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Author: Koichi Takahashi

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Koichi Takahashi
Department of Biology, Faculty of Science, Shinshu University, Matsumoto 390-8621, Japan. koichi@gipac.shinshu-u.ac.jp

Abstract
The effects of climatic conditions on the shoot elongation of alpine dwarf pine (Pinus pumila) were examined at its lower and upper altitudinal limits on Mt. Norikura (2500 and 2840 m a.s.l.) and Mt. Shogigashira (2640 and 2675 m a.s.l.) in central Japan. Altitudinal forest-structural changes were also described. Shoot elongation and stem height of P. pumila increased with decreasing altitude, but its abundance was markedly decreased at the altitudinal ecotone between the upper P. pumila zone and the lower Betula ermanii zone because of the suppression by tall B. ermanii. Thus, the lower altitudinal limit of P. pumila was probably determined by the competition with B. ermanii. The interannual variation in the shoot elongation of P. pumila was related to climatic conditions; long shoot length was associated with high summer temperatures of the previous year at both the upper and lower altitudinal limits on the two mountains. In addition, rates of the increase of shoot elongation in response to the increase of air temperature were not different between the upper and lower altitudinal limits. Thus, the increase of summer temperatures would enhance the growth of P. pumila from its upper to lower altitudinal limits. However, it is harder to predict the altitudinal distribution shift of P. pumila due to environmental change because its lower altitudinal limit is largely affected by competition with B. ermanii. Therefore, this study concluded that long-term monitoring of the population dynamics at the P. pumila–B. ermanii ecotone is necessary to predict the distribution shift of P. pumila.

Introduction
Global warming may affect the distribution shift of altitudinal vegetation zonation. The upper limits of plant distributions are thought to be due to physiological stresses such as cold and insufficient temperature for plant growth and survival, while the lower limits of plant distributions are probably due to competition with species in the lower adjacent vegetation zone (Woodward, 1988; Ohsawa, 1990). In terms of the effects of climatic conditions on the growth of trees, recent studies suggested that limiting effects of low precipitation and/or high temperature on the growth of trees are more significant near the lower altitudinal limits, while the importance of low temperature increases near the upper altitudinal limits (Ettl and Peterson, 1995; Gostev et al., 1996; Buckley et al., 1997; Solomina et al., 1999; Peterson and Peterson, 2001; Takahashi et al., 2001). However, there are few reports from Japan concerning the altitudinal difference in the growth responses to climatic conditions. Increased knowledge of responses to climatic conditions at both the upper and lower altitudinal limits is of great importance for understanding the effects of global warming on the altitudinal distribution shift of plant species, especially in Japan, where there are many high mountains.

In central Japan, dwarf pine scrub (Pinus pumila Regel) is distributed in the alpine zone above the timberlines formed mainly by a deciduous broad-leaved tree species (Betula ermanii Cham.) (Yoshino, 1978). The scrub height and shoot elongation of P. pumila decrease with increasing altitude or near wind-exposed ridges (Okitsu and Ito, 1983; Kajimoto, 1993), apparently as a result of unfavorable environments for the growth of P. pumila. Sano et al. (1977) intensively studied the interannual fluctuation of shoot elongation of P. pumila in relation to climatic conditions and showed that shoot elongation was positively correlated with summer temperatures of the previous year. Okitsu (1988) also reported that the interannual fluctuation of shoot elongation of P. pumila synchronized with one another within the same mountains, irrespective of altitude. Although there is concern about the distribution shift of P. pumila due to global warming (cf. Kajimoto et al., 1996), little information is available to demonstrate how shoot elongation of P. pumila responds to climatic conditions at its upper and lower altitudinal limits. In addition, few attempts have been made to describe the stand structure throughout the altitudinal distribution range of P. pumila, including the ecotone between the upper P. pumila zone and the lower B. ermanii zone. Examination of forest structure at the ecotone is necessary for understanding the formation of the lower altitudinal limit of P. pumila in relation to the competition with B. ermanii.

