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Development of conifer seedlings roots on soil and fallen logs in boreal and subalpine coniferous forests of Japan

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Abstract

To clarify the process of *Abies* seedling establishment on soil and fallen logs, we compared the root systems of conifer seedlings on soil and fallen logs in boreal and subalpine old-growth forests in Japan. Eighteen *Abies* seedlings (nine from soil and nine from fallen logs) were dug up, and for each seedling the diameter and depth of roots, and the length, diameter, and branching of the tap and lateral roots, were assessed. *Abies* seedlings on soil had well-developed roots. By contrast, those on fallen logs had extensive, shallow roots. Some of the roots on fallen logs were asymmetric, due to the shape of the fallen logs, and some seedlings extended their roots beyond the fallen logs. The root penetration of seedlings on fallen logs was influenced by the depth of the decay of the fallen logs on which they were established. Allocation to coarse roots was increased, and the ratio of the tap root length to total root length was higher in soil than on fallen logs. Although the diameters of the first and second lateral roots did not differ between seedlings growing in soil and those growing in fallen logs, some seedlings on fallen logs had longer or more branching roots, indicating that *Abies* seedlings show plasticity in root form in response to the microsites where they become established. On fallen logs, the tap roots of seedlings were prevented from penetrating deeper, leaving the seedlings only the decayed surface to utilize. The shallower, more branching root system of seedlings on fallen logs would be effective for becoming established on the logs.

Keywords: *Abies*; Allocation; Forest floor microsite; Regeneration; Taisetsuzan mountain range; Yatsugatake mountains

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1. Introduction

Evergreen coniferous forests are distributed in the northern parts of Japan and at high elevation, and consist of *Abies*, *Picea*, and *Tsuga* species. Many studies have reported that fallen logs on the forest floor play important roles in the regeneration of these conifers (e.g., Nakamura, 1992; Takahashi, 1994, 1997). *Picea* and *Tsuga* seedlings are established mainly on fallen logs on the forest floor (Christy and Mack, 1984; Harmon and Franklin, 1989; Kubota et al., 1994). A thick litter layer on the forest floor prevents the roots of small seedlings, which germinate from small seeds, from reaching the mineral soil (Knapp and Smith, 1982; Gray and Spies, 1997), and fallen logs appear to offer safe sites for seedling recruitment in boreal and subalpine forests. *Abies* seedlings, which germinate from large seeds, have long roots and can establish on soil or fallen logs (Taylor and Qin, 1988; Szewczyk and Szwagrzyk, 1996; Takahashi, 1997). Pathogenic studies, however, suggest that dark snow blight fungi, *Racodium therryanum* Thuem and *Phacidium abietis* (Dearness)

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Reid et Cain., are important inhibitors of seedling establishment on forest soil in northern Japan (Takahashi, 1979; Cheng and Igarashi, 1987). In such places, seedlings are restricted to fallen logs (Suzuki et al., 1987; Kubota et al., 1994). *Sasa* species, which often form dense undergrowth in boreal and subalpine coniferous forests, also prevent seedling establishment on soil. Therefore, under dense *Sasa* cover, fallen logs become important recruitment sites, not only for *Picea* and *Tsuga* seedlings, but also for *Abies* seedlings (Narukawa and Yamamoto, 2002).

The microsites where seedlings can establish are assumed to be closely related to the root systems of the seedlings. However, few studies have examined the belowground characteristics of seedlings on different microsites (e.g., Heineman et al., 1999). Fallen logs and their bark contain high nutrient concentrations, but not all the nutrients in the fallen logs are available for tree seedlings (Lambert et al., 1980). The nutrient distribution and content in fallen logs change with decay (Grier, 1978; Graham and Cromack, 1982; Sollins et al., 1987; Arthur and Fahey, 1990; Takahashi et al., 2000). Fresh fallen logs have hard bark and wood, and seedlings cannot utilize most such logs as establishment sites (Narukawa and Yamamoto, 2002). *Picea* and *Tsuga* species have shallow root systems (Karizumi, 1979). They are well suited to fallen logs, large roots, or on rocks, where downward penetration by the tap roots may be difficult or impossible. In addition, fallen logs are important establishment microsites for *Abies* seedlings, which develop long tap roots. Root characteristics and allocation to roots vary with environmental factors, such as moisture or nutrient content (e.g., Canham et al., 1996).

