Postfire root distribution of Scots pine in relation to fire behaviour

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Abstract: Fire can potentially have a large direct impact on tree roots and, thus, contribute to reduced vitality. Tree canopy status after fire should have an impact on the postfire production of fine roots, further affecting root function. We analyzed the standing crop of live and dead roots in *Pinus sylvestris* L. with varying degrees of crown scorch, 1 year after fire in northern Sweden. On the burned sites, total *Pinus* live fine-root biomass was 74% of that at the control sites, and it was only 19% of the control for roots <2 mm, indicating an 80% reduction due to fire. Root mortality was highest for high-scorch trees, but this was probably due to greater depth of burn in the organic soil for these trees and not to higher fire intensity per se. Fine-root production was also assessed by an ingrowth experiment. This showed relatively similar fine-root production in both control trees and fire-damaged trees, indicating a high allocation to root growth for the damaged trees, to make up for lost root function. Root dynamics after fire are related to a number of factors, and direct effects are determined by the depth of burn in the organic soil layer. Indirect, long-lasting effects could be due mainly to girdling of coarse roots close to tree stems and canopy loss.

Résumé : Le feu peut avoir un impact direct important sur les racines des arbres et contribuer par conséquent à réduire leur vitalité. Après un feu, l'état de la canopée arborescente devrait avoir un impact sur la production de racines fines, affectant encore davantage la fonction des racines. Nous avons analysé la production existante de racines mortes et vivantes chez des tiges de *Pinus sylvestris* L. affectées par divers degrés de roussissement, un an après un feu dans le nord de la Suède. Dans les stations brûlées, la biomasse totale des racines fines vivantes de *Pinus* représentait 74 % de celle des stations témoins; dans le cas des racines <2 mm, c'était seulement 19 %, indiquant que le feu avait causé une réduction de 80 %. La mortalité des racines était la plus élevée chez les arbres avec le plus de roussissement mais cela était probablement dû à un brûlage plus en profondeur dans le sol organique pour ces arbres et non à une plus forte intensité du feu en soi. La production de racines fines a également été évaluée par une expérience de recrutement. Les résultats ont montré que la production de racines fines était relativement semblable tant chez les arbres témoins que chez les arbres endommagés par le feu, indiquant qu'il y avait une forte allocation vers la croissance des racines dans le cas des arbres endommagés pour compenser la perte de la fonction des racines. Après un feu, la dynamique des racines est reliée à plusieurs facteurs et les effets directs sont déterminés par la profondeur du brûlage dans l'horizon organique du sol. Les effets indirects de longue durée pourraient être dus principalement à l'annelage des grosses racines près du tronc des arbres et à la perte de canopée.

[Traduit par la Rédaction]

Introduction

Trees exposed to fire can suffer injury to the cambium or phloem, to the crown, and to the roots, and these three damage types depend partly on different components of fire behaviour (Ryan and Reinhardt 1988; Dickinson and Johnson 2001; Hély et al. 2003). Cambial damage depends on the bark thickness and duration of the heating (Martin 1963; Ryan and Frandsen 1991; Bova and Dickinson 2005). In contrast, the degree of crown scorch is more directly related to fire intensity and the height of the tree, because of the short exposure time needed to kill small-sized leaves (Van Wagner 1973; Dickinson and Johnson 2001). Finally, root mortality would relate to the amount of soil heating and the depth distribution of roots (Swezy and Agee 1991). For boreal soils with a well-developed organic humus layer, heat penetration is a function of the depth of burn, which is controlled mainly by the moisture content of the forest floor (Schimmel and Granström 1996; Dickinson and Johnson 2001; Miyanishi and Johnson 2002).

It is obvious that root damage from fire can impact on tree vitality directly by reducing postfire uptake of water and mineral nutrients (Dickinson and Johnson 2001), but there are still few studies quantifying fire damage to roots and the subsequent root dynamics. Swezy and Agee (1991) found that fine-root mass decreased by 75% within 5 months after burning of old-growth ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws). Loss was most pronounced in organic soil and in the upper 10 cm of mineral soil. They reported a high degree of smoldering in the organic soil layer because of high litter accumulation close to the stems, although most of the root loss appeared to have occurred between 1 and 5 months after the fire, i.e., was not due to direct heat kill (Swezy and Agee 1991).

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Table 1. Site information: tree characteristics.

Scorch class	n	DBH (cm)	Tree height (m)	Scorch height			Tree bark thickness (cm)
				Stem upper char height (cm)	Scorched crown (m)	Unscorched crown (m)	
Control	6	16.06±0.8	11.1±2.3	Absent	Absent	6.65±0.7	1.07±0.6
Low scorch	8	17.32±0.9	10.5±2.7	84.62±173.9	2.16±8.8	4.81±4.4	0.91±0.5
High scorch	8	16.14±0.9	9.7±1.8	74.5±149.6	3.32±1.1	2.61±1.3	1.1±0.7

Note: Values are means ± SDs. *n*, number of trees; DBH, diameter at breast height.

Fine roots are inherently dynamic, with substantial annual production (Vogt et al. 1996; Persson 1993; Makkonen and Helmisaari 1998). After fire, this would be expected to be even higher because of the need to recuperate lost root function. On the other hand, carbon supply for root growth could be limiting, particularly if there has been a high degree of canopy loss in the fire. Consequently, root growth could be directly related to the degree of fire-caused defoliation. Not much is known of postfire production of roots; however, Sayer and Haywood (2006) found little impact of fire on fine-root production in longleaf pine (*Pinus palustris* P. Mill.), but their stands had been repeatedly burned at 3 year intervals, and there was little foliage damage from the fire.

