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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 proxy for climate in mesic areas.

Location The study was conducted in Switzerland at three forest sites dominated by oak (*Quercus petraea* and *Q. pubescens*). The three sites were in different climatic zones, varying mainly in terms of precipitation regime.

Methods Three 50-year-long site chronologies of mean earlywood vessel size and tree-ring widths were obtained at each site 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 with 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 mesic sites, where it is linked to precipitation during spring, i.e. at the time of vessel formation, and is probably related to the occurrence of only a 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 of mesic sites, where radial growth is not controlled by a single limiting factor.

Keywords

Cell size, climate proxy, earlywood vessels, *Quercus petraea*, *Quercus pubescens*, spring precipitation, Switzerland, tree ring.

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INTRODUCTION

In order to assess the magnitude and to evaluate future scenarios of climate change, a long-term perspective on past climate is crucial. 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 these, 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 of 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. Watson & Luckman, 2001; Brázdil *et al.*, 2002; Cook *et al.*, 2004; Touchan *et al.*, 2005; Wilson *et al.*, 2005; Esper *et al.*, 2007). In addition, the extractable proxy information usually refers to the part of the growing season in which the plant processes are maximized; for example, for radial growth at high altitude, this often corresponds to the temperature during early summer (e.g. Cook *et al.*, 2003; Büntgen *et al.*, 2005, 2006; Frank & Esper,

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2005; Luckman & Wilson, 2005). Consequently, growth processes not subject to a dominant limiting factor, which is the case for many parts of the world and in much of the growing season, are rarely considered in reconstructing past climate from tree rings.

Intra-annual tree-ring features have the potential to provide additional climatic information. They comprise sequences of cells formed at different points in 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; Larson, 1994; Abe *et al.*, 2003; Arend & Fromm, 2007). Since the factors that influence cell development and metrics are not necessarily the same as the 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 where ring width is not an appropriate proxy.

Recent analyses of the year-to-year variability in the dimensions of water-conductive elements of hardwoods confirm the ability of these cells to encode valuable and highly resolved environmental information (e.g. St George & Nielsen, 2000; Eckstein, 2004; Fonti & García-González, 2004; Verheyden *et al.*, 2005; Eilmann *et al.*, 2006). In particular, the earlywood vessels of oaks (*Quercus* spp.) look promising as climatic proxies. 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. In order to do this, their climatic response is analysed in three climatic zones of Switzerland and compared with that of ring width. Specifically, we assess (1) the high-frequency climatic signal of 50-year-long chronologies of mean earlywood vessel area in comparison to ring width in order to (2) discuss the future applicability of this novel climatic proxy.

MATERIALS 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 *c.* 200 km from each other. Climate diagrams (Walter & 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 *c.* 70 years old. At ZUR, dominant (30 m height and 100 cm

