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Ecological and ontogenetic heterogeneity of leaves and its role in insect-plant relationships

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BOGACHEVA, IRINA. Ecological and ontogenetic heterogeneity of leaves and its role in insect-plant relationships. Rep. Kevo Subarctic Res. Stat. 22: 11-17. 1998. - There is high spatial heterogeneity of subarctic trees and shrub leaves depending on abiotic and biotic factors. It causes great variability in herbivory; inter- and intrabiotopical differences, within-crown and within-shoot differences are surveyed here. Disregarding this variation may bias the understanding of insect-plant relationships. Two examples are given: leaf size choice and damaged leaf avoidance of folivorous insects.

KEY WORDS: - folivorous insects - spatial heterogeneity of leaves - leaf size choice - damaged leaf avoidance

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Introduction

Our knowledge on the heterogeneity of phyllophagous insects food resource has considerably increased during the latest decades. Owing to the works of many scientists we have got fruitful information about: geographic and biotopic diversity of leaf chemistry (Depeschko 1959; Haukioja et al. 1978b; Krischik & Denno 1983; MacLean & Jensen 1985), genetic changes in defensive properties of leaves, among them those within one plant (Whitham 1981; 1983; Tuomi et al. 1982; Schultz 1983; Witter 1983), differences between sun and shade leaves (Maiorana 1981; Schultz 1983; Collinge & Louda 1988), among leaves on one shoot (Mooney et al. 1981; Baranchikov 1983; Raupp & Denno 1983; Palo 1984), and among different sites on a

leaf (Zucker 1982; Gall 1987). Leaf chemistry changes throughout the growing season, and leaf quality may even vary diurnally (Haukioja et al. 1978a).

Considering a plant as a heterogeneous resource in time and space (Hodkinson & Hudges 1982; Schowalter et al. 1986), the most investigators are disposed to connect any difference in leaf herbivory with host plant chemistry. Other inner leaf traits being defensive anti-herbivores features (leaf toughness, leaf pubescence, and so on) are discussed more rarely. Variability of food resource is only mentioned as a rule, not discussed; sampling methods used for herbivory evaluation often do not permit to judge about it. I will also discuss whether it is essential

to scrutinize ecological and ontogenetic variability to obtain reliable conclusions on insect-plant relationships.

Methods

My report will refer to diversity and ontogenetic variability in leaf quality and corresponding differences in herbivory in subarctic trees and shrubs. This work was done in the Low Ob' region in 1982-1987, mainly on *Betula pubescens* ssp. *tortuosa*, *B. nana*, some *Salix* species and on *Alnus fruticosa*.

Variation in herbivory was studied at four levels: (1) between trees of different biotopes; (2) among trees in one biotope; (3) among branches within the crown of a tree; (4) among leaves on one shoot. Insect herbivory distribution was studied by recording their feeding marks; for mountain birch in the vicinity of Labytnangi we can distinguish 15 types of such marks (Bogacheva 1984).

Results and Discussion

1. *Interbiotopical differences.* Subarctic areas are extremely heterogeneous in abiotic factors, and it results in high interbiotopic variability of herbivory (Bogacheva 1987). It is often difficult to say what features of biotope cause the observed difference in herbivory because we are not always able to characterize properly the features essential for insects. Leaf consumption on *Salix phylicifolia* on the Polar Urals differs by 5-10 times between the biotopes number 2 and 3 (Table 1), though at first sight they look very similar and are separated only by some hundred meters. Site 3 is flooded by high water in June (as well as site 4) causing later leaf flushing.

In the vicinity of Labytnangi the density (sweep net samples) of different groups of sucking insects (aphids, cicadids, psyllids) on the northern slope of a small brook was 4-10 times lower than that on the southern slope, and the weevil *Polydrusus ruficornis* Bonsd., the main consumer of birch leaves in those places, is entirely absent on the northern slope.

Table 1. Leaf consumption (% of total leaf area) on *Salix phylicifolia* in the Polar Urals. Number of shrubs sampled in each biotope was 4 in 1984, and 5 in other years. Bt = Biotope (see text).