We hypothesized that root architecture plasticity allows *Abies* seedlings to recruit on various microsites in Japan's boreal and subalpine forests. In order to test this hypothesis, we compared root depth and area of extent, the length, diameter, and branching of the tap and each lateral root, and root mass as a function of total plant mass in *Abies* seedlings on soil and fallen logs.

2. Methods

2.1. Study area

This study was conducted in the Taisetsuzan mountain range (43°39′N, 143°06′E) on Hokkaido Island, northern Japan, and in the Yatsugatake Mountains (36°00′N, 138°23′E), in central Japan (Fig. 1). In

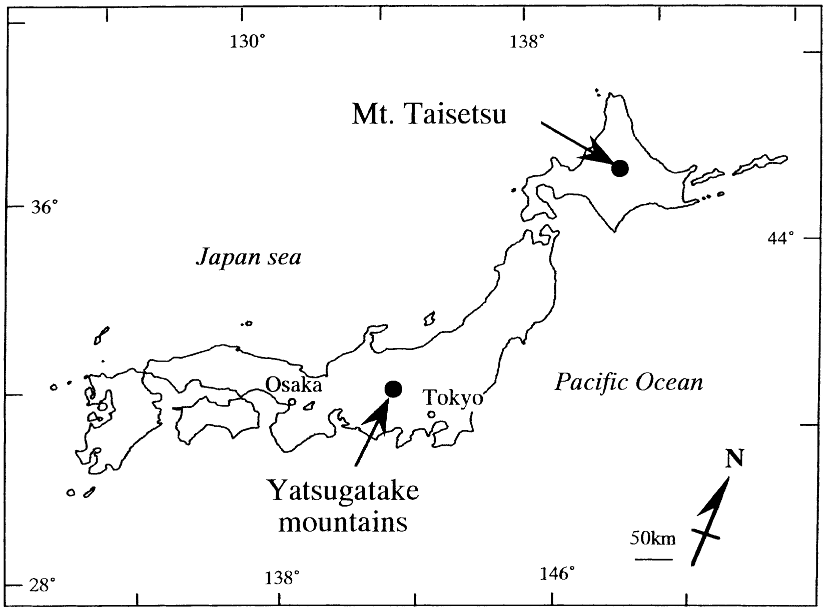

Fig. 1. The location of Mt. Taisetsu and Yatsugatake mountains in Japan.

the Taisetsuzan Range, the mean annual temperature is ca. 5 °C, and August (mean 19 °C) and January (mean −9 °C) are the warmest and coldest months, respectively, at Kamikawa (30 km from the study plot, 350 m a.s.l.). The annual precipitation is 1300 mm at Sounkyo (14 km from the study plot, 600 m a.s.l.). In the Yatsugatake Mountains, the mean annual temperature is ca. 2 °C, and August (mean 21 °C) and February (mean −11 °C) are the warmest and coldest months, respectively. The annual precipitation is 1500–2000 mm (Tsuchida, 1991). In winter, the snow is about 1 m deep in both forests. Both forests grow in moderately moist, dark-brown forest soils (Franklin et al., 1979; Takahashi et al., 1995).

We sampled stands near Lake Taisetsu (about 900 m a.s.l.) in the Taisetsuzan Range and near Shirakomaike Pond (about 2200 m a.s.l.) in the northern Yatsugatake Mountains. Both are extensive old-growth (>300 years) stands. *Abies sachalinensis*, *Picea jezoensis*, and *P. glehnii* dominate the Taisetsu stand, and *Tsuga diversifolia* and *Abies mariesii* dominate the Yatsugatake stand.

