Effects of climate on the radial growth of tree species in the upper and lower distribution limits of an altitudinal ecotone on Mt. Norikura, central Japan

KOICHI TAKAHASHI[1]*, HIROTO AZUMA[1] AND KOH YASUE[2]

[1]*Department of Biology, Faculty of Science, Shinshu University, Matsumoto, Nagano 390-8621, Japan and* [2]*Department of Forest Science, Faculty of Agriculture, Shinshu University, 8304 Minami-Minowa, Nagano 399-4598, Japan*

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*Author to whom correspondence should be addressed. Email: koichi@gipac.shinshu-u.ac.jp

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To show what climatic conditions affect the growth of tree species in the upper and lower distribution limits of an altitudinal ecotone, tree-ring width chronologies were developed for *Abies veitchii*, *Betula ermanii* and *Betula platyphylla* var. *japonica* in their altitudinal ecotone (about 1600 m above sea level) on Mt. Norikura, central Japan. This altitude was the lower distribution limit for *A. veitchii* and *B. ermanii* in the subalpine zone, and was the upper distribution limit for *B. platyphylla* var. *japonica* in the montane zone on Mt. Norikura. The tree-ring widths of the two *Betula* species and *A. veitchii* were positively correlated with the August precipitation of the current year and that of the previous year, respectively. Precipitation in the hottest month of August was less compared with other months during summer. The tree-ring width of *B. platyphylla* var. *japonica* showed no correlation with temperatures of any month in its upper distribution limit. In contrast, the tree-ring widths of *B. ermanii* and *A. veitchii* were negatively correlated with the August temperatures of the current year and of the previous year, respectively, in the lower distribution limit of these species. Therefore, the two *Betula* species and *A. veitchii* responded to climatic conditions of the current year and those of the previous year, respectively. This study also suggests that water deficit in August reduces the growth of the three species in this altitudinal ecotone, irrespective of the upper or lower distribution limit, and that a high August temperature is more detrimental to the growth of *A. veitchii* and *B. ermanii* in their lower distribution limit. Thus, the examined three species with different altitudinal distributions differently responded to climatic conditions in this altitudinal ecotone on Mt. Norikura.

Key words: altitudinal ecotone; central Japan; climatic conditions; dendrochronology; growth; tree-ring width

INTRODUCTION

Forest vegetation changes along altitudinal gradients, accompanied by changes in air temperature. For example, in central Japan, forest vegetation changes from evergreen broad-leaved forests at low altitude to deciduous broad-leaved forests at middle altitude, and to evergreen coniferous forests at high altitude (Yoshino 1978; Ohsawa 1995). Vegetation patterns along altitudinal gradients change markedly in ecotones rather than change gradually with altitude, i.e., an ecotone is a narrow transitional zone between adjacent communities (e.g. Kimura 1963; Harris 1978). Therefore, altitudinal ecotones are the most dynamic sites for investigating altitudinal distributions of plant species under the influences of climatic conditions. However, few studies have investigated the ecotone dynamics in relation to climates, except for the studies on the timberline dynamics (e.g. Wardle 1968; Kullman 1993; Taylor 1995; Camarero & Gutiérrez 1999). Increased knowledge of responses to climate in species of both upper and lower distribution limits that form an altitudinal ecotone is of great importance to understand the effects of global warming on altitudinal distributions of plant species. In this study, we investigated how climatic conditions affect the growth of tree species in the upper and lower distribution limits of an altitudinal ecotone.

Dendrochronological analysis is often used to show what climatic conditions affect tree-ring widths (i.e. radial growth) and to reconstruct past climates (e.g. Schweingruber *et al*. 1978; Hughes *et al*. 1984; Cleaveland 1986; Kienast *et al*. 1987; Sweda & Takeda 1993; Yasue *et al*. 1996, 1997; Gindl 1999). For example, several studies have shown that high summer temperature increases tree-ring widths at high altitude, as well as latitude, and much precipitation increases tree-ring widths at dry sites (Fritts *et al*. 1965; Abrams & Orwig 1995; Gostev *et al*. 1996; Oberhuber *et al*. 1998; Gervais & MacDonald 2000; Rigling *et al*. 2001). Therefore, climatic conditions affecting tree growth are detectable by dendrochronological analysis.

