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Title of paper:

Tree seedling performance on microhabitats along an elevational gradient on Mount Koma, Japan

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Abstract.

Questions: How do biological invasion patterns of larch (*Larix kaempferi*) seedlings change with different microhabitats along an elevational gradient on a volcano? How are seedling attributes such as establishment, competitive ability and morphological plasticity, advantageous to the invasion of stressful disturbed areas?

Location: Mount Koma, Hokkaido, Japan.

Methods: Seed-sowing experiments and natural-seedling censuses were conducted with *L. kaempferi* and the dominant native tree *Betula ermanii*. Seed germination, seedling survival and allocation were investigated on three microhabitats (bareground, *Salix reinii* patch, and *Larix* understory) in three elevational zones for three years.

Results: For the two species, seed germination was higher in *Larix* understories than in bareground and *Salix* patches, but did not differ between elevations. Survival rates were not different between elevations and microhabitats. *Larix* had a higher survival rate than *Betula*. *Larix* showed the highest natural-seedling density in *Salix* patches, independent of elevational differences, while *Betula* density was nearly zero. *Larix* seedlings changed allocations between microhabitats, while the ratio of leaf to total biomass was constant. In bareground *Larix* became more stunted and branched and increased its allocation to the roots. This form is adaptive to windy, nutrient-poor environments. *Larix* seedlings became more tall and slender in *Salix* patch, indicating that the priority was light acquisition in shaded habitats. Little change in *Betula* allocation was detected.

Conclusion: Invasive species establish themselves more efficiently than native species in every microhabitat especially at higher elevations by having higher survival and growth rates derived from superior seedling performance. Plant communities on and above treeline are modified by the biological invasion.

Abbreviations: BA = Bareground. SP = *Salix reinii* patch. LU = *Larix* understory. H, M, and L = high,

middle, and low elevational zones, respectively.

Key words: Allometric relationship, *Betula ermanii*, Biological invasion, Branching pattern, *Larix kaempferi*, Microhabitat, Primary succession, Seed germination, and Seedling survival.

Nomenclature: Ohwi (1975).

Introduction

'Biological invasion' by non-native species is often conspicuous in disturbed and/or harsh habitats such as volcanically devastated landscapes (Burke & Grime 1996; Wearne & Morgan 2004), and modifies plant community structures and successional seres (Richardson & Higgins 1998). Invasive species must have increased performance, defined as seed germination, seedling establishment and growth, competitive ability, and morphological plasticity, than native species (Rejmanek & Richardson 1996; Maurer & Zedler 2002). For example, species that can rapidly change their biomass allocation and/or branching pattern acquire more light and nutrient resources in unstable environments (Baruch *et al.* 2000; Maurer & Zedler 2002). Seedling performance also plays an important role in establishment success because seedlings are generally less tolerant of stress and disturbance than adults (Titus & del Moral 1998). Therefore, research on seedling performance was undertaken here.

Clarifying which species and related environmental characteristics are related to invasion success is required to predict the risks of further invasion and to understand plant community dynamics (Myers & Bazely 2003). Microhabitat often determines seed germination, and seedling establishment and growth (Liang & Seagle 2002), in particular, in disturbed and/or stressful sites (Titus & del Moral 1998). Biotic microhabitats, i.e., patches formed by trees and shrubs, affect seedling establishment via decreased light and increased litter, soil moisture and nutrients, and seed accumulation (Schlesinger *et al.* 1996; Rousset & Lepart 1999; Wearne & Morgan 2004). Therefore, the monitoring of seedling establishment was conducted at the microhabitat scale.

In montane areas, elevational gradients affect seedling establishment patterns by changes in growing season, temperature, snow pack, and wind intensity (Srutek & Leps 1994). Morphological plasticity is related to resource acquisition and the mechanical strength to tolerate wind and snow (Wilson & Oliver 2000; Maurer & Zedler 2002). Wind intensity increasing with elevation promotes the formation of a distinct treeline in Massachusetts, USA (Alftine & Malanson 2004). In contrast, tree densities gradually

decrease with increasing elevation on Mount Koma, northern Japan (Kondo & Tsuyuzaki 1999), indicating that tree survival gradually changes along the elevational gradient. Therefore, elevational gradients are an intrinsic part of biological invasions in mountainous areas.

