Fine-root dynamics in mixed boreal conifer – broad-leafed forest stands at different successional stages after fire

Leena Finér, Christian Messier, and Louis De Grandpré

Abstract: Fine-root (diameter ≤ 10 mm) standing biomass, length, distribution, production, and decomposition were studied in mixed conifer – broad-leafed forest stands 48, 122, and 232 years after fire on clay soils in the southern boreal forest of Quebec. A combination of ingrowth bags, soil cores, and root litter bags was used. Forest composition changed from trembling aspen- (*Populus tremuloides* Michx.) dominated stands in the youngest stage to balsam fir (*Abies balsamea* (L.) Mill.), and then to eastern white-cedar (*Thuja occidentalis* L.) stands in the oldest stage. The fine- and small-root standing biomass did not differ significantly between the forest successional stages. However, the total root length was significantly more developed in the 48-year-old successional stand than in the 232-year-old stand. Within the investigated soil profile (depth =30 cm) most roots (>80%) were found in the 5 to 8 cm thick organic layer and the top 10 cm of the mineral soil. Root biomass in the organic layer increased significantly after fire, and a simultaneous increase in thickness of the organic layer was observed. The ingrowth of roots into ingrowth bags during one and two growing seasons was more than twice as high in the youngest stand as in the oldest one. However, the differences were not statistically significant because of high variation. Fine roots of aspen decomposed significantly faster than those of balsam fir and cedar in all forest stands. The results suggest that root production, the rate of decomposition, and presumably the rate of turnover are higher in forest stands dominated by early successional broad-leafed species such as aspen than in stands composed of late successional coniferous species such as fir, spruce, and cedar. Differences in root dynamics may contribute significantly to the change in the carbon and nutrient cycling often reported with succession in the boreal forest.

Résumé : La biomasse totale, la longueur, la distribution, la production et la décomposition des radicelles (diamètre ≤ 10 mm) ont été mesurées 48, 122 et 232 ans après feu dans des peuplements mixtes de conifères et de feuillus établis sur des sols argileux dans le Sud de la forêt boréale du Québec. Une combinaison de méthodes a été utilisée : des sacs de croissance, des carottes de sol et des sacs de décomposition des radicelles. La composition en espèces forestières passait des peuplements dominés par le peuplier faux-tremble (*Populus tremuloides* Michx.), dans le stade le plus jeune, aux peuplements de sapin baumier (*Abies balsamea* (L.) Mill.) et de thuya occidental (*Thuja occidentalis* L.), dans le stade le plus âgé. Les peuplements des divers stades de succession n'étaient pas significativement différents entre eux quant à la biomasse totale des radicelles et des petites racines. Cependant, la longueur totale des racines dans le peuplement de 48 ans était significativement supérieure à celle du peuplement de 232 ans. Dans le profil de sol étudié (profondeur = 30 cm), la majeure partie des racines (> 80%) était localisée dans la couche organique de 5 à 8 cm d'épaisseur et dans les 10 premiers centimètres du sol minéral. La biomasse des racines situées dans la couche organique augmentait significativement après feu. Un accroissement simultané de l'épaisseur de la couche organique était également observé. Dans le peuplement le plus jeune, après une et deux saisons de végétation, la croissance des radicelles dans les sacs de croissance était plus du double de celle observée dans le peuplement le plus âgé. En raison de la très grande variation, ces différences n'étaient toutefois pas statistiquement significatives. Dans tous les peuplements forestiers, les radicelles du peuplier se décomposaient significativement plus rapidement que celles du sapin et du thuya. Ces résultats suggèrent que la production des radicelles, la vitesse de décomposition, et vraisemblablement la vitesse du turnover, sont plus grandes dans les peuplements forestiers dominés par des espèces feuillues des premiers stades de succession, comme le peuplier faux-tremble, que dans les peuplements composés d'espèces de conifères des stades de succession avancés comme le sapin, l'épinette et le thuya. Ces différences dans la dynamique des radicelles pourraient contribuer aux changements, souvent rapportés en forêt boréale, dans les cycles du carbone et des éléments nutritifs selon les stades de succession.

[Traduit par la Rédaction]

L. Finér. The Finnish Forest Research Institute, Joensuu Research Station, P.O. Box 68, SF80101 Joensuu, Finland.
C. Messier and L. De Grandpré. Université du Québec à Montréal, Groupe de recherche en écologie forestière (GREF), Département des sciences biologiques, CP 8888, Succursale Centre-Ville, Montréal, QC H3C 3P8, Canada.

Introduction

In the southern boreal forests in the Northern Clay Belt of Quebec and Ontario, vegetation types vary in relation to the deposits on soil surface and successional stages (Bergeron and Dubuc 1989). Clay deposits are typical on lowlands where early successional stands are frequently characterized by the abundance of deciduous species such as trembling aspen (*Populus tremuloides* Michx.) and paper birch (*Betula papyrifera* Marsh.). They are replaced in later succession by coniferous

tree species such as white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), and eastern white-cedar (*Thuja occidentalis* L.) (see Bergeron et al. 1982; Bergeron and Dubuc 1989). The growth and structure of the natural forests are controlled by two major types of disturbance, fire and spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks, that occur at regular intervals (Bergeron 1991; Dansereau and Bergeron 1993; Morin et al. 1993). Fires have been less frequent during the last 120 years than before that, and the fire cycle has been prolonged from 60–70 years to about 100 years (Bergeron 1991). But the fire cycles are nevertheless so short that forests seldom reach a steady state in terms of species composition or humus accumulation, but succession still occurs after 200 years on mesic sites (Bergeron and Dubuc 1989).

The aboveground succession of overstorey and understorey species is well documented in boreal forests (Bergeron and Dubuc 1989; De Grandpré et al. 1993; Paré and Bergeron 1995). However, little is known about fine-root production and decompostion during the forest succession. It has been shown that a substantial proportion of the annual net primary production is allocated to fine roots in boreal forest ecosystems (e.g., Ågren et al. 1980; Grier et al. 1981; Keyes and Grier 1981). Indeed, the carbon input from fine roots to the forest soil may be even more substantial than that from the aboveground parts of the trees (e.g., Vogt et al. 1986).

During forest succession not only the species composition changes, but also the soil chemical and physical environment, which may affect the fine-root dynamics. The humus layer at the surface gradually gets thicker, and previously readily available nutrients are immobilized (Flanagan and Van Cleve 1983; Van Cleve et al. 1983; Paré et al. 1993; Brais et al. 1995). Trees respond to low nutrient availability by increasing the proportion of the annual biomass production, which is allocated to fine roots at the expense of other parts of the tree (e.g., Keyes and Grier 1981; Vogt et al. 1983*a*, 1983*b*; Axelsson and Axelsson 1986). Some plant species can even search for new resources by penetrating into deeper soil horizons (Strong and La Roi 1983*a*; Gale and Grigal 1987). Therefore, the role of fine roots in the carbon and nutrient cycling in boreal forests may change with succession.

The aim of our study was to document how fine- and small-root distribution, production, and decomposition vary among different plant species associated with different successional stages after fire in the southern boreal forest of northwestern Quebec.

