



Variation in vessel traits of northern red oak (*Quercus rubra* L.) provenances revealed high phenotypic plasticity to prevailing environmental conditions

Jonathan M. Kormann^{1,2} · Marieke van der Maaten-Theunissen¹ · Lucrezia Unterholzner¹ · Mirko Liesebach² · Katharina J. Liepe^{1,2} · Ernst van der Maaten¹

Received: 28 May 2024 / Accepted: 9 August 2024 / Published online: 21 August 2024
© The Author(s) 2024

Abstract

Key message Red oak provenances responded with high plasticity and intra-annual variability in vessel traits to studied climatic conditions, indicating weak signals of local adaptation and providing opportunities for forest management.

The climate change-induced increase in frequency and severity of extreme events has revealed a high vulnerability of various major tree species in Europe, stressing the need for selecting climate-resilient species for forest management. In this context, adaptive strategies of northern red oak (*Quercus rubra* L.) were examined, using wood anatomical data derived from a provenance trial. We investigated the interannual variation in vessel traits of red oak provenances planted at three sites along a precipitation gradient in Germany. We compared the climate sensitivity of German provenances with those from North America to analyze plasticity and to identify signals of local adaptation in vessel traits. The results revealed variations in vessel traits between all sites, pointing to site-specific responses to prevailing environmental conditions. Differences between provenances were prevalent for vessel size-related traits, with site-specific higher values for German provenances at wet sites. Climate signals, which varied between traits, were strongest for vessel density and the relative conductive area. Vessel traits were found to depend both on previous-year conditions as and on spring climate conditions during the onset of vessel formation. The site-specific response in extreme years deviate significantly between drought and frost events. A trade-off between resistance to extremes and vessel diameter could not be demonstrated, and provenances with larger vessel diameters showed higher frost resistance. The observed high plasticity in vessel traits and the site-specific variation to climate influences point to an adjustment in vessel formation to the prevailing environmental conditions.

Keywords Ring-porous species · Frost hardiness · Drought hardiness · Provenance trial · Climate sensitivity

Introduction

Mortality currently observed in major tree species in European forests demonstrates their vulnerability to global warming. Recent projections indicate a climate-induced bottleneck of suitable species for resilient forest conversion (Wessely et al. 2024). Alternative tree species such as

northern red oak (*Quercus rubra* L.), which is characterized by high growth potential and high climate tolerance, are of great interest to mitigate current tree mortality (Nicolescu et al. 2020). In this regard, tree rings and xylem anatomical traits provide a natural high-resolution data archive that stores trees response to climate variability. This ecological information is essential for understanding and assessing the consequences of climate change on species and ecosystems (Fonti et al. 2010). Besides endogenous drivers (e.g. phytohormones, plant size), xylem formation is controlled by exogenous drivers (e.g. temperature), bringing the focus of current studies to the relationships between environmental variation and the formation of vessel traits (García-González et al. 2016; Giagli et al. 2016). Environmental conditions shape the development in vessels, determining the optimal

Communicated by Sergio Rossi.

✉ Jonathan M. Kormann
jonathan.kormann@thuenen.de

¹ Chair of Forest Growth and Woody Biomass Production, TU Dresden, Dresden, Germany

² Thünen Institute of Forest Genetics, Grosshansdorf, Germany

balance between adaptation to climatic and physiological processes (Chave et al. 2009).

Since water is essential for all physiological processes including photosynthesis, it is considered as a major factor determining tree growth (Tyree and Zimmermann 2002). In red oak, as ring-porous species, water is transported perpendicularly through the vessels (formed mainly during the early growing season) of varying length and diameter, and transferred between vessels through bordered pits (Chave et al. 2009; Fonti et al. 2010). Vessels play therefore a key role in the balance between the water transport efficiency and the resistance to cavitation. However, despite the safety-efficiency is controversial (Gleason et al. 2015), often the maximum water conductance stands in conflict (Hacke and Sperry 2001). In fact, high vessel area is mainly associated with low resistance to both water transport and air embolisms caused by drought-induced cavitation (Sperry 2003; Chave et al. 2009). In addition, wider vessels reduce the resistance also to frost-induced embolism, as freezing water in vessels cause gas embolisms and consequently frost-induced cavitation (Hacke and Sperry 2001). This trade-off between high water conductance and high risk to cavitation provide an important constraint to vessel functions in trees (Baas et al. 2004), implying the need of further investigation (Lens et al. 2022). However, intra-specific differences and variations in vessel characteristics provide insight into how provenances adapt to environmental variability at temporal and spatial scales (Fonti et al. 2010).

In temperate environments, trees are mostly affected by water limitation and extreme events during the growing season, which both increased in frequency and intensity due to climate change, potentially impacting forest resilience (Jump et al. 2017). Consequently, numerous studies analyzed relationships between climate variables and vessel traits (e.g. González-González et al. 2014; García-González et al. 2016; Carrer et al. 2018), in particular to retrospectively quantify responses of vessel traits to extremes (Castagneri et al. 2017; Nola et al. 2020). Besides droughts, in the last decade frost events are also increasing in frequency and intensity (Lamichhane 2021), bringing higher risk of frost plant damages. Due to mild temperatures in winter, the heat sum, which determines the time of bud break, is reached earlier and therefore the growing season starts earlier (Ma et al. 2019). Late frosts during the active growing season impact tree vitality and ultimately growth performance and can cause considerable ecological and economic damage (Vitasse et al. 2014; Ma et al. 2019).

The study of phenotypic plasticity in vessel traits to past extreme events and climate variability is promising for better selecting suitable provenances for adaptive forest management. In this regard, provenance trials present a powerful tool to investigate vessel traits of different species or provenances (Nabais et al. 2018). In this study, we investigated

provenances of the introduced northern red oak (*Quercus rubra* L., hereafter named red oak), that were planted on three sites of a German provenance trial and originate from stands in Canada, the United States, and Germany. We compare vessel characteristics between native (North American) and introduced (i.e. German) provenances and determine the extent of phenotypically plastic response under variable environmental conditions. Further, trait responses to extreme drought and frost events are closely examined. To date, wood anatomical studies considering red oak are rather scarce and concentrated on the comparison either among different oak species (Tardif and Conciatori 2006) or among introduced stands with variable site conditions but unknown seed origin (Matisons et al. 2015).

The provenances investigated in this study have been the subject of previous studies that have identified differences in growth, climate sensitivity, and response to extreme events (Kormann et al. 2023, 2024). According to these studies, provenances from introduced stands in Germany showed a higher growth and a higher climate sensitivity compared to their North American counterparts. Further, they were characterized by a higher frost hardiness and unexpectedly no trade-off between growth and resistance to extreme events was found. However, these studies focused on basal area or tree-ring width, while quantitative wood anatomy has the potential to reveal finer insights into climate–growth associations and resistance dynamics, disentangling the different physiological traits.

The distinct inter- and intra-specific responses in tree rings to climate raise the question of whether provenances are adapted to the prevailing environmental conditions, and how this is reflected in the formation of different vessel traits. To investigate this question, we (i) assessed the relationships among vessel traits and examine their variation between provenances. Further, we (ii) analyzed the plasticity in vessel traits to evaluate the dependency of climate conditions on the differences in trait formation, focusing on the comparison between sites and between North American and introduced provenances. Since vessel formation in red oak, as a ring-porous species, may be influenced by site-specific variability in water availability, emphasis was on intra-specific variation patterns in vessel traits. Finally, we (iii) studied differences in the intra-specific response to both, an extreme drought and an extreme frost year, and the trade-off between resistance to these extremes and vessel diameter.

