

Soil exploitation strategies of fine roots in different tree species of the southern boreal forest of eastern Canada

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Abstract: This study compared the ability of conifers (*Abies balsamea* (L.) Mill., *Picea glauca* (Moench) Voss) and deciduous trees (*Populus tremuloides* Michx., *Betula papyrifera* Marsh.) and shrubs and herbs to exploit soils in a southern boreal forest. Root samples were collected from undisturbed soil and ingrowth cores (disturbed soil) of aspen- and conifer-dominated plots. Total fine-root biomass was similar in aspen and conifer plots but length density was higher under aspen. The low root length density ($0.7 \text{ cm}\cdot\text{cm}^{-3}$) of conifers suggests a dependency on mycorrhizal associations for effective nutrient uptake. Coniferous fine roots were thicker than in the other species. Root tip and internode lengths in deciduous trees showed little differences between undisturbed and disturbed soil, whereas these parameters increased substantially in conifers in disturbed soil. Root growth and architecture in disturbed soil indicated that conifers follow a conservative strategy of optimizing soil exploitation efficiency through the relatively slow development of coarse fine-root systems. In contrast, deciduous trees and understorey shrubs and herbs colonized favourable soil environments to a larger extent maintaining highly ramified thin fine roots to optimize the exploited soil volume. The different soil exploitation strategies may be as important as those differences reported for aboveground growth to explain the coexistence of these species.

Résumé : Cette étude compare la capacité des conifères (*Abies balsamea* (L.) Mill., *Picea glauca* (Moench) Voss) et des feuillus (*Populus tremuloides* Michx., *Betula papyrifera* Marsh.) arborescents, des arbustes et des herbacées à exploiter les sols dans la forêt boréale méridionale. Des échantillons de racines ont été collectés dans le sol non perturbé et dans des sachets de croissance (sol perturbé) prélevés dans des parcelles dominées soit par le peuplier, soit par les conifères. La biomasse totale de racines fines était semblable dans les parcelles de peuplier et de conifères mais la densité linéaire était plus élevée sous le peuplier. La faible densité linéaire des racines ($0,7 \text{ cm}\cdot\text{cm}^{-3}$) des conifères suggère une dépendance des associations mycorrhiziennes pour le prélèvement efficace des nutriments. Les racines fines des conifères étaient plus épaisses que celles des autres espèces. Il y avait peu de différence dans la longueur des apex racinaires et des entre-noeuds chez les arbres feuillus entre le sol perturbé et non perturbé tandis que ces paramètres augmentaient substantiellement chez les conifères dans les sols perturbés. L'architecture et la croissance des racines dans les sols perturbés indiquent que les conifères adoptent une stratégie conservatrice pour optimiser leur efficacité dans l'exploitation du sol via le développement relativement lent d'un système grossier de racines fines. Au contraire, les arbres feuillus, les arbustes en sous-étage et les herbacées colonisent les zones favorables du sol de façon plus extensive en maintenant de minces racines fines fortement ramifiées pour optimiser le volume de sol à exploiter. Les différentes stratégies d'exploitation du sol pourraient être aussi importantes que les différences rapportées dans la croissance aérienne pour expliquer la coexistence de ces espèces.

[Traduit par la Rédaction]

Introduction

In comparison with aboveground plant structures, little is known about differences in fine-root soil exploitation strategies among the different species in the boreal forest. Large quantities of carbon (C) are allocated belowground (Vogt et al. 1986). Plant species are known to differ considerably in

the way they invest C into fine-root systems (Lambers 1987). Such differences in C allocation may be important in explaining the success and failure of the various plant species growing in the boreal forest. The same amount of carbon may produce root systems with very different architecture (Nielsen et al. 1994) and nutrient uptake capacity. This may be critical in the boreal forests where productivity is often nutrient limited, particularly in later successional stages (Van Cleve et al. 1983).

In the southern boreal forest, early successional forests are generally dominated by shade-intolerant deciduous species such as trembling aspen (*Populus tremuloides* Michx.) and paper birch (*Betula papyrifera* Marsh.), whereas late successional stands are dominated by shade-tolerant conifer species such as balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss) (Bergeron and Dansereau 1993). Messier et al. (1999) suggested that basic

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Table 1. Selected chemical and physical characteristics (0–10 cm) of Grey Luvisols (clay) and Humo-Ferric Podzols (till) in trembling aspen- and conifer-dominated plots in forest stands that originated from fires in 1944 (Bauhus et al. 1998).

Stand type	Organic C (g·kg ⁻¹)	Organic N (g·kg ⁻¹)	pH (in H ₂ O)	Ca (exc.) (mg·kg ⁻¹)	P (Bray II) (mg·kg ⁻¹)	Clay (%)
Clay–conifer	40.3	1.5	5.41	2306	10.4	100
Clay–aspen	49.6	1.8	5.40	2623	6.3	84
Till–conifer	37.2	1.4	4.82	130	5.0	47
Till–aspen	53.4	1.9	4.74	311	2.8	54

differences in aboveground growth and crown morphological plasticity in relation to changes in light availability can explain differences in shade tolerance among boreal tree species. However, we do not know whether there are also different strategies with regard to the exploitation of belowground resources among boreal tree species and other plant guilds such as herbs and shrubs. A previous study by Finér et al. (1997) on fine-root dynamics in the mixed boreal forest found no differences in fine-root biomass between forests of different age following fire disturbance, but fine-root length and fine-root growth in early successional stands was higher than in old stands. These differences were attributed to the higher component of trembling aspen in the young stands when compared with old stands. However, since their study did not compare tree species within the same stand, it is not clear whether the differences reported above are the result of differences in tree species or increasing forest age following disturbance. The possible effect of age could be related to site fertility, which tends to decline with time after disturbance (Paré et al. 1993).

In this study we investigated how different tree species and understorey shrubs and herbs differ in their soil exploitation strategies in response to soil type and soil disturbance. For this purpose we compared fine-root biomass, fine-root growth, and some aspects of fine-root architecture of tree, shrub, and herbaceous species at plots dominated by trembling aspen or coniferous species in forest stands that originated from a wildfire in 1944. We were particularly interested in aspects of fine-root architecture that are related to the ability of the different species to compete for belowground resources.

Assuming constant tissue density, C invested in root length contributes more to root surface area than C invested in root diameter. Since the surface area of roots is most important for uptake of water and nutrients, root length per unit of root biomass (cm·g⁻¹ dry mass), specific root length (SRL), is a key component of soil exploitation. We concentrated on the specific root length, root length density (root length per unit volume of soil (cm·cm⁻³)), and the internodal distances of fine roots in disturbed soil patches as indicators of the potential efficiency of root structural carbon to exploit soil. Internodal distances were included in the architectural analysis because the volume of soil effectively exploited by roots also depends on their spatial arrangement. A dense highly branched fine-root system may create many overlaps between soil depletion zones around individual root segments, thus decreasing the efficiency of the C invested in fine roots with regard to nutrient and water uptake (Caldwell and Richards 1986).

The objectives of this study were (i) to compare standing fine-root biomass in undisturbed soil and fine-root growth in a root free soil environment between plots dominated by either coniferous or deciduous species and (ii) to investigate basic fine-root architectural traits among different tree species, herbs, and shrubs in response to soil types and soil disturbance.

Material and methods

Study sites

The field sites were located in a southern boreal forest around Lac Duparquet (48°30'N, 79°20'W) in the Abitibi region of Quebec. The climate is continental and characterized by a mean annual temperature of 0.6°C, mean annual precipitation of 823 mm, and a frost-free period of 64 days. The study area is part of the northern clay belt, where most soils originate from glaciolacustrine clay deposits (Vincent and Hardy 1977). In this region, forests in early successional stages are mostly dominated by trembling aspen and paper birch. The shrub mountain maple (*Acer spicatum* Lam.) and the herbs *Aster macrophyllus* L. and *Aralia nudicalis* L. are commonly found in the understorey. Later during the succession, forests gradually become dominated by shade-tolerant conifers such as balsam fir, white spruce, and white cedar (*Thuja occidentalis* L.) (Bergeron and Dansereau 1993). However, patches of white spruce and balsam fir can also be found in young forests. The age of individual forest stands in the study area has been determined in previous dendrochronological studies (Dansereau and Bergeron 1993).

