Tree Physiology 26, 1289–1296
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Selecting earlywood vessels to maximize their environmental signal

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Received March 15, 2005; accepted December 19, 2005; published online June 30, 2006

Summary The anatomical features of earlywood vessels often reflect information about past climatic conditions. We examined the relationships between mean monthly temperature and mean vessel lumen area (MVA) in various categories of earlywood vessels. Subsets of earlywood vessels of chestnut (*Castanea sativa* Mill.) were selected from a previously reported dataset based on several progressive size-related procedures. To include all earlywood vessels, the minimum size considered was 10,000 μm^2. Changes in the correlations between MVA and the mean air temperature in March are described and discussed. The results show that not all vessels embody the same information. The MVA of a proportion of the largest earlywood vessels in each annual ring was most closely related to March temperature, whereas MVA of the smallest earlywood vessels was better correlated with June temperature. This difference is probably a result of the vessels being formed at different times: early spring for the largest earlywood vessels and later in spring for the smallest earlywood vessels. Analyses combining large and small vessels yielded lower correlations between MVA and monthly temperature. The number, size and distribution of vessels can vary greatly from ring to ring. In making year-to-year comparisons, the best information is provided by observations on vessels of contemporaneous ontogenesis. Criteria for the selection and analysis of vessels in the assessment of temperature during the season of wood formation are proposed and discussed.

Keywords: Castanea sativa, dendrochronology, dendroecology, ring-porous, tree rings, vessel size.

Introduction

Tree rings embody information about past climate. The feature of xylem anatomy most frequently assessed as a measure of past climate conditions is annual ring width. This variable, which can be determined easily and largely nondestructively and which integrates the prevailing environmental conditions during the whole growing season, is inappropriate for reconstructing climatic conditions on time scales shorter than the growing season. For higher temporal resolution, analysis of wood at the cellular level is more suitable. Because cambium produces wood cells throughout the growing season, short-term events can be identified by focusing only on those cells produced at the time of the specific environmental event.

Although the potential of wood anatomy as a source of information about past climate has been long recognized (Eckstein and Frisse 1982, Baas 1986), this approach has been slow to develop because of the lack of convenient techniques for measuring and compiling long chronologies of anatomical features. Recent advances in computer technology and microscopic image analysis (Jagels and Telewski 1990), combined with improved wood-surface preparation (Spiecker et al. 2000), have made the measurements of cell structures across sequences of tree rings much easier. Thus, interest in intra-annual anatomical features as indicators of past environmental conditions is steadily increasing (e.g., Leuschner and Schweingruber 1996, Schweingruber 2001, Wimmer 2002, Masiokas and Villalba 2004).

Recent investigations have concentrated on identifying what ecological information is contained in different features of different cell types. Particularly promising results have been obtained from studies on water conducting elements of several hardwoods (Eckstein 2004). Dendroecological analyses have repeatedly demonstrated the potential of vessels for recording different kinds of information about past environmental conditions, even across species (see Akachuku 1987, Woodcock 1989, St. George et al. 2002, García-González and Eckstein 2003, Corcuera et al. 2004*a*, 2004*b*, Eilmann et al. 2006, for *Quercus* spp.; Pumijumnong and Park 1999 for *Tectona grandis* L.; Fonti and García-González 2004 for *Castanea sativa* Mill.; Tardif 1996 for *Fraxinus nigra* Marsh.; Sass and Eckstein 1995 for *Fagus sylvatica* L.; Schume et al. 2004 for *Populus* × *euramericana* (Dode) Guinier; and Verheyden et al. 2005 for *Rhizophora mucronata* Lam.).

Vessels formed at different times presumably incorporate different information about past climate. In ring-porous woods, vessel size varies considerably across an entire ring. As a rule, the larger the vessel, the closer it is to the ring boundary and the earlier its formation. Vessels of different size should, therefore, embody information about climate at different times of the year. However, dendroecological studies on ring-porous trees have mainly analyzed the characteristics of all earlywood vessels selected from an arbitrarily defined minimal lumen size (e.g., St. George et al. 2002 (1200 μm^2), García-González and Eckstein 2003 (5000 µm^2), Fonti and García-González 2004 (10,000 µm^2), Eilmann et al. 2006 (5000 µm^2)).

