Relationship between Ring Width and Tracheid Characteristics In *Picea crassifolia:* Implication in Dendroclimatology

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Ring width represents the total width of cells in a growing season. Relatively few studies have identified which of the parameters, cell number, size, or wall thickness is the greater contributor to variations in ring width. It is difficult to clearly explain the relationship between the climate in which a tree is located and the ring growth. In this study, the ring width and various tracheid characteristics (radial lumen diameter, double wall thickness, and number) in 298 rings of *Picea crassifolia* wood were investigated. Tree rings were quantitatively categorized based on their width into large, medium, and narrow classes. The tracheid number and lumen diameter were strongly correlated with annual ring width. The tracheid number had the strongest effect on the ring width. The effect of the tracheid number was three times larger than that of the lumen diameter. More earlywood cells were formed in larger rings, while larger earlywood cells were produced in years when narrow rings were formed. Wall thickness had no appreciable effect on ring width. The results of this study help to understand the relationship between the climate and the ring growth from the tree physiology perspective, when ring width is used as a climate proxy.

Keywords: Tracheid number; Tracheid diameter; Tracheid wall thickness; Ring width; Pointer year; Wood science; Dendroclimatology

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INTRODUCTION

Trees record their responses to changes in growth conditions in their wood structure. Tree ring width is a popularly used climate proxy. It has allowed for many advances in the understanding of how trees grow and respond to changing climate conditions (Downes *et al*. 2002). Tree ring formation originates from cell production; after a cell is produced by cell division in the cambium, it grows in the radial and longitudinal directions, and finally, secondary wall formation begins (Gindl *et al.* 2000).

Ring width represents the sum of a growing season's cell production, but conflicting results have been reported. Rossi *et al*. (2008) and Wodzicki *et al*. (1983; 2001) suggested that ring width is determined by cell number, as lesser cell division leads to narrower rings. Deslauriers *et al*. (2008) suggested that cell size contributes more to ring width based on observations of wood formation in *Pinus leucodermis* in two contrasting years. They demonstrated that the difference between narrow rings and large rings was mainly related to cell size, because larger earlywood tracheids were produced in years when larger rings were formed. Reductions in lumen area and cell diameter of up to 50% were observed in the cells produced during dry periods, and fewer cells with narrower rings were observed in non-irrigated *Abies balsamea* seedlings (Rossi *et al*. 2009). The complex, largely unexplored relationship between cell characteristics (cell number and diameter) and ring width have permitted only vague explanations of the effects of climate on ring width.

Picea crassifolia Kom. is an androgynous, evergreen, native Chinese tree species, primarily grown in pure stands or with conifer or broadleaf trees. It is most prevalent at elevations between 1700 and 3500 m in the cold and semi-arid regions of northwestern China. This species has drawn great attention of dendroclimatic studies in China because of its climate sensitivity and distinct tree-ring structure (Fang *et al*. 2009; Gou *et al*. 2005; Liang *et al*. 2006; Zhang *et al*. 2009; 2010). To investigate the contribution of different cell characteristics to ring width and to understand whether the relationship between cell characteristics and ring width varies from narrow to large rings, the ring width and tracheid characteristics (radial lumen diameter, double wall thickness, and number) in 298 rings of a *Picea crassifolia* tree were investigated. The 298 tree rings were quantitatively categorized into large, medium, and narrow rings based on their width.

EXPERIMENTAL

Sample Processing and Measurement

The selected study site was a 300-ha woodland containing semi-natural, pure *P. crassifolia* (38°32′41″N, 100°18′25″E, 2600 m a.s.l.), located on the northern and northwestern slopes of the Qilian mountains at the edge of the Tibetan plateau. The soils are a sandy loam with abundant lichens and few shrubs and grasses. The area has a mean density of around 300 trees/ha and average crown closure of 60 percent. Forty dominant *P. crassifolia* trees of similar diameter were sampled in duplicate by removing a 12-mm diameter, pith-to-bark core at breast height in early September 2009. The annual ring and latewood widths of 60 cores (from 30 trees) without decay or nodes were measured by LINTAB. The measured ring widths of all samples were cross-dated using the COFECHA program (Holmes 1983) to develop a ring width chronology in order to analyze the relationship between climate and the growth of *P. crassifolia* (Xu *et al*. 2011; 2012; 2013). The tracheid characteristics were obtained from a sub-sample of five trees (Table 1) and were highly correlated with the master series used in the dendrochronology analysis.

