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**Clarification of vegetation dynamics in alpine ecosystems
under climate change: Responses of *Pinus pumila* and snow-
meadow communities**

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Summary

Biodiversity of Japanese alpine ecosystems is maintained by the heterogeneity of snow distribution. However, the pattern of snowmelt has been changed under climate warming. Typical alpine vegetation in Japan is largely classified into fellfield plant communities, *Pinus pumila*-dominated communities (i.e. *P. pumila* zone), and late-snowmelt plant communities (i.e. snow-meadow and snowbed communities). The spatial arrangement of these plant communities strongly reflects the local distribution of snow. Among them, *P. pumila* and late-snowmelt plant communities are most sensitive to climate change. Because biomass accumulation of *P. pumila* is extremely large, dynamics of *P. pumila* zone should cause large impacts on alpine vegetation in Japan. The purpose of this study is to quantify the vegetation change during last few decades and to clarify the mechanisms of the dynamics of *P. pumila* and snow-meadow vegetation in the Taisetsu Mountains, Hokkaido of northern Japan.

In Chapter 1, I quantified the canopy dynamics and shoot growth of *P. pumila* with reference to recent climate variations at the fellfield and snow-meadow sides of *P. pumila* zone. Furthermore, I analyzed the trend of shoot growth responding to the temperature conditions during last 19 years across nine sites of six mountain regions in Hokkaido. *Pinus pumila* has expanded the distribution area by 14 % toward both sides during last 32 years. Annual shoot growth was positively related to summer temperature and sunshine duration at both sides, but negatively related to spring temperature at the fellfield side. Shoot growth was larger at the southeastern edge of patches, where snowdrifts were formed. Across the mountain regions in Hokkaido, shoot growth was predicted to increase 10 % per one-degree warming of summer temperature. These results indicate that distribution area of *P. pumila* will be increased by climate warming. However, warm spring may enhance the risk of frost damage at the fellfield side

because of the earlier reduction in cold-resistance. This study suggests the importance of site-specific responses of *P. pumila* to predict the impacts of climate change on alpine vegetation.

In Chapter 2, I analyzed how weather condition (temperature and solar radiation) and habitat type (altitude and timing of snowmelt) can affect the physiological activity and growth of *P. pumila*. The effect of weather condition was quantified by the experimental manipulation of shading, warming and defoliation treatments at branch level. The photosynthetic yield was increased by the shading and warming treatments, but shoot growth was increased only by the warming treatment. These results indicate that physiological activity might be damaged by high radiation under cool temperature conditions, whereas shoot growth was restricted only by cool temperature during the growth season. Recovery of photosynthetic activity took longer time when snowmelt was late. Therefore, warm temperature during the growth season increases the shoot growth, while late snowmelt lengthens the period for the photosynthetic activation after overwintering resulting in shorter photosynthetic period at the snow-meadow side.

In Chapter 3, I analyzed the factors affecting cone production, seedling appearance, and survival of *P. pumila*. All seedling clumps were mapped and traced within a 20 m × 20 m quadrat during 1994–1999 and 2013–2015 at the fellfield habitat, and previous cone scars were counted at seven regions including the mapping plot. The cone production was positively related to summer temperature, and cone production tended to increase at second- or third-year intervals. However, there was no significant relationship between cone production and seedling establishment. Seedling survival was positively related to the temperature soon after germination and that of early growth season of following year. Furthermore, survival rate of seedlings was higher at the place with lichen cover and *P. pumila* litter. The number of seedlings of age 0–5 and the total

number of *P. pumila* individuals tended to decrease recently. In constant, the number of individuals older than age 6 tended to increase, probably because of higher survival rate under warm conditions. Therefore, the increase in summer temperature affects the population structure of *P. pumila*.

In Chapter 4, I quantified the recent changes in snow-meadow vegetation at two locations, Goshikigahara and Koganegahara. The occurrence and dominance of plant species were surveyed in 2012, and compared to the previous vegetation records of 1972 and 1988. I also measured soil moisture of all measurement plots in 2012. During last 40 years, species composition and community structure of alpine snow-meadows have changed but differently between the sites. Generally, the dominant species have changed from tall herbaceous species, such as *Anemone narcissiflora* and *Trollius riederianus*, to graminoid species, such as *Carex blepharicarpa* and *Agrostis flaccid*. The pattern of vegetation change was remarkable at Goshikigahara, where diverse community types existed reflecting the heterogeneous topographic and snow conditions. Soil moisture explained well the spatial variation of species composition at both sites. These results indicate that the significant changes in the vegetation structure have progressed in alpine snow-meadows, probably because of acceleration of snowmelt time and changes in soil water conditions caused by climate warming, but the fragility of vegetation structure is strongly site specific.

These results revealed that the species composition and structure of alpine vegetation have changed rapidly under climate change. However, the factors affecting alpine vegetation highly vary among species or community types depending on the environmental heterogeneity of habitats. Therefore, careful consideration of habitat-specific responses is important to predict the climate change impacts on alpine ecosystems.

Introduction

Global warming is believed to cause profound effects on the structure and function of alpine ecosystems because distribution, survival and reproduction of alpine plants are strongly sensitive to the changes in temperature and water conditions (Nagy and Grabherr 2009). In fact, a number of studies have reported the upward shifts of treeline (Butler et al. 1994; Kullman 2002; Shiyatov 2003; Peñuelas et al. 2007; Gehrig-Fasel et al. 2007; Devi et al. 2008) and shrub expansion in alpine areas as well as in tundra regions (Sturm et al. 2001, 2005; Kullman 2002; Dullinger et al. 2003; Tape et al. 2006; Buras et al. 2012). Comparisons of alpine vegetation records during 1835–1953 and 1990's revealed that the number of plant species inhabiting the summits of nival zone has increased in European Alps (Grabherr et al. 1994; Pauli et al. 2001). Furthermore, the analysis of 68-years vegetation rerecord of alpine sites in Norway revealed a significant upward shift of species distribution along the altitudinal gradient (Klanderud and Birks 2003).

In alpine ecosystems, diverse habitat types are arranged as mosaic pattern reflecting the heterogeneous soil moisture, exposure to wind and snow cover duration, and most of them are related to topography (Nagy and Grabherr 2009; Spasojevic et al. 2013). Typical alpine vegetation in Japan is classified into fellfield communities, snow-meadow or snowbed communities, and *Pinus pumila* (alpine dwarf-pine) dominated communities (Koizumi 1974). In the fellfield habitat, soil surface is almost exposed to strong wind, where soil is completely frozen during the winter and dried in the summer. Thus, plants inhabiting the fellfield habitat are required to have high cold and drought tolerance. In the snowbed habitat, in contrast, a large accumulation of snow protects plants from freezing temperatures during the winter, and snowmelt water maintains moist soil conditions in the summer. *Pinus pumila* inhabits the intermediate habitat

between the fellfield and snowbed, especially on gentle rocky slopes with moderate snow depth in the winter (30–300 cm deep: Okitsu and Ito 1984).

The 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). The invasion and expansion of woody plants having 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 canopy expansion of shrubs are important issues in assessing the global change impacts on alpine ecosystems.

The zonal distribution of *P. pumila* 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* should cause serious impacts on the structure and diversity of alpine ecosystems. Previous studies reported that the net photosynthetic rates of current needles were maximum around at 10–15 °C (Kajimoto 1990), and that the current shoot growth was positively related to the previous summer temperature (Sano et al. 1977; Takahashi 2003; Wada et al. 2005). Annual shoot growth has tended to increase in the mountain regions of the main island of Japan, probably responding to recent climate warming (Wada et al. 2005; Ozeki et al. 2011). In contrast to the field reports, a vegetation

dynamics model based on the climate change scenarios predicts that the potential distribution area of *P. pumila* will decrease to 15–25 % 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.

In the late snowmelt habitats, snow condition limits the distribution of alpine plants (Kudo and Ito 1992; Schöb et al. 2010). The recent changes in species composition and diversity of alpine plant communities were larger in late-snowmelt communities compared with other communities, probably because snow cover period has been changed by climate warming (Spasojevic et al. 2013). Therefore, snow-meadow vegetation may be most sensitive to climate warming among alpine plant communities also in Japan.

The aim of this study is to quantify the recent vegetation change in alpine ecosystems and to clarify the mechanisms, focusing on *P. pumila* and snow-meadow vegetation in the Taisetsu Mountains, Hokkaido of northern Japan. This study is composed of four chapters. In Chapter 1, I quantified the changes in the distribution area of *P. pumila* during last 32 years using aerial photographs, and compared annual shoot growth with reference to various environmental factors between the fellfield side and the snow-meadow side. In Chapter 2, I analyzed shoot growth pattern and physiological activity of *P. pumila* with reference to temperature, solar radiation and snowmelt condition. In Chapter 3, seedling establishment and survival of *P. pumila* were surveyed to evaluate the recent changes in the regeneration process and population structure based on the comparisons of previous data accumulated during 1994–1999 (Wada et al. unpublished data) and present data during 2013–2015. In Chapter 4,

intensive vegetation survey of snow-meadow communities was conducted to reveal the changes in species richness, composition and vegetation structures comparing current vegetation with previous records of 1972 (Sato 2007) and 1988 (G. Kudo, unpublished data). Throughout these studies, I aim to clarify the general pattern of vegetation dynamics and factors affecting the vegetation change in Japanese alpine ecosystems under climate change.

Main study site and climate conditions

This study was mainly conducted in the central part of the Taisetsu Mountains (43° 13'–45' N, 142° 32'–143° 19' E), central part of Hokkaido, northern Japan (Fig.1–1). The Taisetsu Mountains are located in Daisetsuzan National Park, the largest national park in Japan (64 km from north to south, 62 km from east to west). The central part of the Taisetsu Mountains consists of volcanoes of 1750–2300 m height with lava plateau and gentle slope. The treeline is located approximately at 1400–1500 m above sea level (a.s.l.). The alpine zone above the treeline has typical periglacial features, such as polygonal soils, striation soils and stone pavements (Konoya et al. 1968) with perennial snow patches (e.g. Kinoshita et al. 1965) and permafrost (Fukuda and Kinoshita 1974; Takahashi and Sone 1988).

The climate of this region is characterized as cold and snowy winters, and warm, wet and foggy summers. Temperature at 1700 m a.s.l. was 8.7 °C in June, 11.9 °C in July, 12.8 °C in August and –15.9 °C in January, and annual mean temperature was –1.7 °C (means from 2003 to 2012). The precipitation was 149.7 mm in June, 415.5 mm in July, and 316.4 mm in August (means of 2010–2012). Recently, annual mean temperature in alpine area is increasing at the rate of 0.33 °C/10-yr, and the time of snowmelt becomes earlier at the rate of 4.1 days/10-yr (Kudo 2014).

Large snow-meadows are formed at 1600–1800 m a.s.l. in the central part of the Taisetsu Mountains. Reflecting the recent climate warming, populations of typical snow-meadow species have decreased rapidly at the snow-meadow (Kawai and Kudo 2014), while dwarf bamboos (*Sasa kurilensis*) have increased the distribution area (Kudo et al. 2011). These reports indicate that rapid vegetation changes are ongoing in this region under climate change.

Chapter 1. Responses of shoot growth and distribution of *Pinus pumila* to climate variation

1.1 Introduction

In Japanese alpine regions, *Pinus pumila* commonly shows zonal distribution between exposed fellfield and late-snowmelt habitats. Density and plant height of *P. pumila* decline with the increasing intensity of wind exposure, and its growth form changes from zonal to patchy toward the fellfield habitat. On the other hand, density and plant height tend to remain stable toward the snow-meadow side, but *P. pumila* abruptly disappears at typical snow-meadow habitat probably due to too short photosynthetic period (Okitsu and Ito 1984). Therefore, factors affecting the distribution limit may differ between the fellfield side and the snow-meadow side of the *P. pumila* zone.

Distribution and phenology of alpine plants are strongly influenced by snow conditions (Billings and Bliss 1959; Kudo and Ito 1992; Choler 2005; Kudo and Hirao 2006). Global warming may accelerate the growth of alpine plants if harsh climate conditions are mitigated, but the risk of frost damage may also increase early in the season (Inouye 2008; Wheeler et al. 2014). So far, little attention has been paid to the significance of frost damage in Japanese mountains, but it may affect the growth and survival of *P. pumila* (Maruta et al. 1996; Ishida et al. 2001; Nakamoto et al. 2012). Frost damage is expected to occur more frequently at the fellfield habitat than at the snow-meadow habitat because plants are exposed from snow cover early in the spring. If so, climate change impacts on alpine vegetation may vary depending on the proximity to the fellfield and snow-meadow habitat (e.g. Kudo et al. 2010).

The aim of this study is to clarify the growth responses and distribution shift of *P. pumila* during last 20–30 years with reference to the habitat-specific pattern between the

fellfield and snow-meadow sides responding to climate variations. Furthermore, I quantified the growth responses of *P. pumila* to temperature variation at geographical scale across mountain regions in Hokkaido. My specific questions are as follows:

- 1) How extent has the distribution area of *P. pumila* changed in recent years (during last 32 years) at the fellfield side and the snow-meadow side?
- 2) Are environmental factors affecting shoot growth different between the fellfield side and the snow-meadow side?
- 3) Does shoot growth of *P. pumila* respond to temperature variation differently among mountain regions?

1.2 Materials and Methods

1.2.1 Comparisons between fellfield and snow-meadow habitats

Study site

I selected two habitat types as research sites, fellfield side and snow-meadow side of *P. pumila* zone in the central part of the Taisetsu Mountains. The fellfield side habitat (hereafter HF site) is located on a plateau of 1670–1690 m a.s.l. close to Lake Hisago, 2 km south of Mt. Kaun (N 43° 32', E 142° 52'). The snow-meadow side habitat (hereafter GS site) is located on a gentle east-facing slope of 1700–1850 m a.s.l. at Goshikigahara (N 43° 33', E 142° 54'; Fig. 1–1). HF site has typical fellfield vegetation composed of dwarf shrubs (e.g. *Arctous alpinus* var. *japonicus*, *Loiseleuria procumbens*, *Diapensia lapponica* var. *obovata* and *Vaccinium uliginosum*) and lichens (*Cladonia* spp.). GS site has snow-meadow vegetation composed of herbaceous species, such as *Anemone narcissiflora* var. *sachalinensis*, *Trollius riederianus* and *Saussurea riederi* var. *yezoensis*.

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* at 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, I selected large rocks located within the area and used them as ground control points. Clear color photographs taken in September enabled to discriminate *P. pumila* from other vegetation. All works were conducted by 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 at HF site (Fig. 1–2). Canopies of *P. pumila* were easily discernible and 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 my 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* at GS site was observed within a 50 ha (500 × 1000 m) area (Fig. 1–2). The canopies of other shrubs and dwarf bamboos were sometimes difficult to distinguish from *P. pumila* canopies by the non-hierarchical clustering. Therefore, I extracted *P. pumila* canopies 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 distribution 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 HF (25 ha) and GS (50 ha) sites reflected the topographic features of the fellfield and snow-meadow habitats in this region.

Measurements in the field

Because the stems and branches of *P. pumila* retain the annual scars of dormant buds (Fig. 1–3) for approximately 20 years, annual shoot growth 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 last 20 years was measured using a digital caliper at the accuracy of 0.1 mm. I randomly selected 24 patches within the 25 ha area at HF site, and 20 patches within the 50 ha area at GS site. In each patch, I selected four trunks without physical damage and measured branches facing north, south, east, and west.

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

Shoot growth analysis

First, the temporal sequences in annual shoot growth in each habitat over last 20 years were examined using linear regression, following the standardization of annual shoot growths within stems (Fig. 1–4a). Then, factors affecting shoot growth were analyzed using generalized linear mixed-effect models (GLMM) without data standardization. In the first model, environmental and internal variables related to shoot growth were tested in each habitat. Environmental variables 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 growth of *P. pumila* varied among trees depending on the competitive situation (Yasuda and Okitsu 2012). To eliminate these endogenous effects, therefore, I included (6) patch size and (7) stem length during last 20 years (hereafter stem size) as explanatory variables in the GLMM. Patch size, expressed as a 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 every patch 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's information criterion (AIC) in which I adopted the set of variables with the lowest AIC estimate. As there is no long-term meteorological data in the Taisetsu Mountains, I estimated the previous climatic conditions using the data observed in Nukabira Town (N 43° 22.0', E 143° 11.5', 540 m a.s.l.; Japan Meteorological Agency 2012), the nearest weather station to HF and GS sites. A comparison of available temperature records between HF site and Nukabira Gensenkyo revealed that the temperature lapse rate was $-0.5^{\circ}\text{C} / 100$ m elevation. Previous temperatures at HF and GS sites were estimated using this value. The snowmelt day has been recorded since 1988 at a site with similar snow conditions to GS site, located approximately 3 km away from Goshikigahara (G. Kudo,

unpublished data). I used this record for the analysis of GS site. Snowmelt time was not included in the GLMM for HF site because the fellfield habitat received only a small amount of snow accumulation during the winter because of exposure to strong winds.

In the second model, I compared the sensitivity of shoot growth to the direction within patches between 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. I used the R statistical software version 3.2.4 (R Core Team 2016) for all data analyses. The GLMM were performed using the function `glmer` included in the R package `lme4` (Bates et al. 2015).

1.2.2 Shoot growth among mountain regions

Study site

This study was conducted at nine mountain sites from six major mountain regions in Hokkaido (Fig. 1–5, Table 1–1). These sites are Mt. Kaun (hereafter KA), Mt. Aka (AK), Mt. Kuro (KU), Mt. Asahi (AS), Mt. Mekunnai (ME), Mt. Yubari (YU), Mt. Teshio (TE), Mt. Apoi (AP), and Mt. Rausu (RA). Among them, KA (peak altitude is 1954 m a.s.l.), AK (2078 m a.s.l.), KU (1984 m a.s.l.) and AS (2291 m a.s.l.) are located in the Taisetsu Mountains. TE (1557 m a.s.l.) is located in the Kitami Mountain Range, about 40 km north of the Taisetsu Mountains. YU (1668 m a.s.l.) is located about 100 km southwest of the Taisetsu Mountains, geographically characterized by ultrabasic rock in which many endemic and rare plant species exist (Sato 2007). AP (811 m a.s.l.) is located in the southern edge of the Hidaka Mountain Range, also composed of

ultrabasic rock and home to many endemic species (Sato 2007). ME (1202 m a.s.l.) is located in the Niseko Mountains in the western part of Hokkaido and characterized by heavy snowfall. RA (1661 m a.s.l.) is located in the Shiretoko Peninsula at the eastern edge of Hokkaido. This area is characterized by strong winds and foggy climate due to the peninsular topography.

Climate records from the public meteorological station (Japan Meteorological Agency 2012) closest to each site were used for the analyses (Fig. 1–5, 1–6 and Table 1–1). The warmth index (WI: Kira 1948) that is an accumulated value of mean monthly temperature minus five degree for all months warmer than 5 °C was calculated, used temperature at each site was estimated based on the $-0.5\text{ °C} / 100\text{ m}$ lapse rate, for each site.

Measurement in the field

Annual shoot growth for the last 19 years was measured using a digital caliper at the accuracy of 0.1 mm. At each mountain site, I arbitrarily selected 30 (20 at KA and AS) trunks without physical damage at intervals of 5–50 m in 2012. Measurements of all but AS were conducted after late August when current year shoot growth had been completed. Thus, I recorded annual shoot growth from 1994 to 2012. Because measurement at AS was conducted in mid-June when annual shoot might be still growing, I used annual growth data from 1994 to 2011.

Statistical modeling of shoot growth and temperature

In order to reveal the correlation between annual deviations of shoot growth and temperature, I developed a Bayesian state-space model to remove the effects of time-autocorrelations of the time-series data sets. As the model structures for shoot growth

and temperature are common, a generic formulation is described in following. Suppose that $Y_{i,t,*}$ represents an observed value for individual (or data point) i , year t and the “wild card” symbol “*” denoting one of the following: “A” as annual shoot growth (mm), “B1” as spring temperature (°C) and “B2” as mean summer temperature (°C). The range of year t was from 1 to 19 because the start and end year of the analysis is from 1994 to 2012. The observed value $Y_{i,t,*}$ is supposed to follow the normal distribution of mean $\mu_{i,t,*}$ and standard deviation $\sigma_{1,*}$ or observation error, $Y_{i,t,*} \sim N(\mu_{i,t,*}, \sigma_{1,*})$ where the binomial operator “ $Y \sim D$ ” represents a random variable Y follows a probability distribution D . All $\{\sigma_{\text{number},*}\}$ appeared in the following are standard deviations of the normal distributions. The mean value $\mu_{i,t,*}$ is given as,

$$f(\mu_{i,t,*}) = x_{i,t,*} + \beta_{t,*} + \beta_{t \times S,*} + \delta_*,$$

where $f(\cdot)$ is the link function in the style of generalized linear model (GLM), $x_{i,t,*}$ is time-autocorrelation term of which modeling is described later, $\beta_{t,*}$ is the year-specific effect at year t , $\beta_{t \times S,*}$ is the interaction term of year t and observation site S , and δ_* is the monotonic time change that can find a trend either of increase or decrease. Note that both $\beta_{t,*}$ and $\beta_{t \times S,*}$ are the year-specific components without time-autocorrelations.

The details of the model described above were as follows: The functional form of link $f(\cdot)$ was log for annual shoot growth (* “A”) and identity for mean temperature (* is “B1” or “B2”). The autocorrelated time series $\{x_{i,t,*}\}$ was generated by a simple random walk model $x_{i,t,*} \sim N(x_{i,t-1,*}, \sigma_{2,*})$ and $x_{i,1,*} \sim N(m_*, \sigma_{3,*})$. The prior distributions of local parameters of the hierarchical model, i.e. $\{\beta_{t,*}, \beta_{t \times S,*}\}$, were specified as the normal distributions of which means and standard deviations were $\{0\}$ and $\{\sigma_{k,*} \mid k \in \{1, 2, \dots, \text{number of local parameter groups}\}\}$, respectively. On the other hand, those of global parameters, i.e. $\{\delta_*, m_*\}$, were the uniform distributions

ranging $[-10^4, 10^4]$, while the prior distributions of all standard deviations $\{\sigma_{k,*}\}$ were the uniform distributions ranging $[0, 10^4]$.

The Markov chain Monte Carlo (MCMC) method was used to sample from posterior distributions of the parameters with JAGS 4.0.0 (Plummer 2015) and R-3.2.4 (R Core Team 2016). The posterior samples were obtained from three independent Markov chains in which 1000 values (i.e. 3000 samples for each parameter) were sampled with an interval of 100 after a burn-in of 1000 iterations. I evaluated the convergence of the triple sampling chains using $\hat{R}$ statistics (Gelman et al. 2013) for each parameter. The sampling details described above were chosen such that all $\hat{R}$ statistics were smaller than 1.1 or all posterior distributions were well converged.

Using the MCMC posterior samples obtained above, I estimated the correlation between annual shoot growth and mean temperature. The relationship between shoot growth and temperate was estimated by constructing 95% Bayesian confidence intervals of the year-specific components without time-autocorrelations. I chose possible contrasts between deviations in shoot growth (A), temperatures in spring (B1) and in summer (B2) are as follows: $\{\beta_{t,A}, \beta_{t-1,B1}\}$, $\{\beta_{t,A}, \beta_{t-1,B2}\}$, $\{\beta_{t,A}, \beta_{t,B1}\}$ and $\{\beta_{t,A}, \beta_{t,B2}\}$. Note that $\{\beta_{t,A}, \beta_{t-1,B*}\}$ represents the relationship between shoot growth in year t and temperature in year $t-1$ while $\{\beta_{t,A}, \beta_{t,B*}\}$ is that in the same year t . The total sample pairs $\{\beta_{t,A}, \beta_{t,B*}\}$ of which sample size was $19 \text{ years} \times 3000 = 57000$ were divided into 10 uniform-sized clusters to estimate the means and 95% Bayesian confidence intervals for each cluster.

1.3 Results

1.3.1 Changes in distribution area during last 32 years

Projection images of *P. pumila* canopies in 1997 and 2009 are shown in Figure 1–2. At HF site (25 ha), the area occupied by *P. pumila* was 13.1 ha (52 %) in 1977, and 15.0 ha (60 %) in 2009. At GS site (50 ha), it 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 and snow-meadow sides during last 32 years (Table 1–2).

1.3.2 Comparisons of shoot growth between the fellfield side and snow-meadow side

Annual shoot growth was 41.1 ± 5.9 (SD) mm (ranging from 29.8 to 50.9 mm) at HF site, and 52.2 ± 4.0 mm (ranging from 47.1 to 58.9 mm) at GS site. Patch size was 16.4 ± 3.3 (SE) m² (ranging from 2.9 to 70.7 m²) at HF site, and 235.6 ± 86.4 m² (ranging from 6.0 to 1400.0 m²) at GS site. Simple linear regressions based on the standardized shoot growth in each site revealed that annual shoot growth tended to increase from year to year at both HF ($r = 0.54$, $P = 0.013$ by Pearson's correlation test) and GS sites ($r = 0.46$, $P = 0.041$; Fig. 1–4 a). Annual shoot growth had increased on average by 11 mm at HF site, and 6 mm at GS site over the last 20 years.

Stem size, previous summer temperature and sunshine duration were positively related to shoot growth at HF, whereas spring temperature of the current year was negatively related (Table 1–3a). At GS site, stem size, previous summer temperature and sunshine duration were positively related to shoot growth (Table 1–3b). Distance from the *P. pumila* zone and patch size was excluded by AIC at both sites. These results indicate that (1) warm and sunny summers enhanced the shoot growth in the following season at both sites, and (2) warm spring temperatures negatively affected only at the fellfield side.

The responses of shoot growth to the direction within patches were apparent in both sites (Figs. 1–4b and 1–4c; Tables 1–4 and 1–5). Annual shoot growth (mean $\pm$ SD) in each direction was 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) at 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) at GS site. The annual shoot growth tended to increase at the east edges ($r = 0.72$, $P < 0.001$ at HF; $r = 0.58$, $P = 0.008$ at GS by Pearson's correlation test) and south edges ($r = 0.57$, $P = 0.009$ at HF; $r = 0.48$, $P = 0.032$ at GS) and to decrease at north edges ($r = 0.17$, $P = 0.483$ at HF; $r = -0.17$, $P = 0.476$ at GS) and west edges ($r = 0.14$, $P = 0.546$ at HF; $r = 0.11$, $P = 0.648$ at GS). Shoot growth was larger at the eastern and southern sides of patches. Shoot growth at GS site was larger than at HF site, and significant site-direction interactions were detected.

1.3.3 Shoot growth responses to temperature at regional scale

Yearly deviation in shoot growth ($\beta_{t,A}$) showed similar patterns among mountain regions to some extent (Fig. 1–7). However, almost all 95 % BCI of $\beta_{t \times S,A}$ included zero in every mountain region. When all mountains were pooled, significant yearly variation in shoot growth was detected during the 19 years (Fig. 1–8a). Spring and summer temperatures also showed significant yearly variations (Fig. 1–8b, c). The median value of δ_A , deviation in shoot elongation, was 0.013 in which Bayesian confidence interval (BCI) was [0.004, 0.023]. This means a 1.0 % increase in shoot growth during last 19 years. On the other hand, both spring and summer mean temperatures, δ_B , did not change significantly ([–0.078, 0.092] for spring; [–0.030, 0.147] for summer in 95 % BCI).

