Climatic factors affecting the tree-ring width of *Betula ermanii* at the timberline on Mount Norikura, central Japan

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Tree-ring width chronology of Betula ermanii was developed at the timberline (2400 m a.s.l.) on Mount Norikura in central Japan, and climatic factors affecting the tree-ring width of *B. ermanii* were examined. Three monthly climatic data were used for the analysis (i.e., mean temperature, insolation duration, and sum of precipitation). The tree-ring width of *B. ermanii* was negatively correlated with December and January temperatures and with January precipitation prior to the growth. However, why high temperatures and much snow in winter had negative effects on the growth of B. ermanii is unknown. The tree-ring width was positively correlated with summer temperatures during June to August of the current year. The tree-ring width was also positively correlated with the insolation duration in July of the current year. On the contrary, the tree-ring width was negatively correlated with summer precipitation during July to September of the current year. However, these negative correlations of summer precipitation do not seem to be independent of temperature and insolation duration, i.e., much precipitation reduced the insolation duration and temperature. Therefore, it is suggested that much insolation duration and high temperature due to less precipitation in summer of the current year increase the radial growth of *B. ermanii* at the timberline. The results were also compared with those of our previous study conducted in the lower altitudinal limit of *B. ermanii* (approximately 1600 m a.s.l.) on Mount Norikura. This study suggests that climatic factors increasing the radial growth of B. ermanii differ between its upper and lower altitudinal limits.

Key words: *Betula ermanii*; climatic conditions; dendrochronology; Mount Norikura; timberline; tree-ring width chronology.

INTRODUCTION

Timberlines are the most severe climatic conditions such as low temperature, strong winds and short growing season for plants along altitudinal gradients, and therefore, the regeneration of trees at the timberlines is supposed to be sensitive to climatic changes (e.g., Briffa & Osborn 1999; Kusnierczyk & Ettl 2002; Lloyd & Fastie 2002; Chapin et al. 2004; Daniels & Veblen 2004; Dullinger et al. 2004). For example, some researchers have discussed that frequent seedling establishment occurred in warmer and/or more mesic years near the timberlines (Kullman 1986; Taylor 1995; Kajimoto et al. 1998; Camarero & Gutiérrez 1999; Gervais & MacDonald 2000). In addition, many dendrochronological studies have revealed that radial growth of trees near the timberlines increased in ameliorated years with higher temperatures than the average (Ettl & Peterson 1995; Gostev et al. 1996; Buckley et al. 1997; Peterson & Peterson 2001; Wilson & Hopfmueller 2001). Trees may respond to climatic conditions more quickly in growth rather than seedling establishment. Thus, the growth is a useful indicator to examine how climatic conditions affect regeneration of trees at the timberlines. Although many researchers investigated the effects of climatic conditions on the tree growth at the timberlines in North America and Europe (e.g., Kienast et al. 1987; Rolland et al. 1998; Szeicz & MacDonald 1995; Paulsen et al. 2000; Carrer & Urbinati 2004), there are few studies reported in Japan. Increased knowledge of the climate-growth relationships at the timberlines is of great importance for understanding the effects of global warming on the tree regeneration at the timberlines, especially in Japan, where there are many high mountains.

Betula ermanii Cham., a deciduous broad-leaved tree species, is widely

distributed in subalpine coniferous forests in Japan (Tatewaki 1958; Miyawaki 1985). *B. ermanii* dominates over coniferous species in the upper zone of subalpine coniferous forests, and often forms pure stand near the timberlines. Therefore, *B. ermanii* is one of representative tree species at the timberlines in Japan. Takahashi *et al.* (2003) examined the effects of climatic conditions on the tree-ring width of *B. ermanii* in its lower altitudinal limit on Mount Norikura in central Japan. They suggested that less precipitation combined with high temperature in the hottest month of August reduced the tree-ring width of *B. ermanii*. Climatic conditions change with altitude, i.e., air temperature is lower and precipitation is greater at a higher altitude. Therefore, it is expected that climatic factors affecting the tree-ring width of *B. ermanii* are also different between the lower altitudinal limit and the timberline (i.e., the upper altitudinal limit). However, there are no studies that compared the growth responses of *B. ermanii* to climatic conditions between its upper and lower altitudinal limits.

