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Distribution of different mycorrhizal classes on Mount Koma, northern Japan

Abstract To investigate the role of mycorrhizae in nutrient-poor primary successional volcanic ecosystems, we surveyed mycorrhizal frequencies on the volcano Mount Koma (42°04′N, 140°42′E, 1,140 m elevation) in northern Japan. After the 1929 eruptions, plant community development started at the base of the volcano. Ammonia and nitrate levels, along with plant cover, decreased with increasing elevation, whereas phosphorus did not. In total, 305 individuals of 56 seed plant species were investigated in three elevational zones (550–600 m, 650–700 m, and 750–800 m). Five mycorrhizal classes were classified based on morphological traits: ecto- (ECM), arbuscular (AM), arbutoid, ericoid, and orchid mycorrhiza. All plant species were mycorrhizal to at least some extent, with most widespread tree species being heavily ectomycorrhizal. In addition, of 16 tree species collected in all three zones, 6 differed in the frequencies of ECM on roots between elevational zones, and 3 of these 6 species increased in frequency with increasing elevation. These results suggest that ECM colonization in some tree species is related to establishment in nutrient-poor habitats. All species of Ericaceae and Pyrolaceae had ericoid mycorrhizae, and an Orchidaceae species had orchid mycorrhizae. Herbaceous species, except for the low mycorrhizal frequency of *Carex oxyandra* and two Polygonaceae species, and ericoid and orchid mycorrhizal species, were generally AM. Of herbaceous species, *Anaphalis margaritacea* var. *angustior* increased AM frequency and decreased ECM frequency with increasing elevation, and *Hieracium umbellatum* increased ECM frequency. In total,

the establishment of herbaceous species was not sufficiently explained by AM colonization on roots. Tree individuals developed 2–3 classes of mycorrhizae more than herbs at each elevational zone. We conclude that the symbiosis between seed plants and mycorrhizae, ECM in particular, greatly influences plant community structures on Mount Koma. Not only a single mycorrhizal class, but combinations of mycorrhizal classes should be studied to clarify effects on plant community dynamics.

Keywords Arbuscular mycorrhiza · Ectomycorrhiza · Elevational difference · The volcano Mount Koma · Seed plant

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Introduction

Mycorrhizal symbiosis between plants and fungi occurs across a wide range of environments, probably because the mutualism enables plants to obtain nutrients more effectively (Mukerji et al. 2000). Ecological mycorrhizal research focuses on how this mutualism influences community diversity, and ecosystem nutrient and energy flows (van der Heijden et al. 1998). Mycorrhizal relationships are morphologically classified into seven classes: ecto- (ECM), arbuscular (AM), ectendo-, arbutoid, monotropoid, ericoid, and orchid mycorrhiza (Smith and Read 1997). Some fungi have the potential to form different types of mycorrhizae depending on the host species (Sen et al. 1999; Horton and Bruns 2001). However, the morphological classes are the established structural and functional classification, and each class has different roles in the relationship between the plant and the fungi via various nutrient pathways (Allen et al. 2003). For example, ECM fungi are observed mostly on trees and are considered to have a role in the acquisition of nitrogen rather than phosphate, while AM fungi often establish in phosphate-poor environments (Allen 1991; Mukerji et al. 2000). However, laboratory experiments suggest that both ECM and AM fungi may accelerate nitrogen and phosphate uptake (Jones et al. 1990; Hodge et al. 2001).

