

Diversity and Anatomic Structure of Ectomycorrhizas of *Picea obovata* in the Altitudinal Gradient (the Denezhkin Kamen' Mountain Ridge, Central Urals)

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Abstract—Diversity and anatomic structure of ectomycorrhizas of the Siberian spruce in natural communities over the altitudinal gradient from 305 to 800 m above sea level (northern taiga, the Denezhkin Kamen' mountain ridge, the Central Urals) have been investigated. It is established that the relative abundance of fungal mantles of different structure changes substantially with altitude. The cross size of mycorrhizal tips and proportions of their structural parts (fungal mantle, layer of the root cortex parenchyma, and central cylinder) change insignificantly.

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Study of the biological and ecological features of the living organisms at the upper border of their distribution in mountains is a classical model for analysis of the mechanisms of adaptation of the living to extremal environments. A great number of works deal with the upper border of forest and its dynamics, as well as with the reasons for the high mountains being treeless [1–5]. There are five main hypotheses on the mechanisms that control the upper border of forest [3]: 1) low temperatures damaging tissue; 2) mechanical and pathogenic damage of plants; 3) suppressed regeneration; 4) zero carbon balance; 5) inhibition of synthesis. In all cases the main ecological factor considered is unfavorable temperature in alpine habitats, and differences are reduced to determining the most sensitive process. The hypotheses are not incompatible, and different mechanisms of influence on trees can act simultaneously.

The absorbent underground organs of trees — thin roots and ectomycorrhizas — occupy a significant place in two “physiological” hypotheses suggesting that carbon balance and inhibition of synthesis are responsible for treeless alpine habitats [3]. The first hypothesis implies a high cost of the initiation and maintenance of activity of the absorbent organs, which leads to zero carbon balance. The second theory binds the inability of trees to grow with the low effectiveness of the functioning of roots and mycorrhizas on cold soil, which leads to insufficient supply of macrolelements to the plants and inhibition of synthesis against the background of the sufficient supply of photo-assimilates [3, 6]. Meanwhile, there is a significant imbalance between the bodies of information on the structure and functioning of over- and underground organs of trees at the upper border of vegetation, which reflects the much more study given to the former.

Taking this into account, we studied the structure of ectomycorrhizas of the Siberian spruce (*Picea obovata* Ledeb.) in the altitudinal gradient. Our main task was to answer the question whether the activity of ectomycorrhizal associations and/or the share of the resources spent on their formation changes at the upper border of the spruce distribution.

AREA AND METHOD OF STUDY

The key area is the territory of the Denezhkin Kamen' mountain ridge (Central Urals, Denezhkin Kamen' reserve, 60°N, 59°E). Six sample plots were marked on the northern slope in two altitudinal belts (mountain-forest and subgolets) in the interval from 305 to 800 meters above sea level (Fig. 1). The top mark of the gradient corresponds approximately to the upper border of forest communities on the profile. The sample plots were marked in the forests of complex composition (Table 1). From bottom to top, density, average height, and stand stock, as well as the shares (by the number of stems) of Siberian spruce and Siberian fir (*Abies sibirica* Ledeb.) decrease while the shares of West Siberian larch (*Larix sukaczewii* Dyl.) and Siberian pine (*Pinus sibirica* Du Tour) increase.

The Siberian spruce, for which 800 m above sea level is an approximate upper limit for a one-stem tree to form, was chosen as the model species. At a higher altitude, spruces form elfin woods. Lone trees of the Siberian pine and larch, which do not make close communities, occur up to 1000–1050 m above sea level.