To measure the tracheid characteristics, cross-sections of wood with thicknesses of 10 µm and lengths of approximately 20 mm were cut using a sliding microtome. To better distinguish cell lumen from cell walls, sections were stained with safranin and astra blue, dehydrated with alcohol and xylol, and mounted on glass slides. A color CCD digitizing video camera linked to an optical microscope (200x magnification, Olympus, VM-60N, Japan) and a computer was used to measure the tracheid characteristics. The tracheid radial lumen diameter (tracheid diameter) and double wall thickness (tracheid wall thickness) along five radial cell rows were measured individually, from earlywood to latewood, in each tree-ring. The number of tracheids was counted along five radial cell rows in each tree-ring. Only those rows in which the tracheids were approximately in the middle of their lengths were chosen, as shown in Fig. 1.

Table 1. Characteristics of *P. crassifolia* Trees in this Study

Tree Number	Age	DBH (cm)	Height (m)	Ring Width (mm)
1	1948 to 2009	27.4	12.3	1.82 (0.50)
20	1941 to 2009	25.0	16.7	1.30 (0.52)
22	1957 to 2009	25.7	14.3	1.78 (0.34)
28	1951 to 2009	28.5	12.3	1.99 (0.51)
33	1951 to 2009	25.9	11.8	1.82 (0.56)

Values are means (coefficient of variance). DBH: diameter at breast height

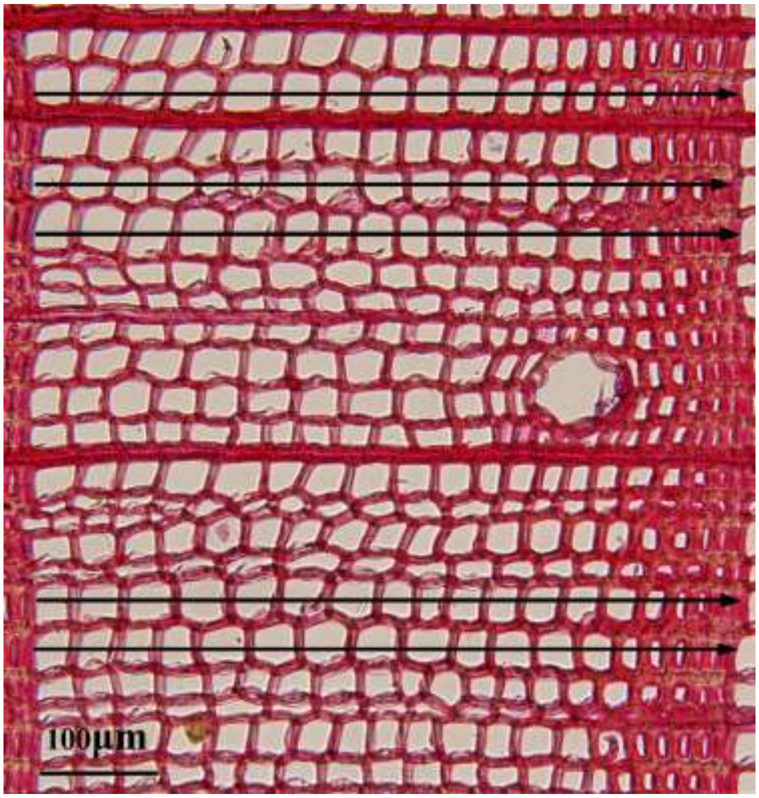

Fig. 1. Image of the structure of a cross-section of *P. crassifolia* wood. The tracheid radial lumen diameter, double wall thickness, and tracheid number were measured along the five directions indicated by the arrows, individually, from earlywood to latewood