The impact of sublethal fire on tree roots would be expected to be twofold. First, immediate mortality should be related to depth of burn. Second, postfire growth of roots should be related to vitality of the tree, largely following the degree of crown scorch. To analyze these relationships, we quantified the spatial root distribution and fine-root production for Scots pine (*Pinus sylvestris* L.) with varying degrees of crown damage from fire.

Methods

Study area and sample trees

Our study area is located in northern Sweden within the Northern Boreal zone. On 17 July 2003, two fires, 8 km apart, were ignited by lightning (approximate position 64°00′N, 20°45′E). There was a long drought period prior to the fires (virtually no precipitation for 30 days prior to 17 July). Each fire eventually covered 115–120 ha before being suppressed. The tree layer within the burns is dominated by *P. sylvestris*, and the understory vegetation of the area is of mesic *Vaccinium* and dry lichen–shrub types. The climate has a continental character with a mean annual precipitation of 700 mm and a growing season that lasts 120–150 days starting in the beginning of June (Sveriges Lantbruksuniversitet (SLU) 2007). The bedrock consists of different granites and is covered by a sandy moraine. The soil is of iron-podzol type and is of relatively low fertility.

Within these burns and on adjacent unburned terrain, we located four pine stands of similar age (ca. 40 years) and density on flat, relatively stone-free ground. Two of the stands were burned, and two were unburned (control) stands; the unburned stands were located in the vicinity of the burned ones. The stands had regenerated naturally from seed trees after clear-felling. They had been subject to precommercial thinning but no management in the last 10 years.

Coarse-root structure and damage pattern

To have a general picture of the mechanisms of fire impact on coarse (diameter >10 mm) pine roots in relation to root architecture, the root system of two scorched pine trees were excavated in one of the stands in August 2004, i.e., 1 year after the fire.

The soil was carefully removed from all coarse roots within a circle, starting from the tree. During excavation we mapped, took photographs, and documented the status of each root along its length: its depth and position in the soil horizon, status of bark and cambium (colour and fungal and insect attack), and presence of stones adjacent to the root. This part of the study was completed to better understand the mechanisms of root mortality, although no quantitative analysis was done.

Fine-root biomass measurements

In July 2004, we selected, within each of the burned areas (B1 and B2), four pine trees that had been subject to a low degree of crown scorch (more than 50% of the canopy remaining) and four trees that had been subject to a high degree of crown scorch (30%–40% of the canopy remaining), for a total of 16 burned trees. On each of the unburned adjacent sites (C1 and C2), we selected three control trees. To minimize the quantity of roots from “nontarget” trees, we choose trees with a minimal distance of 3 m between the studied tree and any neighbouring trees.

The following characteristics were documented for the selected trees: height, diameter at breast height (DBH), scorch height (heat-killed foliage), height of char on two sides of the tree (uppermost and lowermost char height), and bark thickness at 1.3 m height (Table 1). The composition of the understory vegetation was documented by visual estimation around the selected trees. At each tree, soil monoliths for quantification of fine-root biomass were taken along two transects; one on the side of the highest charring of the tree stem and one on the opposite side. Along each transect, three monoliths were taken in the following positions: (*i*) close to the tree stem (10–20 cm from the stem), (*ii*) halfway between the tree stem and the edge of the canopy projection (50–70 cm from the stem, depending on size of the tree), and (*iii*) at the edge of canopy projection (80–130 cm from the stem). The soil monoliths had surface areas of 25 cm × 25 cm and were taken down to 20 cm in the mineral soil. Each monolith was separated into three horizons: organic soil layer, upper mineral soil layer (0–10 cm), and lower mineral soil layer (10–20 cm). Depth of the charcoal–ash layer and of the residual humus layer was measured at four points along the sides of each monolith. Thus, we sampled

Table 2. Site information: soil characteristics.

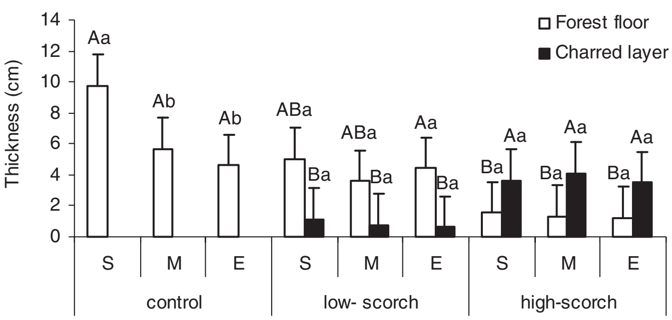
Scorch class	*n*	Mean forest floor thickness (cm)	Mean charcoal layer thickness (cm)	Gravel >16 mm (%)	Coarse sand 5.6–1.6 mm (%)	Fine sand 0.56–0.16 mm (%)
Control	6	6.67±2.7	Absent	5.35±2.1	30.03±14.6	64.39±14.2
Low scorch	8	4.33±0.71	4.34±0.71	4.59±4.1	19.34±19.2	75.64±20.7
High scorch	8	1.36±0.17	3.74±0.32	5.95±3.3	27.08±13.9	66.97±14.6

Note: Values are means ± SDs. *n*, number of trees.