In all mountain regions, last and current spring temperatures and current summer temperature were not significantly related to shoot growth (Fig. 1–9a, b, d). On the other hand, last summer temperature was positively related to shoot growth. With one degree increase in summer temperature, shoot growth increases by 10 % (Fig. 1–9c).

1.4 Discussion

The present study revealed that *P. pumila* in the Taisetsu Mountains has increased the distribution area toward both the fellfield and snow-meadow sides at the same proportion (14 %) over the last three decades. Kudo et al. (2011) reported that dwarf-bamboo (*Sasa kurilensis*) had increased the distribution area by 26 % (1.4 ha) during the same time period at 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 drier soil conditions might be a major driving force of the vegetation change in the alpine moors.

Expansion of shrubs in tundra ecosystems is a worldwide trend of vegetation change responding to the extension of snow-free period and increasing temperature by 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 climate warming, because they can expand their canopies by vigorous clonal growth.

In accordance with the increasing distribution area, shoot growth of *P. pumila* has been accelerated at both sides. The GLMM analysis indicated that the temperature and sunshine duration of previous summer were positively related to the annual growth at both sides. Several studies 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). The resources stored in needles and stems during last growth season 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), and it attains the maximum level in August (Kajimoto 1990; Ishida et al. 2001). Kibe and Masuzawa (1992) demonstrated that the photosynthetic carbohydrate fixed during the summer was transformed into sugar late in the growth season, 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 temperature 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 enhance the risk of exposure to freezing temperatures at night (Bokhorst et al. 2008, 2011; Inouye 2008). The increase in spring temperature, therefore, enhances the risk of frost damage in the fellfield habitat. Needle damage of *P. pumila* was reported in warm and/or early-snowmelt spring at Mt. Tateyama (Maruta et al. 1996) and Mt. Norikura (Nakamoto et al. 2012) in central Japan. A negative effect of spring temperature at the fellfield side might be related to the physiological damage through freezing temperature in warm spring. Indeed, one-third of days during April

and May had above-zero degree temperatures for daily minimums and the remaining two-thirds of days had freezing temperatures. In contrast, spring temperature was excluded by AIC at the snow-meadow side (GS site). Because *P. pumila* is completely protected by snow cover during April and May at GS site, spring temperature has a negligible effect on shoot growth.

The harsh climate conditions at the fellfield side and the restricted growth season at the snow-meadow side are major limiting factors of the expansion of *P. pumila* zone (Okitsu and Ito 1984). Shoot growth is generally decreased 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). Thus, the distance from *P. pumila* zone and patch size may be important factors for the growth at the fellfield side. In contrast, early snowmelt may be beneficial for growth at the snow-meadow side. Nevertheless, all of these variables were excluded by AIC. Probably, microtopographic variation might affect the duration of snow cover more strongly than the simple distance effect for local snow conditions (Holtmeier and Broll 2005).

Larger shoot growth at the snow-meadow side than at 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 at HF site. Protections by snow cover from low temperature, desiccation and mechanical damage by strong winds during the winter and early spring are beneficial for *P. pumila* (Okitsu and Ito 1984; Hadley and Smith 1987). The northwest wind is predominant during the winter in Japanese mountain regions and snowdrifts are formed toward the southeastern direction that accelerates the shoot growth on the east- and south-facing sides within patches. This indicates the great importance of protection by snowdrift at the fellfield side.

In a previous study (Wada et al. 2005), the inter-annual increase in shoot growth ranged from 0.20 to 0.52 mm/yr in central Japan, while a significant trend was not detected in the northern part of Honshu and Hokkaido regions during 1980–2003. In the present study, however, shoot growth has increased by 1 % per year during 1994–2012 across the mountain regions. These results indicate that the shoot growth of *P. pumila* has been accelerated also in northern Japan during last 11 years. Furthermore, I revealed that shoot growth was increased by 10 % with one degree warming in last summer. This is the first report to quantify the shoot responses to temperature change. In addition, shoot growth and summer temperature were well synchronized among research sites. These mountains have various and specific climate conditions and geological situations, but dynamics of *P. pumila* was changed similarly in regional scale within Hokkaido. On the other hand, the factors affecting growth and establishment of *P. pumila* may vary depending on the local habitats even within a same region (e.g. Takahashi 2003). Because of the habitat specific responses, effects of spring temperature might be related to shoot growth across the mountains.

In conclusion, recent climate conditions obviously enhanced the shoot growth and distribution of *P. pumila* in the Taisetsu Mountains at both fellfield and snow-meadow sides and among mountain regions. As mentioned before, the vegetation dynamics model predicts a large reduction in *P. pumila* distribution in the Japanese mountains with climate warming (Horikawa et al. 2009). The discrepancy between the model prediction at a geographic scale and the actual trend at a regional scale suggests that the responses of *P. pumila* to climate change may be strongly specific to region and habitat. Because the dynamics of shrubs may cause great impacts on the biodiversity of alpine ecosystems, monitoring of key species at the regional scale is important for precise prediction, conservation and management of alpine ecosystems under warming climate.

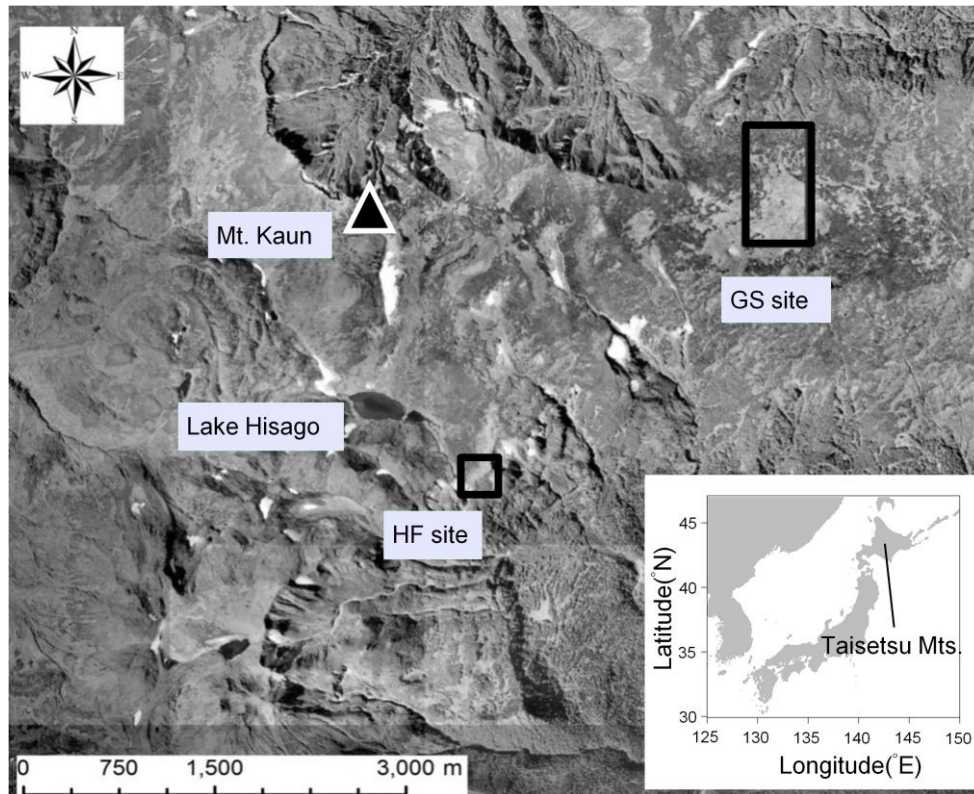


Fig. 1-1 Location of the fellfield habitat (HF site) and the snow-meadow habitat (GS site) of *Pinus pumila* in the Taisetsu Mountains.

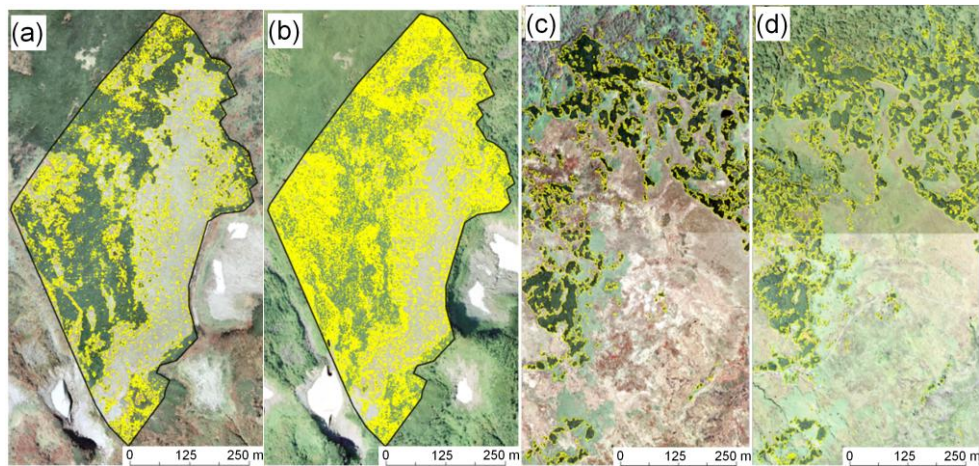


Fig. 1-2 Projections of *Pinus pumila* canopies at the fellfield side (25 ha) on 25 Sept. 1977 (a) and 3 Sept. 2009 (b), extracted using the unsupervised classification of the ISODATA clustering algorithm, and at the snow-meadow side (50 ha) in 1977 (c) and 2009 (d) extracted using visual observation. The fellfield site is located on a plateau close to Lake Hisago, and the snow-meadow site is on a gentle slope at Goshikigahara in the Taisetsu Mountains. Canopies of *P. pumila* are enclosed by yellow lines.

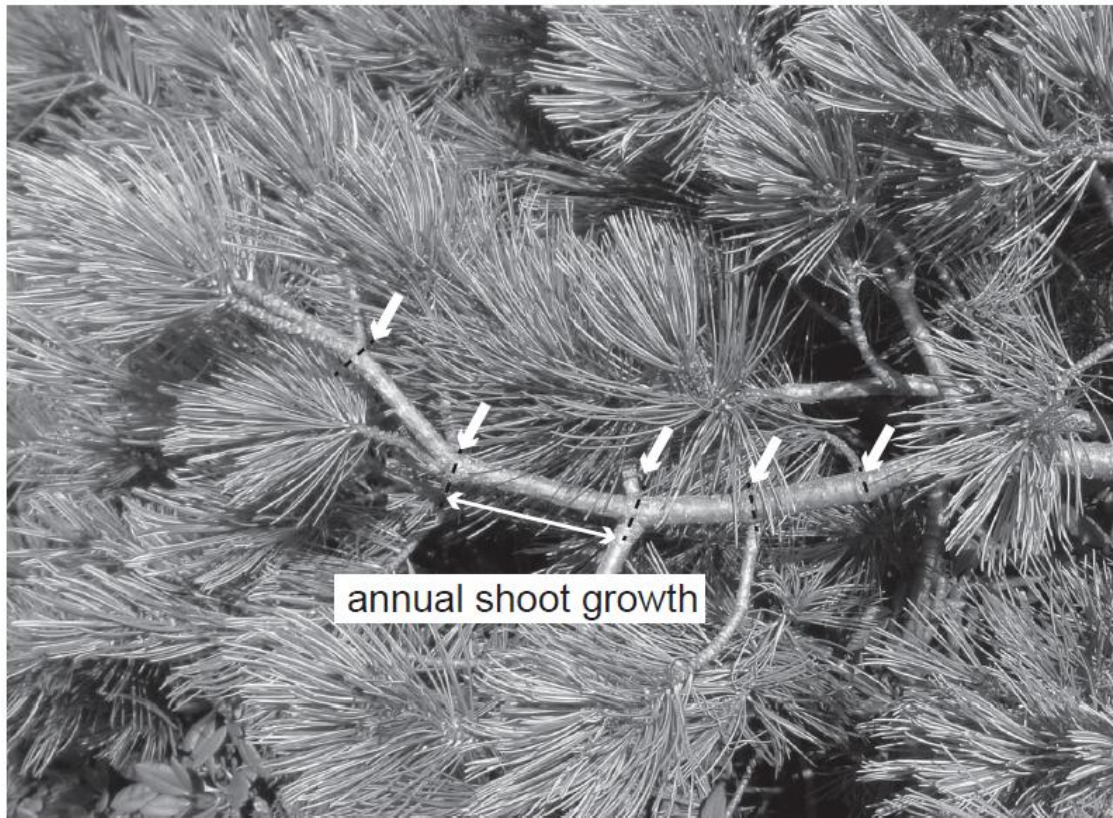


Fig. 1–3 A picture of *Pinus pumila* stem. White arrows indicate the location of bud scars remaining on the stem. Annual shoot growth was expressed as an internodal length between bud scars.

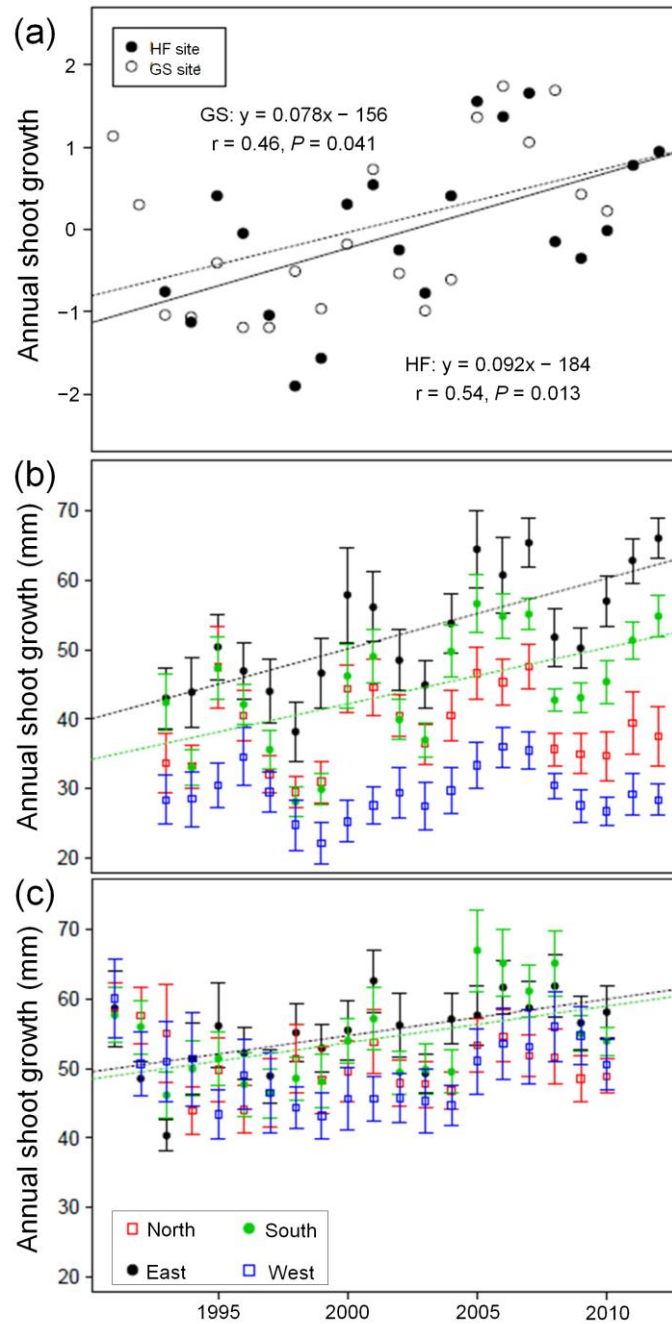


Fig. 1–4 Year-to-year trends of annual shoot growth at the fellfield side (HF site) and the snow-meadow side (GS site) over last 20 years. (a) Results of simple linear regression for standardized values and Pearson’s correlation test are shown. The solid line and broken line indicate HF site and GS site, respectively. The effects of direction on annual shoot growth (vertical bars indicate standard error) at HF site (b) and GS site (c). Results of simple linear regression are shown as significant in the eastern and southern sides of patches.

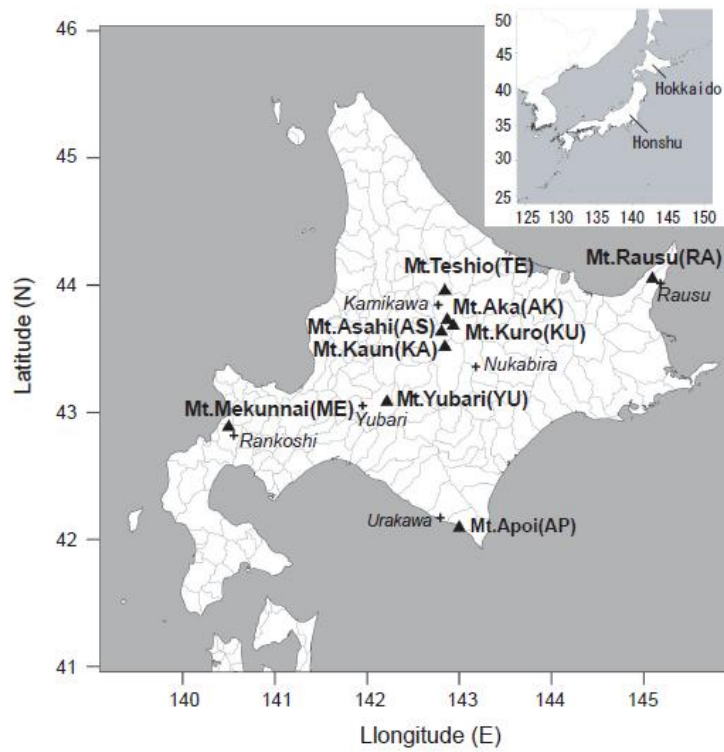


Fig. 1–5 Locations of mountain sites (▲) and reference meteorological stations (+) in Hokkaido.

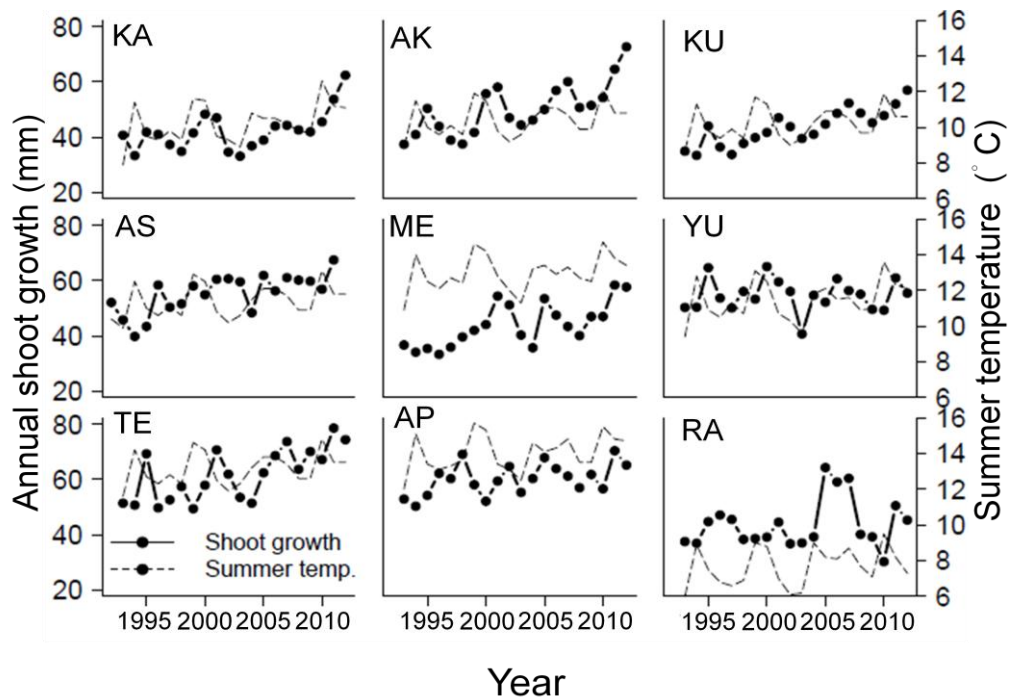


Fig. 1–6 A relationships between the summer temperature and annual shoot growth in each mountain site. Refer Fig. 1–5 for the abbreviation of each site.

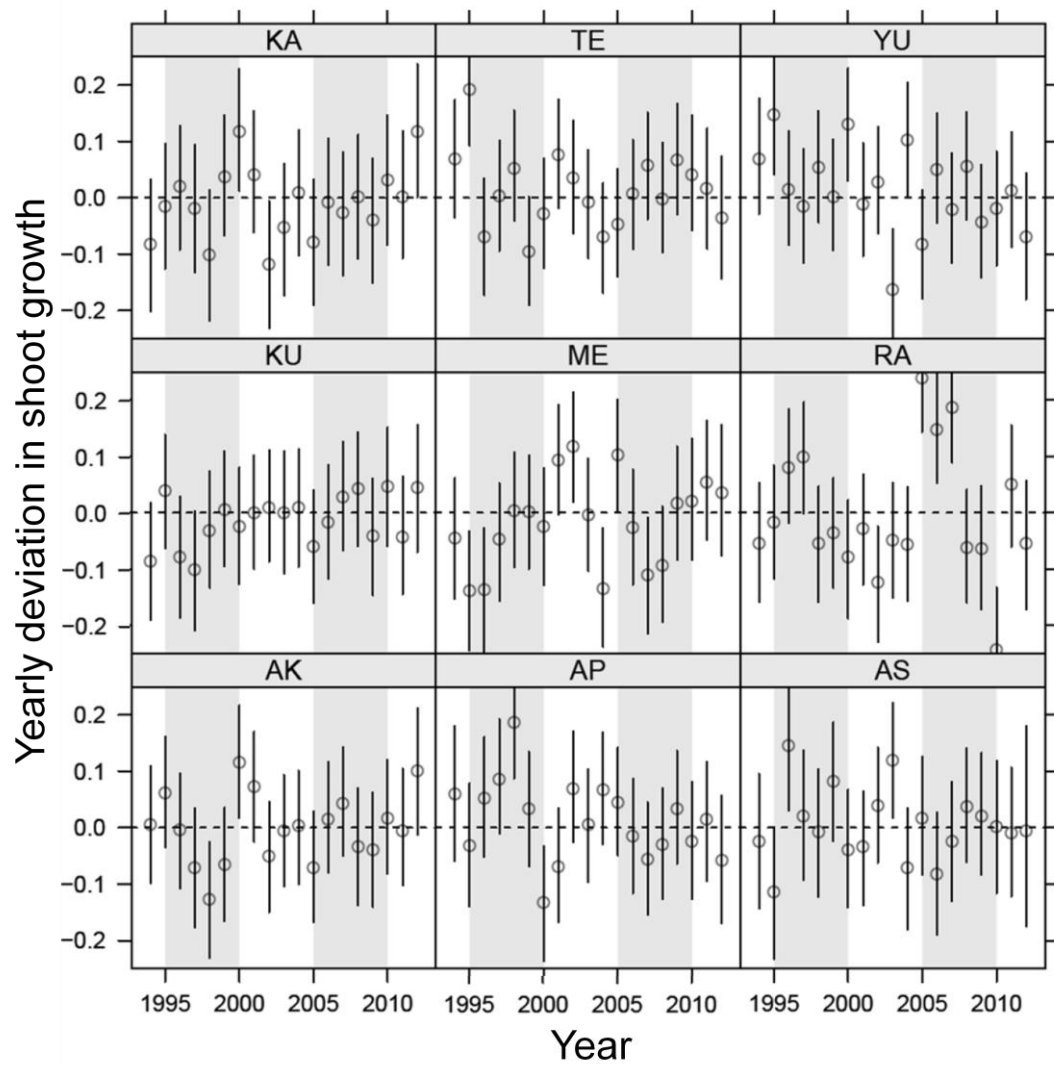


Fig. 1–7 Estimated patterns of annual shoot growth during last 19 years in each mountain site. Refer Fig. 1–5 for the abbreviation of each site.

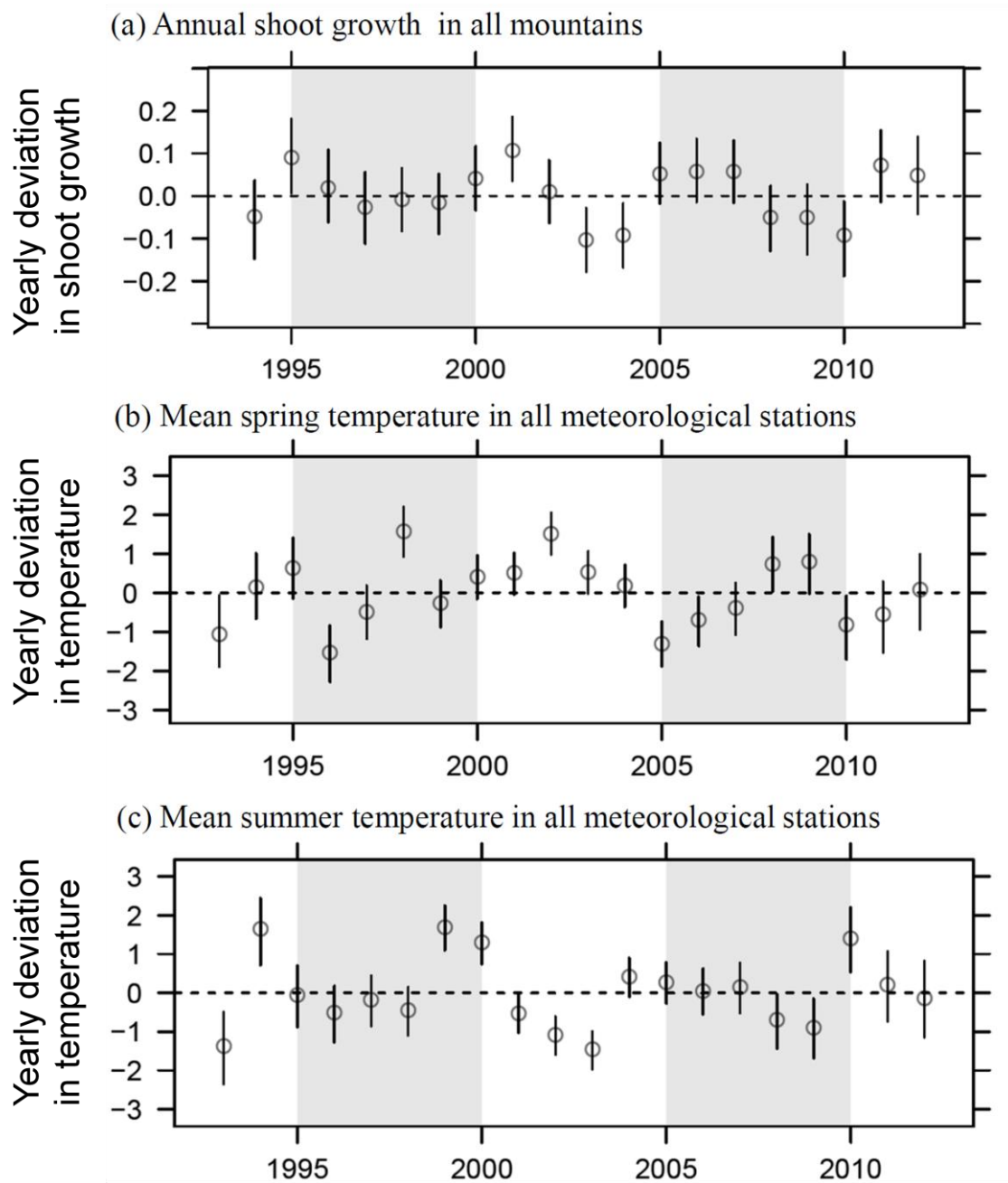


Fig. 1–8 Estimated patterns of annual shoot growth during last 19 years (a), spring temperature (April–May) (b), and summer temperature (June–August) (c) during last 20 years across sites.

