



Xylem Functional Traits as Indicators of Health in Mediterranean Forests

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Abstract

Purpose of Review We conducted a literature survey and meta-analysis to assess, in Mediterranean forests impacted by drought, the role of xylem functional traits as indicators of tree health, and their potential to adjust over a range of climatic conditions to support tree performance and survival. We aimed also to depict the geographic variability of xylem functional traits among Mediterranean forest trees as a tool for regional scale-oriented vulnerability assessment.

Recent Findings Associations were investigated among xylem functional traits, hydraulic safety, and whole plant drought resistance for tree species in Mediterranean-type climates. Variable data were available from a number of study cases of Mediterranean forest communities impacted by intense drought, wherein tree growth and xylem functional traits were investigated along with tree decline and dieback episodes. Variable data were available from a number of studies that analyzed xylem trait adjustments to climatic conditions at different temporal scales.

Summary We observed differing growth patterns and xylem conduit area responses in healthy and unhealthy trees and we sketched hydraulic strategies that may fit observed patterns. Overall, a clear role of xylem conduit size as stand-alone tree health indicator did not emerge. We showed that xylem traits may adjust along different temporal scales and may support the performance and health of Mediterranean tree species over a range of climatic conditions. We outlined substantial geographic variability in xylem traits across the Mediterranean region, suggesting patchy responses to increasing drought. Knowledge gaps and needed lines of research are highlighted.

Keywords Wood anatomy · Conduit area · Conduit density · Drought · Tree mortality

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Introduction

Xylem is a specialized plant tissue that provides mechanical support and water transport from roots to leaves, in order to keep the stomata open and enable photosynthetic CO₂ uptake. Zimmermann's [1] seminal book introduced a new way of looking at xylem anatomy and the intricate network of xylem conduits in the plant vascular system. Xylem functional traits—including conduit size, length, density, spatial arrangement and connectivity, inter-conduit pit properties, ray parenchyma cells—and the segmented plant hydraulic architecture [2] are now considered crucial factors in the modeling of plant water fluxes under fluctuating environmental conditions [3].

In recent years, the health of forest communities has been observed to be frequently harmed by the occurrence of prolonged and intense drought events, which are causing tree decline and mortality due to impaired plant hydraulics and related reductions in carbon assimilation and plant defenses against insect attacks [4, 5]. The Mediterranean region is a

major climate change hotspot likely to exhibit increasingly dry conditions caused by heat and drought waves, which are expected to make forest areas increasingly vulnerable to future climatic conditions [6, 7].

The response of forest tree species to drought is a complex process involving the coordination of multiple physiological mechanisms, as well as substantial long-term structural plasticity [8–10]. Predicting tree death or, alternatively, tree health and survival from the occurrence of drought is challenging since several physiological interactions are at stake, and drought climatic sequences will translate into tree and forest mortality only when physiological tipping points are exceeded [11, 12]. Nonetheless, plant hydraulic system failure may be a convergent mechanism underlying much of the observed vulnerability of trees to drought and reported drought-induced tree mortality [13–15].

Ultimately, hydraulic failure results from an imbalance between plant transpiration and water uptake as a drought period progresses, which causes the pressure in the xylem to become increasingly negative. When xylem pressure drops below a critical threshold, gas bubbles form in xylem conduits in a process called cavitation, and then spread throughout the vascular system in a process (embolism) which blocks xylem water transport, isolating leaves from the soil water source [16]. The vulnerability of xylem conduits to cavitation is largely under the control of the porosity of the inter-conduit membrane, on which the entering of gas bubbles into conduits (the so-called air-seeding process) depends [17]. Xylem functional traits affect the amount and rate of embolism that spreads through the vessel network, and thereby affect water supply impairment to leaves, which can result in crown die-back and tree mortality. Xylem anatomy in the context of whole-tree hydraulic physiology, hydraulic breakdown, and tree mortality mechanisms were the subject of an in-depth review few years ago [18] and will not be addressed here.

Tree species' differential responses to drought may be explored in terms of differences in xylem functional traits and related hydraulic architecture. For a review on hydraulic-related xylem features with respect to woody species' global ecology, the reader is referred to Gleason et al. [19]. Recently, xylem traits were considered as potential functional proxies of hydraulic safety margins, tree drought susceptibility, and as tools for interpreting wide-scale patterns of drought-induced tree mortality risk [20–22]. Quantitative knowledge regarding the intra- and inter-specific diversity in xylem functional traits and their plasticity has been highlighted as requisite information for predicting tree population dynamics and climate change-driven changes in community composition [23]. Xylem traits were also worthy of consideration in the selection of native tree species better adapted to environmental stress conditions for restoration purposes [24].

For the present review, we have focused on xylem functional traits in Mediterranean forests. We conducted a

literature survey and a subsequent meta-analysis aimed at addressing the following topics and research gaps: recent experimental evidence on how xylem functional traits are linked with xylem vulnerability to embolism and drought resistance in Mediterranean tree species; the potential of xylem functional traits to serve as indicators of tree health, performance, and survival in drought-impacted Mediterranean forests; and the potential of xylem functional traits to acclimate throughout an individual tree's life, including plastic responses that may reflect an improved trade-off between xylem safety and efficiency under modified environmental conditions. Finally, a spatial analysis was performed with existing datasets of xylem traits and tree species occurrence to describe Mediterranean forests on a geographical scale based on xylem attributes as a tool for regional-focused vulnerability assessment.

Xylem Functional Traits and Drought Resistance: Evidences for Mediterranean Tree Species

The effectiveness of xylem in conducting water largely depends on its capacity to maximize water transport to leaves while withstanding cavitation and limiting embolism spreading. The hydraulic conductivity of conduits increases with the fourth power of conduit diameter, as represented in the Hagen-Poiseuille laminar flow formulation. However, wider conduits are generally considered to be at elevated cavitation and embolism risk, with the caveat that conduit area is not a good proxy for conduit volume in all circumstances [25, 26]. Plant hydraulic efficiency may rely on structural compensations; for instance, conduit clustering may counterbalance conduit embolism vulnerability and may also be affected by the temporal dynamics of xylem tensions, in that conduit vulnerability to embolism may change across subsequent cycles of drought [11, 27, 28]. Overall, xylem functional traits, plant hydraulic structure, and their plastic adjustments may reflect plant ability to gain a trade-off between xylem efficiency and safety [29].