Fig. 1A–E Five classes of mycorrhizae detected on Mount Koma in 2000. **A** Arbuscular mycorrhizae in the roots of *Elaeanus pungens*. **B** Ectomycorrhizae from the roots of *Salix bakko*. **C** Ericoid mycorrhizae from the roots of *Ledum palustre* var. *diersipoilosum*. **D** Orchid mycorrhizae from *Spiranthes sinensis*. **E** Arbutoid mycorrhizae from *Pyrola incarnata*. *M* Mantle, *H* hyphae, *C* hyphal coil, *V* vesicules, *A* arbuscules, *OH* outer hyphae, *IHC* Intracellular-hyphae-complex. No monotropoid mycorrhizae were observed. *Bars* 50 μm
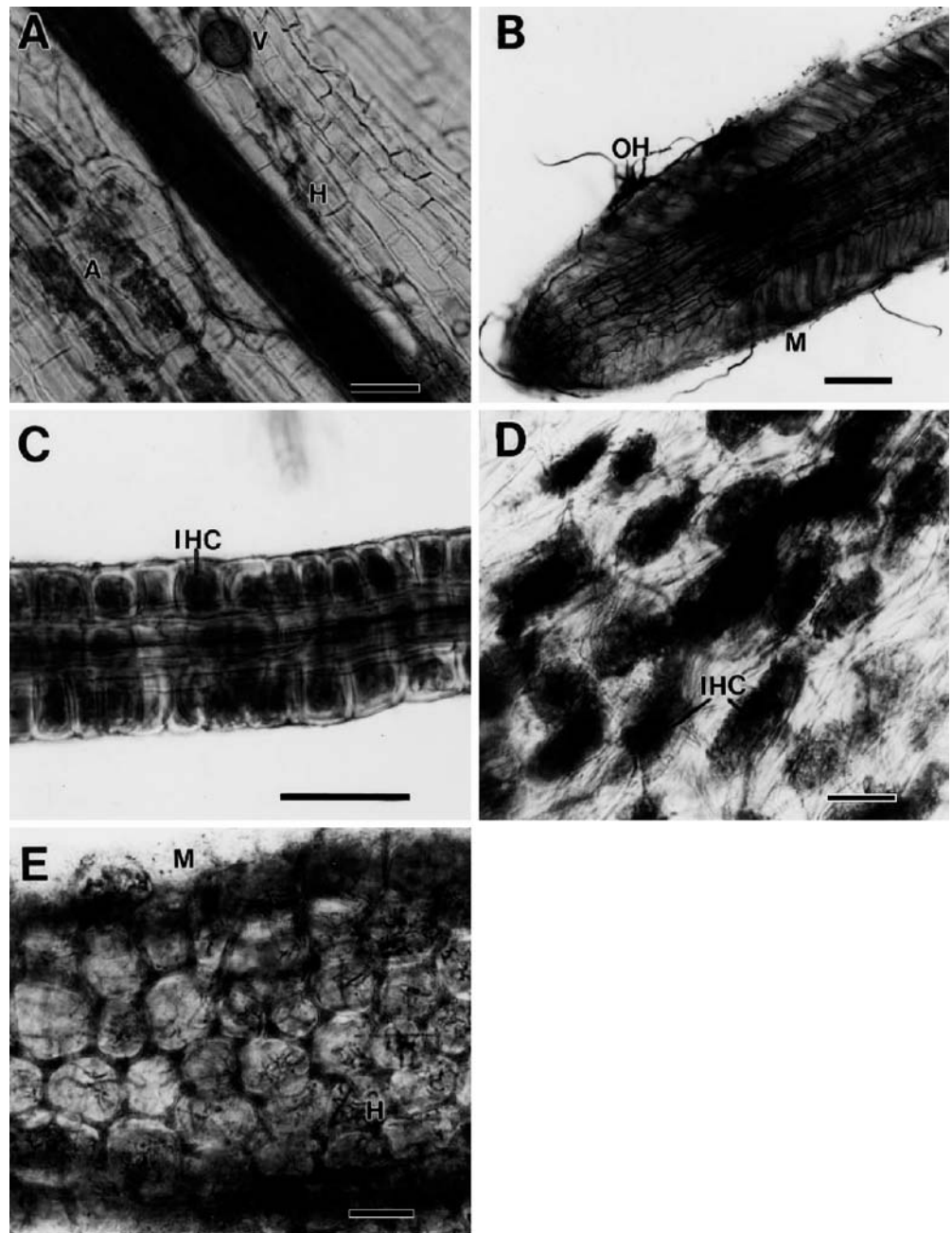
Furthermore, ECM and AM may affect belowground carbon budgets via the alteration of litter quality in different ways (Langley and Hungate 2003). These results suggest that relationships between plants and mycorrhizae are unresolved, and it may be worth evaluating how plant community patterns are related to morphological classes of mycorrhizae in harsh environments.

In the early stages of succession, such as new substrates on volcanoes, pioneer seed plant species are nonmycorrhizal due to a lack of fungal propagules (Allen 1991). In primary successional environments on Mount St. Helens (Wash.), plant establishment was determined by microhabitats such as depressions and near-rock sites rather than the presence of arbuscular mycorrhizal propagules (Titus and del Moral 1998). Subsequently, facultatively myco-

trophic species become mycorrhizal, and eventually obligate mycotrophic species establish (Gange et al. 1990; Titus and del Moral 1998). When more than one class of mycorrhiza, such as AM and ECM, develops on an individual plant, competition or facilitation occurs between the classes (van der Heijden et al. 1998; Hashimoto and Hyakumachi 2000).

The 1929 eruption of Mount Koma in northern Japan produced pumice and ash deposits that created an extensive barren area (Yoshii 1932). Primary succession started at the base of the mountain and proceeded slowly to the summit primarily from plant refugia (Yoshioka 1966). Preliminary investigations showed that nitrates decreased with increasing elevation but phosphates did not. Therefore, this area provides a convenient system to

investigate the relationship between seed plants and mycorrhizae across elevational and nutrient gradients. Our objectives in this study were to determine the following. (1) Which classes of mycorrhizae become established on the sparsely vegetated slopes of the volcano? (2) Which classes are most common? (3) Is the frequency of mycorrhizal relationships related to environmental gradients?

Materials and methods

Study area

Mount Koma is an active andesite composite volcano in the southwestern part of Hokkaido Island, northern Japan (42°04′N, 140°42′E, 1,140 m elevation). The 1929 eruption completely destroyed vegetation on the volcano slopes. The volcano has a 2-km wide horseshoe-shaped caldera opening to the east on the summit. The climate is categorized as warm-cool temperate. Mean annual temperature is 11.6°C, with 24.6°C mean maximum in August and −6.9°C mean minimum in January, measured at Mori Climatological Observatory, 9 km from Mount Koma (10 m elevation). Vegetation recovery proceeded slowly, starting at the base of the mountain, and much of the summit area is still barren today. The non-native *Larix kaempferi* has begun to invade the summit area much more than native tree species (Kondo and Tsuyuzaki 1999). Native pioneer tree species are *Betula* spp. (*B. ermanii* and *B. platyphylla* var. *japonica*), *Populus* spp. (*P. sieboldii* and *P. maximowicizii*), and *Salix* spp. (*S. bakko* and *S. sachalinensis*). Mosses and/or lichens carpet much of the ground surface. Small-scale eruptions occurred on the summit in 1996 and 2000. Damage to the vegetation from these most recent eruptions was restricted to within a few hundred meters of the new crater.

