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Effects of Artificial Warming on Shoot Elongation of Alpine Dwarf Pine (Pinus pumila) on Mount Shogigashira, Central Japan

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Abstract

The effects of artificial warming on shoot elongation of alpine dwarf pine (Pinus pumila) was studied near Mount Shogigashira summit, central Japan, from 2001 to 2003. A nylon windshield net enclosed two experimental plots, 2 × 2 m, each year at the start of the growing season (June, but late July in 2001). The nets were removed at the end of the growing season (late September or early October). Two plots, 1.5 × 1.5 m, without a net were set as controls. In September 2001, the daily mean air temperature differed little between the experimental and control plots: compared to the control plot, the maximum was 4.3°C higher and the minimum was 1.7°C lower in the experimental plot. The annual shoot elongation differed little between the experimental and control plots in 2001 and 2002, but it was greater in the experimental than in the control plot in 2003. Shoot elongation started in June and ended in August in both experimental and control plots, but the rate of the increase was greater in the experimental than in the control plot in 2003, and so shoots had greater elongation in 2003 in the experimental plot. Thus, artificial warming promoted shoot elongation by increasing the daily maximum temperature.

Introduction

Climatic conditions in the alpine zone are severely challenging for the growth and survival of plants; these conditions include extremely low temperatures, short growing seasons, high UV-B radiation, and strong winds (Hadley and Smith, 1983, 1986; Kudo, 1991; Körner, 1999; Phoenix et al., 2000). Global warming is assumed to have strong effects on plant communities in the alpine zone, as well as in the polar and subpolar zones (Kojima, 1994; Henry and Molau, 1997; Myineni et al., 1997; Kullman, 2001; Chapin et al., 2004). Therefore, through the use of experimental manipulations, many studies have examined the effects of climatic conditions on plant performance. For example, the growth of alpine and tundra plants increases for plants growing in open-top chambers (OTCs) that artificially increase local air temperature (e.g., Chapin and Shaver, 1985; Chapin et al., 1995; Molau, 1997; Suzuki and Kudo, 1997; Arft et al., 1999). Although numerous attempts have been made to show the effects of artificial warming on the growth of alpine and tundra plants, few reports exist from Japan. An increased knowledge of plant responses to artificial warming is of great importance to the understanding of the effects of global warming on alpine plant communities in Japan, which has many high mountains.

Many OTC instruments are shorter than 50 cm, and therefore most OTC studies have been on mosses, small herbs, and shrubs (e.g., Jones et al., 1997; Wada et al., 1998; Hollister and Webber, 2000; Dorrepaal et al., 2003). A few OTC studies, however, have examined relatively large plants.

Pinus pumila Regel, a dwarf pine, is the most representative tree species in the alpine zone above timberline in central and northern Japan (Tatwaki, 1958; Wardle, 1977; Yoshino, 1978). This species is also widely distributed in the Russian Far East and eastern Siberia (Nikolov and Helmsaari, 1992). Concern exists about the upward distribution shift of P. pumila along altitudinal gradients as a result of global warming (Kajimoto et al., 1996). Several studies have focused on the growth of P. pumila in relation to climatic conditions (e.g., Sano et al., 1977; Okitsu, 1988; Takahashi, 2003a). For example, a study of the relationship between shoot elongation of P. pumila and monthly climatic data since 1975 showed that shoot elongation is positively correlated with summer temperature of the previous year (Takahashi, 2003a). This finding suggests that P. pumila grows to a greater shoot length if summer temperature increases, as is predicted to happen because of global warming. However, little experimental evidence is available to show whether warming in fact does increase the growth of P. pumila, partly because its relatively large scrub height (up to 2 m) makes experimental studies difficult.

This study attempted to show whether artificial warming increases the growth of P. pumila. Experimental plots were established with and without artificial warming near the summit of Mount Shogigashira, central Japan. The shoot elongations of P. pumila shrubs in each plot were measured several times during the course of the experiment. The values measured in each plot were compared to determine the effect of artificial warming.

Materials and Methods

STUDY SITE

This study was done on a ridge near the summit of Mount Shogigashira (2699 m a.s.l., 35°48’N, 137°50’E), central Japan. P. pumila was distributed only near the summit of Mount Shogigashira. Its altitudinal distribution ranged from the timberline (2630 m a.s.l.) to the summit (2699 m a.s.l.) on the examined slope (Takahashi, 2003a). The mean monthly air temperature was −11.4°C in January and 13.9°C in July, and the annual mean air temperature was 0.8°C at Senjojiki (2650 m a.s.l., 3.5 km from the study area) from October 2001 to September 2002 (Takahashi, 2005). The prevailing wind is from the west in this region (Fukuyo et al., 1998). The growing season of plants at this altitude was estimated as June to September because during those months, the monthly mean air temperature exceeded 5°C, the effective heat for plant growth (Kira, 1948).