In recent years, there has been considerable progress in the methods and techniques, including X-ray micro-computed tomography, for determining xylem anatomical traits and assessing xylem vulnerability to embolism [18]. Experimental evidences from last-year studies on the various links between xylem functional traits, hydraulic safety, and whole plant drought resistance for tree species living in a Mediterranean-type climate are summarized here briefly. An inverse relationship between conduit size and xylem safety (frequently assessed as the xylem water potential that leads to a 50% loss in hydraulic conductivity) has been observed, despite the difficulty of assessing the vulnerability to cavitation of wide and long vessels; positive effects of inter-vessel hydraulic bridges and increased conduit wall strength on xylem safety were also suggested [30, 31]. In-depth review in genus *Quercus* showed that ring-porous xylem of deciduous

tree species has higher hydraulic conductivity; however, it is at higher risk of cavitation compared to diffuse-porous xylem of evergreen tree species [32]. The importance of pit anatomical features (pit aperture size and torus shape) on embolism resistance was also highlighted [36]. However, a tradeoff between hydraulic efficiency and safety was not evidenced in several circumstances [30, 33, 108]. On the other hand, Mediterranean trees may have alternative mechanisms, beyond increasing embolism resistance, to efficiently couple with seasonal changes in soil water availability: for instance, an effective strategy for ring-porous tree species may involve large earlywood vessels, since the advantages associated with an efficient hydraulic pathway during favorable periods might outweigh xylem failure risk during the drought-prone season [108]. Notably, a re-assessment of the vulnerability to drought of long-conduit ring-porous species revealed unexpected levels of embolism resistance, although this result may have been affected by the optical method used to construct vulnerability curves [34]. In Mediterranean shrub-like species, lower xylem vessel area appeared not to provide cavitation resistance, whereas the low conduction efficiency of small vessels was found to be detrimental to recruitment success and competition in some cases [33]. Roots may be the site for relevant xeromorphic adjustments involving different xylem traits like increased vessel number, decreased vessel size, and thinner cell walls that may co-optimize plant water uptake and survival [35]. Observed intra-species differences and geographic patterns in xylem traits suggest that there may be potential for the exploitation of population differences in forest management and breeding programs: in particular, genotype-environment interactions need to be considered with respect to different plant drought resistance strategies across different environmental sites and cultivation conditions [36–38].

The results outlined above are far to provide a coherent description of Mediterranean trees strategy to withstand drought. However, they provide evidence that avoidance of runaway embolism is indeed an important component of drought tolerance in trees and that xylem functional traits are worthy of being explored as predictors of drought-driven tree decline and dieback in Mediterranean forests.

Xylem Functional Traits and Growth Patterns in Healthy and Unhealthy Trees in Drought-Impacted Mediterranean Forests: Literature Survey and Meta-analysis

In the last decades, a number of monitoring and descriptive studies of Mediterranean forest communities impacted by intense droughts and showing tree decline and dieback episodes have been conducted. Based on a literature survey and subsequent meta-analysis of available data, we are here challenging the hypothesis that xylem functional traits can be used as indicators of tree health and survival.

First, we searched the Web of Science database (with different combinations of “Forest, Tree, Mediterranean, Decline, Xylem, Anatomy” as search key-words) for primary research article that have documented forest decline events and explored xylem anatomical traits and tree growth. To refine our search, we checked the literature cited in each article and exploited personal information. Specifically, we sought studies which have developed xylem traits and tree growth chronologies for contrasting populations of trees, i.e., trees showing symptoms of decline or in the process of dying (unhealthy trees, U-trees) versus trees that were able to remain healthy without symptoms of decline (healthy trees, H-trees). As signs of decline, we have considered a wide set of symptoms associated with loss of tree vigor, including reduced growth, reduction in size and quantity of foliage, yellow foliage chlorosis, death of twigs and branches, and ultimately tree death as a part of the decline syndrome (Table 1). We did not consider cases where symptoms were clearly attributed to a single biotic agent, as an insect attack. For our search, sites beyond the strict confines of the Mediterranean eco-region were included if the investigated tree species’ ranges extend to Mediterranean sites; sub-Mediterranean and Mediterranean mountain sites were included. In the end, a total of 22 study cases published between 2004 and November 2019 were selected (Fig. 1), including semi-natural forests, artificial stands, and peri-urban forests. The study cases differed in many aspects: tree species under observation, decline symptoms, site characteristics, management history, experimental conditions, traits investigated, observation and measurement time-spans, explanatory mechanisms for observed tree mortality, or declining phenomena. In several cases, non-replicated or pseudo-replicated experiments were reported. The characteristics of U-trees and H-trees in each selected study are reported in Table S1.

Qualitatively, the results were highly variable with large differences among species and sites, and the observations were not easily constrained to a coherent picture (Table 1). Therefore, a meta-analysis of available growth (tree ring width or basal area increment) and xylem trait data was performed to obtain a quantitative assessment of patterns reported at the selected study sites. Toward this aim, the data were digitized manually, if available in tabular form, or extracted from graphs with a digitizing software (Un-Scan-It 5.0, Silk Scientific, Orem, UT), avoiding interpolations. Juvenile data were excluded and values from 1950 onward were considered in long-term chronologies. Based on descriptions in original articles and inspection of reported patterns, within each chronology, we considered a pre-decline period (20–30 years before the onset of decline symptoms in U-trees) and the period after the onset of tree decline.

Table 1 Selected study cases in which healthy (H-trees: trees that were healthy, without symptoms of decline) and unhealthy trees (U-trees: trees that a certain time showed symptoms of decline and eventually died) were compared in forests impacted mostly by drought. *ID*: site location code (as reported in Fig. 1); *Symptoms*: main symptoms observed in U-trees, as reported in published papers; *Species*: investigated tree species; *Traits*: secondary growth and wood anatomical xylem traits investigated in each study case (*TRW*: tree-ring width, *AC*: conduit area (*ew*: earlywood; *lw*: late-wood); *DHY*, hydraulic diameter; *H*: tree height; *BAI*: basal area

increment. *Diff*: our qualitative estimate of differences between H- and U-trees, based on our personal assessment of results and information reported in the selected papers; with the exception of tree height (*HGH*), the assessment refers to the period before the onset of tree decline; +, ++, +++ indicate the increasing degree to which higher values were apparent in H-trees; -, --, --- indicate the increasing degree to which higher values were apparent in U-trees; = no apparent difference

ID	Symptoms	Species	Trait	Diff	Reference
1	Defoliation, needle/twig drop, microfilia	<i>Pinus halepensis</i>	<i>TRW</i>	=	Bachtobji Bouachir et al. [39]
		<i>Pinus pinea</i>	<i>TRW</i>	=	
2	Defoliation	<i>Abies alba</i>	<i>TRW</i>	+	Bigler [40]
3	Defoliation	<i>Abies alba</i>	<i>BAI</i>	++	Cailleret et al. [41]
4	Defoliation, incidence of pathogens	<i>Abies alba</i>	<i>HGH</i>	+	Camarero et al. [42]
			<i>BAI</i>	++	
		<i>Pinus sylvestris</i>	<i>H</i>	-	
		<i>BAI</i>	+++		
		<i>Pinus halepensis</i>	<i>HGH</i>	+	
5	Defoliation, desiccated shoots/leaves/branches	<i>Quercus faginea</i>	<i>BAI</i>	=/+	Camarero et al. [43]
			<i>HGH</i>	+	
		<i>Quercus ilex</i>	<i>BAI</i>	=/-	
6	Crown transparency defoliation	<i>Quercus frainetto</i>	<i>HGH</i>	+	Colangelo et al. [44]
			<i>BAI</i>	+	
			<i>HGH</i>	++	
			<i>AC ew</i>	-	
7	Shoot dieback, leaf loss, withering, growth decline, high mortality, epicormic shoot formation	<i>Quercus frainetto</i>	<i>AC lw</i>	+	Colangelo et al. [45]
			<i>BAI</i>	=/-	
			<i>AC</i>	+/-	
			<i>BAI</i>	++	
			<i>AC ew</i>	+	
8	Crown transparency, incidence of pathogens	<i>Quercus pubescens</i>	<i>AC lw</i>	+	Colangelo et al. [46]
			<i>BAI</i>	-	
9	Crown dieback and thinning, epicormic shoots, leaf yellowing, incidence of pathogens	<i>Quercus robur</i>	<i>BAI</i>	-	Colangelo et al. [47]
			<i>AC</i>	+	
		<i>Robinia pseudoacacia</i>	<i>HGH</i>	+	
			<i>BAI</i>	++	
10	Rot and canopy dieback, defoliation, incidence of pathogens	<i>Pinus sylvestris</i>	<i>HGH</i>	+	Gea-Izquierdo et al. [48]
			<i>BAI</i>	+/-	
			<i>BAI</i>	++	
11	Defoliation, incidence of pathogens	<i>Pinus pinaster</i>	<i>BAI</i>	+++	Gea-Izquierdo et al. [49]
12	Defoliation	<i>Pinus nigra</i>	<i>TRW</i>	++	Guada et al. (2016)
			<i>TRW</i>	++	
13	Defoliation	<i>Pinus sylvestris</i>	<i>BAI</i>	=/-	Heres et al. [50]
14	Defoliation	<i>Quercus robur</i>	<i>AC</i>	---	Jevsenac and Levanic [51]
15	Defoliation	<i>Quercus robur</i>	<i>AC</i>	--	Levanič et al. [52]
			<i>TRW</i>	--	
			<i>BAI</i>	---	

