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Habitat-specific responses of shoot growth and distribution of alpine dwarf-pine (*Pinus pumila*) to climate variation

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Abstract

Alpine dwarf-pine (*Pinus pumila*) is dominant in the alpine regions of Japan, and often forms the krummholz zone of stunted alpine forest. The distribution of *P. pumila* is strongly related to the distribution of snow, and shoot growth is also sensitive to weather conditions. Changes in temperature and snowmelt regimes may well affect the distribution patterns of the krummholz zone. *P. pumila* usually occupies the habitat between the fellfield and snowbed communities, and responses to climate change may differ depending on whether plants are close to the fellfield or the snowbed. We compared the distribution and shoot growth patterns of *P. pumila* close to both surrounding ecosystems in the Taisetsu Mountains, northern Japan. *P. pumila* has expanded its distribution area by 14 % toward both edges over the last 32 years. Annual shoot growth was positively affected by summer temperature and sunshine duration, but negatively related to spring temperature toward the fellfield side. Shoot growth was greater at the southeastern edge of patches, where snowdrifts were formed. The results indicated that shoot growth and distribution area increased in warm summers. However, warm springs might have a negative influence on shoot growth, probably because the earlier reduction in cold-resistance enhances the risk of frost damage in spring close to the fellfield side. This study suggests the importance of understanding the site-specific responses of shrubs to predict the impacts of climate change on alpine ecosystems.

Keywords Alpine, climate warming, *Pinus pumila*, shoot growth, GIS

Introduction

Rapid vegetation changes with global warming are thought to cause the extinction of many species, especially in the arctic and high mountain regions (Grabherr et al. 1994; IPCC 2007). Increases in shrub biomass, cover, and abundance have been observed in multiple arctic, high-latitude and alpine tundra ecosystems over the past century (Myers-Smith et al. 2011). Upward shifts of tree lines are reported in several montane and sub-alpine regions (Kullman 2002; Wang et al. 2006; Danby and Hik 2007; Peñuelas et al. 2007). The invasion and expansion of woody plants with large biomass and tall canopy structures may have serious impacts on tundra and alpine vegetation (Wilson and Nilsson 2009; Pajunen et al. 2011), because most tundra plants are sensitive to shading stress (Chapin et al. 1995). Furthermore, the reduction in abiotic stress because of global warming may change the biological interactions among plant species from facilitative to competitive relationships (Choler et al. 2001). This may cause a decrease in species diversity through intensive interspecific competition. Therefore, the dynamics of shoot growth and the canopy expansion of shrubs are important issues in assessing global change impacts on alpine ecosystems.

The zonal distribution of *Pinus pumila* (Pallas) Regel, an alpine dwarf-pine, is a characteristic physiognomy of alpine vegetation in Japan (Tatewaki 1958). Biomass accumulation of *P. pumila* at the krummholz zone (Tranquillini 1979) is extremely large in alpine ecosystems (Kajimoto 1989), and its productivity is estimated as being 10 times larger than other alpine plant communities (Okitsu 1985). Therefore, changes in the growth and distribution of *P. pumila* may cause serious impacts to the structure and diversity of alpine ecosystems. Previous studies have reported that the net photosynthetic rates of current needles were high in temperatures of 10–15 °C (Kajimoto 1990), and that the current shoot elongation was positively related to the previous summer temperature (Sano et al. 1977; Takahashi 2003;

Wada et al. 2005). Annual shoot elongation has tended to increase in the mountain regions of the main island of Japan, probably in response to recent climate warming (Wada et al. 2005; Ozeki et al. 2011). In contrast to the field reports, a vegetation dynamics model based on climate change scenarios predicts that the potential distribution area of *P. pumila* will decrease to 14.7–25.0 % of the current suitable area and that *P. pumila* will disappear from many mountain regions in Japan, except for the high mountains in central Japan and Hokkaido (Horikawa et al. 2009). Therefore, it is crucial to understand the relationship between the shoot growth and distribution responses to climatic variation to appreciate the dynamics of *P. pumila* in alpine ecosystems.

