Habitat-Specific Responses of Alpine Plants to Climatic Amelioration: Comparison of Fellfield to Snowbed Communities

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Abstract

Because of the contrastive differences in environment and species composition, climatic amelioration may affect alpine vegetation differently between fellfield and snowbed communities. To test this prediction, the effects of warming on plant growth and vegetation structure were studied in two fellfield and two snowbed communities in northern Japan over 7 years using open-top-chambers (OTCs). OTCs increased the temperature by 1.1–1.8 °C, but the effects on snowmelt time and soil moisture were small. Vegetation height and canopy volume increased substantially at both fellfield sites as a result of the use of OTCs. Deciduous shrubs increased substantially at the lower fellfield and graminoids increased at the upper fellfield. In contrast, the responses of snowbed plants to OTCs were not significant. Because snowbed plants are snow-covered until mid-summer, climatic amelioration during the snow-free period may influence plant growth only slightly if the snow-free period does not change. Species richness and diversity were not changed by OTCs at any of the sites, indicating that the effect of warming alone may not be strong enough to change the species composition and diversity over several years. These results indicate significant variation in the response among alpine communities to warming.

Introduction

The impact of global environmental changes on terrestrial ecosystems is especially significant in arctic and alpine regions (Chapin et al., 1995; Grabherr et al., 1994; Oechel and Vourlitis, 1994; Theurillat and Guisan, 2001). So far, many experiments examining warming, changes in precipitation, nutrient availability, and snow manipulation have been conducted to detect plant responses mainly in polar deserts (Robinson et al., 1998), arctic tundra (Chapin et al., 1995; Hobbie and Chapin, 1998; Jónsdóttir et al., 2005), subarctic (Parsons et al., 1994; Press et al., 1998; Molau, 2001), and mid-latitude alpine regions (Kudo and Suzuki, 2003; Klein et al., 2004; Sandvik et al., 2004; Klanderud, 2008). The results of these studies are highly variable depending on plant species or functional types and among sites and regions (Arft et al., 1999; Walker et al., 2006). For accurate predictions of the response to global changes, consideration of ecological interactions among coexisting species is needed.

In alpine plant communities growing under climatically severe conditions, facilitative relationships exist between neighboring species when microscale environments are mitigated by the existence of other species potentially due to climatic amelioration (Callaway et al., 2002). With decreasing elevation, which causes increasing temperature and decreasing wind speed and desiccation, interspecific relationships may change from facilitative to competitive ones. If warming accelerates competitive situations for alpine plants, changes in species diversity, vegetation structure, and species composition of alpine communities may progress more rapidly at lower rather than upper elevations because plants growing under milder climatic conditions may have potentially higher competitive ability than plants growing under stressful environments (Grime et al., 1986).

Alpine ecosystems located in snowy regions are dominated by two contrasting habitats, fellfield and snowbed. The fellfield habitat is situated on wind-blown ridges and plateaus, where snow disappears early in the season and plants are exposed to cold weather during the winter and spring. In contrast, the snowbed habitat is covered with snow until mid-summer, and the initiation of plant growth is determined by the time of snowmelt (Walker et al., 1994; Arft et al., 1999; Sandvik et al., 2004; Björk and Molau, 2007). Because snowbed plants are protected by snow during winter and start to grow in mid-summer, temperature effects on growth may not be strong, while a short growing season suppresses plant growth (Walker et al., 1994; Björk and Molau, 2007). Thus, the impact of warming on alpine plants may differ between fellfield and snowbed habitats. Species composition is very different between fellfield and snowbed communities in northern Japan; deciduous shrubs are dominant especially in lower alpine conditions, and evergreen dwarf shrubs and lichens are predominant at higher altitudes in the fellfield habitat, while herbaceous plants are common in the snowbed habitat (Kudo and Ito, 1992). The combination of different habitats creates high species diversity in the alpine ecosystem. It is predicted that the responses of dominant species greatly influence community structure as environmental change progresses (Klanderund, 2005). For instance, the expansion of deciduous shrubs is especially obvious in arctic tundra ecosystems under simulated warming (Chapin and Shaver, 1985; Hobbie and Chapin, 1998; Walker et al., 2006). Thus, habitat-specific responses to environmental change should be studied by repeated monitoring of individual species to understand the impact of environmental changes on community structure and species diversity in alpine ecosystems.

In this study, we monitored the growth and vegetation structure of fellfield and snowbed plants in a mid-latitude alpine ecosystem in northern Japan using open-top-chamber (OTC)

experiments combined with a point-frame method over a period of 7 years. Although OTCs modify the microenvironment in a multitude of ways, such as wind-speed reduction, the validity of using an OTC as an analogue of regional climate warming has been examined previously (Hollister and Webber, 2000). Long-term monitoring of vegetation structure in warming experiments has been conducted in only a few arctic regions (e.g. Chapin et al., 1995; Robinson et al., 1998; Hollister et al., 2005), and there are very few studies on mid-latitude alpine ecosystems. In a previous study using the point-frame method for tundra plants, increases in canopy height and plant cover of graminoids and a decrease in species diversity were reported in warming conditions (Hollister et al., 2005). Because changes in canopy height and the composition of canopy-forming species strongly affect the vegetation structure, we particularly focused on studying the dynamics of canopy-forming species in this study.

The goal of the present study was to test the following predictions: (1) climatic amelioration could accelerate vegetation change more rapidly in dry-heath communities near to timberline, where deciduous shrubs dominate, compared with typical fellfield communities located on ridges, where evergreen dwarf shrubs are common, because deciduous shrubs have potentially higher growth rates; and (2) the warming effect of OTCs could be more apparent in fellfield communities than in snowbed communities, because the growth of fellfield plants is limited by low thermal conditions while the growth of snowbed plants is limited by the short growth season.

Materials and Methods

STUDY SITES

This study was conducted in the central part of the Taisetsu Mountains (43°32–34′N, 142°51–53′E) in Hokkaido, northern Japan. The summits are about 1900–2100 m elevation, and timberline is located around 1500–1600 m elevation in this region. The climate of the Taisetsu Mountains is characterized by warm, wet summers and cold, wet winters. Annual mean air temperature at 1700 m elevation is −2.0 °C (mean values of 1995–2007); monthly mean temperature during the summer season is 3.7 °C in May, 9.1 °C in June, 12.9 °C in July, 13.1 °C in August, and 7.8 °C in September. Precipitation during the summer season is 122 mm in June, 171 mm in July, 334 mm in August, and 237 mm in September (mean values of 2002–2007). The plant growth starts in late May or early June in early snowmelt areas, and the growing season lasts until mid-September.

