

# Anatomical Structure of Ectomycorrhiza in *Abies sibirica* Ledeb. and *Picea obovata* Ledeb. under Conditions of Forest Ecosystems Polluted with Emissions from Copper-Smelting Works

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**Abstract**—Changes in the anatomical characters of ectomycorrhiza in Siberian fir and Siberian spruce were studied in natural forests polluted with heavy metals (Cu, Zn, Cd, Pb, As, and Fe) and sulfur dioxide. As technogenic load increased, the total radius of mycorrhiza terminals and plant roots included in them increased in the organic horizon and decreased in the mineral part of the soil. The absolute thickness of fungal mycorrhiza caps and their relative contribution to the total volume of consuming organs increased under pollution. The observed responses were regarded as adaptive, aimed at compensating the adverse effects caused by technogenic pollution.

*Key words:* ectomycorrhiza, roots, heavy metals, *Abies sibirica*, *Picea obovata*, fungal mantle, anatomy.

The responses of ectomycorrhiza, physiologically most active part of the tree root system, to technogenic influences have been studied insufficiently, and this fact reflects general imbalance in the intensity of research on the ecology and composition of above- and underground parts of woody plants (Shvidenko *et al.*, 2000). Presently, there is enough information that gaseous pollutants cause changes in the structure of ectomycorrhizae, leading to the impairment of mycorrhiza formation as estimated from various parameters (Reich *et al.*, 1985; Stroo *et al.*, 1988; Adams and O'Neill, 1991; Shkaraba *et al.*, 1991; Ohtonen *et al.*, 1993; Veselkin, 2002b). The data on the response of ectomycorrhizae to pollution with metal ions are less abundant (Dixon, 1988; Yarmishko, 1990; Leyval *et al.*, 1997), and its mechanism is unclear.

A general response of the fungus–plant system to the influence of any type, including heavy metal pollution, is apparently determined by the severity of stress and the type of individual responses of each symbiont. The response of tree roots proper to the increased concentrations of heavy metal ions in the soil solution is negative, which is expressed in the inhibition of root growth, specific morphological features acquired by roots, and an increased proportion of dead roots in the total biomass (Chernen'kova, 1987; Kabata-Pendias and Pendias, 1989; Yarmishko, 1990; Helmisaari *et al.*, 1999). The ectomycorrhizal fungi possess a relatively high resistance to the toxic effect of metal ions (Willenborg *et al.*, 1990; Wilkinson and Dickinson, 1995), which is due to specific features of their metabolism and the ability to deposit metal ions in the inactive form

on the cell walls or in the vacuoles (Gorbulova and Terekhova, 1995; Leyval *et al.*, 1997). Paradoxically, the physiological and ecological consequences of ectomycorrhiza formation at the increased soil concentrations of heavy metals, indicating that ectomycorrhizae play the role of a barrier to metal ions (Dixon, 1988; Wilkinson and Dickinson, 1995; Leyval *et al.*, 1997), have been studied nearly better than the phenomenology of ectomycorrhiza responses to this type of toxic effect.

This paper deals with the results of research on the anatomical structure of ectomycorrhiza in two tree species dominating in the boreal zone of Eurasia, Siberian fir *Abies sibirica* Ledeb. and Siberian spruce *Picea obovata* Ledeb., under conditions of large-scale pollution of forest ecosystems by emissions from copper-smelting works.

## STUDY REGION AND METHODS

Studies were performed in the southern taiga subzone of the Middle Urals, in natural dark coniferous forests with different degrees of technogenic disturbance. Test plots were situated in the zone affected by emissions from the Middle Ural Copper-smelting Plant, which contained large amounts of solid (Cu, Zn, Cd, Pb, As, and Fe) and gaseous (SO<sub>2</sub>) pollutants. Three zones of technogenic load were delimited around the plant (Vorobeichik *et al.*, 1994): the impact zone (the test plots located 1 and 2 km away from the plant), the buffer zone (4.5 and 7 km), and the background zone (30 km). In the immediate vicinity of the plant, com-

