Tansley review

Plant hydraulics at the heart of plant, crops and ecosystem functions in the face of climate change

Author for correspondence:
José M. Torres-Ruiz
Email: torresruizjm@gmail.com

Received: *4 July 2023*
Accepted: *5 November 2023*

José M. Torres-Ruiz[1], Hervé Cochard[1], Sylvain Delzon[2], Thomas Boivin[3], Regis Burlett[2], Maxime Cailleret[4], Déborah Corso[2], Chloé E. L. Delmas[5], Miquel De Caceres[6], Antonio Diaz-Espejo[7], Pilar Fernández-Conradi[3], Joannes Guillemot[8,9,10], Laurent J. Lamarque[11], Jean-Marc Limousin[12], Marylou Mantova[13], Maurizio Mencuccini[6,14], Xavier Morin[12], François Pimont[3], Victor Resco De Dios[15,16], Julien Ruffault[3], Santiago Trueba[2] and Nicolas K. Martin-StPaul[3]

[1]Université Clermont-Auvergne, INRAE, PIAF, 63000, Clermont-Ferrand, France; [2]University of Bordeaux, INRAE, UMR BIOGECO, Pessac, 33615, France; [3]INRAE, URFM, Avignon, 84140, France; [4]INRAE, Aix-Marseille Université, UMR RECOVER, Aix-en-Provence, 13100, France; [5]INRAE, Bordeaux Sciences Agro, ISVV, SAVE, F-33140, Villenave d'Ornon, France; [6]CREAF, Bellaterra (Cerdanyola del Vallès), Catalonia, E08193, Spain; [7]Instituto de Recursos Naturales y Agrobiología (IRNAS), Consejo Superior de Investigaciones Científicas (CSIC), Seville, 41012, Spain; [8]CIRAD, UMR Eco&Sols, Montpellier, 34394, France; [9]Eco&Sols, Univ. Montpellier, CIRAD, INRAe, Institut Agro, IRD, Montpellier, 34394, France; [10]Department of Forest Sciences, ESALQ, University of São Paulo, Piracicaba, 05508-060, São Paulo, Brazil; [11]Département des sciences de l'environnement, Université du Québec à Trois-Rivières, Trois-Rivières, G9A 5H7, Québec, Canada; [12]CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, 34394, France; [13]Agronomy Department, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL 32611, USA; [14]ICREA, Barcelona, 08010, Spain; [15]Department of Forest and Agricultural Science and Engineering, University of Lleida, Lleida, 25198, Spain; [16]JRU CTFC-AGROTECNIO-CERCA Center, Lleida, 25198, Spain

Contents

New Phytologist (2024) **241:** 984–999
doi: 10.1111/nph.19463

Key words: climate change, crop productivity, drought, mortality, pathogens, plant growth, plant hydraulics, wildfire.

Summary

Plant hydraulics is crucial for assessing the plants' capacity to extract and transport water from the soil up to their aerial organs. Along with their capacity to exchange water between plant compartments and regulate evaporation, hydraulic properties determine plant water relations, water status and susceptibility to pathogen attacks. Consequently, any variation in the hydraulic characteristics of plants is likely to significantly impact various mechanisms and processes related to plant growth, survival and production, as well as the risk of biotic attacks and forest fire behaviour. However, the integration of hydraulic traits into disciplines such as plant pathology, entomology, fire ecology or agriculture can be significantly improved. This review examines how plant hydraulics can provide new insights into our understanding of these processes, including modelling processes of vegetation dynamics, illuminating numerous perspectives for assessing the consequences of climate change on forest and agronomic systems, and addressing unanswered questions across multiple areas of knowledge.

I. Introduction

The field of plant hydraulics examines the capacity of plants to extract water from the soil and transport it up to the aerial organs through the transpiration stream. Moreover, it also considers water exchange between the plant apoplastic and symplastic compartments, determining plant water relations and water status. Variations in plant hydraulic properties, water relations and status (e.g. induced by changes in meteorological conditions or soil water availability) can directly affect key plant functions such as stomatal behaviour, photosynthetic capacity, biomass production and growth. Furthermore, these variations can influence other processes such as the development of plant diseases caused by pathogens, the sensitivity of forests to wildfires or the risk of drought-induced mortality (Fig. 1). As a result, plant hydraulics has garnered increasing attention from diverse scientific fields due to its critical role in addressing relevant questions, especially those related to ecosystem functioning in the face of global changes. The increase in the frequency and severity of drought events is causing irreversible damages to plant productivity and survival, which are further exacerbated by the impacts of pathogens or wildfires (Littell *et al.*, 2016; McDowell *et al.*, 2018, 2022). Thus, many of the mortality events reported world-wide have been related to low water availability and increased atmospheric temperatures (Peng *et al.*, 2011; Hammond *et al.*, 2022; Klein *et al.*, 2022). Such conditions can therefore compromise the contributions of ecosystem services to humankind. Similarly, the intensifying drought conditions are already causing substantial declines in crop yield in most agricultural regions world-wide (Lesk *et al.*, 2016), with important implications for livelihood and food security. It is therefore necessary to identify the physiological traits that explain such variation in plant survival and yield for the maintenance and conservation of our forests and improving crop management.

During the last decades, plant hydraulics has contributed relevant knowledge and tools for understanding biological and ecological processes, such as the susceptibility of forests to fire (Midgley *et al.*, 2011; Ruffault *et al.*, 2022), plant interactions with pathogens and herbivorous insects (Yadeta & Thomma, 2013; Bortolami *et al.*, 2019), and the processes controlling crops and forest productivity and resilience to drought (Flexas *et al.*, 2018; Klein *et al.*, 2022; Morcillo *et al.*, 2022; Fig. 1). Given these pioneering attempts, there is now an opportunity to connect the knowledge generated in plant hydraulics and other disciplines in order to address relevant physiological and ecological questions at large scales (e.g. better prediction of mortality, fire risk, ecosystem functioning or crop production). Significant advances, however, have been made in understanding processes and mechanisms associated with water transport, including cavitation formation and spreading (Tyree & Sperry, 1989; Torres-Ruiz *et al.*, 2016a); hydraulic efficiency and safety within and across species (Choat *et al.*, 2012; Lobo *et al.*, 2018); the role of hydraulic dysfunction in drought-induced mortality (Adams *et al.*, 2017; Mantova *et al.*, 2021, 2022; McDowell *et al.*, 2022); water transport in and out of fruit (Morandi *et al.*, 2007; Torres-Ruiz *et al.*, 2016b); the development of mechanistic models for predicting the consequences of drought-induced hydraulic failure on plant performance (Sperry & Love, 2015; Cochard *et al.*, 2021; Ruffault *et al.*, 2022); and the risk of wildfires (Ruffault *et al.*, 2023). As a result, plant hydraulics provide, at present, a comprehensive framework that represents various aspects of terrestrial plant and ecosystem functioning, including (1) carbon sequestration and productivity of crops and forest ecosystems, as photosynthesis is tightly coordinated with hydraulic functions (e.g. Reichstein *et al.*, 2014); (2) the predictions of plant water status encompassing all components of drought stress using well-established biophysical equations based on simple diffusion laws (e.g. Cochard *et al.*, 2021; De Swaef *et al.*, 2022); and (3) the predictions of plant mortality, demography and the susceptibility to disturbance regimes such as wildfire or pathogen attacks linked to drought (e.g. Gely *et al.*, 2020; Ruffault *et al.*, 2023).

Without attempting to be exhaustive, the goal of this review is to highlight how plant hydraulics can provide relevant insights to other disciplines such as crop sciences, fire ecology, plant pathology and ecology, providing a broad framework highlighting how it can advance unanswered questions and draw future research directions of these fields.

II. Plant hydraulics: a framework for measuring drought impacts

Plant responses to drought are characterized by a sequence of water stress limits for various plant physiological functions, which are linked to hydraulic traits (Bartlett *et al.*, 2016; Blackman

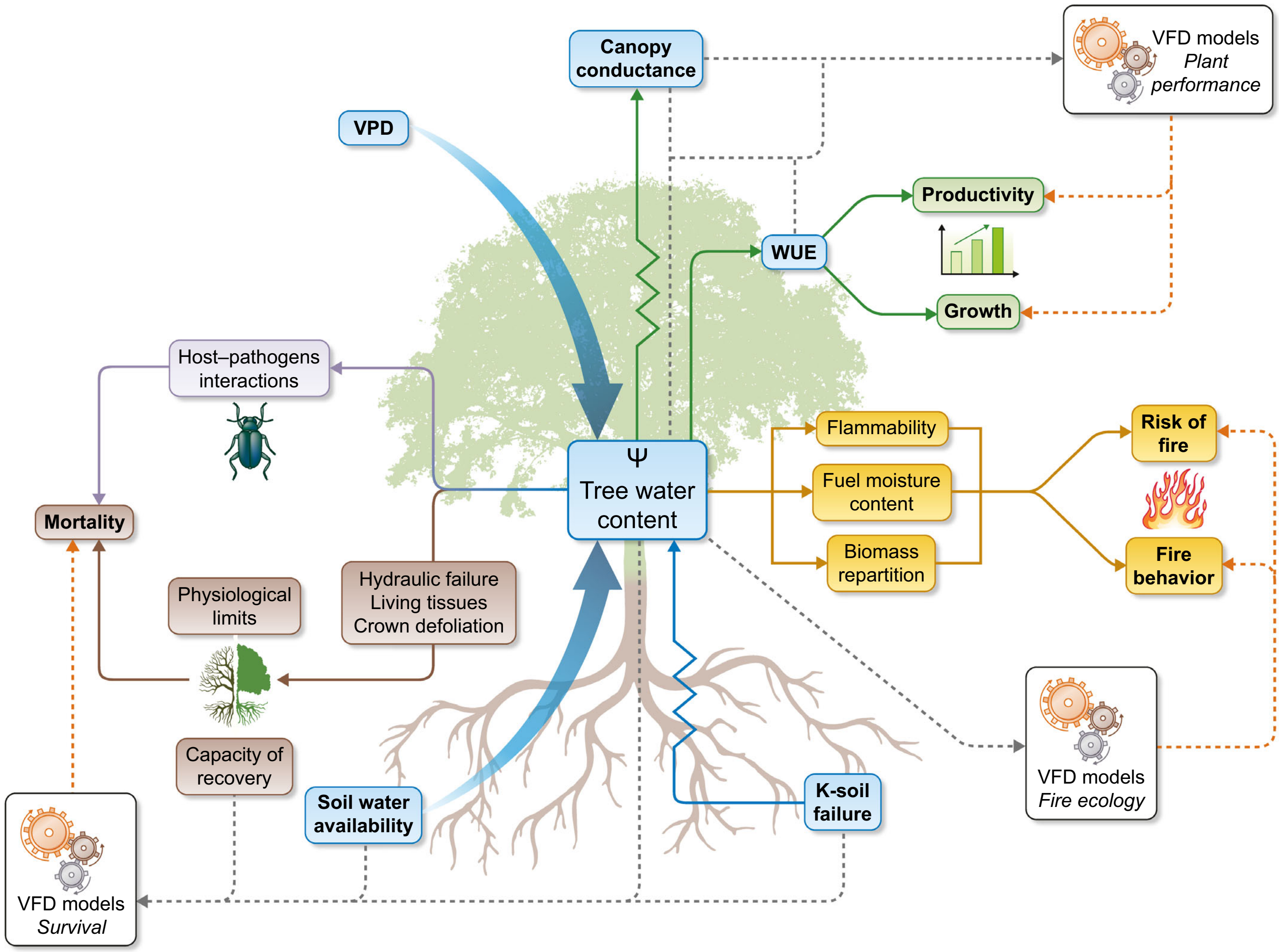

Fig. 1 Conceptual diagram depicting main physiological processes related to tree hydraulic characteristics and their connection to key assessments of climate change impacts in forests and agriculture. Briefly, it shows how vapour pressure deficit (VPD) and soil moisture crucially determine tree water content and, consequently, tree water status (Ψ). The Ψ gradient from roots to leaves, combined with soil conductivity, determines canopy conductance. A Ψ decrease, such as in drought-exposed trees, significantly reduces water use efficiency, impacting both productivity and growth rate. Ψ variation also affects fire risk and behaviour, as it critically determines vegetation flammability, fuel moisture and biomass distribution. Reduced tree water content amplifies pathogen impacts on tree hydraulic capacity, increasing mortality risk. Similarly, low Ψ can cause xylem hydraulic failure, defoliation and damage to living tissues, that could exceed certain tree physiological limits and affect its recovery capacity. Therefore, the use of vegetation function and dynamics (VFD) process-based models is a potent tool for predicting the consequences of a significant Ψ drop on these processes.