We selected two fellfield sites, hereafter site F1 (1710 m elevation) and site F2 (1910 m elevation), and two snowbed sites on southeast-facing gentle slopes, hereafter sites S1 and S2 (1810–1820 m elevation for both sites). These sites are 500 m to 2 km apart. Site F1 was located on a plateau 100 m above timberline, where deciduous shrubs, lichens, and alpine creeping pine (*Pinus pumila*) are common. The vegetation type of F1 was categorized as a dry-heath rather than a typical fellfield in a strict sense (e.g. Sundqvist et al., 2008), but we included this site in the fellfield habitat in this study. Site F2 was located on a ridge, where strong winds prevented the predominance of tall shrubs, but lichens and mat-forming evergreen dwarf shrubs were common. Both sites F1 and F2 were usually exposed from snow cover by mid-April although occasional snowfall lasted until late May. In contrast, herbaceous species were common at the snowbed sites. Snow usually melted in mid-July at site S1 and in late July at site S2.

OTC EXPERIMENT

We selected six warming plots and six control plots of typical vegetation types at each site in 2001. Typical vegetation of each site was characterized by the dominance of deciduous shrubs at site F1, evergreen dwarf shrubs at site F2, and herbaceous plants at snowbed sites S1 and S2 as mentioned before. We set OTCs in the warming plots in late May at sites F1 and F2, and soon after snowmelt (late July) at sites S1 and S2. The OTCs at the fellfield sites were set throughout the year, while the OTCs at the snowbed sites were set only during the snow-free season to prevent damage by thick snow accumulation. For each plot, we set a 50 cm × 50 cm permanent quadrat for measurements of vegetation, and the corners of the quadrat were fixed using steel nails.

The OTCs used in this study were a standard type for International Tundra Experiments (Henry and Molau, 1997): hexagonal enclosures made of clear acrylic boards of 30 cm height and covering 0.65 m² ground area. To evaluate the warming effect of the OTCs, air temperature at 5 cm above the soil surface was measured in 2 or 3 OTCs and 2 or 3 control plots at each site. Measurements were taken at 1-hr intervals by automatic loggers (StowAway Tidbit, Onset Co., U.S.A.). To check the OTC effect on soil moisture conditions, the water content at a depth of 0–5 cm in the soil (in volume %) was measured between the OTC and control plots at each site. Measurements were performed in the late growing season (early to mid-September 2005) after three continuous fine days using a TDR (time domain reflectometer) soil moisture sensor (HydroSense, Campbell Scientific, Australia). Mean values of seven measurements for each plot were used for a comparison between control and OTC plots at each site.

In the middle to late growing season when the growth of plants had been completed (late July at the fellfield sites and late August to early September at the snowbed sites), we recorded the vegetation structure of every plot using a point-frame method (Kent and Coker, 1992). The point-frame method is useful for long-term monitoring of quantitative vegetation information non-destructively (Walker, 1996). A point-frame device was made of a 50 cm × 50 cm square clear acrylic board in which 10 × 10 (=100) small holes were arranged at 5 cm intervals. It was set horizontally over the 50 cm × 50 cm quadrat of individual plots at a height of 15–40 cm depending on vegetation height. For each point of the 100 holes, we vertically set down a graduated steel-stick with a 5 mm diameter, on which a scale with 1 mm accuracy was marked, and every plant species touched by the stick and the height of the top leaves of individual species were recorded. Thus, one plant was represented by 25 cm² of foliage area. In the first year (2001), we recorded only the leaf height of the top-canopy species at each point. However, we recorded the height of every species from the canopy to the soil surface in 2002, 2003, 2005, and 2007 for the analyses of vertical vegetation structure and species diversity. Information obtained from these measurements was the percentage cover of individual species (number of hits for specific species) and plant height (top-leaf height) of individual species at each point. To assess the temporal change of aboveground biomass, we evaluated the canopy volume in a non-destructive manner using the following index: canopy-volume index (cm³) = 25 (cm²) × number of hits (0 to 100) × mean plant height (cm) in each plot. The mean plant height was calculated as an average of the maximum height of target plants (species or canopy-forming plants) within a quadrat. The canopy-volume index is a cubic measure of aboveground biomass. The impact of OTC treatment on vegetation was analyzed by three methods: (1) community structure based on the changes in species diversity and richness, (2) growth of canopy-forming plants based on the changes in canopy
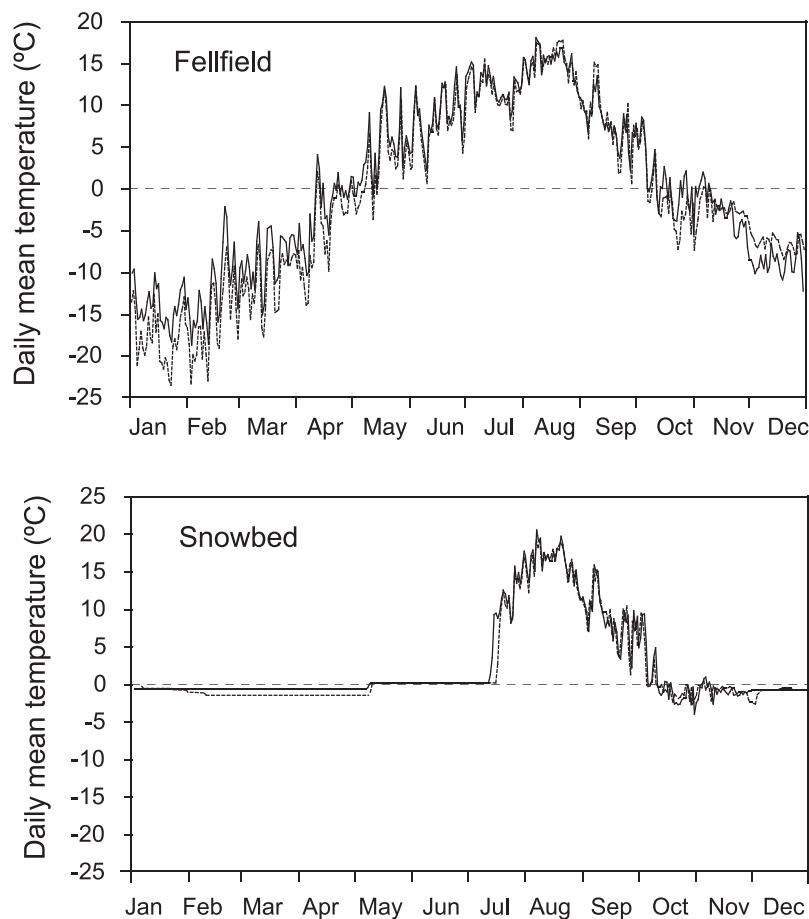
FIGURE 1. Annual variation of daily mean temperature at plant height (5 cm above the ground) at fellfield (upper) and snowbed sites (lower). Mean values of the control plots in 2006 are shown as representative temperatures. Solid lines indicate site F1 (upper) and site S1 (lower), and broken lines indicate site F2 (upper) and site S2 (lower).

height and the canopy-volume index, and (3) the responses of major species based on changes in the canopy-volume index. As indices of species diversity, we used Shannon's H' index ($H = -\Sigma p_i$ (ln [p_i]), where p_i is the proportion of a particular species based on coverage), and species richness per plot (number of vascular species within plots). In the analysis of major species, we selected six dominant species in terms of plant cover at each site in which lichens and mosses were included as a single species category.