Fine roots were sampled from forest stands originating from fires in 1944 (Finér et al. 1997), which comprised patches (hereafter referred to as plots) dominated by trembling aspen or conifers (balsam fir and white spruce) on clay and till soils. The mixed nature of the forest did not permit plots to be located in large monospecific coniferous stands. Therefore, balsam fir and white spruce were grouped together as coniferous plots. Although some distinct differences in their fine-root morphology are apparent (Brundrett et al. 1990), differences in fine-root architecture between them are considerably smaller than between these conifers and either trembling aspen or paper birch. Similarities in growth habits and successional status between white spruce and balsam fir and the difficulties in distinguishing fine roots of the two species suggested that these two coniferous be grouped. Pure paper birch stands were not explicitly included in the study, but since birch was an important component of both conifer and aspen plots, its fine roots were also investigated.

Soils called "clay" were Grey Luvisols with moderate to good drainage, and soils named "till" were Humo-Ferric Podzols that had developed on moraine deposits (Agriculture Canada Expert Committee on Soil Survey 1987). The concentrations of base cations and phosphorus were generally higher in clay than in till soil (Table 1) (Bauhus et al. 1998). Aspen- and conifer-dominated plots were replicated four times for each of the two soil types for a total of 16 plots. At each sample location stand basal area (m²·ha⁻¹) (at

Table 2. Average basal area ($\text{m}^2\text{-ha}^{-1}$) and contribution of trembling aspen, conifers (balsam fir and white spruce), paper birch, and other tree species to basal area in aspen- and conifer-dominated plots in 50-year-old forest stands on clay and till soil.

Stand type	Basal area ($\text{m}^2\text{-ha}^{-1}$)	Aspen (%)	Conifers (%)	Birch (%)	Other species (%)
Clay-conifer	26.91	13	66	16	5
Clay-aspen	54.95	98	1	1	—
Till-conifer	22.70	—	49	46	5
Till-aspen	46.01	92	2	6	—

Note: Other species include *Thuja occidentalis*, *Salix* spp., and *Prunus pensylvanica*.

1.3 m tree height) was determined by measuring all trees (>5 cm diameter at breast height, 1.3 m) within a 10×10 m plot. The basal area derived and the percentage contribution of each species are presented in Table 2. Basal area was measured since a relationship between root biomass of single trees and stem diameter has been demonstrated (Wu et al. 1988; Shepperd and Smith 1993) and consequently stand root biomass is assumed to be related to stand basal area. Basal area is also an indicator of aboveground biomass.

Field sampling

Two different approaches were taken in fine-root samplings. Fine roots were sampled from undisturbed soil using a soil corer (7 cm diameter) and from ingrowth cores (Vogt and Persson 1991) established in holes created in the first sampling. Ingrowth cores were installed to allow fine-root growth in disturbed and unoccupied soil, representing a favourable soil substrate for fine-root growth (Eissenstat 1991). The initial absence of fine roots would presumably allow nutrients mineralized from organic matter to accumulate. Further, soil disturbance, simulated by sieving the soil, usually increases mineralization rates. In the ingrowth cores the root-free soil medium was more homogenous than the undisturbed soil, and so, fine-root architecture should be less influenced by small nutrient rich patches in the soil (Robinson 1994), existing root channels, or competition (Caldwell and Richards 1986).

Soil cores were collected and ingrowth cores installed in early September 1994. The soil was sampled to a depth of 20 cm in the mineral soil. We concentrated on the organic layer and the surface mineral horizons because these contain the vast majority of fine-root biomass and length in these forests (Finér et al. 1997). At each replicate plot, 10 soil cores were extracted along one transect, where soil cores were located approximately 2 m apart. Soil cores were cold stored until washing.

Ingrowth cores were filled with root-free soil. The soil obtained from the site was sieved (5 mm) and roots and rocks were removed before filling mesh bags (4 mm mesh) with soil and placing them into cores. The clay content of the Luvisol was very high (95% clay on average), and previous studies had shown that the structure of the sieved clay soil may deteriorate and thus create a soil environment with limited pore space and oxygen supply. This is partly due to the removal of larger soil aggregates in the sieving process. For this reason the clay soil was mixed with sand (<2 mm) in a 3:1 ratio (clay:sand) before being filled into ingrowth cores to provide a more favourable soil structure. A dense root mat prohibited using root-free forest floor material in the ingrowth cores, and so, peat with approximately the same average thickness and mass as the forest floor material was used instead. The ingrowth cores were collected after 14 months.

Washing and sorting of roots

Fine roots were separated from the soil by washing. Samples were soaked before being repeatedly flushed with water in buckets. The roots floating on top of the water were poured in a sieve (1.0-mm mesh). This procedure, similar to the flotation method

(Böhm 1979), was repeated until only rocks were left in the soil sample. Forest floor samples were also washed gently in a sieve (1.0-mm mesh) to remove fine soil organic matter particles. Then the sieve contents were poured on a tray and dispersed in water to separate roots from the remaining organic material by hand.

An indirect sampling method was employed for root fragments shorter than 5 mm. Once all roots longer than 5 mm were removed, the remaining root fragments in the sample were placed onto a tray with a grid, and roots were collected from 10% of the area. Bauhus and Bartsch (1996) showed that this technique was effective at recovering fine-root mass, particularly of fragile herbaceous roots. In the present study the indirect sampling yielded on average 35% of the total fine-root dry mass in the undisturbed soil cores and 9% in the ingrowth cores.

Until sorting, washed roots were kept frozen. Fine roots were differentiated by size (0–1, 1–2 mm), tree species (trembling aspen, paper birch, or conifers), and by other species (herbs or shrubs). Differentiation of species was facilitated by the use of root reference material from field sites (Finér et al. 1997). Roots from different tree species were usually distinguished by colour and size of smallest roots. Trembling aspen roots were yellow to brown when wet and silver-grey after air drying. Their root tips were narrow (0.1–0.2 mm) in the absence of mycorrhiza, about 1 mm long and often black in colour and thicker (0.2–0.3 mm) after ectomycorrhizal (ECM) infection. First-order fine roots of paper birch (for the ordering system of fine roots refer to Fig. 5) were as fine as trembling aspen roots, but higher order roots of paper birch were dark red. Branching between first- and second-order fine roots was more regular in birch than in aspen and mostly at a right angle. In comparison, the fine roots of balsam fir and white spruce appeared coarser than those of trembling aspen or paper birch. First-order roots were 0.2–0.4 mm in diameter, branched less frequently, and yellow to red-brown in colour. First-order laterals appeared to be shorter in balsam fir than in white spruce. The difference between diameters of first- and second-order fine roots was more pronounced in fir than in spruce. Although it was possible to assign intact fine roots to either white spruce or balsam fir, the determining of individual roots demanded microscopic investigation which was not feasible and thus fine roots of spruce and fir were grouped into conifers. The most frequent shrub species at field sites was *Acer spicatum*. Its fine roots were dark brown and relatively coarse. Most herbaceous species were annuals with soft white or yellow fine roots.

The dead and live fractions of fine roots were separated visually. Live roots were intact, tough and flexible, while dead roots were brittle and fractured easily. Roots that could not be identified by species were categorized as “unknown.” Results for root dry mass and architecture presented in Tables 3–8, and Figs. 1–6 are based on the live fine-root fraction only.

Fine-root fragments recovered by the indirect sampling technique were not differentiated by species, or live and dead roots. Root fragment dry mass was assigned to each root class according to their contribution to the overall fine-root dry mass (live and dead

Table 3. Fine-root (<2 mm) dry mass and length density of different tree species, herbs, and shrubs in undisturbed soil (mineral soil + forest floor) of aspen- and conifer-dominated plots on clay and till soil.