Material and methods

Provenance trial

This research was conducted with 12 provenances planted in a provenance trial in 1991 with two-year-old seedlings

on three sites in northern (Dunkelsdorf; DDF), eastern (Waldsiefersdorf; WSD), and central (Waechtersbach; WBH) Germany, characterized by different environmental conditions. The sites differ in precipitation and elevation (Table 1). Waechtersbach with the highest elevation receives the highest annual precipitation sum, followed by the lower elevation sites Dunkelsdorf and Waldsiefersdorf. Each site was set up as a randomized block design with four replicates. The sites are characterized by a comparable height at stand level, which varies by about 1.2 m at age 29 between the sites, with taller individuals in Dunkelsdorf and smaller in Waldsiefersdorf. Due to the small height differences at stand level, no transformation of vessel size was performed. For the analysis of vessel traits, we selected 12 provenances growing at each site. In 1988, seeds were collected from mature trees in six stands located in North America (each three in Canada and United States) and six in Germany, respectively. The origin locations of the provenances are characterized by different climatic conditions. In particular, two of the United States provenances (P2 and P10) originate from higher elevation, differing especially from introduced provenances in the summer heat:moisture index (SHM; Table 1).

Wood anatomical data

Two increment cores of 16 dominant or co-dominant trees per provenance (i.e. four trees per replicate) were sampled at 1.3 m above ground (diameter at breast height) at each site (Kormann et al. 2024). The sampling took place in spring 2022 before the onset of the growing season. At first, cores were air-dried and cut using a WSL microtome (Gärtner

and Nievergelt 2010). For each increment core, digital high-resolution images were recorded using the ATRICS system (Levanič 2007). Afterwards, annual tree-ring width (TRW) was measured and crossdated using CooRecorder and CDendro software (version 9.6.3, Cybis Elektronik & Data AB, Sweden).

For the analysis of vessel traits, we selected eight cores per provenance and site (two trees per replicate) based upon the quality of the prepared increment cores. For a better detection of vessels and to increase the contrast between vessel lumen and cell wall, the surface of each core was prepared with dark ink (i.e. black felt marker) and chalk (Gärtner and Nievergelt 2010). For the measurements of wood anatomical parameters, images were processed using the image analysis software ROXAS (von Arx and Carrer 2014). This software is specifically designed to measure xylem-related parameters in trees and works with the analysis features of Image-Pro Plus (Media Cybernetics, Rockville, USA).

Xylem anatomical traits initially considered were as follows: mean tree-ring width (TRW, mm), mean vessel area (MVA, μm^2), maximum vessel area (MaxVA, μm^2), number of vessels (VNo), vessel density (VD, no./ mm^2), cumulative vessel area (CTA, mm^2), relative conductive area (RCTA, %), mean hydraulic diameter (Dh2, μm), and the theoretical hydraulic conductivity ($\text{kg}/\text{m}^2/\text{MPa}/\text{s}$) according to the Hagen–Poiseuille law (Tyree and Zimmermann 2002). However, to avoid redundancy and to select the most meaningful traits we run a Pearson correlation matrix between all parameters at site level. Based on the results (Fig. S1), we further selected: TRW, MVA, and MaxVA as an indirect indicator of hydraulic conductivity, VNo and VD as safety-related traits,

Table 1 Description of analyzed sites and provenances

Sites	Code	Country*	Latitude	Longitude	Elevation [a.s.l]	SHM [$^{\circ}\text{C}/\mu\text{m}$]
Waechtersbach	WBH	DE	50.27° N	09.15° E	330	47
Dunkelsdorf	DDF	DE	53.97° N	10.60° E	50	53
Waldsiefersdorf	WSD	DE	52.54° N	14.03° E	80	67
<i>Provenances</i>						
Chattahoochee	P2	US	34.87° N	84.42° W	850	32
Tennessee	P10	US	36.45° N	82.17° W	730	37
Anderson	P18	US	41.17° N	85.67° W	260	46
Constance Bay	P7	CA	45.50° N	76.08° W	260	53
Atomic Energy	P9	CA	46.05° N	77.37° W	180	43
Plaines de Kazabazua	P21	CA	45.93° N	76.10° W	210	51
Bremervoerde	P33	DE	53.25° N	09.18° E	30	50
Borken	P34	DE	51.75° N	06.83° E	40	53
Nidda	P37	DE	50.42° N	09.17° E	240	62
Moerfelden	P38	DE	49.98° N	08.68° E	80	69
Wiesloch	P40	DE	49.27° N	08.58° E	190	61
Bornheim	P44	DE	50.73° N	07.50° E	60	57

*CA = Canada, DE = Germany, US = United States

and RCTA representing the percentage of water conductive area. Further, we selected vessel diameter (Dh2) as proxy for vessel size to study possible trade-offs with resistance.

Climate data

For the analysis of the climate effects on vessel traits, daily climate data of maximum temperature and precipitation were extracted from the 0.25×0.25 E-OBS gridded dataset (Cornes et al. 2018). To identify years with an extreme drought event, the Standardized Precipitation Evapotranspiration Index (SPEI) was calculated using the R package *SPEI* (Beguería and Vicente-Serrano 2023). The driest year per site within the considered period was selected if SPEI exceeded a certain threshold in the summer months June and July ($\text{SPEI} < -2.0$) (McKee et al. 1993), during which most of the tree growth occurs (van der Maaten et al. 2018). The SPEI was calculated at a timescale of 6 months to account for the water availability for tree growth (Vicente-Serrano et al. 2010). The defined drought years according to the SPEI differed between sites, with 2015 for Waechtersbach and 2018 for Dunkelsdorf and Waldsieversdorf, respectively. In addition, the response to a common observed late frost event (May) in 2010 occurring at each site was investigated.

Data analysis

Vessel chronologies were built and detrended using a cubic smoothing spline with frequency cut-off of 50% at 15 years to emphasize a high-frequent climate signal and to remove ontogenetic trends (Cook and Kairiukstis 1990; Carrer et al. 2015). For this procedure, we used the R package *dplR* (Bunn 2008, 2010). The effect of environments, provenances, and their interaction on the selected vessel traits was analyzed with an ANOVA, using each vessel trait as response. To detect site-specific differences between traits, mean comparisons with the non-parametric Kruskal–Wallis test were applied.

Successively, bootstrapped correlation coefficients between daily climate variables (maximum temperature and precipitation) and detrended vessel chronologies were calculated over the period from 1999 to 2021 using the *dendroTools* package (Jevšenak and Levanič 2018; Jevšenak 2020). For the moving-window correlation, we initially tested different time windows (20 days, 40 days, 60 days) to identify the strongest climatic signal. The 40-day time window resulted in highlighting the strongest correlation results; therefore, we decided to present only the 40-day window correlations, whereas results for time windows of 20 and 60 days are presented in Figs. S2 and S3. We considered a 16-month window from previous-year June to current-year September to consider the influence of previous-year climate conditions on vessel formation.