**Table 1.** Characteristics of test plots (range of values)

Parameter	Zone		
	background	buffer	impact
Elevation a.s.l., m	360–380	370–420	360–380
Tree stand composition	6F4S + B; 9F1S + B	6F4S + A, L; 5F5S + B; 7F3S; 8S2F; 7S3F	9F1S + B; 6F4S + B, L; 5F5S; 8F2S
Standing crop*, m <sup>3</sup> /ha	170–314	160–340	28–216
Proportion of dead trees in standing crop*, %	2.5–11.1	3.2–23.7	11.0–37.7
Plant association*	Nemoral–wood sorrel	Nemoral–wood sorrel; wood sorrel–herbaceous	Grass–horsetail; moss–horsetail
Concentrations in A0**, µg/g			
Cu	60–249	94–3134	2437–7969
Cd	2.00–5.75	3.23–18.73	8.27–22.88
Pb	54–120	69–1065	776–1738
Index of litter pollution***	1.13–1.17	4.71–14.62	17.20–32.67

Note: Tree stand composition: (A) aspen, (B) birch, (F) fir, (L) linden, (S) spruce. \*Data of Vorobeichik *et al.*, 1994. \*\*Concentrations of movable forms of metals (extracted with 5% HNO<sub>3</sub>) were measured by E.Kh. Akhunova in an AAS-3 instrument (Carl Zeiss Jena) in the Laboratory of Ecological Toxicology, Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences. \*\*\*Index of litter pollution is the parameter showing an excess over the background pollution level with respect to a complex of pollutants (Cu, Cd, and Pb) in a given place. Substantiation for the choice of this index and the procedure of calculations are described in the paper by Vorobeichik *et al.* (1994).

pared to the background zone, concentrations of acid-soluble Cu forms in the litter were 65 times higher; Pb, 18 times higher; and Cd, 3–5 times higher (Table 1). Technogenic acidification of the soil was recorded (Vorobeichik, 1995). Initially, the test plots were under spruce–fir forests of the linden and wood-sorrel types on gray forest soil, but these forests have undergone a major transformation under the technogenic impact (Vorobeichik *et al.*, 1994).

The roots and ectomycorrhizae of spruce and fir undergrowth were sampled in 1995 without differentiation by soil horizons; sample size was 30 plants and 100 randomly taken root endings from each zone. The root samples of the first-layer fir trees were taken in 1997 from the forest litter, humus horizon (immediately under the litter), and eluvial horizon (from a depth of 15–20 cm) separately. Five root samples were taken from each of 18 test plots (4–10 plots per zone); sample size was 150–300 root endings from every soil horizon in each zone. Mycorrhizae of two-year-old fir seedlings were taken in 1998 from 15 sampling plots; sample size was 30–100 plants and 130–250 root endings in each zone. All samples were taken at the end of the growing period and fixed in 4% formalin.

Cross sections (10–20 µm) of approximately 2700 tips were examined and measured in glycerol, without staining. One section per ending was analyzed. The parameters determined in each section were as follows: the presence of a fungal mantle and its subtype; the total radius of tip ( $r_1$ ), measured from the middle of the central cylinder to the outer edge of the cap; the thick-

ness of fungal mantle ( $m$ ); the radius of plant root within the tip ( $r_2$ ), i.e., the difference of  $r_1$  and  $m$ . The proportion of the cap in the volume of tip ( $d$ ) was calculated from  $r_1$  and  $r_2$  by the formula

$$d = \frac{(r_1^2 - r_2^2)}{r_1^2} 100\%,$$

assuming that the tip represents a cylinder (root) with a sleeve (cap), both with the radius and thickness remaining the same throughout their length. In some cases, the sections were analyzed for the presence or absence of tannin cells—flattened cells with a dark interior—in the external layers of the root bark parenchyma, and the numbers of layers of tannin and “live” cells (retaining their initial isodiametric form) in the root bark was calculated. The endings were considered to be without turgor when all cells of the bark parenchyma had lost the isodiametric form.