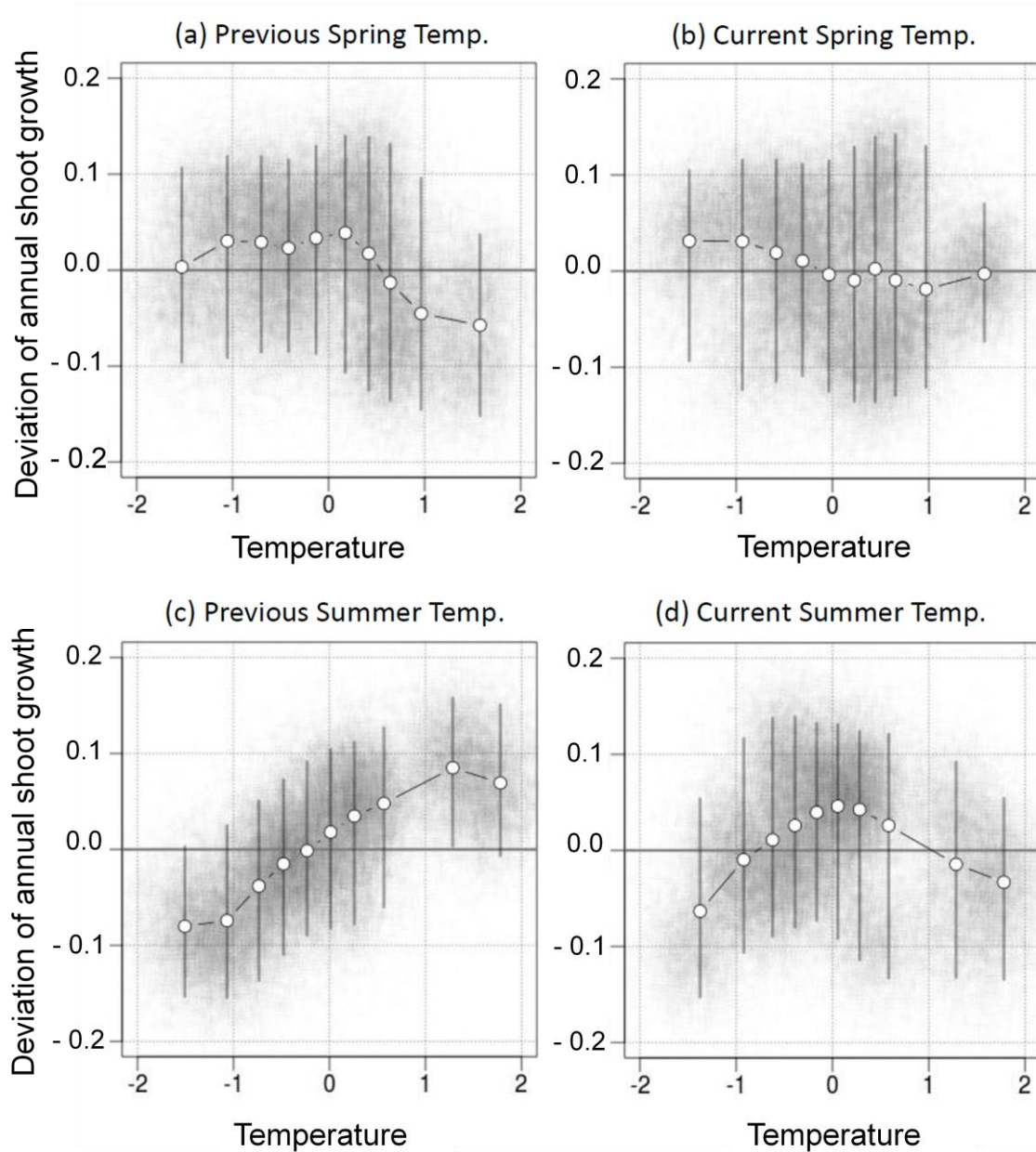


Fig. 1-9 Relationships between the deviation of annual shoot growth of *P. pumila* and temperature regimes. The effects of spring temperature (April-May) of last year (a) and current year (b) year, and the effects of summer temperature (June-August) of last year (c) and current year (d).

Table 1–1 Descriptions of study sites (geographic location and elevation), estimated warmth index (WI), and the nearest meteorological station (MS). For WI, mean values and ranges (maximum–minimum) during last 20 years are indicated. Refer Fig. 1–5 for the abbreviation of each site.

Region	Site	Location	Elevation	WI (°C•month)	Reference MS (elevation)
Taisetsu	KA	N43°32' E142°52'	1680 m	18.2 (25.8–9.7)	Nukabira (540 m)
	AK	N43°40' E142°56'	1840 m	18.4 (23.7–13.1)	Kamikawa (324 m)
	KU	N43°41' E142°54'	1880 m	17.6 (22.9–12.3)	Kamikawa (324 m)
	AS	N43°39' E142°49'	1650 m	22.4 (27.7–17.1)	Kamikawa (324 m)
Niseko	ME	N42°54' E140°31'	1210 m	30.5 (36.3–22.3)	Rankoshi (39 m)
Yubari	YU	N43°06' E142°14'	1540 m	23.8 (30.8–16.6)	Yubari (293 m)
Kitami	TE	N43°58' E142°51'	1310 m	29.9 (35.4–23.9)	Kamikawa (324 m)
Hidaka	AP	N42°06' E143°01'	620 m	42.8 (50.0–33.2)	Urakawa (37 m)
Shiretoko	RA	N44°04' E145°07'	1340 m	12.7 (17.8–6.2)	Rausu (15 m)

Table 1–2 Area occupied by *Pinus pumila* in 1977 and 2009 at the fellfield side (HF site) and the snow-meadow side (GS site), and the percentage of expansion during last 32 years.

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

Table 1–3 Results of generalized linear mixed-effect model (GLMM) for environmental factors related to annual shoot growth at (a) the fellfield habitat (HF site) and (b) the snow-meadow habitat (GS site).

Variables	Coefficient	SE	<i>t</i>	<i>P</i>
(a) HF site				
Intercept	1.69	0.11	15.46	< 0.0001
Stem size	0.001	< 0.001	38.39	< 0.0001
Current summer temperature	−0.017	0.009	−1.86	0.063
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	0.060
Previous summer sunshine	0.004	0.001	6.82	< 0.0001
(b) GS site				
Intercept	2.27	0.11	21.54	< 0.0001
Stem size	0.001	< 0.001	29.43	< 0.0001
Current summer temperature	0.012	0.007	1.77	0.077
Previous summer temperature	0.042	0.009	4.78	< 0.0001
Previous summer sunshine	0.001	< 0.001	2.29	0.022

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

Table 1–4 Annual mean shoot elongation and increasing rate of *Pinus pumila* in the four compass directions at the fellfield habitat (HF site) and the snow-meadow habitat (GS site).

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

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

Table 1–5 Results of the generalized linear mixed-effect models (GLMM) for the analysis of direction within patches related to annual shoot growth between the fellfield habitat (HF site) and the snow-meadow habitat (GS site).

Variables	Coefficient	SE	<i>t</i>	<i>P</i>
Intercept (North, HF)	3.64	0.027	134.88	< 0.0001
East	0.31	0.025	12.23	< 0.0001
South	0.14	0.025	5.46	< 0.0001
West	−0.30	−0.025	−12.23	< 0.0001
Site, GS	0.26	0.040	6.58	< 0.0001
East × GS	−0.22	0.036	−5.94	< 0.0001
South × GS	−0.06	0.036	−1.67	0.095
West × GS	0.27	0.037	7.41	< 0.0001

Chapter 2. Responses of physiological activity and shoot growth of *Pinus pumila* to weather and snowmelt conditions

2.1 Introduction

Summer temperature and sunshine duration are important determinants of shoot growth of *P. pumila* as described in Chapter 1. Photosynthetic activity of *P. pumila* should vary not only among needle ages but also seasonally within a growth period reflecting the seasonal transition of temperature. Generally, photosynthetic rates of 1- to 4-yr-old needles attain at maximum level in August, while that of current needles do in September (Kajimoto 1990). Thus, it takes long period for the physiological maturation of new needles. However, seasonal pattern of photosynthetic activity may depend on the growing habitats if phenological, morphological and anatomical traits of needles vary among habitats. Nagano et al. (2009) demonstrated that *P. pumila* growing at the wind-exposed habitat produced lower cost and shorter life-span needles having higher photosynthetic potential than at the wind-protected habitat. Nevertheless, actual carbon gain at the wind-exposed habitat was restricted by water stress (Nagano et al. 2013). In addition to the habitat-specific weather conditions, the length of growth season in each habitat is highly influenced by the local snow conditions (Kudo 1991). At the late snowmelt habitat, plants are protected from freezing temperature during the winter and strong wind during the growth season, but late snowmelt restricts the photosynthetic period resulting in lower growth rate and late phenological progress (Kammer and Möhl 2002). In the previous studies, the effects of snow conditions on the physiological traits of *P. pumila* have scarcely been considered.

Climate change in alpine ecosystems may cause different physiological impacts on *P. pumila* populations inhabiting different habitats. It is predicted that climate change

causes the changes in not only temperature but also precipitation, sunshine duration and snowmelt regime in alpine ecosystems (Inouye 2008). Warm summer may accelerate the physiological activity and shoot growth of *P. pumila* but early snowmelt and warm temperature during the summer may increase water stress, resulting in lower carbon gain. In contrast, warm spring often increases the risk of frost damage of alpine plants (Nagy and Grabherr 2009), and the risk of frost damage is expected to be high at the fellfield habitat. Because physiological activity highly depends on needle ages, the effects of climate change on physiological impacts may vary between the fellfield side and snow-meadow side habitats reflecting the difference in leafing phenology. Therefore, I focus on the mechanism causing the expansion of *P. pumila* in each habitat with reference to climate and habitat factors affecting the physiological activity and growth of *P. pumila*.

In this study, I conducted three experiments to test how physiological activity and/or shoot growth of *P. pumila* respond to the shading, warming, and defoliation treatments. I expect following responses: (1) the shading treatment may increase the photosynthetic activity if strong radiation (especially in early season) decreases the photosynthetic function, but may decrease the shoot growth if low radiation is a limiting factor for cumulative carbon fixation. (2) The warming treatment may increase the photosynthetic activity and shoot growth if cool temperature is a limiting factor of photosynthetic activity. (3) The defoliation treatment may decrease the shoot growth due to smaller photosynthetic area.

2.2 Material and methods

2.2.1 Measurement of chlorophyll fluorescence

Light intensity and temperature influence the relationship between the light energy

absorbed through a photochemistry process and the energy utilized through metabolism. The energy imbalance between them affects the relative reduction state of photosystem II (Huner et al. 1998). The F_v/F_m value (Kitajima et al. 1975) is calculated with F_o , which is chlorophyll fluorescence value under darkness, and F_m , which is chlorophyll fluorescence value in the state that saturated a chemical reaction ($F_v = F_m - F_o$). Therefore, the F_v/F_m value is yield of the photochemical reaction in the dark-adapted leaf, and it is a reliable measure of the potential quantum yield of photosystem II (Demming et al. 1987; Kooten and Snel 1990).

The photosystem II is easily deactivated under low temperature and high radiation. Photoinhibition decreases photosynthetic capacity, resulting in low daily and annual carbon gain (Long et al. 1994; Hikosaka et al. 2004; Miyazawa et al. 2007). Plants inhabiting alpine environment experience high risk of photoinhibition due to frequent frost event under high irradiation (Streb et al. 1998, Germino and Smith 1999, Manuel et al. 1999). The F_v/F_m values usually indicate from 0.80 to 0.83 without photoinhibition, but the value decreases under the inhibition of photosystem II reaction centers and the increase of heat dissipation (Demmig and Bjorkman 1987; Oquist et al. 1992). In this chapter, I compared F_v/F_m values among habitats throughout the growth period to assess the spatiotemporal variations in photosynthetic capacity of *P. pumila* in the field.

The F_v/F_m was measured for dark-adapted (15 min) needles using portable fluorimeter (MINI PAM, Walz, Effeltrich, Germany) during 31 May to 28 September in 2014. Initial fluorescence (F_o) was measured in the M1-burst mode of the Mini-PAM, maximum fluorescence was measured after a saturating light pulse.

2.2.2 Experimental manipulations of temperature and radiation

To quantify the effects of temperature and radiation on physiological activity and shoot growth, experimental manipulations were conducted at HF site during 2013 and 2014 (Fig. 2-1). I selected 20 patches of *P. pumila* and five shoots in each patch in 2013. All selected shoots were tagged for identification. One of the shoots was assumed as an intact control, and other four shoots were used for manipulations in which lateral branches on the main stems were cut off at the younger than 4-yr-old parts. Then, three kinds of treatment, shading, warming, and defoliation treatments were allocated with a manipulation control (no treatment except for the removal of lateral branches; Fig. 2-2). The removal of lateral branches was conducted to simplify the shoot structure responding to the treatments.

The shading treatment was conducted using the black cheesecloth bags with 51% shading ability. In the warming treatment, I used white non-woven fabric bags with little shading ability ($< 10\%$) but having warming ability. The defoliation treatment means the removal of one-half of the leaves on the branch at the younger than 4-yr-old parts by scissors. The shading and warming treatments, i.e. shoot bagging, were conducted only during the growth season (from 9 June to 10 September in 2013 and from 1 June to 28 September in 2014).

I measured ambient temperature of the shading, warming and control treatments during the growth season in 2013 and 2014. Measurements were done at 1-hr intervals by automatic small loggers fixed on the stems (StowAway Tidbit, Onset Co., USA). To evaluate the effects of treatments on shoot growth, I measured annual shoot growth during 2003 and 2014 using a digital caliper under careful identification of intermodal length between bud-scar marks on the stem.

The F_v/F_m values of 1-yr-old needles were measured in each shoot of each treatment in every patch during the growth season (from 1 June to 28 September) in 2014. To

compare the photosynthetic capacity between different ages, furthermore, the F_v/F_m values of current needles were measured from 29 July to 28 September in 2014 when measurement of current leave was possible. Because the intact control and the manipulation control showed no significant difference for every measurement in the preliminary analyses (i.e. no effect of branch removal), I used the data of the manipulation control for the comparison with the shading, warming and partial defoliation treatments in this study.

2.2.3 Effects of altitude and snowmelt time on photosynthetic activity

The measurement was conducted at Goshikigahara (G site) and the southern slope of Mt. Kaun (K site) (Fig. 2-1). I set five plots in each place across the snowmelt and altitudinal gradients, and measured F_v/F_m values of 1-yr-old needles. I arbitrarily selected and marked six or seven shoots in each plot during the growth season (from 1 June to 29 September) in 2014. The control data at HF site was included in the data analysis, resulting in 11 plots in total.

2.2.4 Data analysis

Seasonal trends of photosynthetic yield of 1-yr-old needles were compared among the treatments using the generalized linear mixed-effect model (GLMM) postulating a Gamma error distribution with log-link functions. In the GLMM, assigned ID of patches was included as a random factor, and treatment and seasonal progress (week number from the first measurement) were treated as explanatory variables in which a quadratic term of week was also included. The effects of needle ages (current vs. 1-yr-old) and treatments on the photosynthetic yield were compared by the GLMM postulating a Gamma error distribution with log-link function in which age and seasonal progress

(week and week²) were set as fixed factors, treatment were included in the explanatory variables, and ID was included in a random factor.

Next, the effects of experimental manipulations on shoot growth were analyzed using the GLMM postulating a Gaussian error distribution with identity-link functions. In the GLMM, assigned ID of patches was included as a random factor. Before the analysis, the annual shoot growth data from 2003 to 2014 were standardized in each shoot. To eliminate the yearly variation during the experiment (2013 and 2014) and endogenous effect, I included year of experiment and mean shoot growth from 2003 to 2012 in the explanatory variables in addition to the treatment effect.

Finally, the effects of altitude and snowmelt time on photosynthetic yield during the growth season in 2014 (May 31–Sep. 29) were analyzed for the measurement data from 11 plots across three locations (HF, G and K sites) in 2014 using the GLMM postulating a Gamma error distribution with log-link function. In the GLMM, location was included as a random factor, altitude and snowmelt time were set as fixed factors, and seasonal progress (week and week²) was treated as explanatory variable. The GLMMs were performed using the function `glmer` (Gamma error distribution) and `lmer` (Gaussian error distribution) included in the R package `lme4` (Bates et al. 2015) using the R statistical software version 3.2.4 (R Core Team 2016).

2.3 Results

2.3.1 Warming effect of the treatments

Temperature fluctuation in each experiment during the growth season was shown in Figure 2-3. Daily mean temperatures of control (mean values 2013 and 2014) were 11.0, 13.2, 12.7 and 8.4 °C in June, July, August and September in daily mean temperature, respectively; daily minimum were 5.9, 8.4, 8.8 and 4.5 °C, respectively; and daily

maximum were 17.7, 19.6, 17.7 and 13.9 °C, respectively. Warming effects of the shading and warming treatments relative to the control were indicated in Table 2-1. The differences in mean temperature were 0.10–0.13 °C (daily mean) in the shading treatment, while 0.38–0.86 °C in the warming treatment.

2.3.2 Changes in photosynthetic yield by the treatments

The seasonal variations in photosynthetic yield (F_v/F_m value) of 1-yr-old needles across the treatments are shown in Figure 2-4, and GLMM results are described in Table 2-2. The F_v/F_m values increased in the shading ($P < 0.001$) and warming treatments ($P < 0.001$), but there was no change in the defoliation treatment ($P = 0.89$). Photosynthetic yield changed as season progressed in which the F_v/F_m values were low in the beginning and end of the growth season ($P < 0.001$), indicating the low photosynthetic capacity in these periods.

The mean values of F_v/F_m of the shading and warming treatments were 0.66 and 0.68 in late May, maintained 0.81–0.85 from late June to mid-September, and decreased to 0.78 and 0.75 in late September, respectively. The F_v/F_m values of the control and partial defoliation treatment were 0.67 in late May, 0.77–0.83 from late June to mid-September, and 0.66 in late September. Therefore, photosynthetic capacity was retained higher in the shading and warming treatments in comparison with the control shoots.

2.3.3 Needle age effect on photosynthetic yield

Seasonal variations in the photosynthetic yield of 1-yr-old and current needles are shown in Figure 2-5, and GLMM results are described in Table 2-3. The F_v/F_m values of 1-yr-old needles were significantly larger than that of current needles ($P < 0.001$). Similar to the 1-yr-old needles (Table 2-3), the F_v/F_m values were increased by the

shading ($P < 0.001$) and warming treatments ($P < 0.001$), but there was no change in the defoliation treatment ($P = 0.41$). The photosynthetic yield changed as season progressed in which the F_v/F_m values were low in the beginning and end of season ($P < 0.001$) also in the 1-yr-old needles, and there were interactions between needle age and season ($P < 0.001$).

The mean F_v/F_m values of current needles of the shading and warming treatments were 0.83–0.84 from late July to mid-August, 0.75–0.78 and 0.80–0.82 from late August to mid-September, and 0.60 and 0.70 in late September, respectively. The F_v/F_m values of current needles of the control and partial defoliation treatments were 0.79–0.82 from late July to mid-August, 0.70–0.71 from late August to mid-September, and 0.50–0.53 in late September. Also for current needles, photosynthetic capacity was retained higher in the shading and warming treatments.

2.3.4 Responses of shoot growth to the treatments

Annual shoot growth was large in 2005–2007 and 2010–2012, while small in 2003, 2004, 2008, 2009, 2013 and 2014. Annual shoot growth was significantly increased in the warming treatment ($P < 0.001$), but there were no significant effects of the shading and defoliation treatments (Fig. 2-6, Table 2-4). There was no significant difference in shoot growth between the years of experiment (2013 and 2014), but previous shoot growth was negatively related to the shoot growth of the experimental years ($P < 0.001$).

2.3.5 Variations in photosynthetic yield among habitats

In the measurements of photosynthetic yield of 1-yr-old needles across plots, the F_v/F_m values tended to decrease at higher altitude ($P < 0.001$) and later snowmelt ($P < 0.001$)

habitats (Fig. 2-7, Table 2-5). Significant interaction was detected between altitude and snowmelt time ($P < 0.001$).

The mean values of F_v/F_m along the altitudinal and snowmelt gradients during the growth season of 2014 were shown in Table 2-6. In the altitudinal comparisons, the F_v/F_m values were 0.67 in late May, 0.77–0.82 from late June to mid-September, and 0.66 in late September at the low-elevation plots; and 0.58 in late May, 0.76–0.82 from late June to mid-September, and 0.72 in late September at the high-elevation plots. In the comparison of snowmelt time, the F_v/F_m values were 0.65 in late May, 0.78–0.83 from late June to mid-September, and 0.71 in late September at the early-snowmelt plots; 0.56 in late May, 0.78–0.83 from late June to mid-September, and 0.71 in late September at the middle-snowmelt plots; and 0.68 from late June to early July, 0.78–0.81 from mid-July to mid-September, and 0.73 in late September at the late-snowmelt plots.

2.4 Discussion

Seasonal changes in physiological activity

The F_v/F_m values showed clear seasonal variations across the treatments and habitats in which the values were commonly low in the beginning and end of the growth season. This might be caused by the seasonal trend of temperature conditions. High irradiance under low temperature during the winter results in the inhibition of photochemical efficiency of photosystem II (Oquist and Ogren 1985; Yamazaki et al. 2003, 2007). The temperature-dependent photoinhibition process sometimes affects the recovery process of photosynthetic capacity after overwintering (Greer et al. 1986). Because conifers retain needles for several years, the photosynthetic apparatus must survive severe winters and recover the photosynthetic capacity quickly in spring (e.g. Oquist and

Huner 2003). Therefore, seasonal trend of the F_v/F_m values in *P. pumila* reflects the recovery process of physiological activity.

Responses to the treatments

Although the F_v/F_m values were low (0.66–0.68) for all treatments in early season (May 31), the shading and warming treatments increased photosynthetic yields. The shading treatment might reduce the negative effects of photoinhibition under low temperature in early season that caused rapid recovery of physiological activity in comparison with control and the defoliation treatment, and maintained physiological activity until late season. Furthermore, the photosynthetic capacity is remained at high level during warmer period (e.g. Oquist and Huner 2003). Therefore, the warming treatment advances physiological recovery from overwintering to growth periods under warm conditions, and maintained physiological activity until late season.

Because shoot growth was increased only by the warming effect, cool temperature during the growth period might restrict the growth of *P. pumila* in this site. On the other hand, shoot growth was not influenced by the shading treatment. The shading treatment reduced irradiation by approximately 51%, but did not change the sunshine duration. Therefore, sunshine duration may be an important factor for shoot growth (Chapter 1, Wada et al. 2005).

Although I expected that annual shoot growth might depend on plant size, i.e. ontogenetic effect, the shoot growth of previous years (2003–2012) was negatively related to the shoot growth of the experimental years (2013 and 2014). Therefore, the positive size effect was not detected in this study. Takahashi (2006) reported that the fluctuation of annual growth was caused by the yearly variation in summer temperature independent on shoot size. Yasuda and Okitsu (2012) reported that there was a positive

correlation between shoot growth and tree-ring growth (as a size index), but the growth pattern varied among individuals. Therefore, shoot growth of *P. pumila* is more sensitive to climate conditions than ontogenetic effect.

Effects of needle age

The responses of current needles to the treatments were similar to that of 1-yr-old needles but the F_v/F_m values of current needles were smaller than that of 1-yr-old needles. Furthermore, interaction was detected between current needles and season progressed. This means that the physiological activity of current needles is more sensitive to the seasonal progress than that of 1-yr-old needles. Net photosynthetic rates of 1-yr-old needles of *P. pumila* attained at maximum in August, while that of current needles did in September (Kajimoto 1990). These differences reflect the physiological maturation process of current needles. A similar trend is reported in another pine, *Pinus sylvestris* (Troeng and Linder 1982). In contrast, the F_v/F_m values of current needles attained at maximum level in the present study, indicating earlier physiological maturation in the Taisetsu Mountains. Nagano et al (2013) reported that the mean photosynthetic rate at the wind-exposed site was 76 % of that at the wind-protected site, and the growth of *P. pumila* at wind-exposed sites was limited by needle production. At the fell-field habitat, strong wind may damage the physiological capacity and decrease the leaf longevity. Thus, relative importance of photosynthesis by current needles may be larger at the fell-field habitat than at the snow-meadow habitat.

Variations among habitats

Photosynthetic activity was sensitive at higher altitude with later snowmelt, where time of growth initiation was late and the length of growth season was short. The recovery of

photosynthetic activity after overwintering takes time when snowmelt was late. Therefore, the acceleration of snowmelt time may positively affect *P. pumila* growth due to not only the extension of photosynthetic period but also shorter recovery period of physiological activity after snowmelt.

In Chapter 1, I demonstrate that *P. pumila* distribution has expanded toward both fellfield and snowbed sides during last a few decades in the Taisetsu Mountains. The expansion toward the fellfield side (HF site) might be due to the increasing temperature during the growth season, while the expansion toward the snow-meadow side (G site) might be partly because of longer snow-free period in addition to the increasing summer temperature. In the fell-field habitat, furthermore, a warm spring may increase the risk of frost damage, while warming summer temperature induced not only shoot growth but also shorter recovery period of physiological activity. Therefore, the negative effect of warm spring may be compensated by warm summer climate.

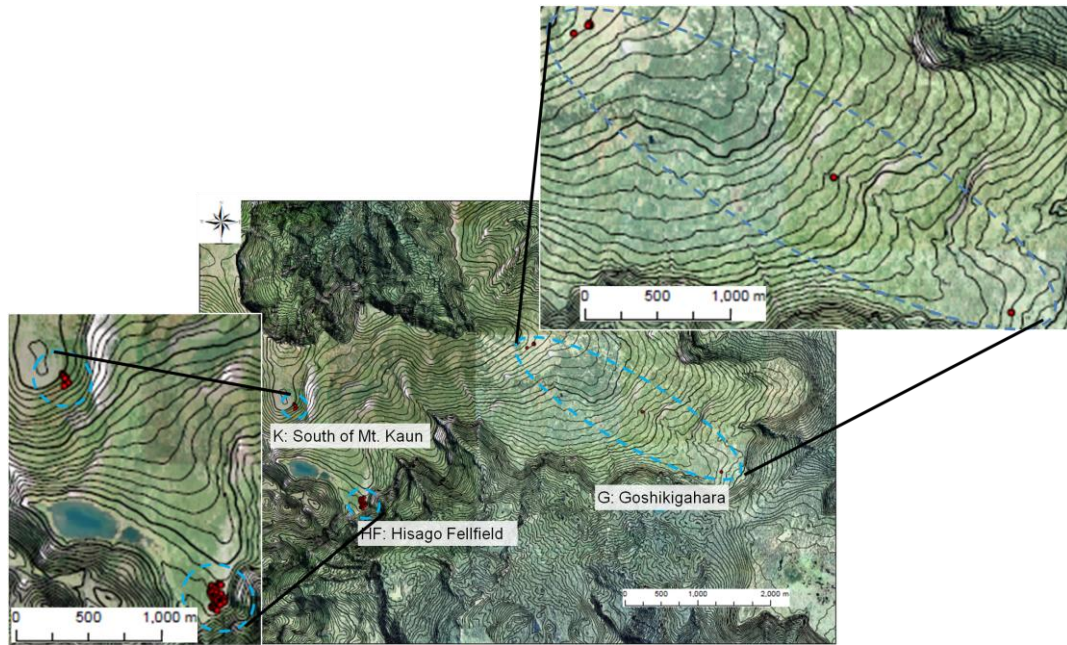


Fig. 2-1 Location of research sites; fellfield (HF) site, Goshikigahara (G) site, and Mt. Kaun (K) site in the Taisetsu Mountains. Plots were selected along the altitudinal and snowmelt gradients in G and K. The measurement of photosynthetic yield was conducted at red points.

