

Earlywood vessels of *Castanea sativa* record temperature before their formation

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Summary

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- The aim of this study was to identify the climatic signal contained in the earlywood vessel size of the ring-porous chestnut (*Castanea sativa*) and the physiological processes involved in the underlying mechanisms.
- In order to assign the encoded signal to a specific physiological process, bud phenology and vessel formation were monitored along an elevation transect and chronologies of the size of the first row of earlywood vessels were retrospectively correlated with 40 yr of early spring temperatures.
- The first vessels appeared in late April to early May, after encoding both a negative temperature signal in February–March (during tree quiescence) and a positive temperature signal in early April (at the time of resumption of shoot growth).
- We hypothesize that February and March temperatures affect cambial sensitivity to auxin, preconditioning tree responses later in the season. Furthermore, April temperature is related to tree activation whereby new hormone production fosters vessel expansion.

Key words: *Castanea sativa*, earlywood, environmental signal, ring porous, southern Swiss Alps, tree rings, vessel size.

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Introduction

Plants actively adjust their growth and development in response to seasonal and annual changes in the environment. Environmental stimuli are ‘read’ by a plant to produce appropriate physiological responses (Heggie & Halliday, 2005), which in the case of wood formation result in permanent morphological characteristics. The use of the width of dated annual tree rings is a well-documented method of gathering interannual environmental information (e.g. Schweingruber, 1996). The anatomical characteristics of wood cells can also provide environmental information with a higher resolution than 1 yr as times of division, expansion, and maturation of wood cells range from days to a few weeks. However, their application as ecological indicators first requires identification of what feature of which cell type contains what signal. This can be accomplished using two approaches. One is to ‘track’

the influence of the environment on wood production through repeated measurements of xylem during its formation (e.g. Suzuki *et al.*, 1996; Farrar & Evert, 1997; Schmitt *et al.*, 2000; Deslauriers *et al.*, 2003; Deslauriers & Morin, 2005); this procedure can be used to clarify the biological basis of wood formation as the phases of cambial cell differentiation can be referred to specific timings and events. The other approach is to obtain environmental information retrospectively; i.e. time series of different anatomical features are screened for their signals (e.g. St George *et al.*, 2002; Wang *et al.*, 2002; García-González & Eckstein, 2003; Kirilyanov *et al.*, 2003; Fonti & García-González, 2004). The combination of the two methods should enable the registered environmental signal to be associated with a specific phase of cell differentiation.

Several dendroecological investigations proved that wood cells contain ecological information (Wimmer, 2002; Eckstein, 2004), although their signals vary among species, climatic

regions, site conditions and anatomical features. For example, the earlywood vessel size of oak (*Quercus* spp.) registered spring precipitation in an oceanic climate (García-González & Eckstein, 2003), temperature in a dry inner-Alpine valley (Eilmann *et al.*, 2006), or periods of flooding along riverbanks (Astrade & Begin, 1997; St George & Nielsen, 2000). Variations in vessel density and diameter in the tropical mangrove *Rhizophora mucronata* were associated with the periodic fluctuation between dry and rainy seasons (Verheyden *et al.*, 2005). Earlywood tracheid dimensions were related to summer temperature in *Larix cajanderi* (Panyushkina *et al.*, 2003) and latewood cell wall thickness was related to summer weather in *Picea glehnii* (Yasue *et al.*, 2000). However, none of these studies included analysis of cambial phenology to support the physiological interpretation of the correlations.

In *Castanea sativa*, a ring-porous tree commonly found in the southern Swiss Alps, Fonti & García-González (2004) revealed a strong negative relationship between earlywood vessel size and temperature in March, which led to the assumption that temperature in March directly affects vessel expansion.

The aim of the present study was to validate this hypothesis by identifying the ecophysiological mechanism responsible for the observed temperature signal. Identification of the developmental stage of the tree coincident with the recording of the signal may allow inferences about how temperature can influence the process of vessel growth. To accomplish this, both the aforementioned approaches were used to relate spring bud and cambial phenological phases in a high-resolution examination of the temperature signal recorded by the earlywood vessels. In particular, the analyses were performed along elevation and aspect transects in order to establish the timing of earlywood vessel formation in relation to the recorded temperature signal, and to elucidate the effects of late winter and early spring temperature on earlywood vessel formation.