Typical alpine vegetation in Japan is classified into fellfield plant communities, snowbed plant communities, and *P. pumila*-dominated communities (Koizumi 1974). In fellfield habitat, the soil surface is exposed throughout the year due to strong winds, and the soil is frozen in the winter and dry in the summer. Thus, plants inhabiting fellfield habitat are required to have high cold and drought tolerance. In the snowbed habitat however, a large accumulation of snow protects plants from freezing temperatures during winter, and snowmelt water maintains moist soil conditions in the summer. However, the length of the growing period is strongly limited due to late snowmelt (Körner 2003). *P. pumila* inhabits the intermediate habitat between the fellfield and snowbed, especially on gentle rocky slopes with moderate snow depth in winter (30–300 cm deep, Okitsu and Ito 1984). The density and plant height of *P. pumila* declines with increasing wind exposure and its growth form changes from zonal to patchy toward the fellfield habitat. Density and plant height tended to be remain stable toward the snowbed but the plant abruptly disappears in typical snowbed habitat probably due to photosynthetic periods that are too short (Okitsu and Ito 1984). Therefore, factors affecting *P. pumila* growth may differ between the fellfield side and snowbed side of the *P. pumila* zone.

The distribution and phenology of alpine plants are strongly affected by snow conditions (Billings and Bliss 1959; Kudo and Ito 1992; Choler 2005; Kudo and Hirao 2006). The effects of global warming on alpine ecosystems include not only increases in plant growth but also an increased risk of frost damage early in the season (Inouye 2008; Wheeler et al. 2014). So far, there has been little attention paid to the significance of frost damage in Japanese mountains, but it needs to be taken into account in the growth and survival of *P. pumila* (Maruta et al. 1996; Ishida et al. 2001; Nakamoto et al. 2012). Frost damage tends to occur more frequently in the fellfield habitat, so climate change may result in different impacts on alpine vegetation depending on their proximity to fellfield and snowbed communities (e.g. Kudo et al. 2010).

The aim of this study is to clarify the growth responses and distribution changes in *P. pumila* during the last 20–30 years in relation to the fellfield and snowbed edges of the *P. pumila* zone, with reference to climate variations. Our specific questions are as follows:

- 1) How has the extent of the distribution area of *P. pumila* been changed in recent years?
- 2) Are environmental factors affecting shoot growth differently depending on proximity to the fellfield or the snowbed edge of the *P. pumila* zone?
- 3) Is there any trend in the direction of the distribution shift? If so, does it reflect the shoot growth pattern between the fellfield side and snowbed side?

Materials and Methods

Study site

This study was conducted in the Taisetsu Mountains (Daisetsuzan National Park) in the central part of Hokkaido, northern Japan (Fig.1). We selected two habitats as research sites, one on the fellfield side and one on the snowbed side of the *P. pumila* zone. The fellfield

tends to not retain snow cover during the winter due to strong winds, whereas the snowbed is covered with thick snow until the middle of summer. The fellfield side habitat (hereafter the HF site) is located on a plateau of 1670–1690 m in elevation close to Lake Hisago, 2 km south of Mt. Kaun-dake (N 43°32', E 142°52'). The snowbed side habitat (hereafter the GS site) is located on a gentle east-facing slope of 1700–1850 m in elevation in the Goshikigahara (N 43°33', E 142°54'; Fig. 1).

The HF site has typical fellfield vegetation composed of dwarf shrubs (*Arctous alpinus* (L.) Niedenzu var. *japonicus* (Nakai) Ohwi, *Loiseleuria procumbens* (L.) Desv., *Diapensia lapponica* (L.) var. *obovata* Fr. Schm. and *Vaccinium uliginosum* (L.)), and lichens (*Cladonia* spp.). In the GS site, snow-meadow vegetation was commonly composed of herbaceous species, such as *Anemone narcissiflora* (L.) var. *sachalinensis* Miyabe et Miyake, *Trollius riederianus* Fisch. Et Mey., and *Saussurea riederi* Herder var. *yezoensis* Maxim. Over recent years, the time of snow melt has become earlier (Kudo and Hirao 2006) and populations of typical snow-meadow species have decreased rapidly since the 1990s in this area, while dwarf bamboos (*Sasa kurilensis* (Rupr.) Makino et Shibata) have increased their distribution area (Kudo et al. 2011). In both sites, *P. pumila* commonly grows as isolated patches of various sizes. The nomenclature follows Ohwi and Kitagawa (1983).