In this study, we concentrated on how the selection of earlywood vessels in ring-porous wood affected correlations between vessel characteristics and monthly mean temperatures during the season of wood formation. In particular, we investigated: (1) whether vessels of different sizes record different information about temperature during the season in which they were formed; and (2) how the expression of information about temperature during a portion of the growing season was influenced by the selection of vessels.

Materials and methods

The original dataset

The analyses were based on previously reported observations on chestnut (*Castanea sativa* Mill.) earlywood vessels (Fonti and García-González 2004). The original data consisted of cross-dated measurements of earlywood vessel lumen areas of 51 trees grown in three plots (Bedano, Novaggio and Gerra) in the southern part of the Swiss Alps. The survey considered all earlywood vessels larger than 10,000 µm^2 within an 8 mm wide radial strip extending across the earlywood width of all rings formed between 1956 and 1995. The results showed a close relationship between the meteorological conditions during earlywood vessel formation and the size of the vessels. In particular, March temperature was inversly correlated with earlywood vessel lumen diameter ($r = -0.63$, $P < 0.001$).

Procedures for vessel selection

Regression analyses were performed to examine the relationships between mean area of the earlywood vessels (MVA) and mean monthly temperature during the season of wood formation. Analyses were performed after application of several size-based procedures of vessel selection.

One analysis (G-Decile) focused on detecting variations in the signal recorded by vessels differing in size. The size distribution of all earlywood vessels in each annual ring was split into 10 groups, each containing 10% of the vessels (decile). Subsequently, chronologies and climate–growth relationships were independently developed for each decile.

We also performed a stepwise selection of large vessels to evaluate the expression of the temperature in March of the year of wood formation. Progressive filters were applied to gradually exclude small vessels from the original dataset, tracking changes in the signal expressed at each step. Three selection procedures were performed retaining only: (1) vessels larger than a given minimal threshold size (F-minValue); (2) the n largest vessels (F-TopX); and (3) the n percent of largest vessels (F-Top%). Figure 1 illustrates the effect of these filtering procedures on two adjacent annual rings.

Chronology building and climate–growth relationships

Relationships between MVA and mean monthly temperature were analyzed by standard dendrochronological procedures (Fritts 1976). For each data subset, individual MVA time series were established and unwanted growth-related trends were removed by adjusting a cubic smoothing spline with a stiffness of 32 years and a 50% cutoff (Cook et al. 1992). The detrended growth indices were averaged into a mean chronology for each site and then a composite chronology was calculated as a mean of the three site chronologies. Climate–growth relationships were also computed from the data subsets using Pearson's correlation coefficient between the chronologies and the monthly records of mean temperature and total precipitation from Lugano, located not more than 20 km from the sites. When the filtering was too strict, such that all earlywood vessels in a ring were removed, that ring was not further considered in the analyses. The years 1956–1959 were not considered at all because too many rings had to be excluded. Fonti and García-González (2004) present a more detailed description of the chronology computation and the establishment of climate–growth relationships.

The climatic signals expressed by the different subsets of earlywood vessels were assessed by plotting the correlations along with the results of the progressive filtering procedures. As each filter generated a new MVA subset for each ring, all processing steps (filtering, establishment of time series, detrending, chronology computation and analysis of climate-growth relationships) had to be recalculated. This was automatically performed by computer programs written specifically for this purpose in Borland Delphi 5.

Results

Variability of vessel number and size

Number and size of earlywood vessels varied greatly from ring to ring. The number of vessels ranged from 14 to 247, depending on earlywood width, with a mean value of 55. The largest measured vessel had a lumen area 16 times the lower size limit fixed at 10,000 µm^2 and less than 1% of vessels (660 out of 95,778 vessels) were larger than 10 times that limit. Figure 2 illustrates the variability in the earlywood vessel size within and between trees and sites. With few exceptions, the distributions were skewed to the left, toward a large number of small vessels.

Signal related to vessel size

Analyses performed separately for each group (G-Decile) show that the growing season temperature signal embodied by the earlywood vessels changed with size. Figure 3 illustrates the correlation between each decile and the mean monthly temperatures from January to June, showing two major climatic signals: a strong inverse relationship with March temperature (as expected), but also, though weaker, a previously undetected positive correlation with June temperature.

