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Arbuscular mycorrhizal distribution in relation to microsites on recent volcanic substrates of Mt. Koma, Hokkaido, Japan

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Abstract Mycorrhizae occur in most terrestrial ecosystems and are crucial to understanding community structure and function. However, their role in primary succession is poorly understood. This study examined the mycorrhizal colonization of six plant species in relation to microsite types on recent volcanic substrates on the summit of Mt. Koma, Hokkaido, Japan. The six microsites were flat, rill, near rock, *Carex* tussock, *Polygonum* patch and *Salix* patch. *Carex oxyandra* was nonmycorrhizal and *Agrostis scabra* and *Campanula lasiocarpa* were arbuscular mycorrhizal (AM) at all microsites examined. *Agrostis* AM colonization levels did not differ across microsites. Near rock *Campanula* roots contained significantly more hyphae than at flat and *Polygonum* patch microsites, and rill and *Carex* tussock *Campanula* more arbuscules than at *Polygonum* patches. *Penstemon frutescens* was found to be facultatively mycotrophic with AM colonization occurring in roots of *Penstemon* growing in *Carex* tussocks, *Polygonum* patches and near rocks. *Polygonum weyrichii* was found to be ectomycorrhizal. *Polygonum* located in rills and in *Polygonum* and *Salix* patches were more colonized than *Polygonum* in *Carex* patches. *Salix reinii* was heavily ectomycorrhizal.

Keywords Arbuscular mycorrhizae · Ectomycorrhizae · Microsites · Primary succession · Volcanoes

Introduction

The focus of this study is the distribution of arbuscular mycorrhizal (AM) colonization of plants in relationship to microsites on the summit of Mt. Koma, Hokkaido, Japan. The relationship between arbuscular mycorrhizae and microsites is important because microsites are critical to colonization dynamics in early primary succession (Titus and del Moral 1998b). This is because initial establishment in primary succession is usually localized in favorable microsites (Oner and Oflas 1977; Tsuyuzaki 1989; del Moral and Bliss 1993). Microsites differ in environmental characteristics at the scale of a seed or seedling and provide relief from stress. For example, rills may be moister due to longer snow retention and near-rock microsites offer more shade.

During primary succession on volcanic substrates, it is unlikely that pioneer species depend on mycorrhizae (Allen 1991; Titus and del Moral 1998a). Only nonhost and facultatively mycotrophic species could invade these sites. Obligate mycotrophic species would be prevented from establishing until a population of AM fungi was present in the soil, presumably having arisen in association with facultatively mycotrophic species. Seral sequences may reflect the mycorrhizal dependence of the colonizing species (Allen 1991). Thus, the pattern of AM distribution across an early primary successional landscape may regulate plant invasion patterns (Allen 1988).

Materials and methods

Mount Koma is an active andesite stratvolcano located in southwest Hokkaido, Japan (42°04′N, 140°42′E, 1,140 m elevation). The summit has a 2-km-wide horseshoe-shaped caldera opening to the east. At least 10 pumice-flow eruptions have been recorded since 1640, including major eruptions in 1640, 1856 and 1929 (Yoshii 1942). The 1-day eruption of 1929 produced 0.38 km^3 of ash and 0.14 km^3 of pumice. The resulting mudflows destroyed most of the vegetation on the slopes of the volcano. More recent small-scale eruptions, such as the latest in 1996 from which total tephra production was about 25,000 tons, covered <25 ha of the summit area, killing most of the vegetation (Ui et al. 1997). This study examines the recovering vegetation in the 1996 eruption impact area at 1,000 m elevation.

Mt. Koma is the centerpiece of the 9,083-ha Onuma Quasi-National Park established in 1958. Quasi-national parks are areas

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of great natural beauty but deemed to be secondary in comparison to national parks. Depending upon the management zone, activities such as forestry and recreational industries are or are not prohibited in a particular area within a park.