The annual mean air temperature of the HF site was –2.0 °C. Mean temperatures during the summer season were 2.9 °C in May, 8.5 °C in June, 11.6 °C in July, 12.5 °C in August, and 7.8 °C in September (mean values from 2002–2010; Kudo et al. 2011).

GIS analysis

Using aerial photographs provided by the Geospatial Information Authority of Japan (on 25 Sept 1977) and Photec Co. Ltd., Sapporo, Japan (on 3 Sept 2009), changes in the

distribution of *P. pumila* in the HF and GS sites were quantified. Vegetation on these photographs was digitized after orthogonal projection transformation at a ground resolution of 25 cm. For orthogonal projection, we selected large rocks located within the area and used them as ground control points. Clear color photographs taken in September enabled us to discriminate *P. pumila* from other vegetation. All works were conducted using the GIS software ArcMap10.0 (ESRI Inc., Redlands, CA, USA) using the Plane Rectangular XII projection system of the Japanese Geodetic Datum 2000.

The distribution of *P. pumila* was observed within a 25-ha area in the HF site (Fig. 2). *P. pumila* canopies were easily discernible in this site and they were extracted as polygons using non-hierarchical clustering with an ISODATA clustering algorithm, which automatically groups pixels based on the reflectance level of each wavelength (Japan Association on Remote Sensing 2001). Each photograph was classified into 20 groups, and the group categorized as a specific color type was taken to represent *P. pumila*. According to our preliminary analysis for testing the accuracy of the vegetation classification, the Kappa coefficient was 0.96 and 0.82 in 1977 and 2009, respectively. The distribution of *P. pumila* in the GS site was observed within a 50 ha (500 × 1000 m) area (Fig. 2). The canopies of other shrubs and dwarf bamboos were sometimes difficult to distinguish from *P. pumila* canopies using non-hierarchical clustering. Therefore, *P. pumila* canopies were extracted as polygons from each photograph by visual observation in which the difference in vegetation height (using a stereoscope), canopy architecture, and leaf color were evaluated. The area of *P. pumila* was calculated. Extracted polygons were verified by field observations to ensure the accuracy of classifications based on the 2009 photographs. The difference in observation area between the HF (25 ha) and GS (50 ha) sites reflected the topographic features of fellfield and snowbed habitats in this region.

Measurements in the field

The stems and branches of *P. pumila* retain the annual scars of dormant buds over the last 20 years on average. Thus, annual shoot elongation can be obtained by measuring the internodal length between bud-scar marks (Sano 1977, Okitsu 1988, Takahashi 2003). Taking advantage of this characteristic, annual shoot growth over the last 20 years was measured using a digital caliper at the accuracy of 0.1 mm. We randomly selected 24 patches within the 25 ha area in the HF site, and 20 patches within the 50-ha area in the GS site. In each patch, we selected four trunks without physical damage and measured branches facing north, south, east, and west.

Measurements in the GS site were conducted in July 2011 and annual shoot elongation was recorded from 1991 to 2010 because the current shoot growth (in 2011) had not been completed yet. Measurement in the HF site was conducted in September 2012 and shoot elongation from 1993 to 2012 was recorded.

Shoot growth analysis

First, the temporal sequences in annual shoot growth in each habitat over the last 20 years were examined using linear regression, following the standardization of annual shoot elongations within stems (Fig. 3 a). Then, factors affecting shoot elongation were analyzed using generalized linear mixed-effect models (GLMMs) without data standardization.