We examined the altitudinal ecotone between deciduous broad-leaved forests and subalpine forests in central Japan. This altitudinal ecotone was formed mainly by *Betula platyphylla* var. *japonica* Hara, *Betula ermanii* Cham. and *Abies veitchii* Lindl. We developed tree-ring width chronologies of the three species, and examined their relationships with climatic conditions of monthly temperature and precipitation. This study aimed to show what climatic conditions affect the radial growth of the three species in their altitudinal ecotone.

METHODS

Site description

This study was carried out on the east slope of Mt. Norikura (3026 m above sea level) in central Japan. On this slope, *Betula platyphylla* var. *japonica* was distributed between about 1100 and 1600 m a.s.l. in the upper zone of deciduous broad-leaved forests, while *Betula ermanii* and four conifers (*Abies veitchii*, *Abies mariesii* Mast., *Picea jezoensis* var. *hondoensis* Rehder and *Tsuga diversifolia* Mast.) were dominants between about 1600 and 2500 m a.s.l. in subalpine forests. Alpine dwarf pine scrub (*Pinus pumila* Regel) was distributed from about 2500 m a.s.l. to near the summit. The forest floor was densely covered with dwarf bamboo (*Sasa senanensis* Rehder), except at dwarf pine scrub sites. The nomenclature follows Ohwi (1961).

We selected an altitudinal ecotone (ca. 1600 m a.s.l., 36˚07'N, 137˚37'E) between the deciduous broad-leaved forests and the subalpine forests, and *B. platyphylla* var. *japonica*, *B. ermanii* and *A. veitchii* growing in the ecotone were examined. This ecotone was the upper distribution limit for *B. platyphylla* var. *japonica*, and was the lower distribution limit for *B. ermanii* and *A. veitchii*. *Betula* species often form pure stands after large disturbances such as forest fires. However, there was no evidence of forest fires around this study area.

The mean annual precipitation was about 1570 mm, according to the meteorological data measured at Nagawato Dam (900 m a.s.l., about 10 km from the study area). The mean annual temperature in this study area (1600 m a.s.l.) was estimated as 4.9˚C from temperatures recorded at Matsumoto Weather Station (610 m a.s.l., about 35 km from the study area) using the lapse rate of –0.6˚C for each +100 m altitude. The mean monthly temperatures in the coldest month of January and the hottest month of August were estimated as –7.3 and 17.7˚C, respectively (Fig. 1).

Sampling and measurement

Thirty trees were cored at 1.3 m trunk height for each species, with one core from each tree, from 5 to 24 November 2000. The diameter at breast height was measured. 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 measurement stage (TA Tree-Ring System, Velmex Inc., NY, USA). The tree-ring boundaries for the two *Betula* species 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 in trees within a species. 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) from correlation coefficients. Of 30 cores for each species, several cores that had low correlations with other trees were eliminated from further analyses.

Growth of trees is affected not only by climatic factors, but also by competition between neighboring trees, i.e., suppression by tall trees and release from suppression. To eliminate competitive effects, all raw ring-width series were standardized by fitting smoothing splines (Cook & Peters 1981) with a 50% frequency-response cutoff of 10 years. This procedure was done by using the ARSTAN program (Cook 1985; Holmes 1994). After standardizing each individual series, the tree-ring width chronology for each species was calculated by averaging the standardized individual series. We used at least 10 cores to make the tree-ring width chronologies in each year.

Responses to climatic conditions

Simple correlation analyses were used to show the effects of monthly mean temperature and total precipitation on the tree-ring widths of the three species. Before the correlation analysis, we compared the meteorological data at Nagawa (1068 m a.s.l., about 7 km southeast of the study site), which was the nearest weather station to the study site, with this data at Nagawato Dam (900 m a.s.l., about 10 km east of the study site) and

