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Research paper

Wood properties in a long-lived conifer reveal strong climate signals where ring-width series do not

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Although tree-ring-width chronologies have been widely used for temperature reconstructions, there are many sites around the world at which there is little evidence of a clear climate signal in the ring-width chronologies. This is the case with the long-lived conifer Huon pine (*Lagarostrobos franklinii* (Hook. F.) Quinn), endemic to Tasmania, Australia, when the species grows at low elevation. In this study, we developed chronologies of several wood properties (e.g., tracheid radial diameter, microfibril angle) from Huon pine growing at a low-elevation site. We found that despite the absence of a climate signal in the ring-width chronologies, there were significant correlations between wood density, tracheid radial diameter and microfibril angle and temperature, stream flow and a drought index, enabling the development of robust chronologies. This novel finding suggests that chronologies based on these wood properties may have important potential for climate reconstructions from sites and species that have not yet been realized. In particular, a relatively extensive resource of ancient, low-elevation Huon pine in western Tasmania, in which climate signals have not been found using ring widths, may now be useful as part of the broader effort to reconstruct Southern Hemisphere climate.

Keywords: dendroclimatology, Huon pine, microfibril angle, SilviScan, Southern Hemisphere, Tasmania, xylem.

Introduction

Tree ring-based reconstructions of past temperature variability are important for putting current changes in regional and global temperatures into a broader historical context (Mann et al. 2008). Typically, climate reconstructions from tree rings are based on samples taken from trees growing at, or near, their environmental limits (e.g., high elevations or dry sites) (Fritts 1976, Salzer et al. 2009). Trees growing at sites that are not perceived to be temperature- or water-limited are largely ignored for climate reconstruction because empirical data and physiological models have shown that the tree-ring series they produce are not highly sensitive to climate variability. The consequence of this sampling approach is that most trees are not considered appropriate for developing temperature reconstructions. In the Southern Hemisphere (SH), where the total area of terrestrial habitat is much smaller than in the Northern Hemisphere (NH), particularly at high latitudes, this is an important issue and has directly limited SH dendrochronological research (Francey 1984, 1985, Cullen and Grierson 2007, Boninsegna et al. 2009, Allen et al. 2012). Consequently, the development of SH climatic reconstructions is based on a very sparse network of long chronologies (Martinelli 2004, Jones et al. 2009, Neukom and Gergis 2011). Identifying new avenues for the development of climate-sensitive SH tree-ring chronologies is a major research priority and is fundamentally important to better understanding regional climate variability as well as inter-hemispheric synchrony in the global climate system.

One of the longest chronologies in the SH is from high-elevation Tasmanian Huon pine, *Lagarostrobos franklinii*

(Hook. F.) Quinn), which spans more than 3000 years (Buckley et al. 1997, Cook et al. 2006). The chronology has successfully been used to develop a summer temperature reconstruction, which has been a critical contribution to efforts to understand past temperature in the SH (Cook et al. 2000, 2006). However, the Huon pine population at Mt Read is an ecological anomaly—it is the only known occurrence of the species above 900 m. Almost all other Huon pine stands are restricted to river valleys at low elevations in western Tasmania, representing a much larger resource that would allow for sampling over a much wider geographic and climatic range and potentially, the development of longer chronologies, than from Mt Read (Buckley et al. 1997). Unfortunately, the low-elevation Huon pine do not crossdate well and the ring-width chronologies that have been developed show a complex but weak temperature signal (Buckley et al. 1997), rendering the ring-width chronologies of little value for temperature reconstruction.

In recent years, a growing body of research has indicated that climate signals can be found in various properties of the wood, but not the ring widths, and that these wood properties can be used to develop climate-sensitive chronologies and proxy climate records from sites that had previously been considered of little or no value for dendroclimatic studies (Poussart and Schrag 2005, Gagen et al. 2006). Most research in this area has focused on variability in cell wall thickness, wood density and stable isotopes (Briffa et al. 2002, McCarroll and Loader 2004, Vaganov et al. 2006, Cullen and Grierson 2007, Sidorova et al. 2012). Very little attention has been given to properties such as tracheid radial diameter and microfibril angle (MFA). Tracheid cross-sectional area has, however, been shown to have a temperature signal (Vaganov et al. 2006, Fonti et al. 2010). A relationship between tracheid diameter and temperature may be caused by low-temperature limitations to the actual physiological processes involved in cell growth and/or reductions in carbohydrate allocation, or due to a reduction in cell turgor or wall extensibility under conditions of drought (Rossi et al. 2007, Hölttä et al. 2010). Microfibril angle is the angle of the cellulose microfibrils in the cell wall, relative to the long axis of the cell. High-resolution radial variation in MFA has hardly been considered in dendroclimatology research at all, owing largely to the difficulty of measurement and interpretation (Xu et al. 2012). Nevertheless, MFA is well known in the wood products literature to be highly sensitive to even short-term changes in environmental conditions in many tree species (Lindström et al. 1998, Wimmer and Grabner 2000, Wimmer et al. 2002, Donaldson and Xu 2005, Donaldson 2008, Drew et al. 2009*b*) and is therefore worthy of greater consideration.

