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## The effects of tracheid dimensions on variations in maximum density of *Picea glehnii* and relationships to climatic factors

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**Abstract** An investigation was made of the effects of tracheid dimensions on variations in the maximum density of *Picea glehnii* Mast., which were associated with climatic changes. Radial cell diameter and the thickness of the tangential cell walls of the last-formed cells in 90 annual rings of nine trees with different annual ring widths were analyzed by image analysis. Correlations between maximum density and tracheid dimensions indicated that changes in maximum density were due mainly to changes in cell wall thickness of the last-formed cells in annual rings and were not due to changes in radial cell diameter. The effects of climatic factors on tracheid dimensions were examined by application of dendroclimatological techniques. A chronology of cell wall thickness that represented common signals among trees was established. Simple correlation and response function analyses of the chronology revealed that cell wall thickness was influenced positively by summer temperature and negatively by precipitation in August, and these responses were similar to those of maximum density. The study demonstrated that variations in maximum density were due to variations in the cell wall thickness of the last-formed cells, which varied depending on the weather in summer.

**Key words** Maximum density · Cell wall thickness · Radial cell diameter · Climatic factors · *Picea glehnii* Mast.

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### Introduction

The maximum density of annual rings of conifers, which can be obtained by densitometric analysis, has been recognized as one of the most important parameters for reconstruction of climatic changes (e.g., Schweingruber et al. 1978; Briffa et al. 1988, 1990, 1995; Hughes et al. 1994). Previous research on the responses of maximum density to climate has revealed positive correlations between maximum density and summer temperatures for the most part at high latitudes and at high altitudes (Parker and Henoch 1971; Kienast et al. 1987; Briffa et al. 1988, 1990, 1995; D'Arrigo et al. 1992). Both positive effects of temperature and negative effects of precipitation in summer have been reported in cool temperate zones (Schweingruber et al. 1978; Kienast et al. 1987; Yasue et al. 1996, 1997; Fujiwara et al. 1999). A positive response of maximum density to temperature and to precipitation during the previous growth period has also been reported in the cool temperate zone of Hokkaido, Japan (Kobayashi et al. 1998). In the case of semiarid regions, the responses of maximum density to the stress of moisture deficit have been reported to be negatively correlated with temperature and positively correlated with precipitation in the southwestern United States (Cleveland 1986; Park 1990) and in north-central China (Hughes et al. 1994). Such strong correlations between maximum density and climatic factors reveal the advantage of the application of maximum density to dendroclimatological studies (Parker and Henoch 1971; Schweingruber et al. 1978; Conkey 1986). However, the anatomical and physiological significance of the relationships between maximum density and climatic factors has not yet been clarified.

In conifers, density depends primarily on the dimensions of tracheids. An increase in density is due to a decrease in radial cell diameter and/or to an increase in cell wall thickness (Saiki 1965; Diaz-Vázquez et al. 1975). The maximum density is found in the last-formed tracheids in an annual ring. Thus, if a good correlation were to exist between maximum density and climatic factors, a change

in climate would be expected to affect the radial enlargement of cells and/or the thickening of cell walls in the last-formed tracheids. Park (1990) made a statistical analysis of the climatic effects on the dimensions of the last-formed tracheids of ponderosa pine (*Pinus ponderosa* Laws.) in southern Arizona. He reported that both cell wall thickness and radial diameter appeared to be good indicators of climatic changes which are negatively influenced by temperature and positively influenced by precipitation. However, relationships between maximum density and tracheid dimensions were not mentioned in Park's report. By contrast, in a preliminary study of two adjacent rings of *Picea glehnii* formed under different summer conditions (cool-wet and warm-dry), we found that the difference in maximum density was due to the difference in thickness of tangential cell walls (Yasue et al. 1996). A similar study on the latewood density of two rings of Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] in western Canada revealed that the difference in latewood density was due to the difference in cell wall thickness (Heger et al. 1974). Verification of such relationships between maximum density and tracheid dimensions requires a statistical analysis based on a large number of samples.

The present study was designed to investigate the ways in which climate influences variations in maximum density in *P. glehnii*. We examined the relationships between maximum density and tracheid dimensions (radial cell diameter and cell wall thickness) of the last-formed tracheids. The dimensions of tracheids were measured by image analysis. Finally, we analyzed the effects of climatic factors on the dimensions of tracheids using dendroclimatological techniques.