Materials and Methods

Study site and tree selection

The study was conducted in 2005 in the Valle Mesolcina (latitude 46°14' N, longitude 9°07' E), an east–west oriented valley located on the southern side of the Swiss Alps. This region is dominated by the nonnative chestnut (*Castanea sativa* Mill.), a tree species that has been intensively cultivated for centuries for both fruit and wood production, and has become the main forest component within the region (Conedera *et al.*, 2004). The six study sites, each of *c.* 1 ha, were located on either a south-facing (S) or a north-facing (N) slope at low, middle or high altitude (L = 300, M = 600 and H = 900 m above sea level (asl), respectively), with the highest site being at the upper limit of the altitudinal range of chestnut. All sites were chestnut stands that had been abandoned for at least 50 yr. In each stand, 10–14 dominant trees (72 trees in total) were selected for the study. The climate

is temperate-humid according to the classification by Walter & Lieth (1964). Prevailing winds are from the north-west and north-east and may produce very dry atmospheric conditions. The meteorological station in Grono (382 m asl), located < 5 km from the study sites, recorded a mean annual temperature of 11.5°C and a total annual precipitation of 1492 mm, with > 80% falling between April and November (data from 1966 to 2004; MeteoSwiss, Locarno-Monti, Switzerland).

Monitoring of spring phenophases, earlywood production and temperature

Site temperature, phenological developmental stages, and earlywood formation were monitored for each site from March to June 2005 in order to quantify differences in the temperature signal of vessel size. Two sensors (Thermochron iButton DS1921G; Maxim Integrated Products Inc., Sunnyvale, CA, USA) stationed at each site 2 m above the ground recorded hourly temperatures. Site temperature differences were calculated from daily averages.

Earlywood vessel formation was monitored at weekly intervals by taking cores (4 mm in diameter) which contained the developing annual layers and a few previously formed tree rings. These samples were extracted from each tree with an increment hammer (Haglof Inc., Madison, MS, USA) following a spiral trajectory down the stem (3 cm right and 2 cm down). Samples were then prepared to track earlywood vessel production. Special care had to be taken to avoid distortions or crushing of newly formed enlarging cells. After sampling, the block of tissue was fixed on a wooden holder, air-dried and sanded. A reflecting light microscope was used for anatomical observations; unambiguous identification of the first earlywood vessel to attain its final size was used to determine the timing of vessel formation (Fig. 1). At the same time, bud-leaf phenology was observed. A phenological phase was assumed to have begun when at least 50% of the study trees at a site showed the first sign of its respective characteristics. In contrast to standard monitoring techniques, which consider a phenological phase to have begun when 50% of the crown buds have attained that stage (Meier, 1997), we observed buds on lower branches because analysis of vessel formation was on samples taken at breast height.

Dendrochronological survey and climate analyses

During the winter of 2004–2005, increment cores of 12 mm in diameter were taken from each study tree 1 m above the ground and perpendicular to the direction of the slope. All cores were mounted, sanded to 400-grit, and cleaned with a high-pressure water blast to remove tyloses and wood dust inside the earlywood vessel lumina. To confirm accurate tree-ring dating, ring widths were first measured using a Lintab measuring device (Rinntech, Heidelberg, Germany) and cross-dating was verified using COFECHA (Holmes, 1983).

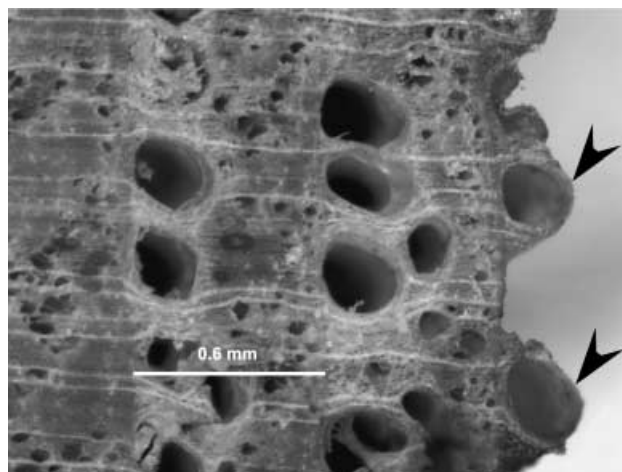


Fig. 1 Cross-section of a core extracted with an increment hammer from the stem of *Castanea sativa*. Two earlywood vessels (arrows) that have attained their final size are clearly visible on the right.