We focused on seed germination, and seedling growth, survival and allocation of *L. kaempferi*. Seedling performance was compared between microhabitats along the elevational gradient. We hypothesize that (1) *L. kaempferi* has higher survival and growth than native tree species in any microhabitat at any elevation, and (2) the high survival and growth of *L. kaempferi* are derived from high seedling performance, such as plastic allometric relationships, that are more adaptive to harsh unstable environments.

Methods

Study sites and materials

Mount Koma, whose latest major eruption in 1929 produced 0.53 km^3 of ash and pumice, is an andesite stratovolcano in southwest Hokkaido, Japan (42º04´N, 140º42´E, 1131 m in altitude). Climate is a warm-cool temperate with 11.6^{o}C mean annual temperature (a maximum of 24.6^{o}C in August and a minimum of -6.9^{o}C in January) and 973 mm annual precipitation (Mori Climatological Observatory, ca 9 km northwest, 10 m a.s.l.). Snow-free period is usually from May to October.

A depressed treeline of *Betula ermanii* Cham. and *Alnus maximowiczii* (Call.) Hult. occurred before the 1929 eruption, but now a non-native larch *L. kaempferi* of which natural northern limit distribution is northern Honshu, 450km south from Hokkaido has become dominant (Kondo & Tsuyuzaki 1999). *L. kaempferi* seeds have immigrated from reforestation efforts at the mountain base since 1953. At present, all tree species naturally regenerate on the slopes. *B. ermanii* was used for comparison with *L. kaempferi* because it is the most dominant native tree. The other common native trees are *Betula platyphylla* Sukatchev var. *japonica* (Miq.) Hara, *Populus sieboldii* Miq., *Populus maximowiczii* Henry,

and *Alnus maximowiczii*. The ground surface is mostly covered with mosses, lichens, shrub patches, or unvegetated pumice. *L. kaempferi* and *B. ermanii* disperse most of their seeds by wind during fall and winter.

To investigate elevational effects on seedling performances, we established seed-sowing experiments in three elevational zones: high = H (725-735 m a.s.l.), middle = M (625-645 m), and low = L (505-515 m). An increase in elevation caused a decrease in growing season open ground surface temperatures from 19.4^{o}C (daily mean) at 450 m to 15.9^{o}C at 800m in 2002 (Nishi & Tsuyuzaki 2004). Soil nitrogen also decreased with increasing elevation, i.e., soil nitrogen at L was double that of H (Tsuyuzaki *et al*. 2005). Therefore, we expected that changes in environmental factors across elevational gradients were fully expressed by this research design.

Three major microhabitats were recognized for plant colonization: *L. kaempferi* understory (LU), *Salix reinii* Franch. et Savat. patch (SP), and bareground (BA). LU is the most shaded but often shows high species diversity (Titus & Tsuyuzaki 2003). *Salix reinii* forms patches having a facilitative effect (Uesaka & Tsuyuzaki 2004). BA was areas where vascular plant cover was < 10%.

Characteristics of microhabitats and establishment of natural seedlings

The cover of each microhabitat was estimated in three 10 m × 10 m plots at each elevational zone. The distribution of each microhabitat was sketched on section papers with 20-cm accuracy, and each microhabitat cover was calculated. Microhabitat type was decided by external physiognomy, and *L. kaempferi* > 30 cm in height was counted as LU.

Photon flux density (PFD), belowground moisture and litter depth were measured in each microhabitat at each elevation in early June, 2003, when leaf flushing had been completed for *L. kaempferi* and *S. reinii*. By using quantatum sensors (LI-190SA, LI-COR, Lincoln), PFD was measured on each seed-sown plot described below at dawn in early June, 2003, to avoid direct solar radiation (Parent &

Messier 1996). Five replications of measurements were simultaneously obtained on the three microhabitats at each elevation. Relative PFD (RPFD) (%) is calculated as: (PFD on the target point)/(PFD on BA) × 100. Volcanic deposits were sampled five times (July, August and October in 2000, and June and August in 2001). At each sampling, three 100-cm^3 cores (20 cm^3 in surface area, and 5 cm in depth) were collected from each site. Samples were transported immediately to the laboratory and weighed, and then dried at 110^oC for > 3 d and weighed. Moisture is calculated as: (fresh weight – dry weight)/(dry weight) × 100. Litter depth was measured at five locations in each seed-sown plot by a ruler in mid-October 2001 after defoliation.