## Materials and methods

### Study site and sample trees

The study site is located in the Teshio Experimental Forest of Hokkaido University (44°57'N, 142°07'E; elevation 300 m) in northern Hokkaido, Japan, where there has been little human disturbance of the forest, such as planting and cutting of trees. Naturally growing *Picea glehnii* trees were chosen from among those

analyzed in a previous study of the responses to climate of ring widths and maximum densities (Yasue et al. 1997). An increment core of 5 mm in diameter was obtained at breast height from each sample tree. Nine trees were selected on the basis of the stability of ring-width series and the absence of reaction wood, in order to minimize the effects of non-climatic factors on tracheid dimensions (Table 1). Differences in ring width were also considered in the selection of samples. We chose trees with average ring widths of 0.30–1.50 mm because it has been reported that narrow rings in suppressed trees are associated with reduced cell wall thickness and/or reduced cell wall area in the latewood (Saiki and Kawake 1980; Kubo 1983; Funada et al. 1995). Moreover, de Kort et al. (1991) also reported that maximum density was significantly reduced in the very narrow rings of non-vital trees. Therefore, we also examined the possible effects of ring width on relationships between maximum density and tracheid dimensions.

The analysis was made for the period from 1901 to 1990 (90 rings), which corresponded to the period for which meteorological data were available. We assumed that all the annual rings used for measurements corresponded to mature wood because of the considerable ages of the sample trees, which were approximately 200–500 years old.

### Preparation of samples and measurements

Increment cores were cut transversely into strips that were 2 mm thick with a twin-bladed saw. The strips were oven-dried and subjected to X-ray analysis together with a calibration wedge described as previously (Yasue et al. 1996, 1997; Kobayashi et al. 1997). The resultant radiographs were scanned at 10 µm intervals with a micro-photo-densitometer (PDS-15; Konika, Japan). The dimensions of the scanning slit were fixed at 30 µm in the radial direction and 100 µm in the tangential direction (Fig. 1). Maximum densities were obtained using a Tree-Ring Analysis Program (Nobori 1989) that was developed for determination of annual ring characteristics, such as ring width, maximum density and minimum density, based on measured density curves.

The same strips as those subjected to X-ray densitometry were also used for image analysis. The strips were cut into segments that were approximately 1 cm long and sectioned transversely at 12 µm on a sliding microtome. The thin sections were stained with a 1% solution of safranin and mounted with a medium (Bioleite; Oken-shoji, Japan). The images (256 levels on a gray scale; 512×512 pixels) of the terminal area of each annual ring were captured with a CCD camera (MXC200; Photometrics, USA) attached to a light microscope (Axiophot; Zeiss, Germany) with an objective lens (×40). The resolution of captured images was 0.47 µm/pixel. The images were processed and analyzed with the NIH-Image program (version 1.60; Rasband 1996) in combination with a Cell Dimension Analysis Macro Program (Kobayashi 1997). The latter program was developed for semi-automatic measurements of tracheid dimensions. In this procedure, the object

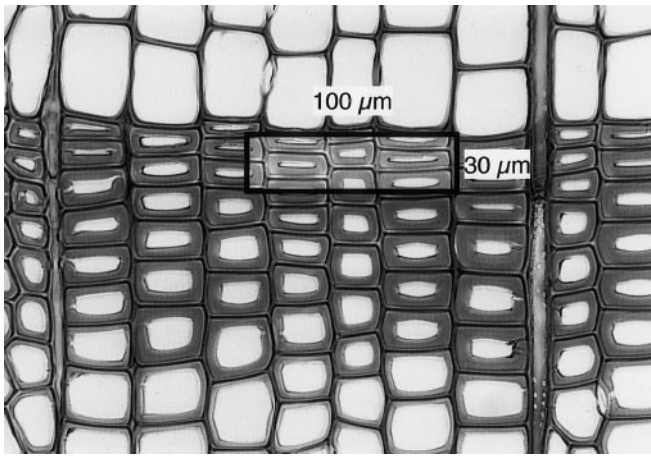
**Table 1** Characteristics of the sample and measured tracheid dimensions. Figures in parentheses are standard deviations