The dated cross-sections were then prepared for vessel measurements. The wood surface was colored black using a marker pen and vessel lumina were filled with white chalk powder to improve vessel detection. Measurements were automatically performed by an image analysis device, which consisted of a combination of a video camera with $\times 18$ magnification and the IMAGE PRO PLUS digital analysis software (Media Cybernetics, Silver Spring, MD, USA). Vessels were measured ring by ring along a 3.8-mm-wide radial strip using digitized images captured with a microscope. Only vessels in the first row and of size $> 0.01 \text{ mm}^2$ were considered, to avoid mixing signals of vessels formed at different times (García-González & Fonti, 2006). An example of an image is shown in Fig. 2. The analysis was performed for the period 1965–2004, which was covered by all trees and allowed the exclusion of juvenile wood from the youngest individuals. To obtain time series, the mean area of these earlywood vessels was calculated for each annual ring. Trends that were not related to climate (mainly age-related trends) were removed from the individual series by fitting a cubic smoothing spline function with 32-yr stiffness and 50% cutoff, retaining mainly year-to-year variability. The series of each site were subsequently averaged into growth indices (Fritts, 1976; Cook & Kairiukstis, 1990).

The statistical quality of each chronology was evaluated by employing four coefficients commonly used in dendrochronology: the mean correlation between trees, the expressed population signal, the mean sensitivity and the first-order autocorrelation. Pearson's correlations were calculated between mean vessel area site chronologies and temperature and precipitation recorded at the nearby Grono weather station (daily average 1966–2004). These correlations were explored using a 14-d moving window technique whereby the climatic variables were shifted across time in daily steps from February to June to investigate if warm and cold conditions from the end

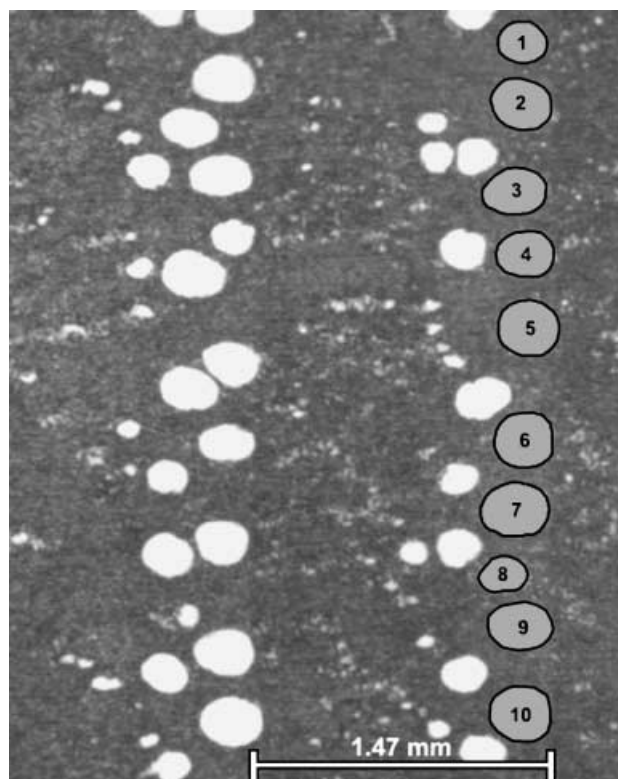


Fig. 2 Example of a digital image used for measurements of vessels of *Castanea sativa*. Numbered vessels correspond to the vessels selected for measurement. The program was executed with filters (morphological 2×2 squares, 1 pass) and an image enhancer (equalize, best fit) in order to optimize contrast and improve recognition of all bright objects (vessel lumina).

of winter through the beginning of spring affected the signal differently, the analyses were repeated by splitting growth years and computing separate correlations. Years with above-average temperature for the period February–April (i.e. $> 7.5^\circ\text{C}$) were considered 'warm early spring years' and vice versa.

