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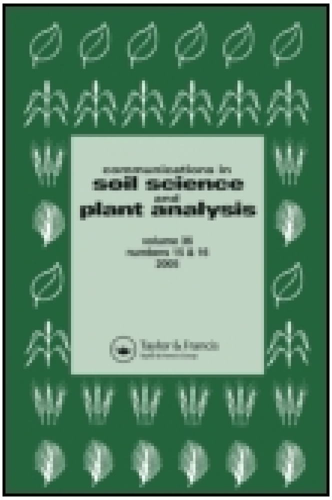

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Abstract: Root ingrowth cores were used to quantify fine root response to nutrient treatments in early and late successional stage black spruce-feathermoss ecosystems that originated from either fire or timber harvesting [cut with protection of regeneration and soils (CPRS)]. Three nutrient treatments (nitrogen, phosphorus, and calcium) were added to ingrowth cores, and root ingrowth was compared with control (water-treated) cores. The efficacy of using a natural substrate from the black spruce-feathermoss organic horizon with the ingrowth core technique was also evaluated. There was an important effect ($p = 0.06$) of nutrient treatment on fine root length and biomass in the cores, and the age of the stand since the time of the disturbance helped to explain differences in root lengths and biomass ($p = 0.05$), with older sites having greater root length and root biomass ingrowth into the cores during the study period. Experience with this technique demonstrated that the choice of fill material, core preparation, and the role of mycorrhizae in root proliferation and nutrient export from the cores are important to consider in future use of this technique.

Keywords: Black spruce, fine root, ingrowth core, feather moss

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INTRODUCTION

Past research has shown that measuring the growth of fine roots into ingrowth cores is a quick and reliable method to compare belowground responses to different experimental treatments (Persson 1990), and this technique has been used in a variety of ecosystems around the world to examine root growth into both fertilized and unfertilized cores (Lukac and Godbold 2001; Finér and Laine 2000; McGrath, Duryea, and Cropper 2000). Some authors also indicated that this technique is an adequate alternative to whole stand fertilization and can be used to test for nutrient limitations in forests (Cuevas and Medina 1988; Raich, Riley, and Vitousek 1994; Stewart 2000).

As with many experimental techniques, several problems associated with ingrowth cores are noted in the literature (Vogt, Vogt, and Bloomfield 1998). Examples include differences in bulk densities and initial soil moistures inside the ingrowth cores compared with surrounding soil (Campbell, Messier, and Bauhus 2002), root injury in the hole where the core is placed (Steingrobe, Schmid, and Claassen 2001), changes in fine root architecture for conifer species (Bauhus and Messier 1999), and the use of fill material that is texturally and mineralogically different from the surrounding soil (Raich, Riley, and Vitousek 1994). In addition to these concerns, mycorrhizal mycelia could be more important than root proliferation in the exploitation of a root-free or fertilized ingrowth core, and the emphasis on fine root growth may overestimate their importance in the exploitation of nutrient rich patches (Tibbett 2000).

This primary objectives of this study were to use the ingrowth core technique to test the efficacy of using a natural organic substrate (from the black spruce-feathermoss organic horizon) in the cores and to quantify the response of fine roots in these systems to nitrogen (N), phosphorus (P), and calcium (Ca) additions compared with control (water-treated) cores. To achieve these objectives, we placed 288 cores in four black spruce disturbance types (12 stands) in central Quebec and measured fine root length and biomass in the cores following one growing season in the field.

MATERIALS AND METHODS

Twelve black spruce stands located near Chibougamau, Québec were used in this study. They were located at latitudes ranging from 49° 9′ to 50° 06′ N and longitudes ranging from 72° 37′ to 75° 39′ W. Each "disturbance type" consisted of three non contiguous stands that were either recently harvested, cut with protection of the regeneration and soils (1988, 1988, 1991), recently burned (1986, 1986, and 1991), burned about 75–85 years previous to the study, or winter harvested approximately 55 years before the study. The four disturbance types will be referred to as the recently burned, recently harvested, old burn, and old harvest sites.

