The role of the intraspecific variability of hydraulic traits for modelling the plant water use in different European forest ecosystems

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Key Points:

- We explore the impact of the intraspecific variability of plant hydraulic traits on the simulated transpiration by CLM5.
- We find that a choice of plant hydraulic traits that reproduces observed plant transpiration also reduces simulated water stress.
- We demonstrate the critical role of the maximum xylem conductance in the model and its dependency on factors other than vegetation type.

Abstract

The drought resilience of forest ecosystems is generally believed to strongly depend on the dominant tree species' hydraulic traits. These traits define the maximum water transport capacity and the degree of vulnerability to hydraulic failure of a given tree species. This work evaluates the effect of the intraspecific variability of hydraulic traits on the simulated tree water use in the Community Land Model (CLM, version 5.0). We selected two broadleaved tree species with contrasting phenologies, geographical distribution, degrees of vulnerability to hydraulic failure, and water use strategies. We performed a series of numerical experiments by modifying the parameters of the plant vulnerability curve and the maximum xylem hydraulic conductance to account for the variability within each tree species. Our prescribed parameter sets represent vulnerable and resistant tree responses to the water deficit. At sites with an ample water supply, the resistant configuration simulates reduced water stress and increased transpiration compared to the vulnerable configuration, whereas at temporarily dry sites, the model results are counter-intuitive when water availability is the limiting factor. The numerical experiments demonstrate the emergent role of the maximum xylem conductance as a modulator of the plant water use strategy and the simulated transpiration. Using the default value for maximum xylem conductance, the model tends to overestimate the spring transpiration at drier sites, forcing the vegetation to experience unrealistic water stress in summer. Our findings suggest that the parameterization of maximum xylem conductance is an important and yet unresolved problem in the CLM and similar land surface models.

Plain Language Summary

The survival of trees under drought conditions depends on their adaptation to water scarcity. Part of this adaptation is characterized by specific plant traits, which are an important component of the Land Surface Models, largely determining the relationship between soil moisture and canopy gas exchange. Our study explores how the variability of specific plant traits of individual tree species may affect the model's ability to reproduce the observed water use by forest stands in Europe. In climates with a pronounced summer dry period, we found that the default model settings overestimate the vegetation water use in the early growing season, when water is abundant, resulting in severe water stress and underestimation of transpiration as the dry season progresses. Specifically, we demonstrate that the rarely considered plant trait representing the maximum water transport capacity plays an essential role in controlling the magnitude of simulated water use and that adjustments to this parameter greatly help to reproduce observed vegetation water use in seasonally dry climates.

1 Introduction

The recent worldwide increase in drought incidence and severity (He et al., 2020) has been associated with high rates of tree mortality (Powers et al., 2020; Senf et al., 2020), altered soil carbon and nitrogen dynamics (Deng et al., 2021), and a diminution in forest evaporation (Lansu et al., 2020; Lindroth et al., 2020). The severity of drought impacts on forest ecosystems and the spatial extent of them depends on the difference between precipitation and potential evaporation, atmospheric water demand, and forest resilience. The latter reflects the lumped vulnerability of individual trees (Haberstroh & Werner, 2022) and is driven by the safety

mechanisms used to overcome disturbances in the whole tree hydraulic system (Arend et al., 2022).

