SELECTING EARLYWOOD VESSELS TO MAXIMIZE THEIR ENVIRONMENTAL SIGNALS

Ignacio García-González[1] and Patrick Fonti[2]

[1] Dep. de Botánica - Univ. Santiago de Compostela,
Escola Politécnica Superior - Campus de Lugo,
E-27002 Lugo, Spain
Tel. +34 982 252361
Fax +34 982 285985
e-mail: bvluigg@lugo.usc.es

[2] WSL, Sottostazione Sud delle Alpi,
Via Belsoggiorno 22,
CH-6504 Bellinzona-Ravecchia, Switzerland
Tel +41 91 821 52 33
Fax +41 91 821 52 39
e-mail: patrick.fonti@wsl.ch

Corresponding author: Ignacio García-González

Running head: Selecting earlywood vessels

This document is the accepted manuscript version of the following article:
García-González, I., & Fonti, P. (2006). Selecting earlywood vessels to maximize their environmental signal. Tree Physiology, 26, 1289-1296.
https://doi.org/10.1093/treephys/26.10.1289

ABSTRACT

The anatomical features of earlywood vessels often contain relevant ecological information. However, the selection of vessels is hampered by the uncertainty of clearly separating earlywood and latewood. This study examines how the definition and selection of earlywood vessels affect the identification of climate-growth relationships. Subsets of earlywood vessels of chestnut (*Castanea sativa* Mill.) were selected from a given dataset using different size-related filtering procedures. In order to include all earlywood vessels, the minimum size considered was 10000 µm^2. Changes in the encoded signal strength, i.e. the correlations between the transversal vessel area and the mean air temperature in March, are described and discussed. The results show that not all vessels bear the same signal nor does the signal have the same intensity. The largest vessels in each annual ring best capture the March temperature signal, whereas the smallest vessels are better correlated with June temperature. This signal divergence is probably due to vessels being formed at different times: early spring for the largest vessels and later in the season for the smallest vessels. Analyses mixing large and small vessels cause undesired noise, which weakens the prominent temperature signal. Therefore, depending on the vessels considered, the strength of the signal can be maximized or understated.

Because the number, size and distribution of vessels can largely vary from ring to ring, it is important to select and analyse vessels bearing the same signal, i.e. that have a contemporaneous ontogenesis. Criteria for the selection and analysis of vessels to optimize their environmental signals are thus proposed and discussed.

Key-words: *Castanea sativa* Mill., dendrochronology, dendroecology, ring-porous, tree rings, vessel size.

INTRODUCTION

Ring width is the most frequently used feature in dendroecology and dendroclimatology since it can be determined easily and largely non-destructively (Schweingruber 1996). This variable, which integrates most positive and negative influences on tree growth during the whole growing season (or even several previous seasons), is, however, problematic for reconstructing environmental events that last for shorter periods. Features at cellular level are expected to be more appropriate for such purposes because of their production throughout the growing season and are therefore now often tested in dendroecology. The capability of tree-ring anatomical features to record environmental signals has been assessed by several authors (e.g. Leuschner and Schweingruber 1996, Schweingruber 2001, Wimmer 2002, Masiokas and Villalba 2004). Recently, the conducting tissue of hardwood trees has been proposed as a further promising feature for retrospective ecological studies (Eckstein 2004).

Dendroecological studies dealing with the vessels of different tree species, such as *Quercus spp.* (Akachuku 1987, Woodcock 1989, St George et al. 2002, García González and Eckstein 2003, Corcuera et al. 2004a, 2004b), *Tectona grandis* L. (Pumijumnong and Park 1999), *Castanea sativa* Mill. (Fonti and García-González 2004), *Fraxinus nigra* Marsh. (Tardif 1996), *Fagus sylvatica* L. (Sass and Eckstein 1995) and *Populus x euramericana* (Dode) Guinier (Schume et al. 2004), have shown that year-to-year variations in vessel features contain ecologically relevant information (Eckstein and Frisse 1982, Baas 1986).

Producing chronologies of anatomical features is, however, often very time-consuming from a methodological point of view. In the past, the large number of cells to be measured meant that extensive research projects were not possible as so much work was involved in measuring cell features using ocular micrometers, screens, or linear micrometers. Recently, computerized image-analysis techniques have evolved quickly and are now revolutionizing measurement and analysis in many scientific disciplines. Within dendrochronology, modern computer technology and microscopic image analysis (Jagels and Telewski 1990), combined with improved wood-surface preparation (Spiecker et al. 2000), are providing the basis for more efficient measurements of cell structures across sequences of tree rings.

The results obtained so far have been promising and surveying intra-annual anatomical features has proved more efficient. Thus relating cellular anatomical features to environmental parameters has become increasingly relevant in dendroecological studies. Since cells are built at different times of year, the optimal selection of the cells for maximizing the signal expression is also important. Choosing only those cells which capture the signal better will both improve the efficiency of the results and reduce the time investment needed.

In ring-porous wood, the size of vessels varies considerably, depending on their position within ring. Usually, the larger the vessel, the closer it is to the ring boundary and the earlier it was formed. Consequently, differently-sized vessels should reflect the different climatic signals that occur during the growing season. In this contribution we intend to analyze further the question of how to select the earlywood vessels to be considered for dendroecological time series. The aim of this study is to verify how the selection of earlywood vessels affects the expression of the signal. In particular, changes in the content and strength of the signal are examined in relation to the size of earlywood vessels.