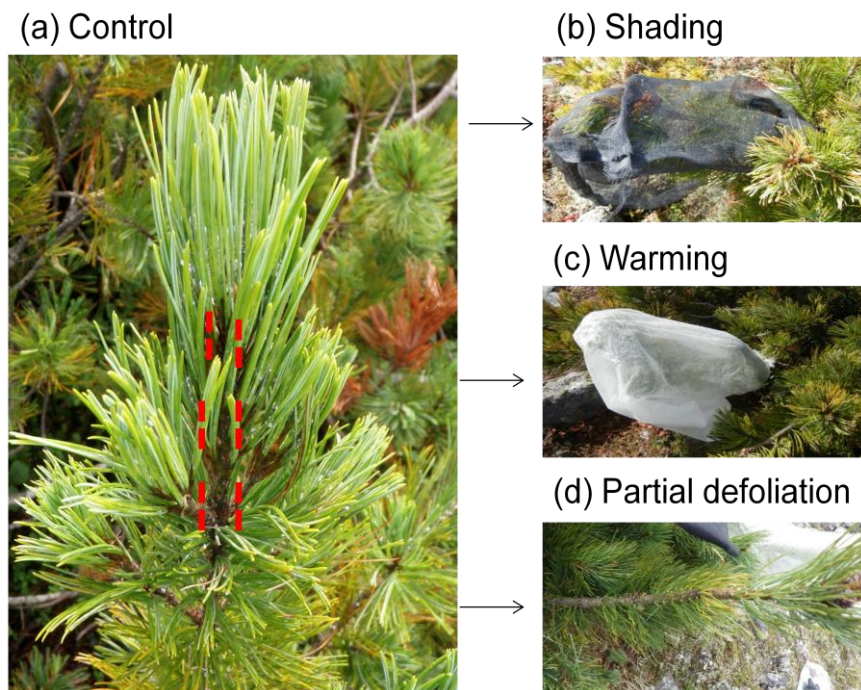


Fig. 2-2 Experimental manipulations of *Pinus pumila*. (a) Control shoot in which lateral branches on the main stems were cut off at the < 4-yr-old parts (red line); (b) the shading treatment was conducted using black cheesecloth bags after cutting of lateral branches; (c) the warming treatment was conducted using non-woven fabric bags after cutting of lateral branches; and (d) defoliation treatment was the removal of one-half needles on the branch of < 4-yr-old parts after cutting of lateral branches.

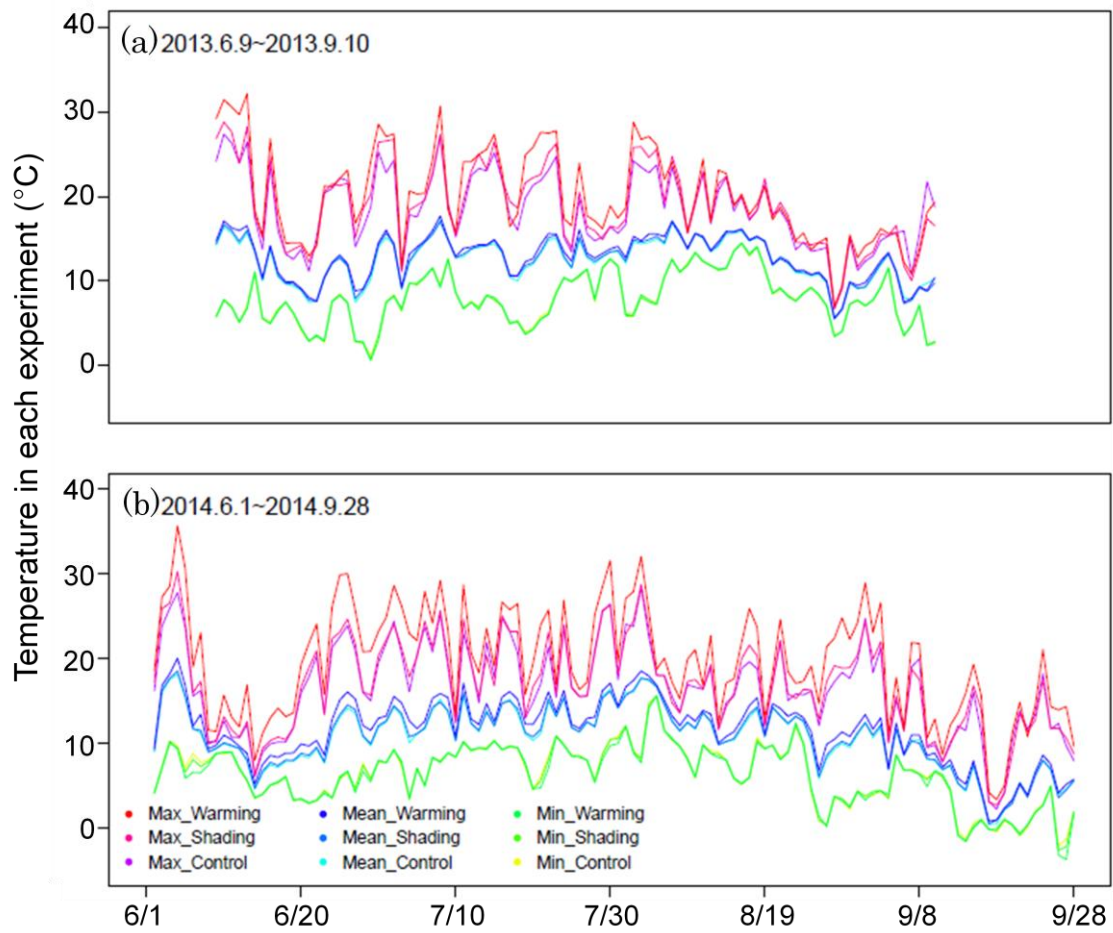


Fig. 2-3 Maximum, mean and minimum temperatures of the control, shading, and warming treatments during the growth season in (a) 2013 (from 9 June to 10 September) and (b) 2014 (from 1 June to 28 September).

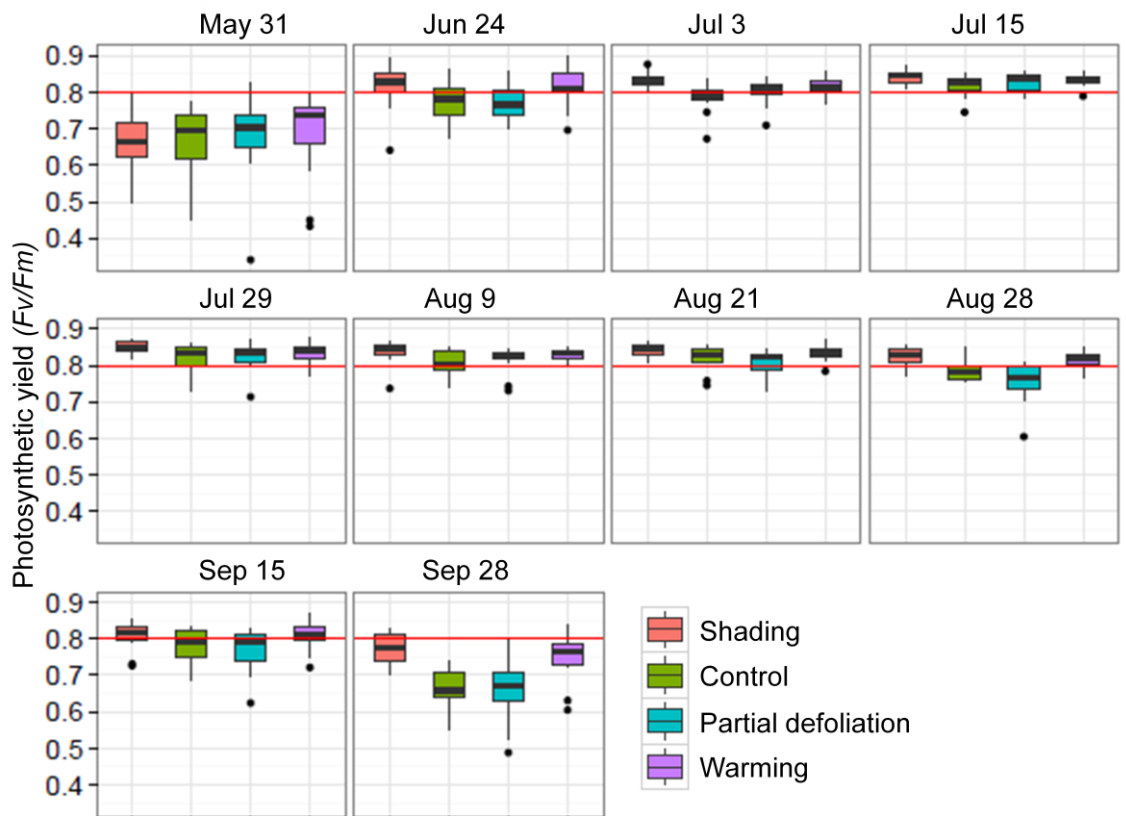


Fig. 2-4 Photosynthetic yield (F_v/F_m) of 1-yr-old needles of the control, shading, warming, and partial defoliation treatments during the growth season in 2014. Box and whisker plot represents the 75th, 50th, and 25th percentile with whiskers from the 90th to 10th percentile. $n = 20$ patches.

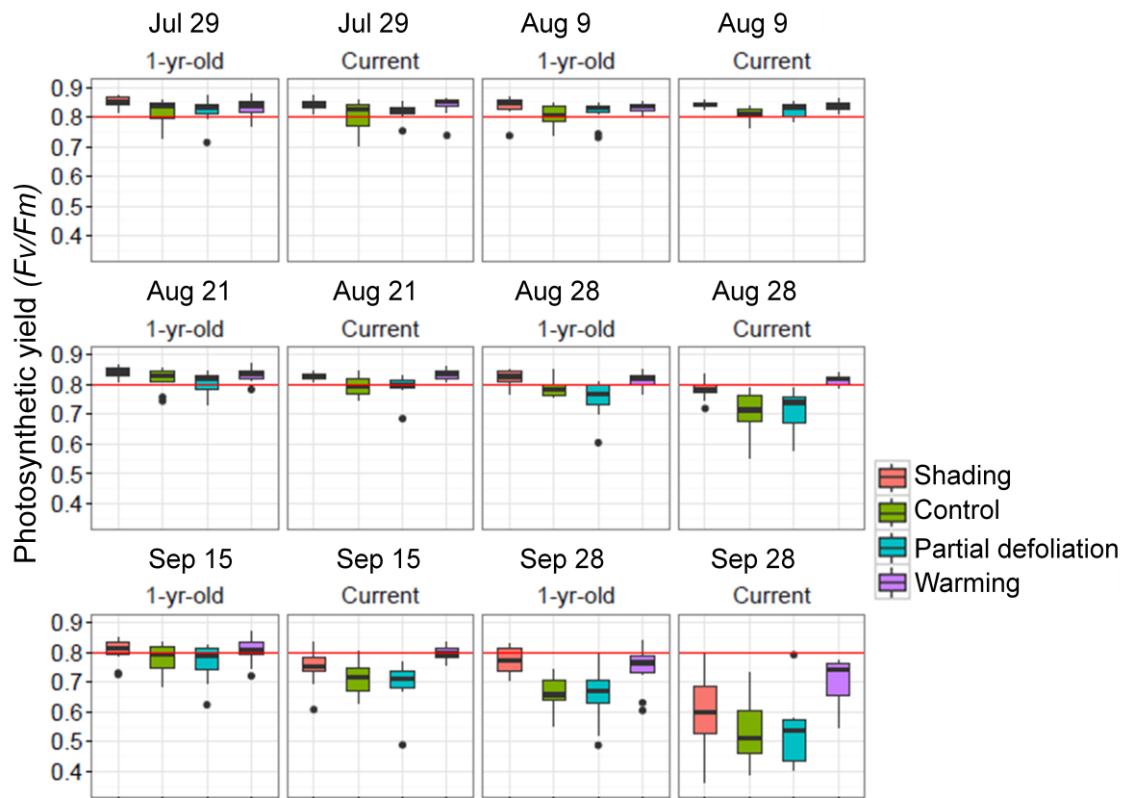


Fig. 2-5 Photosynthetic yield (F_v/F_m) of 1-yr-old and current needles of the control, shading, warming, and partial defoliation treatments during the growth season in 2014. Box and whisker plot represents the 75th, 50th, and 25th percentile with whiskers from the 90th to 10th percentile. $n = 20$ patches.

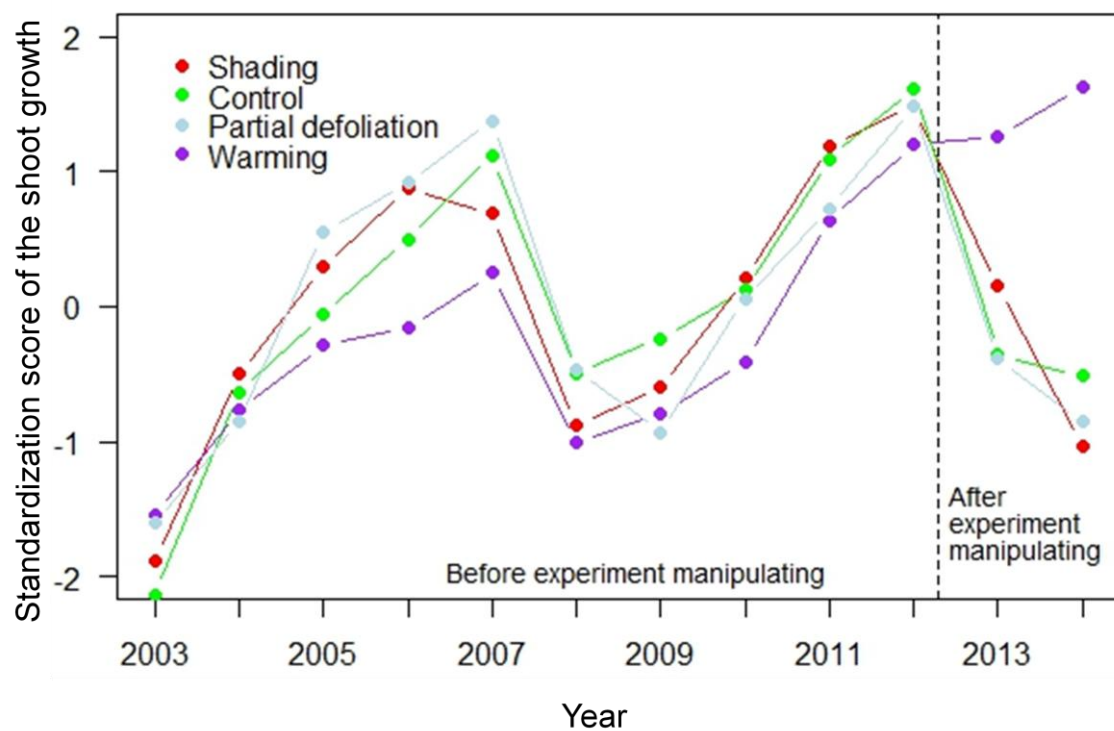


Fig. 2-6 Patterns of annual shoot growth before the experimental manipulation (from 2003 to 2012) and after the manipulation (i.e. control, shading, warming and partial defoliation treatments in 2013 and 2014).

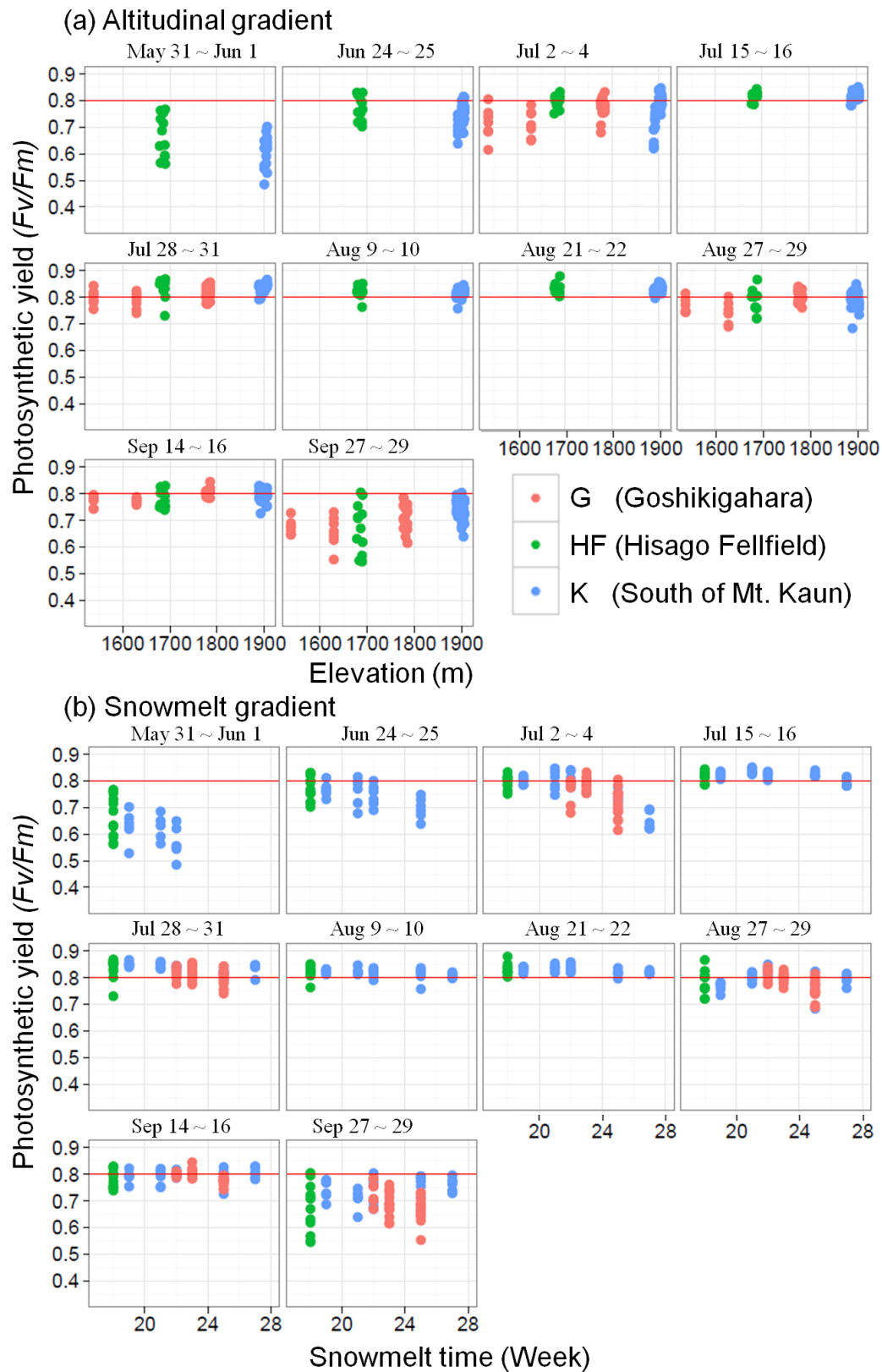


Fig. 2-7 Photosynthetic yield (F_v/F_m) of 1-yr-old needles along the (a) altitudinal and (b) snowmelt gradients during the growth season in 2014 at three locations.

Table 2-1 Warming effects of the shading and warming treatments relative to the control. Mean, maximum and minimum of daily values during the growth season are indicated. Mean $\pm$ SD.

	Year	Mean Temp.	Max Temp.	Min. Temp.
ΔT Shading treatment*	2013	0.13 $\pm$ 0.06	0.58 $\pm$ 0.41	-0.06 $\pm$ 0.03
	2014	0.10 $\pm$ 0.01	0.40 $\pm$ 0.15	-0.04 $\pm$ 0.01
ΔT Warming treatment*	2013	0.38 $\pm$ 0.10	1.72 $\pm$ 1.06	-0.01 $\pm$ 0.02
	2014	0.86 $\pm$ 0.18	3.11 $\pm$ 1.05	-0.14 $\pm$ 0.02

* Difference in daily values between treatment and control during the growth season.

Table 2-2 Result of the GLMM for the effects of treatments (control, shading, warming and partial defoliation) on photosynthetic yield (F_v/F_m) of 1-yr-old needles during the growth season in 2014.

Variables	Coefficient	SE	<i>t</i>	<i>P</i>
Intercept (control)	-2.65	0.027	-99.82	< 0.001
Shading	0.049	0.009	5.22	< 0.001
Warming	0.041	0.009	4.42	< 0.001
Partial defoliation	-0.001	0.009	-0.14	0.89
Season (week)	0.16	0.001	165.28	< 0.001
Season ² (week ²)	-0.003	< 0.001	-167.38	< 0.001

Table 2-3 Result of GLMM for the effects of needle age (current and 1-yr-old) and treatments (control, shading, warming and partial defoliation) on photosynthetic yield (F_v/F_m) during the growth season in 2014.

Variables	Coefficient	SE	<i>t</i>	<i>P</i>
Intercept (1-yr-old needle, control)	-2.98	0.059	-50.6	< 0.001
Current needle	-3.80	0.076	-50.1	< 0.001
Shading	0.062	0.010	6.4	< 0.001
Warming	0.077	0.010	8.0	< 0.001
Partial defoliation	-0.008	0.010	-0.8	0.41
Season (week)	0.18	0.002	92.8	< 0.001
Season ² (week ²)	-0.003	< 0.001	-152.1	< 0.001
Current needle × Season (week)	0.24	0.002	108.0	< 0.001
Current needle × Season ² (week ²)	-0.004	< 0.001	-438.1	< 0.001

Table 2-4 Result of GLMM for the effects of treatments (control, shading, warming and partial defoliation), experimental years (2013 and 2014) and previous shoot growth (2003–2012) on annual shoot growth during 2013 and 2014.

Variables	Coefficient	SE	<i>t</i>	<i>P</i>
Intercept (control, year = 2013)	1.48	0.44	3.40	< 0.001
Year of experiment (2014)	-0.19	0.12	-1.50	0.14
Mean Shoot growth between 2003 and 2012	-0.031	0.008	-3.93	< 0.001
Shading	-0.18	0.18	-0.99	0.32
Warming	0.85	0.18	4.76	< 0.001
Partial defoliation	-0.20	0.18	-1.12	0.27

Table 2-5 Result of GLMM for the effects of altitude and snowmelt gradient on photosynthetic yield (F_v/F_m) during the growth season in 2014.

Variables	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	−2.53	0.073	−34.8	< 0.001
Altitude (10 ³ m)	−0.35	0.039	−8.9	< 0.001
Snowmelt time	−0.039	0.002	−17.6	< 0.001
Season (week)	0.19	0.001	292.4	< 0.001
Seasonality ² (week ²)	−0.003	< 0.001	−667.6	< 0.001
Altitude × Snowmelt	0.019	0.001	16.2	< 0.001

Table 2-6 The mean values of F_v/F_m along the altitude (a) and snowmelt (b) gradients during the growth season in 2014.

Season*	time 1	time 2	time 3	time 4	time 5
(a) Altitude					
Low (1530–1700 m)	0.668	0.767	0.818	0.779	0.662
High (1701–1910 m)	0.580	0.758	0.820	0.797	0.724
(b) Snowmelt time (week)					
Early (18, 19)	0.648	0.784	0.829	0.782	0.708
Middle (22, 23)	0.555	0.776	0.826	0.802	0.710
Late (25, 27)	NA	0.679	0.813	0.784	0.730

* time 1: Mar 31, time 2: Jun 24–Jul 4, time 3: Jul 15–Aug 22, time 4: Aug 27–Sep 16, time 5: Sep 27–29.

Chapter 3. Factors affecting seedling establishment and survival of *Pinus pumila*

3.1 Introduction

Distribution of *P. pumila* has expanded and shoot growth has increased responding to the recent acceleration of snowmelt time and summer temperature as described in Chapters 1 and 2. However, the GIS analysis cannot clarify how population structure has changed under recent climate conditions. Okitsu and Mizoguchi (1990) reported that cone production of *P. pumila* increased with plant size. This means that cone production of *P. pumila* may increase in accordance with the increase in shoot growth and canopy expansion under natural conditions. Changes in cone production may affect seedling establishment pattern, but the relationship between the cone production and seedling occurrence is not clear.

Recruitment of *P. pumila* seedlings primarily depends on the seed dispersal by Japanese nutcrackers (*Nucifraga caryocatactes* var. *japonica*) that store seeds in the soil (Saito 1982; Hayashida 1989). They prefer exposed open habitat near the mature scrubs of *P. pumila* in which soil-moisture tends to be low during the summer (Kajimoto *et al.* 1998). Two major factors affecting seedlings mortality are uprooting caused by frost-heave soil disturbance in spring and drought stress in early summer (Kajimoto 2002). Therefore, seedling establishment of *P. pumila* is strongly determined by the microhabitat of seed caching and environmental conditions at early stage.

Long-term monitoring of seedling dynamics of *P. pumila* has been scarcely conducted. Therefore it is unclear how warm summer temperature, early snowmelt, and dry soil conditions affect the seedling establishment and mortality of *P. pumila*. At the fellfield habitat, where *P. pumila* populations are composed of small patches of

individuals, populations may be maintained by the balance of seedling establishment and mortality. The purpose of this study is to quantify the dynamics of population structure and to clarify the factors affecting cone production, seedling establishment, and survival rate of seedlings based on the 21 years records of seedling dynamics at a fellfield habitat.

3.2 Material and methods

3.2.1 Estimation of cone production

Annual cone production of *P. pumila* during last 20 years was estimated using the cone scar technique (Saito 1983; Nakashinden 1995). I counted cone production of randomly selected 500 stems around the 20 m × 20 m quadrat established in 1994 at HF site (see below). Then, I measured annual shoot growth during last 20 years using a digital caliper to an accuracy of 0.1 mm for 20 stems around the quadrat in order to eliminate the endogenous factor affecting cone production. For the comparison of cone production patterns among other places, furthermore I conducted same measurements at Mt. Ariake (1635 m), Mt. Hirayama (1771 m), Mt. Muri (1876 m), Mt. Muka (1759 m) and Mt. Shiyubetsu (1688 m) in the northern part of the Taisetsu Mountains, and also at Goshikigahara.

3.2.2 Field census of the seedling establishment and population dynamics

All *P. pumila* clumps were labeled using number tape, mapped and traced within a 20 m × 20 m quadrat during 1994–1999 (Wada et al., unpublished data) and 2013–2015 (present survey). All *P. pumila* individuals were classified into three stages: seedling

and younger stem (< 25-yr-old), sapling (older than 25-yr-old but immature plants), and adult (mature plants producing cones).