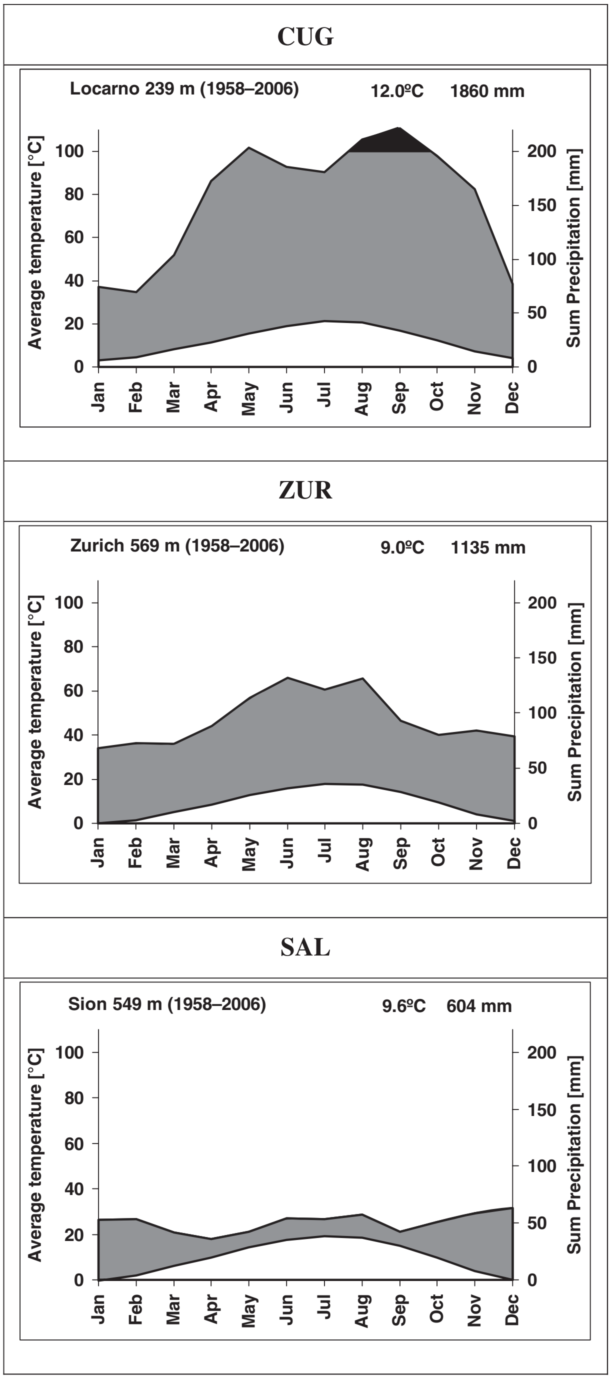

Figure 1 Climate diagrams for Locarno, Zurich and Sion, the closest meteorological stations to the sites of Cugnasco (CUG), Zurich (ZUR) and Salgesch (SAL), respectively (Data MeteoSwiss).

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 in 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-μm grit), the vessel lumina cleaned (with a water pressure blast), and finally the wood surface was coloured black and the 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, Switzerland) connected to a stereomicroscope (Leica MZ 12, Leica microsystem, Heerbrug, Switzerland) with a 12.5× 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 μm^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-year 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 various 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 correlation functions for the width variables and MVA site chronologies with monthly average temperature and total monthly precipitation as 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 considerably among sites (Table 1). Trees subject to dry climate (SAL) have an average RW, LW and EW lower than the corresponding measurements 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 related mainly 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 ± 4199 μm^2, as opposed to 58,804 ± 5867 μm^2 in ZUR and 59,991 ± 6790 μm^2 in CUG.

Quality of chronologies

Table 1 summarizes the statistics used to evaluate chronology quality, and Fig. 2 shows the detrended time series with their

Table 1 Statistical characteristics of chronologies.

	RW			LW			EW			MVA		
	CUG	ZUR	SAL	CUG	ZUR	SAL	CUG	ZUR	SAL	CUG	ZUR	SAL
Mean	2.76	2.15	0.92	1.81	1.06	0.51	0.95	1.09	0.41	59,991	58,804	30,161
SD	0.80	0.55	0.35	0.72	0.44	0.27	0.18	0.21	0.11	6790	5867	4199
MS	0.17	0.19	0.21	0.27	0.36	0.36	0.14	0.14	0.16	0.11	0.10	0.09
AutoR	0.65	0.45	0.64	0.58	0.28	0.55	0.35	0.48	0.61	0.25	0.13	0.52
Rbt	0.57	0.47	0.49	0.56	0.43	0.50	0.22	0.36	0.27	0.27	0.20	0.23
%Var	59.96	51.40	52.32	59.75	48.00	55.05	30.34	41.70	33.60	33.88	27.00	29.08
SNR	19.69	13.19	14.82	19.38	11.38	15.27	4.34	8.32	5.67	5.55	3.74	4.44
EPS	0.95	0.93	0.94	0.95	0.92	0.94	0.81	0.89	0.85	0.85	0.79	0.82

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. A total number of 15 trees was used at each site.

