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Fertilization Effects on Fine Root Biomass, Production, and Turnover Rate in a *Pinus rigida* Plantation

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ABSTRACT : We examined the effects of fertilization [control (C), 200 kg N ha^{-1} + 25 kg P ha^{-1} (LNP), and 400 kg N ha^{-1} + 50 kg P ha^{-1} (HNP)] on fine root (< 2 mm diameter) dynamics using monthly soil coring method in a 39-year-old *Pinus rigida* plantation of central Korea. The average fine root biomass (live + dead) (kg ha^{-1} ± SE) during the first growing season for C, LNP, and HNP was 1301 ± 54, 1084 ± 47, and 1328 ± 22, respectively. The fine root production (kg ha^{-1} ± SE) was 2394 ± 128 for C, 2048 ± 101 for LNP, and 2768 ± 150 for HNP, respectively. Over the same period, fertilization treatments had impact on N and P concentrations of live fine root. Nitrogen and P inputs (kg ha^{-1} yr^{-1}) into the soil through fine root turnover for C, LNP, and HNP were 16.6 and 0.9, 17.2 and 0.9, and 24.1 and 1.6, respectively. There were no significant differences in fine root biomass and production during the first growing season after fertilization. However, fertilization increased fine root N and P concentrations, and in consequence resulted in increased N and P inputs into soil through fine root turnover.

Key words: Biomass, Fine root, Nitrogen, Phosphorus, *Pinus rigida*, Production, Turnover.

INTRODUCTION

Fine roots (< 2 mm diameter) play important roles in water and nutrient absorption and are the important structural and functional components of forested ecosystems (Persson 1983, Cheng and Bledsoe 2002). In order to understand belowground nutrients flux mechanism, it is important to determine temporal and spatial distributions of fine roots. However, due to difficulties in measuring fine root growth, current information about fine root dynamics is limited (Majdi 1996). A large proportion of forest production is allocated to fine roots, resulting in a large flux of carbon and nutrients into belowground system (Marshall 1986, Kurz *et al.* 1996, Cairns *et al.* 1997). Also, fine root turnover represents a major pathway for carbon and nutrient fluxes from plants to soils, but it is not easily or commonly measured (Dilustro *et al.* 2002). Although tree root systems store large amounts of organic matter and nutrients in forest ecosystems, information on the rates and controls of fine root decomposition is scant, especially compared with the aboveground litter decomposition (Fogel and Cromack 1977, Chen *et al.* 2002). To better understand the belowground nutrient cycling in forest ecosystems, more fine root biomass and production studies are needed along with fertilization treatments.

Fertilization is a routine operation in forest management in many regions, and nitrogen (N) and phosphorus (P) are the primary elements used. The impacts of fertilization on fine root dynamics depend on a wide range of factors, including stand composition and structure, and the rate and form of fertilizer. Nitrogen fluxes are a potentially useful method for estimating both turnover and production of fine root in temperate forests and mineral N availability influences fine root growth in natural and managed temperate forests.

There are numerous studies on the effects of fertilization on fine root biomass and production in forests, however, the results are still conflicting in the literature (Hendricks *et al.* 1993). For example, some studies reported increased fine root biomass and production following fertilization (Braekke 1992, Helmisaari and Hallbacken 1999, Majdi 2001). In contrast, the other studies showed that the fine roots responded to fertilization with lower biomass and production (Alexander and Fairley 1983, Gower *et al.* 1992, Majdi and Nylund 1996). The purpose of this study was to determine fine root biomass, production, and turnover with N plus P fertilization treatment in a *Pinus rigida* Mill. plantation of central Korea.