Methods

During June and October 2000, seed plants were excavated at three different elevational zones: low (550–600 m), middle (650–700 m), and high (750–800 m). These areas were not damaged by the most recent eruptions. At each elevational zone, three individuals of each species were collected if possible. Due to restriction on excavating, all tree samples were less than 1 m in height. Root samples were stored in 70% ethanol in the field and brought to the laboratory.

Root samples were stained with 0.05% Trypan Blue in acidic glycerol (50% glycerol in 0.1% HCl) for 3 min at 121°C after tissue clearing in 2.5% KOH and bleaching in alkaline H_2O_2 (2% NH_4OH in 3% H_2O_2), as described by Koske and Gemma (1989). Root samples were mounted on slides with acidic glycerol. On each individual sample, at least ten fine root segments (modules) were randomly selected and observed, if the number of root segments was sufficiently large. The samples were observed microscopically at various magnifications. When mycorrhizae were observed in the root segments, the class of mycorrhizae was recorded based on morphological traits, such as the presence of septum, arbuscule, mantle, Hartig net and/or hyphal coil (Smith and Read 1997) (Fig. 1). If the class was not determined, it was recorded as unknown. The frequency of each mycorrhizal class on each species at each elevational zone was calculated as: (number of mycorrhizal root segments)/(total number of root segments observed) (Quoreshi and Timmer 1998).

In 1998, chemical properties and nutrients in soils were measured from 600 m to 850 m at 50-m intervals. At each elevational zone, 25 volcanic deposit samples were collected in a 20 m ×20 m plot, except at 600 m where 90 samples were collected from three 20 m ×20 m plots. Loss on ignition, pH, ammonium (NH_4^+), nitrate (NO_3^-) and phosphate (PO_4^{3-}) were measured on each sample and averaged for each zone. Volcanic deposits (10 g) were suspended in 20 ml distilled water and filtered. The filtrates were used for determination of pH and content of nitrate, ammonium, and inorganic phosphate. Nitrate and ammonium content were determined using Reflectoquant Nitrate test strips (Merck, Darmstadt, Germany) and Nessler's reagent (Kanto, Tokyo, Japan), respectively. Phosphate content was determined as described by Ames (1966). The same samples of volcanic deposits were then dried at 105°C for 3 days in an oven, and weighed (dry weight). The samples were ignited at 800°C for 8 h in a muffle furnace, and weighed. To estimate organic matter content, loss on ignition of sample was calculated as (weight loss by ignition)/(dry weight) ×100.

Density and dominance of each seed plant species were measured by a line-transect method at each elevational zone in 2000 (Mueller-Dombois and Ellenberg 1974). At each zone, the total length of lines was 150–200 m. When a plant was intersected by a line, the length occupied by the plant occupied on the line was measured. Density per unit length was evaluated from the number of hits, and the dominance from the total length occupied by each species.

Statistical analysis

Occurrence frequencies of mycorrhizae on roots across elevation for each species were investigated by G-test, when the species were distributed in the three elevational zones (Zar 1999). Nutrient conditions between elevational zones were compared by MANOVA. When a significant difference was observed, Scheffe's post-hoc test was applied. The numbers of mycorrhizal classes on individuals were compared between the three elevational zones by two-way ANOVA. Differences in species composition sampled at the three elevational zones were investigated by ANOVA (Zar 1999).

Results

Mycorrhizal classes observed

In total, 305 individuals of 56 seed plant species (23 families and 47 genera) were examined. Of 56 species, 26 were trees. Major families sampled were Asteraceae (8 species), Salicaceae (6), Ericaceae (5), Betulaceae (5), and Poaceae (4). Based on the morphological traits of the 7,403 root segments examined, five mycorrhizal classes were recognized: ECM, AM, ericoid, arbutoid, and orchid mycorrhizae (Fig. 1). Monotropid mycorrhizae were not detected. Ectendomycorrhizae were also observed but were treated as 'unknown' in the analysis, because the distinction of ectendomycorrhizae from ECM and/or AM was somewhat difficult on a few specific host plants. Except for *Carex oxyandra*, which had the lowest mycorrhizal frequency at ~20%, including one individual completely lacking mycorrhizae, all plants examined were mycorrhizal.