In this study we demonstrate the potential for using wood density, tracheid radial diameter and wall thickness and MFA to build robust, climate-sensitive chronologies from trees that exhibit complacent ring-width series. We focus on low-elevation Huon pine because of the potential importance of developing a broader network of Huon pine chronologies to contribute to SH climate reconstructions. We addressed two specific research questions:

(1) Does low-elevation Huon pine exhibit sufficient common variability between series in specific wood properties to allow for the development of robust temporal chronologies?
(2) Is there a significant climate signal in wood properties chronologies from low-elevation Huon pine, even if no signal can be discerned in a ring-width chronology?

Materials and methods

Study site and trees sampled

We conducted this research in low elevation (60 m ASL) temperate rainforest adjacent to the King River, near the town of Queenstown in western Tasmania, Australia. We focused our sampling on the long-lived endemic conifer *L. franklinii* (Huon pine), which was relatively common in our study area. Sample cores 12 mm diameter were extracted from 18 trees (mean diameter at breast height of the sampled trees was 36.2 ± 2.2 cm) using a motorized corer. Although this site was not ideal (it is likely that there had been some disturbance at the site in the late 1800s by nearby mining activity), a major reason for its selection was that we were permitted to take 12-mm diameter wood cores (such sampling is usually not allowed in Tasmania). These larger cores are far better suited for the measurement of wood properties than standard 5 mm cores, as they minimize sample twisting and breakage, which commonly occurs with the 5 mm cores collected by dendrochronologists. Sample preparation is also easier, allowing for more consistent results and minimizing sample loss. We took two cores from 15 trees, and a single core from an additional three trees.

Sample preparation for wood properties measurements

The tree core samples were processed into strips of a standard width (2 mm) in the tangential direction using a custom-designed twin-blade saw. The transverse surface of each strip was polished, as described in Evans (1994), prior to automated cell dimension analysis. Radial variation of wood properties was then measured using SilviScan-3, a rapid-assessment high-resolution technology developed by CSIRO Australia (cf. Evans 1994). Wood density, measured by X-ray densitometry, was measured at a sampling interval of 25 μm. Microfibril angle, the angle of the cellulose microfibrils in the secondary wall relative to the longitudinal cell axis, was measured using a 200-μm pencil beam at a sampling interval of 100 μm, by means of X-ray diffractometry. Tracheid radial diameters were measured over 25 μm intervals using image analysis of the transverse surface. Tracheid wall thickness was calculated from tracheid diameter and wood density. SilviScan adjusted sample orientation by as much as ± 40° to align the rings with the X-ray beam in both densitometry and diffractometry. Earlywood and latewood were defined as the portion of the ring in which wood density was respectively below or above the mean wood density of the ring. In many samples, severe ring curvature near the pith meant that wood property data measured in approximately the first 20 rings was usually not reliable; these data were excluded from analyses.

Climate data

Temperature and precipitation data for the site were obtained from Australian SILO interpolated climate surfaces (Jeffrey et al. 2001). Although the data extend back as far as 1889, no weather stations on Tasmania's west coast recorded data prior to 1900, and the data are most accurate after 1957, when the surfaces were derived from quality-checked data from the Australian Bureau of Meteorology (BOM). At the study site mean summer (December–March) and winter (June–August) temperatures are 14.5 and 8.1 °C, respectively. Mean annual rainfall is ~2400 mm. Summer mean maximum temperature was significantly negatively correlated with total summer rainfall ($r = -0.54$; $P < 0.001$) and relative humidity ($r = -0.76$; $P < 0.001$).

In addition to the climate data, we obtained gauged streamflow data for the King River from a position ~10 km upstream from the research site. More than 50 years of high-quality data were provided by Hydro Tasmania for the period 1924–90. In 1990, the river was dammed and monitoring ceased.

To obtain an indication of drought variability at a broader scale, we used the 12-month standardized precipitation evapotranspiration index (SPEI) (Vicente-Serrano et al. 2010*a*) values (calculated on a 0.5° grid) for the position of the research site. The index is based on a climatic water balance model and accounts for the accumulation of deficits/surpluses at differing timescales. The estimates are spatially and temporally comparable with other datasets (Vicente-Serrano et al. 2010*b*). A high value of the SPEI corresponds to wetter conditions.

Chronology development and climate correlations

In order to develop robust chronologies we must be able to reliably date and crossdate samples. In a tree with no missing or false rings, a simple ring count can establish the date of a particular ring in a particular sample, provided the date of the outer ring is known. Crossdating, in contrast, refers to the matching of ring-width patterns (or patterns of other properties) over time among samples from the same tree, and different trees at the same site. Crossdating also enables identification of missing and false rings in individual samples (Fritts 1976) and confirms precise annual dating of samples. At sites where there is a common broad-scale environmental factor that controls ring-width patterns or patterns of other properties in a common way across the site (e.g., drought at dry sites, temperature at high-elevation sites), it is generally much easier to crossdate samples than at sites less limited by a broad-scale environmental factor.

