How much does VPD drive tree water stress and forest disturbances?

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Abstract

Vapor Pressure Deficit (VPD, atmospheric drought) and soil water potential (Ψsoil, soil drought) have both been reported to affect terrestrial plant water stress, plant functions (growth, stomatal conductance, transpiration) and vulnerability to ecosystem disturbances (mortality or vulnerability to wildfires). Which of atmospheric drought or soil drought has the greatest influence on these responses is yet an unresolved question. Using a state-of-the-art soil-plant-atmosphere hydraulic model, we conducted an in-silico experiment where VPD and Ψsoil were manipulated one at a time to quantify the relative importance of atmospheric vs soil drought on most critical plant functions. The model simulates the combined effects of soil drought and atmospheric drought on plant water potential (ΨPlant), a physiologically meaningful metric of plant water status driving plant turgor, stomatal conductance, hydraulic conductance or water content, and thus mortality and fire risks. Contrary to expectations, we showed that VPD had a weaker effect than Ψsoil on tree water stress and forest disturbances risk (i.e leaf moisture content). While physiological responses associated with low water stress such as stomatal closure or turgor loss could be driven by both VPD or soil drought, consequences of extreme water stress such as hydraulic failure, leaf desiccation and vulnerability to wildfires were almost exclusively driven by low Ψsoil. Our results therefore suggest that most plant functions are affected by VPD through its cumulative effect on Ψsoil via increased plant transpiration, rather than through a direct instantaneous effect on plant water potential. We argue that plant hydraulics provide a strong foundation for predicting tree and terrestrial ecosystem responses to climate changes and propose a list of explanations and testable hypotheses to reconcile plant hydraulic theory and observations of soil and atmospheric drought effects on plant functions.

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Introduction

Over the last decades, the increase in forest disturbances caused by climate change has acted as a catalyst for research on plant responses to drought. While pioneer studies mainly focused on plant responses to reduced precipitation or soil moisture deficit ("soil drought", Beier et al., 2004; Bréda et al., 2006; Limousin et al., 2009; Pangle et al., 2015; Weltzin et al., 2003), the impact of recent massive heat-waves on plants has favored the emergence of the "global-change-type drought" concept (Breshears *et al.* 2005) and shed light on the key role of "atmospheric drought" (or vapor pressure deficit, VPD) on plant functioning (Park Williams *et al.* 2012; Trenberth *et al.* 2014; McDowell *et al.* 2015, 2022; Yuan *et al.* 2019; Grossiord *et al.* 2020). Major efforts are currently underway to unravel the respective roles of VPD and soil drought on the different facets of plant functioning (e.g., gas exchanges, growth, mortality, vulnerability to wildfire) in studies ranging from controlled experiments (Grossiord *et al.* 2017a, b; Schönbeck *et al.* 2022) to analyses of climate impacts at regional (Trotsiuk *et al.* 2021; Dannenberg *et al.* 2022; Grünig *et al.* 2022) and continental scales (Seager *et al.* 2015; Humphrey *et al.* 2021; Bauman *et al.* 2022; Flo *et al.* 2022; Fu *et al.* 2022b, a). In these studies the predominant role of VPD is most of the time invoked as the main driver of plant responses (Grossiord *et al.* 2017a, b; Flo *et al.* 2021, 2022; Humphrey *et al.* 2021; Bauman *et al.* 2022; Fu *et al.* 2022b, a; Grünig *et al.* 2022; Schönbeck *et al.* 2022). These conclusions may seem in contradiction with observational evidence from agricultural irrigation or natural riparian forests in arid zones showing that root access to soil water is a stronger predictor of plant productivity than VPD (Sousa *et al.* 2022). Consequently, there is a strong need to disentangle the role of atmospheric drought (VPD) and soil drought (ψ_{soil}) on different important plant functions which can be done with a plant hydraulic modeling framework.

