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# Nurse-Plant Effects of a Dwarf Shrub on the Establishment of Tree Seedlings in a Volcanic Desert on Mt. Fuji, Central Japan

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## Abstract

We investigated vegetation structure and microenvironments on bare volcanic soil covered by scoria above the forest limit on Mt. Fuji, central Japan, to evaluate the effects of patches of a pioneer dwarf shrub (*Salix reinii*) on the establishment of early successional tree seedlings (*Larix kaempferi*). We analyzed species distribution patterns and the associations among them, and compared the performance (growth and survivorship) of *Larix* seedlings and the local environment (temperature, solar radiation, soil surface stability, soil moisture, and nitrogen) inside and outside *Salix* patches. *Larix* displayed significantly clumped distribution, and the clumping was apparently associated with the preferential occurrence of *Larix* in *Salix* patches. *Salix* patches moderated severe microenvironmental factors, such as drought, high temperature, and movement of the soil surface. *Salix* patches promoted increased height and decreased root:shoot ratio, but not higher rate of biomass accumulation in *Larix* seedlings. Survival rate of *L. kaempferi* inside *Salix* patches was higher than that outside patches at the younger stage, but it was lower at the older stage after *L. kaempferi* emerged from the *Salix* crown. The results indicate *S. reinii* enhances seedling establishment and survival of young *L. kaempferi*, but may compete with it at later stages. The overall net effect of *Salix* patches on *L. kaempferi* is positive, and therefore *S. reinii* appears to accelerate succession from scoria bare land to pioneer woodland.

## Introduction

The nurse-plant effect is a positive interaction in which individuals of one plant species facilitate the establishment and survival of another species by ameliorating the local environment (e.g., McAuliffe, 1988; Valiente-Banuet and Ezcurra, 1991; Franco-Pizana et al., 1996; Walker et al., 2003). Facilitation is usually considered a part of succession (Connell and Slatyer, 1977), but may be especially important in harsh abiotic environments (Bertness and Callaway, 1994; Callaway, 1995; Callaway and Walker, 1997; Holmgren et al., 1997; Flores and Jurado, 2003). In high-elevation plant communities, positive interactions between species are more prevalent than negative interactions (Kikvidze, 1996; Callaway, 1998; Kikvidze and Nakhutsrishvili, 1998; Nuñez et al., 1999; Arroyo et al., 2003; Olofsson, 2004; Kleier and Lambrinos, 2005). In primary succession on bare volcanic soil, an early colonizing plant can provide favorable conditions for the establishment of other species (Veblen et al., 1977; Hirose and Tateno, 1984; del Moral and Wood, 1993; Grishin et al., 1996; Adachi et al., 1996; Titus and Tsuyuzaki, 2003; Uesaka and Tsuyuzaki, 2004).

In subalpine volcanic bare land on Mt. Fuji in central Japan, primary succession is still in progress, and the forest limit appears to be ascending (Tohyama, 1968; Masuzawa, 1985). However, harsh environmental conditions such as an unstable soil-surface substratum (deposited scoria), low soil water availability (Maruta, 1983, 1996), and low soil nutrient concentrations (Hirose and Tateno, 1984; Tateno and Hirose, 1987; Chiba and Hirose, 1993) are likely to delay succession by inhibiting plant establishment, growth, and survival. Facilitation is therefore potentially important in the colonization of these sites by some plant species (Hirose

and Tateno, 1984; Masuzawa, 1985; Adachi et al., 1996). *Larix kaempferi* is the most dominant treeline species that colonizes volcanic bare land (Ohsawa, 1984). The seedlings and saplings of *L. kaempferi* occur not only on bare scoria but also in patches of the dwarf shrub *Salix reinii*, which dominates in bare land just above the forest limit. *Salix* patches promote the formation of ectomycorrhizae in tree seedlings through infection of the fungi species associated with *Salix* on Mt. Fuji (Nara and Hogetsu, 2004). On the volcanic bare land of Mt. Koma in northern Japan, *Salix* patches facilitate establishment of herb and grass species by ameliorating stressful environmental conditions (Uesaka and Tsuyuzaki, 2004). Here we hypothesize that *Salix* patches act as nurse plants for *Larix* seedlings and/or saplings during the early stages of primary succession on the subalpine volcanic bare land of Mt. Fuji.

We investigated spatial distribution patterns of species on subalpine volcanic bare land and compared the growth and survival of *Larix* seedlings inside and outside of *Salix* patches to investigate the facilitative effects of *Salix* on *Larix* seedlings. We also investigated the capacity of *Salix* to ameliorate climatic extremes within its patches and, in this way, to facilitate the establishment and survival of *Larix* seedlings.

