The Iberian vessel chronology network: Obtaining information from oak earlywood anatomy

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The northern Iberian tree-ring and vessel network

More than 150 site chronologies have been obtained for Northern Spain

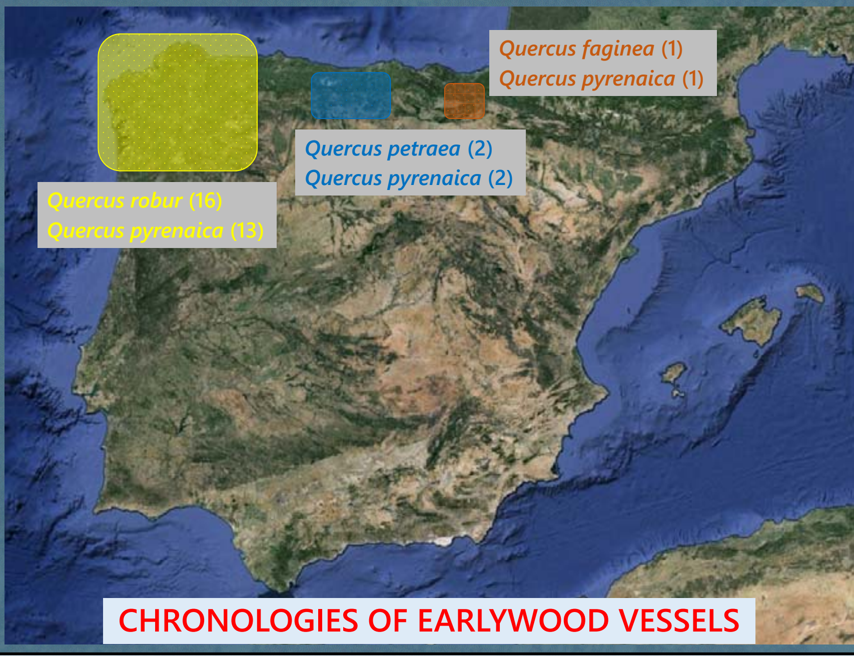
Quercus robur | *Quercus petraea* | *Quercus pyrenaica*

Fagus sylvatica | *Betula alba*

Pinus pinaster | *Pinus pinea*

Other species

The northern Iberian tree-ring and vessel network



A great impact of global change is expected towards the Mediterranean

- Less water availability
- Severe biodiversity losses
- Longer drought periods
- Increment of forest fires

Ecosystems in transition areas between biogeographical regions are particularly sensitive to global change

Many species reach their distribution boundaries along these areas

Stress by rapidly changing conditions can modify species performance

Adaptation | Migration | Evolution

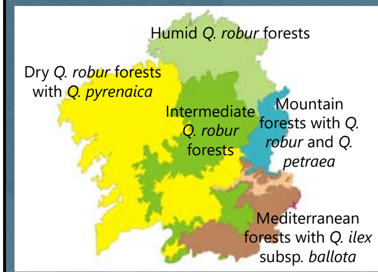
Species distribution around the Mediterranean region is expected to be greatly modified as a result of global change

The Northern Iberian Peninsula is a strong biogeographical boundary

This area constitutes the transition to the Mediterranean region

The distribution limit of many tree species in Europe is found along this area

Variations in the distribution of vegetation can be remarkable within a small region



Quercus forests in NW Spain

Species distributions are dynamic

Relevance for global change studies → Species distribution is expected to be greatly modified as a result of global change

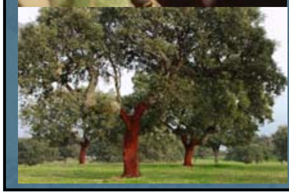
Atlantic forests in the Iberian Peninsula are mainly dominated by deciduous *Fagaceae* (beech and oaks)

Fagus sylvatica	*Quercus petraea*	*Quercus robur*
		
		

These species reach their distribution boundary in Northern Iberia, but some scattered (probably relict) populations occur within the Mediterranean region

Typical Mediterranean forests are dominated by evergreen oaks, although other species occur at higher elevations

Quercus suber



Quercus ilex

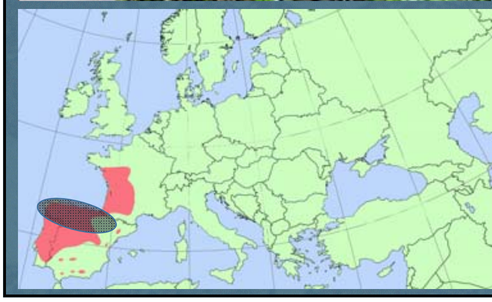
Q. ilex subsp. *ballota*

Q. ilex subsp. *ilex*

These species dominate low and medium altitude forests, mainly in the western Mediterranean area, but they also spread to the southern limit of the Atlantic region

Several marcescent oak species occur within and around the Mediterranean Basin, and are mainly dominant in continental areas

Quercus pyrenaica



Quercus pyrenaica, *Q. pubescens*, *Q. faginea* subsp. *faginea*, *Q. faginea* subsp. *broteroi*, *Q. canariensis*...

Quercus pyrenaica is the main Iberian species of this group

This oak tolerates moderate, but not the strong xeric conditions of many areas of the Iberian Peninsula

It mostly occurs in mid-mountain areas, and is characterized by a delayed budbreak and a short vegetation period to avoid late frost

It constitutes the most common tree along the transition between the Atlantic and Mediterranean region, often coexisting with other species

Deciduous oaks in Northern Iberia provide a unique opportunity to study the possible effects of global change on the distribution of dominant tree species

Mediterranean conditions tend to increase as a consequence of climatic change → *Q. pyrenaica* distribution is mostly Mediterranean, and this species is more tolerant to xeric habitats

Will *Quercus pyrenaica* replace *Quercus robur* in Atlantic areas as conditions become more Mediterranean in the future?

Main sources of stress at the common distribution boundary

1. Higher winter temperatures, increasing respiration during dormancy and thus consumption of reserves → *Quercus pyrenaica*, *Quercus robur*
2. Longer drought episodes during the growing season, mainly in summer time, limiting productivity → *Quercus robur*
3. A very high precipitation, mainly during autumn and winter time, imposed by the Atlantic conditions → *Quercus pyrenaica*

It is necessary to understand the performance of types of oaks under such changing environmental conditions to infer their future behaviour

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Ca. 150 site chronologies have been obtained for Northern Spain →

Quercus robur	*Quercus petraea*	*Quercus pyrenaica*
Fagus sylvatica	*Betula alba*	*Laurus nobilis*
Pinus pinaster	*Pinus pinea*	Other species

Despite the vast network of chronologies, the results obtained so far do not show any strong responses of radial growth to climate

