

# Defining ecologically relevant vessel parameters in *Quercus robur* L. for use in dendroecology: a pointer year and recovery time case study in Central Germany

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## Abstract

**Key message** The most promising and representative earlywood vessel parameters were identified for dendroecological applications in oak.

**Abstract** Recent improvements of methods used in tree-ring and quantitative wood anatomical studies have helped to widen the selection of parameters which contain environmental information. In the present study, we identified the most promising parameters with respect to signal strength, representativeness, and applicability in oak (*Quercus robur* L.) from two sites in Germany with different moisture regimes. We analyzed three tree-ring and 15 vessel parameters. Principal component analysis was used to detect clusters of relatively similar parameters. Correlation analysis and classical dendrochronological methods were used to select the most robust parameters. From the 15 initial anatomical parameters, six proved to be suitable for tree-ring anatomical studies based on our screening criteria. These were mean area of the vessels of the first row, mean of the five largest vessels, total vessel area, total area of the vessels excluding the first row, vessel density, and total vessel area as a percentage of tree-ring

area. These parameters were applied to samples to search for lagged responses to positive and negative pointer years using superposed epoch analysis. Negative, i.e., dry, pointer years provoked no lagged changes in analyzed parameters at either site; whereas positive, i.e., moist, pointer years showed a lagged negative response of all parameters, which was more pronounced at the drier site.

**Keywords** Quantitative wood anatomy · Ring-porous · ROXAS · Superposed epoch analysis (SEA) · Tree-ring anatomy

## Introduction

Time series of wood anatomical features such as vessel size and vessel density have recently been used to obtain valuable information related to past climatic and environmental conditions (e.g., Bryukhanova and Fonti 2013; García-González and Fonti 2006; Sass and Eckstein 1995; Tardif and Conciatori 2006). Vessel features proved to have a different climate signal than tree-ring width. For example, Mediterranean oak species were used to analyze drought impacts on growth and anatomy (Alla and Camarero 2012; Campelo et al. 2010; Corcuera et al. 2004a, b; Corcuera et al. 2006). While the wide use of such tree-ring anatomical approaches has been limited by available resources, recent technical and methodological improvements now enable researchers to perform vessel-based anatomical studies for long time series (Fonti et al. 2009; García-González and Fonti 2008; von Arx and Carrer 2014).

In ring-porous species such as many oaks, the most frequently analyzed anatomical features in recent studies were the mean vessel area or vessel diameter (e.g. Alla and

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Camarero 2012; Campelo et al. 2010; Eilmann et al. 2006; Galle et al. 2010; Gasson 1985; Helińska-Raczkowska 1994). Vessel density and conductive area were often jointly analyzed (Alla and Camarero 2012; Corcuera et al. 2004a; Pumijumnong and Park 1999). In most studies, 2–3 parameters were analyzed; only a few studies used a range of vessel-based features (Galle et al. 2010; González-González et al. 2014). Although a very large range of parameters are potentially available, the most frequently used ones refer only to the wide earlywood vessels for two main reasons: they make the largest contribution to water transport (Fonti et al. 2010), making them crucial to plant survival; and they have been shown to be the most responsive to environmental conditions. The lumen size of earlywood vessels contains climatic signals of the previous year's autumn and current year's spring, i.e., the time of onset of cambial activity and vessel formation (Fonti and García-González 2004).

To discover adaptation strategies of *Quercus robur* L. (pedunculate oak), we wanted to find anatomical parameters based on earlywood vessel features that would provide insights into the environmental information stored in wood structure. We focused on two sites with different water availability in the colline zone of Central Germany. Methods commonly used in dendroecological analyses were applied in this study with earlywood vessel anatomical parameters used as input parameters. Fifteen distinct parameters were tested for their informational content (signal strength), repeatability within the same tree (representativeness), and relevance for the population and sensitivity to environmental conditions (applicability). We hypothesized that individuals of *Q. robur* growing under different water conditions would respond differently in their wood anatomy.

Our specific aims were (1) to compare the performance of different earlywood vessel statistics typically used in dendroecological research, and (2) to use the selected earlywood vessel statistics for a comparison of recovery times of two different oak populations to both positive and negative extreme years. Therefore, we conducted pointer year analysis for each parameter and calculated mid-term growth changes and the necessary recovery time after these extreme years.