Material and methods

The sites

Root sampling was carried out in three southern boreal forest stands at different successional stages after fire around Lake Duparquet (48°30′N, 79°20′W, 300 m above sea level) in northwestern Quebec, Canada. The youngest forest stand, representing the early successional stage, was 48 years old and dominated by trembling aspen with a minor component of paper birch (Table 1). The midsuccessional stand was 122 years old and dominated by trembling aspen and white spruce, with a minor component of balsam fir and paper birch. The oldest, late successional stand was 232 years old and was dominated by eastern white cedar and balsam fir, with some trembling aspen, white spruce, and paper birch. A severe spruce budworm outbreak

from 1970 to 1987 in the area killed most of the balsam fir and white spruce trees (Morin et al. 1993).

The ground layer was characterized by herbs and deciduous shrubs in the early successional stage and yew (*Taxus canadensis* Marsh.) and mountain maple (*Acer spicatum* Lamb.) for the mid and late successional stages (Table 1). The nomenclature of plant species follows the *Flore Laurentienne* (Marie-Victorin 1964). The fire history of the forests in the region was described by Bergeron (1991) and Dansereau and Bergeron (1993), and the succession of the forest vegetation, by Bergeron and Dubuc (1989), De Grandpré et al. (1993), and Paré and Bergeron (1995). The soils consist of clay deposited from postglacial lakes (Grey Luvisol, Canada Soil Survey Committee 1978). The organic layer was on average 5.3, 7.5, and 8.0 cm thick in the 48-, 122-, and 232-year-old stands, respectively. The characteristics of organic layers in these forest stands have been described in detail by Paré et al. (1993) and Brais et al. (1995). The mean annual temperature is 0.6°C, the mean annual precipitation is 823 mm, and the mean annual frost-free period is 67 days at the nearest meteorological station in La Sarre, 35 km north of Lake Duparquet.

The study was carried out in three stands in each of the three successional stages. All sampling was done in one 10×10 m plot in each stand, with a total number of nine plots. All plots were within 20 km from each other. The plots were completely randomly distributed.

Root biomass and length measurements

Fine and small roots were sampled with the core sampling method (Böhm 1979; Vogt and Persson 1991) at the beginning of June 1993. In each plot, eight cylindrical cores (area 38 cm^2, depth 30 cm in mineral soil) were systematically taken with a stainless steel corer (diameter 3.48 cm, length 50 cm). The cores were divided starting from the surface as follows: organic soil layer, 0–10, 10–20, and 20–30 cm in mineral soil. Only every second sample was taken from the deepest soil layer because of the difficulties in sampling. In the laboratory roots were separated into the following diameter classes: <1, 1–2, 2–5, and 5–10 mm, called later in the text as very fine, fine, small, and coarse roots, respectively. The fine, small, and coarse (diameter 1–10 mm) identifiable roots were further separated into the following species or species groups: trembling aspen; white birch; balsam fir and white spruce; Canada yew; eastern white-cedar; deciduous shrubs; and herbs and grasses combined. The identification was done microscopically by comparing the root samples with known roots from the sites. Root characteristics such as colour, smell, taste, resilience, type of mycorrhiza, existence of root hairs, woody structure, and (or) resin were used for species identification. Root mass was determined after drying at 70°C to constant mass. The length of roots was measured with the MacRhizo™ image processing system (Régent Inst., Québec City, Canada). The length of very fine roots (diameter < 1 mm) was estimated for a subsample. "Roots" included both roots and rhizomes.

Root production measurements

A total of 12 root ingrowth bags (see method Vogt and Persson 1991) made of plastic mesh and filled with root-free soil from the stands were installed systematically in all plots in August 1992. Bags (surface area 45 cm^2) were inserted to a soil depth of 30 cm, starting from the surface of the forest floor. A 2–3 cm thick peat layer was put on the top of each bag. Five bags filled with root-free sand were installed adjacent to the other bags to compare the efficiency of sand material with that of soil taken from the stands (clay in this case). The sand all came from a nearby dune. Half of the bags filled with the soil from the stands and all sand bags were taken up from the field in September 1993, 1 year after the installation, and the other half in September 1994, 2 years after installation. In the laboratory, all roots were separated from the bags and divided into two diameter classes (<1 mm and 1–10 mm) and grouped by species as follows: herbs and grasses; balsam fir and white spruce; cedar; Canada yew; and the other woody

Table 1. Tree and field layer characteristics of the forests.

(A) Trees

	48-year-old stand		122-year-old stand		232-year-old stand	
	Stems/ha	Basal area $(m^2 \cdot ha^{-1})$	Stems/ha	Basal area $(m^2 \cdot ha^{-1})$	Stems/ha	Basal area $(m^2 \cdot ha^{-1})$
Populus tremuloides	1831	32.6	1063	13.4	67	9.3
Betula papyrifera	486	3.1	563	3.6	24	1.3
Abies balsamea	418	0.5	888	2.8	1642	13.6
Picea glauca			363	14.4	24	2.5
Thuja occidentalis			538	1.3	1230	17.0
Total	2735	36.2	3415	35.5	2987	43.7

(B) Field layer

	48-year-old stand		122-year-old stand		232-year-old stand	
	Plants/m^2	Cover (%)	Plants/m^2	Cover (%)	Plants/m^2	Cover (%)
Herbs and grasses						
Aster macrophyllus	36.4	46.0	4.5	7.2	0.2	0.1
Aralia nudicaulis	6.9	13.3	1.5	3.4	1.9	7.1
Clintonia borealis	4.3	3.2	4.4	4.4	1.9	1.1
Pteridium aquilium	1.3	10.4	0.0	0.1		
Others	20.0	4.0	29.9	8.3	7.6	2.6
Total	68.9	76.9	40.3	23.4	11.6	10.9
Shrubs						
Taxus canadensis	0.2	1.1	5.5	23.3	9.6	47.6
Acer spicatum	1.9	16.1	2.6	26.3	2.9	17.5
Diervilla lonicera	3.8	7.7			0.1	0.1
Others	9.6	9.5	8.4	8.8	1.1	2.5
Total	15.5	34.4	16.5	58.4	13.7	67.7

Table 2. Total root (diameter ≤ 10 mm) biomass and length in stands at different successional stages after fire and the results of variance analyses, with root biomass and root length on stands of different successional stages as the dependent variables (df = 2).

Stand	Root biomass (g·m^{-2})	Root length (m·m^{-2})
48-year-old	1056 (289)	12 857 (3667)
122-year-old	827 (193)	8 200 (1107)
232-year-old	952 (170)	7 181 (404)
F-value	0.80	5.55
p-value	0.49	0.04

Note: Standard deviation is in parentheses.

deciduous species (e.g., aspen, birch, mountain maple); and all dead roots. The dry mass was determined after drying at 70°C to constant mass.

