ЕКОЛОГІЧНА ЗООЛОГІЯ

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SINGLE OAK TREE AS A HETEROGENEOUS RESOURCE FOR HERBIVORES: INTER-SPECIES' DIFFERENTIATION OF TROPHIC NICHES

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The paper is devoted to the study of differentiation among trophic niches of herbivores within an individual oak tree consortion. Niche partitioning characterizes not only mono- and oligophages, but polyphages as well. The data obtained are discussed in respect to composition and regularities of functioning of natural communities.

Keywords: natural community, herbivore, trophic niche.

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ДУБ – ГЕТЕРОГЕННИЙ РЕСУРС ДЛЯ ФІТОФАГІВ: МІЖВИДОВА ДИФЕРЕНЦІАЦІЯ ТРОФІЧНИХ НІШ

Представлено дані щодо дослідження диференціації трофічних ніш комах-фітофагів у межах індивідуальної консорції дуба. Диференціація поширюється не тількі на моно- та олігофагів, але й на поліфагів. Отримані дані обговорюються з точки зору складу та закономірностей функціонування природного угруповання.

Ключові слова: природне угруповання, комаха-фітофаг, трофічна ніша.

The ecological niche is not a notion of a quantitative population ecology despite several attempts to define it quantitatively. There were numerous definitions of ecological niche. Grinnell (1917, cited after Pianka, 1978) seems to be the first who used the term "niche". He defined it as all the sites where organisms of a species can live (where conditions are suitable for life). Elton (1927, cited after Pianka, 1978) described the niche as the function performed by species in the community of which it is a member. The first definition emphasized the 'address' of the species and the second one emphasized its "profession".

Hutchinson (1957) defined a niche as a region (*n*-dimensional hypervolume) in a multi-dimensional space of environmental factors that affects the welfare of a species. This definition is more close to Grinnell's definition. It became popular because the range of tolerance to ecological factors can be easily measured, whereas species 'profession' is hardly measurable.

Later Odum (1959) defined an ecological niche as a position, or a status of an organism in a natural community, or an ecosystem, which follows from its adaptations, physiological reactions and specific behaviour. Thus, today the term «niche» is awaked wide enough and contains some components, one of which is a trophic or food niche.

Special attention to a trophic niche of a population may be addressed due to its role in determination of matter and energy flow into the given link of food chain.

Some investigations of a host plant – herbivore system showed that a host plant produces highly heterogeneous environment for herbivores, and each of them exploits this environment in one or another way (Semerikov & Glotov, 1980). As the same host plant produces resource for many herbivore species both monophagous and polyphagous, this

causes competition among them for a limited resource, and may result in their trophic niche partitioning. Single tree (individual consortion) with many species, exploiting its resource, serves as a very suitable object for study on trophic niches of herbivores. From another hand, the herbivore niche partitioning in an individual oak consortion may serve as a clear model showing species 'packing up' into the elementary ecosystem.

MATERIALS AND METHODS

The study was done in a testing ground named 'Lavrovoe' (chaparral on southern coast of the Crimean peninsula near Yalta) in 2002. Two oak species, *Quercus pubescens* (Willd) and *Q. petreae* (Mattuschka/Liebl), and their hybrids grow in this general area. One tree of *Q. pubescens* was chosen as a model.

Larvae of all the found herbivores were collected from the tree simultaneously with the leaves, on which they fed. Each larva placed in a separate vial together with a proper leaf. The same day that material was delivered to a laboratory. Species of the larvae were determined, and each leaf was measured (maximal width) and taken to define its stiffness, using device, consisting of a punch on a spring. Leaf stiffness was expressed in symbolic units (distance in mm, which must be passed by a spring, pushing the punch to make a hole in a leaf tissue). Leaf width was used in the study as a measure of a leaf size because larvae usually feed on the top of a leaf and there was impossible to measure its length.