et al., 2023). These hydraulic traits play an important role in shaping critical aspects of plant performance, including growth, photosynthesis, turgor maintenance and overall resilience in the face of drought-induced conditions (Fig. 2). Thus, as soil water availability decreases or atmospheric vapour pressure deficit (VPD) increases, plants commonly reduce stomatal opening to mitigate water stress and hydraulic impairment. However, this adaptive response is associated with the trade-off of limiting photosynthesis and transpiration (Flexas & Medrano, 2002; Martin-StPaul *et al.*, 2017). Drought leads to a decrease in cell turgor pressure due to declining plant water potential, causing plant growth to halt when it reaches values below the minimum pressure required for cell enlargement (Lockhart, 1965). Despite this, only few studies to date have attempted to determine or model the water potential threshold for plant growth (reviewed in Cabon *et al.*, 2020). As for growth, hydraulic limits can be defined for plant gas exchange. In this respect, the turgor loss point (Ψ_{tlp}) appears as a sound water potential limit for characterizing stomatal closure, considering that stomata are completely closed when leaf turgor is equal to zero (Brodribb *et al.*, 2003). However, it should be noted that stomatal closure alone may not be sufficient for assessing the water stress impact on carbon assimilation and economy because photosynthesis is significantly constrained before complete stomatal closure (Fig. 2). The water potential at net zero carbon assimilation ($\Psi A_n = 0$) is therefore crucial for evaluating the effect of drought on plant growth, productivity or carbon sequestration, requiring to consider the roles of the mesophyll conductance to CO_2, the Rubisco carboxylation rate and the chlorophyll electron transport

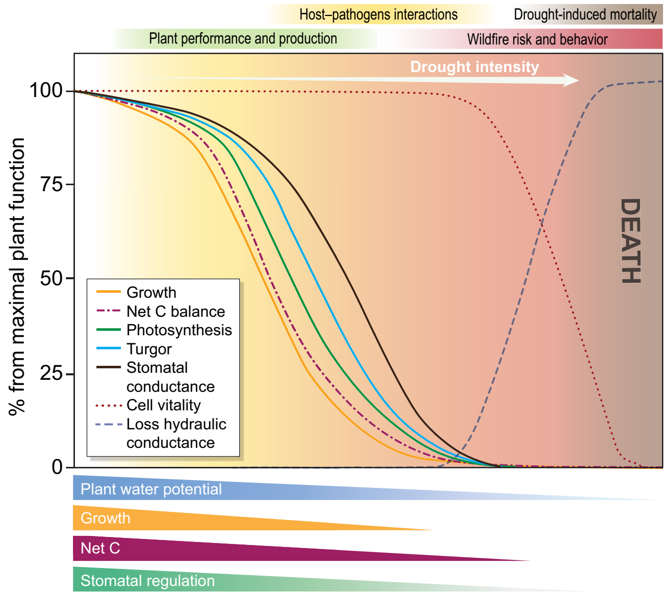

Fig. 2 Conceptual graph illustrating the relative variations in the main physiological functions associated with plant hydraulic traits as plants are exposed to increasing levels of water stress (central panel) and indicating the disciplines for which they can offer valuable insights to address relevant unanswered questions (top panel). The panel at the bottom shows the negative effects of stress intensity on the different physiological functions.

rate on the photosynthetic capacity in addition to the hydraulic traits (e.g. Sperry *et al.*, 2017).

The closure of stomata delays the decline of water potential, preventing it from reaching levels below the critical threshold at which cavitation occurs and maximizing the time in which the plant shows a positive safety margin (i.e. the difference between the actual water potential and water potential at which cavitation starts). It has recently been shown that one of the main causes of this stomatal closure during soil drying is the decrease in soil-root hydraulic conductance which, either by the disconnection of the roots from the soil or by the collapse of the root xylem, also prevents root water losses when the soil water potential becomes very low (Rodriguez-Dominguez & Brodribb, 2020; Abdalla *et al.*, 2022). Despite this, plants continue to dehydrate progressively under limited soil water extraction (soil drought) or higher atmospheric evaporative demand (atmospheric drought) due to the residual water losses from the cuticle and stomata (Machado *et al.*, 2021). This causes the relative water content (RWC) and water potential (Ψ) to decrease, ultimately leading to xylem cavitation and plant hydraulic failure. Hydraulic failure is considered a ubiquitous factor in drought-induced mortality (Adams *et al.*, 2017), so it is important to understand the physiological traits determining hydraulic failure and its link to death for predicting plant responses to climate change. In this regard, recent studies have shown how the loss of hydraulic function is linked to downstream living cell damage (Mantova *et al.*, 2023), which has led to the hypothesis that the loss of meristematic cell integrity induced by hydraulic dysfunction is the possible mechanistic link between hydraulic failure and drought-induced mortality (Mantova *et al.*, 2022).

Xylem resistance to cavitation is conventionally assessed by determining the tension inducing 50% loss of hydraulic conductance (P_{50}), a trait typically well conserved within species (Lamy *et al.*, 2014; Torres-Ruiz *et al.*, 2019), even if acclimation has also been observed for some species across their distribution range or among varieties (Trueba *et al.*, 2017; Stojnić *et al.*, 2018; Dayer *et al.*, 2020). P_{50} represents the point at which the sensitivity of plant hydraulic conductance to water potential is maximum. P_{50} also corresponds to the lethal percentages of loss of conductivity (PLC) for conifers (Brodribb & Cochard, 2009) but not for angiosperms in which death occurs at even more negative water potentials (PLC *c.* 88%, Urli *et al.*, 2013). However, the small number of studies in which these lethal water potential limits were observed, and recent research showing how plants are actually able to recover from drought even when surpassing these values (Hammond *et al.*, 2019; Mantova *et al.*, 2021) questions their use as physiological thresholds for plant mortality.

In summary, plant hydraulic characterization can undoubtedly improve our predictive power for quantifying the impacts of drought and warming on vegetation gas exchange, growth, production and survival. Such information will be highly relevant to assess future species' bioclimatic and growing boundaries, and design species-based conservation and management strategies to alleviate the impact of droughts on natural and managed systems under a changing climate.

III. Hydraulic properties and crop productivity under drought conditions

Significant drought-induced declines in crop production have been witnessed world-wide in recent decades (Howitt *et al.*, 2015; Lesk *et al.*, 2016; Schauberger *et al.*, 2017), prompting crop science researchers to develop cultivars to maintain crop yield under increasing drier conditions. To date, the development of drought-tolerant cultivars/varieties has largely relied on yield potential, on the selection of morpho-anatomical traits or on identifying hormones and proteins that have broad-range effects (De Micco & Aronne, 2012; Fàbregas & Fernie, 2019) but are not fit to context-specific future climates. Yet, an important aspect for increasing drought tolerance in crops is to identify mechanistic traits that preserve the integrity of the hydraulic pathway to maintain productivity and yield under drought conditions.

Plant growth and yield depend not only on photosynthesis capacity but also on the conjunction of several factors that allow the enhancement of the photosynthesis rate to be translated into yield, such as higher hydraulic capacities, sink–source balance and transport of photoassimilates, and the availability of nutrients and environmental conditions (Lawlor, 1995; Araus *et al.*, 2021). The increase in photosynthetic capacity requires the concurrent enhancement of an efficient water transport system (i.e. hydraulic efficiency; Tyree & Sperry, 1989; Brodribb, 2009) and the preservation of its hydraulic integrity (i.e. hydraulic safety), particularly under drought conditions. These interconnected traits play a key role and must progress in parallel to ensure optimal adaptation to drought conditions while maximizing photosynthetic performance. Thus, it has been reported how higher vein

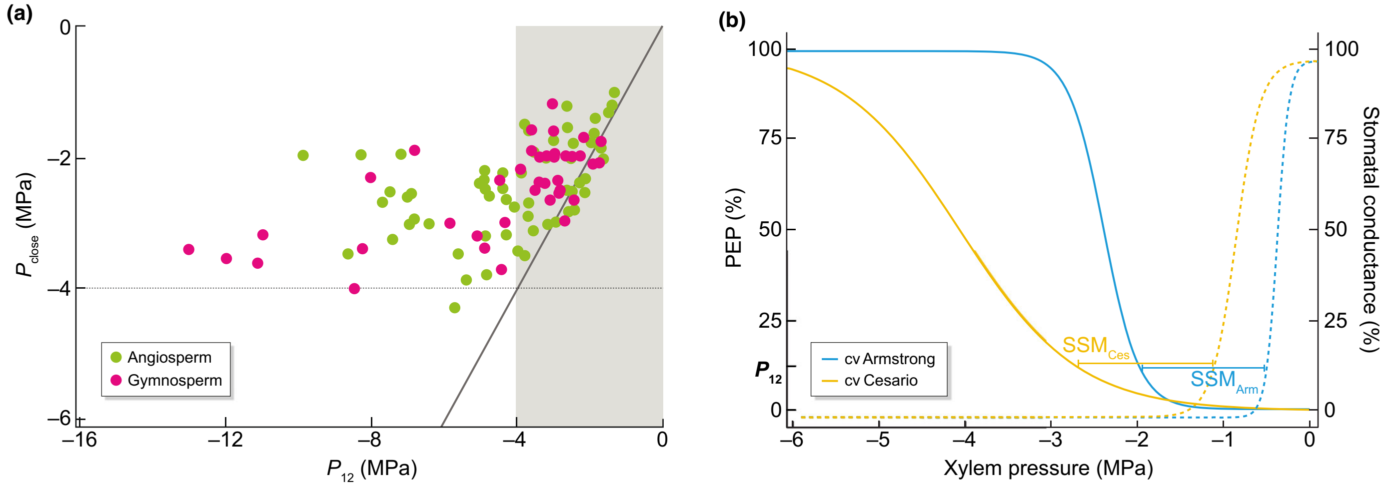

Fig. 3 Crops function with a narrow stomatal safety margin (SSM) that could allow species with a delayed onset of embolism to maintain gas exchange longer under drought. (a) Within the range of pressure-inducing xylem embolism reported in crops (i.e. P_{12} ranging from −1 to −4 MPa; grey area), the linear relationship between P_{close} (pressure-inducing 90% of stomatal closure) and P_{12} is close to the 1 : 1 line (plain line; adapted from Martin-StPaul *et al.*, 2017). The dashed line corresponds to the absolute limit by which stomata closure must occur to avoid rapid death under drought conditions. (b) Cultivars of wheat (*Triticum aestivum*) exhibit differences in xylem vulnerability to cavitation (plain lines). Assuming that SSM is constant in the range of xylem pressure going from −1 to −4 MPa (i.e. $SSM_{Ces} = SSM_{Arm}$), wheat cv Cesario, which shows a delayed P_{12} in comparison to cv Armstrong, would maintain gas exchange under greater water stress (dotted lines).

densities enhance not only photosynthetic gas exchange rates but also stomatal conductance and tolerance to drought-induced disruption of the hydraulic system (Sack & Scoffoni, 2013). However, there is only a weak trade-off between xylem efficiency and xylem safety such that very resistant species to cavitation can show a wide range of hydraulic conductance values (Gleason *et al.*, 2016). An efficient coordination of plant hydraulics and photosynthesis is therefore essential for the synchronized regulation of water loss and carbon dioxide uptake in plants through the stomata. This coordination has recently been evidenced in tomato mutants (Andrade *et al.*, 2022), where a reduction in diameter and number of xylem vessels resulting in lower hydraulic conductivity was associated with a 50% and 25% reduction in stomatal conductance and net photosynthesis, respectively.

Annual crop plants are, in general, relatively vulnerable to embolism, with P_{12} values (i.e. the water potential used as a proxy for the onset of xylem embolism) varying between −1 and −4 MPa, such as in wheat (−1.7 MPa, Corso *et al.*, 2020), sunflower (−2.3 MPa, Ahmad *et al.*, 2018) or maize (−1.6 MPa, Cochard, 2002). Within this range of water potentials, the relationship between complete stomatal closure (P_{close}) and P_{12} is close to the 1 : 1 line (Fig. 3a; Martin-StPaul *et al.*, 2017), which means that there is little to no stomatal safety margin (SSM; i.e. $P_{close} - P_{12}$) for these species. These narrow SSMs allow annual crops to maintain gas exchange up to almost the onset of cavitation under drought conditions. Similar results have been observed in perennial woody crops, like apple trees (Beikircher *et al.*, 2013), for which varieties with a higher resistance to cavitation are able to maintain their stomata open for a wider range of soil water availability. Therefore, if the objective is to ensure crop production and the sustainability of food supply under drought, we need to seek crop species or cultivars with (1) relatively high resistance to embolism and (2) relatively narrow safety margins to maintain gas exchange and maximize the photosynthetic activity even when soil water content starts to be limited (Fig. 3b). However, if our aim is to reduce the risk of drought-induced mortality, it is not only sufficient to identify varieties with higher resistance to embolism and wide safety margins, but we will also have to take into account other physiological traits. This is the case of residual conductance, stomatal closure or capacitance since, as a whole, they will determine the rate of residual water loss and, therefore, the time in which the plant will reach levels of water potential that could start to be detrimental or even fatal. Therefore, when assessing drought tolerance, we cannot focus on one or two traits, but on all those traits (i.e. syndrome of traits) that together will determine the behaviour and response of the plant under drought conditions (Dayer *et al.*, 2022). However, pioneering studies have already shown that this is not an easy task (Tardieu, 2012) since the traits interaction can result in a range of phenotypes. This makes process-based modelling a useful tool for linking the crop's hydraulic properties to plant performance and response to drought (e.g. Wang *et al.*, 2020).