Decomposition experiment

In June 1993, the very fine and fine roots (≤2 mm) of cedar, aspen, and balsam fir were gently collected from mature trees from the three successional stands and carefully cleaned with water. For each plot, ten 10 × 10 cm nylon bags with mesh size of 0.7 mm were filled with 0.7 g of ovendried (dried at 70°C to constant mass) very fine and fine-root material of each species. The bags were placed systematically at a depth of 4 cm from the surface in the replicate plots in June 1993. Half of them were lifted in September 1993 and the other half in September 1994. Dry mass loss was determined in the laboratory. Total nitrogen content of aspen, fir, and cedar roots before incubation was 0.96%, 0.86%, and 0.83%, respectively.

Statistical tests

Mean differences between forest stands at different successional stages were tested by multivariate analysis of variance and paired comparisons with the orthogonal contrasts. Differences between soil layers and successional stages were tested with the repeated measures procedure, because the different layers were not independent. No transformations were made to the data prior to the analysis. All statistical tests were done with the MANOVA procedure of the SPSS/PC+ (SPSS Inc. 1988) statistical package. The biomass and length-weighted diameters (i.e., Σ(diameter × length or biomass)/Σ(length or biomass), respectively) were calculated by assuming that roots in the diameter classes <1, 1–2, 2–5, and 5–10 mm have a mean diameter of 0.5, 1.5, 3.5, and 7.5 mm, respectively.

Results

Root biomass and length

Total standing root biomass did not vary significantly among the three successional forest stands (Table 2). However, root length was significantly greater in the 48-year-old stand. Roots were concentrated near the surface, mostly in the organic layers in all studied forest stands (Fig. 1, Table 3). The depth distribution of root biomass was more superficial in the 232-year-old than in the other younger successional forest stands, but that of root length did not correlate with the age of the forest stand. The very fine roots (<1 mm) accounted for more than 90% of total root length, whereas root biomass was more evenly distributed among the different diameter classes. The

Fig. 1. Standing root (diameter ≤ 10 mm) biomass and length in different soil layers and diameter classes in forest stands at different successional stages after fire.
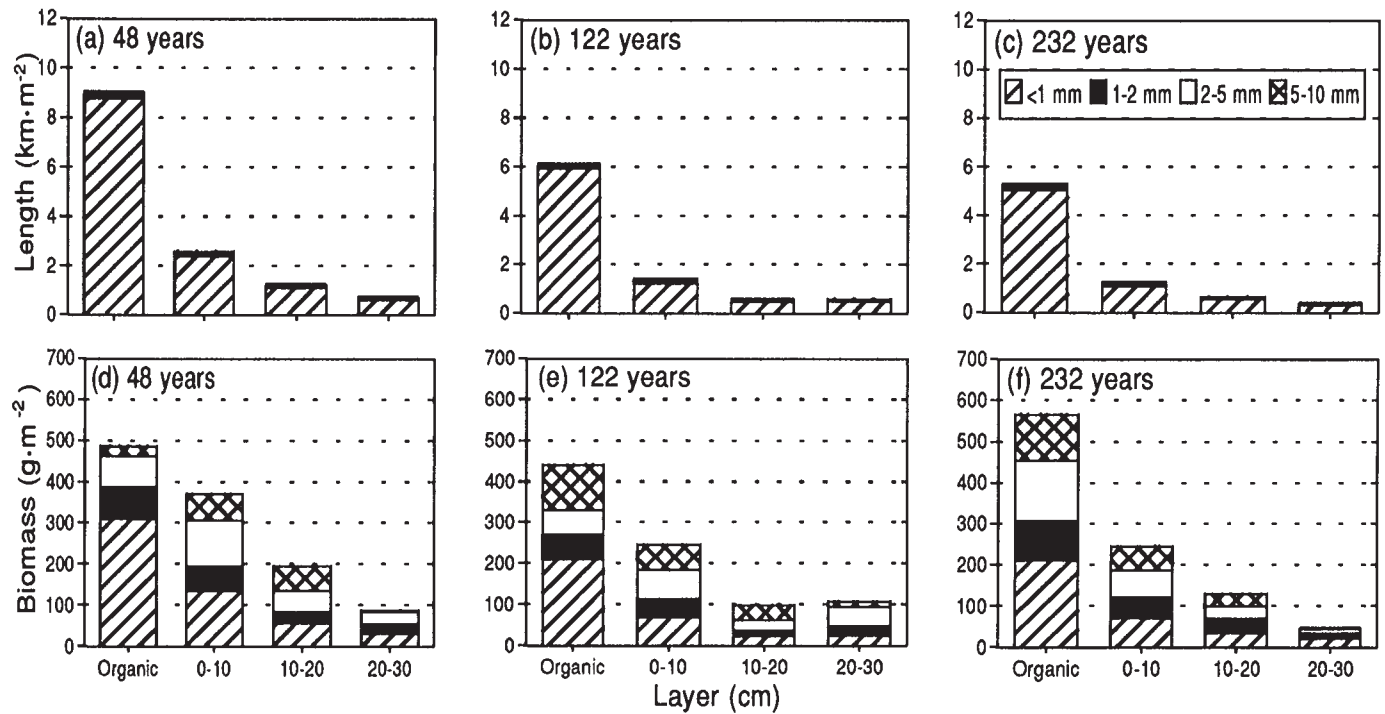

Table 3. The results of repeated measures analysis of variance, with root biomass and root length of different species in different soil layers as the dependent variables (df = 3) and stands of different successional stages as the independent variable (df = 2).

	Root mass		Root length	
	F-value	p-value	F-value	p-value
All species				
Soil layer	81.97	0.00	174.53	0.00
Stand × soil layer	2.30	0.08	4.55	0.06
Populus tremuloides				
Soil layer	5.70	0.06	32.04	0.00
Stand × soil layer	0.49	0.81	4.87	0.00
Betula papyrifera				
Soil layer	1.95	0.16	3.60	0.03
Stand × soil layer	0.71	0.65	1.41	0.26
Shrubs				
Soil layer	14.13	0.00	6.53	0.00
Stand × soil layer	3.61	0.02	1.53	0.22
Herbs and grasses				
Soil layer	22.61	0.00	12.40	0.00
Stand × soil layer	8.28	0.00	2.30	0.08

root length-weighted diameter showed that roots were statistically finer in the organic layer than in the mineral soil layers (Table 4). The root biomass-weighted diameter showed that roots were finer in the 48-year-old forest stand than in the older ones, especially in the surface soil layers (Table 4).

Tree species accounted for 66–80% of the root biomass and 63–71% of the root length (Fig. 2). The proportions did not differ among the successional stages. Aspen dominated tree root biomass and length in the 48- and 122-year-old stands, whereas cedar, aspen, fir, and spruce dominated in the 232-year-old stand. The proportional abundance of birch decreased with succession, and that of spruce and fir increased.

The roots of deciduous shrubs were the most abundant of the ground layer species in the youngest successional stage (Fig. 2). Canada yew replaced deciduous shrubs in the mid-successional stage. Because the roots of Canada yew were thicker than those of shrubs, herbs, and grasses, it dominated more in root biomass than in length. The roots of herbs and grasses were more abundant in the youngest successional stage and were proportionately more important in root length than in biomass.