The resilience of a species to water stress is commonly expressed in the plant vulnerability curve and the recovery patterns shown by the tree species (Klein et al., 2018). This curve postulates a continuous decline of plant organ conductance with declining water pressure in the plant organ (Sperry & Love, 2015; Venturas et al., 2017). The parameters of the curve differ among and within tree species (Rosner et al., 2019), and are influenced by the provenance of the species (Hajek et al., 2016; Lobo et al., 2018) and xylem features such as lignin content (Pereira et al., 2018). This relationship between hydraulic conductivity and pressure has been analyzed across species and biomes (Choat et al., 2012), allowing to quantify the degree of vulnerability to hydraulic failure (Venturas et al., 2017). Vulnerable trees commonly have an early loss of conductance, small safety margins, and low wood density. Resistant trees have vulnerability curves ranging from gradual to steep responses at lower water potentials. These trees commonly have large safety margins and high wood density (Meinzer & McCulloh, 2013; Mrad et al., 2019). The degree of vulnerability to hydraulic failure is related to the trade-off between xylem safety and efficiency (Gleason et al., 2016; Hacke et al., 2006; Venturas et al., 2017). This trade-off requires the coordination of the plant hydraulic traits and water use strategy (WUS), which ranges from aggressive to conservative (Flo et al., 2021; Mrad et al., 2019). Also, the WUS is influenced by the stomatal regulation capacity of the tree species (Konings & Gentine, 2017) and modulated by the vapor pressure deficit irrespective of the soil water content (Fu et al., 2022; Novick et al., 2019).

The plant hydraulic theory is numerically implemented in models using either a plant pipe model, a porous media model, or an electrical analogy model (see Mencuccini et al. (2019) for a more detailed overview). Plant pipe models follow the Hagen-Poiseulle law and require the use of allometric scaling laws (Li et al., 2021; Mrad et al., 2018), whereas porous media models are based on Richards equation assuming that water movement through the xylem mimics an unsaturated porous media flow (Christoffersen et al., 2016; Li et al., 2021). Finally, the electrical analogy models resemble an electrical circuit with resistance and capacitance parameters that control the water flow following Darcy's law (Eller et al., 2018; Li et al., 2021). An electrical analogy model has low to moderate computational requirements making it a suitable model for implementation in large scale Land Surface Models (LSMs). For example, the Community Land Model 5.0 (CLM5, Lawrence et al., 2019) implements an electrical analogy model using the plant vulnerability curve to downscale the segment conductance according to the percent loss of conductance (PLC) (Kennedy et al., 2019). Given its recent implementation, the simulated plant hydraulic response (e.g., vulnerability to hydraulic failure) of CLM5 during drought conditions and across different forested ecosystems has not yet been evaluated in detail. Specifically, it has never been examined in detail to what extent the current (and default) plant hydraulic formulation and parameterization of the model reproduces realistic transpiration rates and plant water status under varying soil moisture availability and atmospheric water demand.

The implementation of the plant hydraulic formulation in LSMs relies on the definition of plant hydraulic traits within the Plant Functional Type (PFT) classification framework (Bonan et al., 2002). This classification assumes that hydraulic traits are spatially homogeneous and temporally fixed within predefined vegetation categories, which is equivalent to assuming the same drought sensitivity within the same PFT class. Several studies have addressed the implications associated with the loss of diversity in the PFT classification in terms of water and

carbon dynamics by using deterministic or stochastic coordinated plant attributes (Christoffersen et al., 2016; Pappas et al., 2016; Wang et al., 2012; Xu et al., 2016) or by exploiting plant trait-climate relationships (Verheijen et al., 2013). A recent study by Butler et al. (2022) showed that the aggregation of allocation and hydraulic traits into PFTs reduces the productivity of the modelled ecosystem with respect to the flux data of sites with a strong dependency on vegetation phenology. Overall, representing the plant trait inter- and intraspecific diversity within the PFT broad classification scheme remains a challenging task requiring the characterization of the emergent plant response by coordinating water use strategies with the xylem vulnerability (Skelton et al., 2015). While the trade-off between plant hydraulic traits has been addressed in previous studies using detailed plant hydrodynamic models (e.g., Mirfenderesgi et al. (2019)), the coordination between hydraulic traits and water use strategies remains unexplored for the plant hydraulic framework implemented in LSMs. Addressing this issue may provide an opportunity to define optimal strategies for large-scale parameterizations of key plant hydraulic traits (e.g., maximum xylem conductance), which are rarely documented in existing hydraulic trait databases.

