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DISTRIBUTION OF PHYLLOPHAGOUS INSECTS IN THE CROWN OF DROOPING BIRCH AT THE NORTHERN BOUNDARY OF TREE VEGETATION

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The susceptibility of various parts of the crown of drooping birch to phyllophagous insects was studied in the Ob forest tundra. It was shown that insects prefer the south part of the crown and certain of its height levels (0-0.5 and 1-2 m). Such an insect distribution in the birch crown and, also, the daily vertical migration of weevils demonstrated by the method of stratified entomological sweeps are largely explained by the requirements for temperature conditions.

The stratification of the insect population declines in moving from the forest zone to polar deserts (Chernov and Matveeva, 1979). This is particularly evident in the fact that whereas the highest-level tree branches are the most thoroughly exploited in the taiga zone (Baranchikov, 1981), plants of the shrub stratum are most thoroughly exploited in forest tundra (Bogacheva, 1979a).

The upper stratum of vegetation in the Ob forest tundra is mainly represented by drooping birch (*Betula tortuosa* Ldb.). Although only a very small part of the birch production is used annually (Bogacheva, 1980), rather complex insect groupings are associated with this birch. This circumstance, as well as the comparatively large vertical extent of the upper stratum (up to 4-5 m), determined the selection of birch as an object for studying the spatial organization of consortia at the northern limit of the distribution of tree vegetation; data were collected for phyllophagous insects.

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TABLE 1. Proportion of Injured Leaves on North and South Sides of Birch Crown, % of Total Number

Type of injury	Labytnangi, field station		Vicinity of Labytnangi		Polar Urals, Sob' valley	
	N	S	N	S	N	S
1	0	0,17	0	0	0	0
2	2,32	9,02	4,75	7,64	4,95	10,62
3	0	0	0	0,48	0,14	0,74
4	2,08	1,82	0,77	1,71	3,23	2,21
6	0,31	1,82	0	0,34	0,07	0,29
7	18,15	19,78	17,17	15,29	0	0
8	0	0,08	0	0	0	0
9	0	0	0	0	0,43	0,22
10	0	0	0,14	0	0	0,07
11	0,23	0,25	0	0,41	0	0,07
12	0,23	1,32	0	0,27	0,14	0,22
13	0	0,25	0	0	0,43	0,59
14	0,07	0,33	0	0,07	0	0,07
15	0,31	0,75	0,07	0,48	0,28	0,22
Total	21,54	32,44	22,06	24,84	9,46	15,25
Surface removed, % of total leaf area	0,82	3,32	1,39	1,98	0,65	1,28
Number of leaves	1295	1208	1433	1465	1393	1356

The study was conducted in 1981-1982 on the lower reaches of the Ob in three regions: 1) territory of Salekhardskii Field Station in the city of Labytnangi, where a portion of sparse birch forest is preserved; 2) sparse birch forest 1.5 km northwest of Labytnangi; 3) birch forest in the valley of the Sob' R., Polar Urals, 50 km northwest of Labytnangi. The vegetation and relief of all areas were earlier described in detail (Bogacheva, 1980).

First of all we studied differences in the distribution of insects in the vicinity of the crown as a function of exposure (north and south sides of the trees) on the basis of an analysis of leaf damage conducted at the end of the growing season (August 5-10, 1981). At each of the three areas, 25 trees were selected, positioned such that they were not shaded by neighboring trees. A branch was cut on the north and south sides of the crown of each tree at 2 m height; all north (as well as all south) branches comprised one common sample of 1200-1500 leaves in volume (Table 1).

In analyzing the samples the damage of each leaf was estimated on a scale of from 0 to 5, while it was also determined what caused the damage. Only injuries due to chewing phyllophages and miners were examined; injuries inflicted by sucking insects (aphids, cicadids, psyllids, and bugs) were not recorded. The method for measuring the removed fraction of leaf area was earlier described in detail (Bogacheva, 1979b).

