that in willow increases. These regular patterns of variability of leaf size within a long shoot lead to the opposite trends in "leaf size selection" in *Polydrusus* and *Gonioctena*. Using leaves of the same age (brachyblast leaves) in birth we have destroyed the phenomenon of "leaf size selection" in weewils. A special procedure of non-random sampling is offered to find the real insect preference to a certain leaf size.

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Leaf size is considered to be one of the criteria used by phyllophagous insects when choosing leaves in a tree crown (Whitham 1978,1983, Fuentes and Etchegaray 1983, Bultman and Faeth 1986a, Auerbach and Simberloff 1989). This has been explained by differences in plant chemistry between large and small leaves, by differences in leaf morphology and anatomy, or by leaf size in itself. The usual way to detect the phenomenon of leaf size selection by insects is by random leaf sampling within a tree crown.

To use random sampling, we must be sure that at least one of two conditions is met: (1) leaves of different size are randomly scattered within the tree crown; (2) insect herbivory is randomly dispersed within the tree crown. Leaves of different sizes are however not randomly dispersed within a tree crown (Semerikov 1986), though this may be better known to botanists than to entomologists. As for the second condition, it has been shown by many authors that the opposite is generally true: insects usually feed only in certain parts of a long shoot (Larsson and Wirén 1982, Baranchikov 1983, Raupp and Denno 1983, Williams et al. 1983, Bogacheva 1990), of a branch (Bultman and Faeth 1986b, Vuorisalo et al. 1989, Bogacheva 1990) or of a tree crown, preferring a certain height level (Medvedev and Kalandadze 1972, Dylis and Nosova 1977, Niemelä 1979, Selman and Lowman 1983, Bogacheva 1984, 1990), or a certain side of tree crown (Carroll and Luck 1984, Bogacheva 1984, 1990, Grossmueller and Lederhouse 1985, Moore et al. 1988).

I intend to show in this report how the phenomenon of "selection of leaf size by insects" is created by random sampling, what the real reasons of this phenomenon may be, and what methods of sampling might help us to find the real leaf size selection, if it does exist.

## Material and methods

The study was done in the Lower Ob region, in the forest tundra zone, at the Salekhard Research Station belonging to the Urals Department of Russian Academy of Sci-

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Fig. 1. Distribution of leaf sizes on long shoots of birch (A) and willow (B). Shoots with different leaf numbers are marked by different symbols. In (A) samples for six birch trees were pooled.

ences, in Labytnangi ( $66^{\circ}40'N$ ,  $66^{\circ}15'E$ ); its territory comprises a birch stand which has been studied since 1977, and willow shrubbery in the lowest part of the territory. A more detailed description of the vegetation has been published earlier (Bogacheva 1980).

Two plant species, the birch, *Betula pubescens* Ehrh. ssp. *tortuosa* (Ledeb.), and the willow, *Salix phylicifolia* L., were used for this study. I chose six trees within the birch stand; from each tree a sample was taken containing 4–7 branches, about 40 cm in length, clipped in the lower (up to 4 m) part of the birch crown. The number of leaves in one sample varied from 379 to 540. Each branch was depicted, so I could know the exact location of each leaf. When necessary, branches were divided into two 20-cm parts, distal and proximal.

I have used leaf mass to characterize leaf size. Each leaf, without its petiole, was weighed within one hour of branch clipping to the nearest milligram. In damaged leaves the area consumed was measured with graph paper; knowing the specific mass of a leaf blade, the leaf area consumed was converted to leaf mass which was then added to the value obtained by weighing. These re-established original leaf masses were used in the analysis of data. The feeding mark types were logged for each damaged leaf (Bogacheva 1984, 1990).

Branches for the willow sample were collected on seven nearby shrubs; the sample contained 593 leaves. The procedure described above for birch was performed also for willow, except the registration of feeding mark types. The samples were collected at the end of July 1989.

I shall use the term "frequency of herbivory" meaning the number of damaged leaves as a percentage of the total number of leaves.

