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Factors affecting the vertical distribution of *Betula platyphylla* var. *japonica* and *Betula ermanii* on Mt. Neko in Nagano Prefecture, Japan

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Betula platyphylla var. *japonica* and *Betula ermanii* segregate vertically at an elevation of approximately 1,850 m on Mt. Neko in Nagano Prefecture, Japan. *B. platyphylla* var. *japonica* and *B. ermanii* were the dominant species below and above this altitude, at which the mean-annual and growing-season air temperatures were 4°C and 14.1°C, respectively. Based on a modification of Kira's warmth index which employs cumulative temperature represented as °C day, leaf unfolding in both species was observed to be initiated at 58°C day and 169°C day, respectively. In 1996, leaf unfolding was initiated on 18 May in *B. platyphylla* var. *japonica* (+/-6 days) and on 5 June in *B. ermanii* (+/-8 days), shortly after the last frost which occurred on 5 May 1995 above 1,850 m; below this elevation there was no risk of frost at the time. At elevations above 1,850 m, the unfolded leaves of *B. platyphylla* were damaged by late frost, while *B. ermanii* escaped injury because the leaves were still protected by winter buds. The optimum temperature for seed germination in both *B. platyphylla* and *B. ermanii* was 30°C. Temperature alternation from 10 to 30°C and moist storage of seeds at 4°C (stratification) prior to incubation increased germination rates in both species. The seedlings of *B. ermanii* had a greater survival rates than those of *B. platyphylla* var. *japonica* when planted above 1,850 m. Comparisons of the timing of leaf unfolding and the latest frost at a site appeared to be the main factors affecting the vertical distribution of these species.

Key words: *Betula ermanii, Betula platyphylla* var. *japonica,* germination, leaf phenology, vertical distribution

INTRODUCTION

Studies on the vertical segregation of plants in Japan were initiated by Imanishi (1949) in the North Alps of central Japan. Thereafter, Takahashi (1962) described the vertical distribution of mountain forests in Central Honshu, and more recently Ohsawa (1984) examined the distribution of forest communities at different elevations on Mt. Fuji. These studies mainly focused on the floristic composition and structure of the forests. *Betula platyphylla* var. *japonica* (Miq.) Hara and *Betula ermanii* Cham. segregate vertically at an elevation of 1,850 m on the southern slope of Mt. Neko in Nagano Prefecture, Japan. The altitudinal change in floristic composition on Mt. Neko was studied first by Tanouchi and Hayashi (1981), but no causative relationship between environmental parameters and the altitudinal distribution of *B. platyphylla* var. *japonica* and *B. ermanii* was discussed. We have attempted to clarify the factors affecting the vertical distribution of these species by relating ecological

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traits such as leaf phenology and seed germination to environmental conditions on the mountain (Kikuzawa 1983, Kudo 1995, Chuine and Beaubien 2001). In this study, those ecological characteristics affecting to the thermal environment of these species were examined through germination, leaf phenology, and the growth of seedlings (Raulier and Bernier 2000)

MATERIALS AND METHODS

Study area

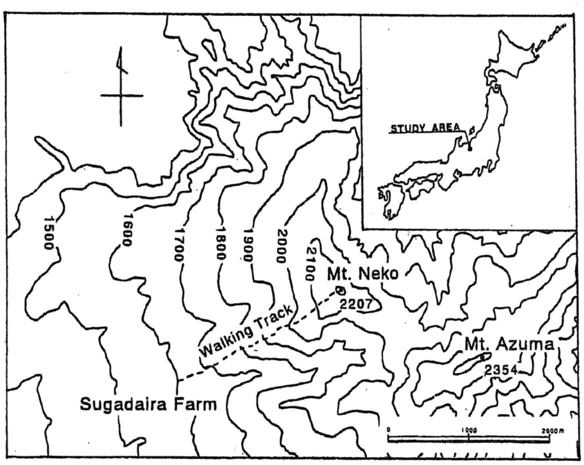

Fig. 1. Location of the study area in Sugadaira, Nagano Prefecture, Japan.

Sugadaira (36°31' N, 138°21' E), located at an elevation of 1,320 m (Fig. 1), has a mean annual air temperature and total annual precipitation of 6.5°C and 1,102 mm, respectively. The area lies in the cool temperate zone and supports a climax forest of summer-green, broad-leaved trees dominated by *Fagus crenata* Blume. Above around 1,850 m, these species are replaced by evergreen conifers such as *Abies veitchii* Lindl. Most of the area in Sugadaira is occupied by secondary forest consisting of *Quercus crispula* Blume, *Pinus densiflora* Sieb. et Zucc., *B. platyphylla* var. *japonica* and *B. ermanii* interspersed with plantations of *Larix leptolepis* Sieb. et Zucc. Gordon, farms, ski slopes and cultivated lands (Tanouchi and Hayashi 1981). The soils are Andosols, which have developed on volcanic deposits from Mt. Azuma and Mt. Neko (2,207 m) slopes gently to the south with steeper slopes on its northern flank, which are associated with the old crater. Distinct forest zones can be observed at different elevations on the mountain, with *P. densiflora* being dominant at 1,300-1,500 m. At 1,500-1,800 m, the forests are mainly composed of *B. platyphylla* var. *japonica* which is then replaced on the upper slopes by *B. ermanii* (1,800-2,100 m). *A. veitchii* is the dominant species at 2,000-2,100 m. Tanouchi and Hayashi (1981) suggested that this zonation reflected the interaction between the forests and environmental conditions and human activities. The study site was located on the southern slope of Mt. Neko, extending from 1,600 m to the summit.