Further, we studied the resistance of vessel traits to extreme drought and frost. Specifically, for each extreme year, we calculated the resistance of each provenance per site as the ratio of the performance of vessel traits in the extreme year compared to the previous year (Lloret et al. 2011). Using the resistance as response, we established linear models to assess differences in the response of traits to extreme events, differences in the impact between drought and frost, provenances, and sites. Based on these results, differences between the responses in extreme events (drought and frost) were quantified using the non-parametric Wilcoxon test.

To investigate whether there are trade-offs between resistance to drought or frost and vessel size, we plotted the resistance of TRW to extreme events against vessel diameter. All calculations were conducted in the R programming environment (R Core Team 2023).

Results

Site-specific response in vessel traits

According to the ANOVA, the selected traits were differently impacted by provenance, sites, and the provenance \times site interaction used as fixed effects (Table S2). TRW and MVA were significantly different between provenances and sites, while VNo, VD, and RCTA were only different between sites. MaxVA, however, differed significantly between provenances. Overall, there was no significant effect of provenance \times site interaction on vessel traits.

The site effect on the vessel traits emerged also when comparing the traits absolute means (Fig. 1, Table S1). We observed the highest TRW in Dunkelsdorf, which differed significantly between all sites, coupled with the lowest mean for MVA and RCTA and the highest VNo. In contrast, MVA was not significantly different between the wet (WBH) and the dry (WSD) site, while MaxVA differed significantly between both sites, indicating the importance of water availability on vessel size formation. The highest variation in MaxVA could be observed in Dunkelsdorf. At the driest site, we found the lowest TRW and VNo (positive correlated) as well as the highest vessel density and RCTA.

Intra-annual climate correlations

Correlation analyses between daily climate variables (maximum temperature and precipitation) and vessel traits revealed different associations between sites, provenances and traits (Figs. 2 and 3). Vessel traits showed a higher climatic response to maximum temperature. Overall, TRW, VD, and RCTA showed the strongest climatic signal at all sites, whereas the response in MVA, MaxVA, and VNo

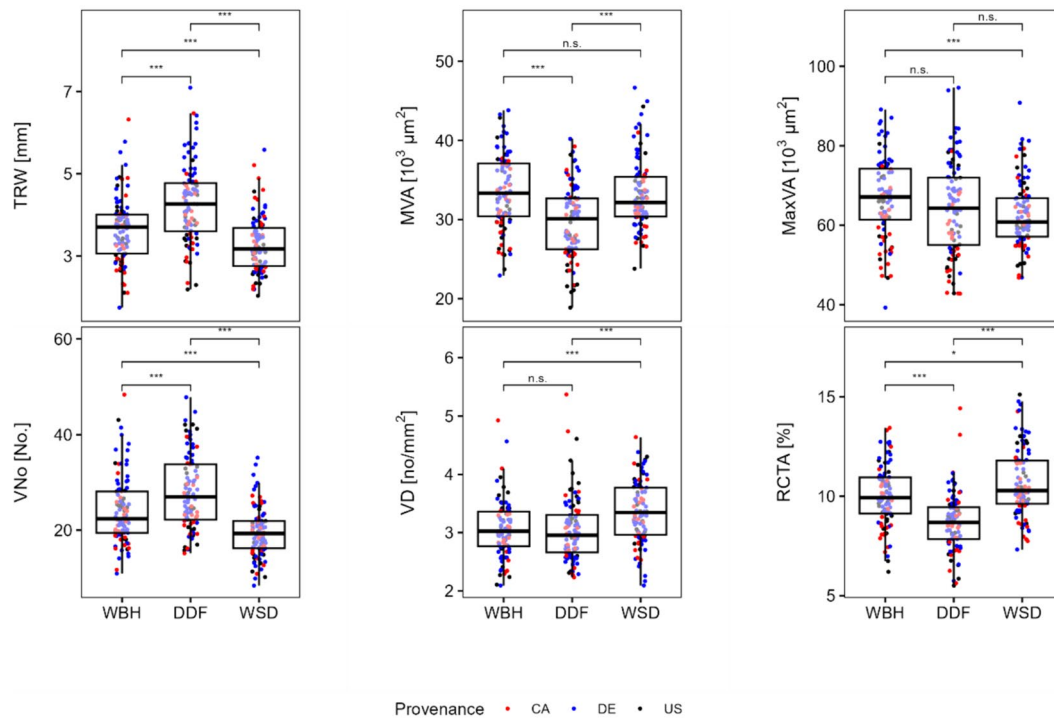


Fig. 1 Boxplots of vessel traits at site level (WBH=Waechtersbach, DDF=Dunkelsdorf, WSD=Waldsieversdorf). Points represent individual trees colored according to their origin (CA=Canada,

DE=Germany, US=United States). Significant differences between site means according to the Kruskal–Wallis test are indicated with asterisk (n.s. not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

was diffuse. Comparable results were found using a different time window for 20 days (Fig. S2a and b) and for 60 days (Fig. S3a and b),

We observed a high dependency of vessel traits on the previous-year (August to September) growing conditions in Waechtersbach and Dunkelsdorf, with positive correlations for maximum temperature (Fig. 2) and negative correlations for precipitation (Fig. 3). At both sites, maximum temperature was negatively correlated in late winter as well as in spring (April to May) of the current year. In Dunkelsdorf, MaxVA and VNo revealed higher dependencies of the previous-year moisture conditions (Fig. 3). In Waldsieversdorf, the response to water availability of the previous year was weak, while maximum temperature had no visible effect on vessel trait formation. In addition, the dependencies of the growing conditions in spring were clearly visible showing low temperature and a high amount of precipitation as main driver for the formation of vessel traits under dry conditions. In Waechtersbach, precipitation in summer (June and July) was positively correlated with VD, RCTA, and MVA, while the response of VNo was similar to the response of TRW. In contrast, precipitation during these months revealed a negative association at the other sites, indicating different dependencies of vessel traits under different moisture conditions.

Differences between provenances were expressed differently depending on climatic variables, sites, and traits. However, responses vary between provenances from different origin, e.g. provenances from the United States showed stronger correlations for MVA and maximum temperature in Waechtersbach (Fig. 2), while MVA of German provenances in Dunkelsdorf was stronger impacted by the amount of precipitation (Fig. 3). In Waldsieversdorf, all provenances revealed a high climate sensitivity for TRW, MVA, VD, and RCTA.

Further, the correlations in the spring months (April–May) varied between sites. The dependence of the previous-year conditions was present at sites with an overall high precipitation sum. The responses of vessel traits varied strongly between sites. VD and RCTA showed a high climate sensitivity at all sites and the opposite response to TRW, whereas VNo revealed a climate response similar to TRW. MVA responds strongly to precipitation, while the response to maximum temperature was diffuse at all sites. No clear pattern was found for MaxVA, suggesting that different factors may influence this trait.



Fig. 2 Bootstrapped correlations between vessel traits (TRW, MVA, MaxVA, VNo, VD, RCTA) and daily maximum temperature. Provenances on the y-axis are colored according to their origin (red = Canada; blue = Germany; black = United States). Sites are ordered along the precipitation gradient from wet (WBH) to dry (WSD). Correla-

tions are indicated in green (positive) and violet (negative) and darker colors indicate significance (correlation > 0.4). Correlations were calculated using a time window of 40 days and over a 16-month window from previous-year June (jun) to current-year September (SEP) for the 1999–2021 period

Response to drought and frost events

The resistance in the identified extreme years differed significantly among vessel traits, extreme events (i.e. drought and frost), and sites, while no effect of provenance or interaction could be distinguished by the ANOVA (Table 2).