Table 1 (continued)

ID	Symptoms	Species	Trait	Diff	Reference
			AC	=	
			DHY	+	
11	Defoliation, incidence of pathogens	<i>Pinus pinaster</i>	BAI	+++	Gea-Izquierdo et al. [49]
16	Defoliation	<i>Abies alba</i>	AC	+++	Pellizzari et al. [53]
	Defoliation	<i>Pinus sylvestris</i>	HGH	++	
			AC	=/+	Pellizzari et al. [53]
			HGH	+	
17	Crown defoliation	<i>Pinus nigra</i>	AC	=/+	Petrucchio et al. [61]
		<i>Pinus nigra</i>	TRW	=/-	
18	Defoliation	<i>Quercus cerris</i>	TRW	+	Romagnoli et al. [54]
19	Crown defoliation, chlorosis	<i>Abies alba</i>	BAI	=/-	Sangüesa-Barreda et al. [55]
20	Desiccation, crown dieback	<i>Pinus nigra</i>	AC	=/-	Savi et al. [56]
			TRW	-	
			DHY	-	
21	Defoliation	<i>Quercus cerris</i>	TRW	=/+	Stojanović et al. [57]
		<i>Quercus robur</i>	TRW	-	
22	Crown defoliation	<i>Pinus sylvestris</i>	BAI	---	Voltas et al. [58]

Meta-analyses on the compiled dataset were conducted with the ‘meta’ and ‘metafor’ packages in the R statistical suite [59, 60], where entry data corresponded to the pre-calculated effect size (i.e., the relative mean difference

between H-trees and U-trees, dimensionless) and their standard errors. Subgroup analysis was performed using the subset of studies reporting data for H-trees and U-trees and for earlywood and latewood, separately. We adopted a random-

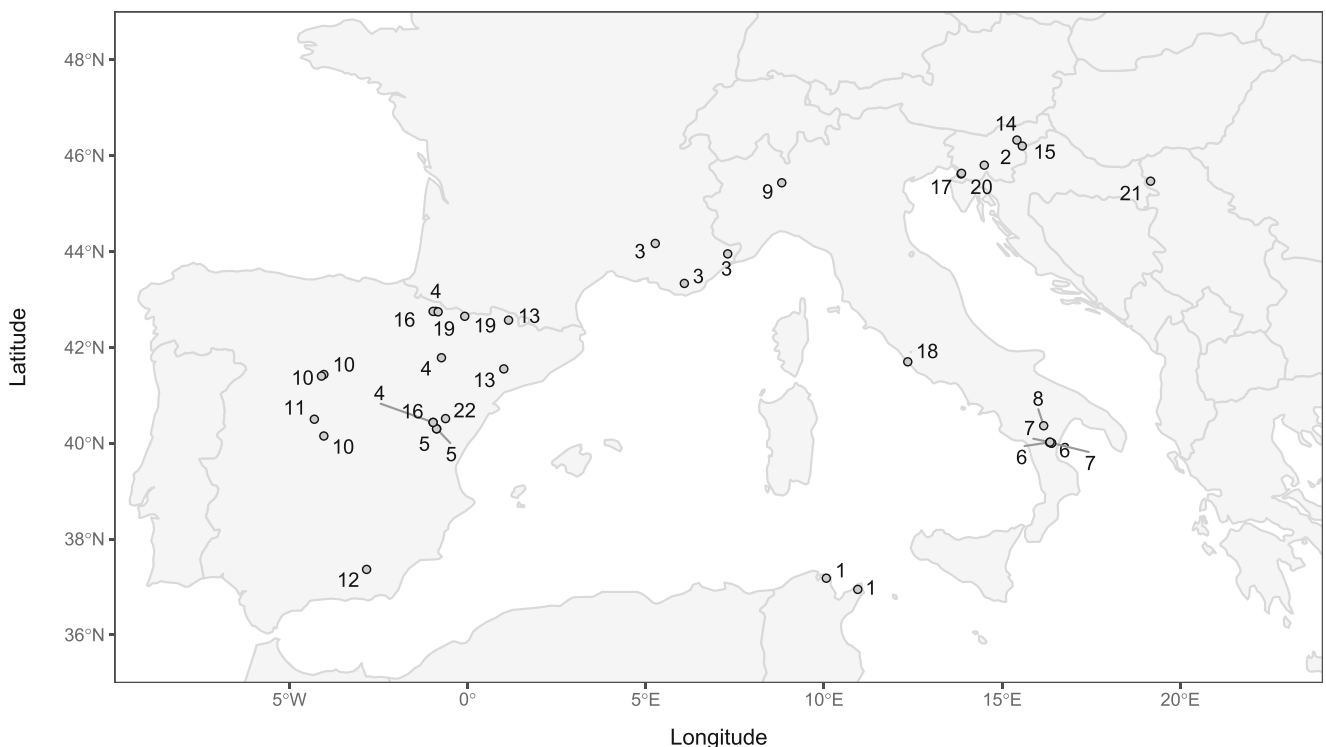


Fig. 1 Geographic distribution of selected case studies with investigated tree species. Numbers in open circles refer to the articles listed in Table 1, from which tree ring width, basal area increment, and xylem trait chronologies were compiled for the present meta-analysis

effects approach in which effect weights are based on within-study and between-study variances. The between-study heterogeneity in effect sizes was assessed using I^2 and Q value statistics while the potential for publication bias was examined by the funnel plot method using Egger's test.

We first examined quantitatively the association between growth rates and tree health status, as assessed in the original articles based on the occurrence of a wide range of declining symptoms (Table 1). In spite of large differences in environmental conditions, intensity and temporal dynamics of symptom progression, a pattern can be recognized wherein U-trees show consistently reduced growth rates (based on tree ring width or basal area increment) with respect to H-trees, as evaluated across the entire tree-ring chronologies (Fig. 2) ([39–41, 49]). Tree ring width was similar in U-trees and H-trees before the onset of drought, whereas lower basal area increments were often recorded in U-trees (Fig. S1). A slowed growth rate in the years preceding drought can then be related to subsequent drought-induced mortality. It is worth noting, however, that time lags between growth reduction and symptoms development were also observed, and higher growth rate in U-trees has been interpreted as an early warning signal of impending drought-induced decline ([42, 52]a, [44, 45]).