The purpose of this study was to examine what climatic factors affect the tree-ring width of *B. ermanii* at the timberline on Mount Norikura in central Japan by using the dendrochronological technique. We also compared the results of this study with those of our previous study (Takahashi *et al.* 2003), conducted in the lower altitudinal limit of *B. ermanii* on Mount Norikura.

MATERIALS AND METHODS

Study site

This study was carried out on Mount Norikura (36°06'N, 137°33'E, 3026 m above sea level) in central Japan. *B. ermanii* and four conifers (*Abies veitchii* Lindl., *Abies*

mariesii Mast., *Picea jezoensis* var. *hondoensis* Rehder, and *Tsuga diversifolia* Mast.) were dominants between approximately 1600 m and 2500 m a.s.l. in the subalpine zone. *B. ermanii* dominated over the four conifers in the upper zone of the subalpine coniferous forests. Alpine dwarf pine scrub (*Pinus pumila* Regel) was distributed above the subalpine zone (Takahashi 2003*a*). In this study, the timberline was defined as the boundary between the subalpine zone dominated by tall trees and the alpine zone dominated by dwarf pine.

The study site was located at about 100 m below the forefront of the timberline in elevation (i.e., 2400 m a.s.l.) on the east slope of Mt. Norikura. This slope was the same slope that our low altitudinal study site (1600 m a.s.l.) was located (Takahashi *et al.* 2003). The horizontal distance between the two study sites was 4.5 km. Trunk height of canopy trees ranged between 10 to 15 m. Mean annual temperature at this study site was estimated to be 0.1°C from the temperature recorded at Nagawa Weather Station (1068 m a.s.l., approximately 11 km from the study site) using the standard lapse rate of -0.6°C for each +100 m altitude. Mean monthly temperatures in the coldest month of January and the hottest month of August were estimated to be -11.5 and 12.3°C, respectively.

Sampling and measurement

Nineteen trees were cored from stems at breast height (1.3 m), with two cores from each tree, during July to August 2002. However, only one core was sampled from one tree of the 19 trees (i.e., total 37 cores were sampled). Stem diameter at breast height was measured for each tree. All cores were dried, mounted, sanded, and then the tree-ring

widths were measured at a precision of 0.01 mm under a microscope by using a sliding measurement stage (TA Tree-Ring System, Velmex Inc., NY, USA) linked to a computer. The tree-ring boundaries of *B. ermanii* were distinguishable by their small diameter cells (terminal parenchyma).

Chronology development

All cores were cross-dated visually by matching characteristic wide and narrow rings that were synchronous within sample trees. Visual cross-dating was statistically verified by using the COFECHA program (Holmes 1983, 1994) that tests each individual series against a master dating series (mean of all series) on the basis of correlation coefficients. Of 37 cores, five cores that had low correlations with other cores were eliminated from further analyses.

Growth of trees is affected not only by climatic factors but also by age, disturbance and competition between neighboring trees. To reduce variations caused by such non-climatic factors, all raw ring-width series were standardized by fitting smoothing splines (Cook & Peters 1981) with a 50% frequency-response cutoff of 40 years. This procedure was done by using the ARSTAN program (Cook 1985; Holmes 1994). After standardizing each individual series, the tree-ring width chronology of *B*. *ermanii* was obtained by averaging the standardized individual series in each year. We used at least five cores to make the tree-ring width chronology in each year.

Statistical analysis

Climatic factors affecting the tree-ring width of B. ermanii were investigated. Three

monthly climatic data were used for the analysis (i.e., mean temperature, insolation duration, and sum of precipitation). The nearest weather station to the study site was Nagawa (1068 m a.s.l., approximately 11 km from the study site). However, the available meteorological data at Nagawa was rather short (i.e., the observation started in 1979). On the contrary, a long-term record was available at Matsumoto (610 m a.s.l., approximately 40 km from the study site). The available meteorological data at Matsumoto began in 1898 for temperature and precipitation, and in 1899 for insolation duration. The correlations of climatic data between the two stations were highly significant (Takahashi *et al.* 2003). Thus, we used the long-term climatic data recorded at Matsumoto.