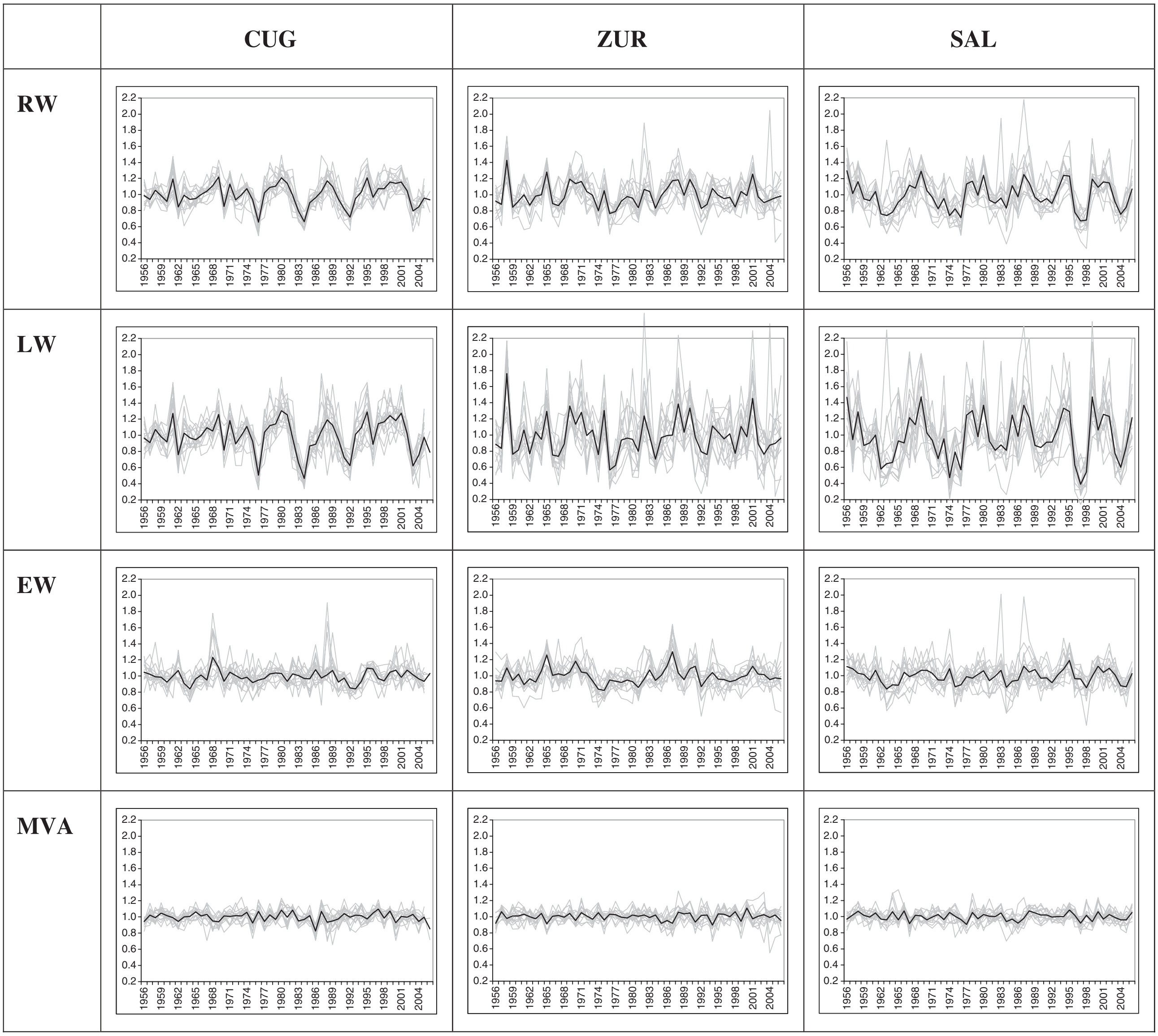

Figure 2 Detrended individual width time series (RW, ring width; LW, latewood width; EW, earlywood width) and mean vessel area (MVA) time series and site chronologies (CUG, Cugnasco; ZUR, Zurich; SAL, Salgesch). Grey lines refer to individual (standard indices), and thick bold lines to the site chronology.

