Original article

Earlywood vessel size of oak as a potential proxy for spring precipitation in mesic sites

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ABSTRACT

Aim In this study, we evaluate the importance of the mean earlywood vessel size of oaks as a potential climatic proxy for mesic areas.

Location The study was conducted at three forest sites dominated by oak (*Quercus petraea* (Mattuschka) Liebl. and *Quercus pubescens* Willd.), and located in different climatic contexts within Switzerland, which mainly differ in their precipitation regime.

Methods Three 50-year long site chronologies of mean earlywood vessel size and tree-ring widths were obtained at the three sites and related to monthly meteorological records in order to identify the main variables controlling growth. The responses of mean vessel size to climate were compared to those of the width variables to evaluate the potential climatic information recorded by the earlywood vessels.

Results The results show that the mean vessel size has a different and stronger response to climate than ring width variables, although its common signal and year-to-year variability are lower. This response is better in particular at the mesic sites, where it is linked to precipitation during spring, i.e., at the moment of vessel formation, and is probably related to the occurrence of only few processes controlling vessel growth, whereas radial increment is controlled by multiple and varying factors.

Main conclusions The mean earlywood vessel size of oak appears to be a promising proxy for future climate reconstructions from mesic sites, where radial growth is not controlled by a single limiting factor.

INTRODUCTION

To assess the magnitude and to evaluate future scenarios of climate change, a long term perspective of past climate is fundamental. Reconstructions of prehistoric climate regimes are based on proxy indicators. Examples of proxies include natural archives such as tree rings, ice cores, corals, lake and ocean sediments, tree pollen, or human archives such as historical records or diaries. Among them, tree-ring records are generally the most accurate, with intra-annual precision, even back thousands of years (IPCC, 2007). However, not all tree rings contain climate relevant information. According to Fritts (2001), the ability to use tree rings to reconstruct past climate depends on the Principle of Limiting Factors, which states that rates of plant processes occur only as fast as allowed by the factor that is most limiting. In this manner, dendroclimatologists generally reconstruct the prevailing climatic conditions throughout the growing period by using a single variable representative for the whole annual ring (usually the total ring width or maximal wood density). For example, if rainfall is the limiting factor, the radial growth of a tree in any single year mostly reflects the amount of rainfall that fell within that growing season (e.g. D'Arrigo & Jacoby, 1991; Stahle & Cleaveland, 1992; Lara *et al.*, 2001; Watson & Luckman, 2001; Brázdil *et al.*, 2002; Cook *et al.*, 2004; Touchan *et al.*, 2005; Linderholm & Chen, 2005; Wilson *et al.*, 2005; Esper *et al.*, 2007). In addition, the extractable proxy information usually refers to the part of the growing season when the plant processes are maximised, e.g. for radial growth at high altitude this often corresponds to the temperature during early summer (e.g. Briffa *et al.*, 2002; Cook *et al.*, 2003; Esper *et al.*, 2003; Frank & Esper, 2005; Luckman & Wilson, 2005; Büntgen *et al.*, 2005, 2006). Consequently growth processes not subject to a dominant limiting factor are rarely considered for reconstructing past

climate from tree rings, as happens with many parts of the globe or a large part of the growing season.

Intra-annual tree-ring features have the potential of providing additional climatic information. They comprise sequences of cells formed at different moments of the growing season whose metrics (e.g. size, shape or wall thickness) respond to external conditions occurring during cell formation (e.g. Denne & Dodd, 1981; Sheriff & Whitehead, 1984; Dünish & Bauch, 1994; Larson, 1994; Abe & Nakai, 1999; Abe *et al.*, 2003; Arend & Fromm, 2007). Since factors that influence cell development and metrics are not necessarily the same as the prevailing factors determining radial growth (i.e. the total amount and types of cells produced during the season), it is expected that additional and more time-resolved climatic information can be gained from anatomical tree-ring features, even for other parts of the season or for other climatic areas.

Recent analyses on the year-to-year variability in the dimensions of water conductive elements of hardwoods confirm the ability of these cells to encode valuable and high-resolved environmental information (e.g. Astrade & Begin, 1997; St George & Nielsen, 2000; García González & Eckstein, 2003; Eckstein, 2004; Fonti & García González, 2004; Verheyden *et al.*, 2005; Eilmann *et al.*, 2006). Among them, the earlywood vessels of oaks (*Quercus* spp.) have promising properties to become a climatic proxy. Their size appears to be sensitive to spring moisture conditions (St George & Nielsen, 2000; García-González & Eckstein, 2003; García González & Fonti, 2008), and some century to millennia long tree-ring chronologies are already available (e.g. Kelly *et al.*, 2002; Leuschner *et al.*, 2002; Spurk *et al.*, 2002; Akkemik *et al.*, 2005; Griggs *et al.*, 2007).