Relationships between climate and tree-ring width were analyzed using a simple correlation analysis. The analysis was done by using the climatic data from the start of the previous growing season to the end of the current growing season because the growth of many tree species is affected not only by the climatic conditions of the current year but also by those of the previous year (cf. Fritts 1962; Sano *et al.* 1977; Okitsu 1988; Eshete & Ståhl 1999; Takahashi *et al.* 2001; Speer *et al.* 2004). The approximate growing season at this study site (2400 m a.s.l.) was estimated to be June to September because the mean monthly temperatures exceeded 5 °C, effective heat for plant growth (Kira 1948), during this period. Thus, the simple correlation analysis was performed using the climatic data from June of the previous year to September of the current year (16 months in total) for the period 1900–2001 (n = 102).

RESULTS

Of 19 trees (37 cores) of B. ermanii, 17 trees (32 cores) were successfully cross-dated, and were used to develop a master chronology having good correlations between trees (Table 1). The span of the tree-ring width chronology of *B. ermanii* was 172 years (Table 1, Fig. 1). The first-order autocorrelation, as a measure of the influence of the previous year's growth on the growth in the current year, was 0.34 (Table 1). The mean sensitivity and standard deviation, as measures of interannual variation in tree-ring width, were 0.23 and 0.25, respectively (Table 1). These values were higher than those of *B. ermanii* in its lower altitudinal limit (approximately 1600 m a.s.l.) of this mountain, i.e., the mean sensitivity and standard deviation were 0.13 and 0.11, respectively. The mean correlation coefficient between B. ermanii individual trees at the timberline was also higher than that in the lower altitudinal limit (0.41 versus 0.13, Table 1). These differences in the basic statistics between the two sites indicate that B. ermanii grew more synchronously and the interannual variation in the tree-ring width was higher at the timberline than in the lower altitudinal limit on Mount Norikura. Probably, severe climatic conditions reflected these growth traits at the timberline. Furthermore, the tree-ring width indices were not significantly correlated between the timberline and the lower altitudinal limit of *B. ermanii* for the period 1943–2000 that corresponded to the span of the chronology in the lower altitudinal limit (r = 0.17, P = 0.20, n = 58, Fig. 1). The difference in growth patterns between the timberline and the lower altitudinal limit appears to reflect the influence of distinct climatic factors on the tree-ring width of B. ermanii.

Correlation coefficients indicate that temperatures of several months were

significantly correlated with the tree-ring width index of *B. ermanii* at the timberline (Fig. 2). December and January temperatures prior to the growth were negatively correlated with the tree-ring width index (P < 0.05, Fig. 2). In addition, January precipitation prior to the growth also showed a negative correlation. During the growing season, the current-year summer temperatures from June to August were positively correlated with the tree-ring width index (P < 0.05, Fig. 2). The tree-ring width index was also positively correlated with the July insolation duration in the current year (P < 0.05, Fig. 2). On the contrary, the tree-ring width index was negatively correlated with the tree-ring width index the current-year summer precipitation from July to September (P < 0.05, Fig. 2). However, these negative correlations of summer precipitation do not seem to be independent of temperature and insolation duration because of the inverse relationships of precipitation with temperature and with insolation duration during the growing season, except for September temperature (Table 2).

DISCUSSION

The correlation analysis showed that the tree-ring width of *B. ermanii* was negatively correlated with December and January temperatures and with January precipitation prior to the growth. However, the underlying mechanism that high temperatures and much snow in winter had negative effects on the tree-ring width of *B. ermanii* is unclear. The correlation analysis showed the positive correlations with summer temperatures and insolation duration, and the negative correlations with summer precipitation in the current year. However, it is harder to consider that much precipitation in summer caused diameter growth reduction of *B. ermanii* by providing much soil water. Taking account

of the negative correlations of precipitation with the insolation duration and temperature, it is plausible that the tree-ring width of *B. ermanii* at the timberline was decreased by less insolation duration and low temperature due to frequent rain events in the summer of current year.