In general, responses obtained to climate are weaker than expected

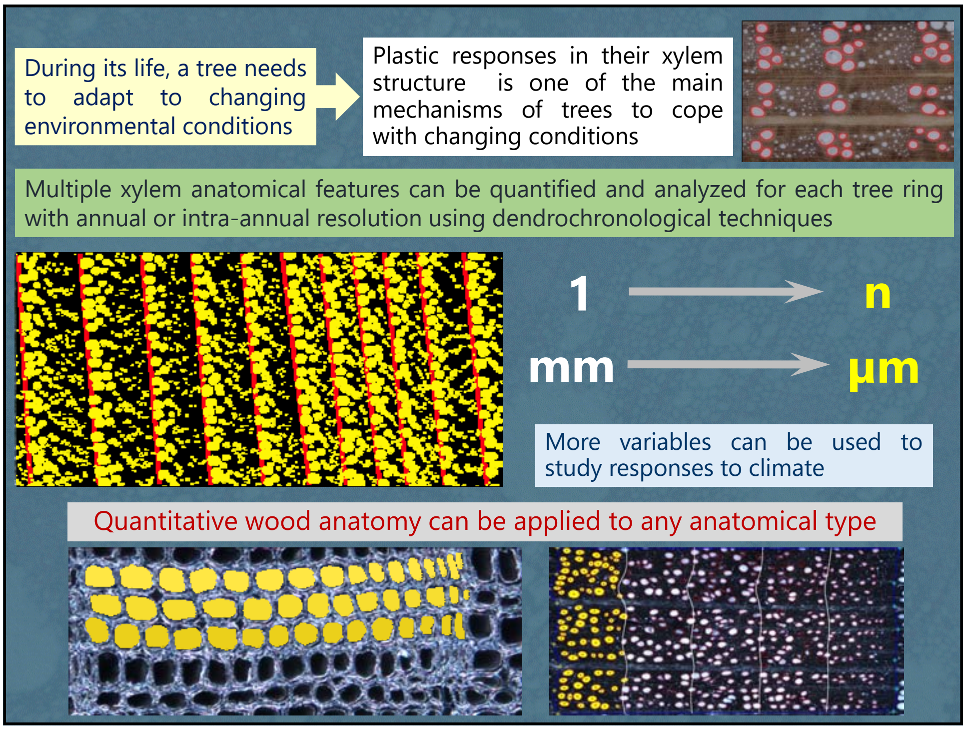
Most climate growth relationships are not stable through time

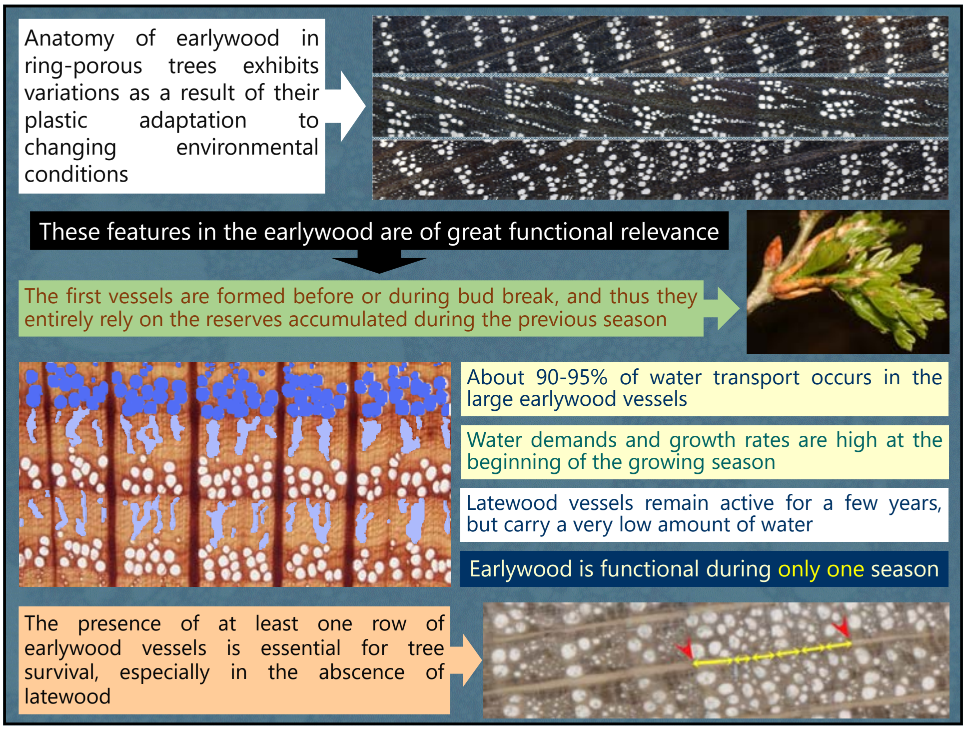
Many factors could be influencing growth in different years → Spring drought; Late frost; Insect outbreaks or mildew; Summer drought; Winter temperature; Human activities

Lack of a prevalent factor limiting growth

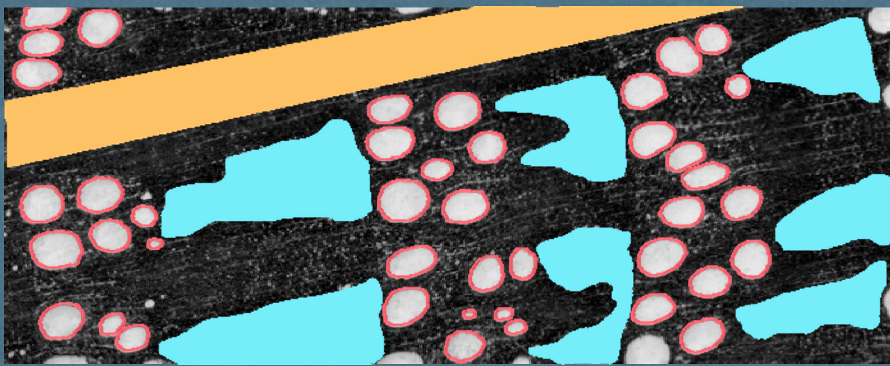
"Classic" dendrochronology (i.e., ring width) does not always work well in transitional areas

Need to look for other variables describing growth


During its life, a tree needs to adapt to changing environmental conditions
Plastic responses in their xylem structure is one of the main mechanisms of trees to cope with changing conditions
Multiple xylem anatomical features can be quantified and analyzed for each tree ring with annual or intra-annual resolution using dendrochronological techniques
1 → n
mm → µm
More variables can be used to study responses to climate
Quantitative wood anatomy can be applied to any anatomical type


Anatomy of earlywood in ring-porous trees exhibits variations as a result of their plastic adaptation to changing environmental conditions
These features in the earlywood are of great functional relevance
The first vessels are formed before or during bud break, and thus they entirely rely on the reserves accumulated during the previous season
About 90-95% of water transport occurs in the large earlywood vessels
Water demands and growth rates are high at the beginning of the growing season
Latewood vessels remain active for a few years, but carry a very low amount of water
Earlywood is functional during only one season
The presence of at least one row of earlywood vessels is essential for tree survival, especially in the abscence of latewood

Anatomy of earlywood in ring-porous trees is also relevant to determine their wood properties and quality



Parenchyma rays

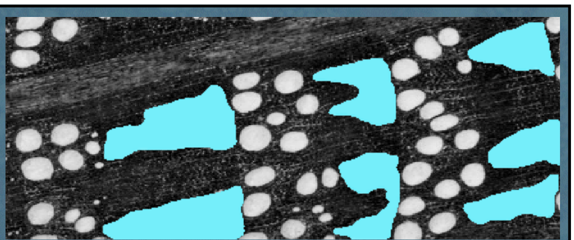
Earlywood vessels

Wood matrix (mostly fibers with axial parenchyma)