MATERIALS AND METHODS

This study was conducted in a 39-year-old *Pinus rigida* Mill. plantation at the Korea University Yangpyeong Experiment Forest

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in central Korea (37°30' N, 127°42' E). Average annual precipitation was 1360 mm and average January and July temperatures were 7.9 and 24.1°C, respectively (Son and Lee 1997, Son *et al.* 2000). For this study, six 15m × 15m plots, which was established on a relatively similar slope, aspect and soil, were randomly selected in 1996. Two replications of three levels of N plus P fertilization treatments [control: C, low N+P (200 kg N ha^{-1}+ 25kg P ha^{-1}: LNP), and high N+P (400 kg N ha^{-1} + 50kg P ha^{-1}: HNP)] were applied. In late March 1996, N [as $(NH_4)_2SO_4$] plus P [as Ca $(H_2PO_4)_2 \cdot H_2O$] fertilizers were broadcasted on the soil surface.

Fine root biomass was estimated by monthly soil coring (intervals of 4 weeks) from April to December at five random locations in each plot (Makkonen and Helmisaari 1999). Although the sequential soil coring method is labor-intensive and limits the frequency of sampling because of time-consuming processing (Majdi 1996), this method is commonly used in forests to estimate fine root biomass, production, and turnover (Makkonen and Helmisaari 2001, Hertel and Leuschner 2002). Especially this method is suitable for studying the annual and seasonal fine root biomass variation. A stainless steel corer (4.5 cm diameter and 30 cm long) was used to take soil cores. Each soil corer was pushed into the soil to about 20 cm (Kim *et al.* 1996). All cores were located at least 1 m away from the stem to avoid possible variation in coarse root biomass (Fredericksen and Zedaker 1995).

Samples were returned to the laboratory and stored at 4°C until they were processed. Roots with ecto-mycorrhizas from mineral soil were wet sieved using a 2 mm mesh screen and fragmented root that passed the screen were hand sorted. Roots were sorted into two diameter classes: coarse roots (> 2 mm diameter) and fine roots (< 2 mm diameter) and classified as live or dead on the basis of morphology, floatation and color with careful microscopic observation. Roots were then dried to a constant mass at 65°C and weighed. Dried fine root samples were ground and digested with sulfuric acid. Nitrogen and P concentrations were determined using an automated analyzer (Bran + Luebbe TRAACS 800, Norderstedt, Germany).

A common approach to measuring fine root production is sequential sampling of root mass and estimating root production by adding increments of standing stocks of living and dead roots (McClaugherty *et al.* 1982). In this study, fine root production was calculated by balancing the monthly live and dead fine root biomass according to the decision matrix presented by Fairly and Alexander (1985). Nutrient fluxes with fine roots were calculated assuming that there was no translocation of nutrients during root senescence (Nambiar 1987). Fine root turnover was calculated as the ratio of fine root production to biomass (Burke and Raynal 1994).

Data were analyzed as a randomized complete block design in a factorial experiment. To test for seasonal trends over sampling dates, analysis of variance using repeated measures was employed. All analyses were conducted using the general linear model procedure of the Statistical Analysis System (SAS 1988). Duncan' s multiple rage test was used to determine whether differences in fine root biomass, production and nutrient concentrations were statistically significant among fertilization treatments at a significance level of 0.05.

RESULTS AND DISCUSSION

Fine root biomass

The average fine root (live + dead) biomass (kg ha^{-1} ± SE) for C, LNP, and HNP was 1301±54, 1084±47, and 1328±22, respectively. These were less than live fine root biomass for high-productivity (45 year: 1871 kg ha^{-1}) and low-productivity (33 year: 2623 kg ha^{-1}) sites in a Douglas-fir plantation (Vogt *et al.* 1987). Fine root biomass for the control plot (1301 kg ha^{-1}) accounted for 0.94% of the total aboveground biomass (138.2 Mg ha^{-1}) for the species (Kim *et al.* 1996). The ratios of live to total fine root biomass were 72% for C, 77% for LNP, and 71% for HNP, respectively, and were similar to those reported for temperate forests (Helmisaari and Hallbåken 1999). Over the entire growing season, average total fine root biomass in LNP was lower than in the control and HNP plots. However, the difference was not statistically significant ($p>0.05$).