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, whereas 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 and RW than for EW and 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 and RW have a much higher common signal than EW and MVA (for example, Rbt is 0.47–0.57 for RW and 0.20–0.27 for MVA, and %Var is in the range 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 the two 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 with the corresponding monthly average temperature and total precipitation (1956–2005, $n = 50$ years) are summarized in

Table 2 Pearson's correlations among chronologies

	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

RW, ring width; LW, latewood width; EW, earlywood width; MVA, mean vessel area; CUG, Cugnasco; ZUR, Zurich; SAL, Salgesch.

Fig. 3. In general, the chronologies are better correlated with precipitation than with temperature. At the driest site (SAL), RW correlates mainly with accumulated precipitation during current spring ($r = 0.41$, $P < 0.01$ with March to May), whereas at the moister sites (CUG and ZUR) the response of RW either covers 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, and those of EW are less consistent. At SAL, both EW and MVA are strongly correlated ($P < 10^{-4}$) with accumulated precipitation during the previous growing season ($r = 0.53$ and $r = 0.51$ for the 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 with precipitation during the period April–May ($r = -0.72$ and $r = -0.57$, $P < 10^{-4}$ for CUG and ZUR, respectively), whereas 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 with temperature are in general weaker. Temperature appears to have little or no influence on RW, LW and EW, but MVA can correlate with (early) spring temperatures; however, correlations are not as strong as those with 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 essential 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 this situation (García-González & Fonti, 2006, 2008). However, 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), to those for *Quercus rubra* L. and *Quercus alba* L. at their northern limit in Canada (Tardif & Conciatori, 2006), and higher than those for *Castanea sativa* in the southern Swiss Alps (Fonti & García-González, 2004; Fonti *et al.*, 2007). Furthermore, the widths are more sensitive than MVA (as shown in earlier works, for example Pumijumnong & Park, 1999; Fonti & García-González, 2004; Tardif & Conciatori, 2006), but they are more affected by previous growth and consequently are 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 than and different from those for the other ring parameters (apart from EW). This result confirms previous findings of similar approaches for other ring-porous species (Fonti & García-González, 2004; Fonti *et al.*, 2007) and in other 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), whereas MVA is not, which could explain why MVA is less autocorrelated and more linked to climate.

Content of the climatic signal and its ecophysiological meaning

The parameters analysed 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 the 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 onset of cambium activity and vessel expansion in spring (Suzuki *et al.*, 1996; Schmitt *et al.*, 2000; Fonti *et al.*, 2007). SAL, however, 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