MATERIALS AND METHODS

The original dataset

The analyses were initiated from a dataset of chestnut (*Castanea sativa* Mill.) earlywood vessels whose suitability for establishing climate-growth relationships had already been demonstrated in a recent study by Fonti and García-González (2004). The original data consisted of cross-dating measurements of vessel lumen areas on 51 trees grown at three different plots (Bedano, Novaggio and Gerra) in the southern part of the Swiss Alps. The survey considered all vessels larger than

10000 µm^2 found within an 8 mm wide radial strip extending across all rings formed between 1956 and 1995. The trees were 45 to 52 years old. The original data set showed a close relationship between the meteorological conditions during earlywood vessel growth and the size of the vessels. In particular, an above-average warm early spring resulted in smaller vessels, and *vice versa*, expressed as a highly significant correlation ($p<0.001$) with March temperatures.

Procedures for vessel selection

The original dataset of earlywood vessels was progressively filtered by size. Filtering was performed to gradually remove undesired vessels in order to determine whether each subset contained the same climatic signal at the same strength. Thus, all vessels in each annual ring were sorted according to their size. Three different selection procedures were applied to the data of each annual ring, retaining only:

- vessels larger than a given minimal threshold size (**F-minValue**);
- the n largest (**F-TopX**) or smallest (**F-BottomX**) vessels;
- the n percent of largest (**F-DecileDown**) or smallest (**F-DecileUp**) vessels.

For both latter procedures, all vessels of each annual ring were first arranged according to size and then selected according to their absolute (F-TopX and F-BottomX) or relative (F-DecileDown and F-DecileUp) ranking position. In addition, the vessels of each annual ring were also split into 10 groups depending on their size, each containing 10% of the vessels (**G-Decile)**. The descriptive parameters of the procedures, i.e. threshold value and filtering progression steps, are summarized in Table 1.

Analyses of climate-growth relationships

Analyses of the relationships between earlywood vessel size and mean monthly temperature were performed using standard dendrochronological procedures (Schweingruber 1988). The growth variable used was the ring's mean vessel area (MVA). With every new data subset, MVA time series were established for each single tree, and undesired growth-related trends were removed from each individual series by adjusting a cubic smoothing spline with a stiffness of 32 years and 50% cutoff (Cook et al. 1992). The detrended growth indices were averaged into a mean chronology for each site and a composite was calculated as an average of the three site chronologies.

Climate-growth relationships were established using Pearson's correlation coefficient between the chronologies and the monthly records of mean temperature and total precipitation from the nearby station of Lugano, not more than 20 km in distance from the sites. The relationship was calculated after each filtering step as the area of all vessels that had been selected in each annual ring. When the filtering was too strict, so that all the vessels in the same ring were removed, the ring concerned was not considered any more in the analyses. The years 1956 to 1959, however, were not considered at all, since too many rings would have been excluded from the calculation. Fonti and García-González (2004) present a more detailed description of the chronology computation and the establishment of climate-growth relationships.

The signal expressed by the different subsets of earlywood vessels was assessed by plotting the correlations along with the results of the progressive filtering procedures. As each filter generated new MVA values for each single 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 programming scripts specifically developed for this purpose using the language 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, with a mean value of 55. The largest measured vessel showed a lumen area 16 times larger than the lower size limit fixed at 10000 µm^2 and less than 1% of them (660 out of 95778 vessels) were larger than 10 times the limit. As an example of the variability in vessel size within and between trees and sites, the frequency distributions in the three sites, five trees from one site and four dated annual rings from one tree are presented in Figure 1. With few exceptions, the distributions are skewed to the left, toward a high number of small vessels.

Filtering based on a minimum threshold value

The original unfiltered dataset shows a highly significant correlation ($p<0.001$) with current March temperature, especially for the composite chronology ($r=-0.63$), which records a stronger signal in comparison to the site chronologies. However, the correlation has important variations when vessels smaller than a given threshold size are progressively removed (Fig. 2). If the smallest vessels (i.e. those smaller than 13000 μm^2) are filtered out, the correlation increases slightly ($r=-0.69$ for the composite) or remains steady (as it was observed for Gerra and Novaggio). A further removal of the smallest vessels, however, results in a rapid decrease in the expression of the climatic signal. This is particular evident when only vessels larger than 40000 μm^2 are retained. In this case, 70% of the vessels and 15% of the rings were removed from the calculations and the correlation dropped to -0.26, which is not significant any more.

Selection based on absolute ranking position

A vessel selection based on only the largest vessels of each ring results in a low correlation in comparison to the whole dataset (Fig. 3). The highest correlation ($r=-0.49$) is obtained when the 18 largest vessels in each ring are considered. A smaller number (5 to 10 vessels) causes lower correlations (below -0.40 for the composite, and even lower for the site chronologies). A higher number (25 to 50) does not enhance the climatic signal.

A similar analysis but performed upwards shows that the smallest vessels are those that reduce the March temperature signal. The correlation is the lowest ($r=-0.21$) when the five smallest vessels are considered, but then increases as larger vessels are included in the calculations. The correlation becomes highly significant ($p<0.001$) when the 48 smallest vessels of each ring are entered in the analysis, which constitutes most of the vessels for many of the rings.

Filtering and grouping based on relative ranking position

The climate-growth relationships after filtering on the relative ranking position of the vessels within the ring are similar to those based on the selection of the ring's top vessels (Fig. 4). The stepwise inclusion of the next smaller decile of vessels shows that the correlations first increase and then decrease. For the composite, the first upper decile is enough to reach a correlation of -0.46, which it keeps increasing until 50% of the vessels are considered ($r=-0.66$). A further addition of smaller vessels has practically no influence on the final result as the correlation decreases very slightly. In contrast, when proceeding upwards, the first lower decile has no significant correlation, but it increases as the following deciles of larger vessels are progressively included. Thus, only when all the vessels are analyzed does the correlation reach its maximum value.