Previous studies reported that fertilization either decreased or increased fine root biomass (Alexander and Fairley 1983, Gower *et al.* 1992, Hendricks *et al.* 1993, Helmisaari and Hallbåken 1999, Majdi 2001). Many factors may have contributed to these conflicting results, including variations in fertilizer treatments (formulation, rate and timing of application), rooting media, tree species and age, and assessment methodology. In general, fertilization may cause short term fluctuations in fine root carbohydrate allocation. Therefore, results from fertilization experiments may represent transient responses rather than permanent changes in allocation. The reasons for no changes in fine root biomass after treatment might be related to the sampling time which was only for the first growing season after fertilization, and the responses of fertilization may be delayed for the following years (Alexander and Fairley 1983).

Seasonal changes in live and dead fine root biomass of *Pinus rigida* were presented in Fig. 1. Fine root biomass varied significantly among sampling times within a treatment and there were two peaks in fine root biomass. Major peak in live fine root biomass was found in May, and the smallest live fine root biomass was occurred in late July (Fig. 1a). The early peak might be related to the peak in fine root production over the same period. The increase in live fine root biomass in the latter part of the growing season might be due to rapid fine root growth following litterfall input and high N mineralization (Son and Lee 1997). Other studies also reported two peaks in fine root biomass during the grow-

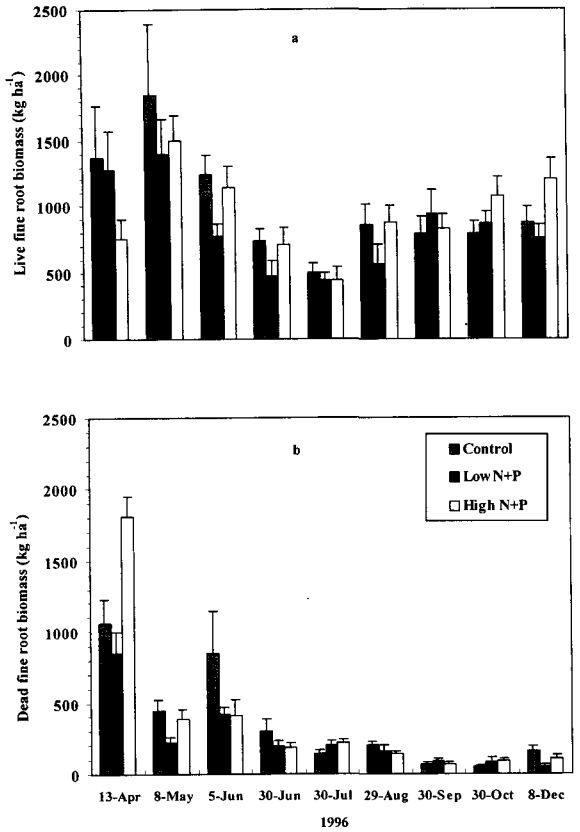

Fig. 1. Live (a) and dead (b) fine root biomass (kg ha^{-1}) of a 39-year-old *Pinus rigida* plantation of central Korea. Error bars represent one standard error.

ing season (Hendrick and Pregitzer 1996). However, dead fine root biomass showed only one peak in early growing season and decreased throughout the rest of the growing season (Fig. 1b). One peak of dead fine root biomass in early spring was

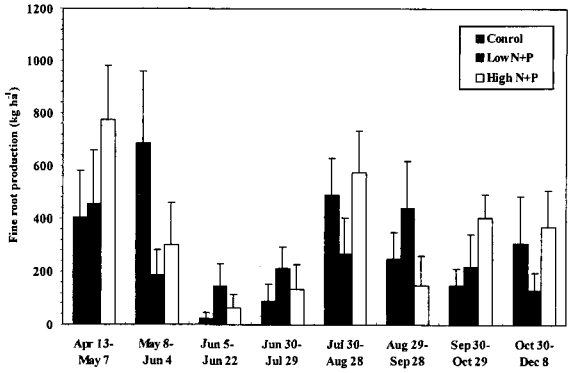

Fig. 2. Fine root production (kg ha-1) of a 39-year-old *Pinus rigida* plantation of central Korea. Error bars represent one standard error.

observed in other temperate coniferous forests (McClaugherty et al. 1982). The seasonal pattern of live fine root biomass seemed to reflect changes in soil moisture which was high in the early growing season, deceased in June and July, and increased again in the late growing season at the study site (Son and Kim 1996).

