Coniferous and non-coniferous fine-root and rhizome production in Scots pine stands using the ingrowth bag method

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TIIVISTELMÄ: HAVUPUIDEN JA MUUN KASVILLISUUDEN OHUTJUURTEN TUOTOS NELJÄSSÄ ERI-IKÄISESSÄ MÄNNIKÖSSÄ JUURISUKKAMENETELMÄLLÄ MITATTUNA

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Coniferous and non-coniferous fine-root and rhizome production was measured after one growing season using the ingrowth bag method in Scots pine (*Pinus sylvestris* L.) stands differing in ages from 7 to 105 years in southern Finland. Total fine-root production decreased from the 7-year to 20-year-old stands, and then increased slightly in the 85- to 105-year-old stands. Most of the total fine-root biomass in the youngest age group came from non-conifer species, whereas most of the total fine-root biomass in the three older age groups came from conifer species. The maximum coniferous fine-root production was found to occur at crown closure in the 11- to 13-year-old stands. Rhizome production was the lowest and highest in the 20- and 85- to 105-year-old stands, respectively. The increase in rhizome production in the 85- to 105-year-old stands was associated with an abundant understory cover of *Vaccinium myrtillus* and *V. vitis-idaea* and an increase in light penetration. The ingrowth bag method was found to be useful in assessing the relative fine-root production among species-group and successional stages of Scots pine stands.

Havupuiden ja muun kasvillisuuden ohutjuurten ja rhizomien yhden kasvukauden aikainen tuotos mitattiin juurisukkamenetelmällä 7–105 vuoden ikäisissä eteläsuomalaisissa männiköissä. Ohutjuurten kokonaistuotos väheni siirryttäessä seitsemänvuotiaista 20-vuotiaisiin männiköihin ja kohosi hieman 85- ja 105-vuotiaissa männiköissä. Nuorimmissa männiköissä muun kasvillisuuden ohutjuurten tuotos oli suurempi kuin havupuiden ja kolmessa vanhemmassa männikössä havupuiden juurten tuotos oli merkittävästi suurempi kuin muun kasvillisuuden. Juurten tuotos oli suurimmillaan latvuskerroksen sulkeutuessa 11–13 vuoden ikäisissä metsiköissä. Rhizomituotos oli pienin 20-vuotiaissa ja suurin 85–105-vuotiaissa männiköissä. Lisääntynyt rhizomituotos 85–105 vuoden ikäisissä männiköissä johtui mustikan ja puolukan runsaudesta kenttäkerroksessa, sillä lajit olivat hyötyneet lisääntyneestä valomäärästä metsiköiden vanhemmalla iällä. Juurisukkamenetelmä osoittautui käyttökelpoiseksi arvioitaessa eri kasvilajiryhmien juurten suhteellista tuotosta eri sukkessiovaiheissa olevissa männiköissä.

Keywords: roots, root systems, fine-root production, forests, ingrowth bag, *Pinus sylvestris*, rhizomes, undergrowth, underwood, vegetation.
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1 Introduction

Following a major disturbance that completely eliminates the overstory canopy, forest ecosystems usually recover quickly through leaf expansion, the uptake of water and nutrients by plants, the retention of nutrients in woody tissues, and an increase in the number of roots in the soil (Gholz 1980; Boring et al. 1981; Bormann and Likens 1981; Bicknell 1982; Gholz et al. 1985). Although the above-ground structural and functional changes that occur during stand development have been extensively studied (Oliver 1981), little is known about the changes occurring below-ground. This is especially true for fine-root production and turnover.