This manuscript aims to evaluate the effect of the intraspecific variability of plant hydraulic traits on the simulated transpiration response of two contrasting tree species in CLM5. The intraspecific variability of plant hydraulic traits defines the spectrum of vulnerability responses to hydraulic failure and the water use strategies of each species. This spectrum considers that individual tree species have different boundaries determining their degree of vulnerability to hydraulic failure. Our hypothesis is that vulnerable trees transpire more than resistant trees under unstressed water conditions and perform poorly during dry periods. On the other hand, resistant trees maintain low transpiration rates but experience less stress on the plant hydraulic system. For each species, we distinguish between a resistant and vulnerable hydraulic trait configuration by extracting from the reported parameter sets for that species the plant vulnerability curve with the minimum and maximum loss of 50% of conductance (Ψ_{p50}) value, respectively. This hypothesis is evaluated for two broadleaved tree species, *Quercus ilex* L. and *Fagus sylvatic*a L., with contrasting phenologies and provenances. The results of point-scale numerical experiments with CLM5 based on each parameterization are compared to the sap flux observed at four experimental sites across Europe. The representation of the simulated vulnerability to hydraulic failure and the water use strategy of each species are interpreted using the simulated leaf water stress factor (β) and percent loss of conductance (PLC) in different plant organs.

2 Materials and Methods

2.1 Tree Species and Experimental Sites

The tree species selected for this study, *Fagus sylvatica* L. and *Quercus ilex* L., belong to the same botanical family (Fagaceae) but differ in their phenology and spatial distribution in Europe (Figure 1). *Fagus sylvatica* is a deciduous broadleaved tree distributed in Central and Western Europe, from Southern Italy to Southern Norway. This tree species grows from sea level to 1000 m a.s.l., with a higher upper elevation limit in dryer regions. It does not survive in locations with poor drainage or stagnant water, and its relatively shallow root system makes it susceptible to drought and high temperatures (Houston Durrant et al., 2016; von Wuehlisch, 2008). *Quercus ilex* is a broadleaved evergreen species that grows as a tree or shrub. It inhabits the Mediterranean basin from the coast up to 1800 m a.s.l., can survive low temperatures, and its

sclerophyllous character allows transpiration to be reduced during dry periods and its resistance to drought to be improved (de Rigo & Caudullo, 2016; Schirone et al., 2019).

Two experimental sites for each species were selected from the SAPFLUXNET database (Poyatos et al., 2020). *Fagus sylvatica* is the dominant tree species in Hesse (France, FR-Hes) and Hinnensee (Germany, DE-Hin), over the sampling periods of 2001-2005 and 2012-2014, respectively (Table 1). Both sites have a temperate oceanic climate (Cfb) according to Köppen-Geiger's climate classification (Beck et al., 2018), with no significant intraseasonal precipitation variability. The stand age marks the main difference between these two sites; trees in FR-Hes were 34 years old during the selected measurement period while those in DE-Hin were more than 200 years old. The mean tree diameter reflects this age difference, with 12.9 cm at FR-Hes and 43.6 cm at DE-Hin. *Quercus ilex* is the dominant tree species in Puechabon (France, FR-Pue) and Alto Tajo (Spain, ES-Alt). These sites cover the monitoring periods 2001-2005 and 2012-2014, respectively. The climate differs slightly between these two sites; FR-Pue has a hot-summer Mediterranean climate (Csa) while ES-Alt has a warm-summer Mediterranean climate (Csb). The different elevations of the sites explain the differences in climate classification (Table 1). Despite a lack of differences in the stand age between these two sites, the diameter recorded for the trees in FR-Pue (9.1 cm) is much smaller than the diameter in ES-Alt (24.4 cm).