The vertical distribution of small roots showed distinct differences among species in succession (Figs. 3, 4 and Table 3). Small roots of aspen were more evenly distributed among the organic, 0–10, and 10–20 cm layers than those of Canada yew, which had roots predominantly in the organic layer. The roots of birch and deciduous shrub were clearly more abundant in the 0–10 cm mineral soil layer than in the organic layer in the 48- and 122-year-old stands (Fig. 3). The root systems of spruce and fir were more superficial in the youngest and oldest stands than in the 122-year-old one. The vertical distribution of the roots of cedar did not much differ from that of aspen in the 232-year-old stand.
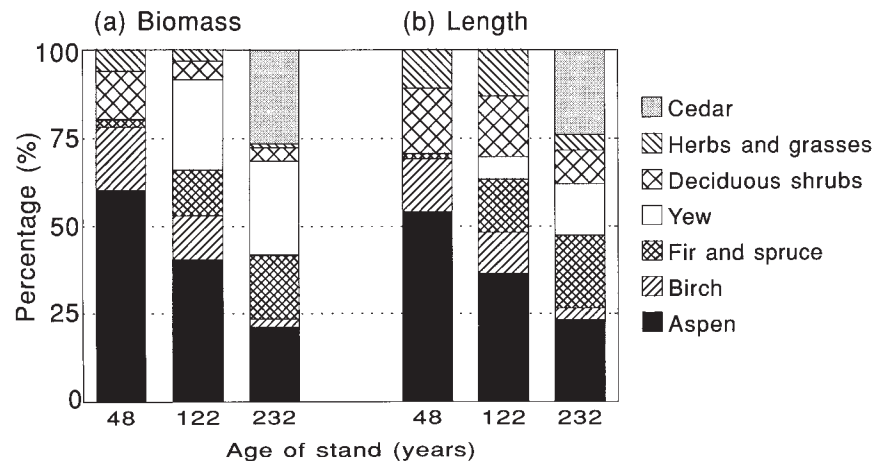
Root production

After 1 and 2 years, most of the roots produced in the ingrowth bags were from woody deciduous and conifer roots (more than

Table 4. The mean root diameter (mm) weighted with root biomass and root length in different soil layers and stands of different successional stages and the results of the repeated measures analysis of variance, with weighted root diameters in different soil layers as the dependent variables (df = 3) and stands of different successional stages as the independent variable.

	Stand				
	48-year-old	122-year-old	232-year-old	F-value	p-value
Root biomass weighted diam. (Σ(diam. $\times$ biomass)/Σ(biomass))					
Organic layer	1.47 (0.11)	2.65 (0.87)	2.82 (0.34)		
0–10 cm	2.72 (0.31)	3.28 (0.09)	3.06 (0.59)		
10–20 cm	2.99 (1.54)	3.52 (1.74)	2.82 (0.69)		
20–30 cm	1.71 (0.66)	2.66 (0.89)	1.47 (0.68)		
Root diam., weighted				4.88	0.01
Stand × root diam., weighted				0.85	0.55
Root length weighted diam. (Σ(diam. $\times$ length)/Σ(length))					
Organic layer	0.54 (0.01)	0.54 (0.01)	0.57 (0.03)		
0–10 cm	0.62 (0.03)	0.66 (0.01)	0.66 (0.05)		
10–20 cm	0.63 (0.05)	0.65 (0.05)	0.68 (0.02)		
20–30 cm	0.63 (0.05)	0.69 (0.05)	0.63 (0.07)		
Root diam., weighted				24.18	0.00
Stand × root diam., weighted				1.68	0.18

Note: Standard deviation is in parentheses.

Fig. 2. Distribution of root (diameter 1–10 mm) biomass and length between different plant species or species groups in forest stands at different successional stages after fire.

85% in all cases, except after 1 year in the youngest stand) (Fig. 5). There was a clear tendency for root production to decrease from the 48-year-old stand to the 232-year-old forest stand after one and two growing seasons. However, the differences were not statistically significant (Table 5). The fine-root production of woody deciduous shrubs and trees combined was more substantial in the 122- and 232-year-old stands (Fig. 5) than the standing root biomass reported in Fig. 2. Similarly, root production of herbs and grasses was greater and that of Canada yew smaller than their share of the root standing biomass in all stands (Fig. 2). The proportion of root production of herbs and grasses decreased and that of fir and spruce increased in all three successional forest stands between the first and second years of study (Fig. 5). There were no significant differences in root production between clay and sand bags (Table 5), although the amounts were consistently less in sand bags.

Decomposition

From 24% to 34% of the root material in litter bags had decomposed after 1 year, and 33% to 45% after 2 years (Fig. 6). The decomposition rate of aspen roots was significantly faster than that of balsam fir and cedar (Fig. 6, Table 6). The decomposition of aspen roots was significantly greater in the 48-year-old stand than in the two older ones. After 2 years, there was a small, but almost significant ($p = 0.06$), interaction between successional stages and species, indicating that the differences in decomposition rates among species were smaller in the oldest successional forest stand.

Discussion

Distribution of root biomass and length

We found that total standing root biomass (diameter ≤ 10 mm) in the successional forest stands was within the ranges reported