## RESULTS

**General responses.** The dynamics of general dimensional parameters (determined for the aggregate of ectomycorrhizal endings) in the toxic gradient is presented in Table 2. An increase in the total radius of tips by 10–27%, compared to that in the background zone, was observed in junior age groups of both species in the impact zone. In the adult plants, this parameter increased under pollution in the litter (by 10%) but decreased in the mineral soil horizon.

**Table 2.** Dimensional parameters of tips in the pollution gradient (general responses)

Parameter	Object	Zone		
		background	buffer	impact
Total radius of ending, $\mu\text{m}$	Spruce, undergrowth	183 $\pm$ 7	211 $\pm$ 5**	209 $\pm$ 8**
	Fir, seedlings	236 $\pm$ 7	270 $\pm$ 5***	299 $\pm$ 5***
	Fir, undergrowth	266 $\pm$ 8	292 $\pm$ 7**	312 $\pm$ 9**
	Fir, A0	281 $\pm$ 6	286 $\pm$ 4	309 $\pm$ 7**
	Fir, A1	277 $\pm$ 6	284 $\pm$ 4	266 $\pm$ 5
	Fir, A1B	277 $\pm$ 6	285 $\pm$ 4	263 $\pm$ 3*
Root radius, $\mu\text{m}$	Spruce, undergrowth	166 $\pm$ 7	189 $\pm$ 5*	185 $\pm$ 7*
	Fir, seedlings	203 $\pm$ 6	236 $\pm$ 4***	250 $\pm$ 4***
	Fir, undergrowth	238 $\pm$ 7	261 $\pm$ 6*	286 $\pm$ 8***
	Fir, A0	252 $\pm$ 6	262 $\pm$ 4	275 $\pm$ 7*
	Fir, A1	250 $\pm$ 5	258 $\pm$ 3	235 $\pm$ 4**
	Fir, A1B	256 $\pm$ 6	258 $\pm$ 4	236 $\pm$ 3***
Cap thickness, $\mu\text{m}$	Spruce, undergrowth	19 $\pm$ 2	25 $\pm$ 3*	27 $\pm$ 3*
	Fir, seedlings	33 $\pm$ 3	36 $\pm$ 2	51 $\pm$ 2***
	Fir, undergrowth	30 $\pm$ 2	35 $\pm$ 2	29 $\pm$ 2
	Fir, A0	30 $\pm$ 1	32 $\pm$ 1	36 $\pm$ 2*
	Fir, A1	28 $\pm$ 2	31 $\pm$ 1	34 $\pm$ 1*
	Fir, A1B	24 $\pm$ 1	30 $\pm$ 1**	30 $\pm$ 1**
Part of cap volume, %	Spruce, undergrowth	18.8 $\pm$ 1.5	21.9 $\pm$ 1.1	23.6 $\pm$ 1.6
	Fir, seedlings	26.1 $\pm$ 1.1	23.9 $\pm$ 0.7	29.8 $\pm$ 0.8**
	Fir, undergrowth	20.7 $\pm$ 1.1	21.6 $\pm$ 0.9	16.9 $\pm$ 1.2*
	Fir, A0	20.1 $\pm$ 0.8	21.6 $\pm$ 0.7	22.4 $\pm$ 0.9
	Fir, A1	19.4 $\pm$ 0.9	20.3 $\pm$ 0.6	22.5 $\pm$ 0.7*
	Fir, A1B	16.9 $\pm$ 0.8	19.8 $\pm$ 0.5**	21.3 $\pm$ 0.4***

Note: Differences from background parameters are significant at \* $p < 0.05$ , \*\* $p < 0.01$ , and \*\*\* $p < 0.001$ .

The change in the absolute radius (in  $\mu\text{m}$ ) of ectomycorrhizal endings resulted primarily from a change in plant root size. Compared to the background values, the average root radius increased under pollution by 9–23%, in seedlings, undergrowth, and in the litter, but decreased by 6–8% in tips of adult plants from the humus (A1) and eluvial (A1B) soil horizons.

