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Specific Features of Root System Morphology and Mycorrhiza Formation in Scots Pine Seedlings from Burned-out Areas

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Abstract—Morphological parameters of the root system (the length of conducting roots and the number of absorbing roots) and the rate of its mycorrhization have been studied in one-year Scots pine seedlings from burned-out areas of cowberry–herb–green moss pine forest in the northern forest–steppe subzone of Western Siberia. The results show that the length of conducting roots in such seedlings increases, whereas the rate and density of mycorrhiza formation in absorbing roots decrease, compared to those in plants from unburned areas. The structure of underground organs in pine seedlings depends not only on fire intensity but also on the type of substrate in the burned-out area.

Key words: Scots pine, forest fires, pyroecology, self-sown seedlings, ectomycorrhiza, morphology.

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Recurrent fires in forests dominated by Scots pine (*Pinus sylvestris* L.) are a key factor accounting for the structure of regeneration and the dynamics of cenopopulations throughout the species range (Melekhov, 1948; Korchagin, 1954; Sannikov, 1973). To date, trends in pyrogenic transformation of environmental factors and the patterns of natural regeneration and postfire dynamics of pine forests in different types of macro- and microbiotopes have been studied comprehensively. However, an important aspect of Scots pine ecology related to the establishment of self-sown seedlings in burned-out areas, namely, relationships with mycorrhizal fungi, have not been studied sufficiently in quantitative terms.

As many other conifers, the Scots pine is a highly mycotrophic plant (Lobanov, 1971; Shubin, 1988; Read, 1998). In nature, root absorption of water and mineral nutrients from the soil is accomplished by Scots pine trees in symbiosis with mycorrhizal (mainly ectomycorrhizal) fungi. Aperiodic fires as a powerful factor transforming all environmental factors and components of forest ecosystems must have an effect on the development, structure, and functions of mycorrhizal symbioses. Today, however, only changes in the diversity of mycorrhizal fungi in burned-out areas are relatively well studied (Torres and Honrubia, 1997; Horton et al., 1998; Grogan et al., 2000; Tuininga and Dighton, 2004; Smith et al., 2004, 2005; Bastias et al., 2006). According to some authors, the rate of mycorrhiza formation in tree roots decreases after fires (de Roman and de Miguel, 2005), while others consider that it remains unchanged (Torres and Honrubia, 1997) or positively correlates with fire intensity (Herr et al., 1994). Little is known about pyrogenic morphological responses of tree roots, except for the fact that the mass of fine roots decreases after creeping fire (Hart et al., 1994; Smith et al., 2004, 2005; Tuininga and Dighton, 2004).

Our previous studies in a burned-out area of cowberry–bilberry–moss pine forest in the pre-forest–steppe zone of Western Siberia showed that the density of mycorrhizae on the roots of pine seedlings growing on a charred litter was only half that in seedlings from an unburned litter (Sannikov, 1965). Moreover, mycorrhizae in the roots located in the upper soil layer (sterilized by fire) were absent during the first two postfire months and then appeared only on the vertical tap roots at depths more than 2.5 cm from the soil surface, spreading to the shallow lateral roots only by autumn.

On the whole, available data on specific features of postfire structure, functions, and significance of mycorrhizal fungi and their relationships with plants in burned-out areas are obviously insufficient and contradictory. The purpose of this study was to analyze and compare specific features of root system morphology and mycorrhiza formation in Scots pine seedlings emerged in the course of natural regeneration of cen-

Table 1. Parameters of plots

Parameter	Group of plots				
	unburned		burned-out		
			creeping fire, burned open stand*	free fire	
				burned dead stand	burned clearcut
	I	II–IV	V, VI	VII–IX	X, XI
Proportion of burned trees, %	0	0	40–50	100	100**
Stocking density	0.6–0.7	0.6–0.7	0.3–0.4	0	0
Soil damage***	Undamaged	Damaged	Undamaged	Undamaged	Damaged
Coverage, %:					
herb–dwarf shrub layer	0–5	0	20–30	30–50	0–10
moss–lichen layer	60–90	0	0	0	0
Illumination level relative to that in open, %*	30	30	50	90	100
Litter depth, cm	3.6	0	1.8–1.9	1.0–1.6	0
pH_{water}	4.98	4.98	5.57	5.72	6.27
Content, mg/100g soil:					
movable P_2O_5	0.33	0.11	0.65	0.66	0.92
movable K_2O	3.16	0.58	3.74	2.01	3.45
easily hydrolysable N	2.24	0.28	1.26	0.98	0.63
Soil mineral richness	5.48	1.00	5.62	4.32	5.52

Notes: * Types of burned-out areas and illumination levels are given according to Sannikov et al., 2004.