We used a two-step process to ensure accurate crossdating of the wood properties data. The first step involved dating rings and traditional dendrochronological crossdating of ring widths. The second step was to examine crossdating of the wood properties data, using dates derived from the observed rings. The purpose of this two-step approach was to see whether samples from low-elevation Huon pine, known to be suboptimal in terms of ring-width crossdating, still contained a site-wide climate signal in the wood properties. If there were site-wide signals in the wood properties but not in ring widths, then variations in wood property profiles could be considered more consistent across the population than variations in ring widths. If a site-wide signal in wood properties is present, then it is reasonable to include samples in developed chronologies based on these wood properties crossdating, whether or not their ring widths can be crossdated.

The visual crossdating of ring widths, using traditional techniques (Stokes and Smiley 1968), was an important part of the first step. Measurements of ring widths were made using a Velmex measuring stage attached to a linear encoder and computer. We then used the data quality control program COFECHA (Holmes 1994), to check visual crossdating of the ring widths. COFECHA is software routinely used in dendrochronology to statistically check visual crossdating. Our previous experience crossdating and measuring Huon pine from both low- and high-elevation sites has indicated that missing and false rings in low-elevation Huon pine are very rare (B. M. Buckley, personal communication and K. Allen, unpublished data). In addition, because our samples were taken from live trees, we know the date of the outermost ring with certainty. We were therefore confident that the combination of our visual crossdating, and the ability to allocate years to rings, allowed us to use these ring-width measurements as a basis for assessing the allocation of rings in the density and tracheid diameter profiles in step two.

In the second step, we generated a full set of the possible ring-width and wood property variables for each ring of each sample. Adjustments to these wood property profiles were required in some cases, particularly to correct for very narrow rings whose widths were below the resolution of the SilviScan measurements. After deriving these wood property profiles, we visually crossdated these wood properties in a manner similar to that used in other dendrochronological studies of wood density (e.g., Parker and Henoch 1971, Jacoby et al. 1988, Sander et al. 1995, Fan et al. 2009). COFECHA was again used to check the crossdating veracity of all samples for each wood property. The software provides statistics enabling the quantitative assessment of whether crossdating is 'stronger' or 'weaker' for wood properties than for ring widths. As a result, we were able to establish whether or not crossdating of various wood properties was superior to crossdating obtainable from ring widths.

These statistics (see Table 1) from COFECHA were used to select samples to be used for chronology development. Only individual samples with consecutive segments that correlated with the master series (constructed from series that crossdated 'well') with a correlation of ≥0.3 at lag 0 (deemed 'sufficiently strongly crossdated') were included in subsequent chronology development (cf. Parker and Henoch 1971). Samples not meeting this criterion were excluded from further analyses. To further guard against spurious relationships, we chose a conservative threshold for including any wood property in chronology development: if more than 50% of the series for a single wood property were excluded from a chronology due to low correlations (i.e., <0.3), that wood property was excluded from all further analyses. The sole exception to this was ring widths. Although <50% of available ring-width series met this criterion, we still developed a ring-width chronology for comparison with the wood property chronologies as it is the most common type of chronology used in dendroclimatic studies.

We developed chronologies from the ring-width and wood properties data that met our conservative selection criteria. We used custom-designed software based on the program ARSTAN (commonly used in dendrochronology to produce standardized and prewhitened chronologies for climate and ecological analyses) (Cook 1985) to develop each of the chronologies. This software enabled us to detrend individual series using detrending methods routinely available in ARSTAN but to do so within a signal-free framework (see Melvin and Briffa 2008). Individual series in our study were detrended using the flexible Friedman 'super-smoother' (Friedman 1984, Friedman and Silverman 1989). For trees growing in mesic forests where forest dynamics may have an important influence on ring-width patterns, stochastic methods of detrending, such as the Friedman supersmoother, are more appropriate than deterministic detrending techniques such as negative exponential or linear regression models (cf. Cook and Kairiukstis 1990). Using a signal-free framework to apply the Friedman supersmoother reduces end-bias that can occur during detrending by removing the common forcing signal in series (Melvin and Briffa 2008). To reduce the effects of outliers on the chronologies, we used a bi-weight robust mean for developing chronologies. Two standard measures of chronology quality, EPS and $\bar{R}$, were

Table 1. Summary of attempted chronologies. *N* refers to the number of trees, while *n* refers to the number of series included in the chronology, EPS and $\bar{R}$ are discussed in the text and inter-series correlation refers to the average correlation between individual series and the 'master series' calculated by COFECHA. Chronology length indicates the start and end year of the final chronology and ASL is the average segment length. In cases where statistical information is omitted, no chronology was developed (see text for more detail on the criteria for chronology development).