For *L. kaempferi*, age was determined by whorl counting, which is accurate for seedlings (Yang *et al.* 1998). Preliminary surveys confirmed that the most stems < 30 cm in height were < 4 years in age. Thus, naturally-emerged seedlings were defined as < 30 cm in height for *L. kaempferi* and *B. ermanii*. Seedlings were measured in the three 10 m × 10 m plots at each elevational zone. Age and microhabitat were determined for each seedling. Based on the relative dominance of each microhabitat and number of seedlings observed seedling densities were evaluated.

Seed-sowing experiment in the field

Two-way factorial experiments were started in June 2000. The design was: (three elevational zones) × (three microhabitats) × (five replicates) for each species. In each 30 cm × 30 cm plot, 900 seeds of either species were sown. These plots were randomly established and ranged over 5 ha at each elevation. *Larix* understories establishing with *Salix reinii* patches were not used to avoid the mixed effects. No treatments were conducted after plot establishment. To estimate natural-seedling emergence in the seed-sown plots, 30 cm × 30 cm non-treated plots (= control) were established adjacent to each sown plot. Seeds of *L. kaempferi* and *B. ermanii* were collected from plantations in northern Japan, and kept at room temperature until planting. Seed viabilities checked by an incubator (25^oC/15^oC, 12hr/12hr) with

continuous light were > 50% for both the species soon after seeds sown in the field.

Seed germination and seedling survival were censused at 10-20 day intervals until snowfall in 2000, soon after snowmelt on May until snowfall in 2001, and soon after snowmelt until seedling excavation in September 2002. Seed germination was recorded when leaves were observed. Every seedling was marked by a thin wire and a small amount of oil paint to leaf or stem. Survival rates were determined as: (the number of seedlings at September 2002)/(the number of seedlings emerged in 2000) in each plot. In September 2002, before defoliation began, all seedlings of *B. ermanii* and *L. kaempferi* were excavated gently from all plots, except four plots in LU where aboveground parts were sampled (L = 2 plots, M = 1, and H = 1) owing to ground conditions. Harvested seedlings were kept in plastic bags, and were transported immediately to the laboratory. We measured height by ruler, basal diameter by calipers, and counted number of branches on each stem collected. The stem, leaf, and root were separated , dried in an oven for 7 d at 70^{o}C and weighed. Here, "leaf" is synonymous with photosynthetically-assimilative organ. Shoot biomass (= stem + leaves) and non-assimilative organ biomass (= stem + root) were calculated. In total, 617 *L. kaempferi* seedlings (441 entire and 224 aboveground) were collected, and 48 *B. ermanii* seedlings were collected.

Data analysis

Belowground moisture and naturally-established *L. kaempferi* seedling density were compared among microhabitats and among elevations by linear mixed model with elevations as main factor, plots as random block factor for each elevation, and microhabitats as nested factor within plots (Pinheiro & Bates 2000). For moisture, sampling date was additionally used as categorical variable. Moisture was arcsine-transformed, and natural *L. kaempferi* seedling density was log-transformed [log(seedling density + 0.5)] to apply the analyses.

RPFD, litter depth, seed germination, seedling survival and total biomass, all of which were

sampled in the seed-sown plots, were compared between microhabitats across elevations by two-way ANOVA followed by Scheffe's test for *post hoc* comparisons. RPFD was compared between SP and LU across elevations. Since litter depth was zero on the plots in BA, the difference was examined between SP and LU and between three elevational zones. RPFD, seed germination and seedling survival percentages were arcsine-transformed, and total biomass and litter depth were log-transformed prior to analysis. Total *B. ermanii* biomass was compared separately among elevations and microhabitats by one-way ANOVA because of small sample sizes. Survival percentages between the two species were compared by one-way ANOVA.

Three allometric relationships were examined in each microhabitat and elevational zone: basal diameter vs height, root vs shoot biomass, and non-assimilative vs assimilative organ biomass. Significant differences in slopes were examined among microhabitats and elevations by ANCOVA. When interaction between an explanatory parameter and microhabitats or elevations was significant, the relationship between the two allometric parameters was different among microhabitats or elevations.

