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Different biomass-allocation patterns among four tree species in heavily disturbed sites on a volcanic mountain in Hokkaido, northern Japan

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Abstract

We have compared biomass-allocation patterns and frequency of sprouting among saplings of four tree species (*Larix kaempferi*, *Betula platyphylla* var. *japonica*, *Populus maximowiczii*, and *Populus sieboldii*) growing on a volcanic mountain in Hokkaido, northern Japan. Growing conditions were very harsh on the mountainside. Leaf mass and fine root mass relative to root mass were larger in *L. kaempferi*, and *L. kaempferi* root mass was less than for the other species. Sprouting ratios were high for the broadleaved species. Different allometries and sprouting ratios among species suggest that survival strategies for *L. kaempferi* were different from those for the broadleaved species. *L. kaempferi* has greater ability to increase leaf mass under harsh growing conditions; this probably results in large photosynthetic production by *L. kaempferi* on the volcano. In contrast, the two *Populus* species and *Betula platyphylla* seem to maintain populations through their ability to produce sprouts from large root systems.

Key words Allometry · *Betula platyphylla* · *Larix kaempferi* · Sprouting · *Populus* species

Introduction

Nutrient limitations affect physiological and morphological traits of plants, including photosynthetic and nutrient absorption rates, specific leaf area and specific root length, and allocation patterns, for example root-to-shoot ratio and leaf-area ratio (Chapin et al. 1993; Berendse 1994; Landhäusser and Lieffers 2001). Two plant strategies as responses to nutrient limitations are recognized; one is the nutrient-conserving strategy (Aerts and van der Peijl 1993; Chapin et al. 1993; Ryser 1996; Silla and Escudero 2004). This strategy is common among plants adapted to nutrient-poor conditions. For example, seedlings of *Quercus* species growing under nutrient-poor conditions in Spain have a long mean nitrogen residence time resulting from increased tissue longevity. Under nutrient-poor conditions these seedlings fare better than those of *Quercus* species from richer, deeper soils (Silla and Escudero, 2004). In general, low tissue turnover is closely related to variations in allocation patterns, for example root-to-shoot ratios, common to species under nutrient-poor conditions (Chapin et al. 1993).

Although biomass-allocation patterns depend primarily on species (Canham et al. 1996), relative allocation patterns to different plant organs change in response to nutrient conditions within a species. Root biomass and root-to-shoot ratios of 1-year-old *Picea abies* seedlings grown hydroponically in a growth chamber increased under conditions of low nutrient availability (Kaakinen et al. 2004). The root-to-shoot ratio of *Betula pendula* seedlings increased under conditions of controlled

nitrogen deficiency (Ericsson 1995). In coniferous stands similar trends have been reported under nutrient-poor conditions, resulting in high net primary production of roots, large root biomass, and a high root-to-shoot ratio (Keyes and Grier 1981; Haynes and Gower 1995).

In woody plants, sprouting behavior has a significant effect on individual persistence and population dynamics (Bond and Midgley 2001). The sprouting frequency of trees is affected by disturbance and by the productivity of the site (Bellingham and Sparrow 2000), and trees, especially broadleaved trees, survive disturbances by sprouting (Sakai et al. 1997). Trees with high sprouting ability have large biomass and carbohydrate reserves in the roots (Sakai et al. 1997; Bond and Midgley 2001; Kabeya and Sakai 2005). It is therefore assumed that biomass-allocation patterns among tree organs depend on the sprouting ability of the trees.

Here, we propose that different biomass-allocation patterns among plant species strongly affect differences between species dominance in a given environment. We also propose that species allocating more biomass to roots and fine roots will be dominant in nutrient-poor sites. We found noticeable dominance differences among four tree species (*Larix kaempferi*, *Betula platyphylla* var. *japonica*, *Populus maximowiczii*, and *Populus sieboldii*) on an active volcano, Mt Komagatake, in northern Japan, where tree growth is severely limited by shallow and gravelly soils with a thin organic layer (Sasaoka et al. 1999, their Table 1). In this study, we examined different biomass-allocation patterns among saplings of these four tree species by analyzing

allometries between the organs of the saplings. We also investigated the sprouting frequency of saplings. In this paper we relate species dominance to allometry differences and discuss survival strategies of the four species on Mt Komagatake.