Results

In the study year 2005, spring was warmer than usual, and the temperature in February to April was 0.68°C higher than the average of the last 40 yr. Temperature differences among sites were stable over the recorded period from March to June. In general, low-elevation sites were up to 4°C warmer than high-elevation sites, whereas the effect of exposition was stronger at lower elevations (Table 1).

Observations of phenology in 2005 showed that the altitude-driven delays in the onset of the different bud-leaf phenophases were not consistent (Table 2). Bud swelling was simultaneous at all sites (week 12, end of March). Depending on the site, bud break occurred 1–3 wk later, with a lag of 4 wk between the first manifestation on the lower branches (mostly epicormic buds) and at the top of the crown. Leaf

Table 1 Temperatures recorded between February and April 2005

Site	Average (and minimum to maximum) temperature (°C)			
	February	March	April	February to March
North High	−0.9 (−5.2 to 4.6)	5.0 (−7.0 to 15.3)	8.4 (3.2 to 16.5)	4.3
South High	−0.9 (−4.9 to 4.9)	5.2 (−6.7 to 16.2)	8.0 (2.2 to 16.9)	4.3
North Middle	0.5 (−4.1 to 5.7)	6.2 (−5.9 to 15.9)	10.0 (4.6 to 18.1)	5.7
South Middle	1.9 (−2.2 to 7.6)	7.9 (−4.0 to 18.4)	10.9 (4.8 to 19.8)	7.1
North Low	1.8 (−3.0 to 6.8)	7.3 (−4.8 to 16)	11.4 (6.3 to 19.0)	7.0
South Low	3.1 (−1.3 to 8.5)	8.9 (−3.1 to 18.2)	12.4 (6.5 to 20.4)	8.3
Grono (weather station)	3.1 (−1.5 to 8.3)	8.9 (−3.3 to 18.1)	12.3 (7.4 to 20.5)	8.3

Table 2 Development of *Castanea sativa* bud-leaf and wood phenology by site during the year 2005

Site	Onset of bud-leaf phenological stage (week of the year)					Onset of vessel appearance (week of the year)	
	Bud swelling	Bud break	Leaf unfolding	Sprouting	Flowering	First vessels	First vessel row complete
NH	12	15	18	21	26	19	24
SH	12	15	18	21	26	19	23
NM	12	13	15	20	24	19	23
SM	12	13	16	19	25	16	21
NL	12	13	15	20	23	17	22
SL	12	13	14	19	23	16	21

NH, North High; SH, South High; NM, North Middle; SM, South Middle; NL, North Low; SL, South Low.

unfolding first occurred in week 14 (6 April) at the south-facing, low-elevation site (SL) and 1 month later (week 18) at the high-elevation sites (SH and NH). A similar delay between low and high elevations (3 wk) was observed for the first appearance of conductive elements (Table 2). The observation of the first earlywood vessels was contemporaneous with the first manifestation of leaf unfolding. The formation of the first row of earlywood vessels occurred over a period of 4–5 wk until the end of May or the beginning of June, depending on the site.

Analyses of the common year-to-year variation of earlywood vessel size indicated that trees growing at the same site only captured a feeble common signal (see values of mean correlation between trees and expressed population signal in Table 3). However, this low intercorrelation appears to be related to the frequent presence of outliers in the individual series, whose influence is minimized by averaging a considerable number of trees at each site. Hence, mean site chronologies reflect a common and robust meso-climatic signal, as suggested