Matsumoto (610 m a.s.l., about 35 km east of the study site). The recording period of the meteorological data at Nagawa was comparatively short (from 1979 to 2000; $n = 22$), while this period at Nagawato Dam and at Matsumoto were from 1969 to 2000 ($n = 32$) and from 1898 to 2000 ($n = 103$), respectively. The records at Nagawato Dam were only for precipitation. The monthly temperatures at Matsumoto showed high correlations with those at Nagawa ($r = 0.89$ to 0.98). However, the monthly precipitation at Matsumoto was not well correlated with that at Nagawa ($r = 0.58$ to 0.95), while the monthly precipitation was highly correlated between Nagawato Dam and Nagawa ($r = 0.75$ to 0.98). The low correlations for precipitation between Matsumoto and the other two stations were probably due to the local variations in rainfall. Thus, we used temperature data at Matsumoto and precipitation data at Nagawato Dam for further analyses because of the short recording period at Nagawa. The calibration period was from 1969 to 2000 ($n = 32$) that corresponded to the recording period at Nagawato Dam.

The correlation analyses between ring widths and climatic data were done from the start of the previous growing season to the end of the current growing season, because growth of many tree species is affected not only by climatic conditions of the current growing season, but also by the climatic conditions of the previous growing season (cf. Fritts 1962; Sano *et al*. 1977; Takahashi *et al*. 2001). The approximate growth period at this study site (1600 m a.s.l.) was estimated as May to Octorber (Fig. 1), because the mean monthly temperatures exceeded 5 ˚C, as effective heat for plant growth (Kira 1949), during this period. Thus, the correlation analysis was performed from May of the previous year to October of the current year (18 month in total).

RESULTS

Tree-ring width chronology

Of 30 core samples for each species, 27, 24 and 23 cores were successfully cross-dated for *B. platyphylla* var. *japonica*, *B. ermanii* and *A. veitchii*, respectively, and were used to develop a master chronology having good correlations between trees of each species (Table 1). Although we sampled from old-looking trees in the study area, the ages of the sampled trees were young. The tree-ring width chronologies for the three species were only for several decades (Table 1, Fig. 2). The mean tree-ring widths of the three species were significantly different from one other (Tukey HSD test, $P < 0.05$). *A. veitchii* had the largest tree-ring width among the three species (Table 1). The mean tree-ring width of *B. platyphylla* var. *japonica* in the upper distribution limit was larger than that of *B. ermanii* in the lower distribution limit. The mean correlation coefficient between trees of *B. ermanii* was lower compared with the other two species (0.21 compared with about 0.4, Table 1). The first-order autocorrelations of standardized chronologies, as measures of the influence of the previous year’s growth on the growth in the current year, were lower than 0.05 for the three species (Table 1). The mean sensitivities and standard deviations, as measures of interannual variation in tree-ring width, were also low (< 0.15) for the three species. These indicate that individual trees of each species grew synchronously in this altitudinal ecotone, but the interannual variation in the tree-ring width was not high.

Each chronology showed several characteristic wide and narrow rings. The tree-ring width indices of the two *Betula* species decreased in 1978 and 1995 (Fig. 2). The indices of *B. ermanii* and *B. platyphylla* var. *japonica* also decreased in 1973 and 1988, respectively, in addition to 1978 and 1995. The characteristic declines of *A. veitchii* (1974, 1979 and 1989) were one-year later than those of the two *Betula* species, except for 1995 that showed a strong decline in all species. Furthermore, *A. veitchii* showed characteristic wide rings in 1977, 1993 and 1999 (Fig. 2). These wide rings of *A. veitchii* were also one-year later than those of the two *Betula* species in 1976, 1992 and 1998. In addition, the index of *B. ermanii* increased in 1980 and 1991, and that of *B. platyphylla* var. *japonica* increased in 1980 and 1982. The tree-ring width index of *A. veitchii* was positively correlated with the 1-year lagged index of *B. ermanii* ($r = 0.38$, $P < 0.01$) and that of *B. platyphylla* var. *japonica* ($r = 0.39$, $P < 0.01$) for 1949 to 2000.

Responses to climatic conditions

The temperatures of all months were not significantly correlated with the tree-ring width index of *B. platyphylla* var. *japonica* in its upper distribution limit (Fig. 3). In contrast, the tree-ring width indices of *B. ermanii* and *A. veitchii* in their lower distribution limit were negatively correlated with the August temperature of the current year and this temperature of the previous year, respectively (Fig. 3).