Parameter	Chronology	*N*, *n*	Average EPS	Average $\bar{R}$	Interseries correlation	Chronology length	ASL
Ring width	Total ring width	8, 11	0.81	0.32	0.38	1790–2009	140
	Earlywood width	10, 12	–	–	0.42	–	–
	Latewood width	–					
	Earlywood width proportion	11, 18	0.84	0.26	0.43	1870–2009	85.1
	Latewood width proportion	7, 11	–	–	0.41	–	–
Wood density	Earlywood wood density	12, 18	0.84	0.3	0.38	1780–2009	93.6
	Latewood wood density	12, 20	0.87	0.3	0.43	1790–2009	98.8
	Average wood density	14, 21	0.87	0.29	0.43	1750–2009	114.1
	Minimum wood density	11, 14	–	–	0.4	–	–
	Maximum wood density	7, 10			0.4	1750–2009	102
Tracheid diameter	Average tracheid diameter	14, 26	0.89	0.32	0.44	1770–2009	107.2
	Maximum tracheid diameter	13, 23	0.87	0.27	0.43	1750–2009	123.6
	Minimum tracheid diameter	–	–	–	–	–	–
	Latewood tracheid diameter	7, 9	–	–	0.38	–	–
	Earlywood tracheid diameter	15, 27	0.9	0.33	0.46	1780–2009	112.6
MFA	Average MFA	12, 19	0.9	0.35	0.46	1770–2009	107.8
	Minimum MFA	11, 19	0.87	0.32	0.42	1860–2009	93.1
	Maximum MFA	14, 21	0.89	0.32	0.43	1830–2009	104.8
Wall thickness	Average wall thickness	14, 20	0.84	0.27	0.42	1790–2009	114.7
	Latewood wall thickness	13, 19	0.87	0.28	0.41	1850–2009	104.2
	Earlywood wall thickness	11, 18	0.86	0.28	0.41	1750–2009	93.9
	Minimum wall thickness	11, 15	–	–	0.41	–	–
	Maximum wall thickness	8, 13	–	–	0.41	–	–

calculated. EPS measures the degree of departure of the chronology from a hypothetical chronology that has been infinitely replicated (Wigley et al. 1984). EPS values >0.85 are generally considered to demonstrate an acceptable level of common signal fidelity. $\bar{R}$ is the mean correlation of all possible pair-wise comparisons over a common time period of tree-ring series that make up the chronology. EPS and $\bar{R}$ were calculated for successive 31-year windows and an average value obtained. Pearson correlations between autoregressively modelled monthly temperature from September of the 'prior' season through to April at the end of the current growing season (a 21-month window) and the auto-regressively modelled wood properties chronologies were calculated for the years 1910–2009.

Results

Crossdating and chronology development

In our study, only 11 out of 33 cores could be successfully included in the ring-width chronology (Table 1) with an additional seven cores indicating weak but insufficient crossdating (i.e., series inter-correlations of < 0.3 for consecutive segments) for inclusion in the chronology. Given such a low number of samples meeting the required standard, we would ordinarily have excluded ring width from chronology development, but it was retained for the purpose of comparison against the wood properties chronologies. In contrast, mean wood density, mean latewood density, wall thickness and MFA exhibited much better crossdating than ring widths in the low-elevation Huon pine that we sampled (> 60% of sampled series were incorporated in the chronologies) (Table 1). Tracheid diameter, both as a ring mean and only in the earlywood, provided the most robust chronologies. In the case of earlywood tracheid diameter, 82% of the series were included in the chronology based on our conservative thresholds. Maximum and latewood tracheid diameter also had sufficiently strong crossdating to allow for chronology development, but did not crossdate as strongly as earlywood tracheid diameter. All of our chronologies had an EPS > 0.8 and most were >0.85, despite the relatively low number of samples (Table 1).

Correlations between wood property variables and ring width were generally weak (Table 2). Ring width was weakly correlated with MFA and tracheid diameter, but not with wood density. Interestingly, the ring-width chronology showed, overall, greater variability than the wood properties chronologies, and exhibited a sudden increase after 1890, later followed by an overall decrease (Figure 1). This occurred in all of the individual ring-width series that extended beyond 1890 (9 out of 11 of the time series), but the year in which the increase started ranged from 1886 to 1909. In contrast, no marked shift was evident in any of the wood property chronologies at that time. The sudden increase and subsequent decrease in ring widths is not related to a high proportion of samples starting around the same date nor a 'juvenile growth' effect (Figure 1). Notably, minimum and maximum MFA were more variable over time than either wall thickness or wood density, and, to a lesser, extent, tracheid diameter.

Correlations with environmental variables

Ring width only correlated significantly with temperature in October ($r = -0.3$; Figure 2). Temperature in December of the 'current' growing season (i.e., the season during which the ring formed) correlated negatively with earlywood wood density, while January–March temperatures were correlated with latewood density. The highest correlation among the various wood properties and the climate data was between latewood density and mean monthly minimum temperature in February ($r \sim -0.6$).

Earlywood tracheid diameter was significantly negatively correlated with temperature in the first half of the growing season ($r > |0.3|$) (November–January) (Figure 2). These correlations were similar for average tracheid diameter of the whole ring, but in this case correlations were also significant ($r < |0.3|$) from February to April. There were significant correlations between minimum MFA and temperatures of all summer months, although the correlations were strongest in the later months of the growing season ($r > |0.4|$) (February and March). The correlation declined markedly in April. There was no evidence of significant correlations between minimum MFA

Table 2. Correlations between ring width (RW), average wood density (AvgWD), latewood density (LWD), average MFA (AvgMFA), minimum MFA (MinMFA), average tracheid radial diameter (AvgTRD), earlywood tracheid radial diameter (EWTRD) and average wall thickness (AvgWT).