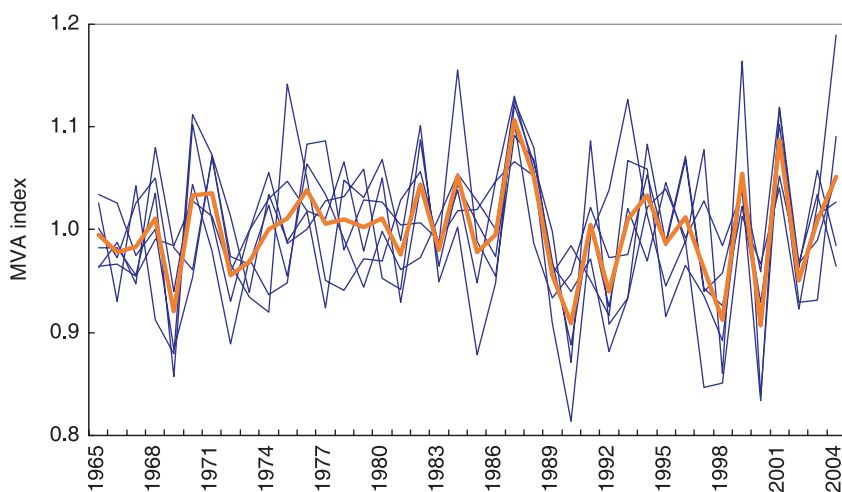
by the consistent pattern among sites (Fig. 3), with correlations raging from 0.25 to 0.62 (data not shown).

The retrospective analyses of climate–growth relationships showed that the signal registered by the annual variation in vessel size was strongly associated with early spring temperatures (not with precipitation; data not shown). In general, the size of earlywood vessels was first negatively correlated with temperature in February and March, then positively correlated with April temperature, and then again negatively correlated with May temperature (Fig. 4). This pattern tended to be consistent among sites, with differences in timing and correlation values. Correlations were strong for high and medium elevations but weak for low elevation. The positive signal in April appeared earlier on the south-facing slope than on the north-facing slope at both the high- and medium-elevation sites, but was not significant ($P > 0.05$) for the lowest sites and was even absent at site NL. However, the transition from negative to positive correlation always preceded the initial vessel appearance, which occurred in mid-April.

Table 3 Statistical quality of mean vessel area (MVA) site chronologies

Coefficient	Site (sample size)						All (72)
	NH (13)	SH (14)	NM (14)	SM (10)	NL (11)	SL (10)	
Rbt	0.088	0.212	0.147	0.204	0.104	0.057	0.095
EPS	0.556	0.790	0.707	0.719	0.560	0.376	0.883
MS	0.065	0.098	0.071	0.098	0.061	0.073	0.057
AutoR	-0.054	-0.358	0.292	-0.233	-0.193	-0.416	-0.243

NH, North High; SH, South High; NM, North Middle; SM, South Middle; NL, North Low; SL, South Low; All, all trees; Rbt, mean correlation between trees; EPS, expressed population signal; MS, mean sensitivity; AutoR, first-order autocorrelation coefficient.

**Fig. 3** Chronologies of *Castanea sativa* mean vessel area (MVA) for each site and the average (bold line) for the period 1965–2004.

The correlation patterns observed for earlywood vessels formed in 'warm early spring' years vs 'cold early spring' years were not different from each other (Fig. 5). Nevertheless, February and March signals were more consistent with milder temperatures, and the positive response in April was delayed by 1–2 wk in cold springs.

Discussion

Phases of tree reactivation

Trees in temperate regions pass through annual periods of activity and dormancy. Dormancy is first maintained by internal factors during rest and later by unfavorable environmental conditions during quiescence (Little & Bonga, 1974). To resume activity, a tree first requires chilling, i.e. exposure to coldness, to enable it to enter the quiescence phase in which it regains the ability to respond to growth-promoting conditions, and then exposure to warmth, to enable it to start cambial cell division (Romberger, 1963; Larson, 1994). During quiescence, only changes at the ultrastructural level occur within a tree (Farrar & Evert, 1997), whereas visible signs of activity appear when the conditions become favorable for tree growth. The

first external characteristic of reactivation is usually bud swelling (Frankenstein *et al.*, 2005) followed by bud break, which is contemporaneous or shortly preceded by the differentiation of the first earlywood vessels in most ring-porous trees (Atkinson & Denne, 1988; Suzuki *et al.*, 1996; Schmitt *et al.*, 2000), including chestnut (Boutin, 1985), even if cambial mitosis has not yet begun. This differentiation only applies to overwintering cambial derivatives, i.e. cells that had divided at the end of the previous season (Imagawa & Ishida, 1972; Kitin *et al.*, 1999; Frankenstein *et al.*, 2005).