Classification of Tree Rings

Tree-rings were classified by ring width as large, medium, or narrow according to the following formulas,

$$\text{Large ring: when } RW_{ij} > \overline{RW_i} + SD_i \quad (1)$$

$$\text{Medium ring: when } \overline{RW_i} - SD_i < RW_{ij} < \overline{RW_i} + SD_i \quad (2)$$

$$\text{Narrow ring: when } RW_{ij} < \overline{RW_i} - SD_i \tag{3}$$

where *RW* is ring width, *SD* is the standard deviation of the ring width, i (i = 1, 2, 3, 4, 5) is the tree number, j (j = 1, 2, 3, …, n) is the annual ring number, and *n* is the tree age. According to the above definitions, there were 44 large rings, 214 medium rings, and 40 narrow rings in the 298 total rings.

Data Analysis

The annual cell lumen diameter, double wall thickness, and tracheid number data used for statistical analysis were the mean values determined from five radial cell rows. Typical latewood cells were characterized by a double cell-wall thickness two times larger than their lumen diameter (Mork 1928).

Linkage and the underlying causes between ring width and tracheid characteristics were studied using path-analysis. Each standardized path coefficient indicates the degree to which a dependent variable is directly affected by an independent variable. In statistical terms, a path coefficient indicates the change expected in the dependent variable, relative to its standard deviation, for one standard deviation change in the independent variable. Because the coefficients are standardized, changes in the dependent variables are directly comparable.

RESULTS AND DISCUSSION

Long-term Trends

At the whole annual ring level, the tracheid number showed similar long-term trends as the ring width, decreasing from 1957 to 1983 and fluctuating between 1984 and 2009 (Fig. 2). The tracheid diameter and wall thickness displayed opposite long-term trends than ring width. The variation patterns of the ring width and the tracheid characteristics of earlywood were similar to those of annual rings, but with less year-to-year fluctuation. Comparing annual rings and earlywood, the long-term trends in latewood width were generally absent, but with parameter-specific variation.

Parameters of Different Tree Rings

The tracheid number for larger rings was significantly larger ($p < 0.001$) than that for narrow rings in both earlywood and latewood. No effects of the tracheid radial lumen diameter or the double wall thickness on ring width were evident. The variation of the same parameter, expressed by the coefficient of variation (CV), tended to increase from earlywood to latewood and was clearly higher for tracheid number than for the other cell parameters in all tree-rings (see Table 2).