The correlation between March temperature and the composite chronology is maximized ($r = -0.68$) when only the vessels in the third decile are considered; then, correlations decrease with vessel size. The lowest value ($r = -0.24$) was not significant and corresponds to the lowest deciles. However, the progressive weakening of the correaltion with March temperature is coupled with the strengthening of the correlation with June temperature, especially in the composite and Bedano

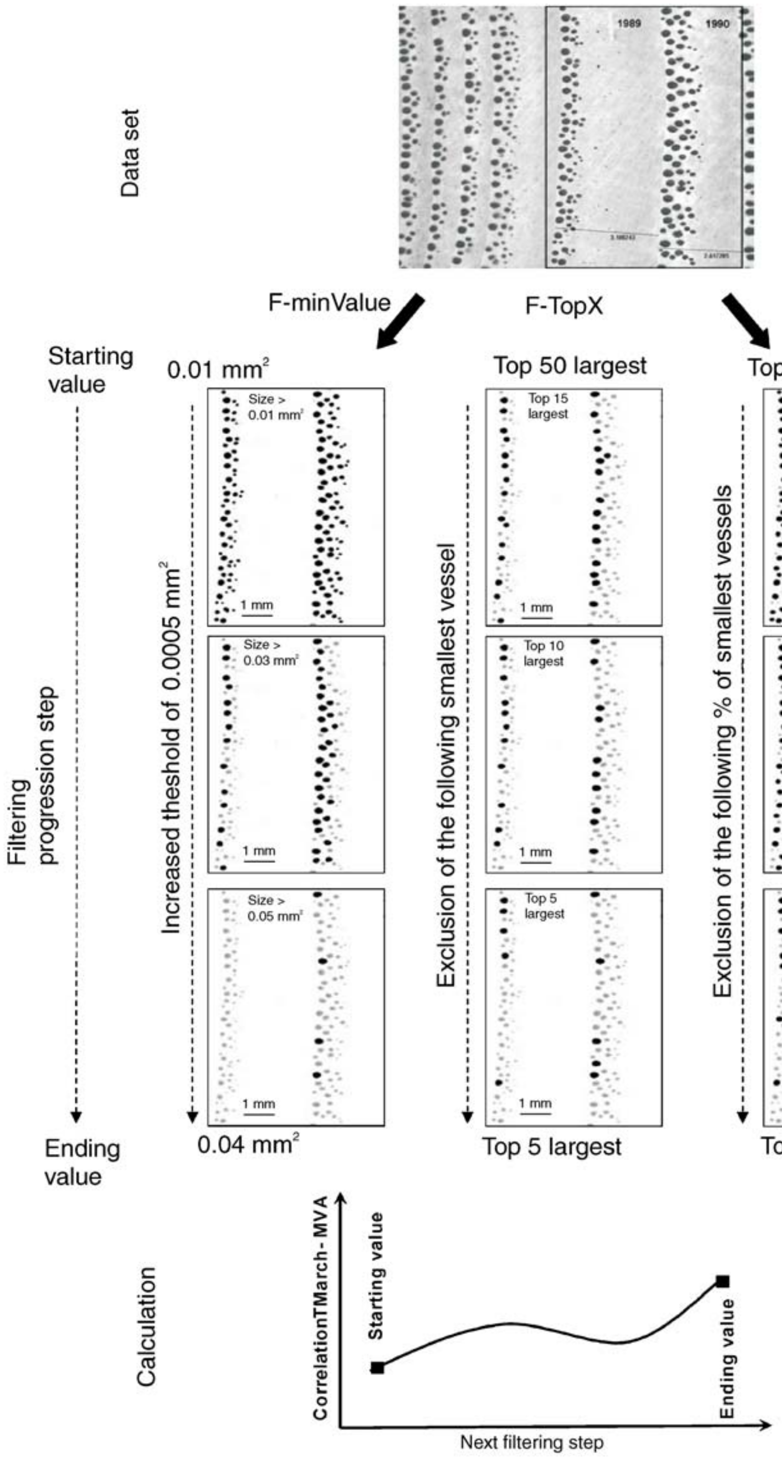


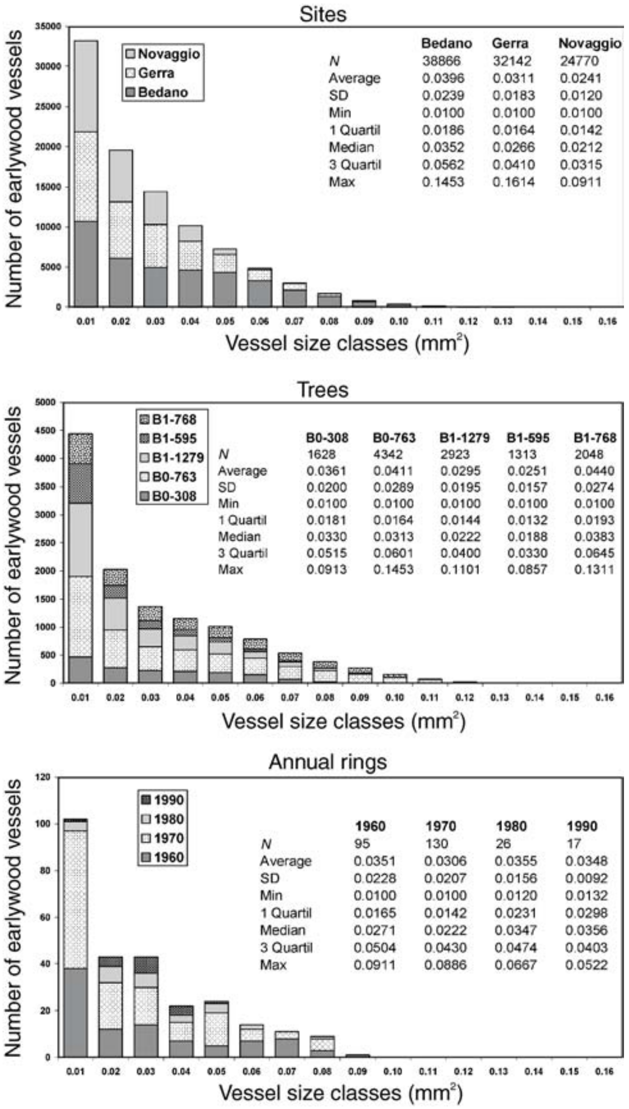
Figure 1. Visual summary of the different filtering procedures applied. The effect of filtering on vessel selection can be observed on two adjacent rings. Black spot refers to selected vessels.

chronologies, shown by a significant correlation ($r = -0.40$, $P < 0.05$) with the 10% smallest vessels.

Signal expression after filtering by size

The original dataset showed a highly significant correlation ($P < 0.001$) with March temperature, especially for the composite chronology ($r = -0.63$), which records a stronger climatic signal than the site chronologies. However, the extent of this correlation varied greatly depending on the selection criteria applied.