Seedlings and younger stems are often composed of clumps (same cohort originated from same seed cache; Kajimoto et al. 1998). Stem age was determined by counting the number of nodes corresponding to yearly growth along a main stem from basal to tip portion (Kajimoto et al. 1998). Seedling age was defined as years after germination, i.e. seedlings germinated in 1993 and 1992 were age 1 and 2 in 1994, respectively (Kajimoto et al. 1998; Kajimoto 2002). The type of micro-habitat of seedling bed was classified into five; cushion plants (*Loiseleuria procumbens* and *Diapensia lapponica*), lichen cover, *P. pumila* litter, mixed (lichen cover and *P. pumila* litter), and other (including bare ground). Field census of population structure was conducted during the middle of August to the middle of September because current seedlings usually appeared after late July.

3.2.3 Data analysis

Effects of environmental factors and endogenous factors on cone production were analyzed using generalized linear model (GLM). In the GLM, following explanatory variables are included: (1) current shoot growth, (2) spring temperature (mean air temperature during April and May), and (3) summer temperature (mean air temperature from June to August) of current and previous years. Negative binomial distribution was assumed with log-link function. Yearly trend of cone production was analyzed by autoregressive analysis in each site.

Factors affecting seedling establishment were analyzed by GLM postulating a negative binomial distribution with log-link function in which the number of seedlings within a plot was a responsible variable and cone production (number of matured cones

on 500 stems in the last year and two years ago) and cumulative soil temperature during the current spring (May to July) were included as explanatory variables.

Year-to-year changes in the survival rates of seedlings during last 21 years were predicted by an asymptotic regression model. The factors affecting seedling survival during one, two, three and twenty years later were analyzed using generalized linear mixed-effect models (GLMMs). In the model of one-year later survival (analyzed data in 1994–1998 and 2013–2014), following explanatory factors were included: (1) clump size, the number of stem per clump, (2) vegetation type around each clump, (3) monthly mean air temperatures that were previous August and September (from germination to overwintering), current April and May (after overwintering) and current June (early growth season). Because there was no data of exact snowmelt day in the survey years, I used (4) the date on which daily mean temperatures exceeded above 5 °C first time as an index of growth initiation. In GLMMs for survival in two (analyzed data in 1994–1997, 2013), three (1994–1996) and twenty (1994–1995) years later, only clump size and vegetation type were included as explanatory variables in which binomial distribution was assumed with logit-link function and survey years as a random factor. Kajimoto (1998, 2002) suggested the importance of precipitation and water conditions for seedling establishment and survival. Although I included precipitation as environmental factor, it did not affect seedling establishment and survival significantly. Thus, it was excluded from the analyses.

Yearly changes in the number of plants in each age class were compared by GLM postulating a Poisson error distribution with log-link function in which observation year was set as an explanatory variable. R statistical software ver. 3.2.4 (R Core Team 2016) was used for data analyses. The GLM of negative binomial distribution analysis was performed using the Mass package (Venables and Ripley 2002), autoregressive analysis

was performed using the tseries package (Trapletti and Hornik 2015), and GLMM of binomial distribution analysis was performed using the glmmML package (Brostrom 2013) in R.

3.3 Results

3.3.1 Cone production

Cone production highly fluctuated from year to year at HF site (Fig. 3-1). The GLM analyses revealed that cone production was positively related to current shoot growth, and current and last summer temperatures, whereas current spring temperature was negatively related (Table 3-1). These results indicate that cone production tends to increase at every second year in this population and it is positively related to summer temperature.

The pattern of cone production differed among populations. The autocorrelation analyses revealed that the cone production of HF site, Mt. Ariake, Mt. Muri, Mt. Muka and Mt. Shiyubetsu showed the periodicity of every second year, while that of Mt. Hirayama and Goshikigahara was every third year (Fig. 3-2).

3.3.2 Seedling establishment

The number of seedlings decreased recently (Fig. 3-3, Table 3-2). All factors included in the GLM, that were cone production in last year and two years before and cumulative soil temperature from May to July, did not affect the seedling establishment significantly (Table 3-3). Clump size (the number of seedlings per clump) was mostly less than five, but some clumps at lichen patches were larger than 25 (Fig. 3-4).

3.3.3 Seedling survival

Seedling survival rate during first year was high at the mixed-type seedling bed, and positively related to clump size, temperatures of August, April and June, and date of growth initiation, whereas May temperature was negatively related (Table 3-4). Survival rate during several years was also high at the mixed-type seedling bed (2, 3 and 20 years later), but it was low at the lichen-type seedling bed (2, 3 and 20 years later), and negatively related to clump size (3 and 20 years later) (Table 3-5). Seedling survival rate at 3 and 20 years later was estimated as 41 % and 13 %, respectively (Fig. 3-5).

3.3.4 Population structure

Total number of individuals and the number of < 5-yr-old seedlings decreased in the recent investigation, while individuals of > 6-yr old tended to increase. The median values of individual age classes were 550, 260, 120, 87, 60, 23, 98 and 25 in 0–2-yr-old, 3–5-yr-old, 6–10-yr-old, 11–15-yr-old, 16–20-yr-old, 21–25-yr old, sapling and adult during 1994 to 1999, while 79, 167, 218, 160, 173, 99, 183 and 22 from 2013 to 2015, respectively (Table 3-2, Fig. 3-6).

3.4 Discussion

Summer temperature and annual shoot growth were positively related to cone production of *P. pumila*. This indicates that cone production is regulated by the assimilative production as suggested by Okitsu and Mizoguchi (1991). Warm summer may increase the resource condition for cone production as well as shoot growth. Optimum air temperatures for net photosynthesis in current and 1-yr-old needles are between 10 and 15 °C (Kajimoto 1990). Mean temperature during the growth period was 8.7 °C in June, 11.9 °C in July, 12.8 °C in August and 8.0 °C in September (means from 2003 to 2012) in this site. Therefore, warm summer temperature enhance the

photosynthetic products of *P. pumila*. On the other hand, warm spring may decrease the freezing resistance early in the season that increased the risk of frost damage (Inouye 2008; Maruta et al. 1996), resulting in lower shoot growth and cone production when physiological activity is damaged by occasional frost temperature.

Interestingly, the periodicity of cone production differed among populations; cone production at HF site, Mt. Ariake, Mt. Muri, Mt. Muka and Mt. Shiyubetsu was enhanced every second year, while cone production at Mt. Hirayama and Goshikigahara was enhanced every third year. Nakashinden (1995) reported that cone production tended to increase at 3- or 4-yr intervals at Mt. Kisokomagatake (2956 m) in central Japan, it was caused by the dynamics of shoot number. Especially, cone production was increased on stems with diameter of 2 to 4 cm in good years, while decreased on stems with diameter of, 5 cm in bad years, because the capacity of cone production might decrease with stem aging (Nakashinden 1995). If the cycle of cone production is determined by resource condition, the length of annual growth period is related to the periodicity of cone production. In early snowmelt place (e.g. HF site), long annual photosynthetic period may shorten the period of resource accumulation for cone production in comparison with late snowmelt places (e.g. Goshikigahara). Similarly, the periodicity of cone production may vary reflecting the local climate conditions and altitudes of individual populations.

Contrary to my expectation, seedling establishment was independent on previous cone production, temperature environment, and precipitation. One possibility is that seedling recruitment may be limited by seed dispersal process. *Pinus pumila* depends on nutcrackers for seed dispersal (Kajimoto et al. 1998; Kajimoto 2002). Only seeds successfully cached in safe site and uneaten can germinate as seedlings. Therefore,

changes in the situations of seed dispersion and/or seed predation pressure may be related to the recent decrease in seedling establishment in HF population.

The present study revealed that warm temperatures soon after germination and early growth season of the next year enhanced the survival rate of seedlings. Temperature in early spring before growth initiation was also related to the survival rate of seedlings. High survival rate was attained when April was warm, May was cool, and growth initiation (first date of $> 5^{\circ}\text{C}$ air temperature) was late. Because April and May temperatures were negatively related to shoot growth (Chapter 1) and cone production, spring temperature differently affected the seedling survival from mature plants. Daily mean air temperature in April ranged from -12 to -6°C (2013–2015) in which soil surface was covered with snow. Mature plants growing at the fellfield habitat are often exposed during winter and early spring because of thin snow depth in fellfield sites. If occasionally warm temperature in early spring decreases the freezing resistance, mature plants increase the risk of frost damage, resulting in lower growth or reproduction. On the other hand, seedlings are mostly protected under snow in April. However, the daily maximum temperature often increases above 0°C in May, which accelerates the snowmelt. Therefore, too early exposure from snow protection increases the risk of frost damage for seedlings. On the other hand, uprooting of seedlings by frost-heave soil disturbance was not common in this site.

The seedling survival of first year was positively related to clump size, while survival rates at third and 20th year were negatively related to clump size. Because a lot of seedlings exist per clump in first year, seedlings are protected by environmental factors such as the wind damage or drying. On the other hand, the mortality of seedlings was increased in later years, because competitive exclusion works as growth advances. Among the types of seedling bed, lichen-moss patches provided favorable microhabitat

for seed germination (Okitsu and Ito 1984). Clumps with many seedlings were common at lichen patches (sometimes > 25). This is because nutcrackers prefer open places for caching (Kajimoto et al. 1998). Lichen patches maintain higher moisture conditions than bare ground (Tanaka et al. 2009), and it is suitable for germination. However, the survival rate at lichen patches is low because seedlings are exposed to severe climate conditions without protection of other vegetation. On the other hand, seedlings at mixed patches showed high survival rate. Litter patches are located under the canopy of *P. pumila*, which is protected from wind but seedlings are shaded. The mixed patches are protected from wind damage around *P. pumila*, and there are moderately open patches. Seedling survival rates were estimated to be 41 % and 13 % at the third and 20th year, respectively. Morihiro (personal communication) reported that only 16 % of 209 seedlings germinated in 1984 survived at the end of third year (1987) at Hyakken-daira, central Japan (2750 m). Therefore, the survival rate at HF site was higher than the previous report.

Cone production and seedling survival rate were enhanced under warm conditions. Reflecting the higher survival rate of seedlings, the number of individuals older than six years tends to increase. On the other hand, the number of seedlings younger than five years tended to decrease regardless of the number of cone production. Warm climate contributes to shoot growth, canopy expansion, cone production, and survival rate of *P. pumila*, whereas seedling recruitment may depend on the activity of nutcrackers and seed predators. As a result, the total number of stems has decreased and population structure has changed recent years. For the prediction of population dynamics of *P. pumila* under climate change, it is important to take into account not only climate conditions and physiological responses but also biological situations through seed dispersal and post-dispersal processes.

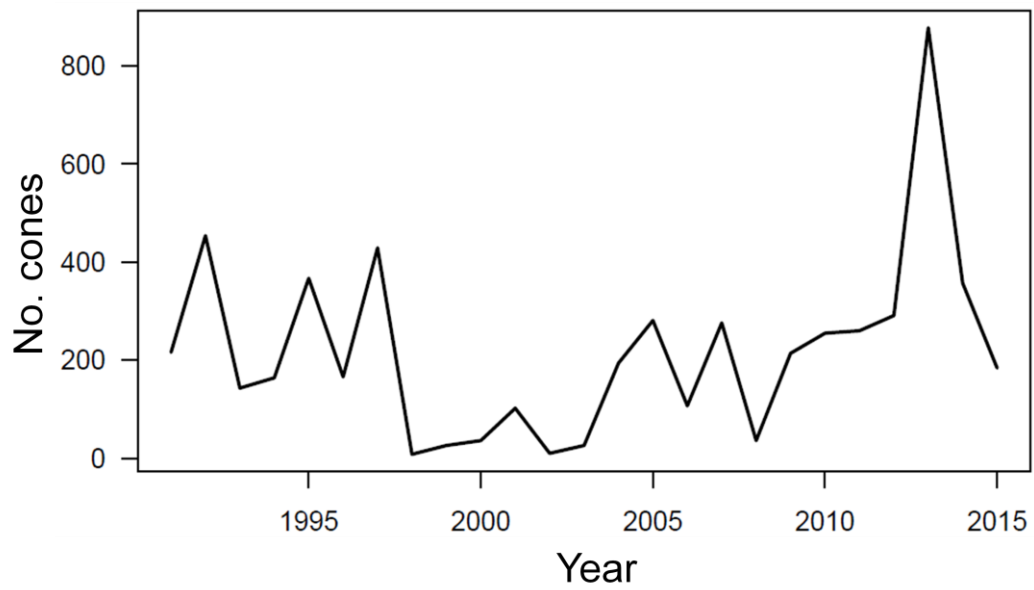


Fig. 3-1 Year-to-year changes in the total number cone scars for 500 shoots (1991–2015) at HF site.

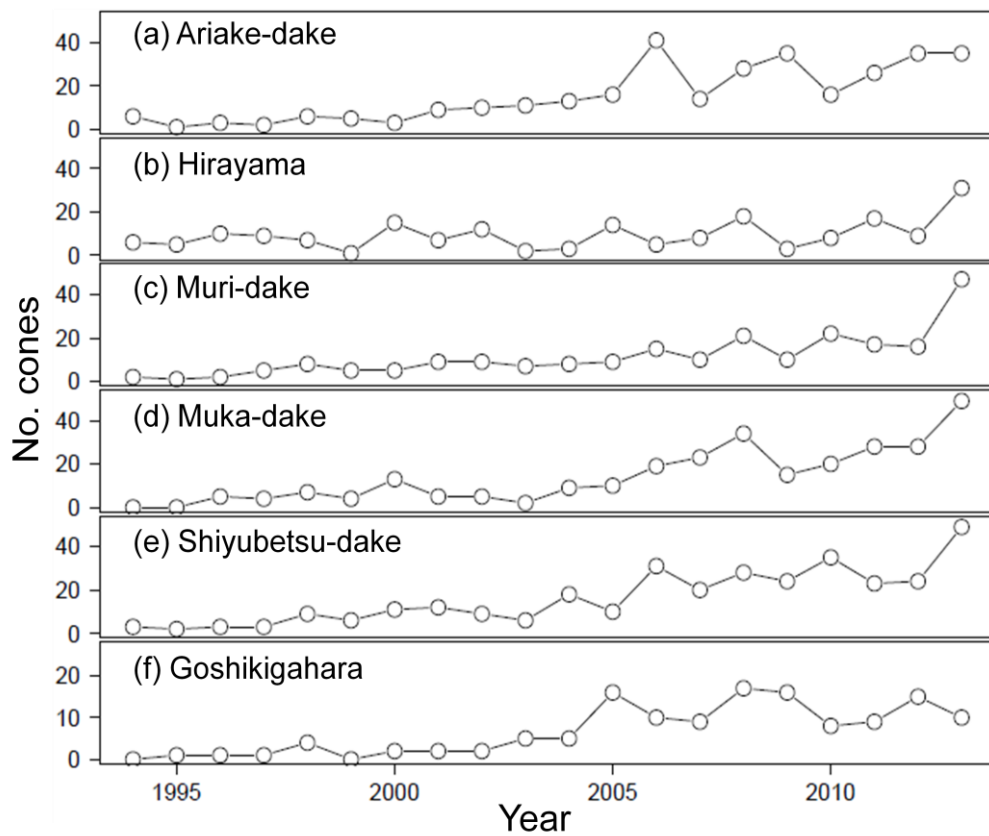


Fig. 3-2 Year-to-year changes in the total number of cone scars for 20 shoots (1994–2015) at Mt. Ariake (a), Mt. Hirayama (b), Mt. Muri (c), Mt. Muka (d) and Mt. Shiyubetsu (e) of the northern part of the Taisetsu Mountains and Goshikigahara site.

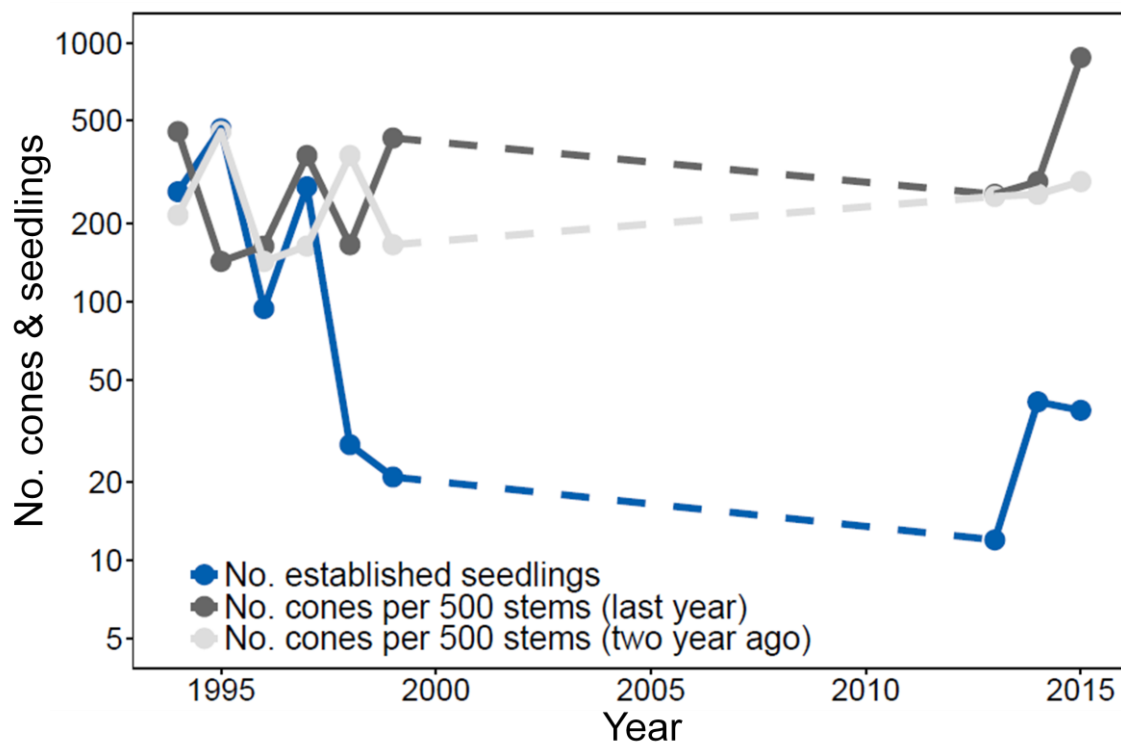


Fig. 3-3 Total number of cones produced by 500 shoots in the one and two years before, and the number of established seedlings at HF site during 1994 to 2015 with an interruption from 2000 to 2012.

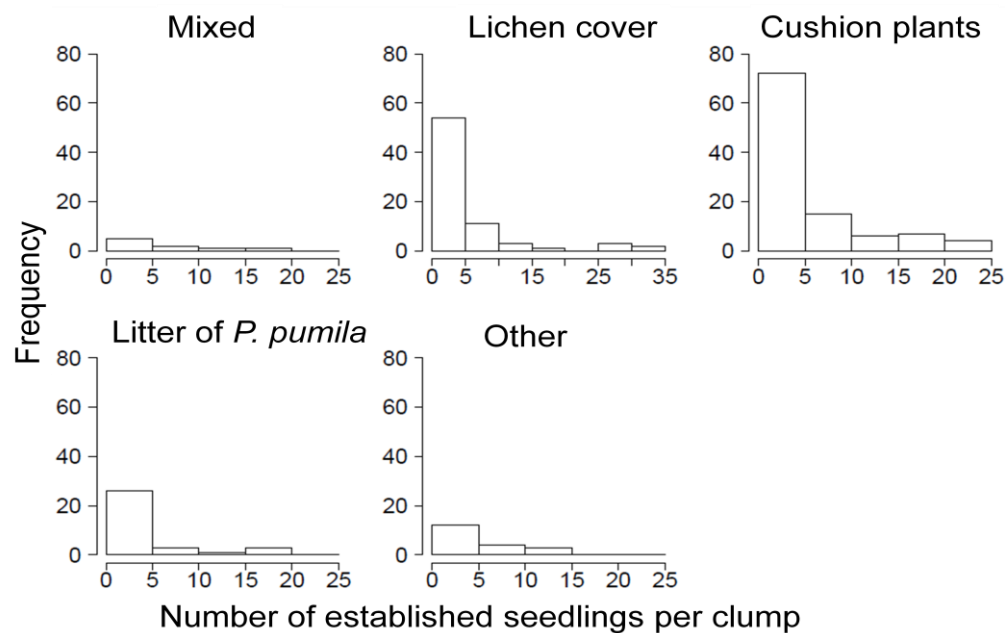


Fig. 3-4 Histogram showing the number of established seedlings per clump among habitat types of seedling bed.

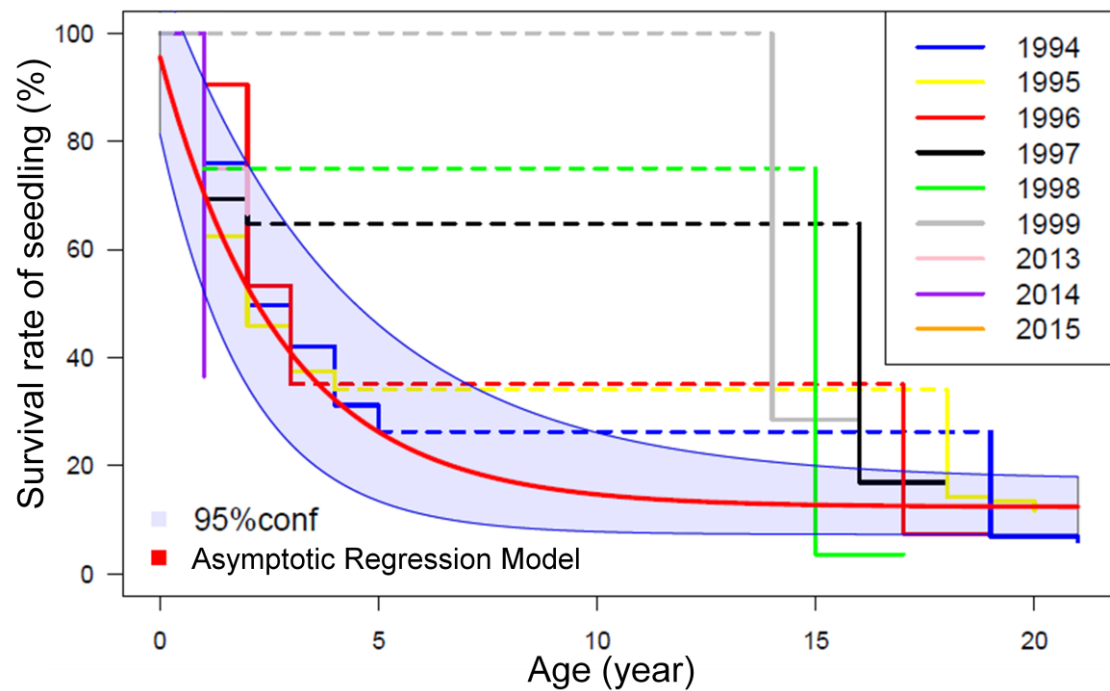


Fig. 3-5 Survival rate of seedlings was predicted by asymptotic regression model (red line). The blue lines show the upper and lower limits of the 95 % confidence interval. Solid lines indicate actual survival rates of seedlings in each survey year at HF site.

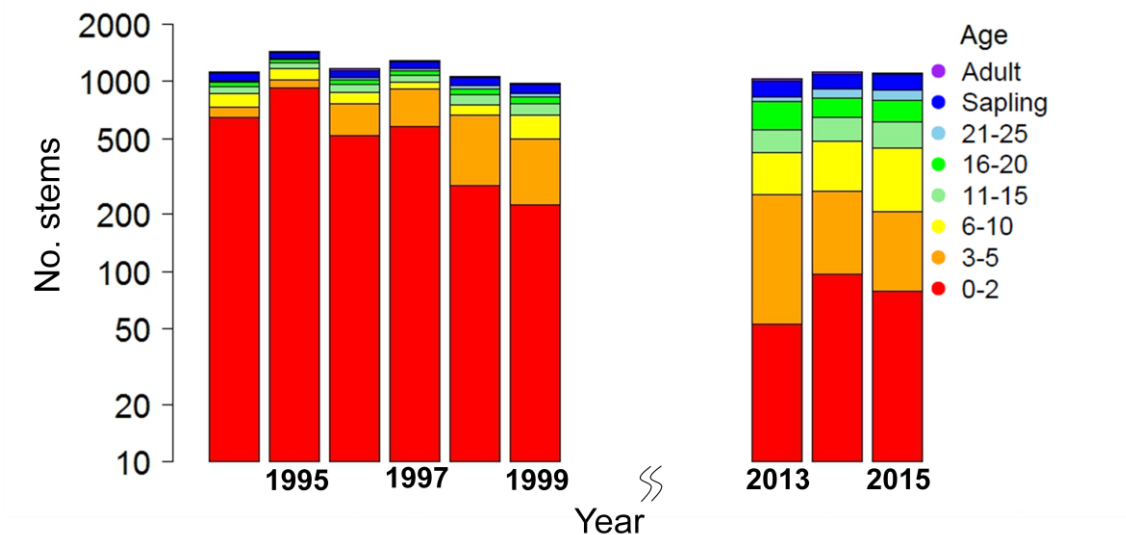


Fig. 3-6 Yearly variation in age structure of the population during 1994–1999 and 2013–2015.

Table 3-1 GLM result for the effects of endogenous factors (shoot growth, cone production in last year and two years before) and temperatures (spring, current and last summer) on cone production from 1993 to 2012.

Variables	Coefficient	SE	z	P
Intercept	2.19	0.71	3.11	0.002
Current shoot growth	0.008	0.003	2.78	0.005
Spring temperature	-0.34	0.038	-9.11	< 0.001
Current summer temperature	0.11	0.042	2.52	0.012
Last summer temperature	0.090	0.041	2.20	0.028

Table 3-2 Seedling survivorships during 1994 and 2015 with an interruption from 2000 to 2012. Seedling age at the beginning of the census (in 1994) is defined as the year after germination.

Age (Years)	Numbers of seedlings								
	1994	1995	1996	1997	1998	1999	2013	2014	2015
-21									38
-20								41	15
-19							12	9	8
-6_-18							497	466	418
-5						21	6	6	6
-4					28	21	1	1	1
-3				278	193	180	47	47	44
-2			94	85	50	33	7	7	7
-1		466	291	214	175	159	66	63	55
0	266	202	132	112	83	70	18	18	16
1	301	249	179	150	123	111	67	66	63
2	82	69	61	60	41	33	16	16	16
3_5	78	64	38	32	29	25	8	8	8
6_10	133	131	118	108	102	95	49	49	48
11_15	77	76	72	71	68	67	22	22	22
16_20	48	47	46	40	34	33	18	18	18
21_25	13	11	9	9	7	6	4	4	4

Table 3-3 GLM result for the effects of cone production (in one and two years ago) and cumulative soil temperature during spring on seedling establishment during 1994–1999 and 2013–2015.

Variables	Coefficient	SE	z	P
Intercept	2.54	5.27	0.48	0.63
Cone production in last year	−0.001	0.002	−0.87	0.39
Cone production in two years before	0.002	0.004	0.58	0.56
Cumulative soil temperature from May to July	0.006	0.012	0.45	0.65

Table 3-4 GLMM result for the effects of habitat type of seedling bed, clump size, temperature (previous August and September, and current April, May and June) and date of growth initiation on seedling survival at one year later during 1994–1999 and 2013–2015. Habitat type of seedling bed was classified as cushion plants, lichen cover, litter of *Pinus pumila*, Mixed (lichen cover and litter of *P. pumila*) and other (e.g. bare ground and forb).