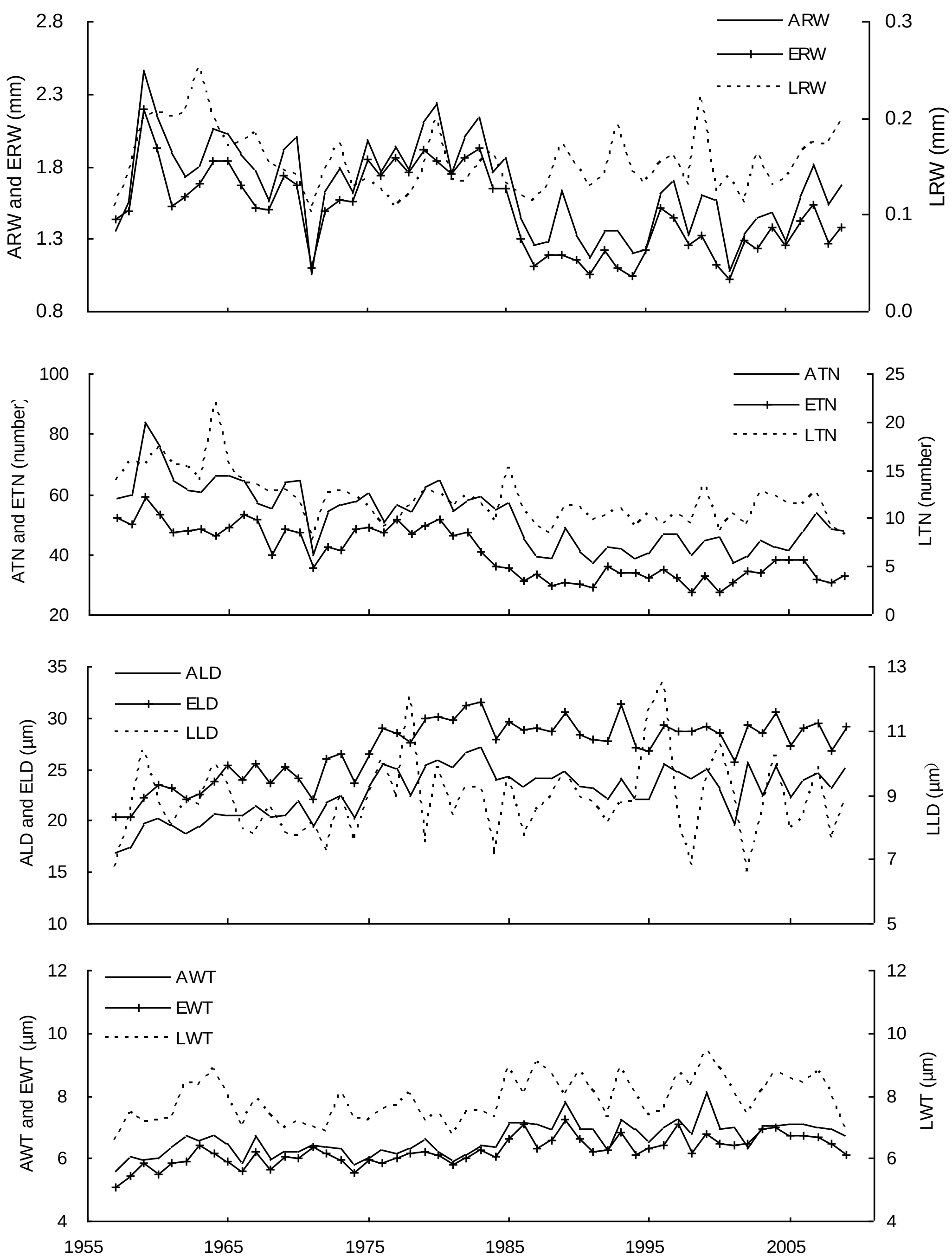

Fig. 2. Time series of tracheid characteristics and ring width in the period from 1957 to 2009. ARW: annual ring width; ERW: earlywood ring width; LRW: latewood width; ATN: annual tracheid number; ETN: earlywood tracheid number; LTN: latewood tracheid number; ALD: annual mean tracheid radial lumen diameter; ELD: earlywood mean tracheid radial lumen diameter; LLD: latewood mean tracheid radial lumen diameter; AWT: annual mean tracheid double wall thickness; EWT: earlywood mean tracheid double wall thickness; and LWT: latewood mean tracheid double wall thickness

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Table 2. Ring Width and Tracheid Characteristics for Annual Ring, Earlywood, and Latewood of the Sampled Trees

Ring Classification		Ring Width (mm)	Tracheid Diameter (µm)	Tracheid Wall Thickness (µm)	Tracheid Count (number)
Annual ring	Large ring	2.38 (0.26)	23.45 (0.17)	5.96 (0.19)	76.68 (0.31)
	Medium ring	1.67 (0.25)	22.33 (0.15)	6.58 (0.17)	55.14 (0.28)
	Narrow ring	1.27 (0.40)	20.79 (0.15)	6.10 (0.15)	47.64 (0.40)
Earlywood	Large ring	2.17 (0.27)	26.53 (0.16)	5.69 (0.16)	62.53 (0.34)
	Medium ring	1.51 (0.26)	26.49 (0.16)	6.20 (0.16)	42.81 (0.36)
	Narrow ring	1.13 (0.44)	25.21 (0.14)	5.77 (0.15)	36.45 (0.45)
Latewood	Large ring	0.20 (0.55)	7.22 (0.22)	9.07 (0.25)	14.15 (0.43)
	Medium ring	0.16 (0.56)	8.73 (0.31)	7.80 (0.18)	12.24 (0.35)
	Narrow ring	0.14 (0.29)	8.36 (0.19)	7.50 (0.18)	11.18 (0.46)

