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

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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*, 2023, 241 (3), pp.984-999. 10.1111/nph.19463 . hal-04601370

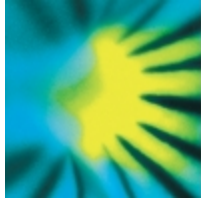
HAL Id: hal-04601370

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

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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Manuscripts

1 Xylem hydraulics at the heart of plant, crops and ecosystem functions in 2 the face of climate change

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30
31 **Words count:** *Summary* - 154 words
32 *Main body* - 6497 words
33 *Figures* - 5 Figures, all in colour.
34 *Supplementary information* - 1 Figure in colour + 1 Table.

35
36 **Contents:** Summary
37 i) Introduction
38 ii) Plant Hydraulics: A Framework for Measuring Drought Impacts
39 iii) Hydraulic properties and crop productivity under drought conditions.
40 iv) Linkage between hydraulics-related plant traits and wildfire risk
41 v) Role of hydraulic traits on plant-herbivore insects-pathogens interactions.
42 vi) Plant hydraulic as a hub for vegetation models.
43 vii) Water-use and drought tolerance strategies in the global spectrum of plant functions
44 Conclusions and prospects
45

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 (Ψ_{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 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 (Ψ) 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_{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_{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_{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*
244 *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 al.*
283 *et al.*, 2018; Pivovarovoff *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
 1043 for 'Vegetation Function and Dynamics' process-based models".

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
 1049 functions.

1050
 1051 **Fig. 3.** Crops function with a narrow stomatal safety margin (SSM) that could allow species with
 1052 a delayed onset of embolism to maintain gas exchanges longer under drought. **A.** Within the range
 1053 of pressure inducing xylem embolism reported in crops (*i.e.* P_{12} ranging from -1 to -4 MPa; grey
 1054 area), the linear relationship between P_{close} (pressure inducing 90% of stomatal closure) and P_{12} is
 1055 close to the 1:1 line (plain line; adapted from Martin-StPaul *et al.* 2017). The dashed line
 1056 corresponds to the absolute limit by which stomata closure must occur to avoid rapid death under
 1057 drought conditions. **B.** Cultivars of wheat (*T. aestivum*) exhibit differences in xylem vulnerability
 1058 to cavitation (plain lines). Assuming that stomatal safety margin is constant in the range of xylem
 1059 pressure going from -1 to -4 MPa (*i.e.* $SSM_{Ces} = SSM_{Arm}$), wheat cv. Cesario, that shows a delayed
 1060 P_{12} in comparison to cv. Armstrong, would maintain gas exchanges under greater water stress
 1061 (dotted lines).

1062
 1063 **Fig. 4.** Impacts of pests and pathogens on plant hydraulic traits (adapted from Martinez-Vilalta *et*
 1064 *al.* 2017). Green and orange arrows represent positive and negative relationships, respectively,
 1065 between variables. The dashed blue line indicates the hydraulic disconnection that occurs
 1066 following severe vessel occlusion (embolism and/or tyloses) and impedes the plant from
 1067 continuing to transpire. Red arrows represent how plant pathogen infections or pest damages may
 1068 also have an antagonistic or synergistic effect on plant response to drought.

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 1070 **Fig. 5.** Diagram summarizing the key advancements and challenges related to integrating plant
 1071 hydraulic models into process-based models of vegetation function and dynamics. The diagram is
 1072 organized both by discipline (hydrology and forestry), by physiological processes and
 1073 disturbances. Green boxes summarize main achievements and pink boxes the main challenges.