From a physiological perspective, plants and ecosystems functions are impaired by "plant water stress" rather than directly by soil drought or atmospheric drought. Plant water stress may be due to difficulty in extracting water from the soil (i.e. « soil drought ») or to difficulty in retaining water in the plant (i.e. "atmospheric drought"). In both cases, the consequences for the plant and, more specifically for the plant water status, are expected to be similar since both result in a drop in its water potential. Plant water stress is typically quantified through the plant water potential (ψ_{plant}). ψ_{plant} a physical measure of the free energy status of water in a plant organ that represents the plant water status and thus allows an unambiguous description of the physiological processes triggered under drought conditions and leading to critical functional impairments in plants. A plant is under water stress when its water potential impairs key physiological functions, such as cell turgor and thus growth, stomatal conductance, integrity of the xylem hydraulic pathway, the water content of plant organs (McDowell 2011; Lempereur *et al.* 2015; Mantova *et al.* 2021). As depicted in Figure 1, only an integrative plant hydraulic framework can, through well-established biophysical laws, predict ψ_{plant} resulting from the interactions between VPD and ψ_{soil}. While the soil retention curves make the links between soil moisture content and ψ_{soil} (van Genuchten 1980), the diffusion laws link the ψ_{soil}, the hydraulic conductance, the plant transpiration and the VPD to the ψ_{plant} (McDowell & Allen 2015) (Figure 1a).

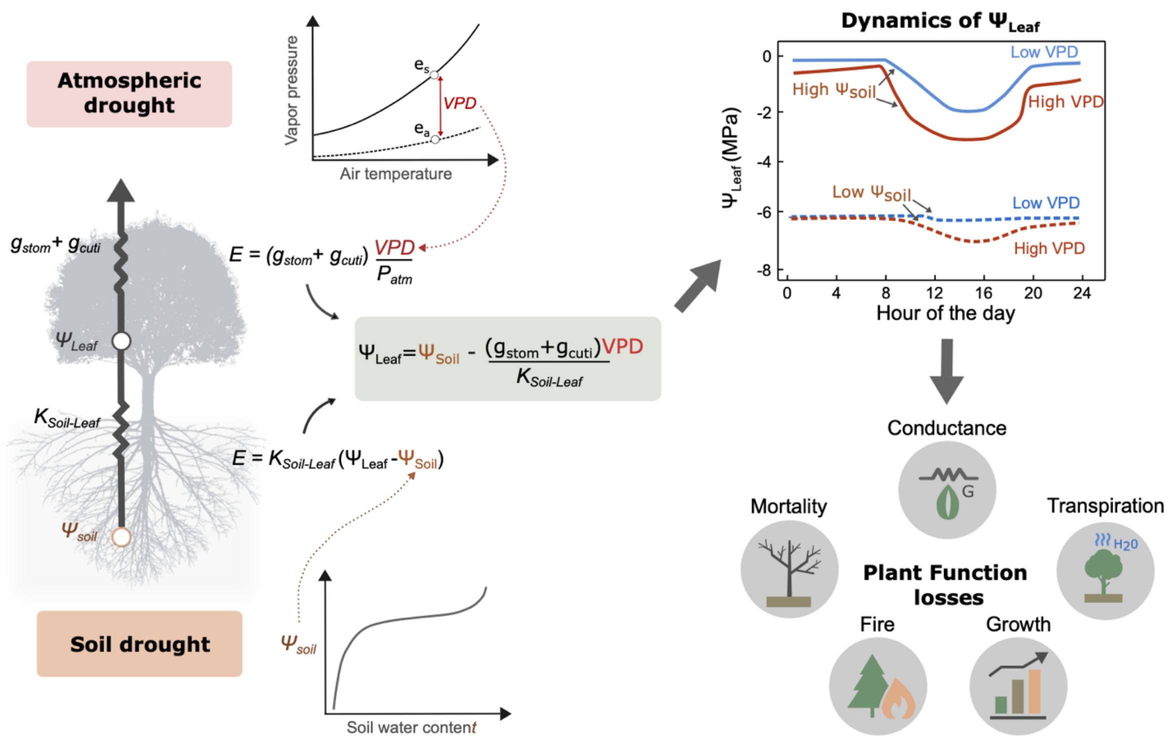

Figure 1: Illustration of how atmospheric drought (VPD) and soil drought (soil water potential, Ψ_{soil}) interact to drive plant water status (a) and water stress (b). Water status triggers water stress by altering various plant functions sequentially. Note that for the sake of clarity, the contribution of capacitance was neglected in the equation of plant water status (leaf water potential, ψ_{leaf}), but it can be integrated (Cochard *et al.* 2021; Ruffault *et al.* 2022b). Other variables include $K_{soil\text{-}leaf}$ (soil-to-leaf hydraulic conductance), G_{leaf} (leaf conductance to water vapour), E_{leaf} (leaf transpiration), P_{atm} (atmospheric pressure).

