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Micro-Environmental Analysis of the Natural Regeneration of Larch Forests in Northern Japan

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Abstract

In order to determine the natural regeneration patterns of Japanese larch (*Larix kaempferi* Sarg.) in volcanic areas of Northern Japan, we analyzed micro-environmental factors, such as temperature (air temperature, surface soil temperature at a depth of 1cm and deep soil temperature at a 10cm depth), soil pH, the ectomycorrhiza infection rate and the nitrogen concentration of the larch plants at the elevation of Mt. Komagatake. We also analyzed the temperature variations in the forest understory and forest gap of the Tomakomai National Forest. Surface soil temperatures showed more temporal variation across the elevation gradient than either air or deep soil temperatures at high elevation or low elevation study sites on Mt. Komagatake. However, the air temperature was greater than the surface soil temperature, which in turn was greater than the 10cm deep soil temperature. With increasing elevation, the ectomycorrhizal infection rate decreased. The ectomycorrhiza of plants was shown to be an important factor affecting larch plant growth. Lower needle nitrogen and phosphorus concentrations reduced the growth of the larch seedlings

Key words: Japanese larch, natural regeneration, micro-environment, temperature

Introduction

The successful natural regeneration of useful species of trees has been pursued in order to save labor costs and conserve of forestlands. However, not many species can regenerate successfully in natural conditions because of high inter-specific and intra-specific competition within forests and in harsh environmental conditions (e.g. Pickett and White 1985, Samejima 1985). Therefore, the promotion and establishment of the natural regeneration of forests for conserving the natural environment has become an important topic of study.

In general, the regeneration success of a tree species is strongly dependent upon natural conditions such as the micro-environment and the growth characteristics of the species. If the physical conditions match the growth traits of the plants, then the seeds and their seedlings can establish themselves under the competitive conditions with other species (e.g. microorganisms, plants, macro-fauna, etc.). Therefore, it is generally accepted that we should know both the capacity of the environment and the growth traits of specific plant species.

Japanese larch trees (*Larix kaempferi* Sarg. = *Larix leptolepis* Gordon) were introduced to Hokkaido, the northernmost island of Japan, at the beginning of the 1900s (Sugimoto 1966) for timber production because of their fast growth characteristics (Asada and Satoo 1981, Koike *et al.* 2000). They are not indigenous to the island of Hokkaido (Tatewaki *et al.* 1965). Although the

Japanese larch originates mainly from central Japan at altitudes ranging from 1100 to 2700m a.s.l. (Asada and Satoo 1981, Asada and Sugawara 1983), there are several possible sites in Hokkaido for establishing the natural regeneration of larch, especially where there is sparse ground vegetation with no litter on the forest floor, or bare soil conditions with full sunlight. Larch trees regenerate fairly well naturally and as a result they have become dominant on disturbed sites following a volcanic eruption of Mt. Komagatake in Hokkaido (Sasaoka *et al.* 1997, Yajima 2000). What kinds of natural conditions allow for the successful natural regeneration of the larch species - a light demanding, deciduous conifer (Gower and Richards 1990, Koike *et al.* 2000)? It is expected that larch will establish itself under sunny, relatively warm soil, moderate-water conditions (Sasaoka *et al.* 2000), without any fungi destroying its seeds and seedlings. Moreover, this species is symbiotic with several kinds of ectomycorrhiza (Yang *et al.* 1998, Qu *et al.* 2003a). In order to clarify the natural regeneration and invasion characteristics of the Japanese larch, we investigated the micro-environment and growth responses of regenerated larch seedlings under different micro-site conditions. To meet these objectives, two study sites on volcanic ash were selected. Firstly, we studied the effect of elevation and nutrient on the growth of the larch seedlings (on Mt. Komagatake). Next, we looked at factors of the forest stand structure affecting seedling establishment (at Tomakomai National Forest).

Materials and Methods

1. Site descriptions

Mt. Komagatake is an active volcano located in the southwestern part of Hokkaido, Japan (42°04'N, 140°42'E, 1133m a.s.l.). The eruption of 1929 produced ash, pumice and mud flows, which destroyed most of the vegetation on the slopes (Yoshii 1932). Pumice-flow eruptions have been recorded many times since 1640. The most recent major eruption was in 1929 (Yoshii 1942). The climate on Mt. Komagatake is temperate. Climatic data (50yr mean) around the base of the volcano indicate a mean annual precipitation of 1138mm. Annual temperatures average 8.3°C, with a mean for January of -3.4°C and for July 19.3°C (Yang et al. 1998).

The present ground layer vegetation is characterized by lichens and scattered shrubs such as *Salix reinii* and *Gaultheria miqueliana* (Kondo and Tsuyuzaki, 1999). Plantations of Japanese larch (*Larix kaempferi*) were intensively established on the lower southwestern slopes of the mountain between 1953 and 1963. The larch is now more abundant towards the summit than any other native woody plant. Although, water conditions at a high elevation can be severe, photosynthesis of the larch saplings are rarely inhibited by water stress due to their xylem water potential (Sasaoka et al. 2000, Yajima 2000). We established three plots (1.5m x 5m) at both low (530 m a.s.l.) and high elevations (768 m a.s.l.).