## Materials and methods

### Study sites

The study involved two sites, Gleichberge and Kyffhäuser, both located in Thuringia, Central Germany (Table 1). Although mean annual temperatures at Gleichberge are about 1 °C warmer than at Kyffhäuser (German Weather

Service DWD), the differences in precipitation, slope orientation and soil properties result in considerably greater water availability for tree growth at the Gleichberge site.

### Preparation of samples for anatomical analyses

The analyses of the anatomical parameters were carried out using increment cores from eight dominant trees of *Q. robur* per site that were at least 137 years old. From each tree, two 5 mm diameter cores were collected at breast height in the line of the slope. The cores were mounted and the surface was cut with a core microtome (WSL, Birnmensdorf) (Gärtner and Nievergelt 2010). Tyloses and wood dust were removed from the vessels with a blast of high-pressure air. Next, the core surface was stained black with a permanent marker and the vessel lumina were filled with white chalk to increase the contrast. The entire cores were scanned using a high-resolution scanner prior to making vessel measurements (Epson Perfection V700 Photo, Seiko Epson Corporation, Nagano, Japan). The cores were scanned with a 24-bit color depth scanner with an optical resolution of 2300 dpi, which has been shown to be sufficient for the analysis of earlywood vessels in *Q. robur* (Fonti et al. (2009)).

### Definition of parameters and measurements

In addition to tree-ring width (TRW), we measured the earlywood (EWW) and latewood (LWW) width. These were assessed using a LINTAB device (Rinntech, Germany) and TSAP-Win v4.69f software (Rinn 2011). The earlywood vessels ( $>6000 \mu\text{m}^2$ , Fonti et al. 2009) were measured and used to derive an array of features (Table 2), including mean vessel area (MVA), largest vessel area (MAX) and total vessel area (TVA, accumulated area of all vessel lumina). Since previous studies found a stronger signal from the vessels of the first row (García-González and Fonti 2008; González-González et al. 2014), these three parameters were applied (1) to all earlywood vessels, (2) only to the first row of earlywood vessels (row) and (3) to the earlywood vessels excluding the first row (rest). Furthermore, the number of vessels (NV), the vessel density (VD), the total vessel area as a percentage of the tree-ring area (TVA%), the mean maximum area of the largest three and five vessels, and of the widest 25 % vessels (MAX3, MAX5, MAX25%, respectively), of all earlywood vessels were measured. VD and TVA% each refer to the total ring width. In total, 18 parameters were tested (Table 2).

The scanned core images were processed with ROXAS v1.5.0.7 software (Fonti et al. 2009; von Arx and Carrer 2014; von Arx and Dietz 2005). The software was applied

**Table 1** Characterization of the study sites

	Gleichberge (moist)	Kyffhäuser (dry)
Forest district	Römhild	Bad Frankenhausen
Coordinates	50°23'N, 10°35'E	51°24'N, 11°06'E
Elevation (m asl)	440–550	427
Slope orientation	NE–NW	SW–NW
Mean annual temperature (°C)	7.6	6.7
Mean annual temperature May–September (°C)	14.5	13.3
Precipitation (mm/year)	650	460
Precipitation May–September (mm)	309	253
Bedrock	Basalt	Sandstone
Soil type	Calcic pelosol	Cambisol
Moisture status	Very fresh—moist	Moderately dry
Nutrition status	Moderate to rich	Moderate

**Table 2** Definitions of earlywood vessel and ring-width parameters used in this study

Acronym	Vessel parameter
MVA	Mean vessel area
MVA <sub>row</sub>	Mean vessel area 1st row
MVA <sub>rest</sub>	Mean vessel area except for 1st row
TVA	Total vessel area
TVA <sub>row</sub>	Total vessel area 1st row
TVA <sub>rest</sub>	Total vessel area except for 1st row
TVA%	Total vessel area in % of tree-ring area
MAX	Maximum vessel area
MAX <sub>row</sub>	Maximum vessel area 1st row
MAX <sub>rest</sub>	Maximum vessel area except for 1st row
MAX3	Mean area of maximum 3 vessels
MAX5	Mean area of maximum 5 vessels
MAX25%	Mean area of maximum 25 % vessels
NV	Number of vessels
VD	vessel density

Acronym	Ring-width parameter
TRW	Tree-ring width
EW	Earlywood width
LW	Latewood width

to recognize the tree-ring borders and measure the vessel dimensions semi-automatically. Some borders and vessels that were mis-recognized by automatic detection were manually corrected using a built-in editing function. Then, chronologies of each parameter were built.