## Materials and Methods

### STUDY SITE

This study was conducted in a volcanic desert above the forest limit on the north-facing slope of Mt. Fuji (35°23′N, 138°44′E; 2400 m a.s.l.). Mt. Fuji (3776 m a.s.l.), a typical strato-volcano in central Japan, has erupted at least 10 times during recorded

history, most recently in 1707. The forest limit on the north-facing slope occurs at 2300–2400 m a.s.l., which is lower than that on high non-volcanic mountains in central Japan. The mean slope inclination of the study site is ca. 18°. The ground surface of the site is covered with a thick basaltic scoria layer and is very unstable. Soil water availability is low due to high drainage in coarse textured soils. Plants are exposed to strong prevailing winds from the west.

Climatic data from the base of Mt. Fuji (860 m a.s.l.; Kawaguchiko Meteorological Observatory, 1971–2000) indicate that mean annual precipitation is 1508 mm and that monthly mean temperatures range from 21.8°C in August to −0.8°C in January. Estimated monthly mean temperatures at 2400 m a.s.l., based on a mean lapse rate of −0.6°C per 100 m increase in elevation, range from 12.6°C in August to −10.0°C in January.

There was sparse and short vegetation at the site, representing an early stage of primary succession. Several tree or shrub species (e.g., *L. kaempferi*, *Betula ermanii*, *Alnus crispa* ssp. *maximowiczii*, and *S. reinii*), as well as several herbs (e.g., *Pleuropteropyrum weyrichii* var. *alpinum* [syn. *Polygonum weyrichii* var. *alpinum*], *Arabis serrata*, and *Stellaria japonica*), occurred at the site. *Salix reinii* was the most dominant species in the vegetation and had developed into low, circular patches (ca. 10 cm in height and <3 m in diameter) by layering.

## FIELD MEASUREMENTS OF PLANTS

A plot was established in the scoria desert just above the forest limit in the summer of 1999 (plot A, 20 m × 20 m = 400 m$^2$). All plants in the plot were marked with numbered tape and were mapped. The height and major and minor axes of the crowns were measured for all individuals, and the basal diameter was measured for trees. Plant cover (percentage of ground area occupied) was determined for each species from the projection area of the plant crown, which was calculated as an ellipse from the major and minor axes. The ages of *L. kaempferi* were determined from bud-scale scars on the main stems. All measurements were performed after mid-August, when the current-year growth of plants had nearly ceased.

Another plot was established in 1999 in the neighborhood of plot A (ca. 30 m away) to provide more data for analyses of the association between *S. reinii* and *L. kaempferi* (plot B, 15 m × 25 m = 375 m$^2$). This plot was not square to avoid gullies and large rocks on the ground. Similar measurements were made in plot B, but only for *S. reinii* and *L. kaempferi*.

In both plots, *S. reinii* and *L. kaempferi* were resurveyed in 2005 to measure the survival rates of *L. kaempferi*.

## SAMPLING OF L. KAEMPFERI

To compare growth patterns and morphology between the microhabitats, *Larix* individuals less than 8 years old were sampled in early September 1999, both inside and outside *Salix* patches around the two plots. In each habitat, eight or more individuals were collected for each age class (0-, 1-, 3-, 5-, and 6-year-old), but few 2-, 4-, and 7-year-old plants were collected because they were rare. For each plant sampled, the length and basal diameter of the trunk were measured. Subsequently, each plant was divided into leaves, stems, and roots, and the dry masses of these parts were measured after drying in an oven at 70°C for 72 h. The concentration of total nitrogen in these samples was determined using an automatic nitrogen-carbon analyzer (Sumigraph NC-900, Sumika Chemical Analysis Service, Japan).

## MICROENVIRONMENT MEASUREMENTS

Light and temperature conditions were examined inside and outside a *Salix* patch in plot A. The photosynthetically active photon flux density (PPFD) was measured on the ground using photon sensors (IKS-27, Koito Industries, Japan). Temperature was measured at the soil surface and underground (5 cm deep) using copper-constantan thermocouples (type K, Hayashi-Denko, Japan). Two sensors were used for each measurement and at each site. The PPFD and temperature measurements were taken at 10-min intervals throughout the growing season in 2000, and the data were stored in a data logger (DS-36IC2, LEAP Science, Japan).

On a sunny day after several rainless days (4 August 2000), samples of surface soil (100 cm$^2$ in area and 5 cm in depth) were collected using a steel can inside and outside of six *Salix* patches around the plots. Each sample was immediately sealed in a polyethylene bag to avoid evaporation and was transported in an insulated box back to the laboratory. The fresh weights of these samples were measured as quickly as possible. For a fraction of each soil sample, concentrations of NO$_3$-N and NH$_4$-N were determined colorimetrically after extraction with distilled water and 1.5 N KCl solution, respectively. The air-dried weight was measured after drying in the laboratory and was used to determine moisture content, and the oven-dried weight was measured after drying at 70°C for more than 72 h. The concentration of total nitrogen in these samples was determined using an automatic nitrogen-carbon analyzer (Sumigraph NC-900).