FIELD METHODS

The 2001–2003 field experiment examined the effects of artificial warming on the shoot elongation of P. pumila at the ridge near the
summit of Mount Shogigashira. The scrub height was 30–50 cm at this ridge (Takahashi, 2003a). Two plots of 2 × 2 m each were established in 2001. To simulate natural warming, a nylon windshield net (0.8 m high) enclosed each plot (Fig. 1). Two other plots of 1.5 × 1.5 m each without the windshield net were also established as controls near the experimental plots. The mesh size of the windshield net was 2 × 2 mm. The windshield net was doubly overlaid to increase the windshield capacity. The percentage of wind-speed reduction by the doubly overlaid windshield net differed according to the wind speed: 89% at 1.8 m/s, 83% at 4.1 m/s, and 72% at 5.7 m/s. The windshield net was set in late July.

Air temperatures at 40 cm above the soil surface in the experimental and control plots were automatically recorded at 1-h intervals in September 2001. This measurement height was nearly equivalent to the scrub height of *P. pumila*. A thermometer that included a data logger (TidbiT, Onset Computer Corporation, Pocasset, Massachusetts, USA) was used; this equipment was completely sealed in epoxy and was very durable. A thermistor having an accuracy was ±0.5°C was placed inside the thermometer. The thermometer was covered with aluminum foil to reduce the effect of direct solar radiation on the thermometer.

About 40–50 terminal-leader shoots of *P. pumila* were randomly selected in each plot. Shoots of *P. pumila* in the experimental plot were chosen in the inner 1.5 × 1.5 m quadrat inside the 2 × 2 m plot to avoid the effect of shading on the shoot elongation by the windshield net. The annual shoot elongation from 1999 to 2003 was determined by measuring the distance between bud scars.

The annual shoot length of *P. pumila* is positively correlated with the size of its winter bud formed in the previous year (Kajimoto, 1993). To show how the artificial warming affects the relationship between bud size and shoot length, the diameter of winter buds formed at the terminal-leader shoots was measured by using a digital caliper at each plot in October 2002. Seasonal changes in shoot length of *P. pumila* were monitored at 1- or 2-wk intervals from the end of June to early August in 2003, to examine the effect of artificial warming on shoot-growth phenology.

**DATA ANALYSIS**

Data recorded for the two plots of each experimental and control plot were pooled for analyses. To examine the shoot-growth phenology of *P. pumila*, the relative growth rate (RGR, d⁻¹) of shoots at time *t* was calculated as

\[ \text{RGR}_t = \frac{(\ln L_t - \ln L_{t-1})}{N_t}, \]

where *L*ₜ and *L*ₜ₋₁ are the shoot length at time *t* and at time *t* − 1 on the previous census day, respectively, and *N*ₜ is the number of days between the two successive census days (i.e., time *t* and time *t* − 1). The relative growth rate at each time was compared between the experimental and control plots by using the Mann-Whitney *U*-test.

Topographic conditions largely influence the shoot growth of *P. pumila* by changing the degree of wind exposure. For example, because wind exposure is greater at convex sites than at concave sites, the shoot elongation and scrub height of *P. pumila* are reduced at convex sites (Okitsu and Ito, 1983). The shoot elongation of *P. pumila* before the start of the experiment of this study differed between the experimental and control plots, reflecting the difference in small-scale topographic conditions. The annual shoot elongation of *P. pumila* in 1999 (before the artificial warming) in the control plot was greater than in the experimental plot (2.85 cm and 2.36 cm, respectively, ANOVA, *F*₁,₁₉₁ = 12.4, *P* < 0.001). Therefore, the effect of artificial warming on shoot elongation cannot be detected by comparing the mean values of shoot elongation between the experimental and control plots. If small-scale topographic conditions regulate the elongation rates of shoots, the shoot-elongation rate in a given year correlates with its previous elongation rate. Therefore, the initial shoot length before the artificial warming must be considered in order to detect the effect of artificial warming on shoot elongation, i.e., the shoot-elongation rate in a given year before the start of artificial warming is assumed to correlate with its previous elongation rate, irrespective of plot. To confirm this assumption, the shoot elongation of *P. pumila* in 2000 (before the artificial warming) was compared between the control and experimental plots by using analysis of covariance (ANCOVA) with the initial shoot length in 1999 as a covariate. If no significant difference was detected, the assumption was confirmed, and then shoot elongation was compared between the experimental and control plots in each year after the start of the experiment from 2001 to 2003. Shoot elongation would be greater in the experimental plot than in the control plot at any initial shoot length if artificial warming increases the shoot elongation of *P. pumila*.

