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Fine-root production in small experimental gaps in successional mixed boreal forests

Campbell, Johanne J.[1], **Finér, Leena**[2] **& Messier, Christian**[1*]

[1]*Groupe de recherche en écologie forestière, Université du Québec à Montréal, C.P. 8888 Succ. Centre-Ville, Montréal, Québec, Canada H3C 3P8; Fax +1 514 987 4648;* [*]*Corresponding author: E-mail messier.christian@uqam.ca;*
[2]*The Finnish Forest Institute, Joensuu Research Station, P.O. Box 68, FIN-80101, Joensuu, Finland*

Abstract. The effects of small 10 m × 10 m experimental above-ground gaps on fine-root production for the first two years were studied in three fire-initiated stands of the north-western mixed broad-leaf-conifer boreal forest of Québec. The 48-yr-old forest is dominated by *Populus tremuloides* (Trembling aspen), the 122-yr-old forest by a mixture of *P. tremuloides*, *Abies balsamea* (balsam fir) and *Picea glauca* (white spruce), and the 232-yr-old forest by *Thuja occidentalis* (eastern white cedar) and *A. balsamea*, with some *P. tremuloides*. 40 root-ingrowth bags were installed in different locations in and around each gap (at gap center, 1 to 2 m either side of gap edge and in adjacent control plots). Half of the ingrowth bags were harvested after one year following gap creation, the other half after two years. Roots were sorted into different species grouping. Fine-root production was statistically ($P < 0.05$) larger in the youngest forest compared to the two older ones after one year, but not after two years. The individual species or groups of species increased, decreased or showed no change in fine-root production in gaps, but overall we did not observe a major shift in species proportion between gap and control plots after two years. Some herbs and also *Taxus canadensis* seemed to benefit in terms of fine-root growth from such small openings after two years. No statistical differences ($P > 0.10$) in total fine-root production were found among locations within and outside gaps in either year. However, there was a clear tendency for fine-root production to be smaller in gap center than in the other locations for the two younger successional forests the first year after gap creation. We conclude that small above-ground gaps (i.e. < 100 m^2) do not produce a significant and long-lasting below-ground gap in terms of total fine-root production in the successional forests investigated.

Keywords: Balsam fir; Eastern white cedar; Root-ingrowth bag; Trembling aspen.

Nomenclature: Marie-Victorin (1964).

Introduction

Within boreal forests, species distribution and composition are continuously changing, due to both catastrophic perturbations (fire and insect outbreaks) and minor ones (single or multiple tree mortality). Minor perturbations create variable-sized canopy gaps that allow different species to establish in the forest understory. Early successional species could replace themselves in large gaps, whereas smaller gaps should favor shade-tolerant species. Many studies in various forest types have investigated effects of gap size on species dynamics (e.g. Brokaw & Scheiner 1989; Lorimer 1989; Veblen 1989; Kneeshaw & Bergeron 1996) and resource availability, especially light (Canham et al. 1990; Lawton 1990; Messier & Puttonen 1995). Above-ground gap formation can also strongly influence below-ground processes, such as nutrient cycling (e.g. Vitousek & Denslow 1986; Mladenoff 1987; Parsons et al. 1994a). In nutrient-poor conifer forests, nutrient limitation can be as important as light for the growth of understory trees (Christy 1986). It is therefore important to determine to what extent above-ground gaps create below-ground gaps in boreal forests.

In tropical forests, Silver & Vogt (1993) and Sanford (1989) observed a decrease in fine-root biomass in gaps of 32 m^2 and 270 m^2, respectively, whereas Sanford (1990) did not find any reduction in gaps ranging in area from 85 to 164 m^2. Wilczynski & Pickett (1993) observed, in a temperate deciduous forest in the eastern United States, a decrease in fine-root biomass in 33 m^2 to 69 m^2-gaps, but no difference in soil temperature and nitrogen availability. In the same kind of forest, Collins & Pickett (1987) observed a small increase in light, soil and air temperature, and soil moisture in 33 m^2 to 151 m^2-gaps. Bauhus & Bartsch (1995) found no difference in soil temperature, but a large increase in nitrification in a 700 m^2-gap, and a gradual shift in fine-root biomass from trees to herbs from the edge to the center of the gap (Bauhus & Bartsch 1996) in a beech forest of Germany. In Rocky Mountain *Pinus contorta* forest, Parsons et al. (1994a) found an increase in nitrate with increasing gap size, and a decrease in fine-root biomass starting at 5 to 6 m from the edge inside the gap (Parsons et al. 1994b). Other studies done in coniferous forests have shown that fine-root biomass (Vogt et al. 1983; Vogt et al. 1987) and production (Messier & Puttonen 1993) changes with stand development and successional stages.