** Burned trees were cut in summer–autumn 2004.

*** Damage to soil involved mechanical removal of its surface horizons together with forest litter and herb–dwarf shrub and moss–lichen layers.

opopulation in areas of bilberry–herb–green moss pine forest affected by fire of different intensities.

OBJECTS AND METHODS

The material was collected in the Iletsko-Ikovskii insular pine forest (Prosvetskii Forest Enterprise, Kurgan oblast, the Tobol region of Western Siberia; 55°36'N, 65°04'E), in the northern forest–steppe subzone. More than 30000 ha of this forest was burned out during the disastrous fire in May 2004. Self-sown pine seedlings aged 11–12 months were collected in 95-year-old bilberry-herb-green moss pine forest on June 3–7, 2005, one year after the fire. This forest type prevails in the study region, occupying gentle slopes and floodplain terraces with deep dryish (periodically moistened), cohesive sandy sod-podzolic soils. In each of 11 plots (Table 1), 30–40 seedlings were collected from the forest litter or exposed mineral soil layers (mineralized substrates) and fixed in 4% formalin solution (total sample size 390 seedlings). Soil samples from the plots were averaged by groups (see Table 1) and analyzed by conventional methods (Arinushkina, 1970) to determine pH_{water}, movable P_2O_5 and K_2O, and easily hydrolysable nitrogen. To compare provision of plants with main mineral nutrients in different plots, we used an integrated index characterizing their contents in the soil (mineral richness), which was calculated as the excess of the total amount of movable P_2O_5 and K_2O and easily hydrolysable nitrogen in plots of a certain group over their minimum amount recorded in the study area.

In the laboratory, each seedling was examined to determine total weight (after drying at 105°C for 24 h) and morphological parameters of underground organs: (1) main root length, mm; (2) the number and (3) length (mm) of lateral conducting roots; (4) the length of all conducting roots, mm; (5) the total number of absorbing roots (both nonmycorrhizal roots and mycorrhizae); (6) the number of mycorrhizae; and (7) the number of mycorrhizal endings. These data were used to calculate the following parameters: (8) the rate of root system mycorrhization, or the percent ratio of the number of mycorrhizae to the number of absorbing roots; the density of (9) absorbing roots, (10) mycorrhizae, and (11) mycorrhizal endings, or the number of corresponding structures per 100 mm of conducting root length (Selivanov, 1981); and (12) the percentage of mycorrhizal endings included in complex mycorrhizae (%).

The term "nonmycorrhizal absorbing root" refers here to a short root uninfected by ectomycorrhizal fungi (i.e., not an extension root), and the term "mycorrhiza," to the organ derived from an absorbing root as a result of its colonization by an ectomycorrhizal fungus. Mycorrhizae were divided into simple (with only one ending) and branched (two or more endings). Nonmycorrhizal roots and mycorrhizae were identified under a binocular microscope (×10–20) by the presence or absence of surface hyphal structures and specific shape, color, and branching pattern.

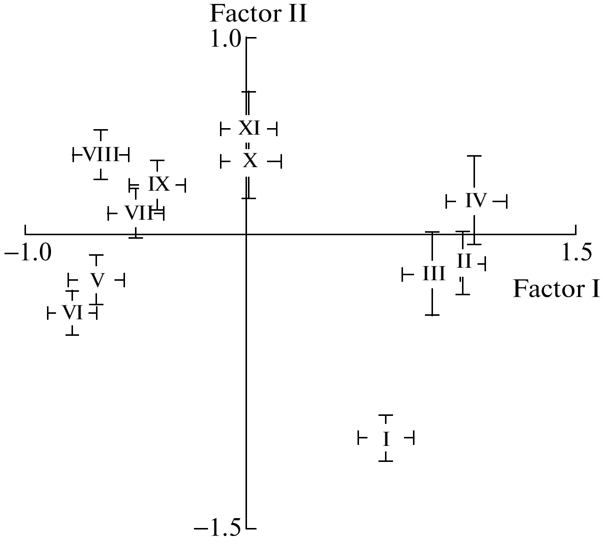
RESULTS AND DISCUSSION

Relatively high values of total weight are characteristic of seedlings from charred or unburned mineralized substrates: 50–66 mg, compared to 32–38 mg in seedlings from the unburned or slightly charred forest litter.

