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Effects of vegetation change and soil disturbance on ectomycorrhizas of *Betula platyphylla* var. *japonica*: a test using seedlings planted in soils taken from various sites

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The occurrence and character of different types of ectomycorrhizas of birch seedlings were investigated in soils from three naturally regenerating birch stands: a forest site, a clear-cut site, and a site recently disturbed by plowing. Birch grown in soil from an evergreen broad-leaved forest without birch was also studied. The rate of ectomycorrhizal formation in the soil from the evergreen broad-leaved forest was lower than that in the soil from the other three sites. The ectomycorrhizal formation of seedlings grown in soil from the clear-cut and plowed sites were the same as or higher than that in soil from the birch forest site. The largest number of ectomycorrhizal types were formed in soil from the birch forest site. In the soil from the plowed site, only one type of ectomycorrhiza was formed, and it was different from the dominant type formed in soils from the birch forest site and the clear-cut site. The results of this investigation showed that equal levels of ectomycorrhizas were formed in soils from the different birch stands, but the types formed were different among those sites. It is likely that the different ectomycorrhizal fungi were better adapted to the soil conditions at each of those sites.

Key Words——birch; clear-cutting; disturbance; ectomycorrhizas; morphological type.

Betula platyphylla Sukatchev var. *japonica* Hara is a major pioneer plant, often found after disturbances such as clear-cutting, plowing, and landslides. Soils at disturbed sites such as these might have temperature, nutrient, and water conditions that are disadvantageous for plant growth compared to forest sites, because of the loss of their organic layer and direct exposure to the elements, such as sun and rain.

The genus *Betula* is known to be ectomycorrhizal (Harley and Smith, 1983). The important roles of ectomycorrhizal fungi in promoting survival and growth of seedlings by enhancing tolerance to drought, shading, or disease and by increasing uptake of nutrients or water have been demonstrated by many researchers (Marx, 1969; Dixon et al., 1984; Abuzinadah and Read, 1989; MacFall et al., 1991; Browning and Whitney, 1993). The ability of *B. platyphylla* var. *japonica* to form mycorrhizal associations might be a factor in its ability to establish itself early at sites with severe conditions.

The amount and type of ectomycorrhizas of birch vary with the conditions of the site (Frankland and Harrison, 1985; Newton, 1991; Newton and Pigott, 1991). A discrepancy between the frequency and abundance of fruit bodies and mycorrhizas in a *Pinus* stand was reported by Gardes and Bruns (1996). Although it is known that there are many fruit bodies of ectomycorrhizal fungi in birch stands in Japan (Ogawa, 1977; Imazeki and Hongo, 1987, 1989), there has been little research about their ectomycorrhizas. There is a need to investigate the quality and quantity of ectomycorrhizas in birch stands to understand the role of ectomycorrhizas in the establishment of birch under natural conditions.

The aim of this study was to determine whether vegetation change and soil disturbance in the field have any effect on ectomycorrhizas of *B. platyphylla* var. *japonica* seedlings that were planted in soils collected from a birch-dominated forest site, a clear-cut site, a site disturbed by plowing, and from an evergreen broad-leaved forest without birch trees.

Materials and Methods

Sampling sites The soil samples were taken from four sites having different vegetation and soil conditions in Gifu Prefecture, Japan. Sites 1–3 were located in the deciduous broad-leaved forest zone (about 1,300 m altitude) of Mt. Norikura (36°08′N, 135°25′E), where the annual mean temperature is about 6.1°C, annual rainfall is 2,788 mm, average monthly rainfall from April through October is 286 mm, and maximum snow depth is about 150 cm. Site 4 was approx. 100 km away from the other three sites, located in the evergreen broad-leaved forest zone (about 30 m altitude) in Gifu City (35°25′N, 136°48 E′), where the annual mean tem-