The hydraulic characteristics of the fruits, which is the final target in fruit tree orchards, have not attracted so much interest as stem or leaf hydraulics. In fruits, both xylem (inflows) and phloem (outflow) fluxes play a major role in their growth rate depending on their developmental stage (Matthews & Shackel, 2005; Clearwater *et al.*, 2012), the irrigation regime (Torres-Ruiz *et al.*, 2016b), irradiance (Boini *et al.*, 2019) or rootstock-scion combinations (Gerbi *et al.*, 2022; Narandžić & Ljubojević, 2022). Understanding the growth strategies of the fruits according to their hydraulic characteristics (i.e. inflows and outflows) can, therefore, help growers optimize their resource management for more sustainable production and higher fruit quality.

Apart from the increasing water scarcity observed in different geographical areas due to climate change, the growing interest in crop hydraulics stems from the recognition that understanding the hydraulic mechanisms responsible for drought resistance in crop plants is important for the development of productive and drought-resistant varieties. This is especially important since improving some morpho-anatomical or physiological traits that could improve drought resistance may not always result in corresponding improvements to hydraulic traits (e.g. Lamarque *et al.*, 2020). Thus, multifaceted approaches are required to develop crop varieties with optimal trait combinations conferring increased hydraulic safety, efficient hydraulic conductance, sustained carbon assimilation and high yield. Now, that hydraulic traits can be easily quantified in crops; it is also possible to integrate this information into existing hydraulic models to predict crop performance under various climate warming scenario and identify traits that can be leveraged to adapt agriculture to climate change (Cochard *et al.*, 2021; Dayer *et al.*, 2022).

Therefore, considering the actual and predicted climate change scenario, identifying or creating crop varieties with an optimal combination of hydraulic safety, efficiency and photosynthetic traits is crucial to ensure crop production under the expected warmer and drier conditions for many areas in the world.

IV. Linkage between hydraulics-related plant traits and wildfire risk

Wildfire is one of the most important natural disturbances affecting ecosystems world-wide (Bowman *et al.*, 2020). As climate warming intensifies, vegetation gets drier (lower moisture content) for longer periods of time (Clarke *et al.*, 2022), thus lengthening the fire season and potentially increasing the frequency of high-intensity fires (Barbero *et al.*, 2015; Dowdy *et al.*, 2019; Ruffault *et al.*, 2020). Plant–fire interactions depend on many physiological mechanisms acting at different temporal and spatial scales (Resco De Dios, 2020). On the one hand, the interplay between biomass production (or fuel accumulation and structure) and its moisture content affects wildfires, at scales ranging from biogeographical patterns of burned area (Boer *et al.*, 2021) to landscape patterns of fire spread (Nelson, 2001). On the other hand, fire effects on ecosystems depend on interactions between fire intensity and plant's resistance and resilience to fire (Karavani *et al.*, 2018).

Live fuel moisture content (LFMC; i.e. the ratio of water mass to dry mass of twigs and leaves within the vegetation) is considered to be one of the most relevant drivers of forest fire behaviour (Nolan *et al.*, 2016; Pimont *et al.*, 2019; Rao *et al.*, 2022). The sensitivity of LFMC to drought depends on plant physiological, structural and hydraulics traits, which differ across species and can vary widely over space and time (Jolly & Johnson, 2018; Ruffault *et al.*, 2018, 2023). Thus, under intense drought conditions, some species can reduce significantly the water flow to the leaves due to a xylem vulnerability segmentation between the leaves and the stems that makes leaf xylem cavitate at higher water potential (i.e. less resistance to cavitation) than stems (Charrier *et al.*, 2016; Levionnois *et al.*, 2020). Apart from exacerbating the dehydration of the leaves, this leaf hydraulic disconnection can trigger leaf senescence and drop (Tyree *et al.*, 1993; Scholz *et al.*, 2014) that will make LFMC to decrease. The same applies when there is significant hydraulic resistance segmentation between the leaves and the stems, for example a high resistance to water flow at the petiole level, which makes the water potential and water content to decay more rapidly in the leaves than in the stems (Tsuda & Tyree, 1997). Yet, despite a growing number of plant hydraulics models (Cochard *et al.*, 2021; Li *et al.*, 2021; Ruffault *et al.*, 2022), attempts to simulate LFMC considering plant hydraulic properties are still scarce (but see Ma *et al.*, 2021; Balaguer-Romano *et al.*, 2022). Recent studies have shown the major role of physiological traits (vulnerability to cavitation, hydraulic segmentation and transpiration regulation) on both leaf and canopy fuel moisture content (Ruffault *et al.*, 2023), but more research is needed to scale up predictions from the leaf or canopy level to the stand or landscape levels. It is also necessary to achieve a better integration between short-term physiological LFMC models (Balaguer-Romano *et al.*, 2022; Ruffault *et al.*, 2023) and microclimatic variation driven by the fire-plume so that this effect can be added to dynamical fire behaviour modelling (Dickman *et al.*, 2023).

Fire effects on plants are tightly linked both to the type of fire and its behaviour as well as to the plant regeneration mode. Thus, crown fires, canopy scorch or consumption by the fire are the main triggers for the mortality of juveniles (Hull Sieg *et al.*, 2006), although there are still some uncertainties about the critical fraction of crown mortality necessary for death (Resco de Dios *et al.*, 2020). Individuals that initially survive fire may succumb in the months or years following the disturbance when the cambium is charred and the tree girdled, due to fire-induced hydraulic dysfunction (Ducrey *et al.*, 1996; Kavanagh *et al.*, 2010; Michaletz *et al.*, 2012). Different mechanisms involving xylem hydraulics have been proposed to potentially explain postfire survival (Michaletz *et al.*, 2012; West *et al.*, 2016; Bär *et al.*, 2019). However, recent studies indicate that vascular cambium is more sensitive to high temperatures than the xylem, making phloem charring a likely candidate to explain postfire survival (Salladay & Pittermann, 2023). This observation is in accordance with the forestry literature, which considers bark thickness (along with canopy scorch) as an indicator of postfire mortality (Resco De Dios, 2020). For resprouting trees, however, fire-induced mortality is more difficult to characterize. It was traditionally considered that stored reserves played a major role for postfire recovery, but recent findings challenge this view and indicate a major effect of plant hydraulics-related processes (Nolan *et al.*, 2021). In this sense, it has been shown how oak trees are unable to resprout if a drought before the disturbance causes a loss of more than 50% in root hydraulic conductance, highlighting the critical role of root hydraulic conductance in the resprouting ability of trees (Resco de Dios *et al.*, 2020).

Improving postfire management requires therefore a better understanding of the mechanisms leading to potential recovery. Nowadays, at least in some Mediterranean countries, forests are often felled after the fire and sprout selection occurs later. This is because the fire is considered to have damaged the vascular tissue leading to stem necrosis. Hydraulic feedbacks could exacerbate the

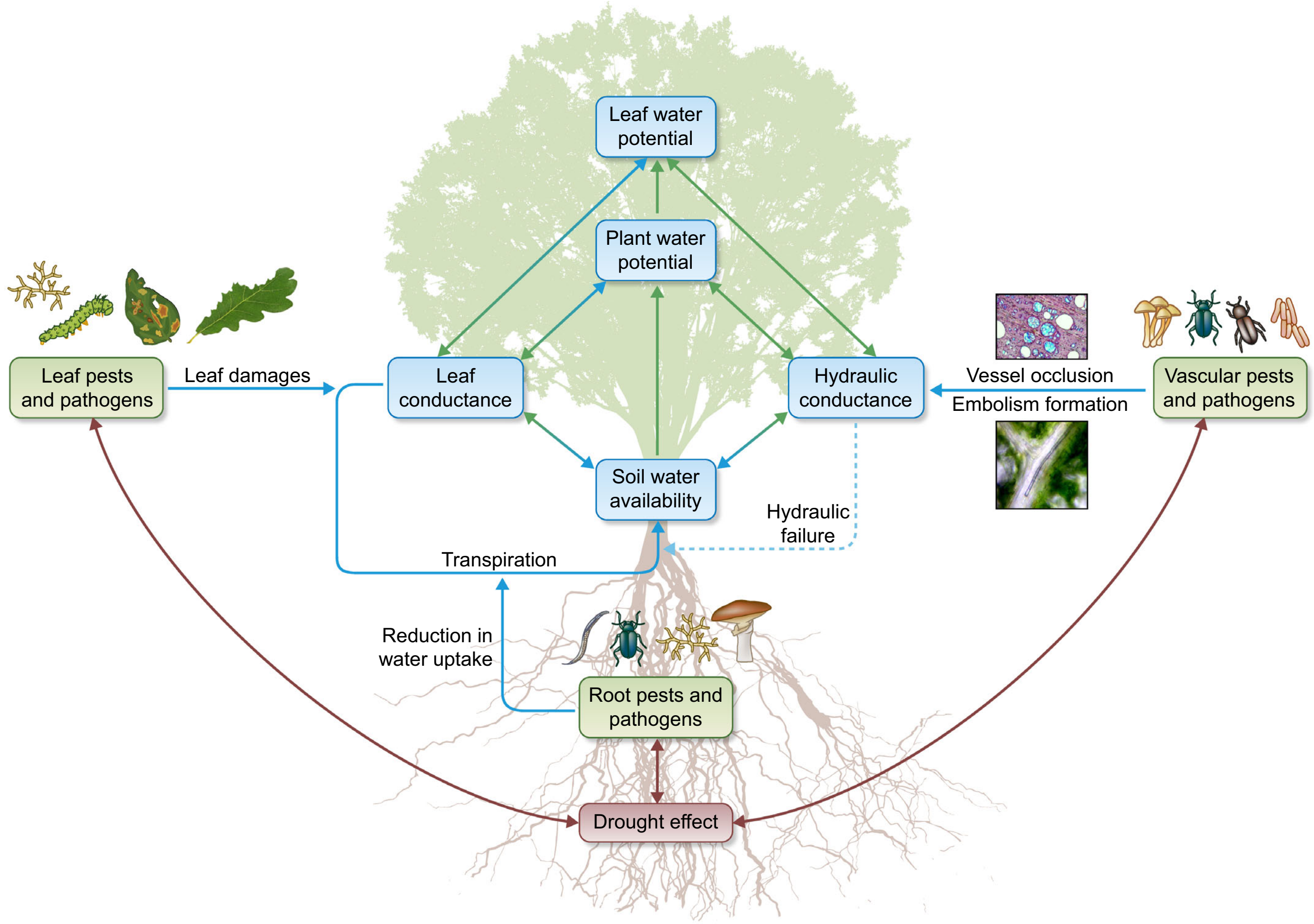

Fig. 4 Impacts of pests and pathogens on plant hydraulic traits. Green and blue arrows represent positive and negative relationships, respectively, between variables. The dashed blue line indicates the hydraulic disconnection that occurs following severe vessel occlusion (embolism and/or tyloses) and impedes the plant from continuing to transpire. Red arrows represent how plant pathogen infections or pest damages may also have an antagonistic or synergistic effect on plant response to drought.

responses when the fire was preceded by a strong drought that defoliated part of the canopy (hence enhancing fire behaviour as previously mentioned). Such feedbacks between prefire drought, fire behaviour and postfire legacy responses should be at the forefront of our research efforts (Karavani *et al.*, 2018).

V. Role of hydraulic traits on plant-herbivore insects–pathogens interactions

The xylem plays a key role in organizing defences against various biotic stresses (Shigo, 1984; Tyree & Zimmermann, 2002), but plant hydraulics is still rarely studied in the context of plant pathology and entomology. Vessel anatomy and compartmentalization, hydraulic conductivity, plant water status and stomatal conductance are traits that underlie plant interactions with insects or pathogens and pathological disturbances (Gely *et al.*, 2020). In addition, interactions between biotic and abiotic stressors can amplify their individual impacts on the capacity of the plants to absorb and transport water (Fig. 4; Griffin-Nolan *et al.*, 2021; McDowell *et al.*, 2022). Hence, it is time to recognize the pivotal role of plant hydraulic traits in plant–pathogen interactions and pave the way for further research in this domain.