The stability of the soil-surface substratum inside and outside *Salix* patches was estimated by a painting method. Three circles, 15 cm in diameter, were drawn with an oil-based spray paint on the ground inside and outside of five *Salix* patches at the end of the growing season in 1999. The initial coverage of the painted area in each circle was defined as 100% of the total area of the circle. After one year, the percent coverage of the painted area remaining in the original circles was judged using a 1-cm-mesh frame measuring 10 × 10 cm. This value was compared between the two microhabitats as a measure of the stability of the soil-surface substratum.

## STATISTICAL ANALYSES

The spatial distribution patterns of each species were quantified using Ripley's *K*-function, $K(t)$ (Ripley, 1977). To facilitate interpretation of the spatial distribution, the *K*-function was transformed into the *L*-function, $L(t) = [K(t)/\pi]^{1/2} - t$, where $t$ was neighbor's distance, as suggested by Ripley (1977). The *L*-function, $L(t)$, is plotted as a function of $t$. When individuals of a species are randomly distributed, the values of $L(t)$ are expected to be zero. A departure from zero indicates a non-random distribution, with positive values indicating clumping, and negative values indicating regularity. To test the significance of departures from a random distribution, we evaluated the 95% confidence intervals from 1000 Monte Carlo simulations. Spatial pattern analyses were conducted with the Splancs Package (Rowlingson and Diggle, 1993) in the R-environment (R Development Core Team; http://www.R-project.org).

To evaluate species associations between *S. reinii* and each of the five dominant species, we looked for significant differences between the frequency with which a species occurred inside and outside *Salix* patches using a randomization test (Kikvidze et al., 2001; Arroyo et al., 2003). From the total frequency of a species and the area covered by *S. reinii*, we generated 10,000 random frequency values of that species inside and outside of *Salix*

TABLE 1

**Abundance (number of individuals) and cover (% of ground surface area occipied by plant canopy) of species in plots A and B. All species were examined in plot A, and two dominant species in plot B.**

| Species | Abundance | Cover (%) |
|---|---|---|
| Plot A (400 m$^2$) | | |
| *Salix reinii* | 61 | 4.81 |
| *Larix kaempferi* | 106 | 2.92 |
| *Betula ermanii* | 59 | 0.47 |
| *Alnus crispa* subsp.*maximowiczii* | 8 | 0.63 |
| *Pleuropteropyrum weyrichii* var. *alpinum* | 286 | 2.51 |
| *Stellaria japonica* | 209 | 0.29 |
| *Arabis serrata* | 137 | 0.06 |
| *Artemisia pedunculosa* | 22 | 0.06 |
| *Deschampsia flexuosa* | 1 | 0.002 |
| Plot B (375 m$^2$) | | |
| *Salix reinii* | 145 | 14.96 |
| *Larix kaempferi* | 287 | 1.34 |

patches. Then we calculated the probability that the observed frequency was generated by chance. The randomization test was conducted in the R-environment (R Development Core Team; http://www.R-project.org).

We tested whether survival rates of *L. kaempferi* differed between microhabitats with Fisher's exact probability test in the R-environment (R Development Core Team). Significant differences in plant size and morphology, nitrogen concentration, and environmental parameters between microhabitats were tested with a one-way ANOVA or Mann-Whitney *U* test (StatView 5.0, SAS Institute Inc.).

## Results

### PLANT DISTRIBUTION PATTERNS

Four woody and five perennial herb species occurred in plot A. The abundance (number of individuals) and cover (percentage of ground area occupied) of each species are shown Table 1. In plot A, *S. reinii* occupied the largest ground cover of all species. The most abundant herb was *P. weyrichii* var. *alpinum* (a dominant herb above the forest limit). *Larix kaempferi* was the most abundant tree. Both *S. reinii* and *L. kaempferi* had higher abundance in plot B than in plot A (Table 1). Current-year seedlings of *L. kaempferi* occurred in small numbers in late summer, whereas seedlings of other species were rarely observed. Six species, including *S. reinii* and *L. kaempferi*, were adequately abundant for distribution pattern analyses.

The index of distribution pattern, $L(t)$, was examined for the six abundant species in plot A and for *S. reinii* and *L. kaempferi* in plot B (Fig. 1). Three species (*L. kaempferi*, *B. ermanii*, and *S. japonica*) had significantly clumped distributions over all scales examined, and *A. serrata* also had a clumped distribution at smaller scales. In contrast, *S. reinii* had a random distribution over all scales in plot B and at the smaller and larger scales in plot A. Further, *P. weyrichii* var. *alpinum* also had a more random than clumped distribution at the smaller and larger scales.

