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### ► To cite this version:

José Torres-Ruiz, Hervé Cochard, Sylvain Delzon, Thomas Boivin, Regis Burlett, et al.. Plant hydraulics at the heart of plant, crops and ecosystem functions in the face of climate change. *New Phytologist*, 2024, 241 (3), pp.984-999. 10.1111/nph.19463 . hal-04601370

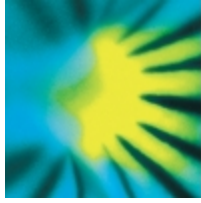
**HAL Id: hal-04601370**

**<https://hal.science/hal-04601370v1>**

Submitted on 4 Jun 2024

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# New Phytologist

## Xylem hydraulics at the heart of plant, crops and ecosystem functions in the face of climate change.

Journal:	<i>New Phytologist</i>
Manuscript ID	NPH-TR-2023-44091
Manuscript Type:	Tansley Review
Date Submitted by the Author:	04-Jul-2023
Complete List of Authors:	Torres-Ruiz, José M.; INRAE, PIAF research unit Cochard, Hervé; PIAF, ECODIV Delzon, Sylvain; University of Bordeaux, Bat B2,, UMR BIOGECO INRA-UB, Biological Sciences Boivin, Thomas; INRAE, URFM Burllett, Regis; University of Bordeaux, Bat B2,, UMR BIOGECO INRA-UB, Biological Sciences Cailleret, Maxime; INRAE, UMR RECOVER; Swiss Federal Institute for Forest Snow and Landscape Research, WSL Corso, Déborah; BIOGECO, INRA, Univ. Bordeaux Delmas, Chloe; INRAE, ISVV De Cáceres, Miquel; Forest Science and Technology Centre of Catalonia, Multifunctional forest management; CREAM, Function Biogeography Diaz-Espejo, Antonio; Universidad de Sevilla, IRNAS-CSIC Fernandez-Conradi, Pilar; INRAE, URFM Guillemot, Joannès; CIRAD, ECO&SOLS Lamarque, Laurent; Université du Québec à Trois-Rivières, Département des Sciences de l'Environnement and Centres d'études nordiques Limousin, Jean-Marc; CNRS, CEFE; Université de Montpellier, CEFE Mantova, Marylou; University of Florida, Agronomy Mencuccini, Maurizio; CREAM, Universidad Autonoma de Barcelona, c/o, CREAM; Pg. Lluís Companys 23, ICREA Morin, Xavier; CEFE-CNRS, Biologie et Fonctionnement des Ecosystèmes; Pimont, François; INRAE, Ecologie des Forêts Méditerranéennes Resco de Dios, Victor; Southwest University of Science and Technology, School of Life Science and Engineering; University of Lleida, Agrotecnio Center Ruffault, Julien; Institut National de la Recherche Agronomique Centre de Recherche d'Avignon, Ecologie Des Forêts Méditerranéennes Trueba, Santiago; Yale University, School of the Environment; University of Bordeaux, BIOGECO Martin-StPaul, Nicolas; INRAE, URFM
Key Words:	Plant Hydraulics, Ecophysiology, Fire Ecology, Plant-Pathogen interactions, Crop Physiology, Vegetation dynamics

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

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**Words count:** Summary - 154 words

Main body - 6497 words

Figures - 5 Figures, all in colour.

Supplementary information - 1 Figure in colour + 1 Table.

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46 **Summary**

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

59

60 **Keywords:** Plant hydraulics; Drought; Wildfire; Pathogens; Crop productivity; Tree growth;  
61 Mortality; Climate Change.

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## 75 **i) Introduction**

76 As for most living organisms, water plays a key role in the functioning of plants. Therefore,  
77 understanding the processes involved in plant water uptake, transport and utilization is  
78 fundamental for comprehending the main ecological processes and plant-related risks. The field  
79 of plant hydraulics examines the capacity of plants to extract water from the soil and transport it  
80 up to the aerial organs through the transpiration stream. Moreover, it also considers water exchange  
81 between the plant apoplastic and symplastic compartments, determining plant water relations and  
82 water status. Variations in plant hydraulic properties, water relations and status (e.g. induced by  
83 changes in meteorological conditions or soil water availability) can directly affect key plant  
84 functions such as stomatal behaviour, photosynthetic capacity, biomass production, and growth.  
85 Furthermore, these variations can influence other processes such as the development of plant  
86 diseases caused by pathogens, the sensitivity of forests to wildfires, or the risk of drought-induced  
87 mortality (Fig. 1). Consequently, there has been a growing interest in plant hydraulics across  
88 various scientific disciplines that have found the knowledge in this field to be crucial for addressing  
89 significant questions, particularly regarding ecosystem functioning in the face of global changes.  
90 The increase in the frequency and severity of drought events are causing irreversible damages to  
91 plant productivity and survival, which are further exacerbated by the impacts of pathogens or  
92 wildfires (Littell *et al.*, 2016; McDowell *et al.*, 2018, 2022). Thus, many of the tree mortality events  
93 reported worldwide have been related to low water availability and increased atmospheric  
94 temperatures (Peng *et al.*, 2011; Klein *et al.*, 2022; Hammond *et al.*, 2022). Such conditions can  
95 therefore compromise the crucial contributions of ecosystem services to humankind. Similarly, the  
96 intensifying drought conditions are already causing substantial declines in crop yield in most  
97 agricultural regions worldwide (Lesk *et al.*, 2016), with important implications for livelihood and  
98 food security. It is therefore crucial to identify the key physiological traits that explain such  
99 variation in plant survival and yield for the maintenance and conservation of our forests and  
100 improving crop management.

101 During the last decades, plant hydraulics has contributed key knowledge and tools for  
102 understanding biological and ecological processes, such as the susceptibility of forests to fire  
103 (Ruffault *et al.*, 2022), plant interactions with pathogens and herbivorous insects (Bortolami *et al.*,  
104 2019), and the processes controlling crops and forest productivity and resilience (Flexas *et al.*,  
105 2018; Klein *et al.*, 2022; Morcillo *et al.*, 2022) (Fig. 1). Despite these pioneering attempts, the

106 connection between plant hydraulics and other disciplines remains limited, preventing relevant  
107 physiological and ecological questions to be addressed at large scales (e.g. better prediction of  
108 mortality, fire risk, ecosystem functioning or crop production). Significant advances, however,  
109 have been made in understanding processes and mechanisms associated with water transport,  
110 including cavitation formation and spreading (Tyree & Sperry, 1989; Torres-Ruiz *et al.*, 2016a);  
111 hydraulic efficiency and safety within and across species (Choat *et al.*, 2012; Lobo *et al.*, 2018);  
112 the role of hydraulic dysfunction in drought-induced mortality (Adams *et al.*, 2017; Mantova *et*  
113 *al.*, 2021, 2022; McDowell *et al.*, 2022); water inflows and outflows to the fruits (Morandi *et al.*,  
114 2007; Torres-Ruiz *et al.*, 2016b) and the development of mechanistic models for predicting the  
115 consequences of drought-induced hydraulic failure on plant performance (Sperry & Love, 2015;  
116 Cochard *et al.*, 2021; Ruffault *et al.*, 2022) and the risk of wildfires (Ruffault *et al.*, 2023). As a  
117 result, plant hydraulics provide, at present, a comprehensive framework that represents various  
118 aspects of terrestrial plant and ecosystem functioning, including (i) carbon sequestration and  
119 productivity of crops and forest ecosystems, as photosynthesis is tightly coordinated with hydraulic  
120 functions, (ii) the predictions of plant water status encompassing all components of drought stress  
121 using well-established biophysical equations based on simple diffusion laws; and (iii) the  
122 predictions of plant mortality, demography and the susceptibility to disturbance regimes such as  
123 wildfire or pathogen attacks linked to drought.

124 Without claiming to be exhaustive, this review intends to bring out how plant hydraulics  
125 can provide relevant insights to other disciplines such as tree physiology, crop sciences, fire  
126 ecology, plant pathology and ecology, providing a broad framework highlighting how it can  
127 advance key questions and draw future research directions of these fields.