Tree no	DBH (cm)	Number of rings <sup>a</sup>	Mean ring width <sup>b</sup> (mm)	Mean maximum density <sup>b</sup> (kg/m <sup>3</sup> )	Mean radial cell diameter <sup>b,c</sup> (µm)	Mean tangential wall thickness <sup>b,c</sup> (µm)
1	50	235	1.50 (0.38)	900 (50)	10.2 (1.0)	3.9 (0.4)
2	33	203	1.14 (0.30)	850 (70)	13.5 (1.4)	4.7 (0.5)
3	40	239	0.79 (0.20)	860 (80)	14.7 (1.3)	5.5 (0.5)
4	52	257	0.77 (0.20)	890 (80)	13.6 (1.4)	4.8 (0.5)
5	34	176	0.74 (0.27)	990 (50)	11.7 (1.1)	4.4 (0.4)
6	44	212	0.60 (0.22)	700 (80)	11.4 (1.2)	4.1 (0.4)
7	45	481	0.50 (0.14)	850 (80)	11.5 (1.4)	4.3 (0.5)
8	44	454	0.50 (0.11)	870 (60)	12.7 (1.4)	4.2 (0.4)
9	36	294	0.30 (0.08)	800 (100)	14.8 (2.3)	3.9 (0.6)

<sup>a</sup> Number of annual rings of each of cores

<sup>b</sup> Values for 1901–1990 ( $n=90$  years)

<sup>c</sup> Mean values for the three last-formed tracheids in annual rings



**Fig. 1** A light micrograph showing the outermost part of an annual ring of *Picea glehnii*. The rectangle indicates the size of the scanning slit for X-ray densitometry

(cell wall area) was separated from the background (cell lumen area) by reference to a threshold gray level. The threshold was chosen manually on the basis of the histogram of gray levels for each scan. The radial diameter of the lumen and the thickness of the tangential cell wall of the two adjacent cells (double cell wall) were measured. Then the radial cell diameter and thickness of a single tangential cell wall were calculated for each cell by application of the following equations, which are modified versions of equations presented Filion and Cournoyer (1995):

$$SWT_i = \frac{1}{2} \left( \frac{DWT_i}{2} + \frac{DWT_{i+1}}{2} \right) \quad (1)$$

$$RCD_i = LUD_i + 2SWT_i \quad (2)$$

where  $SWT_i$  is the thickness of the single tangential cell wall of the  $i$ th cell from the terminal of the annual ring,  $DWT_i$  is the thickness of the double tangential cell wall between adjacent  $i$ -1th and  $i$ th tracheids,  $RCD_i$  is the radial cell diameter, and  $LUD_i$  is the lumen diameter. In the case of the tracheid at the terminal of an annual ring ( $i=1$ ), Eq. 1 was changed to:

$$SWT_1 = \frac{1}{2} \left\{ (DWT_1 - 1.5) + \frac{DWT_2}{2} \right\} \quad (3)$$

We fixed the thickness of the single cell wall of the earlywood tracheid that was adjacent to the last-formed latewood tracheid at 1.5  $\mu\text{m}$  because the cell wall thickness of earlywood tracheids of *Picea* spp. in Hokkaido ranges from 1.0 to 2.0  $\mu\text{m}$  (Wood Industry Editing Committee 1984). We selected five radial files per annual ring. The analyzed radial cell diameter and thickness of a single cell wall were averaged for each of the  $i$ th cells.

#### Relationships between maximum density and tracheid dimensions

The number of cells in a radial row that corresponded to the maximum density was defined subjectively before any relationship between maximum density and tracheid dimensions was examined. The mean value of the sum of radial diameter of the three last-formed cells in all annual rings was 37.9  $\mu\text{m}$  (standard deviation: 6.2  $\mu\text{m}$ ). This value was closest to the radial width of the scanning slit of 30  $\mu\text{m}$  that was used in densitometric analysis (Fig. 1). In addition, maximum percentage of cell wall area were observed only at the last or the second last cells in all annual rings. Therefore, we chose the three last-formed cells for our analysis.