Fine root production

Fine root production (kg ha^{-1} ± SE) of *Pinus rigida* during the growing season was greatest in HNP (2768 ± 150), followed by C (2394 ± 128) and lowest in LNP (2048 ± 101). Other fertilization experiments have estimated that N availability decreased fine root production (Vogt *et al.* 1986, 1987, Hendricks *et al.* 1993), however, the difference in this study was not statistically significant ($p>0.05$). Fine root production values were very similar to those for temperate coniferous forests (1600~2620 kg ha^{-1}, Nadelhoffer *et al.* 1985), but less than those for temperate decid-

Table 1. Live fine root N and P concentrations (%) of a 39-year-old *Pinus rigida* plantation of central Korea. The number in parentheses is one standard error of the mean

	13 Apr.	8 May	5 Jun.	30 Jun.	30 Jul.	29 Aug.	30 Sep.	30 Oct.	8 Dec.	Mean
Nitrogen										
Control	0.67	0.64	0.79	0.75	0.57	0.85	0.69	0.73	0.58	0.70
	(0.01)	(0.04)	(0.10)	(0.01)	(0.06)	(0.03)	(0.07)	(0.03)	(0.01)	(0.02)
LNP	0.89	0.63	0.89	0.75	0.71	0.96	0.72	1.01	1.06	0.84
	(0.13)	(0.06)	(0.09)	(0.13)	(0.05)	(0.07)	(0.06)	(0.04)	(0.08)	(0.04)
HNP	0.96	0.64	1.31	0.72	0.94	0.90	0.64	0.84	0.91	0.87
	(0.06)	(0.14)	(0.17)	(0.05)	(0.10)	(0.17)	(0.01)	(0.11)	(0.08)	(0.05)
Phosphorus										
Control	0.039	0.042	0.053	0.039	0.029	0.046	0.039	0.019	0.024	0.037
	(0.005)	(0.003)	(0.010)	(0.003)	(0.002)	(0.007)	(0.009)	(0.004)	(0.007)	(0.004)
LNP	0.057	0.035	0.047	0.041	0.043	0.065	0.046	0.035	0.046	0.046
	(0.011)	(0.005)	(0.001)	(0.001)	(0.002)	(0.012)	(0.001)	(0.002)	(0.004)	(0.003)
HNP	0.060	0.041	0.087	0.047	0.103	0.076	0.041	0.046	0.025	0.058
	(0.009)	(0.002)	(0.007)	(0.006)	(0.034)	(0.004)	(0.001)	(0.009)	(0.003)	(0.007)

uous forests (3450~9900 kg ha^{-1}, Hendrick and Pregitzer 1993).

The differences in estimates of fine root production between this study and other studies might be, at least to some degree, due to sampling and calculation procedures, definition of fine root size, annual variation, soil sampling depth, soil fertility, proportion of rock fragments, growing season length, and total sampling period (Hendricks *et al.* 1993, Burke and Raynal 1994, Clemensson-Lindell and Persson 1995, Jackson *et al.* 1997, Rytter and Rytter 1998, Makkonen and Helmisaari 1999, 2001).

Fig. 2 showed seasonal changes in fine root production. The highest rates of production occurred in early growing season (April-May). Other studies also reported a peak in that time (Hendrick and Pregitzer 1996, Cheng and Bledsoe 2002). The early peak might be induced by increased soil temperature in the spring (Son and Hwang 2003).