Materials and methods

The study site and species

Mt Komagatake (42°4′N, 140°41′E) is an active stratovolcano located in the cool-temperate vegetation zone of Hokkaido, northern Japan (Fig. 1). The main volcanic cone of the mountain consists of lava and pyroclastics of pyroxene andesite. Layers of andesitic volcanic ash and gravel, avalanche debris deposits, and lava are alternately stratified on the mountain (Katsui et al. 1989). The surface is covered by a layer of volcanic ash and gravel. Mean annual temperature and precipitation from 1982 to 1995 were 8.3°C and 987 mm, respectively (measured at the nearest climatological station, 42° 60′N, 140° 34′E, 19 m a.s.l.; Japan Meteorological Agency 1983–1996). The last devastating eruption of Mt Komagatake occurred in 1929, and most vegetation was destroyed by pyroclastic falls and flows, leaving small patches of live plants (Yoshii 1932). *Larix kaempferi* and broadleaved trees became established in approximately 1945 and 1965, respectively, in areas above 500 m a.s.l., and the current forest stands formed gradually thereafter (Sasaoka et al. 1999). Tree density is low and growth is limited, however. Canopy

height and basal area range from 2.7 to 6.1 m and from 0.8 to 7.8 m² ha⁻¹, respectively, in areas between 500 and 700 m a.s.l. on the south-facing slope of the mountain (Table 1).

We investigated four major tree species, *L. kaempferi* Carr., *B. platyphylla* var. *japonica* Hara, *P. maximowiczii* Henry, and *P. sieboldii* Miquel, in natural stands above 500 m a.s.l. in and around study plots (900–4,900 m² in area) established previously by Sasaoka et al. (1999), in mid-July to late August 1997 at 500, 600, and 700 m a.s.l on the south-facing slope (Fig. 1). Of these, *L. kaempferi* was dominant (Table 1), although the other species occurred frequently in the area. These species are all deciduous, with leaf flush occurring in late April to early May, and leaf fall in October. The species are typical of the pioneers that generally regenerate in open sites (Ishikawa et al. 1978; Koike 1988). *L. kaempferi* is a conifer and was introduced to Hokkaido from central Japan. The other species are broadleaved tree species native to Hokkaido. In areas over 500 m a.s.l. on Mt Komagatake, *L. kaempferi* regenerates naturally from seeds that originate from plantations on the lower slopes (Kondo and Tsuyuzaki 1999; Sasaoka et al. 1999).

Tree sampling

To compare biomass-allocation patterns among these species we investigated allometric relationships among organs (stem, branches, leaves, and fine and coarse roots) of saplings (height < 80 cm) of the four species in and around study plots. Five to six healthy saplings (without

apparent injury or signs of herbivory) of each species were sampled at each elevation (Table 2). *P. maximowiczii* did not occur at 500 m. Mean heights (\pm SD) are shown in Table 2. We usually selected saplings derived from seeds, although several *P. sieboldii* saplings that had sprouted from dead parent stems were also included. Roots were traced from each sapling and dug out with the surrounding soil.

After measurement of stem length in laboratory the sampled saplings were separated into stems, branches, leaves, and roots. Roots were rinsed with tap water over a sieve and cleaned; they were subsequently air-dried and sorted into fine (<1 mm diameter) and coarse (≥ 1 mm diameter) categories. All organ samples were oven-dried at 80 °C for 48–72 h, and dry mass was determined (individual total mass: W , leaf mass: W_l , root mass: W_r , fine root mass: W_{fr}).

For each species, we investigated the frequency of saplings (≥ 50 cm in height) originating from sprouts. Saplings of sprout origin were distinguished morphologically—small stem diameter relative to the root collar and bending of the stem at the root collar.