A more detailed expression of the signal encoded in relation to vessel size is observed when the 10% groups (deciles) are correlated separately with mean monthly temperatures (Fig. 5). The March temperature signal is maximized by the composite ($r=-0.68$) with the vessels belonging to the 3rd decile. Afterwards, correlations decrease as vessel size decreases. The lowest value ($r=-0.24$) is not significant any more and corresponds to the lowest deciles. However, the progressive weakening of the signal in March is coupled to its increase in June, especially for the composite and Bedano chronologies, shown by a significant correlation ($r=-0.40$, $p<0.05$) with the 10% smallest vessels.

DISCUSSION

Determination of earlywood vessels

Ring-porous wood is defined as “wood in which the pores of the earlywood are distinctly larger than those of the latewood and form a well-defined zone or ring” (IAWA Committee 1964). Although this definition is clear, doubts arise when the earlywood vessels have to be selected for measurement. From a methodological point of view, even in typical ring-porous wood species, the differentiation between early- and latewood vessels is not always sharp (Woodcock 1989). As vessels vary considerably in number, size and distribution, it is not always possible to assign them unambiguously to earlywood or latewood (Nola 1996, García González and Eckstein 2003). The criteria used for selecting earlywood vessels are therefore fundamental in ecological studies. Recent studies on ring-porous trees have mainly based the selecting criteria on a minimal vessel lumen size (i.e. St Georg et al. 2002 [1200 µm^2], García González and Eckstein 2003 [5000 µm^2], Fonti and García González 2004 [10000 µm^2], Eilmann et al. in prep. [5000 µm^2]), which has been more or less arbitrarily defined depending on the vessel size distribution and on the accuracy in vessel recognition of the measuring system.

Differences in sites or provenance, position in the tree, presence of juvenile or reaction wood and external environmental factors can affect the structure of the wood (Zobel and van Buijtenen 1989), as well as the vessel size and number. When differences in patterns among annual rings are studied, a selection of earlywood vessels based on only a minimum threshold value can therefore lead to a biased and unbalanced choice of vessels. For example, applying the same minimal threshold size to a ring in juvenile wood or in mature wood will affect vessel selection differently. In this case, vessels will tend to be smaller and more abundant in the younger portion (Helinska-Raczkowska and Fabisiak 1999, 1994). A similar situation can occur in pointer years with abnormally small vessels that are occasionally found in correspondence with extreme events (Fletcher 1975, García González and Eckstein 2003, Eilmann et al. in prep.). In such cases, the vessels in these rings contain a valuable ecological signal that, if an inappropriate minimal size filter is applied, can be over- or underweighted, and result in an incorrect expression of the investigated relationship.

In this dataset the response to March temperature appeared to be greatly influenced by the choice of a minimum threshold. Depending on the size at which this limit was set, the correlation between both variables changed from highly significant to clearly non-significant. Thus, the progressive filtering on a given value allows the identification of the most convenient minimum size that should be used. When vessels smaller than this value are included (in this work, vessels smaller than approx. 13000 µm^2), the signal decreased because of the excessive noise introduced by the smallest vessels, although this fact was not troublesome, as correlations were not far from the maximum. On the other hand, as the filter value increased, larger vessels containing an important signal were excluded, causing a considerable drop in the correlation values.

Vessel size dependence of the signal

Although tree-ring growth variables can be affected by factors preconditioning growth (Fritts 1976), it has often been observed that the main variables affecting the year-to-year variability of vessel size are the weather conditions at the time of vessel formation. This result was shown not only for the earlywood vessels of chestnut (Fonti and García-González 2004), but also for those of pedunculate oak (García González and Eckstein 2003), teak (Pumijumnong and Park 1998), the latewood vessels of bur oak (Woodcock 1989) and even for diffuse-porous species like beech (Sass and Eckstein 1995). It seems therefore that vessels, by means of their size, register the climatic factors that were in force during the phase of vessel expansion, i.e. until the deposition of the secondary cell wall, which determines its final size. It follows that environmental factors can be recorded during this specific period. Nevertheless not all the vessels are formed and completed in the same period and at the same rate. Thus, when studying the influence of a given variable (e.g. temperature in March), it would be desirable to analyze the size of only those vessels whose ontogeny is mostly contemporaneous with that variable. Then these vessels would be recorders of this 'signal', whereas other vessels growing earlier or later in the season would act as a source of 'noise'. Repeating cell analyses during the growing season constitutes one of the best methods for understanding and documenting the intra-annual development of growth rings. The few studies so far performed on conifers (Antonova and Stasova 1993, 1997, Deslauriers et al. 2003) and on broadleaves (Suzuki et al. 1996, Schmitt et al. 2000) supplied essential information on the dynamics of seasonal wood formation. With regards to ring-porous hardwoods, it was observed that the onset of the first earlywood vessels starts before bud-burst and lasts for three to seven weeks afterwards (Suzuki et al 1996, Schmitt et al. 2000).

In the present study, vessel size has been successfully correlated with a variable (mean temperature in March) that applies at the time of vessel growth. Nevertheless, depending on the vessel size classes and on the filtering applied, the strength of the March temperature signal was magnified or understated. Analyses of the correlations from top-down filtering produced different results from those from bottom-up filtering. In the first case, the expression of the largest vessels was highly significant, whereas for the latter the correlations only started to become significant as larger vessels were integrated into the calculations. Size-related differences in the expressions of the response were even more distinct when the analyses were performed separately for each decile, since the signal was maximized (r=-0.68) only when the middle to largest earlywood vessels of each ring were considered. These results clearly indicate that the vessel size affects the signal strength. In particular the smallest vessels, formed later in the season, weaken the signal of March temperature recorded by the largest vessels, which differentiate earlier.