The main objective of this study was to evaluate the effects of experimentally created 10 m × 10 m gaps in three different successional forests that span the whole succession in the north-western boreal forest of Québec on fine-root production using ingrowth bags. Our hypothesis was that such small above-ground gaps also create understory gaps in terms of fine-root production. Root-ingrowth bags have been found to be an efficient method for the comparison of different sites (Yin et al. 1989; Messier & Puttonen 1993). This study complements other research done in the region relating gap effects to tree regeneration (Kneeshaw & Bergeron 1996), understory vegetation (de Grandpré et al. 1993; de Grandpré 1996) and forest floor dynamics (Paré et al. 1993).

Study area

The study includes three different successional forests that burned in 1944, 1870 and 1760. These forests were near the shore of Lake Duparquet, Québec (48° 30' N; 79° 20' W). The youngest forest originated following natural fire 48 yr ago, and was dominated by *Betula papyrifera* (Paper birch) and *Populus tremuloides* (Trembling aspen) in the overstory, and by *Acer spicatum* (Mountain maple) in the understory. The mid-successional forest burned 122 yr ago and was dominated by *Populus*, *Picea glauca* (White spruce) and *Abies balsamea* (Balsam fir) in the overstory and by *Acer*, *Abies* and *Taxus canadensis* (American yew) in the understory. The oldest forest burned 232 yr ago and was dominated by *Thuja occidentalis* (Eastern white cedar), *Abies* and *Populus* in the overstory, and by *Acer*, *Abies* and *Taxus* in the understory. A full description of these stands could be found in Finer et al. (1997) Fire history has been described by Bergeron (1991) and Dansereau & Bergeron (1993), successional pattern of the forest in this region was described by Bergeron & Dubuc (1989) and DeGrandpré et al. (1993), and fine-root dynamics in these same undisturbed successional stands was described by Finér et al. (1997). The last outbreak of spruce budworm *Choristoneura fumiferana* (Clem.), which occurred between 1970 and 1987 (Morin et al. 1993), killed most of the *Abies*. The soil organic layer thickens with forest age, averaging 5.3 cm in the youngest forest and 8.0 cm in the oldest one (de Grandpré et al. 1993). Despite accumulation of organic matter, mineralization of nitrogen is suggested to be high for a boreal forest (Paré et al. 1993). Moss is rare in the understory due to inhibitory effects of *Populus* litter (Paré et al. 1993). Mean annual precipitation and temperature are 823 mm and 0.6 °C, respectively, with an annual frost-free period of 64 days (Bergeron et al. 1983). Soils are classified as a Grey Luvisols (Anon. 1978) (FAO classification: Albic Luvisols).

Material and Methods

Three 10 m × 10 m gaps were clear-cut in May 1992 in each successional forest. All trees were removed from the gap area. Adjacent control plots were established within 100 m from each gap. Soil cores were excavated with a steel corer (∅ = 7 cm) to a depth of 30 cm in each gap and control plot in August 1992. A 30 cm-long 7 mm-mesh bag was installed in a hole. Bags were filled with mineral soil that was passed through a 2-mm sieve to remove all roots. A 2 - 3-cm layer of commercial peat moss was put on top to simulate the organic layer.

For each gap, we installed 30 ingrowth bags (Fig. 1): six bags in the center of the gap, 16 bags 1-2 m from the inside the gap edge, and eight bags at the edge 1 to 2 m outside the gap. 10 additional bags were put in the control plot. Half the bags were harvested after one year, in September 1993, the other half after two years in September 1994. Samples were frozen at – 25 °C until processed. Organic and mineral layers of each sample were separated and all root fragments were removed with a 2-mm sieve using tap water. After picking out the larger root fragments, squares representing 10 % of the surface of a large petri dish containing all remaining