Vegetation survey

Floristic composition, trunk diameter at breast height (DBH) for trees larger than 1 cm diameter, and tree height was assessed in 10 × 10 m quadrats located at elevations of 1,750, 1,800, 1,850, 1,900, 2,000, 2,100, and 2,200 m. Additional quadrats were sampled at 1,845 m and 1,855 m, in the transitional zone between *B. platyphylla* var. *japonica* and *B. ermanii*. The trunks of both *B. platyphylla* var. *japonica* and *B. ermanii* often sprouted from stem bases, and in this survey, such sprouts were considered to be single trees. Field work was conducted from 8-20 September 1995.

Temperature measurements

Auto-recording thermometers (Corner System LcII; Corner System Co Ltd. Sapporo, Japan) were used to measure air and soil temperatures. These were placed in an open area on the summit of Mt. Neko (2,200 m) and at elevations of 1,700 m (mid-elevation of the *B. platyphylla* var. *japonica* zone), 1,850 m (boundary between the *B. platyphylla* var japonica and *B. ermanii* zones) 1,960 m (mid-elevation of the *B. ermanii* zone). Above-ground air temperature (1.3 m) and soil temperature (10 cm depth) were recorded at hourly intervals from June 1995 to August 1997. During the last 10 days of August 1997, soil temperature at a depth 2 cm was also measured at 1,850 m.

Germination tests

Germination tests were conducted on *B. platyphylla* var. *japonica* and *B. ermanii* seeds collected at elevations of 1,750 m (28 September 1995) and 2,050 m (18 September 1995). The seeds of both species were incubated under constant temperature conditions at 10, 15, 20, 25, and 30°C, and under alternating temperature conditions at 10/20, 15/25, and 10/30°C (16 hours in low temperature, 8 hours in high temperature). Germination was conducted under a 16L:8D regime for 40 days, with the light intensity in the chamber being 80 mol m^{-2} s^{-1} for

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the duration of the experiment. Forty seeds were sown in each Petri dish with five replicates performed for both species and seedling emergence was monitored daily. In addition, we examined the germination of seeds which stratified at 4°C for 134 days.

Measurement of seedling growth

Twelve 50-day-old *B. platyphylla* var. *japonica* seedlings and four *B. ermanii* seedlings were planted at uniform distances in a deep plastic pot (10 cm ×Φ9 cm) with four replications. A mixture of a typical Andosol and immature soil (*Akadama-tsuchi*) was used for cultivation. The seedlings were grown under temperature conditions of 10, 14, 20, and 30°C under constant light (60 mol m^{-2} s^{-1}) for 40 days. Seedlings were harvested on days of 21, 47, 67, and 90 after planting and survival rates were calculated before weighing after drying in an oven for 2 days at 70°C. In order to assess seedling establishment under field conditions, we transplanted ten 30-day-old seedlings of each species to elevations of 1,600, 1,850, 2,050, and 2,200 m on 21 July 1997. The seedlings were planted in unglazed pots (Φ14 cm × 14 cm) with the same soil as the that used in the laboratory experiments. We recorded seedling survival for each pot at each altitude on 29 August and 8 October, which were 52 and 92 days after planting, respectively.

Observation of leaf phenology

Leaf unfolding in *B. platyphylla* var. *japonica* and *B. ermanii* trees growing in close proximity was related to a modified Kira's warmth index (WI) (Kojima et al. 2003), which was calculated as the sum of the mean daily temperatures above 5°C expressed as °C day. The annual WI was calculated by summing the mean daily temperature from January 1 for each year. The stages of leaf unfolding identified were as follows (Kojima et al. 2003):

L0: winter bud.

L1: a bud swells and its end splits so that green tissues are exposed.

L2: distal end of leaf open and leaf unfolding has begun.

L3: joint of first leaves opens and a clear leaf shape can be identified.

L4: second leaves begin unfolding.

L5: all leaves completely unfolded and maximum leaf area attained.

RESULTS

Vegetation

Table 1 shows the floristic composition of selected elevations on Mt. Neko. Species dominance of trees changed from *B. platyphylla* var. *japonica* to *B. ermanii* at 1,850 m. The shrub stratum at higher elevations was comprised mainly of *Vaccinium vitis-idaea* Linn. and *Salix reinii* Franch. et Savatit while *Rhododendron japonicum* (A Gray) Suringer, *Sasa senanensis* Franchet et Savatier Rehder var. *senanensis* and *Miscanthus sinensis* Anderss were common at lower elevations. At higher elevations, *Vaccinium uliginosum* Linn was abundant in the shrub layer. *S. senanensis* was the most dominant herbaceous species at all elevations. Except for the tree species, no marked changes in floristic composition were observed at 1,850 m in the transitional zone between the *B. platyphylla* var. *japonica* and *B. ermanii* communities. The change in the relative frequency of *B. platyphylla* var. *japonica* and *B. ermanii* and the abrupt transition in dominance at 1,850 m are shown in Fig. 2. From 2,000 to 2,100 m *B. ermanii* constituted the canopy tree species, but at the summit it grew in association with *A. veitchii* and *A. mariesii* Masters. At around 1,750 m, *Salix bakko* Kimura and *Salix commixta* Hedl. appeared in the understory, resulting in a slight decrease in the relative frequency of *B. platyphylla* var. *japonica.*

The changes in DBH and tree density for *B. platyphylla* var. *japonica* and *B. ermanii* with elevation are shown in Fig. 3. The DBH of most trees ranged between 1 cm and 12 cm, with the density of *B. platyphylla* var. *japonica* decreasing with elevation while that of *B. ermanii* increased. The trees of *B. platyphylla* var. *japonica* have not distributed in the site above 2,000 m. The change in DBH versus tree height at different elevations for *B. ermanii* and *B. platyphylla* var. *japonica* is presented in Fig.