By Poisson regression, relationships between stem height (h) and number of branches (f) were compared among microhabitats and among elevations. The Poisson regression model was: $\mathrm{Prob}\{y = f_i\} = e^{-\mu(h_i)} \times \mu(h_i)^{f_i}/f_i!$, where $\mu(h_i) = \exp(\beta_{i0} + \beta_{i1}h_i)$. β_{i0} and β_{i1} are the regression coefficients of the individual i. A parameter set of β_{i0} and β_{i1} was estimated by a maximum likelihood method (m.l.e.) for discrete distribution on each plot so that the full model has three parameter sets. The selection of parameters to create the best fit model was decided by Akaike's Information Criteria (AIC) (Burnham & Anderson 1998).

All statistical analyses were made by the statistical package R (R Foundation for Statistical Computing, Vienna), except ANOVA and Scheffe's test by StatView (ver. 5.0, SAS Institute Inc., Cary). The level of significance was adjusted to 0.05.

Results

Distribution of microhabitats and the environments

Bareground (BA) was the dominant microhabitat throughout the study area, i.e., > 55% (Table 1). The coverage of *L*arix understory (LU) decreased with increasing elevation and *Salix* patch (SP) increased with increasing elevation. 'Others' sites that were not categorized into the three major microhabitats, mostly consisting of non-*S. reinii* shrub patches, decreased with increasing elevation.

RPFD on BA was four times higher than in SP [23 ± 4% (mean ± SD) at H, 26 ± 7% at M, and 28 ± 11% at L] and seven times higher than in LU (11 ± 4% at H, 15 ± 10% at M, and 13 ± 6% at L). SP showed significantly higher RPFD than LU (n = 15, df = 1, F = 69.25, $p < 0.001$). RPFD was not different among elevational zones (df = 2, F = 2.54, p = 0.085).

Litter depth was significantly greater in SP (2.5 ± 1.0 cm, range: 0.9 to 4.2 cm) than in LU (1.5 ± 0.7 cm, range: 0.4 to 3.5 cm) (df = 1, F = 14.40, $p < 0.001$). BA had no litter. There were no significant differences in litter depth between elevational zones (df = 2, F = 1.06, p = 0.353) without interaction between the two factors (df = 2, F = 1.50, p = 0.226). Litter consisted of broad-leaves in SP and of needle-leaves in LU, indicating that most litter was supplied from proximate sources. Belowground moisture showed significant differences across elevations and across sampling dates (Table 1). In total, the moisture tended to be lower in BA than in LU and SP with increasing elevation, although the moisture did not show significant difference among microhabitats with significant interaction between microhabitats and elevations. Since the relative dominance of LU decreased with increasing elevation and that of BA increased, direct solar radiation affected more of the ground surface and thus belowground moisture should become lower at higher elevation at the landscape level. On microhabitats, therefore, BA was characterized by higher light intensity, lower belowground moisture and lacking litter while SP and LU were by lower light intensity, higher moisture, and thicker litter with different litter qualities.

Seed germination and seedling survival in seed-sowing experiment

Seed germination of *L. kaempferi* and *B. ermanii* started in mid-July 2000, and lasted until snowfall in October 2000. No seedlings emerged in the control plots, thus all seedlings were assumed to come from sown seeds. No morphological damage to seedlings was observed. Seed germination percentages were 5.8% for *L. kaempferi* and 0.9% for *B. ermanii* in 2000. LU was the most suitable microhabitat for seed germination (Table 2).

Seedling survival percentages were > 13% for *L. kaempferi*, and < 24% for *B. ermanii* (Table 2). *L. kaempferi* showed significantly higher percentages than *B. ermanii* (df = 1, F = 20.81, p < 0.0001). Survival percentages did not differ significantly across elevations and microhabitats for both species.

Distribution of naturally-established seedlings

For *L. kaempferi*, natural seedling density was higher in SP at all elevations (df = 2; 16, F = 4.77, p = 0.024) (Table 2), showing that SP was more favorable sites for seedling establishment, *per se*. Likewise, there were no significant differences in seedling densities across elevation (df = 2; 6, F = 0.07, p = 0.930), suggesting that the microhabitat effects on seedling establishment were more critical than the elevational effects. For *B. ermanii* one seedling was recorded on BA at H.