Based on this framework, the relative roles of atmospheric and soil drought on plant functioning result from interacting physiological processes. On the one hand, a decrease in soil water potential in the rooting zone translates into a proportional decline in plant water potential and thus an increase in plant water stress. Because the relationship between ψ_{soil} and soil water content is strongly nonlinear, soil water content must be depleted beyond a certain point before it results in significant decline in ψ_{plant} and causes plant water stress (Granier *et al.* 1999; Martin-StPaul *et al.* 2017) (Figure 1). On the other hand, increase in VPD translates into an increase in transpiration rates and thus into a decrease in ψ_{plant}. However, the decline in ψ_{plant} triggers the down-regulation of gas exchange through a decrease in the stomatal conductance to water vapor, which in turn slows down plant desiccation and the decline in ψ_{plant}. The response of leaf stomatal conductance to ψ_{plant} is species-specific (Klein 2014; Martin-StPaul *et al.* 2017) and effective to regulate water potential up to the point when the stomata are fully closed. Beyond this point, only the leaf cuticular conductance drives the transpiration rate and thus the potential effect of VPD on plant water status and water stress (Duursma *et al.* 2019).

Consequently, the magnitude of the changes in plant water potential induced by a change in VPD or in ψ_{soil} depends on several plant traits (Novick *et al.* 2019). Using a plant hydraulic modeling framework, we explore here the interacting roles of atmospheric drought (VPD) and soil drought (soil water potential) on a suite of key plant functions and derive results and conclusions which can serve as guidelines for future research endeavor.

Materials & Methods: *Using a plant hydraulic model to evaluate how atmospheric and soil drought influence plant functions*

We used the soil plant hydraulic model SurEau (Cochard *et al.* 2021; Ruffault *et al.* 2022b) to explore the relative contributions of soil and atmospheric droughts on several plant physiological processes and related disturbances' risk. SurEau simulates water fluxes and potential through a similar but more elaborated representation of the plant functioning scheme shown in Figure 1. At each time step (typically 30 minutes), the model computes leaf stomatal and cuticular transpiration as the product between leaf-to-air VPD and stomatal and cuticular conductance. Then, stomatal and cuticular fluxes are used to compute ψ_{plant} in the different plant compartments, while accounting for the symplasmic capacitance and the hydraulic conductance losses due to xylem embolism. Stomatal closure is regulated in a feedback manner, as a function of leaf water potential, through empirical relationships (Klein 2014). The soil water potential (ψ_{soil}) and the soil hydraulic conductance are also computed from soil water content. Hence, it can represent different degrees of anisohydry, such as in stomatal optimization gain-risk model (Grossiord et al. 2020). The model is parameterized with measurable plant traits. This includes (i) the traits that determine the water potential for a given soil and atmospheric drought such as plant hydraulic conductance, the stomata sensitivity to water potential, and the cuticular conductance; and (ii) the traits that determine the responses of plant function to water potential such as the plant vulnerability to cavitation, or the pressure-volume curves that drive cell turgor and thus growth (Ali *et al.* 2022) and the moisture content and thus the flammability of the plant organs (Nolan *et al.* 2020; Ruffault *et al.* 2022a).

We performed an *in-silico* experiment with SurEau where soil drought and atmospheric drought were manipulated while keeping constant the other climatic variables (see supplementary matterials). To evaluate the influence of soil drought alone, we prescribed iteratively a range of soil water potential from 0 to -9MPa, using 0.5MPa steps. At each step, we also prescribed iteratively a range of VPD (from 0.5 to 7kPa, corresponding to the range in the field) while keeping temperature constant. To explore the role of plant traits in mitigating the effects of atmospheric drought and soil drought on plant functions, we carried out simulations for two species with very distinct hydraulic traits and climatic niches and on which SurEau was previously assessed (Ruffault et al 2022), namely the Mediterranean oak *Quercus ilex* and the temperate beech *Fagus sylvatica*. Stomatal and hydraulic parameters used for SurEau simulations are reported in supplementary materials.

For each simulation, we extracted six indicators reflecting different aspects of plant functioning: (i) leaf turgor which is related to plant growth, (ii) leaf stomatal conductance which determines photosynthesis and transpiration, (iii) total leaf transpiration rate, taken as the sum of stomatal and cuticular transpiration, (iv) the percent loss of leaf xylem hydraulic conductance which is related to the risk of mortality by hydraulic failure, and (v) leaf moisture content which is related to the flammability of the plant and the risk of wildfires. In addition, we extracted leaf water potential (ψ_{leaf}) which is a taken as an indicator of the overall plant water status (ψ_{plant}).

