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Estimation of Fine Root Production in Coniferous Forests in Japan

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Abstract

It is well documented that fine root production (FRP) in forest ecosystems is large due to rapid turnover in spite of the small standing crop. Several methods have been applied to measure FRP: sequential coring, ingrowth core, nitrogen budget, soil carbon budget, and minirhizotron methods. The processes as well as advantages and disadvantages of each method were briefly reviewed in this report. The soil micromorphological method applied in a Japanese coniferous forest was described. This method enables to determine the fine root distribution and microstructure of the organic layer where fine roots are mostly concentrated. The ability to observe root cross-sections may improve the classification of the physiological status of the roots. The data obtained by this method at one time indicated that those fine and active roots were distributed mostly in the superficial litter layer of the soil. In the fermentation layer below, a smaller number of active types of roots were found. Periodical collections of samples may enable to study seasonal changes of fine roots and supply additional information on root ecology. The most difficult problem in the study of fine root dynamics is still the methodology. Over- and underestimation should be corrected to acquire more accurate information on forest production ecology and the role of forests in carbon and nutrient balance.

Discipline: Forestry and forest products
Additional key words: ecosystem, ingrowth, root free soil core, soil micromorphology, turnover

Introduction

Fine roots (including mycorrhizae) play an important role in the carbon and nutrient economy in temperate forest ecosystems. In many cases, more than 50% of annual net primary production (NPP) is allocated belowground[9,10,17], and nutrient return to the soil by fine root death may exceed that by aboveground litterfall[32]. However, there had been discrepancies in the methods of measuring the fine root production (FRP) and turnover in the past decades[7,8,19,23–26,29,31]. Hendricks et al. (1993)[14] raised an important question: Is belowground NPP positively or negatively correlated to aboveground NPP? They concluded that a positive correlation was more likely, despite many conflicting data.

This review compares several methods used to estimate FRP, examines the contribution of belowground components to the forest productivity, and offers a new approach, that is, micromorphological method of studying the fine root dynamics in a coniferous forest in Japan.

Methods of estimating fine root production

Several methods have been developed to estimate fine root production[27,33,36]. In this paragraph, I will describe each method and the results obtained. First of all, in the "sequential coring" method attempts are made to detect seasonal fluctuations by the following procedures: a certain number of small volumetric soil samples are collected at regular intervals, and the differences in the mean root biomass are summed to represent fine root production. Unexpectedly a large fine root production was first reported by Edwards and Harris (1977)[5] in a mixed deciduous forest. They measured fine root biomass several times over a period of 2 years and found distinct seasonal changes expressing bimodal peaks each year. Persson (1978)[24] suggested that the supply of dead fine root materials to the soil was considerably higher than that conventionally expected. Here it must be noted that some types of calculations give a wide range of values[7,8,29]. In the simplest way, production is estimated by subtracting the minimum from maximum fine root standing crop, while in other cases either all differences or only significant differences are summed. McClaughty et al. (1982)$^{20)}$ developed a decision matrix to account for the simultaneous occurrence of production and death, assuming rapid fine root turnover. They compared some values from different calculations plus decomposition data and suggested that lower estimates of production were more accurate.

In the "ingrowth core" method soil cores are taken, the roots are removed from them and the soil samples are buried after packing them into mesh-bags so that the roots can penetrate into the root-free soil cores through the mesh from the surrounding soil$^{27,33)}$. The advantage of this method is that it enables to compare different experimental treatments and it is less laborious than sequential coring. However it is difficult to convert the data on an area basis$^{33)}$. Persson (1983)$^{26)}$ actually compared FRP estimates based on "sequential coring" and "ingrowth core" method in boreal forests, and found only small differences in magnitude. My preliminary experiment with this method$^{15)}$ in a Japanese cedar (*Cryptomeria japonica* D. Don) plantation showed that fine root regrowth into the root-free soil cores was more abundant from midsummer to late fall than from spring to midsummer (Fig. 1). This finding contrasted with shoot growth which occurred most rapidly from early to midsummer in this stand. Surprisingly, the amounts of very fine roots (less than 1 mm in diameter) in the ingrowth core were considerably larger (more than double) than those in the original soil core after a 4-month incubation period from midsummer to late fall. However, the effect of severing roots in installing the cores and the difference in soil texture as a rooting medium should be considered in interpreting the results from this method.