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Figure 2

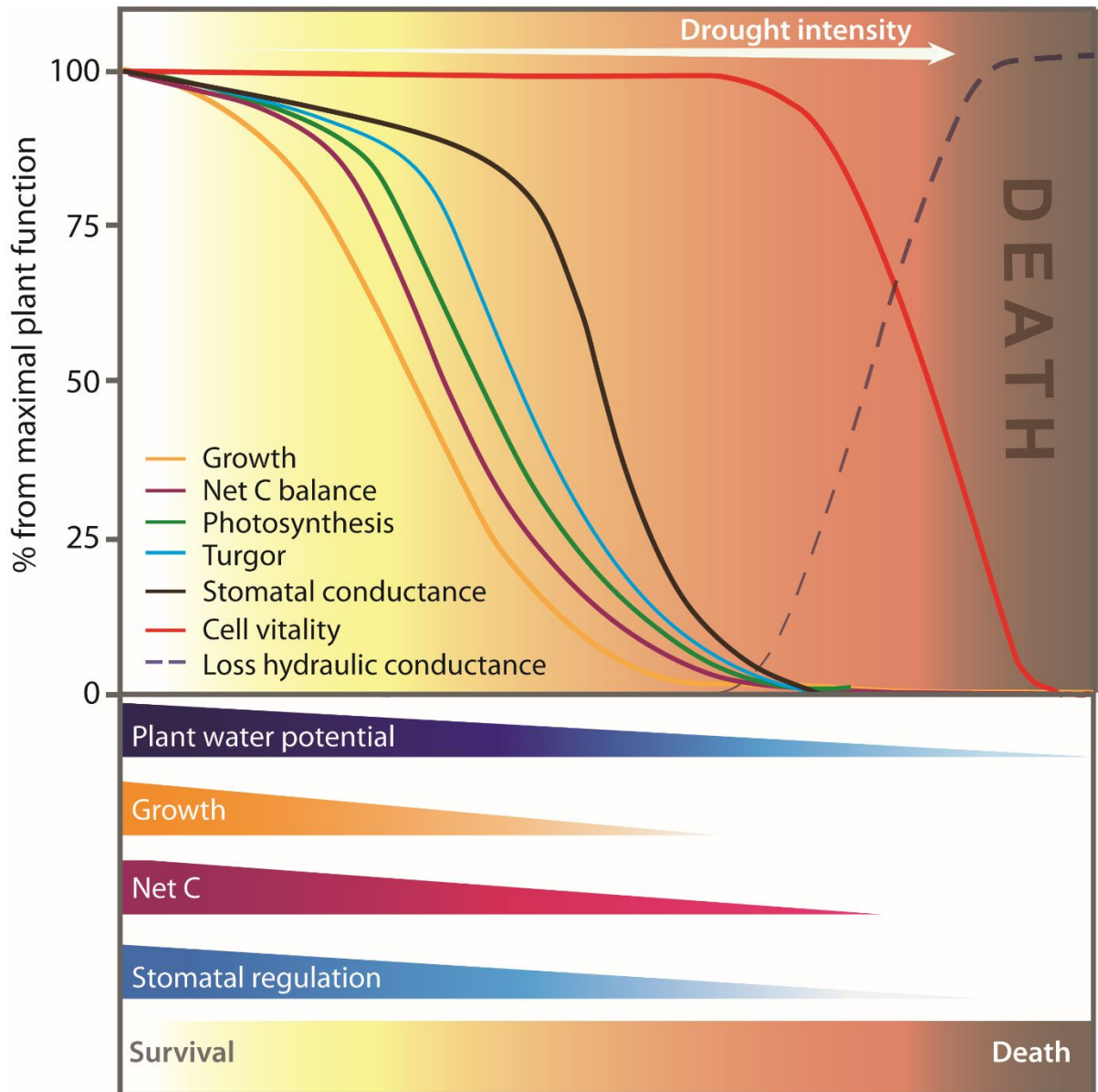


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Figure 3

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