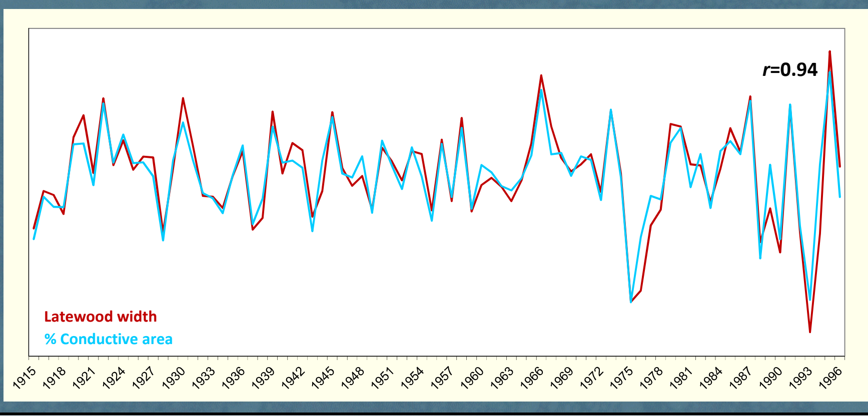
Latewood 'conductive' tissue (mostly vessels, tracheids and parenchyma)

Environmental factors could be controlling some of these features

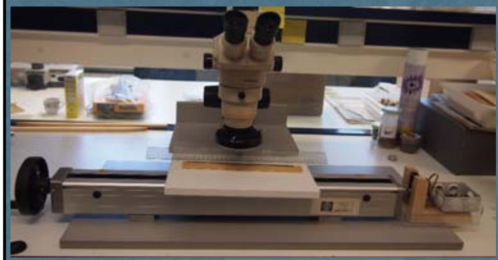
'Conductive area' in the latewood does not appear to contain any relevant environmental information other than the latewood width

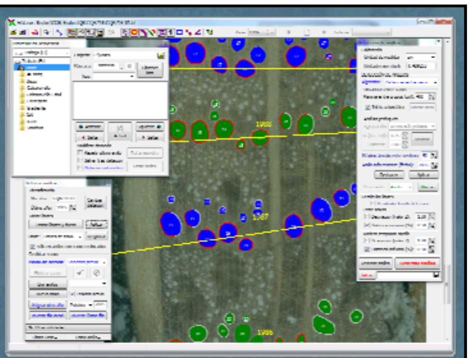


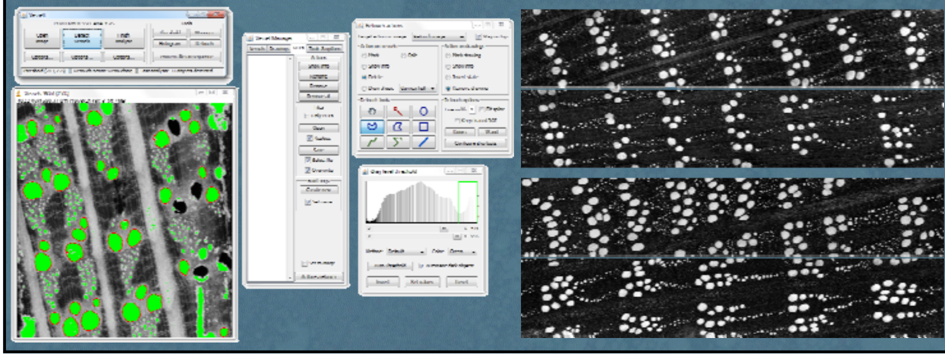
Study case with *Quercus robur* at Caaveiro (NW Spain) for the period 1915-1996 (82 years)



Earlywood characteristics are relatively easy and quick to measure

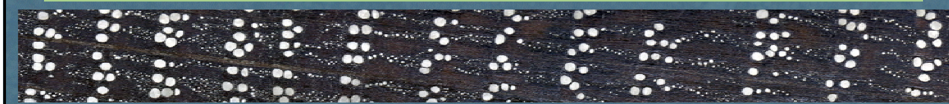






How to extract the environmental information from the earlywood

The plasticity of earlywood anatomical features results in a year-to-year variation, which allows obtaining time series that can studied dendrochronologically



Anatomical traits

Data acquisition

Quantitative variables

Annual values

These variables are usually obtained from the characteristics of the conducting elements (earlywood vessels)

Dimensions/Shape

Number/Distribution

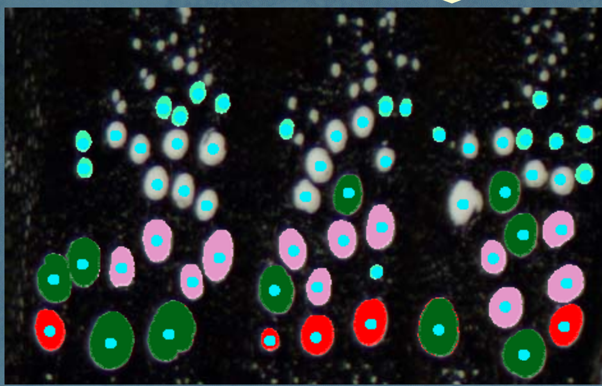
Several variables can be combined into new variables with a physiological meaning

Each variable is expressed as an annual value, and processed using the same analysis procedures as other tree-ring variables (e.g. ring width)

As opposed to tree-ring width, a single ring can be used to obtain multiple anatomical variables

1 → *n*

Environmental signals in the earlywood can be optimized by a proper selection of the response variables



Earlywood variables are based on different aspects of the vessels that can be measured and quantified

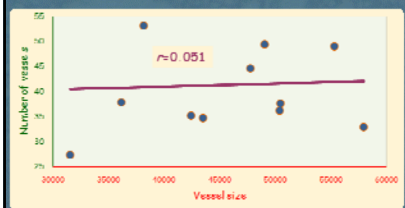
- Vessel dimensions
- Vessel number
- Vessel distribution

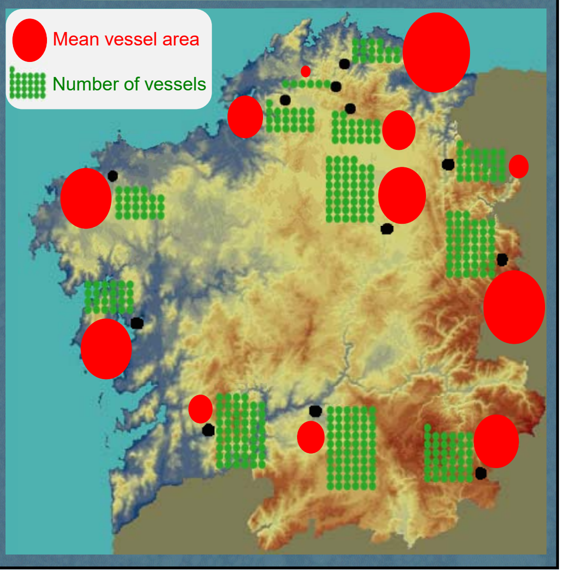
These characteristics can be combined to obtain a variable

Several features and vessel data sets can be used to obtain quantitative variables

Vessel size and vessel number are not necessarily closely related in the earlywood