The vessels size related response is probably related to different climatic signals. Unlike the large vessels, the smallest ones seem to be related with the June rather than with the March temperature. These results have led us to believe that the encoded ecophysiological signals depend on the relative size of the vessels within the growth ring. In ring-porous trees the size of earlywood vessels often tends to decrease the farther they are positioned from the ring boundary to the previous ring (Zobel and van Buijtenen 1989). The moment of formation of the differently-sized earlywood vessels can also be expected to shift slightly with time. Different sized vessels might therefore record the climatic signal differently. The transition of the signal with decreasing vessel size classes from the March to the June temperature can therefore be understood as a physiological transition from vessels belonging to the earlywood (that portion of the annual ring produced early in the year) and those belonging to the latewood (which is produced later in the year).

Practical implications

The analyses performed in this study have shown that the way earlywood vessels are chosen can affect the detection of a given ecological signal. Depending on vessel size classes, the strength and the expression of the signal can vary. There are therefore measures that can be applied in order to improve the identification of eco-physiological relationships between earlywood vessels and climate. Because the number, size and distribution of vessels can sensibly vary from ring to ring, it is important to select and analyse vessels with contemporaneous ontogenesis. Usually ring-porous trees have several vessel rows that are formed at different times during the growing season, so that vessels formed consecutively should respond to consecutive time periods. However, a selection based on the position of vessels within the ring is not straightforward because vessels are not always clearly arranged in rows. Since vessel size in ring-porous woods decreases as the season advances, a selection of vessels with similar sizes would also result in a grouping according to ontogeny criteria. The most commonly used procedure for earlywood vessel selection is based on the minimum threshold value or on a fixed number of large vessels. This has the effect of mixing together vessels from different origins (earlywood or latewood), with the consequence that the environmental signal is reduced by undesired noise.

We therefore propose to perform the analyses in two steps so that the groups of vessels that better respond to the desired signal can be identified. The first step is to make a wide selection of vessels. Here the minimum threshold size has to be low enough to avoid the removal of too many vessels in specific annual rings. Undesired vessels sizes are removed from the calculations only if their negative contribution to the signal expression has been verified. The second step consists of screening the signal encoded by the differently sized vessels. Annual ring vessels have to be grouped according to size. A grouping based on their relative ranking position within the ring is preferred, so that only the vessels from the same position/function within the ring can be compared. If different vessel rows are easily identifiable and constant from ring to ring, it would be worthwhile measuring vessel rows separately. And finally, climate-growth relationships should be performed separately for each group. This procedure is more time-consuming for both measurement and data processing. It does, however, allow an objective selection of only those vessels that maximize the signal, or even identify other climatic signals. Consequently, there is potentially more ecological information that can be gained from earlywood vessels.

ACKNOWLEDGEMENTS

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.

REFERENCES

Akachuku, A.E. 1987. A study of lumen diameter variation along the longitudinal axis of wood vessels in *Quercus rubra* using cinematography. IAWA Bull. 8:41-45.

Antonova, G. and V. Stasova. 1993. Effects of environmental factors on wood formation in Scots pine stems. Trees 7:214-219.

Antonova, G. and V. Stasova. 1997. Effects of environmental factors on wood formation in larch (*Larix sibirica* Ldb.) stems. Trees 11:462-468.

Baas, P. 1986. Ecological patterns in xylem anatomy. *In* On the economy of plant form and function. Ed. T.T. Givnish. Cambridge University Press, New York, pp 327-352.

Corcuera, L., J. Camarero and E. Gil-Pelegrín. 2004a. Effects of severe drought on *Quercus ilex* radial growth and xylem anatomy. Trees 18:83-92.

Corcuera, L., J. Camarero and E. Gil-Pelegrín. 2004b. Effects of severe drought on growth and wood anatomical properties of *Quercus faginea*. IAWA J. 25:185-204.

Cook, E., K. Briffa, S. Shiyatov and V. Mazepa. 1992. Tree-ring standardization and growth trend estimation. *In* Methods of Dendrochronology: Applications in the Environmental Science. Eds. E.R.Cook and L.A. Kairiukstis. International Institute for Applied Systems Analysis. Kluwer Academic Publishers, Boston, pp 104-123.

Deslauriers, A., H. Morin and Y. Bégin. 2003. Cellular phenology of annual ring formation of *Abies balsamea* in the Quebec boreal forest (Canada). Can. J. For. Res. 33:190-200.

Eckstein, D. 2004. Change in past environments - secrets of the tree hydrosystem. New Phytol. 163:1-4.

Fletcher, J.M. 1975. Relation of abnormal earlywood in oaks to dendrochronology and dendroclimatology. Nature 254:506–507.

Fonti, P. and I. García-González. 2004. Suitability of chestnut earlywood vessel chronologies for ecological studies. New Phytol. 163:77-86.

Eckstein, D. and E. Frisse. 1982. The influence of temperature and precipitation on vessel area and ring width of oak and beech. *In* Climate from Tree Rings. Eds. M.K Hughes, P.M. Kelly, J.R. Pilcher and V.C. LaMarche. Cambridge University Press, Cambridge, p 12.

Fritts, H.C. 1976. Tree Rings and Climate. Academic Press, New York, 567 p.

García González, I. and D. Eckstein. 2003. Climatic signal of earlywood vessels of oak on a maritime site. Tree Physiol. 23:497-504.

IAWA Committee. 1964. Multilingual glossary of terms used in wood anatomy. Konkordia, Winterthur, 186 p.

Jagels, R. & F.W. Telewski. 1990. Computer-aided image analysis of tree rings. *In* Methods of Dendrochronology: Applications in the Environmental Science. Eds. E.R.Cook and L.A. Kairiukstis. International Institute for Applied Systems Analysis. Kluwer Academic Publishers, Boston, pp 76-93.

Heliñska-Raczkowska, L. and E. Fabisiak. 1994. Variation of vessel lumen diameter in radial direction as an indication of juvenile wood growth in oak (*Quercus petraea* Liebl.). Ann. Sci. For. 51:283-290.