Data analysis

Allometric relationships among plant organs were analyzed for each species. Comparison of the allometric relationships among elevations was not possible because the sample size was too small. Because visual assessment of the data suggested that the relationship did not differ among elevations within species (Fig. 2), we pooled the data by species

across elevations. For allometric data, reduced major axis (RMA) regression is preferable to ordinal least-squares regression (Wright et al. 2002). In this study, we determined allometric relationships by RMA regression after log-transformation of data and tested homogeneities of slopes and intercepts among the regressions with (S)MATR (<http://www.bio.mq.edu.au/ecology/SMATR/>). The test for homogeneity of slopes in (S)MATR was derived by Warton & Weber (2002). In this study, significant levels for pair-wise comparisons of slopes between species were adjusted by sequential Bonferroni correction. The homogeneity of intercepts was tested by analysis of variance (ANOVA) and then the Tukey-Kramer test after transformation of observed y -values into a form independent of x -values in (S)MATR.

For sprouting frequencies by species, contingency tables by elevation were examined with χ^2 tests. These tests were performed using SPSS ver. 12.0J.

Results

Although data for $W_{fr}-W$ and $W_{fr}-W_r$ allometries were scattered for the two *Populus* species (Figs. 2c, 2d), coefficients of determination for most regressions were fairly high. For W_1-W allometry (Fig. 2a, Table 3), regression coefficients were homogeneous among species ($P>0.05$), although the intercept for *L. kaempferi* was significantly higher than those for the other species ($P<0.01$ in all tests). Regression coefficients of W_r-W allometries (Fig. 2b, Table 3) differed significantly between *L.*

kaempferi and *P. sieboldii* ($P < 0.01$). The intercept for *L. kaempferi* in W_r - W allometry was significantly lower than those for *B. platyphylla* and *P. maximowiczii* ($P < 0.01$ in both tests). Among broadleaved species, regression coefficients and intercepts were homogenous ($P > 0.05$). For W_{fr} - W allometries (Fig. 2c, Table 3), regression coefficients and intercepts were homogenous among species ($P > 0.05$ for both). Regression coefficients for W_{fr} - W_r allometries (Fig. 2d, Table 3) were also homogeneous among species ($P > 0.05$). The intercept for *L. kaempferi* was, however, significantly higher than those for *B. platyphylla* and *P. sieboldii* ($P < 0.01$ for both). The intercept for *P. maximowiczii* was the lowest among species.

The sprouting ratios for *L. kaempferi* were 0% for all plots. The ratios for the remaining study species ranged from 50 to 100% (Table 4). For all elevations, sprouting frequencies depended on species ($P < 0.01$ for all plots), and were significantly larger than expected values for broadleaved species and smaller for *L. kaempferi* ($P < 0.01$ for all plots, Table 4).

Discussion

Variation of allocation patterns among tree organs depends mostly on species identity (Canham et al. 1996; Poot and Lambers 2003; Silla and Escudero 2004). Measurement of differences among allometries revealed W_1 of *L. kaempferi* were the largest among the species studied whereas W_r was the smallest (Figs. 2a, 2b, Table 3). W_{fr} - W allometries were,

furthermore, homogeneous among the species (Fig. 2c, Table 3). We expected larger W_r and W_{fr} for *L. kaempferi* among the species examined, because a high root-to-shoot ratio is usually a response to nutrient-poor conditions (Ericsson 1995; Sack and Grubb 2002; Kaakinen et al. 2004). This expectation was not supported by allometric differences among the species, however. It is concluded that dominance differences among the four tree species on Mt Komagatake were not explained by variations in allometric relationships among the species. We suggest, however, that this conclusion probably resulted from differences between the survival strategies of *L. kaempferi* and broadleaved species. Sprouting ratios in plots at 500, 600, and 700 m a.s.l. were higher for broadleaved species (50–100%) than for *L. kaempferi* (0%; Table 4). We believe, therefore, that sprouting behavior is important for survival of broadleaved species assappling—large root mass (W_r) seems to act as a significant storage organ contributing to sprouting of broadleaved species (Sakai et al. 1997; Bond and Midgley 2001), although we did not examine the relationship between sprouting ability and root mass for the study species on Mt Komagatake. For tree saplings, an increase in total nonstructural carbohydrate reserves (Canham et al. 1999) and increased allocation to roots (DeLagrange et al. 2004) result in higher survival rates under harsh growing conditions. Total nonstructural carbohydrate reserves in roots are, moreover, larger in deciduous broadleaved species than in coniferous species (Kobe 1997).