It should be noted that the samples of roots from seedlings and undergrowth and the samples of adult plant roots from the litter in the impact zone were taken at the sites where pollution was below the maximum level (with a pollution index of 17–20), because root development in the litter was completely suppressed under heavier pollution (Veselkin, 2002a). The samples from the mineral part of soil were taken in the entire range of pollution loads, including the last forest fragments remaining near the plant. The material from the A1 and A1B horizons in the impact zone was divided into two groups: the samples without roots in the litter (heavy pollution), and samples with roots in litter (weaker pollution or better growing conditions). The

radii of roots decreased significantly in the first group of samples—to 232  $\pm$  6  $\mu\text{m}$  (A1) and 235  $\pm$  3  $\mu\text{m}$  (A1B)—but were close to the background values in the second group (256  $\pm$  11 and 240  $\pm$  9  $\mu\text{m}$ , respectively).

The average thickness of fungal caps in all objects increased under maximum pollution by 6–18  $\mu\text{m}$  (20–55%), compared to the background values. The mycorrhizal caps of fir undergrowth were an exception, because their average thickness did not change in the pollution gradient.

The proportion of the cap in total volume of a tip is a parameter that makes it possible to compare the degrees of technogenic transformation of the root proper and of the fungal mantle. In some cases (in spruce undergrowth and in litter), this parameter remained unchanged in the gradient of environmental conditions, because the sizes of both root and cap changed to approximately the same degree. Under pollution, the contribution of the fungus to the total volume of tips increased in seedlings and in the roots

**Table 3.** Qualitative parameters of tips in the pollution gradient (general responses)

Parameter	Object	Zone		
		background	buffer	impact
Frequency of endings with tannin cells, %	Fir, seedlings	36.25	33.51	59.47***
	Fir, A0	63.63	78.60**	90.12***
	Fir, A1	60.95	75.10*	75.84*
	Fir, A1B	59.13	76.28**	77.09**
Frequency of endings with turgor of root bark cells, %	Fir, seedlings	88.75	79.67	79.08
	Fir, A0	71.42	76.61	90.24**
	Fir, A1	82.24	74.69	74.38
	Fir, A1B	83.87	79.21	84.44

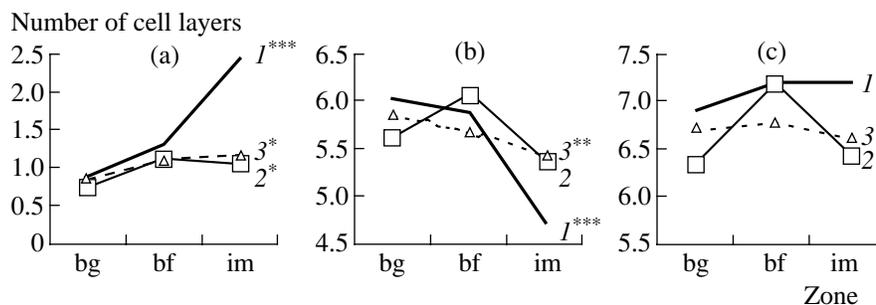
Note: Differences from background parameters are significant at \* $p < 0.05$ , \*\* $p < 0.01$ , and \*\*\* $p < 0.001$ .

found in the A1 and A1B horizons and decreased in fir undergrowth.

If a certain character proved to change already in the buffer zone, its values there were intermediate between those recorded in the impact and background zones, and the effect of emissions in the buffer zone was statistically nonsignificant. In general, the technogenic dynamics of the dimensional parameters of tips in dark coniferous species indicated that the volume of physiologically active absorbing organs increased under the effect of pollution by emissions from the copper-smelting plant. This response was usually accounted for by both partners of ectomycorrhizal associations, and only rarely, by one of the two symbionts.