Despite a significant difference in the absolute heights at which the sample plots are located the root systems of spruce in the altitudinal gradient are formed under similar conditions. All plots present various

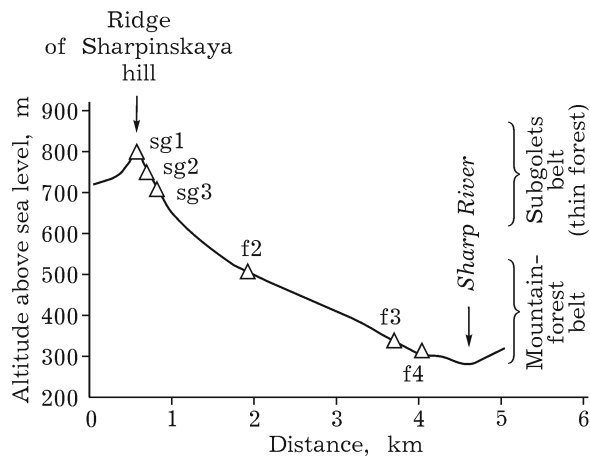


Fig. 1. Scheme of sample plots location.

mountain-forest soils formed on the well-drained eluvium-talus of gabbro. As our observations show, only subramose anchoring roots penetrate soil deeper than 10–15 cm from the day surface on all plots. The samples were taken from either lower layers of organic horizons of the poorly decayed duff densely interwoven with tree and grass roots, or from the upper (1–3 cm) layers of mineral part of soil. In the majority of cases, large clasts of the parental rock weathered to a different degree occurred below the area of sampling, and in the fine earth that filled the spaces between them, the concentration of roots was significantly lower than in the overlying horizons.

The material was collected in August, 2004. To accurately identify the species, the conductive roots with ectomycorrhizas were compared with skeletal roots.

All samples were taken from the undercrown space of the spruce trees of average diameter. The number of samples per one plot is 10–12 (one sample from 10–12 trees). The samples were stored in a 4% formalin solution. Twelve root tips from each sample (120–140 tips from a sample plot) were anatomically analyzed. The tips analyzed total to 750.

The anatomical structure of the ectomycorrhizal tips was studied on thin (10 μm) cross sections prepared on a freezing rotary microtome. At 200–450 \times , the following parameters were recorded for each tip: presence/absence of fungal mantle and its subtype [7]; radius of the vascular cylinder; quantity of tannin-filled cells in parenchyma of the root bark; number of layers and the average size of live cells of parenchyma of the root bark. The percentages of areas under the fungal mantle, parenchyma of bark, and vascular cylinder in the cross section were calculated.

During statistical analysis, sample plot served as a unit for intensity of mycorrhization of root systems and parameters of ectomycorrhizal diversity, while a single tip was a unit for the parameters of anatomical structure of ectomycorrhizas.

RESULTS AND DISCUSSION

Intensity of mycorrhization of the root system of spruce is somewhat higher in the communities of the mountain-forest altitudinal belt. 88–96% of short absorbent roots transform into mycorrhizas, with similar numbers for the subgolets belt — 85–90%. However, the difference of the numbers between the belts is statistically insignificant ($t_{(2)} = 1.55$; $P = 0.197$), and we can speak only about certain tendency toward a change in

Table 1. Characteristics of sample plots.

Sample plot	Altitudinal belt	Altitude above sea level, m	Stand formula	Density, $\text{m}^2/\text{hectare}^*$	Height, m	Stock, $\text{m}^3/\text{hectare}^*$	Vegetative association
mf4	Mountain-forest	305	4S3F2SP1B	25	15	200	long-moss and bilberry
mf3	Mountain-forest	335	4F3P1SP1S1B	43	17	230	cowberry and bilberry
mf2	Mountain-forest	505	3SP3S3B1F	35	12	130	reed-grass and bilberry
sg3	Subgolets	710	4B2F2L1S1SP+P	23	10	110	ledum and bilberry
sg2	Subgolets	750	6B3SP1L+S,P	19	9	100	sedge and bilberry
sg1	Subgolets	800	5SP4B1L+S	3	3	No estimates	*** and bog bilberry

* The data of forest organization.

successfulness of formation of ectomycorrhizas with altitude.