In plots affected by high-intensity fire (burned dead stand and burned clearcut), the number of conducting shoots per plant is 2.2–2.6 times greater, on average, than in seedlings from the unburned litter (Table 2). The number of absorbing roots is minimal in seedlings from the unburned or slightly charred litter and maximal in seedlings from unburned or burned mineralized substrates. The average proportion of absorbing roots transformed into mycorrhizae reaches 84–87% in unburned plots, being 1.5–2 smaller (43–64%) in burned-out plots. It is noteworthy that 5–8% of one-year seedlings in burned-out plots are mycorrhiza-free, but no such individuals have been recorded in control plots. A characteristic feature of the root system in seedlings from burned substrates is that their upper absorbing roots located close to the surface are mainly mycorrhiza-free. On average, the uppermost mycorrhizae in such plants occur at a depth of 18–26 mm, compared to 12–16 mm in seedlings from control plots.

The average absolute number of mycorrhizae and mycorrhizal endings proved to be minimal in seedlings from the charred litter and maximal in seedlings from unburned mineralized substrates. High densities of absorbing roots and of mycorrhizae and mycorrhizal endings on conducting roots are characteristic of seedlings from unburned plots, while these parameters in seedlings from the charred litter are two to five times lower. Thus, at least two independent parameters of growing conditions—the type of substrate and exposure to fire—have an effect on the parameters of root system morphology and mycorrhization in Scots pine seedlings.

The results obtained in a series of two-way ANOVA (Table 3) show that the development of the conducting root system is significantly dependent both on the occurrence/absence of fire and on the type of substrate in the plot: the number of conducting roots is consistently greater in seedlings growing (1) in burned-out plots and (2) on mineralized substrates. The absolute numbers of absorbing organs (roots, mycorrhizae, and mycorrhizal endings) differ depending only on the type of substrate: they are significantly greater in seedlings from mineralized substrates. The rate of mycorrhization depends only on the occurrence/absence of fire in the plot. An increased density of absorbing organs is characteristic of seedlings from unburned plots (compared to burned-out plots) and from mineralized substrates (compared to forest litter).



Positions of centroids for the samples of *Pinus sylvestris* seedling from (I–IV) unburned and (V–XI) burned-out plots in the plane of factors computed without regard to ecological characteristics of the plots (see Table 4, method 2). Vertical and horizontal bars indicate standard deviations.

Factor analysis was performed with regard not only to structural parameters of seedling underground organs but also to ecological characteristics of plots (Table 4, method 1). It can be seen that parameters of root system morphology and mycorrhization form two groups, with their variation within each group being highly concordant. An analysis of factor loadings showed that, in general, the degree of root system mycorrhization and the total number of absorbing organs in seedlings negatively correlate with postfire changes in abiotic conditions, the correlation with mineral nutrient supply (mineral richness) being the strongest. The decrease in substrate acidity in burned-out plots and postfire improvement of light conditions have a favorable effect on the development of conducting roots.

Factor analysis without regard to environmental conditions (Table 4, method 2) yielded similar values of factor loading for structural characters of underground organs. In the plane defined by the axes of two factors (figure), seedlings from burned-out plots (V–XI) segregated from seedlings from control plots (I–IV) mainly along the axis of the first factor, which may be defined as "development of absorbing organs." Within each of these two groups, seedlings from the litter surface

Table 2. Parameters of root system morphological structure and mycorrhization in *Pinus sylvestris* seedlings from different plots