DATA ANALYSES

During the experimental period, one OTC plot at site F1 was destroyed by strong wind; two plots in each of the control and OTC plots at site S1, and one plot each of the control and OTC plots at site S2 were disturbed by deer. These plots were excluded from the analyses. For other plots, disturbance by grazing was negligible during the experiment. In the analyses of species diversity, we used a repeated measures analysis of variance (ANOVA) in which site (F1, F2, S1, S2) and treatment (control, OTC) were considered as fixed factors, and year (2002, 2003, 2005, 2007) within plots was a repeated factor. For canopy data from 2001, 2002, 2003, 2005, and 2007, we compared the changes in canopy height and the canopy-volume index from 2001 between control and OTC plots during 2002 to 2007. First, repeated measures ANOVA was performed over sites in which site and treatment were considered as fixed factors, and year was a repeated factor. When a significant interaction effect was detected between treatment and site, we performed repeated measures ANOVA for each site to elucidate site-specific responses to the OTC treatment. For all layer data measured in 2002, 2003, 2005,

and 2007, we compared the changes in the canopy-volume index of top six dominant species from 2002 between control and OTC plots during 2003 to 2007 by repeated measures ANOVA for each site. For other statistic methods, we denoted in results.

Results

CLIMATE CONDITIONS AND WARMING EFFECT OF OTCS

The annual pattern of temperature at plant height (5 cm) in control plots was different between fellfield sites (F1 and F2) and snowbed sites (S1 and S2; Fig. 1). At the fellfield sites, winter temperature decreased below −10 °C due to sparse snow cover, while daily mean temperature was commonly above 0 °C during mid-May to late September. In contrast, the temperature of the snowbed sites was mostly remained around 0 °C during the snow-covered period from early October to next mid-summer. During the snow-free period, temperatures were similar between fellfield and snowbed sites.

The OTCs increased air temperatures between +1.1 °C and +1.7 °C during the growing season (June to September) and between +0.3 °C and +1.9 °C during the winter at site F1; between +1.2 °C and +1.8 °C during the growing season and between +0.3 °C and +3.4 °C during the winter at site F2; between +1.3 °C and +1.7 °C during the growing season at site S1; and between +1.1 °C and +1.8 °C during the growing season at site S2. Therefore, the effectiveness of warming by the OTCs was similar among sites at least during snow-free periods.

At the fellfield sites (F1 and F2), where OTCs were set throughout the year, first snowmelt day in spring was estimated as the first day on which daily maximum temperature at 5 cm above

TABLE 1

The number of vascular species observed in plots and the composition of functional types based on plant cover, Shannon's species diversity (H'), and species richness per plot (50 cm $\times$ 50 cm) are shown for each site. Measurements were done in the second year (2002) for all OTC and control plots. Functional types are classified into deciduous shrubs (DS), evergreen shrubs (ES), graminoids (G), forbs (F), lichens (L), and mosses (M). Mean values and ranges over plots (in parentheses) are shown for Shannon's H' and species richness.

Site	No. of species	DS	ES	G	F	L	M	H' index	Richness
F1	26	26%	8%	12%	19%	32%	3%	1.98 (1.58–2.28)	11.4 (8–14)
F2	14	4%	38%	14%	13%	21%	10%	1.90 (1.60–2.20)	9.8 (8–13)
S1	18	2%	3%	27%	43%	22%	3%	2.11 (1.97–2.26)	12.1 (10–14)
S2	13	0%	1%	54%	39%	5%	1%	1.68 (0.95–1.99)	8.6 (5–10)

the ground attained ≥ 1.0 °C. First snowmelt day in the control plots at site F1 ranged from 20 February to 19 April (31 March on average), while that in the OTC plots ranged from 20 February to 1 May (7 April on average) during 2002–2007. Similarly, the first snowmelt day in the control plots at site F2 ranged from 23 March to 10 May (12 April on average), while that in the OTC plots ranged from 4 April to 30 April (19 April on average) during 2002–2007. However, the differences in snowmelt time between control and OTC plots were marginally significant at site F1 ($P = 0.07$; Wilcoxon signed rank test) or not significant at site F2 ($P > 0.10$). Because plant growth did not start until late May at the fellfield sites, furthermore, the direct effect of the snowmelt time on phenology might be negligible in this experiment. Snowmelt time at site S1 ranged from 10 July to 29 July (18 July on average), and that at site S2 ranged from 14 July to 4 August (24 July on average) during 2001–2007. At the snowbed sites, OTCs were set within 5 days of snowmelt every year.

Soil moistures during the late growing season were $20 \pm 3.3\%$ (mean $\pm$ SE, $n = 12$) at site F1, $26 \pm 1.2\%$ at site F2 ($n = 12$), $30 \pm 1.4\%$ at site S1 ($n = 8$), and $30 \pm 1.6\%$ at site S2 ($n = 12$), including both control and OTC plots. There were no significant differences between control and OTC plots at any site ($P > 0.10$, Mann-Whitney's U-test). Therefore, the effect of OTCs on soil moisture was negligible in this experiment although information on the seasonal pattern of soil moisture was limited.

SPECIES COMPOSITION AND DIVERSITY

The number of vascular plant species observed in plots at individual sites ranged from 13 to 26 (Table 1; see Appendix for species list). Lichens (*Cladonia* and *Cetraria* spp.) and deciduous shrubs (mainly *Vaccinium uliginosum* and *Arctous alpinus*) dominated at site F1. Evergreen shrubs (mainly *Diapensia lapponica* and *Loiseleuria procumbens*) and lichens dominated at site F2. Major functional types at sites S1 and S2 were forbs (mainly *Potentilla matsumurae* at both sites and *Peucedanum multivittatum* at site S1) and graminoids (mainly Carex *flavocuspis*,

Carex pyrenaica, *Deschampsia caespitosa* var. *festucaefolia* at both sites).

Shannon's H' index varied from 1.68 at site S2 to 2.11 at site S1 among sites in 2002 (Table 1). The H' index varied significantly among sites ($F_{3,36} = 6.91$, $P < 0.001$), but a significant effect of the OTC treatment was not detected ($F_{1,36} = 0.003$, $P = 0.95$). Species richness, i.e. the number of vascular plant species per plot, ranged from 8.6 at site S2 to 12.1 at site S1 in 2002 (Table 1). Similarly, a significant effect of the OTC treatment was not detected on species richness ($F_{1,36} = 0.014$, $P = 0.91$) although it varied significantly among sites ($F_{3,36} = 12.83$, $P < 0.001$). Therefore, species diversity was not influenced by the OTC treatment during the experimental period.