### Chronology building and quality testing

Master tree-ring chronologies consisting of 23 oak trees from Gleichberge and 40 trees from Kyffhäuser (two cores each, including the trees used for the anatomical analyses)

were established. Earlywood and latewood width chronologies were also computed for these 63 trees. Each of these three chronologies covered a time span of 214 years (1797–2010) for Gleichberge and 137 years (1876–2012) for Kyffhäuser, and was replicated by at least six (Gleichberge) and five (Kyffhäuser) trees in any year of the chronologies. The chronologies of the anatomical features based on earlywood vessels were calculated based on the eight oak trees (mean curves of two cores each) per site. With a minimum number of 137 tree rings, we restricted our analyses to the last 111 years (1900–2010), thus excluding the juvenile growth reactions.

All ring width and anatomical series were cross-dated visually with TSAP-Win software (Rinn 2011), and then verified statistically by COFECHA (Holmes 1983). Redundant trends were removed using ARSTAN (Cook 1985). Cubic smoothing splines (Cook and Peters 1981) with 50 % frequency cut off at a stiffness of 60 years were applied to every single series, the variance was stabilized, the autocorrelation was removed by autoregressive modeling, and finally chronologies for each feature were built by averaging the series using a bi-weight robust mean (Cook 1985).

In the following process, all parameters had to pass a quality check by (1) applying principal component analysis (PCA), (2) computing inter-correlations among parameters, (3) checking for within-tree correlations, and (4) calculating the expressed population signal (EPS). Possible similarities and relationships between the chronologies may be presumed based on the high number of parameters used here; therefore, PCA was performed (Richman 1986). PCA has been proven to be an important tool that can be used to test time series of anatomical parameters for possible similarities (Bryukhanova and Fonti 2013). Using SPSS v22.0 software, the loadings for the two first principal components were calculated and orthogonally rotated (varimax method). All 18 parameters

were tested against each other for the years of 1900–2010 (1). To further assess the representativeness of each parameter for oak on these sites, we checked for inter-correlation between the parameters (2), and calculated correlations between the two cores of the same tree (3) (Kniesel et al. 2014). The signal strength of the residual chronologies was checked by calculating the expressed population signal (4) (EPS) (Wigley et al. 1984). Only those parameters with chronologies showing a satisfactory signal were accepted for further analyses. According to Wigley et al. (1984), the EPS should be at least 0.85 to ensure sufficient signal quality. However, since this signal is clearly dependent on the sample size, and because previous studies showed that time series of anatomical traits often show smaller EPSs (Abrantes et al. 2013; Fonti et al. 2007), we defined an EPS of 0.75 as being adequate for a further analysis.

### Pointer-year analysis and recovery time

The parameters chosen with the quality selection process were used for the pointer-year analysis. For each parameter, negative and positive pointer years were assessed individually using the approach following Neuwirth et al. (2007). Hereafter, pointer years were calculated from Cropper values (Cropper 1979) and were divided into three categories based on the intensity of the growth anomaly (weak, strong, extreme). For additional analysis, only pointer years of extreme intensity were selected. As the pointer years were calculated for each parameter individually, the lists of pointer years differ between the parameters.

The recovery time after extreme pointer years was calculated using the superposed epoch analysis (SEA) with a time lag of 4 years (Lough and Fritts 1987). Departures from the mean value of each core for the 4 years prior to each pointer year, and the 4 years immediately after each pointer year, were averaged and plotted to determine if the values for these years were significantly different (Orwig and Abrams 1997). This analysis was carried out with R (R Development Core Team 2013) using the dplR package (Bunn 2008).

To identify the climatological responses of each vessel-based parameter, we used the self-calibrating Palmer Drought Severity Index (scPDSI) (van der Schrier et al. 2006; Wells et al. 2004). We analyzed mid-term responses after dry and moist years according to the scPDSI. Therefore, we followed the approach of Eilmann and Rigling (2012) by calculating mean growth values of 4 years prior to each extreme year; these were compared with the mean growth of the 4 years after the extreme year using a Wilcoxon signed rank test (R Development Core Team 2013).