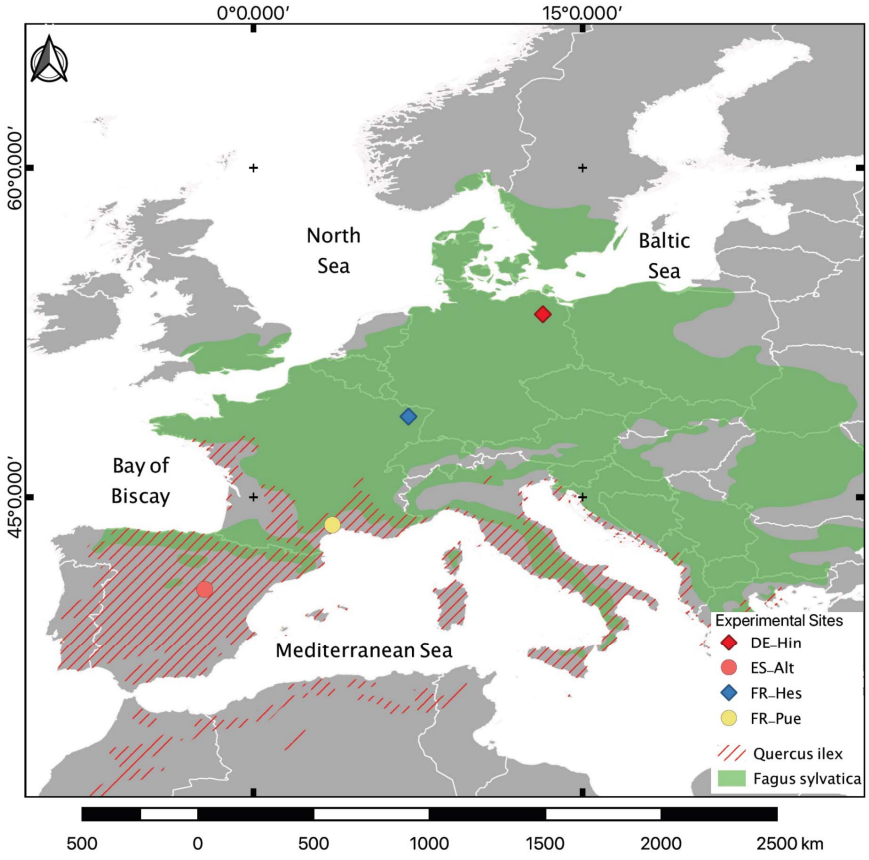

Figure 1. Geographical location of the four experimental sites and the spatial distribution of *Fagus sylvatica* L. and *Quercus ilex* L. across Europe. The spatial distribution of the tree species is based on Mauri et al. (2022).

2.2 Model Setup

The Community Land Model version 5.0 (CLM5, Lawrence et al. (2019)) was implemented at each experimental site using point-scale setups. Hourly atmospheric forcing was retrieved from the SAPFLUXNET dataset. This dataset includes precipitation, wind speed, air temperature, relative humidity, and incoming shortwave radiation. The incoming longwave radiation was calculated according to An et al. (2017) using the vapor pressure deficit and temperature. The COSMO-REA6 reanalysis product (Bollmeyer et al., 2015) was used to fill in the missing variables (i.e., atmospheric pressure) and temporal data gaps for each site. The monthly leaf area index (LAI) in m^2 m^{-2} was determined based on the Global Land Surface Satellite (GLASS) product (Liang et al., 2013, 2014) for the different periods under analysis. The monthly stem area index (SAI) in m^2 m^{-2} was retrieved from the global surface dataset of the model as described in (P. J. Lawrence & Chase (2010). The root area index (RAI) in m^2m^{-2} is calculated in the model (see Equation 2.11.15 of the technical documentation (UCAR, 2020)) based on plant functional type-specific parameters such as the LAI, SAI, root fraction in each soil layer, and the root-to-shoot ratio. The main soil characteristics (e.g., soil texture, organic matter content) were taken from Bonan et al. (2002), while the depth to bedrock was taken from Pelletier et al. (2016). Multi-year spin-up runs were performed for each experimental site by reinitializing soil moisture and soil temperature until a dynamic equilibrium condition was reached. The tree species at the selected sites pertain to two distinctive plant functional types (PFTs), with *Fagus sylvatica* representing the Temperate Broadleaf Deciduous Tree (BDT) in FR-Hes and DE-Hin and *Quercus ilex* representing the Temperate Broadleaf Evergreen Tree (BET) in FR-Pue and ES-Alt; see Table 2 for the default plant hydraulic configuration (DC) of these two PFTs.