Precipitation associated with cloud cover decreases light energy and air temperature, which in turn brings about the reduction of the photosynthetic production of plants in mesic region. Although most dendrochronological and/or dendroclimatological studies have not examined the effects of insolation duration on the tree-ring width, many researchers reported that tree growth was limited by low summer temperatures in high altitudes and high latitudes (Oberhuber et al. 1997; MacDonald et al. 1998; Gervais & MacDonald 2000; Mäkinen et al. 2000; Grudd et al. 2002; Helama et al. 2002; Kirdyanov et al. 2003; Takahashi 2003a; Barber et al. 2004; Takahashi 2005, 2006). Low temperatures reduce the tree growth through several ways. Photosynthetic rates of plants are generally temperature dependent, and therefore, low temperatures during the growing season reduce the photosynthetic production for alpine and subalpine plants (DeLucia & Smith 1987; Körner 1999). Latewood development is also immature under low temperature conditions (Gindl 1999). Furthermore, Gostev et al. (1996) and Solomina et al. (1999) showed that early summer temperature in the current year was positively correlated with the tree-ring width of Dahurican larch (Larix cajanderi Mayr.) in the Kamchatka Peninsula, the Russian Far East. Growth periods for plants are rather short at timberlines or high elevation. High temperature in early summer is effective for the tree growth by prolonging the duration of growing season (Camarero et al. 1998). This view is also supported in this study because of the positive

correlation of the tree-ring width of *B. ermanii* with temperature in June that is the start of the growing season. It is considered that the growth of *B. ermanii* strongly depends on the current-year's photosynthetic production (Kikuzawa 1983). Therefore, the growth of *B. ermanii* is apt to be affected by the current-year's climatic conditions (Takahashi *et al.* 2003). Accordingly, it is no doubt that less insolation duration and low temperature due to frequent rain events in summer of the current year reduce the tree-ring width of *B. ermanii* at the timberline.

The results of this study are different from those of our previous study (Takahashi et al. 2003), conducted for B. ermanii in the lower altitudinal limit (1600 m a.s.l.) on Mount Norikura. Takahashi et al. (2003) suggested that less precipitation combined with high temperature in the current-year August (i.e., drought stress) reduced the tree-ring width of *B. ermanii* in its lower altitudinal limit. August is the hottest month, but precipitation in this month is reduced compared with other months in summer (Takahashi et al. 2003). Although Takahashi et al. (2003) did not analyze the effect of the insolation duration on the tree-ring width, a marginal significant negative relationship was detected between the tree-ring width and the insolation duration in August of the current year in their data set (r = -0.26, P = 0.053, n = 58). This negative relationship supports that growth of *B. ermanii* is reduced by drought stress in its lower altitudinal limit. The discrepancy between the results of this study and those of Takahashi et al. (2003) is apparently due to the difference in climatic conditions between the two sites with different altitude. Precipitation is greater at a higher altitude in this region, associated with the decrease in air temperature (Nagano Meteorological Observatory 1998). In addition, fog often occurs in summer afternoon at high altitudes

in central Japan. Such local-scale climatic conditions hardly cause a water stress for *B. ermanii* at the timberline (Takahashi 2003*b*), but would reduce the photosynthetic production by reducing light energy and temperature. Fujiwara *et al.* (1999) reported that the tree-ring width of *Abies mariesii* was positively correlated with summer temperature at about 2000 and 2200 m a.s.l. on Mount Norikura, and suggested that the reduction of the tree growth in cool summer was due to the insufficient light energy. Therefore, it is considered that negative effects of less insolation duration and low temperature on the growth of *B. ermanii* are more significant near its upper altitudinal limit or the timberline, while less precipitation with high temperature in the hottest month of August reduces the growth of *B. ermanii* near its lower altitudinal limit.

