Introduction

Fine roots of forest trees are, in general, defined as roots less than 2 mm in diameter. Fine roots are physiologically highly active parts of root systems and play a key role in water and nutrient uptake at the tree-soil interface. In addition, recent studies indicate that fine roots have relatively fast turnover rates and fine root uptake at the tree-soil interface. In addition, recent studies indicate that fine roots play a key role in water and nutrient uptake at the tree-soil interface. In addition, recent studies indicate that fine roots have relatively fast turnover rates and fine root uptake at the tree-soil interface.

Increasing nitrogen (N) deposition may affect carbon and nutrient dynamics in forest ecosystems. To better understand the effects of N deposition, we need to improve our knowledge of N effects on fine roots (roots <2 mm in diameter), as they are a key factor in carbon and nutrient dynamics. In the study of fine roots, we fertilized 1 × 2 m plots in a sugi (Cryptomeria japonica) stand (536 kg ha⁻¹ yr⁻¹) for 3 years and evaluated the responses of the fine roots to high N load. After fertilization, the concentration of NO₃⁻-N in the soil of N-fertilized (NF) plots was five times as large as that in the control plots and the effect was more remarkable in the subsurface soil than in the surface soil. The biomass of fine roots was 2 mm in diameter appeared to be greater in the NF plots (88 ± 19 g m⁻²) than in the control plots (66 ± 14 g m⁻²), but this difference was not statistically significant. In both plots, 76% of the biomass was accounted for by fine roots that were <1 mm in diameter. In the surface soil, the specific root length of fine roots <1 mm in diameter was significantly greater, and the diameter of those fine roots was marginally smaller, in the NF plots than in the control plots. In addition, the concentration of N in fine roots <1 mm in diameter was marginally greater in the NF plots than in the control plots. There may have been increased production of thinner fine roots or increased root branching in the NF plots. This study suggests that, in general, high N load is likely to have positive effects on sugi in terms of fine root characteristics and the effects on fine-root morphology are more evident than the effects on fine-root biomass.

**Keywords:** fine-root biomass, fine-root length, fine-root diameter, root tissue density, specific root length, soil depth

Increasing nitrogen (N) deposition may affect carbon and nutrient dynamics in forest ecosystems. To better understand the effects of N deposition, we need to improve our knowledge of N effects on fine roots (roots <2 mm in diameter), as they are a key factor in carbon and nutrient dynamics. In the study of fine roots, we fertilized 1 × 2 m plots in a sugi (Cryptomeria japonica) stand (536 kg ha⁻¹ yr⁻¹) for 3 years and evaluated the responses of the fine roots to high N load. After fertilization, the concentration of NO₃⁻-N in the soil of N-fertilized (NF) plots was five times as large as that in the control plots and the effect was more remarkable in the subsurface soil than in the surface soil. The biomass of fine roots was 2 mm in diameter appeared to be greater in the NF plots (88 ± 19 g m⁻²) than in the control plots (66 ± 14 g m⁻²), but this difference was not statistically significant. In both plots, 76% of the biomass was accounted for by fine roots that were <1 mm in diameter. In the surface soil, the specific root length of fine roots <1 mm in diameter was significantly greater, and the diameter of those fine roots was marginally smaller, in the NF plots than in the control plots. In addition, the concentration of N in fine roots <1 mm in diameter was marginally greater in the NF plots than in the control plots. There may have been increased production of thinner fine roots or increased root branching in the NF plots. This study suggests that, in general, high N load is likely to have positive effects on sugi in terms of fine root characteristics and the effects on fine-root morphology are more evident than the effects on fine-root biomass.

**Keywords:** fine-root biomass, fine-root length, fine-root diameter, root tissue density, specific root length, soil depth
Therefore, fine roots can be used as a sensitive indicator of changes in tree physiological status under changing soil environmental conditions, such as drought and acidification (Hirano et al., 2007; Konojkja, 2007). Fine roots respond to changes in environmental conditions with changes in fine-root biomass and spatial distribution (Helmsaat al., 2007; Finer et al., 2011); fine root morphology, including diameter and specific root length (SRL) (Otonen et al., 2007a,b); and fine root chemistry, such as N content and Al/ Ca molar ratio (Hirano et al., 2007; Vangnseva et al., 2007). Improving our knowledge about the responses of fine roots to N fertilization would help us to better understand the effects of the changing N conditions on forest ecosystems.