ECM established well on tree species. For example, all Betulaceae, Salicaceae, and Pinaceae species were ectomycorrhizal. A few herbaceous species, i.e., *Erigeron acris*, *Polygonum sachalinense*, *Epilobium angustifolium*, *Polygonum weyrichii*, *Hieracium umbellatum* var. *japonicum*, *Anaphalis margaritacea* var. *angustior*, also had high ectomycorrhizal frequencies (Fig. 2). AM were observed on 50 of the 56 species. This accounted for 89% of sampled species. Herbaceous species had the highest frequencies of AM; for example, most species in Poaceae,
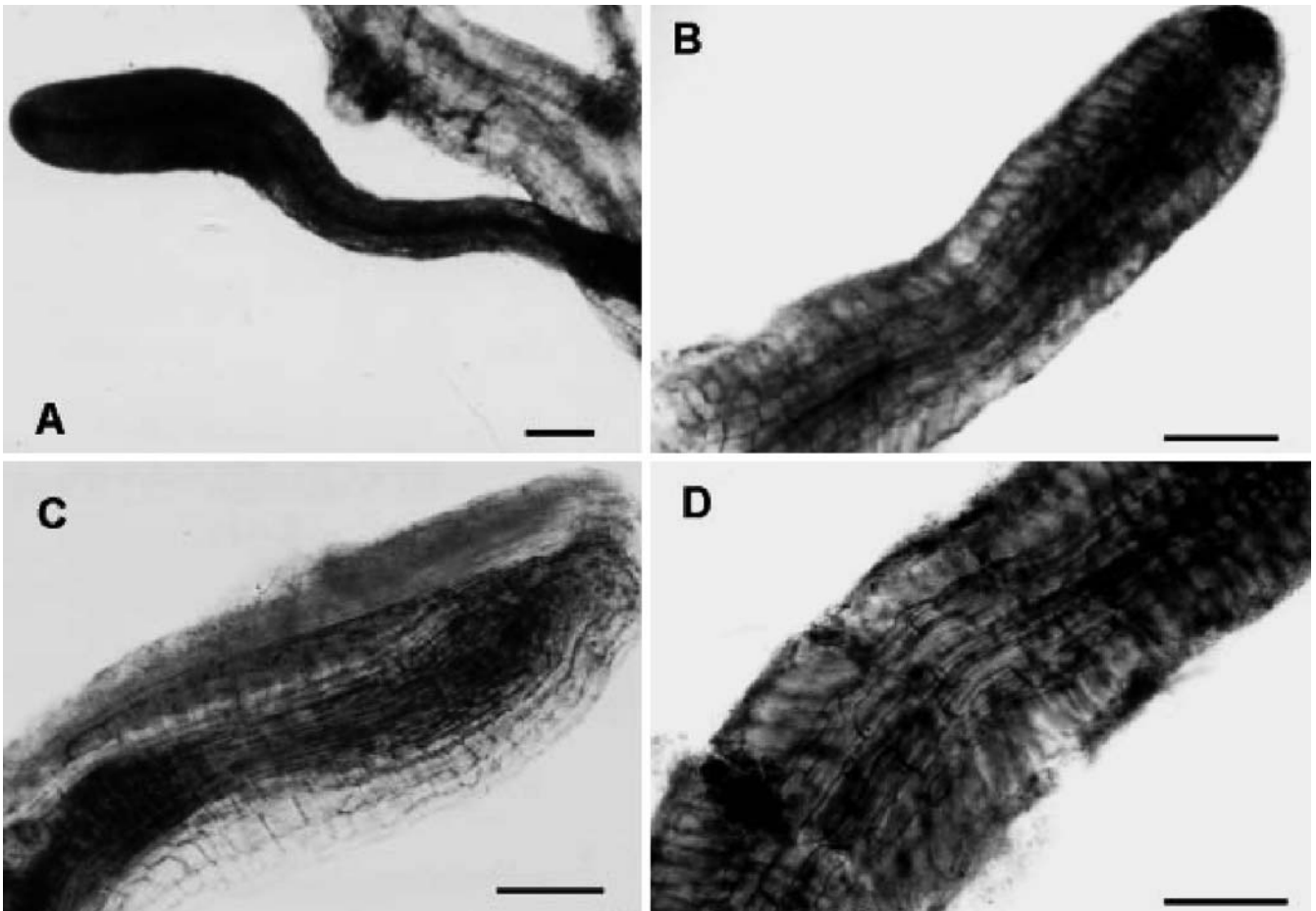
Fig. 2A–D Representative herbaceous plant species with ectomycorrhizae. **A** *Anaphalis margaritacea* var. *angustior*. **B** *Erigeron acris*. **C** *Polygonum sachalinense*. **D** *Polygonum weyrichii*. *Bars* 100 μm

Asteraceae, and Onagraceae showed more than 90% frequencies of AM in roots. In particular, AM were observed in all the root segments of *Calamagrostis langsdorffii*. The following woody species had high frequencies of AM: *Rhus trichocarpa*, *Hydrangea paniculata*, *Rubus phoenicolasius*, *Rubus parivifolius*, *Weigela hortensis*, *Elaeagnus pungens*, and *Sorbus commixta*. Except for *S. commixta*, which is a tree, these are shrubs. Tall tree species developed few AM. In particular, three tree species, *Betula maximowicziana*, *Salix integra*, *Salix sachalinensis*, had no AM.