Thus, the purpose of this study was (1) to describe altitudinal changes in stem height and stem density of P. pumila and B. ermanii from the P. pumila–B. ermanii ecotone to the upper altitudinal limit of P. pumila, and (2) to examine what climatic conditions affect the shoot elongation of P. pumila at its upper and lower altitudinal limits.

Materials and Methods
STUDY SITE
This study was carried out on Mt. Shogigashira and Mt. Norikura in central Japan. The study site on Mt. Shogigashira
was located on the north-facing slope near the summit (2699 m a.s.l., 35°48′N, 137°50′E) in the Nishikoma Experimental Forest of Shinshu University. *P. pumila* was dominant near the summit. One deciduous broad-leaved tree species (*B. ermanii*) and three conifers (*Abies mariesii* Mast., *A. veitchii* Lindl., and *Tsuga diversifolia* Mast.) were distributed from ca. 1400 to 2640 m a.s.l. in the subalpine zone, but the upper altitudinal limits of the three conifers were ca. 100 m below the upper altitudinal limit of *B. ermanii*. The mean monthly air temperature at Senjojiki (2650 m a.s.l., ca. 3.5 km from the study area) ranged between −12.1°C (January) and 11.9°C (August), with the mean annual temperature at 0.8°C during 1990–1992 (Fukuyo et al., 1998). On the east-facing slope of Mt. Norikura (3026 m a.s.l., 36°06′N, 137°33′E), *P. pumila* was distributed from ca. 2500 m a.s.l. to the near summit. *B. ermanii* and four conifers (*A. veitchii*, *A. mariesii*, *T. diversifolia*, and *Picea jezoensis* var. *hondoensis* Rehder) were dominant between ca. 1600 and 2500 m a.s.l. in the subalpine zone, but *B. ermanii* dominated over the four conifers near the timberline on Mt. Norikura. The mean annual temperature at 2500 m a.s.l., the lower altitudinal limit of *P. pumila*, was estimated as −0.5°C from temperatures recorded at Nagawa Weather Station (1068 m a.s.l., ca. 11 km from the study area) using the lapse rate of −0.6°C per each +100 m altitude (cf. Hasegawa, 1970). The mean monthly temperatures in the coldest month of January and the warmest month of August were estimated as −12.1 and 11.7°C, respectively.

**FIELD METHODS**

Interannual fluctuation of shoot elongation of *P. pumila* was examined at the lower and upper altitudinal limits on Mt. Shogigashira (2640 and 2675 m a.s.l.) and Mt. Norikura (2500 and 2840 m a.s.l.) in September 2001. Although small saplings of *P. pumila* were distributed in the *B. ermanii* zone, the density of *P. pumila* was low. Therefore, the lower altitudinal limit of the *P. pumila* zone was defined as the upper altitudinal limit of the *B. ermanii* zone in this study (i.e., the lower altitudinal limit of *P. pumila* does not mean the position of the lowest individual *P. pumila* tree). Annual shoot elongation rate was measured from bud scars for at least 20 yr for each tree. (A simple correlation test was used to show what climatic conditions affect shoot elongation of *P. pumila* at each of the upper and lower altitudinal limits on each mountain. The nearest weather stations to Mt. Norikura and Mt. Shogigashira were Nagawa (36°05′N, 137°41′E, 1068 m a.s.l., ca. 11 km from the study area) and Ina (35°48′N, 137°59′E, 674 m a.s.l., ca. 13 km from the study area), respectively. However, the available meteorological data at Nagawa and Ina began in 1979 and 1993, respectively (i.e., the recording periods at the two weather stations were shorter than the shoot length chronology of *P. pumila*). A long-term record was available at Matsumoto Weather Station (36°15′N, 137°58′E, 610 m a.s.l., ca. 35 to 50 km from the two study sites). Therefore, I used the monthly mean temperature and monthly sum of precipitation recorded at Matsumoto for the correlation test in this study. The shoot elongation of *P. pumila* at each site was compared with the meteorological data from the beginning of the previous growth period to the end of the current growth period. The growing season of *P. pumila* at each site on the two mountains was determined as June to September because the mean monthly temperature exceeded 5°C, an effective heat for plant growth (Kira, 1948), during this period.