2.3 Plant Vulnerability Curve

The plant vulnerability curve (PVC) implemented in CLM5 (Equation 1) determines the plant segment specific hydraulic conductance k (mm_{H2O} $mm_{H2O}^{-1}s^{-1}$) based on three parameters: the xylem pressure inducing 50% loss of hydraulic conductance (Ψ_{p50}, MPa), the non-dimensional sigmoidal shape parameter of the curve (c_k), and the maximum plant hydraulic conductance (k_{max}, mm_{H2O} $mm_{H2O}^{-1}s^{-1}$). CLM5 uses k_{max}, Ψ_{p50} and c_k as static parameters that may differ between plant segments (i.e., root, xylem, and sunlit and shaded leaf) and PFTs. The plant hydraulic system of CLM5 uses k to determine the flux per plant segment by applying a Darcy's law equation, where the reference area varies between plant segments: the leaf area index (LAI, m^2m^{-2}) for the stem-to-leaf, the stem area index (SAI, m^2m^{-2}) for the root-to-stem, and the root area index (RAI, m^2m^{-2}) for the soil-to-root segment. A detailed description of the equations used by the plant hydraulic system of CLM5 is provided in Kennedy et al. (2019) and Lawrence et al. (2019).

$k = k_{max} 2^{-\left(\frac{\Psi}{\Psi_{p50}}\right)^{c_k}}$	Equation 1

2.4. Intraspecific Variability of Plant Hydraulic Traits

The intraspecific variability of both tree species was determined based on the loss of hydraulic conductance at 12%, 50%, 88%, and in some cases at 10% (Ψ_{p12}, Ψ_{p50}, Ψ_{p88}, and Ψ_{p10}, respectively), as reported in the Xylem Functional Traits (XFT) database (Choat et al., 2012). Additional data sources for *Fagus sylvatica* were retrieved from the literature review; see table S1 for a complete list of references for the additional data. The c_k parameter of each dataset was determined by converting the reported slope of the vulnerability curve at Ψ_{p50} to c_k or by solving the CLM vulnerability curve for c_k and inserting any provided combination of PLC and Ψ_{p10}, or Ψ_{p12}, or Ψ_{p88} values reported in the XFT database, with a preference for Ψ_{p10} or Ψ_{p12} if available. The procedure to determine the c_k parameter assumes that Equation 1 follows the Weibull distribution, allowing to use the vulnerability curve formulation from Domec and Gartner (2001). From this formulation, we derived Equation 2 to calculate the c_k parameter based on the Ψ_{p50}, the slope of the curve (s) at Ψ_{p50} (Pa^{-1}), and V as a constant dimensionless value of 34.66. To determine V, we deduced Equation 3 from Domec and Gartner (2001) and inserted the percent loss of conductivity (τ_{50}) of 50%. Equation 4 is used to calculate s (Pa^{-1}) using the slope at any specific loss of conductivity (τ). This indicator is calculated with Equation 5 using τ in %, Ψ_{p50}, and Ψ_x that represents the matric potential at the selected τ. Finally, the two curves with the highest and lowest Ψ_{p50} values were selected for each species to represent the vulnerable (VC) and resistant (RC) response, respectively (Figure 2); see Table 2 for more details on the obtained values.

$$c_k = \frac{\Psi_{p50} \cdot s}{V}$$	Equation 2

$$V = (\tau_{50} - 100) \cdot \ln\left(1 - \frac{\tau_{50}}{100}\right)$$	Equation 3

$$s = -25 \frac{\log\left(\frac{100 - \tau}{\tau}\right)}{\Psi_x - \Psi_{p50}}$$	Equation 4

The xylem water potentials of *Fagus sylvatica* have a narrow distribution, with the Ψ_{p12}, Ψ_{p50}, and Ψ_{p88} values ranging from -2.0 MPa to -5.0 MPa (Figure 2). The two extreme curves obtained from this dataset have a steep decline of hydraulic conductance with the diminution of water potentials, with a small range in c_k (1.73 to 3.33) and Ψ_{p50} (-1.9 MPa to -4.7 MPa) values (Table 2). *Quercus ilex* has a larger range of xylem water potentials than *Fagus sylvatica*, ranging from -0.5 MPa to -7.0 MPa. This species shows a large difference between the extreme vulnerability curves, with c_k values ranging from 1.70 to 8.04 MPa and Ψ_{p50} from -1.23 to -5.72 MPa for the VC and RC, respectively.