All stands were found on slopes less than 10% and were considered mesic sites (well to moderately well drained). The soils of these black spruce sites are classified as humo-ferric podzols (Spodosols). Elevation at these sites ranged from 300 to 400 m. Annual precipitation in this region is approximately 1000 mm, two-thirds in the form of rainfall, one-third as snowfall. Ground cover vegetation was a combination of black spruce [*Picea mariana* (Mill.) B.S.P.], moss [*Pleurozium schreberi* (Brid.) Mitt and *Hylocomium* spp.], and ericaceous shrubs including Labrador tea (*Ledum groenlandicum Retz.)*, northern sheep laurel (*Kalmia angustifolia* L.), and blueberry (*Vaccinium myrtilloides Michx.*).

Core Construction and Nutrient Treatments

The methodology for this study was based on techniques previously described in the literature (Cuevas and Medina 1988; Raich, Riley, and Vitousek 1994). Root ingrowth cores were constructed from plastic (PVC) tubing, 5 cm in diameter and 10 cm tall (196.3 cm^3). Thirty-seven percent of the space on the side of the tubes was open to the outside environment. Holes in the tubing sides were 0.25 cm^2 in size. Cores were filled with organic material (a mixture of feathermoss, tree, and shrub litter) collected from the organic horizon (L, F, and H layers) of each of the four disturbance types. There were no fine roots in the cores at the time of installation in the field (time zero).

The organic material used to fill the cores was originally collected in 1996 and 1997 to characterize nutrient pools and to quantify fine root length and biomass in the 12 stands (4 disturbance types $\times$ 3 replicate stands) used in this study (Smith, Munson, and Coyea 1998; Smith, Coyea, and Munson 2000). After removing all roots for fine root nutrient analyses, this organic material was frozen and then thawed at 4°C in February 1998 (at field moisture contents). The material remained refrigerated until May 1998 when the organic material was air dried for 3 days, mixed, and placed in the manufactured cores at bulk densities similar to those found in the field (0.10 g/cm^3). The cores were then treated with 100 mL of deionized water (control cores), or 100 mL of solutions of urea (1.683 g/L), $CaCl_2$ (2.881 g/L), or NaH_2PO_4 (3.499 g/L). This nutrient treatment was equivalent to an application of 40 g/m^2 (or 400 kg/ha) of N, P, and Ca, respectively.

Core Incubation Period

Four cores from each of the three nutrient treatment groups and the control group were removed for the initial nutrient analyses. Cores were taken to the field sites for installation on May 15 and 16, 1998. To install the cores in each of the 12 experimental stands, three parallel transects were established inside previously established permanent plots (50 m $\times$ 50 m). The transects were located 5 m apart, and in each transect, two N-, two Ca-, and two P-treated cores along with two control cores were randomly placed in 5 cm $\times$ 10 cm holes that were cored into the organic horizon at a 3-m spacing. In the older disturbance types, the living moss layer was placed on top of the core after its installation. Thus, at each stand, six N-, P-, and Ca-treated cores, and six control cores were installed. There were a total of 288 cores installed across all four disturbance types (4 disturbance types X 3 replicate stands X 4 core types X 6 cores per plot = 288). All of the cores were left in place until they were harvested on October 10 and 11, 1998. The installation and harvest dates were chosen to encompass the period of root elongation of the shrub and tree species in this ecosystem (Tyron and Chapin 1983).

Following core collection at the end of the growing season, the cores were stored at 4°C until they were sorted for all fine roots. Sorting required between 20 min and 1.5 hours for each core. All living tree and ericaceous roots that had grown inside the cores were included in the analysis.

Fine roots that had grown into each core were manually separated from the organic material and the total length of all fine roots was estimated by using the grid-intersect technique (Tennant 1975). At the outset of this project, we intended to separate out black spruce root response from ericaceous shrub response. The inability to correctly identify all the roots in the cores combined with a lack of root material for nutrient analyses made this impossible and, therefore, all fine roots were grouped together for analyses by disturbance type, age, and by nutrient treatment. Although we did not quantify the number of roots by species, we estimate that the majority of roots (both in length and biomass) in the cores were from the ericaceous shrubs (through visual inspection of roots).