The land of the Tomakomai region is also on a deep volcanic ash deposit (2m in depth) from the last eruption of Mt. Tarumae in 1739. We selected an approximately 50-year old Japanese larch plantation in Tomakomai National Forest (42°44'N, 141°31'E), Hokkaido, Japan, as a mature forest to be compared with Mt. Komagatake.

The study was carried out in number 1196 and 1198 forestry compartments. The altitude is 115~140m a. s. l., and the average tree height was 18.5m in 2000. Most of the area is covered by volcanic soil (derived from Mt. Tarumae, an active volcano). This forest lies in a cool, temperate forest zone.

We created two monitoring sites at the forest floor in the larch plantation (with a density of 458ha⁻¹, and a mean tree height of 24.3m as of 2002) and its gaps (diameter was ca. 13m), which were formed as a result of the thinning treatment in 1993.

2. Monitoring of the Micro-environment

On Mt. Komagatake, two sets of auto-logged thermometers (Thermo recorder mini, RT-30S, Espec Mic Corp. Osaka) were set up at both the higher altitude and the lower altitude. Three thermometers to monitor the air temperature, temperature at the soil surface and soil temperature at a 10cm depth were set for each altitude from June 2nd to October 9th, 2003. Thermo recorders were also set up in the forest understory and gaps (ambient, soil surface at 1cm and 10cm depths) in the Tomakomai National Forest from June 2nd to October 9th 2003.

In order to investigate the growth status of plants during the growing season in 2003, 20 plots (1m x 1m)

were set up at each altitude. The current year's shoots and total shoot height were measured on June 2nd, July 30th and October 9th, 2003. Twelve seedlings from naturally regenerated larch species, including surface soil and deeper soil (15-20cm depth) among the roots, were sampled from high and low altitudes on Mt. Komagatake. The infection ratio of ectomycorrhiza on roots (r < 2mm) was evaluated using the following formula described by Beckjord et al. (1985):

$$\text{PESR}(\%) = \text{ESR}/(\text{ESR}+\text{NSR}) \times 100,$$

where ESR and NSR are the number of ectomycorrhizal and non-ectomycorrhizal short roots per plant, respectively.

After observing and analyzing the ectomycorrhizal infection rate of the root using a microscope (Olympus, Tokyo), plants were separated into stems, branches, needles, dark roots and fine roots (<2mm) and dried at 60°C for 48hours. Then, samples were milled and homogenized. Fresh soil was separated into surface soil and deeper soil, sieved and the pH was measured using a pH meter (MP 220, TOA Electric Co. Ltd. Tokyo). Finally, soils were dried at 110°C for 48hours. The N concentration of each part of the plant was analyzed using a N-C analyzer (NC900, Shimadzu, Kyoto, Japan). The concentration of P was analyzed using an inductivity coupled plasma, ICP analyzer (IRIS, Jarrel ash, Franklin, MA, USA). The statistical tests were performed with the General Liner Model (GLM) of SAS (SAS Institute, Inc., 1996).

Results

Temperature Fluctuations

From June to October, the maximum air temperature, surface soil temperature at a 1cm depth and deep soil temperature at a 10cm depth on Mt. Komagatake was 28.5, 38.3 and 21.4 °C at a high altitude, and 30.1, 52.2 and 23.3 °C at a low altitude, respectively (Tab. 1). An extremely high temperature of 52.2 °C at the soil surface was instantaneously detected but it did not last a long time. The minimum air temperature, surface soil temperature and soil temperature at a 10cm depth on Mt. Komagatake was 1.0, 0.7 and 7.6 °C at a high altitude and 2.4, 2.5 and 8.6 °C at a low altitude, respectively. The mean temperatures of air, soil surface, and at a 10cm depth in soil were 14.1, 14.6 and 15.1 °C at a high altitude and 15.6, 17.2 and 16.5 °C at a low altitude on Mt. Komagatake. The temperature variation of the surface soil was larger than that of the air temperature and the 10cm deep soil temperature.

Figure 1 shows the daily mean temperature of ambient, soil surface and deep soil at low and high elevations from June to early October, respectively. Daily mean temperatures were higher at the low elevation site than those at the high elevation. The maximum air temperature, and soil temperatures at 1cm and 10cm depths from June to October were 34.9, 25.0 and 24.2 °C at the gap, and 26.4, 26.4 and 20.9 °C at the forest floor at the Tomakomai National Forest. The minimum temperature of these were -0.5, 7.3 and 7.8 °C at the gap and 0.8, 0.8 and 9.7 °C at the forest floor.

Table. 1. Maximum, minimum and mean air temperature, surface soil temperature and in soil temperature at a 10cm depth at high (768m) and low (530m) altitudes on Mt.Komagatake and in the gap and forest of the Tomakomai National Forest from June to October 2003. The values of mean temperature were the means and standard deviations ($n = 1656$).