## 128 *ii) Plant Hydraulics: A Framework for Measuring Drought Impacts*

129 Plant responses to drought are characterized by a sequence of water stress limits for various  
130 plant physiological functions, which are linked to key hydraulic traits (Bartlett *et al.*, 2016;  
131 Blackman *et al.*, 2023). These hydraulic traits play a vital role in shaping critical aspects of plant  
132 performance, including growth, photosynthesis, turgor maintenance, and overall resilience in the  
133 face of drought-induced conditions (Fig. 2). Thus, as soil water availability decreases or  
134 atmospheric vapor pressure deficit (VPD) increases, plants commonly reduce stomatal opening to  
135 mitigate water stress and hydraulic impairment. However, this adaptive response comes at the cost

136 of limiting photosynthesis and transpiration (Flexas & Medrano, 2002; Martin-StPaul *et al.*, 2017).  
137 Drought leads to a decrease in cell turgor pressure due to declining plant water potential, causing  
138 plant growth to halt when it reaches values below the minimum pressure required for cell  
139 enlargement (Lockhart, 1965). Despite this, only few studies to date have attempted to determine  
140 or model the water potential threshold for plant growth (reviewed in Cabon *et al.*, 2020). As for  
141 growth, hydraulic limits can be defined for plant gas-exchange. In this respect, the turgor loss point  
142 ( $\Psi_{tlp}$ ) appears as a sound water potential limit for characterising stomatal closure, considering that  
143 stomata are completely closed when leaf turgor is equal to zero (Brodribb *et al.*, 2003). However,  
144 it should be noted that stomatal closure alone may not be sufficient for assessing the water stress  
145 impact on carbon assimilation and economy because photosynthesis is significantly constrained  
146 before complete stomatal closure (Fig. 2). The water potential at zero carbon assimilation ( $\Psi_{A_n=0}$ )  
147 is therefore crucial for evaluating the effect of drought on plant growth, productivity or carbon  
148 sequestration, requiring to consider the roles of the mesophyll conductance to  $\text{CO}_2$ , the Rubisco  
149 carboxylation rate and the chlorophyll electron transport rate on the photosynthetic capacity in  
150 addition to the hydraulic traits (e.g. Sperry *et al.*, 2017).

151         The closure of stomata delays the decline of water potential, preventing it from reaching  
152 levels below the critical threshold at which cavitation occurs and maximising the time in which  
153 the plant shows a positive safety margin (ie. the difference between the actual water potential and  
154 water potential at which cavitation starts). Despite this, plants continue to dehydrate progressively  
155 under limited soil water extraction (soil drought) or higher atmospheric evaporative demand  
156 (atmospheric drought) due to the water leaks from the cuticle and stomata (Machado *et al.*, 2021).  
157 This causes the relative water content (RWC) and water potential ( $\Psi$ ) to decrease, ultimately  
158 leading to xylem cavitation and plant hydraulic failure. Hydraulic failure is considered a ubiquitous  
159 factor in drought-induced tree mortality (Adams *et al.*, 2017) so understanding the physiological  
160 traits determining hydraulic failure and its link to tree death is crucial for predicting forest  
161 responses to climate change. In this regard, recent studies have shown how the loss of hydraulic  
162 function is linked to downstream living cell damage (Mantova *et al.*, 2023), which has led to the  
163 hypothesis that the loss of meristematic cell integrity induced by hydraulic dysfunction is the  
164 possible mechanistic link between hydraulic failure and drought-induced tree mortality (Mantova  
165 *et al.*, 2022).



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

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

### 184 *iii) Hydraulic properties and crop productivity under drought conditions.*

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

194 In general, it has been assumed that any increase in the rate of photosynthesis per unit leaf  
195 area will automatically translate into higher biomass and yield. However, plant growth and yield  
196 depend not only on photosynthesis capacity but also on the conjunction of several factors that  
197 allows the enhancement of the photosynthesis rate to be translated into yield, such as higher  
198 hydraulic capacities, sink–source balance and transport of photoassimilates, and the availability  
199 and uptake of nutrients (Araus *et al.*, 2021). Also, the relationship between photosynthetic capacity  
200 and yield may not only differ between varieties but also in plants exposed to different  
201 environmental conditions (Lawlor, 1995). The increase in photosynthetic capacity requires the  
202 concurrent enhancement of an efficient water transport system (i.e. hydraulic efficiency) (Tyree &  
203 Sperry, 1989; Brodribb, 2009), and the preservation of its hydraulic integrity (i.e. hydraulic safety),  
204 particularly under drought conditions. These interconnected traits play a key role and must  
205 progress in parallel to ensure optimal adaptation to drought conditions while maximizing  
206 photosynthetic performance. Thus, it has been reported how higher vein densities enhance not only  
207 photosynthetic gas exchange rates but also stomatal conductance and tolerance to drought-induced  
208 disruption of the hydraulic system (Sack & Scoffoni, 2013). However, in trees, there is only a  
209 weak trade-off between xylem efficiency and xylem safety such that very resistant species to  
210 cavitation can show a wide range of hydraulic conductance values (Gleason *et al.*, 2016). An  
211 efficient coordination of plant hydraulics and photosynthesis is therefore essential for the  
212 synchronized regulation of water loss and carbon dioxide uptake in plants through the stomata.  
213 This coordination has recently been evidenced in tomato mutants (Andrade *et al.*, 2022), where a  
214 reduction in diameter and number of xylem vessels resulting in lower hydraulic conductivity was  
215 associated with a 50% and 25% reduction in stomatal conductance and net photosynthesis,  
216 respectively.

217 Annual crop plants are, in general, relatively vulnerable to embolism, with  $P_{12}$  values (*i.e.*  
218 the water potential used as a proxy for the onset of xylem embolism) varying between -1 and -4  
219 MPa, such as in wheat (-1.7 MPa, Corso *et al.*, 2020), sunflower (-2.3 MPa, Ahmad *et al.*, 2018)  
220 or maize (-1.6 MPa, Cochard, 2002). Within this range of water potentials, the relationship  
221 between complete stomatal closure ( $P_{\text{close}}$ ) and  $P_{12}$  is close to the 1:1 line (Fig. 3A; Martin-StPaul  
222 *et al.*, 2017) what means that there is little to no stomatal safety margin (*i.e.*  $P_{\text{close}} - P_{12}$ ) for these  
223 species since they close their stomata at, or just before, the onset of xylem embolism (Creek *et al.*,  
224 2020). These narrow stomatal safety margins allow annual crops to maintain gas exchanges up to

225 almost the onset of cavitation under drought conditions. Similar results have been observed in  
226 perennial woody crops, like apple trees (Beikircher *et al.*, 2013), for which varieties with a higher  
227 resistance to cavitation are able to maintain their stomata open for a wider range of soil water  
228 availability. Thus, as stomata opening depends on the guard cell turgor, plants have a certain  
229 capacity to adjust osmotic potential to shift the turgor loss point close to the onset of cavitation.  
230 However, this coordinated decrease in  $P_{\text{close}}$  and  $P_{12}$  to maximize gas exchange occurs up to a  
231 given  $P_{12}$  value below which increasing embolism resistance is not associated with further decrease  
232 in  $P_{\text{close}}$  that, instead, remains relatively constant at ca. -3.00MPa (Fig. 3A; Martin-StPaul *et al.*,  
233 2017). Therefore, if the objective is to ensure crop production and the sustainability of food supply  
234 under drought, it is crucial to seek crop species or cultivars with i) relatively high resistance to  
235 embolism, and ii) relatively narrow safety margins to maintain gas exchange and maximize the  
236 photosynthetic activity even when soil water content starts to be limited (Fig. 3B). However, this  
237 is not easy task, as it has been observed for some species as maize that the correlation between  
238 stomatal conductance and hydraulic safety is inverse (Gleason *et al.*, 2019), which would imply  
239 that high yield potentials come at the cost of increased vulnerability to xylem embolism in crops.

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

248 Apart from the increasing water scarcity observed in different geographical areas due to  
249 climate change, the growing interest in crop hydraulics stems from the recognition that  
250 understanding the hydraulic mechanisms responsible for drought resistance in crop plants is crucial  
251 for the development of productive and drought-resistant varieties. This is especially important  
252 since improving some morpho-anatomical or physiological traits that could improve drought  
253 resistance may not always result in corresponding improvements to hydraulic traits (e.g. Lamarque  
254 *et al.*, 2020). Thus, multifaceted approaches are required to develop crop varieties with optimal

255 trait combinations conferring increased hydraulic safety, efficient hydraulic conductance,  
 256 sustained carbon assimilation and high yield. Now that hydraulic traits can be easily quantified in  
 257 crops, it is also possible to integrate this information into existing hydraulic models to predict crop  
 258 performance under various climate warming scenario and identify traits that can be leveraged to  
 259 adapt agriculture to climate change (Cochard *et al.*, 2021; Dayer *et al.*, 2022).

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

#### 264 *iv) Linkage between hydraulics-related plant traits and wildfire risk*

265 Wildfire is one of the most important natural disturbances affecting ecosystems worldwide  
 266 (Bowman *et al.*, 2020). As climate warming intensifies, vegetation gets drier (lower moisture  
 267 content) for longer periods of time (Clarke *et al.*, 2022), thus lengthening the fire season and  
 268 potentially increasing the frequency of high intensity fires (Barbero *et al.*, 2015; Dowdy *et al.*,  
 269 2019; Ruffault *et al.*, 2020). Plant-fire interactions depend on many physiological mechanisms  
 270 acting at different temporal and spatial scales (Resco De Dios, 2020). On the one hand, the  
 271 interplay between biomass production (or fuel accumulation and structure) and its moisture content  
 272 affect wildfires, at scales ranging from biogeographical patterns of burned area (Boer *et al.*, 2021)  
 273 to landscape patterns of fire spread (Nelson, 2001). On the other hand, fire effects on ecosystems  
 274 depend on interactions between fire intensity and plant's resistance and resilience to fire (Karavani  
 275 *et al.*, 2018).