The relationships between maximum density, mean single wall thickness, and mean radial diameter of the three last-formed cells

were examined by simple correlation analysis for each individual tree.

#### Development of cell chronologies and analysis of responses to climate

In order to identify the relationships between climatic factors and tracheid dimensions, we developed chronologies of radial cell diameter and cell wall thickness and then calculated simple correlation and response functions (Fritts et al. 1971; Fritts 1976) between climatic data and the chronologies. Individual series of mean radial cell diameter and cell wall thickness of the three last-formed cells were standardized by fitting linear regression lines. The individual standardized series were then averaged to establish the chronologies of radial cell diameter and cell wall thickness. Chronologies were developed with the program ARSTAN (Cook 1985; Holmes 1994). Simple correlation and response function analyses were performed to examine the relationships between cell chronologies and climatic factors. As the homogenized climatic data, we used monthly mean temperature and the monthly total precipitation at Asahikawa (43°47'N, 142°22'E; elevation 112 m), which is located about 140 km south of the study site, from May of the previous growing season to the following September (17 months; Sapporo Meteorological Observatory 1992). The monthly climatic records at Asahikawa show similar tendencies to those near the study site and significant correlations except in the case of December precipitation (Yasue et al. 1997). Calculations were made with the program PRECON (Fritts 1994), which includes a boot-strap method for estimation of the standard errors of each weight of the response function (Guiot 1990). Both analyses were performed for the period from 1901 to 1990 ( $n=90$ ).

## Results

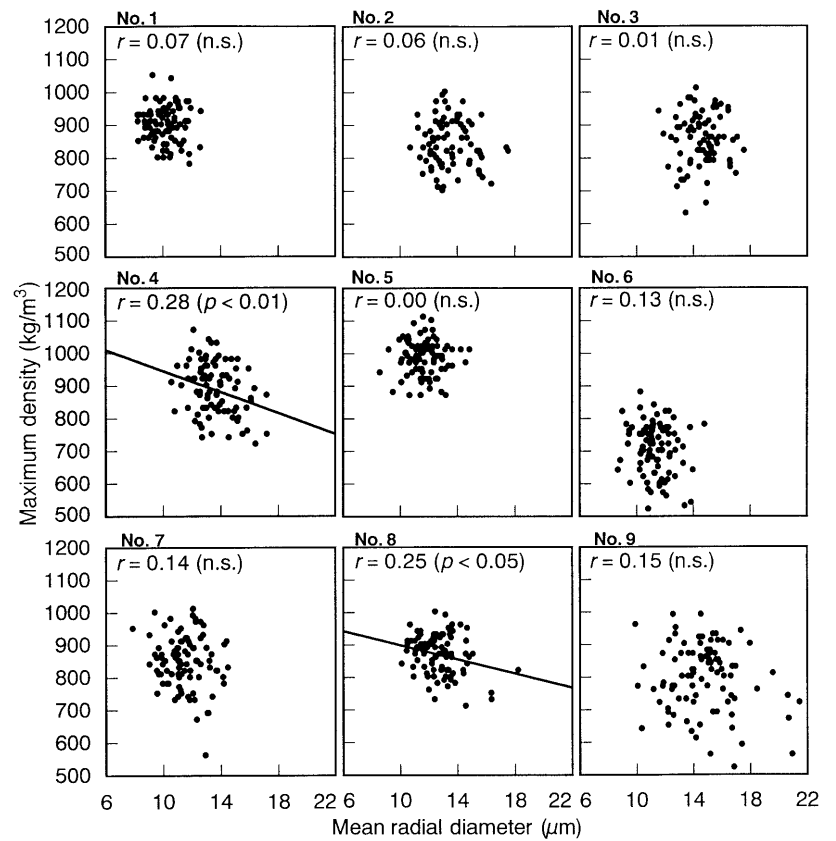
### Effects of tracheid dimensions on maximum density

Mean radial cell diameter and tangential wall thickness are shown in Table 1. No age-related differences in both cell diameter and cell wall thickness were found. All nine trees yield a significant positive correlation between maximum density and the thickness of the tangential cell walls of the three last-formed cells, whereas only two of nine trees yield a significant correlation between maximum density and radial cell diameter (Figs. 2,3). These results indicate that variations in maximum density are due mainly to changes in cell wall thickness of the last-formed cells and not to changes in radial cell diameter. In the tree with the narrowest rings (no. 9 in Figs. 2 and 3), the last three cells in some annual rings include tracheids with a large radial diameter (Fig. 2). However, increases in mean radial diameter make only a limited contribution to decreases in maximum density. Thus, cell wall thickness of the last-formed tracheids is the main factor that affects variations in maximum density, even in narrow rings.