Climate is warm-cool temperate (mean annual temperature 11.6°C, mean maximum in August 24.6°C, mean minimum in January –6.9°C, mean annual precipitation 973 mm, winds primarily from the southwest) (Mori Climatological Observatory, 10 m elevation, 9 km from Mt. Koma). The elevation of the study area would create a much colder climate than at the Observatory. Climax forests in the region are composed of beech, maple and montane conifers (Kojima 1979; Uemura 1993), although vegetation on Mt. Koma has not attained climax.

The study area is open with scattered rock outcrops and gullies with a low cover of herbaceous plants, such as *Polygonum weyrichii*, *Campanula lasiocarpa*, *Carex oxyandra*, and *Penstemon frutescens*, and the shrub *Salix reinii* (Tsuyuzaki et al. 2000). In the study area, the vegetation has colonized primary successional substrates that are too deep for the plants to access pre-eruption soils. The exception is some *Polygonum weyrichii* individuals, which have resprouted from pre-eruption soils exposed in the bottom of deep erosion rills (Tsuyuzaki, unpublished data).

The substrate is composed almost exclusively of fine-grained silica ash (Ui et al. 1997). Levels of N, P, K and organic matter in the substrate are extremely low. The volcanic ejecta was initially alkaline but pH rapidly changed to slightly acidic (5–6.5) due to rain (H. Okada, Usu Volcano Observatory, personal communication).

The six microsite types in this study appear to differ in environmental characteristics on the spatial scale of an individual seed or seedling. These microsites are important to revegetation processes on harsh primary successional sites and were investigated to determine the distribution of AM fungal colonization of plants in the 1996 eruptive substrates. The microsites were as follows:

Flat

Level sites that have heterogeneous gravel, sand and silt substrates. This microsite type is the most common in the study area (Titus unpublished data).

Near-rock

Adjacent to rocks larger than 25 cm in diameter. On exposed surfaces, rocks protect seedlings from direct solar exposure, reduce wind and surface temperatures, and are more likely to trap seeds.

Rill

Small gullies <10 cm deep formed by erosive water action. These are linear habitats that marginally protect seedlings from wind, collect more snow, and have lower solar radiation (del Moral and Bliss 1993). Rill edges are more stable than rill bottoms and drainages. Rills and gullies collectively occupy ca. 30% of the study area (Tsuyuzaki, unpublished data)

Carex tussock

Tussocks of *Carex oxyandra* are common across the study site and are frequently colonized by conspecifics and other species. These tussocks are often colonized when they appear to be in a state of decline, i.e., the *Carex* in sections of the tussock has died.

Polygonum patch

Polygonum weyrichii forms patches across the study site. These are sometimes colonization sites.

Salix patch

Salix reinii, the most common shrub, forms extensive low shrubby mats across the study site that occasionally function as colonization sites.

From 30 July to 10 August the roots of five plants of six major pioneer species were collected from microsite types in which they occurred at different locations across the study site. Not every species was found in every microsite type; a total of 26 species-microsite combinations were collected. Species sampled were *Agrostis scabra*, *Campanula lasiocarpa*, *Carex oxyandra*, *Penstemon frutescens*, *Polygonum weyrichii* and Salix reinii.

Roots were washed, cleared and stained with trypan blue (Brundrett et al. 1994). Percent colonization of arbuscular mycorrhizal roots was estimated by placing a grid of 1-cm squares below a petri plate that contained the root sample under a dissecting microscope. Fifty locations where a root crossed a line on the grid were scored for mycorrhizae. The number of mycorrhizal "hits" is an estimate of the percent of the root colonized (Brundrett et al. 1994). Many samples were examined under higher power to ascertain that the fungus was indeed AM. Vesicles, arbuscules and hyphae were recorded. Percentage ectomycorrhizal colonization was calculated as the number of active root tips divided by the number of total root tips (Gehring and Whitham 1994).

Percent colonization data were arcsine transformed to improve normality and homoscedasticity. Data were analyzed by one-way ANOVA to compare mycorrhizal colonization across microsites (Zar 1984; Norusis 1993). Post-hoc tests were conducted with Tukey's honestly significant difference test. In addition, percent colonization data of biotic and abiotic microsites were contrasted by the *t*-test.