Recent studies have indicated that maximum fine-root biomass in forest ecosystems usually occurs before tree canopy closure, and results mainly from an abundant shrub and herb vegetation cover (Berish 1982; Vogt et al. 1987; Yin et al. 1989; Messier and Kimmins 1991). However, as the tree canopy develops to reach canopy closure, the composition and production of above- and below-ground biomass of these species is strongly modified (MacLean and Wein 1977; Alaback 1982; Kellomäki and Väisänen 1991; Messier 1992). The dynamics of fine-root systems in forest ecosystems need to be studied further to help us interpret descriptions and comparisons of plant productivity and other structural and functional attributes of the ecosystem. Persson (1978) and Fogel (1983) have annually estimated that 4–5 times more organic material is returned to the soil matrix by fine roots than by litter.

Several methods have been used to estimate fine-root biomass, production, and turnover, but none has given us fully satisfactory results (Santantonio and Grace 1987; Hendrick and Pregitzer 1992; Nadelhoffer and Raich 1992). The sequential soil coring method has been used widely (Persson 1980; Persson 1983; Ahlström et al. 1988; Comeau & Kimmins 1989; Yin et al. 1989; Kummerow et al. 1990 a and b), but is believed to underestimate fine-root production (Kurz and Kimmins 1987; Hendrick and Pregilzer 1992). It also requires the separation of dead and live fine-roots – a very difficult task – and is expensive and labour intensive.

An alternative method, the ingrowth bag method, has been used alone or in association with the sequential coring methods to estimate fine-root production (Persson 1979, 1980; Fabiao et al. 1985, Coopersmith 1986; Ahlström et al. 1988; Yin et al. 1989). This method gives similar results to those obtained by the sequential coring method, both quantitatively and qualitatively (Persson 1983; Coopersmith 1986; Symbula and Day 1988; Yin et al. 1989). Although, a major problem with the ingrowth bag method is that it greatly modified the root growth environment, its main advantage is that it allows the direct calculation of fine-root production with much more ease than the sequential coring method. It also allows the estimation of rhizome growth in the understory vegetation. Persson (1979, 1980) found that although the ingrowth bag method took 2 years in boreal forest ecosystems to obtain a quantitative estimate similar to those obtained by the sequential coring method, first-year results gave the same relative values between treatments or stands as occured after 2 years. Similar correlations were obtained by Yin et al. (1989) and Coopersmith (1986). Therefore, the ingrowth of fine-roots after 1 year represents a good relative measure of the differences in fine-root production among different stands or treatments. Vogt and Persson (1991) stated that root studies using the ingrowth bag method should be monitored over at least one growth period.

The aim of the present paper is to compare the relative production of coniferous and non-coniferous fine-roots and rhizomes in Scots pine (*Pinus sylvestris* L.) stands of different ages using the ingrowth bag method.

2 Material and method

2.1 Study area

The study was conducted in eight Scots pine stands divided into four age groups: i) 7 years; ii) 11–13 years; iii) 20 years; and iv) 85–105 years. All 8 stands selected were of the *Vaccinium vitis-idaea* forest site type (Lehto and Leikola 1987). The sites were located within 40 km from each other in and around the municipality of Veikkola some 40 km west of Helsinki (60°15' N, 24°30' E) in southern Finland. The stands of the first two age groups were planted, whereas the third and fourth age groups were naturally regenerated. No silvicultural treatments were done for the first two age groups, but brushing was done in the third age group and brushing and thinning were done in the mature stands. All sites were underlain by deep sandy sediments (mainly of 0–5 mm in size, with a smaller fraction of medium to coarse fragments) of fluvioglacial origin. The soils in all stands were podzolic, with an LFH layer between 4 and 10 cm in thickness, an Ae/Ah of between 2 and 8 cm, and a Bf of between 16 and 40 cm. Most of the fine-roots (< 2 mm in diameter) were found in the forest floor and in the upper Ae/Bf horizon. A detailed description of the structure and composition of the vegetation of the 8 different stands is given in Table 1. All stands were selected based on their homogeneity: similar slope position, aspect, surface material, soil characteristics, site type, tree species composition, and continuous tree cover. This kind of age sequence research assumes that all stands had similar ecological attributes before disturbance (Cole and Van Miegroet 1989).