In studying the distribution of insects with respect to height levels in the crown, four such levels were distinguished: 0-0.5, 0.5-1.0, 1.0-2.0, and 2.0-4.0 m. This work was also done by analyzing leaf injuries at the end of the growing season (August 12-13, 1982), but only in one area, at the field station in Labytnangi. Furthermore, on July 18-19, when the birch-crown population was richest, four sweeps were made at different times of the day every 6 h: 10-11 p.m., 4-5 a.m., 10-11 a.m., and 4-5 p.m. To do this, the field station was divided into four parts, and each sweep was made at a new site. One sample — 50 sweeps of a net — was simultaneously taken from each level distinguished. The obtained results represented not only the association of separate phyllophage groups with specific crown levels, but also the daily vertical migrations of phyllophages. In considering daily migrations, we used materials from 24 h observations of the larval activity of certain phyllophagous species common in the north conducted in different years; their method was described earlier (Bogacheva, 1977).

Injury Identification

Injuries inflicted on birch leaves by leaf-chewing insects were identified in the course of a study of the composition of birch consortia conducted by us in the Ob forest

tundra since 1977. The source of mines was established from the key of M. N. Rimskii-Korsakov (1931) with subsequent refinements from the *Key to Insects of the European USSR* (1978, 1981).

In determining the injury inflicted by phyllophagous insects we strove for the greatest possible definition. In some cases injuries could be definitely assigned by their character to a specific insect species; in others, to a genus or family; while in others identification even to order was impossible. Therefore, we consider it necessary to characterize briefly the types of injury distinguished, indicating their origin.

Type 1. Two birch leaves joined with the upper surfaces inwards, connected along the serrations by a web and skeletonized on the inner surface of the tube that was formed. A characteristic injury associated with the looper *Cidaria hastata* L.

Type 2. Leaf chewings of various size with a simple form of a chewing line, usually starting at the margin of the leaf blade. May belong either to the looper *Oporinia autumnata* Bkh. or to certain solitary sawfly species of the family Tenthredinidae.

Type 3. Intricate chewings of the leaf blade that do not involve the leaf margin and do not cross large veins. Belong to a sawfly of the family Tenthredinidae; green larvae with a black head.

Type 4. Small portions of leaf are skeletonized on the lower surface. Belong to a sawfly of the family Tenthredinidae; small larva, greenish—whitish, semitransparent, with flattened thoracic segment.

Type 5. Several (frequently many) leaves on branch eaten to petiole. They usually include a profoundly skeletonized leaf on which the larvae commence their development. Injuries belong to groups of sawflies (*Croesus* sp. and others) of the family Tenthredinidae.

Type 6. Several (usually three to four) leaves eaten nearly to the petiole; remains of web present on stumps. Injuries belong to the sawfly *Pamphilius* sp. (family Pamphilliidae); apparently, one species.

Type 7. Small, convoluted chewings of the leaf-blade margin. Belong to the weevils *Polydrosus ruficornis* Bonsd. and *Phyllobius maculatus* Tourn.

Type 8. Characteristic "tubes" of the birch leaf roller weevil *Deporaus betulae* L.

Type 9. Small, sometimes significant portions of the leaf are skeletonized on the upper surface. Injury belongs to leaf beetles, most likely one species *Phyllodecta polaris* Schneid.

A description of the characteristic traits of the various types of mines would be a repetition of the types of M. N. Rimskii-Korsakov (1931); therefore, we shall restrict ourselves to the indication of their source.

Type 10. Family Eriocraniidae, genus *Eriocrania.*

Type 11. Family Gracilariidae, genus *Parornix.*

Type 12. Family Lyonetiidae, genus *Lyonetia.*

Type 13. Family Lyonetiidae, genus *Leucoptera.*

Type 14. Family Tenthredinidae, genus *Scolioneura.*

Type 15. Family Tenthredinidae, genus *Fenusa.*

Thus, a total of 15 types of injuries were distinguished, on the basis of which we shall discuss the distribution of insects in the birch crown.

Differences in Insect Distribution in Vicinity of Birch Crown as Function of Exposure

As apparent from Table 1, a whole series of insect groups clearly prefers the south side of the tree crown: most species of the family Tenthredinidae (types 2 and 3), the looper *O. autumnata* (type 2), and *Pamphilius* (type 6); many miners are also attracted to the south side of the birch crown (types 12, 14, and 15). This is explained by the fact that the larvae on the south side of the tree crown are under more favorable temperature conditions; for this same reason sawflies in the montane forests of Western Siberia do more dam-

TABLE 2. Vertical Distribution of Insect Injuries in Birch Crown (in % of total number of leaves)