Several researchers also reported that a major climatic factor enhancing the tree growth was summer precipitation at a low altitude, but was summer temperature at a high altitude in boreal forests and in subalpine forests (Ettl & Peterson 1995; Buckley *et al.* 1997; Peterson & Peterson 2001; Wilson & Hopfmueller 2001; Mäkinen *et al.* 2002). As far as a latitudinal gradient, Lara *et al.* (2001) also showed that the tree-ring width of *Nothofagus pumilio* (Poepp et Endl.) Krasser was positively correlated with summer precipitation and negatively with summer temperature in its northern distribution limit in the central Andes of Chile in Southern Hemisphere, while the summer precipitation had negative effects on the tree-ring width in its southern distribution limit. They described that high temperatures in summer reduced the soil water availability for *N. pumilio* in the northern distribution limits by enhancing evapotranspiration. Therefore, it is suggested that the climatic factors limiting the tree-ring width are different along altitudinal and latitudinal gradients, as found in *B. ermanii* of this study. We presented the first tree-ring width chronology of *B. ermanii* at the timberline, and we concluded that climatic factors increasing the tree-ring width of *B. ermanii* changed from much precipitation in the hottest month of August in its lower altitudinal limit to much insolation duration and high temperature due to less precipitation in summer at its upper altitudinal limit (i.e., the timberline). Thus, the growth of *B. ermanii* along the altitudinal gradient cannot be predicted by temperature alone even under a scenario of global warming. Global circulation models predict that climatic change due to CO_2 doubling increases annual mean temperature at about $4\sim6^\circ$ C and precipitation at about $10\sim15\%$ in the East Asia including Japan (Uchijima & Ohta 1996). Therefore, the expected climatic changes may have both positive and negative effects on the growth of *B. ermanii*: precise prediction of effects of the global warming on the tree growth along the altitudinal gradient still remain uncertain problem. Further studies are necessary to comprehensively predict how global warming causes changes of local weather patterns, and then affect growth of *B. ermanii* along the altitudinal gradient.

ACKNOWLEDGEMENTS

This study was partially supported by grants from the Ministry of Education, Science, Sports and Culture of Japan (Nos. 13760128, 15710007 and 16780123) and from the Sumitomo Foundation for Environmental Research Projects (No. 003280).

REFERENCES

Barber V. A., Juday G. P., Finney B. P. & Wilmking M. (2004) Reconstruction of

summer temperatures in interior Alaska from tree-ring proxies: evidence for changing synoptic climate regimes. *Climatic Change* **63**: 91–120.

- Briffa K. R. & Osborn T. J. (1999) Seeing the wood from the trees. *Science* **284**: 926–927.
- Buckley B. M., Cook E. R., Peterson M. J. & Barbetti M. (1997) A changing temperature response with elevation for *Lagarostrobos franklinii* in Tasmania, Australia. *Climatic Change* 36: 477–498.
- Camarero J. J., Guerrero-Campo J. & Gutiérrez E. (1998) Tree-ring growth and structure of *Pinus uncinata* and *Pinus sylvestris* in the central Spanish Pyrenees. *Arctic and Alpine Research* **30**: 1–10.
- Camarero J. J. & Gutiérrez E. (1999) Structure and recent recruitment at alpine forest-pasture ecotones in the Spanish central Pyrenees. *Ecoscience* **6**: 451–464.
- Carrer M. & Urbinati C. (2004) Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. *Ecology* **85**: 730–740.
- Chapin F. S. III, Callaghan T. V., Bergron Y., Fukuda M., Johnstone J. F., Juday G. P.
 & Zimov S. A. (2004) Global change and the boreal forest: thresholds, shifting states or gradual change?. *Ambio* 33: 361–365.
- Cook E. R. (1985) *A time series analysis approach to tree ring standardization*. Ph.D. dissertation, University of Arizona, Tucson.
- Cook E. R. & Peters K. (1981) The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bulletin* 41: 45–53.

Daniels L. D. & Veblen T. T. (2004) Spatiotemporal influences of climate on altitudinal

treeline in northern Patagonia. *Ecology* **85**: 1284–1296.