The tree-ring width indices of the two *Betula* species were positively correlated with March and August precipitation of the current year (Fig. 3). Also, the tree-ring width index of *B. platyphylla* var. *japonica* was positively correlated with the October precipitation of the current year. *A. veitchii* responded to precipitation differently from the two *Betula* species: its tree-ring width index was positively correlated with the

August precipitation of the previous year, although the two *Betula* species responded to that of the current year (Fig. 3). Therefore, climatic conditions of the previous year affected the tree-ring widths of *A. veitchii*, and climatic conditions of the current year affected the two *Betula* species. This difference between the two genera corresponded to their 1-year difference in the characteristic wide and narrow rings (Fig. 2). August was the hottest month, but its precipitation in this month was less compared with other months between June and September (Fig. 1).

DISCUSSION

One-year difference in tree-ring width variations between *Abies* and *Betula*

We found a 1-year difference in the variations in tree-ring width chronologies between *A. veitchii* and the two *Betula* species. *A. veitchii* responded to climatic conditions of the previous year and the two *Betula* species responded to those of the current year. Clearly, the responses to climatic conditions in the radial growth were different between the two genera. Kikuzawa (1983) categorized deciduous broad-leaved tree species in northern Japan between two extremes according to leaf phenology: leaves emerging simultaneously during a short period at the beginning of a growing season (flush type) or continuously one by one over a long period (succeeding type). He also suggested that the flush-type species grow using the photosynthetic production of the previous year, while the succeeding-type species strongly depend on the photosynthetic production of the current year. The species of the genus *Betula*, including *B. platyphylla* var. *japonica* and *B. ermanii,* are categorized as the intermediate type between the flush and succeeding types (Kikuzawa 1983). In *Betula* species, early leaves, usually one or two, emerge at first, and then late leaves emerge one by one. Thus, it seems that the two *Betula* species largely depend on the photosynthetic production of the current year. Unfortunately, we do not have enough information on the relationship between the growth traits and photosynthetic production for *A. veitchii*. However, several researchers also reported significant correlations between tree-ring width (or shoot elongation) and climatic conditions of the previous year (Fritts 1962; Sano *et al*. 1977; Eshete & Ståhl 1999; Takahashi *et al*. 2001; Takahashi 2003), as seen in *A. veitchii* of this study. For example, the shoot elongation of alpine dwarf pine (*Pinus pumila*) in Japan is positively correlated with the summer temperatures of the previous year (Sano *et al*. 1977; Takahashi 2003). Kibe and Masuzawa (1992) examined the seasonal changes in the amount of carbohydrates in *P. pumila*, and suggested that carbohydrate gained by the photosynthesis in summer is restored in branches and needles as sugar in winter, and is used for the growth in the next year. Their suggestion is consistent with the growth traits of *P. pumila*, i.e. the shoot elongation is affected by climatic conditions of the previous year. Probably, the same is true for *A. veitchii*, i.e. the previous-year's photosynthetic production is used for the current-year's growth. Therefore, the 1-year difference in tree-ring width chronology between the two genera (*Abies* and *Betula*) is probably ascribed to whether the current-year's photosynthetic production is used for the current-year's growth or is restored for the next-year's growth.

Responses to climatic conditions

The tree-ring width indices of the two *Betula* species were positively correlated with the

March precipitation of the current year. The precipitation in March was snow because the temperature was still below zero (Fig. 1). However, why the large amount of snow in March had a positive effect on the growth of the two *Betula* species is unknown. The tree-ring width index of *B. platyphylla* var. *japonica* was positively correlated with the precipitation in October of the current year. This reason is also unknown because their leaves start to fall in October (the end of the growing season), and therefore, the radial growth in this month is probably negligible.

The tree-ring width indices of the three species were positively correlated with the precipitation in the hottest month of August that had less precipitation compared with the other months during summer. Low precipitation coupled with a high temperature causes a drought stress in plants, which in turn reduces the photosynthetic production of plants (Havranek & Benecke 1978; Cienciala *et al*. 1998) because of the stomatal closure in response to the limitation of soil water availability (Cienciala *et al*. 1994; Granier & Loustau 1994; Granier & Bréda 1996; Miller *et al*. 1998). Therefore, much precipitation in August is suggested to increase the growth of the three species in this altitudinal ecotone, irrespective of the upper or lower limit of their distributions.