Fine root N and P concentrations

The average fine root N and P concentrations (% ± SE) during the growing season were 0.70 ± 0.01 and 0.037 ± 0.002 for C, 0.84 ± 0.02 and 0.046 ± 0.002 for LNP, and 0.87 ± 0.03 and 0.058 ± 0.004 for HNP, respectively (Table 1). These values were within the range reported for other coniferous or deciduous forests (Yin and Perry 1991, Burke and Raynal 1994, Jackson *et al.* 1997, Pyo *et al.* 2002). The average fine root N and P concentrations for LNP and HNP were higher than those for C ($p<0.001$) and fine root N and P concentrations varied during the growing season ($p<0.001$). Increases in root nutrient concentration following fertilization were reported from the other studies (Stevenson and Day 1996, Persson *et al.* 1998).

Fine root turnover rate

Fine root turnover rate (yr^{-1}) was highest for HNP (2.08), followed by LNP (1.89) and C (1.84). These values were higher compared with turnover rates (0.6~0.7 yr^{-1}) in *Pinus strobus* plantation reported by Nadelhoffer *et al.* (1985). It was reported that plantations of fast-growing species, where restrictions in water and nutrient availability were kept to a minimum, showed a rapid turnover rate of fine roots (Rytter and Rytter 1998) and fine root turnover may vary with site quality and species composition (Shaver and Billings 1975). Increased fine root turnover rates in *P. rigida* after fertilization was consistent with the previous results that rates of fine roots mortality increased as soil nutrient availability increased (Alexander and Fairley 1983, Pregitzer *et al.* 1995). Low rates of fine root turnover on relatively poor sites may be analogous to the comparatively low rates of leaf turnover in poor sites (Mooney and Gulmon 1982).

Currently two contrasting hypotheses on the effect of nutrient availability on fine root biomass and production were suggested (Hendricks *et al.* 1993). One hypothesis was that fine root biomass and production decreased as nutrient limitation decreased and fine root longevity or turnover rate was not influenced by nutrient availability. The other hypothesis was that fine root growth remained relatively constant across nutrient availability gradients and fine root turnover rate increased with nutrient availability. Our current results showed no significant changes in fine root biomass and production, but indicated increases in fine root turnover rate following fertilization; these supported the second hypothesis (Nadelhoffer *et al.* 1985, Pregitzer *et al.* 1995).

Nitrogen and P inputs

Nitrogen and P (kg ha^{-1}) inputs through fine root turnover during the growing season were 16.6 and 0.87 for C, 17.2 and 0.94 for LNP, and 24.1 and 1.61 for HNP, respectively. These inputs were very similar to 20.3~27.3 kg ha^{-1} of N and 1.2~1.7 kg ha^{-1} of P for a temperate deciduous forest (Burke and Raynal 1994). But the values were lower than 29~62 kg ha^{-1} of N and 3.5~11.1 kg ha^{-1} of P for warm and cold temperate forests summarized by Vogt *et al.* (1986). In the control plot, N input from fine root turnover was greater than that from leaf litter (15.9 kg ha^{-1}) and P input was less important than that from leaf litter (2.40 kg ha^{-1}) in the study site (Kim *et al.* 1996).

It was difficult to suggest firm conclusions on the fine root biomass and production data obtained from this study. First of all, we sampled fine roots for only the first growing season after fertilization and could have missed relative long-term effects (Hendricks *et al.* 1993). If repeated sampling in several years had occurred, the estimation of fine root biomass, production and turnover would have been more accurate (Clemensson-Lindell and Persson 1995, Makkonen and Helmisaari 1998, 1999, Majdi 2001). More comprehensive research on fine root dynamics is needed to understand the role of fine root in carbon allocation and nutrient cycling of *P. rigida* in the region.

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LITERATURE CITED

Alexander, I.J. and R.I. Fairley. 1983. Effects of N fertilization on populations of fine roots and mycorrhizas in spruce humus. Plant and Soil 71: 49-53.