Variables	Coefficient	SE	z	P
Intercept (Cushion plants)	−21.00	5.65	−3.72	< 0.001
Clump size	0.02	0.01	2.96	0.003
Lichen cover	−0.18	0.15	−1.19	0.23
Litter of <i>P. pumila</i>	0.08	0.25	0.33	0.74
Mixed	1.66	0.45	3.69	< 0.001
Others	−0.24	0.27	−0.90	0.37
August temp.	1.02	0.31	3.29	0.001
September temp.	−0.68	0.36	−1.89	0.059
April temp.	2.14	0.56	3.81	< 0.001
May temp.	−1.54	0.46	−3.34	< 0.001
June temp.	1.88	0.46	4.07	< 0.001
Date of growth initiation	0.09	0.03	3.01	0.003

Table 3-5 GLMM results for the effects of habitat type of seedling bed and clump size on seedling survival at two years later (a), three years later (b), and twenty years later (c) during 1994–1999 and 2013–2015.

Variables	Coefficient	SE	<i>z</i>	<i>P</i>
(a) Two years later				
Intercept (Cushion)	0.40	0.19	2.10	0.036
Clump size	−0.004	0.007	−0.62	0.53
Lichen cover	−0.62	0.14	−4.36	< 0.001
Litter of <i>P. pumila</i>	0.33	0.25	1.34	0.18
Lichen and litter	0.72	0.31	2.30	0.022
Other	−0.23	0.26	−0.91	0.37
(b) Three years later				
Intercept (Cushion)	0.17	0.15	1.08	0.28
Clump size	−0.032	0.008	−3.74	< 0.001
Lichen cover	−0.70	0.17	−4.08	< 0.001
Litter of <i>P. pumila</i>	0.14	0.28	0.51	0.61
Lichen and litter	0.67	0.30	2.26	0.024
Other	0.036	0.36	0.10	0.92
(c) Twenty years later				
Intercept (Cushion)	−1.21	0.29	−4.22	< 0.001
Clump size	−0.067	0.017	−3.83	< 0.001
Lichen cover	−0.69	0.31	−2.21	0.028
Litter of <i>P. pumila</i>	−0.78	0.51	−1.54	0.12
Lichen and litter	0.67	0.40	1.67	0.096
Other	−10.12	67.35	−0.15	0.88

Table 3-6 GLM results for yearly changes in the number of individual in each age class during 1994–1999 and 2013–2015.

Variables	Coefficient	SE	z	P
(a) Total individuals				
Intercept	18.50	2.39	7.73	< 0.0001
Year	−0.01	0.001	−4.79	< 0.0001
(b) From 0 to 2 age				
Intercept	252.05	7.89	31.94	< 0.0001
Year	−0.12	0.004	−31.16	< 0.0001
(c) From 3 to 5 age				
Intercept	29.65	5.69	5.22	< 0.0001
Year	−0.01	0.003	−4.27	< 0.0001
(d) From 6 to 10 age				
Intercept	−57.11	6.20	−9.21	< 0.0001
Year	0.03	0.003	10.03	< 0.0001
(e) From 11 to 15 age				
Intercept	−61.28	7.23	−8.47	< 0.0001
Year	0.03	0.004	9.13	< 0.0001
(f) From 16 to 20 age				
Intercept	−127.70	7.7	−16.57	< 0.0001
Year	0.07	0.004	17.20	< 0.0001
(g) From 21 to 25 age				
Intercept	−155.98	12.5	−12.51	< 0.0001
Year	0.08	0.006	12.83	< 0.0001
(h) Sapling				
Intercept	−63.97	6.78	−9.44	< 0.0001
Year	0.03	0.003	10.16	< 0.0001
(i) Adult				
Intercept	15.84	16.71	0.95	0.34
Year	−0.01	0.008	−0.76	0.45

Chapter 4. Vegetation changes in the alpine snow-meadows during last 40 years

4.1 Introduction

Global change causes rapid vegetation change in alpine ecosystems in the world (Nagy and Grabherr 2009). In the Swiss Alps, the number of plant species in the alpine regions has increased since 1985, reflecting the upward migration of lowland species (Walther et al. 2005). On the other hand, Pauli et al (2007) reported that species richness has decreased in the plant communities on subnival to nival summits of the Eastern Alps. Thus, effects of global warming on alpine vegetation may be highly habitat specific. To understand the responses of plant communities to environmental changes, the concept of functional type is available, that is a classification based on the morphological and physiological traits (McIntyre et al. 1999; Hikosaka et al. 2016). Whether species richness increases or decreases would in part depend on the functional types of plants occurring in the focal community, because different functional types respond to environmental conditions in different ways. For example, shrubs and grasses were most responsive to elevated temperature in tundra ecosystems (Dormann and Woodin 2002).

Snow-meadow vegetation is supposed to be the most sensitive vegetation in alpine ecosystems against the climate change. The previous study conducted in the Taisetsu Mountains revealed that large populations of a typical snow-meadow herbaceous species, *Anemone narcissiflora*, replaced with grass predominant vegetation during 17 years (Kawai and Kudo 2014). This rapid change in snow-meadow vegetation might be caused by drier soil conditions owing to recent earlier snowmelt and warmer summer temperature in this region. I predict that the warmer and earlier snowmelt situations may cause diverse vegetation change in terms of species richness and diversity of alpine

plant communities, because the extents of environmental relaxation and competitive situations among species may be highly habitat specific. As a result, mosaic pattern of alpine vegetation (typical alpine vegetation pattern) might have become simpler during last decades. If so, functional types of shrubs and grasses are expected to increase, while forbs might decrease the dominance in snow-meadow sites.

In the Taisetsu Mountains, detail vegetation surveys of snow-meadows were conducted in 1972 (Sato 2007) and 1988 (G. Kudo, unpublished data). These survey records are extremely useful to compare vegetation changes in the snow-meadows sequentially. This chapter aims to (1) quantify the changes in species richness, species diversity, functional types and community types during last 40 years, and to (2) clarify the patterns of vegetation change and habitat fragility of two snow-meadows in different locations.

Nomenclature: Ohwi and Kitagawa (1983) for seed plants; Ohwi and Nakaike (1978) for ferns

4.2 Materials and methods

4.2.1 Study site

In the central part of the Taisetsu Mountains, I selected two snow-meadow sites, Goshikigahara and Koganegahara (Fig. 4-1). These sites are located on gentle slopes at 1650–1850 m elevation; Koganegahara is on a northwest facing slope and Goshikigahara is on an east facing slope. Because of the predominant northeastern winds during the winter season, thick snow-drifts are formed at Goshikigahara, resulting in later snowmelt.

4.2.2 Data set

I conducted vegetation survey in 2012 for the comparisons with the previous vegetation records of 1972 and 1988. A number of sampling plots were selected in the meadows, but the location of plots was not exactly same between present and previous studies; i.e. sampling plots were selected to cover all vegetation types in 1972 (Sato 2007), whereas survey plots in 1988 were mainly distributed at snow-meadow and snowbed habitats. Therefore, I selected datasets obtained at only snow-meadow habitat to minimize the sampling biases between years; 44 plots in 1972 and 103 plots in 1988 for Koganegahara, and 113 plots in 1972 and 103 plots in 1988 for Goshikigahara. In 2012, 85 plots were selected at Koganegahara and 115 plots at Goshikigahara, nearly at the same places with previous records. The plot size was not consistent among years, 1 m × 1 m quadrat was used in 1972 and 2012, while 0.5 m × 0.5 m quadrat in 1988.

The existence of every vascular species in the plots was recorded based on the Braun-Blanquet's dominance scale, “+”: < 1 %, “1”: 1–10 %, “2”: 10–25 %, “3”: 25–50 %, “4”: 50–75 %, and “5”: > 75 % in coverage (Braun-Blanquet 1964). In the 1988 and 2012 surveys, the dominances of lichens and mosses were also recorded, but these data were not used for the analysis and vegetation changes in vascular species were analyzed in this study. The vegetation survey was conducted during July to August in 1971–1972, July 19, August 3 and September 4 in 1988, and July 28–29 in 2012 at Koganegahara; during July and August in 1971–1972, June 22, July 21, August 15 and September 5 in 1988, and August 12–14 at Goshikigahara. In 2012, I also measured volumetric soil water content (%) using a time-domain reflectometry device (TDR, Hydrosence, Campbell Scientific Inc., QLD) connected to a 12-cm probe. The mean value of five measurements in each plot was used for the analysis.

4.2.3 Data analysis

Before the analysis, the values of the Braun-Blanquet's dominance scale were transformed to percentages as follows; “+”: 0.1 %, “1”: 5 %, “2”: 17.5 %, “3”: 37.5 %, “4”: 62.5%, and “5”: 87.5%. First, the Shannon's diversity index (H), the number of species per plot (α diversity) and total number of species per whole site were calculated for each survey in each site. Shannon's H and α diversity were compared between years with generalized linear model (GLM) postulating a Gaussian error distribution with identity-link function.

Second, plant species were divided into seven functional types (deciduous shrub, evergreen shrub, fern, forb, grass, rush and sedge) in advance. The proportion of fern type was very rare and it was excluded from the analyses. Because grass, rush and sedge types showed similar patterns in the preliminary analysis, they were included as a graminoid type in this analysis. I calculated relative dominance that was the summation of dominance percentage of all species in all plots, and allotted the ratio to every species. The relative dominance was summarized for each functional type (here after RDF), and the compositions were compared between years by GLM postulating a Gaussian error distribution with identity-link function.

Third, community structure was subdivided into several community types by the average linkage hierarchic clustering for each survey in each meadow. The number of community types was determined to reflect the typical vegetation types reported in the previous vegetation study (Sato 2007). I calculated relative dominance of individual community types (here after RDC) and allotted the ratio to every species in each community type. The changes in community structure during 40 years were evaluated by comparing main component species (i.e. RDC comprising more than 5 % in focal community type). Furthermore, Shannon's H index and α diversity were calculated for each community type in each survey and each site. These diversities for each survey

were compared between years with GLM postulating a Gaussian error distribution with identity–link function.

Furthermore, vegetation change in each meadow was evaluated comparing the dynamics of common species (i.e. relative dominance comprising more than 1 % at least once in three survey years in either meadow). The dynamics of common species were classified into three categories, increasing (relative dominance coverage increased more than 1.5 times from 1972 to 2012), decreasing (relative dominance coverage decreased less than half during the same period), and changing little (remaining). For the 2012 data, furthermore, the relationship between soil moisture and vegetation was analyzed by the non-metric multi-dimensional scaling (NMDS) and the permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) based on the Bray-Curtis similarity index (Manly 2005). R statistical software ver. 3.2.4 (R Core Team 2016) was used for data analyses. The species diversity, hierarchic clustering, NMDS, and PERMANOVA were performed using the vegan package in R (Oksanen et al. 2016).

4.3 Results

Total number of species was 57, 54 and 57 in 1972, 1988 and 2012 at Koganegahara, and 64, 56 and 64 at Goshikigahara, respectively. A list of species and their dominance scales in each survey year are shown in Table 4-S1. The Shannon's H index increased from 1972 to 2012 in both meadows; the median values are 1.6, 1.6 and 2.2 in 1972, 1988 and 2012 at Koganegahara, and 1.9, 1.7 and 2.3 at Goshikigahara, respectively (Fig. 4-2a; Table 4-S2). The number of species per plot (α diversity) decreased at Koganegahara but increased at Goshikigahara during 40 years; the median values are 13,

12 and 11 in 1972, 1988 and 2012 at Koganegahara, and 8, 10 and 10 at Goshikigahara, respectively (Fig. 4-2 b; Table 4-S2).

The RDF of individual functional types were 5.3–21.5 % in shrub, 60.8–71.4 % in forb, and 9.3–25.0 % in graminoid at Koganegahara, while 7.0–58.4 % in shrub, 23.9–56.5 % in forb, and 17.7–41.8 % in graminoid at Goshikigahara (Fig. 4-3). The major component species in each functional type were as follows (for detail, see Table 4-1):

Shrub type: *Geum pentapetalum* and *Phyllodoce arleutica* at both sites

Forb type: *Fauria crista-galli* and *Anemone narcissiflora* var. *sachalinensis* at Koganegahara; *Trollius riederianus* and *Saussurea riederi* var. *yezoensis* at Goshikigahara

Graminoid type: *Carex blepharicarpa* var. *dueensis* at both sites; *Carex hakkodensis* at Koganegahara; and *Scirpus maximowiczii* at Goshikigahara

The RDF did not change significantly during 40 years for most functional types at Koganegahara (Table 4-S3).

On the basis of the cluster analysis, vegetation was classified into five (1972), five (1988) and four (2012) community types at Koganegahara, and seven (1972), six (1988) and six (2012) at Goshikigahara (Fig. 4-4). The main component species (>5 % in RDC) in these community types are listed in Table 4-2. At Koganegahara, *F. crista-galli* was predominant in K2 (1972), K9 (1988) and K12 (2012); *A. narcissiflora* was predominant in K4 (1972) but highly decreased in 1988 (K8 and K10) and 2012 (K11 and K13); *G. pentapetalum* was predominant in K6 (1988) and K13 (2012) but did not in 1972. At Goshikigahara, *T. riederianus* was predominant in G6 (1972) and common in G13 (1988) and G15 (2012); *G. pentapetalum* was predominant in G8 (1988) and G14 (2012) but did not in 1972 as well as at Koganegahara. *Agrostis flaccida* was predominant in G17 (2012) but there was no recorded in 1972 and 1988. The Shannon's

H index for each community type increased from 1972 to 2012 in both meadows; the median values are 1.6, 1.6 and 2.6 in 1972, 1988 and 2012 at Koganegahara, and 1.9, 1.7 and 2.3 at Goshikigahara, respectively (Tables 4-3, 4-S4). The number of species per community type (α diversity) did not change at Koganegahara ($P = 0.15$; Table 4-S4), but increased at Goshikigahara ($P < 0.05$; Table 4-S4) during 40 years; the median values are 10, 12 and 13 in 1972, 1988 and 2012 at Koganegahara, and 8, 10 and 10 at Goshikigahara, respectively (Table 4-3).

Functional type, frequency (appearance ratio of survey plots) and relative dominance of common species are shown in Table 4-1. At Koganegahara, *F. crista-galli* was predominant in all survey years. Among 23 common species, six species decreased the dominance, while eight species increased the dominance (Table 4-1a). At Goshikigahara, *T. riederians* was a predominant species in 1972, but it was replaced by *G. pentapetalum* in 1988 and 2012. Among 37 species, nine species decreased the dominance, while 18 species increase the dominance (Table 4-1b). In both meadows, the dominance of two species (*A. narcissiflora* and *Ranunculus acris*) decreased, while five species (*G. pentapetalum*, *P. aleutica*, *Coptis trifolia*, *A. flaccid* and *Deschampsia flexuosa*) increased.

In PERMANOVA, soil moisture explained 18 % of total variation in vegetation at Koganegahara, and 11 % of total variation at Goshikigahara (Table 4-4). The NMDS axis was correlated with soil moisture in both meadows in 2012. The analysis by NMDS also indicates that the vegetation structure has changed during last 40 years; community types classified by the cluster analysis were clearly separated from each other in both meadows in 1972, but the separation among community types became unclear in later years (1988 and 2012), indicating the increasing similarity of species composition (Fig. 4-5).

4.4 Discussion

Changes in species composition during 40 years

Although total number of species was retained, Shannon's H index increased during 40 years in both snow-meadow sites. Alpine plant communities are often distributed as mosaic patterns reflecting micro-scale heterogeneity of snowmelt time, soil moisture, nutrient cycling and physical stress (Spasojevic et al. 2013). The mosaic pattern of snow-meadow vegetation at both sites seems to be disturbed by the environmental changes such as earlier snowmelt and drier soil conditions, which might decrease the heterogeneity of micro-habitats resulting in the mixture of species composition among communities.

Although the composition of function types did not change clearly, community structure and the relative dominance of common species changed clearly in each site. The most characteristic changes in species composition were the decrease in typical snow-meadow herbs, *A. narcissiflora* and *T. riederianus*, and the increase in graminoid and shrub species such as *C. blepharicarpa*, *A. flaccid* and *G. pentapetalum*. A previous study reported that *A. narcissiflora* shifted the distribution range toward late snowmelt places in this region (Kawai and Kudo 2014). The trend of increasing dominance of graminoid species in snowbed vegetation has been reported also in the European Alps (Grabherr 2003) and Scandinavian mountains (Virtanen et al. 2003). Increasing summer temperature accelerates the time of snowmelt and drier soil conditions, resulting in the decrease in snowbed vegetation in European alpine ecosystems (Nagy and Grabherr 2009). Therefore, the decrease in soil moisture may be an important factor driving the vegetation change in the snow-meadows.

For other species increasing the relative dominance, such as *G. pentapetalum*, *P. aleutica* and *C. trifolia*, species-specific characteristics may be important to understand

the reason for the expansion of distribution. For instance, *G. pentapetalum* is common in early snowmelt meadows with relatively dry upper slopes (Ide and Oguma 2013). Wada et al. (1998) reported that the artificial warming by open-top chambers positively affected achene size and production of *G. pentapetalum*. This suggests higher reproductive activity under warm conditions in this species. Although *P. aleutica* is an evergreen dwarf shrub, distributed widely along the snowmelt gradients, its growth and reproductive activity tend to decrease at the extremely late snowmelt places (Kudo 1991). Thus, the growth of *P. aleutica* might be promoted by the acceleration of snowmelt time. *Coptis trifolia* commonly grows under coniferous subalpine forests and high moors (Ohwi and Kitagawa 1983). In the alpine zone, *C. trifolia* commonly grow under *P. pumila* canopies (Okitsu and Ito 1989; Takahashi and Miyajima 2010), indicating the preference to shaded conditions for growth. Furthermore, *C. trifolia* prefers relatively early-snowmelt habitat (Kudo and Ito 1992). Therefore, *C. trifolia* might extend the distribution range under accelerating snowmelt conditions without negative effects of shading by other plants.

Difference of two snow-meadows

Although α diversity decreased at Koganegahara, it increased at Goshikigahara. The trends in species richness under climate change are not consistent among alpine regions in the world, from increasing (e.g. Walther et al. 2005) to decreasing (e.g. Pauli et al. 2007). The present study is the first report to detect the different directions of the changes in species richness between snow-meadows within the same mountain region. The RDF was more fluctuated between years at Goshikigahara than at Koganegahara. It means that the structure of plant communities are more complicated at Goshikigahara reflecting the heterogeneous micro-topography and habitat conditions. This trend is

explained by the pattern of ordination diagram of NMDS across years in each snow-meadow; the border of community types became unclear and more monotonous at Koganegahara, while composition of community types became mingled and more complicated at Goshikigahara.

In the European Alps, local extinction of alpine plants has been observed in many locations (Grabherr et al. 1994; Bahn and Korner 2003; Pauli et al. 2003; Walther et al. 2005). Vegetation dynamics model predicts that snowbed vegetation will decrease and shrubby tundra will increase the occupation area (90–200 %) by 2071 (Johnson et al. 2011). Therefore, the vegetation changes observed at both snow-meadows may be at an intermediate phase of ongoing vegetation dynamics under climate warming. At the Goshikigahara, furthermore, dwarf bamboo (*S. kurilensis*) and *P. pumila* have expanded the distribution area (Kudo et al. 2011, Chapter 1) during last 32 years. Because *S. kurilensis* and *P. pumila* have huge biomass in alpine ecosystem, the invasion of these plants should cause a serious impact on other alpine plants, not only through shading effects but also by litter accumulation (Okitsu 1985; Kudo et al. 2011). Changes in the main component species may cause negative effects on species richness through the modification of the plant–plant interactions, such as competition and facilitation (Klein et al. 2004; Klanderud 2005; Kikvidze et al. 2011; Michalet et al. 2014; Olsen and Klanderud 2014). Therefore, the directions of vegetation change may vary among snow-meadows and highly site specific reflecting the local environmental and biological situations.

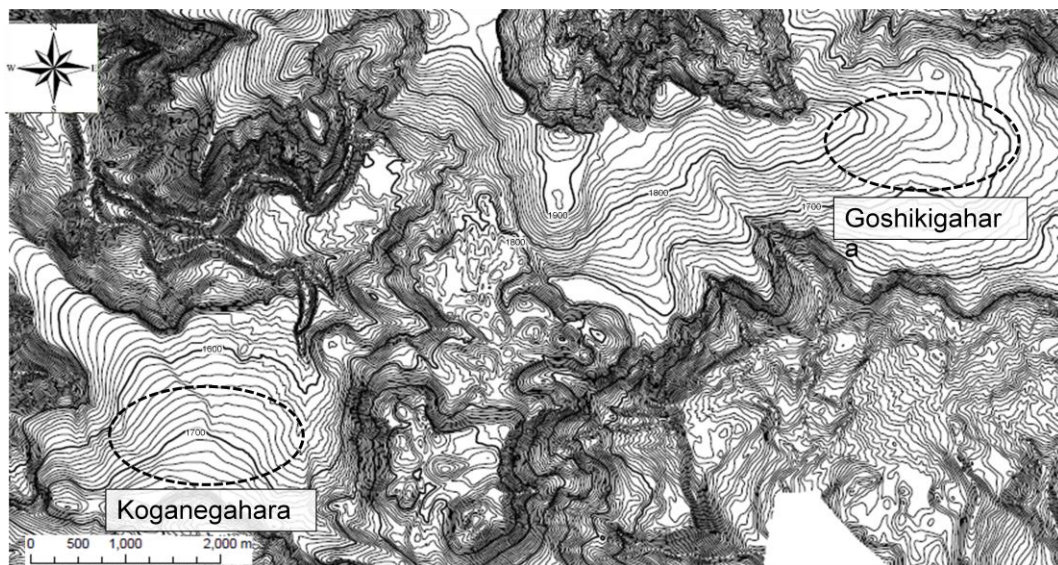


Fig. 4-1 Location of the research sites at Koganegahara and Goshikigahara in the Taisetsu Mountains.

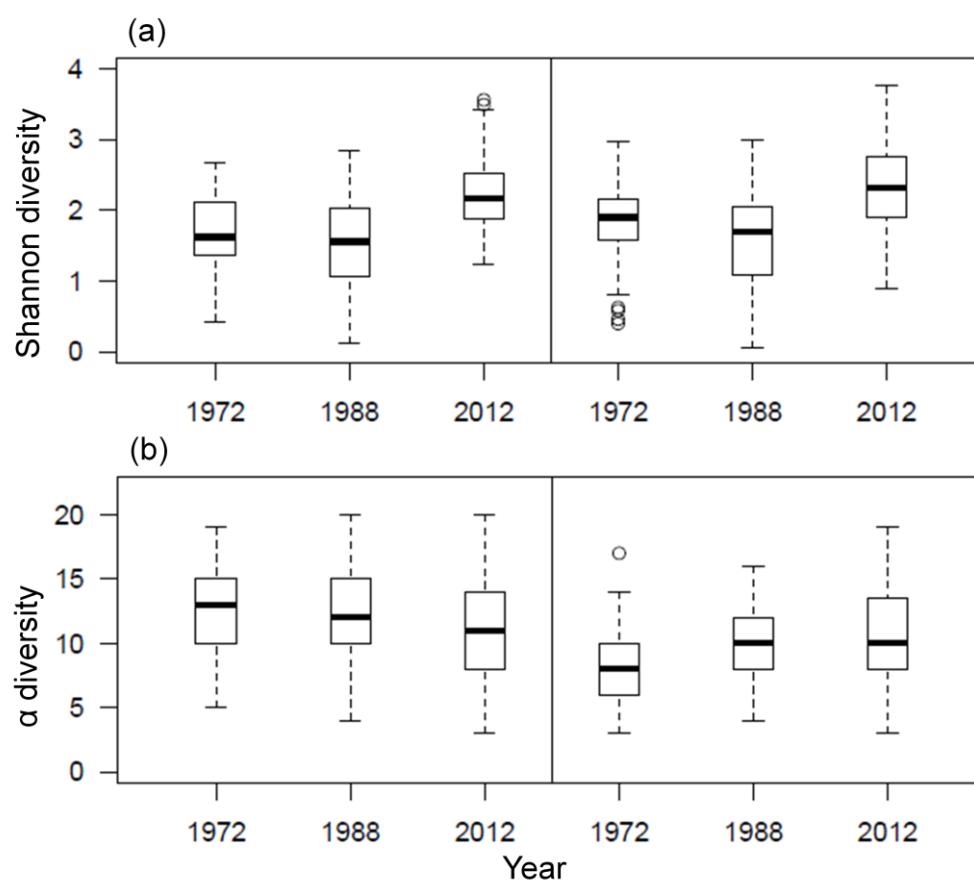


Fig. 4-2 Boxplots showing three survey period transitions of the Shannon's H diversity (a) and α diversity index (b) for each survey period at Koganegahara and Goshikigahara.

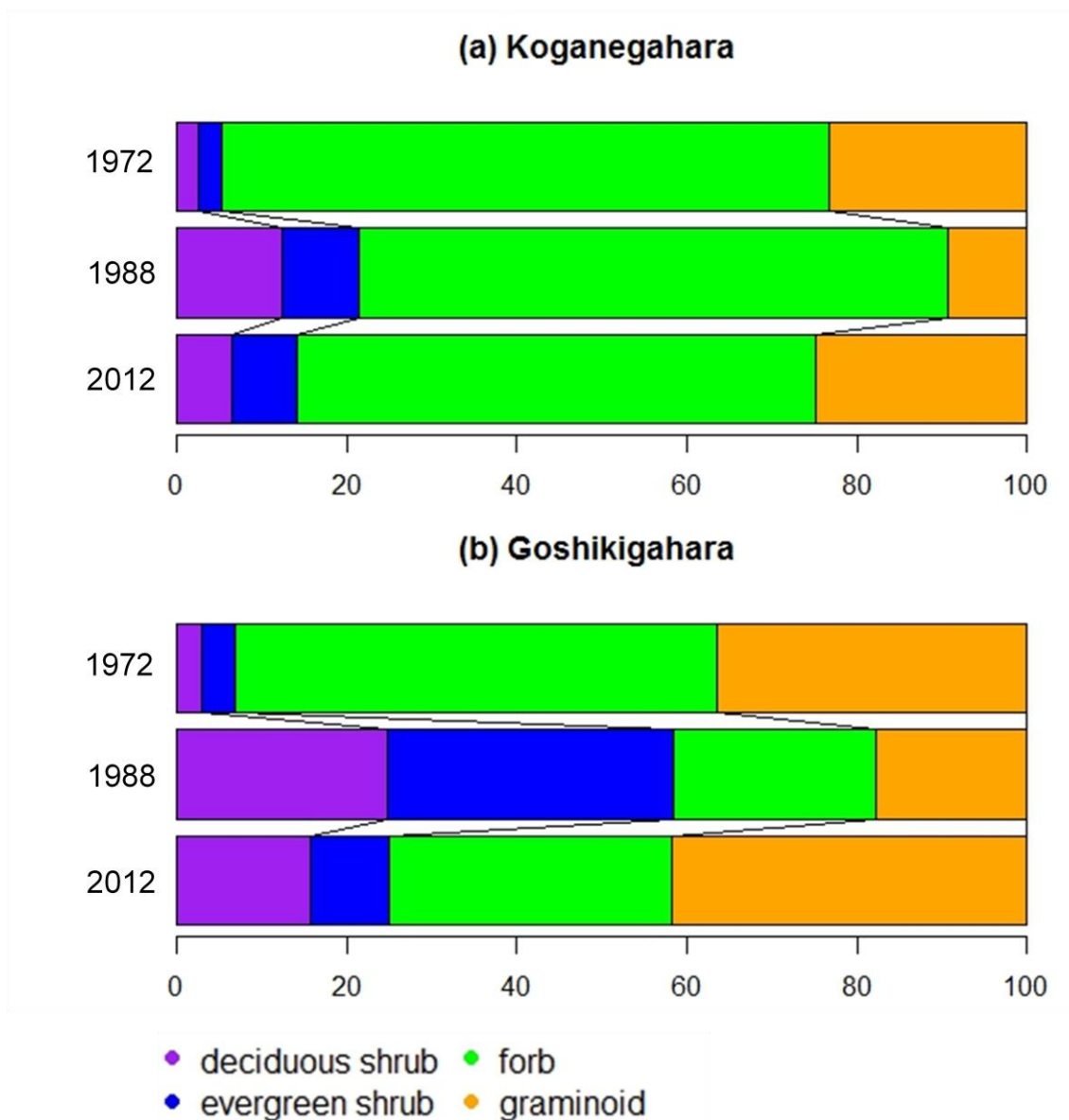


Fig. 4-3 Cumulative relative dominance of each functional type in 1972, 1988 and 2012 at Koganegahara (a) and Goshikigahara (b).