In this explorative study, we evaluate the applicability of oak earlywood vessel size as a potential proxy for spring moisture conditions. For this, their climatic response is

analyzed in three different climatic zones of Switzerland and compared to those of ring width. Specifically, we assess (i) the high-frequency climatic signal of 50-year long chronologies of mean earlywood vessel area in comparison to ring width in order to (ii) discuss the future applicability of this novel climatic proxy.

MATERIAL AND METHODS

Study sites

The three selected oak sites are located within different climatic contexts in Switzerland. Cugnasco (CUG, 46°11'06''N, 8°52'54''E, 560 m a.s.l.) and Zurich (ZUR, 47°22'37''N, 8°26'30''E, 550 m a.s.l.) have mesic climates; Cugnasco experiences a temperate-humid climate typical for the southern part of Switzerland and Zurich, located in northern Switzerland, has humid and cold seasons. The third site, Salgesch (SAL, 46°19'18''N, 7°33'43''E, 880 m a.s.l.), lies in the inner-alpine valley of Valais and is characterized by a temperate and dry climate. The sites are about 200 km apart from each other. Climate diagrams (Walther & Lieth, 1964) for the closest weather stations to the selected sites are shown in Fig. 1.

Trees selected for sampling were sessile oaks (*Quercus petraea* (Mattuschka) Liebl.) at CUG and ZUR, but pubescent oaks (*Quercus pubescens* Willd.) at SAL. At CUG, sessile oaks grow within a mixed forest composed of chestnut coppice (*Castanea sativa* Mill.) and beech (*Fagus sylvatica* L.). The oaks are dominant (22 m height and 60 cm stem diameter) and about 70 years old in age. At ZUR, dominant (30 m height and 100 cm stem diameter) oaks are interspersed in a mixed hardwood forest with mainly beech and some sycamore maple (*Acer pseudoplatanus* L.) and are almost 200 years old. Pubescent oaks at SAL are located at a south-exposed and very dry site with Scots pine (*Pinus sylvestris* L.); they show clear signs of reduced growth, with a maximal height of 12 m and 20 cm stem diameter, although they are up to 110 years old.

Wood preparation and survey

Two cores were sampled at breast height from each of the 15 dominant oak trees selected at each site. The 5-mm cores were air-dried and prepared for ring width measurements and vessel survey. The transversal surface was first sanded (up to a 15 micron grit), the vessel lumina cleaned (with a water pressure blast), and finally the wood surface was coloured black, and vessels filled with white chalk. This procedure increases the contrast between the vessel lumina and the wood matrix, which allows the image analysis software (Image Pro Plus, Media Cybernetics, Silver Spring, MD, USA) to automatically recognize and measure the vessels. Images were captured ring by ring from 1956 to 2005 (50 years) using a digital video camera (Colour view IIIu, Olympus, Volketswil, CH) connected to a stereomicroscope (Leica MZ 12, Leica microsystem, Heerbrug, CH) with a 12.5x objective. For each dated ring, the width of the earlywood (EW), latewood (LW), and the entire ring (RW), as well as the lumen size of all earlywood vessels ($> 10,000 \mu\text{m}^2$) were measured. This corresponded to an average of 33 ± 7 earlywood vessels per annual ring (CUG 32 ± 8 , SAL 29 ± 5 , ZUR 40 ± 8). Finally, time series were built for the width parameters and for the mean vessel area (MVA).

Building site chronologies and computing climate-growth analyses

Individual EW, LW, RW and MVA time series were calculated by averaging the measurements for each tree. To retain only the year-to-year variability, low frequency trends were removed from these series by fitting a cubic smoothing spline function with 32-yr stiffness and 50% cutoff and by dividing by the fitted curve (Cook *et al.*, 1990; Fritts, 2001). The obtained standardized series were finally averaged to build site chronologies.

The statistical properties of the time series were assessed by means of classical dendrochronological parameters (Fritts, 2001), such as the mean sensitivity (MS) and first-order autocorrelation (AR). Chronology quality was achieved according to different indicators of common signal (Wigley *et al.*, 1984; Briffa & Jones, 1990), specifically the mean correlation between trees (Rbt), variance in the first eigenvector (% Var), signal-to-noise ratio (SNR) and expressed population signal (EPS). Climate-growth relationships were established by computing Pearson's correlation functions for the width variables and MVA site chronologies with monthly average temperature and total monthly precipitation registered by the nearby weather stations of Locarno, Sion and Zurich (1956-2005, 50 years).