Table 3. Results from the ANOVA completed on square-transformed forest floor thickness of control, low-scorch, and high-scorch trees and charred layer thickness performed on low- and high-scorch trees.

	Forest floor thickness			Charred layer thickness		
Source of variation	df	*F*	*p*	df	*F*	*p*
Overall model	17	3.08	<0.01	14	4.94	<0.01
Error	113			84		
Site (S)	1	2.38	0.13	1	0.15	0.70
Scorch class (C)	2	5.18	<0.01	1	45.42	<0.01
Distance (D)	2	0.73	0.48	2	1.61	0.21
S × C	2	5.16	<0.01	2	1.05	0.35
S × D	2	0.09	0.91	2	3.04	0.05
C × D	4	4.57	<0.01	3	0.41	0.66
S × C × D	4	1.98	0.10	3	0.08	0.93

Fig. 1. Mean floor and charcoal thickness (cm) along the gradient from the stem (S, near stem; M, middle; E, edge), which were compared using Tukey's multiple comparison tests among scorch classes and distances. Forest floor means were square-transformed prior to analysis; charcoal thickness means were not transformed. Bars with different uppercase letters are significantly different ($p < 0.05$) among the corresponding distances of different scorch classes, and bars with different lowercase letters are significantly different among distances within the same scorch class. Error bars are SDs.



22 trees in total and, around each tree, took six forest floor samples and 12 mineral soil samples (two mineral soil horizons).

Ingrowth experiment

Pine fine-root production was assessed by the ingrowth bag method (Messier and Puttonen 1993; Makkonen 2001). In one of the burned sites and in the adjacent control site, three trees of each scorch severity class, described in Fine-root biomass measurements above, were selected. Cylindrical nylon mesh bags (7 cm diameter and 20 cm long) were filled with 2 mm sieved sand. The mesh size of the bags was 2 mm. At the end of the vegetation season (August 2004), holes of approximately 8 cm diameter were made with a cylindrical corer along the transects at the three distances described above for the soil monoliths. One mesh bag was placed in each hole and covered to a depth of 1 cm with organic material taken from the adjacent soil surface. Thus, in total, we installed 54 mesh bags. Fourteen months later, in October 2005, we were able to recover only 32 of these. The rest were lost because of animal destruction of the markers indicating the bag location.

Laboratory methods

The monoliths were brought into the laboratory, where they were kept at 4 °C. They were then cut in several pieces to facilitate the extraction of roots. The soil was carefully removed from the roots of each monolith piece; afterwards, all roots were washed free of soil with cold water. Pine roots were further separated from the others. Root characteristics such as colour, smell, taste, and presence of resin were used for pine root identification (Vogt et al. 1996; Messier and Puttonen 1993; Finér et al. 1997; Makkonen 2001). Presence and status of ectomycorrhiza (liveor dead) was noted. Then, pine roots were sorted into live and dead roots according to the following diameter classes: <1 mm, 1–2 mm, 2–5 mm, 5–10 mm, and >10 mm (Vogt et al. 1996; Makkonen 2001). The extracted roots were then dried (24 h, 36 °C) and weighed. Texture of the mineral soil from the monoliths was assessed by sieving.

The ingrowth samples were sorted in the laboratory into species without separation into size-classes and with no separation between dead and live roots.

Statistical analysis

Data analyses were done using the SAS statistical package (SAS Institute Inc. 1988). We used a three-way analysis of variance (ANOVA) with the general linear model (GLM) procedure (Lindman 1974; Legendre and Legendre 1998) to test for effects of site, scorch class, and distance from stem on forest floor thickness and the influence of scorch class and distance from stem on charred layer thickness. A preliminary ANOVA with fixed factors (scorch class and scorch side) showed that there was no significant difference in forest floor and charred layer thickness between the low-char side and the high-char side of the trees ($p > 0.05$). Therefore, forest floor thickness values from both sides of the tree were pooled. Square transformation was applied to the forest floor thickness values to satisfy the residual normality assumption (univariate procedure; SAS Institute Inc. 1988), whereas charred layer thickness satisfied the assumption without transformation. The interaction effects among forest floor or charred layer thickness and site, scorch class, and distance were tested; the site variable has been treated as a random factor.

A three-way analysis of variance (ANOVA) was performed using the SAS GLM procedure to test for possible effects of site, scorch class, and distance from stem on root biomass. Different transformations were tested to satisfy the assumptions of normality and homogeneity of variances. Finally, summed and ranked biomass (rank procedure; SAS Institute Inc. 1988) of <1 and 2 mm live and dead roots (<2 mm); biomass of live and dead roots of <2 mm, 2–5 mm, 5–10 mm, and >10 mm diameter classes (2–10 mm); and ranked total live (sumLR) and dead root biomass (sumDR) respected the residual normality assumption. A preliminary ANOVA with fixed factors (scorch class and scorch side) confirmed that there was no significant difference in root biomass between the low-char side and the high-char side of the trees ($p > 0.05$). Therefore, ranked root biomass values from both sides of the stems were pooled.

A two-way analysis of variance (ANOVA) was performed using the SAS GLM procedure to test for possible effects of scorch class and distance from stem on pine root production in the ingrowth experiment. Note that the ingrowth experiment was conducted in only one of the burned sites and the control site adjacent to it; therefore, the site variable has not been included into the model. Because almost one-half of the ingrowth samples were missing, the ingrowth biomass from each tree was pooled according to the corresponding distances. Pine root production values satisfied the normality assumption without transformation.