Parameter*	Plots**										
	unburned				burned						
					burned open stand		burned dead stand			burned clearcut	
	litter	mineralized substrate			litter					mineralized substrate	
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Main root length, mm (Q)	63 ± 4^{a}	74 ± 4^{b}	71 ± 4^{ab}	76 ± 4^{b}	73 ± 3^{b}	75 ± 3^{b}	75 ± 4^{b}	77 ± 4^{b}	79 ± 3^{b}	80 ± 6^{b}	79 ± 4^{b}
Number of lateral conducting roots	3.4 ± 0.4^{a}	5.8 ± 0.5^{abcd}	5.4 ± 0.6^{abc}	6.8 ± 0.6^{bcd}	5.3 ± 0.5^{abc}	4.4 ± 0.5^{ab}	6.1 ± 0.4^{abcd}	7.0 ± 0.4^{bcd}	6.1 ± 0.4^{abcd}	7.9 ± 0.5^{cd}	8.6 ± 0.6^{d}
Length of lateral conducting roots, mm (Q)	34 ± 5^{a}	107 ± 14^{bc}	111 ± 18^{abc}	132 ± 17^{bc}	98 ± 12^{abc}	78 ± 11^{ab}	144 ± 13^{bc}	176 ± 14^{c}	146 ± 14^{bc}	149 ± 17^{bc}	169 ± 20^{bc}
Total length of conducting roots, mm (Q)	97 ± 7^{a}	181 ± 15^{abc}	183 ± 21^{abc}	208 ± 19^{bc}	171 ± 14^{abc}	153 ± 13^{ab}	219 ± 15^{bc}	253 ± 15^{c}	225 ± 14^{bc}	228 ± 19^{bc}	248 ± 22^{bc}
Number of absorbing roots (Ln)	40 ± 3^{abc}	84 ± 8^{de}	77 ± 8^{cde}	96 ± 11^{e}	38 ± 5^{ab}	34 ± 5^{a}	52 ± 6^{abcd}	60 ± 7^{abcde}	62 ± 6^{bcde}	82 ± 9^{cde}	90 ± 7^{e}
Number of mycorrhizae (Ln)	34 ± 3^{abc}	74 ± 7^{c}	68 ± 8^{bc}	86 ± 10^{c}	25 ± 5^{a}	19 ± 5^{a}	36 ± 5^{ab}	40 ± 6^{ab}	40 ± 5^{abc}	57 ± 8^{bc}	58 ± 7^{bc}
Number of mycorrhizal endings (Ln)	53 ± 6^{abcde}	111 ± 11^{de}	101 ± 14^{cde}	136 ± 19^{e}	37 ± 7^{ab}	25 ± 6^{a}	52 ± 7^{abcd}	52 ± 8^{abc}	62 ± 8^{abcde}	78 ± 13^{bcde}	80 ± 10^{cde}
Mycorrhization rate, % (Z)	84 ± 4^{b}	86 ± 1^{b}	84 ± 3^{b}	87 ± 1^{b}	53 ± 6^{a}	43 ± 5^{a}	63 ± 4^{a}	55 ± 4^{a}	59 ± 4^{a}	64 ± 4^{a}	61 ± 4^{a}
Density of absorbing roots, number per 100 mm root length (Q)	41 ± 2^{c}	47 ± 2^{c}	46 ± 2^{c}	47 ± 3^{c}	21 ± 1^{a}	20 ± 2^{a}	23 ± 2^{a}	23 ± 2^{a}	27 ± 2^{ab}	37 ± 2^{bc}	38 ± 2^{bc}
Density of mycorrhizae, number per 100 mm root length (Q)	35 ± 3^{cd}	41 ± 2^{d}	40 ± 3^{cd}	41 ± 2^{cd}	12 ± 2^{a}	10 ± 2^{a}	16 ± 2^{ab}	14 ± 2^{ab}	17 ± 2^{ab}	24 ± 2^{bc}	24 ± 2^{bcd}
Density of mycorrhizal endings, number per 100 mm root length (Q)	53 ± 5^{cd}	60 ± 3^{d}	56 ± 4^{cd}	64 ± 4^{d}	18 ± 3^{ab}	13 ± 3^{a}	23 ± 2^{ab}	19 ± 3^{ab}	26 ± 3^{ab}	33 ± 3^{bc}	34 ± 3^{bc}
Proportion of endings in complex mycorrhizae, % (Z)	50 ± 5^{a}	50 ± 4^{a}	41 ± 4^{a}	55 ± 3^{a}	39 ± 6^{a}	23 ± 5^{a}	44 ± 4^{a}	35 ± 5^{a}	41 ± 4^{a}	41 ± 4^{a}	41 ± 4^{a}

Notes: * Here and in Table 3, letters in parentheses indicate transformations of variables used in calculating significance of differences by Scheffe's test and in ANOVA: (Ln) logarithmic transformation, (Z) arcsine transformation, or (Q) square-root transformation.

** Data are presented as mean values with standard errors. Within the same row, values with similar superscript letters in the same indices do not differ by Scheffe's test at $P < 0.05$.

Table 3. Influence of fire exposure and substrate type on parameters of root system morphological structure and mycorrhization in *Pinus sylvestris* seedlings