Statistical associations between *L. kaempferi* and three herb species and *Salix* patches are shown in Table 2. With the exception of *P. weyrichii* var. *alpinum*, each species was significantly associated with *Salix* patches (randomization test, $P < 0.05$).

### GROWTH, NITROGEN CONTENT, AND SURVIVAL RATE OF *L.* KAEMPFERI

Figure 2 shows the sizes and morphology of *Larix* individuals of different ages collected from *Salix* patches and from nearby bare ground. The length of the main stem, which was nearly equivalent to plant height, was significantly greater inside than outside the patches for most size classes (ANOVA, $P < 0.05$ or 0.01; Fig. 2a). However, the basal stem diameter was smaller inside than outside the patches for 0- and 1-year-old seedlings (ANOVA, $P < 0.05$ or 0.01; Fig. 2b). The mean dry mass of individuals was not significantly different between the two microhabitats for any age examined (Fig. 2c). In 5- and 6-year-old plants, the root:shoot ratio, which indicates the relative allocation of dry matter to below- and aboveground parts, was significantly lower inside than outside the patches (Mann-Whitney *U* test, $P < 0.05$ or 0.01; Fig. 2d). The root:shoot ratio for younger plants did not differ between the microhabitats.

The leaf nitrogen concentration of *Larix* plants of each age was examined in *Salix* patches and bare sites. There were no significant differences in leaf nitrogen concentration between microhabitats for most of the age classes examined, except for 1-year-old plants, in which the leaf nitrogen concentration was lower inside than outside *Salix* patches (Mann-Whitney *U* test, $P < 0.01$; mean ± SE, 1.59 ± 0.07% in patches, 2.00 ± 0.10% in bare sites).

Table 3 shows the survival rates of *L. kaempferi* for 6 years, from 1999 to 2005, inside and outside of *Salix* patches in plots A and B, where all plants were divided into two age classes (younger plants, 0- to 5-year-old; and older plants, 6-year-old and older). There were no significant differences in survival rate between microhabitats in each plot. However, when data from the two plots were pooled, significant differences were detected in both the younger and older plants; the survival rate inside patches was significantly higher than that outside of patches in younger plants, and in contrast it was significantly lower in older plants (Fisher's exact probability test, $P < 0.05$). Significant differences were not detected when both age classes were pooled (Table 3). As for distribution pattern of each age group of *Larix*, both the younger group and older group were significantly associated with the patches not only in 1999 but also in 2006 (randomization test, $P < 0.01$).

### MICROENVIRONMENT INSIDE AND OUTSIDE OF SALIX *PATCHES*

The daily cumulative PPFD inside a patch in early June was similar to that on bare ground and then decreased until the end of June, in conjunction with leaf opening and expansion in *S. reinii* (Fig. 3). The ratio of PPFD inside the patch to that on bare ground was nearly constant throughout July and August (ca. 38%). The mean PPFD between 10 and 14 h during July and August was ca. 200 µmol m$^{-2}$ s$^{-1}$ on cloudy days and ca. 600 µmol m$^{-2}$ s$^{-1}$ on sunny days on the ground in the *Salix* patch.