Root biomass and root production analyses were applied for each soil horizon separately. Interaction effects among root biomass and root production and environmental variables were tested. The site variable was randomized for all ANOVAs. All factor effects and their interactions were tested using type III SS outputs.

Forest floor and charred layer thickness and live and dead root biomass were subjected to Tukey's multiple comparison tests to determine if differences among distances from the stem were significant. Because most of the interactions between root biomass, forest floor, and charred layer thickness of different scorch classes and corresponding distances were significant, Tukey's test was also conducted for each scorch class.

Results

Fire impact on the forest floor

The understory vegetation cover of the control sites was dominated by ericaceous species: *Calluna vulgaris* (L.) Hull (40%), *Empetrum nigrum* ssp. *hermaphroditum* (Lange ex Hagerup) Böcher (32%), and *Vaccinium* spp. (24%). In the burned sites, understory vegetation was almost completely lacking at the time of sampling. There was only sparse recruitment of *Deschampsia flexuosa* (L.) Trin. and *Luzula pilosa* (L.) Willd. and an occasional *Vaccinium* spp. Mean forest floor thickness below the canopies in the control sites was 6.7 cm (Table 2), and forest floor thickness was significantly higher near the stems than at the middle and edge of the canopy projection (Table 3; Fig. 1). In the burned sites, mean forest floor thickness differed between scorch classes. This difference was most pronounced near the stem. For low- and high-scorch trees, the mean thickness of the forest floor did not differ with distance from the stem. There was a statistically significant difference in mean thickness of the charred organic soil between low- and high-scorch trees (Table 3 and Fig. 1). There was no statistically significant difference in the thickness of the charred layer with distance from stem for either the low-scorch or for the high-scorch class.

Coarse-root architecture

The two trees we sampled for coarse-root architecture had DBHs of 10.5 and 14.5 cm, respectively. Most coarse roots were found within approximately a 50 cm radius from the stem, and roots had a diameter of 2–8 cm at their point of attachment to the root collar. There was a maximum of six major tap roots (diameter of each at the collar of approximately 10 cm), and one vertically oriented anchor root of approximately 50 cm depth. The bark thickness of coarse roots did not exceed 2 mm.

Most of the laterally oriented coarse roots were located in the mineral soil or at the interface of the humus and mineral soil. In many cases, the roots with the upper part of the cambium or phloem located in the humus layer had been heat damaged during the fire, whereas the lower side was unaffected and still intact. These initially heat-damaged zones were easily identified because of the charred bark and dark cambium colour.

There were also instances where a short section of the root showed evidence of complete heat girdling, whereas the posterior parts had escaped heat damage. Thus, these parts were cut off from phloem transport and were dying. At the time of sampling (1 year after fire), the inner bark of these cut-off roots had started to die and was easily peeled off but was still distinct from those sections that had been directly heat-killed.

There were several instances where roots growing over large stones in the mineral soil surface had been heat killed because of the lack of the protection of the mineral soil from the heat.

Quantity and spatial distribution of roots

Live roots

For control trees, live root mass of the 2–10 mm diameter class was significantly higher near the stem than at the middle and edge of the canopy projection (Table 4 and Figs. 2*a* and 2*b*), but this was mainly due to a decrease in the larger size fractions with distance from the stem. Further, there was a marked decrease in root mass with depth, particularly

Fig. 2. (*a*) Mean live biomasses (g·m^{-2}) of roots <2 mm (<1 mm + 1–2 mm) diameter, which were compared using Tukey's multiple comparison tests of rank means among scorch classes and distances. Bars with different uppercase letters are significantly different ($p < 0.05$) among the corresponding distances of different scorch classes, and bars with different lowercase letters are significantly different among distances within the same scorch class. Error bars are SDs. (*b*) Mean live biomasses (g·m^{-2}) of roots 2–10 mm (2–5 mm + 5–10 mm + >10 mm) dimaeter, which were compared using Tukey's multiple comparison tests of rank means among scorch classes and distances. Bars with different uppercase letters are significantly different ($p < 0.05$) among the corresponding distances of different scorch classes, and bars with different lowercase letters are significantly different among distances within the same scorch class. Error bars are SDs. Soil layers are as follows: H, humus layer; M1, upper mineral soil (0–10 cm); and M2, lower mineral soil (10–20 cm).