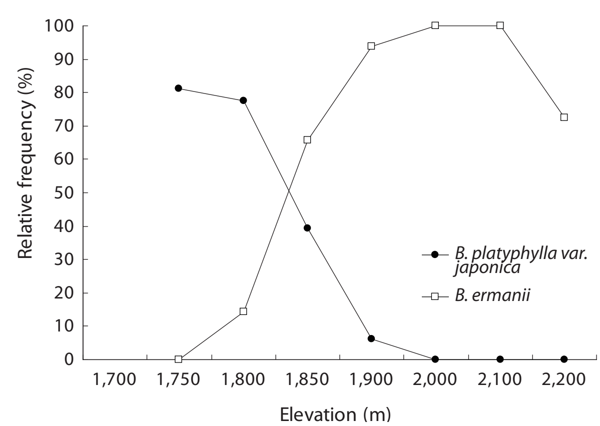

Fig. 2. Relative frequency of *Betula ermanii* and Betula *platyphylla* var. *japonica* at different elevations on Mt. Neko.

Table 1. Floristic composition of the study sites on Mt. Neko

Elevation (m)	**1,750**	**1,800**	**1,845**	**1,850**	**1,855**	**1,900**	**2,000**	**2,100**	**2,200**
Tree height (m)	**4-9**	**4-8**	**4-9**	**4-9**	**4-9**	**4-8**	**4-8**	**> 2**	**> 2**
Percent cover (%)	**70**	**50**	**30**	**50**	**70**	**70**	**50**	**30**	**40**
Shrub height (S) (m)	**1-4**	**1-4**	**1-4**	**1-4**	**1-4**	**1-4**	**1-4**	**1-2**	**0.5-2**
Percent cover (%)	**40**	**30**	**40**	**30**	**20**	**15**	**20**	**10**	**100**
Herb (H)									
Percent cover (%)	**90**	**70**	**90**	**80**	**95**	**100**	**100**	**100**	
Coverage of Tree *									
Betula ermanii		1	2	3	4	4	3	3	3
Betula platyphylla var. *japonica*	3	3	2						
Abies veitchii						+	+		1
Abies mariesii									2
Salix bakko	1								
Coverage of shrub layer*									
B. ermanii		+	2	2	+	2	1		
B. platyphylla var. *japonica*	3	2	3	1	+	+			
Sasa senanensis									5
Salix. reinii	1			+			2	+	
Sorbus commixta		+						+	
Vaccinium smallii				+				+	
S. bakko	1	+		+	+				
Rhododendron japonicum		+	1		+				
Malus sieboldii		+							
Coverage of herb layer*									
S. senanensis	4	4	5	4	5	5	5	4	
R. japonicum	2	1	1	1	1	1	+	+	
S. reinii	1		1				+	3	
Pyrola incarnata		+	+				1	1	
Vaccinium uliginosum							+	1	
Vaccinium vitis-idaea							+	1	
Shortia soldanelloides						+	+	1	
Ixeris dentata								+	
Coptis trifoliolata								+	
Solidago virga-aurea var. *asiatica*								+	
Maianthemum dilataum								+	
Lastrea phegopteris								+	
Calamagrostis langsdorffii								+	
Convallaria keiskei								+	
B. ermanii								+	
V. smallii								+	
Scabiosa japonica							+	+	
Prunus nipponica							+	+	
Astilbe thunbergii							+	+	
Gentiana triflora							+	+	
Gentiana scabra		+					+	+	
Osmunda lancea		+	+					+	
Gaultheria miqueliana			1	1			+	+	
S. commixta							+		
Rosa davurica							+		
Polygonum cuspidatum			+	+	+				
Pteridium aquilinum	1	+	2	+	+				
Athyrium yokoscense		+	+			+	+		
Carex chinoi		+			+	+			
Betula platyphylla var. *japonica*					+				
Carex lanceolata			+						
Miscanthus sinensis	+	+	1						

* Criteria of coverage is Penfound-Howard modified by Numata (1986).