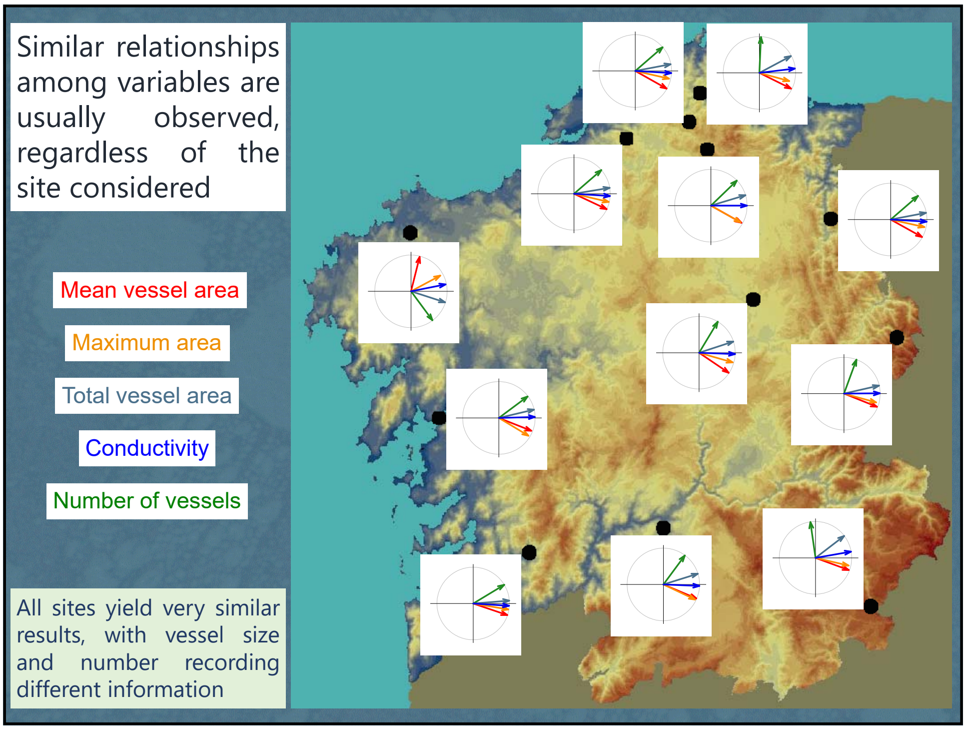
Study case with *Quercus robur* in Galicia (NW Spain) comparing 12 sites along the period 1971-1990 (20 years)

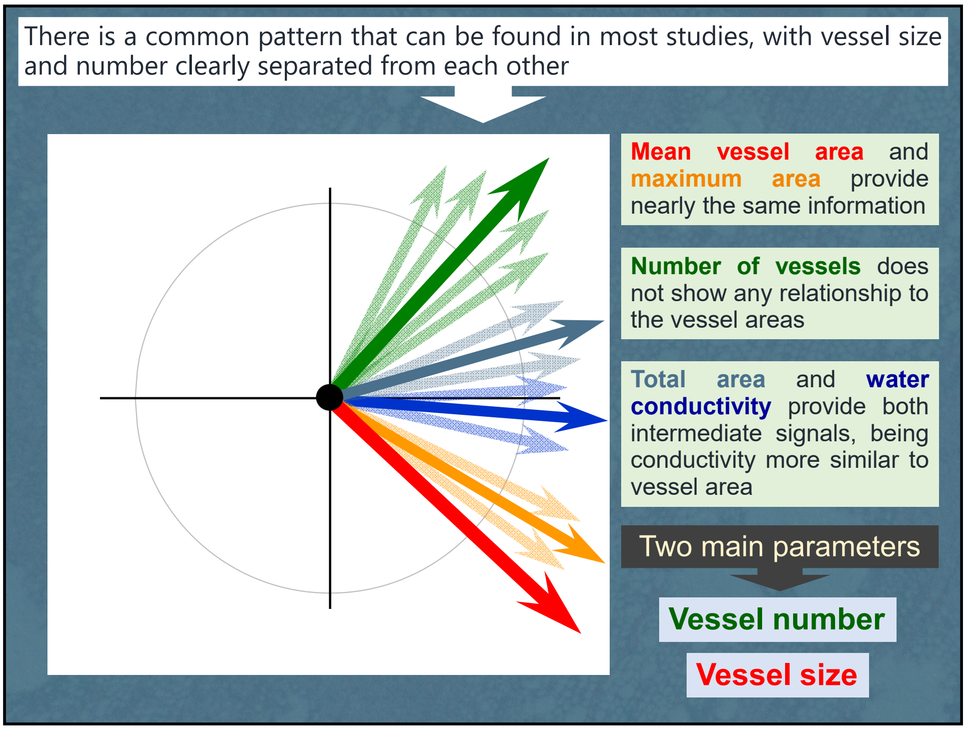




Although an inverse relationship (smaller vessels related to a higher density and viceversa) could be expected *a priori*, no relationship between both variables was found

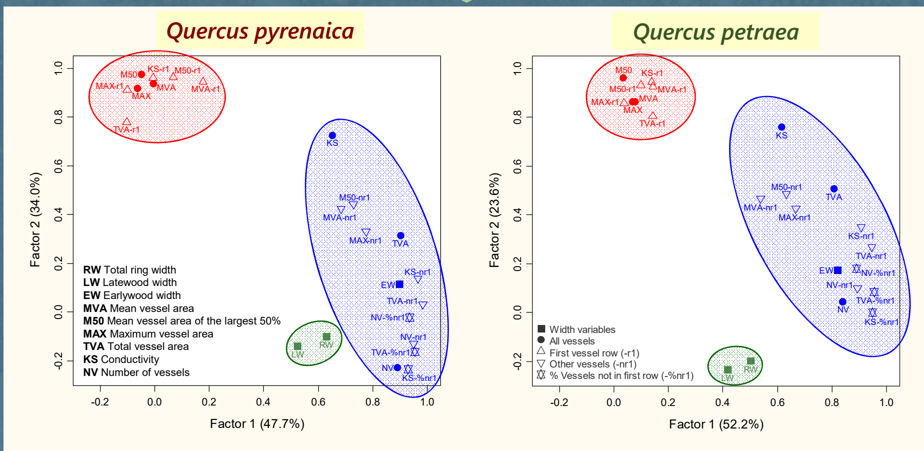
This appears to be the rule when studying earlywood vessels of ring-porous trees


Similar relationships among variables are usually observed, regardless of the site considered
Mean vessel area
Maximum area
Total vessel area
Conductivity
Number of vessels
All sites yield very similar results, with vessel size and number recording different information


There is a common pattern that can be found in most studies, with vessel size and number clearly separated from each other
Mean vessel area and maximum area provide nearly the same information
Number of vessels does not show any relationship to the vessel areas
Total area and water conductivity provide both intermediate signals, being conductivity more similar to vessel area
Two main parameters
Vessel number
Vessel size

The comparison of multiple variables allows optimizing the analyses by determining which ones bear a similar or distinct environmental information

Study case with *Quercus pyrenaica* and *Q. petraea* at Monte Hijedo (Spain) along the period 1937-2006 (70 years), combining multiple variables of vessel size, number and position



Three groups of variables were identified, and the result was the same for both species. These groups can be further analyzed in detail, in order to reduce the number of variables

