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DOES SOIL HETEROGENEITY AND COMPACTION IN INGROWTH-CORES AFFECT GROWTH AND MORPHOLOGY OF BLACK SPRUCE FINE-ROOTS?

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ABSTRACT

Ingrowth-cores are commonly used in studies of fine-root production in forest stands. However, some concerns have been expressed regarding changes in root growth in the artificial soil environment created in ingrowth-cores. In this study, the effects that homogenization and compaction of soil might have on fine-root growth and morphology of black spruce (*Picea mariana* Mill.) were examined. Fine-root (<2 mm) morphology was characterized by diameter and internode length. There was no difference in fine-root biomass and morphology between conventional ingrowth-cores (soil sieved and homogenized) and compacted cores (soil density increased by one third). However,

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fine-root biomass was substantially higher in ingrowth-cores in which the soil was distributed in layers of different fertility (patchy treatment) and both diameter and internode length values were closer to that found in the undisturbed soil cores. In the heterogenous treatment, the root internode length and biomass was significantly higher in rich patches than in poor patches. Our results indicate that fine-root production assessment using conventional ingrowth-cores where the soil is sieved and homogenized may underestimate the true production found in undisturbed soil. Fine-root architectural parameters in the patchy treatment were more similar to those found in the undisturbed soil cores. This study suggests that stratification or increased patchiness of the ingrowth-core growing medium should better mimic the conditions associated in undisturbed soils.

INTRODUCTION

The ingrowth-core method has been used for a long time to assess fine-root production in forest stands (1,2). The method measures the growth of fine-roots in a root free environment to assess the production that is occurring in the adjacent undisturbed soil. For this purpose, soil cores are extracted and the cylindrical hole is refilled with root-free substrate, confined by a mesh of a certain size. The main advantage of the method is the direct calculation of fine-root growth potential. In boreal forests consisting of coniferous tree species, a two-year installation of cores is considered necessary to obtain quantitative results comparable to the sequential coring method (1–5). However, a one-year installation provides a good relative measure of fine-root production between stands (1,2,6). One known disadvantage of the method is an underestimation of fine-root productivity (1). This may be caused by the mortality of fine-roots before the bag is harvested, but the major limitation of the method is the modification of the root growth environment in the bag (4,7,8). These different growth conditions seem to affect conifer fine-root morphology, which can be substantially different in the cores when compared to that found in adjacent undisturbed soil. Bauhus and Messier (7) demonstrated that this architectural change in fine-roots growing in ingrowth-cores is much less pronounced in the deciduous aspen, birch, herbs and shrubs. The reasons for these fine-root architectural changes are not clear, but they may be responsible for inaccurate estimates of fine-root production.

In this study we examined two factors that may influence fine-root morphology and biomass production in ingrowth-cores, namely, soil compaction and heterogeneity in resource distribution.

In studies using ingrowth-cores, the soil is somewhat compacted in order to try to obtain a level of compaction similar to undisturbed soil. However, because the soil is sieved to remove roots, soil structure is affected by the destruction of root channels and the natural macropores. Little is known about the effects of soil compaction on fine-root growth and morphology of forest trees. However, the effects of soil compaction have been studied for a variety of agricultural plants where contrasting effects have been observed depending on species and developmental stage (9–12). A change in soil density through compaction causes variation in soil structure, porosity, and water retention capacity. One study on compaction has found no difference for the internode, the branching angle and the diameter of maize roots (13).

Soil heterogeneity is known to increase fine-root production in rich patches in comparison to poor (14–16). A study by Birch and Hutchings (17) showed that above- and below-ground biomass production of *Glechoma hederacea* increased in heterogeneous soil environments. Fine-roots growing in rich patches are usually finer and more branched than those found in poor patches (3,18–24).

The objective of this study was to evaluate the possible effects of soil compaction and soil heterogeneity on fine-root growth and morphology in a coniferous tree species. For this purpose, the biomass, diameter, and mean internode length of fine-root were examined in both ingrowth cores and undisturbed soil of a black spruce (*Picea mariana* Mill.) stand.

MATERIAL AND METHODS

The field site was located 100 km northwest of Thunder Bay, Ontario, Canada (44°N, 90°W). The study site used in this experiment was a pure black spruce (*Picea mariana*) plantation with more than 90% moss cover in the forest floor stratum. The basal area and stocking of spruce was $20.1\,m^2\,ha^{-1}$ and $1792\,st\,ha^{-1}$, respectively. There was no regeneration and no other tree species were present in the stand.

The effects of three different ingrowth-core treatments were compared with that of undisturbed soil cores: 1) the conventional ingrowth-core treatment consisting of mixed soil (80% sandy soil mixed with 20% of top soil), 2) a compaction treatment where an additional 33% of mixed soil was forced into the same volume as in treatment 1, and 3) a heterogeneous treatment of three alternating layers of sandy soil and three layers of top soil, using the same proportion of sandy soil and top soil as was used in the first 2 treatments. Each treatment was replicated 17 times.