Physiological mechanisms of technogenically induced changes in root size in the tips can be different. For example, tannin cells are usually compressed radially, and a large proportion of these cells in the root may result in the decrease of its diameter. However, this mechanism, being probable in the case of tips from the A1 and A1B horizons (Table 3, figure), is not universal, because the radii of roots in fir seedlings and in litter

increased in the impact zone, although the frequency and abundance of tannin cells in them were markedly greater. Another possible mechanism of increase or decrease in root size is change in the number of living cell layers or in the total number of living cells in the root parenchyma. This possibility is confirmed by the results of multiple regression analysis, which indicate that, in all pollution zones, the number of living cell layers correlates with the root radius positively and more closely, compared to other parameters. However, the analysis of technogenic dynamics of the characters under consideration does not confirm this possibility. There is also some evidence for the assumption that the average root size depends on the degree of disturbance of turgescence in root bark cells. In the tips of adult trees sampled from the litter, the proportion of endings with turgor and the root radius were significantly greater in the impact zone than in the background zone. Marked differences in the sizes of roots from the humus horizon within the impact zone could be explained by the fact that turgor was lost in approximately 30% of tips in the samples from the sites where the roots were



Changes in the number of layers of (a) tannin and (b) "living" cells of root bark and (c) in the total number of these cells in the tips of adult fir trees along the pollution gradient: (1) litter, (2) humus horizon, (3) eluvial horizon; (bg) background, (bf) buffer, and (im) impact zones. Differences between parameters in the background and impact zones are significant at \* $p < 0.05$ , \*\* $p < 0.01$ , and \*\*\* $p < 0.001$ .

**Table 4.** Dimensional and qualitative parameters of tips in the pollution gradient (differential responses)

Object	Type of cap structure and zone								
	plectenchymatous			pseudoparenchymatous			structureless		
	bg	bf	im	bg	bf	im	bg	bf	im
Root radius, $\mu\text{m}$									
Spruce, undergrowth	167	192	186	174	189	178	149	183	168
Fir, seedlings	194	221*	245***	213	238**	251**	158	255**	257**
Fir, undergrowth	245	272**	297***	238	268	327**	212	207	234
Fir, A0	259	258	267	253	250	264	239	237	276
Fir, A1	257	248	226**	241	262**	234	245	233	239
Fir, A1B	248	257	233	250	250	232	239	257	235
Cap thickness, $\mu\text{m}$									
Spruce, undergrowth	15	22**	27**	33	40	30	11	10	13
Fir, seedlings	27	27	45***	37	37	48*	37	45	62
Fir, undergrowth	25	33	30	42	42	38	14	16	19
Fir, A0	27	28	34	32	33	40*	23	35	36
Fir, A1	23	23	36***	33	34	37	26	34	28
Fir, A1B	20	25	28*	27	32	31	20	25	27
Frequency of endings with tannin cells, %									
Fir, seedlings	53.1	23.8***	59.2	18.2	29.7	23.5	100.0	85.7	85.4
Fir, A0	73.0	84.2	88.4	49.2	60.8	88.2	100.0	100.0	100.0
Fir, A1	65.6	83.6	71.9	53.2	62.6	75.7	72.2	100.0*	78.7
Fir, A1B	67.9	87.7	77.2	51.9	71.9**	76.0**	79.0	89.8	88.1

Note: Differences from background parameters are significant at \* $p < 0.05$ , \*\* $p < 0.01$ , and \*\*\* $p < 0.001$ ; (bg) background, (bf) buffer, and (im) impact zones.

absent from the litter, but the proportion of such endings at the sites with more favorable conditions did not exceed 2%.

The abundance of tannin (dead) cell and the proportion of endings without turgor are the parameters characterizing root viability. The dynamics of the first parameter provide evidence for the assumption concerning tree root damage under increasing technogenic load, but the dynamics of the second parameter suggest the absence or insufficient expression of this process.

**Differential responses.** The ectomycorrhizal caps differ in their basic anatomical structure into the pseudoparenchymatous, plectenchymatous, double, and structureless types, and tips with the caps of different types consistently differ from each other, with the main differences concerning cap thickness and the frequency of tannin cells (Veselkin, 2001b). Under increasing technogenic load, the abundance of pseudoparenchymatous caps decreases, whereas the abundance of structureless caps increases in all objects studied in this respect (Veselkin, 1999).