	Clay–conifer	Clay–aspen	Till–conifer	Till–aspen
Biomass (g·m ⁻²)				
Aspen	305 (39) <i>a</i>	567 (51) <i>b</i>	105 (24) <i>c</i>	588 (52) <i>b</i>
Conifers	244 (21) <i>a</i>	10 (9.6) <i>b</i>	253 (47) <i>a</i>	20 (7.4) <i>b</i>
Birch	123 (25) <i>a</i>	40 (20) <i>a</i>	470 (62) <i>b</i>	112 (21) <i>a</i>
Shrubs	15 (3.7) <i>a</i>	80 (14) <i>b</i>	25 (4.9) <i>a</i>	35 (6.0) <i>a</i>
Herbs	7 (2.6)	5 (0.9)	11 (2.9)	13 (3.1)
Unknown	13 (4.9) <i>a</i>	1 (0.6) <i>b</i>	4 (2.2) <i>ab</i>	9 (3.9) <i>ab</i>
Total	707 (41)	703 (58)	868 (106)	777 (48)
Length density (cm·cm ⁻³)				
Aspen	2.66 (0.31) <i>a</i>	5.25 (0.51) <i>b</i>	0.61 (0.13) <i>c</i>	4.33 (0.46) <i>b</i>
Conifers	0.66 (0.07) <i>a</i>	0.02 (0.02) <i>b</i>	0.67 (0.09) <i>a</i>	0.07 (0.02) <i>b</i>
Birch	0.74 (0.17) <i>a</i>	0.23 (0.10) <i>a</i>	1.83 (0.26) <i>b</i>	0.63 (0.12) <i>a</i>
Shrubs	0.19 (0.06) <i>a</i>	1.13 (0.23) <i>b</i>	0.24 (0.05) <i>a</i>	0.30 (0.06) <i>a</i>
Herbs	0.09 (0.04)	0.06 (0.03)	0.10 (0.03)	0.11 (0.03)
Total	4.34 (0.36) <i>ac</i>	6.69 (0.55) <i>b</i>	3.45 (0.30) <i>c</i>	5.44 (0.47) <i>ab</i>

Note: Values are means, with SE given in parentheses, from 40 soil cores for each plot category. Values in a row with the same letter are not significantly different ($P < 0.05$, ANOVA).

roots) in the sample. The root fragments were dried to constant mass at 40°C.

Assessment of architectural traits

After sorting the fine roots, root architecture was investigated on subsamples. Total root lengths, and length over diameter distributions were determined for all samples. Fine-root architectural analysis and length and diameter measurements were carried out using the image analysis software RHIZO™ 3.03 (Régeants Instruments, Quebec). Previous testing of the software showed that root length and diameter is measured with negligible error due to overlap and abutment of fine roots on the scanner (Bauhus and Messier 1998). After measurements roots were dried to constant mass (24 h) at 40°C. Specific root length (SRL) (cm·mg⁻¹) was calculated as the total root length divided by the root dry mass of the sample.

For selected and largely intact root sections showing several orders of branching, length and diameter of all root branches and internodes were determined. Since only fragments of root systems were retrieved, the centripetal Strahler ordering system (Fitter 1982) was used to describe fine-root architecture (see Figs. 5–9). First-order root segments (tips) terminate in a meristem, second-order segments begin at the junction of two first-order segments, third-order segments are those that begin at the junction of two second-order segments, and so on. We further distinguished between long and short order segments of roots, calling the former long first-order root (LR), and the latter short first-order root (SR). This classification was appropriate for the heterorhizic tree root systems investigated. In trees, fine roots are often differentiated into long distributive roots and short laterals, which have determinate growth and form ECM associations more often than long roots (Sohn 1981). This phenomenon has been called heterorhizy (Brundrett et al. 1990), and it is largely absent in trees that form vesicular–arbuscular mycorrhizal associations. Since the trees in our study all form ECM associations (Brundrett et al. 1990), the classification adopted accounted for two obviously different types of first-order roots.

The fine roots recovered from shrubs and herbs were usually too small and fragmented to perform an architectural analysis. Thus only fine-root biomass and length parameters of herbs and shrubs are reported. For the same reasons architectural analysis of birch fine roots could only be performed in the forest floor material.

Statistics

The effects of soil horizons, soil type, and disturbance (ingrowth cores) on fine-root biomass, specific root length, root length density, and internode length and diameter were estimated by means of ANOVA (SYSTAT Inc. 1992). Post-hoc Tukeys HSD multiple comparisons were carried out to test differences between means. In cases when data did not meet the requirements for parametric tests, they were rank transformed (Potvin and Roff 1993). ANOVAs on these ranked data provided identical results for significance and nonsignificance of factors and interactions as the ANOVA on the untransformed data, and F ratios were very similar for the same factors in ANOVAs for untransformed and rank-transformed data.

Regression analysis (General Linear Model (GLM)) was used to investigate whether differences existed between the relationships depicted in Figs. 1–3 for the different species groups, and the 1:1 line.

Results

Fine-root biomass, specific root length, and root length density

Most fine roots were identifiable within the specified species categories (Table 3). Total fine-root (0–2 mm) biomass did not differ significantly ($P < 0.05$) between aspen- and conifer-dominated plots on both soil types (Table 3). The tree fine-root component was clearly dominated by trembling aspen in the aspen plots. However, paper birch and trembling aspen contributed more than 50% of the total fine-root biomass in the coniferous plots. On clay soil, significantly more shrub fine roots were found in aspen plots than in coniferous forest plots (Table 3). The relationship between the percent basal area and percent fine-root biomass for each of the tree species present in each plot shows that the above-ground dominance of trembling aspen in aspen stands is matched belowground (Fig. 1). The percentage of conifer fine roots at conifer-dominated sites was substantially smaller than the percentage of basal area of conifers in the plots. The interaction between tree species and percent basal area in the GLM used to predict the percent fine-root

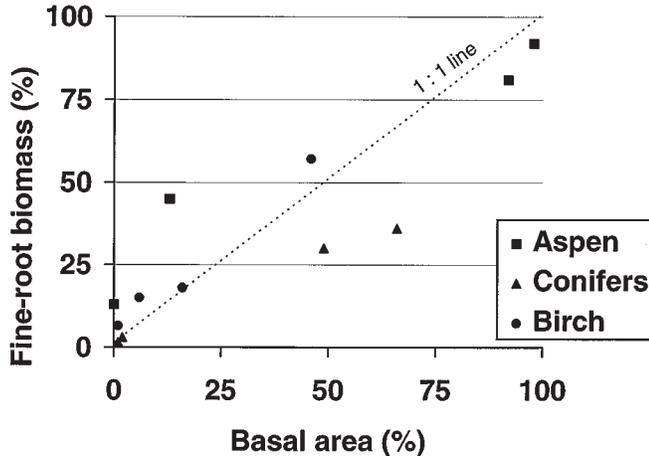
Table 4. Specific root length (SRL) ($\text{cm}\cdot\text{g}^{-1}$) and average fine-root diameter (mm) of different tree species, herbs and shrubs in undisturbed soil.

	Aspen	Conifers	Birch	Shrubs	Herbs
SRL ($\text{cm}\cdot\text{g}^{-1}$)					
Clay	3570 (260) <i>a</i> *	1010 (50) <i>b</i> *	2430 (230) <i>c</i>	3190 (260) <i>ac</i> *	4100 (290) <i>a</i> *
Till	2750 (180) <i>a</i>	1340 (120) <i>b</i>	1830 (200) <i>c</i>	2750 (220) <i>a</i>	2540 (170) <i>a</i>
Diameter (mm)					
Clay	0.35 (0.02) <i>a</i> *	0.60 (0.01) <i>b</i> *	0.38 (0.02) <i>a</i>	0.37 (0.01) <i>a</i> *	0.40 (0.01) <i>a</i> *
Till	0.40 (0.02) <i>a</i>	0.53 (0.01) <i>b</i>	0.40 (0.02) <i>a</i>	0.43 (0.02) <i>a</i>	0.48 (0.01) <i>c</i>

Note: Values are means, with SE given in parentheses. Values in a row with the same letter are not significantly different ($P > 0.05$, ANOVA).

*Significant differences ($P < 0.05$, ANOVA) in SRL and diameter between soil types.

Fig. 1. Relationship between the individual contribution of different tree species to stand basal area (%) versus total tree fine-root biomass (%). Every point represents the average of four plots for each treatment; basal area data are given in Table 1. Only the slope for conifers is different from the 1:1 line ($P < 0.05$).

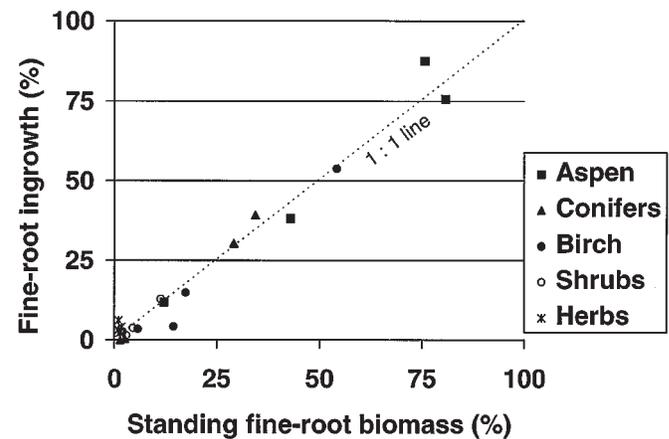


biomass indicated that the slope was different from the 1:1 line only for the conifers. It appeared that trembling aspen contributed more to fine-root biomass in conifer-dominated plots than would be expected from its contribution to the total basal area (Table 2, Fig. 1), but the slope for aspen was not different from the 1:1 line.