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perature is 15.6°C and the annual rainfall is 1,762 mm. Descriptions and soil conditions of the four sampling sites are listed in Table 1. Site 1 was an approx. 40-yr-old secondary forest dominated by *B. platyphylla* var. *japonica*. The forest had an average height of approx. 7 m and a diverse understory. Other common tree species present were *Quercus mongolica* Fischer var. *grosseserrata* Rehder & Wilson, *Acer sieboldianum* Miq., *Kalopanax pictus* Nakai, and *Viburnum furcatum* Blume. The site had a brown forest soil characterized by a 3 cm A_0 horizon, a 7–10 cm A_1 horizon, and a 10–13 cm A_2 horizon. Site 2 was a 10-yr-old, post-clear-cut plantation of *Cryptomeria japonica* D. Don and *Chamaecyparis obtusa* Endlicher. The understory was dominated by grass species such as *Miscanthus sinensis* Anderss, but also included naturally regenerating birch seedlings (0.5–1.0 m height). Soil characteristics of Site 2 were similar to those of Site 1 because the origins of both soils were the same. However, at Site 2, the A_0 to A_2 horizons were less extensive (A_0=0.5 cm, A_1=2.5 cm, A_2=12 cm). Site 3 was located alongside a road, and it had been artificially disturbed by removing of the surface soil 3 yr before. The site had a gravel-mixed mineral soil, and its A_0 and A horizons had been lost because of the disturbance and erosion by rain. The vegetation of Site 3 was limited to a few plant species, but birch seedlings (height <0.2 m) were found among them. Site 4 was a 40-yr-old evergreen broad-leaved forest dominated by *Quercus glauca* Thunberg, *Q. myrsinaefolia* Blume, and *Castanopsis cuspidata* Schottky. *Betula* species were absent in this forest. This site has a brown forest soil with 3 cm A_0 and 7 cm A horizons.

Soil sampling Ten quadrats (50×50 cm) were set randomly in each of the four sites in May 25 and November 2, 1994. Soil inside each quadrat was collected from the top 0–5 cm depth after removing the litter layer. The ten soil samples from each site were fully mixed. Twenty portions of 18 g of soil from each of the four sites, which had been adjusted to 80% of maximum water holding capacity, were put in sterilized test tubes (2×15 cm).

Seedling planting Seeds of *B. platyphylla* var. *japonica*, which had been surface sterilized with 30% H_2O_2 solution for 15 min., were incubated for 30 d on water agar. Seedlings (ca. 1.5 cm in length) were then transferred to the test tubes containing the soil from each of four sites. These seedlings were grown for 120 d in the growth chamber (Nippon Medical & Chemical Instruments, Tokyo) at 23°C in a 13 h light and 11 h dark photoperiod with daytime lighting of 85 μmol/m²/sec.

Evaluation of ectomycorrhiza After 120 d, the seedlings were collected from test tubes, gently washed to remove soil particles, and soaked in distilled water. The entire root system of each seedling was evaluated for the occurrence of ectomycorrhizas. The presence of ectomycorrhizas was confirmed by the observation of a fungal mantle on the root tip using a compound light microscope (×400–×1,000). Ectomycorrhizal types were differentiated by macroscopic (×8–×40) and microscopic (×400–×1,000) appearance of morphological characteristics such as color, size, shape and surface features of mantle tissues, by the method of Ingleby et al. (1990). The lengths of total root and ectomycorrhizal root were measured under a stereomicroscope (×8–×40) using the method of Tennant (1975).

Results

Comparison of the ectomycorrhizal root length among different sites and seasons The percentage of total root length that was ectomycorrhizal (percent ectomycorrhizal root length) was calculated for *B. platyphylla* var. *japonica* seedlings grown in soils collected in May and November from four different sites (Fig. 1). This value, which had a maximum of 30%, was significantly greater in November than in May for Sites 2 and 4. There were no significant differences in percent ectomycorrhizal root length between Site 1 and Site 2 in May, nor between Site 1 and Site 3 in November.

Comparison of ectomycorrhizal types among different

Table 1. Descriptions and soil conditions of four sampling sites.

Site	Altitude (m)	Forest zone	Forest conditions	Age of *Betula platyphylla* var. *japonica* trees	Soil types and horizon thicknesses	Soil content of total C, N, and P (d.w.%)[a]
Site 1	1,300	Deciduous broad-leaved	40-yr-old *B. platyphylla* var. *japonica* and *Quercus mongolica* dominated secondary forest	>40 yr	Brown forest soil A_0, 3 cm; A_1, 7–10 cm; A_2, 10–13 cm	C; 23.0 N; 1.4 P; 0.15
Site 2	1,300	Deciduous broad-leaved	10-yr-old post-clear-cut plantation of *Cryptomeria japonica* and *Chamaecyparis obtusa*	1–10 yr	Brown forest soil A_0, 0.5 cm; A1, 2.5 cm; A_2, 12 cm	NT[b]
Site 3	1,300	Deciduous broad-leaved	Artificially disturbed by plowing 3 yr before. *Miscanthus sinensis* and *B. platyphylla* var. *japonica* dominated site	1–3 yr	Gravel-mixed mineral soil A_0, 0 cm; A, 0 cm; subsoil exposed	C; 0.84 N; 0.09 P; 0.06
Site 4	30	Evergreen broad-leaved	50-yr-old *Quercus glauca*, *Q. myrsinaefolia* and *Castanopsis cuspidata* dominated forest	Absent	Brown forest soil A_0, 3 cm; A, 7 cm	NT