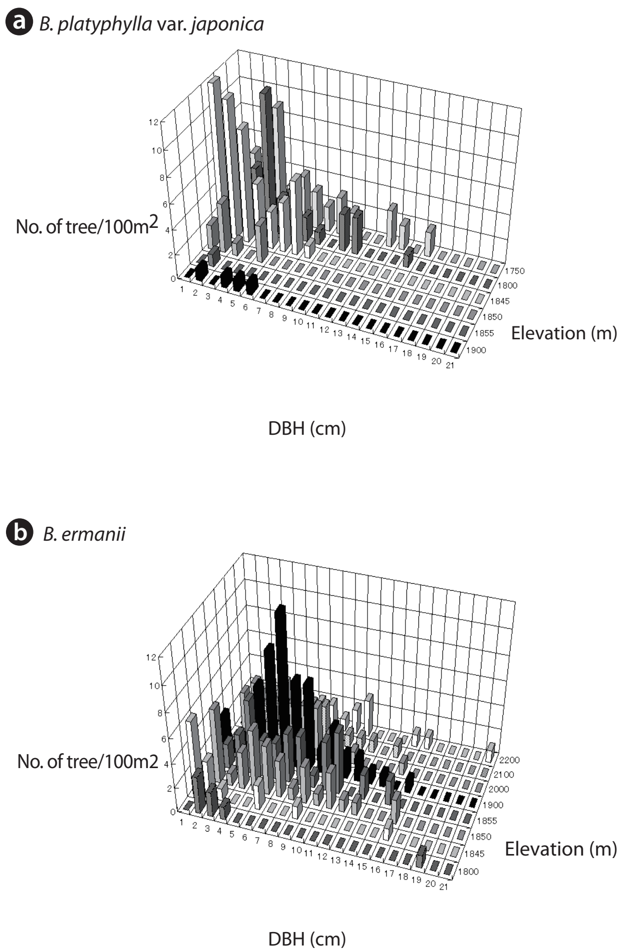

Fig. 3. Relationships between diameter at breast height (DBH) and elevation in Mt. Neko for *Betula ermanii* (a) and *Betula platyphylla* var. *japonic* (b)

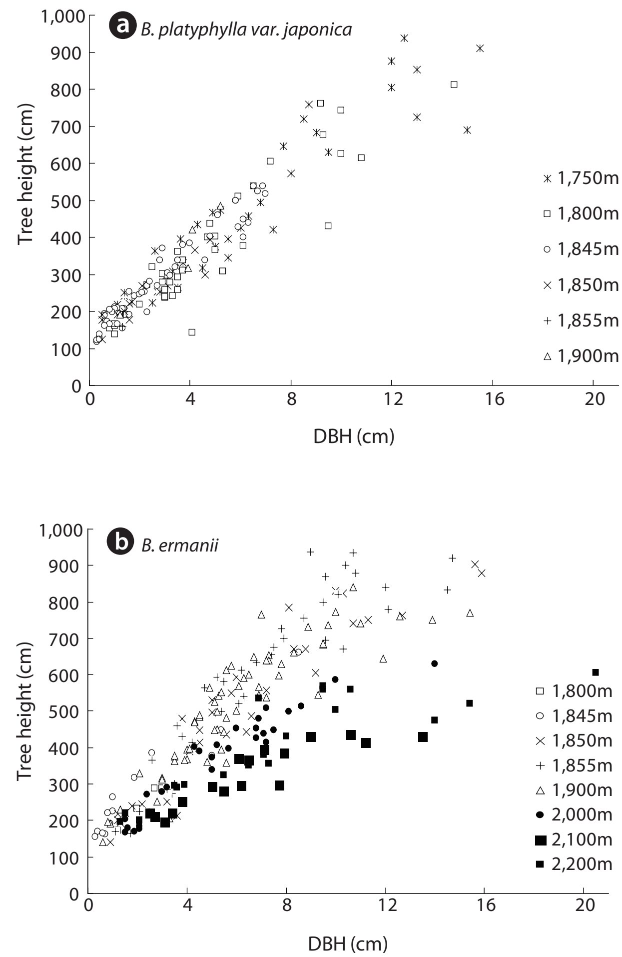

Fig. 4. Relationship between tree height and diameter at breast height (DBH) of *Betula ermanii* (a) and *Betula platyphylla* var. *japonica* at different elevations.

4. The ratio of tree height to DBH was more variable in *B. ermanii* than *B. platyphylla* var. *japonica,* particularly for larger trees. Thus, *B. ermanii* trees with DBHs exceeding 12 cm ranged between about 4 m to 9.5 m in tree height compared to about 7 m to 9.5 m for *B. platyphylla* var. *japonica.* The plasticity in tree growth form of *B. ermanii* was greater than that of *B. platyphylla* var. *japonica.* At the elevation above 2,100 m, the ratio of tree height to stem diameter of *B. ermanii* showed the small value markedly compare to the trees inhabiting in the lower elevations. This suggests an adaptive trait for mountain environments including strong wind.

The rate of sprouting from stumps was 17-80% for *B. ermanii* compared to 33-61% for *B. platyphylla* var. *japonica,* and this was not significant ($P < 0.05$).

Air and soil temperatures

The mean annual temperatures for each elevation were 5.0°C in 1,700 m, 4.0°C in 1,850 m, 3.1°C in 1,950 m and 1.5°C in 2,200 m. The annual average, average highest and average lowest temperatures, as well as the soil temperatures at a depth of 10 cm in growing season from April to September over the elevation range 1,700 to 2,200 m are shown in Fig. 5. Mean air temperature declined linearly with elevation at a lapse rate of 0.7°C per 100 m. In 1996, the mean air temperature during growing season at 1,850 m was 14.1°C

The relationship between mean annual temperature at a given elevation on Mt. Neko and at the Sugadaira Montane Research Centre at Tsukuba University (SMRCT) at 1,320 m was estimated by the following equation:

$$T_a = (T_b + 1.65) - 0.007\,(A - 1320) \quad (1)$$

Where, T_a: mean annual temperature on Mt. Neko (°C)
T_b: mean annual temperature measured at SMRCT (°C)
A: elevation (m)