Fine roots of trembling aspen, paper birch, shrubs, and herbs were also characterized by smaller root diameters and significantly higher specific root lengths than those found in conifers in both soil types (Table 4). Thus, for a similar fine-root biomass, trembling aspen, paper birch, herbs, and shrubs had a much greater length density than conifers (Table 3). Although conifers contributed 27 and 35% to the total fine-root biomass in clay and till soil types, they made up only 19 and 15% of the total length density, respectively.

Root biomass in ingrowth cores left in the field for 14 months was between one third and one half of the standing biomass found in undisturbed soil (Table 5). Both values were strongly correlated ($R^2 = 0.97$), showing that no species was able to produce relatively more root biomass in ingrowth cores than their standing biomass indicated (Fig. 2). This was indicated by the absence of interactions between the percent standing fine-root biomass and the species groups in the GLM used to predict percent fine-root

Fig. 2. Relationship between the individual contribution of different species to the total standing fine-root biomass (%) found in undisturbed cores versus that found in ingrowth cores (%). Every point represents the average of four plots for each treatment.



ingrowth. Significantly ($P < 0.05$) higher values for fine-root biomass and length density were found in ingrowth cores in aspen stands on till compared with the other plot categories (Table 5). Significant effects of tree species, soil type, and the interaction between the two factors (ANOVA table not shown) on root biomass and length density (Table 5) indicate that the till soil was colonized to a larger extent in aspen-dominated plots than in coniferous ones but that no difference was found for the clay soil type.

Root length density in ingrowth cores was between 31 and 33% of that found in undisturbed cores on clay soil, whereas it was 54 and 100% in till soil. This shows that, in till, length density and hence soil occupation had recovered proportionally faster than fine-root biomass. This may be explained by apparently higher specific root lengths of trembling aspen and paper birch in till soil compared with clay (Table 6). However, this difference is only significant for birch roots in mineral soil. The linear relationship ($r^2 = 0.89$) between the contribution of species to the total fine-root length density in undisturbed soil cores versus that in ingrowth cores indicates that herbs have a greater capability to occupy the ingrowth cores than what their standing fine-root length density might suggest (Fig. 3). Apart from the herbs, the slope for other species was not significantly different from the 1:1 line (Fig. 3).

Table 5. Fine-root (<2 mm) biomass (g·m⁻²) and length density (cm·cm⁻³) of different tree species, herbs, and shrubs in disturbed soil (mineral soil + forest floor of ingrowth cores) of aspen- and conifer-dominated plots on clay and till soil.

	Clay–conifer	Clay–aspen	Till–conifer	Till–aspen
Biomass (g·m ⁻²)				
Aspen	35 (14) <i>a</i>	187 (16) <i>b</i>	31 (12) <i>a</i>	392 (27) <i>c</i>
Conifers	94 (12) <i>a</i>	8 (4.4) <i>b</i>	79 (13) <i>a</i>	19 (7.0) <i>c</i>
Birch	91 (15) <i>a</i>	0 (0.0) <i>b</i>	140 (15) <i>c</i>	2 (1.1) <i>b</i>
Shrubs	6 (1.5) <i>a</i>	32 (8.9) <i>b</i>	4 (1.2) <i>a</i>	17 (3.1) <i>ab</i>
Herbs	8 (1.6) <i>a</i>	15 (2.7) <i>b</i>	6 (0.9) <i>a</i>	18 (3.4) <i>b</i>
Unknown	5 (2.1) <i>a</i>	5 (1.6) <i>a</i>	1 (0.6) <i>b</i>	0 (0.0) <i>b</i>
Total	239 (19) <i>a</i>	247 (16) <i>a</i>	261 (23) <i>a</i>	448 (27) <i>b</i>
Length density (cm·cm ⁻³)				
Aspen	0.21 (0.03) <i>a</i>	1.45 (0.21) <i>b</i>	0.16 (0.04) <i>a</i>	4.64 (0.46) <i>c</i>
Conifers	0.24 (0.13) <i>a</i>	0.02 (0.01) <i>b</i>	0.39 (0.07) <i>a</i>	0.02 (0.01) <i>b</i>
Birch	0.54 (0.09) <i>a</i>	0.02 (0.01) <i>b</i>	1.06 (0.16) <i>c</i>	0.07 (0.02) <i>b</i>
Shrubs	0.18 (0.06) <i>ab</i>	0.38 (0.07) <i>b</i>	0.06 (0.02) <i>a</i>	0.38 (0.05) <i>b</i>
Herbs	0.16 (0.04) <i>a</i>	0.33 (0.04) <i>b</i>	0.18 (0.02) <i>a</i>	0.33 (0.03) <i>b</i>
Total	1.33 (0.15) <i>a</i>	2.20 (0.26) <i>a</i>	1.85 (0.17) <i>a</i>	5.44 (0.50) <i>b</i>

Note: Values are means, with SE given in parentheses, from 40 soil cores for each site. Values in a row with the same letter are not significantly different ($P < 0.05$, ANOVA).

Table 6. Specific root length (SRL) (cm·g⁻¹) and average fine-root diameter (mm) of different tree species, herbs, and shrubs in (A) forest floor (peat moss) and (B) mineral soil of ingrowth cores.

(A) Forest floor (peat moss).					
	Aspen	Conifers	Birch	Shrubs	Herbs
SRL (cm·g ⁻¹)					
Clay	4920 (360) <i>a</i>	1330 (78) <i>b</i>	4400 (500) <i>a</i>	4380 (370) <i>a</i>	4830 (490) <i>a</i>
Till	5640 (230) <i>a</i>	1340 (140) <i>b</i>	4680 (280) <i>a</i>	4960 (450) <i>a</i>	4700 (490) <i>a</i>
Diameter (mm)					
Clay	0.36 (0.01) <i>a</i> *	0.70 (0.03) <i>b</i>	0.40 (0.02) <i>ac</i>	0.42 (0.02) <i>c</i>	0.40 (0.02) <i>c</i>
Till	0.32 (0.01) <i>a</i>	0.73 (0.03) <i>b</i>	0.36 (0.02) <i>ac</i>	0.37 (0.02) <i>c</i>	0.42 (0.02) <i>c</i>
(B) Mineral soil.					
	Aspen	Conifers	Birch	Shrubs	Herbs
SRL (cm·g ⁻¹)					
Clay	3150 (260) <i>a</i>	1103 (190) <i>b</i>	2390 (140) <i>c</i> *	3957 (340) <i>a</i>	3560 (390) <i>a</i>
Till	4150 (230) <i>a</i>	1090 (60) <i>b</i>	3830 (390) <i>a</i>	4670 (560) <i>a</i>	4590 (330) <i>a</i>
Diameter (mm)					
Clay	0.40 (0.01) <i>a</i>	0.79 (0.04) <i>b</i>	0.50 (0.02) <i>c</i> *	0.41 (0.03) <i>a</i>	0.47 (0.02) <i>ac</i>
Till	0.38 (0.01) <i>a</i>	0.81 (0.03) <i>b</i>	0.42 (0.02) <i>a</i>	0.41 (0.02) <i>a</i>	0.45 (0.02) <i>a</i>

Note: Values are means, with SE given in parentheses. Values in a row with the same letter are not significantly different ($P < 0.05$, ANOVA).

*Significant differences in SRL and diameter between the soil types ($P < 0.05$, ANOVA).

The length over diameter distribution shown in Fig. 4 indicates that the fine-root length of deciduous trees, herbs, and shrubs was concentrated in the diameter classes smaller than 0.6 mm, whereas fine-root length of conifers was more evenly distributed over the different diameter classes.

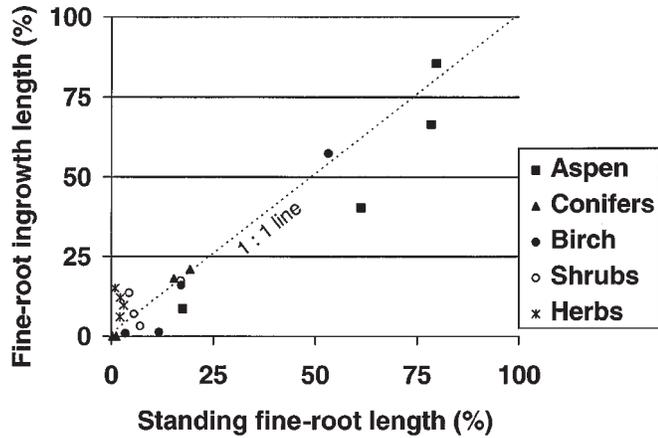
Fine-root architecture

The mean diameters and specific root lengths in both undisturbed soil and ingrowth cores were largely different between fine roots of deciduous and coniferous trees (Tables 4 and 6). Diameters of shrubs and herbs were similar to those of the deciduous tree species.