Representatives of the following most common species were found in the tree: *Tortrix viridana* L. (Lepidoptera; Tortricidae) (larvae of 4-th – 5-th instars), *Toeniocampa gothica* L. (Lepidoptera; Noctuidae) (larvae of 4-th – 5-th instars), *Hybernia defoliaria* Cl. (larvae of 3-rd – 4-th instars), *Operophthera brumata* L. (both Lepidoptera; Geometridae) (larvae of 3-rd – 4-th instars), *Lymantria dispar* L. (Lepidoptera; Lymantriidae) (larvae of 1-st – 2-nd instars), *Neuroterus quercus-baccarum* L (Hymeniptera; cynipidae) (adults). Representatives of some rare species, collected from the tree, were analyzed jointly and formed together the "group of rare species".

The data were processed, using standard statistic procedures (Lakin, 1980). Species frequencies in classes of leaf stiffness and width distribution were used for a graphic presentation of inter-species differentiation of variable food resource.

RESULTS

The pattern of the data collected allowed to describe trophic niches of herbivore species on the width and stiffness of host plant leaves, and to compare these niches among themselves. Statistic parameters for the width of the host plant leaves, on which the larvae of different species fed, are presented in table 1. On the whole, the leaf width distribution for the tree was close to the normal distribution. Significant deviations from the normal distribution were found for width of leaves eaten by *T. viridana*, *T. gothica* and some rare species (Table 1). The width distribution for the leaves eaten by *T. viridana* has a plane top, while those for *T. gothica* and rare species have abrupt tops (as seen from the excess values in Table 1). The data for *T. viridana* and *L. dispar* were found to be significantly deviated from the whole data distribution in respect to variance and mean values correspondingly. The distribution for *T. viridana* has the lowest variance, and *L. dispar* larvae of 1-st–2-nd instars prefer to feed on the smallest leaves.

Statistic parameters for the stiffness of the host plant leaves, on which the larvae of different species fed, are presented in Table 2. Distributions of leaf stiffness for all the species were consistently in agreement with a normal distribution. At the same time, much more statistically significant deviations from the whole tree distribution were found for the stiffness data in comparison with the leaf width data. Leaves, eaten by *T. viridana*, *O. brumata* and *N. Quercus-baccarum*, deviated from the whole stiffness data by their means. The leaf stiffness data for the last species together with *H. defoliaria* also differed from whole tree data by their variances (Table 2). *T viridana* preferred to feed on the leaves less 'stiff' than the whole stiffness' data mean in contrast with *N. Quercus-baccarum* and especially *O. brumata*. Apart from the leaves chosen by *N. Quercus-baccarum*, leaves eaten by *H. defoliaria* were most variable in stiffness in comparison with the whole tree data (Table 2).

Graphic form of the data presentation makes the picture of inter-species differentiation of trophic niches much more clear. The frequencies of all the studied species in the classes of host plant leaf width and stiffness distributions are shown in Figs. 1 and 2. These graphics were obtained as follows: leaves, eaten by representatives of each species were calculated in each of the classes of corresponding distribution, and then their numbers were related to the numbers of corresponding distribution class and expressed in parts of unit. Obtained graphics give obvious picture of the inter-species trophic niche partitioning.

Table 1

Statistic parameters for width of host plant leaves, on which the larvae of different species fed

Species	TOTAL	T. viridana.	T. gothica	H. defoliaria	L. dispar.	Rare species	N. quercus-baccarum
Mean (mm)	30,23	31,29	35,38	27,00	24,00	31,10	29,35
Standard error	0,72	0,89	2,57	8,54	2,27	2,49	1,38
Standard deviation	8,75	6,65	9,28	14,80	8,18	7,87	9,85
Variance	76,56	44,17	86,09	219,00	66,83	61,88	97,03
Excess	-0,08	-0,94**	0,94**	N. A.	0,01	1,82***	-0,17
t_{st}					2,62*		
F		1,73**					
N	146	56	13	3	13	10	51

t_{st} – Student's test estimating significance of differences between means for given species and summarized data; F – Fisher's test estimating significance of differences between variances for given species and summarized data; * – P < 0,05; ** – P < 0,01.

