Introduction

Upper zone of subalpine forests in central Japan is dominated mainly by Betula ermanii Cham., Abies mariesii Mast. and A. veitchii Lindl. (Yoshino 1978). The upper distribution limit of B. ermanii is higher than that of the two Abies species to some extent. A dwarf pine (Pinus pumila Regel) is distributed in the alpine zone above the upper distribution limit of B. ermanii, and therefore, alpine timberline is an altitudinal ecotone between the B. ermanii zone and the P. pumila zone (Takahashi 2003).

Climatic conditions such as low temperature and a short growing season around timberline are generally severe for plant growth and survival. Therefore, many researchers have examined the timberline dynamics in relation to climatic conditions (e.g. Wardle 1968; Okitsu 1984; Kullman 1993; Taylor 1995; Gostev et al. 1996). For example, the growth of several conifer species is positively correlated with summer temperature near or above the timberline in central Japan, while summer rainfall has no or negative influence on the tree growth there (Sano et al. 1977; Okitsu 1988; Fujiwara et al. 1999; Takahashi 2003). Thus, it is suggested that water limitation is weak at the timberline in central Japan. However, there are few ecophysiological studies to examine whether or not water limitation is weak for B. ermanii and P. pumila growing at the timberline. Increased knowledge of water regulation of both species is of great importance for understanding the growth response to climatic conditions at the timberline in central Japan.

Stomatal conductance of leaves decreases in response to water limitation and/or high vapor pressure deficit of air (or low relative humidity) for the control of water loss from plants (e.g. Granier and Loustau 1994; Kallarackal and Soman 1997; Martin et al. 1997). For example, midday stomatal closure is often observed in clear-sky days because of an increase in vapor pressure deficit (Jones and Muthuri 1984; Le Thiec and Dixon 1996). Therefore, the examination of diurnal variations in stomatal conductance provides useful information to elucidate water regulation of B. ermanii and P. pumila at...
the timberline. Furthermore, rainfall events strongly influence stomatal conductance by increasing soil water content. However, available information is still limited about the diurnal variations in the stomatal conductance of *B. ermanii* and *P. pumila*, coupled with the climatic observation. Therefore, the objective of this study was to examine the diurnal variations in the stomatal conductance of *B. ermanii* and *P. pumila* at the timberline on Mt. Shogigashira in central Japan, with the observation of summer rainfall, air temperature and relative humidity of air.

### Materials and methods

This study was carried out near the summit of Mt. Shogigashira (2,699 m above sea level, 35° 48’N, 137° 50’E) in the Nishikoma Experimental Forest of Shinshu University, central Japan. The mean monthly air-temperature at Senjojiki (2,650 m a.s.l., ca. 3.5 km from the study area) ranged between −12.1°C (January) and 11.9°C (August), and the mean annual temperature was 0.8°C during 1990–1992 (Fukuyo et al. 1998). The maximum snow depth around the study area was ca. 3 m (Kajimoto 1989). The prevailing winds come from the west in this region (Fukuyo et al. 1998).

*Pinus pumila* was distributed only near the summit of Mt. Shogigashira. Its altitudinal distribution ranged from the timberline (2,630 m a.s.l.) to the summit (2,699 m a.s.l.). On the contrary, *B. ermanii* was widely distributed from ca. 1,400 m to 2,630 m a.s.l. (timberline) on the east-facing slope of Mt. Shogigashira. This study was conducted at the timberline, which was the altitudinal ecotone between the *B. ermanii* zone and the *P. pumila* zone. The canopy height of *B. ermanii* and that of *P. pumila* were ca. 2.8 m and 1.2 m, respectively, at this timberline (Takahashi 2003).

Air temperature and relative humidity were automatically recorded at the front of the Nishikoma hut near the summit of Mt. Shogigashira at 1-hour intervals from August 7 to October 4 in 2001, by using a thermometer coupled with a humidity sensor (HOB0 H 8 Pro, Onset Computer Corp., Pocasset, MA, USA). The thermometer was set within a radiation shield to prevent exposure to direct solar radiation. Rainfall was also measured by using a rain gauge (Model 7852 M, Davis Corp., USA) with a data logger (HOB0 Event, Onset Computer Corp., Pocasset, MA, USA).

The diurnal variations in the stomatal conductance of *B. ermanii* and *P. pumila* were measured on four days in total (August 14, 25 and September 1, 14 in 2001) by using a null balance porometer (Model Li-1600 with a Model 1600–02 square chamber [2-cm×2-cm], Li-Cor, Lincoln, NE, USA). The porometer measurements were performed from approximately 07:00 to 17:00 hours at about 2-hour intervals, on five replicates for each of *P. pumila* and *B. ermanii* at each measurement time. Leaves were chosen from the top of the canopy for the measurement of each species. Photosynthetic photon flux density (PPFD) was also measured at the porometer measurement.

The current-year shoots of *P. pumila* elongate during June and July, and their needle longevity is ca. 4 years (Kajimoto 1993). The light-saturated photosynthetic rate ($A_{\text{max}}$) of *P. pumila* is higher in the 1-year-old needles than in the other needles by mid-August, but $A_{\text{max}}$ of the current-year needles is higher than $A_{\text{max}}$ of the other older needles thenceforth (Kajimoto 1990), which suggests that current-year needles have fully developed by mid-August. Thus, the current-year needles of *P. pumila* were thought to be mature enough for the measurement of this study because the porometer measurement was started from mid-August. It is important to measure not only the stomatal conductance of the current-year needles but also that of the other older needles for the examination of the water use at the individual-tree level. However, for the practical reason, the porometer measurements of *P. pumila* were conducted only for the current-year needles.