**Results**

The daily maximum air temperature in September 2001 was on average 4.3°C higher in the experimental plot compared with the

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positively correlated with its diameter of the winter bud formed in the previous year (Fig. 4). However, the annual shoot elongation at any diameter of winter bud was greater in the experimental plot compared with the control plot (ANCOVA, $F_{1,172} = 27.3, P < 0.001$, Fig. 4). The shoot-growth phenology in 2003 was compared between experimental and control plots by using shoots emerged from the winter buds with a limited range of diameter between 2.7 and 3.5 mm in 2002, because the diameter of a given winter bud correlated with its shoot elongation (Fig. 4) and because the average diameter of winter buds was significantly greater in the control plot than in the experimental plot (3.6 mm and 3.1 mm, respectively; ANOVA, $F_{1,177} = 35.1, P < 0.001$). In 2003, the shoot elongation of P. pumila in each plot started in June and ended by early August (Fig. 5a). However, the relative growth rate of shoots was higher in the experimental plot than in the control plot by mid-July (Fig. 5b). Therefore, the higher initial growth rate of shoots in the experimental plot resulted in a final greater elongation of shoots compared with the control plot. The statistical significance levels were boundary ($P < 0.1$, Mann-Whitney $U$-test), probably owing to the small number of observations for the control plot ($n = 19$).

**Discussion**

The daily mean air temperature differed little between experimental and control plots because the daily maximum air temperature was higher but the daily minimum air temperature was lower in the experimental plot compared with the control plot. The lower daily maximum air temperature in the control plot is reasonable because of cooling by wind in the day. In this sense, the increase in daily maximum air temperature in the experimental plot was mainly due to wind-speed reduction. Many OTC experiments showed that daily mean and maximum air temperatures increase in OTCs, but daily minimum air temperatures are unchanged (e.g., Chapin and Shaver, 1985; Chapin et al., 1995; Suzuki and Kudo, 1997; Hollister and Webber, 2000). However, some OTC and windshield experiments showed that the daily minimum air temperature is lower in OTC or windshield plots than the ambient air (e.g., Marion et al., 1997; Stenström et al., 1997; Fukuyo et al., 1998; Wada et al., 1998). Therefore, OTC and windshield treatments do not always increase daily minimum or mean air temperatures or both. Although the cause of the reduced daily minimum air temperature in the experimental plot was unknown in this study, radiative cooling is one possible factor. The air temperature near the soil surface decreases at night because of radiative cooling, especially on clear days. On mountain slopes, cold air drainage flows down to the bottom of valleys by gravity. Thus, the night air temperature in the bottom of valleys is lower compared with the upper part of slopes (Yoshino, 1980). In contrast, wind increases the air temperature in the bottom of valleys because of wind pumping (Yoshino, 1980).

**TABLE 1**

<table>
<thead>
<tr>
<th>Year</th>
<th>$a$</th>
<th>$b$</th>
<th>$r^2$</th>
<th>$F$ for $a$</th>
<th>$F$ for $b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2000</td>
<td>0.976</td>
<td>0.595</td>
<td>0.521***</td>
<td>1.086</td>
<td>0.431</td>
</tr>
<tr>
<td>2001</td>
<td>0.395</td>
<td>1.493</td>
<td>0.230***</td>
<td>0.513</td>
<td>1.260</td>
</tr>
<tr>
<td>2002</td>
<td>0.608</td>
<td>0.868</td>
<td>0.341***</td>
<td>0.501</td>
<td>1.336</td>
</tr>
<tr>
<td>2003</td>
<td>0.565</td>
<td>0.953</td>
<td>0.281***</td>
<td>0.706</td>
<td>1.022</td>
</tr>
</tbody>
</table>

**Notes:**

**$P < 0.01$.**

***$P < 0.001$.**
temperature on a ridge and the upper part of slopes by mixing with warm air above (Yoshino, 1980). The windshield nets of this study probably prevented mixing of air. Thus, cold air generated by radiative cooling remained in the experimental plot and reduced the air temperature at night.

The shoot elongation of *P. pumila* differed little between the experimental and control plots in the first and second years of the artificial warming, but a positive effect of the artificial warming on the shoot elongation was detected in the third year. Although shoot elongation of *P. pumila* ends by late July or early August (Kajimoto, 1993), artificial warming started in late July of the first year (i.e., the shoot elongation was almost completed) in this study. Therefore, the windshield experiment hardly influenced the shoot elongation of *P. pumila* in the first year of the experiment.

