THE WITHIN-TREE DISTRIBUTION OF CATERPILLAR MINES

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INTRODUCTION

Lepidoptera is a relatively young order and one of the largest and most diverse in the Insecta. The first paleontological vestiges of moths were found among lower Jurassic deposits, but the most intensive lepidopterous evolution (mainly in suborder Ditrysia = Papilionina) took place in the mid-Cretaceous Period, coterminous with the expansion of angiosperm plants. The flowering plants were a highly determinant factor in the development of the environment, their influence on moth speciation extending beyond provision of food for caterpillars and adults. The greatly increasing heterogeneity of plants in space and time became a base for many potential ecological niches, many of which were afterwards occupied by lepidopterous species. Paleontological data indicate that the mining mode of life was already formed in the first stages of lepidopterous evolution (Kozlov 1988). In recent time, mining caterpillars can be found in nearly all large groups of Lepidoptera. The mining moths are the most specialized ecological group, characterized by important morphological and physiological adaptations at larval stages. They interact very closely with their host plants. Applicability of the term "parasitism" to the mining moths is now under discussion: some authors consider all insects feeding on living plants to be parasites; others question the value of so broad a use of the term. Dogel (1962) wrote, "The parasites are organisms which use other living beings as environment and source of food and make their hosts responsible (partly or completely) for regulation of their interactions with external space." In line with this definition, we consider mining insects true parasites on their host plants.

In this paper, we consider the question how mining caterpillar distribution on host plants reflects topical aspects of the coevolution of insects and plants.

The Heterogeneity of Different Plant Parts and Their Influence on Herbivorous Insects

Leaves on annual shoots differ in morphological, anatomical, and biochemical aspects. This phenomenon is called heterophylly (Serebryakov 1962). Important changes in leaf anatomical structure on annual shoots were described for the first time in Zalensky's (1904) classic work on more than 40 plant species. Apical leaves of all studied plant species are more xeromorphic than basal ones: they have more ribs per surface unit, smaller epidermal cells, smaller mesophyllic cell diameters, thicker epidermal cell membranes, and more developed mechanical tissues.

Krenke (1940) attributed heterophylly to the ontogenetic origin of leaves from structures of different ages. He established the cyclic character of metameric variability: the complete cycle can be described by the unimodal convex curve. This curve reflects changes in morphological and anatomical

BARANCHIKOV, Y.N., MATTSON, W.J., HAIN, F.P., and PAYNE, T.L., eds. 1991. Forest Insect Guilds: Patterns of Interaction with Host Trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. NE-153.

characteristics (leaf size, for example) and physiological processes, but serves only as theoretical background for the primary changes occurring with age. The majority of physiological processes, taking place during the ontogeny of each organ and plant as a whole, follow the unimodal curve; the length of its parts and the maximal point are different for various processes (Gupalo 1975, Klyachko and Kulaeva 1975).

Analyzing the annual shoot structure of *Liriodendron tulipifera*, Vasiliev and Goltsova (1979, 1980) distinguished six characteristic groups by the type of curve describing their changes. They stressed that the variability of external leaf characteristics is more pronounced than that of internal ones. The diversity of organ characteristics is greater than that of tissues and cells.

The structure of a leaf depends both on its location on a shoot and the type of shoot. For example, the leaves of *Populus alba* short shoots are similar to the leaves on the base of the long ones (Pautov 1989). The peculiarities of leaves on different types of shoots are determined not by the differences in the structure of their growing apexes, but by development conditions.

Leaf structure may be affected by environmental factors as well. Zalensky (1904), for example, showed that xeromorphic features increase in leaves as one moves from the basal to the top parts of a shoot.

Initiation of different leaf elements in the bud does not take place not simultaneously. Accordingly, one can distinguish leaf parts different in age and different, therefore, in anatomical, morphological, and biochemical features. Basal and apical parts of a long leaf are known to be distinguished in the same way as basal and apical leaves on the shoot (Tshizhevskaya 1954).

Thus we may conclude that both different leaf parts and different leaves on a shoot are distinguishable by anatomical, morphological, and biochemical features, which may determine their suitability for herbivorous insects. Let us consider, then, the ability of insects to distinguish specific leaf characteristics.

One of the first reports on the ability of females to evaluate the size of host plant leaves demonstrated that egg clutch size of the lilac moth, *Caloptilia syringella* F. (Polejaev 1939), was positively correlated with leaf size. Similar results were obtained for the mining moths inhabiting oak *Quercus emoryi* (Bultman and Faeth 1986b) and for larvae of the mining fly, *Pegomyia nigritarsis* Zett., feeding on different Rumex species (Godfray 1986). The importance of this phenomenon promoting optimal food utilization is obvious, but its mechanisms are still unknown. Leaf preference of attelabid beetles, on the other hand, is determined by length of the leaf margin which the female runs along (Sakurai 1988a, 1988b).

The ability of the papilionid butterfly, *Battus philenor* L., to distinguish leaf shape has also been described. Females of this species prefer to lay eggs either on the wide-leaved *Aristolochia reticulata* or on the narrow-leaved *A. serpentaria*, depending on their individual experience. The leading role of vision in this process is confirmed by the fact that these females also visit nonhost plants with either wide or narrow leaves (Rausher and Papaj 1983, Papaj 1986).

The female orientation to the color of the host plant leaf has been described for the fly, *Pegomyia hyoscyami* Panz., which lays its eggs on the dark, oldest leaves of beets. Leaf color in autumn is the chief criterion in choice of host trees by migrating female aphids *Periphyllus californiensis* Shinji: the majority of females prefer yellow-orange leaves, some of them prefer red, and all ignore yellow-green and green leaves. The species of the host plant, *Acer amoenum* or *A. palmatum*, is not a factor in the choice (Furuta 1986).