## Results

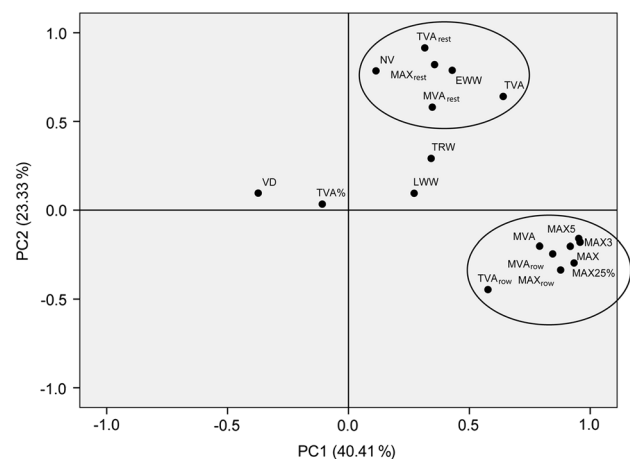
### Principal component analysis and inter-correlation between the parameters

Applying a PCA to all 18 parameters resulted in categorizing two different groups (Fig. 1). The first and second group (Components 1 and 2) explained 40.4 and 23.3 % of the variation, respectively. The first group (i.e. MAX-versions, MVA) included the parameters related mostly to the first row of vessels, whereas the second group (i.e. TVA, EWW, NV) mostly contained parameters of the remainder of the earlywood vessels. Four parameters could not be associated with either group but were clustered in two separate regions, TRW and LWW, as well as VD and TVA%. The results for the Kyffhäuser site were very similar and are therefore not displayed.

The close range among some of the parameters revealed a high level of correspondence and indicates replaceability. Most maximum vessel combinations are rather close together, especially MAX3 and MAX5. The same applies for the mean area of the vessels (MVA) and mean area of the vessels of the first row (MVA<sub>row</sub>). The inter-correlation analysis between all parameters revealed similar results (Table 3). Correlation values of  $r > 0.20$  are already significant ( $p < 0.05$ ), but for our selection process, we preferred the stricter threshold of  $p < 0.001$  with high correlation values of  $r > 0.75$ .

### Within-tree correlations of anatomical features and signal quality

Table 4 shows the within-tree correlations of the cores used for the anatomical parameters. The set of parameters



**Fig. 1** Principal component analysis (PCA) of all 15 anatomical parameters and the three ring-width parameters (TRW, EWW, and LWW) for two components, exemplarily for the Gleichberge site

**Table 3** Inter-correlation among the anatomical parameters; bold values ( $r > 0.75$  and  $p < 0.001$ ) are exemplarily for the Gleichberge site

	TRW	LWW	EWW	MVA	MVA <sub>row</sub>	MVA <sub>rest</sub>	TVA	TVA <sub>row</sub>	TVA <sub>rest</sub>	TVA%	VD	NV	MAX	MAX3	MAX5	MAX25%	MAX <sub>row</sub>	MAX <sub>rest</sub>	
TRW	1																		
LWW	<b>0.96</b>	1																	
EWW	0.48	0.28	1																
MVA	0.05	0.02	0.11	1															
MVA <sub>row</sub>	0.13	0.11	0.18	<b>0.75</b>	1														
MVA <sub>rest</sub>	0.11	-0.01	0.44	0.49	0.10	1													
TVA	0.23	0.04	<b>0.75</b>	0.34	0.42	0.48	1												
TVA <sub>row</sub>	0.00	0.02	-0.11	0.46	0.57	-0.23	0.30	1											
TVA <sub>rest</sub>	0.25	0.04	<b>0.82</b>	0.06	0.09	0.63	<b>0.82</b>	-0.24	1										
TVA%	<b>-0.86</b>	<b>-0.92</b>	-0.12	0.07	0.02	0.12	0.19	0.08	0.13	1									
VD	<b>-0.85</b>	<b>-0.91</b>	-0.17	-0.25	-0.23	-0.04	0.07	-0.07	0.10	<b>0.94</b>	1								
NV	0.18	0.00	0.69	-0.30	-0.08	0.19	<b>0.76</b>	-0.02	<b>0.79</b>	0.15	0.25	1							
MAX	0.16	0.14	0.24	0.69	<b>0.76</b>	0.17	0.46	0.58	0.12	-0.03	-0.27	0.00	1						
MAX3	0.18	0.14	0.27	<b>0.75</b>	<b>0.83</b>	0.20	0.52	0.62	0.16	-0.01	-0.27	0.02	<b>0.96</b>	1					
MAX5	0.18	0.14	0.27	<b>0.79</b>	<b>0.85</b>	0.25	0.53	0.61	0.17	0.00	-0.27	0.00	<b>0.90</b>	<b>0.96</b>	1				
MAX25%	0.13	0.12	0.16	<b>0.81</b>	<b>0.86</b>	0.18	0.41	0.62	0.04	-0.02	-0.29	-0.13	<b>0.93</b>	<b>0.98</b>	<b>0.96</b>	1			
MAX <sub>row</sub>	0.14	0.15	0.11	0.67	<b>0.78</b>	0.06	0.35	0.63	0.00	-0.05	-0.28	-0.10	<b>0.97</b>	<b>0.93</b>	<b>0.88</b>	<b>0.92</b>	1		
MAX <sub>rest</sub>	0.26	0.08	0.73	0.26	0.08	<b>0.80</b>	0.68	-0.25	<b>0.84</b>	0.06	-0.04	0.50	0.16	0.19	0.21	0.10	0.03	1	