The sandy soil was collected from a nearby pit and the rich soil consisted of commercially available topsoil. Ingrowth-cores were made of 8 mm mesh netting and were 30 cm long. Ingrowth-cores were installed in June 1995 and harvested a year later. The corer used in this study had a diameter of 11.5 cm.

Soil analyses (Table 1) were performed on the sandy soil and topsoil used in the ingrowth-cores (three samples each) and on the organic and mineral layers of the undisturbed soil treatment (five samples each). They were analyzed for Bray-II extractable P and for 1 *M* NH_4NO_3 exchangeable cations (25). NH_4 and NO_3 were extracted with 2 *M* KCl. Soil texture was measured with pore size distribution analysis.

Root Processing

Samples were frozen until processed. The fine-roots (<2 mm) were separated from the soil using the flotation method (26); roots were retained with a 2 mm sieve. Roots were collected separately from the rich and poor layers for the heterogeneous treatment. Root sorting was executed in two steps. First, root segments longer than 1 cm were hand sorted and washed. Second, an indirect method was used to account for the mass of smaller roots. Roots were poured on a tray where squares representing 10% of the surface were randomly selected. All root fragments on these squares were picked and classified as a subsample. The weight of these roots was multiplied by ten to estimate the total biomass. Bauhus and Bartsch (27) demonstrated that the small root fractions collected in this way contribute substantially to the calculation of fine-root biomass.

Root morphology was analyzed by measuring mean diameter, total length and number of nodes using RHIZO™ software (28,29). The mean internode length was measured using the ratio of number of nodes divided by total length.

Experimental Design and Statistical Analysis

All three ingrowth-core treatments were installed in 5 rows of 10 or 11 cores each. They were installed in between trees at every 2 m. Seventeen undisturbed soil cores were taken at random in the area of the experiment. There was no formal interspersing of the treatments in this study (30). However, we consider the site homogeneous enough to assume that the statistical mean differences in root biomass and root morphology between treatments were due to the treatments and not to inherent spatial differences in the area of the experiment. This assumption is believed to be realistic because the site is a pure black spruce plantation with virtually no understory vegetation and the substrate in the ingrowth-cores came from one source and was thoroughly mixed before installation. The different treatments were compared using analysis of variance for biomass, diameter, and mean internode length. Bonfferoni pairwise

Table 1. Soil Texture, PO_4, NO_3, NH_4, K, Mg, and Al for Top Soil, Sand, and Black Spruce Site Soil

	Clay (%)	Limon (%)	Sand (%)	PO_4 (ppm)	NO_3 (ppm)	NH_4 (ppm)	K (ppm)	Mg (ppm)	Al (ppm)
Top soil	52.9	7.24	39.9	6.090	6.257	0.271	589.9	61.00	139.00
Sand	37.3	1.9	60.8	4.547	0.127	0.384	28.0	2.99	7.09
Natural organic layer				0.624	0.456	6.938	162.6	34.00	23.90
Natural mineral soil	47.3	32.7	20	1.114	0.229	1.221	28.1	4.07	6.87

comparisons were performed to ascertain statistical differences between individual treatments. No biomass comparison was made between the ingrowth-cores and undisturbed cores. Rich and poor patches in the heterogeneous treatment were compared by paired t-tests. All statistical analyses were performed using the software SYSTAT (31). Mean internode length and biomass data were log-transformed prior to analysis to meet the assumptions of the tests. No transformations were necessary for fine-root diameter data.

RESULTS AND DISCUSSION

As found in other studies (4,7–8), our measured fine-root architectural values were statistically different in the ingrowth-core treatments compared to the undisturbed soil cores (Fig. 1). This confirms that the environment of the ingrowth-core creates "artificial" conditions for the growth of black spruce fine-roots.

Compaction

No statistical differences in fine-root diameter, mean internode length or biomass were observed between conventional ingrowth-cores and the compaction treatment (Fig. 1). These results suggest that compaction is not an important factor in this type of soil (i.e., rather sandy) or at the rate of compaction used in this study (33% more soil). However, it was not possible to evaluate other changes in the physical properties of the soil that result from the installation of ingrowth-cores, such as the reduction in soil aggregation and macro-pores, which may affect root growth.

Heterogeneity of Soil Resources

An increase in overall black spruce fine-root biomass associated with increasing soil heterogeneity (Fig. 1) was observed. A higher fine-root biomass in rich patches compared to poor patches (Table 2) was also observed. An increase in overall biomass in heterogeneous conditions has also been observed by Birch and Hutchings (17). In terms of fine-root diameter and mean internode length, no significant differences were found between the heterogeneous treatment and conventional ingrowth-cores, but in both cases the values were found to be closer to that of the undisturbed soil (Fig. 1).