RESULTS

Mean radial widths and vessel size

Ring-width values differ among sites considerably (Table 1). Trees subject to dry climate (SAL) have an average RW, LW and EW sensibly lower than for the other two sites, ZUR and CUG, and the earlywood comprises a larger proportion of the ring. The difference in RW between ZUR and CUG is mainly related to differences in LW, which is much narrower in ZUR. The size of the earlywood vessels also varies among sites, being clearly smaller at SAL, with a MVA and standard deviation of only $30,161 \pm 4,199 \mu\text{m}^2$, as opposed to ZUR ($58,804 \pm 5,867 \mu\text{m}^2$) or CUG ($59,991 \pm 6,790 \mu\text{m}^2$).

Quality of chronologies

Table 1 summarizes the statistics used to evaluate chronology quality and Fig. 2 shows the detrended time series with their corresponding site chronologies. In general, LW and RW are very similar to each other, with regard to their parameters and the appearance of the chronologies, while EW tends to be more similar to MVA. Year-to-year variation of individual series, expressed by the mean sensitivity (MS), is higher for LW/RW than for

EW/MVA. The first order autocorrelation coefficient, a measure of the influence of previous years upon growth, is larger and highly significant for all width variables (RW, EW and LW), whereas series of MVA are only autocorrelated at SAL.

The similarity between the series of all trees at each site, i.e., the common signal of chronologies, is expressed by the last four parameters (Rbt, % Var, SNR and EPS). At all three sites, LW or RW have a much higher common signal than EW or MVA (e.g., Rbt is 0.47-0.57 for RW and 0.20-0.27 for MVA, or % Var ranges 52.3%-60.0% for RW and 27.0%-33.9% for MVA); however, within the earlywood variables EW has a slightly better common signal than MVA, especially at ZUR.

Chronology curves at each site are very similar for RW and LW ($r=0.94$ to $r=0.98$), showing that both variables yield the same information. Some similarities are also present for RW and EW ($r=0.42$ to $r=0.69$), and for EW and MVA ($r=-0.24$ to $r=-0.46$), but they clearly differ between RW and MVA ($r=-0.35$ to $r=0.17$) (Fig. 2, Table 2).

Climatic signal

Correlations of ring widths and MVA chronologies to the corresponding monthly average temperature and total precipitation (1956-2005, $n=50$ years) are summarized in Fig. 3. In general, the chronologies are better correlated to precipitation than to temperature. At the driest site (SAL), RW correlates mainly to accumulated precipitation during current spring ($r=0.41$, $P<0.01$ with March-May), while at the moister sites (CUG and ZUR) the response of RW either comprises a longer season ($r=0.64$, $P<10^{-6}$ with March to June precipitation for ZUR) or occurs later in summer ($r=0.38$, $P<0.01$ with July precipitation at CUG). Given the high correlation between RW and LW, the climatic signal of LW is practically the same as that of RW.

When considering EW and MVA, significant correlations correspond to different periods and are often stronger than those for RW/LW. Although both variables seem to be related to the same climatic factors, the responses are stronger or better defined for MVA, whereas those of EW are less consistent. At SAL, both EW and MVA are highly correlated ($P < 10^{-4}$) to accumulated precipitation during the previous growing season ($r = 0.53$ and $r = 0.51$ for previous July-September and June-September, respectively), but no response is observed at the moment of earlywood formation in spring. In contrast, EW and especially MVA are clearly related to spring conditions at the mesic sites (ZUR and CUG). MVA shows highly significant negative correlations to precipitation during the period April-May ($r = -0.72$ and $r = -0.57$, $P < 10^{-4}$ for CUG and ZUR respectively), while those of EW are positive and weaker ($r = 0.50$, $P < 10^{-4}$ and $r = 0.34$, $P < 0.01$ for ZUR and CUG respectively).

Correlations to temperature are in general weaker. It appears to have little or no influence on RW, LW and EW, but MVA can correlate to (early) spring temperatures; nevertheless correlations are not as strong as those to precipitation.

DISCUSSION

Statistical quality of the chronologies and strength of climate response

Robust responses among individuals and sites, and a strong relationship to the target climatic variable are essentials for climate reconstruction. The common signal of MVA is lower than that of the ring widths, although previous studies have shown that increasing the number of vessels measured could slightly improve these values (García-González & Fonti, 2006, 2008). But despite the low common signal of MVA, the values are consistent across the three climatic regions, and comparable to those for *Quercus robur* L. from a maritime site in Spain (García-González & Eckstein, 2003), *Quercus*

rubra L. and *Quercus alba* L. at their northern limit in Canada (Tardif & Conciatori, 2006), and higher than for *Castanea sativa* in the southern Swiss Alps (Fonti & García-González, 2004; Fonti *et al.*, 2007). Furthermore, the widths are also more sensitive than MVA (as also shown in earlier works e.g., Pumijumnong & Park, 1999; Fonti & García-González, 2004; Tardif & Conciatori, 2006), but they are more affected by previous growth and consequently highly autocorrelated.