The shape and color of leaves are usually distinguished by the insects remotely. Any additional information about plant chemistry and its surface structure is received by touch. Host plant selection

and orientation on leaf surface depend considerably on composition of the cuticular wax components. These components determine, for example, host plant selection by the aphid *Acyrthosiphon pisum* Harr., stimulate egg laying by the fly *Pegomyiabetae* Curt., and increase the number of feeding probes by the weevil *Sitona lineatus* L. (Klingauf et al. 1978). The cuticular wax composition also influences host plant selection by the aphid *Tuberculoides annulatus* Hart. (Kennedy 1986a), but for this species microrelief of leaf surface is of greater importance. *T. annulatus* inhabits the rough leaves of *Quercus robur*, and does not like the smooth leaves of *Q. ilex*. Tarsi of the aphid *Myzocallis schreberi*, by contrast, can be easily fixed on smooth surfaces with the help of a drawing empodium (Kennedy 1986b). The tarsal morphology of the cicadid *Empoasca fabae* is adapted for fixation on smooth leaf surfaces, which is why this species avoids haired varieties of soya (Lee et al. 1986). Thus host plant preference is often determined by insect tarsus morphology.

Hairs on the leaf surface inhibit insect movements and can prevent feeding or egg laying. Although female *Diaphania nitidalis* and *D. hyalinata* moths are not able to distinguish extracts from hairy and hairless leaves of the cucumber *Cucumis sativus* in experimental conditions, they lay more eggs on smooth leaves. It is thought that this preference is a function of tactile stimulation (Elsey and Wann 1982).

The physiological condition of the host plant also affects insect development. Plant weakening is sometimes known to be accompanied by a decrease in its resistance to pests. Decrease in resistance is caused, in turn, both by reduction of allelochemicals and changes in acidity and osmotic pressure of cellular liquid toward promotion of insect development (Radkevich 1980). Baranchikov (1983) divides factors of plant resistance into two groups: those based on origin--passive and active factors--and those based on direction of effect--general and specific factors. The passive factors are characteristic for a plant independent of its relations with insects, and active factors come into play as a response to damage. General resistance depresses successful development of all herbivorous species, specific resistance that of unspecialized herbivores only. During leaf ontogeny, specific resistance factors are replaced by general ones, accounting for the different food values of young, mature, and old leaves for specialized and nonspecialized consumers.

The specificity in food preference is a general adaptation of phytophagous insects to a heterogenous, "spotted" habitat formed by host plant parts. The first detailed analysis of parasite specificity was made by Dogel (1962). According to Dogel, specificity is a norm of parasite response to environmental conditions or a close connection between parasites and their hosts. Slepyan (1973) extended the concept of specificity. He classified specificity into three forms: hostal, topical, and ontogenetic. Hostal specificity is identical to that defined by Dogel. Slepyan called the preference by parasites for a certain place on or in the host body topical specificity. It is of great importance for less mobile organisms with highly localized feeding, mining moth caterpillars, for example. According to Slepyan, ontogenetic specificity is the ability of parasites to develop in host organs of a certain age and offering certain morphological and physiological conditions. Since in the vigorous plant the individual age of each serial homological part, such as leaves on the shoot, is strongly connected with its place among other metameres, topical and ontogenetic specificity are identical in the context of our work. The influence of host tree age on insect mine distribution has not been investigated.

The irregularity of mine distribution in some spring moth species is connected with the dates of leaf appearance. For example, female Eriocraniidae moths deposit their eggs in birch buds, and that is why the larval mines are usually located on the first or second leaf of a shoot. This phenomenon may be called false topical specificity.

Thus heterophylly and the heterogeneity of leaf parts, together with the ability of phytophagous insects to discriminate almost all morphological and physiological characteristics of host plants, lead to the irregularity of insect mine distribution on leaf parts, on leaves of shoots, and on the types of shoots put forth by host trees.

The objective of this paper is to describe the mine distribution of 34 moth species belonging to the families Nepticulidae, Tischeriidae, Gracillariidae, and Coleophoridae on 22 host tree species.

MATERIALS AND METHODS

Material for this work was collected from 1986 to 1989 in Leningrad, Murmansk, Moscow, Voronezh, Kiev, the Kujbishev districts, the Krasnodar and Primorje areas, and Georgia.

Mine distribution on the parts of a simple leaf was investigated according to the method elaborated by Shevtchenko (1958). The leaf was subdivided into strips of equal area perpendicular to the central leaf rib and in twice the number of strips parallel to this rib. The number of mines was calculated in every rectangle of this net; data for right and left leaf parts were compiled. Equal strip areas allow us to describe the empiric functions of mine distribution along both coordinate axes of the investigated two-dimensional space. The ratio between the mine number and the rectangle area can be used to represent the niche structure in volumetric diagrams (Fig. 1). The height of the columns is related to the number of investigated mines, but the ratio between heights is specific for every insect and its host plant. The simpler method is the calculation of mine number in leaf parts between the lateral ribs. It should be noted that diagrams of mine distribution along the central leaf rib are different for the two described methods.

The leaves on annual shoots, the leaflets of the compound leaf, and the parts of the simple leaf were numbered from the base to the top of the organ. The mine distribution on the crown of a tree is described by their ecological density: the share of mining leaves in a probe. Mine distribution on the different leaf parts was compared by Chi-square and lambda methods and Kholmogorov-Smirnoff criteria (Sachs 1972).

The niche overlap of coexisting species was calculated according to Slobodchikoff and Schultz (1980):

$$\alpha = 1 - \frac{1}{2} \sum_{i=1}^{n} \sum_{j=1}^{k} | p_{ij} - q_{ij} |$$

where p_{ij} and q_{ij} are the mine frequencies of coexisting species in the rectangle with i and j coordinates, and n and k are the number of vertical and horizontal strips of the sample leaf. Mine localization on compound leaves or annual shoots was described by one coordinate (the number of leaves or leaflets), and niche overlap was calculated by the modified formula:

$$\alpha = 1 - \frac{1}{2} \sum_{i=1}^{n} | p_i - q_i |$$

A degree of interaction between coexisting species was measured by D/W ratio, where D is the difference between the mean value of resource consumption and W is the mean standard deviation (Giller 1984). The ratio D/W < I indicates the potentially strong competition between coexisting species. The ratio D/W > 3 indicates that the interaction is all but absent. The D/W criterion can be used for the dome-like function only. Calculating niche overlap for the border values of this criterion we found $\alpha > 0.70$ indicates strong competition and $\alpha < 0.26$ the absence of interaction.

Non-mined leaves with identical numbers gathered from equal annual shoots at the same height and on the same side of a tree crown were used to investigate leaf venation. The leaves were treated for lighting by sulfuric acid and alkali and colored by gentian violet and saphranin (Isakov et al. 1984). Venation density of leaf parts was calculated by measuring the number of crossings of ribs per unit of leaf length with an ocular ruler. The lighting conditions of mined and nonmined leaves were measured by luxmeter. The results were analyzed using standard statistical methods.