Bt	1984 mean	SE	1985 mean	SE	1986 mean	SE	1987 mean	SE
1	23.0	2.4	8.7	1.0	16.8	1.8	19.6	1.4
2	15.6	1.3	13.1	1.3	16.1	0.6	14.9	2.1
3	1.5	0.5	2.7	0.7	1.7	0.4	2.5	0.7
4	4.5	0.6	2.7	0.2	3.9	0.6	3.3	1.2

Considerable differences in microclimatic conditions may be created by small relief alterations; therefore pooling data from several biotopes in one sample is misleading.

2. *Intrabiotopical differences.* This category of differences includes the well-known edge effect of biotope. In birch groves near Labytnangi restricting the sampling on the edge trees makes the mean value of leaf consumption twice as much as the real one.

The other difference within a biotope may be sun or undercanopy position of certain plants; it can essentially alter phyllophages density on these plants. In regions with severe climatic conditions the disposal of a plant on sun-lighted place gives it an elevated level of herbivory (Lincoln & Mooney 1984).

3. *Within-crown differences.* Random variability in resistance among distinct crown elements (branches) and the commensurate heterogeneity of insect population density within tree crown can be impressingly high (Whitham 1983). However, there are some regular patterns of insect distribution within crown created by ecological factors. Only the most active and mobile herbivores - the weevils *P. ruficornis* and *Phyllobius maculatus* Tourn. - caused uniform damage on the leaves of all sides of birch crown. During 24 hours they circuit round the whole perimeter of the crown keeping to its sun-lighted side. Folivores with restricted mobility avoid in some degree the northern side of birch crown. The larval colonies of *Croesus* sp. (Tenthredinidae) occupy the northern side more
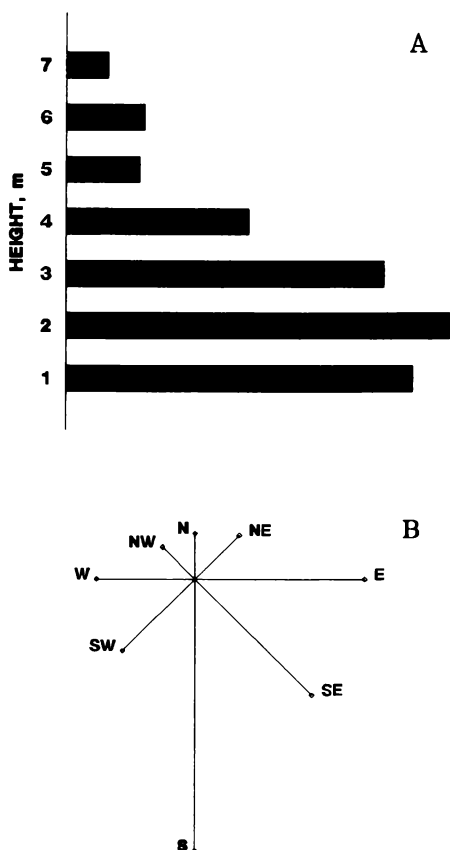
Fig. 1. Distribution of *Croesus* sp. on different
height levels (A) and sides (B) of the mountain birch
crown in Labytnangi in 1987.

rarely than the other sides of the crown (Fig.1);
some other Tenthredinoidea species (e.g.
Pamphilius) may be found on the southern side
only. This phenomenon may be explained by
higher temperatures on that side which
accelerates larval development (Grossmueller &
Lederhouse 1985). The presence of larvae on the
southern side of a crown is insured by adult
behavior; females oviposit mainly in the middle
of a day on sun-lighted leaves. Being in elevated
temperatures during oviposition, a female enables
the same conditions for its progeny.

Most forest tundra folivores prefer the lower
level of tree canopy as illustrated by *Croesus*
distribution (Fig. 1). It may rather depend on
absence of sharp air movements in that part of
the crown than on temperature conditions. Only

Epirrita autumnata Bkh. and some tenthredinid
species inhabit mainly the height level above 2
m from the ground.

4. *Within-shoot differences.* The main trees and
shrubs of the forest tundra produce new leaves
during most of the growing season. So leaves of
different age with uneven nutrients, secondary
substances and physical defence are disposed in
different parts of a long shoot. Ecological
differences of different shoot parts also exist but
they are supposedly of lesser significance for
folivores. Two factors are of special interest for
us. Firstly, ontogenetic differences in nutrients
and defensive substances are regular, and leaves
of different quality coexist in one long shoot.
Secondly, seasonal changes in leaf chemistry are
also quite regular.