Parameter	Parameter value				Significance of factor influence (*P*)*		
	Plots		Substrate				
	unburned	burned-out	litter	mineralized	Fire exposure	Substrate	Fire exposure × substrate
Main root length, mm (Q)	71	77	74	76	0.0005	0.0021	0.0230
Number of lateral conducting roots	5.3	6.5	5.4	6.9	0.0055	0.0035	0.9156
Length of lateral conducting roots, mm (Q)	96	137	112	134	0.0109	0.0312	0.1983
Total length of conducting roots, mm (Q)	167	214	186	210	0.0093	0.0258	0.1775
Number of absorbing roots (Ln)	74	60	47	86	0.7545	0.0033	0.9984
Number of mycorrhizae (Ln)	65	39	33	68	0.1053	0.0068	0.6934
Number of mycorrhizal endings (Ln)	100	55	47	101	0.0916	0.0120	0.7084
Mycorrhization rate, % (Z)	85	57	59	77	0.0000	0.6521	0.3689
Density of absorbing roots, number per 100 mm root length (Q)	45	27	26	43	0.0001	0.0004	0.0143
Density of mycorrhizae, number per 100 mm root length (Q)	39	17	18	34	0.0001	0.0036	0.0925
Density of mycorrhizal endings, number per 100 mm root length (Q)	58	24	25	49	0.0002	0.0143	0.1916
Proportion of endings in complex mycorrhizae, % (Z)	49	38	39	46	0.0924	0.9566	0.8005

* In two-way ANOVA, parameter value in a plot ($n = 11$) was taken as an accounting unit; one factor was "exposure to fire," or the occurrence/absence of fire in the plot ($df = 1$); the other factor was "substrate" (forest litter or a mineralized substrate) ($df = 1$).

(plots I and V–VIII) segregated from seedlings growing on mineralized substrates mainly along the axis of the second factor, "development of conducting roots."

Thus, specific morphological features of root systems revealed in these seedlings appear to result from two relatively independent processes: (1) growth of conducting roots and (2) initiation of absorbing roots. The active growth of conducting roots may be accompanied by initiation of absorbing roots with a high density (on unburned and burned mineralized substrates) as well as with a low density (charred litter). When conducting roots are relatively weakly developed, the density of absorbing roots on them is high (unburned litter). Therefore, when one morphogenetic process is hindered, the other proceeds more actively. In the range of ecological conditions considered in the study, none of the seedlings had poorly developed conducting roots with a low density of absorbing roots. Active mycorrhization positively correlates with the density of absorbing roots and negatively correlates with the growth of conducting roots; i.e., active initiation of absorbing roots, their transformation into mycorrhizae, and subsequent branching of mycorrhizae themselves are processes of the same category (type of morphogenesis), all of them providing for higher abundance of absorbing organs per unit length of conducting roots.

These data provide evidence for the existence alternative types of root system morphogenesis in Scots pine seedlings. The extreme types can be described as follows. The first provides for the development of a compact root system with a high density of absorbing roots, most of them being transformed into mycorrhizae. Such a structure of the absorbing machinery is apparently aimed at the most effective utilization of resources available in a limited soil volume and, therefore, reflects an intensive strategy in the formation of underground organs. In our case, this type of morphogenesis is characteristic of seedlings exposed to strong competition from adult trees growing in unburned plots (figure, plot I). The second type, which reflects an extensive strategy in the formation of underground organs, provides for the development of an extended root system with a relatively sparse arrangement of absorbing roots, many of them nonmycorrhizal. The extensive strategy is aimed at gaining access to resources contained in a large volume of the soil, with the efficiency of their utilization being relatively low. In our case, this is characteristic of seedlings from

Table 4. Factor loadings of parameters characterizing root system morphological structure and mycorrhization in *Pinus sylvestris* seedlings and of environmental parameters

Parameter	Method of analysis*			
	(1) on the basis of average parameter values in a plot, including environmental parameters		(2) on the basis of individual parameter values, without regard to environmental parameters	
	factor 1	factor 2	factor 1	factor 2
Parameters of root system morphology and mycorrhization				
Main root length	–0.11	0.91	–0.06	0.56
Number of lateral conducting roots	0.21	0.95	0.04	0.86
Length of lateral conducting roots	0.00	0.96	–0.01	0.94
Total length of conducting roots	0.00	0.96	–0.02	0.98
Number of absorbing roots (Ln)	0.82	0.55	0.56	0.78
Number of mycorrhizae	0.96	0.22	0.69	0.67
Number of mycorrhizal endings	0.97	0.19	0.68	0.63
Mycorrhization rate	0.86	–0.49	0.82	0.08
Density of absorbing roots	0.95	–0.11	0.91	–0.05
Density of mycorrhizae	0.96	–0.21	0.97	–0.02
Density of mycorrhizal endings	0.96	–0.22	0.94	0.03
Proportion of endings in complex mycorrhizae	0.71	–0.18	0.44	0.02
Environmental parameters				
Fire intensity**	–0.58	0.75		
Illumination level	–0.38	0.80		
Litter depth	–0.59	–0.64		
$\mathrm{pH}_{\mathrm{water}}$	–0.66	0.71		
Soil mineral richness	–0.81	0.08		
Proportion of explained variance	0.50	0.38	0.40	0.36

Notes: * In both cases, factors were identified by the principal component method, using varimax rotation; the first two factors adequately explain the variance of data.