Soil temperatures in the midsurface organic horizon during the period of core installation (mid-May) ranged from 6°C in the older disturbance types to 8°C in the recently disturbed sites. Organic horizon temperatures during the core harvest (mid-October) ranged from 4°C in the recently disturbed sites to 6°C in the older. Maximum growing season temperatures in the organic horizons were reached during mid-July and ranged from 19 to 23°C (during the day) in all four disturbance types (recent harvest, recent fire, old harvest and old fire). Approximately 500 mm of precipitation fell on the sites during the experiment.

Nutrient Analyses

The initial samples (the fill material from 4 cores from each nutrient treatment and 4 control cores) and the root-free organic material left in the cores after the final harvest were analyzed for total N, P, and Ca, exchangeable NH_4^+-N, Bray 2 P_i, and exchangeable Ca. The initial samples were analyzed in triplicate, and the final samples were bulked by stand (6 per treatment) and analyzed in duplicate. Total N was analyzed by using a Tecator 1030 Macro-Kjeldahl Analyzer (Foss Tecator AB), total P and Ca were assayed by using inductively coupled plasma emission (ICP) after ashing and dissolution in 2 mol/L HCl, and filtration. Ammonium-N concentrations were determined by using 2 *M* KCl extractions followed by analysis of the extract with continuous flow in a Lachat QuickChem 8000 Automated Ion Analyzer. Labile inorganic-P (P_i) was estimated by using the Bray 2 procedure (Bray and Kurtz 1945). Exchangeable calcium was determined by using an NH_4Cl-$BaCl_2$ extractant followed by analysis with ICP (Amacher et al. 1990). The pH of the organic material in the harvested cores (October) was determined in a 1:2 soil to water suspension (McLean 1982).

After the fine root length estimation, the roots were then oven dried at 40°C for 3 days and weighed. Fine root length densities and biomass were estimated in cm/cm^3 and g/cm^3, respectively. Some cores experienced compaction or a small portion of the organic material was lost during shipment to the site, and the volume of the organic material in the core was adjusted accordingly.

Statistical Analysis

A one-way analysis of variance of nutrient concentrations as the treatment was conducted on the treated and control fill material in the initial (time zero) cores ($n = 4$). For data collected at the end of the growing season (5 months after core installation), a general linear model using a split plot design was used to separate the effects disturbance-type and age (main plot, random factorial) from significant nutrient treatment effects (sub plot) on root-ingrowth parameters (length and biomass) and nutrient concentrations in the cores (total N, total P, total Ca, exchangeable NH_4^+, labile inorganic P, exchangeable Ca, and pH, $n = 12$). According to tests of normality (Shapiro-Wilk being the most robust) and an examination of residuals, all variables were normal with the exception of exchangeable Ca. Log (x) transformation was used to meet the criteria of normality (Shapiro-Wilk) for this variable.

Tukey's HSD was used to compare treatment effects (disturbance-type, age since disturbance, and nutrient treatment) and their interactions on fine root nutrient concentrations and fine root ingrowth. The data presented in the text, tables, and figures are the nontransformed values. All statistical procedures were performed by using SAS (Version 6.12, SAS Institute, Inc.).

RESULTS AND DISCUSSION

Analyses of the initial nutrient concentrations in the cores indicated that there was an important effect of all nutrient treatments ($p = 0.10$) and that the fertilization raised total and exchangeable nutrient pools to levels that were significantly higher than the control cores (Table 1). After 5 months in the field, the nutrient concentrations in the fertilized cores were dramatically reduced (Table 2). The N, P, and Ca fertilized cores maintained higher concentrations for the specific nutrient applied to each experimental treatment by the end of the growing season; only the cores fertilized with P did not maintain higher total P concentrations compared with one or more of the other cores (Table 2).