The temperature of the hottest month of August was negatively correlated with the tree-ring width indices of *B. ermanii* and *A. veitchii* in their lower distribution limit. However, these negative correlations do not seem to be independent of the precipitation in August. If high temperature reduces the growth of *B. ermanii* and *A. veitchii*, a negative correlation would have been found also for July temperature because July temperature were as high as the August temperature (Fig. 1), but such a negative correlation was not detected. High temperature combined with less precipitation in

August seems to increase the drought stress for these two species in their lower distribution limit. In contrast, *B. platyphylla* var. *japonica* showed no significant correlation with August temperature in its upper distribution limit, which is attributable to its adaptation to high temperature conditions. The optimal temperature for photosynthesis is higher for *B. platyphylla* var. *japonica* (10–24˚C) than in *B. ermanii* (8–20˚C) (Koike 1987). These different optimal temperatures between the two *Betula* species correspond to their altitudinal distribution, i.e. *B. platyphylla* var. *japonica* is distributed more in the lower altitudinal zone than *B. ermanii*. Therefore, high August temperature affects less the growth of *B. platyphylla* var. *japonica* compared with *B. ermanii* in this altitudinal ecotone.

Although the upper distribution limit of *B. platyphylla* var. *japonica* was ca. 1600 m a.s.l. on Mt. Norikura, Takahashi (1962) observed that *B. platyphylla* var. *japonica* was distributed up to ca. 2000 m a.s.l. on Mt. Yatsugatake in central Japan. The mechanism determining the upper distribution limits of this species is unknown. However, it is suggested that the upper distribution limit of *B. platyphylla* var. *japonica* on Mt. Norikura may not be determined by temperature alone.

In this study, a positive correlation was not found between summer temperatures and the tree-ring widths of the three species in this altitudinal ecotone (1600 m a.s.l.). However, Fujiwara *et al.* (1999) found positive relationships between summer temperatures and tree-ring width of *Abies mariesii* at about 2000–2200 m a.s.l. on Mt. Norikura, the site of our study. The discrepancy between the results of our study and those of Fujiwara *et al.* (1999) is probably because the study site of Fujiwara *et al.* (1999) was at a higher altitude than our study site. Precipitation is greater at a higher altitude in this region, associated with the decrease in air temperature (Nagano Meteorological Observatory 1998), suggesting tree growth at the study site of Fujiwara *et al*. (1999) is more limited by low temperature than by precipitation. A similar result was also reported for Dahurican larch (*Larix cajanderi*) on the Kamchatka Peninsula in the Russian Far East. The tree-ring width of larch at low altitude is positively correlated with summer precipitation, while the tree-ring width at high altitude is positively correlated with early summer temperature (Solomina *et al*. 1999; Takahashi *et al*. 2001). Thus, the relative importance of summer temperature for tree growth probably increases with altitude (cf. Wilson & Hopfmueller 2001).

Conclusion

This study showed the effects of climatic conditions on the radial growth of the three species in the upper and lower distribution limits in an altitudinal ecotone between deciduous forests and subalpine forests on Mt. Norikura by using a dendrochronological technique. The radial growth of the three species was affected by drought stress in the hottest month of August in this ecotone. Water deficit combined with high temperature in August was more detrimental to the growth of *B. ermanii* and *A. veitchii* in their lower distribution limit compared with *B. platyphylla* var. *japonica* in its upper distribution limit. Therefore, environmental fluctuation is suggested to affect differently the growth of the three species with different altitudinal distributions in this ecotone on Mt. Norikura.

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FIGURE LEGENDS

Fig. 1. Monthly mean temperatures (circle) at 1600 m a.s.l. in Mt. Norikura, and precipitation (bar) at 900 m a.s.l. (Nagawato Dam). Temperature at 1600 m a.s.l. was estimated from the temperature at 610 m a.s.l. (Matsumoto), by using the lapse rate of –0.6˚C for each +100 m altitude.