Daily changes in the soil-surface temperature inside the patch were smaller than those on bare ground during the growing period (Fig. 4a). The daily maximum soil-surface temperature on sunny days on bare ground was occasionally more than 40°C, and averaged approximately 30°C during the growing season. Within the patch, the daily maximum temperatures were approximately 10°C lower during this period. However, there were no differences in daily minimum temperatures between sites (Fig. 4a). Daily and seasonal changes in belowground temperatures (5 cm deep) were
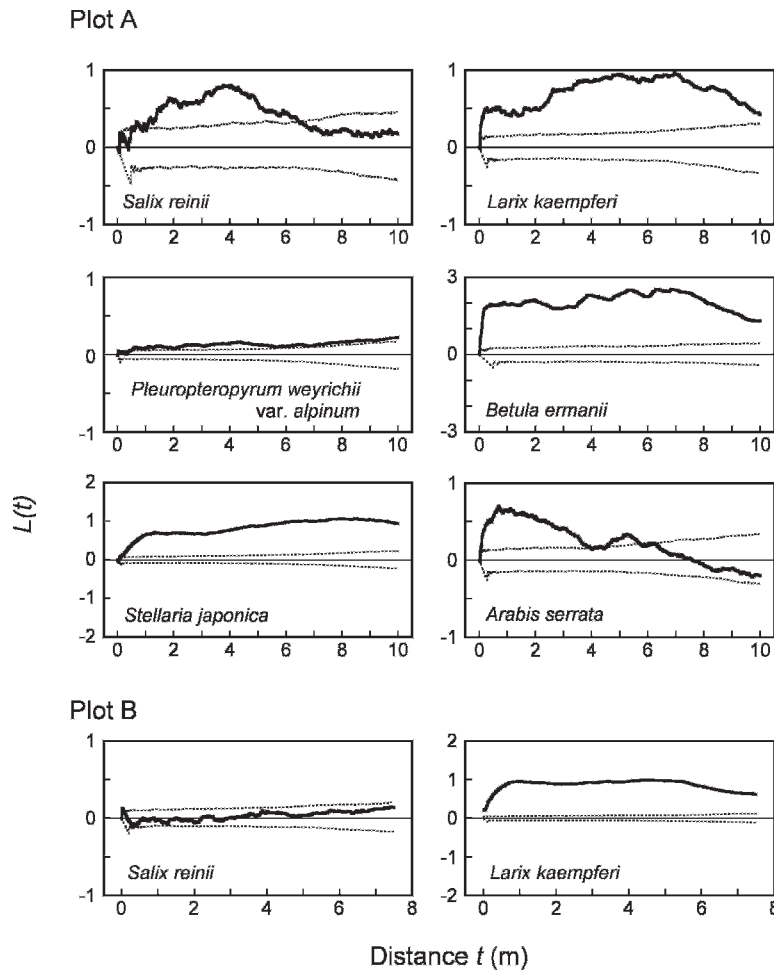
## Plot A



FIGURE 1. Spatial analysis of the distribution pattern of six species in plot A (20 m × 20 m) and two species in plot B (25 m × 15 m). The plot of the derived statistic of Ripley's $K$-function $[L(t) = [K(t)/\pi]^{1/2} - t]$ versus $t$ reveals spatial patterns at increasing values of the neighbor's distance $t$. Positive values of $L(t)$ indicate clumping and negative ones mean regularity. Dotted lines give 95% confidence intervals for complete spatial randomness from 1000 randomizations.

smaller than those in soil-surface temperatures, and differences between sites were relatively small (Fig. 4b).

On a sunny summer day, the soil-surface scoria substratum (0–5 cm depth) in the *Salix* patches contained significantly more moisture and total nitrogen than in bare sites, yet there were no differences in concentrations of $NO_3$-N and $NH_4$-N between the microhabitats (Table 4). Owing to scoria movement, the circles painted on the soil surface lost their shape both inside the patches and in bare sites. After one year, the soil surface area covered by paint in the original circles had decreased from 100% to 58.9% in patches and to 33.7% on bare ground (Table 4). The difference between the microhabitats was statistically significant (Mann-Whitney $U$ test, $P < 0.05$, $n = 15$). Thus, the soil surface inside patches was more stable than that in bare sites.

## Discussion

### DISTRIBUTION PATTERNS AND INTERACTIONS BETWEEN PLANTS

The spatial distribution patterns of wind-dispersed pioneer plants that have colonized bare land may depend primarily on the spatial heterogeneity of the site. In early successional vegetation on Mt. Sakurajima, an active volcano in southern Japan, Tagawa (1965) observed a clumped distribution of pioneer plants, which he attributed to the heterogeneous rocky ground. In contrast, the two dominant pioneer species (*S. reinii* and *P. weyrichii* var. *alpinum*) on the bare scoria on Mt. Fuji had random distributions at some of the scales examined. These species have typical wind-dispersed seeds. The more homogeneous conditions of the scoria desert

### TABLE 2

Density at which species were found inside and outside of *Salix* patches. *P* values are from randomization test. The test was made for four abundant species in plot A, and for *L. kaempferi* in plot B.