Recently, a chronic N fertilization experiment was conducted in a 20-year-old sugi (Cryptomeria japonica) plantation in eastern Japan (Nogakura et al., 2006). In this experiment, inorganic N was supplied at the rate of 336 kg N ha$^{-1}$ y$^{-1}$ for 7 years. Although the N concentration in leaves was higher in the fertilized plots during first 3 years of the experiment, there was no significant effect on aboveground growth of the sugi trees. However, another study showed that 3-year N fertilization at the same rate to small plots (1 m × 2 m) significantly affected fine root dynamics (Nogakura et al., 2013). In that study, the elongation rates and residence time of fine roots increased with N fertilization, whereas stem growth was not significantly affected. This suggests that sugi is tolerant of high N loads. Neither of these reports provided information about fine root parameters, such as morphology and N concentration, and further study on these fine root parameters was needed to better understand how the trees could acclimate to high N load. Therefore, the objective of this study was to determine the responses of the fine roots of sugi trees to 3 years of N fertilization in terms of biomass, morphology, and N concentration.

MATERIALS AND METHODS

SUGI (Cryptomeria japonica)

Sugi is one of the major coniferous species in Japan. Plantations of this species cover half of the plantation area (nearly 20% of all forested area) in the country (Japan FAO Association, 1997) and they are often established on foot slopes or along streams. Rooting depths of sugi trees are about 2–3 m and vertical changes in fine root biomass are moderate (Kurizumi, 1974, 1976). In addition, Fujimaki et al. (2007) reported that sugi stands showed higher coefficients for vertical distribution of fine roots (β; Gale and Grigal, 1987) than shallow-rooting species, such as Chamamaeidopsis obtusa and Picea glauca (0.95–0.99 for sugi vs. 0.91 for Chamamaeidopsis obtusa and 0.89 for Picea glauca). Their results suggest that the proportion of fine root biomass in subsoil is larger for sugi than for shallow-rooting species. However, Fujimaki et al. (2007) also found low β values in a young (4-year-old) sugi stand and in a sugi stand that seemed to be N deficient (0.83 and 0.91, respectively), suggesting that the vertical distribution of sugi fine roots are affected by factors such as stand age and soil conditions (Fujimaki et al., 2007). As for symbioses with mycorrhizal fungi, sugi has been reported to form arbuscular mycorrhiza, but not ectomycorrhiza (Matsuda, 1994).

STUDY SITE

This study was conducted in a 28-year-old sugi (Cryptomeria japonica) plantation in eastern Japan (38°10′N, 140°15′E, 41 m). Mean annual air temperature and mean annual precipitation for 1981–2010 at the Tsushiura weather station, which is located at 10 km south from the study site (Japan Meteorological Agency, http://www.jma.go.jp/jma/menu/report.html), were 14.4°C and 1188 mm, respectively. Stand density at the study site was ca. 4,000 trees ha$^{-1}$. Mean diameter at breast height (DBH) and mean height of the trees were 15.9 cm and 16.9 m, respectively. The soil type was Andosol, according to FAO soil classification (Sakai et al., 2010) and there was only sparse understory vegetation, due to the closed canopy (limited light) and litter that covered the forest floor (Konojkja, 2006).

In August 2003, 12 plots (1 m × 2 m) were established between planting lines. The plots were fertilized with N from October 2003 to November 2006. Each month, 20 L of 10 mM ammonium nitrate solution was sprayed onto 6 of the 12 plots (336 kg N ha$^{-1}$ y$^{-1}$). The remaining six plots were supplied with same amount of tap water that was equivalent to 120 mm rainfall y$^{-1}$ and used as control plots. Among the 12 established plots, 10 (five fertilized and five control plots) were used for this study. Further information on the site characteristics and the design of the N-fertilization experiment can be found in Nogakura et al. (2013) and Sakai et al. (2010).