Results and discussion: *Atmospheric and soil drought are both determinant for plant growth and productivity but soil drought alone determines plant safety*

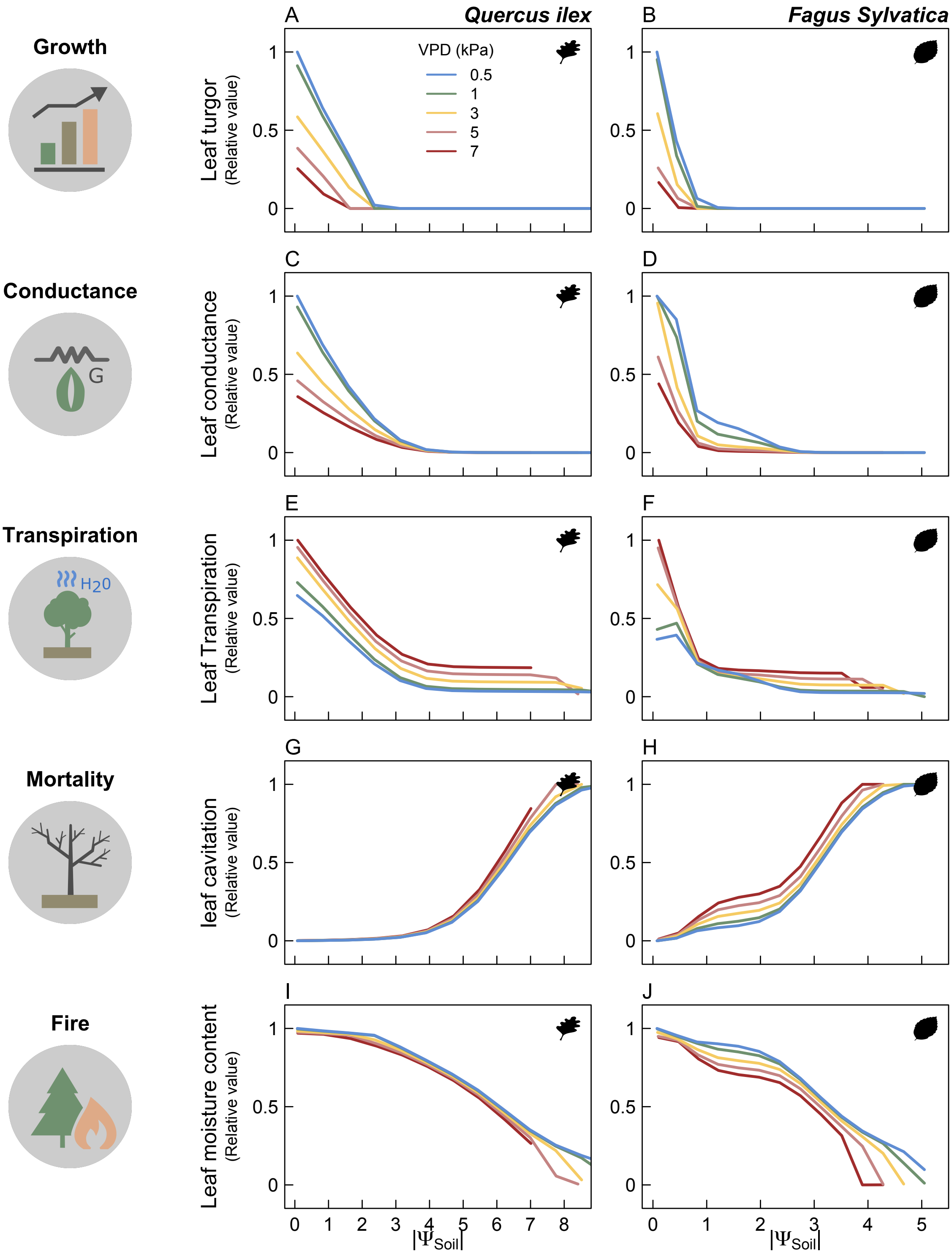

Figure 2 : Simulated dependence of five different plant functions to ψsoil (x axis) and VPD (colors) for Quercus ilex (left) and Fagus sylvatica (right). The different indices were expressed relatively to the value simulated at the maximum atmospheric drought (VPD = 7kPa). Soil water potential is expressed in absolute values (i.e., dry conditions are on the right of each panel). Parameters are provided in Appendix. The range of soil water potential differs because total hydraulic failure which occurs earlier for Fagus sylvatica than for Quercus ilex stops the simulation.