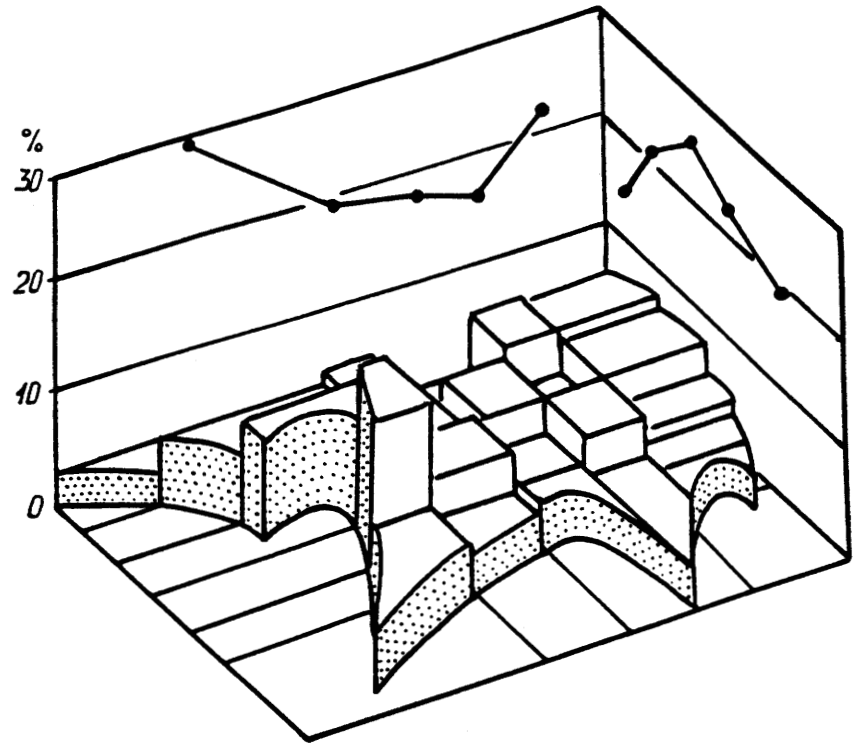

Figure 1. The scheme of leaf subdivision of the strips of equal area and volumetric diagram of niche structure: *Stigmella ultima* Pupl. on *Acer mono* (Primorye Region).

RESULTS

Types of Mine Distribution on the Host Plant

Leaf Parts and Leaflets

The distribution of mines over leaf parts was analyzed for 34 lepidopterous species on 18 host plants. Types of mine distribution over both sectors of simple leaves and over leaflets are similar. They are described by the convex curve with one maximum on 2 to 5 sectors or leaflets (Fig. 2). Two-dimensional analysis shows the pattern of mine distribution over simple leaves to depend on both insect species and host plant species. Significant distinctions in mine distribution are typical both for different moth species inhabiting the same host plant (Fig. 3) and for the single insect species feeding on different types of leaves on the same host plant. For example, the distributional pattern of *Lithocolletis issikii* Kum. mines on the large stool shoot leaves of *Tilia cordata* differs from that on ordinary leaves: χ^2 = 18.19 and 17.85; the level of significance for both coordinate axes is 0.99 (Fig. 4). The mine distribution of *Lithocolletis* sp. on brachyblast and auxyblast leaves of aspen *Populus tremula* also differ significantly (Fig. 5). The distribution of *Lithocolletis issikii* Kum. mines along the midrib of the leaves of *Tilia cordata* from short and long shoots differ with the level of significance 0.999 (χ^2 = 24.32 and 29.89 respectively), as do the leaves of different areas.

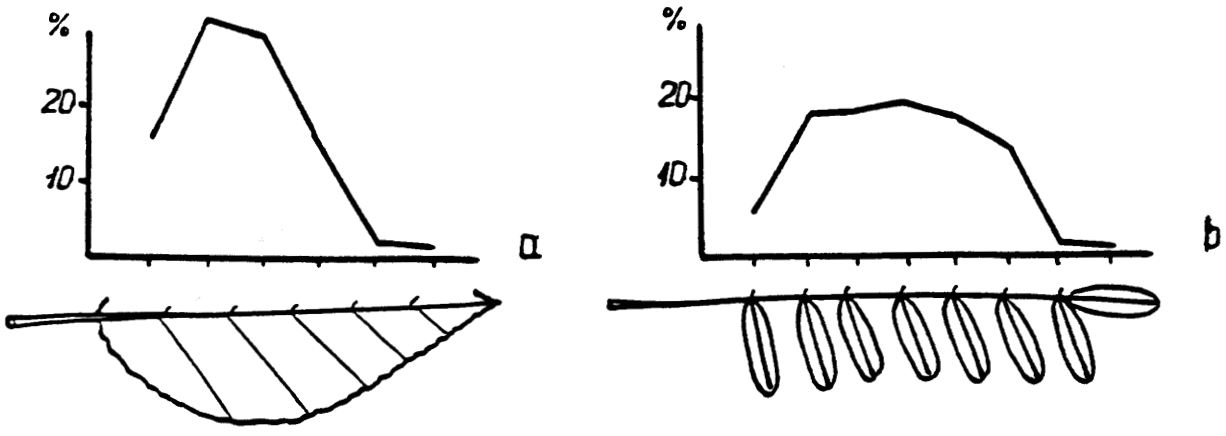

Figure 2. The mine distribution among the leaf parts of simple leaf (a) and among the leaflets of compound leaf (b): a = *Stigmella malella* Stt. on *Malus domestica* (Krasnodar); b = *St. sorbi* Stt. on *Sorbus aucuparia* (Leningrad).