			Maximum (°C)	Minimum (°C)	Mean (°C)
Mt. Komagatake	High altitude	Air temperature	28.5	1	14.1±0.11
		1cm depth in soil	38.3	0.7	14.6±0.14
		10cm depth in soil	21.4	7.6	15.1±0.06
	Low altitude	Air temperature	30.1	2.4	15.6±0.11
		1cm depth in soil	52.2	2.5	17.2±0.17
		10cm depth in soil	23.3	8.6	16.5±0.07
Tomakomai National Forest	Gap	Air temperature	34.9	-0.5	16.6±0.13
		1cm depth in soil	25	7.3	16.8±0.08
		10cm depth in soil	24.2	7.8	16.9±0.07
	Forest	Air temperature	26.4	0.8	16.1±0.1
		1cm depth in soil	26.4	0.8	15.3±0.11
		10cm depth in soil	20.9	9.7	16.3±0.05

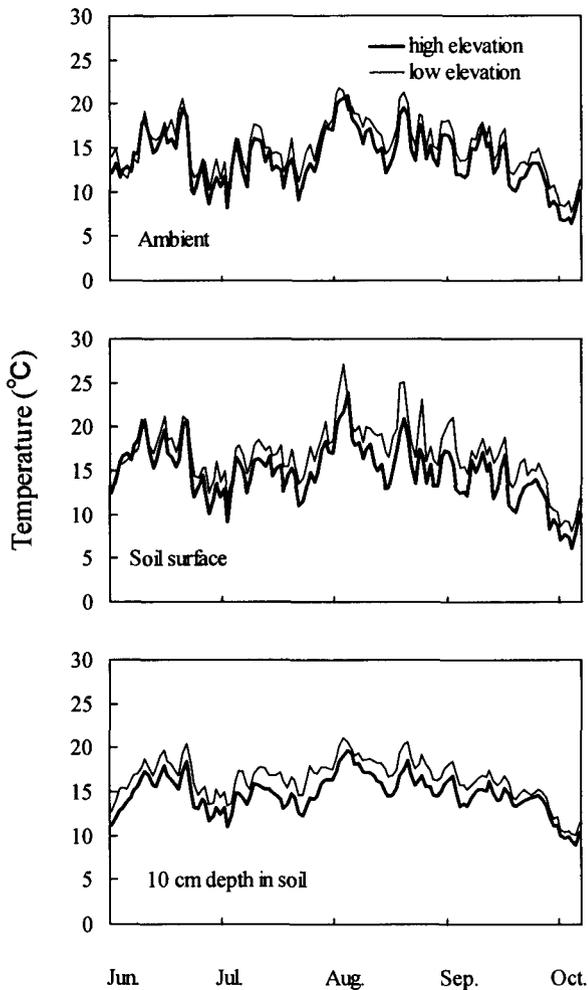


Fig. 1. The daily mean temperature of ambient, soil surface and deep soil at a low elevation (530 m) and a high elevation (768 m) on Mt. Komagatake from June to early October 2003.

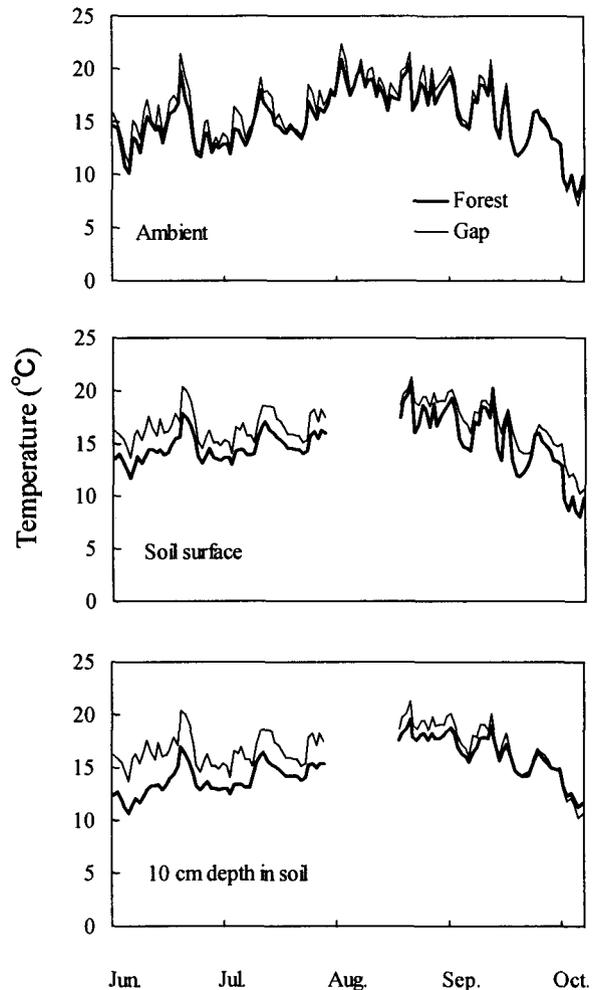


Fig. 2. The daily mean temperature of ambient, soil surface (1 cm) and deep soil (10 cm) at the forest and gap of Tomakomai National Forest from June to early October 2003.