Leaf sizes were compared using t-tests. Correlation coefficients were calculated to find a possible relationship between leaf size and height level within the birch crown. Analysis of variance was used to separate components of leaf size variability within the birch crown (Fisher 1954).

### Results

## Leaf size variability

#### Birch

Variability of leaf size within the birch crown is rather high, especially within long shoots. Coefficients of variance (Cv, %) fluctuate among 6 birch trees from 40.0 to 63.2%. Leaves within short shoots are not equal either, but their variability is random and low (Cv = 18.4– 24.8%). As for long shoots leaf size variability, in addition to a random component, it includes a regular, serial one, caused by leaf position (Semerikov 1986). Large leaves on long shoots are located nearer to the base (Fig. 1), though the largest leaf is usually not the first (counting from the shoot base), but the second or third one; then leaf sizes decrease up to the shoot tip.

Short shoot leaves represent the main part of the fo-



Fig. 2. Some characteristics of short shoots for six birch trees observed. Each point represents mean data for a branch. Tree numbers in legend are the same as in text.



Fig. 3. Frequency of herbivory on long shoots of birch (A) and willow (B) as a function of leaf position. Shoots with different leaf numbers are marked with different line types. A: only the data for tree no. 2 are shown here. B: the data for 6-leaved and 7-leaved shoots were pooled for the plot (solid line), as well as for 8-leaved and 9-leaved shoots (dotted line). The ninth leaves of the last ones are too few to be presented.

liage on a birch tree. All the short shoots leaves appear from buds almost simultaneously; then seasonal changes in leaf quality follow, and in 2–3 wk these leaves may be considered "old". Long shoots, however, continue to grow and to produce young leaves until August (Bogacheva 1990); these leaves are the smallest, both in the long shoots and in the whole birch crown.

Within a birch branch, short shoots with large leaves alternate with small leafed ones. Within-branch variability of short shoots is rather high, exceeding the variability of leaf size within one short shoot (Cv = 24.8-33.1%). Long shoots tend to concentrate in the distal part of a branch, which may be the reason why variability of long shoots within a branch is much less than that of short shoots (Cv = 16.3-24.8%). Leaf sizes differ also between different branches on one tree (Fig. 2: trees 1, 2, 3, 6), though this variability is the lowest one; coefficients of variance do not exceed 16%.

Besides the distinct pattern of leaf size distribution on long shoots, two other patterns of leaf size distribution within tree crowns have been found earlier: (1) leaves in the peripheral zone of tree crowns are smaller than in the central zone (Semerikov 1986); (2) leaves in the upper part of a tree crown are smaller than in its lower part (Semerikov 1986, Machnev 1987). The first of these patterns may be demonstrated easily in our birches: leaves in the distal part of a branch (in the peripheral zone of the birch crown) are 4.4-20.6% smaller than those in the proximal part of a branch (in the central zone of the crown). Differences were significant for 4 trees. As for the other pattern, I failed to find any connection between mean leaf size on a branch and the height of that branch over the ground; the correlation coefficients for all six trees were very low and insignificant. This was probably due to the tops of the birch trees being inaccessible for sampling. Strictly speaking, branches were clipped only in the lower part of the birch trees.

Leaf size fluctuated widely also between birch trees (Fig. 2). This question however is beyond the scope of this report.

#### Willow

Practically all the leaves in willow are disposed in long shoots which grow for a long period. But the pattern of leaf size distribution within a willow shoot is quite opposite to that in birch long shoots: willow leaves increase in size from the shoot base to the tip (Fig. 1). Full-grown tip leaves in willow are the largest both within a shoot and within a bush. The variability of leaf size within a willow shoot is higher than in birch; thus, in a 6-leaved shoot the difference between the largest leaf and the smallest is 7.3-fold in birch and 10.5-fold in willow.

In some respects willow is not so convenient for studying within-crown variability of leaf size as birch. Firstly, in a well-developed willow bush only the distal ends of branches are leafy, so the bush crown cannot be divided into peripheral and central zones. Secondly, a willow bush is formed by ramets of different ages, and ramet age exerts the ultimate influence on shoot length and leaf size (Price et al. 1987). I did not study these questions.