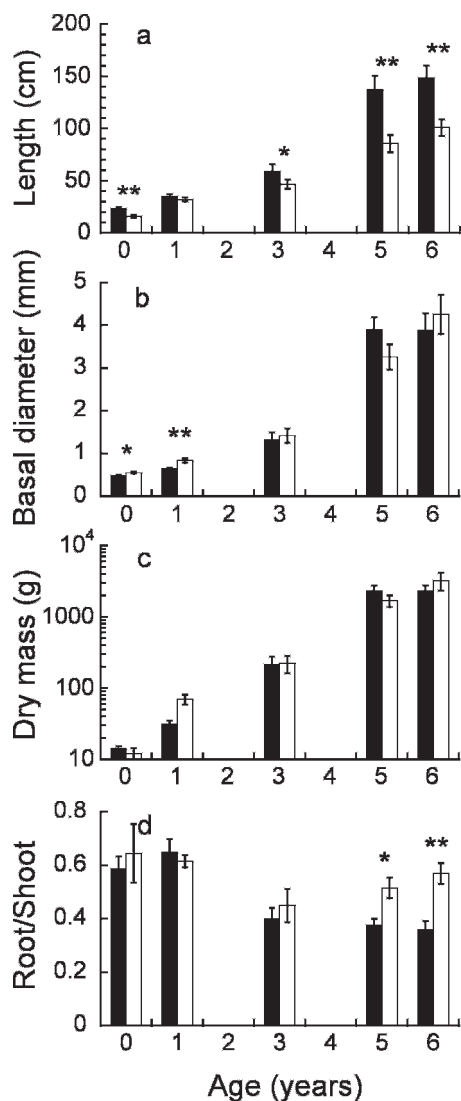| Species | Area examined (m²) | Number of individuals | | Density (m⁻²) | | $P$ |
| --- | --- | --- | --- | --- | --- | --- |
| | | inside patch | outside patch | inside patch | outside patch | |
| *Stellaria japonica* | 400 | 21 | 188 | 1.09 | 0.49 | 0.002 |
| *Arabis serrata* | 400 | 35 | 102 | 1.82 | 0.27 | <0.001 |
| *Pleuropteropyrum weyrichii* var. *alpinum* | 400 | 13 | 273 | 0.68 | 0.72 | 0.638 |
| *Larix kaempferi* | 400 | 18 | 88 | 0.94 | 0.23 | <0.001 |
| *Larix kaempferi* | 375 | 84 | 203 | 1.49 | 0.64 | <0.001 |

**FIGURE 2.** Stem length (a), basal diameter (b), biomass (c), and root:shoot ratio (d) of 0-, 1-, 3-, 5- and 6-year-old *Larix* individuals inside and outside *Salix* patches. Mean and SE are displayed in each panel ($n$ = 8 to 20). Significant differences between microhabitats are shown by asterisks (ANOVA or Mann-Whitney *U*-test); *, $P < 0.05$; **, $P < 0.01$.
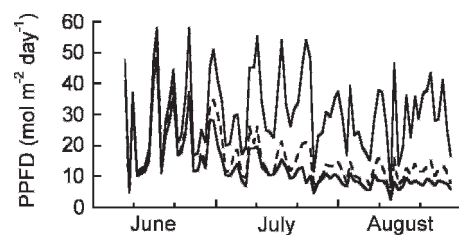


**FIGURE 3.** Seasonal changes in daily cumulative photosynthetically active photon flux density (PPFD) on the soil surface in the *Salix* patches and bare site. The upper solid line indicates the data in bare site, and the broken line and lower solid line indicate the data in the patches, respectively.

relative to rocky ground appear to allow for a random distribution. Several species other than *S. reinii* and *P. weyrichii* var. *alpinum* were clumped, even on scales at which *S. reinii* was randomly distributed. This observation is likely related to the fact that *L. kaempferi*, *S. japonica*, and *A. serrata* occurred more frequently in *Salix* patches than in bare soil (Table 2). These distribution patterns suggest that *Salix* patches have a facilitative effect on the establishment of later colonizers.

A similar distribution pattern has been observed on bare scoria at lower altitudes on the southeastern slope of Mt. Fuji. There, patches of *Reynoutria japonica* (syn. *Polygonum cuspidatum*), the dominant pioneer species, serve as safe sites for the establishment of later colonizers (Masuzawa, 1985; Masuzawa and Suzuki, 1991; Adachi et al., 1996). The facilitative effect of patch-making pioneer plants may be a critical factor in the development of early successional vegetation on both the upper and lower bare scoria lands of Mt. Fuji.

### MICROENVIRONMENTAL MODIFICATIONS BY S. REINII

A nurse plant enhances the establishment and survival of other plants by altering factors such as light, moisture, and nutrient conditions in the local environment (e.g., Valiente-Banuet and Ezcurra, 1991; Uesaka and Tsuyuzaki, 2004). On the volcanic bare ground of Mt. Koma in northern Japan, *Salix* patches act as facilitators for herb species by improving moisture and nutrient conditions, moderating light intensity, and trapping seeds (Uesaka and Tsuyuzaki, 2004). We also verified that *Salix* patches ameliorated several microenvironmental factors (e.g., temperature, soil moisture, soil total nitrogen content, and soil-surface stability) for later-colonizing species.

**TABLE 3**

Survivorship of *L. kaempferi* for 6 years inside and outside of *Salix* patches. Number of individuals in 1999, survivors in 2005, and survival ratio are shown for individuals in two age classes and all individuals. Differences in the survival rate between inside and outside of patches are tested by Fisher's exact probability test.