CANOPY STRUCTURE

The canopy height was significantly influenced by the OTC treatment and a significant site $\times$ treatment interaction was detected, indicating that the effects of OTC on height growth varied among sites (Table 2). During the experimental period, mean canopy height at the fellfield sites increased from 44 mm (2001) to 85 mm (2007) at site F1, and from 29 mm to 60 mm at site F2 in the OTC plots, while mean canopy height in the control plots varied from 46 mm to 45 mm at site F1, and from 33 mm to 36 mm at site F2 (Fig. 2). The repeated measures ANOVA conducted at each site revealed significant effects of treatment and year at both fellfield sites ($F_{1,9} = 10.65$, $P = 0.0098$ and $F_{3,27} = 18.38$, $P < 0.001$ at F1 for treatment and year, respectively; $F_{1,10} = 8.32$, $P = 0.016$ and $F_{3,30} = 35.97$, $P < 0.001$ at F2, respectively). Apparent increases in canopy height in the OTC plots occurred in the second year at site F1, while they occurred in the third year at site F2. The canopy height of control plots decreased in the third year (2003) at both fellfield sites.

At the early-snowmelt snowbed, site S1, canopy height did not change during the first five years (ranging from 54 mm to 63 mm), and then increased in the seventh year in both OTC (91 mm) and control plots (75 mm; Fig. 2). The effect of treatment

TABLE 2

Results of ANOVA of repeated measures for the height growth of canopy-forming plants and the development of canopy volume over sites during the experiment (2001–2007). Δ Height and Δ Canopy volume are the increment of canopy height and canopy-volume index from 2001, respectively.

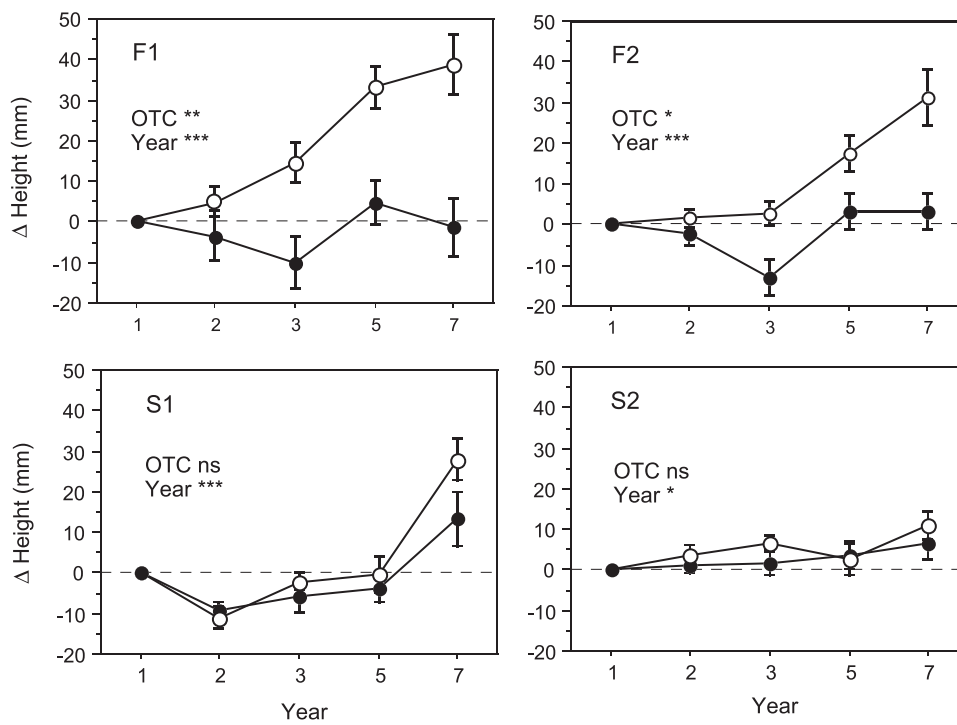| Fixed factor	Δ Height				Δ Canopy volume			
	df	MS	F	P	df	MS	F	P
Site	3	587.5	1.67	0.193	3	733.0×10^5	4.49	0.0095
Treatment	1	5608.4	15.94	0.0003	1	2700.1×10^5	16.55	0.0003
Site $\times$ Treatment	3	1141.6	3.24	0.034	3	744.9×10^5	4.56	0.0088
Error	33	351.9			33	163.7×10^5		

FIGURE 2. Year-to-year pattern of canopy height growth from 2001 (year = 1) to 2007 (year = 7) at each site. Filled and open circles indicate the control and OTC plots, respectively. Vertical bars indicate SE. Significance of OTC treatment and year effects by repeated measures ANOVAs are shown. ns $P > 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

was not significant at site S1 ($F_{1,6} = 0.57$, $P = 0.47$) although significant year variation was detected ($F_{3,18} = 19.78$, $P < 0.001$). At the late-snowmelt snowbed, site S2, canopy height increased gradually from year to year ($F_{3,24} = 4.75$, $P = 0.010$; ranging from 39 mm to 50 mm in the control plots and from 56 mm to 70 mm in the OTC plots), but the effect of treatment was not significant ($F_{1,8} = 0.64$, $P = 0.45$).

Similar to the canopy height, the canopy-volume index was significantly influenced by the OTC treatment and a significant site × treatment interaction was detected, indicating that the effects of OTC on canopy development varied among sites (Table 2). Vegetation cover at site F1 increased from 80% (2001) to 95% (2007) in the OTC plots, while vegetation cover in the control plots varied from 75% to 83%. The canopy-volume index increased $10,571 \pm 2028$ SE cm^3 in the OTC plots during the experimental period (2001–2007) and 660 ± 1286 cm^3 in the control plots. Therefore, canopy expansion as a result of the OTC treatment was 9911 cm^3 at site F1. Vegetation cover at site F2 increased from 86% (2001) to 92% (2007) in the OTC plots, while vegetation cover in the control plots varied from 86% to 95%. The canopy-volume index increased 7650 ± 1764 cm^3 in the OTC plots and 1538 ± 966 cm^3 in the control plots, indicating a 6112 cm^3 canopy expansion as a result of the OTC treatment at site F2. The repeated measures ANOVA conducted for canopy volume at each site revealed significant effects of treatment and year at both fellfield sites: $F_{1,9} = 18.37$, $P = 0.002$ and $F_{3,27} = 17.82$, $P < 0.001$ at F1 for treatment and year, respectively; $F_{1,10} = 6.54$, $P = 0.028$ and $F_{3,30} = 35.05$, $P < 0.001$ at F2, respectively.

Vegetation cover at the snowbed sites (S1 and S2) was consistently large (>90%) among years and plots. At site S1, the canopy-volume index increased 7415 ± 1447 cm^3 in the OTC plots during the experimental period, while it increased 4037 ± 1915 cm^3 in the control plots. At site S2, the canopy-volume index increased 3833 ± 673 cm^3 in the OTC plots and 2466 ± 708 cm^3 in the control plots. The repeated measures ANOVA conducted at each site indicated significant year effect ($P < 0.001$; $F_{3,18} = 32.17$ and $F_{3,24} = 22.76$ at S1 and S2, respectively) but the effect of treatment

was not significant at either snowbed site ($P > 0.10$; $F_{1,6} = 0.04$ and $F_{1,8} = 0.71$ at S1 and S2, respectively).