SOIL ANALYSES

Soil coring was conducted in August 2003 (before N fertilization) and November 2006 (19 days after the last N fertilization) using a soil auger with a 4.8 cm inner diameter (Split tube sampler, Eijkelkamp Agrisearch Equipment, Giesbeek, Netherlands). For initial sampling, three core samples were taken at corners of the 1 m × 2 m plots. Each core sample included soil from 0 to 20 cm below the surface. The soil cores were divided into two depth levels (0–10 and 10–20 cm). The soil samples from the three sampling locations in each plot were pooled before air-drying. For final sampling, a soil core sample was taken from the inside of each plot and divided into two depth levels. Thus, one sample of each depth level was obtained for each plot [i.e., N = 5 for both the N-fertilized (NF) and the control plots]. Samples were air-dried and sieved through a 2-mm mesh. Roots were removed from the samples. Then, 20 g of each soil sample was suspended in 100 mL of 2 mol L$^{-1}$ KCl solution and shaken for 1 h to extract inorganic N. After extraction, the supernatant was clarified by filtration, and the inorganic N concentration was analyzed using flow-injection N analyzers (TN-30 for NH$_4$-N and TN-50 for NO$_3$-N, Mitsubishi Chemical Analytech, Tokyo, Japan).

FINE ROOT ANALYSES

Soil coring for fine root analyses were conducted in November 2006 with the same soil auger used for soil analyses. Two 20-cm deep soil cores were obtained from each plot. The soil cores were divided into two depth levels (0–10 and 10–20 cm) and the soil samples from the two sampling locations in each plot were pooled before root sample preparation. Thus, one sample of each depth level was obtained for each plot (i.e., N = 5 for both the NF and the control plots). The soil samples were washed with tap water on a sieve that...
Analyses of fine root parameters were performed separately for in the surface soil.

The fine roots were divided into diameter classes of <1 mm and 1–2 mm and were subjected to image analysis. The image analysis was conducted using a root image analysis system that included image analysis software and an image scanner (WinRHIZO Pro 2003b, Regent Instruments, Quebec, QC, Canada). To obtain the images, fine root samples were placed in tap water in a transparent plastic tray and were scanned at 400 dpi using the scanner and a transparency unit. Root length, diameter, and volume were used in further analyses. Data were analyzed separately for diameter classes of <0.5, 0.5–1.0, and 1.0–2.0 mm. After the scanning, fine root samples were dried at approximately 70°C for more than 48 h and were weighed.

Specific root length and root tissue density (RTD) were calculated by following equations:

\[ \text{SRL} (\text{m g}^{-1}) = \text{fine root length (m m}^{-2})/\text{fine root biomass (g m}^{-2}) \]

\[ \text{RTD} (\text{g cm}^{-3}) = \text{Fine root biomass (g m}^{-2})/\text{fine root volume (cm}^3 \text{ m}^{-3}) \]

After weighing, the N concentration of the fine roots was measured using an NC analyzer (Sumigraph NC-22F, SCAS, Tokyo, Japan). Fine roots 1–2 mm in diameter at soil depths of 10–20 cm were not subjected to this N analysis due to limited sample quantity.

**STATISTICS**

Split-plot ANOVA was conducted to examine the effects of N fertilization and soil depth on fine root parameters and soil inorganic N contents. Sampling plots were considered as a random effect. Analyses of fine root parameters were performed separately for each fine root diameter class. In addition, one-way ANOVA was conducted to examine effects of N fertilization at each soil depth. A Wilcoxon rank sum test was performed to examine effects of N fertilization on the proportion of fine root length in different diameter classes of <0.5, 0.5–1.0, and 1.0–2.0 mm. In further analyses, data were analyzed separately for diameter classes of <0.5, 0.5–1.0, and 1.0–2.0 mm. After the scanning, fine root samples were dried at approximately 70°C for more than 48 h and were weighed.

**RESULTS**

**INORGANIC N IN THE SOIL**

In August 2003, prior to fertilization, concentrations of NH₄-N and NO₃-N were similar in the control and NF plots (Tables 1 and 2). In November 2006, 19 days after the final fertilization, NO₃-N concentrations were significantly greater in the NF plots than in the control plots, but NH₄-N concentrations did not significantly differ between NF and control plots (Tables 1 and 2). The increase in NO₃-N concentration was more evident in subsurface soil than in the surface soil.