Values are means (CV).

The ratio of earlywood width to the whole annual ring width was 85%. The ratio of earlywood width to the whole annual ring width of the tracheid wall thickness for large rings was almost equal to that for narrow rings. The ratio of earlywood width to whole annual ring width of the tracheid number and ring width for large rings was significantly higher than those for narrow rings, while the ratio of earlywood width to whole annual ring width of tracheid diameter for narrow rings was significantly higher than that for large rings. This indicates that more earlywood cells were formed in larger rings than in narrower rings, while larger earlywood cells were produced in years when narrow rings were formed (Table 3).

Table 3. ANOVA of Ratio of Earlywood to Annual Ring (E/A) between Large Rings and Narrow Rings

Ring Width	Tracheid Diameter	Tracheid Wall Thickness	Tracheid Number
Large ring>narrow ring**	Large ring<narrow ring**	NS	Large ring >narrow ring***

NS: non-significant; *: significant at p = 0.05; **: significant at p = 0.01; ***: significant at p = 0.001.

Relationships between Tracheid Characteristics and Ring Width

The number of tracheids had the strongest correlation with the annual ring width. Tracheid wall thickness was negatively correlated with ring width, while tracheid diameter did not exhibit any significant correlation. Tracheid diameter had a negative relationship with earlywood width. In latewood, the number of tracheids and their diameter were significantly related to the latewood width for both medium and narrow rings. Tracheid wall thickness was not significantly correlated with ring width for any latewood width (Table 4). Tracheid diameter was positively related to wall thickness. The tracheid number was negatively correlated with the tracheid diameter and wall thickness in annual rings and earlywood, but positively correlated in latewood (Table 5). Cell number and size have a degree of plasticity that are dependent on the environmental conditions (Thomas *et al*. 2006); a negative relationship between cell number and cell lumen diameter in earlywood was shown (Table 5).

Table 4. Pearson's Correlation of Ring Width to Tracheid Characteristics for Annual Rings, Earlywood, and Latewood

Ring Classification		Tracheid Diameter	Tracheid Wall Thickness	Tracheid Number
Annual ring	Large ring	-0.17	-0.11	0.90***
	Medium ring	0.06	-0.04	0.81***
	Narrow ring	0.06	-0.36**	0.86***
Earlywood	Large ring	-0.27*	-0.22	0.84***
	Medium ring	-0.04	-0.02	0.76***
	Narrow ring	-0.20	-0.30*	0.90***
Latewood	Large ring	0.16	-0.14	0.23
	Medium ring	0.13*	0.06	0.34***
	Narrow ring	0.38**	0.05	0.26*

*: significant at p=0.05; **: significant at p=0.01; ***: significant at p=0.001 (two-tailed).

Table 5. Pearson's Correlation between Different Tracheid Characteristics of Annual Rings, Earlywood, and Latewood

Ring Classification		Diameter vs. Wall Thickness	Diameter vs. Number	Wall Thickness vs. Number
Annual ring	Large ring	0.41**	-0.54***	-0.23
	Medium ring	0.48***	-0.31***	-0.29***
	Narrow ring	0.11	-0.37*	-0.38*
Earlywood	Large ring	0.46**	-0.58***	-0.38*
	Medium ring	0.55***	-0.42***	-0.32***
	Narrow ring	0.23	-0.50***	-0.35*
Latewood	Large ring	0.12	0.37*	0.17
	Medium ring	0.33***	0.26***	0.12
	Narrow ring	0.13	0.44**	- 0.08

Correlation between tracheid diameter and tracheid wall thickness (Diameter vs. Wall Thickness), between tracheid diameter and tracheid number (Diameter vs. Number), between tracheid wall thickness and number (Wall Thickness vs. Number). *: significant at p=0.05; **: significant at p=0.01; ***: significant at p=0.001 (two-tailed).