276 Live fuel moisture content (LFMC) (i.e. the ratio of water mass to dry mass of twigs and  
 277 leaves within the vegetation) is considered to be one of the most relevant drivers of forest fire  
 278 behaviour (Nolan *et al.*, 2016; Pimont *et al.*, 2019; Rao *et al.*, 2022). The sensitivity of LFMC to  
 279 drought depends on plant physiological, structural and hydraulics traits, which differ across species  
 280 and can vary widely over space and time (Jolly & Johnson, 2018; Ruffault *et al.*, 2018). This is the  
 281 case for the pressure-volume curves that link the leaf water status and cell relative water content  
 282 (Tyree & Hammel, 1972), and that have been recently transferred for LFMC predictions (Nolan *et*  
 283 *al.*, 2018; Pivovarov *et al.*, 2019; Ruffault *et al.*, 2023). Also, under intense drought conditions,  
 284 some species can reduce significantly the water flow to the leaves due to a vulnerability

285 segmentation between the leaves and the stems that makes leaf xylem to cavitate at higher water  
286 potential (i.e. less resistance to cavitation) than stems (Charrier *et al.*, 2016; Levionnois *et al.*,  
287 2020). Apart from exacerbating the dehydration of the leaves, this leaf hydraulic disconnection  
288 can trigger leaf senescence and drop (Tyree *et al.*, 1993; Scholz *et al.*, 2014) that will have an  
289 impact on LFMC and therefore fire behaviour. The same applies when there is significant  
290 hydraulic segmentation between the leaves and the stems, e.g. at the petiole level, which makes  
291 the water potential and water content to decay more rapidly in the leaves than in the stems (Tsuda  
292 & Tyree, 1997). Yet, despite a growing number of plant hydraulics models (Li *et al.*, 2021;  
293 Cochard *et al.*, 2021; Ruffault *et al.*, 2022), attempts to simulate LFMC considering plant hydraulic  
294 properties are still scarce (but see Ma *et al.*, 2021; Balaguer-Romano *et al.*, 2022). Recent studies  
295 have shown the major role of physiological traits (leaf area, vulnerability to cavitation, hydraulic  
296 segmentation, transpiration regulation) on both leaf and canopy fuel moisture content (Ruffault *et*  
297 *al.*, 2023) but more research is needed to upscale predictions from the leaf or canopy level to the  
298 stand or landscape one. It is also necessary to achieve a better integration between short-term  
299 physiological LFMC models (Balaguer-Romano *et al.*, 2022; Ruffault *et al.*, 2023) and micro-  
300 climatic variation driven by the fire-plume so that this effect can be added into dynamical fire  
301 behaviour modelling (Dickman *et al.*, 2023).

302 Fire effects on plants are tightly linked both to the type of fire and its behaviour as well as  
303 to the plant regeneration mode. Thus, crown fires, canopy scorch or consumption by the fire are  
304 the main triggers for the mortality of seedling trees (Hull Sieg *et al.*, 2006), although there are still  
305 some uncertainties about the critical % of crown mortality necessary for tree death (Resco de Dios  
306 *et al.*, 2020). Trees that initially survive fire may succumb in the months or years following the  
307 disturbance when the cambium is charred and the tree girdled, due to fire-induced hydraulic  
308 dysfunction (Ducrey *et al.*, 1996; Kavanagh *et al.*, 2010; Michaletz *et al.*, 2012). Different  
309 mechanisms involving xylem hydraulics have been proposed to potentially explain post-fire  
310 survival (Michaletz *et al.*, 2012; West *et al.*, 2016; Bär *et al.*, 2019). However, recent studies  
311 indicate that vascular cambium is more sensitive to high temperatures than the xylem, making  
312 phloem charring a likely candidate to explain post-fire survival (Salladay & Pittermann, 2023).  
313 This observation is in accordance with the forestry literature, which considers bark thickness  
314 (along with canopy scorch) as a key indicator of post-fire mortality (Resco De Dios, 2020). For  
315 resprouting trees, however, fire-induced mortality is more difficult to characterise. It was

316 traditionally considered that stored reserves played a major role for post-fire recovery, but recent  
317 findings challenge this view and indicate a major effect of plant-hydraulics related processes  
318 (Nolan *et al.*, 2021). In this sense, it has been shown how oak trees are unable to resprout if a  
319 drought prior to the disturbance causes a loss of more than 50% in root hydraulic conductance,  
320 highlighting the critical role of root hydraulic conductance in the resprouting ability of trees (Resco  
321 de Dios *et al.*, 2020).

322 Improving post-fire management requires therefore a better understanding of the  
323 mechanisms leading to potential recovery. Nowadays, at least in some Mediterranean countries,  
324 forests are often felled after the fire and sprout selection occurs later. This is because the fire is  
325 considered to have damaged the vascular tissue leading to stem necrosis. Hydraulic feedbacks  
326 could exacerbate the responses when the fire was preceded by a strong drought that defoliated part  
327 of the canopy (hence enhancing fire behaviour as previously mentioned). Such feedbacks between  
328 pre-fire drought, fire behaviour and post-fire legacy responses should be at the forefront of our  
329 research efforts (Karavani *et al.*, 2018).

#### 330 *v) Role of hydraulic traits on plant-herbivore insects-pathogens interactions.*

331 The xylem plays a key role in organising defences against various biotic stresses (Shigo,  
332 1984; Tyree & Zimmermann, 2002), but plant hydraulics is still rarely studied in the context of  
333 plant pathology and entomology. Vessel anatomy and compartmentalization, hydraulic  
334 conductivity, plant water status, and stomatal conductance are key traits that underlie plant  
335 interactions with insects or pathogens and pathological disturbances (Gely *et al.*, 2020). In  
336 addition, interactions between biotic and abiotic stressors can amplify their individual impacts on  
337 the capacity of the trees to absorb and transport water (Fig. 4) (Griffin-Nolan *et al.*, 2021;  
338 McDowell *et al.*, 2022). Hence, it is high time to recognize the pivotal role of plant hydraulic traits  
339 in plant-pathogen interactions and pave the way for further research in this domain.

340 Xylem vessels host a large breadth of endophytic microorganisms and some of them are  
341 vascular pathogens (Pearce, 1996). Plant responses to vascular fungi or bacteria, and the toxins  
342 they often produce, can lead to compartmentalization of the xylem in order to block the spread of  
343 the pathogen (Shigo, 1984; Yadeta & Thomma, 2013). This highlights the key role of xylem  
344 anatomical characteristics in plant-pathogen interactions, for example, through the size of the  
345 vessels or the pits (Venturas *et al.*, 2014). Pathogenesis can induce losses in hydraulic conductance



346 resulting from pathogen clogging of the xylem conduits (Deyett *et al.*, 2019; Ingel *et al.*, 2022),  
347 cavitation (Pérez-Donoso *et al.*, 2007), or vessel occlusion by gums and tyloses (Sun *et al.*, 2013;  
348 Bortolami *et al.*, 2019). These losses can lead to the xylem hydraulic failure and induce irreversible  
349 dehydration of the distal organs (Mensah *et al.*, 2020; Bortolami *et al.*, 2021a). Recently, the use  
350 of X-ray microtomography coupled with the contrasting agent iohexol revealed an induced  
351 production of tyloses and/or gels and the subsequent loss in hydraulic conductivity in vivo, which  
352 shed new lights on xylem functioning during vascular pathogenesis (Bortolami *et al.*, 2019,  
353 2021a). As plant hydraulic functioning is directly linked to gas exchange and carbon metabolism  
354 (Pinheiro & Chaves, 2011; McDowell, 2011), these losses in hydraulic conductance induced by  
355 vascular pathogenesis can affect stomatal regulation (Bortolami *et al.*, 2021b).

356 Vascular dysfunction may also be linked to insect damages leading to the abnormal  
357 production of xylem (Lipshitz & Mendel, 1987), the alteration of xylem fibre anatomy  
358 (Hillabrand *et al.*, 2019b), the increase of vulnerability to embolism (Aguadé *et al.*, 2015), or the  
359 alteration of hydraulic conductivity (Hillabrand *et al.*, 2019a) (Fig. 4). Also, insect mining  
360 damages induce the partial closure of the stomata, enriching leaf  $\delta^{13}\text{C}$  and reducing plant  
361 transpiration (Bansal, 2015; Peschiutta *et al.*, 2016; Wagner *et al.*, 2020). In the short term, this  
362 may have some positive effects for the plant as it would reduce water losses and thus its risk of  
363 hydraulic failure (Wagner *et al.*, 2020), however, it would also reduce considerably carbon  
364 assimilation. Leaf mining insects not only compromise the leaf's water-retaining properties by  
365 feeding on both superficial and deeper living tissues, but epidermis mining can also result in cuticle  
366 breaks. This, in turn, leads to an increase in plant residual transpiration (Raimondo *et al.*, 2013),  
367 significantly elevating the risk of hydraulic failure in infected plants (Billon *et al.*, 2020; Blackman  
368 *et al.*, 2023).