**Table 4** Within-tree correlations (mean corr.), their significance [sign. corr. (%)], and expressed population signal (EPS) for all anatomical parameters and tree-ring width; bold parameters were accepted for further analyses based on their high values

	Gleichberge (moist)			Kyffhäuser (dry)		
	Mean corr.	Sign. corr. (%)	EPS	Mean corr.	Sign. corr. (%)	EPS
<b>MVA</b>	0.38	75	0.75	0.34	75	0.73
<b>MVA<sub>row</sub></b>	0.38	87.5	0.77	0.36	75	0.78
<b>MVA<sub>rest</sub></b>	0.31	62.5	0.76	0.28	50	0.74
<b>TVA</b>	0.43	87.5	0.80	0.36	75	0.83
<b>TVA<sub>row</sub></b>	0.18	12.5	0.67	0.16	25	0.58
<b>TVA<sub>rest</sub></b>	0.47	87.5	0.86	0.45	87.5	0.86
<b>TVA%</b>	0.70	100	0.92	0.72	100	0.95
MAX	0.32	50	0.71	0.28	37.5	0.75
MAX <sub>row</sub>	0.31	50	0.73			
MAX <sub>rest</sub>	0.34	62.5	0.80			
MAX3	0.39	75	0.78			
<b>MAX5</b>	0.39	75	0.83	0.38	75	0.81
MAX25%	0.39	75	0.78			
NV	0.38	75	0.83			
<b>VD</b>	0.67	100	0.92	0.66	100	0.94
TRW	0.60	100	0.96	0.73	100	0.98

analyzed from Kyffhäuser site is already reduced for replaceable features based on the PCA results. Only two anatomical parameters showed a strong correlation throughout all trees on both sites (TVA% and VD). However, the other parameters showed a rather weak mean correlation, and the values for TVA<sub>row</sub> did not even exhibit any within-tree correlation. Parameters were accepted for further analyses if at least 75 % showed significant correlations of  $r > 0.34$ .

The EPS was used as a criterion to assess the signal strength and quality of the different chronologies (Wigley et al. 1984). When applying the adapted threshold of 0.75, nearly all parameters (12 out of 15 anatomical parameters) showed a satisfying signal quality (Table 4) on both sites. The EPS values provided similar results as the mean correlations: TVA% and VD had the highest values and TVA<sub>row</sub> had the lowest. For comparison, the within-tree correlations of the TRW are included, and have high values as expected.

### Selection of suitable anatomical parameters

Fifteen anatomical parameters based on earlywood vessels were tested for signal quality, representativeness, and applicability. After passing a quality check by calculating the EPS, applying a PCA, computing inter-correlations among the parameters, and checking for within-tree correlations, six parameters seemed to be suitable for the further dendroecological analysis: **TVA**, **TVA<sub>rest</sub>**, **MVA<sub>row</sub>**, **MAX5**, **TVA%**, and **VD**. We decided to also include the frequently used **MVA** parameter to allow the comparison of results

with other studies. In addition, we considered all tree-ring width parameters (TRW, LWW, and EWW) for further analyses. In this selection, each of the two groups and the two additional clusters of PCA are represented by at least two parameters.

### Superposed epoch analysis (SEA) and mid-term growth deviations

The effects of positive pointer years were extremely short-dated; this applied to all vessel-based and tree-ring width parameters. In most cases, the SEA revealed significantly higher values in the positive pointer year itself, but no effect on the following years (data not shown). In contrast, the impact of extremely negative pointer years lasted longer. All parameters (except for MVA and MVA<sub>row</sub> Kyffhäuser) showed significantly lower values in the pointer years (Table 5). MVA and MVA<sub>row</sub> were affected at the Gleichberge site, but this effect did not show up in the following years. TVA<sub>rest</sub> was affected, but differently on both sites. While the oak trees at the dry site (Kyffhäuser) needed 3 years to recover in this parameter, at the moist site (Gleichberge) oak trees showed much higher values the following year. The values of TVA% and VD are of interest, because at the Kyffhäuser site, no recovery time was needed, but at the Gleichberge site, 2 years were necessary. For unknown reasons, even 1 year prior to the pointer year, the values were lower.