a) Soil samples which were collected from top 0–5 cm depth were analyzed by the Environmental Analysis Center of Sankyo Co., Aichi, Japan.
b) NT, not tested.

sites and seasons Sixteen different morphological types (Types 1 to 16) of ectomycorrhizas were found among the four soils (Tables 2, 3). The numbers of different types of ectomycorrhiza recorded in roots of 20 seedlings from the soils of Sites 1, 2, and 4 in May were 6, 2 and 3, while those from Sites 1, 2, 3, and 4 in November were 9, 5, 1, and 4, respectively. We were unable to identify any of these ectomycorrhozal fungi except Type 16. Type 1 was the most abundant one (>70%) associated with seedling roots grown in soils of Site 1 and

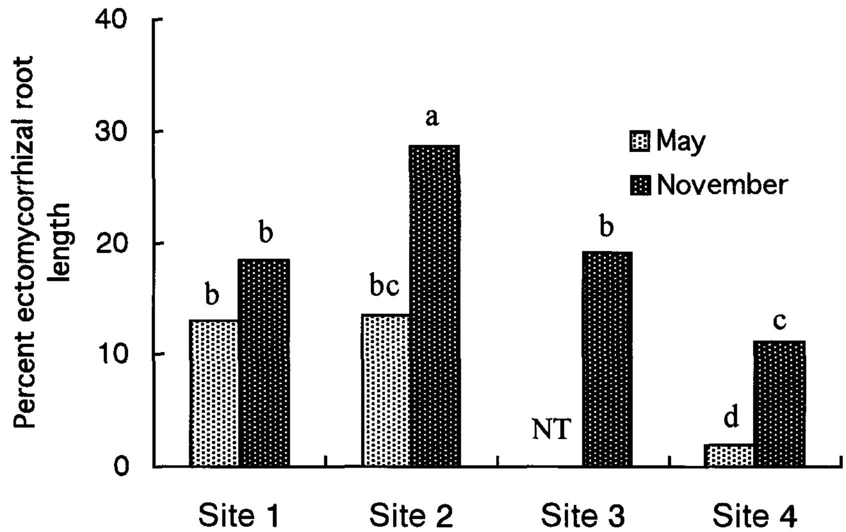


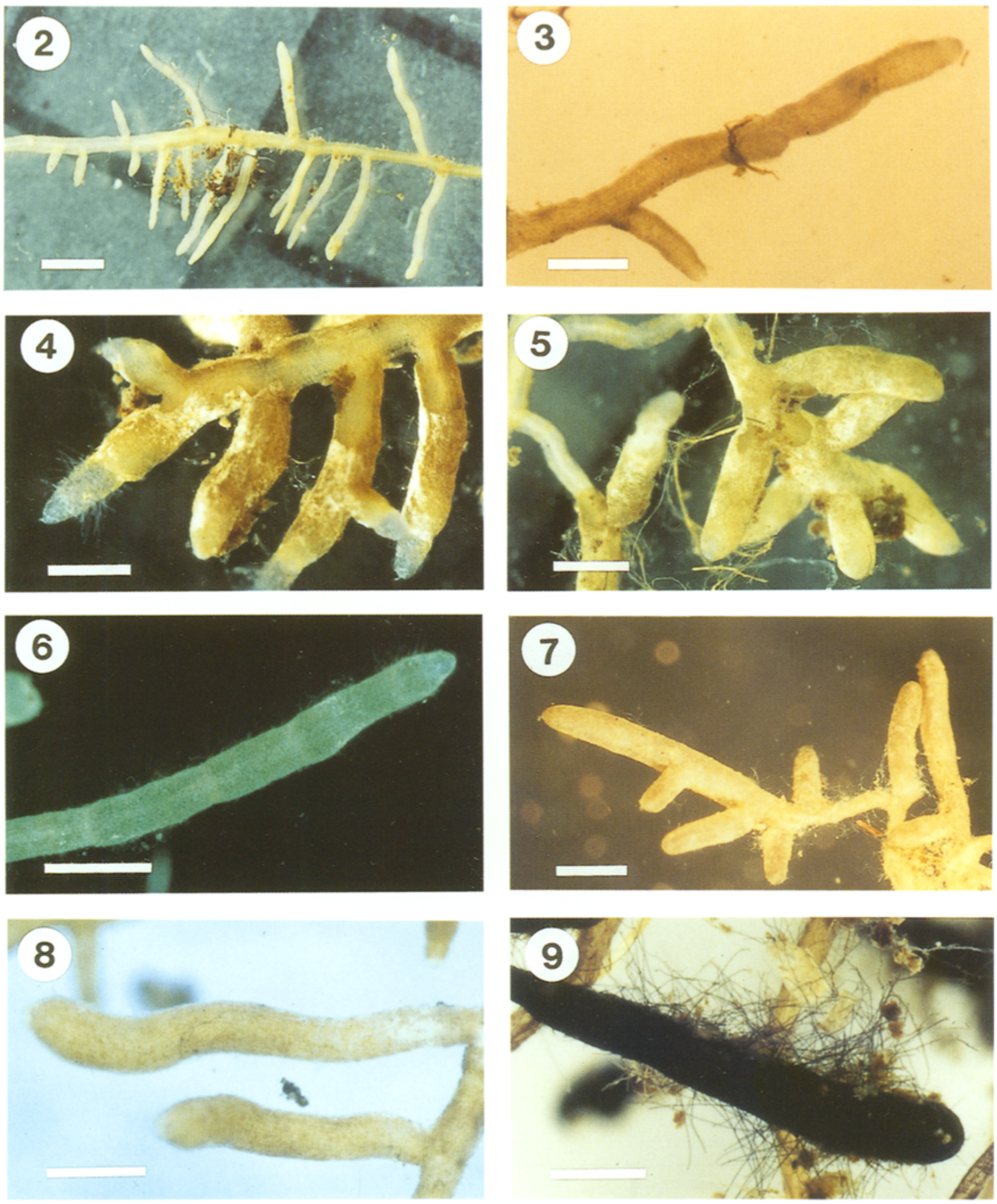
Fig. 1. Percent ectomycorrhizal root length of *Betula platyphylla* var. *japonica* seedlings grown for 120 d in soils collected from 4 different sites in May and November, 1994.
Columns with the same letter are not significantly different ($P=0.05$) according to Duncan's multiple range test. NT is not tested.