*P. pumila* is assumed to grow by using the photosynthetic production gained in the previous year (Kibe and Masuzawa, 1992). The photosynthetic rate of plants is generally temperature dependent (e.g., DeLucia and Smith, 1987). The optimal temperature for the photosynthetic rate of *P. pumila* is 10–15°C (Kajimoto, 1990). The growing season of *P. pumila* is from June to September, and the day air temperatures of June and September are usually lower than the optimal temperature for the photosynthesis of *P. pumila* (Takahashi 2003b, 2005). Therefore, the increase in daily maximum air temperature by the windshield treatment would increase the photosynthetic production by *P. pumila*, especially in the early and late growing season (i.e., June and September). However, the delayed installation of the windshield nets in the first year probably did not increase the annual photosynthetic production so much. Therefore, artificial warming hardly influenced the shoot elongation of *P. pumila* in the second year. Windshield nets were installed at the beginning of the growing season in the second and third years. Therefore, a higher relative growth rate of shoots in the experimental plot than in the control plot in the third year suggests that photosynthetic production gained in the second year was greater in the experimental plot. Shoot elongation at any diameter of winter buds was greater in the

**FIGURE 3.** Annual shoot elongation (cm/yr) of *Pinus pumila* from 2000 to 2003 in relation to its initial shoot length in 1999. Solid circles and solid line represent the control plot, and open circles and broken line represent the experimental plot in each diagram. Table 1 lists regression results for these data.

**FIGURE 4.** Relationship between shoot elongation of *Pinus pumila* and the diameter of the shoot’s bud formed in the previous year. Solid circles and solid line represent the control plots, and open circles and broken line represent the experimental plots. The regression equations are $Y = 1.94X - 1.59$ ($r^2 = 0.48, P < 0.001, n = 95$) and $Y = 2.21X - 1.59$ ($r^2 = 0.39, P < 0.001, n = 80$) for the control and experimental plots, respectively.
The results of this study contribute to a prediction of the effect of global warming on the growth of *P. pumila*. Thus, the higher daily maximum air temperature in the experimental plot than in the control plot in the third year. This result suggests that the higher daily maximum air temperature in the experimental plot compared to the control plot probably accelerated cell division of the apical meristem of *P. pumila* in the experimental plot (cf. Woodward, 1979), which contributes to an increase in shoot elongation. Thus, artificial warming is considered to promote shoot elongation of *P. pumila*.

Although this study showed the positive effect of artificial warming on shoot elongation of *Pinus pumila* on Mount Shogigashira, central Japan. The examined shoots originated from buds of diameters between 2.7 and 3.5 mm. Solid and open circles are the control and experimental plots, respectively. The number of observations was 19 and 40 for the control and experimental plots, respectively. The dagger symbol (†) in b is the boundary statistical level of significance (0.05 < P < 0.1).

FIGURE 5. Seasonal changes in (a) shoot length and (b) relative growth rate of shoots of *Pinus pumila* on Mount Shogigashira, central Japan. The examined shoots originated from buds of diameters between 2.7 and 3.5 mm. Solid and open circles are the control and experimental plots, respectively. The number of observations was 19 and 40 for the control and experimental plots, respectively. The dagger symbol (†) in (b) is the boundary statistical level of significance (0.05 < P < 0.1).

experimental plot than in the control plot in the third year. This result suggests that the higher daily maximum air temperature in the experimental plot compared to the control plot probably accelerated cell division of the apical meristem of *P. pumila* in the experimental plot (cf. Woodward, 1979), which contributes to an increase in shoot elongation. Thus, artificial warming is considered to promote shoot elongation of *P. pumila*.

Although this study showed the positive effect of artificial warming on shoot elongation of *Pinus pumila*, the results must be treated with caution because the effect of artificial warming cannot be separated from the effect of wind-speed reduction. The shoot elongation and scrub height of *P. pumila* are reduced at windswept sites (Okitsu and Ito, 1983; Kajimoto, 1993; Takahashi, 2003a). Net assimilation rates and growth rates of alpine-arctic plants are lower at windswept summits compared with sheltered hollows (Warren Wilson, 1959). Accordingly, in a strict sense, this study showed the effect of wind-speed reduction, not of artificial warming. However, the interpretation of the results of this study cannot be denied because wind decreases plant growth and production by reducing the leaf temperature (Jones, 1992), i.e., the cause of the increase in shoot elongation of *P. pumila* was the temperature in the wind-reduced experimental plots.

In conclusion, artificial warming promoted shoot elongation of *P. pumila* by increasing the daily maximum air temperature. Thus, the results of this study contribute to a prediction of the effect of global warming on the growth of *P. pumila* that is the most representative species in the alpine zone in Japan, i.e., global warming would increase the shoot growth of *P. pumila*.

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