Diversity of ectomycorrhizas was estimated by the diversity of fungal mantles. Classification of T. Dominik–I. A. Selivanov was used, which is based on two groups of features: 1) type of the mantle (plecten-, pseudoparenchymatic (in the given work all mantles with pseudoparenchymatic elements were labeled pseudoparenchymatic: transitional, pseudoparenchymatic proper, double), or unstructured); 2) presence of specific hyphal formations on the mantles.

Six to eleven subtypes of mantles were recorded on sample plots (Table 2), but no relation of the choice of mantles to the altitudinal belt was revealed. Judging by Shannon's index of diversity, the mantles in the subgolets belt are somewhat more diverse, but the belt differences are related mostly to the change of the ratio between the abundant subtypes. The level of domination of sparse species is higher in the mountain-forest belt, which is evident from large values of the Berger-Parker index and from the abruptly dropping curves of the distribution of the abundance of subtypes (Fig. 2).

In their structure, the suites of mantles on various sample plots within one belt are much more close to each other than to the suites of mantles of another belt (Fig. 3; diagram is based on the estimates of abundance of mycorrhizas with mantles of various subtypes). In the mountain-forest belt, mycorrhizas with plectenchymatic mantles dominate, while mycorrhizas with complex pseudoparenchymatic are predominant in alpine habitats. The ratio of mantles of the three basic types differs significantly in the two belts (when combining the data on all plots within a belt $\chi^2_{(2)} = 19.82$, $P < 0.001$).

The average cross size of ectomycorrhizal tip (radius) is slightly higher for the trees that grow in the subgolets belt (Table 3). The size of the whole tip grows as a result of an insignificant increase in the average thickness of the fungal mantle in the given conditions, while the thickness of the layer of cells of root parenchyma, average number of parenchyma layers, and the average size of its cells do not depend on altitude.

Change in the linear dimensions of the structural parts of the tips naturally leads to the change of the ratio of their areas in cross section. In the subgolets belt, as

Table 2. Parameters of diversity of ectomycorrhizal mantles

Parameter		Altitudinal belt and sample plot					
		Mountain-forest			Subgolets		
		mf4	mf3	mf2	sg3	sg2	sg1
<i>Abundance of mycorrhizas with the a certain subtype of mantle, %:</i>							
plectenchymatic	B	39	45	49	30	30	33
transitional	BF	—	—	1	2	1	—
	F	23	14	9	18	20	16
pseudoparenchymatic	G	4	9	7	15	19	19
	I	—	—	—	—	—	2
	K	—	1	—	—	—	2
	L	—	3	—	—	2	—
double	N	1	3	—	—	1	2
	O	2	1	2	2	2	1
	P	—	1	—	—	1	4
	Q	2	1	—	2	—	—
unstructured	SR	27	21	32	31	24	20
HN*		2	1	—	—	—	1
<i>Percentage of mantles, %:</i>							
plectenchymatic		39	45	49	30	30	33
pseudoparenchymatic		32	33	19	39	46	46
unstructured		27	21	32	31	24	20
Total of subtypes		8	11	6	7	9	10
Shannon index of diversity		1.46	1.61	1.23	1.55	1.64	1.76
Berger-Parker index		0.39	0.45	0.49	0.31	0.30	0.33

* Tips without external fungal mantle but with a well-developed Hartig net.

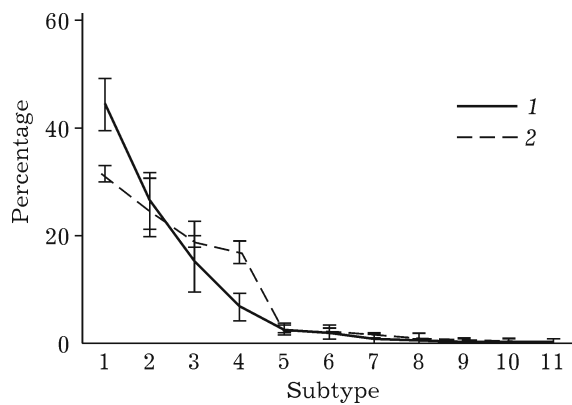


Fig. 2. Distribution of abundance of subtypes of fungal mantles in mountain-forest (1) and subgolets (2) belts. Averaged values for three plots within the zone are given; vertical bars stand for range of deviation.