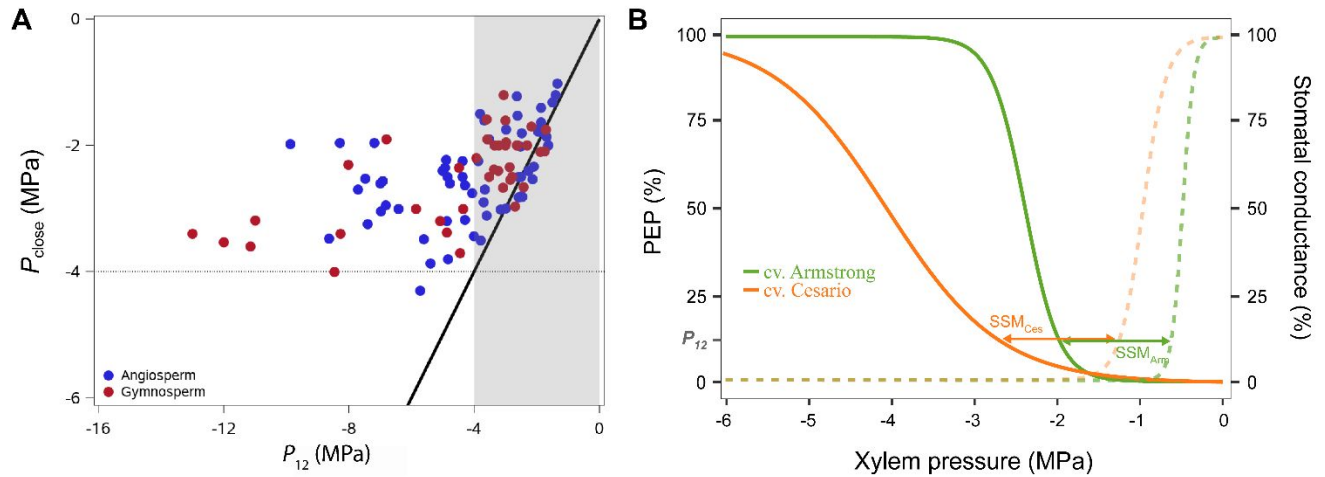


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Figure 4

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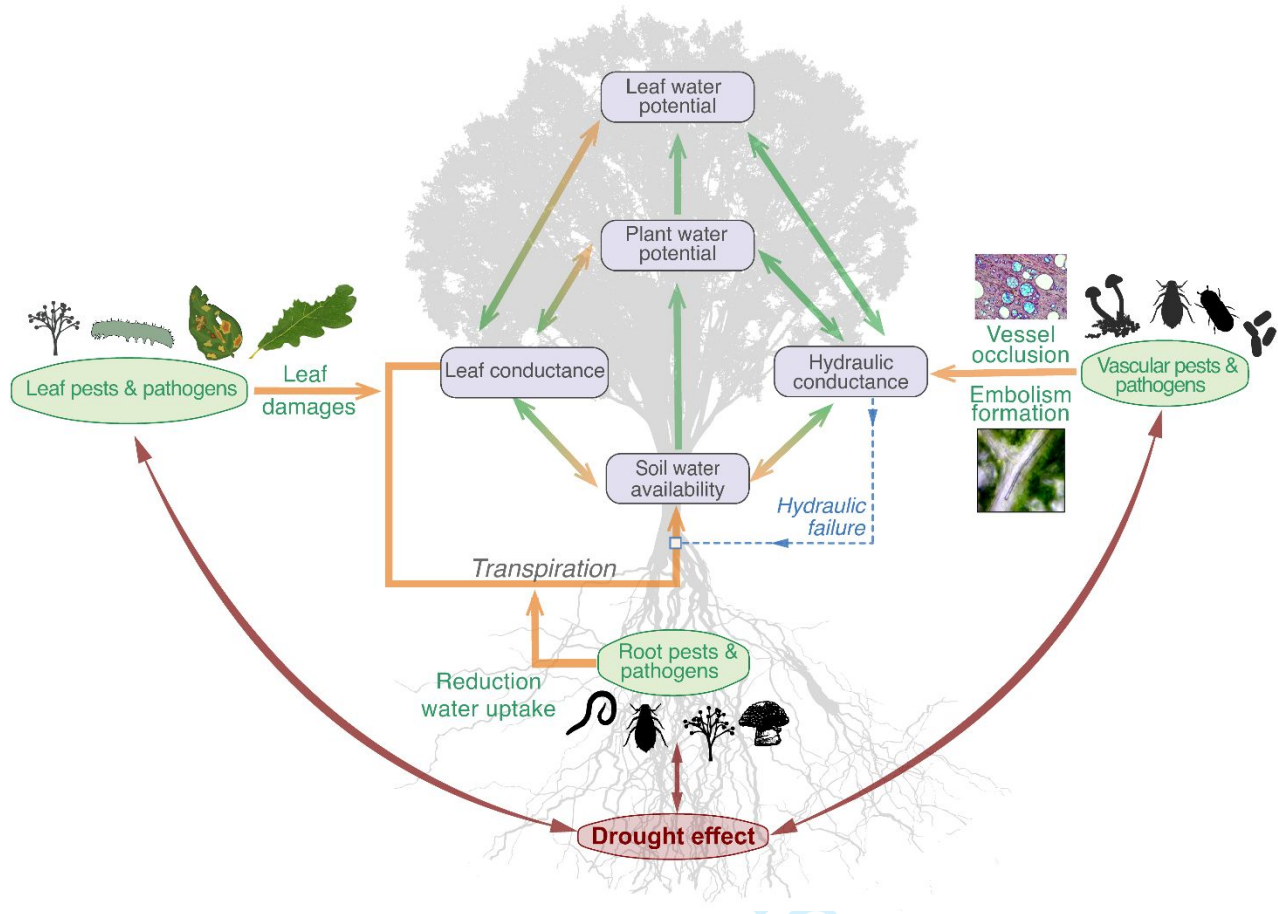