2.2. Sampling seedlings

We selected seven conifer species in the Taisetsu and Yatsugatake stands; *A. sachalinensis* (Fr. Schm.) Masters, *Picea glehnii* (Fr. Schm.) Masters, and *P. jezoensis* (Sieb. et Zucc.) Carriere in the Taisetsu stand and *A. mariesii* Masters, *A. veitchii* Lindley, *P. jezoensis* var. *hondoensis* (Sieb. et Zucc.) Carriere, and *T. diversifolia* (Maxim.) Masters in the Yatsugatake stand. For each species, 18 well-established seedlings between 20 and 40 cm tall were sampled randomly; nine seedlings in each species were on fallen logs, which were in decay class 3 or 4 (Christy and Mack, 1984), and nine seedlings were on soil near fallen logs. Since few *Picea* or *Tsuga* seedlings were established on soil, they were sampled only on fallen logs. Therefore, we only compared *Abies* seedlings on soil and fallen logs. In nine seedlings of each species on each microsite, six seedlings were used for the investigation of root systems and other three were for the detailed investigation of lateral roots. Fallen log profiles were described by measuring the diameter where the seedlings were established, the height from the ground, and the mean thickness of decayed wood at three points around the seedlings.

2.3. Excavation and measurement procedures

Before digging up the roots, we measured all seedlings for height, basal diameter, and maximum crown length and width perpendicular to the length. Six seedlings in each species on each microsite were carefully dug up with a small shovel and fingers in September or October 2000. The root area was then determined for each seedling, and the maximum

Table 1
Diameter (mean ± S.D., mm) at rootcollar, crown and root area (mean ± S.D., cm^2), and rood depth (mean ± S.D., cm) of seedlings on soil and fallen logs in the boreal (Taisetsu) and subalpine (Yatsugatake) old-growth forests of Japan

Species	Microsite	Diameter (mm)	Crown area (cm^2)	Root area (cm^2)	Root depth (cm)
A. sachalinensis	Soil	5.44 ± 1.53 n.s.[a]	676.3 ± 473.9 n.s.	393.9 ± 276.0 n.s.	17.7 ± 5.5*
A. sachalinensis	Fallen logs	5.32 ± 1.26	720.3 ± 342.1	945.7 ± 729.9	11.2 ± 2.7
A. mariesii	Soil	7.34 ± 1.59 n.s.	800.0 ± 222.3 n.s.	717.0 ± 382.5 n.s.	17.5 ± 5.2**
	Fallen logs	7.51 ± 1.64	969.7 ± 394.1	1646.2 ± 1138.6	7.8 ± 2.0
A. veitchii	Soil	6.92 ± 1.13 n.s.	891.3 ± 497.2 n.s.	709.5 ± 347.4 n.s.	18.0 ± 2.6**
	Fallen logs	6.99 ± 3.03	862.9 ± 576.5	1951.1 ± 1809.2	9.2 ± 4.1
P. glehnii	Fallen logs	4.41 ± 1.22	309.3 ± 188.0	532.8 ± 199.3	9.2 ± 5.0
P. jezoensis	Fallen logs	4.46 ± 0.94	409.4 ± 231.4	1094.4 ± 979.3	7.8 ± 3.3
P. jezoensis var. *hondoensis*	Fallen logs	4.65 ± 1.13	478.0 ± 267.0	2036.8 ± 2846.9	6.0 ± 3.3
T. diversifolia	Fallen logs	6.81 ± 1.95	1051.5 ± 530.2	1958.4 ± 1884.9	7.0 ± 3.7

[a] *t*-Test, non-significant at $P > 0.05$.

* Significant difference in *Abies* seedlings between soil and fallen logs at $P < 0.05$.