** Fire intensity was estimated in grades: (0) unburned plots, (1) creeping fire, and (2) free fire.

open, burned-out plots, where growing conditions are close to optimal (figure, plot VIII).

The series of test plots arranged in order of increasing fire intensity (unburned—burned open stand—burned dead stand—burned clearcut) may be interpreted as a complex pyrogenic gradient of increasingly favorable growing conditions for self-sown Scots pine, which is a typical pyrophyte adapted to regeneration in totally burned-out areas (Sannikov, 1983). Optimization of growing conditions in such areas is accounted for by the improvement of illumination level, suppression of phytocenotic competition, and abundant provision with mineral nutrients (Sannikov, 1992). As for the development of underground organs, however, pyrogenic transformation of the above factors hay produce opposite effects: higher illumination activates the growth of roots and mycorrhizae (Tsel'niker, 1978; Noland et al., 1997; Bucking and Heyser, 2003; van Hees and Clerkx, 2003), whereas the improvement of mineral nutrition is usually accompanied by a decrease in the number of roots and the activity of mycorrhizal fungi (Shemakhanova, 1962; Lobanov, 1971; Rii, 1981; Nakvasina, 1983; Brunner and Brodbeck, 2001; Baar et al., 2002; Bucking and Heyser, 2003). In the context of aforementioned general concepts, it is difficult to explain why seedlings growing at a relatively low illumination level (unburned plots) are characterized by active formation of absorbing roots and mycorrhizae, whereas those growing at a high illumination level, under almost optimal edaphic conditions (burned-out plots), produce mainly conducting roots.

A probable explanation of this contradiction is that specific morphological features of root systems in mycotrophic plants are determined in part by their fungal symbionts. Thus, hormones produced by ectomycorrhizal fungi have an effect on initiation of absorbing roots, increasing their density (Shemakhanova, 1962; Wullschleger and Reid, 1990; Scagel and Linderman, 1998). The observed positive correlation between the plot average values of characters “mycorrhization rate” and “absorbing root density” ($r = 0.85$, $P = 0.0009$) is evidence for the hypothesis concerning a probable effect of fungal activity on root branching in seedlings. Hence, it may well be that the decreased density of initiation of absorbing roots in seedlings from burned out plots, compared to those from unburned plots, is explained by low activity of ectomycorrhizal fungi in areas affected by fire (this unequivocally follows from the reduced proportion of absorbing roots colonized by fungi).

Apparently, the activity of ectomycorrhizal fungi in burned-out areas decreases because heat and fire destroy their mycelium and propagules (Sannikov, 1965; Bruns et al., 2002). It should be noted that the assemblage of ectomycorrhizal fungi colonizing the soil sterilized by fire markedly differs from the initial assemblage. In particular, it includes a large proportion of Ascomycetes fungi (Torres and Honrubia, 1997; Horton et al., 1998; Grogan et al., 2000; Tuininga and Dighton, 2004; Smith et al., 2004, 2005; Bastias et al., 2006). Some properties of pioneering species pertain to the explerent strategy, and they appear to be less active in establishing symbiosis than ectomycorrhizal fungi characteristic of unburned forest soils.

CONCLUSIONS

The establishment and growth of Scots pine seedlings in habitats affected by fire are accompanied by consistent changes in the structure of root systems and the degree of their association with ectomycorrhizal fungi. Depending on combination of environmental factors, seedlings produce either mainly conducting roots (in burned-out areas) or absorbing roots (in unburned areas), with the initiation of absorbing roots being accompanied by their active transformation into ectomycorrhizae. These two trends may be regarded as two different strategies, extensive and intensive, in the formation of underground organs. Structural modifications of underground organs in such habitats are conditioned by pyrogenic changes in abiotic and biotic environmental factors, primarily the improvement of mineral nutrient supply and reduction of the activity of ectomycorrhizal fungi.

The occurrence of completely mycorrhiza-free individuals and a low degree of root system mycorrhization among seedlings growing in burned-out areas provide evidence that they are capable of autonomous consumption of nutrients from the soil. The observed specific features of root system morphology and mycorrhization in Scots pine confirm the hypothesis concerning two pathways of adaptation of its underground organs to alternative edaphic complexes characteristic of mineral or pyrogenic habitats (Sannikov, 1983, 1992).