Fig. 3. The relative distribution of root (diameter 1–10 mm) biomass of herbs and grasses, deciduous shrubs, Canada yew, aspen, birch, fir and spruce, and cedar between different soil layers in forests stands at different successional stages after fire.
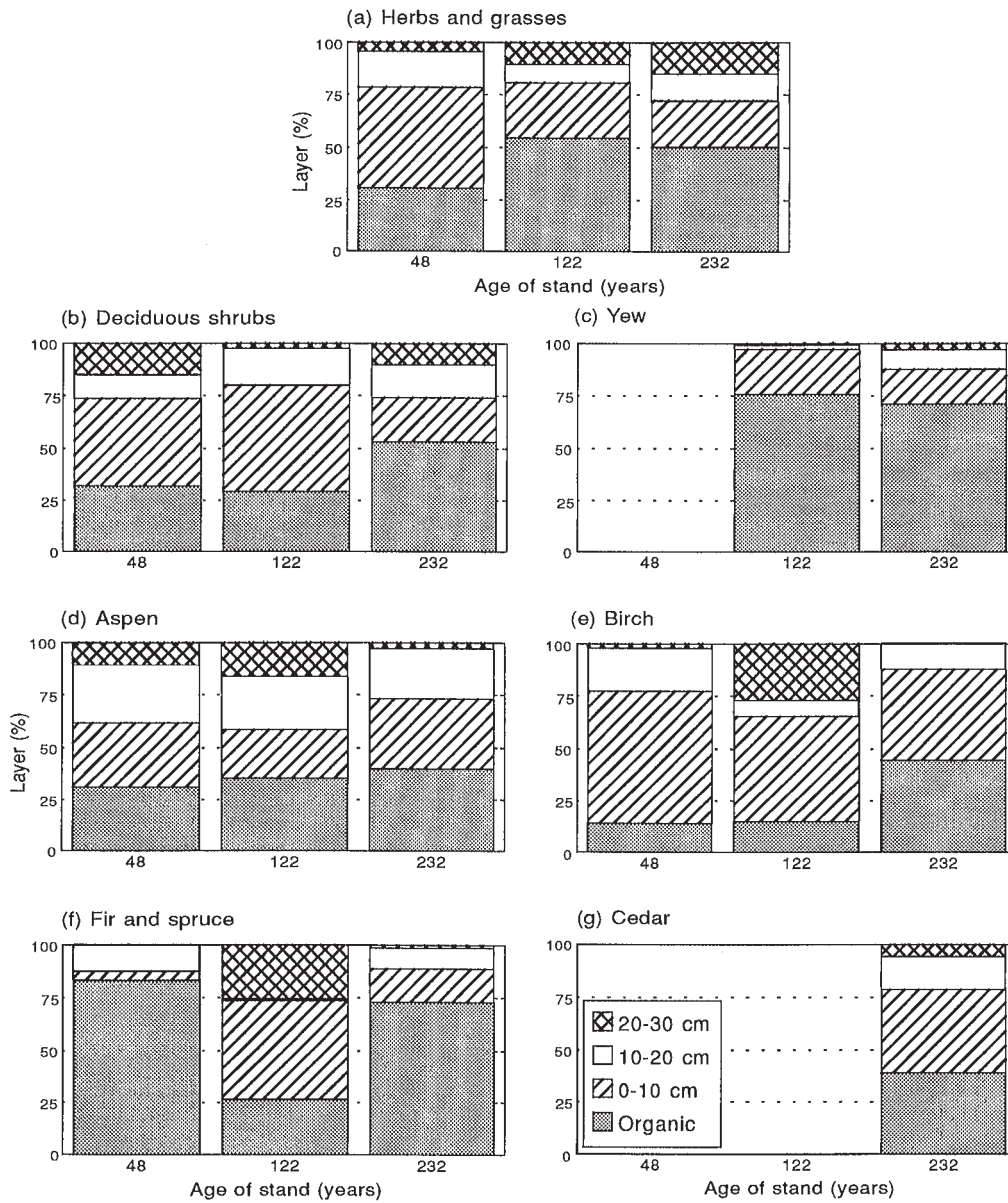

for other boreal forest ecosystems (e.g., Grier et al. 1981; Persson 1983, Finér 1991). The image analysis system utilized in this study made it possible to measure the length of even the very fine roots. Thus, the total root length estimates (Table 2) were greater than that of other root length estimates for tree roots made in other boreal forests (Håland and Brække 1989; Finér 1991).

Our results did not show significant differences in total standing root biomass among the three successional forest stands. Our results are in accordance with Ruark and Bockheim's (1987) observations from an age series of young aspen stands in Wisconsin, U.S.A., and those of Vogt et al. (1983*a*) from 13- to 160-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands in Washington, U.S.A. However, Grier et al. (1981) and Persson (1983) found an increase in fine-root biomass from 23- to 180-year-old *Abies amabilis* (Dougl. ex

Loud.) Dougl. ex J. Forbes stands in Washington, U.S.A., and from 20- to 120-year-old *Pinus sylvestris* L. stands in Sweden, respectively. In this study, tree stand density and basal area (Table 1) were similar in all succesional stages. The results of Paré and Bergeron (1995) in the same stands show that differences in the aboveground tree biomass do not significantly differ between the 48-, 122-, and 232-year-old stands. Therefore, our results suggest that in these successional stands, similar amounts of aboveground tree biomass sustain equal amounts of root biomass.

Unlike root biomass, root length decreased from the youngest to the oldest successional stages possibly as a result of changes in species composition (Table 1) and (or) site overall fertility with succession. In effect, Paré et al. (1993) showed for the same stands that there was a decrease in available P and K with succession. Nutrient-rich sites have been found to promote the

Fig. 4. Relative distribution of root (diameter 1–10 mm) length of herbs and grasses, deciduous shrubs, Canada yew, aspen, birch, fir and spruce, and cedar between different soil layers in forest stands at different successional stages after fire.
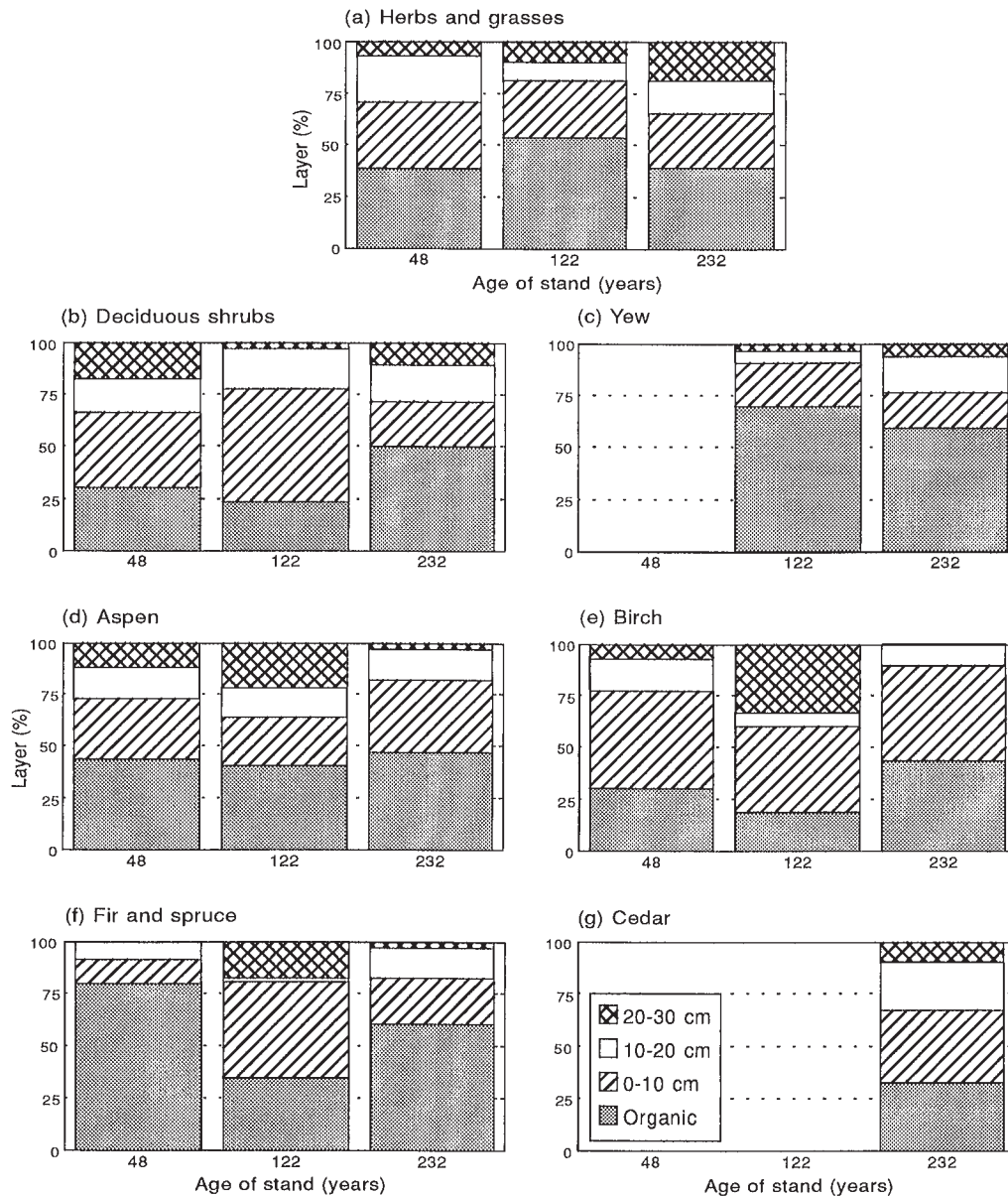
development of thinner roots for a similar total root biomass (Persson 1980). A greater root length for a similar standing root biomass should improve the cost–benefit ratio of obtaining both water and nutrients.