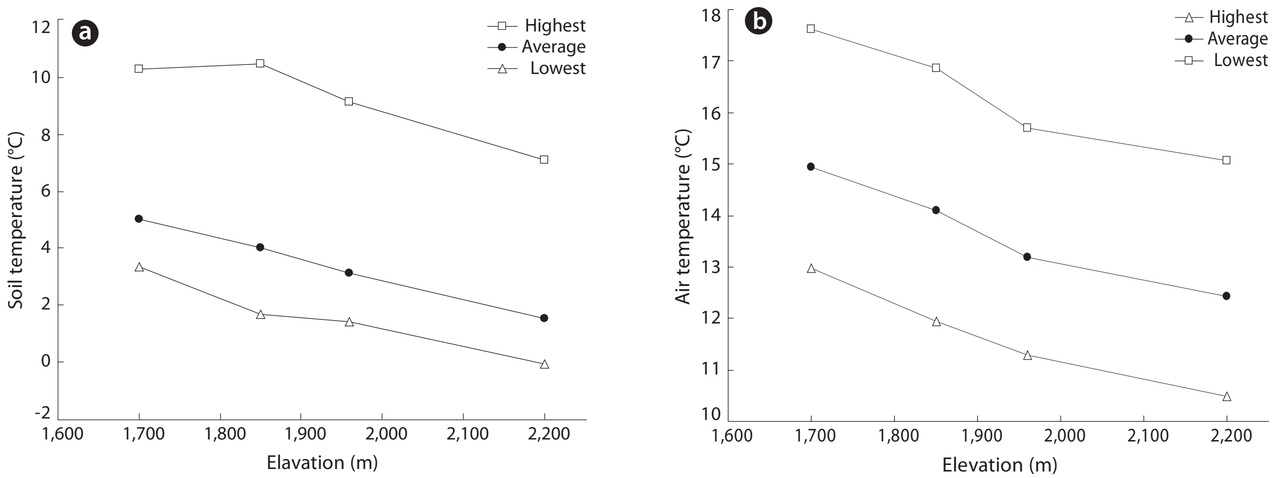

Fig. 5. Changes of temperatures in mean annual, average maximum and average minimum in air (a) and soil at 10 cm depth (b) from June to October, 1996 in the slope of Mt. Neko.

Given the strong correlation between the temperatures at both sites ($r = 0.98$) this equation was used to estimate the mean air temperature at any elevation using the measured values obtained at SMRCT. Using this method, the mean annual temperature at 1,850 m was estimated to be 4°C and 14.1°C during growing season between 1991 and 1996. These findings closely corroborated the values measured in 1996. Average annual minimum and maximum air temperatures also decreased with elevation, being 10°C and 20°C, respectively.

Mean air temperature (T_a) and mean soil temperature (T_s) at depths of both 2 cm and 10 cm were strongly correlated at all elevations. For example, at 1,850 m, soil and air temperatures could be represented as follows:

$$T_{s(10\ cm)} = 0.88\ T_a + 3.02 \qquad r = 0.97 \qquad (2)$$

$$T_{s(2\ cm)} = 0.90\ T_a + 4.48 \qquad r = 0.87 \qquad (3)$$

Similar correlation coefficients were obtained for all elevations. We used equation (3) to elucidate which soil temperature conditions where important for seed germination. At 1,850 m, the difference between the mean daily air and soil temperatures at a depth of 2 cm were ≥ 10°C for 25 days, ≥ 15°C for 17 days and ≥ 20°C for 5 days for during May to October 1996. The average daily difference in soil temperature was 15°C at 1,850 m.

Germination

The germination rates of *B. platyphylla* var. *japonica* and *B. ermanii* under different temperature regimes are given in Table 2. For both species, the maximum germination rate at a constant temperature was observed at 30°C when 74.0% and 42.5% of *B. platyphylla* var. *japonica* and *B. ermanii* germinated, respectively. At a constant temperature of 10°C, only 0.5% of the *B. platyphylla* var. *japonica* germinated. No seeds of *B. ermanii* germinated below 20°C. Indeed, under the same temperature conditions, germination *B. platyphylla* var. *japonica* was consistently higher than that observed in *B. ermanii*. Under the condition of alternating temperature, 77-89% of *B. platyphylla* var. *japonica* germinated. For *B. ermanii*, 82% of seedlings germinated under the 10-30°C regime. The germination rates after cold stratification at 4°C are shown in Table 3. Stratification greatly promoted the germination in both species, but was particularly effective for *B. ermanii* in which 66% and 43% of seedlings germinated under constant temperatures of 15°C and 20°C, respectively.

Seedling growth

The dry weight of the *B. ermanii* and *B. platyphylla* var. *japonica* seedlings grown under different temperature conditions is given in Fig. 6; both species showed enhanced growth at higher temperatures. The relative growth rates (RGRs) at 14.1°C (the mean annual temperature at 1,850 m during the growing season) were 0.031 g/day for *B. platyphylla* var. *japonica* and 0.029 g/day for *B. ermanii*, respectively, and these values did not differ significantly. The percentage survival of both species at constant temperatures of 10°C and 14°C and under natural conditions at different elevations on Mt. Neko are shown in Table 4a and 4b. The percentage survival of *B. platyphylla* var. *japonica* and *B. ermanii* seedlings was 50%

Table 2. Germination rates (%) of *Betula platyphylla* var. *japonica* and *Betula ermanii* with standard errors

	Germination rate and standard error	
Temperature (°C)	*B. platyphylla* var. *japonica*	*B. ermanii*
10	0.5 ± 0.2	0.0 ± 0.0
15	7.5 ± 1.8	0.0 ± 0.0
20	23.0 ± 1.7	0.0 ± 0.0
25	64.0 ± 2.4	13.0 ± 0.9
30	74.0 ± 2.1	42.5 ± 2.0
10/20*	77.0 ± 1.2	29.0 ± 4.5
15/25*	89.0 ± 1.5	35.0 ± 6.2
10/30*	89.0 ± 0.9	82.0 ± 5.5

*Low temperature, 16 hours; High temperature, 8 hours.