Orchid mycorrhizae, arbutoid mycorrhizae and ericoid mycorrhizae were observed on the respective seed plant taxa. Ericoid mycorrhizae were observed on all Ericaceae species collected (*Gaultheria miqueliana*, *Ledum palustre* var. *diversipilosum*, *Leucothoe grayana* var. *oblongifolia*, *Rhododendron branchycarpum*, and *Tripetaleia paniculata*). The occurrence frequencies on roots averaged ~50%, but varied greatly between species. Two Pyrolaceae species, *Chimaphila japonica*, and *Chimaphila umbellata*, both of which are sometimes categorized as shrubby herbs, also had ericoid mycorrhizae. One herbaceous Pyrolaceae species, *Pryola incarnata*, developed arbutoid mycorrhizae. One Orchidaceae species, *Spiranthes sinensis*, had extensive orchid mycorrhizae, as would be expected.

Nutrient status and seed plant species composition

Organic matter, expressed as loss on ignition of volcanic deposits, ranged from 0.96 to 9.86, and was higher at lower elevations (Fig. 3), even though the highest value was lower than in soils on the forests and grasslands of Japan. The volcanic deposits were acidic, ranging from pH 3.9 to 5.5. The increase in elevation roughly paralleled the decrease in total nitrogen, while phosphorus was lowest in mid-elevation. Ammonium was more than double at the lowest than at the highest elevation. Nitrate also fluctuated with elevation, although the difference was not significant except at the lowest value at 750 m. Roughly, nutrients in volcanic deposits decreased with increasing elevation, principally due to the decline of nitrogenous nutrients.

The most common species were woody species, such as *Salix reinii*, *Gaultheria miqueliana*, and *Larix kaempferi* (Table 1). *Salix reinii*, a shrub, increased in density and dominance with increasing elevation, while tall trees, i.e., *L. kaempferi*, *Populus sieboldii*, *Betula ermanii*, etc., were restricted to low and middle elevational zones. Herbaceous species consisted mostly of grasses, sedges, and rushes. Most of these herbs, in particular *Calamagrostis langsdorffii* and *Carex oxyandra*, increased in density and
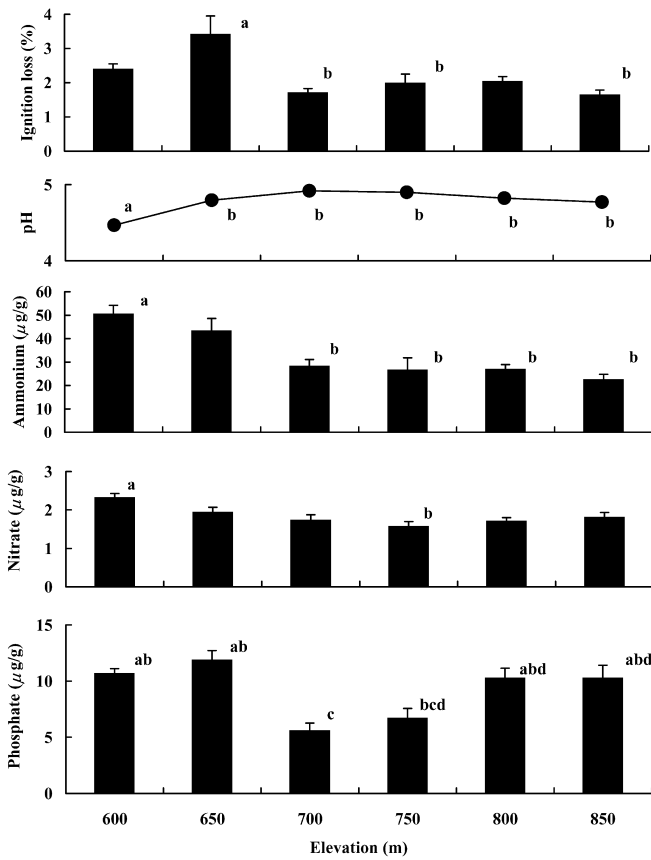
Fig. 3 Changes in environmental factors with elevation in 1999. Same letters indicate values not significantly different between elevations at $P>0.05$ (Scheffe's test after MANOVA). Columns indicate mean with standard error. $n=25$ in each elevation, except $n=90$ at 600 m

dominance with increasing elevation. Forbs were sparsely distributed, except for *Anaphalis margaritacea* var. *angustior*.

Elevational differences in mycorrhizae

Of 16 tree species collected from all the elevational zones, 6 differed in the frequency of ECM on roots between the elevational zones, and 3 of the 6 species, *Salix bakko*, *Weigela hortensis*, and *Gaultheria miqueliana*, increased in frequency with increasing elevation (Table 2). These results suggest that ECM colonization in trees is related to establishment for some tree species on nutrient-poor habitats. Of herbaceous species, *Anaphalis margaritacea* var. *angustior* increased AM frequency and decreased ECM frequency with increasing elevation, while *Hieracium umbellatum* increased ECM frequency. AM frequency did not increase with increasing elevation for any herbaceous species. In total, therefore, the establishment of herbaceous species could not be sufficiently explained by AM colonization on roots.