The k_{max} values used by default in CLM5 are assumed constant for the different PFTs and homogeneous across the different plant organs (i.e., root, xylem, and leaf). k_{max} values for each plant segment can be determined based on the experimental specific hydraulic conductance ($k_{s,}$

kg $m^{-2}MPa^{-1}s^{-1}$), which is defined as the flow rate per cross sectional area per unit of pressure difference along a plant segment (kg $m^{-2}MPa^{-1}s^{-1}$) (Eamus et al., 2016). However, a standard procedure for determining k_{max} for its use in CLM5 (i.e., at PFT level and for each plant segment) from tree- and plant organ-specific information existing in literature has not been specified yet. Therefore, considering the large uncertainty in estimating this parameter and the unknown effect of its variability, we arbitrary choose a range of values between one order of magnitude above (2.0 x 10^{-7} mm_{H2O} $mm_{H2O}^{-1}s^{-1}$) and below (2.0 x 10^{-9} mm_{H2O} $mm_{H2O}^{-1}s^{-1}$) the default value (2.0 x 10^{-8} mm_{H2O} $mm_{H2O}^{-1}s^{-1}$) of the model. The upper and lower values of this variability range are referred to from now as high (Hk_{max}) and low (Lk_{max}) xylem conductance, respectively.

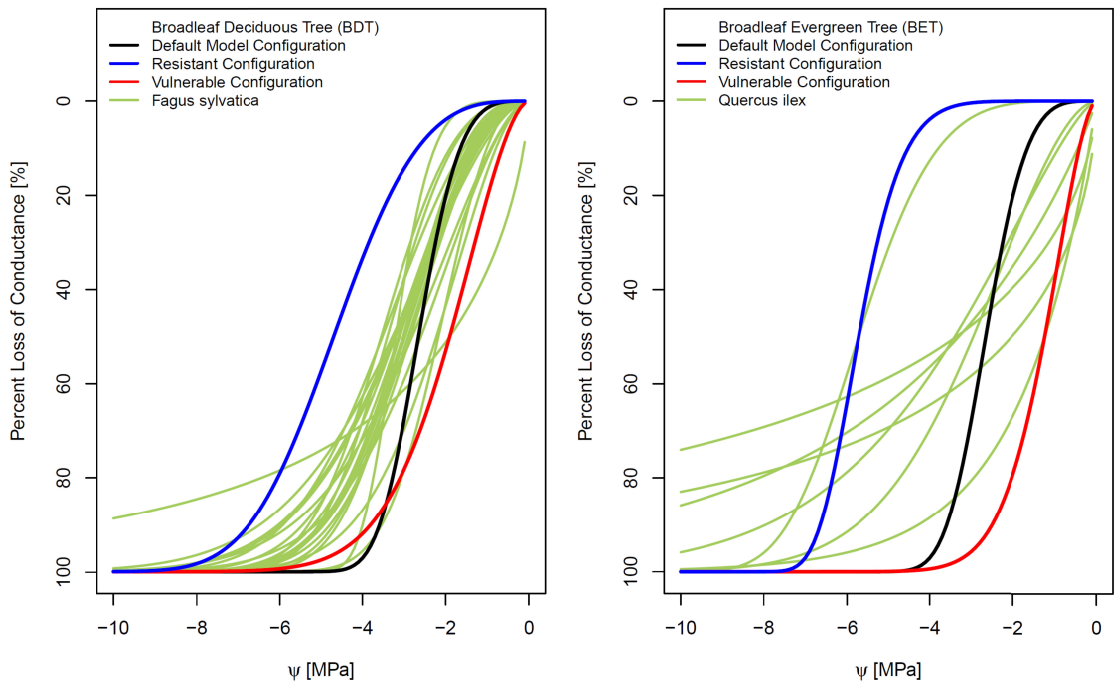

Figure 2. Spectrum of the vulnerability curves of *Fagus sylvatica* L. (left plot) and *Quercus ilex* L. (right plot). The solid blue, red, and black lines represent the resistant, vulnerable, and default vulnerability curves used in the numerical experiments, respectively. The solid green lines show the full set of vulnerability curves for each species.