The qualitative findings of systematic assessment of xylem functional traits in a handful of selected study cases are summarized in Table 1, whereas the quantitative assessment of differences between H-trees and U-trees in xylem conduit areas measured before the drought-induced tree decline on wood chronologies are shown in the so-called 'forest plot' (Fig. 3). Note that both increased and decreased xylem conduit areas can be observed in U-trees, relative to H-trees. Given the limited availability of data and their variability, contrasting tree strategies can be sketched only speculatively. We may consider a 'low-hydraulics' L-strategy, in cases where U-trees show a reduced growth rate, conduit size, and theoretical hydraulic efficiency compared to H-trees. Tree species growing in harsh environmental conditions may exhibit an excessively conservative L-strategy, wherein low hydraulic efficiency associated with small-sized conduits and a limitation of carbon capture and plant growth may lead to reduced plant water uptake and, eventually, tree decline due to a combination of carbon starvation and hydraulic failure under increased environmental stress. In our dataset, an excessively conservative L-strategy may be attributed to conifer species ([53, 61]); however, similar findings have been reported for oak as well ([44], in case of earlywood vessels). The experimental observations of Bernadier and Clark [62] and Camarero et al. [42] seem compatible with this interpretation, and Gentilesca et al. [63] considered this behavior in declining Mediterranean oaks.

Alternatively, a 'high-hydraulics' H-strategy may be considered in cases where large conduit size, high potential hydraulic conductivity, and high growth rates are found in U-

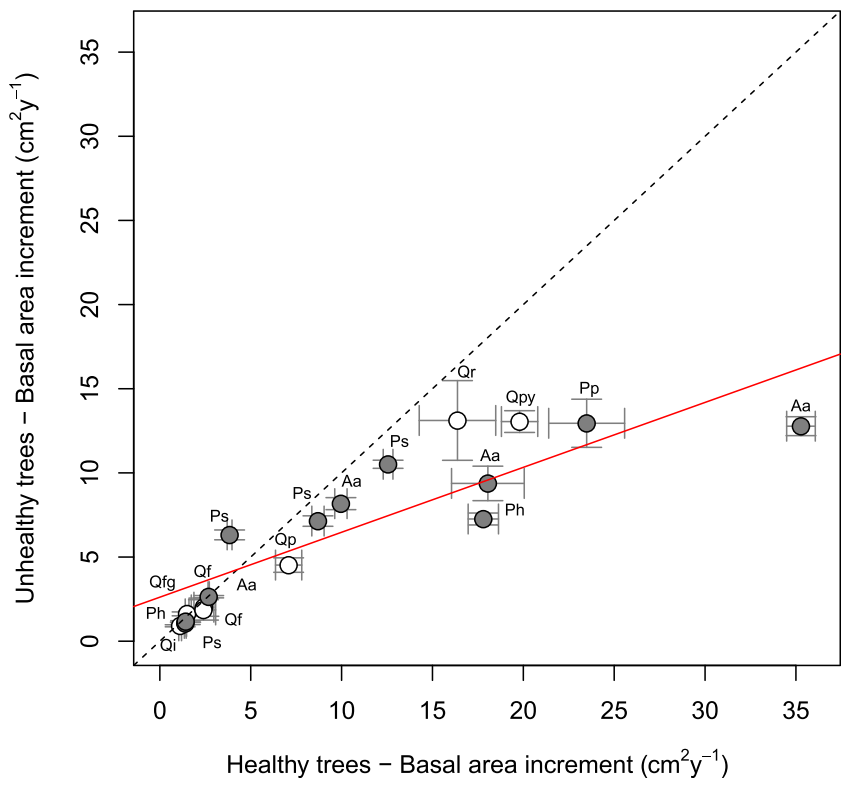
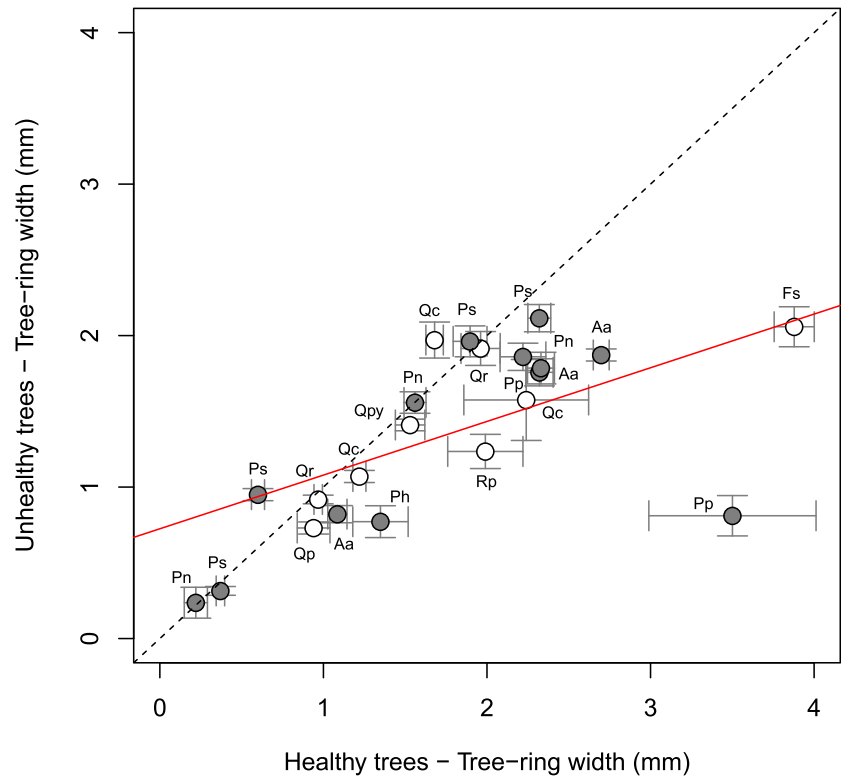
trees, compared to H-trees, before the onset of drought-induced tree decline. Although large xylem conduits favor transport efficiency, they carry risk of hydraulic dysfunction due to cavitation [64]. Sudden changes in transpiration demand by increasingly drier atmospheric conditions, and reduced soil water availability, may result in run-away embolism in large xylem conduits, leading to increased risk of tree decline due to hydraulic failure in H-strategy tree species. In our dataset, this large conduit circumstance may be mainly attributed to ring-porous oak species [44, 51, 52].

Altogether, the limited and unbalanced datasets that are currently available seem to preclude a thorough assessment of investigated xylem functional traits as stand-alone forest health indicators at specific Mediterranean sites. Differences in xylem conduit area may define different strategies of tree species to cope with drought. However, to gain scientific relevance, this approach will require more in-depth eco-physiological assessment, such as more data describing variability among and within species and more data related to environmentally driven spatial patterns. There is still much to be learned regarding likely interactions between structural plant strategies and drought intensity and duration. Additionally, time lags in ecological responses at the community level should be considered by means of long-term observations. For instance, it is possible that large conduit strategies may imply more vulnerability in the short-term but may support vitality in post-drought conditions, favoring resilience and survival in the long term [42].