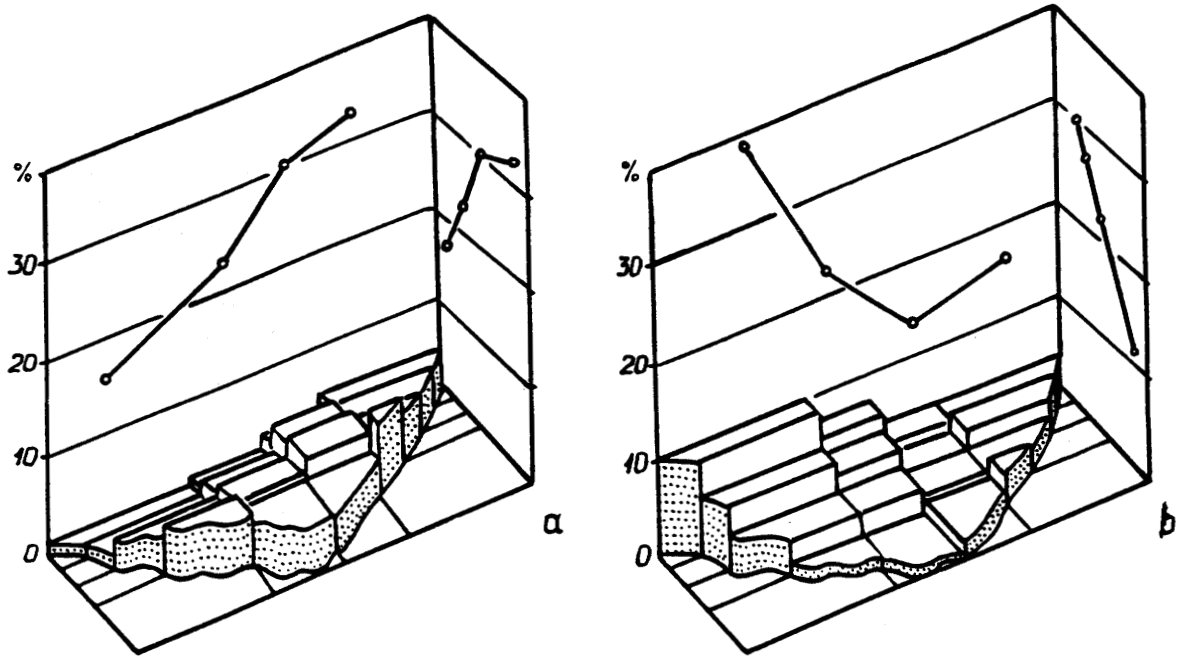

Figure 3. The mine distribution of coexisting species on leaf parts: a = *Stigmella* sp. and b = *Lithocolletis malella* Gram., both on *Mespilus germanica* (Georgia).

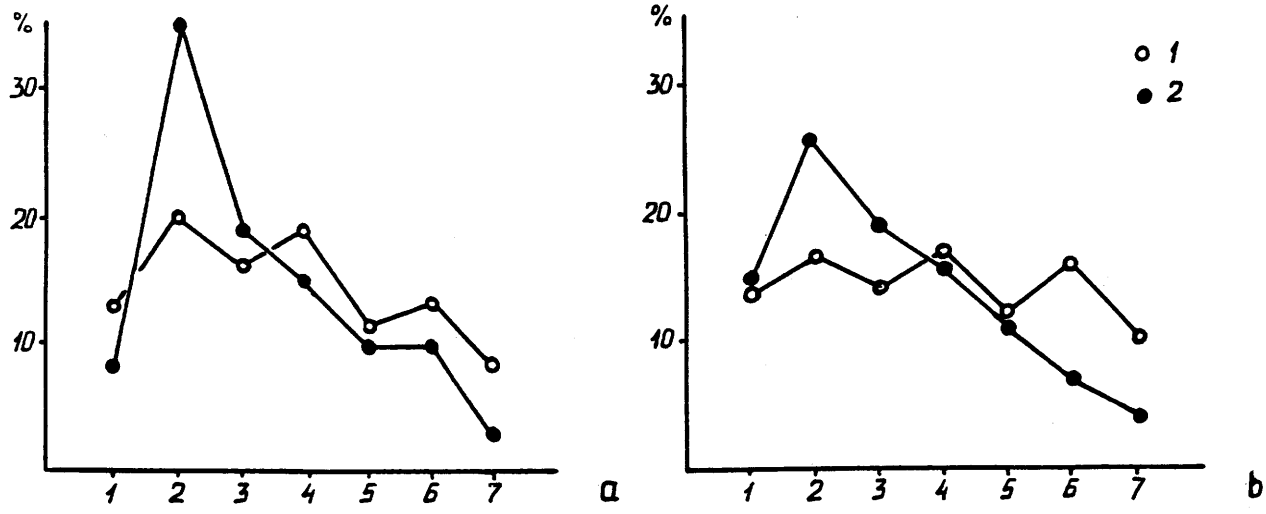

Figure 4. The mine distribution on leaf parts of two leaf types: *Lithocolletis issikii* Kum. on *Tilia cordata* (Kiev). 1 - shoot leaves, and 2 - ordinary leaves; a - parallel to central vein and b - perpendicular to it.

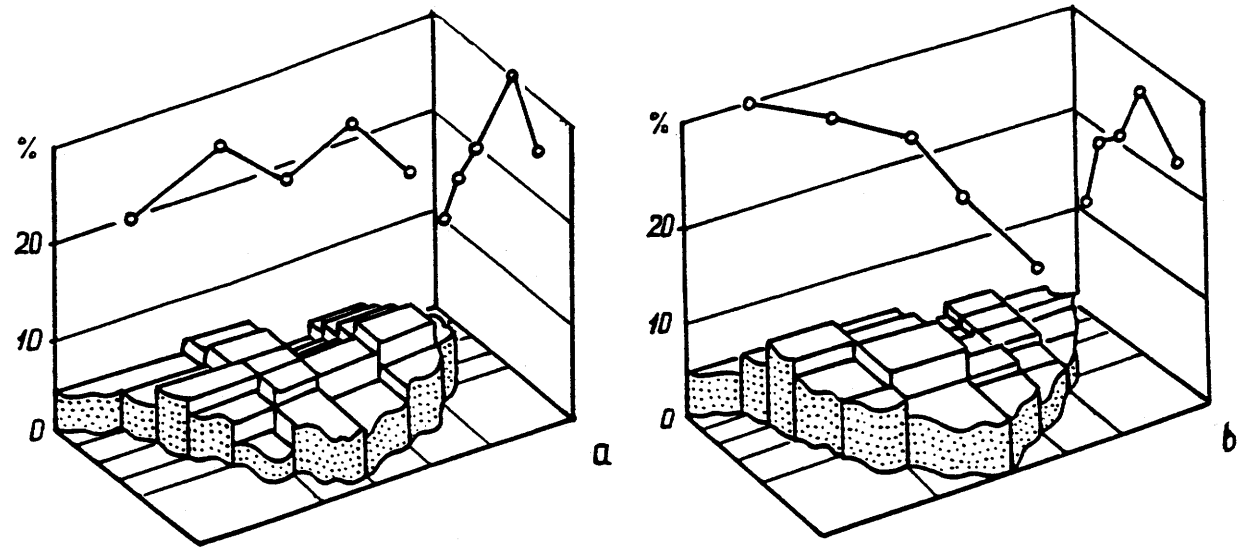

Figure 5. The mine distribution on leaf parts of leaves from two shoot types, *Lithocolletis* sp. on *Populus tremula* (Leningrad): a - auxyblasts; b - brachyblasts.