The first filter (F-minValue) removed the smallest vessels progressively by increasing the minimum threshold size (Figure 4). Only when the smallest earlywood vessels (i.e., those smaller than 13,000 μm^2) had been filtered out, did the correlation coefficient increase slightly ($r = -0.69$ for the composite) or remain constant (as observed for Gerra and Novaggio).



	Bedano	Gerra	Novaggio
N	38866	32142	24770
Average	0.0396	0.0311	0.0241
SD	0.0239	0.0183	0.0120
Min	0.0100	0.0100	0.0100
1 Quartil	0.0186	0.0164	0.0142
Median	0.0352	0.0266	0.0212
3 Quartil	0.0562	0.0410	0.0315
Max	0.1453	0.1614	0.0911

	B0-308	B0-763	B1-1279	B1-595	B1-768
N	1628	4342	2923	1313	2048
Average	0.0361	0.0411	0.0295	0.0251	0.0440
SD	0.0200	0.0289	0.0195	0.0157	0.0274
Min	0.0100	0.0100	0.0100	0.0100	0.0100
1 Quartil	0.0181	0.0164	0.0144	0.0132	0.0193
Median	0.0330	0.0313	0.0222	0.0188	0.0383
3 Quartil	0.0515	0.0601	0.0400	0.0330	0.0645
Max	0.0913	0.1453	0.1101	0.0857	0.1311

	1960	1970	1980	1990
N	95	130	26	17
Average	0.0351	0.0306	0.0355	0.0348
SD	0.0228	0.0207	0.0156	0.0092
Min	0.0100	0.0100	0.0120	0.0132
1 Quartil	0.0165	0.0142	0.0231	0.0298
Median	0.0271	0.0222	0.0347	0.0356
3 Quartil	0.0504	0.0430	0.0474	0.0403
Max	0.0911	0.0886	0.0667	0.0522

Figure 2. Examples of earlywood vessel lumen area distributions within sites, trees and growth increments.