Two main groups of anatomical variables were identified, which were clearly distinct from tree-ring width

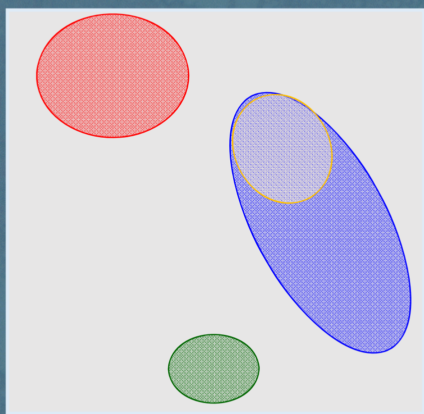
Variables related to vessel size

Variables related to cell production

There appears to be no relationship between vessel size and number

'Intermediate' variables (total vessel area, earlywood width, conductivity) are affected by both characteristics, but more related to cell production

All earlywood variables are different from **tree-ring width**



There appears to be a shift along the growing season

Variables in the first row are highly related to vessel size

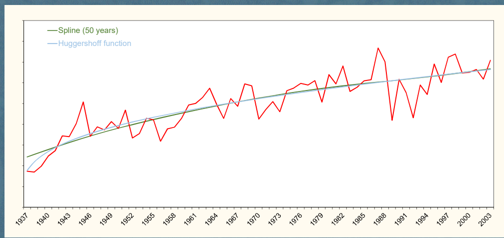
Variables not in the first row are related to vessel number

This pattern of variables tends to be always present, regardless of the species or site

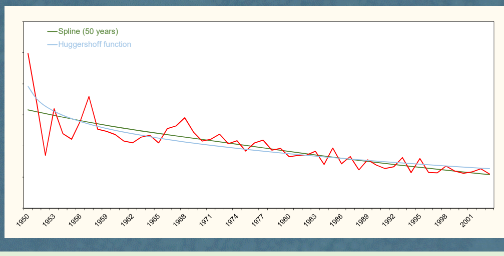
Series of anatomical features also exhibit growth trends, but much less remarkable than in ring width, and the should be detrended in a similar way

As trends are in general gently, detrending is usually successful with relatively rigid curves, or even deterministic methods, including trend lines

Vessel size usually shows a slightly ascending trend, which tends to stabilize afterwards



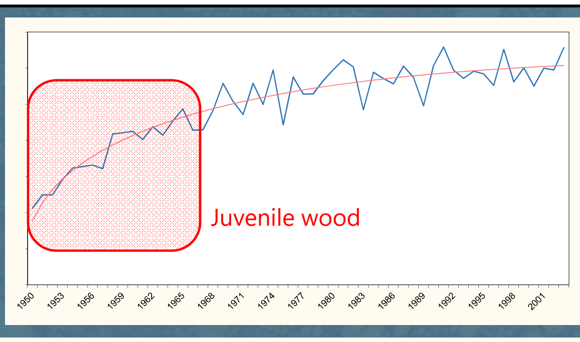
On the contrary, age trend of **vessel number** is descending, but it also tends to stabilization

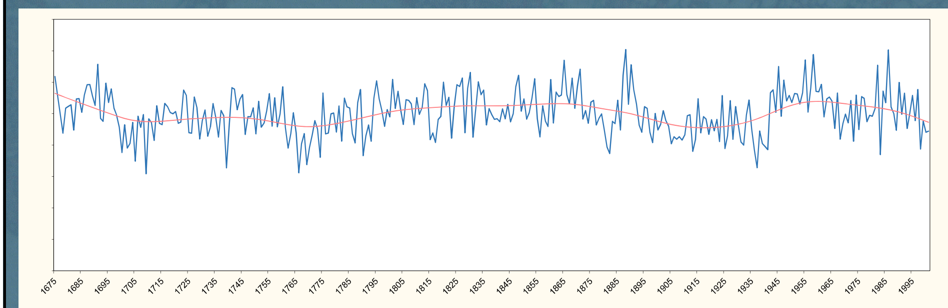


A fairly rigid spline or even a Huggershoff function usually fit well to most anatomical series

Trends are much more pronounced in juvenile wood, and in general it should be avoided to obtain chronologies

On the contrary, trends are weak in long series in comparison to ring width





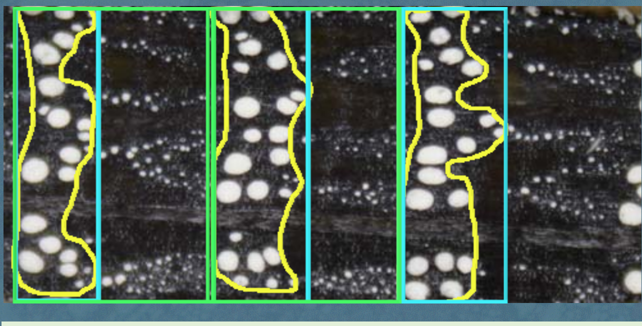
Some periods of growth changes are present, but transitions are usually not abrupt, and much more gently than in ring-width series

The quantification of earlywood vessel production is not straightforward, and presents some methodological difficulties

Vessel number vs. vessel density

Vessel number without considering radial distance can be too highly related to width, mainly earlywood width

In general, it is not possible to define a reasonable earlywood boundary to compute vessel density



Different criteria to delimit earlywood can lead to very different values of density

Vessel density referred to the whole ring is surely mixing up different environmental signals, and is not recommended

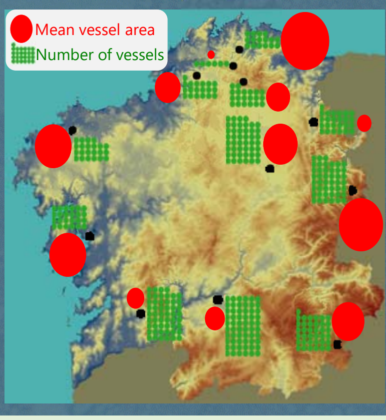
Variables based on the number of vessels are highly related to earlywood width, and these variables are probably a better estimator of earlywood production than earlywood width itself (especially the number of vessels and the total vessel area)

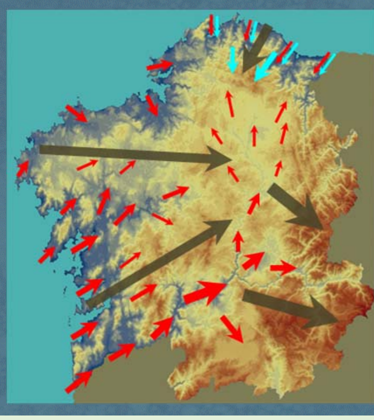
The plasticity of the earlywood can be achieved by studying different anatomical characteristics along with their variation through space and time

Study case with *Quercus robur* in Galicia (NW Spain) comparing 12 sites along the period 1971-1990 (20 years)

Prevailing climatic gradients

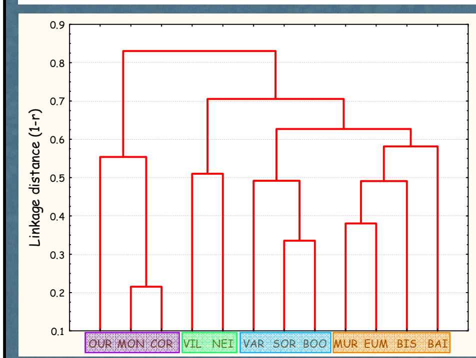
- More Mediterranean conditions
- Increasing continentality
- Moist summer conditions