compared with the mountain-forest belt, the contribution of fungal mantle and vascular cylinder to the formation of total area of section increases, and the relative contribution of the layer of bark parenchyma drops. If only the area of root section (vascular cylinder and layer of root parenchyma) rather than the area of the whole tip is taken as 100%, as in Tables 3 and 4, then the area under vascular cylinder in the mountain-forest belt will be $19.83 \pm 0.46\%$, and in the subgolets belt $22.16 \pm 0.50\%$ of the area of section ($F_{(1;658)} = 11.93$; $P < 0.001$). In general, the differences between the average size parameters of ectomycorrhizas from different altitudinal belts are small (no more than 9–13% of the values of the corresponding parameter in one of them).

The sizes of ectomycorrhizal tips and their structural parts (mantle, parenchyma, vascular cylinder) vary significantly depending on which kind of mantle was formed [8]. In our case, Table 3 illustrates how the type of mantle influences all parameters of the tip structure and Table 4 characterizes the structure of ectomycorrhizas with different mantles. The absolute sizes of the tip, root, and mantle are largest in the case of pseudoparenchymatic mantles, and the smallest, of unstructured ones. In the groups of tips with similar mantles only the radius of vascular cylinder depends on altitude (in the subgolets belt it is higher in the tips with plecten- and pseudoparenchymatic mantles).

The ectomycorrhizal tips from the subgolets belt show fewer tannin-filled (dead) cells as compared with the tips from the mountain-forest belt. This regularity is observed in the whole suite of tips as well as in groups of tips with plectenchymatic and unstructured mantles.

The conditions in the subgolets belt are a priori unfavorable for spruce growth, since they constrain the growth and development of the trees. The annual temperature is 2–3 °C lower, vegetation period is short, and the soils are immature and cold with unstable moistening [1].

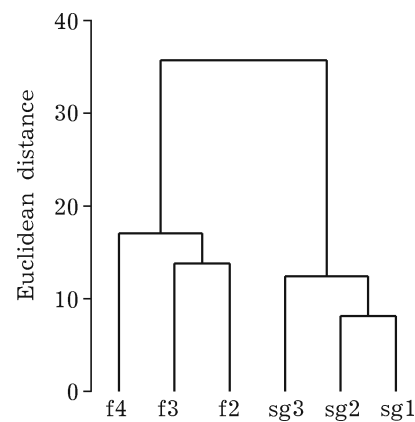


Fig. 3. Similarity of sets of fungal mantles on sample plots (sg1–sg3 — subgolets, f2–f4 — mountain-forest belt).

This change of living conditions is most evidently coupled with the change of diversity and structure of fungal mantles. Although it is often impossible to identify the species of the fungus that formed the mycorrhiza using morphological and anatomic features, it is the fungus species that determine the type of mantle and its structure [8, 9]. Thus, it can be stated with certainty that the altitudinal peculiarity of mantles is coupled with differences in the species composition of ectomycorrhizal fungi. In this connection, worthy of note are mycorrhizas with the G mantle, which are much more abundant in the subgolets belt (15–19% mycorrhizas), than in the mountain-forest belt (4–9%). G-mycorrhizas is the only subtype for which we can with certainty indicate at least the genus of the fungal symbiont – g. *Cenococcum* (species – *C. geophilum* or *C. graniforme*). G-mycorrhizas are supposed to be unproductive [10] for they contain a lot of dead tissues of both symbionts [11], and their increased abundance is frequently recorded in unfavorable ecological conditions [12, 13].

Biological diversity is usually decreased in the extreme environmental conditions [14, 15]. As a result, the diversity of ectomycorrhizas in the subgolets belt might be supposed to decrease, too. However, this is not the case. On the contrary, the diversity of mantles increases. It is explained mostly by the change of ratio of a few of widespread mantles rather than by the appearance or disappearance of some subtypes.