Tree reactivation was observed simultaneously at all study sites by the end of March (week 12) as bud swelling, but the rate of bud break and leaf unfolding differed according to slope and elevation, suggesting that it is modulated by temperature. Unfolding was delayed by up to 3 wk at the upper sites, and occurred slightly earlier on south-facing slopes than on north-facing slopes. Similar differences in timing among sites were observed for the completion of the first earlywood vessels, which were clearly visible between mid-April and mid-May (week 16–19), always when leaf unfolding had already begun. The time lag between bud break and the formation of the first vessel elements was consistent with the findings of Suzuki *et al.* (1996) for several ring-porous species.

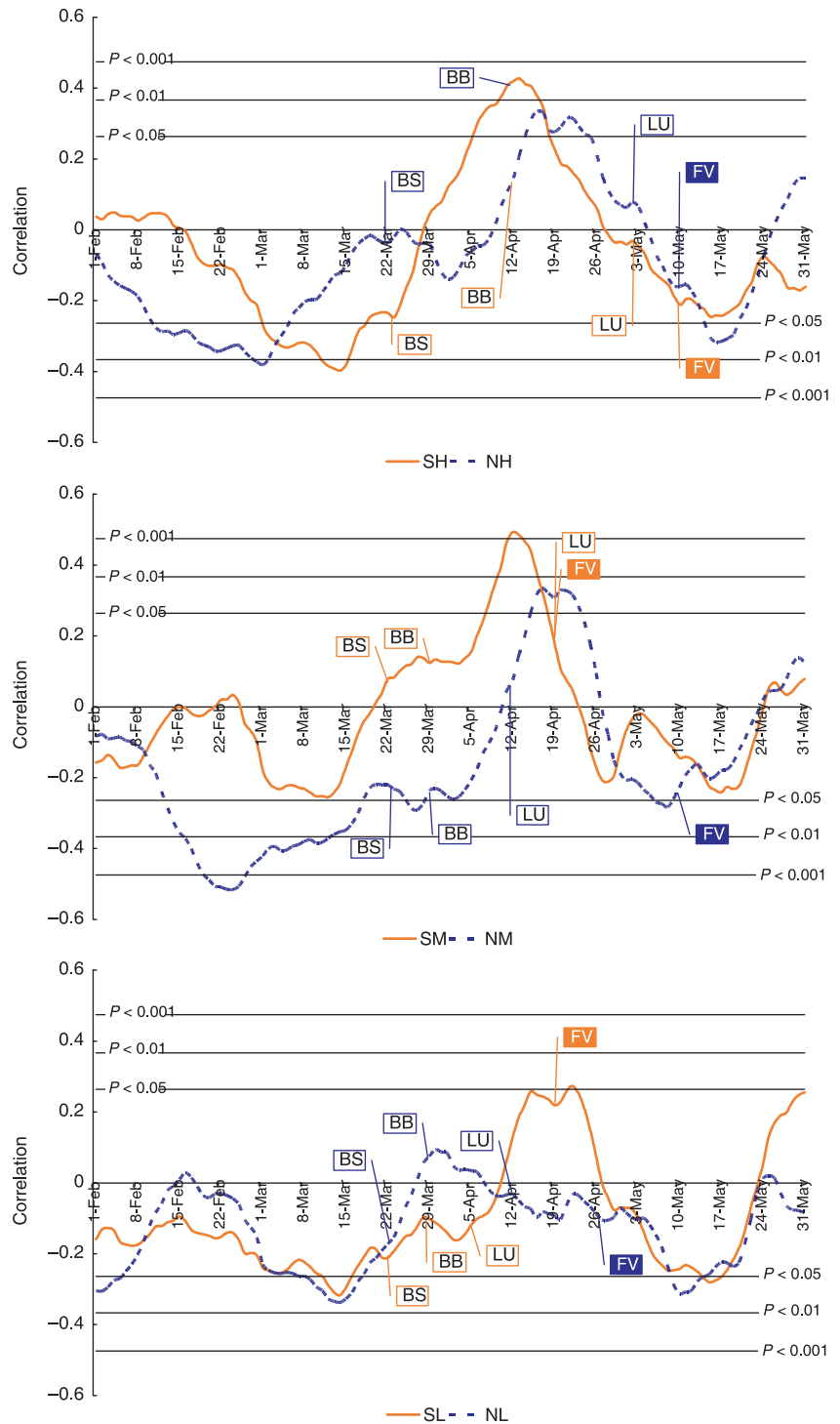


Fig. 4 Variation of the Pearson's correlation coefficient between mean vessel area (MVA) site chronologies and temperature based on a 14-d moving window from February to June. Data refer to the period 1965–2004. Horizontal lines indicate significance at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively. Sites were as follows: SH, South High; SM, South Middle; SL, South Low; NL, North Low; NM, North Middle; NL, North Low. BS, bud swelling; BB, bud break; LU, leaf unfolding; FV, appearance of first vessels.

Timing of vessel formation and temperature signal

Climate–growth analyses showed a significant relationship between the size of earlywood vessels and the temperature in early spring, confirming the ability of this ring-porous species to register environmental information (e.g. St George *et al.*, 2002; García-González & Eckstein, 2003; Eilmann *et al.*, 2006).