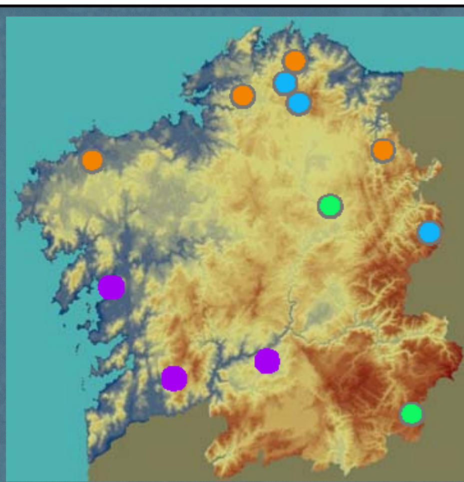




Site variations in anatomical features are remarkable, but no pattern could be explained as related to the prevailing climatic conditions of the region

Chronologies of mean vessel area were compared to each other, and their grouping proved to be coherent with the bioclimatological conditions





Low southern sites, with a strong summer drought and a clear Mediterranean trend

Mountain areas with a mild summer due to altitude or low insolation

Northern valleys towards the coast, at low elevation, with warm but moist summer

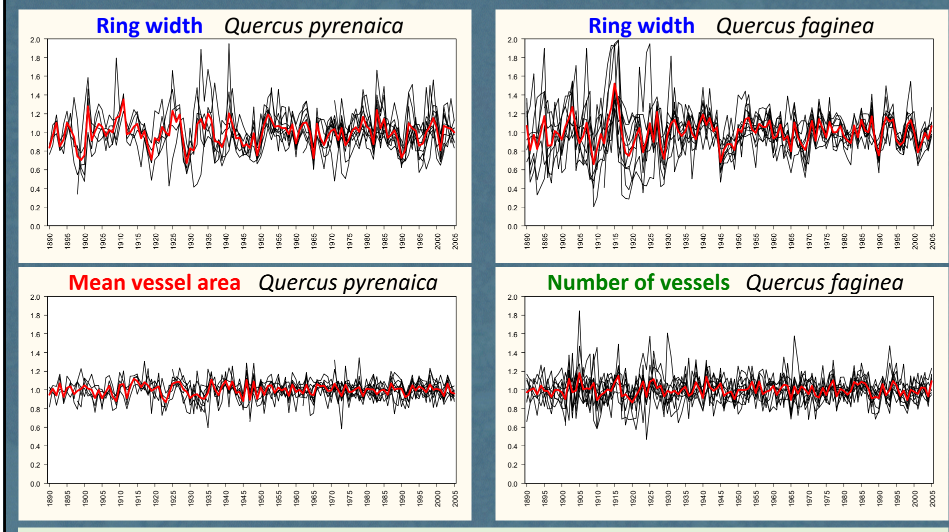
Inland sites having more intermediate conditions in summer

Earlywood vessel size is very powerful recording local environmental information, but when analyzed as time series rather than site-related values, because only the year-to-year variability was able to reflect the prevailing climatic gradients

Time series of earlywood vessel features present characteristics that allow using them to build chronologies

Year-to-year variability

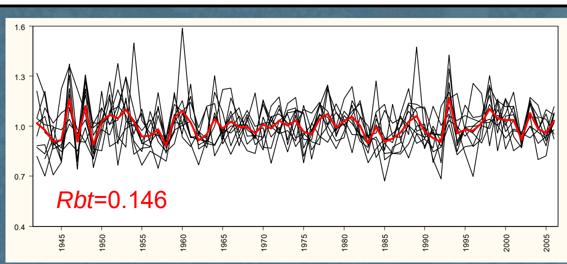
Common variation among trees



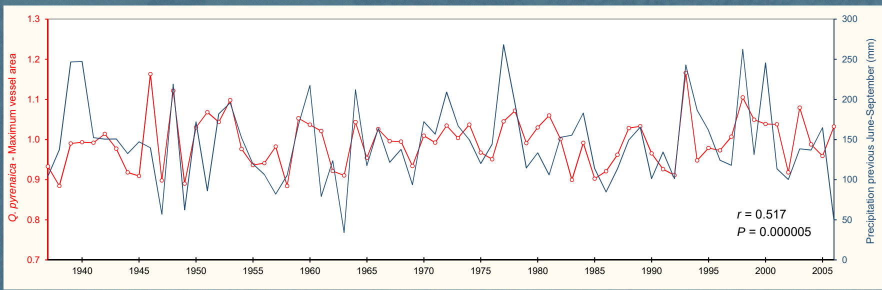
Both sensitivity and common signal are usually considerably lower than in tree-ring width, especially when considering vessel size

Variations among individuals is high, which results in a much lower common signal than in ring width

Other statistical methods rather than the classical assessment of common signal should be explored



Despite the low common signal, climatic responses are usually extraordinarily high



Anatomical series mostly reflect high-frequency variation

Autocorrelations in raw series can be high, but they are mostly due to trend; series of indices exhibit low or even absent autocorrelations, especially when vessel size is considered

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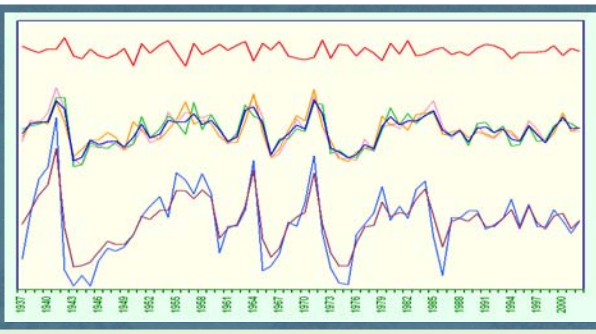
Very often, strong recurrent growth reductions, probably related to non-climatic events (e.g. insect outbreaks), are not recorded by anatomical series

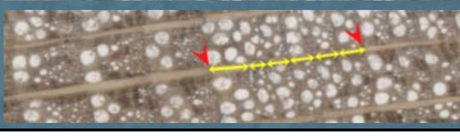
Analysis of chronologies of *Q. pyrenaica* in Sanabria, NW Spain



- Mean vessel area
- Total vessel area
- Vessel number
- Conductivity
- Total ring width
- Earlywood width
- Latewood width

This lower variation can result in a high robustness against disturbances, which can enhance the climatic signal of anatomical variables

These reductions were very remarkable when latewood was considered, and moderate for several earlywood variables affected by the number of vessels



The effect of the reductions was completely absent when mean vessel area was considered

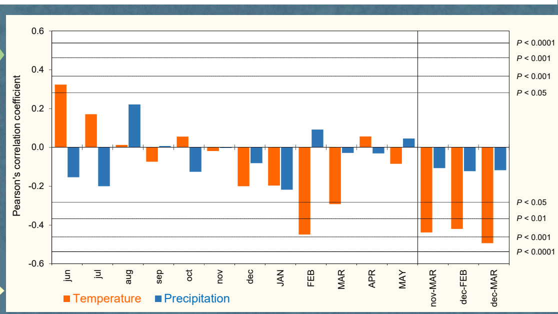
Tree-ring studies based on earlywood anatomy (mainly mean vessel area) proved to be successful in many cases