These two reasons together with particular
requirements of phyllophagous insects cause an
uneven damage of different leaf categories. Early
spring species as *Epirrita autumnata* on birch
feed mainly on short-shoot leaves and basal
leaves of long-shoots; the rest leaves will appear
later and will be exploited to a lesser degree.
Summer species have a real choice; those which
feed on old leaves (some tenthredinids, the leaf
beetle *Phyllodecta polaris* Schneid.) prefer leaves
on short-shoots. The other summer species, as
weevils, prefer young leaves and therefore
selectively exploit tip leaves of long shoots. Total
damage of leaves depends on food requirements
of dominant herbivore group.

I have shortly envisaged here the ecological
and ontogenetic heterogeneity of the food
resource of folivores. Now I shall show two
examples of disregard of this heterogeneity and
its consequences for understanding of insect-plant
relationships.

Not only nutrients and secondary substances
but also leaves of different size have a certain
distribution pattern along the shoot. Therefore
preference of a certain shoot part means at the
same time the using of a distinct leaf size. This
phenomenon may be properly demonstrated on
birch. *Epirrita autumnata* caterpillars damaging
short-shoot leaves use mainly the largest leaves
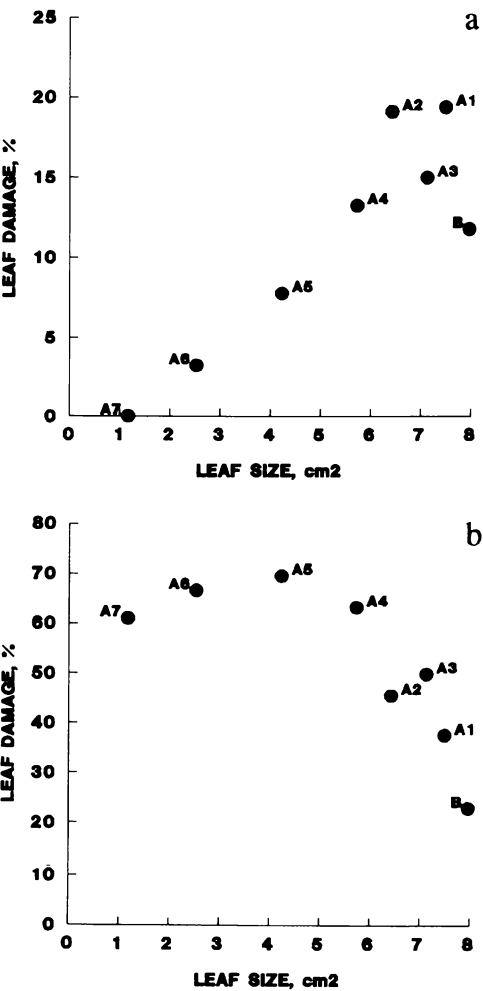in birch crown; but, as we have already shown in

Fig. 2. The relationship between birch leaf size and leaf damage by *Epirrita autumnata* (a) and by *Polydrusus ruficornis* (b). B = average leaf from short shoot; A1-A7 leaves from long shoots, beginning from the base.
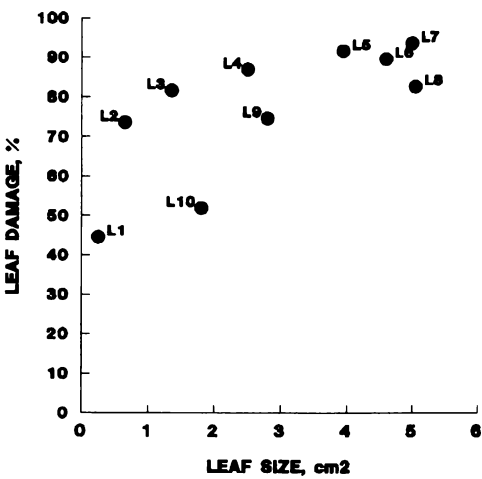
Fig. 3. The relationship between willow leaf size and leaf damage by *Phytodecta pallidus*. L1-L10 = numbers of leaves, beginning from shoot base.

fact they have no choice. Weevils feed on tip leaves of long shoots, as though they would choose the smallest ones. Damage by both species has been shown to be closely tied with leaf size (Fig. 2).