** Significant difference in *Abies* seedlings between soil and fallen logs at $P < 0.01$.

length and width of the root area were measured. Depth of penetration was measured as the depth of the deepest root. Once excavated, seedlings were separated to above- and belowground parts at the root collars. In the laboratory, we determined the following variables for the belowground part: (i) length of the tap root; (ii) total number of first-order lateral roots; (iii) length of the first-order lateral roots. First-order lateral roots are defined as roots branching from a tap root. Above- and belowground biomass were obtained by drying the specimens at 70 °C for 24 h to a constant mass; stems, leaves, coarse roots (diameter $\geq$ 8 mm), and fine roots (diameter $<$ 8 mm) were each weighed separately. Quadrats, each 1×1 m^2, were located around three seedlings of each species in each microsite, and all soil and roots were excavated to a depth of 10 cm in each quadrat. The roots were washed carefully, and the following variables were measured: (iv) base diameter, length of first-order lateral roots, and number of branches on each first-order lateral root; (v) base diameter of second-order lateral roots and number of branches on second-order lateral roots. Second-order lateral roots are defined as roots branching from a first-order lateral root.

The crown and root areas were derived as an ellipse from their lengths and widths. To compare variables of

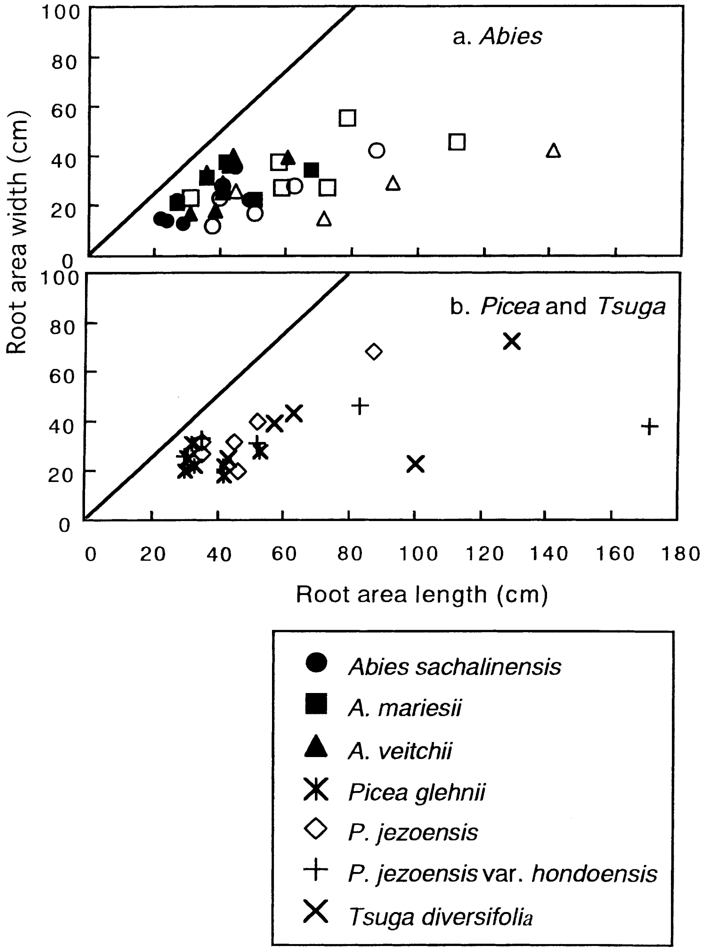

Fig. 2. The relationship between root area length and width of seedlings in the boreal (Taisetsu) and subalpine (Yatsugatake) old-growth forests of Japan. For *Abies*, open symbols indicate seedlings on soil and black symbols indicate seedlings on fallen logs. The lines indicate root area length = root area width.

Abies seedlings between microsites, we used Student's *t*-test.

3. Results

3.1. Root area and distribution

The mean diameter of seedlings at ground level differed among species, but did not differ between *Abies* seedlings on soil and fallen logs (Table 1, *t*-test, $P > 0.05$). The mean crown and root areas of seedlings were not significantly different between microsites ($P > 0.05$). Seedlings on soil had symmetric root systems, while some seedlings on fallen logs developed asymmetric root systems (Fig. 2). The crown area of seedlings was positively correlated with stem basal diameter ($R^2 = 0.71$, $P < 0.05$), but the root area of seedlings was not ($R^2 = 0.24$, $P > 0.05$). This trend did not vary among species or microsites. The roots of seedlings on fallen logs occupied a larger area than the crown (Table 2).