RESPONSES OF MAJOR SPECIES

Six dominant species at each site are indicated in Figures 3–6. These dominant species occupied 72–85% of the total plant cover at each site. The analyses of canopy-volume index were performed for these species. At site F1, a significant positive effect of the OTC treatment was detected for *Potentilla matsumurae*, *Vaccinium uliginosum*, and *Arctous alpinus* (Fig. 3). A significant year effect was detected for all species. At site F2, a significant positive effect of the OTC treatment was detected for lichens, *C. stenantha* var. *taisetsuensis*, and mosses (Fig. 4). A significant year effect was detected for all species except *P. matsumurae*. The canopy-volume index of the control plots tended to be lower in 2003 and higher in 2007. In contrast, none of the species showed a significant effect of the OTC treatment at site S1, while all species showed significant effect of year and most of them tended to increase the canopy-volume index during the experimental period (Fig. 5). Also at site S2, none of the species showed a significant effect of the OTC treatment (Fig. 6). A significant year effect was detected for *P. matsumurae*, *C. flavocuspis*, *C. pyrenaica*, and lichens, but their response patterns were not consistent among species.

Discussion

GENERAL TRENDS

The results of the present experiment largely supported our hypothesis on the site-specific responses of alpine plant communities to climatic amelioration. The growth of canopy-forming plants responded to the OTC treatment more rapidly in the lower fellfield community dominated by deciduous shrubs near to the timberline than in the upper fellfield community dominated by evergreen dwarf shrubs on a ridge. Furthermore, responses to the OTC treatment were more apparent in the fellfield communities
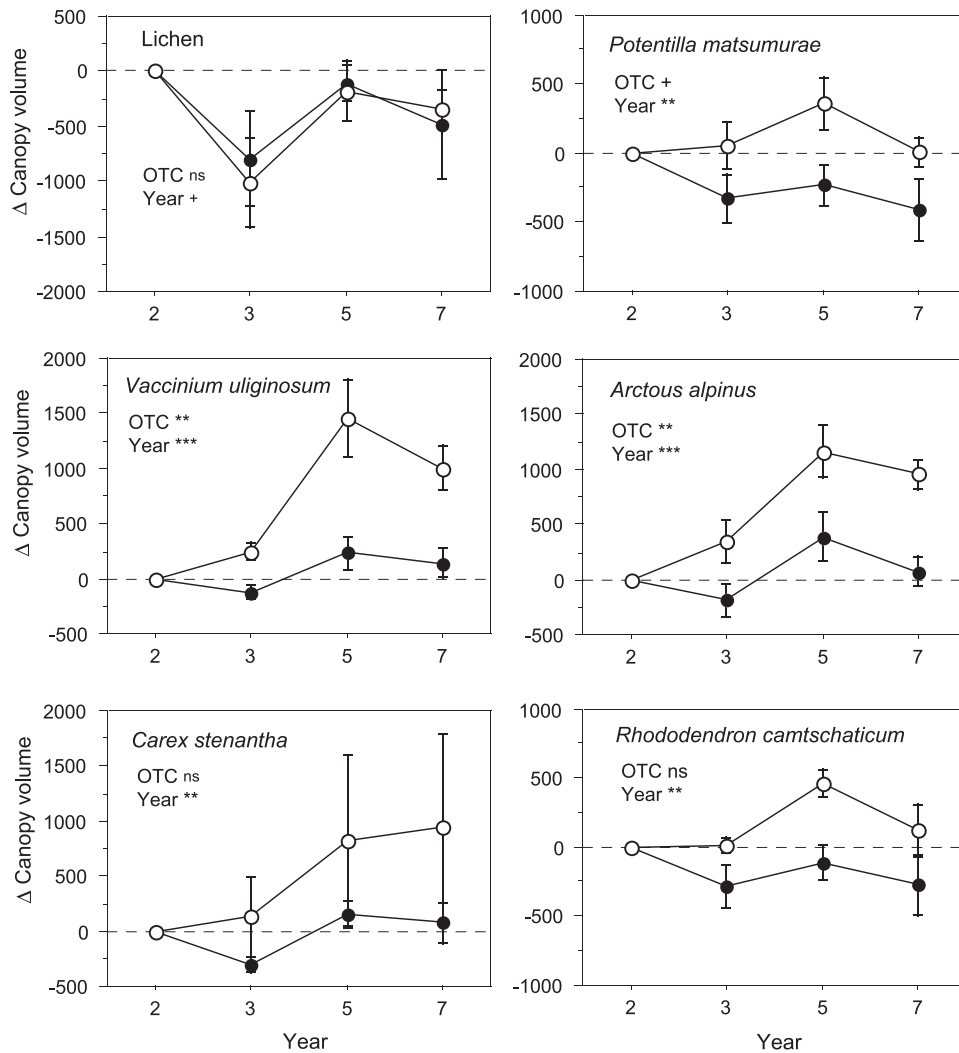
FIGURE 3. Year-to-year patterns of the canopy-volume index (cm³) of major species at site F1 from 2002 (year = 2) to 2007 (year = 7). Filled and open circles indicate the control and OTC plots, respectively. Vertical bars indicate SE. Significance of OTC treatment and year effects by repeated measures of ANOVAs are shown. ns $P > 0.10$, + $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

than in the snowbed communities. However, significant effects on species diversity were not detected in our experiment, indicating that competitive exclusion had not occurred during the OTC treatment.

The effects of experimental warming on species diversity differ among different studies. Rapid declines in species richness and diversity as a result of artificial warming were reported in Alaskan arctic tundra (Chapin et al., 1995; Hollister et al., 2005) and a Tibetan alpine region (Klein et al., 2004). In contrast, significant effects on species composition and diversity were not detected in subarctic tundra in Iceland (Jónsdóttir et al., 2005) and Norwegian alpine heath communities (Klanderud and Totland, 2005) during a 3- to 5-year warming experiment. Various responses of tundra plant communities to climatic amelioration may depend on the species composition of dominant plants (Chapin and Shaver, 1985; Press et al., 1998; Jónsdóttir et al., 2005; Klanderud, 2008). For instance, expansion of a deciduous shrub *Betula nana* is a major reason for the rapid decline in species diversity in tussock tundra of northern Alaska (Chapin and Shaver, 1985; Hobbie and Chapin, 1998). Therefore, the modification of interspecific relationships within communities may strongly depend on the behavior of a few dominant species. In the present study, *Vaccinium uliginosum* and *Arctous alpinus* at site F1 and *Carex stenentha* var. *taisetsuensis* at site F2 showed significant increase in plant cover by the OTC treatment. These

species occupied 12–19% of total plant cover at each site and may cause significant effects on other species under climatic amelioration. Furthermore, combinations of warming treatment and fertilization treatment or plant removal and introduction treatment may be useful to elucidate the warming impact on interspecific relationship because warming treatment alone may be too moderate to influence species diversity during a short period (Choler et al., 2001; Klanderud, 2005, 2008; Klanderud and Totland, 2005).