Comparison of mine distribution in four populations of *L. issikii* Kum. (from Kiev, Kuibyshev, Voronezh, and Moscow) showed geographical variability of this feature (Fig. 6); it is probably dependent on morphological and biochemical differences in leaves of host plant populations. The distribution of *Stigmella nylandriella* Tengstr. mines on leaflets of a compound rowan tree leaf differ

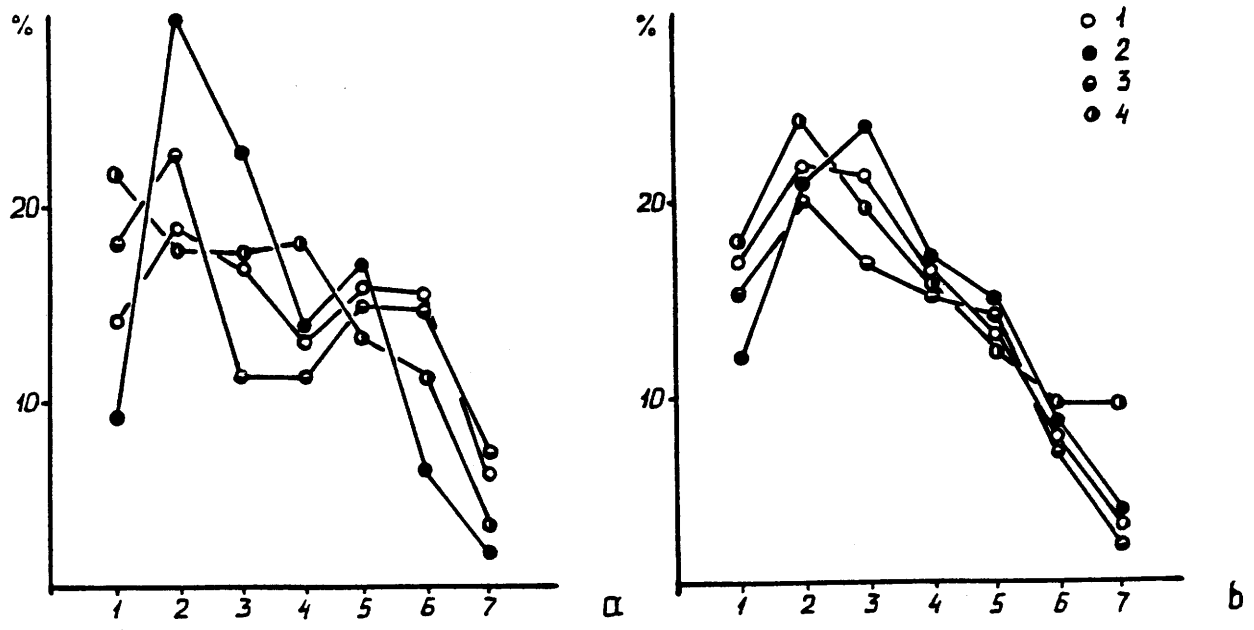

Figure 6. The mine distribution of leaf parts in various geographical regions, *Lithocolletis issikii* Kum. on *Tilia cordata*: 1 = Voronezh district, 2 = Moscow district, 3 = Kujbyshev, 4 = Kiev; a = parallel to central vein and b = perpendicular to it.

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significantly in Murmansk and Leningrad (χ^2 = 16.67 and 16.05; level of significance 0.95). That may be explained by climatic particularities of these regions or by the differences between host plants (*Sorbus aucuparia* in Leningrad and *S. gorodkovii* in Murmansk).

Annual Shoots

Mine distribution over the leaves of annual shoots was investigated for 18 lepidopterous species on 13 host plants. In most cases, this distribution is described by the convex unimodal curve or its segments (Fig. 7). The polymodal character of some empirical distributions may be explained by insufficient number of calculated mines.

Some empirical curves may approximate power, normal, or Poisson function, but the change of curve with the leaf number increase on the shoot is specific for every species, which is why their typification is nearly impossible. The mean number of injured leaves (calculated as arithmetic mean of injured leaf numbers) is the only comparable parameter of distribution. In most cases, the mean value increases with leaf number on the annual shoot. But for three species--*Stigmella sorbi* Stt., *Caloptilia syringella* F., and *Lithocolletis issikii* Kum. first generation--the maximum is observed on the shoots of the middle length.

The pattern of mine distribution on annual shoots is connected with the systematic positioning of phytophagous insect species. Accordingly, the nepticulid moths prefer first leaves of shoots (Fig. 7a), while the gracillariid moths choose leaves in the middle of shoots (Fig. 7b). On the other hand, host plant species can also be a factor in the mine distribution. For example, in Murmansk Territory, over