- DeLucia E. H. & Smith W. K. (1987) Air and soil temperature limitations on photosynthesis in Engelmann spruce during summer. *Canadian Journal of Forest Research* 17: 527–533.
- Dullinger S., Dirnböck T. & Grabherr G. (2004) Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invisibility. *Journal of Ecology* 92: 241–252.
- Eshete G. & Ståhl G. (1999) Tree rings as indicators of growth periodicity of acacias in the Rift Valley of Ethiopia. *Forest Ecology and Management* **116**: 107–117.
- Ettl G. J. & Peterson D. L. (1995) Growth response of subalpine fir (*Abies lasiocarpa*) to climate in the Olympic Mountains, Washington, USA. *Global Change Biology* 1: 213–230.
- Fritts H. C. (1962) The relation of growth ring widths in American beech and white oak to variations in climate. *Tree-Ring Bulletin* **25**: 2–10.
- Fujiwara T., Okada N. & Yamashita K. (1999) Comparison of growth response of *Abies* and *Picea* species to climate in Mt. Norikura, central Japan. *Journal of Wood Science* 45: 92–97.
- Gervais B. R. & MacDonald G. M. (2000) A 403-year record of July temperatures and treeline dynamics of *Pinus sylvestris* from the Kola Peninsula, northwest Russia. *Arctic, Antarctic and Alpine Research* 32: 295–302.
- Gindl W. (1999) Climate significance of light rings in timberline spruce, *Picea abies*, Austrian Alps. *Arctic, Antarctic and Alpine Research* **31**: 242–264.

Gostev M., Wiles G., D'Arrigo R., Jacoby G. & Khomentovsky P. (1996) Early summer

temperatures since 1670 A.D. for Central Kamchatka reconstructed based on a Siberian larch tree-ring width chronology. *Canadian Journal of Forest Research* **26**: 2048–2052.

- Grudd H., Briffa K. R., Karlén W., Bartholin T. S. Jones P. D. & Kromer B. (2002) A
 7400-year tree-ring chronology in northern Swedish Lapland: natural climatic
 variability expressed on annual to millennial timescales. *The Holocene* 12:
 657–665.
- Helama S., Lindholm M., Timonen M., Meriläinen J. & Eronen M. (2002) The supra-long Scots pine tree-ring record for Finnish Lapland: Part 2, interannual to centennial variability in summer temperatures for 7500 years. *The Holocene* 12: 681–687.
- Holmes R. L. (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-ring Bulletin* **43**: 69–78.
- Holmes R. L. (1994) *Dendrochronology program library version 1994*. Laboratory of Tree-Ring Research, University of Arizona, Tucson.
- Kajimoto T., Onodera H., Ikeda S., Daimaru H. & Seki T. (1998) Seedling establishment of subalpine stone pine (*Pinus pumila*) by nutcracker (*Nucifraga*) seed dispersal on Mt. Yumori, northern Japan. *Arctic, Antarctic, and Alpine Research* **30**: 408–417.
- Kienast F., Schweingruber F. H., Bräker O. U. & Schär E. (1987) Tree-ring studies on conifers along ecological gradients and the potential of single-year analyses. *Canadian Journal of Forest Research* 17: 683–696.

Kikuzawa K. (1983) Leaf survival of woody plants in deciduous broad-leaved forests. 1.

Tall trees. Canadian Journal of Botany 61: 2133–2139.

- Kira T. (1948) On the altitudinal arrangement of climatic zones in Japan. *Kanti-Nogaku*2: 143–173 (in Japanese).
- Kirdyanov A., Hughes M., Vaganov E., Schweingruber F. & Silkin P. (2003) The importance of early summer temperature and date of snow melt for tree growth in the Siberian Subarctic. *Trees* 17: 61–69.

Körner Ch. (1999) Alpine Plant Life. Springer, Berlin.