The extremely negative pointer years were calculated for each parameter separately and each parameter was



**Table 5** Superposed epoch analysis (SEA): deviations of the extremely negative pointer years from the mean values of each parameter, deviations before the pointer years and necessary recovery

time after pointer years (changes of values: – lower, – – much lower, + higher, ++ much higher than the mean)

	Gleichberge (moist)									Kyffhäuser (dry)								
	-4	-3	-2	-1	Pointer year	+1	+2	+3	+4	-4	-3	-2	-1	Pointer year	+1	+2	+3	+4
TRW					--									--				
LWW					--	--								--				
EWW					-									-				
TVA					--									--				
TVA <sub>rest</sub>					-	++								--	-	-	-	
MVA					-													
MVA <sub>row</sub>					--													
Max5					-									-	+			
TVA%					-	--		-	-					-				
VD					-	--		-	-					--				

influenced by different biotic and abiotic conditions. Hence, the reasons why each parameter showed extreme values were diverse. There was only one similarity: TVA% and VD were mainly influenced by particularly moist years at both sites.

Mid-term deviations in growth after dry and moist years based on the scPDSI revealed very different results. While no significant changes were observed after dry years (data not shown), different changes among parameters and between sites were evident after moist years (Fig. 2). TRW, LWW, and EWW were negatively affected on both sites, EWW had similar values, but LWW and consecutively TRW were more reduced at the Gleichberge site.

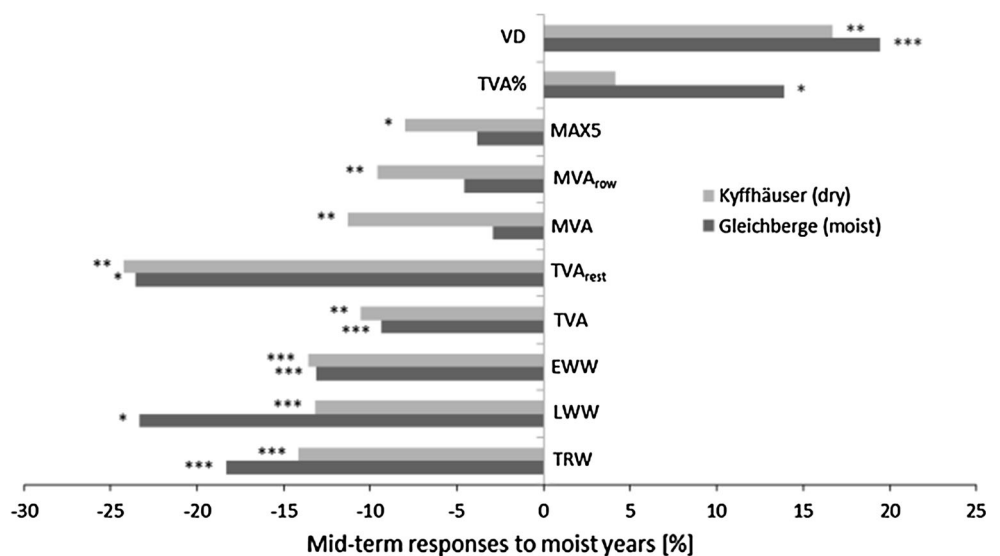
TVA and especially TVA<sub>rest</sub> were strongly reduced on both sites equally. MVA, MVA<sub>row</sub>, and MAX5 were

slightly but insignificantly reduced at the Gleichberge site, while they were stronger and significantly reduced at Kyffhäuser site.

### Discussion

In this study, we tested 15 anatomical and three tree-ring width parameters in *Q. robur* for signal quality, representativeness, replaceability and applicability. This approach yielded 10 suitable parameters organized in four different groups with respect to replaceability, i.e. distinctiveness of information. The selected parameters proved useful for discriminating different response patterns to moisture availability for trees growing on different sites.