369 Overall, biotic damage can increase on water-stressed trees, but the interactions between  
370 drought and biotic stressors likely depend on the pathogen lifestyle (biotrophic, hemibiotrophic,  
371 vascular, necrotrophic (Jactel *et al.*, 2012, 2019) (supplementary Fig. S1), the insect feeding guild  
372 (xylem-tappers, bark or wood borers, leaf chewers or miners and gall formers) (Gely *et al.*, 2020),  
373 and both the timing and intensity of water stress. Thus, too negative water potentials can limit the  
374 development of the xylem inhabiting micro-organisms (Beattie, 2011) and sap-feeding insects  
375 (Huberty & Denno, 2004) but also increase the susceptibility of conifers to bark beetle attacks

376 through a decrease in duct and resin volume production (Gaylord *et al.*, 2013). Different pathogen  
377 and insect guilds can interact with plant hydraulic functioning (vessel occlusion; loss of hydraulic  
378 conductivity; stomatal regulation) and/or carbon balance (carbohydrate consumption or activation  
379 of the plant defence response), which could impair maintenance of carbon-dependent metabolic,  
380 defence or hydraulic functions (Anderegg, 2015; Jactel *et al.*, 2019; McDowell *et al.*, 2022). For  
381 example, insect defoliation can alter xylem fibre anatomy more consistently and severely than  
382 drought alone, likely leading to a reduced structural support to vessels and an increased  
383 vulnerability of defoliated trees to drought-induced cavitation when leaf area recovers (Hillabrand  
384 *et al.*, 2019b). These interactions between biotic and abiotic stresses may be synergistic (Croisé *et*  
385 *al.*, 2001; Gao *et al.*, 2017, p. 201; Lima *et al.*, 2019), antagonistic (Arango-Velez *et al.*, 2016;  
386 Bortolami *et al.*, 2021b), or neutral (Lopisso *et al.*, 2017), and they likely vary with stress intensity  
387 and the measured hydraulic traits (Bansal, 2015).

388 Therefore, hydraulic traits play a key role in understanding the interaction between  
389 drought-induced decrease in plant water potential and plant functional response to biotic stressors,  
390 but they are rarely monitored in this context. In fact, among 62 reviewed studies on drought and  
391 cryptogamic disease interactions in plants (see Supplementary material), only 60% of them used  
392 an unambiguous metric of plant water status (leaf or stem water potential) to quantify drought  
393 intensity, while only 11% measured hydraulic traits (hydraulic conductance, gas exchange, or  
394 relative water content). Considering the interacting effects between biotic and abiotic stressors  
395 across latitudes and cropping systems is crucial to predict plant functioning under the actual  
396 climate change context, especially in the long term when abiotic and biotic factors can interact to  
397 predispose, incite, or contribute directly or indirectly to plant death (i.e. the “death spiral”, Manion,  
398 1981; Griffin-Nolan *et al.*, 2021). Pathologists and entomologists should therefore explicitly  
399 quantify the plant water status in general, and plant hydraulic traits in particular, if we are to better  
400 understand the mechanisms involved in insect- or pathogen-plant interactions.

#### 401 *vi) Plant hydraulic as a hub for vegetation models.*

402 Vegetation function and dynamics process-based models (VFDM) are becoming necessary  
403 tools to predict the impact of climatic change on vegetation dynamics and associated ecosystem  
404 services. Historically, VFDM were primarily based on modeling the gas exchanges between the  
405 canopy and the atmosphere, with a primary focus on carbon dynamics (Fatichi *et al.*, 2019). More



406 recently, the implementation of plant hydraulics in VFDM has gained in popularity with strong  
407 expectations to improve predictions of the impact on tree physiology and thus on forests'  
408 response to climate change (Rowland *et al.*, 2021; Trugman, 2022).

409 Whole-tree hydraulic models simulating plant water use and transport (Sperry *et al.*, 1998),  
410 embolism and refilling (Edwards & Jarvis, 1982; Sperry *et al.*, 2003) and even drought-related  
411 mortality (Martínez-Vilalta *et al.*, 2002) have long been available. However, it is only recently that  
412 such models have been framed with the goal of being operational to predict ecosystem functions  
413 and dynamics at global (Eller *et al.*, 2020) and local scales (De Cáceres *et al.*, 2021; Ruffault *et*  
414 *al.*, 2023). There are key potential benefits of such integration, in particular the possibility to  
415 improve climate change impact simulations by mechanistically accounting for the combined effect  
416 of atmospheric and soil drought on the plant water status (e.g. water potential, Allen *et al.*, 2015;  
417 Martin-StPaul *et al.*, 2023); see Introduction section, Fig. 1). In fact, when implemented in  
418 multilayer vegetation models, this also allows to represent microclimatic effects on plant water  
419 status (De Cáceres *et al.*, 2021). In addition, the possibility of accounting for plant hydraulic traits  
420 and environmental conditions - increasingly available in different databases - enables the  
421 integration of knowledge and data to generalize predictions of the sequence of plant responses to  
422 drought (see section 1). For instance, the explicit representation of plant water potentials allows to  
423 account for sink limitations (i.e. cambial activity) when simulating secondary growth (Hayat *et al.*,  
424 2017). More specifically, turgor effects can now be included, along with temperature effects, when  
425 predicting cambium division and cell expansion (Cabon *et al.*, 2020), although there are still some  
426 questions to address about the integration of these sink limitations with other determinants of  
427 xylogenesis, such as hormonal control (Hartmann *et al.*, 2017) or sugar availability (Carteni *et al.*,  
428 2018). In addition, thanks to their traits-based approach and the increasing knowledge of traits  
429 coordination and syndromes (section 6) hydraulic models have also the potential to help identify  
430 trade-offs between productivity and stress tolerance (section 2) and improve the representation of  
431 succession and forest dynamics (Morin *et al.*, 2021). Plant hydraulic models also allow to model  
432 gas exchanges during drought by accounting for plant water status (Fig. 5), opening the door to  
433 new stomatal behaviour models based on optimization criteria by balancing the carbon gain of  
434 opening stomata *vs.* the risk of hydraulic failure (Wolf *et al.*, 2016; Sperry *et al.*, 2017).

435 Plant hydraulic modelling is seen as a promising tool to predict the disturbances related to  
436 water stress in VDFM. Firstly, it enables the evaluation of drought-induced tree mortality caused  
437 by hydraulic failure and/or plant desiccation (De Kauwe *et al.*, 2020; Cochard *et al.*, 2021; Ruffault  
438 *et al.*, 2022), thanks to empirically-determined thresholds (section 1). Furthermore, it can predict  
439 moisture content in different plant organs, which proves to be a better factor in explaining mortality  
440 (Mantova *et al.*, 2021) (section 1) and could also be associated with other disturbances such as  
441 wildfire risk (see section 3). However, empirical models currently tend to be more accurate in  
442 predicting tree mortality events within their calibration context compared to hydraulic-based  
443 models (Adams *et al.*, 2013). Nevertheless, this accuracy is expected to improve with a more robust  
444 parameterization of traits and environmental variables, particularly concerning micro-local  
445 edaphic conditions such as soil depth or percent rock content. Another important aspect is gaining  
446 a better understanding of the interdependency between water and carbon processes and their role  
447 in mortality (McDowell *et al.*, 2022). In this sense, available models can simulate both xylem and  
448 sugar phloem transport (De Schepper & Steppe, 2010; Hölttä *et al.*, 2017), but a more precise  
449 mechanistic coupling is still required between water and carbon economies concerning water  
450 transport and stomatal behaviour. Additionally, simulating the legacies of previous drought  
451 impacts is challenging as it necessitates an explicit representation of functional sapwood area and  
452 accurate predictions of growth following drought events. While models incorporating plant  
453 hydraulics can simulate plant competition for water resources, advancements are needed to  
454 understand to what extent plants coexisting in the same stand share the same water pools.  
455 Furthermore, the linkage of plant hydraulic physiology to pathogens and pest attack risk (as  
456 mentioned in section 4) is currently poorly implemented.

457 Apart from this, one of the most crucial challenges for the plant hydraulic models is  
458 appropriately parameterizing plant hydraulics, taking into account both inter-specific and intra-  
459 specific variability. Global plant trait databases serve as essential data sources for this task.  
460 However, additional knowledge is required in cases where further scaling of tissue-level  
461 measurements to organ- or plant-level parameters is needed (see section 6). Strategies such as  
462 utilizing trait-trait relationships or other approaches to fill missing trait data (De Cáceres *et al.*,  
463 2023) and considering plastic trait responses to changing environmental conditions are essential  
464 in this process.