	RW	AvgWD	LWD	AvgMFA	MinMFA	AvgTRD	EWTRD	AvgWT
RW	1.00							
AvgWD	0.12	1.00						
LWD	0.05	0.69***	1.00					
AvgMFA	0.22**	0.21	0.20**	1.00				
MinMFA	−0.01	0.19**	0.25**	0.77***	1.00			
AvgTRD	−0.32***	−0.33***	−0.08	0.18**	0.29***	1.00		
EWTRD	−0.20**	−0.24**	−0.01	0.14*	0.23**	0.88***	1.00	
AvgWT	−0.12	0.81***	0.57***	0.21**	0.21**	0.06	0.06	1.00

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

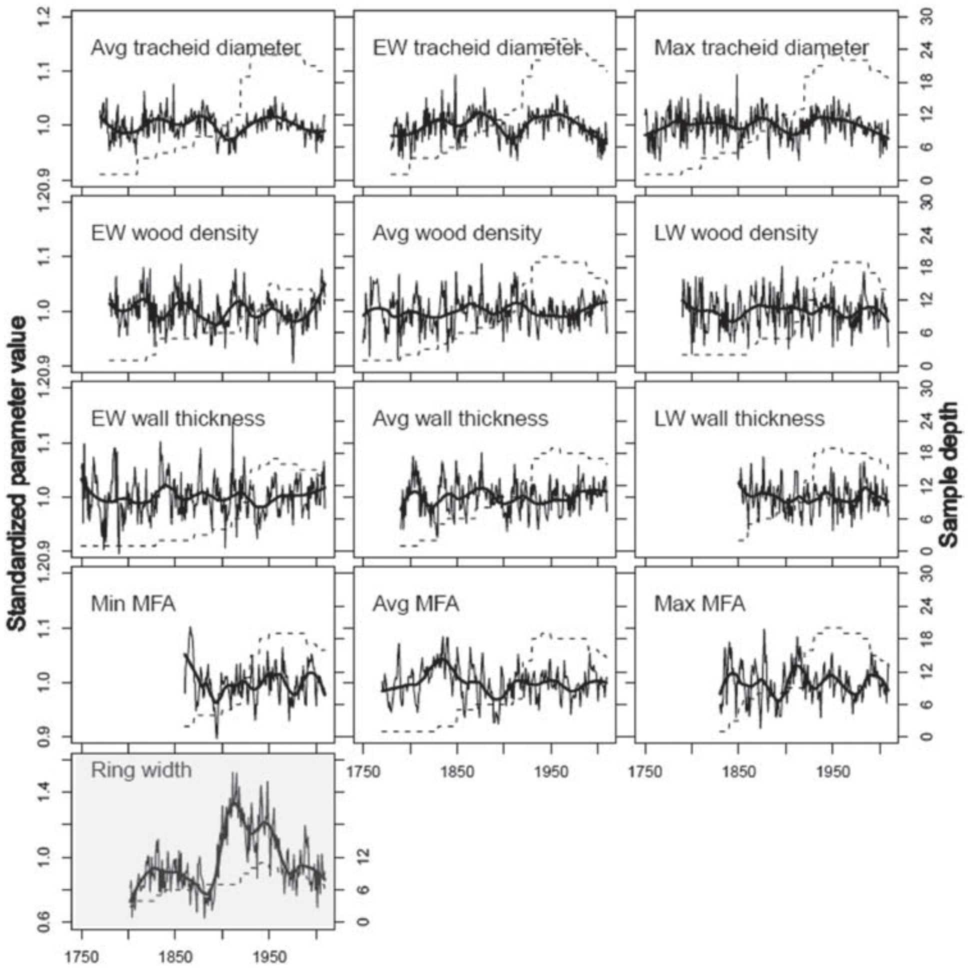

Figure 1. Standardized chronologies are shown for all variables for which chronologies were created. Note the differing scales for ring width compared with other variables. Sample depth is shown for each chronology as a dashed line. The smoothed trend is shown as the bold line.

and prior season temperatures (i.e., temperatures in the season prior to the formation of the growth ring). Maximum MFA, by comparison, was significantly correlated most strongly with temperatures in November and December of the current growing season ($r > |0.3|$), and with temperatures in the prior growing season ($r > |0.4|$). Correlations were generally slightly higher between minimum temperature and wood density and wall thickness, than maximum temperature. Microfibril angle, on the other hand, generally correlated more strongly with maximum than minimum temperature.

Tracheid diameter and MFA also correlated significantly ($r > 0.25$) with streamflow and SPEI across most months of the current growing season (Figure 3). Ring width, wood density and wall thickness, although exhibiting relatively high correlations with SPEI and stream flow in some months, did not show the same broad correlations across the season (Figure 3). There was a significant correlation between ring width and April (negative) and June (positive) streamflow of the prior year, and September streamflow of the current year. There was also a significant, strong and positive correlation between streamflow in January of the current growing season and latewood wood density and wall thickness. Average MFA and mean tracheid diameter of the ring were significantly correlated with streamflow in at least three months of the current growing season, but had their highest correlations with December streamflow ($r > |0.3|$). There was also a significant correlation between maximum MFA and mid-summer streamflow during the prior growing season. There was no evidence of a significant correlation between ring width, wood density and latewood wall thickness and SPEI. There were, however, significant correlations between average tracheid diameter, minimum and maximum MFA and SPEI in almost all summer months. The strongest correlation ($r \sim 0.5$) was between March SPEI and minimum MFA.