Thus, this study supports a previously observed negative correlation with February and March temperatures (Fonti & García-González, 2004) and, with the application of a more sensitive 14-d moving window, highlights a new positive relationship with early April temperature. This positive correlation was stronger where temperature was more limiting, i.e. at high-elevation sites and on north-facing slopes, and also

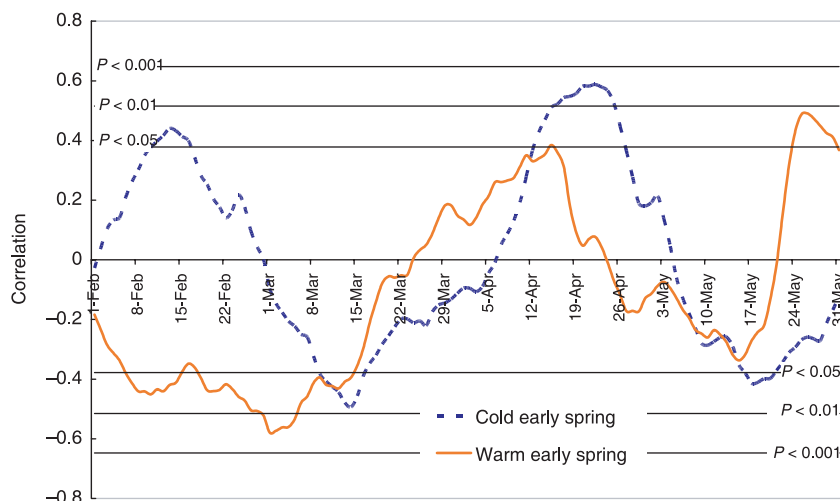


Fig. 5 Variation of the Pearson's correlation coefficient between mean vessel area (MVA) chronologies of cold (dashed line) and warm (solid line) early spring years and temperature, based on a 14-d moving window from February to June. Data refer to the period 1965–2004. Horizontal lines indicate significance at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

occurred earlier at warmer sites (south-facing slopes). The timing of the April signal also preceded the detection of the first earlywood vessels, which were observed 1–4 wk after this positive signal. These vessels originate from overwintering cambial derivatives that undergo expansion for a few weeks before lignification, so their differentiation seems to be synchronous with the positive temperature signal in early April but does not coincide with the prior negative signal in February and March. The positive effect of April temperature in triggering activity is supported by observations of temperature-induced cambial reactivation on locally heated stems (e.g. Oribe *et al.*, 2001, 2003; Gričar *et al.*, 2006). In contrast, the registration of the negative signal in February–March anticipates the beginning of vessel differentiation.