The data obtained show that young *L. dispar* larvae preferred to feed on little leaves, *T.viridana* larvae of late instars tended to occupy middle parts of the distribution, and *T. gothica* larvae fed on large leaves (Fig 1) Other species did not show consistent patterns in relation with the size of fodder leaves. More regular picture was obtained when studying leaf stiffness as a factor. The *L dispar* larvae predominated in low stiffness classes of the distribution in contrast to the *O. brumata* larvae exploiting high stiffness classes of the leaf stiffness distribution (Fig. 2). Other species, excluding only *H. defoliaria*, formed a range of intermediate distributions between these two extreme cases, substituting each other in a following order: *T. gothica*, *T. viridana*, Rare species and *N. quercus-baccarum*. Distribution of the *H. defoliaria* was bimodal with two peaks in extreme classes of the leaf stiffness distribution.

Fig. 3 presents the data on the frequencies of four species in different zones of two-dimensional leaf width-stiffness distribution. Zones of the distribution were picked out as Yu. P. Altukhov (1989) described it. These zones have following means: M– – leaves with small values of both the features, M0 – moderate leaves, M+ – leaves with high values of both the features, Mw – disproportional leaves with high values of width and low values of stiffness, Ms – disproportional leaves with low values of width and high values of stiffness. It is seen right away from Fig. 3 that *T. viridana* and *T. gothica* from one hand, and *N. quercus-baccarum* from another hand have opposite trends of their frequencies in the zones of two-dimensional leaf width-stiffness distribution. The first two species

predominated in the M- and Mw zones while frequencies of the last species were high in the M+ and Ms zones. Such trends mean that these three species were much more susceptible to the leaf stiffness than to the leaf size. Another was peculiar to a new *L. dispar* larvae. Both leaf features influenced the species occurrence in the zones of host plant leaf distribution (Fig. 3).

Table 2

Statistic parameters for stiffness of host plant leaves, on which the larvae of different species fed

Species	TOTAL	T. viridana.	T. gothica	H. defoliaria	L. dispar	Rare species	O. brumata	N. quercus-baccarum
Mean (simb. units)	33,64	32,52	32,13	33,83	31,93	34,37	38,50	35,12
Standard error	0,25	0,39	0,87	2,89	1,10	0,62	0,96	0,25
Standard deviation	3,35	3,17	3,46	7,08	4,10	2,71	1,91	1,97
Variance	11,25	10,04	11,98	50,17	16,84	7,36	3,67	3,87
Excess	0,09	0,02	0,76	0,39	–0,62	–0,20	–1,29	0,30
t_{st}		2.4**					4.9**	4,2***
F				4,5***				2.9***
N	185	66	16	6	14	19	4	60

t_{st} – Student's test estimating significance of differences between means for given species and summarized data; F – Fisher's test estimating significance of differences between variances for given species and summarized data; ** – $P < 0,01$; *** – $P < 0,001$.
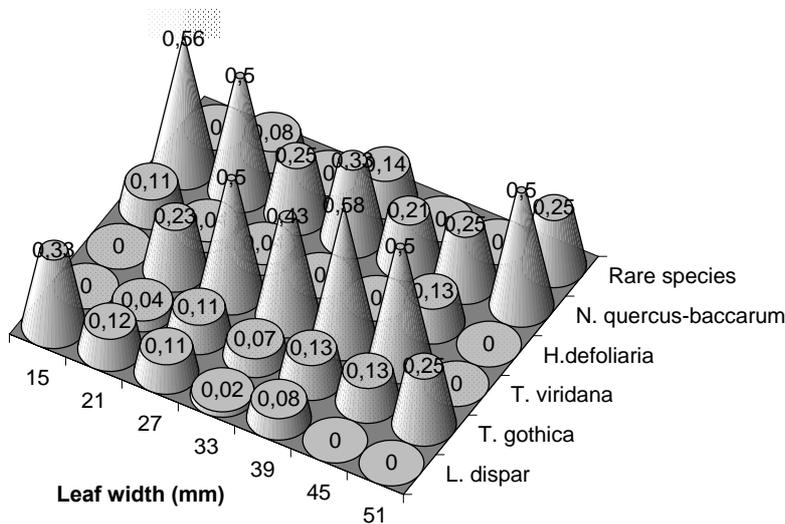

Fig. 1. **Frequencies of the studied species in the classes of fodder-leaf width distribution**
Significant correlations: *L. dispar* – $R = –0,84$, $P < 0,05$; *T. gothica* – $R = 0,91$, $P < 0,01$