In spite of the higher statistical quality for the width chronologies (i.e., higher sensitivity and common agreement), Pearson's correlations between MVA chronologies and monthly climatic variables are stronger and different than for the other ring parameters (apart from EW). This result confirms previous findings of similar approaches on other ring-porous species (Fonti & García González, 2004; Fonti *et al.*, 2007) or climatic contexts (García-González & Eckstein, 2003). A higher chronology quality does not necessarily guarantee a better climatic signal, since other non climatically-related disturbances (e.g., forest dynamics or insect outbreaks) could cause synchronic changes in radial growth, increasing common signal and autocorrelation, but obscuring climate-growth relationships. In the present study, RW appears to be affected by growth reductions (especially at CUG) while MVA is not, which can explain why MVA is less autocorrelated and more linked to climate.

Content of the climatic signal and its ecophysiological meaning

The parameters analyzed encode different climatic signals which also vary according to the climatic regime. At CUG and ZUR, the response of RW (or LW) is weak and unclear, which confirms the difficulties of identifying a consistent climatic signal from RW of oak at mesic sites (e.g. Kelly *et al.*, 1989; Lebourgeois *et al.*, 2004; Rozas, 2005). In contrast, the earlywood (mainly MVA) has a stronger and reliable response to spring precipitation, i.e., during the moment of cambial reactivation and vessel

expansion in spring (Suzuki *et al.*, 1996; Schmitt *et al.*, 2000; Fonti *et al.*, 2007). On the other hand, SAL is very prone to drought, and the main response to climate is related to accumulated precipitation during the second half of the previous growing season, which mostly affects RW; in this case, the response of MVA is more indirect and occurs mainly during the previous growing season.

These differences among parameters and regions can be explained if one considers the processes involved in registering the climatic signal. Radial increment is controlled by climatic factors (i.e., temperature and precipitation) whose relevance, in particular in the mesic sites, can differ from year to year and among sites. Thus, RW embodies the sum of various processes regulating the amount of wood formation throughout the whole growing season, but fails to clearly identify a single prevailing factor, which constitutes a major limitation to reconstruct climate from tree rings in many temperate areas (Schweingruber, 1996). In contrast, the response of MVA is limited to a shorter time span and linked to fewer crucial physiological processes (e.g. vessel expansion). Therefore the response of MVA seems to be controlled by climate even if there is no single prevailing factor limiting tree growth, as occurs at mesic sites. However, more specific studies are required to decipher the ecophysiological mechanism responsible for the negative correlation with precipitation, including phenological observations of both foliar and cambial development, as it has been done in other studies (e.g. Fonti *et al.*, 2007; Rossi *et al.*, 2007). For the case of SAL, we hypothesize that the signal in the water conductive cells is linked to the accumulation of reserves during the second half of the previous summer. Under such conditions of drought, cambial growth ceases at early- or mid- summer (see correlation of RW to climate, Weber *et al.*, 2007), and subsequent water availability determines reserve storage for the following growing season (Barbaroux & Bréda, 2002; Zweifel *et al.*, 2006). Thus, a rainy late summer

could foster assimilation of carbohydrates, which would be used at the beginning of the following season to develop the photosynthetic apparatus (Yang & Midmore, 2005), and therefore, in expectation of a higher need of water, the tree would have prepared itself by producing larger earlywood vessels. As opposed to MVA, the response of RW at this site appears to be directly linked to the availability of water to assimilation and therefore to wood production during the first half of the growing season.

Evaluation of the applicability of MVA as a climate proxy

As a rule, the stronger the climatic response is, the more reliable the climate reconstruction. For this reason, dendroclimatic reconstructions have been traditionally based on the Principle of Limiting Factors (Fritts, 2001), i.e., trees and sites are selected in order to maximize the effect of a specific climatic factor (LaMarche, 1982; Schweingruber *et al.*, 1992; Fritts, 2001). Such tree-ring time series exhibit a high year-to-year variability with an optimal agreement between trees, which strongly reflects the prevailing climatic factor of interest. But it has the restriction that most trees need to be sampled at the Alpine or boreal timberlines or in semidesertic areas, where trees are close to their distribution boundaries.