Low soil water potential (ψ_{soil}) and high vapour pressure deficit (VPD) had different impacts on water stress, and their relative contribution were overall consistent among both study species (Figure 2). Both soil water potential (ψ_{soil}) and vapour pressure deficit (VPD) were strongly influent on plant functions that are very sensitive to water status, such as turgor and stomatal conductance. In particular, rising VPD induced a decrease of up to 50% in these functions in the absence of soil drought. This is consistent with empirical observations that VPD negatively influence stomatal conductance (López *et al.* 2021) and with the widely reported negative effects of VPD on primary productivity (Novick *et al.* 2016; Yuan *et al.* 2019; Dannenberg *et al.* 2022; Flo *et al.* 2022; Fu *et al.* 2022b; Grünig *et al.* 2022) or growth (Trotsiuk *et al.* 2021). However, our results suggest that this effect operates only in the first phase of the drought (moderately negative water potential): as ψ_{soil} decrease and stomatal conductance and turgor become close to *nill,* no further influences of soil or atmospheric drought were observed for turgor and stomatal conductance (Figure 2A to 2D).

Model outputs indicate that VPD caused an increase in transpiration, in agreement with empirical observations of positive effect of VPD on transpiration (López *et al.* 2021) and with the predictions of different stomatal conductance models (Grossiord *et al.* 2020). By contrast, rising ψ_{soil} caused a systematic decrease in transpiration due to stomatal closure. The contradictory effects that soil and air drought have on transpiration are explained by the fact that stomatal conductance decreases cannot fully limit the flow dictated by high VPD, as the cuticular conductance still allows some water losses.

Regarding embolism formation, which is among the latest processes to be affected by water stress in vascular plants (Delzon & Cochard 2014; Creek *et al.* 2020), the role of VPD was low until ψ_{soil} has reached substantially negative values. Therefore, VPD effect is small compared to the soil drought effect in our simulations (Figure 2G and 2H). This response disagrees with many empirical observations suggesting that VPD is the main driver of tree mortality (Park Williams *et al.* 2012; Breshears *et al.* 2013; Bauman *et al.* 2022) and can lead to increased embolism independently from soil drought (Schönbeck *et al.* 2022; Wagner *et al.* 2022). Similarly, for leaf moisture content, we also found a low sensitivity to VPD compared with the sensitivity to ψ_{soil}, except at high soil drought levels (Figures 2I and 2J). In particular, to reach leaf moisture content levels associated with high wildfire danger (ca. < 60% on dry mass basis, Pimont et al., 2019; Nolan et al., 2016), a very severe soil drought is required (from -3 to -4MPa). Here again, this result suggests that the effect of VPD on live fuel moisture content is not responsible for increased fire activity under high VPD conditions.

In summary, it appears that the effect of VPD on leaf water status is maximal at high ψ_{soil}, before full stomatal closure, due to transpiration response to VPD with a greater sensitivity of beech compare to oak, which is linked to difference of total hydraulic conductance for a given flow. For intermediate level of ψ_{soil} VPD sensitivity decreases and becomes strong again for low ψ_{soil}, right before hydraulic failure. Overall, by exploring the full range of ψ_{plant} until hydraulic failure, we found that VPD had a weaker effect on ψ_{leaf} than ψ_{soil} (figure 3).

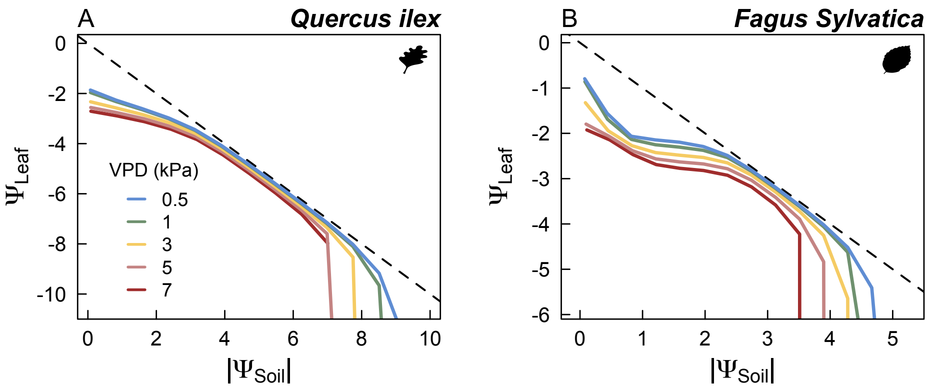

Figure 3 : Simulated dependence of plant water status (here simulated using leaf water potential, MPa) to soil drought (soil water potential, MPa) and atmospheric drought (VPD) for two contrasted species. The colors represent the VPD gradient.