Since the plant species composition of the samples used to investigate mycorrhizae was not significantly different at the three elevational zones (ANOVA, $P<0.05$), the frequency of mycorrhizae could be compared between the three elevational zones, without consideration of differences in species composition. A maximum of three classes of mycorrhizae was observed in an individual species (Fig. 4). All of the species that had all three classes belonged to Ericaceae (*G. miqueliana*, *Ledum palsture* var. *diversipilosum*, and *Leucothoe grayana*), and the three mycorrhizal classes were ericoid mycorrhiza, ECM and AM. For species with two mycorrhizal classes, the classes were usually ECM and AM. Plants developing more than one mycorrhizal class composed 20–40% of the plants

Table 1 Number of vascular plant individuals intersected per 100 m transect line at three different elevational zones. Percentage dominance (total length of plants occupied on lines by total length of surveyed lines ×100) is shown in parentheses

Elevational zone Total length measured (m)	Low 200	Middle 150	High 170	Total
Salix reinii	10.5 (5.8)	86.3 (20.5)	122.6 (23.4)	73.1 (16.6)
Gaultheria miqueliana	57.0 (10.1)	95.6 (14.0)	1.7 (0.0)	51.4 (8.1)
Calamagrostis langsdorffii	2.5 (0.1)	17.3 (0.5)	45.9 (1.3)	21.9 (0.6)
Larix kaempferi	21.5 (19.3)	26.6 (17.2)	9.3 (3.3)	19.1 (13.2)
Salix integra	12.5 (5.3)	11.9 (1.7)	16.3 (3.1)	13.6 (3.4)
Carex oxyandra	4.5 (0.1)	11.9 (0.3)	15.1 (0.6)	10.5 (0.3)
Miscanthus sinensis	14.5 (1.5)	2.0 (0.0)	6.4 (1.0)	7.6 (0.9)
Populus sieboldii	5.5 (0.8)	4.0 (0.4)	2.9 (0.2)	4.1 (0.5)
Luzula capitata		4.6 (0.1)	4.6 (0.1)	4.6 (0.1)
Betula ermanii	2.0 (0.8)	5.3 (2.0)		3.7 (1.4)
Weigela hortensis	2.0 (0.2)	4.0 (0.4)	0.6 (0.1)	2.2 (0.3)
Betula platyphylla var. *japonica*	3.5 (2.3)	2.7 (0.7)		3.1 (1.5)
Hydrangea paniculata	2.5 (0.8)	1.3 (0.2)	2.3 (0.3)	2.1 (0.4)
Anaphalis margaritacea var. *angustior*	3.0 (0.1)	0.7 (0.0)	2.3 (0.0)	2.0 (0.1)
Populus maximowiczii	1.5 (0.3)	2.7 (0.5)	1.7 (0.1)	2.0 (0.3)
Salix bakko		3.3 (0.5)	0.6 (0.0)	1.9 (0.3)
Others (20 species)	6.5 (0.5)	2.0 (0.5)	8.7 (0.5)	5.7 (0.5)
Total	149.5 (47.9)	282.1 (59.6)	241.1 (33.9)	224.2 (47.2)

Table 2 Seed plant species that were collected from all the elevational zones and showed significant differences of mycorrhizal colonization among three elevational zones. Percentage frequency of root segments that were ectomycorrhizal and arbuscular mycorrhizal are shown. Significant differences of relative frequencies of ectomycorrhiza and arbuscular mycorrhiza along elevation were confirmed by *G*-test (*P*<0.01). All the species examined are shown in the Appendix

Elevational zone	Low	Middle	High
Percentage frequency of ectomycorrhiza			
Herbs and forbs			
Hieracium umbellatum var. *japonica*	0	40	48
Anaphalis margaritacea var. *angustior*	0	27	56
Trees and shrubs			
Salix bakko	36	53	67
Populus maximowiczii	46	80	57
Weigela hortensis	0	12	60
Gaultheria miqueliana	15	24	39
Larix kaempferi	80	57	67
Alnus maximowiczii	73	47	53
Percentage frequency of arbuscular mycorrhiza			
Herbs and forbs			
Luzula capitata	43	13	50
Polygonum weyrichii	20	29	2
Anaphalis margaritacea var. *angustior*	63	48	23
Trees and shrubs			
Populus maximowiczii	9	0	0
Weigela hortensis	54	55	24
Larix kaempferi	0	10	5
Rhus tricocarpa	76	67	34

examined at each elevational zone. Trees tended to develop more mycorrhizal classes than herbs.

Discussion

Characteristics of mycorrhizal classes and plant species

At least five classes of mycorrhizae were observed in the present study. Ericoid, orchid and arbutoid mycorrhizae were selectively observed within the host seed plant taxa. Ericoid mycorrhizae were observed in all Ericaceae species and also in two Pyrolaceae species. Only *Spiranthes sinensis* had orchid mycorrhizae. Arbutoid mycorrhizae were only found in one Pyrolaceae species, *Pyrola incarnata*. The other two classes, ECM and AM, were common. Furthermore, all plants except one *Carex oxyandra* individual developed mycorrhizal roots. In a previous study on Mount Koma, ECM fungi on the roots of *Larix kaempferi* seedlings were recognized as 12 morphological classes (Yang et al. 1998). Furthermore, the present study shows that all the sampled plant species had mycorrhizae and, in particular, ECM frequency was high in the species of Cyperaceae, Polygonaceae and Juncaceae
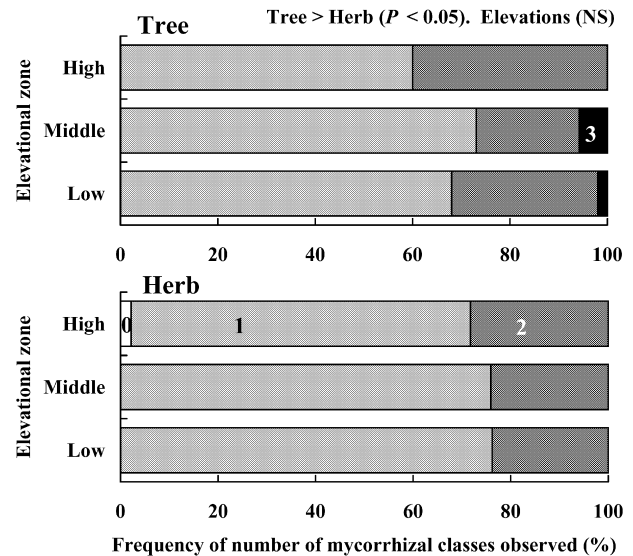
Fig. 4 Relative frequencies of number of mycorrhizal classes observed on individual plants, summarized by two life forms (trees and herbs). Numbers indicate numbers of mycorrhizal classes observed. The frequencies are significantly different between the life forms at *P*<0.05 and not significantly different among the elevational zones (two-way ANOVA)