Seedling biomass

L. kaempferi total seedling biomass averaged 7.0 ± 1.2 mg, which was five-times higher than *B. ermanii* (1.2 ± 1.0 mg), and differed among microhabitats (df = 2, F = 222.01, p < 0.001) and elevations (df = 2, F = 21.69, p < 0.001) (Table 2). The total biomass averaged 13.1 ± 19.1 mg in BA and 9.7 ± 9.4 mg in SP. Seedlings in LU were extremely smaller. *L. kaempferi* total biomass increased with increasing elevation where open areas were more common. Significant interaction between elevation and microhabitat (df = 2, F

= 10.16, $p < 0.001$) implied that difference in total biomass became higher between BA and SP with increasing elevation. *B. ermanii* did not change total biomass among elevations ($df = 2$, $F = 0.86$, $p = 0.431$) and microhabitats ($df = 2$, $F = 0.03$, $p = 0.975$).

Allometric changes with microhabitats and elevations

For *L. kaempferi* in microhabitats, the best Poisson regression model of the relationship between stem height and number of branches was obtained when BA was used in separate analysis ($y = e^{0.09x-6.62}$) and the data on SP and LU were merged ($y = e^{0.05x-6.62}$) (Fig. 1a). On elevation, the best model obtained when H was used in separate analysis ($y = e^{0.06x-5.39}$) and the data on L and M were merged ($y = e^{0.04x-5.39}$) (Fig. 1b). These indicated that seedlings in BA at higher elevations produced more branches. *B. ermanii* did not develop branches.

L. kaempferi allocation ratios between the biomass of assimilative and non-assimilative organs was not significantly different among elevations (ANCOVA, $df = 2$, $F = 2.33$, $p = 0.060$) or microhabitats ($df = 2$, $F = 2.58$, $p = 0.140$), indicating that the proportion of resources allocated to produce leaves was constant. The allometry between stem diameter and height indicated that seedlings in SP allocated more to height increase and those in BA allocated more to diameter increment ($df = 2$, $F = 16.42$, $p < 0.001$) (Fig. 2a). The allometric relationship slopes decreased from L to H ($df = 2$, $F = 5.19$, $p = 0.006$) (Fig. 2b). In summary, *L. kaempferi* formed thicker stems with increasing elevation, in particular in BA. The slopes of lines fitted to shoot-root biomass relationships were significantly different among microhabitats ($df = 2$, $F = 6.03$, $p = 0.003$) (Fig. 2c), but were not different among elevations ($df = 2$, $F = 2.84$, $p = 0.059$). The slope on SP was lower, indicating that seedlings allocated more resources to aboveground organs in SP than in BA and LU.

For *B. ermanii*, except for diameter to height relationships among elevation ($df = 2$, $F = 3.30$, $p = 0.046$), there were no significant differences among elevations and microhabitats for all three allometric

relationships (Fig. 2d). Therefore, allocation patterns of *B. ermanii* changed little between microhabitats and elevations.

Discussion

Microhabitat effects on seed germination

Low light (1.5% RPFD) decreases seedling emergence, growth and survival for *Betula* spp., and has smaller effects on two needle-leaved species, hemlock and white pine (Catovsky & Bazzaz 2000). RPFD > 10%, even on LU, seemed to be enough to allow seed germination for the two species examined. *Betula ermanii* seed germination is restricted by high solar radiation (Katsuta *et al*. 1998). In addition, BA tends to be drier than LU and SP (Uesaka & Tsuyuzaki 2004). Therefore, the examined two species showed low seed germination rates in BA because of ground dryness and/or high light.

Thick litter accumulation often restricts seed germination and the resultant seedling establishment (Tolliver *et al.* 1995). Litter accumulated more in SP than in LU. In addition, broad-leaved litter inhibits seedling emergence more than needle-leaved litter (Peterson & Pickett 2000). SP showed lower seed germination rates than LU, probably not only because of litter depth but also because litter quality determined seed germination patterns.