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Figure 5

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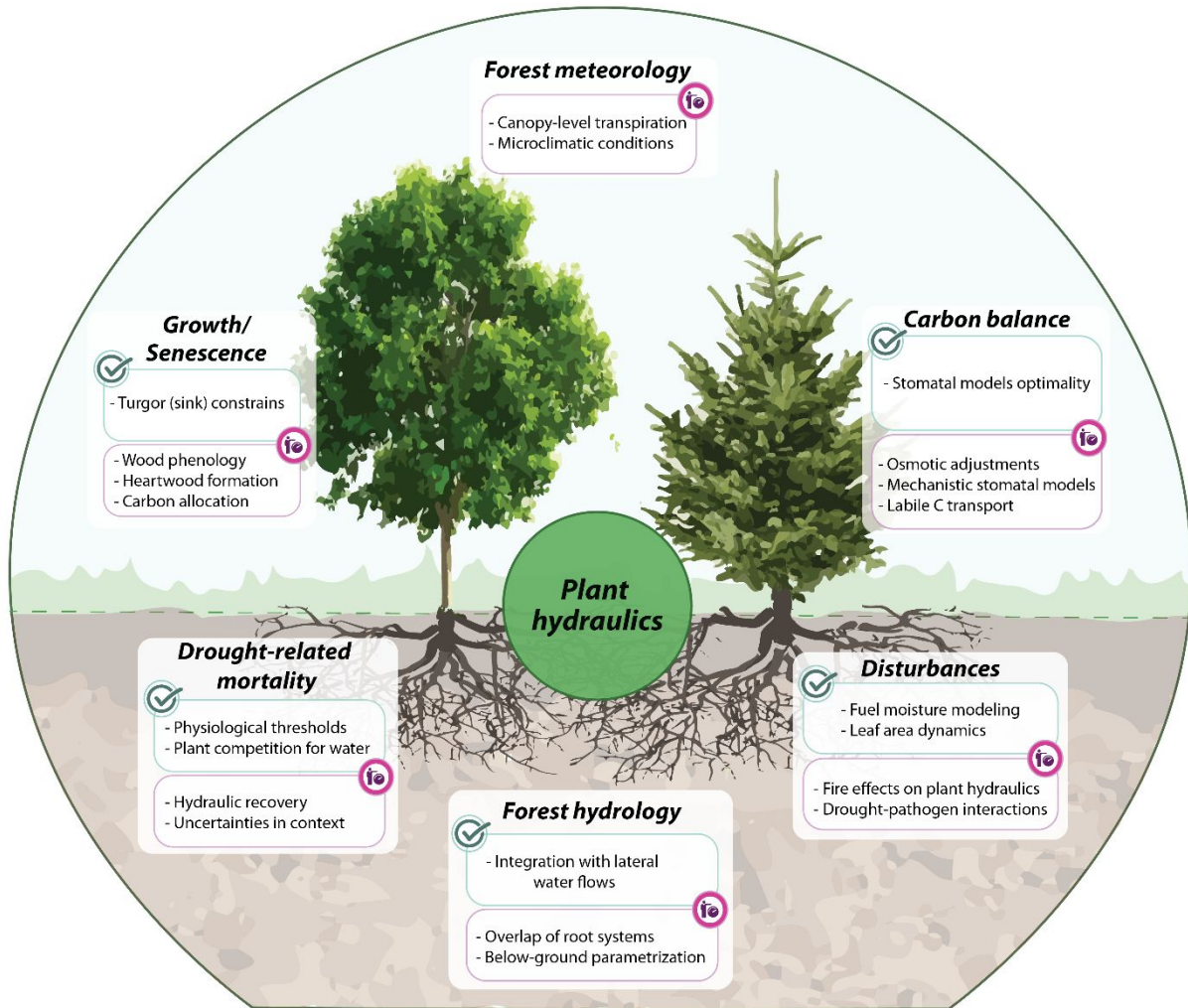