#### Leaf damage by insects

#### Birch

The main consumer of birch leaves in the study site is the weevil *Polydrusus ruficornis* Bonsd. It damages usually no less than 50% of the leaves, eating about 1-2% of the total leaf area. The geometrid *Epirrita autumnata* Bkh., sawflies and leaf beetles are responsible for another 1-2%. The narrow, tortuous feeding marks by *P. ruficornis*, starting from the leaf edge, are easily distinguished from those of the other folivores (Bogacheva 1984, 1990).

In a typical year, adult *P. ruficornis* appear in the middle of July, reach their highest density by the end of the month and disappear by 10 August (Bogacheva 1988). They preferably feed on sun-lit leaves; looking for optimal light conditions they tend to follow the sun



Fig. 4. Frequency of herbivory in birch (A) and willow (B) as a function of leaf size. Black bars indicate long shoots, hatched bars birch short shoots. The heaviest leaf mass category represents all the leaves over 350 mg (in A) and over 120 mg (in B). In A only the data for tree no. 2 are shown.

around the birch crown visiting all its sides and height levels (Bogacheva 1984, 1990). The distribution of weevils in the territory was very heterogeneous (Bogacheva 1988). Only two of our six trees (Fig. 2, trees 2 and 4) were inhabited by large numbers of weevils; the frequency of herbivory for these trees was 36.7% and 36.6%, respectively. In the other four trees it varied from 0% to 7.1%. Only one tree (tree no. 2) will be used for future demonstration of food preference in weevils.

Weevils show a clear preference for younger leaves

which are found on the distal ends of long shoots (Fig. 3). Since these leaves are small, an apparent "choice of small leaves" may be demonstrated for long shoots. In short shoots, the leaves of all weight classes were damaged evenly (Fig. 4). But the phenomenon found for long shoots would be maintained also for the whole sample pooling both long and short shoots (Table 1). On tree no. 2 the mass of a leaf damaged by weevils is, on average, 179.5 mg, while the mean leaf mass in this sample is 201.3 mg; a 10.8% difference is obtained (p < 0.05).

#### Willow

The main phyllophagous insect on many willow species in the Lower Ob region is the leaf beetle *Gonioctena pallida* L. We cannot distinguish feeding marks by this species from many others with confidence but *G. pallida* dominates the willow insect guild, consuming no less than 75–80% of the whole leaf area lost, or 7–10% of the total leaf area. So, I have used all damaged willow leaves even though some feeding marks were not made by *G. pallida*. This does not obscure, however, the pattern created by *G. pallida*.

This leaf beetle is a flush feeder. Adults begin to feed on willow plants at the end of June when there are only 1-2 leaves on the shoots. Some days later the first larvae appear: G. pallida is a viviparous insect, so instead of laying eggs small larvae emerge (Bogacheva and Dubeshko 1975); this phenomenon is rather common in some chrysomelid genera. Willow shoots grow fast, especially in warm summers, and several basal leaves by the beginning of larval feeding are already too old for neonate larvae. The larvae feed on the youngest leaves of the shoot moving towards the growing shoot tip. Only adults and final instar larvae can gnaw basal leaves, although they also prefer the younger ones. Such a food preference leads to more intensive damage on the distal, and larger, leaves of a shoot (Fig. 3). This apparent preference for large leaves can be demonstrated also for the whole sample, in which all shoots are pooled (Fig. 4). The mean damaged leaf in this sample is 31.9% larger than the mean leaf of the sample (61.1 mg vs 46.3 mg; p < 0.001).

Table 1. Mean masses (mg) of any leaf vs damaged leaf in different leaf categories within tree no. 2. 40-cm branches were divided into two equal-length parts, distal and proximal. Frequency of herbivory is the percentage of damaged leaves. \* p < 0.05; all others are not significant.