Although allometric relationships for two *Populus* species were scattered (Fig. 2), possibly because of sampling of saplings of *P. sieboldii*,

of sprout-origin, we found no distinctive difference among allometric relationships for organs among broadleaved species (Table 3). Allocation patterns of *L. kaempferi* differed markedly from those of broadleaved species, however. The most important trait of *L. kaempferi* that is related to its dominance on Mt Komagatake is its great ability to increase leaf mass under unsuitable growing conditions. This trait may result in large photosynthetic production of *L. kaempferi* compared with the other species, because photosynthetic capacity (light-saturated photosynthesis) was homogenous among *L. kaempferi*, *B. platyphylla*, and *P. maximowiczii* saplings on Mt Komagatake (unknown for *P. sieboldii*; Sasaoka et al. 2000). In contrast, broadleaved species seem more vulnerable to harsh site conditions, but maintain populations by high sprouting ability sustained by a large root mass. Plant characteristics such as physiological (e.g. photosynthetic and nutrient absorption rates) and morphological (e.g. specific leaf area) traits and tissue longevity are, however, also closely related to plant adaptation to harsh growing conditions (Chapin et al. 1993; Berendse 1994; DeLagrange et al. 2004; Silla and Escudero 2004). It is important to investigate these different plant traits and allocation pattern to examine plant adaptation to harsh conditions.

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Figure Legends

Fig. 1. Map of the study site and plot locations on Mt Komagatake, Hokkaido, northern Japan.

Fig. 2. Allometric relationships among saplings on Mt Komagatake: *filled circles*: *L. kaempferi*, *open squares*: *B. platyphylla* var. *japonica*, *pluses*: *P. maximowiczii*, *open triangles*: *P. sieboldii*. *Solid lines*, *dotted lines*, *broken lines with dots*, and *broken lines* represent regressions for *L. kaempferi*, *B. platyphylla*, *P. maximowiczii*, and *P. sieboldii*, respectively. Data from 500, 600, and 700 m a.s.l. were pooled by species. Abbreviations; W : individual total mass, W_l : leaf mass, W_r : root mass, W_{fr} : fine root mass.

Table 1 General description of stands investigated (modified from Sasaoka *et al.* 1999)

Elevation (m)	Density ^a (ha ⁻¹)	Canopy height ^b (m)	BA ^c (m ² ha ⁻¹)	Dominant species (% BA)	Canopy closure (%)
500	2111	6.1	7.8	Lk (59)	40
600	1538	3.1	2.3	Lk (92)	15
700	600	2.7	0.8	Lk (80)	5

Lk: *Larix kaempferi*.

^a Tree density taller than 0.5 m.

^b Mean height of the highest 10% of trees.

^c Basal area at ground level.

Table 2 General description of saplings sampled

Species	Elevation (m)	N ^a	Height ^b (cm)
Lk	500	5	41.6±21.6 (15–80)
	600	5	
	700	5	
Bp	500	5	48.8±21.6 (10–80)
	600	5	
	700	5	
Pm	500	0	35.7±17.2 (9–66)
	600	5	
	700	5	
Ps	500	6	35.6±11.1 (20–56)
	600	5	
	700	5	

Abbreviations; Lk: *Larix kaempferi*, Bp: *Betula platyphylla* var. *japonica*,
Pm: *Populus maximowiczii*, Ps: *Populus sieboldii*

^a Number of saplings

^b Mean±standard deviation with range (min.-max.) in parentheses

Table 3 Allometric regressions ($\log_{10}y = a + b \log_{10}x$) for saplings on Mt Komag