FUNCTIONAL TYPE RESPONSES IN FELLFIELD COMMUNITIES

The responses of canopy-forming plants to the OTC treatment were faster and stronger at site F1 than at site F2. Site F2 was located 200 m higher than site F1, and the daily mean temperature was 1.2 °C lower at site F2 throughout the year ranging from 0.5 °C to 1.7 °C as a monthly mean (G. Kudo, unpublished data). Although the seasonal pattern of temperature transition was similar between the two fellfield sites (Fig. 1), the composition of functional types was very different. Deciduous shrubs were common at site F1, while evergreen shrubs with mat-forming growth forms dominated at site F2 (Table 1). The difference in species composition may be a major factor contributing to the site-specific responses. In the analyses of a 6-
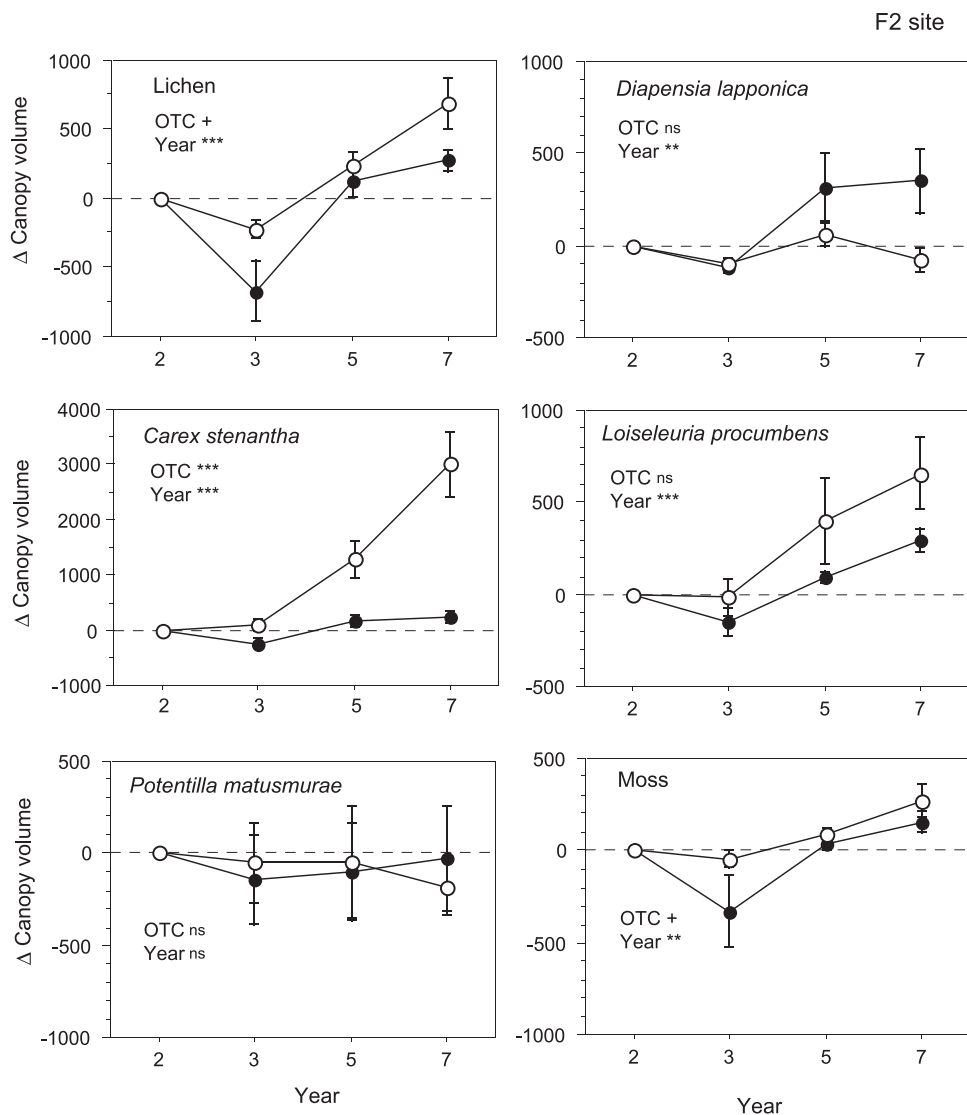
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FIGURE 4. Year-to-year patterns of the canopy-volume index (cm³) of major species at site F2 from 2002 to 2007. Filled and open circles indicate the control and OTC plots, respectively. For details, refer to Figure 3.

year OTC experiment in the tundra biome, height and plant cover of deciduous shrubs and graminoids increased especially in comparison with other functional types (Walker et al., 2006). Similar responses were reported in several other experiments in the field (Press et al., 1998; Jónsdóttir et al., 2005; Wahren et al., 2005; Hollister et al., 2005; Van Wijk et al., 2003), indicating that deciduous shrubs and graminoids have potentially high growth ability under moderate conditions (Dormann and Woodin, 2002). Thus, the initial composition of major species is important to predict the vegetation responses to climate change (Press et al., 1998; Jónsdóttir et al., 2005). In contrast, mosses and lichens have low growth potential and tended to decrease their plant cover in several experiments due to the acceleration of interspecific competition (Klanderud, 2008; Walker et al., 2006; Jónsdóttir et al., 2005; Hollister et al., 2005; Van Wijk et al., 2003). However, negative responses of these functional types to the OTC treatment were not detected in the present study. Because species diversity did not change in the present experiment, the interaction among co-occurring species might have not changed greatly.

Site-specific responses were detected even within the same species between sites F1 and F2. *Carex stenantha* var. *taisetsuensis* highly increased its canopy volume with the OTC treatment at site F2, while OTC effect was not detected at site F1. Similarly, canopy-volume index for lichens increased with the OTC

treatment only at site F2 although its significant level was marginal. In contrast, *Potentilla matusmurae* increased its canopy-volume index during the OTC treatment at site F1 but did not change at site F2. These various intraspecific responses indicate that the sensitivity to climatic change varied among species. For lichens and *C. stenantha* var. *taisetsuensis*, for example, climatic conditions at site F1 may not be severe but those at site F2 may be stressful for their growth due to upper elevation, thus climatic amelioration by OTCs resulted in the acceleration of growth only at site F2. We observed that *Diapensia lapponica* decreased its plant mass in the OTC plots at site F2 although a statistically significant difference was not detected (Fig. 4). This was because of die-back of the canopy due to earlier growth as a result of the OTC treatment and subsequent frost damage in the early season. A decline in *D. lapponica* populations was reported in northern Sweden, in which climate warming might cause physiological stress for this species (Molau, 1996).