Xylem vessels host a large breadth of endophytic microorganisms and some of them are vascular pathogens (Pearce, 1996). Plant responses to vascular fungi or bacteria, and the toxins they often produce, can lead to compartmentalization of the xylem in order to block the spread of the pathogen (Shigo, 1984; Yadeta & Thomma, 2013). This highlights the role of xylem anatomical characteristics in plant–pathogen interactions, for example, through the size of the vessels or the pits (Venturas *et al.*, 2014). Pathogenesis can induce losses in hydraulic conductance resulting from pathogen clogging of the xylem conduits (Deyett *et al.*, 2019; Ingel *et al.*, 2022), cavitation (Pérez-Donoso *et al.*, 2007) or vessel occlusion by gums and tyloses (Sun *et al.*, 2013; Bortolami *et al.*, 2019). These losses can lead to xylem hydraulic failure and induce irreversible dehydration of the distal organs (Mensah *et al.*, 2020; Bortolami *et al.*, 2021a). Recently, the use of X-ray microtomography coupled with the contrasting agent iohexol revealed an induced production of tyloses and/or gels and the subsequent loss in hydraulic conductivity *in vivo*, which shed new light on xylem functioning during vascular pathogenesis (Bortolami *et al.*, 2019, 2021a). As plant hydraulic functioning is directly linked to gas exchange and carbon metabolism (McDowell, 2011; Pinheiro & Chaves, 2011), these losses in hydraulic conductance induced by vascular pathogenesis can affect stomatal regulation (Bortolami *et al.*, 2021b).

Vascular dysfunction may also be linked to insect damages leading to the abnormal production of xylem (Liphschitz & Mendel, 1987), the alteration of xylem fibre anatomy (Hillabrand *et al.*, 2019b), the increase in vulnerability to embolism (Aguadé *et al.*, 2015) or the alteration of hydraulic conductivity (Hillabrand *et al.*, 2019a; Fig. 4). Also, insect mining damages induce the partial closure of the stomata, enriching leaf δ13C and reducing plant transpiration (Bansal, 2015; Peschiutta *et al.*, 2016; Wagner *et al.*, 2020). In the short term, this may have some positive effects for the plant as it would reduce water losses and thus its risk of hydraulic failure (Wagner *et al.*, 2020); however, it would also reduce considerably carbon assimilation. Leaf-mining insects not only compromise the leaf's water-retaining properties by feeding on both superficial and deeper living tissues, but epidermis mining can also result in cuticle breaks. This, in turn, leads to an increase in plant residual transpiration (Raimondo *et al.*, 2013), significantly elevating the risk of hydraulic failure in infected plants (Billon *et al.*, 2020; Blackman *et al.*, 2023).

Overall, biotic damage can increase in water-stressed plants. However, such damages also depend on the interactions between drought and biotic stressors, which, as the same time, are influenced by the pathogen's lifestyle (biotrophic, hemibiotrophic, vascular, necrotrophic; Jactel *et al.*, 2012, 2019; Supporting Information Fig. S1; Table S1; Notes S1), the insect feeding guild (xylem-tappers, bark or wood borers, leaf chewers or miners and gall formers; Gely *et al.*, 2020), as well as both the timing and intensity of water stress. Thus, too negative water potentials can limit the development of the xylem-inhabiting microorganisms (Beattie, 2011) and sap-feeding insects (Huberty & Denno, 2004) but also increase the susceptibility of conifers to bark beetle attacks through a decrease in duct and resin volume production (Gaylord *et al.*, 2013). Different pathogen and insect guilds can interact with plant hydraulic functioning (vessel occlusion; loss of hydraulic conductivity; and stomatal regulation) and/or carbon balance (carbohydrate consumption or activation of the plant defence response), which could impair maintenance of carbon-dependent metabolic, defence or hydraulic functions (Martínez-Vilalta, 2014; Anderegg, 2015; Jactel *et al.*, 2019; McDowell *et al.*, 2022). For example, insect defoliation can alter xylem fibre anatomy more consistently and severely than drought alone, likely leading to a reduced structural support to vessels and an increased vulnerability of defoliated plants to drought-induced cavitation when leaf area recovers (Hillabrand *et al.*, 2019b). Drought-induced stomatal closure can lead to a reduced production of carbon-based defensive compounds leading to amplified pathogen and insect attacks and damages (McDowell *et al.*, 2008). For example, low kino, resin or latex production have been shown to reduce tree capacity to resist secondary bark beetles and wood borer attacks (Gaylord *et al.*, 2013; Gely *et al.*, 2020) and low carbon availability for defence will reduce plant resistance to necrotrophs and vascular pathogens in particular (Oliva *et al.*, 2014). However, reduced nonstructural carbohydrate content on water-stressed trees may also alter host quality for insects and pathogens. For example, during severe drought conditions, the concentration of soluble sugars in phloem decreases, reducing nutritional compounds availability for sap-sucking and leaf-feeding insects (Gely *et al.*, 2020) as well as for biotroph pathogens that directly depend on the quality of the infected tissue (Oliva *et al.*, 2014).

The interactions between biotic and abiotic stresses may be synergistic (Croisé *et al.*, 2001; Gao *et al.*, 2017, p. 201; Lima *et al.*, 2019), antagonistic (Arango-Velez *et al.*, 2016; Bortolami *et al.*, 2021b), or neutral (Lopisso *et al.*, 2017), and they likely vary with the ecology of the biotic agent, abiotic stress intensity and the measured hydraulic traits (Bansal, 2015). Therefore, hydraulic traits play a key role in understanding the interaction between drought-induced decrease in plant water potential and plant functional response to biotic stressors, but they are rarely monitored in this context. In fact, among 62 reviewed studies on drought and cryptogamic disease interactions in plants (see Supporting Information), only 60% of them used an unambiguous metric of plant water status (leaf or stem water potential) to quantify drought intensity, while only 11% measured hydraulic traits (hydraulic conductance, gas exchange or RWC). Considering the interacting effects between biotic and abiotic stressors across latitudes and cropping systems is crucial to predict plant functioning under the actual climate change context, especially in the long term when abiotic and biotic factors can interact to predispose, incite, or contribute directly or indirectly to plant death (i.e. the 'death spiral', Manion, 1981; Griffin-Nolan *et al.*, 2021). Pathologists and entomologists should therefore explicitly quantify the plant water status in general, and plant hydraulic traits in particular, if we are to better understand the mechanisms involved in insect– or pathogen–plant interactions.

VI. Plant hydraulics as a hub for vegetation models

Vegetation function and dynamics process-based models (VFDM) are becoming necessary tools to predict the impact of climatic change on vegetation dynamics and associated ecosystem services. Historically, VFDM were primarily based on modelling the gas exchange between the canopy and the atmosphere, with a primary focus on carbon dynamics (Fatichi *et al.*, 2019). More recently, the implementation of plant hydraulics in VFDM has gained in popularity with strong expectations to improve predictions of the impact on tree physiology and thus on forests' response to climate change (Rowland *et al.*, 2021; Trugman, 2022).

Whole-plant hydraulic models simulating plant water use and transport (Sperry *et al.*, 1998), embolism and refilling (Edwards & Jarvis, 1982; Sperry *et al.*, 2003) and even drought-related mortality (Martıínez-Vilalta *et al.*, 2002) have long been available. However, it is only recently that such models have been framed with the goal of being operational to predict ecosystem functions and dynamics at global (Eller *et al.*, 2020) and local scales (De Cáceres *et al.*, 2021; Ruffault *et al.*, 2023). There are potential benefits of

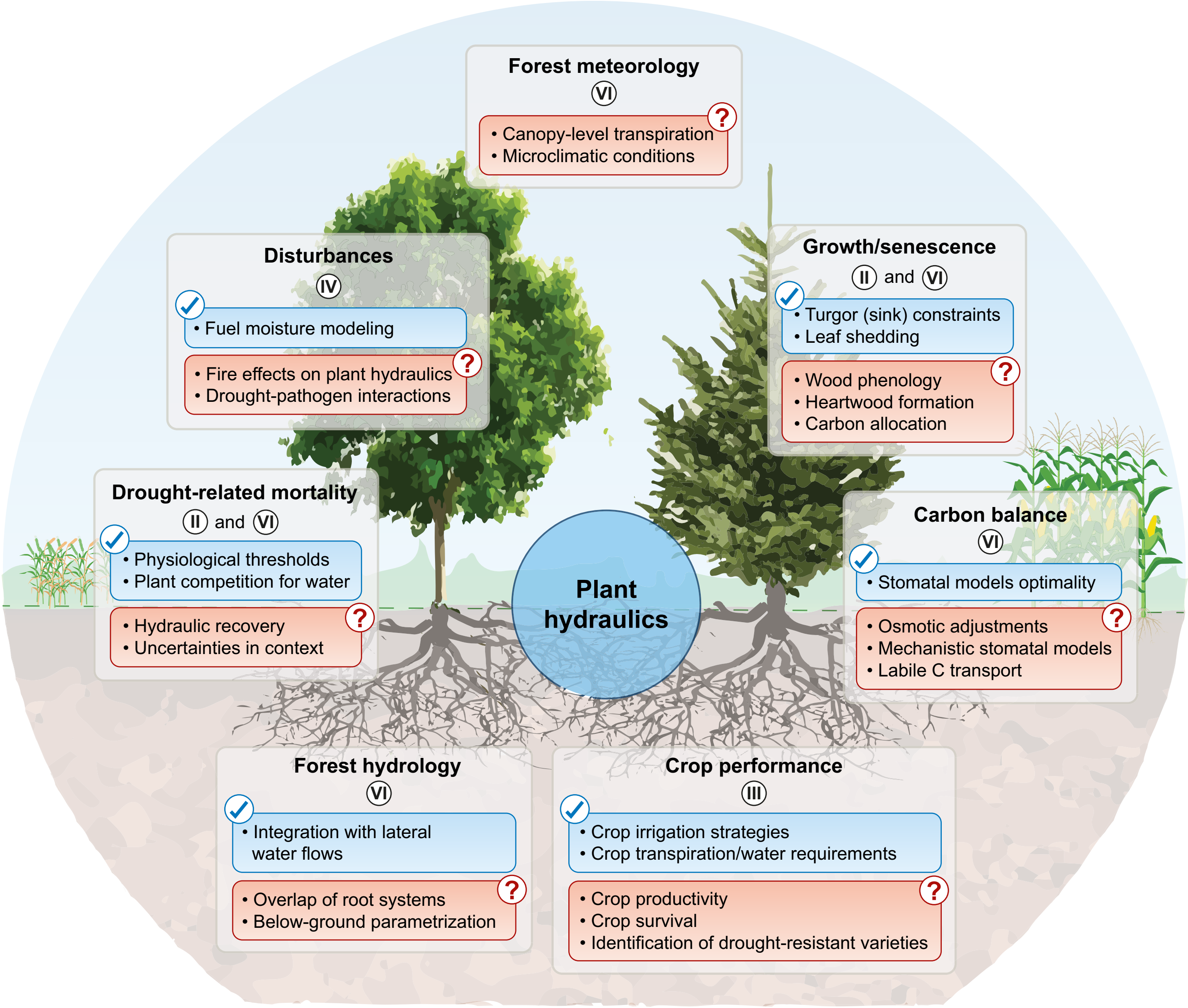

Fig. 5 Diagram summarizing the key advancements and challenges related to integrating plant hydraulic models into process-based models of vegetation function and dynamics. The diagram is organized both by discipline (hydrology and forestry), and by physiological processes and disturbances. Blue boxes summarize the main achievements and red boxes the main challenges. Numbers indicate the section in which the different processes are mainly, but not exclusively, discussed.

such integration, in particular the possibility to improve climate change impact simulations by mechanistically accounting for the combined effect of atmospheric and soil drought on the plant water status (e.g. water potential, Allen *et al.*, 2015; Martin-StPaul *et al.*, 2023; see Section I; Fig. 1). In fact, when implemented in multilayer vegetation models, this also allows to represent microclimatic effects on plant water status (De Cáceres *et al.*, 2021). In addition, the possibility of accounting for plant hydraulic traits and environmental conditions – increasingly available in different databases – enables the integration of knowledge and data to generalize predictions of the sequence of plant responses to drought (see Section I). For instance, the explicit representation of plant water potentials allows to account for sink limitations (i.e. cambial activity) when simulating secondary growth (Hayat *et al.*, 2017). More specifically, turgor effects can now be included, along with temperature effects, when predicting cambium division and cell expansion (Cabon *et al.*, 2020), although there are still some questions to address about the integration of these sink limitations with other determinants of xylogenesis, such as hormonal control (Hartmann *et al.*, 2017) or sugar availability (Cartenì *et al.*, 2018). In addition, thanks to their traits-based approach and the increasing knowledge of trait coordination and syndromes (Section VI) hydraulic models have also the potential to help identify trade-offs between productivity and stress tolerance (Section II) and improve the representation of succession and forest dynamics (Morin *et al.*, 2021). Plant hydraulic models also allow to model gas exchange during drought by accounting for plant water status (Fig. 5), opening the door to new stomatal behaviour models based on optimization criteria by balancing the carbon gain of opening stomata vs the risk of hydraulic failure (Wolf *et al.*, 2016; Sperry *et al.*, 2017).