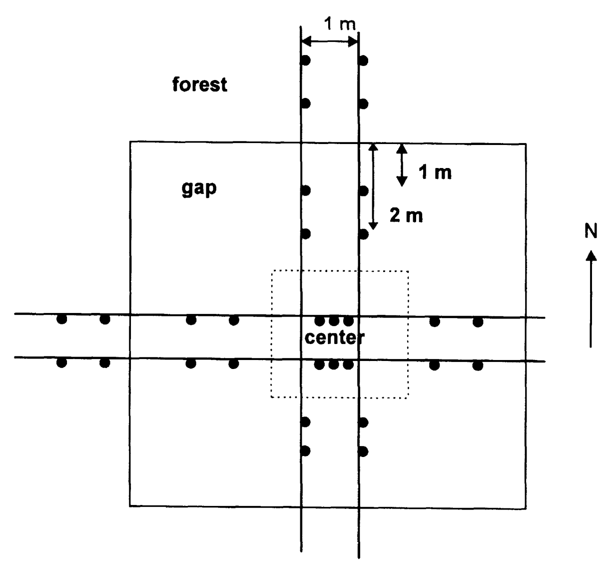

Fig. 1. Orientation pattern for the root-ingrowth bags installed in the autumn of 1992 in each gap. Control plots are within 100 m away from each of these gaps.

fragments were randomly selected and all remaining root fragments on these squares were picked and classified separately as a subsample. The weight of these roots was multiplied by 10 to estimate total biomass. Roots were classified as herbs, *Abies* + *Picea*, *Thuja*, *Taxus*, and woody deciduous species. Species identifications were made by comparing harvested roots with some samples of the species taken from the same sites. When necessary, a binocular was used to better differentiate the roots; the main identification criteria were morphology, color and surface aspect. Roots were oven-dried at 70 °C for 24 h prior to biomass determination. All roots smaller than 2 mm in diameter were considered as fine roots. No roots larger than 2 mm were found in the bags after two years.

The experimental design was a completely randomized experiment with plots as replicates and in-growth bags as subsamples of each replicate. Differences in fine-root biomass (all species combined) among forests (48, 122, and 232 yr since fire) and among locations (center, edge-gap, edge-forest and control) were tested by Two-way Analysis of Variance. For comparison of individual species or species groups, gap centers, edge-gaps and edge-forests were combined into one location (gap) and compared with control plots. Tests were performed using SYSTAT (Anon. 1992).

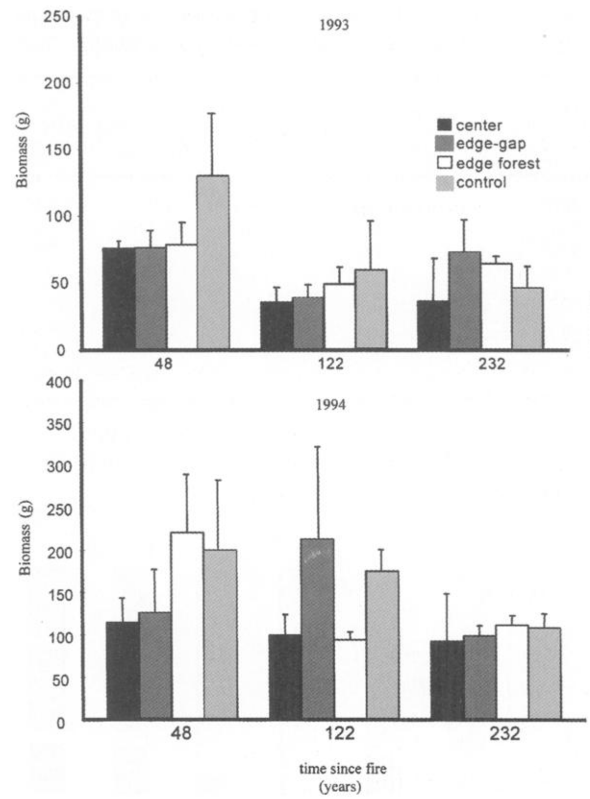

Fig. 2. Total fine-root biomass (g/m^2) found in in-growth bags in the center of the gap, inside gap edge, outside gap edge and control in each of the 48-, 122- and 232-yr-old stands for samples harvested after one year (1993) and two years (1994). Vertical lines on each bars are standard errors of the means.

Results

Overall forest and location effects

Fine-root biomass production (all species combined) was significantly higher one year post-treatment in the youngest forest than in the older two forests (Table 1), but not the second year. There was no significant location effect on either year, but fine-root production was always the lowest in the center of the gap (Fig. 2).