The use of anatomical variables, such as MVA, can overcome part of the site-related limitations imposed by the classical dendrochronological reconstructions. This study on three climatically different oak sites in Switzerland shows that the year-to-year variability in the size of earlywood vessels (MVA) of oak contains both a common signal and a strong correlation to climate. This response changes according to the climatic regimes, but it is always related to physiological processes controlling vessel formation. In the case of trees at sites where conditions can be considered ‘intermediate’ (mesic sites), the response of RW is unstable, but that of MVA is directly linked to specific physiological processes in the tree and limited to a short seasonal time span.

Processes regulating vessel growth differ from those controlling radial increment, which explains why valuable climatic information can be gained from MVA chronologies taken from trees growing at intermediate areas of their distribution range, where tree growth is not determined by a single climatic factor. MVA can also respond to different factors than RW at sites with more limiting conditions, and thus extend the sources of information where climate has a strong influence upon RW. In addition, under a similar climatic context (e.g., both mesic sites), the response also appears to be consistent across regions, which makes MVA a promising proxy for climate reconstructions, especially considering that some millennia long oak chronologies are already available for intermediate sites.

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BIOSKETCHES

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Tables

Tab. 1: Statistical characteristics of chronologies. RW = Ring width [mm], LW = Latewood width [mm], EW = Earlywood width [mm], MVA = Mean vessel area [μm^2], CUG = Cugnasco, ZUR = Zurich, SAL = Salgesch. SD = Standard deviation, MS = Mean sensitivity, AutoR = Autocorrelation, Rbt = Mean correlation between trees, %Var = Percentage of variance in the first eigenvector, SNR = Signal-to-noise ratio, EPS = Expressed population signal.

	RW			LW		
	CUG	ZUR	SAL	CUG	ZUR	SAL
Mean	2.76	2.15	0.92	1.81	1.06	0.51
SD	0.80	0.55	0.35	0.72	0.44	0.27
MS	0.17	0.19	0.21	0.27	0.36	0.36
AutoR	0.65	0.45	0.64	0.58	0.28	0.55
Rbt	0.57	0.47	0.49	0.56	0.43	0.50
%Var	59.96	51.40	52.32	59.75	48.00	55.05
SNR	19.69	13.19	14.82	19.38	11.38	15.27
EPS	0.95	0.93	0.94	0.95	0.92	0.94

	EW			MVA		
	CUG	ZUR	SAL	CUG	ZUR	SAL
Mean	0.95	1.09	0.41	59,991	58,804	30,161
SD	0.18	0.21	0.11	6,790	5,867	4,199
MS	0.14	0.14	0.16	0.11	0.10	0.09
AutoR	0.35	0.48	0.61	0.25	0.13	0.52
Rbt	0.22	0.36	0.27	0.27	0.20	0.23
%Var	30.34	41.70	33.60	33.88	27.00	29.08
SNR	4.34	8.32	5.67	5.55	3.74	4.44
EPS	0.81	0.89	0.85	0.85	0.79	0.82

Tab. 2: Pearson’s correlations among chronologies. RW = Ring width, LW = Latewood width, EW = Earlywood width, MVA = Mean vessel area, CUG = Cugnasco, ZUR = Zurich, SAL = Salgesch.

	CUG			ZUR			SAL		
	LW	EW	MVA	LW	EW	MVA	LW	EW	MVA
RW	0.98	0.42	-0.02	0.94	0.68	-0.35	0.98	0.69	0.17
LW		0.26	0.04		0.40	-0.22		0.54	0.07
EW			-0.24			-0.43			0.46

Figures' legends

Fig. 1: Climate diagram of Locarno, Zurich and Sion, the closest meteorological stations to the site of Cugnasco (CUG), Zurich (ZUR) and Salgesch (SAL) respectively.

Fig. 2: Detrended individual width series (RW, LW, EW) and mean vessel area (MVA) time series and site chronologies (Cugnasco = CUG, Zurich = ZUR, Salgesch = SAL). Grey lines refer to individual time-series (standard indices) and thick bold lines to the site chronology.

Fig. 3: Pearson's correlations for sites' width chronologies (RW, LW, EW) and mean vessel area (MVA) as compared with monthly average temperature (T) and sum precipitation (P) for the period 1956-2005. White bars = Cugnasco (CUG), grey bars = Zurich (ZUR), black bars = Salgesch (SAL). Horizontal lines indicate the significance levels for $P < 0.001$, $P < 0.01$, $P < 0.05$ ($n=50$), respectively.

508 **Figure 1**

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511 **Figure 2**

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514 **Figure 3**