Allometric changes in Larix kaempferi

Total nitrogen in the volcanic deposits on BA was approximately one third of that on SP (Uesaka & Tsuyuzaki 2004). Seedlings in BA should allocate more to roots in order to obtain water (Yura 1989) and nutrients (Qu *et al.* 2003). Invasive plants allocating more resources to belowground have advantages in the acquisition of nutrients and water in infertile and/or drought conditions (Baruch *et al.* 2000; Maurer &

Zedler 2002). Furthermore, wind intensity affects stem form, i.e., large belowground organs and stunted stems are advantageous in tolerating high wind (Wilson & Oliver 2000; Henry & Thomas 2002). Wind intensity in BA should be highest because of few obstacles to windblast. High wind intensity decreases photosynthesis, but branching reduces wind intensity within the canopy (Tranquillini 1979). Therefore, a stunted, branching stem with higher root allocation on *L. kaempferi* is an adaptation to bareground by the effective acquisition of light, water, nutrients, and high tolerance to wind. Morphological plasticity, including allometric changes, in invasive species has advantages in seedling establishment not only due to resource acquisition (Baruch *et al.* 2000; Maurer & Zedler 2002) but also because of increased tolerance to physical stress.

Total seedling biomass was not different between SP and BA, although light intensity was lower in SP. These results suggest that light intensity in SP restricted seedling growth the least. Furthermore, *L. kaempferi* stems were more slender in SP than in BA. For trees height growth often has priority over diameter growth in shaded habitats in order to overcome light competition (Canham 1989; Wang *et al.* 1994; Chen & Klinka 1998).

Little change in allocation pattern was observed for *B. ermanii* between habitats. *Betula pubescens* and *B. pendula* do not greatly change allocation patterns under different light conditions (Messier & Puttonen 1995). Owing to low seedling performance, *B. ermanii* is considered to be weaker in its response to stress and disturbance, both of which fluctuate across space and time.

Changes in plant community development

Higher seedling performance by *L. kaempferi* contributes to its successful invasion of this stressful and harsh environment. *L. kaempferi* modifies areas at the upper limit of treeline (Kondo & Tsuyuzaki 1999), indicating that the biological invasion greatly alters plant community structure. The *L. kaempferi* canopy facilitates the establishment of native herbs when the canopy size becomes large enough

for cohabitants to establish (Titus & Tsuyuzaki 2003), showing that the larch becomes one of the major components of the present plant community. Biological invasions also alters underground nutrient cycling (Ehrenfeld 2002), although little consideration has been given to potential impacts.

In total, *L. kaempferi* could invade everywhere except larch undercanopy via high seedling performances, i.e., germination, stress tolerance, and plasticity. Those characteristics of species in genus *Larix* may allow (biological) invasion to various, in particular, for disturbed and/or stressful, ecosystems (Richardson & Higgins 1998, Peterken 2001).

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Table 1. Relative dominance of microhabitat and moisture of volcanic deposits at three elevational zones. Moisture (n = 135) was significantly different among elevational zones (df = 2; 6, F = 5.17, p = 0.05) and among sampling dates (df = 4; 116, F = 18.76, p < 0.0001), and was not significant among microhabitats (df = 2; 116, F = 1.89, p = 0.156). The interaction between elevational zones and microhabitats was significant (df = 4; 116, F = 2.97, p = 0.022).

	Low	Middle	High	Total mean
Relative dominance (%)				
Bareground (BA)	56.4	63.5	67.8	63.3
Salix reinii patch (SP)	6.1	24.3	25.0	17.3
Larix understory (LU)	16.4	8.5	6.3	9.4
Others	21.1	3.7	0.9	10.0
Moisture (%)				
Bareground (BA)	22.0 ± 5.6	22.9 ± 4.3	19.7 ± 3.3	21.5 ± 4.6
Salix reinii patch (SP)	21.0 ± 5.6	23.5 ± 5.1	21.0 ± 5.6	23.0 ± 6.6
Larix understory (LU)	21.5 ± 5.6	27.0 ± 7.5	21.4 ± 5.9	23.3 ± 6.8
Total mean	21.5 ± 5.5	24.5 ± 5.9	21.9 ± 6.4	22.6 ± 6.1

Table 2. Germination percentages of *Larix kaempferi* and *Betula ermanii* in 2000, percent survival and total seedling biomass three years after sowing, and natural seedling densities in 2000 in different microhabitats and elevational zones. Different superscripts with small letters indicate significant differences between microhabitats and different capital letters indicate differences between elevational zones. For *L. kaempferi*, an interaction between microhabitat and elevational zone is significant for total seedling biomass ($df = 2$, $F = 10.16$, $p < 0.001$). Significance was determined by ANOVA and Scheffe's test. Values are mean ± standard deviation.