There was no significant effect of soil type on fine-root

tip and internode lengths or internode diameter in the species investigated. Thus, the data for the two soil types were pooled. Figures 5–8 depict schematically the fine-root systems of trembling aspen and conifers in the undisturbed soil and ingrowth cores based on average internode length and diameter of different orders of fine roots. Since no branching angles could be established on roots extracted from the soil, we used constant orthogonal branching angles for all species and soil environments in these figures. Although tip lengths were listed separately for long and short first-order fine roots, their diameters were not distinguished because they were not significantly different. A comparison between long and short first-order fine-root lengths and their different

Fig. 3. Relationship between the individual contribution of different species to the total standing fine-root length density (%) found in undisturbed cores versus that found in ingrowth cores (%) Every point represents the average of four plots for each treatment.



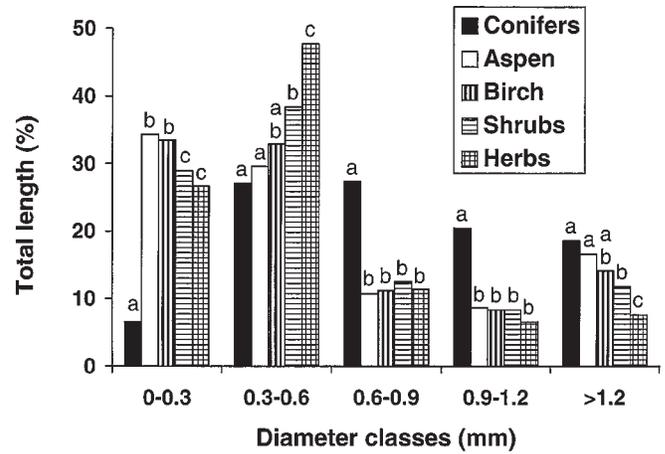
response to soil disturbance underscores the importance of differentiating the two root types in heterorhizic systems. In undisturbed soil, long root first-order links were, on average, between two and four times as long as short root first-order links. This difference was accentuated in conifer fine roots in ingrowth cores by one order of magnitude (Table 7, Figs. 7 and 8).

Trembling aspen root tips (first-order) and second-order internodes were generally shorter and thinner than those of conifers (Tables 7 and 8). Trembling aspen fine-root diameter increased abruptly from the third to the fourth order in forest floor material and from the second to the third order in mineral soil, whereas fine-root diameter of conifers increased more gradually from first- to fourth-order internodes (Table 8). In undisturbed soil, aspen fine-root third- and fourth-order internodes were equally long (third order in mineral soil) or longer than coniferous root internodes of the same order (Table 7). However, in ingrowth cores the third-order internodes of conifers were longer than those of trembling aspen.

In summary, in undisturbed soil trembling aspen fine-root systems were more intensive in the first two orders but more extensive in the third and fourth orders than coniferous fine-root systems. The dimensions of birch first- and second-order fine roots were similar to those of trembling aspen (Tables 7 and 8). Third- and fourth-order diameters of birch fine roots in undisturbed forest floor were smaller than in trembling aspen. Unfortunately, architectural analysis of birch fine-root systems could only be performed in the forest floor material, because those roots retrieved from the mineral soil were mostly in the form of small pieces that did not allow the analysis of root systems from the first to the fourth order.

The response to the initially root-free soil environment provided by ingrowth cores was different between species. Because of the large variation in tip and internode length, only a few of the differences between ingrowth cores and undisturbed soil were significant. The analysis of variance showed that ingrowth cores had the strongest influence on first-order long root and third- and fourth-order internode length, whereas the tree species was the most significant fac-

Fig. 4. Percentage of total fine-root length in different diameter classes among conifers, trembling aspen, paper birch, shrubs, and herbs in the forest floor of ingrowth cores ($n = 57-80$). Bars with the same letter within a diameter range were not significantly different ($P < 0.05$, ANOVA and post-hoc Tukey test).



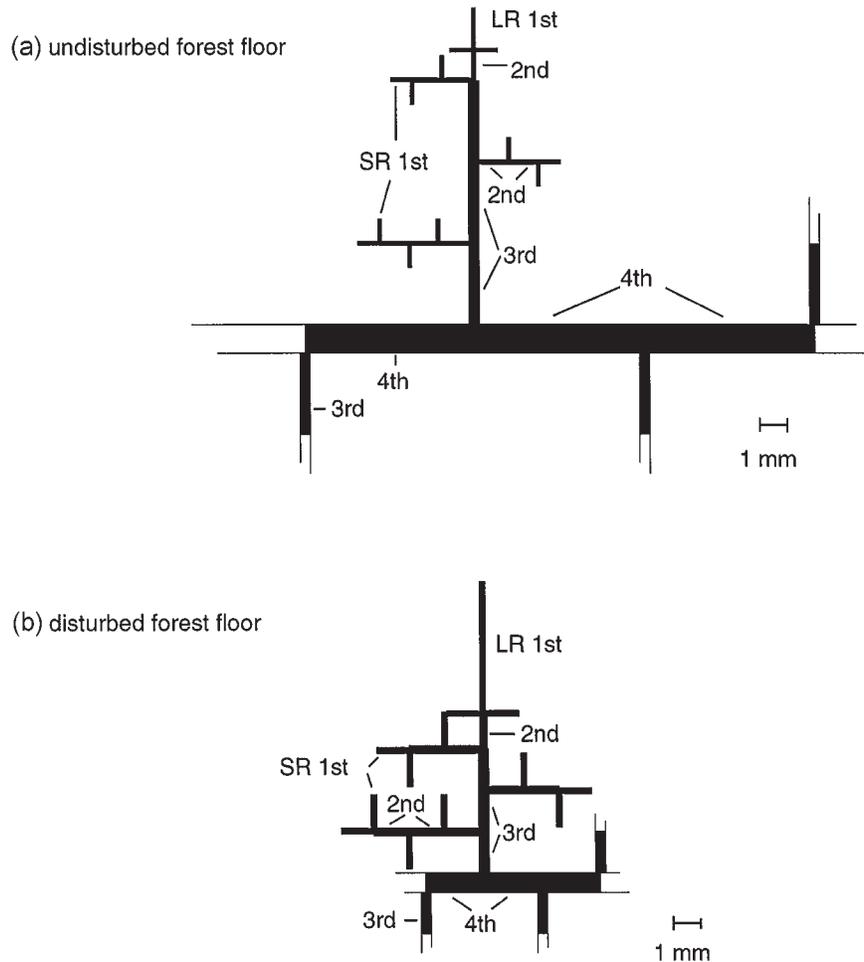
tor for first-order short root and second-order internode lengths. The effect of horizon on tip and internode lengths and diameter was generally small to nonsignificant. Tree species, ingrowth cores, and the soil horizon had a significant influence on the diameter of all orders of roots. First-, second-, and fourth-order roots were most strongly affected by tree species and ingrowth cores, whereas ingrowth core was the most significant factor for third-order internode diameter.

Conifer fine-root architecture was strongly affected by the change in soil environment brought about by ingrowth cores. Long root tip length increased significantly in the mineral soil and was also highly variable in both the forest floor and mineral soil of ingrowth cores (Table 7). Maximum long root tip lengths in the forest floor and mineral soil of ingrowth cores were 75 and 98 mm, respectively. No fourth-order fine roots developed in ingrowth cores. In contrast to aspen, second- and third-order internode lengths of conifers were consistently longer in the disturbed soil environment. Short root tip length showed the smallest response to the disturbed soil environment. Conifer fine-root diameters increased in the ingrowth core soil environment (Table 8). In general, conifers developed a less ramified, coarser fine-root system in the ingrowth cores (Figs. 7 and 8).

In the forest floor, aspen fine roots appeared to have responded to the ingrowth core environment with extended first-order links and reduced third- and fourth-order internodes (Table 7, Fig. 5). Response of internode length of trembling aspen fine roots in the mineral soil was similar as internode lengths increased for the first two orders but were shorter for the third- and fourth-order internodes. As indicated by the standard deviations (Table 7) the variability of internode length in ingrowth cores was higher than that in undisturbed soil, and thus only a few differences were significant.