Table 2. Ectomycorrhizal types and their characteristics on *Betula platyphylla* var. *japonica* seedlings.

Type	Color[a]	M.t.[b]	Specialized elements on the mantle surface[c]	Emanating hyphae[d]		Ectomycorrhizal species
				Cc[e]	Diam (μm)	
1	LB	NP	−	+	1.0–3.0	
2	LB-B	NS	−	−	4.5–9.0	
3	B	NP	−	+	2.0–4.0	
4	PW	NP	−	+	1.0–3.0	
5	PW	FP	−	+	1.5–4.5	
6	LB	NP	−	+	2.0–4.0	
7	DB	IS.B	−	+	2.0–3.5	
8	DB	IS.A	+[f]	+	1.5–3.5	
9	LB	NP	−	+	1.5–3.0	
10	B	IS.A	+[g]	−	3.0–4.0	*Tuber* sp. ?
11	B-BL	IS.B	−	+	2.0–3.0	
12	LB	NP	−	+	1.9–2.8	
13	LB	NP	−	+	2.0–4.0	
14	PW	FP	−	+	2.0–4.0	
15	W-LB	NS	−	+	2.0–5.5	
16	BL	NS	−	−	3.0–4.0	*Cenococcum geophilum*

a) PW, pale or white; B-BL, brown to black; LB, light brown; B, brown; DB, dark brown; BL, black.
b) Structural mantle types of the fungal sheath surface: FP, felt prosenchyma; NP, net prosenchyma; NS, net synenchyma; IS.A, interlocking irregular synenchyma; IS.B, not interlocking irregular synenchyma.
c) +, present; −, absent.
d) Emanating hyphae which dispersed from the fungal sheath surface.
e) Cc, clamp connection.
f) Obclavate to club-like (15–35 μm in length).
g) Acicular and thick wall (>90 μm in length, 3.0–4.0 μm in diam).