Correlations between wood properties chronologies and precipitation were generally not significant over consecutive months. A notable exception was minimum MFA, which correlated with rainfall from February to April. There were, however, significant correlations evident between all of the measured wood properties and rainfall in at least one month of the current or prior growing seasons.

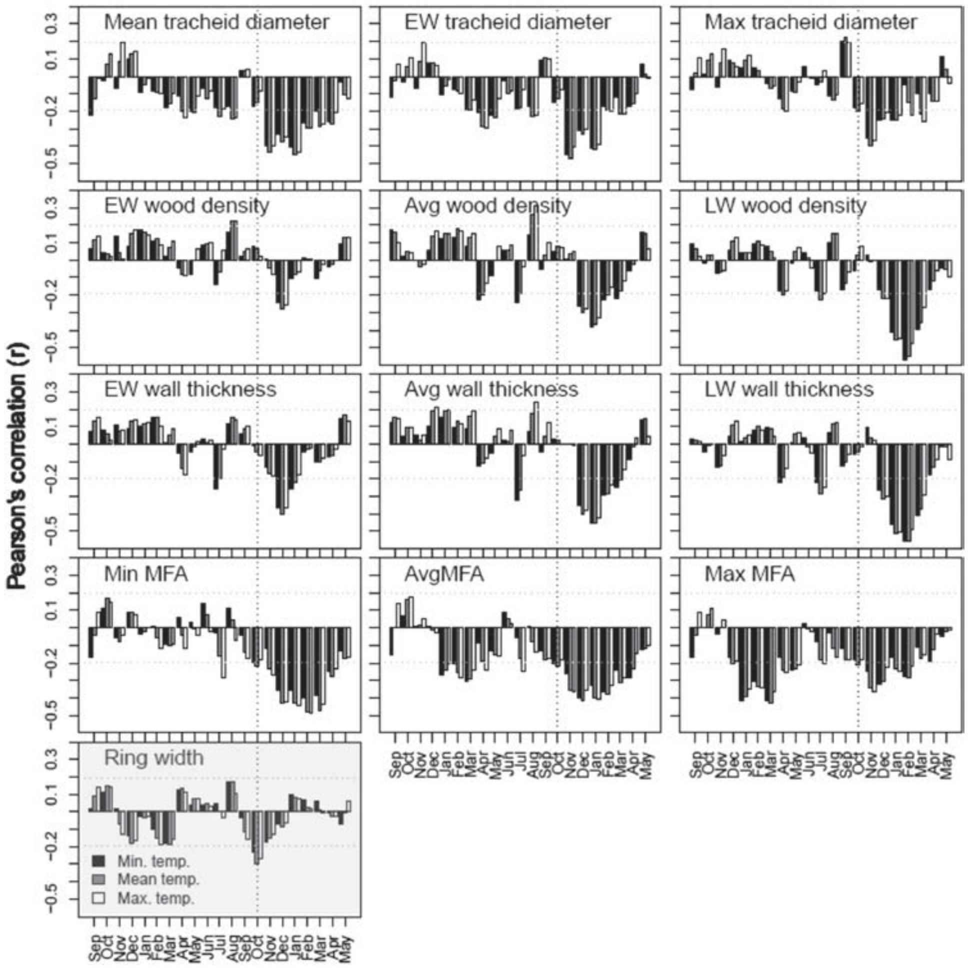

Figure 2. Correlations between temperature (averaged daily minimum, mean and maximum for the month) and chronologies shown in Figure 1. Points to the right of the vertical dashed line (at October) indicate correlations with conditions in the 'current' growing season of each year, while points to the left are indicate correlations with conditions in the 'prior' growing season. Correlations significant at $\alpha = 0.05$ indicated by the horizontal dotted lines.

Discussion

For nearly a century, dendroclimatologists have used tree-ring-width series, taken from trees growing in relatively extreme environmental conditions, to reconstruct historical climate patterns. The rationale is straightforward: where trees are growing at the limits of their environmental tolerance, seasonal stem growth will be most sensitive to fluctuations in those environmental conditions (e.g., temperature) which are most limiting to growth. However, most trees grow in forests that are not at the altitudinal or latitudinal limits of their distributions, where controls on stem growth are less direct and obvious. Consequently, large areas of the forested biomes of the world are ignored for dendroclimatic research because the ring-width patterns in the trees are not sufficiently sensitive to local climate variability to be of use in developing historical climate reconstructions.

Our study on low elevation Huon pine, however, demonstrates that properties of the wood other than ring width may be strongly correlated with climate even when the ring widths are not. Neither our ring-width chronology, nor other existing ring-width chronologies of low-elevation Huon pine that are both longer and better replicated than ours, have shown evidence of a clear climate signal (Buckley et al. 1997). We found that various wood properties of the low-elevation Huon pine exhibited clear, significant correlations with temperature, streamflow and a standardized drought index (SPEI). These correlations indicate that there is significant potential for using these wood properties for understanding past temperature and drought variation at sites that would traditionally be ignored for dendroclimatic studies. This possibility is further supported by at least two other recent studies. Xu et al. (2012) found that MFA of *Picea crassifolia* Kom. on the Tibetan peninsula was more sensitive to temperature than ring widths (Xu et al. 2012) and Sidorova et al. (2012) demonstrated strong regional correlations between cell wall thickness and summer temperatures in Tuva, Russia. If wood properties exhibit similar climate sensitivity in other areas where ring-width chronologies do not,