In this study only the fine, small, and coarse root (1–10 mm) biomass and length were studied by species because of the difficulty in identifying the origin of the very fine roots. The proportions of woody deciduous tree species out of root biomass and length (Fig. 2) found in the 122- and 232-year old stands were greater, and those of coniferous species smaller, than their relative abundance as indicated by their aboveground basal area (Table 1). The total proportion of tree roots to those of other vegetation did not vary with succession, supporting observations from young aspen stands (Ruark and Bockheim 1987). The contribution of understorey species to total root

biomass has been correlated with tree canopy status (Grier et al. 1981; Persson 1983; Vogt et al. 1983a) and changes in understorey light availability (Messier and Puttonen 1993).

The root systems were shallow in all successional forest stands, which seems to be a general phenomenon in northern forest ecosystems (e.g., Persson 1983; Gale and Grigal 1987; Kimmins and Hawkes 1978). The roots were also thinner in the organic layer than deeper in the mineral soil, which was also the case in mixed conifer – broad-leafed forests studied by Ehrenfeld et al. (1992). The proportionately larger amount of fine roots in the organic layer, compared with the mineral soil layers, emphasizes the importance of the organic layer for the nutrition in boreal forests.

The amount of root biomass in the organic soil layer increased with increasing age of the stands. This appears to be

Fig. 5. Distribution of root (diameter ≤ 10 mm) production among different species and species groups after 1 (I) and 2 (II) years in forest stands at different successional stages after fire.
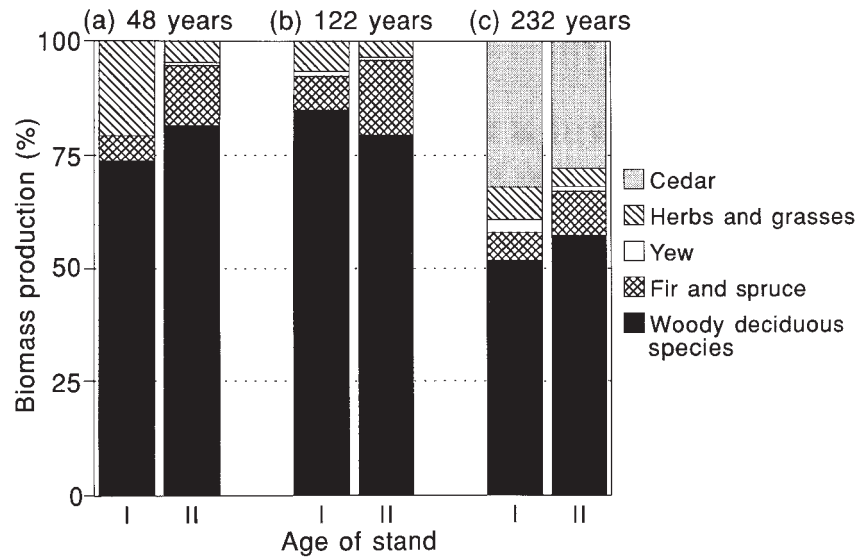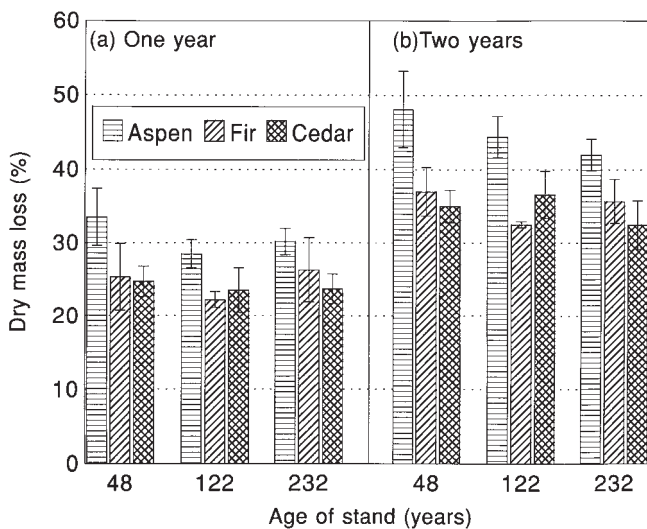

Fig. 6. Dry mass loss of fine-root litter in litter bags after 1 and 2 years in forest stands at different successional stages after fire.

related to an increased accumulation of organic matter, because the ratio between root biomass and the depth of the organic layer even decreased with succession, being 92, 59, and 67 g·m^{-2}·cm^{-1} in the 48-, 122-, and 232-year-old stands, respectively. Vogt et al. (1981) and Ehrenfeld et al. (1992) have also suggested that increased organic matter accumulation during stand development provides new space for root growth.

In this study aspen, which is an early successional species, had similar vertical distribution of roots in all studied successional stages, and it did not differ from that of cedar in the 232-year-old stand. In contrast, the roots of birch grew deeper in the 48- and 122-year-old stands than in the oldest stand. The firs and spruces in the 48-year-old stand were mainly saplings, which could explain the superficial distribution of their roots in that stand. In the 232-year-old stand fir was more dominant

than spruce and in the 122-year-old stand spruce was more dominant (Table 1). That may indicate that fir has a more superficial root system than spruce. However, our study did not cover the distribution of very fine roots. Our findings are not fully in accordance with some earlier results, which have suggested that early successional species have deeper root systems than late successional species (Grier et al. 1981; Gale and Grigal 1987) and that even the same species can grow roots deeper in soil in early successional forest stands than in older ones (Grier et al. 1981). This has been seen as an adaptation by intolerant tree species, which often grow in soil with a thin organic layer, to tap the soil more deeply to obtain water and nutrients. Strong and LaRoi (1983a) found that rooting depth may also increase with the aging of a stand. The depth of rooting may also be explained by resource competition and partitioning, and may be dependent on the texture of the soil (Strong and LaRoi 1983a, 1983b). The different proportion of roots found in the different soil layers among species within each successional stage and for the same species among successional stages (Figs. 3 and 4) could, therefore, be seen as an acclimatization for the coexistence of different plant species in order to minimize competition for water and nutrients. For example, it might be hypothesized that deep organic layers are advantageous for an understorey species such as Canada yew that produces most of its roots in that layer (Fig. 3). Root partitioning among coexisting species is still poorly understood, but a recent paper by Brisson and Reynold (1994) has shown that there exists a strong intraspecific competition for rooting space for creosotebush (*Larrea tridentata*) shrubs in the Chihuahuan desert of New Mexico, U.S.A.