Results

Species differed in habitat preference for establishment. *Agrostis* was not found in the biotic microsites. *Campanula* and *Penstemon* were frequent in all microsites except for *Salix* patches. *Polygonum* established in all microsites examined. *Salix* was most common in large patches.

Carex was nonmycorrhizal in all sites. *Agrostis* and *Campanula* were found to be mycorrhizal at all microsites when present (Table 1). *Agrostis* AM colonization levels did not differ across microsites. Near-rock *Campanula* roots contained significantly more hyphae than did *Campanula* in near rock and *Polygonum* patches, and rill and *Carex* tussock *Campanula* roots contained more arbuscules than did *Campanula* roots in *Polygonum* patches. *Penstemon* was found to be facultatively mycotrophic with AM colonization occurring at the biotic microsites and near rocks. *Penstemon* roots at near-rock sites contained significantly more hyphae than did *Penstemon* roots at flat and rill sites.

Polygonum and *Salix* were found to be exclusively ectomycorrhizal (Table 2). *Polygonum* roots at rill and *Polygonum* and *Salix* patches were more colonized than *Polygonum* at the other microsites. *Salix* was heavily ectomycorrhizal in *Salix* patches.

Campanula, *Penstemon* and *Polygonum* plants occurred in both biotic and abiotic microsites. No significant differences were found between biotic and abiotic sites in mycorrhizal colonization levels of AM structures or ectomycorrhizae (results not shown).

Table 1 Percent arbuscular mycorrhizal (*AM*) colonization of plant species collected from microsites on Mount Koma, Hokkaido, Japan (mean ± standard deviation, *n*=5). Significance was tested by one-way ANOVA on arcsine transformed percent data. For the structures where significant differences were found, the microsites with different superscripts are significantly different by Tukey's post-hoc test at $P \leq 0.05$. *Carex oxyandra* is not included because all colonization values were zero. *Salix* patches are also not included because none of these AM species were detected in *Salix* patches

Microsite	*Agrostis scabra*			*Campanula lasiocarpa*			*Penstemon frutescens*		
	% Hyphae	% Arbuscules	% Vesicles	% Hyphae	% Arbuscules	% Vesicles	% Hyphae	% Arbuscules	% Vesicles
Flat	31±13	7±5	2±2	18 ± 7^{a}	5 ± 3^{ab}	1±1	0^{a}	0	0
Rill	33±16	10±7	2±2	36 ± 17^{ab}	12 ± 6^{b}	2±2	0^{a}	0	0
Near rock	13±10	6±4	3±3	46 ± 14^{b}	9 ± 3^{ab}	3±2	10 ± 3^{b}	2±2	0.4±0.9
Carex tussock	–	–	–	32 ± 13^{ab}	12 ± 5^{b}	2±2	4 ± 5^{ab}	0	0
Polygonum patch	–	–	–	15 ± 10^{a}	4 ± 4^{a}	1±2	6 ± 9^{ab}	4±9	0
F	3.381	0.542	0.256	5.221	4.119	0.683	3.932	0.951	–
P	0.068	0.595	0.778	0.005	0.014	0.612	0.016	0.455	–

Table 2 Percent ectomycorrhizal colonization of plant species collected from microsites on Mount Koma, Hokkaido, Japan (mean ± standard deviation, *n*=5). Significance was tested by one-way ANOVA on arcsine transformed percent data. Different superscripts are significantly different by Tukey's post-hoc test at $P \leq 0.05$

Microsite	*Polygonum weyrichii*	*Salix reinii*
Flat	8 ± 6^{ab}	–
Rill	13 ± 4^{b}	–
Near rock	10 ± 3^{ab}	–
Carex tussock	4 ± 3^{a}	–
Polygonum patch	12 ± 3^{b}	–
Salix patch	12 ± 2^{b}	80±8
F	3.956	–
P	0.009	–

Discussion

Some of the pioneer species examined differed in mycorrhizal colonization depending on the microsite colonized. However, unlike Mount St. Helens the biotic microsites did not harbor the more heavily colonized AM and ectomycorrhizal plants. Most AM plant species that colonize primary successional substrates appear to be facultatively mycotrophic (Allen 1991; Titus and del Moral 1998a; Titus et al. 1998). This status supports a broad range of tolerance to AM, from rarely mycorrhizal to nearly always colonized depending upon the species, neighboring species and site conditions (Boerner 1992). In this study, *Penstemon* was the only species that was clearly facultatively mycotrophic. The other species surveyed were mycorrhizal in all microsites in which they were found, except for *Carex*, which appeared to be nonmycotrophic.