In Fig. 3, the path-analysis model shows standardized partial regression coefficients, or path coefficients that indicate the degree to which the independent variables (tracheid characteristics) had direct effects on the dependent variable (ring width). The coefficients indicate the change expected in the dependent variable for a 1 standard deviation change in the independent variable. For example, a 1 standard deviation increase in tracheid number caused a 1.04 standard deviation increase in earlywood width for large rings. Because the coefficients are standardized, changes in the dependent variables can be directly compared. Path coefficients are influenced by correlations among predicting variables. In Fig. 3, the tracheid characteristic variables are connected through curved, two-headed arrows that represent simple correlations. The strongest direct effect of a tracheid characteristic on ring width was that of the tracheid number. The direct effect of the tracheid number was three times larger than that of the lumen diameter. Wall thickness had no appreciable effect on the ring width. There was a positive correlation between the radial lumen diameter and the wall thickness for large rings. A greater variance in the annual ring width (R^2 = 0.93) was explained by tracheid characteristics than that of earlywood width (R^2 = 0.77) in large rings, while similar variances of annual ring and earlywood widths were explained by tracheid characteristics.

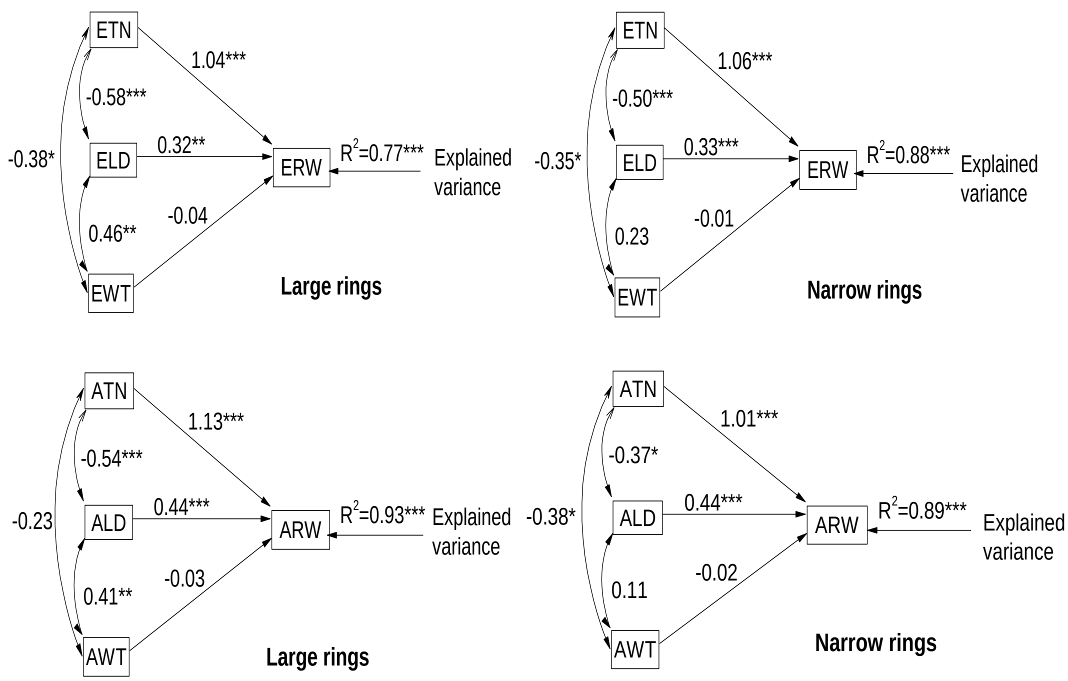

Fig. 3. Path-analysis model tests of the relationships between annual ring width (ARW) and earlywood width (ERW) and tracheid characteristics. Curved arrows indicate correlations between tracheid characteristics. Straight arrows point from independent to dependent variables, implying causation. Path coefficients are the direct effects of the variable at the tail-end of the arrow on the variable at the head of the arrow. Relationships between latewood width and tracheid characteristics were not shown in this diagram because no significant influence of tracheid characteristics on latewood width were found

Long-term Trends and Variation of Parameters

Distinctive long-term trends were shown for all parameters at annual ring and earlywood levels, which were in agreement with typical trends for conifers. These long-term trends have often been considered "noise" in the domain of dendroclimatology, since they are believed to be largely influenced by non-climatic factors. Numerous sophisticated statistical methods have been developed to filter out these trends (Cook and Kairiukstis 1990; Fritts 1976). The high variabilities, expressed by high coefficients of variance, of the tracheid number and latewood cell parameters without apparent long-term trends are particularly interesting to dendroclimatological studies as they are influenced more by climate (Mäkinen *et al*. 2002; Park and Spiecker 2005). The greater coefficient of variance of all parameters in narrow rings reinforces the important role of narrow rings in dendroclimatological studies.

Relationships between Cell Characteristics and Ring Width