Site 2 (Figs. 2, 3). Macroscopically, it was characterized by light-brown color and fairly straight, slender, and infrequently short-branched hyphae. Microscopically, Type 1 had torturous emanating hyphae (1.0–3.0 μm in diam) bearing clamp-connections. Type 10 from Site 2 had straight, unbranched and slightly thick-walled setae on the mycorrhizal mantle surface, which are features very similar to those of *Tuber* sp. (Ingleby et al., 1990). Type 12 was observed on seedlings grown in Site 3 soil (Fig. 7), and was the only type observed on this soil. Its



Figs. 2–9. Ectomycorrhizas of *Betula platyphylla* var. *japonica* seedlings that were planted in soils collected from four different sites. Figs. 2, 3. Type 1 was the dominant ectomycorrhizal type (>70%) in both Site 1 and Site 2 soils. Fig. 4. Type 3 in Site 1 soil. Fig. 5. Type 5 in Site 1 soil. Fig. 6. Type 9 in Site 2 soil. Fig. 7. *This type of ectomyorrhiza (Type 12) was the only type found in* soil from Site 3. Fig. 8. Type 13 was the dominant ectomycorrhizal type in soil from Site 4. Fig. 9. Type 16 was identified as *Cenococcum geophillum*. This type of ectomycorrhiza appeared in soils from Site 1, Site 2, and Site 4. Scale bars: Fig. 2=1 mm; Figs. 3–9=0.5 mm.

Table 3. Percentage occurrence of 16 types of ectomycorrhiza on roots of *Betula platyphylla* var. *japonica* seedlings grown in soils collected from various sites in May and November, 1994.

Sites	Mo	Ectomycorrhizal types															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Site 1	May	76.1	0.3	3.5	1.4	8.4	—[a]	—	—	—	—	—	—	—	—	—	14.0
	November	87.8	0.5	0.1	0.1	3.5	3.9	0.1	2.5	—	—	—	—	—	—	—	1.4
Site 2	May	94.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.6
	November	75.4	—	—	—	—	—	—	—	17.4	4.2	0.1	—	—	—	—	2.9
Site 3	November	—	—	—	—	—	—	—	—	—	—	—	100.0	—	—	—	—
Site 4	May	—	—	—	—	—	—	—	—	—	—	—	—	64.7	34.1	—	1.2
	November	—	—	—	—	—	—	—	—	—	—	—	—	58.0	23.6	16.9	1.5

a) — denotes absence.

macroscopic features were beige coloration, and short, stubby mycorrhizas with an irregular branching pattern. Microscopically, it showed torturous emanating hyphae (1.9–2.8 μm in diam) bearing clamp-connections. Type 13 appeared abundantly in soil from Site 4 (Fig. 8). Macroscopically, it was similar to Type 1, but its microscopic characteristics differed in the texture of the mantle surface and the width of emanating hyphae (2.0–4.0 μm in diam). Type 16 was characterized by abundant coarse, dark brown to black emanating hyphae (Fig. 9). This type was identified as *Cenococcum geophilum* Fr. on the basis of its black color, projecting hyphae, and pseudoparenchymatous sheath (Pigott, 1982). This type was observed from Sites 1, 2, and 4.

The average numbers of morphological types of ectomycorrhiza found per seedling ranged from 0.6 to 3.0 (Table 4). The number of types varied with the site and season of soil collection. For example, it was significantly greater in soils collected in November than in May. Among the four sites, Site 1 had the highest number, followed by Site 2. The numbers from Site 4 in May and Site 3 were lower (Table 4).

Table 4. Average number of ectomycorrhizal types on *Betula platyphylla* var. *japonica* seedlings grown in the soils from Sites 1–4 collected in May and November, 1994.

Site	Mo	Number of ectomycorrhizal types per seedling
Site 1	May	2.7 b[a]
	November	3.0 a
Site 2	May	1.9 c
	November	2.5 b
Site 3	November	0.8 de
Site 4	May	0.6 e
	November	1.0 d

a) Values followed by the same letter are not significantly different ($P=0.05$) according to Duncan's multiple range test.