2.5. Numerical Experiments

The role of the intraspecific variability of plant hydraulic traits in contrasting tree species was examined based on a series of numerical experiments. These experiments aimed to assess to what extent the plant hydraulics representation of CLM5 reproduces the measured transpiration of each experimental site based on the spectrum of vulnerability to the hydraulic failure of each tree species (Table 2).

The first set of experiments compared the effect of the PVC shape on the distribution of PLC values, leaf water stress (β), and the transpiration simulated by the model. The PVC shape parameters determine the steepness of the hydraulic response (c_k) and the range of water potentials at which the plant will start experiencing extreme water stress (Ψ_{p50}). We hypothesized

that the RC describes a plant response less affected by low soil water potentials, while the VC describes a plant response with a high susceptibility to hydraulic failure at low water potentials.

The second set of experiments explored the role of k_{max} in constraining the whole plant water use strategy of the different tree species. This was achieved by changing the k_{max} value to the high (Hk_{max}) and low (Lk_{max}) xylem conductance while keeping the default model configuration for the shape parameters (Table 2). Finally, two additional intermediate values were added to this experiment representing a half order of magnitude difference between the boundaries and the default k_{max} (1.1 x 10^{-7} mm_{H2O} $mm_{H2O}^{-1}s^{-1}$ and 1.1 x 10^{-8} mm_{H2O} $mm_{H2O}^{-1}s^{-1}$) and are referred to as intermediate-high (IHk_{max}) and intermediate-low (ILk_{max}) xylem conductance, respectively.

The third set of experiments aimed to evaluate the role of coordinated changes in safety (i.e., shape parameters) and transport capacity (i.e., maximum xylem conductance). We analyzed the plant hydraulic response simulated by CLM5 using the best fitted k_{max} value obtained for each site in the second set of experiments together with both Ψ_{p50} and c_k values used in the first set of experiments (Table 2). That is, the response of each vulnerable and resistant model configuration was evaluated across a wide spectrum of xylem conductance. We hypothesized that a resistant tree species (i.e., with low Ψ_{p50}) associated with high k_{max} values would experience more stress (i.e., large degree of vulnerability) than a vulnerable tree species having a low k_{max}.

2.6. Data Analysis

2.6.1. Reference Evaporation

Equation 5 is based on Equation 6 from Allen et al. (1998), and calculates the reference evaporation (E_o) used as a descriptive variable of the atmospheric water demand for each experimental site. Equation 5 assumed a reference crop of 0.12 m height, a surface resistance of 70 s m^{-1}, and an albedo of 0.23. This equation requires wind speed (u) in m s^{-1}, net radiation (R_n) and ground heat flux (G) both in MJ $m^{-2}d^{-1}$, air temperature (T) in C, and the actual and saturated vapor pressures (e_a and e_s, respectively) in kPa. G was extracted from the modeled results of the default configuration of each experimental site. The slope of the saturation vapor pressure curve at air temperature (Δ, kPa K^{-1}) was computed using Equation 6, based on Equation 13 from Allen et al. (1998). The psychrometric constant (γ) was estimated with Equation 7 based on Equation 8 from Allen et al. (1998), where λ is the latent heat of vaporization (2.45 MJ kg^{-1}), c_p is the specific heat at constant pressure (1.013 x 10^{-3} MJ kg^{-1} K^{-1}), p is the atmospheric pressure (kPa), and ϵ is the molecular weight ratio of water vapor and dry air (0.622).