that have been generally considered nonmycotrophic (Smith and Read 1997). These results suggest that high fungal diversity is one of the characteristics of mycorrhizal composition on Mount Koma.

Carex oxyandra had low AM colonization levels in the study area, but no mycorrhizae were found on *C. oxyandra* plants growing in the 1996 eruption blast area, which was covered with new tephra (Titus and Tsuyuzaki 2002). *Carex* species are generally nonmycorrhizal (Miller et al. 1999). For example, out of 100 *Carex* plants examined on Mount St. Helens only 2 individuals contained a trace of AM (Titus et al. 1998). These differences suggest that, even on a single mountain, AM colonization on *Carex* is flexible with respect to nutrient status. AM colonization was also observed on four *Carex* and other Cyperaceae species in the Western Ghats, India (Muthukumar and Udaiyan 2000). *Calamagrostis langsdorffii*, of which dominance and density increased with increasing elevation, was highly arbuscular mycorrhizal. Another grass, *Agrostis scabra*, was found to be facultatively mycorrhizal both on Mount Koma in this study and on Mount St. Helens (Titus et al. 1998).

Distribution patterns of mycorrhizae and plants of the community level

The different classes of mycorrhizae affect plant uptake of N and P differently (Smith and Read 1997). On Mount Usu, located near Mount Koma, soil nutrients in the volcanic deposits were measured 8 years after the eruptions (Haruki and Tsuyuzaki 2001). Loss on ignition was ~1%, total nitrogen ranged from 30 to 310 μg/g, and available phosphorus from 170 to 300 μg/g. The loss on

ignition was 2–3 times higher on Mount Koma than on Mount Usu, while phosphorus was lower. These results suggest that soil nutrient conditions on Mount Koma are somewhat higher than on Mount Usu. However, soil nutrient levels, including N and P, are much lower than in disturbed forest soils (Hashimoto and Hyakumachi 2000). Mount Koma is a nutrient-poor environment. In particular, nitrogen decreased with increasing elevation while phosphate does not.

AM fungi have been reported to improve plant growth and survival in disturbed environments, particularly by the improvement of phosphate uptake (Allen and Allen 1980; Stahl et al. 1988). However, the effects of AM on plant establishment were masked on Mount Koma; i.e., the frequencies of AM for most plant species did not change in the three elevational zones, whereas plant species abundances did change. A laboratory experiment with ^{32}P-labelled soil has shown that phosphate uptake by AM fungi is highly variable and can sometimes be negligible (Jakobsen et al. 2001). The frequency of AM did not change across elevation, suggesting that AM colonization level is not linked to nitrogen levels on Mount Koma. Further studies on interactions between AM fungi and plants, and between different AM fungi are required (Allen et al. 2003).

In contrast, ECM on trees increased in frequency with increasing elevation or fully colonized even at lower elevation, suggesting that tree establishment patterns were influenced by ECM more than by other classes. Even in the 1996 eruption blast area, *Salix reinii*, which increased in dominance with increasing elevation, was heavily ectomycorrhizal (Titus and Tsuyuzaki 2002). ECM occur with AM on the roots of *Betula platyphylla* var. *japonica* after disturbance (Hashimoto and Hyakumachi 2000), and there is apparent competition between ECM species (Yang et al. 1998). AM fungi working together often promote plant growth (van der Heijden et al. 1998), and mycorrhizal symbiosis is important for plant performance in N-limited successional environments (Aikio et al. 2000). Greater ectomycorrhizal diversity per se, rather than colonization or composition, increased mycorrhizal root biomass at the expense of shoot biomass and increased P uptake of *Betula populifolia* seedlings (Baxter and Dighton 2001). This may mean that mycorrhizal fungal communities manipulate seed plant communities over time, although further studies are needed to reveal the role of ECM and AM associations on the same host (Maremmani et al. 2003).