Discussion

Occurrence of ectomycorrhizas The percent ectomycorrhizal root length and number of morphological types of ectomycorrhizas on *B. platyphylla* var. *japonica* grown in soils collected from Sites 1, 2, and 4 in November were higher than those in May (Fig. 1, Tables 3, 4). These data suggest that the activity of ectomycorrhizal fungi varied seasonally, with more advanced activity of the ectomycorrhizal propagules in November than in May. Vogt et al. (1980) reported that mycorrhizal root biomasses were highest in fall in 23-yr-old and 180-yr-old pacific silver fir stands. The peak of occurrence of fruiting bodies of ectomycorrhizal fungi in Site 1 was also found in October (Kamiya, personal communication).

Site 4 has a diverse vegetation, mature trees, a well developed forest soil, and some ectomycorrhizal tree species such as *Q. glauca* and *Q. myrsinaefolia*. Although conditions at this site seem to be advantageous for ectomycorrhizal fungi (Dighton and Mason, 1985; Last et al., 1987), the percent ectomycorrhizal root length was lower for the *B. platyphylla* var. *japonica* seedlings grown in Site 4 soils than in soils of the other three sites (Fig. 1). The reason for this discrepancy seems to be the absence of *Betula* spp. in Site 4. Thus, the distribution of ectomycorrhizal fungi might be more closely related to the distribution of the host plants than to the site conditions.

The percent ectomycorrhizal root length on seedlings grown in soils collected from the sites that had been artificially disturbed by clear-cutting or plowing surface soil (Sites 2 and 3) appeared the same as or even higher than that from the undisturbed birch forest (Site 1). This suggested that in cases where host plants remained or regenerated, the ectomycorrhizal inoculum in soils might be preserved after disturbance. In coniferous forests, several researchers have reported a diminished soil inoculum potential or mycorrhizal development after clear-cutting (Harvey et al., 1980; Perry et al., 1982; Schoenberger and Perry, 1982). However, we did not observe this negative impact of clear-cutting. In our Site 2, ectomycorrhizal inocula were maintained after clear-cutting, because of the prompt regeneration of trees from seeds buried in the soil or blown in from neighboring birch forest. Pilz and Perry (1984) reported the same tendency, with more ectomycorrhizas formed in clear-cuts than in undisturbed forest. They also suggested that prompt regeneration might be important to secure adequate formation of indigenous mycorrhizas.

The morphological types of ectomycorrhizas The total number of the morphological types of ectomycorrhizas of *B. platyphylla* var. *japonica* seedlings grown in the soils collected from Sites 1, 2 and 3 in November was 9, 5, and 1, respectively (Table 3). The mean number of ectomycorrhizal types per seedling was 3.0, 2.5, and 0.8, respectively (Table 4). Thus, the diversity of ectomycorrhizas of *B. platyphylla* var. *japonica* seedling might be decreased after disturbance, and it seems that plowing was particularly critical. Pilz and Perry (1984) also demonstrated the presence of more types of ectomycorrhizas of Douglas-fir seedlings in undisturbed forest soils than in soils at clear-cut sites. The humus and litter layer of the soil surface might play an important role in maintaining the diversity of ectomycorrhizal fungi, as ectomycorrhizas can develop better in soils with humus and litter than in mineral soil (Harvey et al., 1979).

Because more open stands are subject to increased sunlight and more rainfall reaching the forest floor directly, the soil temperature and moisture conditions at Site 2 were different from those of Site 1. The A_0 horizon of Site 2 was only one-sixth as thick as that of the undisturbed forest at Site 1. Both Sites 1 and 2 have, however, the same dominant ectomycorrhizal type (Type 1) on *B. platyphylla* var. *japonica*. This suggests that the dominant ectomycorrhizal fungi might retain their inoculum potential in soil after the environmental changes caused by forest clear-cutting. Alternatively, inocula of this fungus might have been transferred from the adjacent forests to the clear-cut site.

In Site 3, only one type of ectomycorrhiza was formed on seedlings, and the dominant ectomycorrhizal type (Type 12) was different from that of Site 1 and Site 2 (Table 3). The reason for this change might be the complete loss of surface soil by artificial disturbance: when the surface soil was removed from Site 3, so Type 1, which was dominant in Site 1 and Site 2, might also have been removed. However, when the regeneration of host plants occurs after disturbance, the dominant type of ectomycorrhizas might be changed by severe disturbance of the ground, such as removal of the surface soil. Ectomycorrhizal fungi that are better adapted to the soil conditions after disturbance would be expected. The ectomycorrhizal fungus that caused Type 12 at Site 3 could be better adapted to these changed soil conditions.