2.2 Measurements of fine-root and rhizome production

We assessed the fine-root production using the ingrowth bag method described by Persson (1979, 1980). Root-free mesh bags (7 × 5 mm mesh size), filled with 2 mm sieved mineral soil taken outside the plot, were placed into 8.2 cm diameter holes made with a long cylindrical root corer. A cylindrical (diameter 7 cm) plastic pipe was used to fill the mesh bags with the sieved sand up to the forest floor surface. In all, 8 cylindrical mesh bags were installed in each stand to a depth of 30 cm in early May 1991, for a total of 64 bags. The bags were installed in all four cardinal directions from the center of the plot at 3 and 8 m in the younger stands (age groups I to III) and 6 and 15 m in the mature stands (age group IV), respectively. The bags were left in the soil for 6 months until the beginning of November 1991. They were then brought to the laboratory and stored at 2 °C. All of the root measurement was done within 2 months.

The sand in the bags was carefully washed through a 2-mm sieve, and the roots and rhizomes were separated and sorted by hand into different sizes (0–2 mm and > 2 mm) and into two groups: coniferous (Scots pine and Norway spruce [*Picea abies*, (L.) Karst.]) and non-coniferous (dwarf shrubs, herbaceous, graminaceous, *Betula* and *Sorbus* species). Separation of fine-roots between the two groups was possible because of the differences in root morphology, resilience when bent, and colour. Most of the roots greater than 2 mm in diameter were rhizomes produced from *Vaccinium* and fern species. After sorting, the roots were dried at 70 °C for 24 h and weighed to determine the oven-dry biomass per hectare.

2.3 Statistics

The experiment was a completely randomized design in which two Scots pine stands were nested within each age group. Square-root-transformed values were used when the variances were not homogeneous according to Bartlett's test. Both transformed and untransformed data were checked for homogeneity of variances and normality of distribution. Only the untransformed means are presented, but the statistics of some of the means were performed on transformed means. The significant mean differences between the four different age groups ($P < 0.05$) were compared using the Tukey HSD multiple test (Wilkinson 1987).

Table 1. Structure and composition of the eight Scots pine stands investigated.

Stand age (years)	Conifer a) density (stems/ha)	Birch (>4 m) b) density (stems/ha)	Dominant b) tree basal area (m²)	Birch (<4m) density (stems/ha)	Shrub c) density (stems/ha)	Light d) penetration (% PPFD)	Conifer crown cover (%)	Understory ground cover (%) e)							
								VM	VV	DF	CA	PA	MP	M	O
7	3318 (98)	—	—	15590	3700	80.0	30	3	23	48	7	1	6	43	10
7	4461 (93)	—	—	4950	13800	78.5	35	3	22	48	8	3	5	17	12
11	3725 (79)	2546	12.2 (86)	20112	8400	21.8	65	0	13	38	21	0	3	34	16
13	2865 (92)	1750	22.2 (94)	8568	2400	20.3	70	1	13	30	8	0	3	54	11
20	2438 (97)	1251	28.3 (81)	3380	7000	9.2	80	8	20	28	5	16	0	23	16
20	2520 (86)	875	20.5 (87)	4600	11800	8.3	85	3	13	36	14	9	0	33	7
85	405 (75)	8	30.7 (97)	1130	9700	14.5	60	53	21	3	8	10	2	76	3
105	447 (77)	136	35.1 (96)	720	3800	17.1	55	52	24	3	1	0	1	37	6

a) The number in parentheses is the percentage of Scots pine.
b) Tree greater than 4 m tall; the number in parentheses is the percentage of basal area of the dominant tree in Scots pine.
c) Mainly Sorbus aucuparia L.
d) Measured at 1 m above the forest floor using three point and one 1 m long quantum sensors that measure the photosynthetic photon flux density (PPFD = 400–700 nm).
e) Species: VM = Vaccinium myrtillus L.; VV = Vaccinium vitis-idaea L.; DF = Deschampsia flexuosa L.; CA = Calamagrostis arundinaceae (L.) Roth; PA = Pteridium aquilinum (L.) Kuhn; MP = Melampyrum pratense L.; M = Mosses; O = Other species.