At the time of core harvest, there was an important effect ($p = 0.06$) of nutrient treatment on fine root biomass and fine root length (Table 3). The Ca- and P-treated cores had significantly higher fine root length densities than the control and N-treated cores across the sites ($p = 0.10$). For fine root biomass, the Ca- and P-treated cores had significantly higher fine root biomass than the N-treated cores across all sites, but none of the nutrient treated cores were significantly higher than the control cores (data not shown).

There was a significant effect of time ($p = 0.05$) since disturbance (age of stand) on root length densities and root biomass in the cores (Table 3) with significantly greater lengths and biomass in the older stands than in stands disturbed more recently. Ingrowth cores placed at the old fire sites had the highest root biomass and root lengths (0.68 g/cm^3 and 290.9 cm/cm^3, respectively) of all the sites. In a previous study at these sites, the older disturbance types had higher mean root biomass in the organic horizon and surface mineral soils, but these values were not significantly greater than those in the younger disturbance types (Smith, Coyea, and Munson 2000). This same study indicated that the ericaceous shrubs had significantly higher root lengths than the black spruce in the younger disturbance types, whereas black spruce roots dominated the older disturbance types. Thus, the comparison of ericaceous shrub and black spruce ingrowth into treated cores should be an important consideration in future studies.

Methodological Considerations

The presence of significantly higher pools of exchangeable N, Ca, and P in the ingrowth-cores after dosage (time zero) and at the time of final harvest indicated that the fertilizer treatment of the natural substrate was successful because we were able to maintain the intended differences in nutrient concentrations over an entire growing season. It was believed that the fertilizer dosage (40 g/cm^3) was too high for this environment, and the concentration would be reduced if this technique were used in the future. Previous studies used calcine clay, vermiculite, or perlite as fill material for the ingrowth cores, to take advantage of their high CEC (so that nutrient treatments persist) or low background concentrations of potential growth-limiting nutrients. Previous authors discouraged the use of root-free soils (native substrate) with this method to avoid filling the cores with soils that have

Table 1. Nutrient concentrations in the treated and control organic material used to fill the ingrowth cores before placement in the field, $n = 4$, ± 1 standard error

Nutrient treatment	Nutrient concentration					
	Total N (%)	Total Ca (ppm)	Total P (ppm)	NH_4^+-N (ppm)	Exch. Ca[a] (ppm)	Bray 2 P_i (ppm)
Control	1.0 ± 0.01 b	3553 ± 229 b	568 ± 18 b	201 ± 8 b	1427 ± 63 bc	51 ± 4 b
Nitrogen	1.2 ± 0.03 a	4065 ± 502 b	614 ± 25 b	2120 ± 321 a	1256 ± 96 c	67 ± 1 b
Calcium	0.9 ± 0.01 c	6399 ± 289 a	560 ± 26 b	201 ± 14 b	3111 ± 339 a	60 ± 1 b
Phosphorus	1.0 ± 0.01 b	4275 ± 254 b	2664 ± 159 a	145 ± 7 b	1603 ± 56 b	1715 ± 219 a

Note: In each column, mean values followed by different letters indicate significant differences among the cores for nutrient concentrations ($p = 0.10$, Tukey's HSD).

[a]Exchangeable Ca.

Table 2. Nutrient concentrations in the control and treated ingrowth cores after removal from the field, $n = 12$, ± 1 standard error

Nutrient treatment	Nutrient concentration					
	Total N (%)	Total Ca (ppm)	Total P (ppm)	NH_4^+-N (ppm)	Exch. Ca[a] (ppm)	Bray 2 P_i (ppm)
Control	0.91 ± 0.02 a,b	2772 ± 198 b	637 ± 48 a	175 ± 20 b	1643 ± 68 b	26 ± 3 b
Nitrogen	0.95 ± 0.02 a	3350 ± 297 a	847 ± 106 a	267 ± 33 a	1723 ± 144 b	23 ± 4 b
Calcium	0.88 ± 0.01 b	3646 ± 282 a	717 ± 79 a	139 ± 16 b	2195 ± 32 a	22 ± 2 b
Phosphorus	0.89 ± 0.02 b	2695 ± 221 b	691 ± 51 a	156 ± 13 b	1580 ± 33 b	47 ± 4 a

Note: In each column, mean values followed by different letters indicate significant differences among the cores for nutrient concentrations ($p \leq 0.10$, Tukey's HSD).