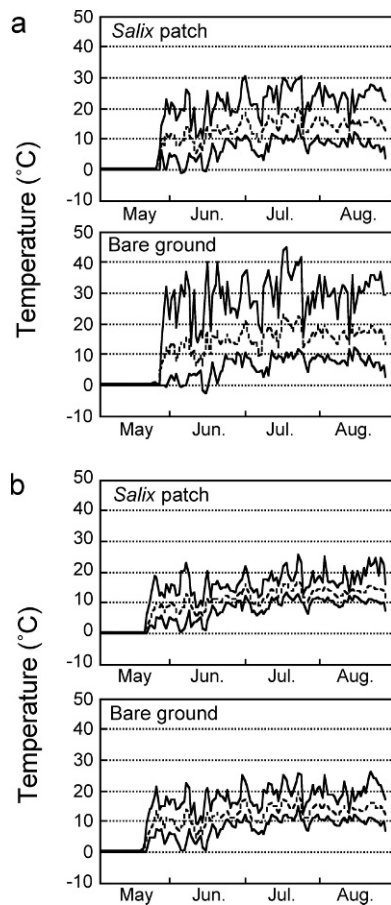| Plot | Age (yr) in 1999 | In *Salix* patches | | | Outside patches | | | |
|---|---|---|---|---|---|---|---|---|
| | | Plants in 1999 | Survivors in 2005 | % | Plants in 1999 | Survivors in 2005 | % | *P* |
| A | 0–5 | 5 | 5 | 100 | 36 | 17 | 47 | 0.051 |
| | 6+ | 13 | 12 | 92 | 52 | 51 | 98 | 0.363 |
| | All | 18 | 17 | 94 | 88 | 68 | 77 | 0.116 |
| B | 0–5 | 53 | 33 | 62 | 157 | 76 | 48 | 0.111 |
| | 6+ | 31 | 21 | 68 | 46 | 37 | 80 | 0.282 |
| | All | 84 | 54 | 64 | 203 | 113 | 56 | 0.191 |
| A and B | 0–5 | 58 | 38 | 66 | 193 | 93 | 48 | 0.025 |
| | 6+ | 44 | 33 | 75 | 98 | 88 | 90 | 0.038 |
| | All | 102 | 71 | 70 | 291 | 181 | 62 | 0.189 |

M. ENDO ET AL. / 339

**FIGURE 4.** Seasonal changes in the soil-surface temperatures (a) and belowground temperatures (b) in the *Salix* patches and bare ground. Daily maximum and minimum temperatures are shown by upper and lower solid lines, respectively. Daily means are shown by broken lines.

On bare scoria, most seedlings of pioneer plants die from severe desiccation during mid-summer, when solar radiation is high and precipitation is low (Maruta, 1976; Yura, 1988). The interception of solar radiation by the *S. reinii* crown did not depress the growth of *Larix* seedlings. Instead, it effectively prevented temperature increases in the patch on sunny days. The moisture content of the soil-surface stratum was significantly higher inside *Salix* patches than in bare sites on a sunny summer day. These temperature and moisture conditions apparently moderated water stress for *L. kaempferi* growing in the patches. The effect of *Salix* patches in lowering desiccation may enhance the survival of *Larix* seedlings.

Available nitrogen is the main factor limiting plant growth during primary succession in volcanic deserts (Hirose and Tateno,

1984; Tateno and Hirose, 1987; Chiba and Hirose, 1993). Hirose and Tateno (1984) suggested a facilitative effect of *R. japonica* patches on primary succession, demonstrating that soil organic nitrogen, ammonium, and nitrate in *R. japonica* patches were all higher than in surrounding bare sites. However, neither soil ammonium nor nitrate levels in *Salix* patches were higher than those in the surrounding sites, although total nitrogen was higher in *Salix* patches. Mineralization rates of organic nitrogen are highest in mid-summer in a volcanic desert (Hirose and Tateno, 1984). The accumulated nitrogen inside *Salix* patches might be mineralized and then lost immediately through absorption and leaching. Thus, more detailed investigations of soil nutrient dynamics are needed to verify that *S. reinii* improves the soil nutrient conditions inside the patches.

On exposed alpine gravel fields, movement of the surface substratum severely limits plant survival, and only species that develop large subterranean organs are found in these regions (Koizumi, 1979; Chujo, 1983). The movement of scoria gravel in the volcanic desert on Mt. Fuji may frequently injure or kill small plants. *Salix reinii* appears to have a high tolerance for surface gravel movement, and the highly branched prostrate stems decrease substratum movement within patches of this species. This surface stabilizing capability is likely one component of the nurse-plant effect of *S. reinii* on *L. kaempferi*.