3 Results and discussion

3.1 Stand structure and composition

Table 1 summarizes the structural and compositional characteristics of the 8 research stands. The two 7-year-old stands have a very open overstory canopy dominated by 2–3 m tall Scots pines, birches, and Sorbus aucuparia (L.) shrubs, and a fairly dense ground vegetation dominated by Deschampsia flexuosa (L.) and Vaccinium vitis-idaea (L.). The 11- and 13-year-old stands are characterized by a closed overstory canopy of mainly 4–6 m tall Scots pines with some dominant spruces and birches, a very dense subcanopy of birches and S. aucuparia, and a fairly thin ground vegetation dominated by D. flexuosa, Calamagrostis epigejos (L.) and V. vitis-idaea. The two 20-year-old stands are characterized by a very closed overstory canopy of mainly 7–9 m tall Scots pines with some dominant spruces and birches, a fairly thin subcanopy of birches and S. aucuparia, and a thin ground vegetation dominated by D. flexuosa, C. epigejos, Pteridium aquilinum (L.), and V. vitis-idaea. The 85- and 105-year-old stands have a fairly closed overstory canopy of 20–25 m tall Scots pines with some dominant spruces and birches, a very thin subcanopy of birches and S. aucuparia, and a dense ground vegetation fully dominated by V. myrtillus and V. vitis-idaea.

The four age groups of Scots pine stands studied here have a similar post-clearcutting stand development sequence as the ones described in Alaska by Alaback (1982), in central Sweden by Bråkenhielm and Persson (1980), and in eastern Canada by MacLean and Wein (1977). The changes in structure and composition during stand development have been divided by Oliver (1981) into four distinct stages: 1) tree initiation, when trees from the new stand invade the newly available space; 2) early tree dominance with competitive tree-stem exclusion, when new stems are excluded and there is a vertical stratification by species in the existing stand; 3) tree dominance with an opening of the canopy, when shrubs and advanced regeneration reinvade the understory and the overstory becomes more mature and open; and 4) stand maturation, when tree-height growth stops, the overstory gradually dies, and the understory slowly fills in to replace it. This classification is based only on above-ground components, and predicts that, at the competi-tive tree-stem exclusion stage, foliage biomass, litterfall, net primary production and nutrient accumulation in above-ground tree components will generally reach a plateau (Oliver 1981; Vogt et al. 1987). The competitive tree-stem exclusion stage begins at crown closure and usually occurs, depending on plant species and stand density, anywhere from 5 to 60 years after tree initiation.

According to Oliver's (1981) classification, the 7-year age group was at the tree initiation stage, the 11- to 13-year age group was at the beginning of the tree-stem exclusion stage, the 20-year age group was at the tree-stem exclusion stage, and the 85- to 105-year age group was at the late tree dominance stage when the stand starts to open up.

3.2 Fine-root production

No significant differences ($P > 0.364$) were found between the two stands within each of the age groups for all root variables studied (Table 2). Therefore, only the differences among age groups are discussed in this study. Significant differences ($P < 0.01$) occurred in coniferous fine-root, non-coniferous fine-root, rhizome, and total fine-root production among the four age groups of Scots pine stands (Table 2).