Fine-root biomass on a volume basis was much higher (6 times higher) in rich patches than in poor patches in the heterogeneous treatment. However, mean

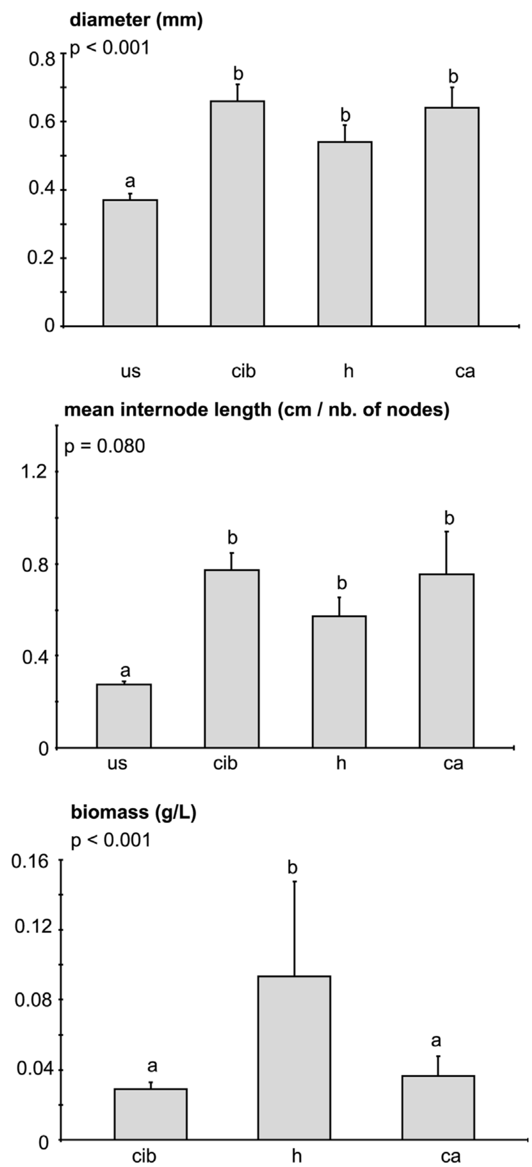

Figure 1. Comparison of average diameter (mm), mean internode length (cm/nb. of nodes), and biomass (g/L) for black spruce fine-roots for undisturbed soil (us), conventional ingrowth bag (cib), heterogenous (h), and compaction (ca) treatments. Lines above bars represent the standard errors of the means, and bars with different letters differ significantly ($p < 0.05$) by the variance analysis.

Table 2. Means, Standard Errors of the Means (SE), and p-Value for the Paired t-Test in Rich and Poor Patches for Diameter, Mean Internodes Length, and Biomass for Black Spruce

	Diameter (mm)		Mean Internode Length (cm/nodes)		Biomass (g/L)	
	Means	SEM	Means	SEM	Means	SEM
Black spruce						
Poor	0.061	0.013	0.435	0.058	0.023	0.017
Rich	0.049	0.005	0.788	0.175	0.129	0.021
p	0.432		0.032		0.004	

diameter increased, though not statistically significant, and mean internode length significantly increased in the rich patches. This means that in a rich patch, fine-roots increased their overall biomass, but decreased their branching. A decreasing branching in ingrowth bags compared to undisturbed soil is a well-known phenomenon (1,7). What is not known is why fine-root density increases while branching decreases in rich patches. Decreasing branching has been associated with increasing soil exploitation efficiency (21), while increasing density has been associated with increasing soil exploitation potential (7). Exploitation potential is defined as the total volume of soil exploited by the root system, while exploitation efficiency is defined as the soil volume the depletion zones around roots occupy per unit volume of root tissue. Based on these definitions, black spruce's fine roots in the poor patches have a high soil exploitation efficiency, but a very low soil exploitation potential. On the other hand, black spruce's fine-roots in the rich patches have a very high soil exploitation potential, but not necessarily a high soil exploitation efficiency. Although interesting, it was not the objective of this paper to evaluate the ecological advantage of this particular strategy as acknowledged by Fitter (20).

Appraisal of the Ingrowth-Core Method

Neither factors investigated in this study, soil compaction and a heterogeneous distribution of soil resources, had a significant effect on modifying our measured values of fine-root morphology compared to the conventional ingrowth-core treatment. However, we suggest that the heterogeneous treatment, because it increased the total amount of biomass and produced fine-root morphological values that are closest to that of the undisturbed soil cores, produced growth conditions that are closest to those found in undisturbed soils. This study suggests, therefore, that stratification or increased patchiness of the ingrowth-core growing medium better mimics the conditions associated with undisturbed soils. It is possible that plants have evolved different root types that can find an optimum set of conditions for their development to make use of the natural patchiness found in soils.

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