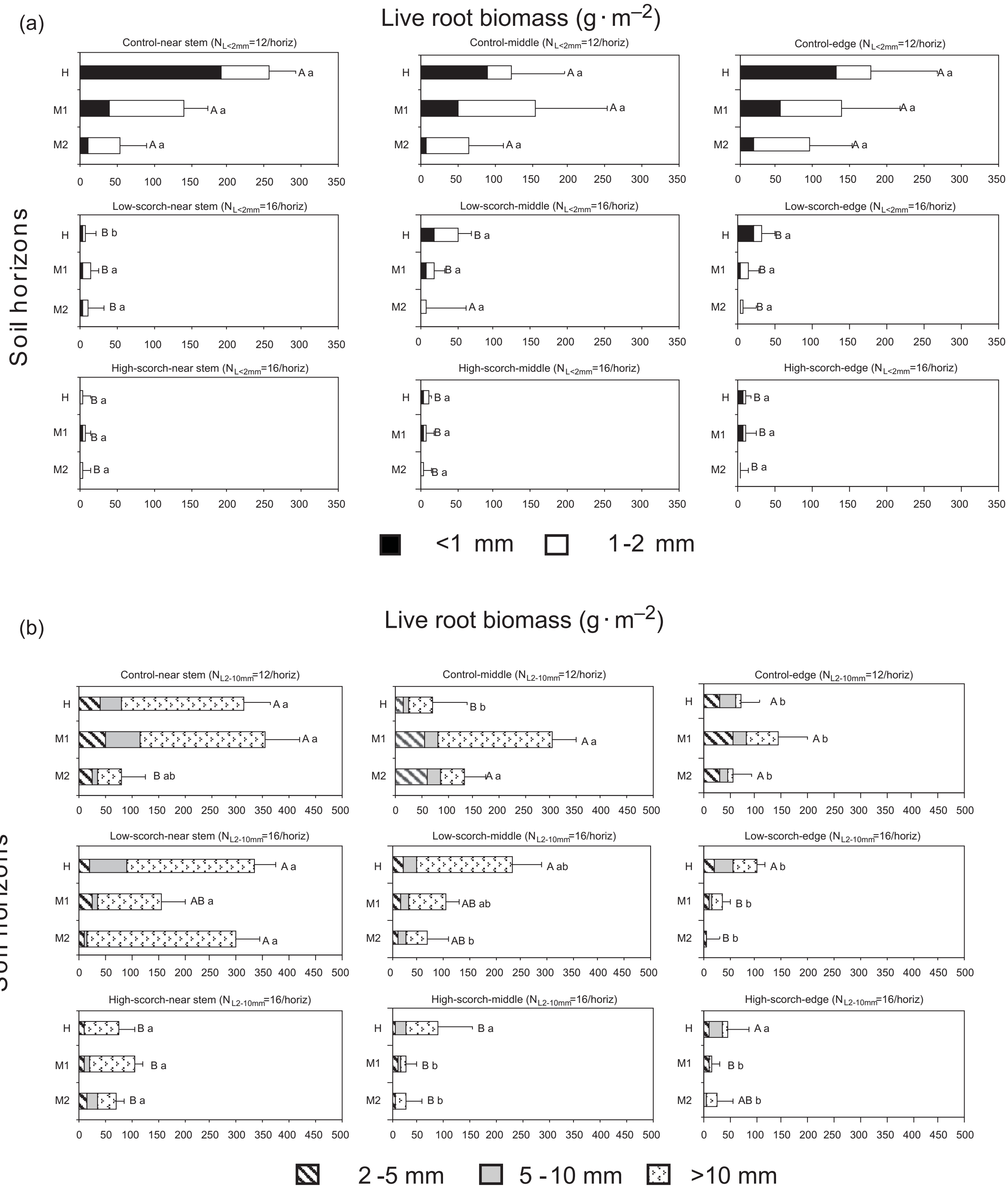


Table 4. Results from the ANOVA performed on ranked diameter classes of live-root biomass.

		Diameter <2 mm		Diameter 2–10 mm		Total live-root biomass	
Soil horizon and source of variation	df	*F*	*p*	*F*	*p*	*F*	*p*
Organic horizon							
Overall model	17	7.56	<0.01	1.51	0.03	3.5	<0.01
Error	114						
Site (S)	1	1.91	0.17	2.55	0.11	1.91	0.17
Scorch class (C)	2	52.69	<0.01	6.13	<0.01	21.84	<0.01
Distance (D)	2	0.25	0.78	2.62	0.04	3.12	0.04
S × C	2	2.73	0.06	2.24	0.08	3.02	0.05
S × D	2	0.25	0.78	0.38	0.69	0.30	0.74
C × D	4	9.87	0.03	1.55	0.07	1.82	0.07
S × C × D	4	0.47	0.75	0.72	0.58	0.12	0.98
Upper mineral horizon							
Overall model	17	6.84	<0.01	3.15	<0.01	5.18	<0.01
Error	114						
S	1	0.16	0.69	1.23	0.27	0.21	0.65
C	2	18.12	<0.01	12.79	<0.01	21.95	0.01
D	2	0.11	0.89	7.94	0.02	2.82	0.05
S × C	2	31.99	<0.01	7.74	0.01	11.18	<0.01
S × D	2	0.02	0.98	1.20	0.31	0.94	0.39
C × D	4	12.14	0.03	8.43	0.01	10.07	0.01
S × C × D	4	0.23	0.92	0.44	0.78	1.09	0.37
Lower mineral horizon							
Overall model	17	4.55	<0.01	4.74	<0.01	4.21	<0.01
Error	114						
S	1	8.56	<0.01	20.13	<0.01	18.54	<0.01
C	2	15.88	<0.01	7.38	<0.01	10.17	<0.01
D	2	0.16	0.85	2.13	0.05	1.66	0.09
S × C	2	14.13	<0.01	13.13	<0.01	8.60	<0.01
S × D	2	0.89	0.41	0.85	0.43	1.34	0.27
C × D	4	5.06	0.03	6.31	0.04	3.64	0.06
S × C × D	4	0.36	0.84	2.10	0.08	1.59	0.18

for finer root fractions: control trees had the most roots with diameter <1 mm in the organic soil layer, fewer roots in the upper mineral soil, and very few roots in the lower (10–20 cm) mineral soil. Abundant ectomycorrhiza was observed on the control tree fine roots in the humus layer.