Fig. 1 shows coniferous and non-coniferous fine-root biomass and rhizome biomass found in the ingrowth bags after one growing season in the four age groups of Scots pine stands. The coniferous fine-roots were mainly long roots, typical of those growing in poor mineral soils. This was also found by Persson (1980) and Coopersmith (1986) in their ingrowth bag studies. The total fine-root production decreased in the 7- to 20-year age groups, and increased slightly in the 85- to 105-year age group (Fig. 1). A similar trend was found for the non-coniferous fine-root biomass. Most of the total fine-root biomass in the 7-year age group was from non-conifer species, whereas most of the total fine-root biomass in the older age groups was from the conifer species. The large non-coniferous fine-root production found on the 7-year age group was caused mainly by the abundance of grass species. Vogt et al. (1987) and Yin et al. (1989) also found the maximum standing fine-

Table 2. A summary of the analysis of variance showing variance ratios (F), P-values, and error mean-square for coniferous fine-root, non-coniferous fine-root, and non-coniferous rhizome biomass produced after one growing season in the eight Scots pine stands of four different age groups. The eight stands are nested within the four age groups. Variances were made homogeneous with a square-root transformation.

Source	Df	Coniferous fine-root		Non-coniferous fine-root		Rhizome		Total fine-root	
		F-ratio	P	F-ratio	P	F-ratio	P	F-ratio	P
Age groups	3	4.19	0.010	35.8	0.000	6.09	0.001	9.46	0.000
Stands {Age groups}	4	1.11	0.364	0.29	0.882	0.52	0.722	0.38	0.821
Error mean-square	51	0.046		0.023		0.019		0.055	

root biomass to occur early in stand development, the result of high amounts of fine-roots from shrub and herb species. Using the same method, Persson (1983) found similar amounts of fine-roots in 18- and 120-year-old Scots pine stands in central Sweden after 1 year, as in the 20- and 85- to 105-year old stands in this study.

The sharp decrease in the non-coniferous fine-root production of mainly grass species from the 7-year to 11- to 13-year age groups (Fig. 1) did not correspond to a similar decrease in grass above-ground cover (Table 1). This suggests that there was a shift in biomass allocation in these grass species from below- to above-ground organs – a shift that was presumably associated with the closing of the conifer tree canopy (Table 1). A similar result was reported by Vogt et al. (1987) for *Gaultheria shallon* Pursh growing under developing Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands in Oregon. In this study, non-coniferous fine-root production contributed between 16 and 25 % of the total fine-root production in the three oldest age groups. These values are comparable with those reported by Vogt et al. (1981) for the contribution of understory vegetation to total fine-root biomass in a 23-year-old *Abies amabilis* (Dougl.) Forbes stand in the Pacific Northwest of USA. However, they are much lower than those reported by Persson (1979, 1983) for 18- and 120-year-old Scots pine stands in central Sweden, presumably because those stands were more open than the ones reported in this study. Vogt et al. (1981) reported non-coniferous fine-root values as low as 2 % in a very closed 180-year-old *A. amabilis* stand.

Vogt et al. (1987) found Douglas-fir fine-root biomass to peak at canopy closure in both low- and high-productivity stands in western Wash-
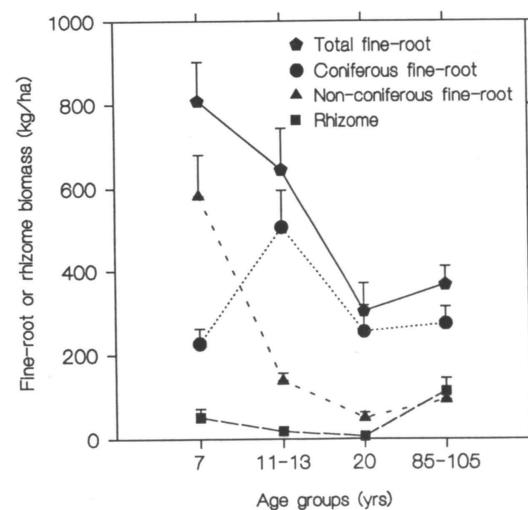

Fig. 1. Fine-root and rhizome biomass production of coniferous and non-coniferous species in four age groups of Scots pine (*Pinus sylvestris* L.) stands after one growing season in southern Finland, using the ingrowth bag method. The vertical bars are one standard error of the mean with n = 16.