In all *Abies* species, the seedling roots were shallower on fallen logs than on soil (Table 1, *t*-test, $P < 0.05$). Root penetration was influenced by the depth of decay of fallen logs where seedlings were established (Fig. 3). Some of the roots extended beyond the fallen logs and penetrated the soil.

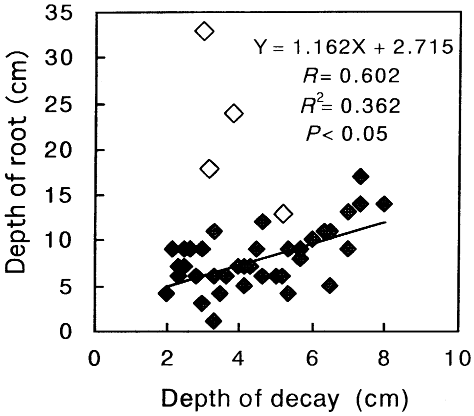

Fig. 3. The relationship between root depth of conifer seedlings and depth of decay of fallen logs, where the seedlings established, in the boreal (Taisetsu) and subalpine (Yatsugatake) old-growth forests of Japan. Open marks indicate root penetration beyond fallen logs. The correlation coefficient of the black symbols is 0.602.

Table 2
Ratio of crown area to root area of seedlings on soil and fallen logs in the boreal (Taisetsu) and subalpine (Yatsugatake) old-growth forests of Japan

Species	Microsite	Crown area/root area, mean ± S.D.
A. sachalinensis	Soil	1.80 ± 0.47[*]
	Fallen logs	0.97 ± 0.60
A. mariesii	Soil	1.33 ± 0.58 n.s.[a]
	Fallen logs	0.78 ± 0.44
A. veitchii	Soil	1.29 ± 0.40[**]
	Fallen logs	0.54 ± 0.26
P. glehnii	Fallen logs	0.58 ± 0.25
P. jezoensis	Fallen logs	0.48 ± 0.27
P. jezoensis var. *hondoensis*	Fallen logs	0.52 ± 0.33
T. diversifolia	Fallen logs	0.83 ± 0.49

[a] *t*-test, non-significant at $P > 0.05$.

[*] Significant difference in *Abies* seedlings between soil and fallen logs at $P < 0.05$.

[**] Significant difference in *Abies* seedlings between soil and fallen logs at $P < 0.01$.

3.2. Root architecture

Abies seedlings tended to have longer tap roots in soil than on fallen logs, although there were no significant differences in *A. sachalinensis* and *A. veitchii* (Table 3, *t*-test, $P > 0.05$). On the other hand, *Abies* seedlings tended to have longer lateral roots on fallen logs than in soil. Consequently, the ratio of tap root length to total root length was higher in seedlings in soil than on fallen logs in seedlings of *A. sachalinensis* and *A. mariesii* (*t*-test, $P < 0.05$). The diameters of the first and second lateral roots did not differ between those in soil and those on fallen logs (*t*-test, $P > 0.05$). Seedlings on fallen logs had comparatively longer lateral roots than those growing in soil, especially in *A. veitchii* (Fig. 4). The lateral roots of seedlings on fallen logs also branched more per unit diameter, than those in soil, especially in *A. mariesii*.

3.3. Root biomass

Allocation patterns to leaf and stem in *Abies* seedlings did not differ among microsites (Fig. 5; *t*-test, $P > 0.05$). Of the total biomass, 40% was allocated to stems, ~30% to leaves, and ~30% to root biomass.