The mean air temperature and soil temperatures at 1cm and 10cm depths in the Tomakomai National Forest were 16.6, 16.8 and 16.9 °C at the gap and 16.1, 15.3 and 16.3 °C at the forest floor (Tab. 1). Figure 2 shows the daily mean soil temperatures at the gap and the forest floor. The mean temperature of ambient, surface soil at a 1cm depth and at a 10cm depth at the forest floor was lower than those at the gap.

Plant Growth Survey

The plant growth during the growing season (from June to October) and shoot height relationship at the low and high elevation sites are shown in Figure 3. When the current year's shoot height was above the regression line, the plants were defined as "good-growth-plants". In contrast, the plants with a

shoot height lower than the regression line, were defined as "poor-growth-plants". The growth rate of plants at the high altitude site was higher than that at the low altitude site. However, there was no significant difference between the two altitudes.

Soil pH and Ectomycorrhiza Infection

The pH values of the surface soil were lower than those of the deeper soil (about 15-20cm depth) regardless of the locations and plant growth conditions (Tab. 2). The pH of the surface soil of the poor-growth-plant sites were significantly lower than the good-growth-plant sites at a high altitude. However, there is no significant difference in the value at a low altitude.

Table. 2. The soil pH and infection rate (%) of ectomycorrhiza of Japanese larch seedlings at a high altitude (768m) and a low altitude (530m) on Mt. Komagatake. Values with the same letter (*a*, *b* and *c*) within columns are not significantly different from each other at $P < 0.05$ separated by the Least Squares Means using the GLM model of SAS analysis. All values are means and the standard deviations of six replicates.

Locations	Plant condition	Infection rate of ectomycorrhiza (%)	Soil pH	
			Surface soil	Deeper soil (15-20cm)
High altitude	Good	72.09(6.51) ^b	5.63(0.06) ^a	5.73(0.04) ^{NS}
	Poor	51.13(5.05) ^c	5.54(0.01) ^b	5.74(0.14) ^{NS}
Low altitude	Good	89.62(2.49) ^a	5.64(0.06) ^a	5.70(0.13) ^{NS}
	Poor	56.18(1.29) ^c	5.63(0.03) ^a	5.71(0.01) ^{NS}

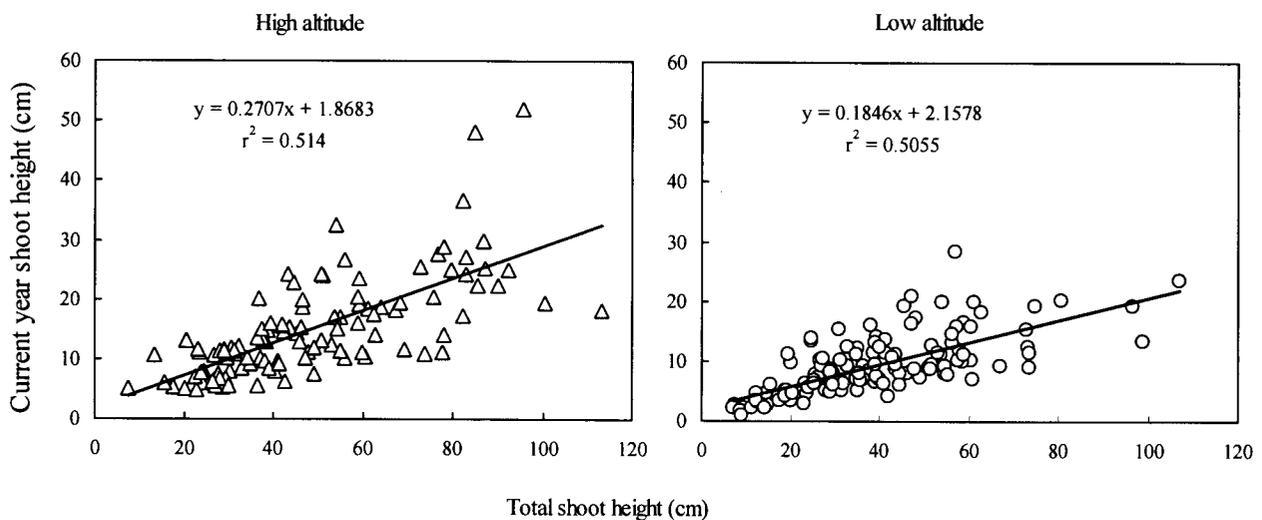


Fig. 3. The relationship between the height of current year's shoot (cm) and total shoot height (cm) at a high altitude and a low altitude on Mt. Komagatake.

The infection ratio of ectomycorrhiza of roots of good-growth-plants was higher in the low altitude location than in the high one (Tab. 2). At both altitudes, the roots of good-growth-larch plants had a significantly higher infection ratio of ectomycorrhiza than those of the poor-growth-plants. Although the pH of surface soil at a high altitude was slightly lower ($P < 0.05$), there was no difference in the infection rate of ectomycorrhiza (Tab. 2).