ington. Following canopy closure, Douglas-fir fine-root biomass remained relatively constant in the low-productivity stands, but decreased significantly in the high productivity stands. Based on that study and others, Vogt et al. (1987) suggested that the competitive tree-stem exclusion stage may be the period at which maximum coniferous fine-root biomass is reached. The findings of our study concurs with such a hypothesis, and showed that young 11- to 13-year-old Scots pine stands produced significantly more

fine-roots than did ecologically similar, but older and younger, Scots pine stands. The attainment of early maximum coniferous fine-root biomass or production may be related to the fact that trees are expanding their fine-roots rapidly to occupy the space left vacant by the declining understory ground vegetation biomass. It is also possible that the decline in coniferous fine-root production in the 20-year age group compared to that in the 11- to 13-year age group was associated with an onset of tree mortality in the 20-year age group. In the latter both the above- and below-ground environment is presumably occupied by the dominant coniferous canopy, and little new space is available for fine-root expansion. New fine-roots are only produced to replace dead ones. Ågren et al. (1980) estimated that 63 % of the annual carbon budget of a 14-year-old Scots pine stand in central Sweden is allocated to below-ground production. The early achievement of maximum coniferous fine-root production could therefore be related to the above-ground production of leaves. In effect, many studies have shown leaf area index to reach maximum values rather early in the development of a stand (Aber 1979; Oliver 1981; Vogt et al. 1987). The results also validate the prediction of a forest growth model that used the pipe theory and principles of functional balance (Nikinmaa 1990).

3.3 Rhizome production

Rhizome production was the lowest and highest in the 20- and 85- to 105-year age groups, respectively. The increase in rhizome production in the 85- to 105-year age group was associated with a very abundant understory cover of *V. myrtillus* and *V. vitis-idaea*, and an increase in light penetration from 8–9 % of above photosynthetic photon flux density (PPFD) under the 20-year stands to 14–17 % under the 85- to 105-year stands. In a pot experiment, Messier (1993) found that *Gaultheria shallon* allocated biomass preferentially to leaves at the expense of both fine-root and rhizome production under 5–10 % full sunlight compared to 30 %. Patterson (1980) reported similar results for *Imperata cylindrica*, a rhizomatous perennial grass growing in the southern United States. Tappeiner and Alaback (1989) showed that several understory species found in the conifer forests of coastal Alaska produced 5 to 13 times less rhizome when growing under an old conifer forest transmitting be-

tween 2.8 and 6.4 % full sunlight than when growing in a recent clearcut. In the same study, they found little rhizome production under a dense young conifer stand transmitting between 0.6 and 2.3 % full sunlight. Similarly, Tappeiner et al. (1991) reported rhizome extension in *Rubus spectabilis* to be very sensitive to overstory tree canopy density.

3.4 Assessment of the ingrowth bag method

The main problems associated with the use of the ingrowth bag method are: 1) the bulk density of the soil in the bags will differ from that naturally present in the soil; 2) the lack of competition in the root ingrowth bag initially; 3) the possible disappearance of fine-roots produced in the bags before harvesting; 4) the absence of roots in the bags at the beginning of the incubation period; and 5) the presence of injured roots around the bags after their installation which favored the growth of adventitous roots. After root ingrowth bags are installed, fine-roots grow into the root-free soil where competition for water and nutrients may be less than in the surrounding soil. This may increase fine-root branching and production. If mortality and decomposition occur in the bags before they are collected, production may be underestimated. This appears not to be important, however, because only a few dead fine-roots are usually found in the bags in the first 2 years (Persson, 1980; Coopersmith, 1986; this study). Installation of the root bags may also heavily disturb the soil, severing many roots and possibly influencing subsequent fine-root production. Futhermore, the absence of roots inside the bags at the beginning of the incubation period may explain the initial lag in fine-root growth often found with this method (Persson, 1980; Coopersmith, 1986; this study). In spite of all of these problems, we believe that the ingrowth bag method is a good method to compare fine-root production between different sites or treatments, especially when the values are compared in relative terms.