In the first model, environmental and internal factors related to shoot growth were tested in each habitat. Environmental factors in the GLMM included: (1) summer temperature (mean air temperature from June to August) of the current and previous years; (2) sunshine duration during the summer season of the current and previous years; (3) snowmelt time of the current

year; (4) spring temperature (mean air temperature during April and May) of the current year; and (5) distance from the closest *P. pumila* zone to the specific patches. Shoot growth of *P. pumila* may indicate size-dependency (Takahashi and Yoshida 2009). A previous study reported that the relationship between tree-ring width and shoot elongation of *P. pumila* varied among trees depending on the competitive situation (Yasuda and Okitsu 2012). To eliminate these endogenous factors, therefore, we included (6) patch size; and (7) the length of the stem over the last 20 years (hereafter stem size) as explanatory factors in the GLMM. Patch size, expressed as the canopy projection area, represented total plant size, while stem size represented the ontogenetic and/or growth situation of individual stems. In the GLMM, assigned the number to each patch which we investigated (hereafter patch ID) was included as a random factor, and a Gamma error distribution was assumed with log-link function. To detect the site-specific factors affecting shoot growth in each habitat, the GLMM was performed for each habitat, and factors were selected in each model based on the Akaike information criterion (AIC) in which we adopted the set of factors with the lowest AIC values. There is no long-term meteorological data in the Taisetsu Mountains, so we estimated the previous climatic conditions using the data observed in Nukabira Town (N 43°22.0', E 143°11.5', 540 m elevation; Japan Meteorological Agency 2012) which was the nearest weather station to the HF and GS sites. A comparison of the available temperature records between the HF site and Nukabira Gensenkyo revealed that the temperature lapse rate was – 0.5 °C/100 m elevation. Previous temperatures in the HF and GS sites were calculated using this value. The snowmelt day has been recorded since 1988 at a site with similar snow conditions to the GS site, located approximately 3 km away from Goshikigahara (G. Kudo, unpublished data). We used this record for the analysis of the GS site. Snowmelt time was not included in the GLMM for the HF site because the fellfield-side habitat received only a small amount of snow accumulation during the winter because of exposure to strong winds.

In the second model, we compared the sensitivity of shoot growth to the direction within patches between the HF and GS sites. Direction influences the microenvironment for shoots, such as solar radiation and snow condition, and it may determine the direction of patch expansion. Analysis was performed using a GLMM with a postulated Gamma error distribution with log-link function, in which site (HF, GS) and direction within a patch (N, S, W, E) were set as fixed factors, and patch ID as a random factor. We used the R statistical software version 2.15.2 (R Core Team 2012) for all data analyses. The GLMMs were performed using the function glmer included in the R package lme4 (Bates et al. 2013).

Results

Changes in distribution over the past 32 years

Projection images of *P. pumila* canopies in 1997 and 2009 are shown in Figure 2. In the HF site (25 ha), the area occupied by *P. pumila* was 13.1 ha (52 %) in 1977, and 15.0 ha (60 %) in 2009. In the GS site (50 ha), the area occupied by *P. pumila* was 8.8 ha (18 %) in 1977, and 10.1 ha (20 %) in 2009. These results indicate that *P. pumila* has increased its distribution by almost the same proportion (14 %) toward the fellfield side and snowbed side over the last 32 years (Table 1).

Comparisons of shoot growth between the fellfield side and snowbed side

Annual mean shoot elongation was 41.1 ± 5.9 (SD) mm (ranging from 29.8 to 50.9 mm) in the HF site and 52.2 ± 4.0 mm (ranging from 47.1 to 58.9 mm) in the GS site. Patch size was 16.4 ± 3.3 (SE) m² (ranging from 2.9 to 70.7 m²) in the HF site and 235.6 ± 86.4 m² (ranging

from 6.0 to 1400.0 m²) in the GS site. Simple linear regressions based on the standardized shoot elongation in each site revealed that annual shoot growth tended to increase from year to year in both the HF ($r = 0.54$, $P = 0.013$ by Pearson's correlation test) and GS sites ($r = 0.46$, $P = 0.041$; Fig. 3 a). Annual shoot growth had increased on average by 11 mm in the HF site and 6 mm in the GS site over the last 20 years.

The results of the GLMMs with the smallest AIC are described in Table 2. In the HF site, stem size, previous summer temperature and sunshine duration were positively related to shoot growth, whereas spring temperature of the current year was negatively related (Table 2 a). In the GS site, stem size, previous summer temperature and sunshine duration were positively related to shoot growth (Table 2 b). In both sites, distance from the *P. pumila* zone and patch size were excluded by AIC. These results indicated that (1) warm and sunny summers enhanced the shoot growth in the following season at both sites, and (2) warm spring temperatures negatively affected plants only at the fellfield side.