Plant hydraulic modelling is seen as a promising tool to predict the disturbances related to water stress in VDFM. First, it enables the evaluation of drought-induced mortality caused by hydraulic failure and/or plant desiccation (De Kauwe *et al.*, 2020; Cochard *et al.*, 2021; Ruffault *et al.*, 2022), thanks to empirically determined thresholds (Section I). Furthermore, it can predict moisture content in different plant organs, which proves to be a better factor in explaining mortality (Mantova *et al.*, 2021; Section I) and could also be associated with other disturbances such as wildfire risk (see Section III). However, the most recent studies attempting to apply hydraulic models to predict mortality at a large scale, showed relatively modest improvements compared with more simple empirical approach (Venturas *et al.*, 2021). Nevertheless, this accuracy is expected to improve with a more robust parameterization not only of trait variability, but also of the structural properties of the stands and other environmental variables such as local edaphic conditions such as soil depth or percent rock content (Trugman *et al.*, 2021; Venturas *et al.*, 2021; Trugman, 2022). Another important aspect is gaining a better understanding of the interdependency between water and carbon processes and their role in mortality (McDowell *et al.*, 2022). In this sense, available models can simulate both xylem and sugar phloem transport (De Schepper & Steppe, 2010; Hölttä *et al.*, 2017), but a more precise mechanistic coupling is still required between water and carbon economies concerning water transport and stomatal behaviour. Additionally, simulating the legacies of previous drought impacts is challenging as it necessitates an explicit representation of functional sapwood area and accurate predictions of growth following drought events. While models incorporating plant hydraulics can simulate plant competition for water resources, advancements are needed to understand to what extent plants coexisting in the same stand share the same water pools. Furthermore, the linkage of plant hydraulic physiology to pathogens and pest attack risk (as mentioned in Section IV) is currently poorly implemented.

Apart from this, one of the most relevant challenges for the plant hydraulic models is appropriately parameterizing plant hydraulics, taking into account both interspecific and intraspecific variability. Global plant trait databases serve as essential data sources for this task. However, additional knowledge is required in cases where further scaling of tissue-level measurements to organ- or plant-level parameters is needed (see Section VI). Strategies such as utilizing trait relationships or other approaches to fill missing trait data (De Cáceres *et al.*, 2023) and considering plastic trait responses to changing environmental conditions are essential in this process.

VII. Water-use and drought tolerance strategies in the global spectrum of plant functions

Trait-based ecology posits that functional traits describe the ecological strategies of individuals and species, influence their performance and fitness and, therefore, allow predictions of population-level demographic rates, community dynamics and ecosystem functioning (Violle *et al.*, 2007). Among the different functional traits, tree hydraulics properties influence tree water use, photosynthesis and growth, while also crucially determining tolerance to drought. This makes hydraulic traits good candidates to predict tree behaviour and forest dynamics under actual climate change scenarios. However, a fundamental question remains: how are hydraulic traits related to the trait trade-off axes governing tree functions and forest demography? (Volaire, 2018; Guillemot *et al.*, 2022).

Current knowledge states that plant function can be largely captured by a fundamental axis differentiating the acquisitive and conservative strategies: the 'fast–slow' axis (Reich, 2014). The fast–slow axis was originally described as a leaf economic axis (Wright *et al.*, 2004), contrasting fast and slow return on investments of nutrients and dry mass in leaves, and was later proposed to apply at the whole-plant scale to explain individual performances and demography (Reich, 2014). Consequently, in this axis, leaf photosynthesis can be interpreted as a return on a building investment. As water mainly runs through the soil–plant–atmosphere continuum, this interpretation may not apply, and there is still an open debate on how to expand the axes related to carbon and nutrients to whole-plant water relations. Various studies suggested that species exhibiting high growth and/or acquisitive leaf traits tended to have lower hydraulic safety margin and xylem hydraulic resistance (Oliveira *et al.*, 2021; Guillemot *et al.*, 2022). This suggests that drought tolerance is, to some extent, aligned with the fast–slow axis, but the mechanisms involved remain elusive. In this sense, at least three nonexclusive mechanisms could be involved:

1. A direct trade-off among xylem traits

The hydraulic safety–efficiency trade-off states that species evolving xylem able to efficiently transport water are also more vulnerable to cavitation, due to inherent structural constraints. However, the relationship between safety and efficiency is very weak (Gleason *et al.*, 2016). Studies on this topic mostly considered efficiency as the ability to transport an amount of water in a small cross-section of living wood (i.e. space-use efficiency). However, other definitions of xylem hydraulic efficiencies exist (Bittencourt *et al.*, 2016; Mencuccini *et al.*, 2019) and deserve to be better explored in relation to drought tolerance, such as hydraulic energy efficiency (the energy invested – production and maintenance – in the hydraulic system) or the hydraulic nutrient efficiency (hydraulic conductance by unit nutrient invested). If these alternative definitions of efficiency show a clearer trade-off with drought tolerance, they would be compatible with the return-on-investment concept of the leaf economics, and would pertain to the mechanisms described in the next paragraph.

2. A trade-off between water relations and carbon and/or nutrient investment

A stomatal safety–efficiency trade-off was recently proposed (Henry *et al.*, 2019), where species with greater maximum stomatal conductance show greater sensitivity to closure during leaf dehydration, that is, a higher leaf water potential at which stomatal conductance is reduced. This trade-off potentially relates to the observation that species with high stomatal conductance at low VPD show a greater sensitivity to VPD, as originally described by (Oren *et al*., 1999). Overall, this implies that acquisitive species show greater isohydricity, that is, they have a narrower leaf operating range under water stress, which implies a higher (less negative) turgor loss point. Variation of turgor loss point between species is known to be largely driven by leaf osmolality (Bartlett *et al*., 2012), which is related to the nutrient and carbon investment in organic and/or inorganic solutes (Patakas *et al*., 2002). Therefore, anisohydry, that is wider leaf operating range under water stress, may come at the cost of higher structural and osmotic carbon and/or nutrient investment, which may align water relation strategies on the fast–slow axis.

3. An indirect effect of carbon or nutrient scarcity on water relation traits

Recent studies reported that tropical woody species with more resistant xylem occur preferentially on P-poor soils and they show low leaf P concentration (Oliveira *et al*., 2019; Guillemot *et al*., 2022). Although this pattern could arise from the mentioned energy or nutrient cost of water transport, it could also merely result from the fact that nutrient-poor soils impose slow conservative strategies that favour efficient nutrient use and low tissue turnover. This results in species growing dense, small-vessel wood (Heineman *et al*., 2016), which may also exhibit high xylem resistance to embolism. In such a case, the association between drought tolerance and slow strategy would not arise from adaptive trade-offs but rather from an exaptive result of resource scarcity (Laughlin *et al*., 2020). Understanding the mechanisms by which nutrient limitation affects xylem anatomy and function in plants could significantly improve predictions of plant survival during drought across different locations, environments and even taxonomic groups (Cary *et al*., 2020).

In resume, future research needs to link root-scale, xylem-scale and leaf-scale water relation traits and processes to plant growth, reproduction and mortality. This will allow us, on the one hand, to better predict forest dynamics under climate change and, on the other hand, to unveil the evolutionary and physiological constraints within which breeding programs can seek to improve plant species performances.

VIII. Conclusions and prospects

Variations in plant hydraulic properties, such as conductivity and resistance, can have a profound impact on plant water relations. These changes can directly affect critical plant functions, such as stomatal behaviour, photosynthetic capacity, growth and susceptibility to environmental stressors and disturbances such as drought, pathogens and wildfires. The purpose of this review is to highlight the increasing significance of plant hydraulics in diverse scientific disciplines that have recognized hydraulic traits as critical components. Thus, the integration of the plant hydraulic properties into studies and vegetation models aimed at understanding the functioning and response of ecosystems under drought conditions is crucial for the evaluation of plant response to drought and its impacts on forest and agronomic ecosystems. Indeed, this will provide novel information for selecting and breeding more resilient and productive species or varieties to maintain their productivity even under drought conditions. Similarly, plant hydraulics-related processes are key for evaluating fire activity, encompassing biogeographical patterns of burned areas, fuel dynamics and the interplay between prefire drought, fire behaviour and postfire effects. It can also significantly improve our understanding of the mechanisms involved in insect– or pathogen–plant interactions and of the influence of drought on them. Also, understanding the relationship between hydraulic traits and the trade-offs defining a more acquisitive or conservative strategy for the different species is a fundamental question to plant behaviour and forest dynamics in the face of climate change. Therefore, expanding the use of these hydraulic aspects to other fields and disciplines offers promising perspectives for assessing and predicting the effects that climate change and, more specifically, drought will have on both forestry and agricultural systems through its influence on both abiotic and biotic factors.

Acknowledgements

This article is an output of the international network ‘PsiHub’ funded and supported by the ECODIV department of INRAE. This review was partly supported by the H2020 Project FORGENIUS (Improving access to FORest GENetic resources Information and services for end-USers) #862221.

Competing interests

None declared.

ORCID

Thomas Boivin https://orcid.org/0000-0003-1694-2425
Regis Burlett https://orcid.org/0000-0001-8289-5757
Maxime Cailleret https://orcid.org/0000-0001-6561-1943
Hervé Cochard https://orcid.org/0000-0002-2727-7072
Déborah Corso https://orcid.org/0000-0002-3797-0153
Miquel De Caceres https://orcid.org/0000-0001-7132-2080
Victor Resco De Dios https://orcid.org/0000-0002-5721-1656
Chloé E. L. Delmas https://orcid.org/0000-0003-3568-605X
Sylvain Delzon https://orcid.org/0000-0003-3442-1711
Antonio Diaz-Espejo https://orcid.org/0000-0002-4711-2494
Pilar Fernández-Conradi https://orcid.org/0000-0001-7025-2623
Joannes Guillemot https://orcid.org/0000-0003-4385-7656
Laurent J. Lamarque https://orcid.org/0000-0002-1430-5193
Jean-Marc Limousin https://orcid.org/0000-0002-2734-2495
Marylou Mantova https://orcid.org/0000-0003-4445-3100
Nicolas K. Martin-StPaul https://orcid.org/0000-0001-7574-0108
Maurizio Mencuccini https://orcid.org/0000-0003-0840-1477
Xavier Morin https://orcid.org/0000-0003-1961-8700
François Pimont https://orcid.org/0000-0002-9842-6207

Julien Ruffault https://orcid.org/0000-0003-3647-8172
José M. Torres-Ruiz https://orcid.org/0000-0003-1367-7056
Santiago Trueba https://orcid.org/0000-0001-8218-957X

References

Abdalla M, Ahmed MA, Cai G, Wankmüller F, Schwartz N, Litig O, Javaux M, Carminati A. 2022. Stomatal closure during water deficit is controlled by below-ground hydraulics. *Annals of Botany* **129**: 161–170.

Adams HD, Zeppel MJB, Anderegg WRL, Hartmann H, Landhäusser SM, Tissue DT, Huxman TE, Hudson PJ, Franz TE, Allen CD *et al.* 2017. A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature Ecology & Evolution* **1**: 1285–1291.

Aguadé D, Poyatos R, Gómez M, Oliva J, Martínez-Vilalta J. 2015. The role of defoliation and root rot pathogen infection in driving the mode of drought-related physiological decline in Scots pine (*Pinus sylvestris* L.). *Tree Physiology* **35**: 229–242.

Ahmad HB, Lens F, Capdeville G, Burlett R, Lamarque LJ, Delzon S. 2018. Intraspecific variation in embolism resistance and stem anatomy across four sunflower (*Helianthus annuus* L.) accessions. *Physiologia Plantarum* **163**: 59–72.

Allen CD, Breshears DD, McDowell NG. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**: art129.

Anderegg WRL. 2015. Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. *New Phytologist* **205**: 1008–1014.

Andrade MT, Oliveira LA, Pereira TS, Cardoso AA, Batista-Silva W, DaMatta FM, Zsögön A, Martins SCV. 2022. Impaired auxin signaling increases vein and stomatal density but reduces hydraulic efficiency and ultimately net photosynthesis. *Journal of Experimental Botany* **73**: 4147–4156.

Arango-Velez A, El Kayal W, Copeland CCJ, Zaharia LI, Lusebrink I, Cooke JEK. 2016. Differences in defence responses of *Pinus contorta* and *Pinus banksiana* to the mountain pine beetle fungal associate *Grosmannia clavigera* are affected by water deficit. *Plant, Cell & Environment* **39**: 726–744.

Araus JL, Sanchez-Bragado R, Vicente R. 2021. Improving crop yield and resilience through optimization of photosynthesis: panacea or pipe dream? *Journal of Experimental Botany* **72**: 3936–3955.

Balaguer-Romano R, Díaz-Sierra R, De Cáceres M, Cunill-Camprubí À, Nolan RH, Boer MM, Voltas J, Resco de Dios V. 2022. A semi-mechanistic model for predicting daily variations in species-level live fuel moisture content. *Agricultural and Forest Meteorology* **323**: 109022.