References

Aber, J.D. 1979. Foliage-height profiles and succession in northern hardwood forests. Ecology 60: 18–23.

Ågren, G.I., Axelsson, B., Flower-Ellis, J.G.K., Linder, S., Persson, H., Staaf, H. & Troeng, E. 1980. Annual carbon budget for a young Scots pine. Ecol. Bull. (Stockholm) 32: 307–313.

Ahlström, K., Persson, H. & Börjesson, I. 1988. Fertilization in a mature Scots pine (Pinus sylvestris L.) stand – effects on fine roots. Plant and Soil 106: 179–190.

Alaback, P.B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. Ecology 63: 1932–1948.

— & Hermann, F.R. 1988. Long-term response of understory vegetation to stand density in Picea-Tsuga forests. Can. J. For. Res. 18: 1522–1530.

Berish, C.W. 1982. Root biomass and surface area in three successional tropical forests. Can. J. For. Res. 12: 699–704.

Bicknell, S.H. 1982. Development of canopy stratification during early succession in northern hardwoods. For. Ecol. Manage. 4: 41–51.

Boring, L.R., Monk, C.D., & Swank, W.T. 1981. Early regeneration of a clear-cut southern Appalachian forest. Ecology 62: 1244–1253.

Bormann, F.H. & Likens, G.E. 1981. Pattern and process in a forested ecosystem. Springler-Verlag, New York. N.Y. 253 p.

Bråkenhielm, S. & Persson, H. 1980. Vegetation dynamics in developing Scots pine stands in central Sweden. Ecol. Bull. (Stockholm) 32: 139–152.

Cole, D.W. & Van Miegroet, H. 1989. Chronosequences: a technique to assess ecosystem dynamics. In: Dyck, W.J. & C.A. Mees, C.A. (eds.). Research strategies for long-term site productivity. Proc., IEA/BE A3 Workshop, Seattle, Wash., August 1988. Rep. No. 8. For. Res. Inst. N.Z. Bull. 152: 5–23.

Comeau, P.G. & Kimmins, J.P. 1989. Above- and below-ground biomass and production of lodgepole pine on sites with differing soil moisture regimes. Can. J. For. Res. 19: 447–454.

Coopersmith, D.J. 1986. Root and fungal biomass production on low, medium and high productivity second-growth Douglas-fir stands on Vancouver Island. M.Sc. thesis, Univ. of B.C. Faculty of Forestry, Vancouver, B.C. 189 p.

Fabiao, A., Persson, H.A. & Steen, E. 1985. Growth dynamics of superficial roots in Portuguese plantations of Eucalyptus globulus Labill. studied with a mesh bag technique. Plant and Soil 83: 233–242.

Fogel, R. 1983. Root turnover and productivity of coniferous forests. Plant and Soil 71: 75–85.

Gholz, H.L. 1980. Production and the role of vegetation in element cycles for the first three years on an unburned clearcut watershed in western Oregon. Bull. Ecol. Soc. Am. 61: 149–157.

— , Hawk, G.M., Campbell, A. & Cromack, K., Jr. 1985. Early vegetation recovery and element cycles on a clear-cut watershed in western Oregon. Can. J. For. Res. 15: 400–409.

Hendrick, R.L. & Pregitzer, K.S. 1992. The demography of fine roots in a northern hardwood forest. Ecology 73: 1094–1104.

Kellomäki, S. & Väisänen, H. 1991. Applications of a gap model for the simulation of forest ground vegetation in boreal conditions. For. Ecol. Manag. 42: 35–47.