465 *vii) Water-use and drought tolerance strategies in the global spectrum of plant functions*

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

475 Current knowledge states that the functions of trees can be largely captured by a  
 476 fundamental axis differentiating the acquisitive and conservative strategies: the “fast-slow” axis  
 477 (Reich, 2014). The fast-slow axis was originally described as a leaf economic axis (Wright *et al.*,  
 478 2004), contrasting fast and slow return on investments of nutrients and dry mass in leaves, and was  
 479 later proposed to apply at the whole-plant scale to explain individual performances and  
 480 demography (Reich, 2014). Consequently, in this axis, leaf photosynthesis can be interpreted as a  
 481 return on a building investment. As water mainly runs through the soil–tree–atmosphere  
 482 continuum, this interpretation may not apply, and there is still an open debate on how to expand  
 483 the axes related to carbon and nutrients to whole-plant water relations. Various studies suggested  
 484 that tree species exhibiting high growth and/or acquisitive leaf traits tended to have lower hydraulic  
 485 safety margin and xylem hydraulic resistance (Oliveira *et al.*, 2021; Guillemot *et al.*, 2022). This  
 486 suggests that drought tolerance is, to some extent, aligned with the fast-slow axis, but the  
 487 mechanisms involved remain elusive. In this sense, at least three non-exclusive mechanisms could  
 488 be involved:

489 **i) A direct trade-off among xylem traits.** The hydraulic safety-efficiency trade-off states  
 490 that species evolving xylem able to efficiently transport water are also more vulnerable to  
 491 cavitation, due to inherent structural constraint. However, the relationship between safety and  
 492 efficiency, despite significant, is very weak (Gleason *et al.*, 2016). Studies on this topic mostly  
 493 considered efficiency as the ability to transport an amount of water in a small cross-section of  
 494 living wood (i.e., space-use efficiency). However, other definitions of xylem hydraulic efficiencies

495 exist (Bittencourt *et al.*, 2016; Mencuccini *et al.*, 2019) and deserve to be better explored in relation  
496 with drought tolerance, such as hydraulic energy efficiency (the energy invested - production and  
497 maintenance - in the hydraulic system) or the hydraulic nutrient efficiency (hydraulic conductance  
498 by unit nutrient invested). If these alternative definitions of efficiency show a clearer trade-off with  
499 drought tolerance, they would be compatible with the return-on-investment concept of the leaf  
500 economics, and would pertain to the mechanisms described in the next paragraph.

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

514       iii) **An indirect effect of carbon or nutrient scarcity on water relation traits.** Recent  
515 studies reported that tropical woody species with more resistant xylem occur preferentially on P-  
516 poor soils and they show low leaf P concentration (Oliveira *et al.*, 2019; Guillemot *et al.*, 2022).  
517 Although this pattern could arise from the mentioned energy or nutrient cost of water transport, it  
518 could also merely result from the fact that nutrient-poor soils impose slow conservative strategies  
519 that favour efficient nutrient use and low tissue turn-over. This results in species growing dense,  
520 small-vessel wood (Heineman *et al.*, 2016), which may also exhibit high xylem resistance to  
521 embolism. In such a case, the association between drought tolerance and slow strategy would not  
522 arise from adaptive trade-offs but rather from an exaptive result of resource scarcity (Laughlin *et*  
523 *al.*, 2020).

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

## 529 **Conclusions and prospects**

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

## 551 **Acknowledgements**

552 This article is an output of the international network "PsiHub" funded and supported by the  
553 ECODIV department of INRAE.

554

555 **Author contributions**

556 The conception of this manuscript and the identification of the different sections was carried out  
 557 by J.M.T-R and N.M. All authors have contributed equally to the different sections and to the  
 558 revision and correction of the final version. M.M. and J.M.T-R developed the conceptual figures  
 559 of this article, which were subsequently improved with the contributions of all the authors.

560

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1039 **Figure legends**

1040 **Fig. 1.** Conceptual diagram depicting the main physiological processes related to the hydraulic  
 1041 characteristics of plants and how they are linked to other processes crucial for assessing the  
 1042 consequences of climate change in forest and agricultural systems. The abbreviation VFD stands  
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1044  
 1045 **Fig. 2.** Conceptual graph showing the relative variation in the main physiological functions linked  
 1046 to plant hydraulic traits as plants are subjected to increasing levels of water stress. The intensity of  
 1047 stress increases along the x-axis until reaching levels at which their survival is compromised and  
 1048 plant death is induced by drought due to the negative effects on the different physiological  
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 1051 **Fig. 3.** Crops function with a narrow stomatal safety margin (SSM) that could allow species with  
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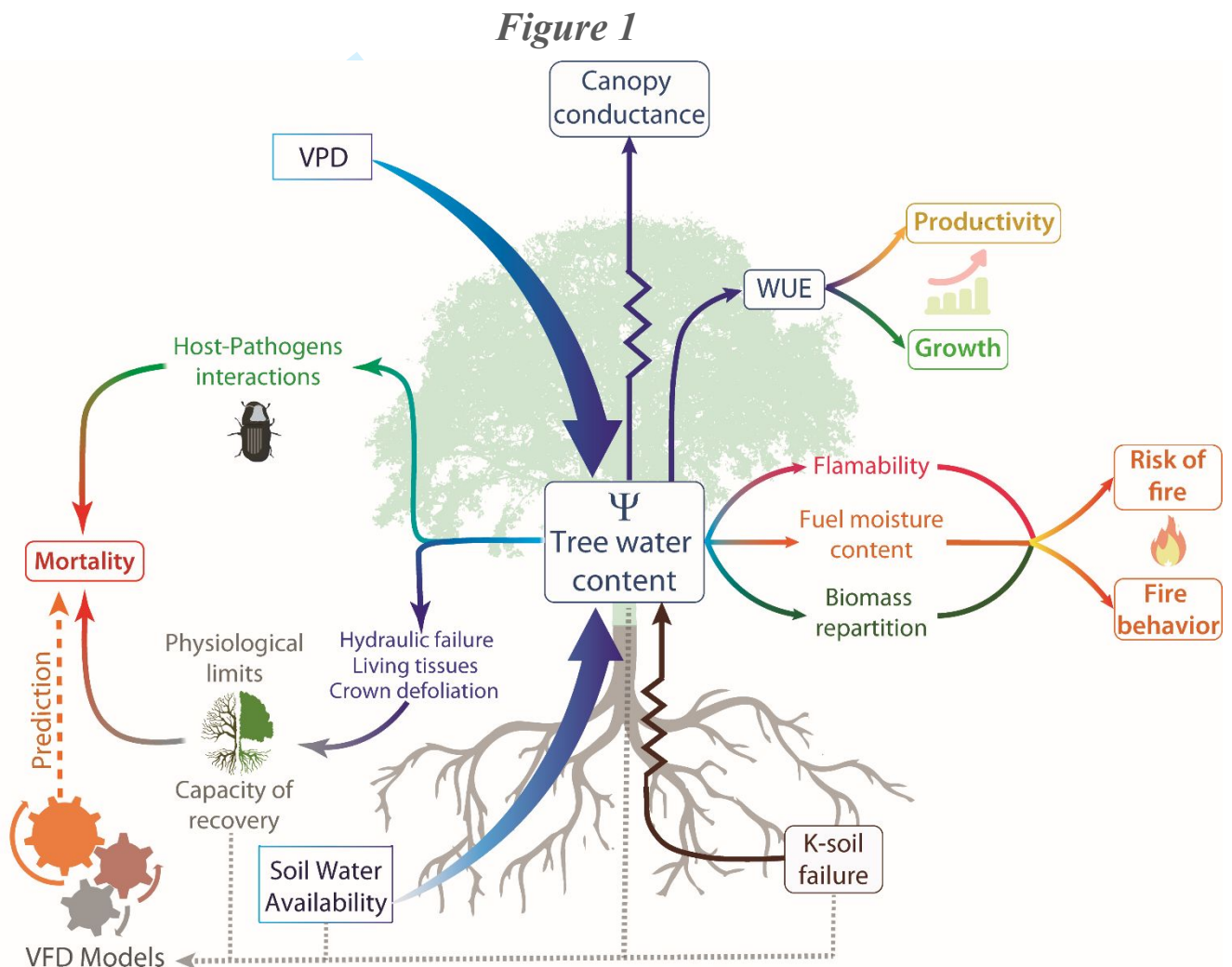
# Figures

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## 1077 Xylem hydraulics at the heart of plant, crops and ecosystem functions in 1078 the face of climate change 1079