Table 3. Germination rates (%) of *Betula platyphylla* var. *japonica* and *Betula ermanii* with standard errors under stratification of 4°C for 134 days

	Germination rate and standard error	
Temperature (°C)	*B. platyphylla* var. *japonica*	*B. ermanii*
10	0.0 ± 0.0	0.0 ± 0.0
15	56.0 ± 5.2	66.0 ± 7.8
20	79.3 ± 2.8	43.0 ± 8.6
25	92.7 ± 1.0	81.0 ± 4.1
30	92.7 ± 1.2	80.0 ± 1.7
10/20*	90.0 ± 0.8	88.0 ± 1.1
15/25*	88.7 ± 1.4	88.0 ± 2.7
10/30*	96.7 ± 0.7	92.0 ± 0.5

*Low temperature, 16 hours; High temperature, 8 hours.

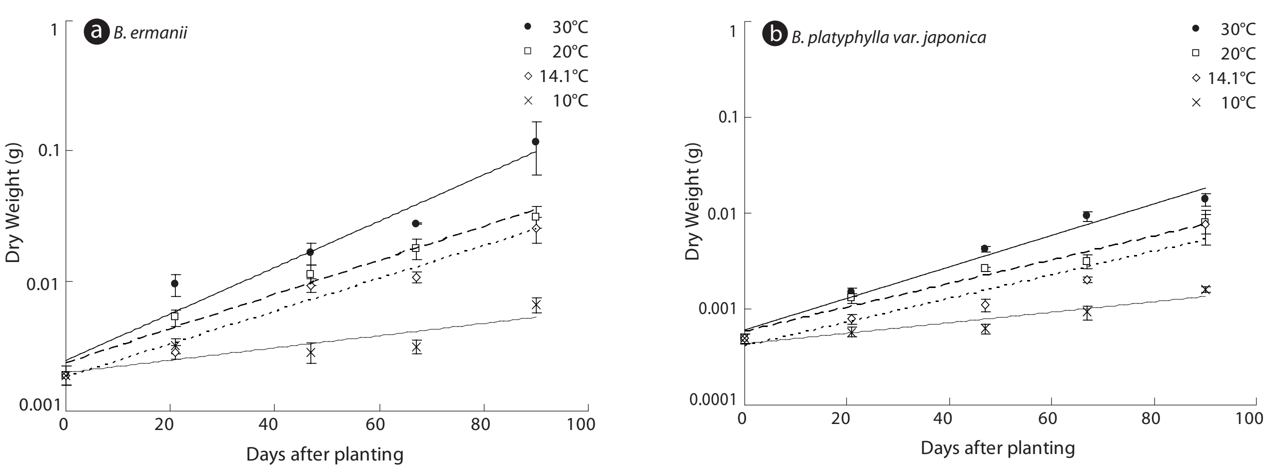

Fig. 6. Growth of seedlings of *Betula ermanii* (a) and *Betula platyphylla*var. *japonica* (b) incubated in a growth chamber at 10, 14, 20 and 30°C. Vertical bars are standard error.

Table 4a. Survival rate (%) of seedlings of *Betula platyphylla* var. japonica and *Betula ermanii* at temperatures of 10°C and14°C in the labotratory

	Survival rate (%)			
	B. platyphylla var. japonica		*B. ermanii*	
	Temperature (°C)			
Days after planting	10	14	10	14
0	100.0	100.0	100.0	100.0
21	66.7	100.0	100.0	100.0
47	16.7	58.3	75.0	100.0
67	33.3	50.0	100.0	75.0
90	50.0	83.3	100.0	100.0

Table 4b. Survival rate (%) of seedlings of *Betula platyphylla* var. *japonica* and *Betula ermanii* on Mt. Neko

	Survival rate (%)			
	Elevation (m)			
	B. platyphylla var. *japonica*			
Days after planting	1600	1850	2050	2200
0	100.0	100.0	100.0	100.0
52	10.0	10.0	30.0	20.0
92	0.0	10.0	10.0	20.0
	B. ermanii			
Days after planting	1600	1850	2050	2200
0	100.0	100.0	100.0	100.0
52	60.0	80.0	90.0	70.0
92	40.0	80.0	90.0	60.0

and 100% at 10°C after 90 days of planting. Conversely, at 14°C, percentage survival among seedlings was 80% in *B. platyphylla* var. *japonica* and 100% in *B. ermanii* (Table 4a). Under a constant temperature of 10°C, 75% of the *B. ermanii* seedlings were still healthy by 47 days after planting. Under natural condition, the survival rates of seedlings of *B. platyphylla* var. *japonica* were 10% at both 1,850 m and 2,050 m and of *B. ermanii* seedlings were 80% and 90% at the same elevations after 92 days of planting (Table 4b).