Heliñska-Raczkowska, L. and E. Fabisiak. 1999. Radial variation of earlywood vessel lumen diameter as an indicator of the juvenile growth period in ash (*Fraxinus excelsior* L.). Holz Roh-Werkstoff 57:283-286.

Masiokas, M. and R. Villalba. 2004. Climatic significance of intra-annual bands in the wood of *Nothofagus pumilio* in southern Patagonia. Trees 18:696-704.

Nola, P. 1996. Climatic signal in earlywood and latewood of deciduous oaks from northern Italy. *In* Tree Rings, Environment and Humanity. Eds. J.S. Dean, D.M. Meko and T.W. Swetnam. Radiocarbon. Dept. of Geosciences, Univ. Arizona, Tucson, pp 249–258.

Leuschner, H.H. and F.H. Schweingruber. 1996. Dendroökologische Klassifizierung und Auswertung häufig auftretender intraannueller holzanatomischer Merkmale bei Eichen und Kiefern. Dendrochronologia 14:273–285.

Pumijumnong, N. and W.-K. Park. 1999. Vessel chronologies from teak in northern Thailand and their climatic signal. IAWA J. 20:285–294.

Sass, U. and D. Eckstein. 1995. The variability of vessel size in beech (*Fagus sylvatica* L.) and its ecophysiological interpretation. Trees 9:247–252.

Schmitt, U., R. Möller and D. Eckstein. 2000. Seasonal wood formation of beech (*Fagus sylvatica* L.) and black locust (*Robinia pseudoacacia* L.) as determined by the ‘pinning’-technique. J. Appl. Bot. 74:10-16.

Schume H, M. Grabner and O. Eckmuellner. 2004. The influence of an altered groundwater regime on vessel properties of hybrid poplar. Trees 18:184-194.

Spiecker, H, M. Schinker, J. Hansen, Y. Park, T. Ebding and W. Doell. 2000. Cell structure in tree rings: novel methods for preparation and image analysis of large cross sections. IAWA J. 21:361-373.

St. George.S, E. Nielsen, F. Conciatori and J. Tardif. 2002. Trends in *Quercus macrocarpa* vessel areas and their implications for tree-ring paleoflood studies. Tree-Ring Research 58:3-10.

Suzuki, M., K. Yoda and H. Suzuki. 1996. Phenological comparison of the onset of vessel formation between ring-porous and diffuse-porous deciduous trees in a Japanese temperate forest. IAWA J. 17:431-444.

Schweingruber, F.H. 1988. Tree rings: Basics and applications of Dendrochronology. Kluwer Academic Publishers, Dordrecht, Netherlands, 276 p.

Schweingruber, F.H. 1996. Tree Rings and Environment. Dendroecology. Swiss Federal Institute for Forest, Snow and Landscape Research, Paul Haupt, Birmensdorf and Berne, 609 pp.

Schweingruber, F.H. 2001. Dendroökologische Holzanatomie: Anatomische Grundlagen der dendrochronologie. Paul Haupt, Berne, 472 pp.

Tardif, J. 1996. Earlywood, latewood and total ring width of a ring-porous species (*Fraxinus nigra* Marsh) in relation to climatic and hydrologic factors. *In*: Tree Rings, Environment and Humanity. Eds. J.S. Dean, D.M. Meko and T.W. Swetnam. Radiocarbon. Dept. of Geosciences, The University of Arizona, Tucson, pp 315-324.

Wimmer, R. 2002. Wood anatomical features in tree-rings as indicators of environmental change. Dendrochronologia 20:21-36.

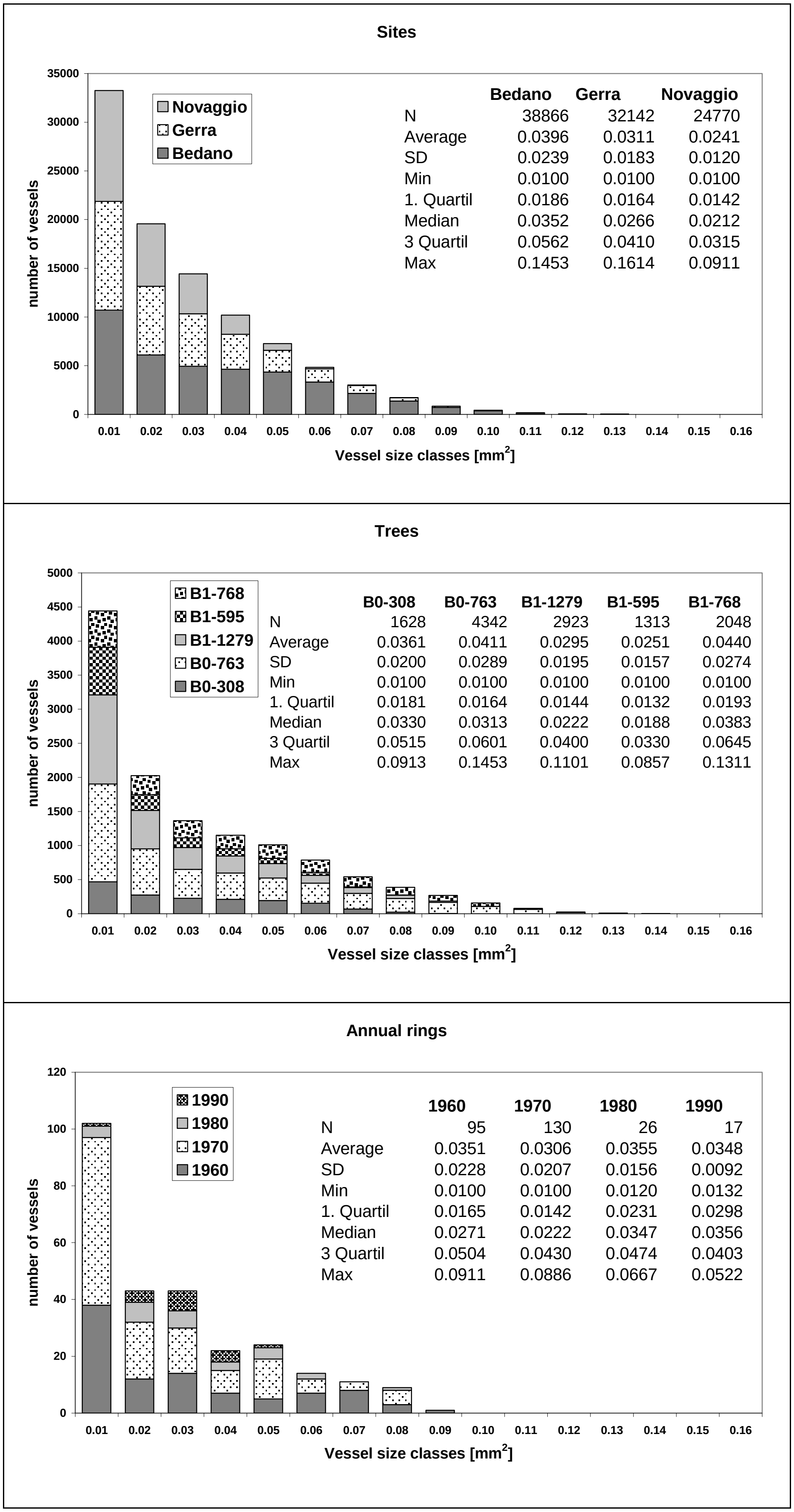
Woodcock, D.W. 1989. Climate sensitivity of wood anatomical features in a ring-porous oak (*Quercus macrocarpa*). Can. J. For. Res. 19:639-644.