For trees at the burned sites, mass of live fine roots <2 mm was very low in all soil horizons compared with control trees (Fig. 2*a*). For larger roots, the difference was not as dramatic. Thus, both high- and low-scorch trees had significantly lower fine-root mass than control trees for all soil horizons, and in many cases, fire also significantly decreased root mass of diameters >2 mm. Total live root mass of the high-scorch trees was only one-third of that of the control trees, whereas low-scorch and control trees did not differ (Figs. 2*a* and 2*b* and Table 4). Similar to control trees, scorched tree root mass was higher near the stems than farther away. Distance from low-scorched trees significantly influenced live fine-root (<2 mm) mass (Table 4 and Figs. 2*a* and 2*b*).

There was no significant difference either in root mass or in the depth of burn between the two different sides of the sampled tree (windward and leeward sides). Little ectomycorrhiza was found on the fine roots of low-scorch trees in the forest floor, and only some remnants of dead ectomycorrhiza were left on the roots of severely scorched trees.

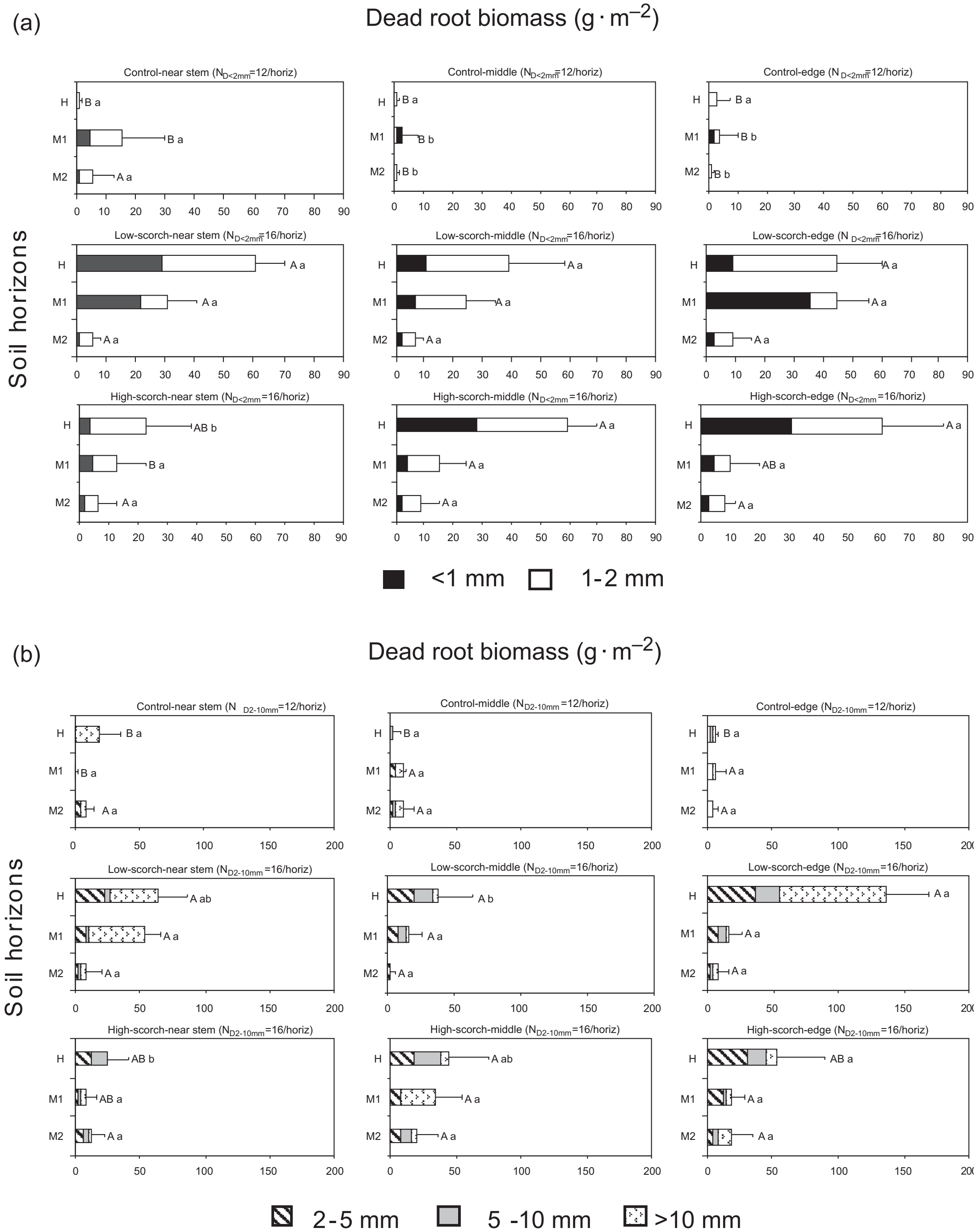
Dead roots

For the control trees, the quantity of dead roots was less than 5% of that of live roots. For low- and high-scorch trees, the quantities of total dead roots were 41% and 82% of that of total live roots, respectively; and for roots <2 mm, the proportion of dead roots was even higher: 160% and 317%, respectively (Figs. 3*a* and 3*b*). Dead root mass of high-scorched trees was approximately 20 times higher than that of the control. Dead-root biomass of all classes and of the total dead-root biomass differed significantly among scorch severity classes (Table 5). A substantial amount of dead roots were also found at a depth of 10–20 cm (horizon M2) in the mineral soil.