In accordance with the ANOVA, the variability of the resistance between provenances in both drought and frost years was low (Fig. 4). In contrast, we found differences in the resistance between sites, traits, and extreme events (drought and frost). TRW showed the overall lowest resistance to drought and frost and frost resistance was significantly different to drought resistance in Waechtersbach and Waldsieversdorf. The resistance of MVA, MaxVA, and VNo showed a similar trend between Dunkelsdorf and Waldsieversdorf, with lower resistance to frost for all traits. In Waechtersbach, the response of MVA was slightly higher during the frost year, while differences between drought and frost years were absent for MaxVA and VNo. The resistance of VD and RCTA was completely different between all sites with contradictory responses between

Dunkelsdorf (higher resistance to drought) and Waechtersbach (higher resistance to frost), while the response between extremes was not distinguishable in Waldsieversdorf. At this site, we observed the highest resistance for both traits.

According to the ANOVA, vessel diameter varied significantly between provenances ($p < 0.001$) and sites ($p < 0.001$; cf. Table S2) and provenances revealed a high plasticity in vessel diameter, even between sites (Fig. S4). To investigate the trade-off between resistance to extreme events and vessel size, we plotted the resistance of TRW in the extreme drought and frost year, respectively, against the mean vessel diameter per provenance and site (Fig. 5). The relationship between the two parameters was not correlated during the drought year at all sites, and the variability in resistance between provenances was low. On the other hand, we observed a significant positive relationship between frost resistance and vessel diameter in Dunkelsdorf, i.e. provenances with a higher mean vessel diameter showed higher resistance to frost. In Waldsieversdorf, no significant relationship was found.



Fig. 3 Bootstrapped correlations between vessel traits and daily precipitation sum. For detailed description of the figure, please refer to Fig. 2

Table 2 Results of the ANOVA using the resistance to extreme events as response

	<i>p</i> value	Expl. variance [%]
Vessel trait	< 0.001	64.4
Extreme event	< 0.001	2.2
Provenance	0.872	0.4
Site	< 0.001	2.5
Extreme event × provenance	0.716	0.6
Site × provenance	0.555	1.5
Residual		28.4

Bold *p* values indicate significant differences between the tested effects

Discussion

Plasticity of vessel traits

Differences in vessel traits were present among all sites (Fig. 1), highlighting the dependence of the respective environmental conditions on vessel formation (e.g.

Abrantes et al. 2013). This is supported by the findings of the ANOVA (Table S2), indicating significant differences between provenances in vessel size-related traits. One explanation might be the relationship between vessel size and tree height, as taller individuals were associated with larger vessel size according to the tapering ratio (Rosell et al. 2017; Olson et al. 2018; Fajardo et al. 2020). Therefore, it cannot be dismissed out of hand that differences in the individual height have implications on vessel trait variation, although differences in height appear to be small (i.e. 1.2 m between Dunkelsdorf and Waldsiefersdorf). Thereby, it is unexpected that despite the larger TRW in Dunkelsdorf (and taller individuals), MVA as indirect proxy for hydraulic conductivity was significantly larger in the dry environment (Waldsiefersdorf) with overall smaller individuals (cf. Figure 1). For red oak as ring-porous species, this may be related to the dependence of hydraulic conductivity on VNo rather than on vessel size, since a larger TRW results in a higher formation of wide and narrow vessels (Buttó et al. 2021). The advantages of wide and narrow vessels are a simultaneously high hydraulic efficiency and safety to embolism, respectively (Kitin and Funada 2016). Therefore, individuals in Dunkelsdorf, who are characterized by a large TRW and high

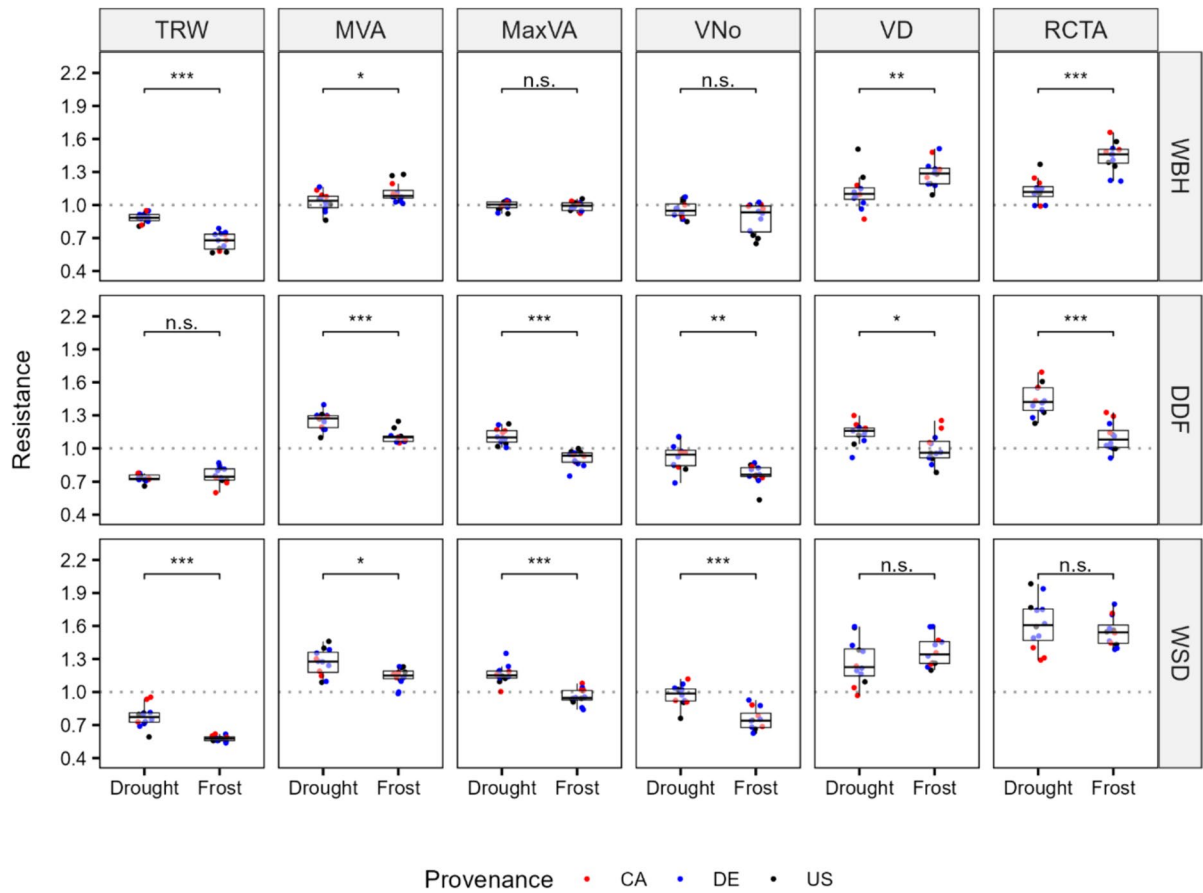
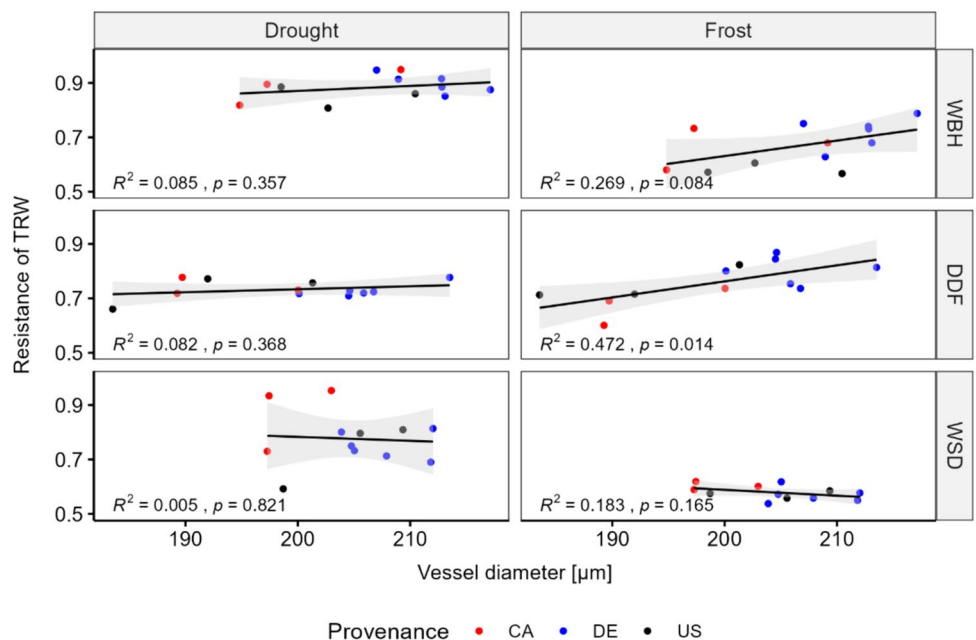