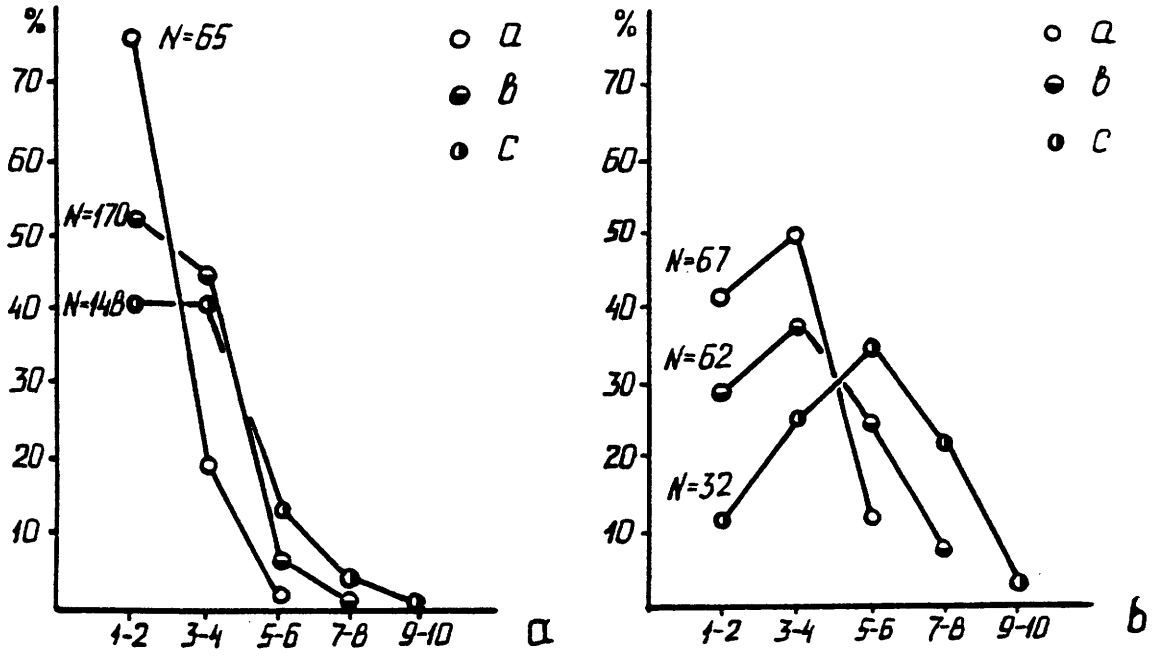

Figure 7. The mine distribution among the leaves of annual shoots of (a) *Stigmella malella* Stt. and (b) on *Malus domestica* (Krasnodar): a = shoots with 4 to 5 leaves, b = 6 to 7 leaves, and c = 8 to 9 leaves. Horizontal scale = the leaf number; N = number of investigated mines.

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90 percent of *Stigmella sorbi* Stt. mines can be found on the first or second leaf of mountain ash shoots, but on the second or third leaf of *Cotoneaster* shoots (Kozlov and Koricheva 1989).

Significant distinctions in mine distribution were discovered between three populations of *Caloptilia syringella* F. on common lilac and two populations of *Lithocolletis issikii* Kum. on small-leaf linden on shoots with five or more metameres.

In some cases, the location of mines is determined by sequence of leaf blossom. In Voronezh Territory, the seventh leaf on the shoot of small-leaf linden blossoms out after egg laying by females from the hibernated generation of *Lithocolletis issikii* Kum. and so is not damaged by caterpillars of the first generation. Maximums of curves for mine distribution of the second generation are shifted toward the top of long shoots. That is why the mine distribution on shoots with six to seven leaves differs considerably for the first and second moth generations.

Comparison of mine distributions over leaf sectors on common beech *Fagus silvatica* on shoots of different length and over leaves of different numbers on shoots of equal length, which was carried out for *Lithocolletis maestingella* Müller showed no significant distinction between them. Thus the distribution of mines on the leaf does not depend on leaf position on the shoot. For five species, we compared the frequency of mines on the shoots of different length with the frequency of occurrence of these shoots on the host plant. These frequencies differ significantly for *Lithocolletis* sp. on speckled alder, *Lithocolletis maestingella* Müller on common beech, and *Caloptilia syringella* F. on common lilac, which indicates a distinct preference for shoots with a certain number of metameres.

Crown Layers

Mine distribution over crown layers was studied for four lepidopterous species. Most *Caloptilia syringella* F. mines are concentrated on the *Syringa vulgaris* and *S. josikae* bushes in the lower and middle layers of the crown, at a height of 40 to 120 cm above ground surface, where shoots with 3 to 5 pairs of leaves are predominant. The upper layer of the crown consists of longer shoots with 7 to 12 metameres, where mines seldom occur.

The maximal ecological density of *Lithocolletis blancardella* F. and *Stigmella malella* Stt. mines on the apple has been recorded at a height of 1.5 m (the normal tree height is about 4.5 m).

Ecological density of first-generation mines of *L. maestingella* Müller on common beech trees, about 25 to 30 m high, decreases in the upper layer of the crown. This may be explained by a temperature gradient (in the spring the ground warms up more rapidly than the air). Ecological density of the second generation increases up to 25 m, then falls abruptly, probably because of the wind, which can blow the female moths away. In this case, mine distribution over both leaf sectors and annual shoots is similar in the various crown layers. This fact allows us to consider topical specificity and vertical changes in ecological density to be independent parameters jointly determining the distributional pattern of mining moths over a tree.

Factors Influencing Mine Distribution Over the Host Plants

Unlike other phyllophagous insects, mining caterpillars have no opportunity for food choice. Even nepticulid caterpillars, which make long serpentine mines, occur mainly near the place of egg laying. So, in both *Stigmella oxyacanthella* Stt. on *Crataegus caucasica* and *St. confusella* Wood. on *Betula pendula*, there are no distinctions in distribution of mines or eggs over the leaf surface (λ = 0.40 and 0.98 respectively). Thus preference of place for oviposition by the female coincides with the food preferendum of caterpillars.

Significant differences between distribution of mines with dead and living caterpillars of *L. issikii* Kum. on leaves of small-leaf linden (χ^2 = 12.68, level of significance 0.95) indicate the importance of the choice of oviposition place by this species. The survival of caterpillars is likely to depend on mine location on a leaf.

Caterpillar distribution on the host plant can also be influenced by abiotic factors, among which illumination particularly important. Females of *Malacosoma californicum* pluviale Dyar are shown to prefer the sunny side of the tree (Moore et al. 1988), moths of *Stigmella malella* Stt. prefer the shady leaves (Chambon 1968). *Caloptilia syringella* F., which occurs in the lower layer of the shrub crown, is known to damage most heavily the common lilac growing in shadow (Lazareva et al. 1985). Comparison of lighting conditions of leaves with and without mines, as well as our experiments with moth females, showed that the lilac moth lays eggs on less illuminated leaves.

Biotic factors influencing mine distribution are diverse: leaf structure, density of herbivorous insect populations, and interspecific competition, among others.