Larix kaempferi	Bareground (BA)				*Salix reinii* patch (SP)				*Larix* understory (LU)			
Elevational zone	Germination (%)	Survival (%)	Total biomass (mg)	Natural density (stem m^{-2})	Germination (%)	Survival (%)	Total biomass (mg)	Natural density (stem m^{-2})	Germination (%)	Survival (%)	Total biomass (mg)	Natural density (stem m^{-2})
High	2.8 ± 1.2^{a}	31.8 ± 25.8	23.8 ± 31.5^{bB}	$0.08 \pm 0.09^{*}$	4.7 ± 3.5^{ab}	20.9 ± 11.5	13.5 ± 11.9^{bB}	0.24 ± 0.37	10.8 ± 10.7^{b}	12.9 ± 13.7	1.6 ± 0.7^{aB}	0.09 ± 0.16
Middle	2.5 ± 1.0^{a}	22.1 ± 11.3	15.2 ± 16.5^{bB}	0.09 ± 0.05	2.6 ± 2.6^{ab}	33.7 ± 39.4	8.5 ± 5.2^{bB}	0.26 ± 0.19	6.6 ± 8.0^{b}	20.3 ± 21.5	2.7 ± 1.3^{aB}	0.08 ± 0.14
Low	3.2 ± 1.9^{a}	46.4 ± 19.9	7.3 ± 5.9^{bA}	0.07 ± 0.03	4.4 ± 3.3^{ab}	27.7 ± 16.9	6.6 ± 7.4^{bA}	0.26 ± 0.19	14.6 ± 4.6^{b}	32.1 ± 13.1	1.8 ± 0.9^{aA}	0.18 ± 0.23
Betula ermanii	Bareground (BA)				*Salix reinii* patch (SP)				*Larix* understory (LU)			
Elevational zone	Germination (%)	Survival (%)	Total Biomass (mg)	Natural density (stem m^{-2})	Germination (%)	Survival (%)	Total biomass (mg)	Natural density (stem m^{-2})	Germination (%)	Survival (%)	Total biomass (mg)	Natural density (stem m^{-2})
High	0.7 ± 0.5^{ab}	16.4 ± 15.1	1.6 ± 1.1	0.00 ± 0.01	0.3 ± 0.2^{a}	5.0 ± 10.0	0.5***	-	1.6 ± 0.9^{b}	1.0 ± 2.2	0.4	-
Middle	1.2 ± 2.0^{ab}	0.0 ± 0.0	-**	-	0.4 ± 0.7^{a}	7.1 ± 10.1	1.4 ± 0.7	-	1.2 ± 1.2^{b}	23.6 ± 32.3	1.1 ± 0.4	-
Low	0.9 ± 1.1^{ab}	18.8 ± 7.6	1.0 ± 1.1	-	0.5 ± 0.8^{a}	0.0 ± 0.0	-	-	1.6 ± 1.8^{b}	15.6 ± 14.0	1.2 ± 1.2	-

*: Multiple comparisons were not conducted for natural *L. kaempferi* seedling density.