Aber et al. (1985)$^{1)}$ and Nadelhoffer et al. (1985)$^{22)}$ presented in the same year another approach to estimate FRP, namely, the "nitrogen (N) budget" method. Raich and Nadelhoffer (1989)$^{28)}$ introduced an innovative "soil carbon (C) budget" method. These 2 methods can be combined and are referred to as the "budget" method. N budget method determines the amount of N mineralized in soil by soil incubation, N uptake by aboveground part of plants, N content in the aboveground litterfall. FRP estimates can then be calculated. Soil carbon budget can only set the upper limits to FRP, but it can verify the overestimation of FRP. The upper limits can be obtained by subtracting the C amount in litterfall from that of soil respiration. The resultant limits are referred to as total root allocation which expresses live root respiration plus belowground detritus production. These authors were able to define the relationship between aboveground litterfall data and FRP from N budget, and they suggested that annual FRP increases with aboveground production$^{23)}$. Also their analysis showed that FRP

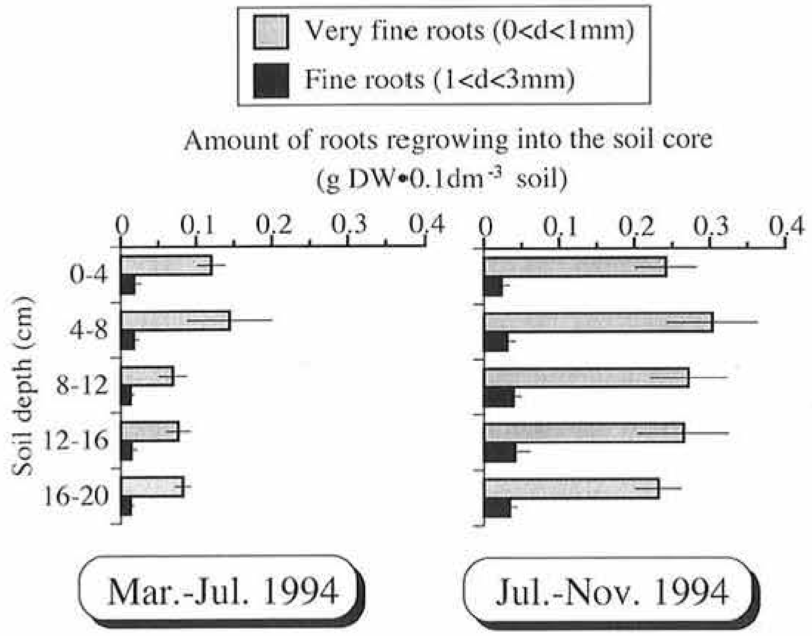

Fig. 1. Amount of roots which regrew into root-free soil cores during 2 periods
d = diameter of roots. Bars indicate standard errors of the mean.

values from "sequential coring" exceeded the predicted upper limits by "soil C budget" in some cases, which may suggest overestimation.

"Minirhizotron" experiments were carried out in North American hardwood forests[11-13]. This method requires facilities such as glass tubes inserted into the soil, borescopes equipped with a video camera, and the software suitable for processing data to periodically record root images and analyze them. The most striking feature is that it can provide demographic data, though the root growth may perhaps be different on the interfaces between the soil and the glass tube. Hendrick et al. (1993)[12] converted their data on a mass basis and obtained FRP estimates of 8,000 and 7,300 $\mathrm{kg \cdot ha^{-1} \cdot yr^{-1}}$ at the 2 sites, which illustrated the important role of fine roots in forest production.

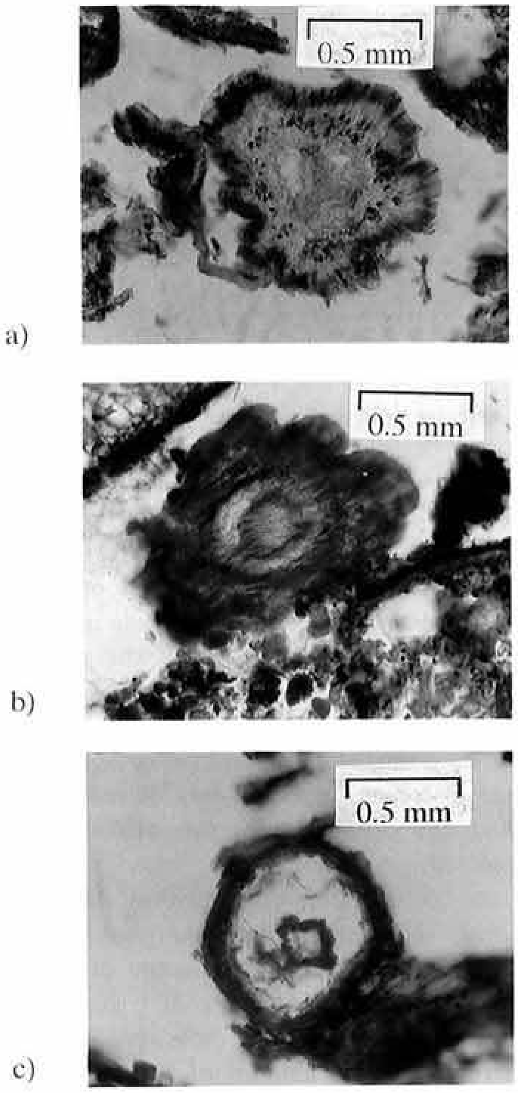

Fig. 2. Photographs of cross-sections of roots in soil thin sections
a) Type 2, only epidermis is brown.
b) Type 3, fecal pellets in the lower part.
c) Type 6, cortical tissues missing.