Experimental study of the behavior of *Stigmella malella* Stt. females before egg laying (Chambon 1968) showed the moths of this species to prefer the prominent relief of ribs (lower side of a leaf). The degree of vascular system development and the peculiarities of leaf venation are of great importance for mining caterpillars. The investigation of leaf venation carried out on different parts of the leaf for *Tilia cordata.*, *Mespilus germanica*, *Fagus sylvatica*, and *Carpinus betulus* showed a negative correlation between mine number and rib density for four of the 11 species of mining moths inhabiting these plants (Fig. 8). The coefficient of this correlation is not high (r = -0.14 to -0.24), but it is statistically significant.

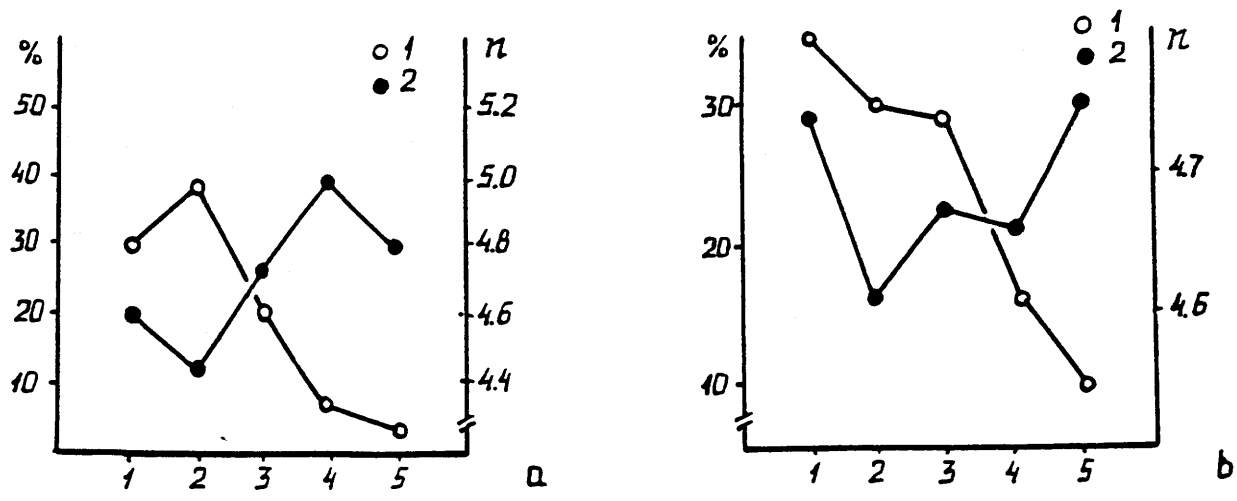

Figure 8. The connection between vein density and mine distribution among the leaf parts, *Coleophora* sp. on *Carpinus betulus* (Kiev): a = perpendicular to central vein and b = parallel to it; 1 = the mine distribution (left scale, percent) and 2 = the vein density (right scale, the number of vein crosses with 1 mm scale).

In one case (*Coleophora* sp. on *Carpinus betulus*, r = -0.12), the choice of place for mine was made not by the moth, but by the caterpillar. Last instar caterpillars of this species leave the mine, build the case, and move freely on a leaf surface. They bore a hole in the epidermis and feed on mesophyll tissues, forming a bilateral mine. A negative correlation between mine number and density of ribs has been found for *Stigmella* sp. on *Fagus silvatica* and *St. microtheriella* Stt. and *St. carpinella* Hein. on *Carpinus betulus*, taking into account only initial parts of serpentine mines (r is -0.2 and -0.16 respectively). If we consider all leaf parts with a mine, the correlation becomes insignificant. Obviously, for caterpillars of the genus *Stigmella* Schr., the low density of leaf venation is necessary at early stages of mine formation only, when larval mandibles cannot penetrate the hard cover of leaf veins. The important role of moth females in choice of place with low rib density is confirmed by their peculiar behavior (Strokov 1956) and by the presence of sensory elements on the end of their abdomen (Chambon 1968).

The pattern of mine distribution may depend on population density of herbivorous insects. For example, if the ecological density of *Stigmella nylandriella* Tengstr. in Voronezh Territory is low (about 1 mine per a compound leaf of mountain ash), the distribution of leaflet areas and mines differs significantly (λ = 2.32); if insect density increases up to 18 mines per leaf, distribution of the two becomes equal (λ = 0.48) (Kozlov and Koricheva 1989). Analogous "substrata saturation" was described for the gall midge *Miciola fagi* Hart., inhabiting beech, when its ecological density was increasing (Dajoz 1981).

If the ecological density of herbivorous insects is low, their food resources are practically unlimited. Therefore, in case of joint utilization by a few species, food preferendums may coincide. But many phytophages and miners in particular sometimes become enormously abundant, damaging up to 90 percent of leaves (Petrenko 1967, Tshagelishvili 1972). In that case, the degree of environmental resource saturation decreases and, according to the competitive exclusion principle, the coexistence of species is possible only if there are some ecological distinctions between them. Coexisting species of mining moths have a similar food source; thus repeated resource utilization is impossible if there are temporal confines

between coexisting species. In that case, evidently, those dimensions of the niche which are connected with heterogeneity of host plant, i.e. the site parameters, must play the main role.

The study of mine distribution in seven moth complexes on the leaves of annual shoots and the parts of leaves indicates some interaction between coexisting species. In Kiev Territory, six species inhabiting the european hornbeam, *Carpinus betulus*, have in most cases strong coincidence in one leaf dimension and considerable discrepancy in the other. Mine distribution of *Parornix carpinella* Frey and *Coleophora* sp. differs significantly in both dimensions from the many other species, and, conversely, distribution of mines *Stigmella microtheriella* Stt. and *Lithocolletis quinnata* Geoffroy show no distinctions in either dimension. The last pair of species, in addition to four other species inhabiting european hornbeam, have a coefficient of niche overlap of more than 0.7, which suggests strong competition. Distinctions in both dimensions of a leaf are significant for pairs of species coexisting on elm, common beech, small-leaf linden, and medlar; the coefficient of niche overlap for them is less than 0.7.