The responses of shoot growth to direction within patches were apparent in both sites (Fig. 3 b, c, Table 3 and Table 4). Annual shoot elongations (mean $\pm$ SD) were 38.8 ± 5.7 mm (north), 52.7 ± 8.3 mm (east), 44.2 ± 8.5 mm (south) and 29.3 ± 3.5 mm (west) in the HF site, and 50.5 ± 4.0 mm (north), 55.0 ± 5.4 mm (east), 54.0 ± 6.5 mm (south) and 49.3 ± 4.7 mm (west) in the GS site. The annual shoot growth tended to increase at the east edges ($r = 0.72$, $P < 0.001$ in the HF site; $r = 0.58$, $P = 0.008$ in the GS site by Pearson's correlation test) and south edges ($r = 0.57$, $P = 0.009$ in the HF site; $r = 0.48$, $P = 0.032$ in the GS site) and to decrease at north edges ($r = 0.17$, $P = 0.483$ in the HF site; $r = -0.17$, $P = 0.476$ in the GS site) and west edges ($r = 0.14$, $P = 0.546$ in the HF site; $r = 0.11$, $P = 0.648$ in the GS site) in both sites. Shoot growth was larger in the eastern and southern sides of patches. Shoot growth in the GS site was larger than in the HF site, and significant site-direction interactions were detected.

Discussion

The present study revealed that *P. pumila* in the Taisetsu Mountains has increased its distribution area toward both the fellfield and snowbed edges in the same proportion (14 %) over the last three decades. Our previous study (Kudo et al. 2011) reported that dwarf-bamboo (*Sasa kurilensis*), an evergreen shrubby bamboo forming dense clonal patches, had increased its distribution area by 26 % (1.4 ha) during the same time period in the GS site. Therefore, about 33 % of this area is occupied by *P. pumila* (20 %) and dwarf bamboo (13 %), and the shrubby area has increased by 5 %, corresponding to a 2.6 ha decrease in snow-meadow vegetation. The invasion of dwarf bamboo was prominent in places with low soil moisture (Hoshino et al. 2009; Kudo et al. 2011). The invasion of *P. pumila* and dwarf bamboo toward late-snowmelt habitat was reported also in the alpine moors of central Japan (Yasuda and Okitsu 2001). They speculated that the ongoing soil aridification might be a driving force of the vegetation change on alpine moors. Expansion of shrubs in tundra ecosystems is a worldwide vegetation pattern owing to the extension of the snow-free period and the increase in temperature resulting from climate change (Sturm et al. 2001, 2005; Dullinger et al. 2003; Tape et al. 2006). In Japanese mountain regions, dwarf bamboo and *P. pumila* are thought to be key species causing rapid vegetation change under warming climate, because they can expand their canopies by vigorous vegetation growth of shoots.

In accordance with the increase in distribution, shoot growth of *P. pumila* has been accelerated at both habitat edges. The GLMM analysis indicated that the temperature and sunshine duration of the previous summer were positively related to the annual growth at both sides. Several studies have reported the positive effects of temperature and/or sunshine duration of previous summer on current shoot growth of *P. pumila* (Sano et al. 1977;

Takahashi 2003, 2006; Wada et al. 2005; Yasuda and Okitsu 2007; Ozeki et al. 2011). It indicates that the resources stored in needles and stems during the last growing period may be used for shoot growth in the current season. Shoot growth of *P. pumila* commonly starts in early June and terminates in late July (Kajimoto 1993). Photosynthetic activity of *P. pumila* is generally low in the early season (May and June), then it increases to its maximum level in August (Kajimoto 1990; Ishida et al. 2001). Kibe and Masuzawa (1992) demonstrated that photosynthetic carbohydrate fixed during the summer was transformed into sugar in the late growing period, and reserved in branches and needles during the winter. Therefore, old needles and branches of *P. pumila* act as storage organs, and shoot growth from June to July may strongly depend on stored resources.