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REFERENCES

Arinushkina, E.V., *Rukovodstvo po khimicheskomu analizu pochv* (Manual of Soil Chemical Analysis), Moscow: Mosk. Gos. Univ., 1970.

Baar, J., Bastiaans, T., van de Coevering, M.A., and Roelofs, J.G.M., Ectomycorrhizal Root Development in Wet Alder Carr Forests in Response to Desiccation and Eutrophication, *Mycorrhiza*, 2002, vol. 12, no. 3, pp. 147–151.

Bastias, B.A., Xu, Z.H., and Cairney, J.W.G., Influence of Long-Term Repeated Prescribed Burning on Mycelial Communities of Ectomycorrhizal Fungi, *New Phytol.*, 2006, vol. 172, no. 1, pp. 149–158.

Brunner, I. and Brodbeck, S., Response of Mycorrhizal Norway Spruce Seedlings to Various Nitrogen Loads and Sources, *Environ. Pollut.*, 2001, vol. 114, no. 2, pp. 223–233.

Bruns, T., Tan, J., Bidartondo, M., et al., Survival of *Suillus pungens* and *Amanita francheti* Ectomycorrhizal Genets Was Rare or Absent after a Stand-Replacing Wildfire, *New Phytol.*, 2002, vol. 155, no. 3, pp. 517–523.

Bucking, H. and Heyser, W., Uptake and Transfer of Nutrients in Ectomycorrhizal Associations: Interactions between Photosynthesis and Phosphate Nutrition, *Mycorrhiza*, 2003, vol. 13, no. 2, pp. 59–68.

de Roman, M. and de Miguel, A.M., Postfire, Seasonal, and Annual Dynamics of the Ectomycorrhizal Community in a *Quercus ilex* L. Forest over a 3-Year Period, *Mycorrhiza*, 2005, vol. 15, no. 6, pp. 471–482.

Grogan, P., Baar, J., and Bruns, T.D., Below-Ground Ectomycorrhizal Community Structure in a Recently Burned Bishop Pine Forest, *J. Ecol.*, 2000, vol. 88, no. 6, pp. 1051–1062.

Hart, S.C., Classen, A.E.T., and Wright, R.J., Long-Term Interval Burning Alters Fine Root and Mycorrhizal Dynamics in a Ponderosa Pine Forest, *J. Appl. Ecol.,* 1994, vol. 42, no. 4, pp. 752–761.

Herr, D.G., Duchesne, L.C., Tellier, R., et al., Effect of Prescribed Burning on the Ectomycorrhizal Infectivity of a Forest Soil, *Int. J. Wildland Fire*, 1994, vol. 4, no. 2, pp. 95–102.

Horton, T.R., Cazares, E., and Brubs, T.D., Colonization of Bishop Pine (*Pinus muricata*) Seedlings in the First 5 Months of Growth after Wildfire, *Mycorrhiza,* 1998, vol. 8, no. 1, pp. 11–18.

Korchagin, A.A., Forest Vegetation: Impact of Fires and Postfire Regeneration in Northern Europe, *Tr. Bot. Inst. Akad. Nauk SSSR: Geobot.,* Leningrad, 1954, vol. 9, pp. 75–149.

Lobanov, N.V., *Mikotrofnost’ drevesnykh rastenii* (Mycotrophicity of Woody Plants), Moscow: Lesnaya Promyshlennost’, 1971.

Melekhov, I.S., *Vliyanie pozharov na les* (Impact of Fires on Forest), Moscow: Goslestekhizdat, 1948.

Nakvasina, E.N., Effect of Additional Mineral Nutrition on the Quality of Spruce Planting Stock, in *Lesovodstvo, lesnye kul'tury i pochvovedenie* (Forest Management, Forest Cultures, and Soil Science), Leningrad: Leningr. Lesotekhn. Akad., 1983, pp. 90–93.

Noland, T.L., Mohammed, G.H., and Scott, M., The Dependence of Root Growth Potential on Light Level, Photosynthetic Rate, and Root Starch Content in Jack Pine Seedlings, *New Forests*, 1997, vol. 13, nos. 1–3, pp. 105–119.

Read, D.J., The Mycorrhizal Status of *Pinus, in Ecology and Biogeography of Pinus,* Richardson, D.M., Ed., Cambridge: Cambridge Univ. Press, 1998, pp. 324–340.

Rii, V.F., Fertilizers, Mycorrhization, and Plant Survival Rate, in *Mikoriza i drugie formy konsortivnykh otnoshenii v prirode* (Mycorrhiza and Other Forms of Consortive Relationships in Nature), Perm, 1981, pp. 18–22.