[a]Exchangeable Ca.

Table 3. Probability results (p values) for the effects of nutrient treatment, disturbance type, and age of stand along with their interactions (data collected from cores left in the field for one growing season)

Source	df	Root length (cm/cm^3)	Root biomass (g/cm^3)	Total N (%)	Total P (ppm)	Total Ca (ppm)	Labile inorganic P (ppm)	Exchangeable NH_4^+-N (ppm)	Exchangeable Ca (ppm)
Disturbance	1	0.55	0.35	0.83	0.91	0.96	0.80	0.59	0.38
Age	1	0.02	0.03	0.52	0.63	0.48	0.68	0.05	0.26
Disturbance ∗ age	1	0.95	0.07	0.94	0.40	0.23	0.87	0.02	0.32
Rep(disturbance ∗ age)	8	0.0001	0.16	0.0001	0.78	0.93	0.0001	0.60	0.10
Nutrient	3	0.06	0.06	0.01	0.39	0.09	0.0001	0.005	0.0001
(Disturbance ∗ nutrient)	3	0.62	0.78	0.77	0.85	0.94	0.73	0.88	0.53
(Age ∗ nutrient)	3	0.07	0.26	0.13	0.84	0.54	0.07	0.46	0.44
(Disturbance ∗ age ∗ nutrient)	3	0.29	0.47	0.31	0.77	0.73	0.21	0.99	0.28

low CEC, which would prohibit the retention of cations useful for study (Raich, Riley, and Vitousek 1994). It was believed that use of the native organic material was suitable because the CEC of the organic horizon of upland black spruce sites ranges from 26 to 79 cmol(+)/kg, which is high compared to mineral soil (Ruess et al. 1996; Steele et al. 1997). Previous studies also have indicated that most of the fine root biomass in black spruce ecosystems is found in the organic horizon (Tyron and Chapin 1983; Ruess et al. 1996; Steele et al. 1997), and it was thought that this also supported the use of the natural substrate.

Another potential problem with this methodology included the preparation of the cores. Although our N-treated cores had significantly higher NH_4^+-N concentrations compared to the control and other treated cores, the preparation of this substrate (removal of fine roots, storage at 4°C, placement in cores, transportation to the site) was in effect, a long-term incubation (albeit at low temperatures). By the time the cores were ready for placement in the field, they had higher background NH_4^+-N concentrations than the surrounding undisturbed substrate at each disturbance type (Smith, Coyea, and Munson 2000).

In addition to concerns about fill material and core preparation, the assumption that root proliferation (increase in root length density or biomass) in nutrient-treated ingrowth cores is related to increased uptake of a limiting nutrient may not always hold true (Caldwell 1994). For example, N uptake was not correlated with increases in root length of *Plantago* in N-enriched substrates (Hodge, Robinson, and Fitter 2000). In addition, the relationship between P uptake and root length is not always proportional, with a shrub (*Artemesia*) obtaining up to 8 times more P than a grass (*Pseudoroegneria*) despite having smaller root length densities (Caldwell 1994).

Finally, because mycorrhizae play a large role in nutrient uptake by the tree and shrub components in boreal systems (Stribley and Read 1980; Carleton and Read 1991), the role of mycorrhizae in root proliferation and nutrient uptake may also confound results of this type of bioassay (Tibbett 2000). Black spruce-associated mycorrhizae are known to aid the export of P from the moss and litter layer (Chapin et al. 1987), results that suggest a potentially important, but unquantified mechanism of P export from our cores. In addition, if mycorrhizal fungi concentrate hyphae in nutrient-rich zones such as our fertilized cores, root proliferation could be reduced (Cui and Caldwell 1996). This is important to consider with the ingrowth core experiment, particularly when fertilized cores have much higher nutrient concentrations than the surrounding substrate.

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