Type of injuries	Crown levels, m			
	0—0,5	0,5—1,0	1,0—2,0	2,0—4,0
2	4,13	5,44	3,38	5,59
3	0,95	0	0	0
4	1,64	1,89	0,54	5,72
5	0,86	0,38	0	0,20
6	0,34	0,53	0	0
7	65,55	46,41	74,11	36,42
11	0,60	0,08	0,42	0,39
12	0,86	0,76	0,42	0,20
13	0,09	0,08	0	0,39
14	0,34	0,38	0,30	0,39
Total	70,28	53,29	75,98	45,69
Surface removed, % of total . . .	3,31	2,80	3,61	2,29
Number of leaves . .	1161	1323	1657	1521

age to vegetation on slopes of southern exposure (Stroganova, 1980). The presence of larvae on the south side of the crown is insured by the behavior of the imagos, which mainly oviposit during the first half of the day on leaves illuminated during this time by the sun. Being under elevated temperature conditions during oviposition, the female thus insures the same conditions for her future progeny. We have never observed oviposition in the sawflies Tenthredinidae and Pamphiliidae, while Williams (1981) demonstrated an analogous behavior in the butterfly *Euphydryas gillettii* Barnes under montane conditions. Probably, this is an adaptation typical of insects of arctic and montane habitats that are unable to complete long migrations in the crown during feeding. At the same time, such active and mobile phyllophages as the weevils *P. maculatus* and *P. ruficornis* show no preference for any side of the birch crown (Table 1).

Distribution of Insects With Respect to Height Levels of Birch Crown

We used the method of the stratified study of injuries and the method of stratified sweeps to study the vertical distribution of insects in the crown. The first method is convenient in that it results in a summation of all injuries inflicted on birch during the season. The second, given the appropriate repeatability of sweeps, makes it possible to demonstrate more precise (seasonal or daily) differences in the distribution of insects with respect to crown levels.

It is apparent from Table 2 that the insects more or less clearly fall into two groups with respect to vertical distribution in the crown: 1) Those occupying the lower part of the crown, comprising certain species of solitary sawflies of the family Tenthredinidae (type 3), the sawflies Pamphiliidae (type 6), moths of the genus *Lyonetia* (type 12); 2) those preferring the upper part of the crown, associated primarily with injuries of types 4 and 13. The social sawflies Tenthredinidae (type 5), judging by the data of Table 2, are found primarily in the lower part of the crown; but the results of Table 3 contradict this conclusion. On the basis of our observations we also know that some social sawfly species inhabit a height of 2 m and more, since the distribution in the crown apparently differs in different species.

Injuries of type 2, which may belong to either solitary species of Tenthredinidae or the looper *O. autumnata*, are found nearly equally at all crown levels. However, it is apparent from Table 3 that sawflies prefer the lower part of the crown of birch, while *O. autumnata*, according to our observations and the data of Niemelä (1979), prefer the upper part (third and fourth levels).

Weevils were the only group of insects completing true vertical daily migrations; in the morning they ascended to the upper part of the crown, and in the second half of the day

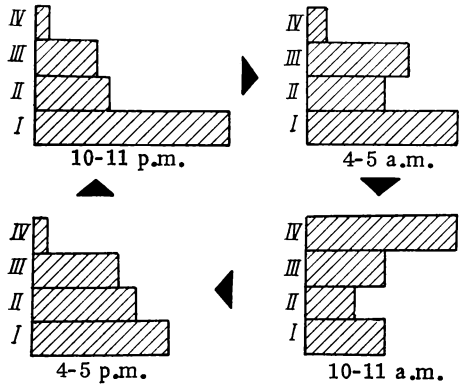

Fig. 1. Distribution of the weevil *P. ruficornis* to crown height levels at various times of day: I-IV) levels: 1) 0-0.5 m; II) 0.5-1.0 m; III) 1.0-2.0 m; IV) 2.0-4.0 m.

returned to the lower horizons. Figure 1 presents the vertical daily migrations of the weevil *P. ruficornis*; the migrations of another species, *P. maculatus*, were completely analogous. Data on the distribution of weevils to the upper levels (Table 3) in general coincide with data on the weevil leaf injury at these levels (Table 2). However, if weevil feeding is not judged on the basis of leaf injury but by the consumed fraction of the leaf surface (respectively 1.7, 1.1, 2.8, and 1.0% of the leaf area at levels I-IV), it can be concluded that they feed most intensively during the first half of the day when they are at height level III. The clear preference for this same part of the crown by the aphids *E. punctipennis* (see Table 3) permits the hypothesis that a large reserve of elongated, long-growing shoots with young leaves, which, as is known, are preferentially eaten by weevils, is located here. This hypothesis, however, is still in need of verification.