Spring temperatures negatively affected shoot growth at the fellfield side (HF site). The freezing resistance of dwarf shrubs rapidly decreases under the exposure to warm conditions (Sakai and Larcher 1987). The early phenological responses to the increase in daytime temperature may also enhance the risk of exposure to freezing temperatures at night (Bokhorst et al 2008, 2011; Inouye 2008). The increase in spring temperatures then enhances the risk of frost damage in the fellfield-side habitat. Needle damage of *P. pumila* was reported in warm and/or early-snowmelt springs on Mt. Tateyama (Maruta et al. 1996) and Mt. Norikura (Nakamoto et al. 2012) in central Japan. A negative effect of spring temperatures at the fellfield side might be related to physiological damage through freezing temperature in warm springs. Indeed, we confirmed that one third of days during April and May showed above-zero degree temperatures for daily minimums and the remaining two thirds of days had freezing temperatures. However, spring temperature was excluded by AIC at the snowbed side (GS site). In these sites, *P. pumila* is completely protected by snow cover during April and May when frost damage may happen, so the effect of spring temperatures is negligible in the GS site.

The harsh climate conditions in the fellfield-side habitat and the restricted growing period in the snowbed-side habitat are major limiting factors to the establishment of the *P. pumila* zone (Okitsu and Ito 1984). Shoot growth generally decreases at wind-exposed places with little snow cover (Okitsu and Ito 1984). Large patches can trap more snow resulting in more protection from the harsh winter climate (Essery and Pomeroy 2004), so significant effects of distance from *P. pumila* zone and patch size were expected at the fellfield side. In contrast, early snowmelt may be beneficial for growth in the snowbed-side habitat. Thus, significant effects of snowmelt time and distance from the *P. pumila* zone were expected at the snowbed side. Nevertheless, all of these factors were excluded by AIC in both habitats. One reason for this is that microtopography might affect the duration of snow cover more strongly than the simple distance effect for local snow conditions (Holtmeier and Broll 2005).

The larger shoot growth at the snowbed side in comparison with the fellfield side indicates that the snow-covered habitat is more suitable for the growth of *P. pumila* than the exposed habitat. Furthermore, annual shoot growth was accelerated at the east- and south-facing edges within patches, especially in the HF site. Protection by snow cover from low temperature, desiccation, and mechanical damage by strong winds during winter and early spring is beneficial for *P. pumila* (Okitsu and Ito 1984; Hadley and Smith 1987). The northwest wind is predominant during the winter in Japanese mountain regions, so snowdrifts are formed in a southeastern direction, accelerating shoot growth on the east- and south-facing sides within patches. This indicates the great importance of protection by snowdrifts at the fellfield side. In conclusion, recent climate conditions obviously enhanced the shoot growth and distribution of *P. pumila* in the Taisetsu Mountains toward both fellfield and snowbed habitats. However, the relationship between shoot growth and distribution area is not clear in the present study. Further studies on the population dynamics of *P. pumila* are necessary. As mentioned before, the vegetation dynamics model predicts a large reduction in the distribution of *P. pumila* in

338 the Japanese mountains with climate warming (Horikawa et al. 2009). The discrepancy
339 between the model prediction at a geographic scale and the actual trend at a regional scale
340 suggests that responses of *P. pumila* to climate change may be strongly specific to the region
341 and habitat. The dynamics of shrubs may cause great impacts on the biodiversity of alpine
342 ecosystems, so monitoring of key species at the regional scale is important for precise
343 prediction, conservation and management of alpine ecosystems under a warming climate.

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Figure legends

Fig.1. Location of the fellfield-side habitat (HF site) and the snowbed-side habitat (GS site) in the Taisetsu Mountains, Hokkaido, northern Japan.

Fig.2. Projections of *Pinus pumila* canopies in the fellfield-side habitat (25 ha) on 25 Sept 1977 (a) and 3 Sept 2009 (b), extracted using the unsupervised classification of the ISODATA clustering algorithm, and in the snowbed-side habitat (50 ha) in 1977 (c) and 2009 (d) extracted using visual observation. The fellfield-side habitat is located close to Lake Hisago and the snowbed-side habitat is located in Goshikigahara, Taisetsu Mountains, Hokkaido, northern Japan. Patches of *P. pumila* are enclosed by yellow lines.