The pattern of leaf distribution along birch long shoot is simple: basal leaves are the largest, tip leaves the smallest (Fig. 2 - see the legend). On willow (*Salix phylicifolia*) shoots we find quite different and more complicated pattern: the largest leaves are situated nearer to the distal end of the shoot (Fig. 3 - see the legend). Willow leaves damage by leaf beetle *Phytodecta pallidus* L. correlates with the leaf size as well (Fig. 3). The reason of this correlation is plant phenology and different suitability of leaves to *Phytodecta* larvae. The largest leaves are those expanding at

Table 2. The comparison of expected and observed numbers of leaves with co-occurring folivorous and sucking insects, Labytnangi in 1987. Total number of leaves was 734-768.

Date	Average leaf damage (%) folivorous insects mean	S.E.	sucking insects mean	S.E.	Coefficient of variation (%) foli-vores	sucking	Correlation coefficient (r)	Numbers of co-occurred leaves Expected, according to Poisson distrib.	Real distrib.	Observed
26 June	4.2	2.8	22.9	4.3	228	66	+0.68	7.1	12.8	8
3 July	6.9	4.2	43.5	6.6	211	52	+0.66	23.0	37.5	35
10 July	16.3	5.5	58.9	6.8	116	40	+0.58	73.6	89.0	85
16 July	37.7	7.1	70.0	5.3	65	26	+0.32	202.3	206.6	208
8 August	76.1	4.6	70.2	5.4	21	27	+0.19	409.0	413.5	425

the time of *Phytodecta* highest density; they are soft and fit for insect feeding. Tough basal leaves are less palatable, tip leaves will appear later. All these patterns of damage distribution (Figs. 2, 3) can be explained without any hypothesis on leaf size choice by folivorous insects, in spite of clear correlations obtained.

The study on relationships between leaf size and herbivory begins in practice from random sampling within tree crown. Within-shoot leaf size diversity is however the main component of within-crown heterogeneity, and the choice of certain leaf size means really the choice of certain shoot part. I believe it is more correct to solve the problem of leaf size selection only with leaves belonging to one leaf category; but random sampling surely makes it impossible.

The second problem I would like to discuss here may be formulated shortly as follows: do folivorous insects avoid previously damaged leaves? One of the methods to investigate this problem is studying of different species co-occurence on one leaf. It is also done sometimes on random sample which can't give us any idea on spatial leaf heterogeneity (Putman 1984); even data from different tree species are pooled afterwards for calculations (Bultman & Faeth 1985). Estimating the expected number of interspecific associations for all leaves of the sample according to the Poisson distribution we suppose that the distribution of folivores on their host plants is random. But it is known to be not true: on the contrary, insects prefer certain biotopes, microhabitats within biotopes, trees, parts of tree crown and sections of shoots. If food requirements of two species are similar, their densities would be correlated positively; if their requirements are different, the correlation would be negative.

A negative correlation doesn't prove interspecific competition, as some authors (Rafes & Sokolov 1976) believe. And different feeding marks in this case meet on one leaf more rarely than we would expect according to the Poisson distribution. In some cases they do not meet on one leaf at all, as leaf mining lepidopteran *Lyonetia* on short-shoot leaves and *Leucoptera* on tip leaves of long-shoots, or as leaf mining

tenthredinids *Messa* and *Fenusa* (DeClerck & Shorthouse 1985). We can not conclude on these grounds about the existence of competition or about damaged leaf avoidance by folivorous insects. Higher number of co-occured leaves in a sample compared to the Poisson distribution is expected in the case of positive correlation.

How can we deal with ontogenetic and ecological variability of our data? To remove ontogenetic variability we analyse only short-shoots leaves in our birch samples. The material would be delivered from all forms of ecological variability if we calculate the expected number of co-occured feeding marks on leaves (according to the Poisson distribution) not for the total sample but for the individual branches. The result for the whole sample is calculated as the sum of numbers expected for branches. If sample heterogeneity and correlation coefficient of the two species densities are high, this calculated number would differ notably from random (Table 2). This method of calculation was described in detail earlier (Bogacheva 1989).

Ecological and ontogenetic variability of leaves and corresponding differences of herbivory are rather high in nature. Studying the insect-plant relationships we have to keep the role of these factors in mind as an alternative to plant chemistry. Refusing from random sampling, we must get and maintain all the data on ecological and ontogenetic variability of our sampling material.

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