RESPONSES OF FELLFIELD AND SNOWBED COMMUNITIES

Slow and moderate responses of snowbed plants to OTC treatment indicated that cool temperature conditions might not restrict the growth of snowbed plants. The limiting factor for the
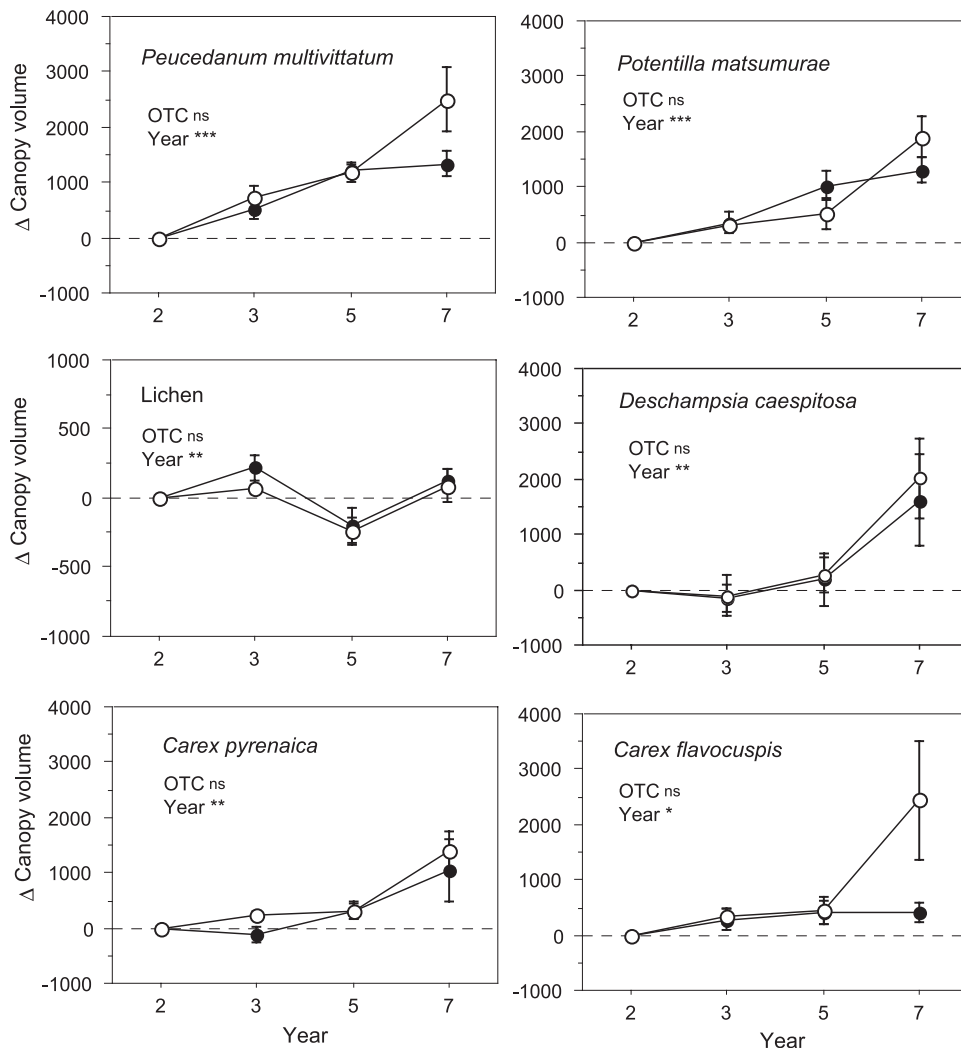
FIGURE 5. Year-to-year patterns of the canopy-volume index (cm³) of major species at site S1 from 2002 to 2007. Filled and open circles indicate the control and OTC plots, respectively. For details, refer to Figure 3.

growth of snowbed plants may be the short growing period due to late snowmelt (Walker et al., 1994; Björk and Molau, 2007), which we did not manipulate. Sandvik et al. (2004) reported similar results in which a 5-year OTC treatment in Norway did not influence snowbed vegetation. Therefore, warming during summer may cause little impact on growth and vegetation change in snowbed communities if snowmelt conditions do not change.

Walker et al. (1994) demonstrated that factors correlated with variation in the aboveground biomass of alpine plants varied among fellfield, dry meadow, moist meadow, wet meadow, and snowbed communities in the Rocky Mountains: annual phytomass in the fellfield and dry meadow communities was associated with precipitation in the previous year, while that of moist and wet meadows was related to the current soil moisture, and that of the snowbed community was determined by the time of snowmelt. Inter-annual variation in the canopy-volume index was detected also in the control plots in the present experiment, which might reflect climatic fluctuation from year to year. At sites F1 and F2, canopy height and the canopy-volume index decreased in the third year (2003) only in the control plots but not in the OTC plots (Fig. 2). Because the temperature in July 2003 was the lowest during the experimental period, i.e. 2.4 °C lower than the average

of the last 10 years (12.9 °C), the growth of fellfield plants might have been limited due to the cool weather conditions in that year.

The composition of plant functional types may determine the responses of the communities to environmental change (Chapin et al., 1996; Walker et al., 2006) even when the responses of plant species are largely individualistic (e.g. Dormann and Woodin, 2002; Klanderud, 2008). Shrubs and lichens were common in the fellfield communities, while graminoids and forbs dominated in the snowbed communities (Table 1). Several studies demonstrated that the growth of graminoids was especially sensitive to fertilization more than simple warming treatment (Dormann and Woodin, 2002; Van Wijk et al., 2003; Klanderud and Totland, 2005). Thus, effects of warming on soil nutrient conditions may influence the vegetation dynamics in snowbed communities. Because the OTCs had little effects on soil temperature in our previous study at site F1 (Kudo and Suzuki, 2003; see also Marion et al., 1997) and soil moisture in the present study, edaphic conditions in the OTCs might be small in the present experiment, resulting in little impact on the snowbed communities.