Study case with *Quercus petraea* at Monte Hijedo (Spain) along the period 1937-2006 (70 years)

Strong relationships to climate are usually found

These responses clearly differ from the information contained in tree-ring width

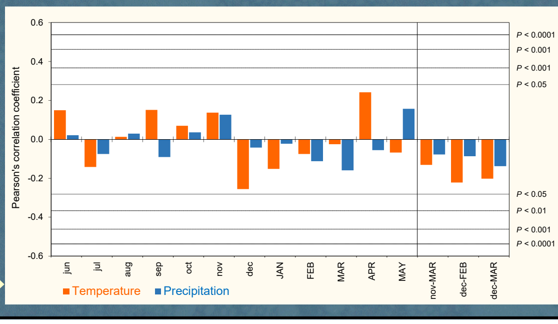
Number of vessels



The responses are of high ecological relevance, and also physiological meaningful in most cases

Relationships to climate area identified even under an apparently lack of a prevailing limiting factor for tree growth

Total ring width



The size of the earlywood vessels of *Quercus robur* can be strongly related to climatic factors (example at two contrasting sites in Galicia, NW Spain)

Trees growing on a valley at low altitude near the coastline (200 m a.s.l), and Mediterranean influence

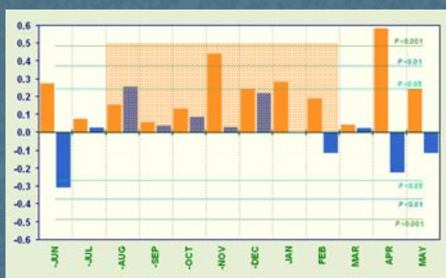
Trees growing on inland mountains close to the altitudinal range of the species (1,400 m a.s.l.)

Late February-March

Late April-May

Low temperature is not a limiting factor, whereas short recurrent droughts can occur in spring

Low temperature can be a limiting factor to initiate cambial activity due to the high elevation

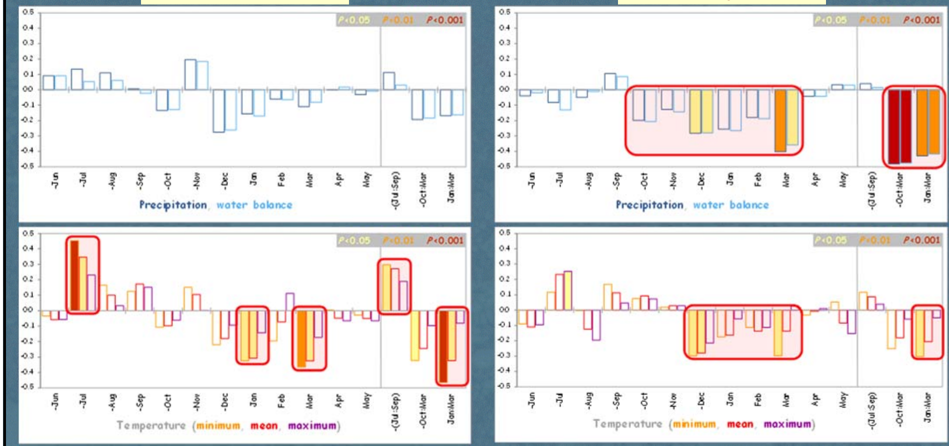


Trees at both sites respond to different factors; in addition, the role of temperature is of opposite sign

Time series of earlywood are very useful to study differences across species

Study case on coexisting *Quercus robur and Q. pyrenaica* at Cortegada Island (NW Spain), using chronologies of **mean vessel area** along the period 1956-2005 (50 years)

Quercus robur | *Quercus pyrenaica*

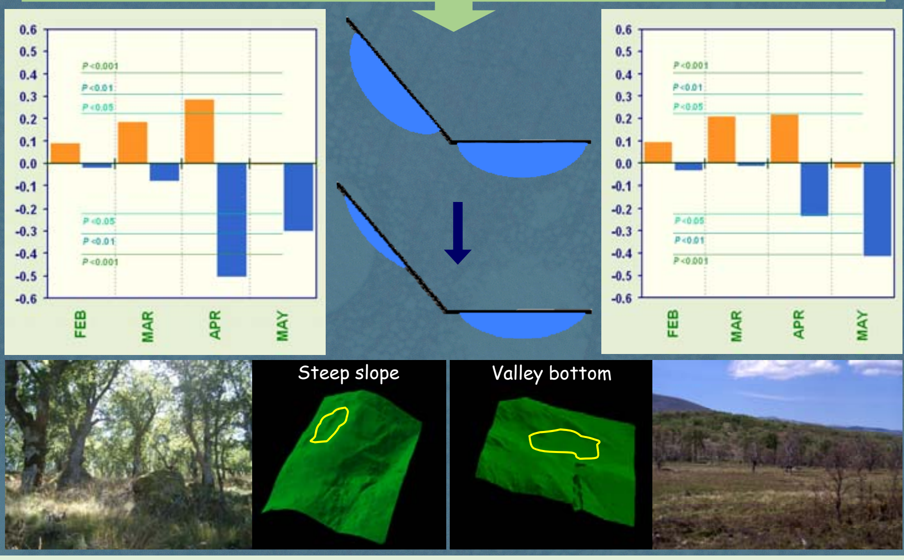


Earlywood vessel size is related to the main stress factors operating on each species along their distribution boundary, which has a great biogeographical relevance

Q. robur responds to a 'Mediterranean' summer and *Q. pyrenaica* to Atlantic winter conditions

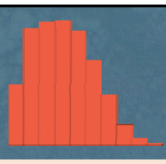
Local ecological conditions can also be easily evidenced in earlywood series

Study case with *Quercus pyrenaica* at Sanabria (NW Spain) at two neaby sites differing in soil water regime, using chronologies of **mean vessel area** for 1937-2002 (65 years)



Response to water availability occurs earlier on the steeper slope, as soil water reserve is reduced

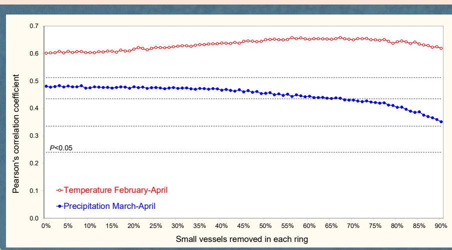
The distribution of vessel size within a ring can be used to define multiple size variables



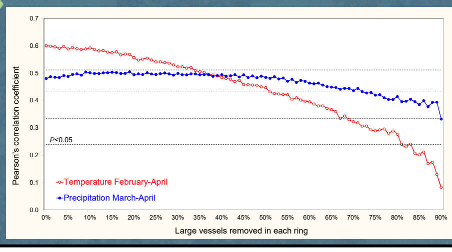
Mean vessel area is the most used variable, but it does not yield the best and more robust results in all cases

Environmental responses of vessel size can be evidenced or optimized by filtering the earlywood vessels according to their size

Smallest vessels can be in general removed, and this often leads to a maximization of the climatic signal when only a small proportion of large vessels is retained