**Results**

Saplings of the two conifers (*Abies veitchii* and *A. mariesii*) were found in the *P. pumila*–*B. ermanii* ecotone on Mt. Shogigashira, but their abundance was negligible. *B. ermanii* and *P. pumila* were distributed exclusively from each other (Figs. 1, 2a). The stem height of *B. ermanii* gradually decreased with increasing altitude, and its density was markedly lower at 35 m from the lower side of the plot (ca. 2645 m a.s.l.) (Figs. 2a, 2b). More than half of *B. ermanii* showed the multistemmed form with apparent scars of past breakage on the main trunk, probably because of snow pressure. *P. pumila* dominated over *B. ermanii* above the distance 35 m (Fig. 2a). The stem height of *P. pumila* was highest between 35 and 55 m (i.e., above the upper altitudinal limit of *B. ermanii*) and gradually decreased with increasing altitude (Fig. 2b). The stem height of *P. pumila* increased again at about the distance 90 m because this site was relatively leeward compared with the site between the distances 70 and 90

**DATA ANALYSIS**

The 10 × 35 m plot was divided into seven 10 × 5 m quadrats. Mean stem height, stem density, and mean shoot elongation rate of *P. pumila* were calculated for each 10 × 5 m quadrat to reveal the altitudinal forest-structural changes. However, this quadrat size of 10 × 5 m was not large enough for *B. ermanii* because of the low density (a few trees per this quadrat size). Thus, the stem density of *B. ermanii* was calculated for each 10 × 10 m quadrat, instead of the 10 × 5 m quadrat. Although the size of the uppermost quadrat was 10 × 5 m, there were no trees of *B. ermanii* in this quadrat because this quadrat was located in the *P. pumila* zone. Most of *B. ermanii* reached to canopy layer and its saplings were rare in this ecotone (i.e., the variation in stem height was rather small). Therefore, the mean stem height of *B. ermanii* was calculated for each 10 × 5 m quadrat. The shoot length chronology of *P. pumila* at each site (i.e., the upper or lower altitudinal limit on Mt. Norikura or Mt. Shogigashira) was calculated by averaging the shoot length among the examined *P. pumila* trees in each year, according to Sano et al. (1977). The shoot length chronology at each site was determined from 1975 to 2001 (n = 27). A simple correlation test was used to show what climatic conditions affect shoot elongation of *P. pumila* at each of the upper and lower altitudinal limits on each mountain. The nearest weather stations to Mt. Norikura and Mt. Shogigashira were Nagawa (36°05′N, 137°41′E, 1068 m a.s.l., ca. 11 km from the study area) and Ina (35°48′N, 137°59′E, 674 m a.s.l., ca. 13 km from the study area), respectively. However, the available meteorological data at Nagawa and Ina began in 1979 and 1993, respectively (i.e., the recording periods at the two weather stations were shorter than the shoot length chronology of *P. pumila*). A long-term record was available at Matsumoto Weather Station (36°15′N, 137°58′E, 610 m a.s.l., ca. 35 to 50 km from the two study sites). Therefore, I used the monthly mean temperature and monthly sum of precipitation recorded at Matsumoto for the correlation test in this study. The shoot elongation of *P. pumila* at each site was compared with the meteorological data from the beginning of the previous growth period to the end of the current growth period. The growing season of *P. pumila* at each site on the two mountains was determined as June to September because the mean monthly temperature exceeded 5°C, an effective heat for plant growth (Kira, 1948), during this period.
m. The altitudinal change in the shoot elongation of *P. pumila* corresponded well to that in stem height (Fig. 2c).

The annual shoot elongation of *P. pumila* fluctuated at both the upper and lower altitudinal limits on Mt. Norikura and Mt. Shogigashira (Fig. 3). Although the shoot elongation was always higher at the lower altitudinal limits than at the upper altitudinal limits on the two mountains, the interannual fluctuation in the shoot elongation showed a similar trend between the upper and lower altitudinal limits on each mountain ($r = 0.591$, $P = 0.001$ for Mt. Norikura, and $r = 0.666$, $P < 0.001$ for Mt. Shogigashira).