Table 4 shows technogenic transformations of some anatomical characters in the groups of mycorrhizae with caps of different structural types, and Table 5

shows the results of two-way ANOVA performed to estimate the proportions of the total variance of some characters accounted for by the effects of two factors: the type of cap structure (plectenchymatous, pseudoparenchymatous, and structureless) and site of sampling (the impact, buffering, and background zones).

Root radius depended on the pollution level (zone) more strongly than on the structure of the cap formed on its surface, so that the dynamics of this parameter in the gradient of environmental conditions appeared to be unrelated to changes in the proportions of structurally different caps. The characters "frequency of endings with tannin cells" and "frequency of endings with turgor of root bark cells" had a different mechanism of transformation in this model, depending mainly on the type of cap structure rather than on the degree of habitat disturbance. The dynamics of both these characters in the pollution gradient were largely determined by the increasing abundance of structureless caps and the decreasing abundance of plectenchymatous caps (tannin cells and the loss of turgor occurred very often in the former but were relatively rare in the latter).

As estimated for the aggregate of root endings, the mechanism of changes in the characters "cap thick-

**Table 5.** Average proportion (%) of variance in the parameters of ectomycorrhizal ending structure accounted for by influences of the type of cap structure and the zone of technogenic load (figures in parentheses show the range of values)

Parameter	Factor		
	Type of cap structure	Zone of load	Interaction of factors
Root radius	1.27 (0.02–5.05)	4.45 (1.44–10.07)	1.15 (0.29–2.22)
Cap thickness	8.14 (2.59–18.39)	3.02 (0.33–7.99)	1.76 (0.09–3.92)
Part of cap volume	8.39 (3.92–15.66)	2.93 (0.49–5.58)	2.09 (0.05–5.18)
Frequency of endings with tannin cells	6.67 (2.38–11.75)	0.96 (0.19–1.62)	1.85 (0.51–3.45)
Frequency of endings with turgor of root bark cells	5.36 (0.34–8.49)	0.71 (0.20–1.29)	0.57 (0.33–0.92)

ness” and “the part of cap volume” in response to pollution was intermediate. In the two-way model, these characters proved to depend both on the type of cap structure (strongly) and the zone (level) of pollution (relatively weakly). It should be noted that the increase in thickness was characteristic mainly of poorly structured plectenchymatous caps and, to a lesser extent, of pseudoparenchymatous caps. The structureless caps manifested only a tendency toward thickening, which could be explained by their low abundance in many samples and, hence, low reliability in estimating average values.

## DISCUSSION

Thickening is a well-known symptom of the toxic effect of copper ions on plant roots (Kabata-Pendias and Pendias, 1989). In our case, this phenomenon was observed in two species of dark conifers in the natural ecosystems polluted with heavy metal particles. It should be noted that the increase in the cross section of tips does not mean a simultaneous increase in their absolute volume when the size of a hypothetical “average” ending is estimated. This is explained by the fact that the length of root endings of the last order of branching significantly decreases in the impact zone (Veselkin, 1999, 2001a). The data obtained in this study are difficult to interpret unambiguously, because the increase in root radius along the pollution gradient is observed only in the upper soil horizons, where most roots of seedlings and undergrowth concentrate, whereas root radius in the mineral soil horizon decreases. The causes of these differences are as yet unclear.

Root mortality increases under the effect of heavy metals (Yarmishko, 1990; Helmisaari *et al.*, 1999). Although root formation continues in polluted areas, most new thin roots quickly die off (Helmisaari *et al.*, 1999). Therefore, the life span of roots apparently decreases under conditions of heavy metal pollution. It should be noted that the rates of new root formation and dying off depend on many environmental factors, including season, conditions of the growing period as a whole, nutrient supply, soil moisture content, and soil toxicity (Orlov and Koshel'kov, 1971; Makkonen and

Helmisaari, 1998; Helmisaari *et al.*, 1999). Hence, each zone of technogenic load and every soil horizon are probably characterized by a specific life span of root endings and the period of their renewal, and this may account for the specific dynamics of many characters considered above.