The diameter of first- and second-order links in forest floor of ingrowth cores was 154% and 193% of the diameter in undisturbed forest floor, respectively (Table 8). Fourth-order

Fig. 5. Schematic representation of the fine-root system of trembling aspen in the forest floor of (a) undisturbed soil cores and (b) ingrowth cores. Drawings are based on average link lengths and diameters of long root (LR) and short root (SR) tips and internodes of second-, third-, and fourth-order roots ($n = 148-175$).



root diameter was only 68% of that in the original forest floor. No increase in aspen fine-root diameter was observed in the mineral soil of ingrowth cores (Fig. 6). Third-order internodes were significantly thinner than in undisturbed soil, however.

In the forest floor, birch fine roots showed no significant change in link lengths. However, the diameter of the first three root orders increased significantly (Table 8).

There was a negative curvilinear relationship between the average diameter of tree fine-root systems grown in various soil conditions and specific root length (Fig. 9; for clarity only data for trembling aspen and conifers are presented). The graph illustrates that changes in root diameter result in small changes in SRL for conifers, located at the flat end of the curve, whereas the same diameter changes in trembling aspen roots (which are even smaller changes if expressed on a root volume basis), result in strong changes of SRL because aspen is located at the steep section of the curve.

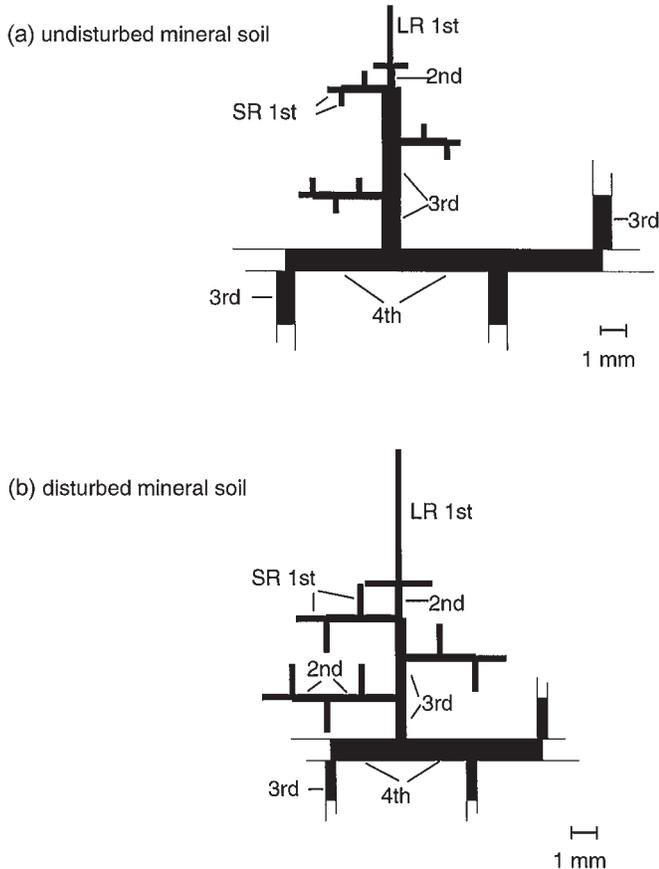
Discussion

Fine-root biomass and root length density

The measured quantities of fine-root biomass (<2 mm in diameter) are within the range reported elsewhere in the lit-

erature for comparable forest ecosystems and species (Messier and Puttonen 1993; Ruark and Bockheim 1987; Vogt et al. 1986; Makkonen and Helmisaari 1988). Our values are similar to the ones reported by Finér et al. (1997) for trembling aspen – paper birch forest of the same age sampled several hundred metres to some kilometres away from our sites. The percent contribution of conifers to the total fine-root biomass in conifer-dominated plots was less than their contribution to total basal area, a surrogate of above-ground biomass. The strong belowground presence of trembling aspen in conifer-dominated patches may be explained by the strong dominance of trembling aspen in areas surrounding the conifer plots and the intensive and far reaching network of lateral roots maintained by trembling aspen to facilitate sprouting of suckers and thus rapid site occupancy following forest disturbance (Lavertu et al. 1994). Thin and relatively unbranched trembling aspen laterals can be found at large distances from aspen trees in the forests at field sites (J. Bauhus, unpublished data) and in other aspen forests (Peterson and Peterson 1992). Our results show that fine-root biomass in conifer-dominated patches is not lower than in pure or almost pure aspen-dominated plots. The high fine-root biomass and length density produced by trembling aspen and paper birch in conifer-dominated plots indicates that

Fig. 6. Schematic representation of the fine-root system of trembling aspen in the mineral soil of (a) undisturbed soil cores and (b) ingrowth cores. Drawings are based on average link lengths and diameters of long root (LR) and short root (SR) tips and internodes of second-, third-, and fourth-order roots ($n = 136-184$).



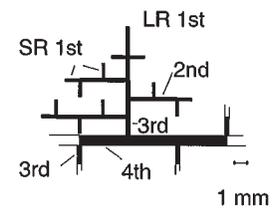
belowground competition must be intense in such coniferous patches within a matrix of otherwise deciduous-dominated forests. These results also suggest that overall soil exploitation is higher in mixed forests than in pure coniferous stands. This may also have implications for stand productivity in mixed versus pure conifer stands in this type of forest. It has been suggested that the decline in aboveground biomass (Paré and Bergeron 1995) and decreasing root length density (Finér et al. 1997) following the aggradation phase in the southern boreal forest was related to decreasing proportions of trembling aspen as stands age.

From our study it is not clear whether the very high root density of trembling aspen in ingrowth cores in till soil was a result of changed soil nutrient status resulting from soil disturbance or improved soil texture. However, it is important to note that only trembling aspen fine roots responded to those changes, whereas conifers did not, indicating a higher plasticity in fine-root growth of trembling aspen.

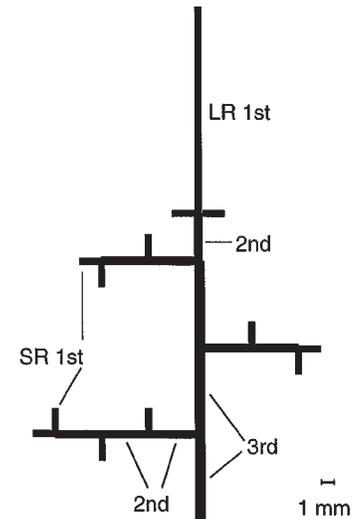
Eissenstat (1991) proposed that species with a high SRL also have the potential for high fine-root production rates in favourable soil environments. This had been confirmed by Fitter (1994) who found that species with thin fine roots proliferate more strongly in nutrient-enriched soil patches than species with larger mean root diameters. The above studies

Fig. 7. Schematic representation of the fine-root system of conifers (white spruce and balsam fir) in the forest floor of (a) undisturbed soil cores and (b) ingrowth cores. Drawings are based on average link lengths and diameters of long root (LR) and short root (SR) tips and internodes of second-, third-, and fourth-order roots ($n = 143-201$). The scale used is half that in Figs. 5 and 6.

(a) undisturbed forest floor



(b) disturbed forest floor

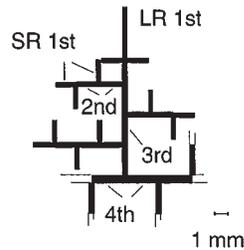


suggest that the proliferation of trembling aspen fine roots in till was a response to improved soil conditions. However, the proportion of aspen fine-root biomass and length in ingrowth cores was not higher than those proportions found in undisturbed soil (Figs. 2 and 3). A ratio greater than one in Figs. 2 and 3 would indicate a positive response of a given species to favourable soil patches. The highest ratios, which were particularly pronounced when expressed as length density, were found in herbaceous species, which may indicate a greater precision in allocating root carbon to favourable soil patches. This observation supports Grime's (1979) finding that root foraging is more precise in subordinate species within a community. The survival of understorey plants may depend on mechanisms to locate and effectively exploit favourable soil environments.