Table 3

Root architecture (mean ± S.D.) of conifer seedlings on soil and fallen logs in the boreal (Taisetsu) and subalpine (Yatsugatake) old-growth forests of Japan

Species	Microsite	Data	Tap root length (cm)	First-order lateral root			Ratio of tap root[a] (%)
				Length (cm)	Number	Density[b] (cm^{-1})	
A. sachalinensis	Soil	6	18.8 ± 6.4 n.s.[c]	14.4 ± 8.8 n.s.	5.7 ± 2.3 n.s.	0.30 ± 0.07 n.s.	22.5 ± 7.3[*]
	Fallen logs	6	15.0 ± 4.4	17.8 ± 11.7	8.0 ± 2.8	0.59 ± 0.31	11.7 ± 6.4
A. mariesii	Soil	6	20.3 ± 4.8[*]	11.5 ± 7.7 n.s.	15.7 ± 4.2 n.s.	0.80 ± 0.26 n.s.	10.4 ± 1.8[**]
	Fallen logs	6	13.3 ± 3.5	15.9 ± 11.3	12.8 ± 2.5	0.99 ± 0.17	6.4 ± 1.6
A. veitchii	Soil	6	22.8 ± 9.3 n.s.	12.0 ± 8.9 n.s.	15.7 ± 2.8[*]	0.79 ± 0.34 n.s.	12.1 ± 5.9 n.s.
	Fallen logs	6	14.0 ± 3.7	15.7 ± 14.2	12.0 ± 1.4	0.89 ± 0.18	7.5 ± 2.6
P. glehnii	Fallen logs	6	10.5 ± 5.6	14.8 ± 6.6	6.5 ± 2.9	0.64 ± 0.09	10.4 ± 1.8
P. jezoensis	Fallen logs	6	11.7 ± 3.4	16.9 ± 9.3	6.5 ± 1.2	0.62 ± 0.29	9.6 ± 2.3
P. jezoensis var. *hondoensis*	Fallen logs	6	6.5 ± 2.1	20.7 ± 19.8	8.5 ± 2.1	1.34 ± 0.22	5.8 ± 4.4
T. diversifolia	Fallen logs	6	18.0 ± 11.3	14.8 ± 15.6	12.7 ± 5.9	0.94 ± 0.54	8.5 ± 4.8

[a] The ratio of tap root length as a function of total root length.

[b] The density of first-order lateral root in tap root length.

[c] *t*-test, non-significant at $P > 0.05$.

[*] Significant difference in *Abies* seedlings between soil and fallen logs at $P < 0.05$.

[**] Significant difference in *Abies* seedlings between soil and fallen logs at $P < 0.01$.