Several previous studies simulating warming revealed that the responses of tundra plant communities to specific environmental factors varied substantially between community types within
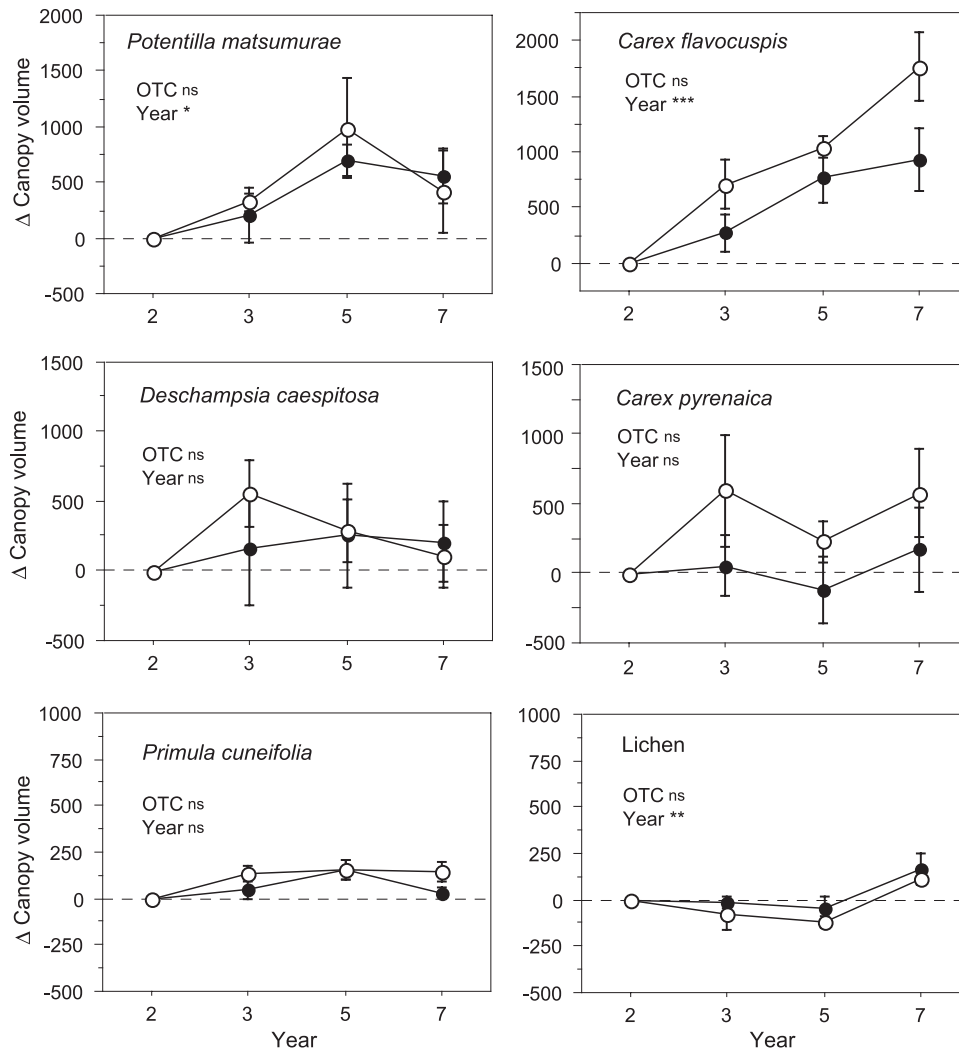
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FIGURE 6. Year-to-year patterns of the canopy-volume index (cm^3) of major species at site S2 from 2002 to 2007. Filled and open circles indicate the control and OTC plots, respectively. For details, refer to Figure 3.

regions (Chapin and Shaver, 1985; Hollister et al., 2005; Jónsdóttir et al., 2005; Wahren et al., 2005). These results indicated that limiting factors of plant growth and performance are highly specific to local habitats (Chapin and Shaver, 1985; Walker et al., 1994) and that indirect effects of warming such as soil nutrition, soil moisture, and snowmelt time are extremely important for the prediction of vegetation dynamics. Results from the present study suggest that deciduous shrubs will dominate in the lower-alpine fellfield and graminoids will dominate in the typical alpine fellfield on ridges, while snowbed vegetation may experience little impact if warming results in moderate thermal conditions without considerable changes in other edaphic conditions. If warming results in earlier snowmelt, drier soil conditions, and/or changes in nutrition situations as predicted (Van Wijk et al., 2003; Klanderud and Totland, 2005; Wahren et al., 2005; Walker et al., 2006; Björk and Molau, 2007), its impact may be accelerated over wider vegetation types but differently in each habitat. It is obvious that changes in snowmelt timing and snow depth are occurring with warming in high latitude and alpine regions (Dye, 2002; Beniston, 2003; IPCC, 2007). In addition, in the Taisetsu Mountains, snowmelt time of alpine meadows has occurred earlier during the last decades (Kudo and Hirao, 2006). Therefore, it is possible that warming may cause large impacts on snowbed vegetation by advancing growing season and changes in edaphic conditions due to earlier snowmelt (Heegaard, 2002; Hiller et al., 2005; Huelber et al., 2006;

Schöb et al., 2009). Even allowing for the limitations of the present experiment, the results stress the significance of the heterogeneous structure of alpine vegetation in predicting the impact of warming on the alpine ecosystem.

Acknowledgments

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APPENDIX

List of vascular species observed in the plots of individual sites.

Family	Species	F1	F2	S1	S2
Deciduous shrub					
Ericaceae	*Arctous alpinus*	X	X		
Ericaceae	*Rhododendron camtschaticum*	X			
Ericaceae	*Vaccinium uliginosum*	X			
Rosaceae	*Siversia pentapetala*	X	X	X	
Rosaceae	*Spiraea betulifolia*	X			
Evergreen shrub					
Ericaceae	*Phyllodoce aleutica*			X	X
Ericaceae	*Phyllodoce caerulea* f. *yesoensis*				X
Ericaceae	*Empetrum nigrum*	X	X		
Ericaceae	*Vaccinium vitis-idaea*	X			
Ericaceae	*Arcterica nana*	X	X	X	
Ericaceae	*Harrimanella stelleriana*				X
Ericaceae	*Bryanthus gmelinii*	X	X		
Ericaceae	*Ledum decumbens*	X			
Ericaceae	*Loiseleuria procumbens*	X	X		
Diapensiaceae	*Diapensia lapponica*	X	X		
Pinaceae	*Pinus pimila*	X	X		
Graminoid					
Cyperaceae	*Carex pyrenaica*			X	X
Cyperaceae	*Carex stenantha* var. *taisetsuensis*	X	X		
Cyperaceae	*Carex flavocuspis*	X		X	X
Juncaceae	*Luzula oligantha*			X	
Juncaceae	*Juncus beringensis*			X	X
Poaceae	*Calamagrostis langsdorffii*	X		X	X
Poaceae	*Deschampsia flexuosa*			X	X
Poaceae	*Deschampsia atropurpurea*				X
Poaceae	*Deschampsia caespitosa* var. *festucaefolia*			X	X
Poaceae	*Festuca ovina*	X	X		
Poaceae	*Hierochloe alpina*	X			
Forb					
Apiaceae	*Tilingia ajanensis*	X	X	X	
Apiaceae	*Peucedanum multivittatum*			X	
Apiaceae	*Bupleurum triradiatum*	X			
Asteraceae	*Saussurea yanagisawae*	X	X		
Asteraceae	*Artemisia arctica*	X			
Campanulaceae	*Campanula chamissonis*	X			
Gentianaceae	*Gentiana nipponica*			X	X
Parnassiaceae	*Parnassia palustris*			X	
Primulaceae	*Primula cuneifolia*			X	X
Ranunculaceae	*Anemone narcissiflora*			X	
Rosaceae	*Potentilla matsumurae*	X	X	X	X
Scrophulariaceae	*Penstemon frutescens*	X			
Scrophulariaceae	*Pedicularis chamissonis*			X	
Valerianaceae	*Patrinia sibirica*	X			