Plant species composition on Mount Usu after the 1977–1978 eruptions is close to that on Mount Koma (Tsuyuzaki 1989). For example, most of the woody species are observed on both the mountains. The common species on Mount Koma often establish in early successional stages on Japanese volcanoes (Yoshii 1939–1940). At the global level, species that can establish in the early stages of succession have similar vegetative, life history, and seed-biology traits (Tsuyuzaki and del Moral 1995). Some of these traits may be explained by the relationship between the plants and the mycorrhizal fungi, particularly for the ectomycorrhizal relationship when tree establishment is proceeding.

Appendix

Seed plant species used for evaluation of mycorrhizal colonization on Mount Koma, northern Japan.

When mycorrhizal frequencies observed on root segments were more than 20%, the classes are indicated by the following abbreviations: *ECT* ecto-, *AM* arbuscular, *ORCD* orchid, *ERIC* ericoid, *ARBT* arbutoid. Nomenclature of seed plants follows Ohwi and Kitagawa (1983).

Herbs and forbs: *Agrostis flacca* Hack. [Poaceae] AM. *Agrostis scabra* Willd. [Poaceae] AM. *Anaphalis margaritacea* (L.) Benth. et Hook. fil. var. *angustior* (Miq.) Nakai [Asteraceae] ECT, AM. *Artemisia japonica* Thunb. [Asteraceae] AM. *Calamagrostis langsdorffii* (Link) Trin. [Poaceae] AM. *Campanula lasiocarpa* Cham. [Campanulaceae] AM. *Carex oxyandra* (Franch. et Savat.) Kudo [Cyperaceae] AM. *Chimaphila japonica* Miq. [Pyrolaceae] ERIC. *Chimaphila umbellata* (L.) W. Barton [Pyrolaceae] ERIC. *Erigeron acris* L. [Asteraceae] AM. *Epilobium fauriei* Lev. [Onagraceae] AM. *Epilobium angustifolium* L. [Onagraceae] ECT, AM. *Geranium thunbergii* Sieb. et Zuc. [Geraniaceae] AM. *Hieracium umbellatum* L. var. *japonica* Hara [Asteraceae] AM. *Hypericum erectum* Thunb. [Hypericaceae] AM. *Hypochaeris radicata* L. [Asteracaee] AM. *Ixeris dentata* (Thunb.) Nakai var. *amplifolia* Kitam. [Asteraceae] AM. *Lotus corniculatus* L. var. *japonicus* Regel [Fabaceae] AM. *Luzula capitata* (Miq.) Nakai [Juncaceae] AM. *Miscanthsus sinensis* Anderss. [Poaceae] AM. *Oenothera biennis* L. [Onagraceae] AM. *Penstemon frutescens* Lamb. [Scrophulariaceae] AM. *Picris hieracioides* L. var. *glabrescens* (Regel) Ohwi [Asteraceae] AM. *Plantago asiatica* L. [Plantaginaceae] AM. *Polygonum sachalinense* Fr. Schm. [Polygonaceae] ECT, AM. *Polygonum weyrichii* Fr. Schm. [Polygonaceae] ECT, AM. *Pyrola incarnata* Fisch. [Pyrolaceae] ARBT. *Rumex acetosella* L. [Polygonaceae] AM. *Solidago virga-aurea* L. var. *leiocarpa* (Benth.) Miq. [Asteraceae] ECT, AM. *Spiranthes sinensis* (Pers.) Ames [Orchidaceae] ORCD.

Trees and shrubs: *Acer japonicum* Thunb. [Aceraceae] ECT, AM. *Alnus maximowiczii* Callier [Betulaceae] ECT. *Betula ermanii* Cham. [Betulaceae] ECT. *Betula maximowicziana* Regel [Betulaceae] ECT. *Betula platyphylla* Sukatchev var. *japonica* (Miq.) Hara [Betulaceae] ECT. *Carpinus cordata* Blume [Betulaceae] ECT, AM. *Elaeagnus pungens* Thunb. [Elaegnaceae] AM. *Gaultheria*

miqueliana Takeda [Ericaceae] ECT, ERIC. *Hydrangea paniculata* Sieb. [Saxifragaceae] ECT. *Larix kaempferi* (Lamb.) Carr. [Pinaceae] ECT. *Ledum palustre* L. var. *diversipilosum* Nakai [Ericaceae] ERIC. *Leucothoe grayana* Maxim. var. *oblongifolia* Nakai [Ericaceae] ERIC. *Pinus densiflora* Sieb. et Zucc. [Pinaceae] ECT. *Populus maximowiczii* Henry [Salicaceae] ECT. *Populus sieboldii* Miq. [Salicaceae] ECT. *Rhus tricocarpa* Miq. [Anacardiaceae] AM. *Rhododendron branchycarpum* D. Don [Ericaceae] ERIC. *Rubus parvifolius* L. [Rosaceae] AM. *Rubus phoenicolasius* Maxim. [Rosacaee] AM. *Salix bakko* Kimura [Salicaceae] ECT. *Salix integra* Thunb. [Salicaceae] ECT. *Salix reinii* Franch. et Savat. [Salicaceae] ECT. *Salix sachalinensis* Fr. Schm. [Salicaceae] ECT. *Sorbus commixta* Hedl. [Rosaceae] AM. *Tripetaleia paniculata* Sieb. et Zucc. [Ericaceae] ERIC. *Weigela hortensis* (Sieb. et Zucc.) K. Koch [Caprifoliaceae] ECT, AM.

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