However, a further removal of vessels resulted in a rapid decrease in the correlation. This was particularly evident if only vessels larger than 40,000 μm^2 were retained; in this case, when 70% of the vessels and 15% of the rings were removed from the calculation, the correlation coefficient dropped to –0.26, which was not significant.

The second filter (F-TopX) selected only a fixed number of the largest earlywood vessels (Figure 5). In no case did it provide a closer correlation than the whole data set. The highest correlation coefficient (r = –0.49) was obtained when the 18 largest vessels in each ring were considered. A smaller number of vessels (5–10 vessels) resulted in a decline in the correlation coefficient (below –0.40 for the composite, and even less for the site chronologies), but a greater number of vessels (25–50 vessels) did not enhance the strength of the climatic signal.

The last filter (F-Top%) retained the largest vessels by progressively removing the lowest percentile of earlywood vessels (Figure 6). For the composite, filtering down to only 35% of the large vessels did not affect the correlation coefficient noticeably (r = –0.63 to –0.66). The maximum value was achieved when the largest half of earlywood vessels was considered (r = –0.66). Removing more vessels resulted in a lower expression of the signal. Nevertheless, the first upper decile yielded a correlation coefficient of –0.46.

Discussion

Vessel size dependence of the signal

Weather conditions during the season of vessel formation appear to be largely responsible for year-to-year differences in vessel size. This has been observed not only in the case of the earlywood vessels of chestnut (Fonti and García-González 2004), but also for earlywood vessels of *Quercus robur* L. (García-González and Eckstein 2003), *T. grandis* (Pumijumnong and Park 1999), the latewood vessels of *Quercus macrocarpa* Minchx. (Woodcock 1989) and even for diffuse-porous species like *F. sylvatica* (Sass and Eckstein 1995). These results led to the hypothesis that vessel size reflects the climatic factors prevailing during the time of vessel expansion, i.e., until the complete deposition of the secondary cell wall, which determines their final size.

Successive analyses of wood formation during the growing season constitute one of the best methods for understanding the processes of cell production. Various investigations with conifers (Antonova and Stasova 1993, 1997, Deslauriers et al. 2003, Deslauriers and Morin 2005) and on broadleaf species (Suzuki et al. 1996, Schmitt et al. 2000, Frankenstein et al. 2005) have already supplied essential information on the mechanisms of xylem growth. For ring-porous hardwoods, the formation of the first earlywood vessels starts before bud burst and lasts for 3 to 7 weeks (Suzuki et al. 1996, Schmitt et al. 2000). When studying the effect of a given environmental variable, it is desirable to analyze only those vessels whose ontogeny is contemporaneous with that variable, for only contemporaneously formed vessels are likely to embody the climatic signal of interest, in which case inclusion in the analysis of vessels formed earlier or later in the season will only obscure the signal.

In our study, earlywood vessel size was correlated with mean March temperature, i.e., during the period of vessel growth. But when we partitioned the whole dataset into size classes (G-Decile), significant variations in the correlations were found. Unlike MVA of large vessels, MVA of the smallest vessels was more closely related to June temperature than to March temperature. This can be explained by the fact that, in ring-porous trees, the size of the earlywood vessels decreases as the distance of the previous ring's boundary increases (Zobel and van Buijtenen 1989). Because the formation of smaller earlywood vessels occurred later than the formation of the larger vessels, they are probably responding to temperature during a different portion of the growing season.