Discussion: *(2) Remaining questions on how VPD affects plant water stress and disturbances*

With the exception of stomatal conductance and growth, for which high VPD can cause a decrease and thus limit photosynthesis and productivity in the absence of soil drought, our model simulations depart from recent empirical evidence that high VPD alone can actually trigger strong water stress. In particular, model simulations disagree with the possibility that VPD can, in the absence of severe soil drought, lead to profound disturbances such as increase in embolism and mortality through hydraulic failure or increase in vulnerability to wildfire through plant desiccation. In the following, we propose explanations and testable hypotheses on the way VPD could accelerate extreme water stress in conjunction or not with significant soil drought.

1- *Differentiating instantaneous VPD to VPD integrated over time*

VPD may have instantaneous effects on plant functions or act through its cumulated effect over time (*time*VPD*). *time*VPD* includes a temporal dimension accounting for the role of higher VPD on the faster depletion of the soil water reserves because of increased cumulated transpiration (Novick et al 2016; Grossiord et al 2020; Also illustrated in Fig. 3 of this study). Moreover, the drier the soil the stronger this effect is, because of the highly non-linear relationship between soil water content and water potential (Martin-StPaul et al 2017). Therefore, care should be taken when drawing conclusions from correlations between averaged VPD values over time and tree or ecosystem functions losses, as the pattern found may in fact be directly driven by soil drought and only indirectly by atmospheric drought. It should be emphasized that the variations of soil drought and VPD have different temporal scales, which makes them difficult to compare on the same ground (Novick et al 2016). Indeed, the variations of soil moisture available to plants occur on a weekly to seasonal scale depending on the water balance of the ecosystem (cumulative transpiration and rainfall) and the soil water storage capacity, whereas VPD variations occurs at hourly to daily scales according to variations in air temperature and relative humidity. It can be emphasize, that soil drought has also been proven to exert a control on instantaneous VPD by modifying the ratio between latent and sensible heat fluxes (Whan *et al.* 2015)

2- *Mechanisms possibly explaining why plant extreme water stress is exacerbated under high VPD*

It is also likely that several mechanisms that are not implemented in this version of SurEau are at play in plant responses to VPD or could eventually accelerate VPD effects on plant extreme water stress such as xylem embolism and leaf desiccation, regardless of the level of soil drought.

In particular, it is noteworthy that high VPD is most generally correlated with elevated temperature, which may directly influence plant hydraulic and water fluxes should also be considered. The different ways by which temperature can influence plant water relations have recently been reviewed and tested in a modeling experiment (Cochard 2021). Results from this analysis suggested that the steep increase in leaf cuticular conductance in response to high temperature that have been reported empirically (Schuster *et al.* 2016; Slot *et al.* 2021) could profoundly accelerate water losses and plant desiccation. However, here again, this effect is expected to produce significant effects on xylem embolism and desiccation only under soil drought conditions (Cochard, 2021), as water availability compensates the increased demand of the leaves. Such effect is independent but interactive with the effect of VPD and still has to be quantified experimentally.

Alternatively, rapid changes in hydraulic conductance somewhere in the soil-to-leaf pathway – other than drought induced xylem embolism, which is accounted for in the SurEau model – could exacerbate the effect of VPD on water potential drops and thus on hydraulic failure and desiccation risk. For instance, it has been recently suggested that fine, absorbing roots can be partially or totally uncoupled from the soil during drought (Rodriguez-Dominguez & Brodribb 2020; Duddek *et al.* 2022). This phenomenon would be linked to root shrinkage, which could increase soil to leaf hydraulic resistance (Duddek *et al.* 2022) and reduce plant water potential and stomatal conductance (Rodriguez-Dominguez & Brodribb 2020). It remains to be seen if such process is widespread among plants species. If plants could be disconnected from a dry soil while being subjected to the same atmospheric drought, they could desiccate faster under high VPD, their internal water store acting as a capacitor.