After volcanic eruptions, certain microsite types increase in organic matter and nutrient content faster than others. For example, biotic microsites accumulate organic matter and N from the plant that comprises the microsite and by trapping windblown material. Likewise rocks and rills trap windblown material and the soils at these microsites increase in organic matter and nutrients faster than flat sites (del Moral and Bliss 1993; del Moral and Wood 1993; Titus and del Moral 1998b; Titus et al. 1998). However, the nutrient accumulation process is slow and nutrient levels across the Mt. Koma study site are likely to still be extremely low.

After the 1996 eruption, the newly emplaced volcanic substrates on Mt. Koma would have been free of AM fungal propagules (Allen 1988; Titus et al. 1998). The AM and ectomycorrhizal colonization detected in this study show that dispersal and erosional forces have brought mycorrhizal propagules to the landscape. In addition, mycorrhizal plant rootstock of *Polygonum weyrichii* survived below the newly emplaced substrate and grew up through this new substrate or were exposed by gully formation (Tsuyuzaki, unpublished data). The roots of this ectomycorrhizal species could serve as a source of mycorrhizal propagules (Antos and Zobel 1985; Tsuyuzaki 1989). On Mount St. Helens, the invasion of AM propagules across the primary successional landscape is sporadic as some microsites contain more mycorrhizal propagules and more heavily colonized plants than do other microsites (Titus et al. 1998). The primary successional landscape on Mt. Koma is <25 ha in extent (Ui et al. 1997). Dispersal barriers to AM fungal propagules would not be great and it is assumed that after 5 years AM propagules would have dispersed across the devastated landscape from the surrounding vegetation (Allen 1987). Due to small spore size, dispersal barriers for ectomycorrhizal fungi would be nonexistent and dispersal of ectomycorrhizal propagules into the study site would be rapid. For ectomycorrhizal plants establishment may result from a simultaneous plant and ectomycorrhizal fungal invasion. For AM plants it may be that the volcanic substrates are initially colonized by facultatively mycotrophic plants that are initially nonmycorrhizal and these plants are subsequently colonized by AM fungi (Doerr et al. 1984; Allen 1987, 1988, 1991; Gange et al. 1990; Boerner 1992).

Carex spp. are generally considered to be nonhosts (Powell 1975; Anderson et al. 1984; Harley and Harley 1987; Miller et al. 1999), although mycorrhizal wetland *Carex* have been found (Turner et al. 2000), and mycorrhizal upland *Carex* spp. have been found in the alpine (Read and Haselwandter 1981; Allen et al. 1987; Fontenla et al. 2001), and in grasslands (Read et al. 1976; Miller et al. 1999), and a few AM *Carex mertensii* plants were found at Mount St. Helens (Titus et al. 1998). Dark septate intracellular colonizations have been found in *Carex* species (Treu et al. 1996; Miller et al. 1999). No arbuscular mycorrhizal or dark septate fungal colonization were observed in *Carex oxyandra*.

Some *Agrostis* species appear to be important in primary succession in harsh environments. This is because they colonize the initially nonmycorrhizal environments, subsequently become mycorrhizal, and then provide a source of AM inoculum for later successional species (Titus et al. 1998; Greipsson and El-Mayas 1999). *Agrostis scabra* was found to be facultatively mycotrophic on Mount St. Helens with the level of AM colonization differing across different microsites (Titus et al. 1998). However, on Mt. Koma the level of AM colonization was similar across the three microsites where the species was found.