Fig. 2. Standardized tree-ring width chronologies and sample depths of (a) *Abies veitchii*, (b) *Betula ermanii* and (c) *Betula platyphylla* var. *japonica* in the altitudinal ecotone (1600 m a.s.l.) on Mt. Norikura, central Japan. Each chronology was constructed using at least 10 cores. Arrows indicate the characteristic years that growth of many trees decreased or increased synchronously.

Fig. 3. Correlation coefficients between the standardized tree-ring width chronologies and monthly climate data (precipitation and temperature). Shaded bars indicate a significant correlation ($P < 0.05$).

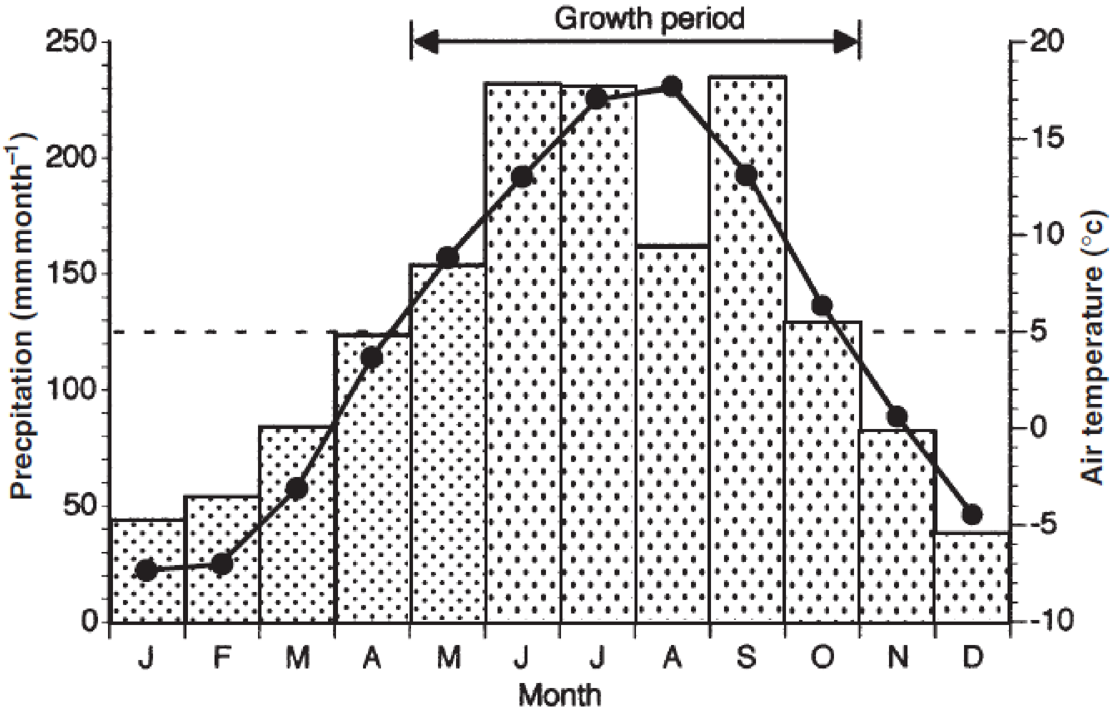
Growth period
Precpitation (mm month^{-1})
250
200
150
100
50
0
Air temperature (°c)
20
15
10
5
0
-5
-10
J
F
M
A
M
J
J
A
S
O
N
D
Month