Bansal S. 2015. The interactive effects of drought and herbivory on ecophysiology of trees. In: Mahalingam R, ed. *Combined stresses in plants.* Cham, Switzerland: Springer International Publishing, 245–259.

Bär A, Michaletz ST, Mayr S. 2019. Fire effects on tree physiology. *New Phytologist* **223**: 1728–1741.

Barbero R, Abatzoglou JT, Larkin NK, Kolden CA, Stocks B, Barbero R, Abatzoglou JT, Larkin NK, Kolden CA, Stocks B. 2015. Climate change presents increased potential for very large fires in the contiguous United States. *International Journal of Wildland Fire* **24**: 892–899.

Bartlett MK, Klein T, Jansen S, Choat B, Sack L. 2016. The correlations and sequence of plant stomatal, hydraulic, and wilting responses to drought. *Proceedings of the National Academy of Sciences, USA* **113**: 13098–13103.

Bartlett MK, Scoffoni C, Sack L. 2012. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecology Letters* **15**: 393–405.

Beattie GA. 2011. Water relations in the interaction of foliar bacterial pathogens with plants. *Annual Review of Phytopathology* **49**: 533–555.

Beikircher B, De Cesare C, Mayr S. 2013. Hydraulics of high-yield orchard trees: a case study of three *Malus domestica* cultivars. *Tree Physiology* **33**: 1296–1307.

Billon LM, Blackman CJ, Cochard H, Badel E, Hitmi A, Cartailler J, Souchal R, Torres-Ruiz JM. 2020. The DroughtBox: a new tool for phenotyping residual branch conductance and its temperature dependence during drought. *Plant, Cell & Environment* **43**: 1584–1594.

Bittencourt PRL, Pereira L, Oliveira RS. 2016. On xylem hydraulic efficiencies, wood space-use and the safety-efficiency tradeoff: comment on Gleason *et al.* (2016) 'Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species'. *New Phytologist* **211**: 1152–1155.

Blackman CJ, Billon L-M, Cartailler J, Torres-Ruiz JM, Cochard H. 2023. Key hydraulic traits control the dynamics of plant dehydration in four contrasting tree species during drought. *Tree Physiology* **43**: 1772–1783.

Boer MM, Dios VRD, Stefaniak EZ, Bradstock RA. 2021. A hydroclimatic model for the distribution of fire on earth. *Environmental Research Communications* **3**: 35001.

Boini A, Bresilla K, Perulli GD, Manfrini L, Corelli Grappadelli L, Morandi B. 2019. Photoselective nets impact apple sap flow and fruit growth. *Agricultural Water Management* **226**: 105738.

Bortolami G, Farolfi E, Badel E, Burlett R, Cochard H, Ferrer N, King A, Lamarque LJ, Lecomte P, Marchesseau-Marchal M *et al.* 2021a. Seasonal and long-term consequences of esca grapevine disease on stem xylem integrity. *Journal of Experimental Botany* **72**: 3914–3928.

Bortolami G, Gambetta GA, Cassan C, Dayer S, Farolfi E, Ferrer N, Gibon Y, Jolivet J, Lecomte P, Delmas CEL. 2021b. Grapevines under drought do not express esca leaf symptoms. *Proceedings of the National Academy of Sciences, USA* **118**: e2112825118.

Bortolami G, Gambetta GA, Delzon S, Lamarque LJ, Pouzoulet J, Badel E, Burlett R, Charrier G, Cochard H, Dayer S *et al.* 2019. Exploring the hydraulic failure hypothesis of esca leaf symptom formation. *Plant Physiology* **181**: 1163–1174.

Bowman DMJS, Kolden CA, Abatzoglou JT, Johnston FH, van der Werf GR, Flannigan M. 2020. Vegetation fires in the Anthropocene. *Nature Reviews Earth and Environment* **1**: 500–515.

Brodribb TJ. 2009. Xylem hydraulic physiology: the functional backbone of terrestrial plant productivity. *Plant Science* **177**: 245–251.

Brodribb TJ, Cochard H. 2009. Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiology* **149**: 575–584.

Brodribb TJ, Holbrook NM, Edwards EJ, Gutiérrez MV. 2003. Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. *Plant, Cell & Environment* **26**: 443–450.

Cabon A, Fernández-de-Uña L, Gea-Izquierdo G, Meinzer FC, Woodruff DR, Martínez-Vilalta J, De Cáceres M. 2020. Water potential control of turgor-driven tracheid enlargement in Scots pine at its xeric distribution edge. *New Phytologist* **225**: 209–221.

Cartenì F, Deslauriers A, Rossi S, Morin H, De Micco V, Mazzoleni S, Giannino F. 2018. The physiological mechanisms behind the earlywood-to-latewood transition: a process-based modeling approach. *Frontiers in Plant Science* **9**: 1053.

Cary KL, Ranieri GM, Pittermann J. 2020. Xylem form and function under extreme nutrient limitation: an example from California's pygmy forest. *New Phytologist* **226**: 760–769.

Charrier G, Torres-Ruiz JM, Badel E, Burlett R, Choat B, Cochard H, Delmas CEL, Domec J-C, Jansen S, King A *et al.* 2016. Evidence for hydraulic vulnerability segmentation and lack of xylem refilling under tension. *Plant Physiology* **172**: 1657–1668.

Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG *et al.* 2012. Global convergence in the vulnerability of forests to drought. *Nature* **491**: 752–755.

Clarke H, Nolan RH, De Dios VR, Bradstock R, Griebel A, Khanal S, Boer MM. 2022. Forest fire threatens global carbon sinks and population centres under rising atmospheric water demand. *Nature Communications* **13**: 7161.

Clearwater MJ, Luo Z, Ong SEC, Blattmann P, Thorp TG. 2012. Vascular functioning and the water balance of ripening kiwifruit (*Actinidia chinensis*) berries. *Journal of Experimental Botany* **63**: 1835–1847.

Cochard H. 2002. A technique for measuring xylem hydraulic conductance under high negative pressures. *Plant, Cell & Environment* **25**: 815–819.

Cochard H, Pimont F, Ruffault J, Martin-StPaul N. 2021. SurEau: a mechanistic model of plant water relations under extreme drought. *Annals of Forest Science* **78**: 55.

Corso D, Delzon S, Lamarque LJ, Cochard H, Torres-Ruiz JM, King A, Brodribb T. 2020. Neither xylem collapse, cavitation, or changing leaf conductance drive stomatal closure in wheat. *Plant, Cell & Environment* **43**: 854–865.

Croisé L, Lieutier F, Cochard H, Dreyer E. 2001. Effects of drought stress and high density stem inoculations with *Leptographium wingfieldii* on hydraulic properties of young Scots pine trees. *Tree Physiology* **21**: 427–436.

Dayer S, Herrera JC, Dai Z, Burlett R, Lamarque LJ, Delzon S, Bortolami G, Cochard H, Gambetta GA. 2020. The sequence and thresholds of leaf hydraulic traits underlying grapevine varietal differences in drought tolerance. *Journal of Experimental Botany* **71**: 4333–4344.

Dayer S, Lamarque LJ, Burlett R, Bortolami G, Delzon S, Herrera JC, Cochard H, Gambetta GA. 2022. Model-assisted ideotyping reveals trait syndromes to adapt viticulture to a drier climate. *Plant Physiology* **190**: 1673–1686.

De Cáceres M, Mencuccini M, Martin-StPaul N, Limousin J-M, Coll L, Poyatos R, Cabon A, Granda V, Forner A, Valladares F *et al.* 2021. Unravelling the effect of species mixing on water use and drought stress in Mediterranean forests: a modelling approach. *Agricultural and Forest Meteorology* **296**: 108233.

De Cáceres M, Molowny-Horas R, Cabon A, Martínez-Vilalta J, Mencuccini M, García-Valdés R, Nadal-Sala D, Sabaté S, Martin-StPaul N, Morin X *et al.* 2023. MEDFATE 2.9.3: a trait-enabled model to simulate Mediterranean forest function and dynamics at regional scales. *Geoscientific Model Development* **16**: 3165–3201.

De Kauwe MG, Medlyn BE, Ukkola AM, Mu M, Sabot MEB, Pitman AJ, Meir P, Cernusak LA, Rifai SW, Choat B *et al.* 2020. Identifying areas at risk of drought-induced tree mortality across South-Eastern Australia. *Global Change Biology* **26**: 5716–5733.

De Micco V, Aronne G. 2012. Morpho-anatomical traits for plant adaptation to drought. In: Aroca R, ed. *Plant responses to drought stress*. Berlin, Heidelberg, Germany: Springer Berlin Heidelberg, 37–61.

De Schepper V, Steppe K. 2010. Development and verification of a water and sugar transport model using measured stem diameter variations. *Journal of Experimental Botany* **61**: 2083–2099.

De Swaef T, Pieters O, Appeltans S, Borra-Serrano I, Coudron W, Couvreur V, Garré S, Lootens P, Nicolaï B, Pols L *et al.* 2022. On the pivotal role of water potential to model plant physiological processes. *In Silico Plants* **4**: diab038.

Deyett E, Pouzoulet J, Yang J-I, Ashworth VE, Castro C, Roper MC, Rolshausen PE. 2019. Assessment of Pierce's disease susceptibility in *Vitis vinifera* cultivars with different pedigrees. *Plant Pathology* **68**: 1079–1087.

Dickman LT, Jonko AK, Linn RR, Altintas I, Atchley AL, Bär A, Collins AD, Dupuy J-L, Gallagher MR, Hiers JK *et al.* 2023. Integrating plant physiology into simulation of fire behavior and effects. *New Phytologist* **238**: 952–970.

Dowdy AJ, Ye H, Pepler A, Thatcher M, Osbrough SL, Evans JP, Di Virgilio G, McCarthy N. 2019. Future changes in extreme weather and pyroconvection risk factors for Australian wildfires. *Scientific Reports* **9**: 10073.

Ducrey M, Duhoux F, Huc R, Rigolot E. 1996. The ecophysiological and growth responses of Aleppo pine (*Pinus halepensis*) to controlled heating applied to the base of the trunk. *Canadian Journal of Forest Research* **26**: 1366–1374.

Edwards WRN, Jarvis PG. 1982. Relations between water content, potential and permeability in stems of conifers. *Plant, Cell & Environment* **5**: 271–277.

Eller CB, Rowland L, Mencuccini M, Rosas T, Williams K, Harper A, Medlyn BE, Wagner Y, Klein T, Teodoro GS *et al.* 2020. Stomatal optimization based on xylem hydraulics (SOX) improves land surface model simulation of vegetation responses to climate. *New Phytologist* **226**: 1622–1637.

Fàbregas N, Fernie AR. 2019. The metabolic response to drought. *Journal of Experimental Botany* **70**: 1077–1085.

Fatichi S, Pappas C, Zscheischler J, Leuzinger S. 2019. Modelling carbon sources and sinks in terrestrial vegetation. *New Phytologist* **221**: 652–668.

Flexas J, Carriquí M, Nadal M. 2018. Gas exchange and hydraulics during drought in crops: who drives whom? *Journal of Experimental Botany* **69**: 3791–3795.

Flexas J, Medrano H. 2002. Drought-inhibition of photosynthesis in C3 plants: stomatal and non-stomatal limitations revisited. *Annals of Botany* **89**: 183–189.

Gao X, Zhou X, Wang H, Kong X, Zhang S, Wang Z, Wu W, Zhang Z, Lieutier F. 2017. Influence of severe drought on the resistance of *Pinus yunnanensis* to a bark beetle-associated fungus. *Forest Pathology* **47**: e12345.

Gaylord ML, Kolb TE, Pockman WT, Plaut JA, Yepez EA, Macalady AK, Pangle RE, McDowell NG. 2013. Drought predisposes piñon–juniper woodlands to insect attacks and mortality. *New Phytologist* **198**: 567–578.

Gely C, Laurance SGW, Stork NE. 2020. How do herbivorous insects respond to drought stress in trees? *Biological Reviews* **95**: 434–448.

Gerbi H, Paudel I, Zisovich A, Sapir G, Ben-Dor S, Klein T. 2022. Physiological drought resistance mechanisms in wild species vs rootstocks of almond and plum. *Trees* **36**: 669–683.

Gleason SM, Westoby M, Jansen S, Choat B, Hacke UG, Pratt RB, Bhaskar R, Brodribb TJ, Bucci SJ, Cao K-F *et al.* 2016. Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist* **209**: 123–136.

Griffin-Nolan RJ, Mohanbabu N, Araldi-Brondolo S, Ebert AR, LeVonne J, Lumbsden-Pinto JI, Roden H, Stark JR, Tourville J, Becklin KM *et al.* 2021. Friend or foe? The role of biotic agents in drought-induced plant mortality. *Plant Ecology* **222**: 537–548.