Onset and regulation of vascular differentiation

The delay between the negative temperature signal and vessel enlargement can be explained by considering that wood formation is the result of a complex system of plant internal signals which are regulated by the environment. The major role in the control of cambial activity is played by auxin, indole-3-acetic acid (IAA), which is involved in all aspects of vascular differentiation, from cell division in the cambial meristem to cell expansion and maturation of the cambial derivatives (for detailed reviews, see Lachaud *et al.*, 1999; Mellerowicz *et al.*, 2001; Ye, 2002; Friml, 2003; Fukuda, 2004; Scarpella & Meijer, 2004; Kepinski, 2006). Auxin concentrations and gradients determine the rate and duration of cell developmental phases (Little & Pharis, 1995; Uggla *et al.*, 1996; Tuominen *et al.*, 1997; Savidge, 2000; Sundberg *et al.*, 2000) and thus influence the final size of the water-conducting elements (Aloni & Zimmermann, 1983).

Auxin is often present in the dormant cambium (Savidge & Wareing, 1982; Sundberg *et al.*, 1991; Uggla *et al.*, 1996) but it is not able to induce the resumption of wood formation in

early spring by itself if the cambial cells have not yet regained their capability to respond to the stimulator (Lachaud, 1989). This responsiveness is usually referred to as 'auxin sensitivity' (Trewavas & Cleland, 1983) and is linked to the ability of the cambial cells to carry out polar transport of the regulator (Lachaud, 1989), mediated by the action of auxin efflux carriers (Berleth *et al.*, 2000; Fukuda, 2004; Paponov *et al.*, 2005). The presence of cytokinins may be required to trigger the cambial responsiveness to auxin (Baum *et al.*, 1991; Aloni *et al.*, 2006). Auxin carriers, deactivated during dormancy (Riding & Little, 1984; Moyle *et al.*, 2002; Schrader *et al.*, 2004), are re-established during quiescence, from January to March (Lachaud, 1989), whereas cytokinins supplied by root apices (Aloni, 2001) are produced only later under favorable environmental conditions.

Role of temperature in controlling vessel size

The process of regaining auxin sensitivity during quiescence may explain the relationship between the negative signal of February and March temperature and vessel size in chestnut. In particular, a warm late winter would increase the sensitivity of overwintering cambial derivatives by fostering the reactivation of auxin carriers. Schrader *et al.* (2003) found that rising temperature before bud break increased the expression of genes involved in polar auxin transport, providing evidence that auxin sensitivity can be modulated by temperature. When triggered later in the season, this higher cell sensitivity to auxin signals would result in smaller vessels as a consequence of an earlier and faster process of differentiation (Aloni & Zimmermann, 1983).

The positive correlation with April temperature corresponds to the beginning of active growth following favorable conditions in early spring. Comparison of the different responses at sites with different elevation and slope, together with comparison of years with a 'warm' or a 'cold' spring,

showed that higher temperatures produced an earlier reactivation and a sooner appearance of the positive April signal. Warm conditions in this period promote the production of cytokinins followed by the synthesis of auxin in the apical region of active shoots (Aloni *et al.*, 2003; Friml, 2003). Temperature influences these processes by both triggering auxin synthesis (Gray *et al.*, 1998) and affecting auxin transport (Schrader *et al.*, 2003), but would not be able to maintain cambial activity by itself without a continuous supply of auxin (Oribe *et al.*, 2003). Consequently, previously differentiating earlywood vessels are exposed to a new basipetal flux of *de novo* produced auxin, which is responsible for the re-establishment of mitoses in the cambial zone. All these processes result in changes in auxin gradients that facilitate further expansion of these vessels (Uggla *et al.*, 1996).

The combination of temperature signals in the earlywood vessels with tree phenological observations suggests that late winter and early spring temperatures influence the physiological processes involved in earlywood vessel differentiation, determining the final size of these vessels. We hypothesize that, depending on the stage of the seasonal cycle, temperature may (i) influence cambial sensitivity to auxin, (ii) determine when cambial derivatives start to differentiate, and (iii) regulate the duration of vessel enlargement. This study on forest trees complements previous studies at the cellular or molecular level carried out under controlled conditions, and provides new insights into cambial activity and its regulation by environmental factors.

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