Acclimation of Xylem Functional Traits: a Plant Strategy to Maintain Tree Health in Mediterranean Forests

The potential of xylem hydraulic structures to cope with changing environmental conditions can be assessed from long- to short-term temporal scales. Thanks to improved anatomical techniques, in recent years, there were increased opportunities to explore and interpret even rapid responses to

Fig. 2 Results of meta-analyses of tree-ring width (TRW, upper panel) and basal area increment (BAI, lower panel) values compiled from study cases listed in Table 1. The relationship between H-trees and U-trees is represented in both panels. Circles and bars represent mean values and standard deviations for each investigated tree species, respectively. The dashed lines show 1:1 relationship. The solid red lines are the regression predictions obtained from the applications of a linear mixed-effect model in which tree species were considered as random terms (TRW: Y -intercept = 0.72, slope = 0.35, R^2 marginal = 0.36; R^2 conditional = 0.76, $p < 0.01$; BAI: Y -intercept = 2.61, slope = 0.38, R^2 marginal = 0.78; R^2 conditional = 0.98, $p < 0.001$). Grey and white circles are conifer and hardwoods, respectively. Ps, *Pinus sylvestris*; Pn, *Pinus nigra*; Ph, *Pinus halepensis*; Pp, *Pinus pinaster*; Aa, *Abies alba*; Qr, *Quercus robur*; Qc, *Quercus cerris*; Qp, *Quercus pubescens*; Qpy, *Quercus pyrenaica*; Qf, *Quercus frainetto*; Qfg, *Quercus faginea*; Qi, *Quercus ilex*; Fs, *Fagus sylvatica*; Rp, *Robinia pseudoacacia*



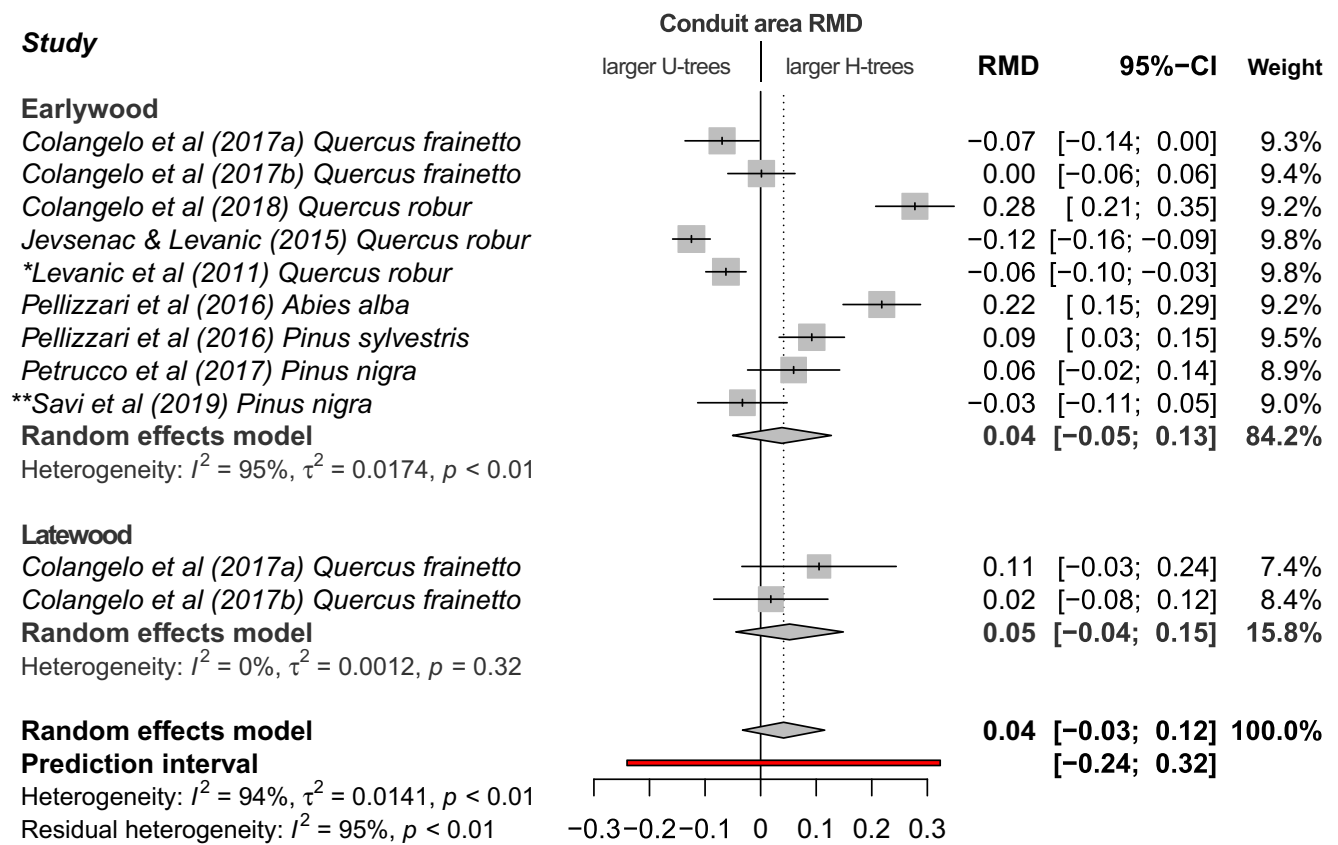


Fig. 3 Meta-analysis results for xylem conduit areas (average lumen size) assessed before the drought-induced tree decline on wood chronologies from study cases listed in Table 1. Results for earlywood conduits and latewood conduits are shown in the upper panel and lower panel, respectively. From left to right, columns report authors, year of publication, and investigated tree species for selected cases. Graphical representation of the relative mean difference (RMD = MD/x, where MD is the mean difference of samples and x is the sample mean) between H-trees (trees that did not show symptoms of decline) and U-trees (trees that showed symptoms of decline or were dying); error bars

indicate 95% confidence intervals (CIs), the vertical dashed line represents the no effect line. The diamonds represent summary RMDs, such that the lateral diamond tips show associated CIs; I^2 is the variability percentage independent of sampling error; τ^2 is the between-study variance. For each study, the weight is computed as the inverse of within-studies squared standard error plus the between-studies variance, τ^2 . The red line shows the range in which we can expect the effects of future studies to fall based on the current meta-analysis. *, hydraulic diameter; **, radial lumen diameter

suddenly occurring extreme climatic events, such as those recently documented for the Mediterranean region [7].

Much of the information available to date describes long-term patterns investigated on dated tree-rings at annual resolution over a tree’s life. At this scale, effective xylem functional trait adjustments have been reported frequently for Mediterranean tree species across climatic conditions. Notably, in most cases, variations in conduit size and density with precipitation and temperature showed xylem structure plasticity allowing trees to cope with fluctuating environmental boundaries and eco-physiological demands [28, 65–69]. In a large-scale analysis of long-term environmental constraints on xylem functional traits—including functionally interpretable indexes like the ratio (vessel composition) and product (vessel frequency) of conduit size and density—descriptions of general adjustment patterns are suggestive of at least some coordination of xylem traits towards functional homeostasis across fluctuating environmental conditions, balancing

transport efficiency, safety, and mechanical strength [70]. Much of the available information is related to conduit size and density, whereas adjustments involving conduit spatial arrangement have been less frequently investigated. Some available data indicate that conduit clustering occurs in Mediterranean habitats suffering from drought conditions, as a possible strategy to improve hydraulic efficiency by allowing water to bypass air-filled conduits through inter-vessel pit membranes [28, 71].