**BIOMASS AND LENGTH OF FINE ROOTS**

Mean biomass of total fine roots (i.e., fine roots <2 mm in diameter at soil depths of 0–20 cm) was 56 and 88 g m⁻² in the control and the NF plots, respectively. Fine roots <1 mm in diameter accounted for 76% of the total fine root biomass in both plots (Table 3). Although mean biomass of the fine roots <1 mm in diameter in the NF plots was 1.6-times as large as that in the control plots, the difference was not statistically significant (Table 4). On the other hand, the effect of soil depth on the biomass of fine roots <1 mm in diameter was significant: fine root biomass decreased in the surface soil; the fine root biomass in the surface soil were four-times and 2.5-times as large as those in the control plots (56%) and the NF plots, respectively. Fine roots 1–2 mm in diameter at soil depths of 10–20 cm were not subjected to this N analysis due to limited sample quantity.

**Table 1 | Concentration of inorganic nitrogen in the soil before and after N fertilization.**

| Soil depth (cm) | August 2003 | November 2006 |
|----------------|-------------|---------------|
| NH₄-N (mg kg⁻¹) | 0–10        | 10–20         |
| Control        | 30 ± 1      | 23 ± 3        |
| NF             | 31 ± 1      | 17 ± 1        |
| NO₃-N (mg kg⁻¹) | 0–10        | 10–20         |
| Control        | 16 ± 1      | 10 ± 2        |
| NF             | 15 ± 1      | 8 ± 0         |

**Table 2 | Results of split-plot ANOVA examined for effects of N fertilization (treatment) and soil depth (depth) on concentrations of inorganic nitrogen (NH₄-N and NO₃-N).**

| Parameter Effect | August 2003 | November 2006 |
|-----------------|-------------|---------------|
| NH₄-N Treatment | 0.6         | 0.48          |
| Depth           | <0.01       | <0.01         |
| Treatment x depth | 1.5      | 4.3           |
| NO₃-N Treatment | 0.9         | 0.36          |
| Depth           | <0.01       | <0.01         |
| Treatment x depth | 0.0       | 0.92          |
| Data shown are means ± SE (N = 5).
Table 3 | Biomass and length of fine roots of sugi at control and nitrogen-fertilized (NF) plots.

| Diameter class | Soil depth (cm) | Biomass (g m⁻²) | Length (m m⁻²) |
|----------------|----------------|-----------------|---------------|
|                |                | Control | NF     | Control | NF     |
| Diameter < 1 mm| 0–10           | 34.1 ± 8.0   | 47.8 ± 10.1 | 557 ± 146 | 912 ± 148 |
|                | 10–20          | 8.6 ± 5.6    | 19.4 ± 6.3  | 1245 ± 329 | 311 ± 100 |
| Diameter 1–2 mm| 0–10           | 12.2 ± 4.1   | 10.5 ± 3.1  | 21 ± 7    | 24 ± 7   |
|                | 10–20          | 1.1 ± 0.7    | 10.8 ± 8.3  | 6 ± 4     | 27 ± 17  |

Data shown are means ± SE (N = 5).

Table 4 | Results of split-plot ANOVA examined for effects of N fertilization (treatment) and soil depth (depth) on biomass and length of fine roots.

| Parameter | Diameter class | Effect | F-value | P-value |
|-----------|----------------|--------|---------|---------|
| Biomass   | Diameter < 1 mm| Treatment | 1.8     | 0.21    |
|           |                | Depth    | 19.7    | <0.01   |
|           |                | Treatment × depth | 0.1 | 0.82    |
| Length    | Diameter < 1 mm| Treatment | 3.0     | 0.12    |
|           |                | Depth    | 23.1    | <0.01   |
|           |                | Treatment × depth | 0.6 | 0.45    |
| SRL       | Diameter 1–2 mm| Treatment | 0.8     | 0.13    |
|           |                | Depth    | 0.8     | 0.41    |