The monthly mean temperatures (July to September or July to October) of the previous year were positively correlated with the shoot elongation rates at both the upper and lower altitudinal limits on the two mountains (Fig. 4). The January and March temperatures of the current year were also positively correlated with the shoot elongation rates of *P. pumila* at the upper and lower altitudinal limits, respectively, on Mt. Norikura (Fig. 4). In addition, the shoot elongation rates were negatively correlated with precipitation (monthly sum) in summer of the previous year (July or August, or both), except for the upper altitudinal limit on Mt. Norikura (Fig. 4).

To compare shoot elongation rates of *P. pumila* in response to air temperature between the upper and lower altitudinal limits, mean temperature between July and September was used as an independent variable because the shoot elongation rates were positively correlated with monthly mean temperatures during this period at each site. The shoot elongation rate of *P. pumila* at its lower altitudinal limit was higher than that at its upper altitudinal limit at any mean temperature between July and September ($F_{1,51} = 123.4$, $P < 0.001$ for Mt. Norikura, and $F_{1,51} = 84.3$, $P < 0.001$ for Mt. Shogigashira). Furthermore, the slopes of the regressions were not different between the upper and lower altitudinal limits of *P. pumila* on each mountain ($P > 0.05$, Fig. 5). This indicates that the rates of increase in shoot elongation of *P. pumila* in response to the increase of summer temperatures were not different between its upper and lower altitudinal limits on the two mountains.

**FIGURE 1.** The Pinus pumila–Betula ermanii ecotone on Mt. Shogigashira in central Japan on 5 October 2002. Pinus pumila (dark gray) and Betula ermanii (light gray) dominate the upper and lower parts of the slope, respectively. The leaves of B. ermanii have turned completely yellow.

**Discussion**

The stem height and the shoot elongation of *P. pumila* decreased with increasing altitude, and long shoot length of *P. pumila* was associated with high summer temperatures of the previous year, irrespective of the upper or lower altitudinal limit. Shorter shoot length at the upper altitudinal limit than at the lower altitudinal limit was probably attributable to its wind-exposed environments near the summit because the altitudinal difference between the upper and lower altitudinal limits of *P. pumila* on Mt. Shogigashira was only 35 m. It is known that shoot growth of alpine plants is reduced by wind (Kajimoto, 1993; Fukuyo et al., 1998), probably due to the decrease of leaf temperature by wind (Jones, 1992). Wind also possibly affects plant growth by winter desiccation at timberlines (Hadley and Smith, 1983, 1986; Wardle, 1968, 1985). However, the needles of *P. pumila* are hardly damaged by winter desiccation (Maruta et al., 1996), because *P. pumila* is completely covered with snow in winter (Okitsu and Ito, 1983) and because *P. pumila* has a high freezing tolerance up to $-70^\circ$C (Sakai and Kurahashi, 1975). Thus, winter desiccation does not strongly affect the shoot growth of *P. pumila* even in wind-exposed environments. Although Sano et al. (1977) showed that summer temperatures regulated shoot elongation of *P. pumila*, the present study revealed that this relationship is applicable to the whole of its altitudinal distribution range.

The growth responses of several tree species to climatic conditions have been examined in the subalpine zone on Mt. Norikura. Fujiwara et al. (1999) found a positive correlation between August temperature and the tree-ring width in Abies mariesii, but not in *Picea jezoensis* var. hondoensis at 2000–2200 m a.s.l. (the upper zone of their distribution). In contrast, Takahashi et al. (unpublished data) showed negative correlations between the August temperature and the tree-ring widths of *A. veitchii* and *B. ermanii* at 1600 m a.s.l. (the lower limit of their distribution), while positive correlations of August precipitation were found in the two species. It seems that importance of summer temperatures to the tree growth decreases with decreasing altitude at least on the scale between 1600 and 2840 m a.s.l. on Mt.
Norikura. Therefore, the similar responses in the shoot elongation to climatic conditions between \( P. \) \( pumila \) growing at its upper and lower altitudinal limits are ascribed to its narrow altitudinal distribution range in the alpine zone.