Overall, there are few data available exploring the effect of VPD independently of soil drought or temperature on the physiological responses to severe drought (embolism, hydraulic failure, desiccation). To date, we are aware of only one experimental evidence of significant hydraulic effects of VPD for Fagus sylvatica (Schonbeck et al. 2022). This is the only study that we know that aimed to separate the effects of VPD from those of soil drought and high temperature, so such studies should be replicated and investigated in more depth before conclusions can be drawn.

3- Mechanisms possibly explaining why wildfire activity is exacerbated under high VPD

While it is well documented that wildfire danger increases in periods of prolonged droughts (Abatzoglou *et al.* 2018), increasing evidence also shows that large wildfires preferentially occur under high VPD (high atmospheric drought) (Seager *et al.* 2015; Abram *et al.* 2021; Clarke *et al.* 2022; Grünig *et al.* 2022). Two, non-mutually exclusive, hypothesis have been put forwards to explain these observations. First, VPD being a reliable predictor of dead fuel moisture content (Resco de Dios *et al.* 2015), wildfire danger is higher under high VPD. Second, high VPD could also drive the decline of the moisture content of live fuels and plant mortality, both factors also known to increase wildfire danger (Nolan *et al.* 2016; Pimont *et al.* 2019). Contrasting with the conclusions by (Griebel *et al.* 2023), our results suggest that the decrease in dead fuel moisture content but not in live plant moisture content of living leaves and vegetation mortality is likely to mediate this relationship (Figure 3). The emergence of plant hydraulic approaches to fuel moisture prediction (Balaguer-Romano *et al.* 2022; Ruffault *et al.* 2022a), which can better represent the mechanisms driving both live and dead fuel variations, will help in interpreting and predicting climate change effects on wildfire danger.

Conclusion

Soil-Plant hydraulic framework integrates the effects of water deficit on plants in one metric, water potential, which sequentially triggers a stress on different functions. Under such hypothesis, soil drought and atmospheric drought impact plant water stress and hydraulic functions through the same mechanisms and it becomes possible to integrate and explore the independent and combined effects of soil and atmospheric drought on plants functions. A sensitivity analysis using a plant hydraulic model informed with measured plant traits indicates that VPD is mostly acting on plant hydraulics through interactive effects with soil drought. We thus argue that using a unifying plant hydraulic framework based on plant water stress rather than opposing the relative influences of atmospheric and soil drought would provide a stronger foundation for predicting tree and terrestrial ecosystem responses to climate changes.

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Supplementary Materials

Model run and parametrization

Implementation

We used the SurEau-Ecos version of the model (Ruffault et al 2022b) developed in R and available from Github (https://zenodo.org/record/5878978#.ZDb9PuxBzmE). The model has been modified to work in a "steady state mode". This means that we allowed to set the boundary conditions in terms of soil drought (i.e. soil water potential) and atmospheric drought (i.e. air VPD) at the desire value. On the one hand, for the soil, the model includes three soil layers that were set identical and filled with a volume of water corresponding to the target water potential. This is used to initialized the water potential and the hydraulic conductivity in the different soil layers. On the other hand, for the atmosphere, radiation was set to a constant saturating value (PAR = 2000 umol/m2/s) and the wind speed was set with non-limiting conditions of 2m/s. VPD manipulation was done by setting temperature at a constant 40°C (typical of what can be expected during a heatwave under temperate and Mediterranean climate) and by changing the air relative humidity (from 0 to 100%). This allows to explore the role of VPD independently from the effect of temperature, which could also influences processes such as hydraulic conductance, osmotic potential and cuticular conductance (Cochard, 2021). The model was run a first times to equilibrate the internal water stores and the leaf temperature, and a second time to obtain the values for the five indicators (turgor, stomatal conductance, transpiration, percent loss of embolism and leaf water content).

Parameterization

The most sensitive plant parameters, that define the drought responses strategies, were extracted from the two species by following the guidelines developed in (Ruffault et al 2022), while other values, less sensitive were let as default and constant for the two species. All values are reported in Table S1. The parameters defining the vulnerability curves to cavitation (VC) as well as the pressure volume curves parameters (PV) were extracted from the database published in Martin-StPaul et al 2017. The minimal conductance (g_{min}) is a sensitive parameter in the models and for which we have relatively little data available with homogeneous method (Duursma et al 2019). To be conservative, we thus choose to use the average value reported for the Fagale taxonomic group of 4mmol/m2/s (Duursma et al 2019), that we applied for the two species. For these three types of parameters (VC, PV, gmin), we applied the same values to leaves and stems assuming no segmentation. The response of the cuticular conductance to temperature, which is still under exploration, was also offset for this exercise.