Nitrogen and Phosphorus Concentrations in Larch Plants

The plant nitrogen (N) concentration at a high elevation was higher than that at a low elevation. However, there was no significant difference between the two elevations. The N concentration of the needles was significantly higher in the good-growth-plants than in the poor-growth-plants at both altitudes and the N concentration of the stem and the fine root was also significantly higher in the good-growth-plants than in the poor-growth-plants at a low altitude (Fig. 4). For the branches and the dark root organs, the N concentrations did not differ significantly between the good-growth-plants and the poor-growth-plants at either the high and low altitude sites.

The phosphorus (P) concentration was higher in the needles in comparison to the branches, stems, fine roots and dark roots. For all the organs, P concentration was higher in the good-growth plants than it was in the poor-growth plants. Moreover, there were significant differences in the P concentration in needles of the good-growth and the poor-growth plants. However,

there were no significant differences in the phosphorus concentration of plants at the high altitude and the low altitude sites (Fig. 5).

Discussion

Originally, the dominant tree species in the Mt. Komagatake area were birch, poplar and willow (Yoshii, 1942). The larch plantation on Mt. Komagatake was established between 1953 and 1963. Larch trees generally grow fast and produce large amounts of seeds, which is well suited to colonizing volcanic slopes and other areas after disturbances (Tatewaki *et al.* 1965, Koike *et al.* 2000). Kondo and Tsuyuzaki (1999) reported the distance from the seed source was the primary factor influencing the colonization of *L. kaempferi*, particularly in the early stages.

Soil temperature is an important factor affecting both the root and shoot growth of plants (Boucher *et al.* 2001, Kaspar and Bland 1992). On Mt. Komagatake, surface soil temperatures showed more temporal variation across the gradient than either air or deep soil temperatures at both high and low elevation study sites. If this temperature fluctuation is very large, then plant growth (e.g. photosynthesis) will be suppressed (Larcher 2003). The mean temperature at a low elevation on Mt. Komagatake was 1.5 °C higher than that of the high elevation (Tab. 1, Fig. 1). However, this slightly higher temperature did not promote the growth of current shoots (Fig. 3). Current shoot length at a high altitude was longer than that of a low altitude. This seems to be a contradiction. In general, the leaf and shoot elongation is accelerated by daily maximum

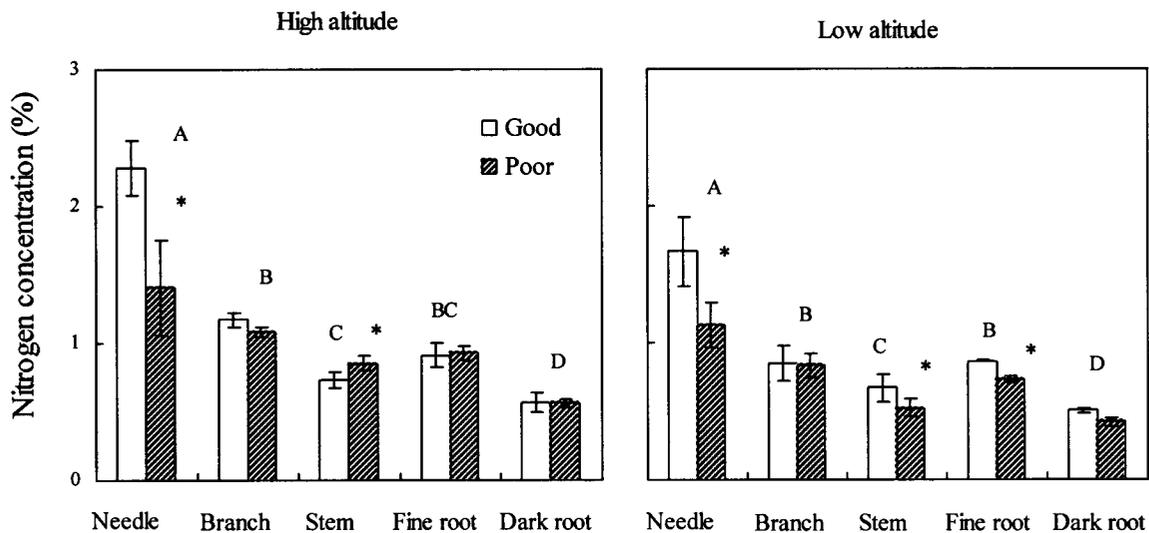


Fig. 4. N concentration (%) of Japanese larch plants in the needle, branch, stem, fine root (<2mm) and dark root at a high altitude and a low altitude on Mt. Komagatake. Values with the same letter (A, B and C) are not significantly different from each other at $P < 0.05$ separated by Least Squares Means using GLM model of SAS analysis. All values are means of six replicates.

* means significant difference between good growth and poor growth plants within the same organ.