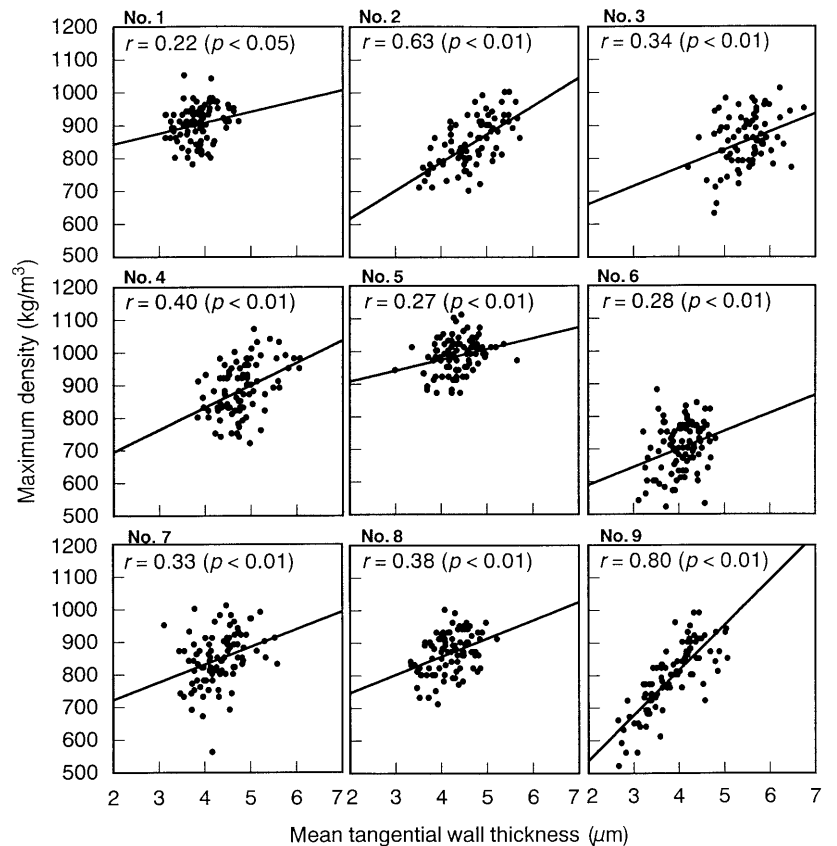
### Effects of climatic factors on tracheid dimensions

The statistical analysis of chronologies of tracheid dimensions reveal relatively low mean sensitivities (0.04 and 0.05) and standard deviations (0.04 and 0.05) for both radial cell diameter and cell wall thickness (Table 2). Thus,

**Fig. 2** Correlations between the mean radial diameter of the last-formed three tracheids and maximum density. A total of 810 annual rings (90 annual rings of each of 9 trees) were analyzed. The number in each panel refers to the tree whose characteristics are given in Table 1

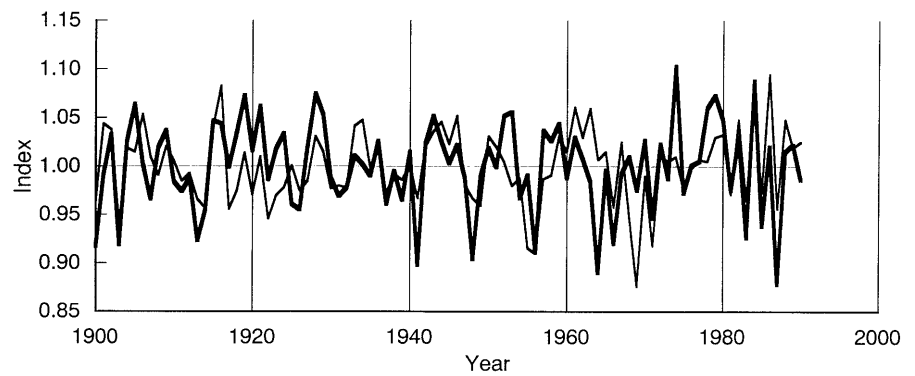


**Fig. 3** Correlations between mean thickness of tangential cell walls of the last-formed three tracheids and maximum density. A total of 810 annual rings (90 annual rings of each of 9 trees) were analyzed. The number in each panel refers to the tree whose characteristics are given in Table 1