For the purpose of the present review, we have updated and reanalyzed previously examined long-term wood anatomical data from time-series dated woody rings [70]. By a search in the Web of Science database, we have included results published from the beginning of 2016 through February 2020 and considered Mediterranean tree species (Table 2). In case of studies showing results for different tree vigor classes, only healthy trees were considered. Subsequently, we have fitted those data to a Bayesian model to inspect the response of

Table 2 Data set used for investigating the long-term adjustments of xylem conduit area. Latitude (*Lat*) and longitude (*Long*) are expressed in decimal degrees, positive numbers indicate north and east, respectively; *Int*: time intervals covered by conduit area tree-ring chronologies

	Lat	Long	Int	Reference
<i>Quercus ilex</i>	38.600	−7.250	1942–2001	Abrantes et al. [65]
<i>Quercus faginea</i>	42.317	−0.413	1975–2007	Alla and Camarero [66]
<i>Quercus ilex</i>	41.333	1.833	1984–2005	Campelo et al. [67]*
<i>Quercus frainetto</i>	40.022	16.346	1980–2014	Colangelo et al. [44]*
<i>Quercus frainetto</i>	40.022	16.346	1980–2014	Colangelo et al. [45]
<i>Quercus faginea</i>	41.117	−1.650	1970–2000	Corcuera et al. [72]
<i>Quercus ilex</i>	41.117	−1.650	1970–2000	Corcuera et al. [72]
<i>Quercus pyrenaica</i>	41.117	−1.650	1970–2000	Corcuera et al. [72]
<i>Quercus canariensis</i>	36.520	−5.520	1975–2008	Gea-Izquierdo et al. [73]
<i>Erica arborea</i>	40.850	−3.941	1968–2009	Gea-Izquierdo et al. [74]
<i>Pinus nigra</i>	40.283	−1.983	1960–2006	Martin-Benito et al. [75]
<i>Pinus sylvestris</i>	40.283	−1.983	1960–2006	Martin-Benito et al. [75]
<i>Pinus halepensis</i>	41.783	−0.717	1970–2010	Pacheco et al. [68]**
<i>Pinus sylvestris</i>	40.433	−0.967	1900–2012	Pellizzari et al. [53]**
<i>Abies alba</i>	40.433	−0.967	1940–2012	Pellizzari et al. [53]**
<i>Fagus sylvatica</i>	44.100	10.700	1928–2015	Pericolo et al. unpublished data
<i>Ilex aquifolium</i>	39.930	16.320	1930–2012	Rita et al. [28]
<i>Alnus cordata</i>	39.930	16.320	1930–2012	Rita [28]
<i>Acer pseudoplatanus</i>	39.930	16.320	1930–2012	Rita [28]
<i>Quercus cerris</i>	39.950	16.176	1926–2012	Rita et al. [76]

Only control (*) or healthy (**) trees were considered in these cases

xylem conduit area and conduit density to changes in SPEI (standardized precipitation evapotranspiration index) values; the SPEI is a multi-scalar drought index that represents a balance between precipitation and potential evapotranspiration [77]. Time series of SPEI were extracted from the Global SPEI data base (https://spei.csic.es/spei_database/), based on the CRU TS 3.24.01 climate data set, and annual averaged.

The series from each site/species were first detrended and standardized using the “dplr package” in R [78]. Detrending involved fitting a 32-year cubic smoothing spline curve function, with 50% frequency cut-off, to amplify the climatic (high frequency) and remove the non-climatic (low frequency) signals. Series were then standardized by transforming raw xylem measurement values into a dimensionless index by dividing the observed by the expected values given by the spline function. Subsequently, models were run with four chains of 1000 warm-up and 4000 sampling steps and weak informative priors using ‘rstanarm’ package in the R statistical suite [79], wherein sampling id was included as a random term. Model convergence, effective posterior sample size, Monte Carlo standard error, and posterior predictive checks were performed using the ‘shinystan’ R package [80]. Then, we calculated mean values and the 95% highest posterior density (HPD) intervals using the ‘coda’ R package [81].

In the model, we observe an increase in conduit area with increasingly positive SPEI values (i.e., more favorable site

water balance conditions), as observed elsewhere [82]. Positive responses were found for diffuse-porous and conifer species, whereas an opposite response was recorded for ring-porous tree species (Fig. 4, left upper panel). In ring-porous species, the analysis was restricted to earlywood vessels and might not represent xylem plasticity accurately over an annual temporal scale because potential compensatory effects are neglected, associated for instance with modifications in latewood vessel characteristics [45, 83]. Additionally, earlywood vessel area of ring-porous species might be dependent, mostly at xeric sites, on previous year’s climate conditions (Martínez-Sancho et al. 2017). Conversely, xylem vessel density decreased with SPEI in both ring-porous and diffuse-porous tree species (Fig. 4, left lower panel). Altogether, plastic adjustments towards narrower and denser conduits with increasingly dry environmental conditions are suggested.

Based on compiled chronologies obtained from articles listed in Table 1, we have also assessed inter-annual changes in xylem conduit area recorded in Mediterranean forest areas impacted by drought. The right panel in Fig. 4 is a simplified ‘forest plot’ that presents the results of a meta-analysis of xylem conduit area variation across drought periods in U-trees and H-trees studied at selected sites. Overall, the forest plot only shows a significant difference for H-trees. In particular, H-trees seem to maintain, or sometimes increase, their xylem conduit areas during the drought period whereas U-