1080 JM Torres-Ruiz<sup>1\*</sup>, H Cochard<sup>1</sup>, S Delzon<sup>2</sup>, T Boivin<sup>3</sup>, R Burlett<sup>2</sup>, M Cailleret<sup>4</sup>, D Corso<sup>2</sup>, CEL  
1081 Delmas<sup>5</sup>, M De Caceres<sup>6</sup>, A Diaz-Espejo<sup>7</sup>, P Fernández-Conradi<sup>3</sup>, J Guillemot<sup>8,9,10</sup>, LJ Lamarque<sup>11</sup>, JM  
1082 Limousin<sup>12</sup>, M. Mantova<sup>13</sup>, M Mencuccini<sup>6,14</sup>, X Morin<sup>12</sup>, F Pimont<sup>3</sup>, V Resco De Dios<sup>15,16</sup>, J Ruffault<sup>3</sup>,  
1083 S Trueba<sup>2</sup>, N K Martin-StPaul<sup>3</sup>

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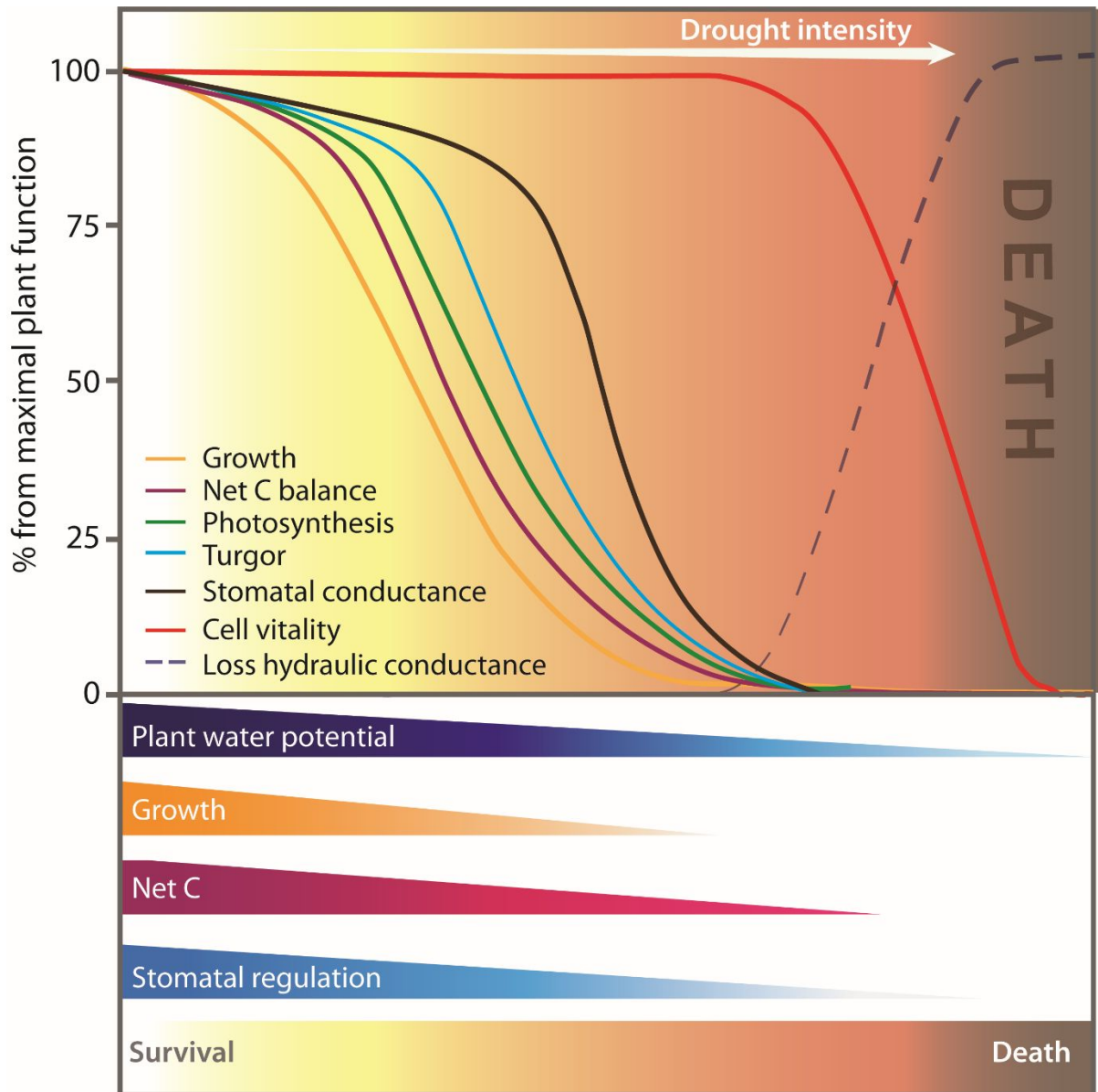


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Figure 2

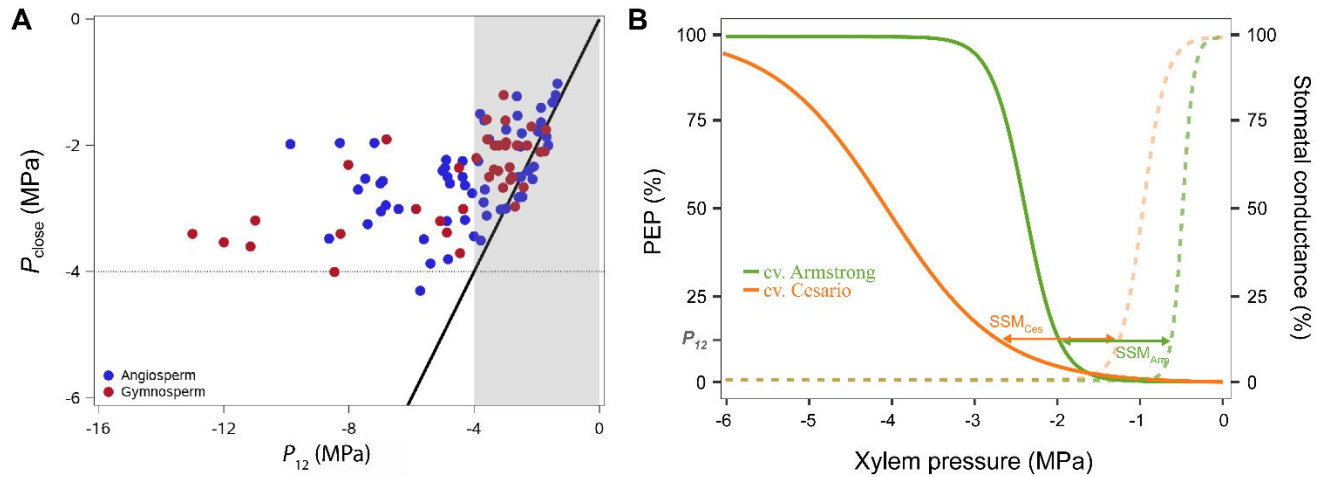


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Figure 3

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**Fig. 3.** Crops function with a narrow stomatal safety margin (SSM) that could allow species with a delayed onset of embolism to maintain gas exchanges 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 (*T. aestivum*) exhibit differences in xylem vulnerability to cavitation (plain lines). Assuming that stomatal safety margin is constant in the range of xylem pressure going from -1 to -4 MPa (*i.e.*  $SSM_{Ces} = SSM_{Arm}$ ), wheat cv. Cesario, that shows a delayed  $P_{12}$  in comparison to cv. Armstrong, would maintain gas exchanges under greater water stress (dotted lines).