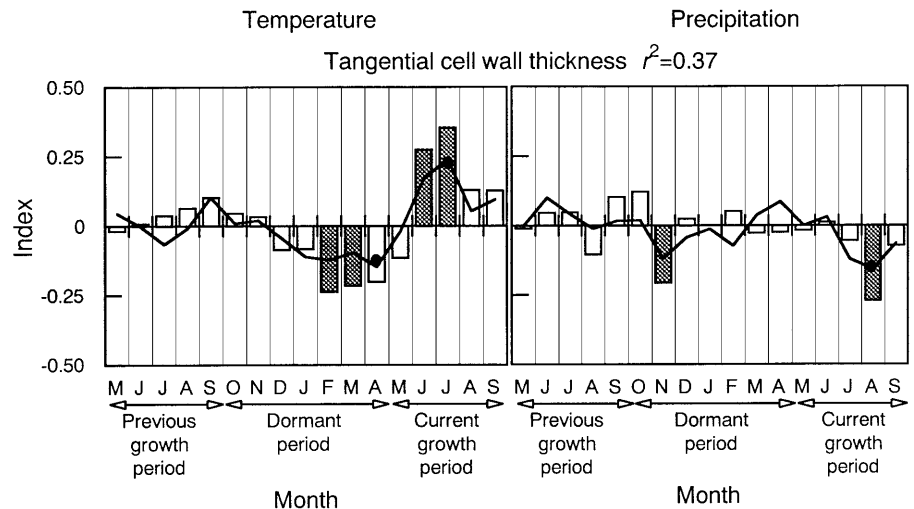




**Fig. 4** Standardized chronologies of tangential cell wall thickness (*thick line*) and maximum density (*thin line*) of the nine sample trees of *P. glehnii* in Teshio in northern Hokkaido. Each chronology was established with a standardization method fitting linear regression line. The thicknesses of tangential cell walls are mean value for the three last-formed tracheids in annual rings. Correlation between the two chronologies is 0.55 ( $P < 0.01$ )



**Fig. 5** Responses to climate of the chronology of tangential cell wall thickness of the three last-formed tracheids in annual rings of *P. glehnii* in Teshio in northern Hokkaido, obtained from response function (*lines*) and simple correlations (*columns*), calculated for the period from 1901 to 1990. The shaded columns and circles indicate significant variables ( $P < 0.05$ ).  $r^2$  is the squared multiple-correlation coefficient of the regression equation of the response function



**Table 2** Summary of statistical data for chronologies of radial cell diameter and tangential cell wall thickness in *P. glehnii*

	Radial cell diameter <sup>a</sup>	Tangential cell wall thickness <sup>a</sup>
Trees in chronology ( <i>n</i> )	9	9
Spans of chronology	1901–1990	1901–1990
<i>Standardized chronology</i>		
Mean sensitivity	0.04	0.05
Standard deviation	0.04	0.05
First-order autocorrelation	0.13	-0.04
Mean correlation between trees	0.00	0.14
Signal to noise ratio	0.03	1.45
Variance in first eigenvector (%)	21.8	25.3

<sup>a</sup> Mean values for the three last-formed tracheids in annual rings

there is low year-to-year variability in radial diameter and cell wall thickness. The mean correlation between trees for cell wall thickness (0.14) indicates that the sampled trees give moderately common signals. The mean correlation is the same as that obtained for maximum density (0.14) in a previous study of *P. glehnii* (Yasue et al. 1997). A chronology of cell wall thickness was established, as shown in Fig. 4. By contrast, the mean correlation between trees with respect to radial cell diameter is

zero, indicating that there are no common signals among trees. Because of the lack of synchronization of inter-tree variations in radial cell diameter, no chronology of radial cell diameter could be established. The chronology of cell wall thickness revealed a similar pattern to that of maximum density (Fig. 4). This also indicates that variations in maximum density are due mainly to changes in cell wall thickness of the last-formed cells.