Differences between individual species and species groups

Differences in fine-root production for root category among forests and between gap and control plots are shown in Tables 2 and 3 and in Fig. 3. We grouped together the samples from the various locations in and around the gap into a category called gap for analysing species effects, since effects of an above-ground gap extend well beyond the edge of the gap (Lieberman et al. 1989). After one year, herbs and *Taxus* fine-root biomass were higher in gap than in control areas, although this difference was not significant ($p > 0.05$). *Abies* + *Picea* had significantly lower fine-root production in gaps for the 48- and 232-yr-old forests in both 1993 and 1994. Woody deciduous species had slightly lower biomass in gaps than in the undisturbed controls, especially for the 48- and 122-yr-old forests, although these differences were not significant. After two years, all species showed similar trends, but most of the significant first year differences disappeared by year 2. Species proportions varied between gap and control plots much more during the first than the second year post-treatment (Fig. 3).

Table 1. Analysis of Variance: summary table showing variance F-ratio, p-value and mean square error (MSE) terms of total fine-root biomass production among the three successional forests and four locations (gap center, inside gap edge, outside gap edge and control) for samples harvested after one year (1993) and two years (1994).

		1993		1994	
	df	F-ratio	p	F-ratio	p
Forest	2	4.827	0.017	2.177	0.130
Location	3	1.815	0.171	1.519	0.229
Forest × Location	6	1.025	0.433	0.728	0.631
MSE	24	0.363		0.453	

Table 2. Fine-root production (g/m^2) for herb, fir plus spruce, yew and woody deciduous species in three different successional forests (48-, 122- and 232-year-old stands) for samples harvested after one year (1993) and two years (1994).

Site/age	Herb		*Abies* + *Picea*		*Thuja*		*Taxus*		Woody deciduous	
	Control	Gap	Control	Gap	Control	Gap	Control	Gap	Control	Gap
1993										
48 yr	26.7	29.3	7.1	2.4	-	-	0.1	2.4	94.2	42.6
122 yr	4.0	10.0	4.5	5.4	-	-	0.7	3.6	50.9	22.4
232 yr	3.6	10.6	2.9	0.7	14.0	14.8	1.4	2.7	24.3	28.8
1994										
48 yr	14.1	13.9	37.8	4.8	-	-	1.9	0.1	223.8	133.5
122 yr	6.5	11.4	26.7	15.3	-	-	1.0	4.0	133.3	102.6
232 yr	5.2	6.3	11.4	5.9	33.1	20.2	1.4	7.3	66.6	57.2

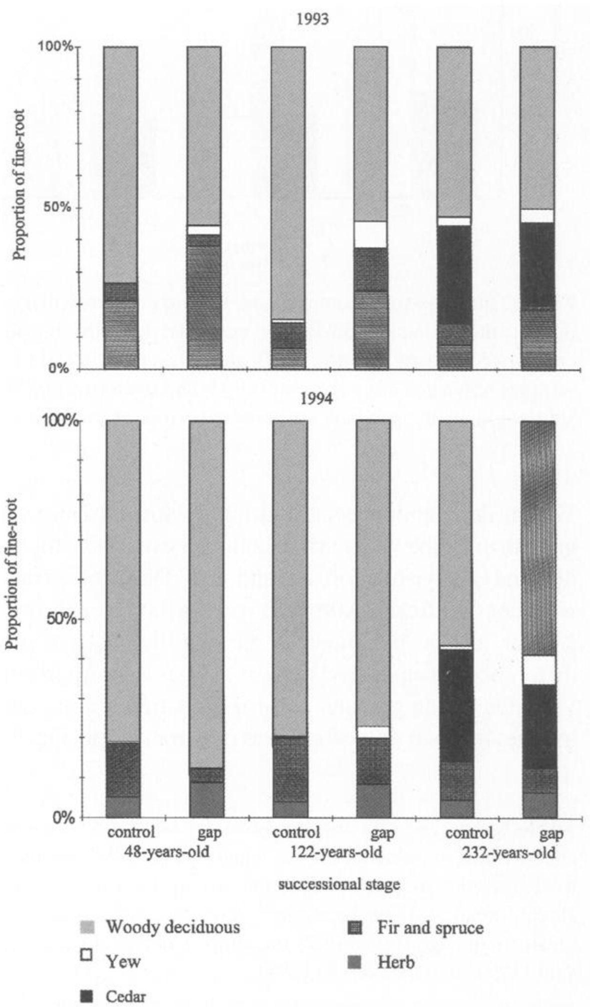

Fig. 3. Proportion of fine roots in herbs, *Abies* + *Picea*, *Thuja*, and woody deciduous species categories in gap and control plots in the 48-, 122- and 232-yr-old forest stands for samples harvested after one year (1993) and two years (1994).