**Fig. 2** Mid-term deviations of the 4 years after moist years and from the 4 years prior to moist years (based on scPDSI) in %, significance after Wilcoxon signed rank test



### Selecting the most suitable anatomical parameters for dendroecological studies

The relatively high number of vessel-based parameters with an EPS above 0.75 (12 out of 15) indicates that the sample trees were well selected and showed a rather strong signal when compared with other studies using anatomical chronologies (Abrantes et al. 2013; Fonti et al. 2007; Matisons et al. 2013).  $TVA_{\text{row}}$  showed a considerably lower EPS value than any other parameter, which may indicate a higher degree of noise, e.g., because of substantial circumferential variability when taking 5-mm-wide cores. Such an explanation is also supported by the observed poor within-tree correlation.

The PCA and correlation analysis revealed a high level of correspondence among some of the parameters (i.e., MAX3, MAX5 and MAX25%). This indicated replaceability of parameters having similar initial values and validity (González-González et al. 2014), as well as the necessity of splitting some parameters for different regions of the earlywood because of intermixed signals (e.g. MVA, MVA of the first row of vessels, MVA of remaining vessels). Several studies have already shown the importance of analyzing the earlywood vessels of the first row separately from the following vessels; while the climatic signal of these different vessels varies, it is often more pronounced in first-row vessels (Fonti et al. 2007; García-González and Fonti 2008; González-González et al. 2014). In addition, our PCA results strongly support the concept that anatomical parameters contain complementary information to ring width (TRW, LWW) (Campelo et al. 2010; García-González and Eckstein 2003; Matisons et al. 2013). Our grouping of parameters containing a similar signal is very much in line with a recent study of González-González et al. (2014), who chose 23 anatomical and growth variables for a comparison between two *Quercus* species growing at the same site. However, they did not include earlywood vessel density (VD) and the total vessel area as a percentage of the tree-ring area ( $TVA\%$ ) that interestingly formed a fourth group in our analysis. Preston et al. (2006) studied wood density and vessel traits of 51 species in California, and found that a negative correlation existed between MVA and VD. Both parameters were inversely related, which was also found in the present study ( $r = -0.25$ ,  $p < 0.01$ , Table 3). The higher the MVA, the fewer vessels are arranged in a tree ring and the VD decreases.

A poor within-tree correlation indicates a high circumferential variability. This is rather problematic because any particular core would not seem to be representative for the entire tree. The correlation between two cores of the same tree indicated representativeness of only a few parameters (i.e.,  $TVA\%$ , VD). However, both parameters include the

overall constant component TRW. Conducting a partial correlation without TRW as a stabilizing factor would potentially lead to lower correlation values. Aside from  $TVA_{\text{row}}$  (see above), the single largest vessel also did not perform well as a parameter. An increase in stochasticity was observed when using extreme values, but also potential effects of small measurement inaccuracies may be responsible for this result. The implications of a poor within-tree correlation also depend on the aims of the study. If a comparison of populations or sites is the goal, it is a problem indeed, but could be solved by thicker cores and/or increasing the number of trees. If comparing the changes over time is the goal, the problem is somewhat smaller because the relative changes within one core will still reflect the responses to internal and external factors.

### Recovery time after negative pointer years

*Quercus robur* is adapted to dry to moist soils. While growth reactions following extreme events can be detected in TRW, LWW, and EWW, the underlying adaptation strategy is likely to be more easily visible in xylem structure. An approximation to this wide field is the analysis of earlywood vessel dimensions and densities. The selected vessel parameters were analyzed for the necessary recovery time after extreme pointer years. The results revealed differences in the adaptation of pedunculate oak to the dry (Kyffhäuser) and the moist (Gleichberge) sites.

$MVA_{\text{row}}$  was unaffected in negative pointer years at the drier site (Kyffhäuser), but strongly reduced at Gleichberge (Table 5). The first row of earlywood vessels is especially important for ring-porous species as it is the basis for water uptake for leaf unfolding (Sass-Klaassen et al. 2011). Regardless of whether the reason for a negative pointer year was a cold winter or a dry summer, the first vessels were unspoiled at the Kyffhäuser site in contrast to Gleichberge. Summer conditions, especially late summer conditions have a great influence on the first row of earlywood vessels, because it is confirmed that the first row of earlywood vessels originates from overwintering cambial derivatives (Fonti et al. 2007).