Change of the ratio of mantles of different types is the basic mechanism that governs the dynamics of the average size parameters of the ectomycorrhizal tips in the altitudinal gradient. This conclusion is evidently illustrated by Table 3, which shows that only some parameters of structure of the root that is part of an ectomycorrhiza such as radius of vascular cylinder, ratio of bark parenchyma and vascular cylinder, and ratio of the number of layers of live and dead cells of bark are determined both by the altitudinal belts and the features of the mantle structure. The differences in the values of

Table 3. Sizes and features of anatomical structure of ectomycorrhizal tips

Parameter	Average values		Relevance of differences in ANOVA											
	Mountain-forest	Subgolets	One-way; factor — altitudinal belt, $df = 1$; $df_{err} = 622$						Two-way ($f_{err} = 658$)					
			Altitudinal belt, $df = 1$			Type of mantle, $df = 2$			Altitudinal belt, $df = 1$			Type of mantle, $df = 2$		
			F	P		F	P		F	P		F	P	
<i>Lateral dimensions, μm</i>														
Tip radius	144	151	6.69	0.010	1.28	0.258	21.91	< 0.0001	2.17	0.115				
Mantle thickness	15	17	4.55	0.033	0.07	0.795	122.87	< 0.0001	4.20	0.015				
Thickness of root parenchyma	74	73	0.47	0.493	1.83	0.177	17.30	< 0.0001	1.48	0.229				
Radius of vascular cylinder	55	61	22.55	< 0.0001	15.94	0.0001	10.55	< 0.0001	0.81	0.447				
Diameter of live cell of root parenchyma	18	17	0.28	0.593	2.21	0.138	47.86	< 0.0001	2.91	0.055				
<i>Percentage of area in cross section, % of total area of cross section of tip</i>														
Mantle	18.36	20.16	5.65	0.018	0.34	0.560	114.99	< 0.0001	2.64	0.072				
Root bark	65.61	62.22	16.55	0.0001	7.98	0.005	43.28	< 0.0001	0.70	0.498				
Vascular cylinder	16.13	17.60	6.78	0.009	9.87	0.002	18.47	< 0.0001	0.86	0.424				
<i>Number of the cell layers</i>														
Dead cells	2.33	2.06	10.17	0.02	8.97	0.003	21.10	< 0.0001	8.63	0.0002				
Live cells	2.81	3.01	5.74	0.017	6.20	0.013	8.00	0.0004	2.78	0.063				
Total	5.14	5.06	0.94	0.334	0.39	0.534	3.63	0.027	1.78	0.170				

Note: Bold-typed are cases with significant influence of factors.

Table 4. Sizes and features of anatomical structure of ectomycorrhizal tips with mantles of different types

Parameter	Type of mantle and altitudinal belt					
	Plectenchymatic		Pseudoparenchymatic		Unstructured	
	mountain-forest	subgolets	mountain-forest	subgolets	mountain-forest	subgolets
<i>Lateral dimensions, μm</i>						
Mantle thickness	12	14	25	22	9	10
Thickness of root parenchyma	72	73	82	76	68	64
Radius of vascular cylinder	53	60***	60	65**	55	58
<i>Percentage of area in section, % of total area of cross section of tip</i>						
Mantle	16.24	17.78	26.76	25.04	13.25	14.60
Root bark	67.70	65.14*	59.36	58.37	68.54	65.25
Vascular cylinder	16.06	17.08	13.84	16.50***	18.63	20.15
<i>Number of cell layers</i>						
Dead cells	2.31	1.94**	1.77	2.00	2.90	2.28**
Live cells	2.83	3.08	3.09	3.04	2.44	2.87*
Total	5.15	5.00	4.86	5.03	5.33	5.15

Note: Significance of differences in parameters between altitudinal belts: * — $P < 0.05$; ** — $P < 0.01$; *** — $P < 0.001$.