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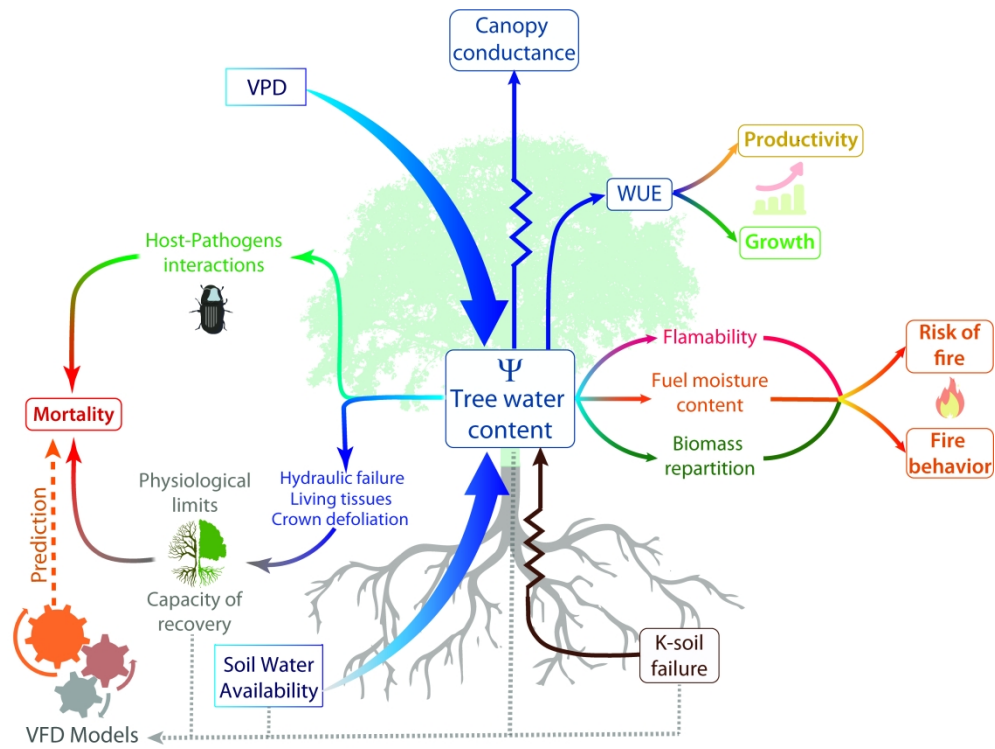