Root production

All ingrowth soil cores contained pine roots 14 months after deployment, and all ingrowth pine roots were <2 mm in diameter. Ingrowth root mass did not differ substantially between control and either of the scorch classes (Fig. 4), and there were no significant differences (Table 6). Root mass was similar overall for both upper and lower parts of the ingrowth soil cores (Fig. 4). Also, there was no statistically significant difference in ingrowth root mass with distance from the stem, either for the control or for the scorched trees.

Fig. 3. (*a*) Mean dead biomass (g·m^{-2}) of roots <2 mm (<1 mm + 1–2 mm) diameter, which were compared using Tukey's multiple comparison tests of rank means among scorch classes and distances. Bars with different uppercase letters are significantly different ($p < 0.05$) among the corresponding distances of different scorch classes, and bars with different lowercase letters are significantly different among distances within the same scorch class. Error bars are SDs. (*b*) Mean dead biomass (g·m^{-2}) of roots 2–10 mm (2–5 mm + 5–10 mm + >10 mm) diameter, which were compared using Tukey's multiple comparison tests of rank means among scorch classes and distances. Bars with different uppercase letters are significantly different ($p < 0.05$) among the corresponding distances of different scorch classes, and bars with different lowercase letters are significantly different among distances within the same scorch class. Error bars are SDs. Soil layers are as follows: H, humus layer; M1, upper mineral soil (0–10 cm); and M2, lower mineral soil (10–20 cm).



Discussion

Fire had a dramatic impact on *Pinus* tree roots at these study sites. One year after fire on the burned sites, mean mass of live roots <2 mm diameter in all soil horizons was <19% of that at control sites. The degree of fire-caused root death should relate to both root depth distribution and heat input into the soil but may result from different mechanisms, such as direct heat-kill and indirect killing due to cut-off from phloem transport of girdled roots. The latter could be

Table 5. Results from the ANOVA performed on ranked diameter classes of dead-root biomass.

		Diameter <2 mm		Diameter 2–10 mm		Total dead-root biomass	
Soil horizon and source of variation	df	*F*	*p*	*F*	*p*	*F*	*p*
Organic horizon							
Overall model	17	6.83	<0.01	3.05	0.01	5.02	<0.01
Error	114						
Site (S)	1	8.04	0.01	0.93	0.34	2.31	0.13
Scorch class (C)	2	50.02	<0.01	14.21	<0.01	35.74	<0.01
Distance (D)	2	1.24	0.29	0.13	0.88	0.66	0.52
S × C	2	1.40	0.25	4.68	0.01	2.08	0.13
S × D	2	0.31	0.73	0.53	0.59	0.49	0.61
C × D	4	8.13	<0.01	3.11	0.01	8.31	0.01
S × C × D	4	1.24	0.30	1.28	0.29	0.47	0.76
Upper mineral horizon							
Overall model	17	2.67	<0.01	1.97	0.02	1.26	0.07
Error	114						
S	1	0.21	0.65	4.94	0.03	2.89	0.05
C	2	14.96	<0.01	4.24	0.02	5.76	0.02
D	2	1.21	0.30	2.81	0.05	0.19	0.52
S × C	2	0.91	0.41	3.37	0.04	0.74	0.14
S × D	2	0.75	0.48	1.24	0.29	0.43	0.31
C × D	4	7.20	0.01	2.13	0.05	0.38	0.54
S × C × D	4	0.84	0.50	1.03	0.40	0.21	0.63
Lower mineral horizon							
Overall model	17	3.41	<0.01	1.16	0.13	2.22	0.01
Error	114						
S	1	0.57	0.45	4.54	0.04	4.65	0.03
C	2	19.08	<0.01	1.69	0.19	11.09	<0.01
D	2	0.04	0.96	0.18	0.84	0.46	0.64
S × C	2	0.31	0.74	0.32	0.73	0.82	0.44
S × D	2	0.93	0.40	2.11	0.13	0.65	0.52
C × D	4	2.17	0.05	1.12	0.08	0.64	0.64
S × C × D	4	1.32	0.27	1.08	0.37	0.33	0.86

the main cause of death here, at least for roots in deeper soil layers, where lethal temperatures during fire are unlikely (Schimmel and Granström 1996).

Fire intensity (sensu Byram 1959) is reflected in the scorch height on the trees (Van Wagner 1973) and, thus, has a direct effect on tree canopy status after fire and, ultimately, on the capacity of the tree to supply roots with carbon. However, fire intensity should not have a direct influence on depth of burn, because the deeper organic layers are too compact to burn in flaming combustion (Johnson 1992). Nevertheless, for our sample trees, there was a significant relationship between scorch type and depth of burn, which makes it difficult to separate the effects of these two fire-behaviour variables on postfire root dynamics.