The formation of annual rings occurs due to the production of cells by the cambium, the growth of cambial derivatives by expansion, and secondary wall thickening. The former two processes determine the annual increment width. The latter determines the accumulation of biomass in cell walls, which increments the total biomass of wood (Antonova and Stasova 1993). Ring width is a measure of the sum of a growing season's cell division and cell enlargement activity in the direction of the xylem (Gindl *et al*. 2000). It depends mainly on the rate of periclinal cell division and the cell enlargement phase in the cambial region (Wimmer and Grabner 2000).

In this study, correlation and path-analysis indicated that the tracheid number was the most important predictor of ring width. The direct effect of tracheid number was three times larger than that of the trachied lumen diameter. Put another way, cell number and size defined tree-ring width (Deslauriers and Morin 2005), but cell number contributed much more to ring width than cell size did.

Earlywood accounts for about 85% of the total ring width in *P. crassifolia* trees, therefore earlywood width is very important to the total ring width. Variations in earlywood width depend on the start of the growing season (early or late) and the time of the early- to latewood transition (Deslauriers *et al*. 2003). Delaying the beginning of cell formation commonly leads to narrow rings. This occurs because the beginning of the growing season varies considerably, depending mostly on climate variation (Creber and Chaloner 1984; Vaganov *et al*. 1994). Cambial activity is influenced by temperature and water availability throughout the growing season; the more intense of the two is the decisive factor (Horacek *et al*. 1999). The earlywood-to-latewood transition time varies depending on the start of the growing season and on the cell formation rate. Year-to-year climatic variations, such as soil or water deficits (Eilmann *et al*. 2009), have been found to explain the variation in the earlywood-to-latewood transition time. In this study, the ratio of earlywood to latewood tracheid numbers in larger rings was significantly higher than that in narrower rings, while the reverse was true for the tracheid lumen diameter. This suggested that more earlywood cells were formed in larger rings, while larger earlywood cells were produced in years when narrow rings were formed.

CONCLUSIONS

1. The tracheid number and lumen diameter showed strong correlations with the annual ring width.
2. The tracheid number had the strongest effect of any of the tracheid characteristics on the ring width. The direct effect of tracheid number on the ring width was three times larger than that of the lumen diameter.
3. More earlywood cells were formed in larger rings, while larger earlywood cells were produced in years when narrower rings were formed.

4. Wall thickness had no effect on ring width. This result is helpful in understanding the relationship between tree growth and climate from a tree physiology perspective, when ring width is used as a climate proxy.

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