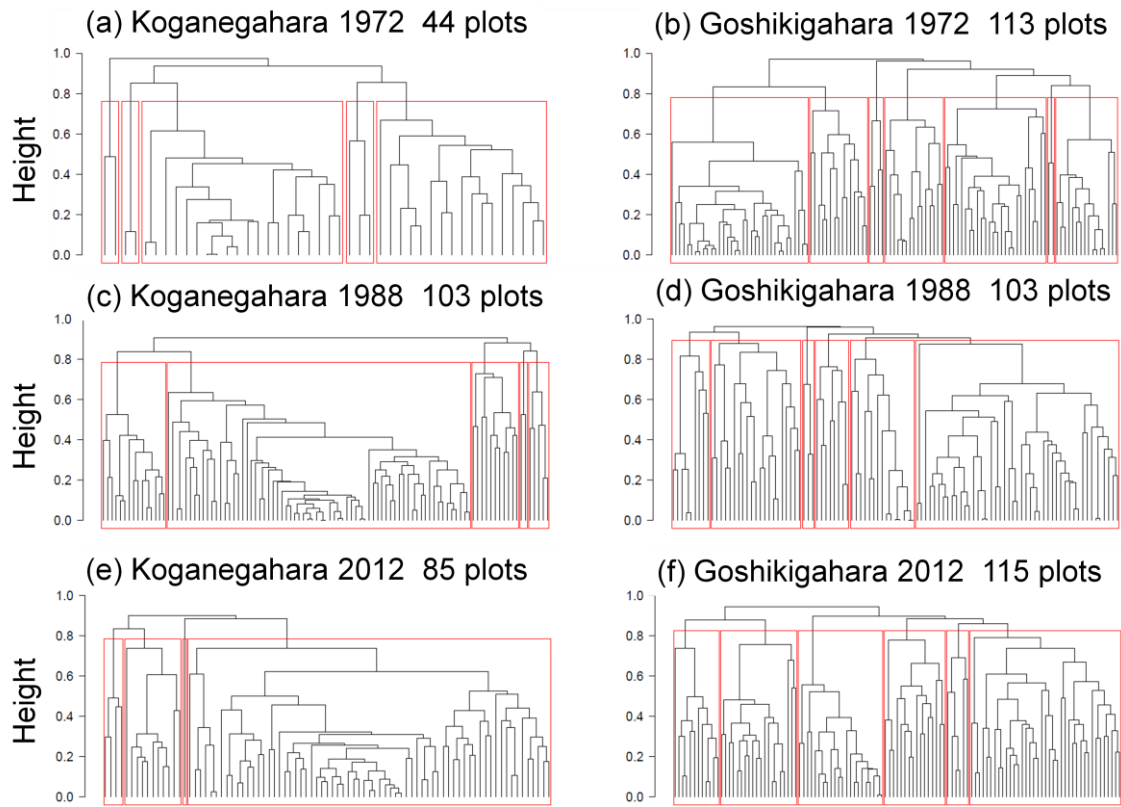


Fig. 4-4 Results of the cluster analysis for sampling plots in each snow-meadow site (Koganegahara, Goshikigahara) in each year (1972, 1988, 2012). The number of sampling plots used for analysis is indicated in each cluster.

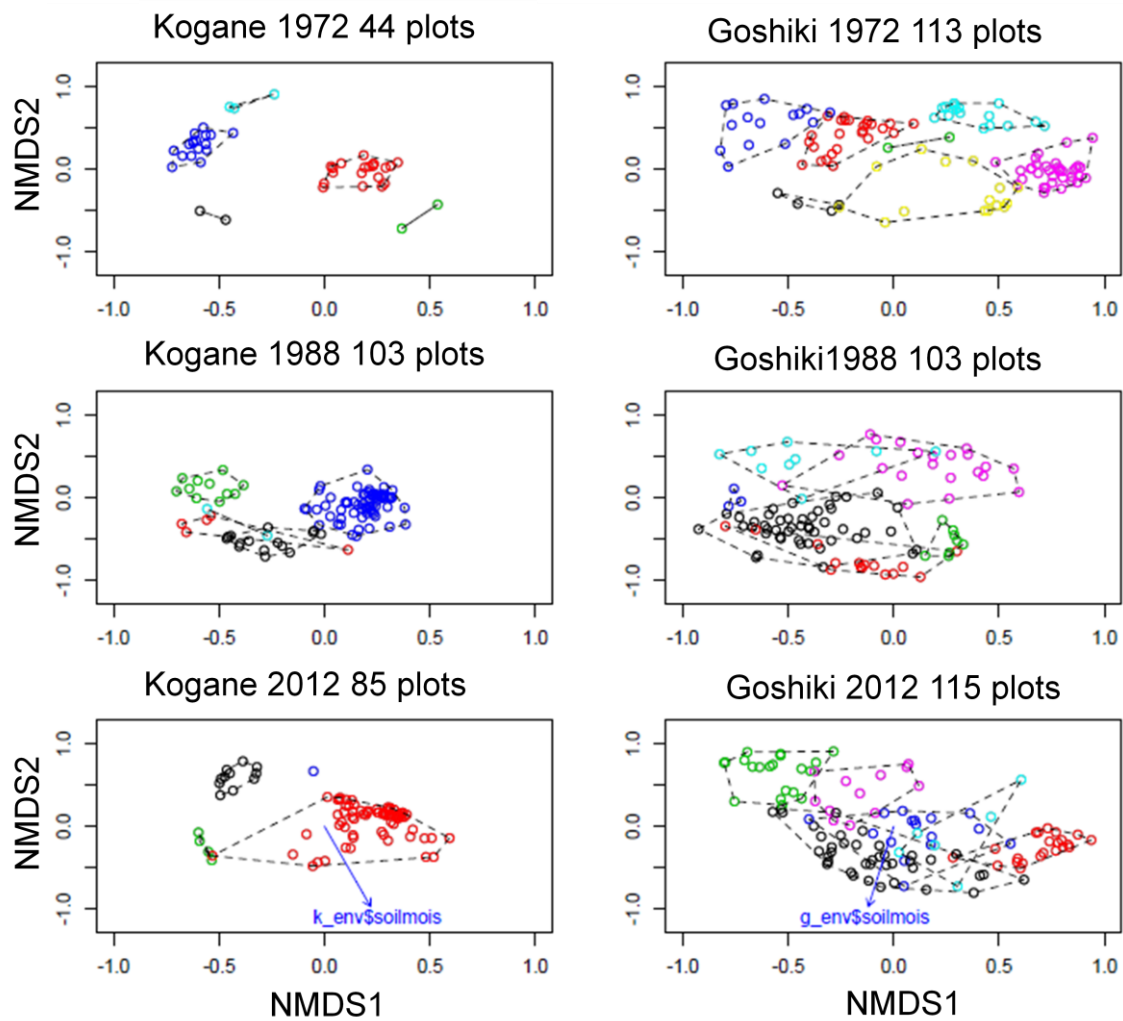


Fig. 4-5 Ordination diagram of a non-metric multi-dimensional scaling (NMDS) of the vegetation composition in each snow-meadow site (Koganegahara, Goshikigahara) in each year (1972, 1988, 2012). The number of sampling plots used for analysis is indicated in each cluster. The group surrounded by the dashed line was distributed by a cluster classification (Fig. 4-4). Arrows in 2012 indicate the gradient of soil moisture.

Table 4-1 Changes in relative dominance of major species across three survey periods at Koganegahara (a) and Goshikigahara (b). Species with small relative dominance (less than 1 % across three survey records) were excluded as rare species. The trend of dynamics was classified as increase (relative dominance increased more than 1.5 times), decrease (relative dominance decreased less than half), and stable (remaining) from 1972 to 2012.

(a) Koganegahara

Species	Type	Frequency (%)			Relative dominance (%)			Dynamics
		1972	1988	2012	1972	1988	2012	
<i>Anemone narcissiflora</i> var. <i>sachalinensis</i>	Forb	54.5	35.0	35.3	18.59	3.13	2.49	Decrease
<i>Peucedanum multivittatum</i>	Forb	56.8	35.9	20.0	4.45	3.34	0.51	Decrease
<i>Potentilla matsumurae</i>	Forb	61.4	40.8	35.3	3.97	1.99	1.60	Decrease
<i>Scirpus maximowiczii</i>	Sedge	4.5	0	8.2	3.51	0	0.99	Decrease
<i>Ranunculus acris</i> var. <i>nipponicus</i>	Forb	25.0	10.7	15.3	1.56	0.31	0.45	Decrease
<i>Deschampsia caespitosa</i> var. <i>festucaefolia</i>	Grass	6.8	40.8	5.9	0.28	1.66	0.12	Decrease
<i>Fauria crista-galli</i>	Forb	54.5	82.5	80.0	27.56	48.36	35.89	Stable
<i>Carex blepharicarpa</i> var. <i>dueensis</i>	Sedge	54.5	16.5	41.2	11.94	1.10	11.56	Stable
<i>Saussurea riederi</i> var. <i>yezoensis</i>	Forb	18.2	7.8	25.9	4.21	0.94	3.95	Stable
<i>Carex hakkodensis</i>	Sedge	45.5	83.5	57.6	3.38	3.64	4.63	stable
<i>Trollius riederianus</i>	Forb	6.8	1.9	9.4	2.59	1.20	1.81	stable
<i>Arnica unalascensis</i>	Forb	54.5	57.3	49.4	1.73	3.50	2.13	stable
<i>Juncus beringensis</i>	Rush	13.6	10.7	14.1	1.07	0.31	0.78	stable
<i>Rhododendron aureum</i>	evergreen	18.2	9.7	11.8	1.00	1.24	1.32	stable
<i>Solidago virga-aurea</i> var. <i>leiocarpa</i>	Forb	25.0	55.3	40.0	0.79	2.68	0.81	stable
<i>Phyllodoce aleutica</i>	evergreen	18.2	38.8	37.6	1.56	7.71	6.11	increase
<i>Geum pentapetalum</i>	deciduous	34.1	36.9	28.2	2.41	12.07	5.86	increase
<i>Primula cuneifolia</i>	Forb	52.3	76.7	57.6	2.41	1.59	4.11	increase
<i>Gentiana nipponica</i>	Forb	43.2	80.6	58.8	0.05	0.12	1.94	increase
<i>Deschampsia flexuosa</i>	Grass	45.5	62.1	35.3	1.09	0.83	1.72	increase
<i>Agrostis flaccida</i>	Grass	0	0	41.2	0	0	1.41	increase
<i>Coptis trifolia</i>	Forb	25.0	53.4	32.9	0.03	0.16	1.33	increase
<i>Tilingia ajanensis</i>	Forb	36.4	62.1	36.5	0.59	0.10	1.08	increase

(b) Goshikigahara

Species	Type	Frequency (%)			Relative dominance (%)			Dynamics
		1972	1988	2012	1972	1988	2012	
<i>Trollius riederianus</i>	Forb	32.7	8.7	18.3	17.72	2.04	5.39	decrease
<i>Ranunculus acris</i> var. <i>nipponicus</i>	Forb	38.9	18.4	16.5	7.03	2.13	0.30	decrease
<i>Anemone narcissiflora</i> var. <i>sachalinensis</i>	Forb	25.7	29.1	24.3	4.93	2.62	0.71	decrease
<i>Juncus beringensis</i>	Rush	44.2	41.7	36.5	4.62	0.77	2.10	decrease
<i>Tilingia ajanensis</i>	Forb	38.1	30.1	38.3	3.71	0.79	1.69	decrease
<i>Primula cuneifolia</i>	Forb	36.3	34.0	27.8	2.79	0.69	1.20	decrease
<i>Carex scita</i> var. <i>riishirensis</i>	Sedge	16.8	5.8	14.8	1.09	0.35	0.44	decrease
<i>Poa yezoalpina</i>	Grass	19.5	0	17.4	1.01	0	0.31	decrease
<i>Arnica unalascensis</i>	Forb	15.9	22.3	7.8	0.93	1.95	0.15	decrease
<i>Carex blepharicarpa</i> var. <i>dueensis</i>	Sedge	35.4	29.1	36.5	16.73	1.69	10.99	stable
<i>Lagotis stelleri</i> var. <i>yesoensis</i>	Forb	25.7	14.6	19.1	6.28	2.01	3.47	stable
<i>Saussurea riederi</i> var. <i>yezoensis</i>	Forb	34.5	3.9	28.7	4.88	2.54	6.31	stable
<i>Carex hakkodensis</i>	Sedge	35.4	36.9	33.9	3.96	5.51	3.20	stable
<i>Scirpus caespitosus</i>	Sedge	9.7	1.9	15.7	2.10	0.08	1.16	stable
<i>Peucedanum multivittatum</i>	Forb	26.5	26.2	41.7	2.09	1.42	1.57	stable
<i>Swertia cuspidata</i>	Forb	14.2	15.5	8.7	1.10	0.88	1.03	stable
<i>Phyllodoce caerulea</i>	evergreen	2.7	23.3	7.8	0.82	8.29	0.45	stable
<i>Hypericum kamtschaticum</i>	Forb	8.8	10.7	20.0	0.29	1.56	0.33	stable
<i>Loiseleuria procumbens</i>	evergreen	0	1.9	0	0	1.89	0	stable
<i>Geum pentapetalum</i>	deciduous	25.7	63.1	46.1	2.68	21.15	11.74	increase
<i>Scirpus maximowiczii</i>	Sedge	20.4	12.6	25.2	4.36	5.68	6.86	increase
<i>Sasa kurilensis</i>	Grass	0.9	2.9	18.3	0.00	0.15	5.95	increase
<i>Rhododendron aureum</i>	evergreen	16.8	33.0	38.3	1.32	7.12	4.30	increase
<i>Phyllodoce aleutica</i>	evergreen	3.5	38.8	20.9	1.69	16.17	3.85	increase
<i>Calamagrostis langsdorffii</i>	Grass	14.2	14.6	43.5	1.09	0.10	3.16	increase
<i>Sanguisorba stipulata</i>	Forb	27.4	13.6	24.3	0.86	1.07	2.93	increase
<i>Spiraea betulifolia</i>	deciduous	1.8	6.8	9.6	0.00	0.38	2.39	increase
<i>Coptis trifolia</i>	Forb	15.9	41.7	41.7	0.32	0.07	2.13	increase
<i>Geranium erianthum</i> f. <i>pallens</i>	Forb	28.3	10.7	47.0	0.60	0.54	1.93	increase
<i>Eriophorum vaginatum</i>	Sedge	6.2	2.9	14.8	0.37	0.15	1.78	increase
<i>Agrostis flaccida</i>	Grass	0	0	20.0	0	0	1.65	increase
<i>Solidago virga-aurea</i> var. <i>leiocarpa</i>	Forb	8.0	10.7	38.3	0.31	0.58	1.58	increase
<i>Deschampsia flexuosa</i>	Grass	8.0	48.5	24.3	0.39	0.15	1.48	increase
<i>Deschampsia caespitosa</i> var. <i>festucaefolia</i>	Grass	12.4	35.0	21.7	0.66	1.67	1.42	increase
<i>Salix reinii</i>	deciduous	0.9	3.9	7.8	0.14	0.49	1.22	increase
<i>Potentilla matsumurae</i>	Forb	7.1	26.2	11.3	0.35	1.65	0.84	increase
<i>Vaccinium uliginosum</i>	deciduous	1.8	15.5	0.9	0.08	2.74	0.22	increase

Table 4-2 List of major component species with >5 % in RDC in 1972, 1988 and 2012 at Koganegahara (a) and Goshikigahara (b).

(a) Koganegahara

1972			Species		RDC (%)	1988		Species		RDC (%)	2012		Species		RDC (%)
No. of plots		Type	No. of plots		Type	No. of plots		Type	No. of plots		Type	No. of plots		Type	
K1	2	<i>Rhododendron aureum</i>	32.2	K6	15	<i>Geum pentapetalum</i>	52.9	K11	11	<i>Carex blepharicarpa</i> var. <i>dueensis</i>	39.8				
		<i>Geum pentapetalum</i>	20.7			<i>Phyllodoce aleutica</i>	19.6			<i>Saussurea riederi</i> var. <i>yezoensis</i>	20.3				
		<i>Deschampsia flexuosa</i>	20.7			<i>Fauria crista galli</i>	6.5			<i>Trollius riederianus</i>	8.0				
		<i>Anemone yezoensis</i>	16.1			<i>Rhododendron aureum</i>	5.1			<i>Anemone narcissiflora</i> var. <i>sachalinensis</i>	7.1				
						<i>Deschampsia caespitosa</i> var. <i>festucaefolia</i>	49.0	K12	69	<i>Fauria crista galli</i>	45.8				
K2	20	<i>Fauria crista galli</i>	62.8	K7	5	<i>Carex hakkodensis</i>	19.4			<i>Phyllodoce aleutica</i>	7.8				
		<i>Carex hakkodensis</i>	7.2			<i>Solidago virga aurea</i> var. <i>leiocarpa</i>	9.0			<i>Carex blepharicarpa</i> var. <i>dueensis</i>	6.8				
		<i>Primula cuneifolia</i>	5.6			<i>Deschampsia flexuosa</i>	8.9			<i>Carex hakkodensis</i>	5.5				
K3	2	<i>Scirpus maximowiczii</i>	81.7			<i>Peucedanum multivittatum</i>	24.0			<i>Primula cuneifolia</i>	5.2				
		<i>Fauria crista galli</i>	14.7	K8	11	<i>Anemone narcissiflora</i> var. <i>sachalinensis</i>	14.9	K13	4	<i>Geum pentapetalum</i>	36.3				
K4	17	<i>Anemone narcissiflora</i> var. <i>sachalinensis</i>	41.3			<i>Solidago virga aurea</i> var. <i>leiocarpa</i>	14.2			<i>Rhododendron aureum</i>	13.1				
		<i>Carex blepharicarpa</i> var. <i>dueensis</i>	21.2			<i>Potentilla matsumurae</i>	10.4			<i>Anemone narcissiflora</i> var. <i>sachalinensis</i>	11.2				
		<i>Peucedanum multivittatum</i>	9.3			<i>Saussurea riederi</i> var. <i>yezoensis</i>	9.5			<i>Deschampsia flexuosa</i>	6.5				
K5	3	<i>Carex blepharicarpa</i> var. <i>dueensis</i>	30.9			<i>Fauria crista galli</i>	65.9	K14	1	<i>Arnica unalascensis</i>	43.0				
		<i>Trollius riederianus</i>	28.5	K9	70	<i>Phyllodoce aleutica</i>	6.2			<i>Juncus beringensis</i>	12.0				
		<i>Saussurea riederi</i> var. <i>yezoensis</i>	28.5							<i>Ranunculus acris</i> var. <i>nipponicus</i>	12.0				
		<i>Juncus beringensis</i>	11.6	K10	2	<i>Arnica unalascensis</i>	71.7			<i>Carex hakkodensis</i>	12.0				
						<i>Deschampsia caespitosa</i> var. <i>festucaefolia</i>	6.6								
						<i>Carex hakkodensis</i>	6.6								
						<i>Fauria crista galli</i>	6.5								
						<i>Anemone narcissiflora</i> var. <i>sachalinensis</i>	6.5								

(b)Goshikigahara

1972		Species	RDC (%)	1988		Species	RDC (%)	2012		Species	RDC (%)		
Type	No. of plots			Type	No. of plots			Type	No. of plots				
G1	4	<i>Phyllodoce aleutica</i>	40.5	G8	47	<i>Geum pentapetalum</i>	39.0	G14	39	<i>Geum pentapetalum</i>	27.9		
		<i>Phyllodoce caerulea</i>	21.6			<i>Phyllodoce aleutica</i>	31.2			<i>Sasa kurilensis</i>	15.2		
		<i>Geum pentapetalum</i>	12.4			<i>Rhododendron aureum</i>	6.7			<i>Rhododendron aureum</i>	8.2		
		<i>Coptis trifolia</i>	7.0			<i>Phyllodoce caerulea</i>	50.4			<i>Phyllodoce aleutica</i>	6.2		
		<i>Deschampsia flexuosa</i>	5.9			<i>Rhododendron aureum</i>	23.1	G15	22	<i>Carex blepharicarpa</i> var. <i>dueensis</i>	37.6		
		<i>Lagotis stelleri</i> var. <i>yesoensis</i>	33.5			<i>Vaccinium uliginosum</i>	15.9			<i>Saussurea riederi</i> var. <i>yezoensis</i>	21.7		
		<i>Carex hakkodensis</i>	14.7			G10	8			<i>Hypericum kamtschaticum</i>	21.0	<i>Trollius riederianus</i>	19.0
		<i>Primula cuneifolia</i>	12.0							<i>Anemone narcissiflora</i> var. <i>sachalinensis</i>	20.2	<i>Calamagrostis langsdorffii</i>	5.2
		<i>Tilingia ajanensis</i>	10.9			<i>Carex blepharicarpa</i> var. <i>dueensis</i>	15.4	G16	20	<i>Scirpus maximowiczii</i>	55.1		
		<i>Geum pentapetalum</i>	7.8			<i>Rhododendron aureum</i>	10.5			<i>Eriophorum vaginatum</i>	10.9		
		<i>Swertia cuspidata</i>	5.8			<i>Solidago virga aurea</i> var. <i>leiocarpa</i>	8.9			<i>Scirpus caespitosus</i>	8.6		
		<i>Peucedanum multivittatum</i>	36.9			<i>Peucedanum multivittatum</i>	6.5			<i>Lagotis stelleri</i> var. <i>yesoensis</i>	4.1		
G3	2	<i>Sanguisorba stipulata</i>	18.5	G11	3	<i>Potentilla matsumurae</i>	47.4	G17	16	<i>Agrostis flaccida</i>	12.9		
		<i>Juncus beringensis</i>	17.2			<i>Primula cuneifolia</i>	26.8			<i>Phyllodoce aleutica</i>	11.2		
		<i>Primula cuneifolia</i>	8.6			<i>Carex flavocuspis</i>	12.0			<i>Deschampsia caespitosa</i> var. <i>festucaefolia</i>	9.7		
		<i>Deschampsia caespitosa</i> var. <i>festucaefolia</i>	8.6			<i>Anemone narcissiflora</i> var. <i>sachalinensis</i>	5.9			<i>Solidago virga aurea</i> var. <i>leiocarpa</i>	7.3		
G4	15	<i>Scirpus maximowiczii</i>	49.3	G12	9	<i>Veronica stelleri</i> var. <i>longistyla</i>	5.9			<i>Potentilla matsumurae</i>	6.5		
		<i>Scirpus caespitosus</i>	27.0			<i>Scirpus maximowiczii</i>	51.4			<i>Carex hakkodensis</i>	6.2		
G5	16	<i>Ranunculus acris</i> var. <i>nipponicus</i>	46.3			<i>Deschampsia caespitosa</i> var. <i>festucaefolia</i>	12.9			<i>Peucedanum multivittatum</i>	5.2		
		<i>Juncus beringensis</i>	21.4			<i>Arnica unalascensis</i>	12.1			G18	6	<i>Sanguisorba stipulata</i>	38.5
		<i>Tilingia ajanensis</i>	11.3			<i>Juncus mertensianus</i>	5.7					<i>Juncus beringensis</i>	13.4
G6	35	<i>Trollius riederianus</i>	42.3	G13	21	<i>Carex hakkodensis</i>	25.6			<i>Rhododendron aureum</i>	10.2		
		<i>Carex blepharicarpa</i> var. <i>dueensis</i>	34.2			<i>Saussurea riederi</i> var. <i>yezoensis</i>	13.1			<i>Calamagrostis langsdorffii</i>	8.4		
		<i>Saussurea riederi</i> var. <i>yezoensis</i>	9.6			<i>Trollius riederianus</i>	10.9			<i>Carex hakkodensis</i>	6.3		
G7	15	<i>Anemone narcissiflora</i> var. <i>sachalinensis</i>	32.1			<i>Ranunculus acris</i> var. <i>nipponicus</i>	9.7	G19	12	<i>Lagotis stelleri</i> var. <i>yesoensis</i>	31.0		
		<i>Carex blepharicarpa</i> var. <i>dueensis</i>	18.3			<i>Lagotis stelleri</i> var. <i>yesoensis</i>	9.5			<i>Carex hakkodensis</i>	16.8		
		<i>Peucedanum multivittatum</i>	9.2							<i>Geum pentapetalum</i>	12.9		
		<i>Saussurea riederi</i> var. <i>yezoensis</i>	6.5							<i>Swertia cuspidata</i>	10.2		
		<i>Rhododendron aureum</i>	5.3							<i>Tilingia ajanensis</i>	8.6		

Table 4-3 Transitions of the Shannon's H diversity and α diversity across survey periods in each community type at Koganegahara (a) and Goshikigahara (b).

(a) Koganegahara

1972			1988			2012		
type	H	α	type	H	α	type	H	α
K1	2.0	10.5	K6	1.6	11.3	K11	2.4	11.4
K2	1.5	12.2	K7	1.8	10.6	K12	2.2	10.8
K3	0.7	5.0	K8	2.4	16.8	K13	2.8	15.5
K4	2.0	14.6	K9	1.4	11.8	K14	2.7	15.0
K5	1.6	8.3	K10	1.3	11.5			

(b) Goshikigahara

1972			1988			2012		
type	H	α	type	H	α	type	H	α
G1	1.9	6.8	G8	1.5	10.0	G14	2.4	11.7
G2	2.1	8.8	G9	1.2	8.3	G15	2.1	9.2
G3	2.1	8.0	G10	2.1	10.6	G16	1.7	6.7
G4	1.3	5.9	G11	1.6	9.0	G17	3.1	14.8
G5	1.8	6.8	G12	1.7	9.9	G18	2.2	9.5
G6	1.8	8.5	G13	1.9	10.0	G19	2.4	10.7
G7	2.2	11.7						

Table 4-4 Results of PERMANOVA for vegetation type responses to the soil moisture at Koganegahara (a) and Goshikigahara (b).