DISCUSSION

The natural community composition and functioning could be understood with the help of a good knowledge of niche structures of community participants (Putman & Wratten, 1984), especially analysing niche separation or niche overlapping in the reality. This is usually a difficult task because of complexity of interactions among organisms or species in a community or population. It is well known that two species could not occupy the same niche at the same time. Direct competition between two species for the same ecological niche results in one of three possible outcomes: extinction, exclusion, or character displacement (Chapman & Reiss, 1999).
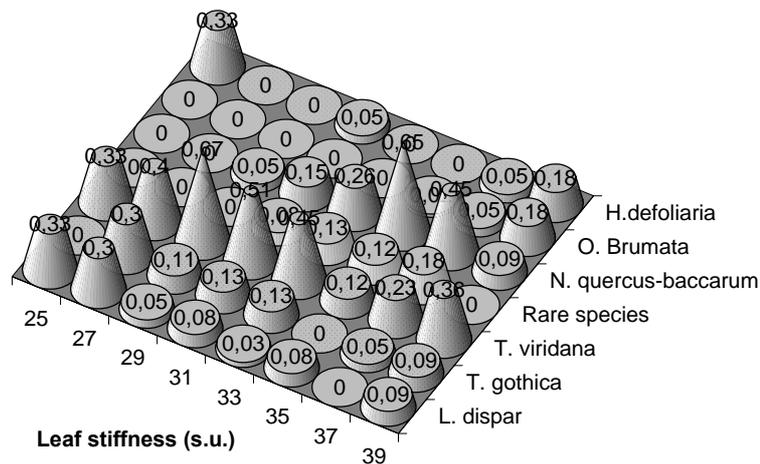

Fig. 2. **Frequencies of the studied species in the classes of fodder-leaf stiffness distribution**
Significant correlations: *L. dispar* – R = –0,74, P < 0,05; O. *brumata* – R = 0,73, P < 0,05;
N. quercus-baccarum (correlation with the class numbers) – Rr = 0,77; P < 0,05

The results herein reported show distinct evidence of partitioning of resources among the species exploiting the same host tree. Even individual tree produces highly heterogeneous environment for herbivores feeding on it (Ivashov, 2001). This partitioning seems to be the result of the previous strong inter-specific competition. Niche heterogeneity may lead to frequency-dependent fitnesses among competing species, even if every species is able to exploit every niche (Ayala, 1972). In this case, competition becomes weak, the community becomes stable and these species can coexist in the same habitat.

Some non-trivial sight could be obtained if with the niche concept the genetic composition of the competing species would be considered. A species or population often is treated as if it is a set of individuals having the same ecological properties. Yet natural populations, particularly populations of sexually reproducing organisms, are highly polymorphic genetically. The ecological, behavioral and other properties of an individual result in the interaction between its genotype and the environment. The existence of so many and such different genotypes in a population means that individuals in the population differ, among others, in their ability to utilize different environmental resources.

It was found earlier by *T.viridana* (Simchuk *et al.*, 1999) that larval Pts-4 and Est-4 genotypes showed relationships with pH and stiffness of host plant leaves. Both the studied loci were polyallelic in *T. viridana*, and many genotypes divided population trophic niche into narrow micro-niches. Each genotype had its own micro-niche, to which it was most adapted, i. e. larvae of given genotype might eat only leaves of certain properties and did not eat other leaves (Simchuk *et.al*, 1999). If to consider these data with the results herein reported, it may be concluded that not the whole population competes with populations of other species sharing the same or close resources, but only separate genotypes do it. In other words, individuals of some genotype, eating leaves with corresponding properties, have much higher probability to conflict with representatives of another species preferring

leaves with the same properties than individuals of other genotypes. For instance, the *T. viridana* individuals of 'soft-leaf-eating' genotypes (see Simchuk *et al.*, 1999) have higher probability to compete with *L. dispar* and *T. gothica* larvae than with *N. quercus-baccarum* and *O. brumata* in comparison with individuals of "stiff-leaf-eating" genotypes and *vice versa*.