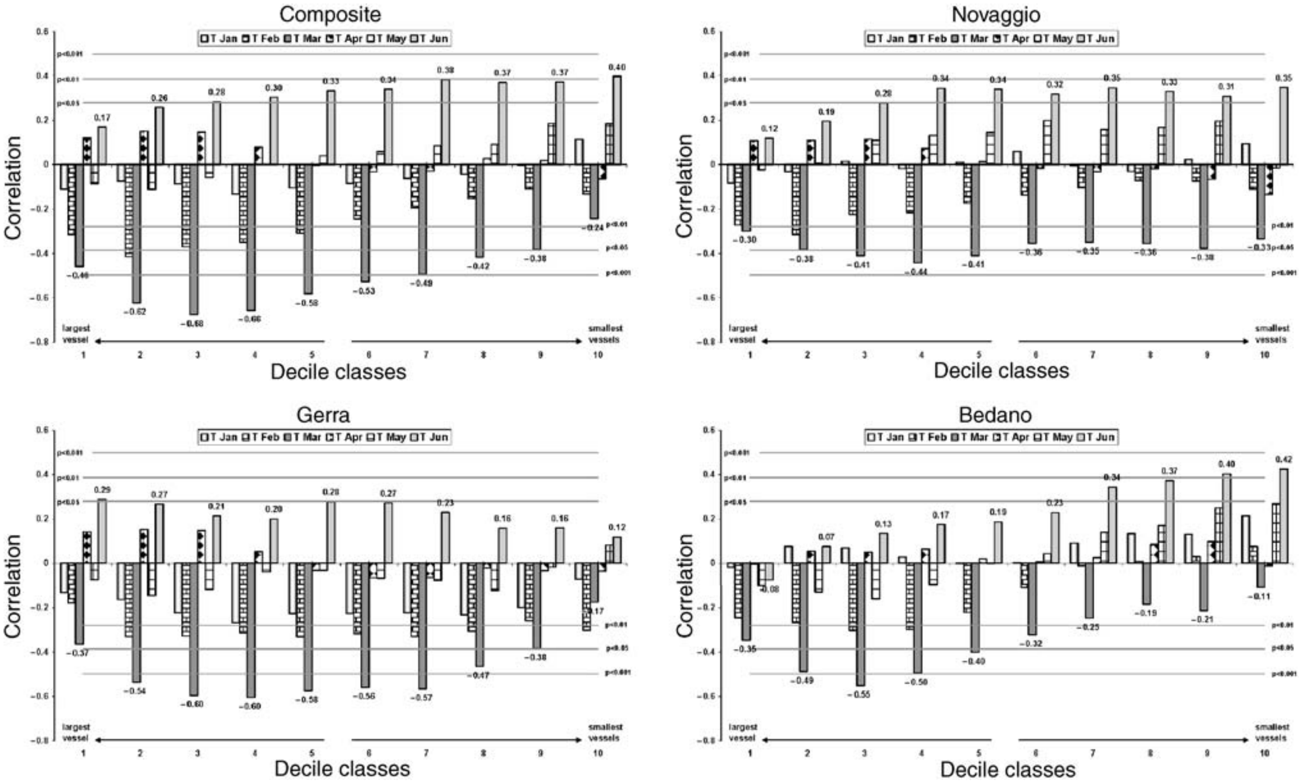


Figure 3. Pearson's correlation between January to June temperatures and the mean earlywood vessel area (MVA) for each of the ten decile groups. Results are presented for the composite chronology and for the individual sites. Horizontal lines indicate the significance levels ($P < 0.05$; $P < 0.01$; and $P < 0.001$) and values refer to the correlations for the March and June temperatures.

Influence of vessel selection criteria on signal expression

Because not all earlywood vessels register the same climatic signal, it is essential that chronologies are built from vessels formed during the same span of time under the same environmental conditions. However, arbitrarily defining a lower size limit for the selection of earlywood vessels may not always respect this principle. For example, applying the same minimal threshold size to a ring in juvenile wood or in mature wood will affect vessel selection differently because earlywood vessels differ in size and abundance (Helińska-Raczkowska and Fabisiak 1999, 1994). A similar situation may occur in years with abnormally small earlywood vessels (Fletcher 1975,