Sannikov, S.H., Ecological Assessment of Pine Regeneration in Green Moss Pine Forests along the Pyshma River, *Cand. Sci. (Biol.) Dissertation*, Sverdlovsk: Inst. Plant Anim. Ecol., Ural Branch, USSR Acad. Sci., 1965.

Sannikov, S.N., Forest Fires As an Evolutionary–Ecological Factor of Pine Population Regeneration in the Transural Region, in *Gorenie i pozhary v lesu* (Combustion and Fires in Forests), Krasnoyarsk: Inst. Lesa Dreves., Sib. Otd. Akad. Nauk SSSR, 1973, pp. 236–277.

Sannikov, S.N., Cyclic Erosion–Pyrogenic Theory of Scots Pine Natural Regeneration, *Ekologiya*, 1983, no. 1, pp. 10–20.

Sannikov, S.N., *Ekologiya i geografiya estestvennogo vozobnovleniya sosny obyknovennoi* (Ecology and Geography of Natural Regeneration of Scots Pine), Moscow: Nauka, 1992.

Sannikov, S.N., Sannikova, N.S., and Petrova, I.V., *Estestvennoe lesovozobnovlenie v Zapadnoi Sibiri (ekologo-geograficheskii ocherk)* (Natural Forest Regeneration in Western Siberia: An Ecogeographic Synopsis), Yekaterinburg: Ural. Otd. Ross. Akad. Nauk, 2004.

Scagel, C.F. and Linderman, R.G., Relationships between Differential in Vitro Indoleacetic Acid or Ethylene Production Capacity by Ectomycorrhizal Fungi and Conifer Seedling Responses in Symbiosis, *Symbiosis*, 1998, vol. 24, no. 1, pp. 13–34.

Selivanov, I.A., *Mikosimbiotrofizm kak forma konsortivnykh svyazei v rastitel'nom pokrove Sovetskogo Soyuza* (Mycosymbiotrophism As a Form of Consortive Relationships in the Plant cover of the Soviet Union), Moscow: Nauka, 1981.

Shemakhanova, N.M., *Mikotrofiya drevesnykh porod* (Mycotrophism in Tree Species), Moscow: Akad. Nauk SSSR, 1962.

Shubin, V.I., *Mikoriznye griby Severo-Zapada evropeiskoi chasti SSSR. Ekologicheskaya kharakteristika* (Mycorrhizal Fungi in the Northwestern European Part of the Soviet Union: Ecological Characteristics), Petrozavodsk: Karel. Fil. Akad. Nauk SSSR, 1988.

Smith, J.E., McKay, D., Niwa, C.G., et al., Short-Term Effects of Seasonal Prescribed Burning on the Ectomycorrhizal Fungal Community and Fine Root Biomass in Ponderosa Pine Stands in the Blue Mountains of Oregon, *Can. J. For. Res.*, 2004, vol. 34, no. 12, pp. 2477–2491.

Smith, J.E., McKay, D., Brenner, G., et al., Early Impacts of Forest Restoration Treatments on the Ectomycorrhizal Fungal Community and Fine Root Biomass in a Mixed Conifer Forest, *J. Appl. Ecol.,* 2005, vol. 42, no. 3, pp. 526–535.

Torres, P. and Honrubia, M., Changes and Effects of a Natural Fire on Ectomycorrhizal Inoculum Potential of Soil in a *Pinus halepensis* Forest, *For. Ecol. Manag.*, 1997, vol. 96, no. 3, pp. 189–196.

Tsel'niker, Yu.L., *Fiziologicheskie osnovy tenevynoslivosti drevesnykh rastenii* (Physiological Bases of Share Tolerance in Woody Plants), Moscow: Nauka, 1978.

Tuininga, A.R. and Dighton, J., Changes in Ectomycorrhizal Communities and Nutrient Availability Following Prescribed Burns in Two Upland Pine–Oak Forests in the New Jersey Pine Barrens, *Can. J. For. Res.*, 2004, vol. 34, no. 8, pp. 1755–1765.

van Hees, A.F.M. and Clerkx, A.P.P.M., Shading and Root–Shoot Relations in Saplings of Silver Birch, Pedunculate Oak, and Beech, *For. Ecol. Manag.*, 2003, vol. 176, nos. 1–3, pp. 439–448.

Wullschleger, S.D. and Reid, C.P.P., Implication of Ectomycorrhizal Fungi in the Cytokinin Relations of Loblolly Pine (*Pinus taeda* L.), *New Phytol.*, 1990, vol. 116, no. 4, pp. 681–688.