x	y	Species	a	b	r^2
W	W_l	Lk	-0.283 ^a	0.924(NS)	0.987 ^{**}
		Bp	-0.595 ^b	0.859(NS)	0.918 ^{**}
		Pm	-0.699 ^b	0.869(NS)	0.923 ^{**}
		Ps	-0.673 ^b	0.865(NS)	0.828 ^{**}
W	W_r	Lk	-0.556 ^a	0.944 ^a	0.991 ^{**}
		Bp	-0.357 ^{b,c}	1.011 ^{a,b}	0.967 ^{**}
		Pm	-0.394 ^{b,c}	1.051 ^{a,b}	0.952 ^{**}
		Ps	-0.377 ^c	1.101 ^b	0.980 ^{**}
W	W_{fr}	Lk	-0.989(NS)	0.778(NS)	0.932 ^{**}
		Bp	-1.202(NS)	0.970(NS)	0.836 ^{**}
		Pm	-1.401(NS)	1.048(NS)	0.498 [*]
		Ps	-0.957(NS)	0.660(NS)	0.570 ^{**}
W_r	W_{fr}	Lk	-0.531 ^a	0.825(NS)	0.919 ^{**}
		Bp	-0.857 ^b	0.958(NS)	0.816 ^{**}
		Pm	-1.009 ^{a,b}	0.998(NS)	0.506 [*]
		Ps	-0.728 ^b	0.597(NS)	0.562 ^{**}

Regressions are significant at 1% (^{**}) and 5% (^{*}) levels

Abbreviations; W : individual mass, W_l : leaf mass, W_r : root mass, W_{fr} : fine root

NS: not significant, abbreviations for species: see in Table 2

^{a,b,c} significant differences ($P < 0.05$ or $P < 0.01$: see in text)

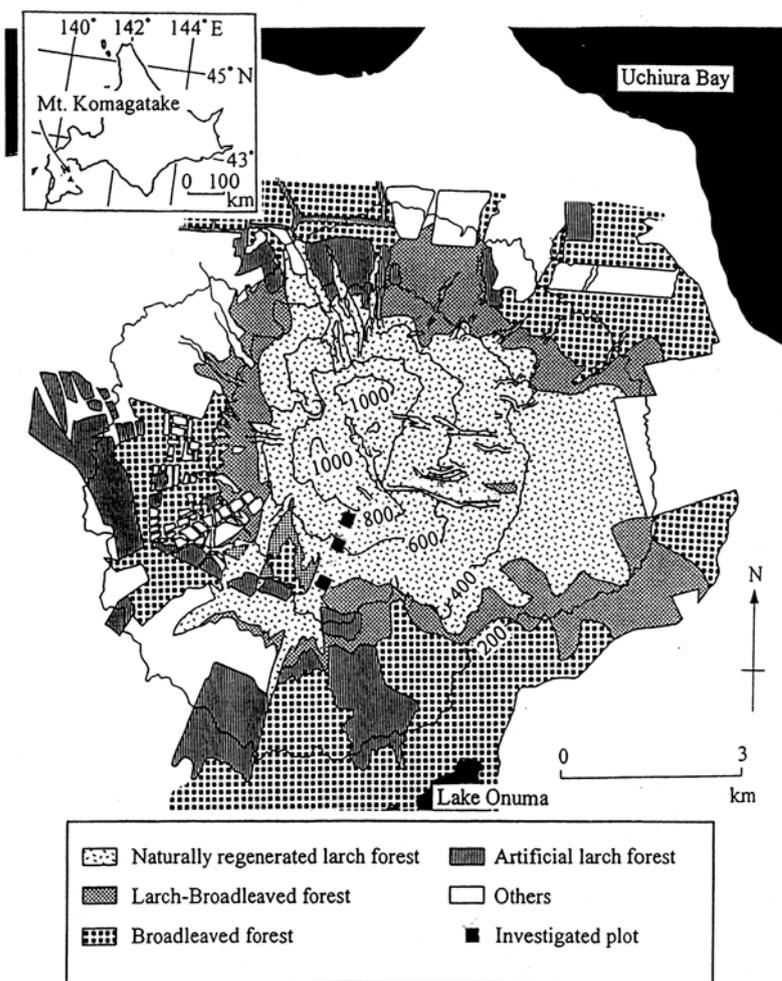
Table 4 Sprouting ratio by species

Species	Elevation (m)	Sprouting ratio (%)	N ^a
Lk	500	0	100
	600	0	83
	700	0	39
Bp	500	80	46
	600	66	38
	700	92	25
Pm	500	50	6
	600	93	15
	700	94	161
Ps	500	73	15
	600	100	5
	700	75	20

For explanation of abbreviations see Table 2

^aNumber of saplings observed

Shibuya et al. Fig. 1



Shibuya et al.: Figure 2