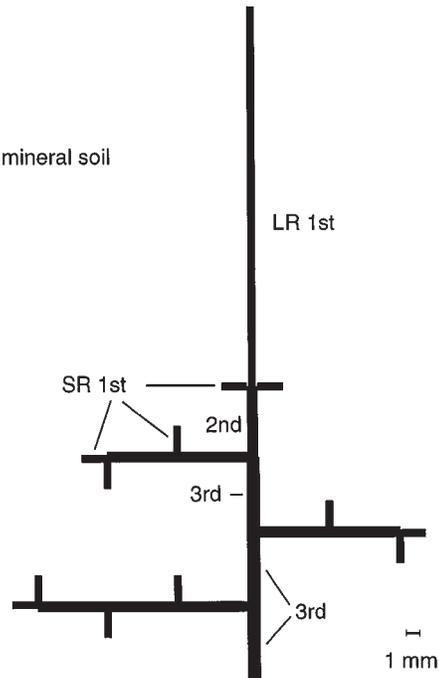
The ability to effectively take up mobile and poorly mobile nutrients from the soil depends on soil properties such as nutrient content and diffusion and on the root length density. The fine-root density of trembling aspen in aspen plots ($4.33-5.25 \text{ cm}\cdot\text{cm}^{-3}$) was high and appears to be sufficient to access even poorly mobile nutrients (Barley 1970), whereas

Fig. 8. Schematic representation of the fine-root system of conifers (white spruce and balsam fir) in the mineral soil of (a) undisturbed soil cores and (b) ingrowth cores. Drawings are based on average link lengths and diameters of long root (LR) and short root (SR) tips and internodes of second-, third-, and fourth-order roots ($n = 129-183$). The scale used is half that in Figs. 5 and 6.

(a) undisturbed mineral soil



(b) disturbed mineral soil



the low root density of conifers ($0.66-0.67 \text{ cm}\cdot\text{cm}^{-3}$) suggests that there might be a high dependency on ectomycorrhizal associations to produce higher length densities for effective nutrient uptake.

Fine-root architecture

Specific root lengths of trembling aspen and paper birch were similar to those reported for other northern hardwood species (Fahey and Hughes 1994; Pregitzer et al. 1997), and SRL of conifers was similar to values reported for Norway spruce (*Picea abies* (L.) Karst.) in Sweden (Clemensson-Lindell and Persson 1995). The fine-root diameters corresponded with values given by Brundrett et al. (1990). Specific root length was substantially higher in trembling aspen, paper birch, shrubs, and herbs than in balsam fir and

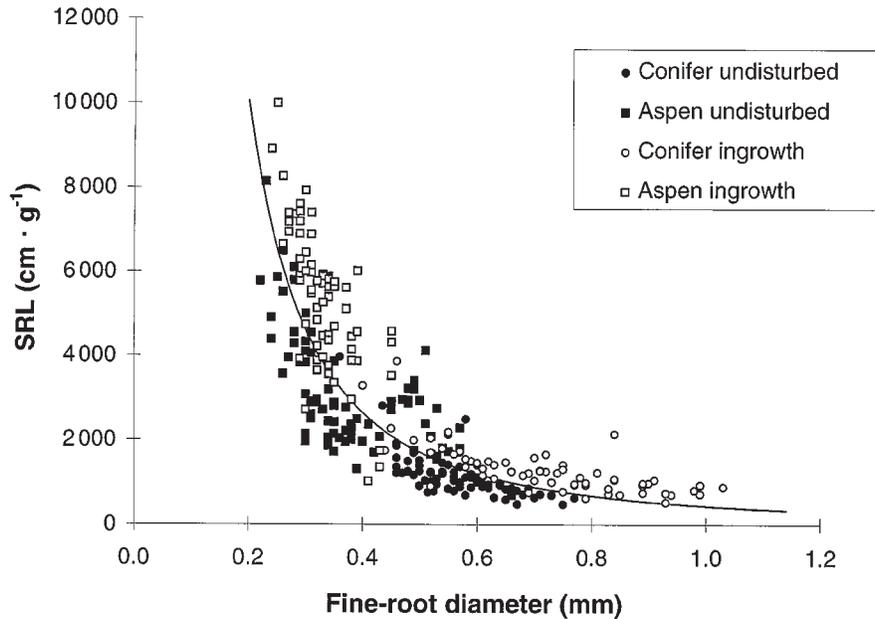
white spruce. Therefore, the first species group can exploit larger soil volumes per unit of C used in root construction than can the conifers. The location of aspen and conifers on the curve depicting the negative curvilinear relationship between root diameter and SRL indicates that diameter has a stronger influence on aspen SRL than on conifer SRL (Fig. 9). The increase in fine-root diameter of conifers in ingrowth cores when compared with undisturbed soil entailed no significant decrease in SRL (Fig. 9). This morphological change would represent an advantageous adaptation if thicker roots resulted in higher uptake and transport capacity for water and nutrients. If thick roots were white and unsuberized, increased root surface area would facilitate higher nutrient uptake per unit root length and increase the depletion zone area (Barber 1984). However, this would be an inefficient way to increase the depletion zone since the ratio of root depletion zone to root volume for a single root is always greater for thin roots. The underlying reason for the increase of fine-root diameter of conifers in disturbed soil obviously deserves further research. Clemensson-Lindell and Persson (1995) proposed that an increase in SRL of spruce fine roots was indicative of improved root vitality, whereas a decrease in SRL was attributed to adverse soil chemical conditions. The addition of high quantities of ammonium reduced SRL by more than 40% in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings, indicating that N supply, the form of mineral N, and rhizosphere pH may have a strong influence in SRL (Olsthoorn et al. 1991).

Although the ratio of C cost of root construction to root surface area is more favourable in thin than in thick roots, the production of thin fine roots may not be a more efficient means of soil exploitation than the production of thick roots. Despite a more favourable SRL in thin roots, the overall C cost may be higher because of higher rates of respiration and root turnover (Reynolds 1975; Eissenstat 1992; Pregitzer et al. 1997). In addition, thin fine roots have a limited growth potential and transport capacity (Fitter 1987). The rate of mycorrhizal infection may determine whether thick and long-lived or thin and short-lived roots are more advantageous in terms of C costs. Plants may only benefit from mycorrhizal infection on roots with greater longevity since this association provides more long-term than immediate benefits (Fitter 1985).

Thin fine roots in deciduous trees and coarser fine roots in coniferous trees may be analogous to needles and leaves of evergreen and deciduous trees. In generalized terms, needles of shade-tolerant conifers have a higher longevity, lower respiration costs, and lower photosynthetic capacity than leaves of shade-intolerant deciduous trees (Stenberg et al. 1995).

The average internode length of trembling aspen's second-order and third-order roots, 1.1 mm in forest floor and 0.91 mm in mineral soil and 2.95 mm in the forest floor and 2.09 mm in mineral soil, respectively, correspond well with the internode lengths of aspen given by Lyford (1975). Using a different root branch classification, Lyford reported equivalent values of 1.25 mm for second-order roots and 2.5 mm for third-order roots. Lyford's values for internode length of yellow birch (*Betula alleghaniensis* Britt.) are 2.00 mm for second-order roots and 3.33 mm for third-order roots. The similarity in values measured between our study

Fig. 9. Relationship between fine-root diameter (mm) and specific root length (SRL) ($\text{cm}\cdot\text{g}^{-1}$) for fine-root systems of trembling aspen and conifers in the forest floor of undisturbed soil cores and ingrowth cores. The regression equation is $y = 1/[0.009(d/2)^2]$, where d is diameter ($r^2 = 0.90$).



and that of Lyford (1975) suggest that internode lengths in these species is relatively insensitive to different soil environments. This assumption is corroborated by the finding that few significant differences in aspen internode lengths occurred among different soil types, among horizons, and between ingrowth cores and undisturbed soil. Link lengths of black birch (*Betula lenta* L.) measured by Crabtree and Berntson (1994) were substantially longer than those we measured for paper birch. However, Crabtree and Berntson (1994) determined root architecture on seedlings grown in 70% shade, which may have influenced root C allocation and thus fine-root architecture.

The response of coniferous root systems to the ingrowth core soil environment, namely extended tip and internode lengths, can be seen as an increase in exploitation efficiency sensu Fitter et al. (1991) and Berntson (1994). Soil "exploitation efficiency" can be defined as the soil volume the depletion zones around roots occupy per unit volume of root tissue (Fitter et al. 1991). The radius of the depletion zone depends largely on the mobility of a specific nutrient, and thus, for the same root the extent of the depletion zone varies for the different nutrients. The potential overlap of depletion zones within a fine-root system increases with the radius of depletion zones around individual roots. Based on our study we cannot quantify these depletion zones and their overlaps, but it is possible to discuss the implications that the different fine-root systems may have for resource acquisition.

Berntson (1994) proposed that the optimization of soil exploitation efficiency to increase the amount of soil exploited per unit of root volume was the most important adaptive response in plants with root growth limited by carbon allocation belowground. Simulation models of root growth and resource acquisition (Fitter et al. 1991; Berntson 1994; Nielsen et al. 1994) have shown that there are trade-offs between

soil exploitation efficiency and exploitation potential. "Exploitation potential" is defined as the total volume of soil exploited by the root system. Soil exploitation potential is increased through the development of greater root length.