The parameters  $TVA\%$  and VD were only slightly affected at the Kyffhäuser site, but were very strongly affected at the Gleichberge site, where 2 years of recovery time were necessary before the parameters returned to normal values. The reason for the occurrence of extremely negative pointer years for  $TVA\%$  and VD was the occurrence of especially moist years. Both parameters refer to TRW: the total vessel area as a percentage of the respective tree-ring area and the vessel density as the number of vessels divided by the respective tree-ring area. Therefore, the smaller the values (which is the case for negative pointer years), the wider is the tree ring, and the better is



the growth. So in this case, small values of TVA% and VD caused by increased moisture should be assessed as positive responses. Hence, the effect was very positive at the Gleichberge, even for the following 2 years, but it is negligible at Kyffhäuser. The oak trees at Kyffhäuser were not able to transform a higher supply of water into increased stem growth. An excess of soil water can definitely hinder wood formation (Pallardy 2008). Additional reasons for a missing positive effect at the Kyffhäuser site might be increased growth in other parts than the stem such as growth in the crown, a poor water-holding capacity of the site, a lack of solar radiation resulting from increased cloud cover or a higher occurrence of mildew (Butin 2011). Expressed more positively, the oaks at Kyffhäuser seem to be well adapted to dry conditions.

Furthermore,  $TVA_{rest}$  was immensely disturbed at the Kyffhäuser site after negative pointer years, and needed 3 years to recover; in contrast, at the Gleichberge site,  $TVA_{rest}$  seemed to even over-compensate the following year. Recall that  $TVA_{rest}$  refers to all vessels except for the first row. The first row was important in trees at the Kyffhäuser site since often there were no following vessels in the tree ring. This earlywood element was especially variable and sensitive at the Kyffhäuser.

### Mid-term growth deviations after moist years

By looking at the climatic response of the parameters after exceptionally moist years (scPDSI), it was very obvious that the oak trees suffered at both sites. Based on scPDSI, dry years did not affect oak growth as strongly as did years with too much moisture; TRW, LWV, and EWW declined significantly (especially LWV in Gleichberge), as did TVA and  $TVA_{rest}$  (Fig. 2). A variety of conditions may cause a decrease in growth and vessel area, such as low temperatures and/or solar radiation, mildew, or disturbed root respiration and growth due to increased ground water level.

TVA% and VD are both inversely related to TRW; therefore, their values increase as TRW becomes smaller. Therefore, the values of those parameters increase after exceptionally moist years, although conditions are worse at Gleichberge than at Kyffhäuser. With that in mind, it should be mentioned that a higher number of vessels is not necessarily combined with smaller vessels (González-González et al. 2014); although in another study, a correlation between a high earlywood vessel density and a lower earlywood vessel area was recognized (Gricar et al. 2013), both in ring-porous *Quercus* species.

A difference was found in the reactions of MVA,  $MVA_{row}$ , and MAX5. In this context, the largest vessels can also be expected to be found in the first row (González-

González et al. 2014). These are the parameters that were especially important to the trees at the Kyffhäuser site. All of them were significantly reduced, in contrast to the Gleichberge site, where the reductions were minor and insignificant. Cold winters or drought do not really affect these parameters in the oak trees at Kyffhäuser, but they seem to be affected under moist conditions.

### Conclusions

Thanks to the technological advances, currently a range of parameters can be easily obtained from the earlywood vessels in a ring-porous species such as *Quercus robur*. However, our study showed that only a few of these parameters meet the requirements for dendroecological analyses, concerning reliability, robustness, and representativity. While the identification of the most suitable parameters may depend on the species and the specific context of the study, we think that the procedure as presented here could be generally valid. Distilling the most suitable parameters for each study (by a principal component analysis, inter-correlations among parameters, within-tree correlations and the expressed population signal) in advance will improve the validity of the results and enable a broader, deeper understanding of trees and their adaptation to different growing conditions. In the present study, both oak populations (and especially that from a dry site Kyffhäuser) seemed to be well adapted to dry conditions, whereas extremely moist conditions cause stress. The effects were especially apparent in the vessel area in the first row and in vessel density. However, we must be aware of the limitations when trying to generalize such results. Nevertheless, this study again demonstrates the value of vessel chronologies in the interpretation of the ability of a species to adapt to different sites. The approaches used in this study to quality check anatomical parameters appear to be necessary before every dendroecological study.

**Author contribution statement** All authors made substantial contributions to conception and design of the study. BK and BG conducted sampling. BK performed lab work and data analysis and interpretation. All authors drafted the manuscript. AR and GvA gave final approval of the version to be submitted.

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