Kummerow, J., Kummerow, M. & Trabaud, L. 1990a. Root biomass, root distribution and the fine-root growth dynamics of Quercus coccifera L. in the garrigue of southern France. Vegetatio 87: 37–44.

— , Castillanos, J., Maas, M. & Larigauderie, A. 1990b. Production of fine roots and the seasonality of their growth in a Mexican deciduous dry forest. Vegetatio 90: 73–90.

Kurz, W.A. & Kimmins, J.P. 1987. Analysis of some sources of error in methods used to determined fine root production in forest ecosystems: a simulation approach. Can. J. For. Res. 17: 909–912.

Lehto, J. & Leikola, M. 1987. Käytännön metsätyypit. Kirjayhtymä.

MacLean, D.A. & Wein, R.W. 1977. Changes in understory vegetation with increasing stand age in New Brunswick forests: species composition, cover, biomass, and nutrients. Can. J. Bot. 55: 2818–2831.

Messier, C. 1992. Growth and biomass allocation of Gaultheria shallon in coastal British Columbia (CANADA): ecological and silvicultural implications. In: Root ecology and its practical application. 3rd International ISRR Symp., Vienna, 1991. Verein für Wurzelforschung, A-9020, Klagenfurt. p 513–516.

— 1993. Effects of neutral shade and growing media on growth, biomass allocation, and competitive ability of Gaultheria shallon. Can. J. Bot. 70: 2271–2276.

— & Kimmins, J.P. 1991. Above- and below-ground vegetation recovery in recently clearcut and burned sites dominated by Gaultheria shallon in coastal British Columbia. For. Ecol. Manage. 46: 275–294.

Nadelhoffer, K.J. & Raich, J.W. 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology 73: 1139–1147.

Nikinmaa, E. 1990. Application of cost-benefit principles on stand growth; a carbon budget model approach. Silva Carelica 15: 155–166.

Oliver, C.D. 1981. Forest development in North America following major disturbances. For. Ecol. Manage. 3: 153–168.

Patterson, D.T. 1980. Shading effects on growth and partitioning of plant biomass in cogongrass (Imperata cylindrica) from shaded and exposed habitats. Weed Science 28: 735–740.

Persson, H. 1978. Root dynamics in a young Scots pine stand in central Sweden. Oikos 30: 508–519.

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

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

— 1983. The distribution and productivity of fine-roots in boreal forests. Plant and Soil 71: 87–101.

Santantonio, D. & Grace, J.C. 1987. Estimating fine-root production and turnover from biomass and decomposition data: a compartment-flow model. Can. J. For. Res. 17: 900–908.

Symbula, M. & Day, Jr. F.P. 1988. Evaluation of two methods for estimating belowground production in a fresh-water swamp forest. Am. Midland Naturalist 120: 405–415.

Tappeiner II, J.C. & Alaback, P.B. 1989. Early establishment and vegetative growth of understory species in the western hemlock – Sitka spruce forests of southeast Alaska. Can. J. Bot., 67: 318–326.

Tappeiner, J., Zasada, J. Ryan, P. and Newton, M. 1991. Salmonberry clonal and population structure: the basis for a persistent cover. Ecology 72: 609–618.

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

— & Persson, H. 1991. Measuring growth and development of roots. In: Hincley, T. & Lassoie, J.P. (eds.). Techniques and approaches in forest tree ecophysiology. CRC-Press, Inc., Florida. p. 477–501.

— , Vogt, D.J., Moore, E.E., Fatuga, B.A., Redlin, M.R. & Edmonds, R.L. 1987. Conifer and angiosperm fine-root biomass in relation to stand age and site productivity in Douglas-fir forests. J. Ecol. 75: 857–870.

Wilkinson, L. 1988. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL.

Yin, X., Perry, J.A. & Dixon, R.K. 1989. Fine-root dynamics and biomass distribution in a Quercus ecosystem following harvesting. For. Ecol. Manage. 27: 159–177.

Total of 44 references