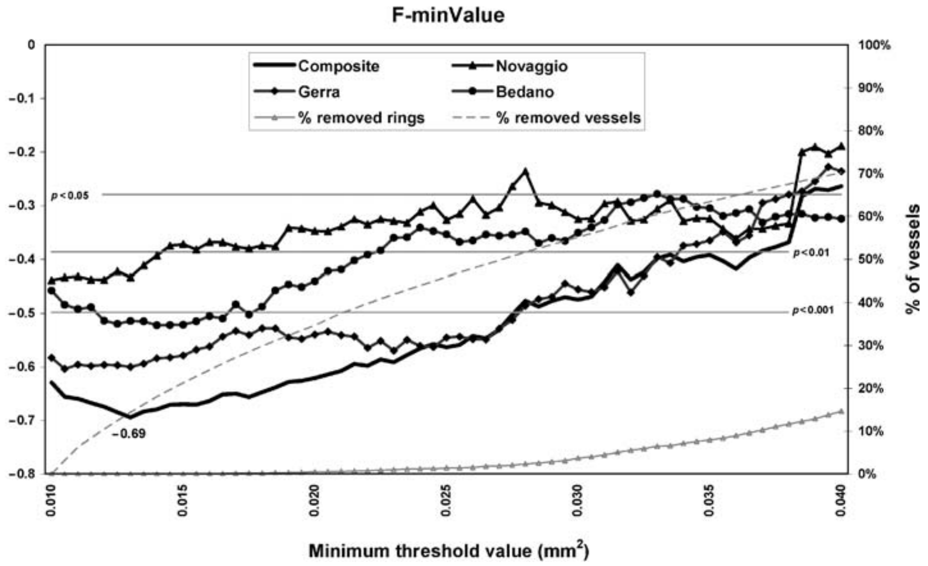


Figure 4. Variation in Pearson's correlation between March temperature and mean earlywood vessel area (MVA) as the minimum threshold value filtering progresses (F-minValue). Results are presented for each site and for the composite chronology. Horizontal lines indicate the significance levels ($P < 0.05$; $P < 0.01$; and $P < 0.001$).

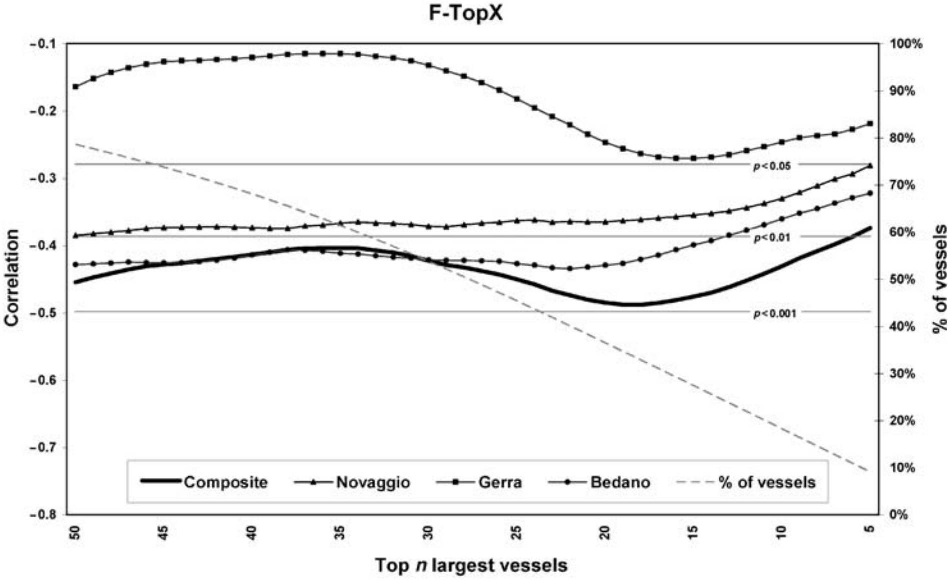


Figure 5. Variation in Pearson's correlation between March temperature and mean earlywood vessel area (MVA) as the number of top largest vessels is progressively reduced (F-TopX). Results are presented for each site and for the composite chronology. Horizontal lines indicate the significance levels ($P < 0.05$; $P < 0.01$; and $P < 0.001$).

García-González and Eckstein 2003, Eilmann et al. 2006). In such rings, the vessels contain an environmental signal that may be over- or underweighted if an inappropriate minimal size filter is applied.

In our data set, the response to March temperature was greatly influenced by the selection criteria applied. An adequate selection, aimed at maximizing the proportion of vessels that bear only the March temperature signal, increased the correlation to values close to −0.70 (r = −0.69 for vessels > 13,000 μm^2 when using F-MinValue or r = −0.66 for 50% of the vessels in F-Top%). However, application of the wrong criteria causes the same correlation to be considerably reduced (e.g., when considering too few vessels or a great number of small vessels).

The filter most prone to produce changes is the F-minValue, which showed values ranging from highly significant to non-significant. Two reasons explain the weakening of the signal expression. If the threshold limit is set too low (F-minValue < 13,000 μm^2), the introduction of the smallest vessels adds noise; whereas, if the limit is set too high, an important proportion of the signal is lost as a result of the unequal removal of vessels among rings (an example is shown in Figure 1), i.e., the largest earlywood vessels are excluded in rings with a below-average vessel size, whereas relatively small vessels are retained in other rings. Because the optimal minimum vessel size can only be identified a posteriori by progressive filtering, omitting this procedure by arbitrarily choosing the limit will risk missing an explicit signal.