The maximum stomatal conductance and initial hydraulic conductance were taken from Aranda et al (2005) for Fagus sylvatica and from Limousin et al (2009, 2010) for Quercus ilex. The parameters defining the stomatal response curve to water potential were retrieved from Martin-StPaul et al 2017. The response of stomata to light and temperature were not relevant for this exercise and were offset. Plant sizable properties, in terms of leaf and bark area and water volume, were set equal for the two species assuming an idealized small tree with a leaf area index of 2.2 m2/m2 and a total stem volume of water of 15l/m2. Rooting length was set to obtain a root area proportional to the leaf area assuming and the root distribution was .

The moisture retention curves of the three soil layers were defined with the same values using parameters typical of a clay loamy soil.

Table 1 : List of parameters used for the two species to produce the simulation of this paper

Symbol	Definition	Unit	*Fagus sylvatica*	*Quercus ilex*	Reference
		Stomatal and hydraulic traits			
ε_L	Leaf modulus of elasticity of the leaf symplasm (same value for the stem)	MPa	-1.80	-2.5	Martin-StPaul et al 2017
π_{0_L}	Leaf osmotic potential at full turgor of the leaf symplasm (same value for leaf and the stem)	MPa	11	15	Martin-StPaul et al 2017
$\psi_{50,L}$	Parameter of the vulnerability curves to cavitation of the leaf (water potential causing 50% loss of conductance) (same value for leaf and the stem)	MPa	-3.15	-6.9	Martin-StPaul et al 2017
$slope_L$	Slope of the vulnerability curve to cavitation at the inflexion point of the sigmoid. (same value for leaf and the stem)	%/ MPa	70	30	Martin-StPaul et al 2017
g_{cuti20}	Leaf cuticular conductance at 20°C (same value for leaf and the stem)	mmol/m2/s	4	4	Duursma et al 2019
g_{stom_max}	Maximal stomatal conductance	mmol/m2/s	240	200	Aranda et al 2005 for *Fagus sylvatica*; Limousin et al 2009, 2010 for *Quercus ilex*
$K_{plant,max}$	Maximal plant axial hydraulic conductance	mmol/m2/s/MPa	2	0.8	Aranda et al 2005 for *Fagus sylvatica*; Limousin et al 2009, 2010 for *Quercus ilex*
K_{SSym}	Stem radial hydraulic conductance (between symplasm and apoplasm)	mmol/m2/s/MPa	0.26	0.26	Ruffault et al 2022b
$\psi_{gs,12}$	Water potential causing 12% stomatal closure	MPa	-1.3	-1	Martin-StPaul et al 2017
$\psi_{gs,88}$	Water potential causing 88% stomatal closure	MPa	-2.0	-2.7	Martin-StPaul et al 2017
		Sizable and morphological traits (water volumes)			
LDMC	Leaf dry matter content	g/g	514	500	Personal data
LMA	Leaf mass per area	g/m2	91	190	Personal data
α_{LApo}	Leaf apoplasmic fraction	-	0.4	0.4	Ruffault et al 2022
LAI_{max}	Leaf area index	m2/m2	3	3	Ruffault et al 2022
β	Root distribution	-	0.98	0.98	Ruffault et al 2022
V_S	Stem water volume	l/m2			Ruffault et al 2022
α_{SApo}	Stem water volume fraction of the apoplasm	-	0.4	0.4	Ruffault et al 2022
α_{SSym}	Stem water volume fraction of the symplasm	-	0.4	0.4	Ruffault et al 2022
fBarkToLeaf	Bark to leaf area ratio	-	0.8	0.8	Ruffault et al 2022
$RaLa$	Root to leaf area ratio	-	1	1	Ruffault et al 2022
		Soil moisture retention curve			
α	Shape parameters of the moisture retention curve	cm-1	0.0111		Ruffault et al 2022
n	Shape parameters of the moisture retention curve	-	1.47		Ruffault et al 2022
k_{sat}	Saturated hydraulic conductivity	mmol/m/s/MPa	12.7		Ruffault et al 2022

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