Leaf phenology

The stage of leaf unfolding in *B. platyphylla* var. *japonica* and *B. ermanii*, and the modified Kira's WI are shown in Fig. 7. Leaf expansion began (stage L2) at 58°C day in *B. platyphylla* compared to 169°C day in *B. ermanii*. *B. platyphylla* var. *japonica* required 240°C day for full leaf expansion (stage L5) compared to 330°C day for *B. ermanii*.

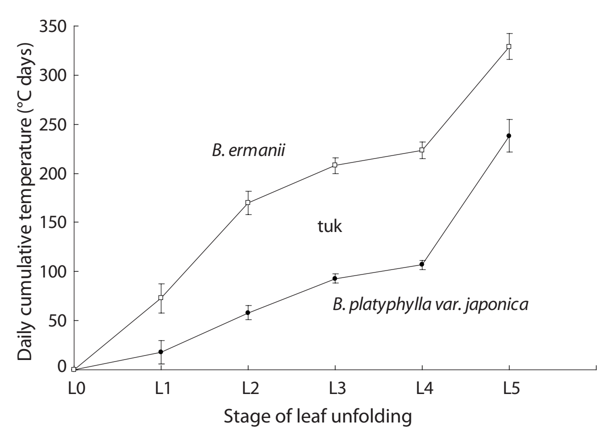

Fig. 7. Leaf unfolding stages related to the modified Kira's warmth index for *Betula ermanii* and *Betula platyphylla* var. *japonica*. Vertical bars are standard error.

B. ermanii thus required higher daily cumulative temperatures for the initiation of leaf unfolding compared to *B. platyphylla* var. *japonica*, which meant that *B. platyphylla* var. *japonica* unfolded its leaves earlier than *B.*

Table 5a. Dates of each leaf unfolding stage with standard errors at 1,850 m on Mt. Neko, 1997

Stage	*Betula platyphylla var. japonica*		*Betula ermanii*	
L1	29 Apr	± 3.5 days	21-May	± 2.1 days
L2	18 May	± 2.0 days	05-Jun	± 0.9 days
L3	27 May	± 0.6 days	12-Jun	± 0.4 days
L4	29 May	± 2.2 days	13-Jun	± 1.5 days
L5	15 Jun	± 3.3 days	26-Jun	± 3.2 days

Table 5b. Dates of late spring frosts and associated minimum air temperature at 1,850 m on Mt. Neko, 1997

Date of latest frost	Minimum air temperature (°C)
05 May	-2
06 May	-13
07 May	-4.1
09 May	-2.5
10 May	-1.7
12 May	-0.3
13 May	-1.6
15 May	-1.3

ermanii (Watanabe 1996). However, the WI of L4 stage needed 106°C day in *B. ermanii,* whereas 131°C day *B. platyphylla* var. *japonica*. Leaves of *B. ermanii* thus expanded comparatively quickly once unfolding started and attained full development. Compared to *B. platyphylla* var. *japonica*, it took 15 days longer for *B. ermanii* to pass from the L1 to the L2 stage, but 8 days less to pass from the L4 to the L5 stage (Kojima et al. 2003, Kato and Hayashi 2008).

The dates when each leaf stage was reached at an altitude of 1,850 m are given in Table 5a. The L1 stage when the bud swells and the terminal end splits to expose the green tissues inside was reached on 29 April in *B. platyphylla* var. *japonica* and on 21 May in *B. ermanii*, a difference of more than 20 days. The L2 stage was reached on 18 May in *B. platyphylla* var. *japonica* and on 5 June in *B. ermanii* and the final stage (L5) was attained on 15 June in *B. platyphylla* var. *japonica* and on 26 June in *B. ermanii*.

Table 5b shows the dates of late spring frosts at 1,850 m and the minimum air temperatures on those days. The last frost occurred on 15 May 1997, after the leaves of *B. platyphylla* var. *japonica* had begun to unfold. By this date *B. platyphylla* var. *japonica* was between the L1 and L2 stages, whereas *B. ermanii* was still in the winter bud stage (L0), implying that they escaped the potential damage associated with late spring frost.

The biological characteristics of both species are summarised in Table 6. Briefly, *B. ermanii* germinates and/or grows at temperatures lower than those preferred by *B. platyphylla* var. *japonica.* Cold stratification for seeds and temperature alternation from 10 to 30°C increased germination rates in both species. Non-stratified *B. ermanii* seeds did not germinate below 20°C, while germination occurred in *B. platyphylla* var. *japonica* at temperatures ranging from 10 to 30°C. The seedlings of both species grew best at 30°C. Below 14.1°C the survival rate of *B. ermanii* was higher than that of *B. platyphylla* var. *japonica* under both experimental and field conditions. Leaf unfolding in *B. platyphylla* var. *japonica* commenced after 60°C day of modified Kira's WI before the equivalent 160°C day required for *B. ermanii* (Fig. 7). Finally, it was noted that the ratio of tree height versus DBH in *B. ermanii* varied considerably more than in *B. platyphylla* var. *japonica* with increasing elevation.

DISCUSSION

There are two possible hypotheses for the transition from *B. platyphylla* var. *japonica* to *B. ermanii* on Mt. Neko. The first hypothesis is that any discontinuous environmental conditions, including temperature in particular, exist along the altitudinal gradient. However, no such discontinuity was observed in either air or soil temperature gradients, or in mean air temperatures which decreased linearly with increasing elevation (Fig. 5). Thus, the first hypothesis was not supported by observed environmental conditions.