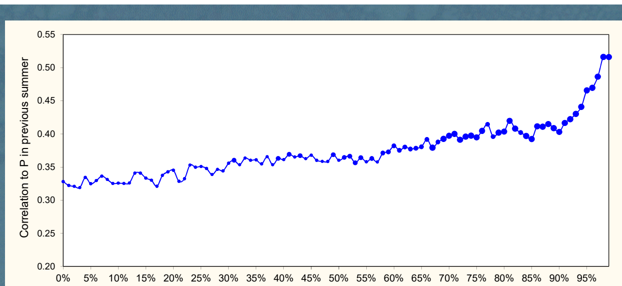
Study case with *Quercus robur* at Caaveiro (NV Spain) along the period 1925-1996 (72 years)



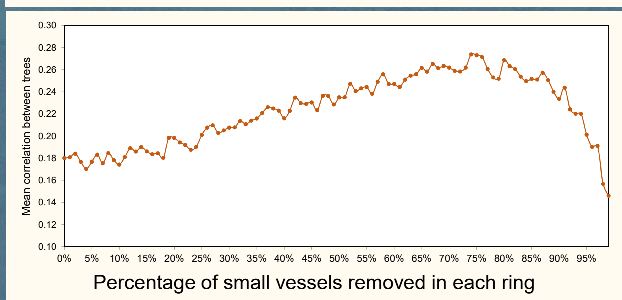
Removal of large vessels usually has very negative influence on the signal; in most cases, the relationship is immediately lost, and only occasionally it can be retained in some vessels of intermediate size

The use of the largest vessels is optimal to identify the influence of environmental variables on vessel size in many cases; therefore, only a small proportion of vessels is enough to unmask the prevailing signal

Study case on *Quercus pyrenaica* at Monte Hijedo (Spain) along the period 1937-2006 (70 years)



In many cases, only very few largest vessels (upper quartile, 95th percentile, or even the maximum vessel) provide the best relationship to climate

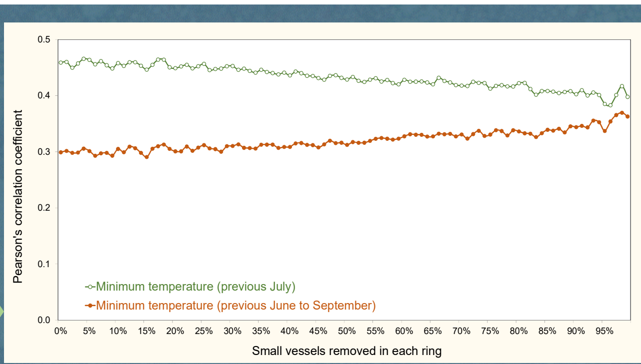


When filtering out small vessels, the climatic signal is usually maximized, but common signal tends to be even lower

The main signal of vessel size is usually retained by the largest vessels, regardless of being maximized or not

But sometimes a larger proportion of vessels should be considered for an optimal signal, although the largest vessels identify the relationship

Study case on *Quercus robur* at Ribeiro do Bispo (Spain) along the period 1937-2006 (70 years)



A filtering to optimize the climatic signal of vessel size should always be performed

Lower limit for considering vessels can be rather flexible, avoiding the tedious measurement of small vessels

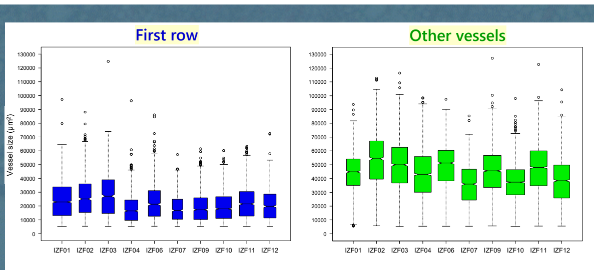
Smallest vessels can be in general removed without the risk of loosing environmental signals

As large vessels tend to be found at the beginning of the ring, size filtering is also highly related to vessel position, namely to the consideration of the first row separately

Considering vessel position, namely vessel row, is fundamental to optimize the environmental signal of earlywood vessels

Vessel distribution usually differs between the first row and the other earlywood vessels

Vessels in the first row are larger and the distribution more symmetrical



Responses of vessel size are mostly determined by the first row of earlywood vessels

Considering other rows usually lowers the signal, especially if large vessels are not filtered

Vessel number/density is mostly dependent on the rest of the vessels, and constant in the first row

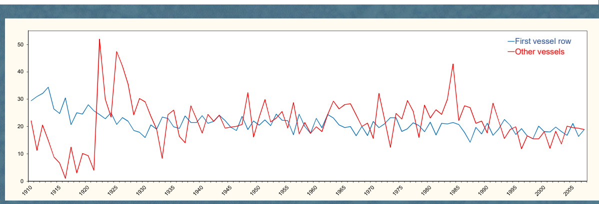
All variables influenced by vessel number should be only considered for all earlywood vessels

"Intermediate" variables are more robust if conductivity is considered, due to the influence of large vessels

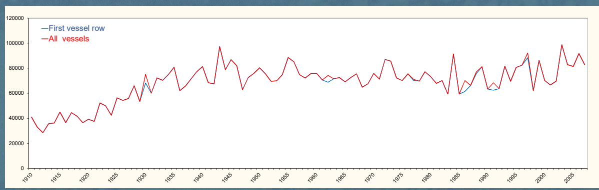
These variables can be useless if number and size are controlled by different factors

Not all variables need to be considered for all vessel positions within the ring

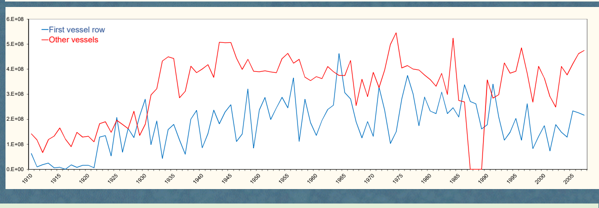
The number of vessels scarcely varies in the first row and should be considered neglectible



Maximum vessel area is determined by the first vessel row, as the largest lie nearly always within this row



Vessels not in the first row can lead to somehow erratic behaviour of the series, especially if conductivity is considered



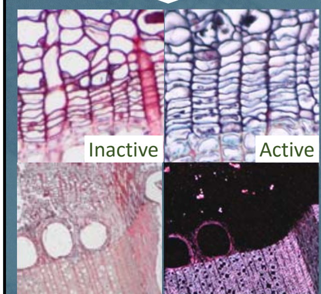
This is a common behaviour in most series of earlywood variables, and therefore can already be considered *a priori* to avoid analyzing an excessive number of variables

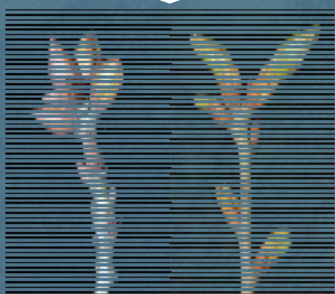
The correct interpretation of climate-growth relationships in tree rings and vessel elements requires a detailed understanding of wood formation dynamics

Seasonal cambial activity

Leaf phenological phases

Non-structural carbohydrates





The development of new tools allowed the establishment of long chronologies of vessel characteristics