Leaf categories	All leaves			Frequency	Damaged leaves		
	n	x	S.E.	herbivory	n	x	S.E.
Leaves in short shoots on proximal parts of branches	171	225.33	5.96	27.49	47	233.79	10.63
Leaves in short shoots on distal parts of branches	141	211.68	7.41	26.95	38	213.11	14.55
All short shoot leaves	312	219.16	4.68	27.24	85	224.47	8.87
Long shoot leaves	170	168.50	8.64	54.12	92	137.96*	11.68
All leaves	482	201.29	4.44	36.72	177	179.50*	8.15

# Discussion

Two insect species with different feeding phenologies (a summer feeding weevil and a spring feeding leaf beetle) showed the same food preference for young, not fully expanded leaves of their host plants, birch and willow. So they tended to feed on distal leaves of long shoots. Different patterns of leaf size distribution on long shoots of birch and willow, however, create the impression that the weevil discriminates against large leaves, and the leaf beetle against small ones. This pattern would be found using a random sample, assuming that all categories of foliage are sampled according to their natural proportion. Leaf size in itself, therefore, is not a criterion for insect choice; the real criterion is leaf age. The weevil P. ruficornis damages short shoot leaves of all size classes evenly, as leaf size in this case is not correlated with leaf age; this connection exists only in long shoots. And since leaves of different age have different traits (water, nitrogen and phenol content, leaf toughness etc.), these traits would also have a certain pattern of distribution within long shoots. Using random sampling we would find these traits to correlate also with leaf size and hence with insect herbivory.

I took an interest in the problem of "leaf size selection by insects" after reading the papers by Whitham (1978, 1983). He demonstrated high correlations between leaf size in poplar, and the performance and density on poplar leaves of Pemphigus aphids. But how can stem mothers choose the proper (large) leaves for themselves and their progeny? At the time of their galling, the preferred leaves are still small. Phenol content is believed to be a criterion for leaf selection (Zucker 1982). I think, however, that Rhomberg (1984) is nearer to the truth believing that the stem mother chooses for galling any leaf young enough to form a gall; non-random distribution of leaf sizes within long shoots and non-random availability of these leaves to *Pemphigus* create the phenomenon of "large leaves choice". The situation with Pemphigus and Populus is quite similar to our one with Gonioctena and Salix. If poplar and willow were to have the "birch pattern" of leaf size distribution, we would find "small leaves choice" by both Pemphigus and Gonioctena.

Different strategies in leaf age preference within insect guilds permit us to find the opposite trends in "leaf size selection" in different species. Some species feeding on birch at the same time as *P. ruficornis* (e.g. leaf beetle *Phratora polaris* Schneid.) prefer old leaves in short shoots and on the base of long shoots; "large leaves choice" may be demonstrated for them. Species with opposite trends in leaf size selection exist even within narrow ecological groups of folivores, e.g. among Lepidoptera mining oak leaves (Bultman and Faeth 1986a). The possible source of this phenomenon is understandable from the data by DeClerck and Shorthouse (1985); they showed that the sawfly *Messa nana* mining birch leaves chooses those in short shoots and (rarely) on Finally, the phenomenon of "leaf size selection" might be found when insects have no choice at all. Thus, *Epirrita autumnata* caterpillars develop on mountain birch so early that they feed mainly on short shoot leaves (Haukioja 1980). Long shoots only begin to grow at that time; their small distal leaves, not damaged by *Epirrita*, will be found in later samples. They decrease the mean size of birch leaves in a random sample and create the impression of "large leaves choice" by *Epirrita*.

The variability of leaves within long shoots is the highest component of within-crown variability. We must however keep in mind two other patterns of leaf size dispersion within tree crown. Together with insect preference to a certain part of tree crown, they may have their effect on "leaf size selection".

It is reasonable to surmise that it would be useful for miners and other immobile insects to have the real capacity to choose large leaves for larval development. Random sampling however is not a relevant method for proving the existence of such a capacity; leaves of the same age belonging to one part of tree crown have to be collected. Such a sample would not include any leaf size variability except the random one. In trees bearing large quantity of short shoots, such as birch, it is suitable to use the leaves collected on proximal parts of branches in the lower part of the crown; in some other trees, as poplar and willow, leaf position on the long shoots has to be taken into consideration.

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