Fig. 1

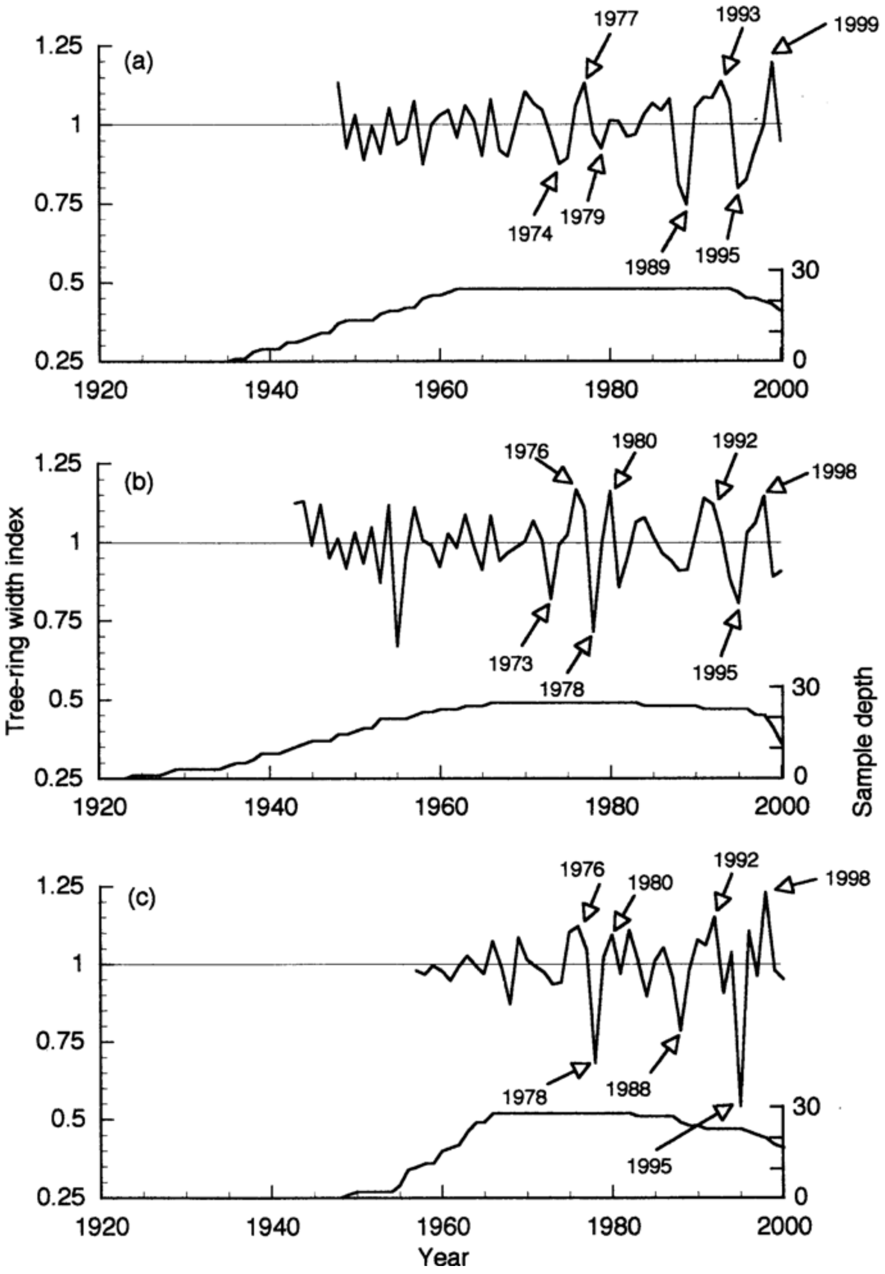
(a)
1977
1993
1999
1974
1979
1989
1995
(b)
1976
1980
1992
1998
1973
1978
1995
(c)
1976
1980
1992
1998
1978
1988
1995
1.25
1
0.75
0.5
0.25
30
0
1920
1940
1960
1980
2000
Tree-ring width index
Sample depth
Year