Newton (1991) reported that the dominant type of ectomycorrhiza in a 50-yr-old birch forest was *Paxillus involutus* (Batsch) Fr., based on its morphological characteristics. It seems that *P. involutus* was not a dominant ectomycorrhizal fungus at our site, because its characteristics differ from those of Type 1, the dominant type at Site 1 and Site 2. Furthermore, fruiting bodies of *P. involutus* were not present at Site 1 (Kamiya, personal communication).

In the present study, 16 morphological types of ectomycorrhizas were found in soil from four sites. Although a number of morphological characteristics of ectomycorrhiza that are associated with birch were reported by Ingleby et al. (1990) and Agerer (1994), the only identifiable ectomycorrhizal fungus that appeared in this study was *C. geophilum* (Type 16). Different ectomycorrhizal types are found under different environmental conditions (Frankland and Harrison, 1985; Newton, 1991; Newton and Pigott, 1991), and many unknown types of ectomycorrhizas might exist on birch seedlings, as suggested by Newton (1991).

Betula platyphylla var. *japonica* is a pioneer plant that can establish itself at a disturbed site immediately after disturbance. The soil conditions at a disturbed site might be more severe than those of undisturbed forest soils. For example, in this study, the amounts of the total organic matter, nitrogen, and phosphorus in the disturbed soil at Site 3 were extremely low, being 1/27, 1/16, and 1/3 of those at Site 1, respectively (Table 1). The present investigation showed that the ectomycorrhizal formation of *B. platyphylla* var. *japonica* seedlings grown in soil from disturbed sites, such as after clear-cutting or removal of the surface soil, was the same as or higher than that in soil from an undisturbed *B. platyphylla* var. *japonica* forest site. Furthermore, our results suggested that certain ectomycorrhizal types can be dominant in a birch-dominated stand. Seedlings are susceptible to environmental stresses. Christy et al., (1982) reported that ectomycorrhizal conifer seedlings grew better than non-ectomycorrhizal seedlings in the field. Mycorrhizal associations are favorable for seedlings to overcome some environmental stresses, especially at sites with environmentally severe conditions such as Site 3. Thus, it would be interesting to know if Type 12, which was the only type of ectomycorrhiza that appeared in soil from Site 3, plays an important role in the establishment of *B. platyphylla* var. *japonica* seedlings at this site. It has been reported that the influences of ectomycorrhizas on plant growth differ according to the species of ectomycorrhizal fungi (Cline and Reid, 1982; Dixon et al., 1984; Tyminska and Tacon, 1986). It is necessary to investigate the influences of those dominant ectomycorrhizal fungi on the growth of *B. platyphylla* var. *japonica* seedlings in order to understand the establishment of these trees under severe conditions.

In the present study, the sites investigated were few and restricted to a small region. To know the distribution of the dominant ectomycorrhizal types that appeared in the present investigation, it will be important to extend the investigation to a wider area where secondary growth of *B. platyphylla* var. *japonica* is found.

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Literature cited

Abuzinadah, R. A. and Read, D. J. 1989. Carbon transfer associated with assimilation of organic nitrogen sources by silver birch (*Betula pendula* Roth.). Trees **3**: 17–23.

Agerer, R. 1994. Colour atlas of ectomycorrhizae. Einhorn-Verlag, Schwabisch Gmünd.

Browning, M. H. R. and Whitney, R. D. 1993. Infection of containerized jack pine and black spruce by *Laccaria* species and *Thelephora terrestris* and seedling survival and growth after outplanting. Can. J. For. Res. **23**: 330–333.

Christy, E. J., Sollins, P. and Trappe, J. M. 1982. First-year survival of *Tsuga heterophylla* without mycorrhizae and subsequent ectomycorrhizal development on decaying logs and mineral soil. Can. J. Bot. **60**: 1601–1605.

Cline, M. L. and Reid, C. P. P. 1982. Seed source and mycorrhizal fungus effects on growth of containerized *Pinus contorta* and *Pinus ponderosa* seedlings. Forest Sci. **28**: 237–250.

Dighton, J. and Mason, P. A. 1985. Mycorrhizal dynamics during forest tree development, pp. 117–139. Cambridge University Press, Cambridge.

Dixon, R. K., Garrett, H. E., Cox, G. S., Marx, D. H. and Sander, I. L. 1984. Inoculation of three *Quercus* species with eleven isolates of ectomycorrhizal fungi. I. Inoculation success and seedling growth relationships. Forest Sci. **30**: 364–372.