For species of *Stigmella centifoliella* Z. and *Tischeria angusticolella* Zett. in Kiev Territory, there is no difference in mine distribution on leaflets of compound leaves (λ = 0.86, 0.99, and 0.51 for leaves with 3, 4, and 5 leaflets respectively); coefficients of niche overlap are more than 0.7 (α = 0.79, 0.84, and 0.75). Among three species inhabiting mountain ash, *Sorbus aucuparia*, mine distribution over leaflets of compound leaves differs significantly only in two species; the coefficient of niche overlap is more than 0.7. However, mine distribution of these species on annual shoots overlaps considerably less (α = 0.53 - 0.65). Distinctions between *Stigmella sorbi* Stt. and *St. nylandriella* Tengstr. gradually increase with growth of leaf number on mountain ash shoots, reaching their maximum on shoots with 7 to 8 leaves. The most considerable distinction between *Stigmella sorbi* Stt. and *Lithocolletis sorbi* Frey was recorded on shoots with 3 to 4 and 7 to 8 leaves respectively. Thus niche overlap of these species is maintained at a minimal level on all shoot types.

If we assume that mine distribution is controlled by interspecific competition, our data should satisfy several criteria (Brown and Davidson 1977, Addicott 1978). First, the potential competition between species should be factored into analysis of their niche structure. In our case, the coexistence of species under the large overlap of mine distribution functions on leaf parts of simple and compound leaves can be explained by divergence of these species along other dimensions of resources, such as mine distribution over the leaves of annual shoots in three moth species mining the mountain ash. Moreover, ecological density of the majority of studied species was rather low (about 1 mine per leaf) and preferendum coincidence may be explained by the excess of resources. However, the tendency of optimum to diverge at least along one dimension is observed in general.

The second criterion is the utilization of mutual resources by the competitors. The method of material collection (at one time on one host plant) and the detection of mines of different moth species on a leaf show that this criterion is correct for mining caterpillars.

Third, the behavior of a certain species in nature must verify intraspecific competition. Its presence in the case of mining larvae is proved by the fact that more uniform mine distribution over the leaf is observed by an increase in ecological density of the species (Kozlov and Koricheva 1989). The increase in *Lithocolletis* Hbn. (= *Cameraria* Chapm.) mortality has been shown experimentally to depend on high caterpillar density (Bultman and Faeth 1986a).

These data confirm the importance of competition in the mining moth guild, albeit indirectly. They have prompted some authors to propose the alternative hypothesis on the mechanisms of species diversity regulation in folivorous insects (Lawton and Strong 1981). They suppose that the population density of herbivorous insects is usually lower than the quantity of resources allows and that intensification of competition during outbreaks cannot play the decisive role in formation of community structure. Individual ecological reactions--to climate, host plant phenology, biochemistry, and distribution--together with isolation, migration, and the influence of predator and parasite, are of principal importance.

According to this view, the coexistence of species became possible not as a result of the mutual adaptation of potential competitors, but owing to the initial differences in their ecology.

However, there is direct evidence of interspecific competition in coexisting herbivorous insect species. For example, it has been shown for four aphid species that the growth rate of each is higher in the absence of competitors than in the presence of other species on the host plant (Addicott 1978). Besides, among folivorous insects the competition for food can be observed even at low ecological density, since plants, and in particular their vegetative organs, have low nutritional value and contain secondary metabolites. Such a situation might be typical when competitors are abundant. In nature one usually finds only a slight competition between a few species in the community. This can probably be explained by the fact that competition is too powerful a factor, one which during the evolution process either forces out one of the competing species or causes them to diverge into different niche dimensions. The study of Far-Eastern *Lithocolletis issikii* Kum., which suddenly appeared some years ago in the European part of the U.S.S.R., is of particular interest in this regard.

Irregularity of distribution of mining caterpillars is based on differences in the structure of various leaves (or their parts) and their location on host plants; it can be regarded as a result of insect-plant coevolution. Mine distribution reflects the specific oviposition behavior of females, which discriminate different features of a host plant. One of the mechanisms regulating mining moth diversity is species competition. The presence of competition is confirmed by the above-mentioned tendency toward differentiation of ecological niches of potentially competing species. The role of different factors in the formation of associated mining moth structures is a question requiring further study.

CONCLUSIONS

Mine distribution over a simple leaf and over the leaflets of a compound leaf is irregular and specific for each moth and plant species. Mine distribution of a certain species can differ if the host plant's leaves are very heterogenous, as are the leaves of auxyblasts and brachyblasts, stoll shoots leaves, and ordinary leaves, and if the leaves are of different size and located on shoots of different length.

For four moth species, the geographical variability of mine distribution on leaf parts and leaves of annual shoots is shown. In the majority of cases, the mine distribution on leaves of annual shoots can be described by a convex unimodal curve or its rising or descending part. Species of the family Nepticulidae prefer the basal leaves of a shoot independent of host plant species; the family Gracillariidae prefers leaves from the middle part of a shoot. The species of host plant can also be an influential factor in the distributional pattern of mines, however.

The mine frequency of three among five studied moth species on shoots of different length does not coincide with the frequency of these shoots on host plants. We can conclude that females choose a certain shoot type. Ecological density of mines at a certain crown layer is determined by light conditions and possibly by different distribution modes of shoots in the crown. For 4 out of 11 studied species of mining moths, a significant negative correlation between mine number and vein density on leaf parts was discovered. This correlation can become insignificant with development of a mine.

Significant distinctions in damage frequency of lilac leaves by *Caloptilia syringella* F. mines were discovered in different light conditions. The moths of this species prefer shadowed leaves. Significant distinctions in mine distribution along at least one resource dimension were discovered for coexisting species. The irregularity of mine distribution on host plants results from active choice of the ovipositional place by moth females. This choice is influenced by both biotic factors, such as veins density, herbivorous insect population density, and interspecific competition, and abiotic factors, such as light conditions.

ACKNOWLEDGMENTS

We are grateful to Drs. V. Kuznetzov (Zoological Institute, Leningrad), A. Sazonov (All-Union Research Institute for Plant Protection, Leningrad), and A. Stekolnikov (Leningrad State University) for critical analysis of the manuscript, to Drs. A. Frolov, R. Noy, L. Danilkina (Leningrad State University), and V. Isakov (Botanical Garden of the Latvijan Academy of Sciences, Riga) for help in leaf preparation. Dr. E. Zvereva (All-Union Research Institute for Plant Protection) provided invaluable assistance in manuscript editing and translation.

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