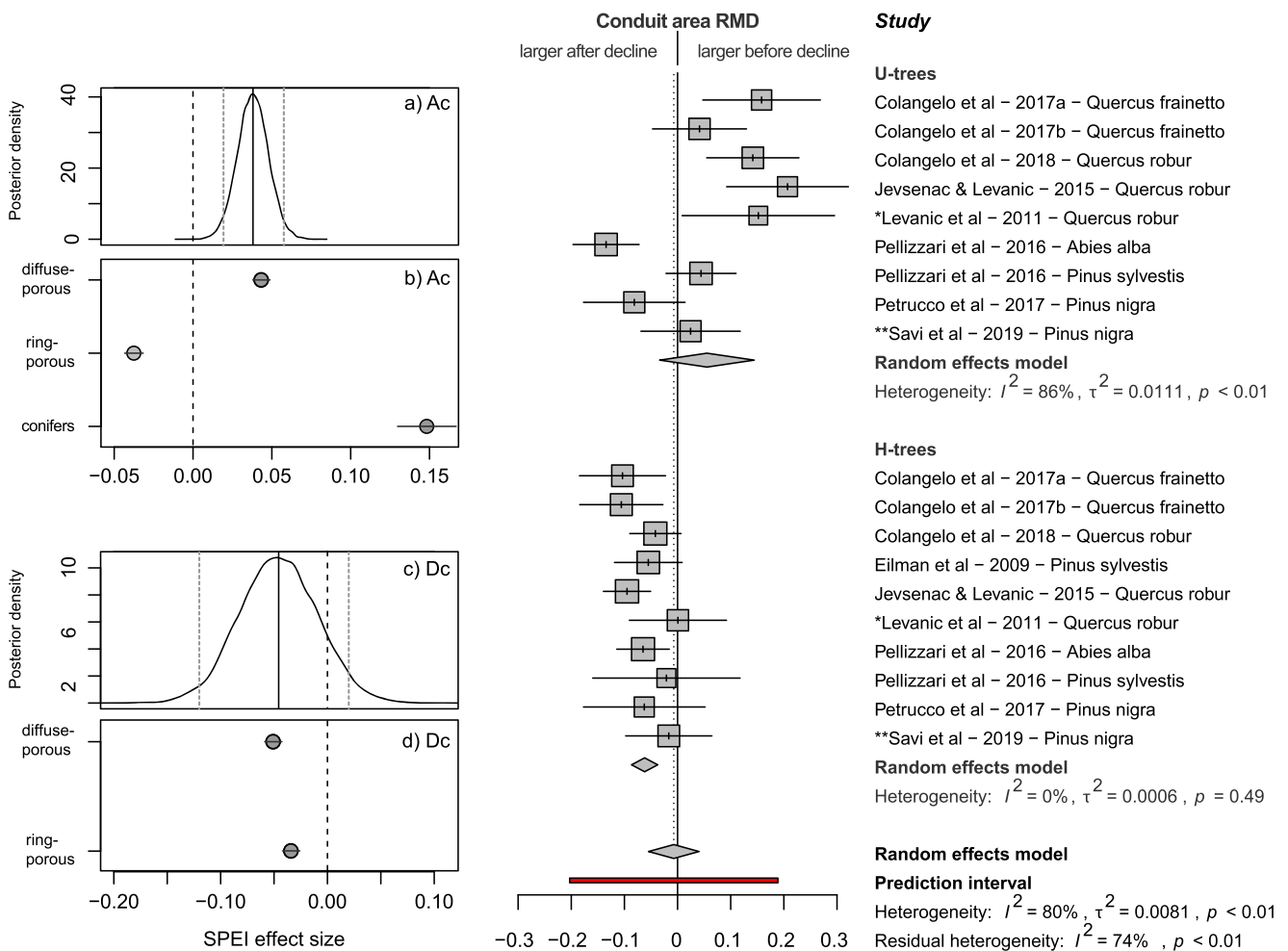


Fig. 4 Long- and short-term adjustments of xylem conduit area (average lumen size). On the left side: Bayesian posterior distributions of the relationship between SPEI (where higher value means higher ratio of rainfall to PET hence more favorable water balance conditions) and xylem conduit area (Ac) and xylem conduit density (Dc, de-trended) values (**a**, **c**), respectively. X-axis shows the predicted SPEI effect size, the y-axis the Bayesian posterior density. Gray dashed lines show 95% uncertainty interval of the posterior distribution. **b**, **d** Circles represent the slope of the conduit area and conduit density response to SPEI, respectively, dashed line represents the zero line, bars are 95% confidence intervals of the slope (CIs). On the right side: a ‘forest plot’ that shows relative mean difference (RMD = MD/x, where MD is the

mean difference of samples and x is the sample mean) between xylem conduit area values measured before and after the onset of drought-induced decline for H-trees and U-trees from selected study cases. Grey squares indicate the RMD and bars are 95% CIs. I^2 is the variability percentage independent of sampling error; τ^2 is the between-study variance. For each study, the weight is computed as the inverse of within-studies squared standard error plus the between-studies variance, τ^2 . Diamonds represent summary RMDs between the values measured before and after the onset of tree decline. The vertical dashed line represents the line of no effect and the red line shows the range in which we can expect the effects of future studies to fall based on the current meta-analysis. *, hydraulic diameter; **, radial lumen diameter

trees show more variable responses with conduit area reductions occurring in ring-porous species and conduit area increases being apparent in conifer species. Notably, drought-related increases in lumen areas in conifer species have been associated with reduced cell-wall thickness under conditions that limit carbon uptake and constrain xylem construction costs, resulting in a reduced resistance to cavitation in tracheids [84, 85]. Overall, from these data, it remains unclear whether the maintenance of tree health is consequent to a homeostatic hydraulic strategy (e.g., [86, 87]) or vice-versa.

In recent years, intra-ring anatomical techniques have increasingly been applied to highlight short-term adjustments of xylem structure and morphogenetic responses to intra-annual

climate variability in Mediterranean tree species. Studies applying these techniques have yielded the following notable outcomes: frequent bimodal seasonal patterns of morphogenetic processes and legacy effects of previous climatic conditions [68, 88, 89]; synchronization of cambial activity around relatively wet periods to mitigate the impact of summer drought Viera et al. [109]; differential control of environmental conditions depending on the characteristics of different populations of conduits produced throughout the growing season (e.g., early vs. latewood conduit size and shape) [90]; a strong effect of water availability during tracheid enlargement on final tracheid diameter [91]; differing response strategies between co-existing tree species suggesting that hydraulic-

driven selective effects depend on climate change directionality [92]; major vulnerability of ring-porous wood structures that become less (or not) sustainable under drier conditions [93]; feasibility of mechanistic biophysical modeling of short-term drought-induced xylem conduit adjustments [94].

Altogether, acclimation studies performed at different time scales are producing a convergence of evidence regarding the plasticity of xylem traits that may support the performance and health of Mediterranean tree species over a range of climatic future conditions. Progress in this line of research will benefit greatly from major experimental efforts; for instance, common-garden multi-species replicated experiments over a broad range of climatic conditions, including the warm and dry margins of species' ranges, wherein environmental manipulations could be performed; standardized sampling and anatomical techniques applied over seasonal and annual scales; tree height-cambial age relationships properly reconstructed to account for the tapering effect and extract climatic signals on xylem functional traits; genetic and environmental effects that mediate traits plastic responses could be dissected.

Xylem Functional Traits as Descriptors of the Mediterranean Forest

Xylem and wood characteristics have been up-scaled spatially to interpret land-ecosystem properties, understand species range limits in ecological regions, forecast vegetation changes driven by climate change, and map areas poorly suited for tree growth [95–97]. The rationale underlying and current evidence supporting the use of xylem functional traits as indicators of tree health in Mediterranean forests have been elaborated in previous chapters. Here, we have conducted a simple exercise aimed at developing a geographic scale description of Mediterranean forests in terms of xylem functional traits and wood properties, which might be used as model inputs for large-scale studies or evaluating changes in hydraulic traits over time.

Spatial interpolation methods were used to generate Mediterranean region-wide raster maps, by melding georeferenced occurrences of Mediterranean tree species obtained from Brus et al. [98] with species-averaged wood density values, xylem conduit size data, and specific hydraulic conductivity data obtained from extensive records of xylem functional traits and wood properties [19, 99–101].