As for the porometer measurement of *P. pumila*, five current-year needles from one fascicle were placed in the chamber, and their stomatal conductance was measured as one replicate. Needle diameter was measured for part of the needles used for the porometer measurements by using a digital caliper. The average diameter of needles was 0.61 mm (n = 32). Total
surface area of five needles inside the chamber was calculated as the product of the number of needles (i.e. five needles) and the surface area per single needle inside the chamber. The surface area of a single needle inside the chamber was estimated as a cylinder ($\pi \times 0.061 \times 2 \text{ cm}^2$). The stomatal conductance of $P. \text{pumila}$ was calculated on the basis of the actual leaf area inside the chamber.

**Results and discussion**

Weather conditions at the timberline on Mt. Shogigashira were usually clear sky in early morning, but foggy or cloudy from late morning or noon during early August and mid-September in 2001. Rainfall also frequently occurred in late afternoon or evening. Rainfall (>1 mm/day) was observed in total 20 days from August 7 to September 15 (total 40 days), and the total rainfall during this period was 450.4 mm (Fig. 1). Thus, entire clear-sky days were infrequent at the timberline on Mt. Shogigashira during the examined period.

Stomatal conductance was measured during the four days (August 14, 25 and September 1, 14). However, the measurement could not be conducted throughout the daytime on September 14 because of the rainfall from the morning (Fig. 1). The diurnal changes in PPFD on August 14 were similar to those on September 1 (Fig. 2). PPFD was high in the early morning on both days, but had decreased by 10:00 hours due to the occurrence of fog (Fig. 2). On the contrary, the diurnal changes in PPFD on August 25 were different from those on the other two days (Fig. 2). PPFD increased from the early morning to the noon on August 25, but abruptly decreased at the noon by the occurrence of fog. However, high PPFD was observed again at around 15:00 hours because of the temporal clearance of fog.

The diurnal variations in the stomatal conductance of $B. \text{ermanii}$ and $P. \text{pumila}$ were not large during the three days (Fig. 3). The stomatal conductance of $P. \text{pumila}$ on August 25 was tended to be more variable than that on the other two days (Fig. 3), although the reason was unknown. Thus, this study showed that stomatal closure of $B. \text{ermanii}$ and $P. \text{pumila}$ seems to occur infrequently at the timberline on Mt. Shogigashira, at least, during the examined period because of foggy and rainy climatic conditions. However, intra- and interannual fluctuation of climatic conditions may be large. For example, the total rainfall between August 7 and September 15 in 2002 was only one-thirds of the rainfall observed during the same period in 2001 at this timberline (Takahashi unpublished). In addition, midday stomatal closure was observed in $P. \text{pumila}$ on an entirely clear-sky day in summer of 2002 (Takahashi unpublished). Ishida et al. (2001) also reported the importance of stomatal control for $P. \text{pumila}$ during snow-melting period. Solar radiation is high, but soil temperature is still low (ca. 0°C) at this period (Maruta et al. 1996). $Pinus \text{pumila}$ needs to avoid needle desiccation during the snow-melting season because $P. \text{pumila}$ hardly absorbs soil water. Therefore, the results of this study do not mean that stomatal control is less important for $B. \text{er-}

Fig. 1. Seasonal changes in air temperature (upper figure) and daily rainfall (lower figure) recorded near the summit of Mt. Shogigashira in central Japan. The upper figure shows the daily range between the maximum and minimum air-temperatures (vertical bar) with the daily mean temperature (solid circle). Arrows in the lower figure indicate the days that porometer measurement was performed.
Fig. 2. Diurnal changes in air temperature (open circle) and relative humidity (RH, solid circle) on August 14, 25 and September 1 near the summit of Mt. Shogigashira in central Japan (upper figures), and diurnal changes in photosynthetic photon flux density (PPFD) at the porometer measurement for *Betula ermanii* (open circle) and *Pinus pumila* (solid circle) (lower figures). The lower figure shows the observed range between the maximum and minimum PPFD (vertical bar) with the mean PPFD (circle) at each measurement time.

Fig. 3. Diurnal changes in stomatal conductance in *Betula ermanii* (upper) and *Pinus pumila* (lower) on August 14, 25 and September 1 at the timberline on Mt. Shogigashira in central Japan. The mean value (solid circle) with the observed range between the maximum and minimum values (vertical bar) was shown. Note that ordinate scales are different between the upper and lower figures.
manii and *P. pumila* at this timberline. Further studies are necessary to reveal how these two species respond to climatic conditions in terms of the stomatal control for water regulation by the examination of the stomatal conductance in various climatic conditions.

**Acknowledgements**

This study was partially supported by a grant from the Ministry of Education, Science, Sports and Culture of Japan (No. 13780418).

**References**


Taylor, A.H. 1995. Forest expansion and climate change in the mountain Hemlock (*Tsuga mertensiana*) zone, Lassen Volcanic National Park,


(Received January 21, 2003; accepted May 18, 2003)