Fig. 2

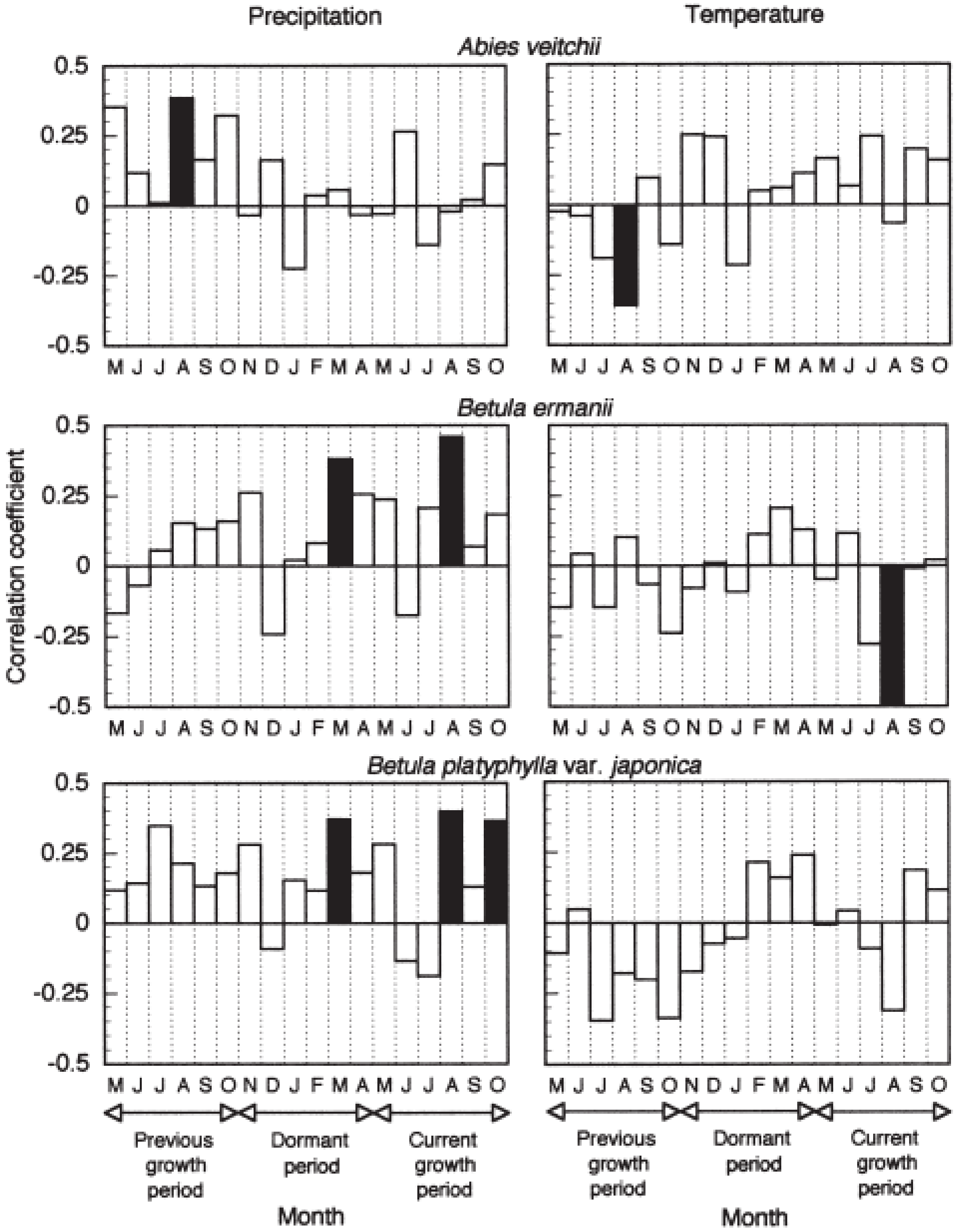
Precipitation
Temperature
Abies veitchii
Betula ermanii
Betula platyphylla var. japonica
Correlation coefficient
0.5
0.25
0
-0.25
-0.5
M J J A S O N D J F M A M J J A S O
Previous growth period
Dormant period
Current growth period
Month

Fig. 3

Table 1 Basic statistics of tree-ring width chronologies of *Abies veitchii* (Av), *Betula ermanii* (Be) and *Betula platyphylla* var. *japonica* (Bp) in the central Japan.

	Av	Be	Bp
Number of samples	23	24	27
Range of DBH[†] (cm)	25–45	21–42	19–40
Range of chronology (years)	65	77	52
Mean tree-ring width[‡] (mm)	3.10	2.51	2.93
Standardized chronology			
Mean sensitivity	0.105	0.128	0.150
Standard deviation	0.093	0.113	0.135
First-order autocorrelation	0.042	0.023	–0.043
Mean correlation between trees[#]	0.404	0.211	0.381
Signal-to-noise ratio[#]	15.6	3.5	11.1

[†] Diameter at breast height.

[‡] Mean tree-ring widths of the three species were significantly different from each other (Tukey HSD test, $P < 0.05$).

[#] Calculated for the common intervals.