absolute and relative thickness of mantles and radius of the tips between the altitudinal belts are completely explained by the increased percentage of tips with thick pseudoparenchymatic mantles on the upper hypsometrical levels, while the abundance of the less developed plectenchymatic mantles decreases. The following reasoning is pertinent here. Given the ratio of plecten- and pseudoparenchymatic and unstructured mantles in the subgolets belt to those of the mountain-forest belt is constant and only the average thickness of the mantles of various types changes (as indicated in Table 4), then the average thickness for the whole suite of mantles will make up 15 μm as in the mountain-forest belt. If, on the contrary, we suppose that the thickness of mantles of each type in both belts is constant and only their ratio changes, then the average thickness of the mantles in the subgolets belt would be 17 μm , as on high-altitude plots.

Thus, the changes in the structure in the sets of mantles can be considered one of the ways of adaptation of ectomycorrhizal symbionts to the conditions of high altitudes. Most likely, mycorrhizas with mantles of different types have different levels of physiological activity [11].

Some of the established features of structure of ectomycorrhizas can be due to the change of thermal regime of habitats. For example, the low temperatures of soil both below and above the optimum lead to a drop in intensity of mycorrhization of root systems [16–18]. In-

tensity of mycorrhization of seedlings of white spruce (*Picea glauca*) dropped from 92 in the valley to 80% in alpine habitats [4]. Low temperatures, even in the experimental conditions, lead to a change in the ratio of mycorrhizas of different morphological types [17, 18], in particular, to an increased percentage of G-mycorrhizas [18]. The low temperatures can result in the change of proportions between vascular cylinder and the bark parenchyma: in the experiments by Prokushkin [19] the absolute thickness of the layer of the bark parenchyma decreased on cold soils, when the total diameter of the leader roots of pine (mostly due to the decreased number of layers of cells, with the cell size relatively stable), while the vascular cylinder and tracheids grew in diameter.

The conclusions drawn from analysis of the obtained data disagree with the known facts of the increased share of underground organs in the biomass of trees in the extreme conditions of the upper border of forest [4, 20, 21] or in the low temperature conditions [22]. These changes evidence that the functional activity of the absorbent organs becomes weaker in the extreme conditions and are interpreted as adaptive rearrangements [21]. The altitude-dependent changes in the structure of ectomycorrhizas are insignificant. They do not indicate significant changes in activity of mycorrhiza formation or in the level of development of symbionts along the altitudinal gradient. To compare, the amplitude of changeability of the thickness of man-

tle, which is controlled by environmental conditions, can be significantly higher than in the studied altitudinal gradient by a factor of 1.4–1.7 [23].

To understand why the structure of ectomycorrhizas of spruce does not change significantly along the altitudinal gradient, we must take into account the following. First of all, over the whole gradient the samples were taken from the undercrown area, i.e., in more or less similar microbiotopic conditions. It is possible that edificating action of trees, which is most noticeable in the near-stem and undercrown parts, moderates abiotic and biotic conditions and promotes decrease in potential differences in structure of ectomycorrhizas from different altitudinal belts. Second, ectomycorrhizas from different altitudinal belts were collected at different stages of their seasonal dynamics. Taking into account that during the period of sampling the growth of roots and formation of ectomycorrhizas had not been yet finished, the hypothesis that roots and mycorrhizas at different altitudes were at different stages of their development seems to be sound. Unfortunately, nothing is known about the character of variability of ectomycorrhizas in horizontal mosaics of phytocenosis and in time. Thus, these considerations are hypothetical and require special study.

CONCLUSION

The main reaction of ectomycorrhizal associations of the Siberian spruce to the altitude above sea level in the studied gradient is the change of diversity of types of fungal mantles. Change of the abundance of mantles of various types leads to insignificant changes of the average sizes of ectomycorrhizas and of the ratio of symbionts in them. The parameters characterizing the state of vegetative symbiont change irrespective of the ratio of mantles of different types. With altitude the absolute and relative sizes of vascular cylinder grow, and the number of dead cells of the bark of the root parenchyma drops.