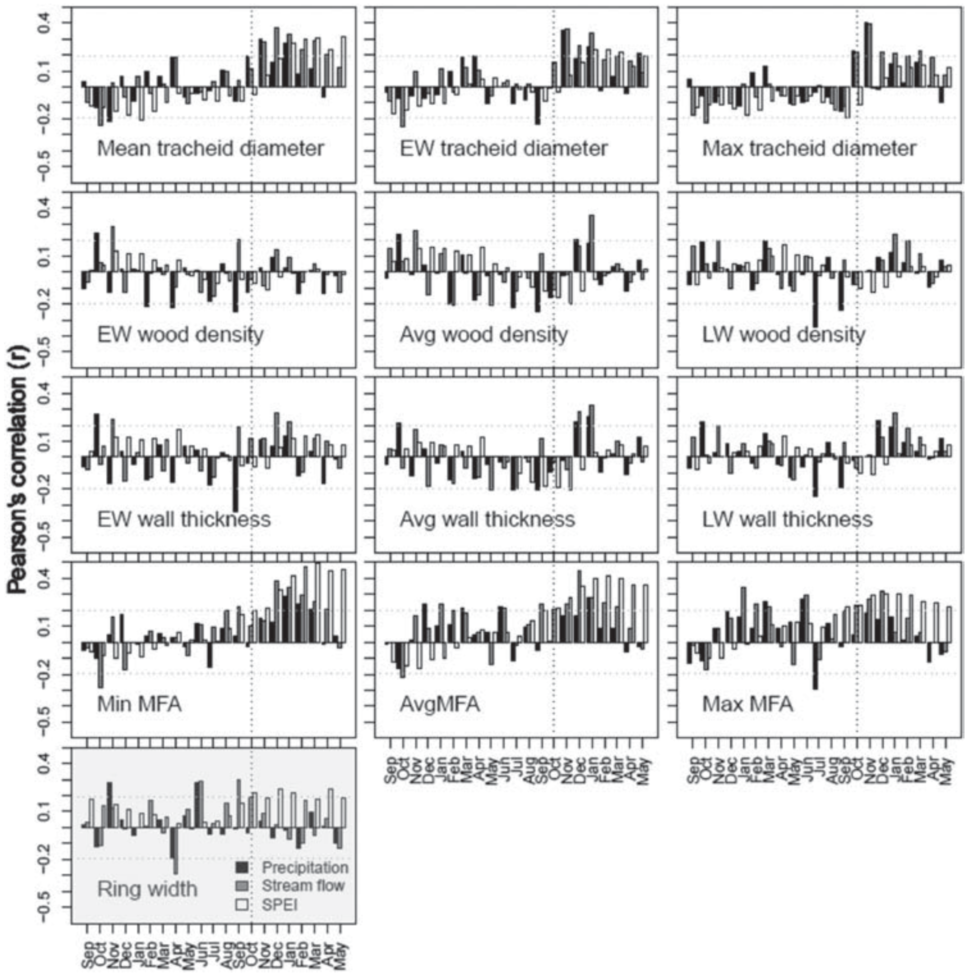

Figure 3. Correlations between local streamflow, SPEI and precipitation and chronologies shown in Figure 1. Points to the right of the vertical dashed line (at October) indicate correlations with conditions in the 'current' growing season of each year, while points to the left are indicate correlations with conditions in the 'prior' growing season. Correlations significant at $\alpha = 0.05$ indicated by the horizontal dotted lines.

climate-sensitive reconstructions from a much wider range of sites than is currently possible, both geographically and environmentally, may become broadly achievable.

Our data also show that within-ring variation in wood properties provides information about climatic variation in different portions of the growing season, yielding a finer level of inference than ring widths alone. In particular, earlywood tracheid diameter related to conditions in the first 3 months of the growing season (when tracheids are most actively expanding) (cf. Hölttä et al. 2010), while latewood wood density was most strongly correlated with conditions in the mid to late part of the growing season (when the latewood forms). Similarly, minimum MFA was more strongly correlated with late-season conditions than maximum MFA. There is thus great potential to consider parameters in concert for maximum insight into past climatic variability. It is still not clear, however, why certain wood properties exhibit a significant climate signal where ring widths do not. One reason may be the apparent insensitivity of tracheid diameter, MFA and wood density to some localized, environmental disturbances (e.g., the possible effects of mining activities on the forest in our study) when compared with the ring-width series. Another likely reason is because the conditions that limit and determine processes of xylem cell differentiation operate over only a brief window of time (days to weeks) (Barnett 1981), while total ring width, which is accumulated over several months during the full growing season, represents the integration of a much broader set of conditions. To understand these issues further, our research group is involved in several ongoing research projects studying xylem developmental patterns and short-term growth responses in Huon pine and other species.