## FACILITATION AND COMPETITION WITH NURSE PLANTS

On occasion, nurse plants can exert a negative effect on the nursed species (Callaway and Walker, 1997; Holmgren et al., 1997). Desert nurse species, which protect understory plants from low temperatures or freezing, also inhibit the growth of these plants through competition for available water and solar radiation (Franco and Nobel, 1988, 1989; Valiente-Banuet et al., 1991). In a glacier foreland community, negative and positive impacts of willow canopies on species occurrence cancel each other out (Totland et al., 2004). The growth of *L. kaempferi* was not facilitated by *S. reinii*, even though survival was enhanced through the nurse-plant effect. *Larix* seedlings in *Salix* patches had more slender main stems and lower root:shoot ratios than those in bare sites. Similar results were observed on another volcanic desert (Akasaka and Tsuyuzaki, 2005). These morphological features clearly show etiolation in *Larix* seedlings, which is their response to shading by *S. reinii* and indicates competition for light. In addition, the leaf nitrogen concentration of *L. kaempferi* in *Salix* patches was similar to or lower than that in bare sites. This seems to indicate competition for nitrogen. The formation of ectomycorrhizae on *Larix* seedlings is enhanced when the seedlings are transplanted near established *S. reinii* (Nara and Hogetsu, 2004). Our data indicate that the facilitative effect on ectomycorrhizal

**TABLE 4**

Water and nitrogen contents and stability of ground surface substratum in *Salix* patches and bare ground. Mean $\pm$ SE are shown ($n = 6$ for water and nitrogen contents and $n = 15$ for the stability of surface scoria).

|  | *Salix* patch | Bare ground | Mann-Whitney *U*-test |
|---|---|---|---|
| Water content (%) | 7.23 $\pm$ 0.60 | 5.30 $\pm$ 0.57 | $P < 0.05$ |
| Total N (mg g$^{-1}$) | 0.37 $\pm$ 0.03 | 0.19 $\pm$ 0.01 | $P < 0.01$ |
| NO$_3$$-$N ($\mu$g g$^{-1}$) | 0.09 $\pm$ 0.03 | 0.14 $\pm$ 0.02 | ns |
| NH$_4$$-$N ($\mu$g g$^{-1}$) | 1.61 $\pm$ 0.24 | 1.90 $\pm$ 0.18 | ns |
| Unmoved surface scoria (% yr$^{-1}$) | 58.9 $\pm$ 6.1 | 33.7 $\pm$ 8.8 | $P < 0.05$ |

ns: not significant.

formation does not result in higher leaf nitrogen content in *Larix* seedlings.

The effect of a nurse plant on the nursed species may change from positive to negative (or neutral) as the nursed plant grows (Kellman and Kading, 1992; Pugnaire et al., 1996; Callaway and Walker, 1997). Although the survival rate of *L. kaempferi* inside *Salix* patches was higher than that outside of patches during younger stages, it was lower during older stages. This appears to be associated with the extent of protective effects of *Salix* patches on *Larix* seedlings against severe environmental conditions, such as strong winds. Flying gravel during high winds causes stem injuries that are substantial contributions to moisture stress in *L. kaempferi* on the bare lands of Mt. Fuji (Maruta, 1996). The protective effects of *Salix* patches seems to be very important for the survival of young *L. kaempferi* growing under the *Salix* crown, but less important for the survival of older *L. kaempferi* emerging from the *Salix* crown. Therefore the competitive effects of *Salix* patches on *Larix* seedlings may be more dominant than the protective effects during the older stages, thus resulting in a lower survival rate within patches.

### ROLES OF *S. REINII* IN PRIMARY SUCCESSION

The pioneer species that accelerate primary succession vary with altitude. The forest limit on the southeastern slope of Mt. Fuji, where the most recent eruption occurred, is about 1000 m lower than on the northern slope. On the southeastern side, bare scoria spreads out below the subalpine zone. *Reynoutria japonica* is the dominant pioneer species on bare ground at lower altitudes but rarely occurs on the northern slope, where the bare ground is beyond the altitudinal upper limit of this species (Maruta, 1994). Here, *S. reinii* is one of the important pioneers accelerating primary succession in the subalpine zone.

The identity of the facilitative species also appears to change throughout the successional sequence. In early successional stages, *S. reinii* facilitates seedling establishment of tree species that dominate the treeline vegetation. In the next successional stage, *L. kaempferi* develops a krummholz form and dominates (Maruta, 1996). During this process, *S. reinii* cover decreases owing to increasing competition with *L. kaempferi* for some resources (nutrients, moisture, and light), in which light may be increasingly important as vegetation develops. As a cover of krummholz vegetation increases, *L. kaempferi* develops elect trunks to form an early successional forest. Several plant species, including later successional, shade-tolerant species such as *Abies veitchii*, are frequently observed under the *Larix* canopy. Thus, *L. kaempferi* may serve as a nurse plant during early stages of forest development.

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