Zobel, B.H.and J.P. van Buijtenen. 1989. Wood variation: its causes and control. Springer series in wood science, New York, 363 p.

Filter	**Starting threshold value**	**Progression step**	**Ending threshold value**	**Total number of steps**
F-minValue	0.01 mm^2	0.0005 mm^2	0.040 mm^2	60
F-TopX	Top 5 largest	Next largest	Top 50	45
F-BottomX	Top 5 smallest	Next smallest	Bottom 50	45
F-DecileDOWN	Largest 10% vessels	Next 10% largest vessels	Tenth largest 10% vessels	10
F-DecileUP	Smallest 10% vessels	Next smallest 10% vessels	Tenth smallest 10% vessels	10

Group	**Minimal value**	**Maximal value**	**Group width**	**Number of groups**
G-Decile	1st largest decile	10th largest decile	Decile	10

Table 1. Description of filtering and grouping procedures



Sites

	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

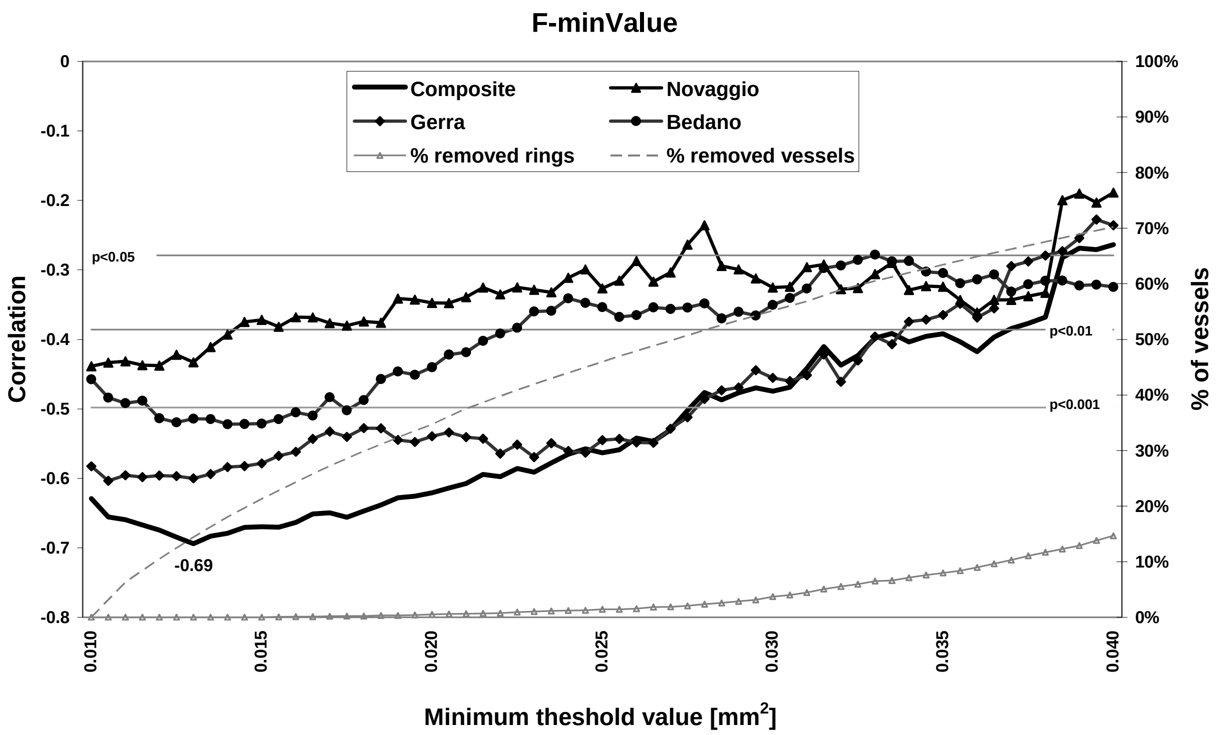
Trees

	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

Annual rings

	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 1: Examples of vessels lumen area distributions within sites, trees and growth increments.