MORPHOLOGY OF FINE ROOTS

The mean diameter of fine roots < 1 mm in diameter ranged from 0.52 to 0.57 mm and was significantly smaller in the surface soil than in subsurface soil (Tables 5 and 6). In the surface soil, root diameter was marginally smaller in the NF plots than in the control plots (Table 5; One-way ANOVA, P = 0.06). Mean RTD of fine roots < 1 mm in diameter ranged from 0.23 to 0.26 cm⁻¹ and was not significantly affected by either soil depth or N fertilization (Tables 5 and 6). Mean SRL of fine roots < 1 mm in diameter ranged from 16.0 to 19.2 m g⁻¹ (Table 5). Although the effects of soil depth and N fertilization on SRL were not significant, their interactive effect was marginally significant (P = 0.05; Table 6), indicating that N fertilization affected SRL differently at different soil depths. At soil depths of 0–10 cm, SRL was significantly greater in NF plots than in control plots (One-way ANOVA, P = 0.01). SRL did not differ significantly between NF and control plots at soil depths of 10−20 cm.

The diameter, RTD, and SRL of fine roots 1–2 mm in diameter in the surface soil were similar in control and NF plots and were not significantly different. Statistical analyses were not performed for the fine roots 1–2 mm in diameter in the subsurface soil, because there were no fine roots in this diameter class in the three of five control samples.

DISCUSSION

EFFECTS OF N FERTILIZATION ON THE SOIL

After the 3 years of N fertilization, there was a greater concentration of NO₃⁻N in the soil of NF plots than in control plots, whereas NH₄⁺-N concentration was not significantly different between the plots. Soil pH decreased in NF plots (from 7.7 to 7.0 in roots that were 1–2 mm in diameter (Table 7). The N concentration of fine roots < 1 mm in diameter in the surface soil was marginally higher in NF plots than in control plots (One-way ANOVA, P = 0.06). However, there was no significant difference between control and NF plots in the N concentration of roots in the subsurface soil or the N concentration of roots 1–2 mm in diameter (data not shown). The effects of soil depth on N concentrations in fine roots were also not significant (data not shown).
Table 5 | Morphological parameters of fine roots of sugi at control and nitrogen-fertilized (NF) plots.

| Diameter class | Soil depth (cm) | Diameter (mm) | RTD (g cm⁻³) | SRL (m g⁻¹) |
|----------------|----------------|---------------|--------------|-------------|
|                | Control        | NF            | Control      | NF          | Control     | NF          |
| diameter <1 mm | 0–10           | 0.55 ± 0.02   | 0.52 ± 0.01  | 0.26 ± 0.01 | 0.25 ± 0.01 | 16.0 ± 0.9  | 19.2 ± 0.3 |
|                | 10–20          | 0.57 ± 0.03   | 0.57 ± 0.01  | 0.23 ± 0.01 | 0.24 ± 0.01 | 17.9 ± 2.1  | 16.1 ± 0.5 |
| diameter 1–2 mm| 0–10           | 1.4 ± 0.1     | 1.3 ± 0.1    | 0.33 ± 0.03 | 0.33 ± 0.03 | 2.2 ± 0.4   | 2.3 ± 0.3  |
|                | 10–20          | 0.9 ± 0.0     | 1.2 ± 0.1    | 0.17 ± 0    | 0.20 ± 0.07 | 5.1 ±       | 70 ± 3.0   |

Data shown are means ± SE (N = 2–4).

* Standard error (SE) was not shown because the number of replication was 2 for these data.

Table 6 | Results of split-plot ANOVA examined for effects of the N fertilization (treatment) and soil depth (depth) on diameter, root tissue density (RTD) and specific root length (SRL) of fine roots <1 mm in diameter.

| Parameter       | Effect         | F-value | P-value |
|-----------------|----------------|---------|---------|
| Diameter        | Treatment      | 0.8     | 0.41    |
|                 | Depth          | 11.5    | 0.01    |
| Treatment x depth| Treatment      | 3.7     | 0.09    |
| RTD             | Treatment      | 0.0     | 0.90    |
|                 | Depth          | 3.4     | 0.10    |
| Treatment x depth| Treatment      | 1.7     | 0.23    |
| SRL             | Treatment      | 0.3     | 0.62    |
|                 | Depth          | 0.3     | 0.60    |
| Treatment x depth| Treatment      | 5.2     | 0.05    |