Simple correlation analysis of the relationships between cell wall thickness and climatic factors reveals that cell wall thickness is negatively correlated with temperature in the February and March that preceded the radial growth and is positively correlated with temperature in the June and July of the current year. It is also negatively correlated with precipitation during the previous November and the current August (Fig. 5). Similarly, the response function reveals a positive correlation with temperature in the current July and a negative correlation with precipitation during the current August. Moreover, 37% of the variance of indices of cell wall thickness can be explained by the regression equation of the response function. These statistical results indicate that the cell wall thickness of the last-formed cells is mainly influenced in a positive manner by temperature and in a negative manner by precipitation in summer during the current growing season.

## Discussion

Our anatomical examination of relationships between maximum density and tracheid dimensions revealed that changes in maximum density were due mainly to changes in cell wall thickness. In addition, the statistical analyses of the response to climate indicated that the cell wall thickness of the last-formed cells was influenced positively by temperature and negatively by precipitation during the summer of the current growing season. This pattern of responses is the same as that reported previously for maximum density (Yasue et al. 1997). These results suggest that variations in maximum density of *P. glehnii* are due to differences in the cell wall thickness of the last-formed cells that were influenced by the climate in summer. Thus, our observations of the way in which climate influences variations in maximum density confirm that the maximum density of *P. glehnii* is useful as an indicator of changes in climate.

During the seasonal radial growth of *P. glehnii* in Teshio, cell division occurs from the beginning of May to the middle of August, and the thickening of the cell walls of tracheids continues until the end of September (Yasue et al. 1994). The period during which the last-formed cells mature corresponds to the months that yielded significant correlations between climatic factors and cell wall thickness. Thus, the climate in summer might directly affect the thickening of cell walls of the last-formed tracheids. The physiological significance of these correlations is not fully understood, even though there have been many experimental studies of the effects of environmental factors on tracheid dimensions (e.g., Denne and Dodd 1981). In general, cell wall thickness has been shown to be determined by the duration of cell wall thickening (Wodzicki 1971; Skene 1972; Jenkins 1975; Denne 1976). By contrast, studies of the direct effects of temperature on tracheid dimensions have indicated that higher temperatures accelerate the rate of cell wall thickening (Denne 1971; Wodzicki 1971). However, the net effect of elevated temperature on cell wall thickness seems to be relatively minor since the duration of cell wall thickening is decreased at higher temperatures (Denne 1971; Denne and Dodd 1981; Antonova and Stasova 1993, 1997). Thus, the observed positive effect of temperature in summer on cell wall thickness was probably due to an increase in the duration of cell wall thickening rather than to an increase in the rate of thickening.

We also found a negative correlation between cell wall thickness and August precipitation. There have been few reports, to our knowledge, on the negative effects of precipitation on cell wall thickness but there have been several reports of positive relationships between cell wall thickness and the light quantity (Denne and Smith 1971; Smith 1975; Denne 1976). These reports have revealed that a decrease in day length or in light intensity results in a rapid decline in cell wall thickness (Denne and Smith 1971; Smith 1975; Denne 1976). The meteorological data for Asahikawa revealed a strong correla-

tion between the duration of sunshine in August from 1891 to 1980 ( $n=90$ ) and August precipitation ( $r=-0.52$ ;  $P<0.01$ ); however, the homogeneity of the data with respect to the duration of sunshine has not been verified. Thus, the negative correlation with August precipitation might be attributable to an effect of the duration of sunshine rather than to a direct effect of rainfall on cell wall thickness. The longer duration of sunshine in late summer, which is associated with low precipitation, might increase cell wall thickness by increasing in the duration of cell wall thickening.

In summary, it appears that both temperature and the duration of sunshine of summer affect the cell wall thickness of the last-formed cells and, as a consequence, they cause variations in the maximum density of *P. glehnii*. The present results can explain how climate affects maximum density in a cool temperate zone and confirm the usefulness of changes in maximum density as indicators of changes in climate.

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