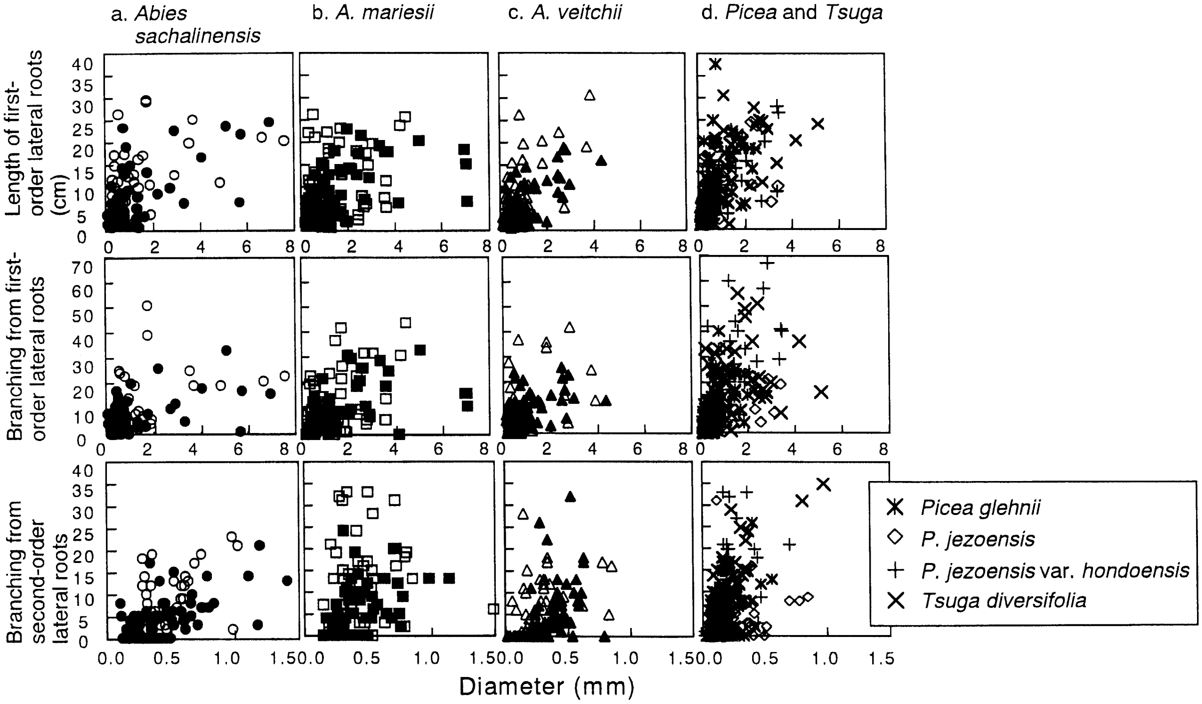

Fig. 4. Relation of lateral root length and number of branching with each base diameter in conifer seedlings in the boreal (Taisetsu) and subalpine (Yatsugatake) old-growth forests of Japan. Open and black symbols mean *Abies* seedlings on fallen logs and soil, respectively.

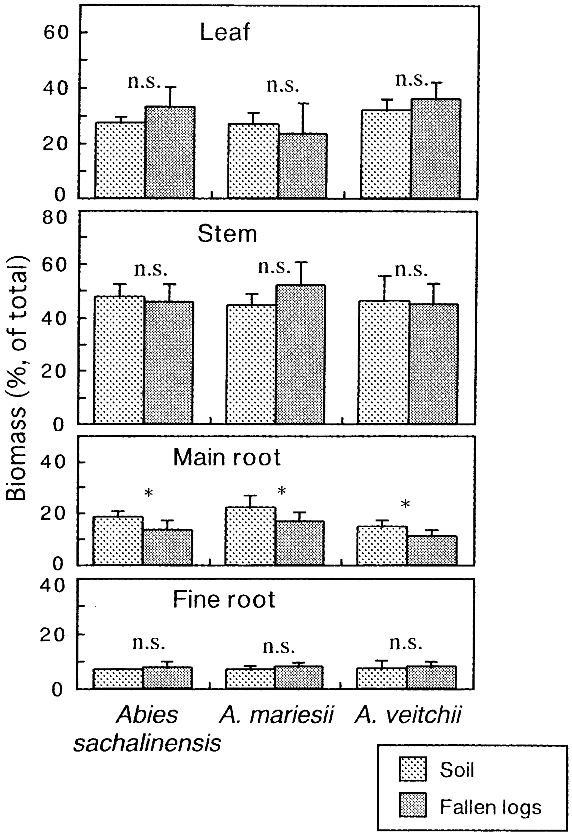

Fig. 5. Leaf, stem, coarse root (diameter $\geq$ 8 mm), and fine root (diameter $<$ 8 mm) biomass ratios to total biomass of conifer seedlings established on soil and fallen logs in the boreal (Taisetsu) and subalpine (Yatsugatake) old-growth forests of Japan. Symbols: n.s., $P > 0.05$; * $P < 0.05$; (t-test, d.f. = 1).

The biomass of coarse roots was about twice that of fine roots. The coarse root biomass of *A. mariesii* and *A. veitchii* seedlings growing on fallen logs was less than that of seedlings growing in soil (t-test, $P < 0.05$). There were no significant differences in fine root biomass between the microsites (t-test, $P > 0.05$). The top/root (T/R) ratios of seedlings did not differ between the microsites in any *Abies* species (t-test, $P > 0.05$).