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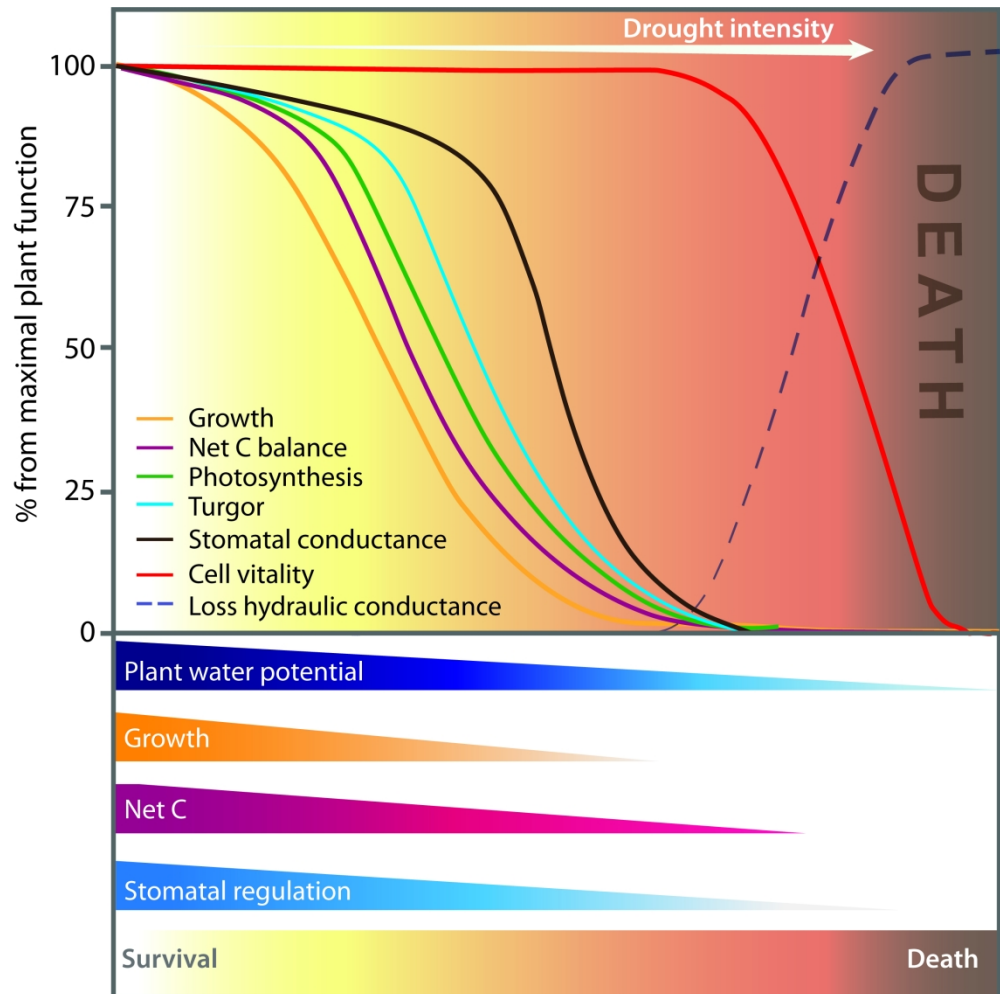


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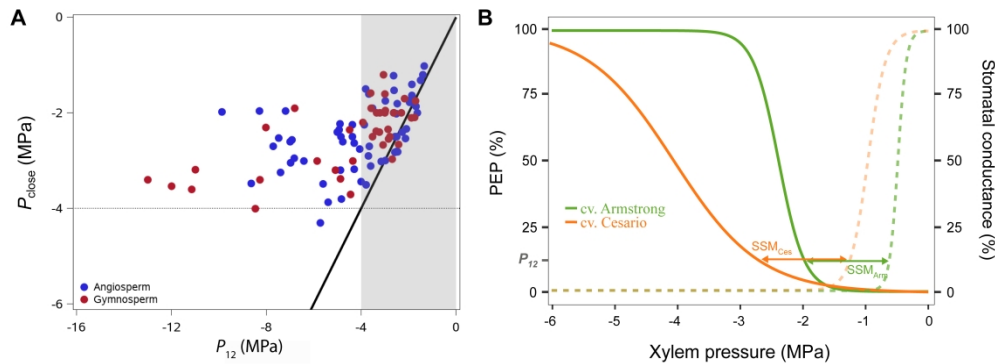