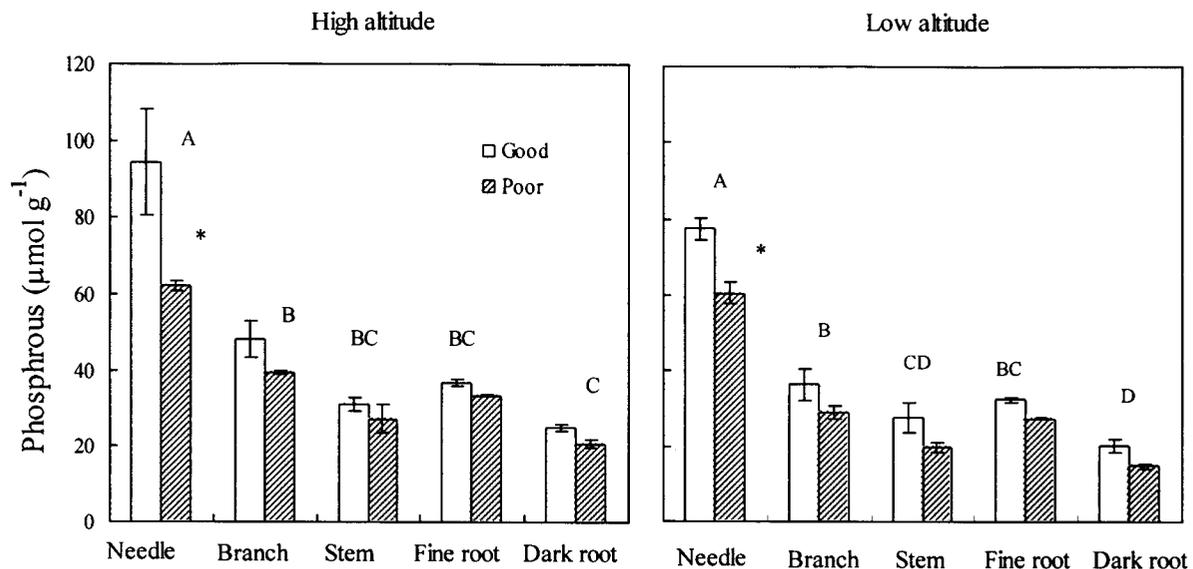


Fig. 5. The phosphorus concentration ($\mu\text{mol per g}$) of Japanese larch plants in the needle, branch, stem, fine root ($<2\text{mm}$) and dark root at a high altitude and a low altitude on Mt. Komagatake. Values with the same letter (A, B and C) are not significantly different from each other at $P<0.05$ separated by Least Squares Means using the GLM model of SAS analysis. All values are means of six replicates.

* means significant difference between good growth and poor growth plants within the same organ.

temperature (Biscoe and Gallagher 1977). At high altitudes, the respiratory consumption of larch seedlings during the night may be suppressed. As a result, the shoots at a high altitude were longer than those at a low altitude even though the maximum photosynthetic rate at a high altitude is slightly lower (Kayama *et al.* 2004).

The water condition is also an essential factor for the growth, survival and establishment of tree seedlings on Mt. Komagatake (Sasaoka *et al.* 2000). They concluded that the light saturated net photosynthetic rate at ambient CO_2 (Psat) of larch shows a higher value during high water stress of xylem water potential (XWP) at -1.65MPa than that of poplar and white birch at XWP at -1.20MPa . Therefore, larch behaved as a drought tolerant species by sustaining its photosynthetic activity in higher Psat during high water stress conditions as compared to the other two species.

In many respects, temporal variation in soil temperatures is qualitatively similar to the PFD (photon flux density) variation as reported by Bazzaz and Wayne (1994) in a deciduous broad-leaf forest in the northeastern US. Across the continuum, ambient temperatures are generally greater than surface soil temperatures at 1cm depth, which are greater than deep soil temperatures for the entire 24-hr period (e.g. Sipe 1990). Our results showed a similar temperature pattern in the forest and gap of Tomakomai National Forest. In other words, the air temperature was higher than the surface soil temperature, which was in turn higher than the deep soil temperature (10cm) (Fig. 2). However, the fluctuation of surface soil temperatures on Mt. Komagatake was higher than that of air temperatures, which was higher than that of deep soil temperatures

(Fig. 1). This clearly demonstrated that the fluctuation of surface soil temperatures was higher than that of air temperatures and deep soil temperatures. Soil temperatures are influenced by numerous factors such as soil texture, porosity, humus content, soil moisture, heat conductivity, heat storage capacity, exposure to radiation and wind (Holtmeier 2003).

The soil pH level is also considered to be an important factor for larch establishment in relation to the symbiosis of ectomycorrhizae formation. Activities of ectomycorrhizae are usually accelerated at slightly lower pH levels (Smith and Read 1997). In this sense, however there was no difference in the infection ratio and ectomycorrhiza (Tab. 2). We found large differences in the infection ratio as affected by the growth (good vs. poor) of seedlings. Determining how soil pH influenced the ectomycorrhizae formation and growth on Mt. Komagatake still requires further study. Yang *et al.* (1998) assessed the types, occurrence patterns and diversity of ectomycorrhizae in *L. kaempferi* seedlings along an elevation gradient on Mt. Komagatake. They found that the correspondence between the type and frequency of mycorrhiza, the elevation gradient and litter accumulation suggested that a change in the litter accumulation along the gradient might affect the types of mycorrhiza and their occurrences. They considered that the lower infection ratio of ectomycorrhiza at a high elevation might be the result of less litter at a high altitude. Moreover, larch seedlings usually grow near shrubs such as *Salix reinii* and *Gaultheria miqueliana*, especially at the high elevation (Kondo and Tsuyuzaki 1999). We also found ectomycorrhizae with these ground layer plants. It may

clarify that the nutrients and carbon translocate within the mycelial network. We hypothesize that the mycelial network may be important and essential to the natural regeneration of larch, particularly at an early stage (Qu *et al.* 2003a). This will be investigated in future studies.