Variable	df	SS	MS	F value	R^2	P
(a) Koganegahara						
Soil moisture	1	3.55	3.55	17.63	0.18	0.0001
Residuals	83	16.71	0.20		0.82	
(b) Goshikigahara						
Soil moisture	1	4.83	4.83	14.31	0.11	0.0001
Residuals	113	38.12	0.34		0.89	

Table 4-S1 A list of vascular plant species and the number of plots included in each predominance scale in each survey period at Koganegahara (a) and Goshikigahara (b).

(a) Koganegahara

Species	Type	1972, 44 plot						1988, 103 plot						2012, 85 plot					
		Braun-Blanquet's dominance scale						Braun-Blanquet's dominance scale						Braun-Blanquet's dominance scale					
		+	1	2	3	4	5	+	1	2	3	4	5	+	1	2	3	4	5
<i>Phyllodoce aleutica</i>	evergreen	6	0	1	1	0	0	8	17	8	6	1	0	2	6	11	11	1	1
<i>Phyllodoce caerulea</i>	evergreen	7	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Lycopodium sitchense</i> var. <i>nikoense</i>	fern	1	1	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0
<i>Harrimanella stelleriana</i>	evergreen	0	0	0	0	0	0	2	1	0	0	0	0	0	1	0	0	0	0
<i>Primula cuneifolia</i>	forb	11	10	2	0	0	0	59	20	0	0	0	0	8	20	18	3	0	0
<i>Carex pyrenaica</i>	sedge	11	0	0	0	0	0	55	4	0	0	0	0	14	14	0	0	0	0
<i>Deschampsia caespitosa</i> var. <i>festucaefolia</i>	grass	1	2	0	0	0	0	32	7	2	1	0	0	2	3	0	0	0	0
<i>Pedicularis chamissonis</i> var. <i>hokkaidoensis</i>	forb	7	0	0	0	0	0	25	0	0	0	0	0	9	2	0	0	0	0
<i>Fauria crista-galli</i>	forb	2	1	3	9	8	1	3	9	17	27	27	2	0	0	7	10	14	37
<i>Swertia cuspidata</i>	forb	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Scirpus maximowiczii</i>	sedge	0	0	0	0	2	0	0	0	0	0	0	0	2	0	3	2	0	0
<i>Scirpus caespitosus</i>	sedge	0	1	0	0	0	0	2	0	0	0	0	0	0	1	5	0	0	0
<i>Eriophorum vaginatum</i>	sedge	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Drosera rotundifolia</i>	forb	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Platanthera tipuloides</i>	forb	2	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
<i>Trollius riederianus</i>	forb	0	0	1	2	0	0	0	0	1	0	1	0	0	1	3	3	1	0
<i>Saussurea riederi</i> var. <i>yezoensis</i>	forb	1	1	4	2	0	0	2	5	0	1	0	0	1	6	8	4	3	0
<i>Carex blepharicarpa</i> var. <i>dueensis</i>	sedge	8	2	8	4	2	0	9	7	0	1	0	0	0	11	6	4	2	12
<i>Heloniopsis orientalis</i>	forb	19	1	0	0	0	0	13	0	0	0	0	0	7	7	0	0	0	0
<i>Geranium erianthum</i> f. <i>pallidum</i>	forb	8	0	0	0	0	0	2	3	1	0	0	0	5	3	0	0	0	0
<i>Rumex arifolius</i>	forb	8	0	0	0	0	0	0	1	0	0	0	0	1	4	0	0	0	0
<i>Polygonum viviparum</i>	forb	9	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
<i>Luzula plumosa</i> var. <i>macrocarpa</i>	rush	3	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Viola biflora</i>	forb	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Juncus beringensis</i>	rush	5	0	0	1	0	0	7	4	0	0	0	0	2	6	4	0	0	0
<i>Sanguisorba stipulata</i>	forb	14	2	1	0	0	0	10	3	1	0	0	0	7	8	3	0	0	0
<i>Ranunculus acris</i> var. <i>nipponicus</i>	forb	5	4	2	0	0	0	7	4	0	0	0	0	4	8	1	0	0	0
<i>Poa yezoalpina</i>	grass	6	3	0	0	0	0	0	0	0	0	0	0	7	4	0	0	0	0
<i>Veratrum grandiflorum</i>	forb	0	0	0	0	0	0	5	3	0	0	0	0	1	0	0	0	0	0
<i>Thalictrum aquilegifolium</i>	forb	0	0	0	0	0	0	5	0	0	0	0	0	1	1	0	0	0	0
<i>Viola allariaefolia</i>	forb	0	0	0	0	0	0	7	0	0	0	0	0	1	0	0	0	0	0
<i>Tilingia ajanensis</i>	forb	12	4	0	0	0	0	64	0	0	0	0	0	11	17	3	0	0	0
<i>Geum pentapetalum</i>	deciduous	8	3	4	0	0	0	5	10	8	13	2	0	2	5	3	10	2	2
<i>Gentiana nipponica</i>	forb	19	0	0	0	0	0	83	0	0	0	0	0	13	32	5	0	0	0
<i>Arnica unalascensis</i>	forb	17	5	2	0	0	0	32	21	5	1	0	0	14	21	6	0	1	0
<i>Carex hakkodensis</i>	sedge	5	13	1	1	0	0	46	37	3	0	0	0	3	20	24	2	0	0
<i>Tofieldia okuboi</i>	forb	5	0	0	0	0	0	15	0	0	0	0	0	5	7	0	0	0	0

<i>Anemone narcissiflora</i> var. <i>sachalinensis</i>	forb	3	2	8	7	4	0	7	24	5	0	0	0	3	17	7	3	0	0
<i>Hypericum kamtschaticum</i>	forb	5	0	0	0	0	0	10	3	0	0	0	0	3	6	0	0	0	0
<i>Luzula oligantha</i>	rush	21	4	0	0	0	0	29	1	0	0	0	0	11	10	1	0	0	0
<i>Parnassia palustris</i>	forb	11	0	0	0	0	0	15	0	0	0	0	0	2	0	0	0	0	0
<i>Carex scita</i> var. <i>riishirensis</i>	sedge	3	5	0	0	0	0	12	6	0	0	0	0	11	14	0	0	0	0
<i>Veronica stelleri</i> var. <i>longistyla</i>	forb	13	1	0	0	0	0	21	0	0	0	0	0	7	8	1	0	0	0
<i>Gaultheria miqueliana</i>	evergreen	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vaccinium ovalifolium</i> var. <i>alpinum</i>	deciduous	11	0	0	0	0	0	0	0	0	0	0	0	2	11	2	0	0	0
<i>Rhododendron camtschaticum</i>	deciduous	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Shortia soldanelloides</i> f. <i>alpina</i>	forb	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Juncus filiformis</i>	rush	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Potentilla matsumurae</i>	forb	14	7	6	0	0	0	21	19	2	0	0	0	4	20	6	0	0	0
<i>Deschampsia flexuosa</i>	grass	15	4	1	0	0	0	54	10	0	0	0	0	6	16	8	0	0	0
<i>Solidago virga-aurea</i> var. <i>leiocarpa</i>	forb	8	2	1	0	0	0	36	17	3	1	0	0	16	17	1	0	0	0
<i>Peucedanum multivittatum</i>	forb	11	7	7	0	0	0	22	5	9	1	0	0	4	13	0	0	0	0
<i>Coptis trifolia</i>	forb	11	0	0	0	0	0	54	1	0	0	0	0	4	20	4	0	0	0
<i>Calamagrostis langsdorffii</i>	grass	0	0	0	0	0	0	18	4	0	0	0	0	0	10	1	0	0	0
<i>Platanthera chorisiana</i>	forb	2	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
<i>Orchis aristata</i>	forb	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Tilingia holopetala</i>	forb	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carex flavocuspis</i>	sedge	2	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0
<i>Vaccinium uliginosum</i>	deciduous	0	0	0	0	0	0	13	4	0	0	0	0	0	0	0	0	0	0
<i>Vaccinium ovalifolium</i> var. <i>coriaceum</i>	deciduous	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Spiraea betulifolia</i>	deciduous	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Anemone yezoensis</i>	forb	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vaccinium vitis-idaea</i>	evergreen	3	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
<i>Rhododendron aureum</i>	evergreen	6	0	2	0	0	0	1	6	3	0	0	0	0	2	7	1	0	0
<i>Rubus pedatus</i>	deciduous	1	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
<i>Sasa kurilensis</i>	grass	1	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0
<i>Lastrea quelpaertensis</i>	fern	6	0	0	0	0	0	1	1	0	0	0	0	1	2	0	0	0	0
<i>Boykinia lycoctonifolia</i>	forb	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Streptopus amplexifolius</i> var. <i>papillatus</i>	forb	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Deschampsia atropurpurea</i> var. <i>paramushirensis</i>	grass	0	0	0	0	0	0	7	0	0	0	0	0	19	12	0	0	0	0
<i>Carex thunbergii</i> var. <i>appendiculata</i>	sedge	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0
<i>Carex omiana</i> var. <i>monticola</i>	sedge	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Platanthera ophrydioides</i>	forb	0	0	0	0	0	0	0	0	0	0	0	0	14	3	0	0	0	0
<i>Agrostis flaccida</i>	grass	0	0	0	0	0	0	0	0	0	0	0	0	9	22	4	0	0	0
<i>Epilobium palustre</i> var. <i>lavandulaefolium</i>	forb	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

(b) Goshikigahara

Species	Type	1972, 113plot						1988, 103 plot						2012, 115 plot					
		Braun-Blanquet's dominance scale						Braun-Blanquet's dominance scale						Braun-Blanquet's dominance scale					
		+	1	2	3	4	5	+	1	2	3	4	5	+	1	2	3	4	5
<i>Phyllodoce aleutica</i>	evergreen	0	0	1	1	1	1	5	6	10	14	4	1	1	5	8	5	5	0
<i>Phyllodoce caerulea</i>	evergreen	1	0	0	1	1	0	2	9	3	7	3	0	1	5	3	0	0	0
<i>Lycopodium sitchense</i> var. <i>nikoense</i>	fern	3	1	0	0	0	0	0	1	0	0	0	0	0	4	0	0	0	0
<i>Harrimanella stelleriana</i>	evergreen	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
<i>Primula cuneifolia</i>	forb	11	15	15	0	0	0	29	5	1	0	0	0	3	24	5	0	0	0
<i>Carex pyrenaica</i>	sedge	2	1	0	0	0	0	34	1	0	0	0	0	3	3	0	0	0	0
<i>Deschampsia caespitosa</i> var. <i>festucaefolia</i>	grass	3	9	2	0	0	0	30	3	1	2	0	0	4	15	4	1	1	0
<i>Pedicularis chamissonis</i> var. <i>hokkaidoensis</i>	forb	18	2	0	0	0	0	20	1	0	0	0	0	8	7	0	0	0	0
<i>Lagotis stelleri</i> var. <i>yezoensis</i>	forb	7	1	4	15	2	0	1	9	5	0	0	0	1	5	5	8	3	0
<i>Swertia cuspidata</i>	forb	6	5	4	1	0	0	7	8	1	0	0	0	1	4	4	0	0	1
<i>Scirpus maximowiczii</i>	sedge	1	6	10	2	4	0	3	4	1	0	4	1	0	5	7	6	6	5
<i>Scirpus caespitosus</i>	sedge	1	4	2	2	2	0	1	1	0	0	0	0	1	11	4	2	0	0
<i>Eriophorum vaginatum</i>	sedge	3	2	2	0	0	0	1	2	0	0	0	0	0	6	8	2	1	0
<i>Drosera rotundifolia</i>	forb	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Platanthera tipuloides</i>	forb	6	0	0	0	0	0	7	0	0	0	0	0	11	0	0	0	0	0
<i>Trollius riederianus</i>	forb	0	0	3	12	11	11	0	5	2	2	0	0	1	2	4	5	5	4
<i>Saussurea riederi</i> var. <i>yezoensis</i>	forb	8	4	22	5	0	0	0	1	0	1	2	0	0	9	9	5	7	3
<i>Carex blepharicarpa</i> var. <i>dueensis</i>	sedge	0	1	3	15	17	4	13	15	2	0	0	0	2	9	8	4	4	15
<i>Heloniopsis orientalis</i>	forb	13	7	0	0	0	0	4	6	0	0	0	0	9	3	0	0	0	0
<i>Geranium erianthum</i> f. <i>pallidum</i>	forb	23	7	2	0	0	0	4	7	0	0	0	0	10	35	9	0	0	0
<i>Rumex arifolius</i>	forb	9	0	0	0	0	0	2	0	0	0	0	0	6	1	0	0	0	0
<i>Polygonum viviparum</i>	forb	3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
<i>Juncus beringensis</i>	rush	12	18	14	6	0	0	36	6	1	0	0	0	10	21	9	1	1	0
<i>Sanguisorba stipulata</i>	forb	17	13	0	1	0	0	5	7	2	0	0	0	6	14	2	2	1	3
<i>Ranunculus acris</i> var. <i>nipponicus</i>	forb	10	15	3	12	3	1	5	10	3	1	0	0	14	3	2	0	0	0
<i>Poa yezoalpina</i>	grass	5	14	3	0	0	0	0	0	0	0	0	0	12	7	1	0	0	0
<i>Veratrum grandiflorum</i>	forb	18	6	5	0	0	0	3	5	1	0	0	0	11	1	0	0	0	0
<i>Viola repens</i>	forb	1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Platanthera hyperborea</i>	forb	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thalictrum aquilegifolium</i>	forb	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Salix reinii</i>	deciduous	0	0	1	0	0	0	0	3	1	0	0	0	0	5	2	0	1	1
<i>Conioselinum filicinum</i>	forb	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tilingia ajanensis</i>	forb	11	14	16	1	1	0	21	10	0	0	0	0	11	23	10	0	0	0
<i>Geum pentapetalum</i>	deciduous	10	7	8	4	0	0	17	10	14	16	8	0	6	10	8	8	12	9
<i>Gentiana nipponica</i>	forb	23	4	0	0	0	0	50	0	0	0	0	0	10	18	1	0	0	0
<i>Arnica unalascensis</i>	forb	3	12	3	0	0	0	10	8	5	0	0	0	4	5	0	0	0	0
<i>Carex hakkodensis</i>	sedge	6	14	17	3	0	0	13	18	2	3	2	0	1	17	16	5	0	0
<i>Tofieldia okuboii</i>	forb	1	0	0	0	0	0	3	0	0	0	0	0	7	2	0	0	0	0
<i>Anemone narcissiflora</i> var. <i>sachalinensis</i>	forb	10	4	3	9	3	0	8	17	5	0	0	0	6	21	1	0	0	0

<i>Hypericum kamtschaticum</i>	forb	3	7	0	0	0	0	2	6	2	1	0	0	12	11	0	0	0	0
<i>Luzula oligantha</i>	rush	6	1	0	0	0	0	12	0	0	0	0	0	11	9	0	0	0	0
<i>Parnassia palustris</i>	forb	16	2	0	0	0	0	11	0	0	0	0	0	8	14	0	0	0	0
<i>Carex scita</i> var. <i>riishirensis</i>	sedge	5	9	5	0	0	0	4	1	1	0	0	0	2	15	0	0	0	0
<i>Veronica stelleri</i> var. <i>longistyla</i>	forb	2	0	0	0	0	0	7	1	0	0	0	0	2	0	0	0	0	0
<i>Vaccinium ovalifolium</i> var. <i>alpinum</i>	deciduous	3	0	0	0	0	0	0	0	0	0	0	0	1	9	0	0	0	0
<i>Potentilla matsumurae</i>	forb	2	5	1	0	0	0	13	11	3	0	0	0	2	7	2	2	0	0
<i>Agrostis mertensii</i>	grass	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Deschampsia flexuosa</i>	grass	2	6	1	0	0	0	49	1	0	0	0	0	2	16	10	0	0	0
<i>Solidago virga-aurea</i> var. <i>leiocarpa</i>	forb	4	4	1	0	0	0	6	4	1	0	0	0	11	26	6	1	0	0
<i>Peucedanum multivittatum</i>	forb	14	7	6	3	0	0	11	15	1	0	0	0	9	33	6	0	0	0
<i>Coptis trifolia</i>	forb	13	4	1	0	0	0	43	0	0	0	0	0	7	28	13	0	0	0
<i>Calamagrostis langsdorffii</i>	grass	2	9	5	0	0	0	14	1	0	0	0	0	5	21	23	1	0	0
<i>Platanthera chorisiana</i>	forb	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Senecio kawakamii</i>	forb	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tilingia holopetala</i>	forb	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carex flavocuspis</i>	sedge	0	0	0	0	0	0	16	7	0	0	0	0	1	0	0	0	0	0
<i>Loiseleuria procumbens</i>	evergreen	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
<i>Arctica nana</i>	evergreen	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0
<i>Vaccinium uliginosum</i>	deciduous	0	2	0	0	0	0	8	4	2	0	2	0	0	0	0	1	0	0
<i>Spiraea betulifolia</i>	deciduous	2	0	0	0	0	0	2	5	0	0	0	0	0	2	3	3	1	2
<i>Streptopus streptopoides</i>	forb	2	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
<i>Anemone yezoensis</i>	forb	0	0	0	0	0	0	3	0	0	0	0	0	2	0	0	0	0	0
<i>Pinus pumila</i>	evergreen	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
<i>Vaccinium vitis-idaea</i>	evergreen	6	5	0	0	0	0	30	0	0	0	0	0	4	15	1	0	0	0
<i>Rhododendron aureum</i>	evergreen	7	4	8	0	0	0	5	11	13	5	0	0	2	11	25	5	1	0
<i>Sasa kurilensis</i>	grass	1	0	0	0	0	0	1	2	0	0	0	0	1	1	2	9	2	6
<i>Cirsium kamtschaticum</i>	forb	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
<i>Cirsium pectinellum</i> var. <i>alpinum</i>	forb	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carex limosa</i>	sedge	1	1	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0
<i>Saxifraga fusca</i>	forb	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Deschampsia atropurpurea</i> var. <i>paramushirensis</i>	grass	0	0	0	0	0	0	1	0	0	0	0	0	6	2	0	0	0	0
<i>Ixeris dentata</i> var. <i>kimurana</i>	forb	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Juncus mertensianus</i>	rush	0	0	0	0	0	0	1	2	2	0	0	0	1	6	1	0	0	0
<i>Carex thunbergii</i> var. <i>appendiculata</i>	sedge	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
<i>Carex omiana</i> var. <i>monticola</i>	sedge	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0
<i>Platanthera ophrydioides</i>	forb	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Agrostis flaccida</i>	grass	0	0	0	0	0	0	0	0	0	0	0	0	4	7	10	2	0	0
<i>Lilium medeoloides</i>	forb	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
<i>Rhynchospora alba</i>	sedge	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Carex curta</i>	sedge	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Table 4-S2 GLM results of Shannon's H and α diversity during 1972 to 2012 at Koganegahara (a) and Goshikigahara (b).

Variables	Coefficient	SE	t value	P value
(a) Koganegahara				
Shannon				
(Intercept)	-33.80	5.12	-6.60	< 0.0001
year	0.018	0.003	6.96	< 0.0001
α diversity				
(Intercept)	82.38	31.62	2.61	0.0098
year	-0.035	0.016	-2.23	0.027
(b) Goshikigahara				
Shannon				
(Intercept)	-24.10	4.05	-5.95	< 0.0001
year	0.013	0.002	6.43	< 0.0001
α diversity				
(Intercept)	-98.31	20.68	-4.75	< 0.0001
year	0.054	0.010	5.22	< 0.0001

Table 4-S3 GLM results of relative dominance in each functional type during 1972 to 2012 at Koganegahara (a) and Goshikigahara (b).

	(a) Koganegahara				(b) Goshikigahara			
Variable	Coefficient	SE	T	P	Coefficient	SE	t	P
Deciduous shrub								
(Intercept)	-136.81	470.41	-0.29	0.82	-519.59	946.64	-0.55	0.68
year	0.072	0.24	0.31	0.81	0.27	0.48	0.56	0.67
Evergreen shrub								
(Intercept)	-208.58	246.55	-0.85	0.55	-58.31	1559.05	-0.04	0.98
year	0.11	0.12	0.87	0.54	0.037	0.78	0.05	0.97
Forb								
(Intercept)	606.32	113.45	5.34	0.12	1043.98	1317.75	0.79	0.57
year	-0.27	0.057	-4.75	0.13	-0.51	0.66	-0.76	0.59
Graminoid								
(Intercept)	-160.93	830.41	-0.19	0.88	-366.08	1187.94	-0.31	0.81
year	0.09	0.42	0.22	0.86	0.20	0.60	0.34	0.79

Table 4-S4 GLM results of Shannon's H and α diversity during 1972 to 2012 at Koganegahara (a) and Goshikigahara (b).

Variables	Coefficient	SE	t	P
(a) Koganegahara				
Shannon				
(Intercept)	-46.89	14.63	-3.21	0.0076
year	0.025	0.007	3.34	0.006
α diversity				
(Intercept)	-136.74	96.24	-1.42	0.18
year	0.075	0.048	1.54	0.15
(b) Goshikigahara				
Shannon				
(Intercept)	-21.00	11.08	-1.9	0.075
Year	0.012	0.006	2.07	0.054
α diversity				
(Intercept)	-105.79	53.53	-1.98	0.065
year	0.058	0.027	2.15	0.046

General discussion

The present study revealed that recent climate warming influences the alpine vegetation at various scales. First, the GIS analysis showed that the distribution area of *P. pumila* has increased by 1.88 ha toward fellfield side within the 25 ha area, and by 1.27 ha toward snow-meadow side within the 50 ha area during last 32 years; the expansion rate was 14 % at both habitats (Chapter 1). Therefore, *P. pumila* zone has expanded in the Taisetsu Mountains. This is the first report to quantify the expansion rate of *P. pumila* in the Japanese mountain ecosystems. However, dynamics of *P. pumila* zone may vary among mountain regions. Horikawa et al. (2009) predict that the potential distribution area of *P. pumila* may be decreased in many mountain regions under climate warming. In fact, Oguma (personal communication) find that the distribution of *P. pumila* has decreased and replaced by dwarf bamboo on Mt. Rishiri, northern Hokkaido. These studies indicate the importance of site-specific responses of *P. pumila* to climate warming for the prediction of vegetation dynamics in alpine ecosystems.

Second, the shoot growth analysis among mountain regions and the measurement of photosynthetic activity along the environmental gradients successfully explained the factors affecting the dynamics of *P. pumila*. Although warm summer is positively related to the shoot growth at every site (Chapters 1 and 2), warm spring occasionally brings about the disappearance of cold resistance early in the season that results in the increasing risk of frost damage in early season at the fellfield habitat. Although the negative impact of warm spring on shoot growth existed only at the exposed fellfield habitat, the expansion rate of *P. pumila* distribution was similar between the fellfield and snow-meadow side habitats. This means that recent warm summer accelerates the shoot growth more than the negative effect of warm spring temperature. In the Taisetsu Mountains, summer temperature is increasing at the pace of 0.04 °C/yr during last 34

years, while the increasing rate of spring temperature is only 0.01 °C/yr (G. Kudo, unpublished data), indicating apparent warming during the summer more than during the spring. Photosynthetic yield changed as season progressed at the both sites, but the recovery of photosynthetic activity after overwintering took time at the late snowmelt places (Chapter 2). This indicates that short growth period is a major limiting factor determining the distribution of *P. pumila* toward late-snowmelt places. The expansion of *P. pumila* at the snow-meadow side, therefore, may be related to the longer snow-free period in addition to the increasing summer temperature.

Third, the approach of population ecology indicated that the frequency of seedling establishment and survival rate could affect the population structure of *P. pumila* (Chapter 3). Cone production was positively related to the summer temperature but negatively to spring temperature as shown in shoot growth. Furthermore, survival rate of seedlings was positively related to the summer temperature but negatively to spring temperature. Nevertheless, seedling establishment was independent on the cone production and soil temperature in my study. Beside, seedling establishment has decreased recent years. Therefore, other factors than physiological factors affecting the growth, reproduction and survival of *P. pumila* may prevent the seedling establishment. One possibility is that the changes in the situation of seed dispersal process and/or predation pressure are related to the seedling establishment. For the prediction of population dynamics of *P. pumila* under climate change, therefore, it is important to take into account not only the direct effects of climate conditions on cone production and seedling survival rate but also biological factors through seed dispersal and post-dispersal stages.

Finally, the chronological comparisons of vegetation records revealed that species composition of snow-meadow communities have been changed during last 40 years but

differently between snow-meadows even within a same mountain area (Chapter 4). Dominant species have changed from typical snow-meadow plants (*Anemone narcissiflora* var. *sachalinensis* and *Trollius riederianus*) to graminoid (*Agrostis flaccida* and *Carex blepharicarpa* var. *dueensis*) or shrubby species (*Geum pentapetalum* and *Phyllodoce arleutica*). In accordance with the site-specific changes in species composition, the types of plant communities have also changed differently between Koganegahara and Goshikigahara; plant communities at Koganegahara have shifted more monotonously, while those at Goshikigahara have shifted more complicatedly. The most contrastive topographic features are slope direction and snowmelt pattern; Koganegahara is located on a west-facing gentle slope in which snowmelt progress relatively uniformly during short period, while Goshikigahara is located on an east-facing slope with micro-topographic undulations in which snowmelt pattern highly varies reflecting the micro-topography. Thus, diverse habitats are formed at Goshikigahara, where various types of plant communities are formed. As reported by Kudo and Hirao (2006), time of snowmelt has been accelerated during last 30 years in the Taisetsu Mts. Earlier snowmelt might decrease the heterogeneity of micro-scale environmental conditions at Koganegahara, but diverse environmental conditions might be maintained at Goshikigahara if the heterogeneity of snowmelt pattern was remained due to topographic determination of snow distribution. Acceleration of snowmelt time is common at relatively early-snowmelt places, but there is little evidence of earlier snowmelt trend at the late-snowmelt places like snowbed habitat (Kudo and Hirao 2006). Therefore, the effects of climate warming on alpine vegetation are strongly habitat-specific, and it is difficult to predict without consideration of habitat-specific responses.

The most explosive vegetation change in the snow-meadows is the decrease in typical snow-meadow herb, *A. narcissiflora*. Kawai and Kudo (2014) reported that a large *A. narcissiflora* population disappeared in early 90's at Goshikigahara and replaced by graminoid species (*A. flaccida*). These vegetation changes might be caused by the acceleration of snowmelt time and soil desiccation (Chapter 4). Furthermore, Kudo et al. (2011) reported that dwarf bamboo has increased the distribution area by 1.36 ha at the snow-meadow side during the same period. As a result of *P. pumila* and dwarf bamboo expansion, snow-meadow vegetation decreased by 2.6 ha at Goshikigahara. These results clearly indicate the ongoing vegetation change in the Taisetsu Mountains at landscape scale during a few decades.

In the snowy Japanese alpine ecosystems, heterogeneous snow accumulation and snowmelt patterns are key factors creating and maintaining species diversity of plant communities. As the direct effects of climate change, warm temperature, longer snow-free period and soil desiccation accelerate the growth and distribution of *P. pumila*, and the invasion of dwarf bamboo, graminoids and shrubs into snow-meadows. However, the responses of plants greatly vary depending on the regions, habitat types, and locations. Furthermore, the decrease in seedling establishment of *P. pumila* might be related to the seed dispersal and predation pressure caused by the changes in biological interactions, and snow-meadow vegetation area was decreased by the expansion of *P. pumila* and dwarf bamboo. The present studies strongly suggest the importance of investigations at various scales in each mountain region and habitat type to evaluate the climate change impacts on alpine ecosystems.

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