Fig. 4 Boxplots of resistance of vessel traits for one drought and one frost year. Sites are ordered along the precipitation gradient from wet (WBH) to dry (WSD) and provenances are colored according to their origin (CA = Canada, DE = Germany, US = United States). Significant

site-specific differences between the response to drought and frost are determined by the Wilcoxon test (n.s. not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

Fig. 5 Relationship between resistance of TRW and vessel diameter [μm] in one extreme drought (left) and frost year (right) per site (rows), respectively. Each point represents one provenance (mean of eight trees) colored according to their origin (CA = Canada, DE = Germany, US = United States)



VNo, indicate a different adaptive behavior under favorable environments, while MVA seems to increase under dry environmental conditions. However, these findings accentuate the high phenotypically plastic response in vessel traits to the site-specific climate variability. Together with the absence of the provenance \times site interactions for all studied vessel traits, the assumption of weak signals for local adaptation is supported, which is in line with similar studies on red oak (Leites et al. 2019; Leites and Benito Garzón 2023) and European beech (Gárate-Escamilla et al. 2019). In conclusion, the plasticity may be a result of the site-specific phenotypic differentiation between and within provenances, presumably due to natural selective processes that have taken place, shaping the adaptive capacity of provenances to local climate.

Furthermore, the significant differences in vessel size between provenances suggest that these are under some degree of genetic control, which, for example, may partly explain differences in MaxVA between introduced and North American provenances at humid sites (Table S1). Previous studies analyzing the genetic differentiation in vessel traits of provenances of European oak species revealed no genetic differentiation in xylem-related traits, while a stronger genetic control of leaf development could be observed (Torres-Ruiz et al. 2019; George et al. 2020). On the other hand, the analysis of beech provenances revealed differences in vessel traits and the hydraulic system between provenances, manifesting in a more efficient water transport during a drought event (Eilmann et al. 2014). Although these species have distinct vessel characteristics, the results highlight the further need of research to better understand the underlying genetic mechanisms of vessel traits. The extent to what vessel traits is genetically controlled in red oak cannot be finally answered, since comparable studies are not available. However, variation in vessel traits was observed at both sites with higher water availability. At these sites, differences between North American and introduced provenances were apparent, pointing to a variation in TRW as a more comprehensible explanation (Kormann et al. 2024).

Environmental influence on vessel formation

The relationships with climate indicate differences in the climate sensitivity between traits (Figs. 2 and 3). We observed a high climatic signal in VD and RCTA at all sites, indicating a high climatic sensitivity of these traits (Oladi et al. 2014). In contrast, the weak response of MVA, MaxVA, and VNo suggest that these traits are less susceptible to climate variability and not limited by maximum temperature or precipitation, at least in the studied environments. This could be linked to the high climatic tolerance of red oak (Duveneck et al. 2014; Nicolescu et al. 2020) or to the optimal environmental growing condition, in fact climate sensitivity may

vary geographically (i.e. Matfás et al. 2017). Accordingly, the correlations between daily climate variables and vessel traits indicated a different response between traits along the environmental gradient. Again, there was a strong differentiation in the sensitivity between the sites on an intra-annual level. In general, the results indicate climatic dependencies of vessel traits during two physiologically essential phases for vessel formation: first, the storage of nutrients and carbohydrates at the end of the previous-year growing season, and second, the onset of vessel formation (cell division) in spring of the current-year, which was also observed in previous studies (e.g. Fonti and García-González 2004). The importance between climate and the identified periods on vessel formation could be proved for red oak growing in the natural distribution, indicating water scarcity in the early growing season as main limiting factor hampering vessel formation (Tardif and Conciatori 2006; Kormann et al. 2024). Following, a strong temporal variability in the climate sensitivity between sites was apparent, which may be related to differences in leaf phenology and the onset of vessel formation between the sites as well as between provenances, as northern red oak provenances (Canada) showed an earlier bud break compared to those from the south (Kriebel et al. 1976; Lindback et al. 2023). The influence of the previous-year conditions was predominant at both sites with higher water availability, while this relationship was absent at the continental site, indicating a higher reactivity and dependency of short-term weather conditions on vessel formation.

Besides these relationships, the negative association with precipitation in summer (June and July) in Dunkelsdorf and Waldsiedersdorf indicates a variable response between sites and highlights different strategies of provenances to cope with environmental variability. In Waechtersbach, this observation was reversed, suggesting a positive effect of precipitation on vessel formation during this period under high water availability. These may reflect the storage of nutrients and carbohydrates for the vessel formation in the following year (Barbaroux and Bréda 2002), as discussed in the previous paragraph. Studies analyzing red oak in the natural distribution and in the introduced range found comparable patterns in the climate sensitivity (Tardif and Conciatori 2006; Matisons et al. 2015).

Different strategies to cope with extreme events

The examination of wood anatomical characteristics at species, and even closer at provenance level, provides essential insights to evaluate their adaptability to retrospective climate extremes (Chave et al. 2009; Olson et al. 2018). The results revealed site-specific differences in the resistance of vessel traits to a drought and late frost event (Fig. 4), revealing no provenance differentiation (Table 2). However, the response of provenances to drought or frost differed significantly

between sites and we observed an overall higher resistance of vessel traits in the drought year. Generally, the high resistance indices of vessel traits are difficult for interpretation compared to TRW, since the formation of vessels is mainly affected by years prior to the respective extreme event. Yet, the high resistance in the drought and frost year indicate an adjustment in vessel formation (e.g. higher VD and RCTA) to cope with the extreme conditions (e.g. Fonti et al. 2013). The site-specific differences in the response of vessel traits to extreme events may be related to the prevailing environmental conditions and further factors affecting the respective extreme event (duration, timing, severity) and consequently the susceptibility of the respective trait.