Factors Conditioning the Distribution of Insects in Birch Crown

In studies devoted to the distribution of insects in the tree crown, differences in the composition of insect communities and in crown injury at various height levels are considered as a result of differences in the microclimatic conditions developed at these levels and in the ecological requirements of the individual species (for example, Medvedev and Kalandadze, 1972). However, in those cases where some factor is directly limiting for many insect groups it acts unidirectionally on their distribution in the crown and as a result determines the structure of the community and the crown injury. Thus, it has been shown (Nosova et al., 1976), that on filbert growing in spruce forest under conditions of severe shading the leaf injury steadily increases from the lower crown levels to the upper.

Under Subarctic conditions this limiting factor is temperature. The selection of parts of the crown with the most favorable temperatures is very important for northern phyllophages insect species. Two paths of adaptation in this direction are possible. The first is the use of the near-ground part of the crown, where the air temperature and moisture are usually higher, while the wind velocity is markedly lower. Such a path of adaptation is characteristic, for example, of the leaf beetle *Melasoma collaris* L. in alpine habitats of Norway (Hagvar, 1975), the larva of which dies when deposited on a bush higher than 40 cm. The second path is the use of the upper part of the crown; this enables the larva to warm itself at the expense of solar radiation, which is highly characteristic of species of arctic and montane habitats (Strel'nikov, 1940; Downes, 1964; Kevan et al., 1982). For this same reason the larvae prefer the southern side of the tree crown.

Insects capable of active movement in the crown (weevils) use both paths simultaneously, descending during the second half of the day to the lower part of the crown into the layer of air warmed during the day, and in the morning, after nighttime cooling, ascending into the upper part illuminated by the sun. We found similar vertical migrations, only of smaller scale, in the larvae of several phyllophagous species that during the early morning hours make their way to the terminal leaves of shoots illuminated by the sun. We observed such behavior in 1982 in the caterpillars *O. autumnata*, and in 1971-1972, in larvae of the leaf beetle *Phytodecta pallidus* L. on willow. The larvae of solitary sawfly species do not make such migrations.

Thus, the distribution of insects in the birch crown under Subarctic conditions is mainly controlled by their requirements for temperature conditions. The selection of regions of the

TABLE 3. Vertical Distribution of Insects in Birch Crown, Average for Four Determinations (insects per 50 sweeps of net)

Group of insects	Type of injuries	Height levels, m			
		0—0,5	0,5—1,0	1,0—2,0	2,0—4,0
Solidarity sawflies					
Tenthredinidae	2	2,5	1,2	0,5	0,8
Looper *O. autumnata*	2	0	0,2	0,2	0
Solidarity sawfly					
Tenthredinidae	3	0,5	0	0	0,2
Social sawflies					
Tenthredinidae	5	0	0	1,8	0
Pamphiliidae	6	1,8	0,2	0,2	0,2
Weevil *P. ruficornis*	7	91,2	47,0	52,2	23,8
Weevil *P. maculatus*	7	3,2	2,2	3,5	4,2
Aphid *Euceraphis punctipennis* Zett.	—	24,5	27,0	58,2	23,5
Cicada Cicadellidae	—	16,5	6,2	11,2	7,2
Psyllidae Psyllidae	—	1,0	0	0,2	0
Bugs Hemiptera	—	0,5	0	0,5	0,2
Total		141,5	84,2	129,2	60,2

crown with the most favorable temperature regimen explains the greater damage of the southern part of the crown, as well as certain of its height levels (0-0.5 and 1.0-2.0 m). Each species, possessing a limited mobility, occupies a fully defined part of the birch crown; the difference in the paths of adaptation of the species even within systematically and ecologically similar groups precludes relating these groups to any of the distinguished parts of the crown. At the same time, the various modes of distribution in the crown of immobile species, on the one hand, and the existence of mobile species completing daily vertical migrations, on the other, results in a rather uniform exploitation of all parts of the birch crown.

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