Braekke, F.H. 1992. Root biomass after drainage and fertilization of a low-shrub pine bog. Plant and Soil 143: 33-43.

Burke, M.K. and D.J. Raynal. 1994. Fine root growth phenology,

production, and turnover in a northern hardwood forest ecosystem. Plant and Soil 162: 135-146.

Cairns, M.A., S. Brown, E.H. Helmer and G.A. Baumgardner. 1997. Root biomass allocation in the world' s upland forests. Oecologia 111: 1-11.

Chen, H., M.E. Harmon, J. Sexton and B. Fasth. 2002. Fine-root decomposition and N dynamics in coniferous forests of the Pacific Northwest, U.S.A. Canadian Journal of Forest Research 32: 320-331.

Cheng, X. and C.S. Bledsoe. 2002. Contrasting seasonal patterns of fine root production for blue oaks (*Quercus douglassi*) and annual grasses in California oak woodland. Plant and Soil 240: 263-274.

Clemensson-Lindell, A. and H. Persson. 1995. The effects of nitrogen addition and removal on Norway spruce fine-root vitality and distribution in three catchment areas at Gårdsjo . Forest Ecology and Management 71: 123-131.

Dilustro, J.J., F.P. Day, B.G. Drake and C.R. Hinkle. 2002. Abundance, production and mortality of fine roots under elevated atmospheric CO_2 in an oak-scrub ecosystem. Environmental and Experimental Botany 48: 149-159.

Fairley, R.I. and I.J. Alexander. 1985. Methods of calculating fine root production in forests. In: Ecological Interactions in the Soil. pp. 37-41. Special Publication No. 4 of the British Ecological Society, London.

Fogel, R. and K.Jr. Cromack. 1977. Effect of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. Canadian Journal of Botany 55: 1632-1640.

Fredericksen, T.S. and S.M. Zedaker. 1995. Fine root biomass, distribution, and production in young pine-hardwood stands. New Forests 10: 99-110.

Gower, S.T., K.A. Vogt and C.C. Grier. 1992. Carbon dynamics of Rocky Mountain Douglas-fir: influence of water and nutrient availability. Ecological Monographs 62: 43-65.

Helmisaari, H.-S. and L. Hallbäken. 1999. Fine-root and necromass in limed and fertilized Norway spruce (Picea abies (L.) Karst.) stands. Forest Ecology and Management 119: 99-110.

Hendricks, J.J., K.J. Nadelhoffer and J.D. Aber. 1993. Assessing the role of fine roots in carbon and nutrient cycling. TREE 8: 174-178.

Hendrick, R.L. and K.S. Pregitzer. 1993. The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. Canadian Journal of Forest Research 2507-2520.

Hendrick, R.L. and K.S. Pregitzer. 1996. Applications of minirhizotrons to understand root function in forests and other natural ecosystems. Plant and Soil 185: 293-304.

Hertel, D. and C. Leuschner. 2002. A comparison of four different fine root production estimates with ecosystem carbon balance data in a *Fagus - Quercus* mixed forest. Plant and Soil 239: 237-251.

Jackson, R.B., H.A. Mooney, and E.D. Schulze. 1997. A global budget for fine root biomass, surface area, and nutrient contents. Proceedings of National Academy of Science 94: 7362-7366.

Kim, J.S., Y. Son, J.H. Lim and Z.S. Kim. 1996. Aboveground biomass, N and P distribution, and litterfall in *Pinus rigida* and *Larix leptolepis* plantations. Journal of Korean Forestry Society 85: 416-425.

Kurz, W.A., S.J. Beukema and M.J. Apps. 1996. Estimation of root biomass and dynamics for C budget model of the Canadian forest sector. Canadian Journal of Forest Research 26: 1973-1979.

Majdi, H. 1996. Root sampling methods - applications and limitations of the minirhizotron technique. Plant and Soil 185: 255-258.