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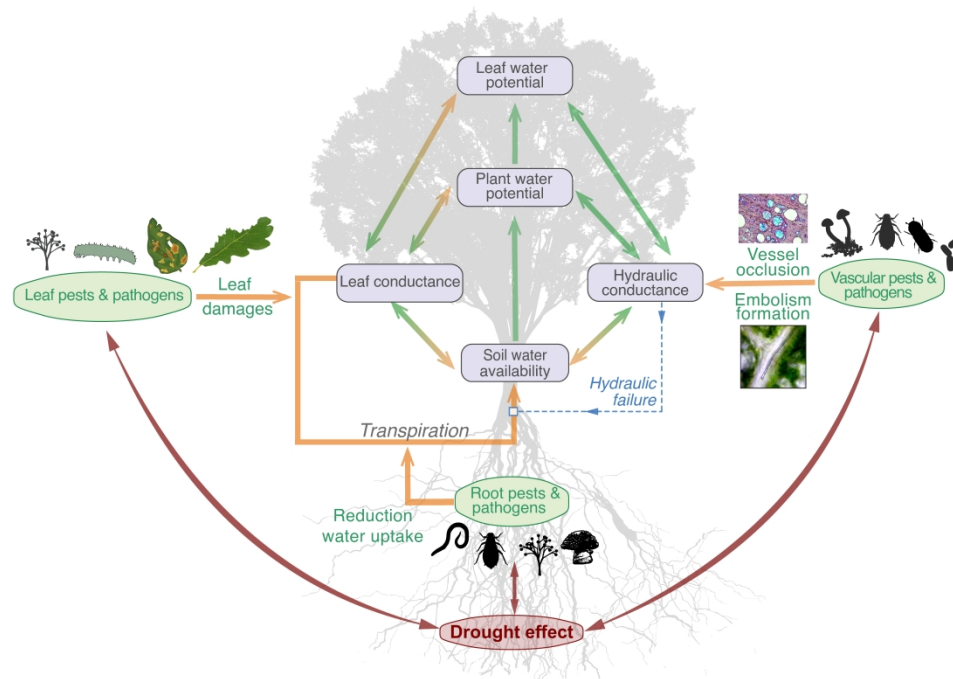


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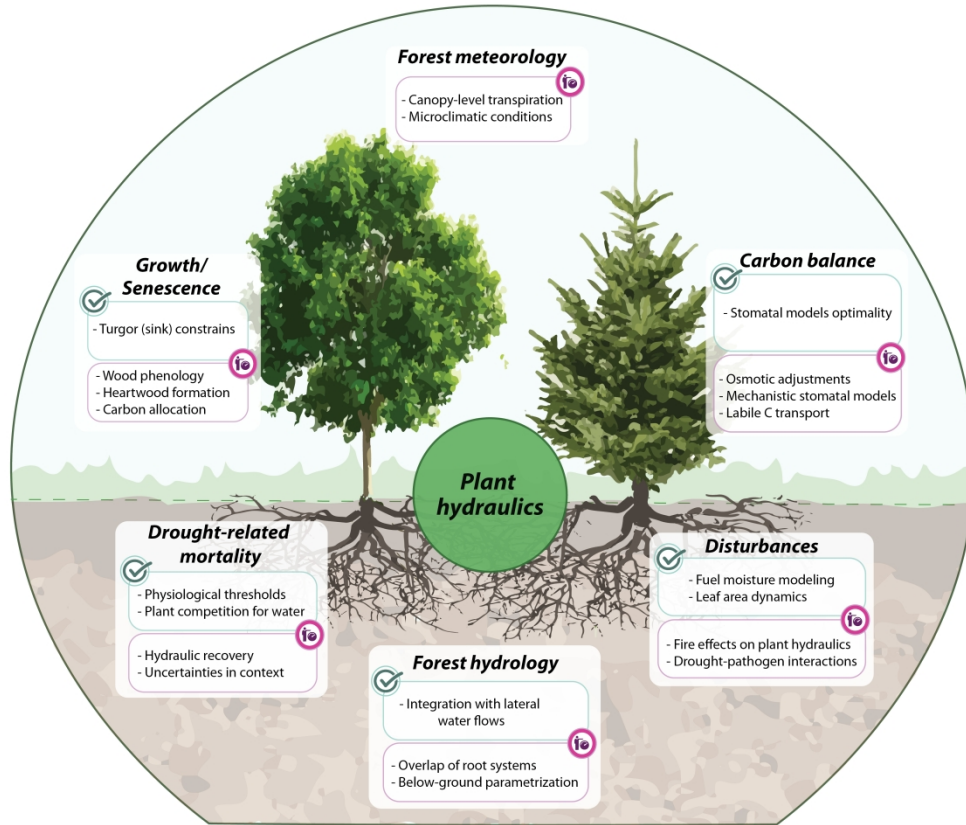


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