Other oak herbivores also may have different genotypes preferring leaves of different properties as food. In this case we obtain much more complex picture of competition in which interaction occur between concrete genotypes of different species. Competitive relations among genotypes of different species may be considered as system-creating ties joining genofonds of interacting populations into a new extra-populative genetic system – a genetic system of a community. For such genetic system of a community M.A. Holubets (1982) proposed the term "genoplast". This term includes a couple of genotype-genotype interaction among representatives of different species in a community. Such repeating interactions (in great number of variants) form stochastically regular community structure, in which species are optimally "packing up".
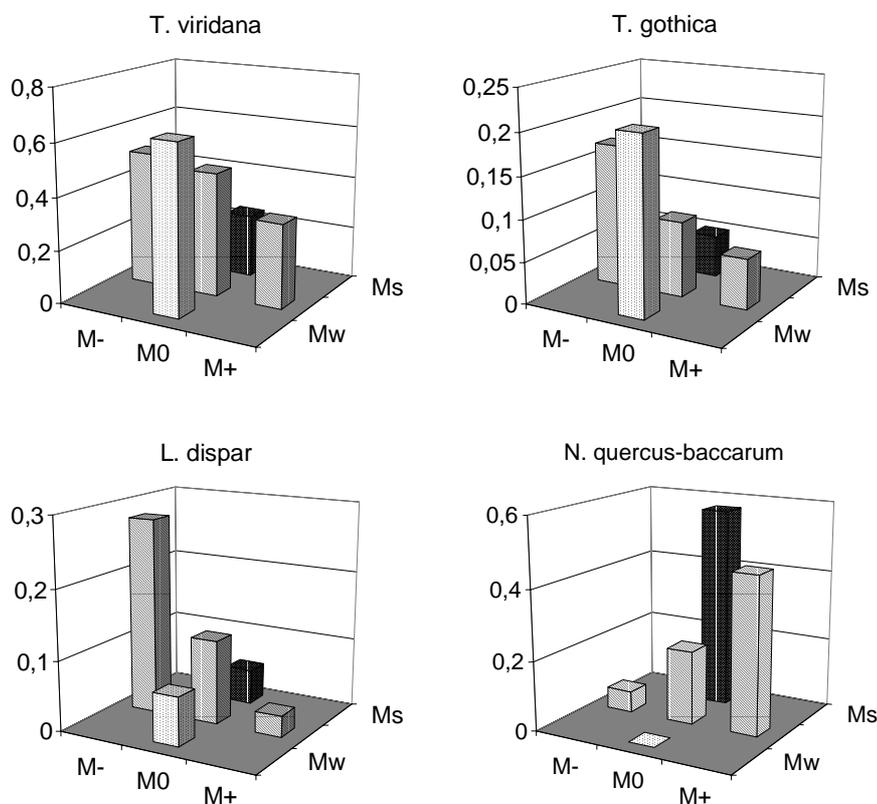

Fig 3. **Frequencies of four herbivore species in different zones of two-dimensional fodder-leaf distribution on stiffness and width**

M- – leaves with small values of both the features; M0 – moderate leaves; M+ – leaves with high values of both the features; Mw – disproportional leaves with high values of width and low values of stiffness; Ms - disproportional leaves with low values of width and high values of stiffness: *T. viridana* – $\chi^2 = 8,02$; df = 3; P < 0,05; *T. gothica* – $\chi^2 = 3,84$; df = 3; P > 0,05; *L. dispar* – $\chi^2 = 8,50$; df = 3; P < 0,05; *N. quercus-baccarum* – $\chi^2 = 26,0$; df = 3; P < 0,001; χ^2 – test estimates significance of the frequencies heterogeneity (after Altukhov, 1989).

CONCLUSIONS

1. Leaves of a single oak tree as a trophic niche of insect herbivore show strong consistent partitioning among herbivores in mean values and variances.

2. Herbivore species substitute each other in order when distributing in respect to features of leaves which they eat

3. Polyphagous insects have the size of a trophic niche that does not exceed that of mono and olygophagous herbivores.

4. Not the whole population competes with populations of other species sharing the same or close resources, but only separate genotypes do it.

5. Competitive relations among genotypes of different species may be considered as system-creating ties joining genofonds of interacting populations into a new extra-populative genetic system – a genetic system of a community, which is named genoplast.

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