Following from the above, the extension of root tip and internode lengths results in less overlap of depletion zones around roots and thus in increased exploitation efficiency. A comparison of aspen tip and internode lengths between ingrowth cores and undisturbed soil indicates little change in exploitation efficiency and the maintenance of a dense fine-root system. The same may be said for paper birch since no change in tip and link lengths was observed. Because the older fine roots in undisturbed soil may have lost or shed root branches leading to an increase in the apparent internode length, the differences in internode lengths of higher order roots between disturbed and undisturbed soil are difficult to interpret and will not be further discussed.

The underlying cause of reduced ramification in conifers in ingrowth cores is unknown. It is important to remember that the fine-root systems as depicted in Figs. 7 and 8 are only a picture in time. It can be assumed that, with time, the fine-root systems of conifers in ingrowth cores would fill in and assume a structure similar to that in undisturbed soil. In addition the changed physical soil conditions in ingrowth cores may also cause significant deviations from the development of fine-root structures in the undisturbed soil.

The marked increase in length of first-order long root tips of conifers in ingrowth cores is contrasted by the small increase in length of first-order short root tips. This points to different functions of long and short roots. It has been suggested that slow growth of short roots is necessary to facilitate the development of ECM (Sohn 1981). If this is in fact an evolutionary adaptation to facilitate the establishment of the symbiotic relationship between plant and fungus, it may explain our observations.

Table 7. Fine-root internode length (mm) of trembling aspen, conifers, and paper birch in forest floor and mineral soil of undisturbed soil cores and ingrowth cores.

Species	Horizon	Sample type	LR first	SR first	Second	Third	Fourth
Aspen	Forest floor	Undisturbed soil core	1.58 (0.73) <i>a</i>	0.81 (0.39) <i>ab</i>	1.10 (0.87) <i>a</i>	2.95 (2.01) <i>a</i>	6.23 (4.89) <i>a</i>
		Ingrowth core	4.76 (4.48) <i>ab</i>	1.27 (1.01) <i>bc</i>	1.29 (0.68) <i>a</i>	1.50 (0.91) <i>a</i>	2.14 (1.48) <i>b</i>
	Mineral soil	Undisturbed soil core	2.31 (1.30) <i>ab</i>	0.53 (0.30) <i>a</i>	0.91 (0.49) <i>a</i>	2.09 (1.42) <i>a</i>	4.17 (2.88) <i>ab</i>
		Ingrowth core	5.21 (3.78) <i>ab</i>	1.18 (0.85) <i>b</i>	1.35 (0.85) <i>a</i>	1.57 (0.98) <i>a</i>	2.78 (1.95) <i>b</i>
Conifers	Forest floor	Undisturbed soil core	2.42 (1.15) <i>ab</i>	1.18 (0.86) <i>b</i>	1.85 (1.44) <i>a</i>	1.45 (1.28) <i>a</i>	3.91 (4.69) <i>ab</i>
		Ingrowth core	16.2 (16.5) <i>b</i>	1.75 (1.81) <i>c</i>	5.78 (3.71) <i>b</i>	6.83 (8.96) <i>b</i>	
	Mineral soil	Undisturbed soil core	4.11 (2.02) <i>ab</i>	1.67 (1.57) <i>c</i>	1.77 (1.33) <i>a</i>	2.37 (2.30) <i>a</i>	2.61 (2.61) <i>b</i>
		Ingrowth core	29.4 (26.4) <i>d</i>	2.02 (1.87) <i>c</i>	5.50 (7.91) <i>b</i>	5.78 (6.37) <i>b</i>	
Birch	Forest floor	Undisturbed soil core	3.49 (3.84) <i>ab</i>	0.96 (0.54) <i>ab</i>	1.81 (1.49) <i>a</i>	1.94 (1.54) <i>a</i>	2.48 (1.79) <i>b</i>
		Ingrowth core	5.38 (4.28) <i>ab</i>	0.99 (0.48) <i>ab</i>	1.64 (1.68) <i>a</i>	1.57 (1.31) <i>a</i>	2.31 (1.72) <i>b</i>

Note: Values are means, with SD given in parentheses. Internode length is given for first-, second-, third-, and fourth-order roots. First-order roots of ectomycorrhizal tree fine roots were categorized as long roots (LR) and short roots (SR). Coniferous fine roots of the fourth order had not developed in ingrowth cores. Values in a column with the same letter are not significantly different ($P < 0.05$, ANOVA).

Table 8. Fine-root internode diameter (mm) of trembling aspen, conifers, and paper birch in forest floor and mineral soil of undisturbed soil cores and ingrowth cores.

Species	Horizon	Sample type	First	Second	Third	Fourth
Aspen	Forest floor	Undisturbed soil cores	0.13 (0.04) <i>a</i>	0.14 (0.04) <i>a</i>	0.37 (0.09) <i>ac</i>	1.04 (0.31) <i>a</i>
		Ingrowth cores	0.21 (0.06) <i>b</i>	0.27 (0.08) <i>b</i>	0.37 (0.10) <i>ac</i>	0.71 (0.13) <i>b</i>
	Mineral soil	Undisturbed soil cores	0.20 (0.05) <i>b</i>	0.28 (0.07) <i>b</i>	0.73 (0.16) <i>b</i>	0.86 (0.26) <i>ac</i>
		Ingrowth cores	0.21 (0.06) <i>b</i>	0.27 (0.05) <i>b</i>	0.41 (0.12) <i>c</i>	0.84 (0.38) <i>ac</i>
Conifers	Forest floor	Undisturbed soil cores	0.24 (0.08) <i>b</i>	0.28 (0.08) <i>b</i>	0.34 (0.12) <i>a</i>	0.80 (0.21) <i>c</i>
		Ingrowth cores	0.50 (0.16) <i>c</i>	0.62 (0.23) <i>c</i>	0.79 (0.33) <i>d</i>	
	Mineral soil	Undisturbed soil cores	0.35 (0.12) <i>d</i>	0.41 (0.13) <i>d</i>	0.43 (0.16) <i>c</i>	0.60 (0.15) <i>d</i>
		Ingrowth cores	0.57 (0.21) <i>e</i>	0.80 (0.30) <i>e</i>	0.99 (0.30) <i>e</i>	
Birch	Forest floor	Undisturbed soil cores	0.14 (0.05) <i>a</i>	0.18 (0.05) <i>a</i>	0.21 (0.05) <i>f</i>	0.58 (0.18) <i>d</i>
		Ingrowth cores	0.24 (0.05) <i>b</i>	0.29 (0.06) <i>b</i>	0.41 (0.07) <i>c</i>	0.66 (0.07) <i>b,d</i>

Note: Values are means, with SD given in parentheses. No architectural analysis of birch roots from the mineral soil was carried out. Internode diameter is given for first-, second-, third-, and fourth-order roots. Coniferous fine roots of the fourth order had not developed in ingrowth cores. Values in a column with the same letter are not significantly different ($P < 0.05$, ANOVA).

Conclusions

Our results indicate very different strategies of soil exploitation in conifers, such as balsam fir and white spruce, on one hand and deciduous tree species, such as trembling aspen and paper birch, and herbs and shrubs on the other hand. The conifers appear to follow a conservative strategy of relatively slow development of a coarse and presumably long-lived fine-root system. This may be indicative of an adaptation to conditions where root growth is limited by C and plants develop fewer roots with longer internodes and root tips and a low degree of branching because they cannot afford to develop many roots in parts of the soil that may not prove profitable enough. Both balsam fir and white spruce are considered shade tolerant, and this adaptation might be beneficial for the period of time when they grow and develop beneath the canopy of the shade-intolerant deciduous trees. In contrast, shade-intolerant tree species, such as trembling aspen and paper birch, and shade-tolerant understory herbs and shrubs seem capable of rapid colonization of favourable soil environments while maintaining highly ramified thin fine roots to maximize the volume of soil exploited. Whether or not the former or the latter strategy is more effi-

cient in terms of the C invested per unit of water and nutrients obtained depends among other things on the longevity, respirational C cost, C exudation, C allocated to mycorrhizae, and the uptake capacity of the fine-root system for different nutrients and water. These aspects were not addressed in this study, but they require further investigation. The differences in fine-root soil exploitation strategies among tree species, herbs, and shrubs reported in this study might be as important as those reported for aboveground growth to explain intraspecific competition and coexistence in different environments of the boreal forest ecosystem.

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