425 Figure 2: Evolution of Pearson's correlations between the March temperature and the 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).

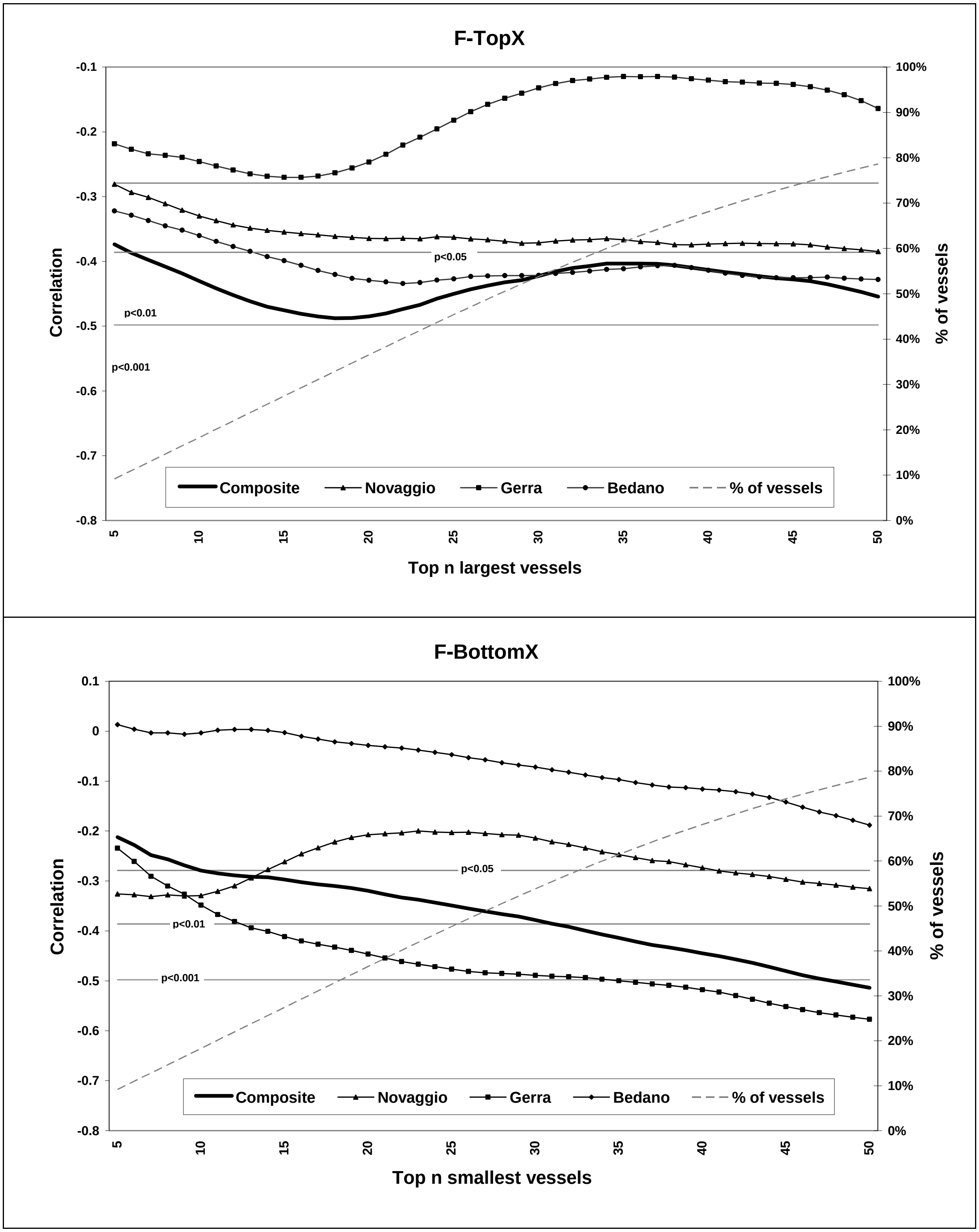


Figure 3: Evolution of Pearson’s correlations between the March temperature and the mean earlywood vessel area (MVA) as the absolute ranking position filtering progresses (above for F-TopX and below for F-BottomX). Results are presented for each site and for the composite chronology. Horizontal lines indicate the significance levels (p<0.05, p<0.01 and p<0.001)