The vulnerability during extreme events is considered to increase proportional with vessel diameter (Baas et al. 2004), and thus, wider vessels tend to be more susceptible to drought- or frost-induced cavitation (Hacke and Sperry 2001; Wheeler et al. 2005; Sperry et al. 2008). The resistance to cavitation is described as an essential adaptive trait to assess the climate suitability of trees (Fonti et al. 2013; Hacke et al. 2017). To investigate whether provenances with wider vessels may have lower drought or frost hardiness, we chose hydraulic vessel diameter as a proxy. This trait considers the importance of hydraulic water transport, the vulnerability to drought- or frost-induced embolism, and pathogen spreading (Gleason et al. 2015; Hacke et al. 2017).

The findings indicate the absence of a safety-efficiency trade-off between vessel diameter and resistance to drought (Fig. 5). Here, provenances showed no clear differentiation in drought resistance, whereas variable patterns in vessel diameter were observed. Again, the variation in vessel diameter may be attributed to slight differences in tree size (Anfodillo et al. 2006; Olson et al. 2018) and underlines the phenotypically plastic response of provenances to prevailing environmental conditions (Schreiber et al. 2015). In contrast, we observed a significant relationship between frost resistance and vessel diameter in Dunkelsdorf. Here, introduced provenances show higher frost hardiness and higher vessel diameter, underlining the importance of a high VNo (wide and narrow vessels) associated with a larger TRW, enabling an efficient water transport (Buttó et al. 2021). For the other sites, no significant relationship could be detected (Fig. 5). The overall lowest frost resistance of provenances growing in the dry environment may be related to the higher MVA (Fig. 1), to ensure an efficient hydraulic conductivity. On the other hand, the higher MVA increases the susceptibility to frost embolism, resulting in an impaired water uptake and consequently in higher growth declines (Gleason et al. 2015; Hacke et al. 2017; Olson et al. 2018). While site-specific differences were obvious, no unequivocal differentiation in cavitation resistance was detected on a provenance level, which is comparable to findings for maritime pine (Lamy et al. 2011).

The consideration of vessel diameter for the investigation of the trade-off hypothesis is controversially discussed. While some studies recommend this trait as an informative vessel trait (Gleason et al. 2015; Hacke et al. 2017), other studies plead for a more comprehensive view, because using vessel diameter only as a comparative trait can be misleading. On one hand, the formation of the vessel diameter is subject to a variety of unknowns (e.g. xylem chemistry, cell wall thickness, local temperature or pressure differences), and on the other hand, the relationship of the trade-off at the whole-plant level shows strong variation (e.g. in the xylem between roots and stems or branches) (Lens et al. 2022). Therefore, considering adaptations in pit membranes and other mechanical wood properties provides deeper insight into resistance to air embolism (Lens et al. 2011, 2013), which further complicates the understanding at whole-plant level (Lens et al. 2022). The results presented in this study may serve as an indicator of how provenances respond to environmental conditions in the introduced range. However, there is need for further research including differences in drought- or frost-induced cavitation at the whole tree level, since differences in vessel diameters between trunk, branches and roots may occur (Lens et al. 2022).

Conclusions

Although red oak was introduced in Europe over 300 years ago, the knowledge of how this species responds at wood anatomical level to climate variability and extreme events in the introduced range is scarce. In times of increasing temperatures and altered precipitation regimes, this knowledge can be used to provide the best suited reproductive material for adaptive forest management. The evaluation of different vessel traits as ecological indicators to study adaptability (Campelo et al. 2010), and their association with climate parameters at provenance level is an unprecedented comparison for this species, highlighting a high plasticity of these traits to local environmental conditions. The different trait formation under favorable and dry environments indicates an adaptive behavior to the respective climate (VNo vs. MVA). However, the implications of the different strategies were manifested in the response to an extreme late frost event, being detrimental for individuals with higher MVA according to the safety-efficiency trade-off (Gleason et al. 2015). In contrast to the site-specific variability, provenance differentiation was only detected for vessel size-related traits and under humid conditions. Here, (introduced) provenances with high vessel size show higher frost hardiness, providing opportunities for forest management. The observed high plasticity and associated weak signals of local adaptation reflect the behavior of this species in its natural distribution (Leites et al. 2019; Leites and Benito Garzón 2023),

allowing this species to thrive under different environmental conditions in the introduced range.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00468-024-02557-y>.

Acknowledgements The authors acknowledge the technical staff for the long-term support and measurement of the sites including the data acquisition, which enables studies like this, and the forest enterprises offering and managing the trial sites. Further, they are grateful to Georg von Arx, who helped us to adjust the configuration file for red oak as prerequisite for the analysis with ROXAS. They would also like to thank all those who have contributed to this study, whether in the form of comments or answering questions.

Author contribution statement All authors contributed to the study conception and the design. Sampling was performed by JMK as well as the statistical analysis and visualization. MMT, EM, and LU contributed to the statistical analysis. ML and KJL were responsible for the conceptualization and funding acquisition. EM had the supervision. All authors reviewed the manuscript and approved the final version to be published.

Funding Open Access funding enabled and organized by Projekt DEAL. This study is part of the project “RubraSelect” funded by the German Federal Ministry of Food and Agriculture and the Federal Ministry of the Environment, Nature Conservation, Nuclear Safety and Consumer Protection following a decision of the German Bundestag (Waldklimafonds, Grant No. 2220WK03C4).