Woody deciduous was the most abundant species or species group in all three forests, especially in the two youngest forests.

First-year herb fine-root biomass production was significantly higher ($p < 0.001$) in the youngest forest compared to the two older ones (Table 3). Fine-root production of *Taxus* increased from the youngest to the oldest forests, but the differences were not significant ($p > 0.05$). *Thuja* was only present in the oldest forest. After two years, woody deciduous fine roots were significantly less abundant in the oldest forest than in the two younger ones (Table 3).

Discussion

The experimental 100-m^2 above-ground gap used in this study reduced, although not significantly ($p > 0.05$), total fine-root biomass production during the first and second year in the center of the gap (Fig. 2): this was especially true for the 48- and 122-yr-old forests. The lack of significance was probably due to the high variability typical of fine-root research. The various individual species or species group increased, decreased or showed no change in fine-root production in gaps (Table 2). Therefore, we cannot conclude from this study that 10 m × 10 m gaps in the mixed broad-leaf-conifer boreal forest actually produce a significant and long-lasting (i.e. at least two years) below-ground gap in terms of total fine-root production in either successional forest. These results concur with those of Sanford (1990) in a tropical forest and Parsons et al. (1994b) in a *Pinus lodgepole* forest that showed that gaps of less than 100 m^2 have little or no effect on fine-root biomass production.

Overall we did not observe a major shift in species proportions between gap and control plots after two years (Fig. 3), although herbs and species such as *Taxus* seemed to benefit in terms of fine-root growth from such

Table 3. Analysis of Variance: summary table showing F-statistics, p-values, and mean square error (*MSE*) terms of fine-root biomass production for herb, fir plus spruce, yew and woody deciduous species among the three successional forests and between gap and control plots for samples harvested after one year (1993) and two years (1994).

		Herb		*Abies* + *Picea*		*Taxus*		Woody deciduous	
	df	F-ratio	p	F-ratio	p	F-ratio	p	F-ratio	p
1993									
Forest	2	10.613	0.000	4.471	0.020	0.465	0.465	2.379	0.110
Plot	1	1.873	0.181	7.964	0.008	0.070	0.070	2.099	0.158
Forest × Plot	2	0.613	0.548	2.450	0.103	0.803	0.803	0.220	0.803
MSE	30	0.740		0.552		1.065		1.104	
1994									
Forest	2	2.561	0.094	1.540	0.231	1.007	0.377	4.186	0.025
Plot	1	0.087	0.770	15.499	0.000	0.677	0.417	1.697	0.203
Forest × Plot	2	0.555	0.580	1.092	0.349	1.869	0.172	0.097	0.908
MSE	30	0.928		1.022		1.246		0.750	

small openings in the short term. Because we were not able to easily differentiate fine roots of the woody understory shrubs from those of aspen, we were not able to verify the possibility that they increased their presence in gaps while fine roots of *Populus* declined.

Total fine-root production found in our three successional forests was within the range reported for other boreal forests studied with the ingrowth bag method (Persson 1983; Ahlström et al. 1988; Messier & Puttonen 1993). Also, the tendency for the early successional forest to produce more fine-root biomass supports earlier findings by Vogt et al. (1983, 1987). However, we cannot rule out the possibility that trends observed in this study were due to changes in soil fertility induced by species differences (Paré & Bergeron 1995) and not due to intrinsic species differences. The greater proportion of fine-root produced by the woody deciduous species (which includes *Populus*) than any other species or species group in all three forests confirmed the findings of Finér et al. (1997). This was true even in the oldest forest that was dominated by *Thuja* and *Abies* among trees and *Taxus* among understory plant species. This shows the explosive fine-root growth potential of the woody deciduous category that is presumably dominated by the overstory *Populus* and understory *Acer* roots.

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