The abundance of \( P. \) \( pumila \) was markedly decreased at the \( P. \) \( pumila-B. \) \( ermanii \) ecotone on Mt. Shogigashira, although the stem height and shoot elongation of \( P. \) \( pumila \) were highest at its lower altitudinal limit. In addition, no negative correlations between summer temperatures and the shoot elongation of \( P. \) \( pumila \) were detected even at its lower altitudinal limits. These suggest that \( P. \) \( pumila \) physiologically can grow at lower altitude than the current lower altitudinal limit, but tall \( B. \) \( ermanii \) suppresses the growth and invasion of \( P. \) \( pumila \) at lower altitude. Therefore, the lower altitudinal limit of \( P. \) \( pumila \) seems to be determined by the competition with \( B. \) \( ermanii \). Although increase of summer temperatures enhances the growth of \( P. \) \( pumila \) throughout much of its altitudinal distribution, the growth of \( B. \) \( ermanii \) at its upper altitudinal limit also may be enhanced by the increase of the summer temperatures. The increase of crown area of the present \( B. \) \( ermanii \) trees may suppress the growth of more trees of \( P. \) \( pumila \) in the \( P. \) \( pumila-B. \) \( ermanii \) ecotone, which in turn brings about the upward distribution shift of \( P. \) \( pumila \) to some extent.

However, the possible effects of future global warming on the altitudinal distribution of \( P. \) \( pumila \) are harder to predict; i.e., the upward shift of \( P. \) \( pumila \) scrub due to competition with \( B. \) \( ermanii \) is uncertain for the following two reasons. First, \( B. \) \( ermanii \) is a typical light-demanding species with very small seeds and cannot establish unless mineral soil is exposed in sunlit conditions such as canopy gaps (Seiwa and Kikuzawa, 1996). \( P. \) \( pumila \) densely covers the forest floor and regenerates by vegetative growth such as layering (Kajimoto, 1992). The repetitive vegetative growth allows long-term persistence of \( P. \) \( pumila \), which prevents the seedling establishment of \( B. \) \( ermanii \). Kajimoto et al. (1996) also pointed out the importance of habitat competition between \( P. \) \( pumila \) and other subalpine conifers on the distribution shift of \( P. \) \( pumila \). Second, Okitsu and Ito (1989) suggested that the altitudinal distribution range of \( P. \) \( pumila \) is associated with strong wind, heavy snow accumulation, and rocky substrate rather than with air temperature because the \( P. \) \( pumila \) zone is formed near mountain summits, irrespective of the height of the mountains (ranging between ca. 1050 and 2150 m a.s.l. in northern Japan). This indicates that the altitudinal position of the \( P. \) \( pumila-B. \) \( ermanii \) ecotone is not determined by air temperature alone. Therefore, the effects of global warming on the distribution shift of \( P. \) \( pumila \) will be complex.
FIGURE 4. Correlation coefficients between the annual shoot elongation of Pinus pumila and the monthly climatic conditions (monthly sum of precipitation and monthly mean temperature) at the upper and lower altitudinal limits on Mt. Norikura (2840 and 2500 m a.s.l.) and Mt. Shogigashira (2675 and 2640 m a.s.l.), central Japan. Shaded bars indicate significant correlation (P < 0.05 by Pearson correlation test).
This study concluded that the increase of the summer temperatures enhances the growth of *P. pumila* throughout its altitudinal distribution range, and the formation of the lower altitudinal limit of *P. pumila* largely depends on competition with *B. ermanii*, which forms the lower adjacent vegetation zone. Therefore, long-term monitoring of the population dynamics at the *P. pumila*-*B. ermanii* ecotone is necessary to predict the distribution shift of *P. pumila* scrub due to environmental change.

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