Table 7 | Biota concentration of fine roots of sugi in control and nitrogen-fertilized (NF) plots.

| Diameter class | Soil depth (cm) | N concentration (g kg⁻¹) |
|----------------|-----------------|--------------------------|
|                | Control         | NF                       |
| diameter <1 mm | 0–10            | 16.6 ± 0.5               | 18.2 ± 0.5               |
|                | 10–20           | 17.9 ± 1.1               | 16.2 ± 1.1               |
| diameter 1–2 mm| 0–10            | 7.7 ± 0.6                | 9.0 ± 0.6                |
|                | 10–20           | N.A.                     | N.A.                     |

Data shown are means ± SE (N = 4–6).

N.A., not analysed.

The effects of N fertilization were more evident in fine root morphology than in fine root biomass. We found that the 3 years of N fertilization significantly increased the SRL of fine roots <1 mm in diameter in the surface soil (Table 5). The SRL can be described as a function of the diameter and RTD of fine roots (Ostonen et al., 2007b). Our results showed that diameter of fine roots <1 mm in diameter in the surface soil was marginally smaller in NF plots than in control plots (0.52 vs. 0.55 mm, Table 5), whereas there was no effect of N fertilization on the RTD of these fine roots (Tables 5 and 6). Furthermore, in the surface soil, the proportion (by length) of “very” fine roots (diameter <0.5 mm) was significantly greater in the NF plots than in the control plots (Figure 1). These results suggest that the N fertilization in this study increased the amount of thinner fine roots relative to the amount of thicker fine roots or increased branching of fine roots. Branching of fine roots can result from proliferation of lower-order roots with small diameter (Pregitzer et al., 2002).
for 1st- and 2nd-order roots (Vang et al., 2013). On the other hand, under heterogeneous soil nutrient conditions, root proliferation often occurs in nutrient rich patches and rapid root proliferation is linked to high SRL (Eissenstat, 1991; Hodge, 2004). SRL has often been used as an index of the cost and benefit of fine roots, assuming that root length is proportional to resource acquisition (benefit) and root mass is proportional to construction and maintenance (cost; Eissenstat and Yanai, 1997). In addition, SRL is reported to be positively correlated with root respiration and N uptake (Roel et al., 1999; Makita et al., 2009). Therefore, the increased SRL of fine roots <1 mm in diameter that was observed in the present study may be a cost-effective response of sugi to increase acquisition of soil resources from N-rich sites.

It is, however, still difficult to explain why SRL increased in the NF plots only in the surface soil and not in the subsurface soil (Table 5). Increased N availability is not the only reason because the concentration of inorganic N was much greater in the subsurface soil than in the surface soil (Table 3). This vertical pattern of N concentration in the soil is also not consistent with the vertical pattern of N concentrations in fine roots (Table 7). In the NF plots, most of inorganic N in the subsurface soil was present as NO3−, whereas the concentration of inorganic N was much greater in the subsurface soil than in the surface soil (Table 3). This vertical pattern of N concentration in the soil is also not consistent with the vertical pattern of N concentrations in fine roots (Table 7). In the NF plots, most of inorganic N in the subsurface soil was present as NO3−, whereas the concentration of inorganic N was much greater in the subsurface soil than in the surface soil (Table 3). This vertical pattern of N concentration in the soil is also not consistent with the vertical pattern of N concentrations in fine roots (Table 7).

In conclusion, this study suggests that the effect of high N load was more evident in the root morphology than in fine root biomass. Fine root biomass tended to increase under high N load, although the effect was not statistically significant. The increase in SRL in the surface soil may reflect a cost-effective means of acquiring soil resources from N-rich patches. However, the observed differences in SRL could not be fully explained by increased N availability, given their vertical patterns. A better understanding of sugi responses to high N load may be gained from future studies in which chemical and physical characteristics of the soil, such as cation leaching or porosity, are examined together with fine root characteristics.

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