The N concentration of plants at the high altitude was significantly higher than those at the low altitude. It may be an acclimation of adaptation for the larch at high elevations to keep a relatively high photosynthetic rate during the shorter growth period (Körner 1999, Larcher 2003). The N concentration of the needles differed significantly between the good-growth-plants and the poor-growth-plants. Moreover, the P concentration of the needles was significantly higher in good-growth-plants than it was in poor-growth-plants (Fig. 4). This demonstrated that the N and P concentrations of the needles could be a key factor in influencing the growth of larch seedlings (Qu *et al.* 2003b). Since foliage nitrogen is one of the most important resources determining photosynthetic capacity (e.g. Evans 1989, Larcher 2003), the lower N and P concentrations of needles of poor-growth-plants may suppress the photosynthetic rate and may in turn reduce plant carbon allocation to roots because symbiotic microorganisms require photosynthates of the host plants (Smith and Read 1997). The N and P concentration of needles and branches in good-growth-plants were higher at high altitudes than at low altitudes. This tendency is also found in alpine plants because plant size at high altitudes is small with a high concentration of nutrients (Körner 1999). At low altitudes, phosphates in the stem may be an essential storage location for growth. We must detect the seasonal trends of P and N in seedlings under field conditions to analyze different growth patterns.

Although our research period was limited, we showed that the fluctuation of temperatures was different on Mt. Komagatake compared to the Tomakomai National Forest. The fluctuation of soil surface temperature was higher than that of air temperatures, which was higher than that of deep soil temperatures on Mt. Komagatake. Moreover, the large fluctuation of soil surface temperatures may not benefit larch growth at the low altitude. However, in Tomakomai National Forest, the temperature at the gap was higher than at the forest floor, which may accelerate the growth of regenerated larch seedlings. Ectomycorrhizae infection is revealed to be an important element for establishing larch growth. Even though N uptake was not limited by elevation, the lower N and P content of the needles reduced the growth of the larch seedlings. Further study will be needed to assess the effect of soil pH on the ectomycorrhizae formation and the succession of ectomycorrhiza-plant relations *in situ*.

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References

- Asada, S. and Satoo, T. (1981) Silviculture in Larch, Norin-shuppan. Pp 289, Tokyo.
- Asada, S. and Sugawara, S. (1983) Japanese larch of Shinshu (Nagano Prefecture). Rinkei Shimbunsha (Newspaper of Economic of Wood industry and Forestry). (In Japanese).
- Bazzaz, F.A and Wayne, P.M. (1994) Coping with Environmental Heterogeneity: The physiological ecology of tree seedlings regeneration across the gap-understory continuum. In: Caldwell, M.M. and Pearcy, R.W. (eds.) Exploitation of Environmental heterogeneity by plants. Academic Press, San Diego, USA, 349-390.
- Beckjord, P.R., Melhuish, J.H. and McIntosh, M.S. (1985) Effects of nitrogen and phosphorus fertilization on growth and formation of ectomycorrhizae of *Quercus alba* and *Q. rubra* seedlings by *Pisolithus tinctorius* and *Scleroderma aurateum*. Can. J. Bot. 63: 1677-1680.
- Biscoe, P.V. and Gallagher, J.N. (1977) Weather, dry matter production and yield. In: Landsberg, J.J. and Cutting, C.V. (eds.) Environmental effects on crop physiology. Academic Press, London, New York, 75-100.
- Boucher, J.-F., Bernier, P.Y. and Munson, A.D. (2001) Radiation and soil temperature interactions on the growth and physiology of eastern white pine (*Pinus strobes* L.) seedlings. Plant Soil, 236: 165-174.
- Evans, J.R. (1989) Partitioning of nitrogen between and within leaves grown under different irradiances. Australian Plant Physiol., 16: 533- 548.
- Gower, S.T. and Richards, J.H. (1990) Larches: deciduous conifers in an evergreen world. BioScience 40: 818-826.
- Holtmeier, F.K. (2003) Mountain timberlines: ecology, patchiness, and dynamics. Kluwer Academic Publishers, Netherlands. Pp369.
- Kaspar, T.C. and Bland, W.L. (1992) Soil temperature and root growth. Soil Sci. 154:290-299.
- Kayama, M., Qu, L., Kitahashi, Y., Eguchi, N, Akasaka, M. and Koike, T. (2004) Photosynthetic characteristics of seedlings of Japanese larch regenerated on Mt. Komagatake in Hokkaido. Transaction of the meeting in Hokkaido branch of the Japanese Forestry Society 52, 60-62, (In Japanese).
- Koike, T., Yazaki, K., Funada, R., Maruyama Y., Mori Y. and Sasa K. (2000) Forest health and vitality in northern Japan – A history of larch plantation. Res. Note, Fac. Forestry, Univ. of Joensuu, 92: 49-60.
- Kondo, T. and Tsuyuzaki, S. (1999) Natural regeneration patterns of the introduced larch, *Larix kaempferi* (Pinaceae) on the volcanic Mt.