**: No seedlings were observed.

***: Standard deviation was not obtained because of one seedling survived

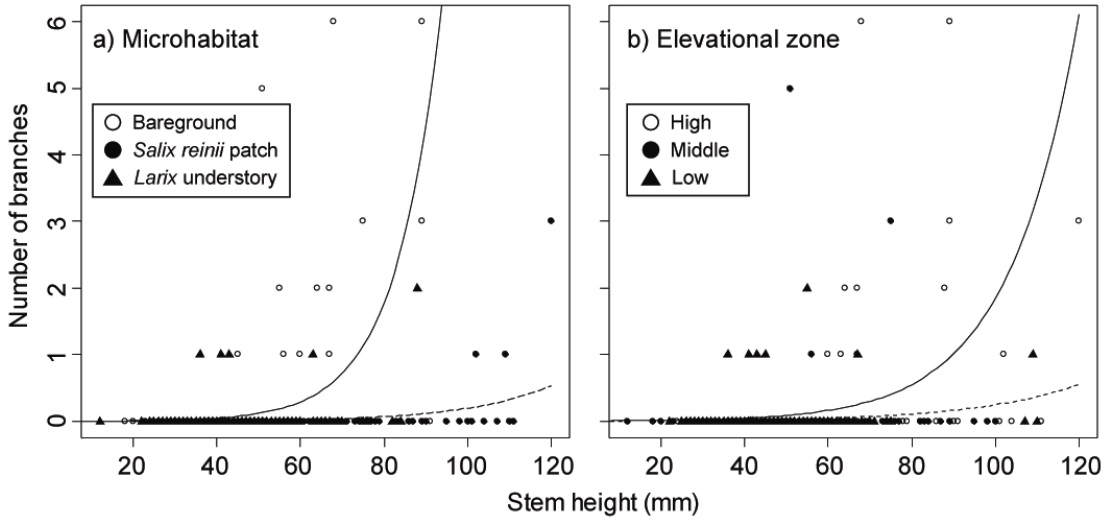


Fig. 1. Changes in relationships between number of branches and stem height on *Larix kaempferi* seedlings across a) microhabitats and b) elevational zones. Poisson regression lines ($y = e^{ax + b}$) are fitted to the relationships between stem height (x) and number of branches (y). The best fitted models are shown. For a) microhabitats, the regression line for bareground is shown by a slolid line, and that for *Salix reinii* plus *Larix* understory is shown by an interrupt line, and for b) elevational zones, a solid line for high elevational zone and an interrupt line for middle plus low elevational zones.

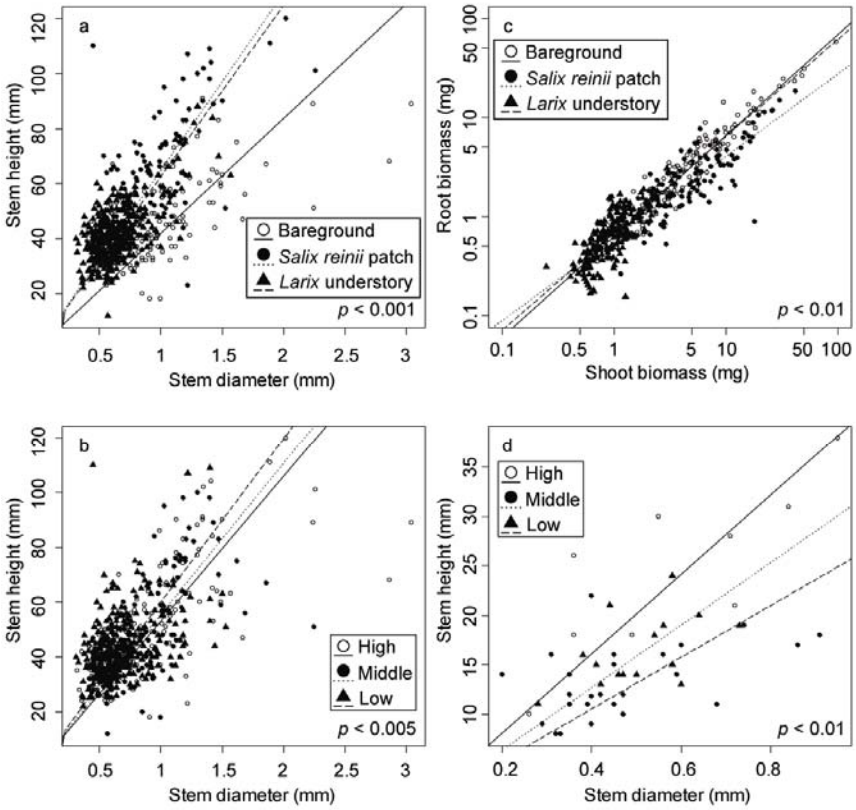


Fig. 2. Allometric relationships on *Larix kaempferi* (a-c) and *Betula ermanii* (d) on microhabitats (a, c) and on elevational zones (b, d). Of the twelve allometric relationships examined, the four relationships of which slopes are significanltly different are shown. The significance among the slopes is indicated on each microhabitat or elevational zone.