Deep smoldering frequently occurs beneath tree canopies (Miyanishi and Johnson 2002), in particular close to tree stems (Miyanishi 2001). Our observations from the excavations of fire-damaged trees suggest that the upper layer coarse roots are subjected to direct fire girdling especially at the root collar, because there they are not covered by mineral soil. In addition, large roots that were forced by stones to grow near the surface were severely damaged. In contrast to stem bark, coarse root bark is thinner (Makkonen 2001), thus offering little heat protection to the coarse root cambium. Indirect effects resulting from cut-off of phloem transport in girdled roots appear to have resulted in massive loss, not least for roots in deep mineral soil layers and at the edge of the canopy projection, where depth of burn was low.

Fire affected the root diameter classes differently. Thus, the most severe losses were observed for the small diameter classes (<2 mm), for all soil horizons, which is in accordance with the study by Swezy and Agee (1991).

The ingrowth experiments were used as a measure of postfire root production. Because photosyntate is the main source of energy for conifer root metabolism (Iivonen et al. 2001; Helmisaari et al. 2007), it would be expected that root production should depend on fire damage to foliage. Surprisingly, our results from the ingrowth experiment did not show any significant difference in root production between damaged and undamaged trees. This suggests a high priority for regenerating root function after fire, probably at the expense of stem growth (Sayer and Haywood 2006).

Scots pine is a moderately fire-resistant species widely distributed throughout northern Eurasia. In northern Sweden, fire-history studies have documented life spans of several hundred years, with repeated scarring in low-intensity fires (Engelmark et al. 1994; Niklasson and Granström 2000). This species should be expected to be well adapted to fire, but our results nevertheless show the potential for severe root loss, mainly because of a shallow root distribution. This pattern of rooting

Fig. 4. Mean pine fine-root mass (g·m^{-2}) in the ingrowth soil cores after 14 months. Error bars are SDs.

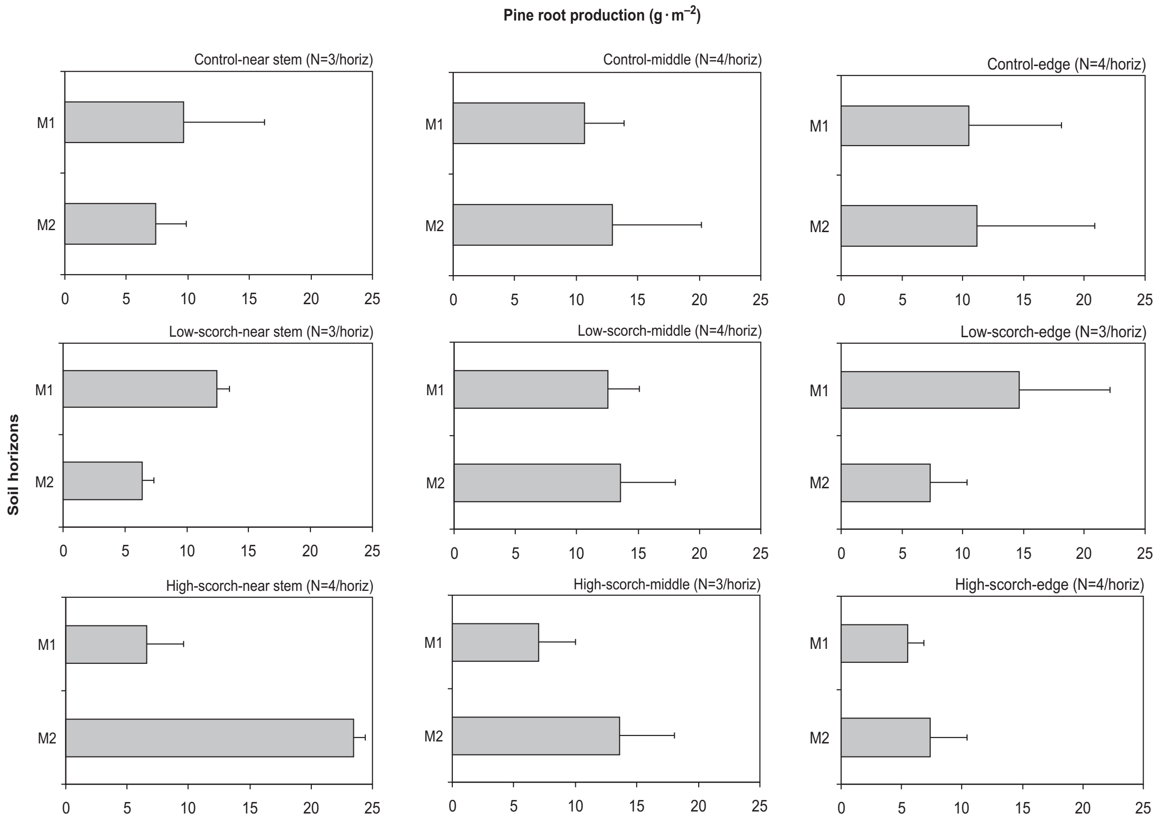


Table 6. Results from the ANOVA performed on pine root production.

	Production		
Soil horizon and source of variation	df	*F*	*p*
Upper mineral horizon			
Overall model	8	0.76	0.64
Error	22		
Scorch class (C)	2	1.20	0.32
Distance (D)	2	0.03	0.97
C × D	4	0.78	2.41
Lower mineral horizon			
Overall model	8	1.74	0.15
Error	22		
C	2	0.74	0.49
D	2	0.33	0.72
C × D	4	2.41	0.09

appears to be typical for boreal soils (Persson 1993; Taskinen et al. 2003) and is likely a response to the vertical distribution of nutrient release (Lindahl et al. 2007).

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