Finally the method of "soil micromorphology" is often used in pedogenesis and soil taxonomy. In the next section, I will present an example of this method in a Japanese coniferous forest.

Application of soil micromorphology to fine root dynamics study

The experimental site was a natural Hinoki cypress (*Chamaecyparis obtusa* Endl.) forest. The stand density (larger than 2 cm in diameter at breast height) was 2,700 ($\mathrm{no. \cdot ha^{-1}}$) and the basal area was 46.5 $\mathrm{m^2 \cdot ha^{-1}}$. The soil samples were collected in October 1993, and impregnated with polyethylene glycol (molar mass 4,000) at the site and again in the laboratory and cut with a rock slicer. The sampling depth was limited to the organic layer because of the hardness of the resin used. Fine roots were, however, mostly concentrated in the organic layer. Thus the soil thin sections were stained with methylene blue. The detailed description is presented in the reports of Takeda (1987)[30] and Kasuya, Takeda & Iwatsubo (1992)[16]. The roots that appeared in the soil thin sections were examined under a microscope and classified by the degree of staining, suberization and decomposition (Table 1, Fig. 2). The diameters of roots of each type are depicted in Fig. 3. As anticipated, type 1 which shows secondary thickening displayed the largest diameter, while other types, which all consisted of absorbing roots, did not exhibit any difference in the pattern of distribution of root diameter values. Type 2 (the most active roots in terms of absorption capacity) was concentrated in the shallowest layer (Fig. 4). This

Table 1. Classification of roots in soil thin sections

Root type	Characteristic
Type 1	Showing annual growth ring(s)
Type 2	Both stele and cortex stained (blue)
Type 3	Only stele stained (blue) and cortex suberized (brown)
Type 4	Both stele and cortex suberized (brown)
Type 5	Part of stele and/or cortex decomposed (missing)
Type 6	Only epidermis and endodermis remaining

A larger number of root types reflect the status of roots with low activity, except for type 1, which has a thick xylem layer.

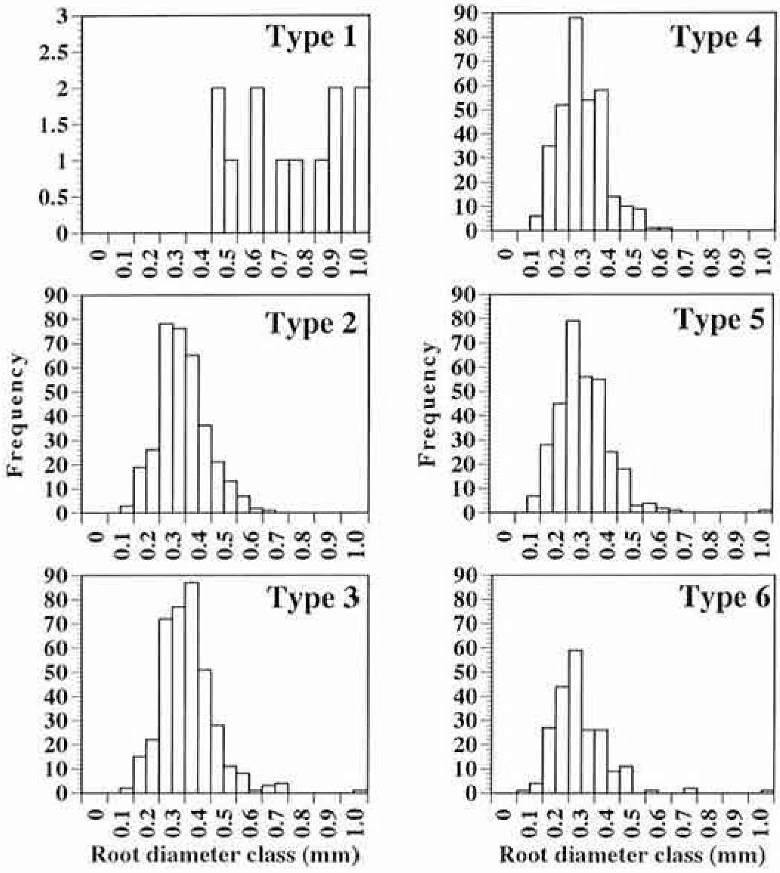

Fig. 3. Frequency distribution of root diameter in soil thin sections

layer corresponded to the litter layer of the forest floor (about 1 cm thick), and the fermentation layer was 3 to 4 cm thick. Although the results were recorded at one time and not in a time series, this method enabled to obtain an accurate classification of root activity by observing directly a cross-section of roots and the fine distribution of roots especially in ecosystems showing distinct seasonal changes in growth. Takeda (1987)[30] proposed the use of the method in the classification of organic layers of soil. Also the method can be applied to mycorrhizal research and soil biology after improvement of staining or microscopic techniques[8].