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Abrantes J, Campelo F, García-González I, Nabais C (2013) Environmental control of vessel traits in *Quercus ilex* under Mediterranean climate: Relating xylem anatomy to function. *Trees Struct Funct* 27:655–662. <https://doi.org/10.1007/s00468-012-0820-6>
- Anfodillo T, Carraro V, Carrer M et al (2006) Convergent tapering of xylem conduits in different woody species. *New Phytol* 169:279–290. <https://doi.org/10.1111/j.1469-8137.2005.01587.x>
- Baas P, Ewers FW, Davis SD, Wheeler EA (2004) Evolution of xylem physiology. In: Hemsley AR, Poole I (eds) *The evolution of plant physiology*. Elsevier Academic Press, London, pp 273–295
- Barbaroux C, Bréda N (2002) Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. *Tree Physiol* 22:1201–1210. <https://doi.org/10.1093/treephys/22.17.1201>
- Beguéría S, Vicente-Serrano SM (2023) SPEI: calculation of the standardized precipitation-Evapotranspiration Index
- Bunn AG (2008) A dendrochronology program library in R (dplR). *Dendrochronologia* 26:115–124. <https://doi.org/10.1016/j.dendro.2008.01.002>
- Bunn AG (2010) Statistical and visual crossdating in R using the dplR library. *Dendrochronologia* 28:251–258. <https://doi.org/10.1016/j.dendro.2009.12.001>
- Buttó V, Millan M, Rossi S, Delagrange S (2021) Contrasting carbon allocation strategies of ring-porous and diffuse-porous species converge toward similar growth responses to drought. *Front Plant Sci* 12:1–14. <https://doi.org/10.3389/fpls.2021.760859>
- Campelo F, Nabais C, Gutiérrez E et al (2010) Vessel features of *Quercus ilex* L. growing under Mediterranean climate have a better climatic signal than tree-ring width. *Trees Struct Funct* 24:463–470. <https://doi.org/10.1007/s00468-010-0414-0>
- Carrer M, Unterholzner L, Castagneri D (2018) Wood anatomical traits highlight complex temperature influence on *Pinus cembra* at high elevation in the Eastern Alps. *Int J Biometeorol* 62:1745–1753. <https://doi.org/10.1007/s00484-018-1577-4>
- Carrer M, Von Arx G, Castagneri D, Petit G (2015) Distilling allometric and environmental information from time series of conduit size: the standardization issue and its relationship to tree hydraulic architecture. *Tree Physiol* 35:27–33. <https://doi.org/10.1093/treephys/tpu108>
- Castagneri D, Regev L, Boaretto E, Carrer M (2017) Xylem anatomical traits reveal different strategies of two Mediterranean oaks to cope with drought and warming. *Environ Exp Bot* 133:128–138. <https://doi.org/10.1016/j.envexpbot.2016.10.009>
- Chave J, Coomes D, Jansen S et al (2009) Towards a worldwide wood economics spectrum. *Ecol Lett* 12:351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>
- Cook ER, Kairiukstis LA (1990) *Methods of dendrochronology*. Springer, Dordrecht
- Cornes RC, van der Schrier G, van den Besselaar EJM, Jones PD (2018) An ensemble version of the E-OBS temperature and precipitation data sets. *J Geophys Res Atmos* 123:9391–9409. <https://doi.org/10.1029/2017JD028200>
- Duveneck MJ, Scheller RM, White MA (2014) Effects of alternative forest management on biomass and species diversity in the face of climate change in the northern Great Lakes region (USA). *Can J for Res* 44:700–710. <https://doi.org/10.1139/cjfr-2013-0391>
- Eilmann B, Sterck F, Wegner L et al (2014) Wood structural differences between northern and southern beech provenances growing at a moderate site. *Tree Physiol* 34:882–893. <https://doi.org/10.1093/treephys/tpu069>
- Fajardo A, Martínez-Pérez C, Cervantes-Alcayde MA, Olson ME (2020) Stem length, not climate, controls vessel diameter in two trees species across a sharp precipitation gradient. *New Phytol* 225:2347–2355. <https://doi.org/10.1111/nph.16287>
- Fonti P, García-González I (2004) Suitability of chestnut earlywood vessel chronologies for ecological studies. *New Phytol* 163:77–86. <https://doi.org/10.1111/j.1469-8137.2004.01089.x>
- Fonti P, Heller O, Cherubini P et al (2013) Wood anatomical responses of oak saplings exposed to air warming and soil drought. *Plant Biol* 15:210–219. <https://doi.org/10.1111/j.1438-8677.2012.00599.x>
- Fonti P, Von Arx G, García-González I et al (2010) Studying global change through investigation of the plastic responses of xylem

- anatomy in tree rings. *New Phytol* 185:42–53. <https://doi.org/10.1111/j.1469-8137.2009.03030.x>
- Gárate-Escamilla H, Hampe A, Vizcaíno-Palomar N et al (2019) Range-wide variation in local adaptation and phenotypic plasticity of fitness-related traits in *Fagus sylvatica* and their implications under climate change. *Glob Ecol Biogeogr* 28:1336–1350. <https://doi.org/10.1111/geb.12936>
- García-González I, Souto-Herrero M, Campelo F (2016) Ring-porosity and earlywood vessels: a review on extracting environmental information through time. *IAWA J* 37:295–314. <https://doi.org/10.1163/22941932-20160135>
- Gärtner H, Nievergelt D (2010) The core-microtome: a new tool for surface preparation on cores and time series analysis of varying cell parameters. *Dendrochronologia* 28:85–92. <https://doi.org/10.1016/j.dendro.2009.09.002>
- George JP, Theroux-Rancourt G, Rungwattana K et al (2020) Assessing adaptive and plastic responses in growth and functional traits in a 10-year-old common garden experiment with pedunculate oak (*Quercus robur* L.) suggests that directional selection can drive climatic adaptation. *Evol Appl* 13:2422–2438. <https://doi.org/10.1111/eva.13034>
- Giagli K, Gričar J, Vavričik H et al (2016) The effects of drought and wood formation in *Fagus sylvatica* during two contrasting years. *IAWA J* 37:332–348. <https://doi.org/10.1163/22941932-20160137>
- Gleason SM, Westoby M, Jansen S et al (2015) Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytol* 209:123–136. <https://doi.org/10.1111/nph.13646>
- González-González BD, Rozas V, García-González I (2014) Earlywood vessels of the sub-Mediterranean oak *Quercus pyrenaica* have greater plasticity and sensitivity than those of the temperate *Q. petraea* at the Atlantic-Mediterranean boundary. *Trees - Struct Funct* 28:237–252. <https://doi.org/10.1007/s00468-013-0945-2>
- Hacke UG, Sperry JS (2001) Functional and ecological xylem anatomy. *Perspect Plant Ecol Evol Syst* 4:97–115. <https://doi.org/10.1078/1433-8319-00017>
- Hacke UG, Spicer R, Schreiber SG, Plavcová L (2017) An ecophysiological and developmental perspective on variation in vessel diameter. *Plant Cell Environ* 40:831–845. <https://doi.org/10.1111/pce.12777>
- Jevšenak J (2020) New features in the dendroTools R package: Bootstrapped and partial correlation coefficients for monthly and daily climate data. *Dendrochronologia*. <https://doi.org/10.1016/j.dendro.2020.125753>
- Jevšenak J, Levanič T (2018) dendroTools: R package for studying linear and nonlinear responses between tree-rings and daily environmental data. *Dendrochronologia* 48:32–39. <https://doi.org/10.1016/j.dendro.2018.01.005>
- Jump AS, Ruiz-Benito P, Greenwood S et al (2017) Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. *Glob Chang Biol* 23:3742–3757. <https://doi.org/10.1111/gcb.13636>
- Kitin P, Funada R (2016) Earlywood vessels in ring-porous trees become functional for water transport after bud burst and before the maturation of the current-year leaves. *IAWA J* 37:315–331. <https://doi.org/10.1163/22941932-20160136>
- Kormann JM, Liesebach M, Liepe KJ (2023) Provenances from introduced stands of Northern Red Oak (*Quercus rubra* L.) outperform those from the natural distribution. *For Ecol Manage* 531:1–8. <https://doi.org/10.1016/j.foreco.2023.120803>
- Kormann JM, van der Maaten E, Liesebach M et al (2024) High risk, high gain? Trade-offs between growth and resistance to extreme events differ in northern red oak (*Quercus rubra* L.). *Front Plant Sci* 15:1–14. <https://doi.org/10.3389/fpls.2024.1374498>
- Kriebel H, Bagley W, Deneke F et al (1976) Geographic Variation in *Quercus rubra* in North Central. *Silva Genet* 25:118–122
- Lamichhane JR (2021) Rising risks of late-spring frosts in a changing climate. *Nat Clim Chang* 11:554–555. <https://doi.org/10.1038/s41558-021-01090-x>
- Lamy JB, Bouffier L, Burlett R et al (2011) Uniform selection as a primary force reducing population genetic differentiation of cavitation resistance across a species range. *PLoS ONE*. <https://doi.org/10.1371/journal.pone.0023476>
- Leites L, Benito Garzón M (2023) Forest tree species adaptation to climate across biomes: Building on the legacy of ecological genetics to anticipate responses to climate change. *Glob Chang Biol* 29:4711–4730. <https://doi.org/10.1111/gcb.16711>
- Leites LP, Rehfeldt GE, Steiner KC (2019) Adaptation to climate in five eastern North America broadleaf deciduous species: growth clines and evidence of the growth-cold tolerance trade-off. *Perspect Plant Ecol Evol Syst* 37:64–72. <https://doi.org/10.1016/j.ppees.2019.02.002>
- Lens F, Gleason SM, Bortolami G et al (2022) Functional xylem characteristics associated with drought-induced embolism in angiosperms. *New Phytol*. <https://doi.org/10.1111/nph.18447>
- Lens F, Sperry JS, Christman MA et al (2011) Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus *Acer*. *New Phytol* 190:709–723. <https://doi.org/10.1111/j.1469-8137.2010.03518.x>
- Lens F, Tixier A, Cochard H et al (2013) Embolism resistance as a key mechanism to understand adaptive plant strategies. *Curr Opin Plant Biol* 16:287–292. <https://doi.org/10.1016/j.pbi.2013.02.005>
- Levanič TOM (2007) Research report ATRICS - A new system for image acquisition in dendrochronology. *Tree-Ring Res* 63:117–122. <https://doi.org/10.3959/1536-1098-63.2.117>
- Lindback EC, Rauschendorfer JK, Burton AJ et al (2023) Common garden study reveals frost-tolerant northern seed sources are best suited to expand range of *Quercus rubra*. *For Ecol Manage* 539:120985. <https://doi.org/10.1016/j.foreco.2023.120985>
- Lloret F, Keeling EG, Sala A (2011) Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 120:1909–1920. <https://doi.org/10.1111/j.1600-0706.2011.19372.x>
- Ma Q, Huang JG, Hänninen H, Berninger F (2019) Divergent trends in the risk of spring frost damage to trees in Europe with recent warming. *Glob Chang Biol* 25:351–360. <https://doi.org/10.1111/gcb.14479>
- Matías L, Linares JC, Sánchez-Miranda Á, Jump AS (2017) Contrasting growth forecasts across the geographical range of Scots pine due to altitudinal and latitudinal differences in climatic sensitivity. *Glob Chang Biol* 23:4106–4116. <https://doi.org/10.1111/gcb.13627>
- Matisons R, Jansons J, Katrevičs J, Jansons Ā (2015) Relation of tree-ring width and earlywood vessel size of alien *Quercus rubra* L. With climatic factors in Latvia. *Silva Fenn* 49:1–14. <https://doi.org/10.14214/sf.1391>
- McKee TB, Doesken NJ, Kleist J (1993) The relationship of drought frequency and duration to time scales. American Meteorological Society, Anaheim, California
- Nabais C, Hansen JK, David-Schwartz R et al (2018) The effect of climate on wood density: what provenance trials tell us? *For Ecol Manage* 408:148–156. <https://doi.org/10.1016/j.foreco.2017.10.040>
- Nicolescu VN, Vor T, Mason WL et al (2020) Ecology and management of northern red oak (*Quercus rubra* L. syn. *Q. borealis* F. Michx.) in Europe: a review. *Forestry* 15:481–494. <https://doi.org/10.1093/forestry/cpy032>
- Nola P, Bracco F, Assini S et al (2020) Xylem anatomy of *Robinia pseudoacacia* L. and *Quercus robur* L. is differently affected by