Of the *Campanula* species that have been surveyed for mycorrhizal colonization most are AM and a few appear to be nonmycotrophic (Harley and Harley 1987). *Campanula lasiocarpa* was found to be AM in all microsite types where it was present. Hyphae were less abundant in *Campanula* roots from flat sites, similar to observations of other species on Mount St. Helens (Titus et al. 1998), but unlike Mount St. Helens the biotic sites did not have more heavily colonized roots. The ectomycorrhizae of *Polygonum* patches may suppress AM colonization of *Campanula* in these patches. *Campanula* are, however, fairly common in *Polygonum* patches so the lower hyphal and arbuscular levels were not impacting the colonization of this microsite by *Campanula* in a major way.

Scrophulariaceae is in a family with a wide range of mycotrophic states (Harley and Harley 1987; Fontenla et al. 2001). *Penstemon cardwellii*, a pioneer species on Mount St. Helens, was found to be facultatively mycotrophic with the level of AM colonization varying depending upon the microsite in which the plant was located (Titus et al. 1998). In this present study, a similar pattern was observed with the species being nonmycorrhizal in flat and rill microsites and mycorrhizal in the biotic microsites. However, AM colonization levels in biotic and abiotic microsites were not significantly different because of the AM colonization levels of *Penstemon* in near-rock microsites. Neither of the two biotic microsites were AM, which may account for the relatively low AM colonization levels at these sites.

Many *Polygonum* species appear to be nonmycotrophic (Harley and Harley 1987; Rickerl et al. 1994; Treu et al. 1996; Ishi et al. 1998; Titus et al. 1998), some species are AM (Harley and Harley 1987), and some species have been found to be ectomycorrhizal (Treu et al. 1996; Massicotte et al. 1998). In this study, *Polygonum weyrichii* was ectomycorrhizal. *Polygonum* growing amongst ectomycorrhizal species, i.e., with itself or with *Salix*, exhibited higher ectomycorrhizal colonization levels than did *Polygonum* growing in nonmycotrophic *Carex* tussocks. This may be because prior presence of the fungi resulted in higher colonization. Ectomycorrhizal colonization of *Polygonum* was also high in rill sites where erosion may be causing pre-eruption soil to become available to the roots. Presumably, *Polygonum* have accessed pre-eruption soils only in rill microsites (Tsuyuzaki, unpublished data).

Salix species can be either ectomycorrhizal or AM (Harley and Harley 1987; Lodge and Wentworth 1990; Jones et al. 1991; Dhillon 1994; Treu et al. 1996; van der Heijden and Vosátka 1999). *Salix reinii* was heavily ectomycorrhizal and no AM colonization was found. Due to the greater dispersal abilities of ectomycorrhizal fungi *Salix* species are often found to be ectomycorrhizal in primary successional environments such as glacial forelands (Jumpponen et al. 1999). AM plant species in this study were not detected in *Salix* patches, whereas the ectomycorrhizal *Polygonum* was common. This may be because of competition from the dense *Salix* growth; however, it may be that the ectomycorrhizal fungi assist in competitive exclusion of AM species.

Microsites were found to have smaller effects upon mycorrhizal colonization levels on Mt. Koma than on Mount St. Helens. This may be due to the much smaller scale of the blast on Mt. Koma, which did not present AM fungi with vast dispersal distances. Also, higher mycorrhizal colonization levels were not observed in biotic microsites. Flat sites, which do not trap propagules well, did not show lower colonization levels in *Campanula* and *Penstemon*. The ectomycorrhizal microsites did appear to cause a reduction in AM colonization in *Campanula*. In some cases, higher colonization levels were observed in rills, where erosion may provide access to propagules and near rock, which are effective at trapping propagules. To a seedling, biotic microsites may be very different from each other; for example, *Carex* tussocks would most likely be very different microsites than a *Polygonum* patch, likewise for abiotic microsites a rill is a very different microsite than a near-rock or flat site. This is supported by the lack of certain plant species in certain microsite types; for example, *Agrostis* was not found in *Carex* tussocks or *Polygonum* patches. Differences in mycorrhizal propagules would be only one of many differences between microsites; other factors such as seed trapping ability, soil moisture and nutrients, and light availability would affect plant distribution across microsites.

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