The thickening of fungal caps under the effect of emissions from the copper-smelting plant is a response that has been determined reliably, because the decrease of thickness has been observed neither in any object studied nor within any group of tips with the caps of the same type. This phenomenon has not been described in available publications. On the contrary, there are data that the cap thickness decreases under the technogenic impact (Shkaraba *et al.*, 1991; Veselkin, 2002b). The cause of such an inconsistency is in the type of technogenic load. In the works cited above, the conclusion concerning the decrease in the cap thickness was drawn for the case of environmental pollution with gaseous substances. In our case, the maximum effect on ecosystems as a whole and on the underground plant organs had soil toxicity resulting from the accumulation of high concentrations of Cu, Cd, Pb, and Zn ions.

Gaseous pollutants (mainly SO<sub>2</sub>) in the zone affected by emissions from the Middle Ural Copper-Smelting Plant obviously have a damaging effect on both above- and underground organs of plants. In the second case, this effect can be both direct, through acidification of soil solution and the resulting increase in the toxicity of metal ions (Vorobeichik, 1995), and indirect, through the change in the amounts of photosynthetic products transferred to the underground organs (Ohtonen *et al.*, 1993). The latter mechanism can be used to explain the decrease of root size in tips observed under the heaviest pollution, assuming that the strongest effect on plants under these conditions is exerted by sulfur dioxide. However such an interpretation should be regarded with caution, because if this were the case, the resources available for the fungal partner would decrease as well, but this is not confirmed by our data. It is noteworthy that both the fungal mantle thickness and the radius of consuming roots proved to decrease in the tips of pine under pollution with gaseous emissions from a cryolite plant (Veselkin, 2002b).

It is important that, together with the signs of better development of the fungal and plant components of ectomycorrhizae under conditions of pollution, there are signs of their damage and impaired physiological activity, which clearly manifest themselves at the anatomical level. These are the loss of turgescence, the increasing frequency of dead cells in the roots, whose number negatively correlates with the physiological activity of mycorrhizae (Qian *et al.*, 1998), and the increasing frequency of structureless caps (Veselkin, 1999) associated with last stages of ectomycorrhiza development (Semenova, 1980). A similar spectrum of responses has been observed by morphological characters: at higher loads, the length of conductive roots and the numbers of sucking roots and mycorrhizae with obvious signs of damage increase (Veselkin, 1999, 2002b). Similar trends of root system transformation in the seedlings of coniferous species under pollution with heavy metals were described by Stavrova (1990) in a greenhouse experiment.

Taking into account that underground organs of trees develop more quickly under unfavorable edaphic conditions than under optimal conditions (Abrazhko, 1973; Bobkova, 1987; Prokushkin *et al.*, 2000), a feasible explanation to the observed trends may be as follows. Technogenic deterioration of conditions for the growth and functioning of tree roots and the direct adverse effect of increased soil toxicity on these organs evoke adaptive responses manifested as the increase in the numbers and size of sucking roots and ectomycorrhizae. At the anatomical level, both partners of the ectomycorrhizal association are involved in these responses, but the response of the fungal symbiont is often more pronounced under the maximum loads. This conclusion agrees with data on the high resistance of symbiotrophic macromycetes to the influence of heavy metals (Willenborg *et al.*, 1990; Wilkinson and Dickinson, 1995), on the one hand, and confirms the basic concept of ectomycorrhizal associations as the efficient instrument for improving the adaptive potential of tree plants, on the other hand. Moreover, the observed responses of the fungal component do not contradict the concept of ectomycorrhiza as a specific adaptation responsible for the formation of root barrier to the entry of heavy metal ions from the soil into the above-ground plant organs (Wilkinson and Dickinson, 1995; Leyval *et al.*, 1997).

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