- climate in a temperate alluvial forest. *Ann for Sci* 77:1–16. <https://doi.org/10.1007/s13595-019-0906-z>
- Oladi R, Bräuning A, Pourtahmasi K (2014) “Plastic” and “static” behavior of vessel-anatomical features in Oriental beech (*Fagus orientalis* Lipsky) in view of xylem hydraulic conductivity. *Trees Struct Funct* 28:493–502. <https://doi.org/10.1007/s00468-013-0966-x>
- Olson ME, Soriano D, Rosell JA et al (2018) Plant height and hydraulic vulnerability to drought and cold. *Proc Natl Acad Sci U S A* 115:7551–7556. <https://doi.org/10.1073/pnas.1721728115>
- R Core Team (2023) A language and environment for statistical computing
- Rosell JA, Olson ME, Anfodillo T (2017) Scaling of xylem vessel diameter with plant size: causes, predictions, and outstanding questions. *Curr for Reports* 3:46–59. <https://doi.org/10.1007/s40725-017-0049-0>
- Schreiber SG, Hacke UG, Hamann A (2015) Variation of xylem vessel diameters across a climate gradient: Insight from a reciprocal transplant experiment with a widespread boreal tree. *Funct Ecol* 29:1392–1401. <https://doi.org/10.1111/1365-2435.12455>
- Sperry JS (2003) Evolution of water transport and xylem structure. *Int J Plant Sci* 164:115–127. <https://doi.org/10.1086/368398>
- Sperry JS, Meinzer FC, McCulloh KA (2008) Safety and efficiency conflicts in hydraulic architecture: scaling from tissues to trees. *Plant Cell Environ* 31:632–645. <https://doi.org/10.1111/j.1365-3040.2007.01765.x>
- Tardif JC, Conciatori F (2006) Influence of climate on tree rings and vessel features in red oak and white oak growing near their northern distribution limit, southwestern Quebec, Canada. *Can J for Res* 36:2317–2330. <https://doi.org/10.1139/X06-133>
- Torres-Ruiz JM, Kremer A, Carins Murphy MR et al (2019) Genetic differentiation in functional traits among European sessile oak populations. *Tree Physiol* 39:1736–1749. <https://doi.org/10.1093/treephys/tpz090>
- Tyree MT, Zimmermann MH (2002) Xylem structure and the ascent of sap, 2nd edn. Springer, Berlin Heidelberg, Heidelberg
- van der Maaten E, Pape J, van der Maaten-Theunissen M et al (2018) Distinct growth phenology but similar daily stem dynamics in three co-occurring broadleaved tree species. *Tree Physiol* 38:1820–1828. <https://doi.org/10.1093/treephys/tpy042>
- Vicente-Serrano SM, Beguería S, López-Moreno JI (2010) A multi-scalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *J Clim* 23:1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>
- Vitasse Y, Lenz A, Körner C (2014) The interaction between freezing tolerance and phenology in temperate deciduous trees. *Front Plant Sci* 5:1–12. <https://doi.org/10.3389/fpls.2014.00541>
- von Arx G, Carrer M (2014) Roxas -A new tool to build centuries-long tracheid-lumen chronologies in conifers. *Dendrochronologia* 32:290–293. <https://doi.org/10.1016/j.dendro.2013.12.001>
- Wessely J, Essl F, Fiedler K et al (2024) A climate-induced tree species bottleneck for forest management in Europe. *Nat Ecol Evol*. <https://doi.org/10.1038/s41559-024-02406-8>
- Wheeler JK, Sperry JS, Hacke UG, Hoang N (2005) Inter-vessel pitting and cavitation in woody Rosaceae and other vesselless. *Plant Cell Environ* 28:800–812

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.