- Kullman L. (1986) Recent tree-limit history of Picea abies in the southern Swedish Scandes. Canadian Journal of Forest Research 16: 761–771.
- Kusnierczyk E. R. & Ettl G. J. (2002) Growth response of ponderosa pine (*Pinus ponderosa*) to climate in the eastern Cascade Mountains, Washington, U.S.A.:
 Implications for climatic change. *Ecoscience* 9: 544–551.
- Lara A., Aravena J. C., Villalba R., Wolodarsky-Franke A., Luckman B. & Wilson R. (2001) Dendroclimatology of high-elevation *Nothofagus pumilio* forests at their northern distribution limit in the central Andes of Chile. *Canadian Journal of Forest Research* **31**: 925–936.
- Lloyd A. H. & Fastie C. L. (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change* **52**: 481–509.
- MacDonald G. M., Case R. A. & Szeicz J. M. (1998) A 538-year record of climate and treeline dynamics from the lower Lena River region of northern Siberia, Russia. *Arctic and Alpine Research* **30**: 334–339.
- Mäkinen H., Nöjd P. & Mielikäinen K. (2000) Climatic signal in annual growth variation of Norway spruce (*Picea abies*) along a transect from central Finland

to the Arctic timberline. Canadian Journal of Forest Research 30: 769–777.

- Mäkinen H., Nöjd P., Kahle H.P., Newmann U., Tveite B., Mielikäinen K., Röhle H. &
 Spiecker H. (2002) Radial growth variation of Norway spruce (*Picea abies* (L.)
 Karst.) across latitudinal and altitudinal gradients in central and northern Europe. *Forest Ecology and Management* 171: 243–259.
- Miyawaki A. (1985) Vegetation of Japan. 6. Chubu. Shibundo Co. LTD. Publishers, Tokyo (in Japanese).
- Nagano Meteorological Observatory (1998) Annual report on weather conditions of Nagano Prefecture in 1998. Nagano Branch Office of Japanese Meteorological Society, Nagano (in Japanese).
- Oberhuber W., Pagitz K. & Nicolussi K. (1997) Subalpine tree growth on serpentine soil: a dendroecological analysis. *Plant Ecology* **130**: 213–221.
- Okitsu S. (1988) Geographical variations of annual fluctuations in stem elongation of *Pinus pumila* Regel on high mountains of Japan. *Japanese Journal of Ecology*38: 177–183 (in Japanese).
- Paulsen J., Weber U. M. & Körner Ch. (2000) Tree growth near treeline: abrupt or gradual reduction with altitude? *Arctic, Antarctic, and Alpine Research* 32: 14–20.
- Peterson D. W. & Peterson D. L. (2001) Mountain hemlock growth responds to climatic variability at annual and decadal time scales. *Ecology* **82**: 3330–3345.
- Rolland C., Petitcolas V. & Michalet R. (1998) Changes in radial tree growth for *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus uncinata* near the alpine timberline since 1750. *Trees* 13: 40–53.

- Sano Y., Matano T. & Ujihara A. (1977) Growth of *Pinus pumila* and climate fluctuation in Japan. *Nature* **266**: 159–161.
- Solomina O. N., Muravyev Y. D., Braeuning A. & Kravchenko G. N. (1999) Two new ring width chronologies of larch and birch from the Kamchatka peninsula (Russia) and their relationship to climate and volcanic activities. In: *Cryospheric Studies in Kamchatka II* (ed. R. Naruse) pp. 111–124. Institute of Low Temperature Science, Hokkaido University, Sapporo.
- Speer J. H., Orvis K. H., Grissino-Mayer H. D., Kennedy L. M. & Horn S. P. (2004) Assessing the dendrochronological potential of *Pinus occidentalis* Swartz in the Cordillera Central of the Dominican Republic. *The Holocene* 14: 563–569.
- Szeicz J. M. & MacDonald G. M. (1995) Recent white spruce dynamics at the subarctic alpine treeline of north-western Canada. *Journal of Ecology* **83**: 873–885.
- Takahashi K. (2003*a*) Effects of climatic conditions on shoot elongation of alpine dwarf pine (*Pinus pumila*) at its upper and lower altitudinal limits in central Japan. *Arctic, Antarctic, and Alpine Research* 35: 1–7.
- Takahashi K. (2003b) Diurnal variations in stomatal conductance of *Betula ermanii* and *Pinus pumila* at the timberline on Mt. Shogigashira, central Japan. *Journal of Phytogeography and Taxonomy* **51**: 159–164.
- Takahashi K. (2005) Effects of simulated warming on shoot elongation of alpine dwarf pine (*Pinus pumila*) on Mt. Shogigashira, central Japan. *Arctic, Antarctic, and Alpine Research* (in press).
- Takahashi K. (2006) Shoot growth chronology of alpine dwarf pine (*Pinus pumila*) in relation to shoot size and climatic conditions: a reassessment. *Polar Bioscience*