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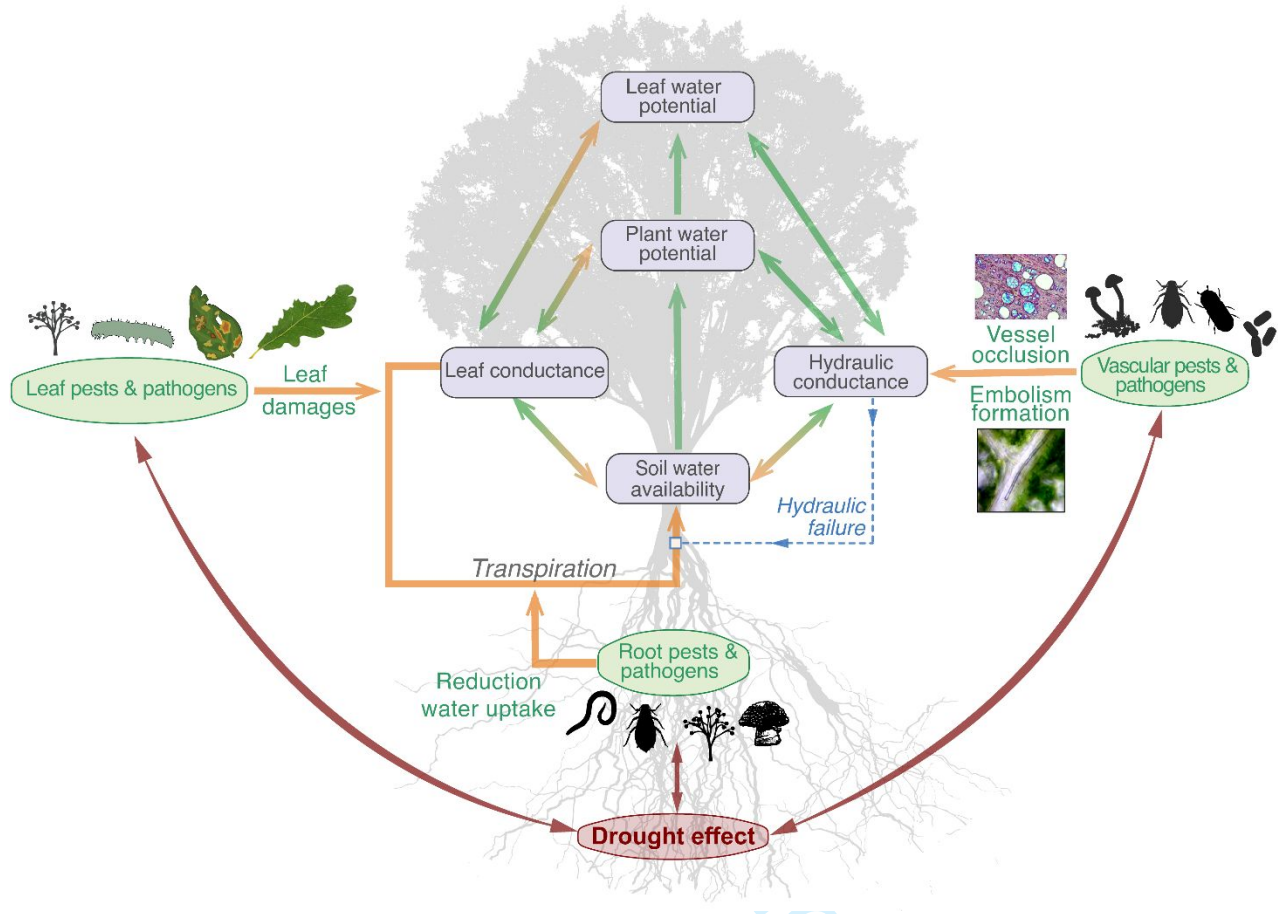
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Figure 4

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**Fig. 4.** Impacts of pests and pathogens on plant hydraulic traits (adapted from Martinez-Vilalta *et al.* 2017). Green and orange 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.

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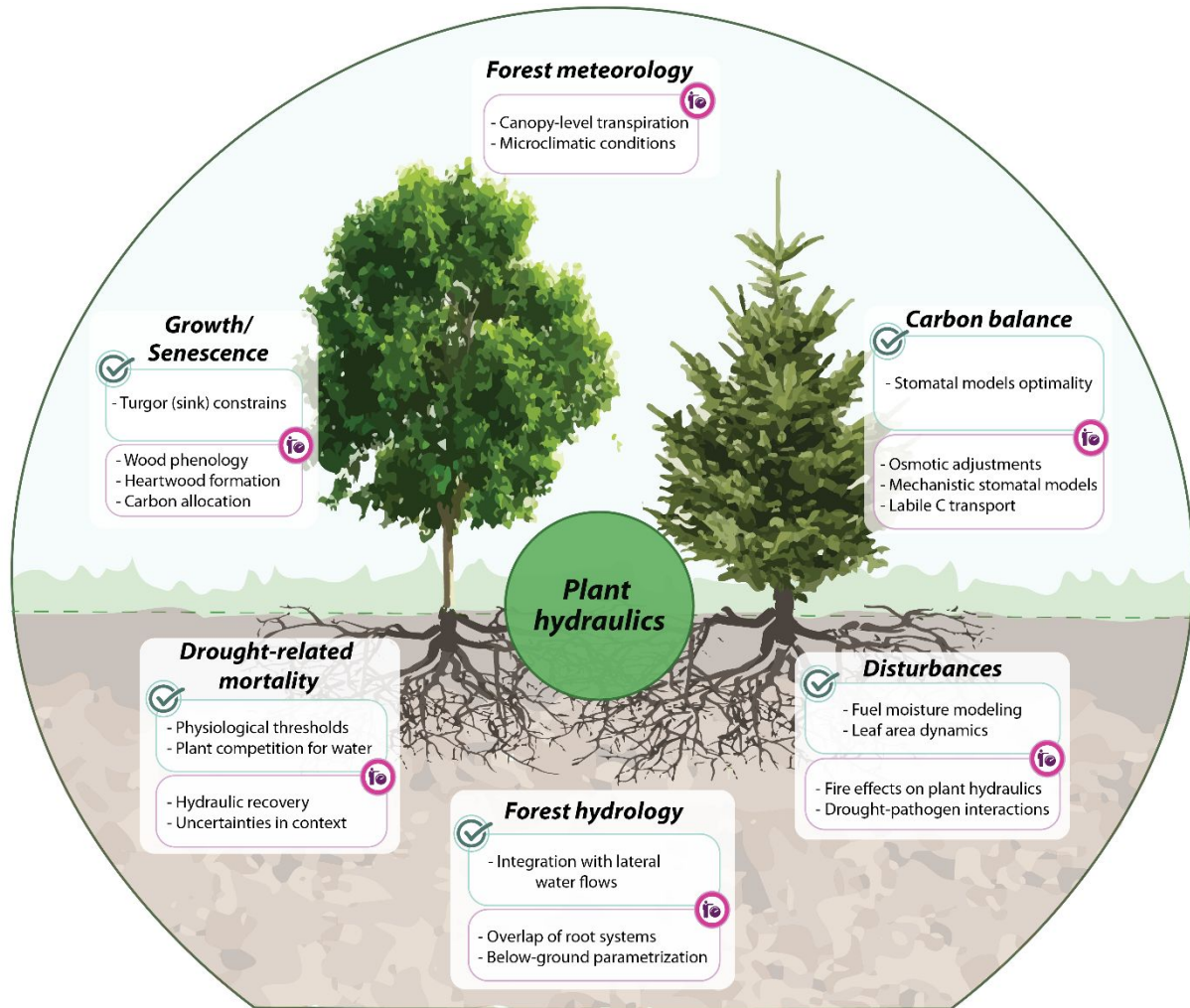
Figure 5

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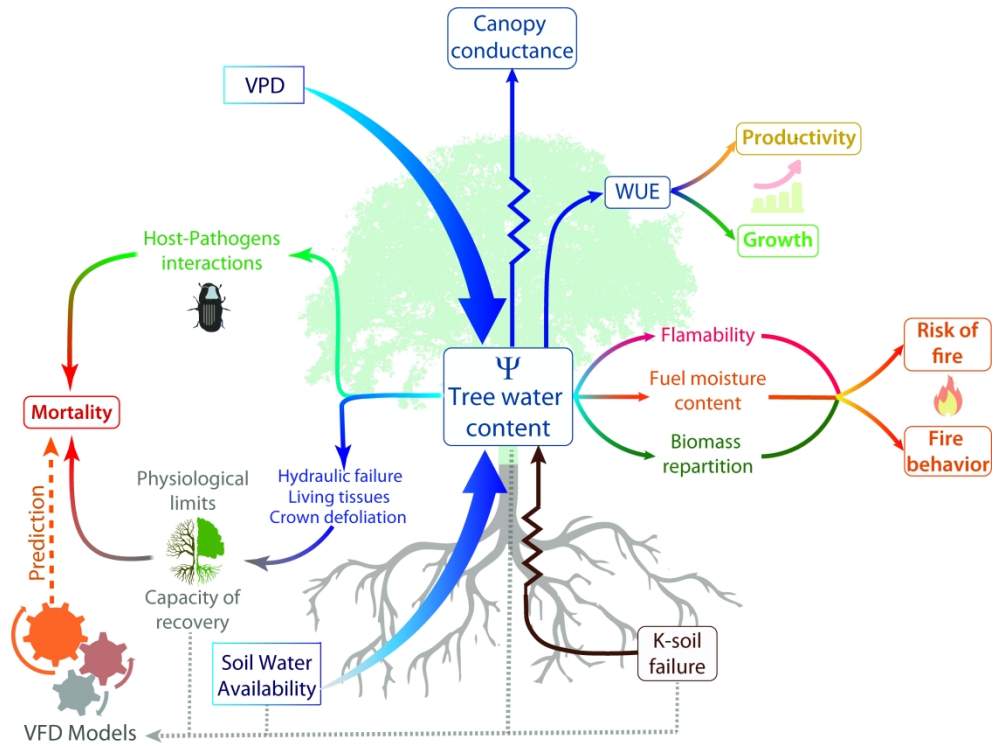