Guillemot J, Martin-StPaul NK, Bulascoschi L, Poorter L, Morin X, Pinho BX, le Maire G, Bittencourt PRL, Oliveira RS, Bongers F *et al.* 2022. Small and slow is safe: on the drought tolerance of tropical tree species. *Global Change Biology* **28**: 2622–2638.

Hammond WM, Williams AP, Abatzoglou JT, Adams HD, Klein T, López R, Sáenz-Romero C, Hartmann H, Breshears DD, Allen CD. 2022. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nature Communications* **13**: 1761.

Hammond WM, Yu K, Wilson LA, Will RE, Anderegg WRL, Adams HD. 2019. Dead or dying? Quantifying the point of no return from hydraulic failure in drought-induced tree mortality. *New Phytologist* **223**: 1834–1843.

Hartmann FPK, Rathgeber CB, Fournier M, Moulia B. 2017. Modelling wood formation and structure: power and limits of a morphogenetic gradient in controlling xylem cell proliferation and growth. *Annals of Forest Science* **74**: 1–15.

Hayat A, Hacket-Pain AJ, Pretzsch H, Rademacher TT, Friend AD. 2017. Modeling tree growth taking into account carbon source and sink limitations. *Frontiers in Plant Science* **8**: 182.

Heineman KD, Turner BL, Dalling JW. 2016. Variation in wood nutrients along a tropical soil fertility gradient. *New Phytologist* **211**: 440–454.

Henry C, John GP, Pan R, Bartlett MK, Fletcher LR, Scoffoni C, Sack L. 2019. A stomatal safety-efficiency trade-off constrains responses to leaf dehydration. *Nature Communications* **10**: 3398.

Hillabrand RM, Hacke UG, Lieffers VJ. 2019a. Defoliation constrains xylem and phloem functionality. *Tree Physiology* **39**: 1099–1108.

Hillabrand RM, Lieffers VJ, Hogg EH, Martínez-Sancho E, Menzel A, Hacke UG. 2019b. Functional xylem anatomy of aspen exhibits greater change due to insect defoliation than to drought. *Tree Physiology* **39**: 45–54.

Hölttä T, Lintunen A, Chan T, Mäkelä A, Nikinmaa E. 2017. A steady-state stomatal model of balanced leaf gas exchange, hydraulics and maximal source–sink flux. *Tree Physiology* **37**: 851–868.

Howitt R, MacEwan D, Medellín-Azuara J, Lund J, Sumner D. 2015. *Economic analysis of the 2015 drought for California Agriculture*. Davis, CA, USA: Center for Watershed Sciences, University of California – Davis.

Huberty AF, Denno RF. 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology* **85**: 1383–1398.

Hull Sieg C, McMillin JD, Fowler JF, Allen KK, Negron JF, Wadleigh LL, Anhold JA, Gibson KE. 2006. Best predictors for postfire mortality of ponderosa pine trees in the intermountain west. *Forest Science* **52**: 718–728.

Ingel B, Caldwell D, Duong F, Parkinson DY, McCulloh KA, Iyer-Pascuzzi AS, McElrone AJ, Lowe-Power TM. 2022. Revisiting the source of wilt symptoms: X-ray microcomputed tomography provides direct evidence that *Ralstonia* biomass clogs xylem vessels. *PhytoFrontiers* **2**: 41–51.

Jactel H, Koricheva J, Castagneyrol B. 2019. Responses of forest insect pests to climate change: not so simple. *Current Opinion in Insect Science* **35**: 103–108.

Jactel H, Petit J, Desprez-Loustau M-L, Delzon S, Piou D, Battisti A, Koricheva J. 2012. Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology* **18**: 267–276.

Jolly WM, Johnson DM. 2018. Pyro-ecophysiology: shifting the paradigm of live wildland fuel research. *Fire* **1**: 8.

Karavani A, Boer MM, Baudena M, Colinas C, Díaz-Sierra R, Pemán J, de Luis M, Enríquez-de-Salamanca Á, Resco de Dios V. 2018. Fire-induced deforestation in drought-prone Mediterranean forests: drivers and unknowns from leaves to communities. *Ecological Monographs* **88**: 141–169.

Kavanagh KL, Dickinson MB, Bova AS. 2010. A way forward for fire-caused tree mortality prediction: modeling a physiological consequence of fire. *Fire Ecology* **6**: 80–94.

Klein T, Torres-Ruiz JM, Albers JJ. 2022. Conifer desiccation in the 2021 NW heatwave confirms the role of hydraulic damage. *Tree Physiology* **42**: 722–726.

Lamarque LJ, Delzon S, Toups H, Gravel A-I, Corso D, Badel E, Burlett R, Charrier G, Cochard H, Jansen S *et al.* 2020. Over-accumulation of abscisic acid in transgenic tomato plants increases the risk of hydraulic failure. *Plant, Cell & Environment* **43**: 548–562.

Lamy J-B, Delzon S, Bouche PS, Alia R, Vendramin GG, Cochard H, Plomion C. 2014. Limited genetic variability and phenotypic plasticity detected for cavitation resistance in a Mediterranean pine. *New Phytologist* **201**: 874–886.

Laughlin DC, Delzon S, Clearwater MJ, Bellingham PJ, McGlone MS, Richardson SJ. 2020. Climatic limits of temperate rainforest tree species are explained by xylem embolism resistance among angiosperms but not among conifers. *New Phytologist* **226**: 727–740.

Lawlor DW. 1995. Photosynthesis, productivity and environment. *Journal of Experimental Botany* **46**: 1449–1461.

Lesk C, Rowhani P, Ramankutty N. 2016. Influence of extreme weather disasters on global crop production. *Nature* **529**: 84–87.

Levionnois S, Ziegler C, Jansen S, Calvet E, Coste S, Stahl C, Salmon C, Delzon S, Guichard C, Heuret P. 2020. Vulnerability and hydraulic segmentations at the stem–leaf transition: coordination across Neotropical trees. *New Phytologist* **228**: 512–524.

Li L, Yang Z-L, Matheny AM, Zheng H, Swenson SC, Lawrence DM, Barlage M, Yan B, McDowell NG, Leung LR. 2021. Representation of plant hydraulics in the NOAH-MP land surface model: model development and multiscale evaluation. *Journal of Advances in Modeling Earth Systems* **13**: e2020MS002214.

Lima LKS, de Jesus ON, Soares TL, de Oliveira SAS, Haddad F, Girardi EA. 2019. Water deficit increases the susceptibility of yellow passion fruit seedlings to Fusarium wilt in controlled conditions. *Scientia Horticulturae* **243**: 609–621.

Liphschitz N, Mendel Z. 1987. Histological studies of *Pinus halepensis* stem xylem affected by *Matsucoccus josephi* (Homoptera: Margarodidae). *IAWA Journal* **8**: 369–376.

Littell JS, Peterson DL, Riley KL, Liu Y, Luce CH. 2016. A review of the relationships between drought and forest fire in the United States. *Global Change Biology* **22**: 2353–2369.

Lobo A, Torres-Ruiz JM, Burlett R, Lemaire C, Parise C, Francioni C, Truffaut L, Tomášková I, Hansen JK, Kjær ED *et al.* 2018. Assessing inter- and intraspecific variability of xylem vulnerability to embolism in oaks. *Forest Ecology and Management* **424**: 53–61.

Lockhart JA. 1965. An analysis of irreversible plant cell elongation. *Journal of Theoretical Biology* **8**: 264–275.

Lopisso DT, Knüfer J, Koopmann B, von Tiedemann A. 2017. The vascular pathogen *Verticillium longisporum* does not affect water relations and plant responses to drought stress of its host, *Brassica napus. Phytopathology* **107**: 444–454.

Ma W, Zhai L, Pivovaroff A, Shuman J, Buotte P, Ding J, Christoffersen B, Knox R, Moritz M, Fisher RA *et al.* 2021. Assessing climate change impacts on live fuel moisture and wildfire risk using a hydrodynamic vegetation model. *Biogeosciences* **18**: 4005–4020.

Machado R, Loram-Lourenço L, Farnese FS, Alves RDFB, de Sousa LF, Silva FG, Filho SCV, Torres-Ruiz JM, Cochard H, Menezes-Silva PE. 2021. Where do leaf water leaks come from? Trade-offs underlying the variability in minimum conductance across tropical savanna species with contrasting growth strategies. *New Phytologist* **229**: 1415–1430.

Manion PD. 1981. *Tree disease concepts.* Englewood Cliffs, NJ, USA: Prentice-Hall.

Mantova M, Cochard H, Burlett R, Delzon S, King A, Rodriguez-Dominguez CM, Ahmed MA, Trueba S, Torres-Ruiz JM. 2023. On the path from xylem hydraulic failure to downstream cell death. *New Phytologist* **237**: 793–806.

Mantova M, Herbette S, Cochard H, Torres-Ruiz JM. 2022. Hydraulic failure and tree mortality: from correlation to causation. *Trends in Plant Science* **27**: 335–345.

Mantova M, Menezes-Silva PE, Badel E, Cochard H, Torres-Ruiz JM. 2021. The interplay of hydraulic failure and cell vitality explains tree capacity to recover from drought. *Physiologia Plantarum* **172**: 247–257.

Martínez-Vilalta J. 2014. Carbon storage in trees: pathogens have their say. *Tree Physiology* **34**: 215–217.

Martı́nez-Vilalta J, Piñol J, Beven K. 2002. A hydraulic model to predict drought-induced mortality in woody plants: an application to climate change in the Mediterranean. *Ecological Modelling* **155**: 127–147.

Martin-StPaul N, Delzon S, Cochard H. 2017. Plant resistance to drought depends on timely stomatal closure. *Ecology Letters* **20**: 1437–1447.

Martin-StPaul N, Ruffault J, Guillemot J, Barbero R, Cochard H, Cailleret M, Caceres MD, Dupuy J-L, Pimont F, Torres-Ruiz JM *et al.* 2023. How much does VPD drive tree water stress and forest disturbances? *Preprints.* doi: 10.22541/au.168147010.01270793/v1.

Matthews MA, Shackel KA. 2005. 9 - Growth and water transport in fleshy fruit. In: Holbrook NM, Zwieniecki MA, eds. *Physiological ecology. Vascular transport in plants.* Burlington, NC, USA: Academic Press, 181–197.

McDowell N, Allen CD, Anderson-Teixeira K, Brando P, Brienen R, Chambers J, Christoffersen B, Davies S, Doughty C, Duque A *et al.* 2018. Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytologist* **219**: 851–869.

McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG *et al.* 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* **178**: 719–739.

McDowell NG. 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology* **155**: 1051–1059.

McDowell NG, Sapes G, Pivovaroff A, Adams HD, Allen CD, Anderegg WRL, Arend M, Breshears DD, Brodribb T, Choat B *et al.* 2022. Mechanisms of woody-plant mortality under rising drought, CO_2 and vapour pressure deficit. *Nature Reviews Earth and Environment* **3**: 294–308.

Mencuccini M, Rosas T, Rowland L, Choat B, Cornelissen H, Jansen S, Kramer K, Lapenis A, Manzoni S, Niinemets Ü *et al.* 2019. Leaf economics and plant hydraulics drive leaf: wood area ratios. *New Phytologist* **224**: 1544–1556.

Mensah JK, Sayer MAS, Nadel RL, Matusick G, Eckhardt LG. 2020. Physiological response of *Pinus taeda* L. trees to stem inoculation with *Leptographium terebrantis. Trees* **34**: 869–880.

Michaletz ST, Johnson EA, Tyree MT. 2012. Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires. *New Phytologist* **194**: 254–263.

Midgley JJ, Kruger LM, Skelton R. 2011. How do fires kill plants? The hydraulic death hypothesis and Cape Proteaceae "fire-resisters". *South African Journal of Botany* **77**: 381–386.

Morandi B, Rieger M, Grappadelli LC. 2007. Vascular flows and transpiration affect peach (*Prunus persica* Batsch.) fruit daily growth. *Journal of Experimental Botany* **58**: 3941–3947.

Morcillo L, Muñoz-Rengifo JC, Torres-Ruiz JM, Delzon S, Moutahir H, Vilagrosa A. 2022. Post-drought conditions and hydraulic dysfunction determine tree resilience and mortality across Mediterranean Aleppo pine (*Pinus halepensis*) populations after an extreme drought event. *Tree Physiology* **42**: 1364–1376.

Morin X, Bugmann H, de Coligny F, Martin-StPaul N, Cailleret M, Limousin J-M, Ourcival J-M, Prevosto B, Simioni G, Toigo M *et al.* 2021. Beyond forest succession: a gap model to study ecosystem functioning and tree community composition under climate change. *Functional Ecology* **35**: 955–975.

Narandžić T, Ljubojević M. 2022. Size-controlling cherry rootstock selection based on root anatomical characteristics. *Horticulturae* **8**: 615.

Nelson RM. 2001. Chapter 4 – Water relations of forest fuels. In: Johnson EA, Miyanishi K, eds. *Forest fires.* San Diego, CA, USA: Academic Press, 79–149.