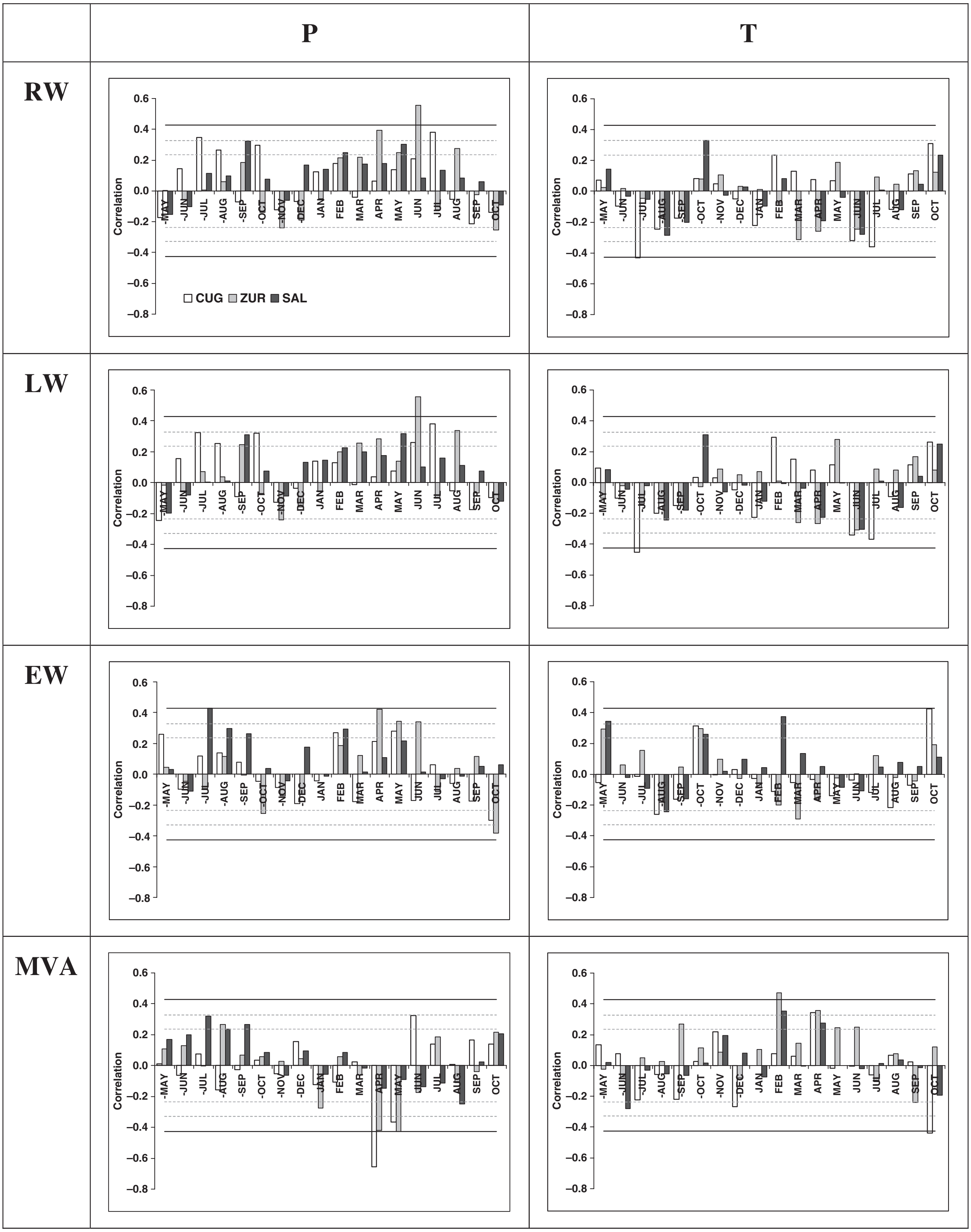

Figure 3 Pearson's correlations for the widths (RW, ring width; LW, latewood width; EW, earlywood width) and mean vessel area (MVA) sites chronologies as compared with monthly average temperature (T) and sum precipitation (P) for the period 1956–2005. White bars, Cugnasco (CUG); grey bars, Zurich (ZUR);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

dominant factor, which constitutes a major limitation to efforts 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 dominant factor limiting tree growth, as is the case 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 (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 the correlation of RW with 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 the accumulation 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 greater need of water, the tree would have prepared itself by producing larger earlywood vessels. In contrast to MVA, the response of RW at this site appears to be directly linked to the availability of water for physiological processes, 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, the more reliable the climate reconstruction. For this reason, dendroclimatic reconstructions have been traditionally based on the principle of limiting factors (Fritts, 2001); that is, 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. However, it has the restriction that most trees need to be sampled at the Alpine or boreal timberlines or in semi-desert 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 with climate. This response changes according to the climatic regime, but 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 timespan. 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 in temperate areas, 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 increase the sources of information in areas where climate has a strong influence on RW. In addition, in similar climatic contexts (e.g. both mesic sites), the response 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 mesic sites.

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