Root production

Root production measured with the ingrowth bag method did, although not significantly, decrease from the early to late successional stages. Root production has also been found to be more substantial in 20-year-old, or young, Scots pine stands than in older ones (Persson 1983; Messier and Puttonen 1993). However, in *A. amabilis* stands, fine-root production was found

Table 5. Fine-root production (g·m^{-2}) after 1 and 2 years measured with the ingrowth bag method and the results of variance analyses, with the root production in stands of different successional stages as the dependent variable.

Stand	One year		Two years	
	Clay bags	Sand bags	Clay bags without dead roots	Clay bags with dead roots
48-year-old	130 (75)	88 (67)	289 (166)	530
122-year-old	61 (36)	—	168 (95)	223 (37)
232-year-old	47 (18)	37 (12)	133 (56)	151 (24)
F-value	2.43		1.52	
p-value	0.17		0.29	

Note: Standard deviation is in parentheses.

Table 6. The results of variance analyses, with the decomposition of root litter after 1 and 2 years as the dependent variables.

Independent variable	One year		Two years	
	F-value	p-value	F-value	p-value
Stand	6.11	0.00	3.56	0.03
Species	34.95	0.00	42.28	0.00
Stand × species	1.62	0.17	2.34	0.06

to be greater in mature than in young stands (Grier et al. 1981). In our study, however, both species composition and soil characteristics (Paré et al. 1993; Brais et al. 1995) vary from the youngest to the oldest successional stage. Thus the decrease in root production could not be attributed solely to the aging of the stand. According to earlier studies that were not supported by ours, the decrease in the fertility of site, which is associated also with succession, increases the investment on fine roots (Keyes and Grier 1981). However, we did not have an estimate of biomass production of the other parts of trees and cannot make judgement on changes in the relative allocation of biomass production into roots with succession.

The discrepancy between the proportion of the total standing root biomass and production in ingrowth bags among the different species or species groups suggests different root production and turnover rates. For example, Canada yew made up approximately 25% of the standing root (diameter 1–10 mm) biomass in the 232-year-old forest stand (Fig. 2), but only less than 5% of total root biomass production (Fig. 5). By contrast, aspen, birch, and woody deciduous shrubs made up only approximately 25% of the standing root biomass in the 232-year-old stand, but made up to 50% of the root biomass production. As well, for a unit of standing root biomass, herbs and grasses had greater root production than the woody species combined. These findings suggest that root production and turnover rates are more substantial in early successional stages dominated by herbs and grasses and woody deciduous species than in late successional stages with more coniferous shrubs and trees. In late successional stages the herbs and grasses and woody deciduous species have greater importance in the dynamic processes attributed to roots when judged solely by their share of root biomass.

We used the ingrowth bag method for studying root production, which is known to give quantitative results similar to the sequential coring method if the time elapsed from the installation of bags to sampling is long enough (Persson 1979;

Joslin and Henderson 1987; Neill 1992). In boreal coniferous forest ecosystems that time has been found to be 2 years (Persson 1979). However, after the first year the two methods appear to yield similar relative differences between treatments or stands (Persson 1979; Messier and Puttonen 1993). This later observation was also supported by the results of this study, although the living root mass in the ingrowth bags was only between 5–12% and 14–27% of the mass found in the cores after 1 and 2 years, respectively: the proportion decreasing from the early to late successional stands. The magnitude of total root production after 2 years (Table 5) was at the lower end of the range measured with the same method in other forest ecosystems (Joslin and Henderson 1987; Persson 1993; Messier and Puttonen 1993). These results suggest that root mass has not reached steady state in the ingrowth bags even after 2 years and would probably stabilize earlier in young than in old successional stages. This also suggests that the results reported in this study, even after 2 years, are more a measure of root growth potential than an exact measure of root production.

The growth medium used in the ingrowth bags was also tested by comparing root production in bags filled with sand versus clay. After 1 year, root production did not differ significantly between the sand-filled and clay-filled bags, although production was systematically smaller in the sand bags. The relative differences found between the 48- and 232-year-old forest stands were also similar for both sand and clay bags. Therefore, as a measure of fine-root growth potential, sand-filled bags could be used rather than clay-filled bags. The advantages of sand bags are obvious. It is relatively easy to find root-free sand materials. Sand is also much easier to wash in the laboratory than clay. The smaller production found in sand bags than in clay bags should be explained by the low nutrient availability expected to be found in pure sand compared with clay. Sand bags were also found to have better contact with the surrounding soil than clay-filled bags. The easy availability of root-free sand and the fast and accurate sorting of roots from bags in the laboratory would favour the use of sand in further experiments.

Decomposition

We found that the rate of dry mass loss in litter bags after one and two growing seasons was within the range reported for fine-root decomposition in other forest ecosystems (Berg 1984; McClaugherty et al. 1984). The decomposition of tree root litter, as for leaf litter, has been related to the chemical composition of the decaying material (Berg and Staaf 1980; Berg 1984). The first stage of decomposition has been reported to be regulated by the nutrient content in the litter, and the second stage, by the content of lignin (Berg and Staaf 1980; Berg 1984). In this study, aspen roots had a higher nitrogen content than roots of fir and cedar, and were found to decompose faster than the roots of the other species. We also found that site factors were less important than the quality of litter in controlling root decomposition. This has also been reported from field incubation studies (Flanagan and Van Cleve 1983; McClaugherty et al. 1984). Only aspen roots were found to decompose faster in the younger than in older forest stands. Vogt et al. (1983b) also found that similar substrates decompose faster in younger stands. Such results suggest that root decompostion would be faster in forest stands dominated by aspen than in those dominated by conifer species, such as the 232-year-old forest stand investigated in

this study. These differences in fine-root decomposition rate among species may contribute to the increasing humus layer often found beneath late successional conifer-dominated stands (Flanagan and Van Cleve 1983; Van Cleve et al. 1983; Paré et al. 1993; Brais et al. 1995).

Acknowledgements

References

Ågren, G.I., Axelsson, B., Flower-Ellis, J.G.K., Linder, S., Persson, H., Staaf, H., and Troeng, E. 1980. Annual carbon budget for a young Scots pine. Structure and function of northern coniferous forest—an ecosystem study. Ecol. Bull. (Stockholm), **32**: 307–313.

Axelsson, E., and Axelsson, B. 1986. Changes in carbon allocation patterns in spruce and pine trees following irrigation and fertilization. Tree Physiol. **2**: 189–204.

Berg, B. 1984. Decomposition of root litter and some factors regulating the process: longterm root litter decomposition in a Scots pine forest. Soil Biol. Biochem. **16**: 609–617.