Nolan RH, Boer MM, Resco de Dios V, Caccamo G, Bradstock RA. 2016. Large-scale, dynamic transformations in fuel moisture drive wildfire activity across southeastern Australia. *Geophysical Research Letters* **43**: 4229–4238.

Nolan RH, Collins L, Leigh A, Ooi MKJ, Curran TJ, Fairman TA, Resco de Dios V, Bradstock R. 2021. Limits to post-fire vegetation recovery under climate change. *Plant, Cell & Environment* **44**: 3471–3489.

Oliva J, Stenlid J, Martínez-Vilalta J. 2014. The effect of fungal pathogens on the water and carbon economy of trees: implications for drought-induced mortality. *New Phytologist* **203**: 1028–1035.

Oliveira RS, Costa FRC, van Baalen E, de Jonge A, Bittencourt PR, Almanza Y, Barros FV, Cordoba EC, Fagundes MV, Garcia S *et al.* 2019. Embolism resistance drives the distribution of Amazonian rainforest tree species along hydro-topographic gradients. *New Phytologist* **221**: 1457–1465.

Oliveira RS, Eller CB, Barros F d V, Hirota M, Brum M, Bittencourt P. 2021. Linking plant hydraulics and the fast–slow continuum to understand resilience to drought in tropical ecosystems. *New Phytologist* **230**: 904–923.

Oren R, Sperry JS, Katul GG, Pataki DE, Ewers BE, Phillips N, Schäfer KVR. 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit: intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant, Cell & Environment* **22**: 1515–1526.

Patakas A, Nikolaou N, Zioziou E, Radoglou K, Noitsakis B. 2002. The role of organic solute and ion accumulation in osmotic adjustment in drought-stressed grapevines. *Plant Science* **163**: 361–367.

Pearce RB. 1996. Antimicrobial defences in the wood of living trees. *New Phytologist* **132**: 203–233.

Peng C, Ma Z, Lei X, Zhu Q, Chen H, Wang W, Liu S, Li W, Fang X, Zhou X. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change* **1**: 467–471.

Pérez-Donoso AG, Greve LC, Walton JH, Shackel KA, Labavitch JM. 2007. *Xylella fastidiosa* infection and ethylene exposure result in xylem and water movement disruption in grapevine shoots. *Plant Physiology* **143**: 1024–1036.

Peschiutta ML, Bucci SJ, Scholz FG, Goldstein G. 2016. Compensatory responses in plant-herbivore interactions: impacts of insects on leaf water relations. *Acta Oecologica* **73**: 71–79.

Pimont F, Ruffault J, Martin-StPaul NK, Dupuy J-L, Pimont F, Ruffault J, Martin-StPaul NK, Dupuy J-L. 2019. Why is the effect of live fuel moisture content on fire rate of spread underestimated in field experiments in shrublands? *International Journal of Wildland Fire* **28**: 127–137.

Pinheiro C, Chaves MM. 2011. Photosynthesis and drought: can we make metabolic connections from available data? *Journal of Experimental Botany* **62**: 869–882.

Raimondo F, Trifilò P, Gullo MAL. 2013. Does citrus leaf miner impair hydraulics and fitness of citrus host plants? *Tree Physiology* **33**: 1319–1327.

Rao K, Williams AP, Diffenbaugh NS, Yebra M, Konings AG. 2022. Plant-water sensitivity regulates wildfire vulnerability. *Nature Ecology & Evolution* **6**: 332–339.

Reich PB. 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**: 275–301.

Reichstein M, Bahn M, Mahecha MD, Kattge J, Baldocchi DD. 2014. Linking plant and ecosystem functional biogeography. *Proceedings of the National Academy of Sciences, USA* **111**: 13697–13702.

Resco De Dios V. 2020. *Plant-fire interactions: applying ecophysiology to wildfire management.* Cham, Switzerland: Springer International Publishing.

Resco de Dios V, Arteaga C, Peguero-Pina JJ, Sancho-Knapik D, Qin H, Zveushe OK, Sun W, Williams DG, Boer MM, Voltas J *et al.* 2020. Hydraulic and photosynthetic limitations prevail over root non-structural carbohydrate reserves as drivers of resprouting in two Mediterranean oaks. *Plant, Cell & Environment* **43**: 1944–1957.

Rodriguez-Dominguez CM, Brodribb TJ. 2020. Declining root water transport drives stomatal closure in olive under moderate water stress. *New Phytologist* **225**: 126–134.

Rowland L, Martínez-Vilalta J, Mencuccini M. 2021. Hard times for high expectations from hydraulics: predicting drought-induced forest mortality at landscape scales remains a challenge. *New Phytologist* **230**: 1685–1687.

Ruffault J, Curt T, Moron V, Trigo RM, Mouillot F, Koutsias N, Pimont F, Martin-StPaul N, Barbero R, Dupuy J-L *et al.* 2020. Increased likelihood of heat-induced large wildfires in the Mediterranean Basin. *Scientific Reports* **10**: 13790.

Ruffault J, Limousin J-M, Pimont F, Dupuy J-L, De Càceres M, Cochard H, Mouillot F, Blackman CJ, Torres-Ruiz JM, Parsons RA *et al.* 2023. Plant hydraulic modelling of leaf and canopy fuel moisture content reveals increasing vulnerability of a Mediterranean forest to wildfires under extreme drought. *New Phytologist* **237**: 1256–1269.

Ruffault J, Martin-StPaul N, Pimont F, Dupuy J-L. 2018. How well do meteorological drought indices predict live fuel moisture content (LFMC)? An assessment for wildfire research and operations in Mediterranean ecosystems. *Agricultural and Forest Meteorology* **262**: 391–401.

Ruffault J, Pimont F, Cochard H, Dupuy J-L, Martin-StPaul N. 2022. SurEau-Ecos v.2.0: a trait-based plant hydraulics model for simulations of plant water status and drought-induced mortality at the ecosystem level. *Geoscientific Model Development* **15**: 5593–5626.

Sack L, Scoffoni C. 2013. Leaf venation: structure, function, development, evolution, ecology and applications in the past, present and future. *New Phytologist* **198**: 983–1000.

Salladay RA, Pittermann J. 2023. Using heat plumes to simulate post-fire effects on cambial viability and hydraulic performance in *Sequoia sempervirens* stems. *Tree Physiology* **43**: 769–780.

Schauberger B, Archontoulis S, Arneth A, Balkovic J, Ciais P, Deryng D, Elliott J, Folberth C, Khabarov N, Müller C *et al.* 2017. Consistent negative response of US crops to high temperatures in observations and crop models. *Nature Communications* **8**: 13931.

Scholz FG, Bucci SJ, Goldstein G. 2014. Strong hydraulic segmentation and leaf senescence due to dehydration may trigger die-back in *Nothofagus dombeyi* under severe droughts: a comparison with the co-occurring *Austrocedrus chilensis*. *Trees* **28**: 1475–1487.

Shigo AL. 1984. Compartmentalization: a conceptual framework for understanding how trees grow and defend themselves. *Annual Review of Phytopathology* **22**: 189–214.

Sperry JS, Adler FR, Campbell GS, Comstock JP. 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant, Cell & Environment* **21**: 347–359.

Sperry JS, Love DM. 2015. What plant hydraulics can tell us about responses to climate-change droughts. *New Phytologist* **207**: 14–27.

Sperry JS, Stiller V, Hacke UG. 2003. Xylem hydraulics and the soil–plant–atmosphere continuum: opportunities and unresolved issues. *Agronomy Journal* **95**: 1362–1370.

Sperry JS, Venturas MD, Anderegg WRL, Mencuccini M, Mackay DS, Wang Y, Love DM. 2017. Predicting stomatal responses to the environment from the optimization of photosynthetic gain and hydraulic cost: a stomatal optimization model. *Plant, Cell & Environment* **40**: 816–830.

Stojnić S, Suchocka M, Benito-Garzón M, Torres-Ruiz JM, Cochard H, Bolte A, Cocozza C, Cvjetković B, de Luis M, Martinez-Vilalta J *et al.* 2018. Variation in xylem vulnerability to embolism in European beech from geographically marginal populations. *Tree Physiology* **38**: 173–185.

Sun Q, Sun Y, Walker MA, Labavitch JM. 2013. Vascular occlusions in grapevines with pierce's disease make disease symptom development worse. *Plant Physiology* **161**: 1529–1541.

Tardieu F. 2012. Any trait or trait-related allele can confer drought tolerance: just design the right drought scenario. *Journal of Experimental Botany* **63**: 25–31.

Torres-Ruiz JM, Cochard H, Mencuccini M, Delzon S, Badel E. 2016a. Direct observation and modelling of embolism spread between xylem conduits: a case study in Scots pine: embolism formation and spread in Scots pine. *Plant, Cell & Environment* **39**: 2774–2785.

Torres-Ruiz JM, Kremer A, Carins Murphy MR, Brodribb T, Lamarque LJ, Truffaut L, Bonne F, Ducousso A, Delzon S. 2019. Genetic differentiation in functional traits among European sessile oak populations. *Tree Physiology* **39**: 1736–1749.

Torres-Ruiz JM, Perulli GD, Manfrini L, Zibordi M, Lopéz Velasco G, Anconelli S, Pierpaoli E, Corelli-Grappadelli L, Morandi B. 2016b. Time of irrigation affects vine water relations and the daily patterns of leaf gas exchanges and vascular flows to kiwifruit (*Actinidia deliciosa* Chev.). *Agricultural Water Management* **166**: 101–110.

Trueba S, Pouteau R, Lens F, Feild TS, Isnard S, Olson ME, Delzon S. 2017. Vulnerability to xylem embolism as a major correlate of the environmental distribution of rain forest species on a tropical Island. *Plant, Cell & Environment* **40**: 277–289.

Trugman AT. 2022. Integrating plant physiology and community ecology across scales through trait-based models to predict drought mortality. *New Phytologist* **234**: 21–27.

Trugman AT, Anderegg LDL, Anderegg WRL, Das AJ, Stephenson NL. 2021. Why is tree drought mortality so hard to predict? *Trends in Ecology & Evolution* **36**: 520–532.

Tsuda M, Tyree MT. 1997. Whole-plant hydraulic resistance and vulnerability segmentation in *Acer saccharinum*. *Tree Physiology* **17**: 351–357.

Tyree MT, Cochard H, Cruiziat P, Sinclair B, Ameglio T. 1993. Drought-induced leaf shedding in walnut: evidence for vulnerability segmentation. *Plant, Cell & Environment* **16**: 879–882.

Tyree MT, Sperry JS. 1989. Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology* **40**: 19–36.

Tyree MT, Zimmermann MH. 2002. *Xylem structure and the ascent of sap*. Berlin, Heidelberg, Germany: Springer.

Urli M, Porte AJ, Cochard H, Guengant Y, Burlett R, Delzon S. 2013. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiology* **33**: 672–683.

Venturas M, López R, Martín JA, Gascó A, Gil L. 2014. Heritability of *Ulmus minor* resistance to Dutch elm disease and its relationship to vessel size, but not to xylem vulnerability to drought. *Plant Pathology* **63**: 500–509.

Venturas MD, Todd HN, Trugman AT, Anderegg WRL. 2021. Understanding and predicting forest mortality in the western United States using long-term forest inventory data and modeled hydraulic damage. *New Phytologist* **230**: 1896–1910.

Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! *Oikos* **116**: 882–892.

Volaire F. 2018. A unified framework of plant adaptive strategies to drought: crossing scales and disciplines. *Global Change Biology* **24**: 2929–2938.

Wagner D, Wheeler JM, Burr SJ. 2020. The leaf miner *Phyllocnistis populiella* negatively impacts water relations in aspen. *Tree Physiology* **40**: 580–590.

Wang DR, Venturas MD, Mackay DS, Hunsaker DJ, Thorp KR, Gore MA, Pauli D. 2020. Use of hydraulic traits for modeling genotype-specific acclimation in cotton under drought. *New Phytologist* **228**: 898–909.

West AG, Nel JA, Bond WJ, Midgley JJ. 2016. Experimental evidence for heat plume-induced cavitation and xylem deformation as a mechanism of rapid post-fire tree mortality. *New Phytologist* **211**: 828–838.

Wolf A, Anderegg WRL, Pacala SW. 2016. Optimal stomatal behavior with competition for water and risk of hydraulic impairment. *Proceedings of the National Academy of Sciences, USA* **113**: E7222–E7230.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M *et al.* 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

Yadeta K, Thomma B. 2013. The xylem as battleground for plant hosts and vascular wilt pathogens. *Frontiers in Plant Science* **4**: 97.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Drought impacts on symptoms and damages of plant disease caused by fungi and oomycete.

Notes S1 Effects of water stress on plant diseases caused by fungi and oomycetes were reviewed using vote-counting approach.

Table S1 List of articles that tested the effect of water stress on plant diseases caused by fungi and oomycetes.