Future research

Since belowground NPP is positively correlated with aboveground NPP based on data obtained by the "budget" method, the most difficult problem is to determine why fine root decomposition is slow (usually less than 30% per year, from data compiled by Vogt et al. (1991)[34]) though many data indicate the large contribution of fine roots to annual NPP. Bloomfield and Vogt (1996)[4] reported that the higher lignin content of fine roots than that of senescent foliage may inhibit decomposition in coniferous as well as in other forest ecosystems. Fahey (1994)[6] attributed the slow decomposition rate of fine roots to the disturbance effect of the litterbag method used for measuring the decomposition, whereas Vogt et al. (1991)[34] compared litterbag and other methods such as trenching, and suggested that the former method gave smaller decomposition rates. It is hoped that the discrepancies in the data of rapid turnover rate and slow decomposition rate of fine roots will be resolved. Atkinson (1992)[3] also pointed out that root consumption by herbivores should be reexamined. In the current micromorphological study, it appeared that a substantial amount of roots were grazed since many fecal pellets of collembola were found all around the root cross-sections (Fig. 2). Furthermore, if the amount of fine root biomass is low in high productivity sites[35], how can a tree compensate for the decrease in surface area for absorbing water and nutrients? Some researchers have suggested that woody coarse roots must be responsible for these functions[2,18]. Hendricks et al. (1993)[14] noted that the pattern of antiherbivore

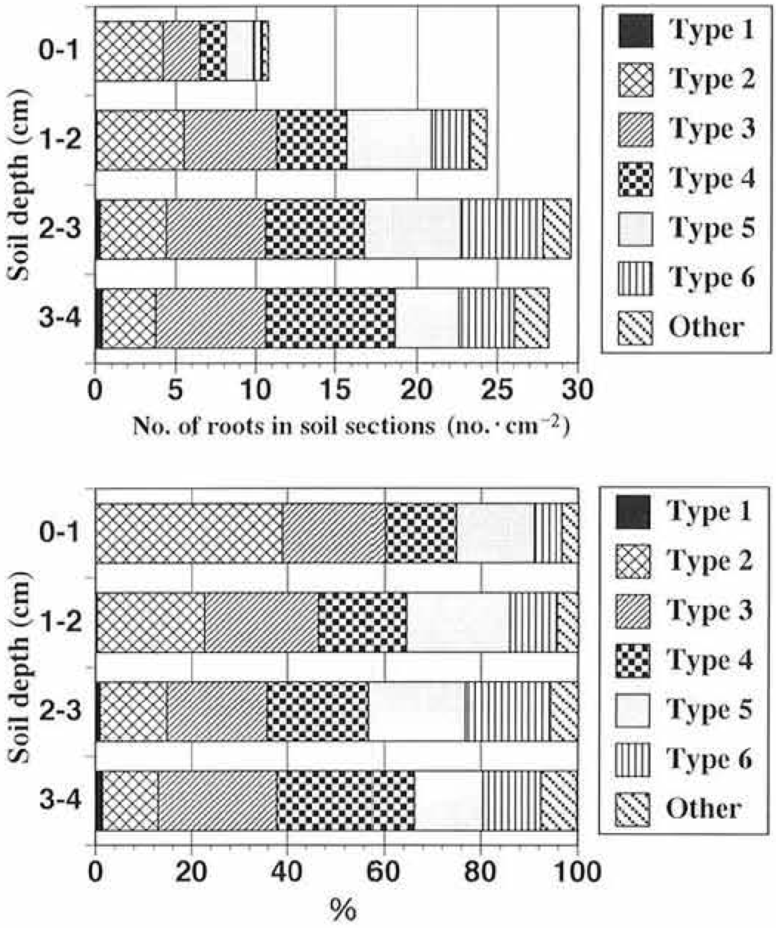

Fig. 4. Number and percentage of roots of each type in soil cross-sections at each soil depth
The type with a low number represents the roots with a more vigorous appearance.

compound allocation and retranslocation along a N availability gradient remained unknown, since 40–70% of the macronutrients were reabsorbed in fine roots prior to senescence in some coniferous forests[21].

It remains to be determined whether there is a positive or negative correlation between belowground and aboveground NPP not only in forest production studies but also in relation to the global climatic changes in the near future since forests can mitigate the carbon dioxide increase by acting as a sink.

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