Fig.3. Year-to-year trends of annual shoot growth of *Pinus pumila* in the fellfield-side habitat (HF site) and the snowbed-side habitat (GS site) over the last 20 years. (a) Results of simple linear regression for standardized values and Pearson's correlation test are shown. The solid line and broken line indicate the HF site and the GS site, respectively. Comparison of the effects of direction on annual shoot growth (vertical bars standard error) in HF site (b) and GS site (c). Results of simple linear regression are shown as significant in the east and south sides of patches.

Table 1. Area occupied by *Pinus pumila* in 1977 and 2009 in the fellfield-side habitat (HF site) and the snowbed-side habitat (GS site), and the percentage of expansion over the past 32 years.

Site	Plot area (ha)	Canopy cover area of <i>P. pumila</i> (ha)		
		1977	2009	Δ area (%)
HF	25	13.08	14.96	14.4
		(52.3%)	(59.8%)	
GS	50	8.80	10.07	14.4
		(17.6%)	(20.1%)	

Table 2. Results of generalized linear mixed-effect model (GLMM) for environmental factors related to annual shoot growth in (a) the fellfield-side habitat (HF site), and (b) the snowbed-side habitat (GS site).

Variables	Coefficient	SE	<i>t</i>	<i>P</i>
(a) HF site				
Intercept	1.687	0.109	15.46	< 0.0001
Stem size	0.001	< 0.001	38.39	< 0.0001
Current summer temperature	−0.017	0.009	−1.86	0.0632
Previous summer temperature	0.038	0.009	4.18	< 0.0001
Spring temperature	−0.089	0.009	−9.89	< 0.0001
Current summer sunshine	0.001	0.001	1.88	0.0599
Previous summer sunshine	0.004	0.001	6.82	< 0.0001
(b) GS site				
Intercept	2.273	0.106	21.54	< 0.0001
Stem size	0.001	< 0.001	29.43	< 0.0001
Current summer temperature	0.012	0.007	1.77	0.0773
Previous summer temperature	0.042	0.009	4.78	< 0.0001
Previous summer sunshine	0.001	< 0.001	2.29	0.0222

Variables were selected based on the smallest Akaike information criterion (AIC).

Table 3. Annual mean shoot elongation and shoot growth increasing rate of *Pinus pumila* in the four compass directions in the fellfield-side habitat (HF site) and the snowbed-side habitat (GS site).

Direction	HF site		GS site	
	Shoot elongation	Increasing rate	Shoot elongation	Increasing rate
	Mean $\pm$ SD (mm)	(mm year ⁻¹)	Mean $\pm$ SD (mm)	(mm year ⁻¹)
North	38.8 $\pm$ 5.7	0.16	50.5 $\pm$ 4.0	-0.12
East	52.7 $\pm$ 8.3	1.02 ***	55.0 $\pm$ 5.4	0.53 **
South	44.2 $\pm$ 8.5	0.81 **	54.0 $\pm$ 6.5	0.53 *
West	29.3 $\pm$ 3.5	0.09	49.3 $\pm$ 4.7	0.09

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$ (by Pearson's correlation test)

Table 4. Results of the generalized linear mixed-effect models (GLMM) for the analysis of direction within patches related to annual shoot growth between the fellfield-side habitat (HF site) and the snowbed-side habitat (GS site).

Variables	Coefficient	SE	<i>t</i>	<i>P</i>
Intercept (North, HF)	3.643	0.027	134.88	< 0.0001
East	0.305	0.025	12.23	< 0.0001
South	0.135	0.025	5.46	< 0.0001
West	−0.300	−0.025	−12.23	< 0.0001
Site, GS	0.262	0.040	6.58	< 0.0001
East × GS	−0.217	0.036	−5.94	< 0.0001
South × GS	−0.061	0.036	−1.67	0.0954
West × GS	0.271	0.037	7.41	< 0.0001