The maps generated in this exercise (Fig. 5) depict substantial variability across the Mediterranean region with respect to wood properties and xylem functional traits and can be regarded as a sketch of wide-scale hydraulic functionality. Conduit size and hydraulic conductivities, which show quite concordant spatial patterns with reduced values towards low latitudes, may be used tentatively as proxies of hydraulic vulnerability in locally patchy spatial distributions, and on a wide geographic scale. The wood density patterns displayed in our maps are more difficult to interpret. Wood density is an

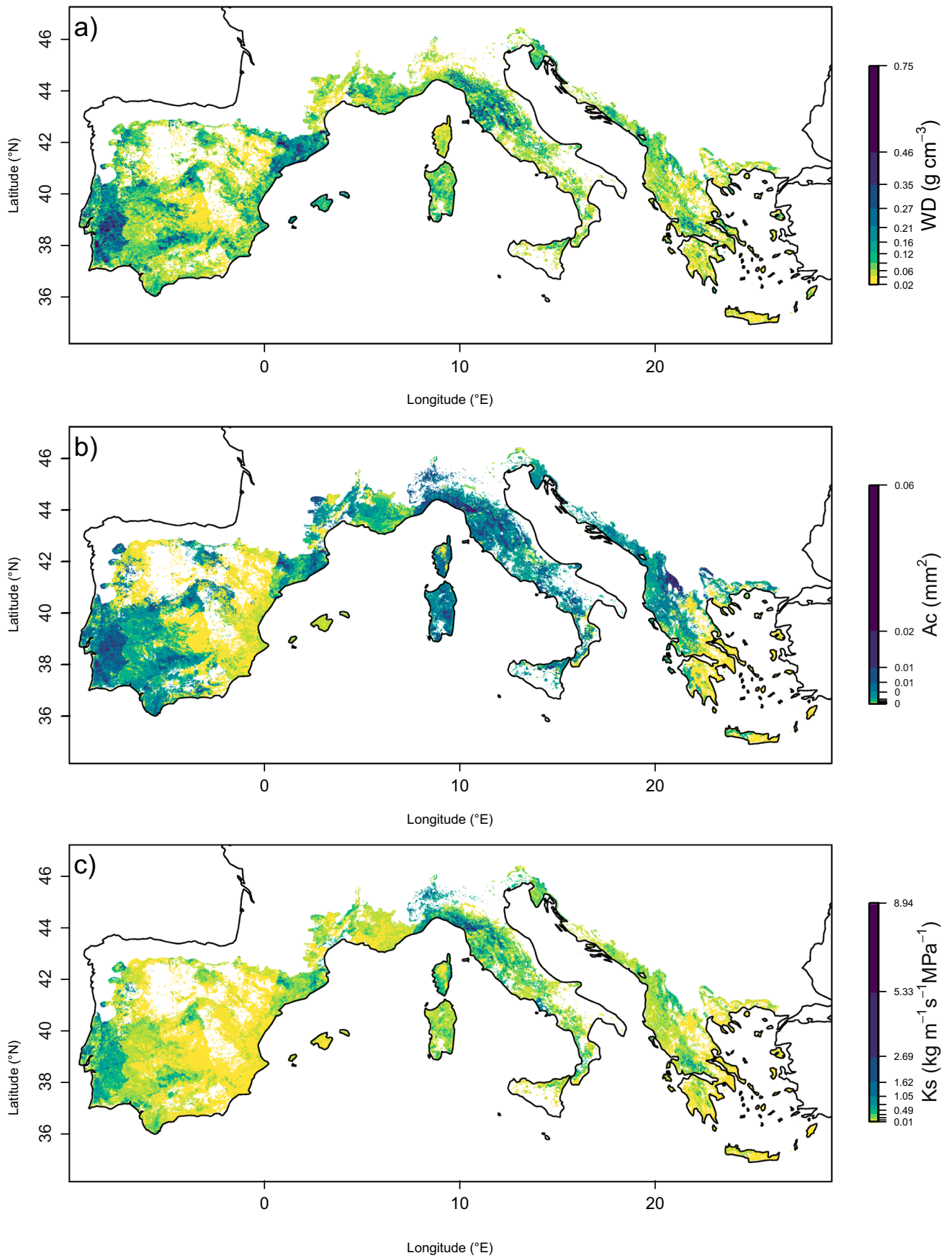
emerging xylem property, whose determinants and functional significance have been discussed in depth by Chave et al. [99]. However, in a global assessment of wood density as a putative determinant of tree mortality across biome, it explained less than 10% of the variation in forest responses to drought [20]. Efforts aimed at clarifying operational xylem trait biogeography in the Mediterranean region are currently impaired by insufficient information on inter- and intra-specific variability in xylem functional properties of relevant forest tree species, which is resulting in low-resolution and uncertain spatial patterns. Reducing this uncertainty could be envisaged as a research direction for regional-oriented assessments of Mediterranean forest vulnerability.

Conclusions

Our literature survey shows that xylem functional traits have not been investigated in drought-impacted Mediterranean forests fully and systematically. In our survey of recent evidence on the relationship between xylem anatomy and hydraulic vulnerability in Mediterranean trees, we did not find convergent changes for xylem functional traits in drought-impacted trees. Our associated meta-analysis did not reveal a totally coherent role of xylem conduit size as a tree-health indicator at sites where H-trees and U-trees were compared. We developed a simple scheme of different hydraulic strategies that may fit observed conduit area response patterns. There were some indications, in ring-porous species, that high growth rates and large conduit areas may be linked to tree's drought vulnerability. However, a thorough evaluation will require more in-depth ecological assessments, especially assessments that can yield enhanced datasets describing intra- and inter-species variability, environmentally driven spatial patterns, and long-term tree and community resilience.

The hypothesis that other xylem functional traits may perform better as indicators of Mediterranean forest decline and dieback under increasing drought than the traits examined here cannot be ruled out. Future research may address this point, hopefully with common-garden replicated experiments in which wider ranges of xylem traits are studied, possibly including less frequently investigated traits, such as porosity and surface characteristics of pit membranes connecting xylem conduits [102, 103], with more careful attention being paid to plant hydraulic segmentation [2], junction-constricted zones and root tissues, changes in the allometry of xylem traits [104]. Also, the increasingly available evidence that hydraulic vulnerability is likely to involve extra-xilary variables should be considered [105, 107].

On the levels of a whole tree and or a tree stand, a large body of evidence suggests that hydraulic performance and safety arises from the coordination of multiple traits and from the plasticity of tree structure, as a result of variable resource



◀ **Fig. 5** Geographic maps of wood density (WD, upper panel), xylem conduit area (Ac, middle panel), and hydraulic specific conductivity (Ks, lower panel) for the Mediterranean region. The pixel level values were weighted on the relative abundance of each species/genus in the pixel. WD values of *Castanea* spp., *Eucalyptus* spp., *Pseudotsuga* spp., and *Robinia* spp. are from extra Mediterranean areas. Missing Ks values of *Quercus robur/petraea* were filled with the average *Quercus* spp. values

allocation between transpiring foliage, conductive sapwood, and absorbing roots [9]. Our survey suggests that xylem traits may adjust over different temporal scales and may support the performance and health of Mediterranean tree species over a range of future climatic conditions. However, convincing evidence on the proportion of genetically and environmentally driven xylem traits that exhibit variability remains poor so far, with the exception of wood density, which has been investigated extensively and has been incorporated frequently in forest-tree genetic studies and breeding programs [106]. Extending the depth of knowledge for other xylem functional traits is needed to enable ecological and evolutionary predictions on population and community levels.

Studies on xylem functional traits may gain perspective if focus is up-scaled spatially. On a geographic scale, the Mediterranean eco-region displays spatial variability in pixel-averaged values of xylem functional traits, reflecting variability in species composition and suggesting patchy responses to increasing drought. Enhanced knowledge on the inter-specific and intra-specific variability of xylem functional traits will support the up-scaling of model predictions from an individual to a community scale, where the consequences of forecasted droughts are likely to affect a range of values and functions associated with Mediterranean forests.

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Compliance with Ethical Standards

Conflict of Interest Marco Borghetti, Tiziana Gentilesca, Michele Colangelo, Francesco Ripullone and Angelo Rita declare they have no conflict of interest.

Human and Animal Right and Informed Consent This article does not contain any studies with human and animal subjects performed by any of the authors.

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