In general, the structure of ectomycorrhizas of the Siberian spruce does not undergo any significant changes (those that could be characterized as qualitative) against the considerable contrast of ecological conditions on the opposite ends of the altitudinal gradient and pronounced differences in vitality of trees. With possible changes in the life span and intensity of physiological processes in ectomycorrhizas not taken into account, the obtained results show no increase in the share of resources spent on the formation of ectomycorrhizal tips at the upper border of spruce distribution. They do not give grounds for a statement that the activity of ectomycorrhizas changes in the given condition, either.

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REFERENCES

1. P. L. Gorchakovskii and S. G. Shiyatov, *Phytoindication of Environmental Conditions and Natural Processes in High Altitudes* (Nauka, Moscow, 1985) [in Russian].
2. S. G. Shiyatov, in *The Plants of Urals and Their Anthropogenic Changes* (Sverdlovsk, 1985), pp. 32–58 [in Russian].
3. Ch. Korner, *Oecologia* **115** (4), 445 (1998).
4. B. Sveinbjörnsson, *Ambio* **29** (7), 388 (2000).
5. F.-K. Holtmeier, *Mountain Timberlines. Ecology, Patchiness and Dynamics* (Kluwer Academic Publishers, Dordrecht; Boston, 2003).
6. W. K. Smith, M. J. Germino, T. E. Hancock, and D. M. Johnson, *Tree Physiology* **23** (16), 1101 (2003).
7. I. A. Selivanov, *Mycosymbiotrophism as a Form of Consortive Relations in the Vegetation Cover of the USSR* (Nauka, Moscow, 1981) [in Russian].
8. D. V. Veselkin, *Mikologiya i Fitopatologiya* **37** (1), 22 (2003).
9. I. Ostonen, K. Löhmus, and R. Lash, *Plant and Soil* **208** (2), 283–292 (1999).
10. V. I. Shubin, *Mycorrhizal Fungi of the Northwest of the European Part of the USSR (Ecological Characteristics)* (Karelian Branch of the USSR AS, Petrozavodsk, 1988) [in Russian].
11. X. M. Qian, I. Kottke, and F. Oberwinkler, *Plant and Soil* **199** (1), 91 (1998).
12. C. D. Pigott, *New Phytol.* **92** (4), 501 (1982).
13. T. Holopainen, in *Ecol. and Appl. Aspects of Ecto- and Endomycorrhizal Assoc.* (Praha, 1989), Part 1, pp. 185–190.
14. R. Whittaker, *Communities and Ecosystems* (Macmillan, New York, 1970; Progress, Moscow, 1980).
15. E. Odum, *Fundamentals of Ecology*, 3rd ed. (W. B. Saunders Company, Philadelphia, 1971; Mir, Moscow, 1986).
16. C. Theodorou and G. D. Bowen, *Aust. J. Bot.* **19** (1), 13–20 (1971).
17. J. L. Parke, R. G. Lindermann, and J. M. Trappe, *Can. J. For. Res.* **13** (4), 657 (1983).
18. T. Domisch, L. Finner, T. Lehto, and F. Smolander, *Plant and Soil* **239** (2), 173 (2002).
19. S. G. Prokushkin, *Mineral Nutrition of Pine (on Cold Soils)* (Nauka, Siberian Branch, Novosibirsk, 1982) [in Russian].
20. V. A. Usol'tsev, O. A. Krapivina, S. V. Maksimov, and V. E. Vlasenko, *Forest of Urals and Their Management* **24**, 144 (2004).
21. C. Li, S. Liu, F. Berninger, *Trees*, **18** (3), 277 (2004).
22. A. C. Balisky and P. Burton, *New Forests* **14** (1), 63 (1997).
23. D. V. Veselkin, *Ekologiya* **36** (2), 90 (2004) [Russ. J. Ecol. **36** (2), 71 (2004)].