The effect of temperature and drought on tracheid diameter

Our study site has a relatively mild climate, with a mean temperature during the growing season of about 14 °C, and a very low frost risk. As a result, the lowest monthly temperatures during the growing season (mean monthly minimum air temperature >7.6 °C from November to February) are unlikely to severely limit physiological processes like xylem development, or carbohydrate sequestration and allocation, in Huon pine (Read and Busby 1990, Rossi et al. 2007), as they would at a higher elevation site like Mt Read. On the other hand, xylem expansion is highly drought-sensitive in Huon pine: whole tree and stem conductivity are well known to become critically limiting to growth under only moderately hot and dry conditions (Brodribb and Hill 1998, Brodribb and Cochard 2009) because the irreversible process of tracheid development is largely determined by the ability of the cell to generate and maintain positive turgor (Hölttä et al. 2010). Our finding that tracheid diameter was correlated not only with temperature, but also with variation in the calculated drought index (SPEI) and local streamflow is consistent with these known physiological and developmental patterns. Even relatively short-term maintenance of high water-deficit conditions would impact on the characteristics of tracheids by suppressing the capacity of the developing xylem to generate positive turgor, reducing wall extensibility and ultimately reducing cell expansion rates (Sheriff and Whitehead 1984, Nonami and Boyer 1990, Abe et al. 2003, Bouriaud et al. 2005, Rossi et al. 2009). These changes would lead to critical adjustments in the hydraulic properties of the tracheids which form the water-conducting system of the gymnosperm stem (Fonti et al. 2010). In this context, it is worth noting that none of the wood properties we considered were strongly correlated with precipitation. This may merely reflect the lack of nearby precipitation data for the area, or, rather, that streamflow and SPEI provide a superior, more integrated signal of seasonal landscape and ecosystem water availability (Milly et al. 2005), variation in which is captured by the developing xylem.

Effects of temperature on latewood wall thickness and wood density

Although many dendroclimatological studies have found a positive relationship between wood density and temperature, the majority of these have looked at trees growing at high altitudes or latitudes, typically where low temperatures limit growth and cell wall development (Briffa et al. 2002, Rossi et al. 2008). We found the opposite pattern in our low-elevation Huon pine. One likely cause of the negative correlation between latewood tracheid wall thickness and temperature is the reduction in the duration of the process of secondary wall thickening in warmer conditions. Wood density is determined by both the tracheid wall thickness and the tracheid diameter. Importantly, however, the effect of tracheid diameter on wood density tends to be greatest in the earlywood, while the density of the latewood can be expected to be more closely associated with variation in wall thickness (Yasue et al. 2000). The duration of secondary thickening plays a critical role in determining final wall thickness (Skene 1972, Denne 1976, Dodd and Fox 1990) and higher temperatures have been shown to decrease the duration of the process, such that the cell walls may be thinner when differentiation occurs under higher temperatures (Denne 1971, Antonova and Stasova 1993, 1997).

An environmental signal in MFA variation

We found a strong correlation between MFA and drought in our low elevation Huon pine, which is consistent with other studies (conducted using a variety of species) where drought conditions and lower rates of tree growth and xylem element differentiation were associated with lower MFA (Barnett and Bonham 2004, Lundgren 2004, Donaldson 2008, Drew et al. 2009*a*).

Interpreting these findings is not elementary. Although there is a large body of research that explores the processes and mechanisms behind the environmental control of MFA in the primary cell wall (Boyd 1985, Baskin 2001, Barnett and Bonham 2004), the causes of MFA variation in the secondary wall are poorly understood (Barnett and Bonham 2004, Donaldson 2008). Importantly, however, factors that control MFA during tracheid growth may be related to the subsequent orientation of MFA in the secondary cell wall (Boyd 1985). For example, in *Pseudotsuga menziesii* (Mirb.) Franco, Wardrop and Preston (1950) found that MFA tended to be higher when the rate of extension of the cambial initial (from which the mature tracheid develops) was more rapid. It is possible, then, that understanding growth-determined MFA can offer clues to microfibril orientation in subsequent wall layers, after cell expansion has ceased. Recent research indicates that microfibril orientation in the developing cell is closely linked to mechanisms and processes determining the direction of transport of growth-modulating hormones, particularly auxin, and associated adjustments in the cell cytoskeleton (Chan 2011, Korbei and Luschnig 2011). The extent to which these mechanisms operate only during the tracheid expansion phase, or even into the stage of secondary thickening, is still unknown, however, and presents an important area for further research

Potential for using low-elevation Huon wood properties for temperature reconstruction

Based on our results, we suggest longer and better replicated chronologies developed from the wood properties we have studied here could potentially be used to develop temperature and other climate reconstructions from sites where it has not been possible, or even attempted, before. For the endemic Tasmanian conifer, Huon pine, our findings potentially open the way to make use of the relatively extensive network of low-altitude sites in Tasmania to contribute to research efforts to understand past temperature variation in the SH. Low-elevation Huon pine sites have never before been used for climate reconstruction purposes due to the poor quality and complexity of the climate signal contained in the ring widths (Buckley et al. 1997). But by utilizing information in wood properties, these sites may yield even longer climate records than the 3600-year summer temperature reconstruction from Mount Read (Cook et al. 2006). Such an advance is particularly significant in the SH, where there are very few long chronologies containing a strong climate signal (Briffa 2000). Our findings strongly suggest that the analysis of radial variation in tracheid diameter and MFA, in concert with wood density, show great potential as a powerful new tool for dendroclimatic research.

Conflict of interest

None declared.

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