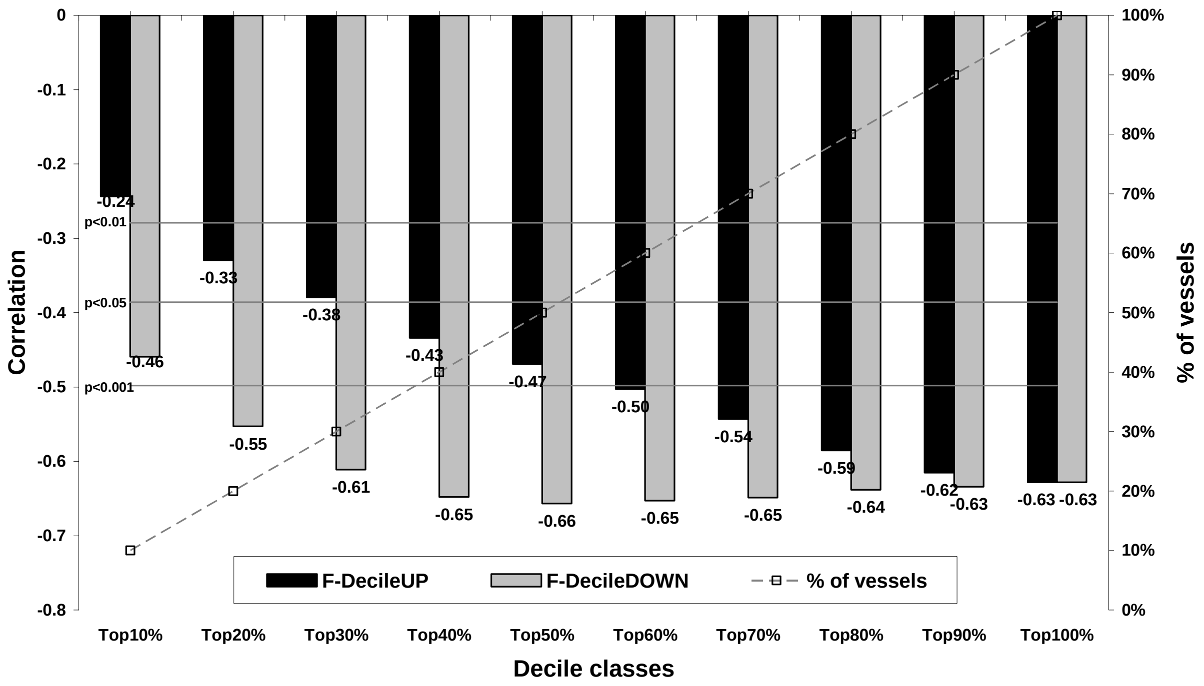


Figure 4: Evolution of Pearson's correlation between the March temperature and the mean earlywood vessel area (MVA) as the relative ranking position filtering progresses (black for F-DecileUP and grey for F-DecileDOWN). Results are presented for the composite chronology. Horizontal lines indicate the significance levels ($p<0.05$, $p<0.01$ and $p<0.001$).

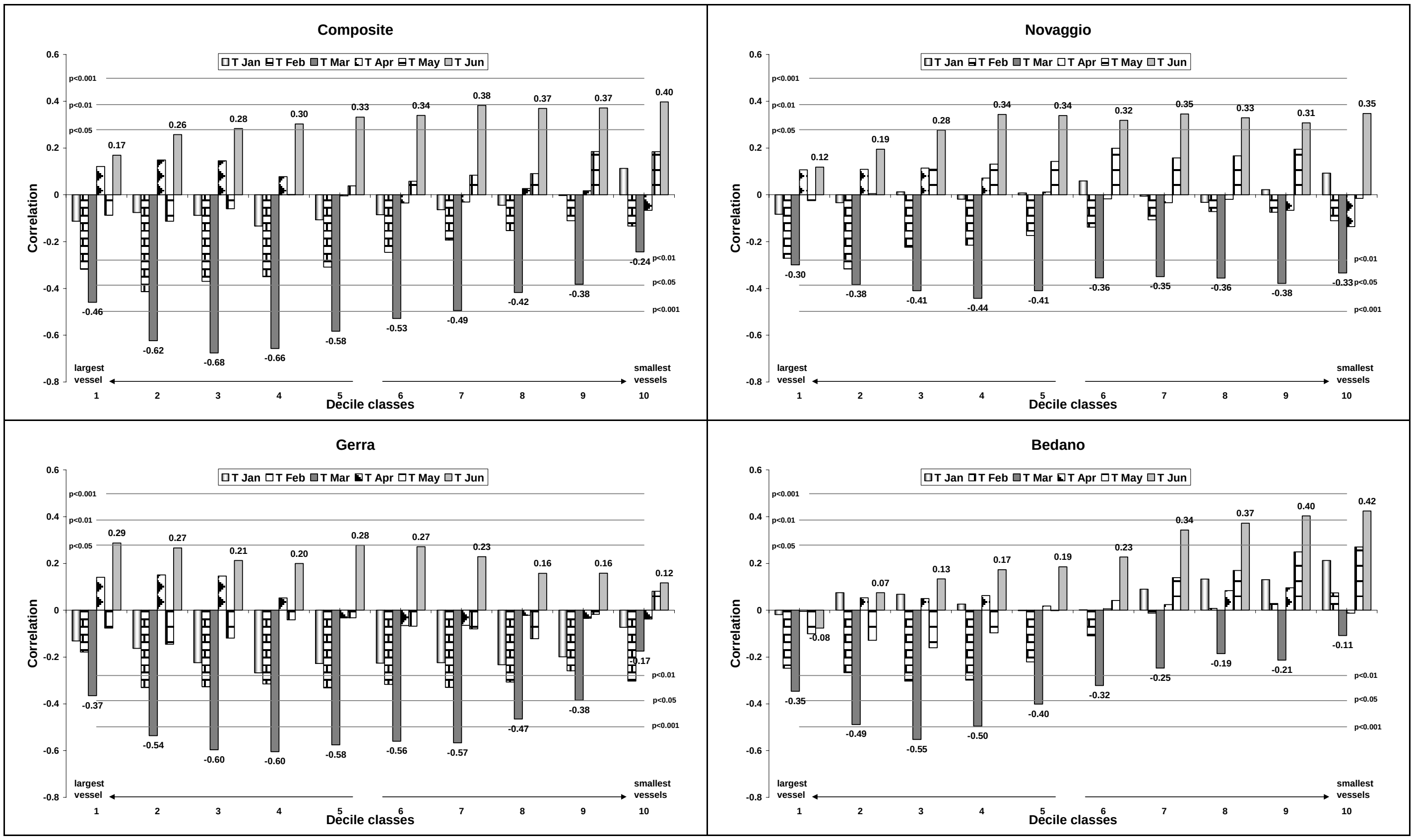


Figure 5: Evolution of the Pearson's correlation between the January to June temperatures and the mean earlywood vessel area (MVA) for each of the ten decile classes (G-Decile). Results are presented for the composite chronology and for the individual sites. Horizontal lines indicate the significance levels (p<0.05, p<0.01 and p<0.001), and values refer to the correlations for the March and June temperatures.