The second hypothesis was that these species respond differently to the same environmental cues due to their different biological characteristics such as timing of leaf unfolding, seed germination, frost avoidance and tolerance to heavy wind (Table 6) (Maruyama 1978, Linkosalo et al. 2000, Arora and Boer 2005). For example, leaf unfolding was initiated at a modified Kira's WI of 160°C day in *B. ermanii* whereas leaf unfolding in *B. platyphylla* var. *japonica* occurred at 60°C day at the same elevation. In other words, *B. platyphylla* var. *japonica* began leaf unfolding earlier than *B. ermanii* at the same elevation. At sites above 1,850 m, where late-spring frosts were recorded from 5 May until 14 May 1997 and WI was 60°C day, the leaves of *B platyphylla* var. *japonica* were observed to have unfolded whereas the leaves in *B. ermanii* were still in winter buds. This meant that *B. ermanii* could avoid damage due to late frost while *B. platyphylla* var. *japonica* could not. No frosts occurred in the lower zone at this critical point in the growing season, which determines leaf unfolding in *B. platyphylla* var. *japonica*. Thus, the second hypothesis appears to offer a more likely reason for the transition between *B. platyphylla* var. *japonica* and *B. ermanii* at 1,850 m on Mt. Neko.

The principal difference in the vertical distribution of these two species was the timing of leaf unfolding and how this related to the occurrence of late spring frosts. According to field observations, frost damage to the young leaves of *B. platyphylla* var. *japonica* appeared to arrest leaf growth. However, during the same period, the leaves of *B. ermanii* were not damaged because the buds remained in their winter state until the risk of frost had passed.

Kojima et al. (2003) exposed buds of *F. crenata* in the winter bud stage (stage L0) and in early stage of leaf unfolding (stages L2-L3) to artificial frost. While the winter buds were not damaged by the frost and began unfolding normally afterwards, the L2-L3-stage buds did not unfold. This is likely to be the main reason why *B. platyphylla* var. *japonica* cannot become established above 1,850 m. On 5 May 1997, ice crystals were observed to have formed on the ends of upper branches of *B. ermanii* growing above 1,900 m. The frost did not damage the leaves of *B. ermanii* because they were protected by their winter buds, however, the unfolding leaves (stage L3) of *B. platyphylla* var. *japonica* were observed to be damaged.

The seeds of both species were produced in September (Table 6). Only a few seeds of *B. ermanii* germinate in autumn of the current year because they require moist stratification. These seeds contribute to the buried seed population and normally germinate in the following spring. On the other hand, the seeds of *B. platyphylla* var. *japonica* germinate soon after production, as they do not require stratification. The resulting seedlings cannot endure the cold winter conditions at high elevations and therefore cannot become established; in the areas where there is no late frost, such germination behaviour is considered advantageous. The seedlings of *B. ermanii* must be more tolerable for cold environment than that of *B. platyphulla* var. *japonica* because the seeds of former species are heavier than the latter species.

The thick, stunted growth form of *B. ermanii* trees growing near the summit of Mt. Neko, is well adapted to the strong winds and snow conditions (Okitsu and Satomi 1989). This morphological adaptation of trees to wind, which has been reported in several tree species (Larson 1965, Neel and Harris 1971, Lawton 1982), enables *B. ermanii* to survive on mountain summits (Ohsawa 1984)

Table 6. Biological characteristics of *Betula platyphylla* var. *japonica* and *Betula ermanii*

	B. platyphylla var. japonica	*B. ermanii*
Distribution (elevation, m)	1,750-1,850	1,850-2,000
Growth plasticity of tree	Not plasticized	Plasticized
Temperature maximum germination occurred (°C)	30	30
Temperature alternation maximum germination occurred (°C)	Alternate 10/30°C	Alternate 10/30°C
Germination rate cold stratification applied	Promoted	Promoted
Leaf unfolding time (elevation of 1,320 m)	Beginning of May	Beginning of June
Leaf unfolding speed	Slow	Quick
Time attained maximum leaf size	May	June
Time seed matured	September	September
Seed dispersal type	Wind	Wind
Air dried seed weight (g)	0.0906	0.5940
Number of seed in one bunch	817	383
Ratio of wing weight /intact seed weight (%)	16.5	8.1
Daily cumulative temperature for leaf unfolding (°C day)	238	329
No. of day of leaf unfolding (days)	43.4	36.9
No. of day of surplus production (days)	115.8	119.6
No. of day of leaf fall	64.8	28.9

and is an important factor affecting the establishment of the *B. ermanii* zone in Hokkaido (Okitsu 1999). The absence of this form in *B. platyphylla* var. *japonica* further limits the success of this species in high mountain environments.

Taken together, these biological characteristics of *B. platyphylla* var. *japonica* and *B. ermanii* affect the transition between the two species at an elevation of 1,850 m on Mt. Neko, where the mean annual air temperature is 4°C. These same environmental factors, which favour the segregation of *B. platyphylla japonica* and *B. ermanii* at high elevations are also considered to affect the geographic distribution of these two species. Indeed, the 4°C mean annual isotherm passes between Hokkaido and Sakhalin and coincides with the boundaries of their ranges (Kojima 1994). The distribution of *B. ermanii* on Hokkaido is primarily that area where the mean annual air temperature is 4 .

On a large geographic scale, temperature is considered to be the primary environmental factor determining the vertical and horizontal distributions of these species. On a more local scale, the interrelationship between the biological and ecological characteristics of plants and their physical environments affect species segregation within a stand.

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