Correlations produced for F-TopX were more stable, but always much lower than those for the whole data set. A few of the very largest vessels are insufficient to achieve an optimal signal because they are not the best recorders (see Figure 3),

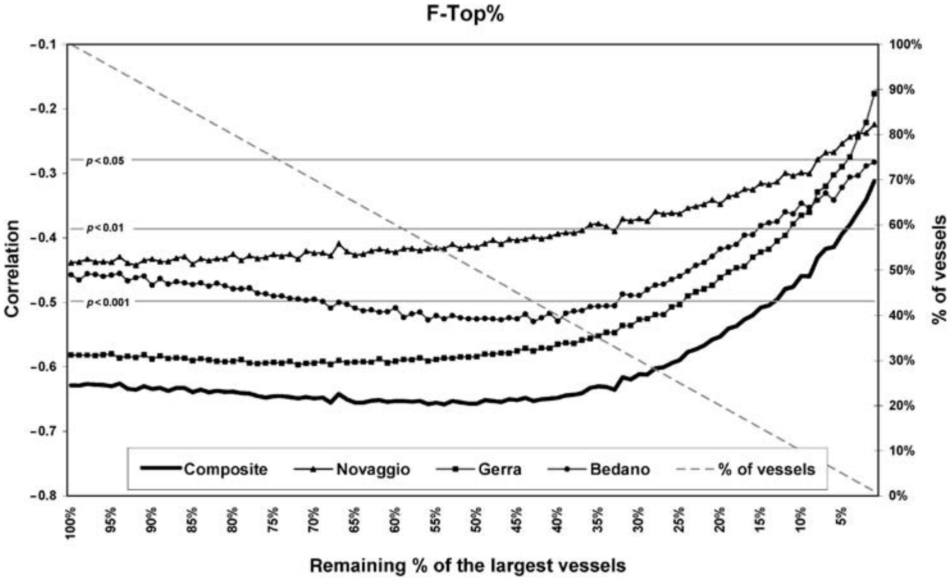


Figure 6. Variation in Pearson's correlation between March temperature and mean earlywood vessel area (MVA) as percentiles of large vessels are progressively removed. Horizontal lines indicate the significance levels ($P < 0.05$, $P < 0.01$ and $P < 0.001$).

whereas selecting too many of them will result in unequal vessel selection among rings; in this case, the presence of rings with few vessels will obscure the relationship, but information will be lost from rings with numerous large vessels.

Analyses performed with F-Top% overcome the problems of previous filters. This filter provides a selection that is proportional to the size and number of vessels within each ring and groups vessels formed within the same period. The main advantage is that an optimal signal expression is achieved with a few of the largest vessels (35%), and remains mostly unaffected by the introduction of most of the small vessels. Additionally, the risk of influencing the final result by application of incorrect selection criteria is reduced because many of the smallest vessels can be removed.

Practical implications

Based on our results, we propose two possible procedures for selecting earlywood vessels as a measure of temperature during the season of wood formation. A first approach consists of selecting earlywood vessels by their position within the ring. Because earlywood vessels in ring-porous trees are often arranged in tangential lines, consecutive rows of contemporaneous vessels are expected to show a shift in the climate information that they embody. For this reason, it would be convenient to analyze only vessels belonging to the same row. Unfortunately, the selection of single rows is not straightforward because vessels are not always arranged in tangential rows, especially those formed later in the season.

The other approach is to make a selection according to size because earlywood vessel size decreases as the season progresses. In this case, we propose that the analyses be performed in two steps so that the subsets of vessels responding to the desired signal can be identified. The first step is to make a wide selection of vessels, with a threshold size low enough to avoid the exclusion of too many vessels in specific annual rings. The second step consists of screening the signal recorded by the vessels of different size. For this, vessels should be grouped within each ring according to their size (e.g., as we did with G-Decile) and climate–growth relationships should be performed only considering the vessels that embody the relevant signal. Although this procedure is more time-consuming, it allows an objective selection of only those vessels that maximize the expression of the signal. As a result, the evaluation of the climate information embodied in earlywood vessels is improved.

Acknowledgments

The authors thank Andreas Rigling and Hans Beeckman for their helpful comments and feedback on an earlier version of the manuscript. The English was revised by Silvia Dingwall.

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