4. Discussion

4.1. Root systems of Abies seedlings

The root systems of adult trees have been categorized. For warm-temperate rain forests, Hinds and Reid (1957) reported 'tap-rooted', 'plate-rooted' (i.e., with spreading laterals and variously developed peg or sinker roots) and 'heart-rooted' (i.e., several major roots descending obliquely from the base of the trunk) categories. Mature *Abies* trees have long taproots, while *Picea* and *Tsuga* develop plate-roots (Karizumi, 1979). Root architecture associated with seed size is recognized as adaptive in terms of the microsite at which establishment occurs (Knapp and Smith, 1982; Gray and Spies, 1997). Large-seeded species, such as *Abies*, can grow down through deep litter to the mineral soil, which is a more secure source of water, and these species are suited to microsites with soft, deep soil. On the other hand, small-seeded species, such as *Picea* and *Tsuga*, do not have a clear tap root and are commonly seen on microsites elevated above the forest floor. Variability in root architecture is related to both genotype and environment (Eissenstat, 1991). For example, the root pattern and allocation to roots are affected strongly by variation in soil N availability (Hilbert, 1990; Canham et al., 1996; Pregitzer et al., 1997). In this study, aspects of the root architecture of *Abies* seedlings differed by microsite. *Abies* seedlings on soil developed deep tap roots, but they extended lateral roots and had shallow root systems on fallen logs, where downward penetration by a tap root might be difficult or impossible. This suggests that the root systems of *Abies* seedlings have plastic responses to microsites. In this study, the mean depth of decay on the fallen logs where the seedlings were established was 4.3 cm (2.0–9.2 cm). Therefore, the tap root of most of the seedlings on fallen logs was prevented from penetrating deeply, and instead it bent and followed the hard sapwood.

4.2. Root system of seedlings on fallen logs

Conifer seedlings established on fallen logs had extensive, relatively fine lateral roots. The root system affects anchoring of the seedling and the absorption of nutrients and water. Coutts (1983) noted the importance of several attributes of root architecture to stability. For instance, root diameter is directly related to root strength, and by its fourth power to root stiffness. Therefore, branching decreases total stiffness. A wide angle between roots decreases the distance from the stem and uprootings can occur. However, fine roots are effective for water and nutrient uptake (Nye and Tinker, 1977). Not all fallen logs on the forest floor are available for seedlings (Takahashi et al., 2000; Narukawa and Yamamoto, 2002). Hofgaard (1993) showed that fallen logs older than ca. 40 years carried regenerating seedlings of all tree species. With decay, the moisture and chemical contents of fallen logs vary (Lambert et al., 1980; Graham and Cromack, 1982; Harmon et al., 1986). Nevertheless, water extracts from decayed fallen logs are acidic and have quite low mineral nutrient concentrations (Takahashi et al., 2000). Extensive fine roots are effective for absorbing the modest amounts of nutrients that become available in fallen logs with decay. In subboreal forests of Japan, we can find stilt-rooted trees. They may be the results of the collapse of fallen logs where young seedlings established.

The development of seedling root systems is not simply correlated with one variable in the shoot system. The belowground factors determining anchorage and absorption and the aboveground means of shade-tolerance or avoidance are realized independently (Kohyama and Grubb, 1994). Kajimoto et al. (1999) reported that the horizontal rooting zone of *Larix gmelinii* on permafrost soil expanded far beyond the projection area of each canopy. In our study, the roots of seedlings on fallen logs occupied a larger area than the crowns. This suggests that competition among roots on the surface of decayed logs starts before competition among shoots. The roots of some seedlings on fallen logs penetrated the soil beyond the fallen logs. If seedlings regenerate on fallen logs, they may need to extend their roots well beyond the fallen logs to escape competition and to absorb sufficient water and nutrients to grow.

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