Berg, B., and Staaf, H. 1980. Decomposition rate and chemical changes of Scots pine needle litter. II. Influence of chemical composition. Structure and function of northern coniferous forest—an ecosystem study. Ecol. Bull. (Stockholm), **32**: 373–390.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology, **72**: 1980–1992.

Bergeron, Y., and Dubuc, M. 1989. Succession in the southern part of Canadian boreal forest. Vegetatio, **79**: 51–63.

Bergeron, Y., Camieré, C., Bouchard, A., and Gangloff, P. 1982. Analyse et classification des sols pour une étude écologique intégrée d'un secteur de l'Abitibi, Québec, Geogr. Phys. Quat. **36**: 291–305.

Böhm, W. 1979. Methods of studying root systems. Springer-Verlag, Berlin. Ecol. Stud. 33.

Brais, S., Camiré, C., Bergeron, Y., and Paré, D. 1995. Changes in nutrient availability and forest floor characteristics in relation to stand age and forest composition in the southern part of the boreal forest of northwestern Quebec. For. Ecol. Manage. **76**: 181–189.

Brisson, J., and Reynolds, J.F. 1994. The effect of neighbors on root distribution in a creosotebush (*Larrea tridentata)* population. Ecology, **75**: 1693–1702.

Canada Soil Survey Committee. 1978. The Canadian system of soil classification. Can. Dep. Agric. Publ. 1646.

Dansereau, P.-R., and Bergeron, Y. 1993. Fire history in the southern boreal forest of northwestern Quebec. Can. J. For. Res. **23**: 25–32.

De Grandpré, L., Gagnon, D., and Bergeron, Y. 1993. Changes in the understorey of Canadian boreal forest after fire. J. Veg. Sci. **4**: 803–810.

Ehrenfeld, J.G., Kaldor, E., and Parmelee, R.W. 1992. Vertical distribution of roots along a soil toposequence in the New Jersey Pinelands. Can. J. For. Res. **22**: 1929–1936.

Finér, L. 1991. Root biomass on an ombrotrophic pine bog and the effects of PK and NPK fertilization. Silva Fenn. **25**: 1–12.

Flanagan, P.W., and Van Cleve, K. 1983. Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. Can. J. For. Res. **13**: 795–817.

Gale, M.R., and Grigal, D.F. 1987. Vertical root distributions of northern tree species in relation to successional status. Can. J. For. Res. **17**: 829–834.

Grier, C.C., Vogt, K.A., Keyes, M.R., and Edmonds, R.L. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Can. J. For. Res. **11**: 155–167.

Håland, B., and Brække, F.H. 1989. Distribution of root biomass in a low-shrub pine bog. Scand. J. For. Res. **4**: 307–316.

Joslin, J.D., and Henderson, G.S. 1987. Organic matter and nutrients associated with fine root turnover in a white oak stand. For. Sci. **33**: 330–346.

Keyes, M.R., and Grier, C.C. 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Can. J. For. Res. **11**: 599–605.

Kimmins, J.P., and Hawkes, B.C. 1978. Distribution and chemistry of fine roots in a white spruce – subalpine fir stand in British Columbia: implications for management. Can. J. For. Res. **8**: 265–279.

Marie-Victorin, F. 1964. Flore Laurentienne. 2nd ed. Les Presses de L'Université de Montréal, Montreal.

McClaugherty, C.A., Aber, J.D., and Melillo, J.M. 1984. Decomposition dynamics of fine roots in forested ecosystems. Oikos, **42**: 378–386.

Messier, C., and Puttonen, P. 1993. Coniferous and non-coniferous fine-root and rhizome production in Scots pine stands using the ingrowth bag method. Silva Fenn. **27**: 209–217.

Morin, H., Laprise, D., and Bergeron, Y. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. Can. J. For. Res. **23**: 1497–1506.

Neill, C. 1992. Comparison of soil coring and ingrowth methods for measuring belowground production. Ecology, **73**: 1918–1921.

Paré, D., and Bergeron, Y. 1995. Above-ground biomass accumulation along a 230-year chronosequence in the southern portion of the Canadian boreal forest. J. Ecol. **83**: 1001–1007.

Paré, D., Bergeron, Y., and Camiré, C. 1993. Changes in the forest-floor of Canadian southern boreal forest after disturbance. J. Veg. Sci. **4**: 811–818.

Persson, H. 1979. Fine-root production, mortality and decomposition in forest ecosystems. Vegetatio, **41**: 101–109.

Persson, H. 1980. Fine-root dynamics in a Scots pine stand with and without near optimum nutrient and water regimes. Acta Phytogeogr. Suec. **68**: 101–110.

Persson, H. 1983. The distribution and productivity of fine roots in boreal forests. Plant Soil, **71**: 87–101.

Ruark, G.A., and Bockheim, J.G. 1987. Below-ground biomass of 10-, 20-, and 32-year-old *Populus tremuloides* in Wisconsin. Pedobiologia, **30**: 207–217.

SPSS Inc. 1988. SPSS/PC+ advanced statistics V 2.0 for IBM PC/XT/AT and PS/2. Marija J. Norusis/SPSS Inc., Chigaco, Ill.

Strong, W.L., and La Roi, G.H. 1983a. Rooting depths and successional development of selected boreal forest communities. Can. J. For. Res. **13**: 577–588.

Strong, W.L., and La Roi, G.H. 1983b. Root-system morphology of common boreal forest trees in Alberta, Canada. Can. J. For. Res. **13**: 1164–1173.

Van Cleve, K., Oliver, L.K., Schlentner, R., Viereck, L.A., and Dyrness, C.T. 1983. Productivity and nutrient cycling in taiga forest ecosystems. Can. J. For. Res. **13**: 747–766.

Vogt, K.A., and Persson, H. 1991. Measuring growth and development of roots. *In* Techniques and approaches in forest tree ecophysiology. *Edited by* J.P. Lassoie and T.M. Hinckley. CRC Press, Boca Raton, Fla. pp. 477–501.

Vogt, K.A., Edmonds, R.L., and Grier, C.C. 1981. Seasonal changes in biomass and vertical distribution of mycorrhizal and fibrous-textured conifer roots in 23- and 180-year-old subalpine *Abies amabilis* stands. Can. J. For. Res. **11**: 223–229.

Vogt, K.A., Moore, E.E., Vogt, D.J., Redlin, M.J., and Edmonds, R.L. 1983a. Conifer fine root and mycorrhizal root biomass within the

forest floors of Douglas-fir stands of different ages and site pro-
ductivities. Can. J. For. Res. **13**: 429–437.

Vogt, K.A., Grier, C.C., Meier, C.E., and Keyes, M.R. 1983*b*. Or-
ganic matter and nutrient dynamics in forest floors of young and
mature *Abies amabilis* stands in western Washington, as affected
by fine-root input. Ecol. Monogr. **53**: 139–157.

Vogt, K.A., Grier, C.C., and Vogt, D.J. 1986. Production, turnover,
and nutrient dynamics of above- and belowground detritus of world
forests. Adv. Ecol. Res. **15**: 303–377.