Majdi, H. 2001. Changes in fine root production and longevity in relation to water and nutrient availability in a Norway spruce stand in northern Sweden. Tree Physiology 21: 1057-1061.

Majdi, H. and J.-E. Nylund. 1996. Does liquid fertilization affect fine root dynamics and lifespan of mycorrhizal short roots? Plant and Soil 185: 305-309.

Makkonen, K. and H.-S. Helmisaari. 1998. Seasonal and yearly variations of fine-root biomass and necromass in a Scots pine (*Pinus sylvestris* L.) stand. Forest Ecology and Management 102: 283-290.

Makkonen, K. and H.-S. Helmisaari. 1999. Assessing fine-root biomass and production in a Scots pine stand-comparison of soil core and root ingrowth core methods. Plant and Soil 210: 43-50.

Makkonen, K. and H.-S. Helmisaari. 2001. Fine root biomass and production in Scots pine stands in relation to stand age. Tree Physiology 21: 193-198.

Marshall, J.D. 1986. Drought and shade interact to cause fine root mortality in Douglas-fir seedlings. Plant and Soil 91: 51-60.

McClaugherty, C.A., J.D. Aber and J.M. Melillo. 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 63(5): 1481-1490.

Mooney, H.A. and S.L. Gulmon. 1982. Constraints on leaf structure and function in relation to herbivory. BioScience 32: 198-206.

Nadelhoffer, K.J., J.D. Aber and J.M. Melillo. 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. Ecology 66: 1377-1390.

Nambiar, E.K.S. 1987. Do nutrients retranslocate from fine roots? Canadian Journal of Forest Research 17: 913-918.

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

Persson, H., K. Ahlstr m and A. Clemensson-Lindell. 1998. Nitrogen addition and removal at Gårdsjdsjön-effects on

fine-root growth and fine-root chemistry. Forest Ecology and Management 101: 199-205.

Pregitzer, K.S., D.R. Zak, P.S. Curtis, M.E. Kubiske, J.A. Teeri and C.S. Vogel. 1995. Atmospheric CO2, soil nitrogen and turnover of fine roots. New Phytologist 129: 579-585.

Pyo, J.H., C.H. Shin, J. Namgung, J.H. Kim and H.T. Mun. 2002. Weight loss and nutrients dynamics during the decomposition of fine roots. Korean Journal of Ecological Sciences 25(1): 41-44.

Rytter, R.-M. and L. Rytter. 1998. Growth, decay, and turnover rates of fine roots of basket willows. Canadian Journal of Forest Research 28: 893-902.

SAS. 1988. SAS/STAT User' s Guide. 6.03 edition. SAS Institute. Cray, NC, USA.

Shaver, G.R and W.D. Billings. 1975. Root production and root turnover in a wet tundra ecosystem, Barrow, Alaska. Ecology 56: 401-409.

Son, Y. and H.W. Kim. 1996. Soil respiration in Pinus rigida and *Larix leptolepis* plantations. Journal of Korean Forestry Society 85: 496-505.

Son, Y. and I.K. Lee. 1997. Soil nitrogen mineralization in adjacent stands of larch, pine and oak in central Korea. Annales des Sciences Forestieres 54: 1-8.

Son, Y. and J.H. Hwang. 2003. Fine root biomass, production, and turnover in a fertilized Larix leptolepis plantation in central Korea. Ecological Research (in press).

Stevenson, M.J. and F.P. Day. 1996. Fine-root biomass distribution and production along a barrier island chronosequence. The American Midland Naturalist 135: 205-217.

Vogt, K.A., C.C. Grier and D.J. Vogt. 1986. Production, turnover, and nutritional dynamics of above- and below-ground detritus of world forests. Advances in Ecological Research 15: 303-377.

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

Yin, X. and J.A. Perry. 1991. Factors affecting nitrogen concentration of fine roots in forest communities: regression analysis of literature data. Forest Science 37(1): 374-382.

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