- Komagatake, Northern Japan. Diversity and Distributions, 5: 223-233.
- Körner, C. (1999) Alpine Plant Life: Functional plant ecology of high mountain ecosystem. Springer, Berlin, Germany, Pp.338.
- Larcher, W. (2003) Physiological Plant Ecology: Ecophysiology and stress physiology of functional groups. Springer, Berlin, Germany, 185-230.
- Pickett, S.T.A. and White, P.S. (1985) The Ecology of Natural Disturbance and Patch Dynamic. Academic Press, San Diego. Pp.472.
- Qu, L., Qureshi, A.M., Iwase, K., Tamai, Y., Funada, R. and Koike, T. (2003a). *In vitro* ectomycorrhiza formation on two larch species of seedlings with six different fungal species. Eurasian J. For. Res. 6:65-73.
- Qu, L., Qureshi, A.M. and Koike, T. (2003b). Root growth characteristics, biomass and nutrient dynamics of seedlings of two larch species raised under different fertilization regimes. Plant Soil, 255:293-302.
- Samejima, J. (1985) Consideration on natural forests in Hokkaido. Association of Hoppo Ringyo (Northern Forestry), Sapporo. Pp. 128 (in Japanese).
- Sasaoka, E., Yajima, T., Nakamura, F., Shibuya, M. and Shimizu, O. (1997) The invasion processes and stand structure of *Larix kaempferi* forests on Mt. Komagatake. The proceeding of the 108th annual meeting of Japanese forest society 115. (In Japanese)
- Sasaoka, E., Yoshida, M., Yajima, T., Shibuya, M. and Takahashi, K. (2000) Soil moisture and xylem water potential of tree saplings on Mt. Komagatake, Hokkaido. Res. Bull. Hokkaido University Forests. 105-112. (In Japanese with English summary).
- SAS Institute Inc. (1996) SAS/STAT user's guide. SAS Institute INC. Cary, N.C.
- Sipe, T.W. (1990) Gap partitioning among maples (Acer) in the forests of central New England. Ph.D. Thesis, Harvard University, Cambridge, MA.
- Smith, S.E. and Read, D.J. (1997) Mycorrhizal Symbiosis. 2nd Eds. Academic Press, London, U.K. Pp605.
- Sugimoto, S. (1996) Considering about larch forests. Association of North Forestry (Hoppo Ringyo) Society, Sapporo (In Japanese).
- Tetewaki, M., Ito, K., and Tohyama, M. (1965) Phytosociological study on the forests of Japanese larch (*Larix leptolepis* Gordon). Res. Bulls College Exp. Forests, Hokkaido University. 26:1-176. (In Japanese with English summary).
- Yajima, T. (2000) Difference in the disturbance regimes caused by eruption and its influencing on revegetation processes in forests. Research Report of JSPS (H8-10), Fac. Agr., Hokkaido University, Sapporo, pp. 41 (in Japanese).
- Yang, G., Cha, J.Y., Shibuya, M., Yajima, T. and Takahashi, K. (1998) The occurrence and diversity of ectomycorrhizas of *Larix kaempferi* seedlings on a volcanic mountain in Japan. Mycol. Res., 102: 1503-1508.
- Yoshii, Y. (1932) Re-vegetation of Volcano Komagatake after great eruption in 1929. Bot. Mag. Tokyo 46:208-215.
- Yoshii, Y. (1942) Plant communities of Volcano Komagatake after eruptions. Ecol. Rev., 8:170-220. (In Japanese).

Appendix



Photo. 1. A view of larch plantations of Mt. Komagatake (Dark green parts of lower slope)

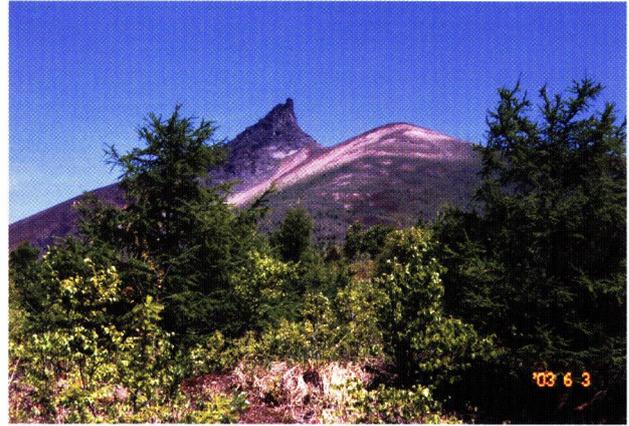


Photo. 2. Young larch stand developed on the slope



Photo. 3. primary succession of larch near the summit



Photo. 4. Ectomycorrhiza of root of larch seedlings



Photo. 5. A view of Tomakomai National Forest with litter trap



Photo. 6. A view of thinning for estimation of net primary production, which will make a forest gap