(in press).

- Takahashi K., Azuma H. & Yasue K. (2003) Effects of climate on the radial growth of tree species in the upper and lower distribution limits of an altitudinal ecotone on Mount Norikura, central Japan. *Ecological Research* 18: 549–558.
- Takahashi K., Homma K., Shiraiwa T., Vetrova V. P. & Hara T. (2001) Climatic factors affecting the growth of *Larix cajanderi* in the Kamchatka Peninsula, Russia. *Eurasian Journal of Forest Research* 3: 1–9.
- Tatewaki M. (1958) Forest ecology of the islands of the North Pacific Ocean. *Journal of Faculty of Agriculture, Hokkaido University* **50**: 371–486.
- Taylor A. H. (1995) Forest expansion and climate change in the mountain Hemlock (*Tsuga mertensiana*) zone, Lassen Volcanic National Park, U.S.A. Arctic and Alpine Research 27: 207–216.
- Uchijima Z. & Ohta S. (1996) Climatic change scenarios for Monsoon Asia based on 2 × CO₂-GCM experiments. In: Climate Change and Plants in East Asia (eds K. Omasa, K. Kai, H. Taoda, Z. Uchijima & M. Yoshino) pp. 3–12. Springer, Tokyo.
- Wilson R. J. S. & Hopfmueller M. (2001) Dendrochronological investigations of Norway spruce along an elevational transect in the Bavarian Forest, Germany. *Dendrochronologia* 19: 67–79.

Figure legends

Fig. 1. Standardized tree-ring width chronology and sample depth of *Betula ermanii* at the timberline on Mount Norikura in central Japan (solid lines). The chronology was constructed using at least five cores in each year. A dotted line indicates the standardized tree-ring width chronology of *B. ermanii* (since 1943) at its lower altitudinal limit (redrawn from Takahashi *et al.* 2003).

Fig. 2. Results of the simple correlation analysis for the relationships between the standardized tree-ring width chronology of *Betula ermanii* and monthly climatic data (mean temperature, insolation duration, and sum of precipitation). Significant relationships (P < 0.05) were indicated by shaded bars.



Fig. 1



Table 1 Basic statistics of tree-ring width chronology for *Betula ermanii* at thetimberline on Mount Norikura in central Japan.

Statistics	Value
Number of trees (cores)	17 (32)
Range of DBH^{\dagger} (cm)	19–41
Range of chronology (years)	172
Mean tree-ring width (mm)	0.65
Standardized chronology	
Mean sensitivity	0.23
Standard deviation	0.25
First-order autocorrelation	0.34
Mean correlation between trees [#]	0.41
Signal-to-noise ratio [#]	10.22

[†]Stem diameter at breast height.

[#]Calculated for a common interval from 1891 to 1997.

Table 2 Correlation coefficients of monthly sum of precipitation with monthly mean temperature and with monthly insolation duration at Matsumoto Weather Station in central Japan, during 1900–2001 (n = 102). Correlation test was performed for the four months during the growing season of plants at the timberline on Mount Norikura (2400 m a.s.l.).

Month	Temperature	Insolation duration
June	-0.20^{*}	-0.56***
July	-0.52^{***}	-0.61***
August	-0.47^{***}	-0.42***
Septembe	er –0.078	-0.67^{***}

*: *P* < 0.05, ***: *P* < 0.001.