Frankland, J. C. and Harrison, A. F. 1985. Mycorrhizal infection of *Betula pendula* and *Acer pseudoplatanus*: relationships with seedling growth and soil factors. New Phytol. **101**: 133–151.

Gardes, M. and Bruns, T. D. 1996. Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: above- and below-ground views. Can. J. Bot. **74**: 1572–1583.

Harley, J. L. and Smith, S. E. 1983. Mycorrhizal symbiosis. Academic Press, London.

Harvey, A. E., Larsen, M. J. and Jurgensen, M. F. 1979. Comparative distribution of ectomycorrhizae in soils of three Western Montana forest habitat types. Forest Sci. **25**: 350–358.

Harvey, A. E., Larsen, M. J. and Jurgensen, M. F. 1980. Partial cut harvesting and ectomycorrhizae: early effects in Douglas-fir-larch forest of western Montana. Can. J. For. Res. **10**: 436–440.

Imazeki, R. and Hongo T. 1987. Colored illustration of mushrooms of Japan, I. Hoikusha, Osaka. (In Japanese.)

Imazeki R. and Hongo T. 1989. Colored illustration of mushrooms of Japan, II. Hoikusha, Osaka. (In Japanese.)

Ingleby, K., Mason, P. A., Last, F. T. and Fleming, L. V. 1990. Identification of ectomycorrhizas. HMSO, London.

Last, F. T., Dighton, J. and Mason, P. A. 1987. Succession of sheathing mycorrhizal fungi. Trees **2**: 157–161.

MacFall, J., Slack, S. A. and Iyer, J. 1991. Effects of *Hebeloma arenosa* and phosphorus fertility on root acid phosphatase activity of red pine (*Pinus resinosa*) seedlings. Can. J. Bot. **69**: 380–383.

Marx, D. H. 1969. The influence of ectotrophic mycorrhizal fungi on the resistance of pine roots to pathogenic infections. I. Antagonism of mycorrhizal fungi to root pathogenic fungi and soil bacteria. Phytopathology **59**: 153–163.

Newton, A. C. 1991. Mineral nutrition and mycorrhizal infection of seedling oak and birch III. Epidemiological aspects of ectomycorrhizal infection, and the relationship to seedling growth. New Phytol. **117**: 53–60.

Newton, A. C. and Pigott, C. D. 1991. Mineral nutrition and mycorrhizal infection of seedling oak and birch I. Nutrient uptake and the development of mycorrhizal infection during seedling establishment. New Phytol. **117**: 37–44.

Ogawa, M. 1977. Ecology of higher fungi in *Tsuga diversifolia* and *Betula ermani-Abies mariesii* forests of subalpine zone. Trans. Mycol. Soc. Japan **18**: 1–19.

Perry, D. A., Meyer, M. M., Egeland, D., Rose, S. L. and Pilz, D. 1982. Seedling growth and mycorrhizal formation in clearcut and adjacent, undisturbed soils in Montana: A greenhouse bioassay. For. Ecol. Manage. **4**: 261–273.

Pigott, C. D. 1982. Fine structure of mycorrhiza formed by *Cenococcum geophilum* FR. on *Tilia cordata* Mill. New Phytol. **92**: 501–512.

Pilz, D. P. and Perry, D. A. 1984. Impact of clearcutting and slash burning on ectomycorrhizal associations of Douglas-fir seedlings. Can. J. For. Res. **14**: 94–100.

Schoenberger, M. M. and Perry, D. A. 1982. The effect of soil disturbance on growth and ectomycorrhizae of Douglas-fir and western hemlock seedlings: a greenhouse bioassay. Can. J. For. Res. **12**: 343–353.

Tennant, D. 1975. A test of a modified line intersect method of estimating root length. J. Ecol. **63**: 995–1001.

Tyminska, A. and Tacon, F. L. 1986. Effect of three ectomycorrhizal fungi on growth and phosphorus uptake of *Pinus silvestris* seedlings at increasing phosphorus levels. Can. J. Bot. **64**: 2753–2757.

Vogt, K. A., Edmonds, R. L., Grier, C. C. and Piper, S. R. 1980. Seasonal changes in mycorrhizal and fibrous-textured root biomass in 23- and 180-year-old Pacific silver fir stands in western Washington. Can. J. For. Res. **10**: 523–529.