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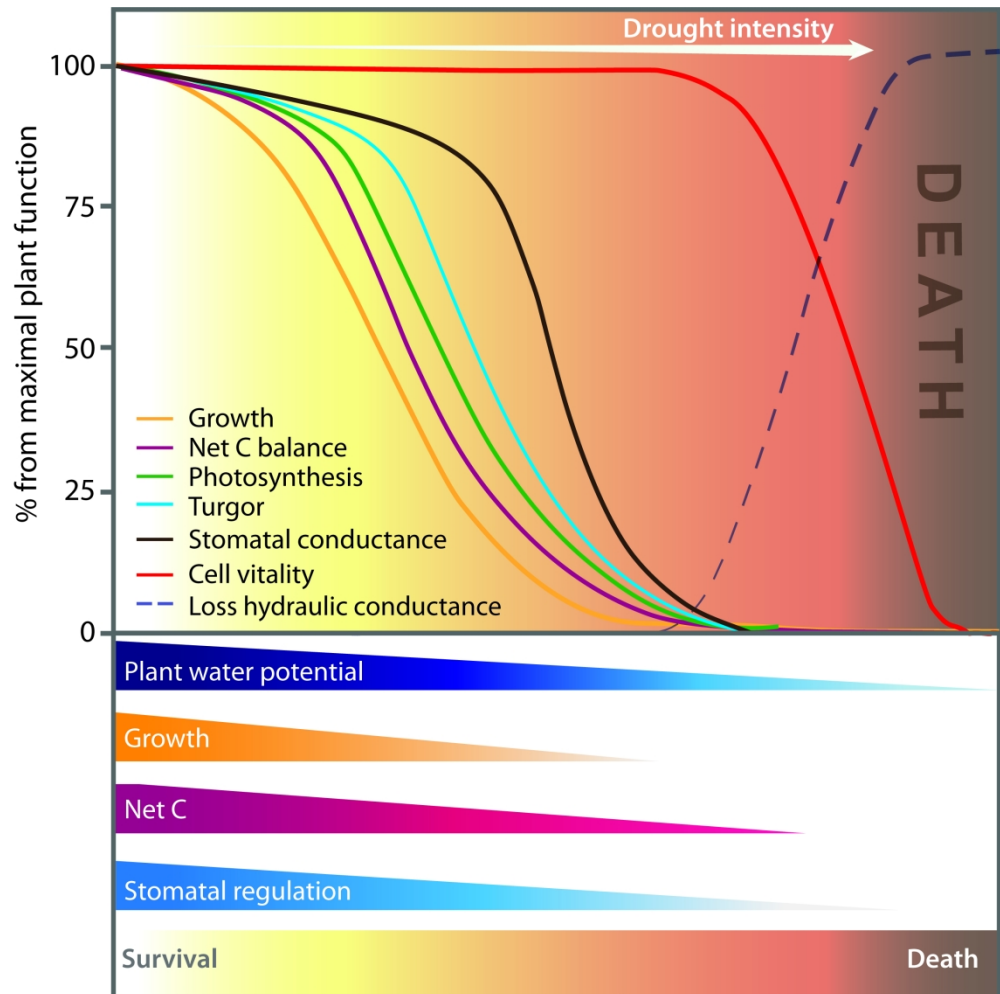


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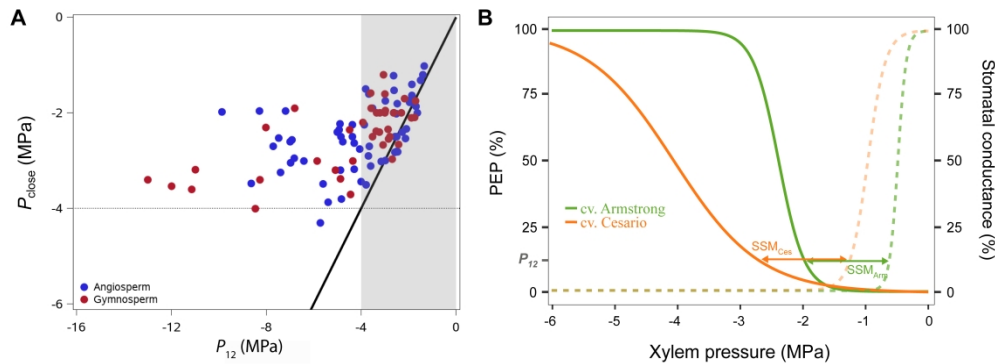


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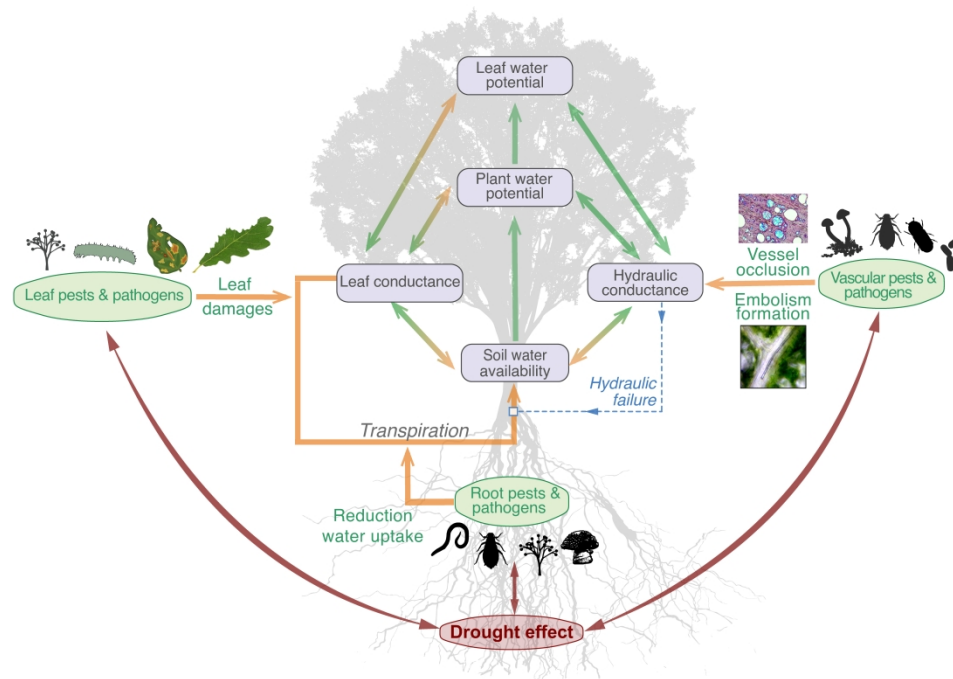


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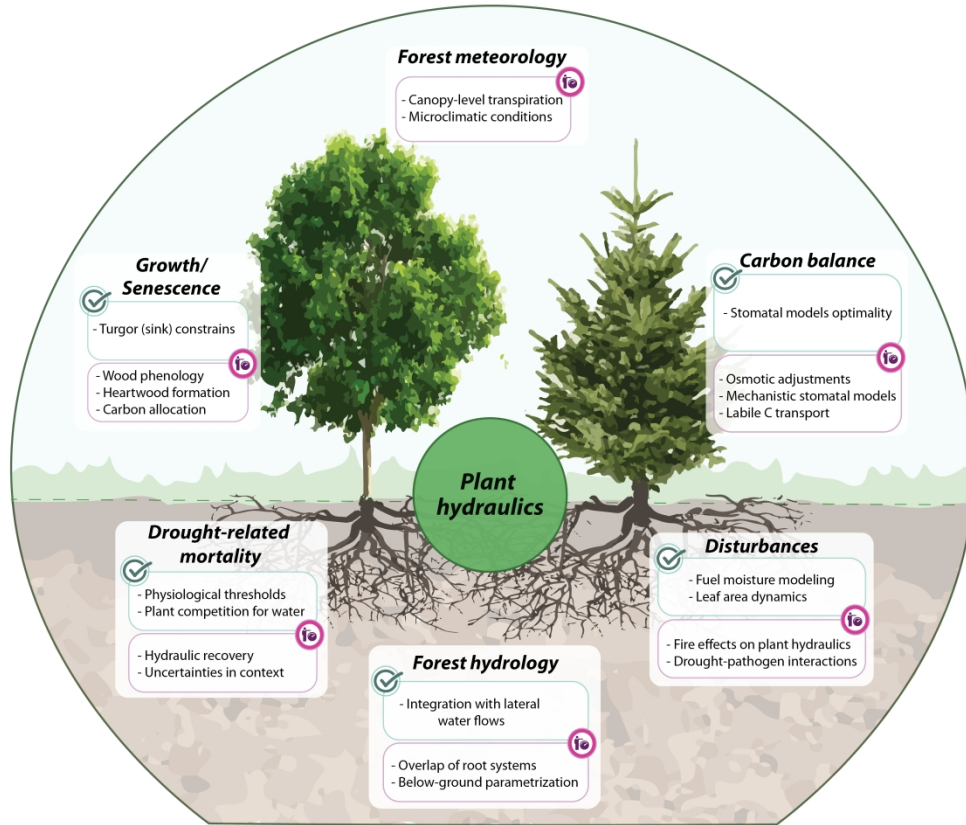


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