$$E_o = \frac{0.408 \cdot \Delta \cdot (R_n - G) + \gamma \frac{900}{T + 273} \cdot u \cdot (e_s - e_a)}{\Delta + \gamma \cdot (1 + 0.34 \cdot u)}$$	Equation 5

$$\Delta = \frac{4098 \cdot \left(0.6108 \cdot exp^{\left(\frac{17.27 \cdot T}{T + 273.3}\right)}\right)}{(T + 237.3)^2}$$	Equation 6

$$\gamma = \frac{c_p p}{\epsilon \lambda}$$	Equation 7

2.6.2. Upscaled Transpiration

Observed forest transpiration (E_T) in mm hr^{-1} was calculated based on the hourly and sub-hourly sap flux of individual trees (Q_{tree}) in cm^3 hr^{-1} available on the SAPFLUXNET data set (Poyatos et al., 2020). We used equation 8 to obtain E_T and summarized it in daily time steps following the recommendations of Nelson et al. (2020). Equation 8 requires Q_{tree} aggregated in hourly fluxes per tree (m^3 hr^{-1}tree^{-1}), the basal tree area (Ω_{tree}) in m^2 tree^{-1}, the stand basal area (Ω_{stand}) in m^2 m^{-2}, and the number of measured trees (n). All the information required in Equation 8 is available on the SAPFLUXNET data set for each site. The stand basal area of DE-Hin was missing in the SAPFLUXNET data set, so we obtained it from Moreno et al. (2017) according to the geographical location of the plot.

$$E_T = \frac{\Omega_{stand}}{n \cdot 10^3} \cdot \sum_{tree=1}^{n} \frac{Q_{tree}}{\Omega_{tree}}$$	Equation 8

2.6.3 Plant Water Stress

The plant water stress was evaluated by comparing the percent loss of conductance (PLC) and the transpiration water stress parameter (β). The PLC was calculated using Equation 9 at the root-stem (hereafter named stem) and stem-leaf (hereafter named leaf) plant segments. This equation uses the simulated (k) and the maximum (k_{max}) plant organ conductance. The water stress parameter β was calculated as a weighted average of shade and sunlit components according to their corresponding LAI components. Further details on the mathematical formulation of the water stress factor of CLM5 are provided in Kennedy et al. (2019).

$$PLC = 100 \cdot \left(1 - \frac{k}{k_{max}}\right)$$	Equation 9

3. Results

The impact of the different plant hydraulic parametrizations was investigated by comparing the simulated time series of transpiration (E_{Tm}) to the upscaled sap flux measurements (E_T). The comparison was carried out for the spring, summer, and autumn seasons. Furthermore, a comprehensive insight into the simulated plant hydraulic response was gained by analyzing the temporal evolution and probability density of PLC, the transpiration water stress parameter (β), and the water potentials across the soil-vegetation continuum (Ψ).

3.1. Reference Evaporation and Measured Transpiration

Figure 3 shows the seasonal distribution of E_o and E_T for the four sites and two tree species selected. For most of the seasons, the atmospheric water demand is two- and four-times larger than the E_T in FR-Hes/DE-Hin and FR-Pue/ES-Alt, respectively. It is worth noticing that

despite belonging to the same climate classification, the DE-Hin and FR-Hes sites have highly contrastingly E_o values. This difference is explained by a lower mean annual precipitation (606.4 mm yr^{-1}) and temperature (8.7 °C) at DE-Hin compared to FR-Hes, which receives 1003.8 mm yr^{-1} of precipitation and experiences a mean annual temperature of 9.97 °C. Seasonal E_T patterns differ strongly among species and seasons, with sites dominated by *Fagus sylvatica* (i.e., FR-Hes and DE-Hin) showing values close to 0 in spring and autumn due to the deciduousness of the forest species. In contrast, the evergreen *Quercus ilex* at FR-Pue and ES-Alt express smaller intraseasonal variations, with greater spring and autumn E_T, but smaller values in summer compared to the *Fagus sylvatica* sites.

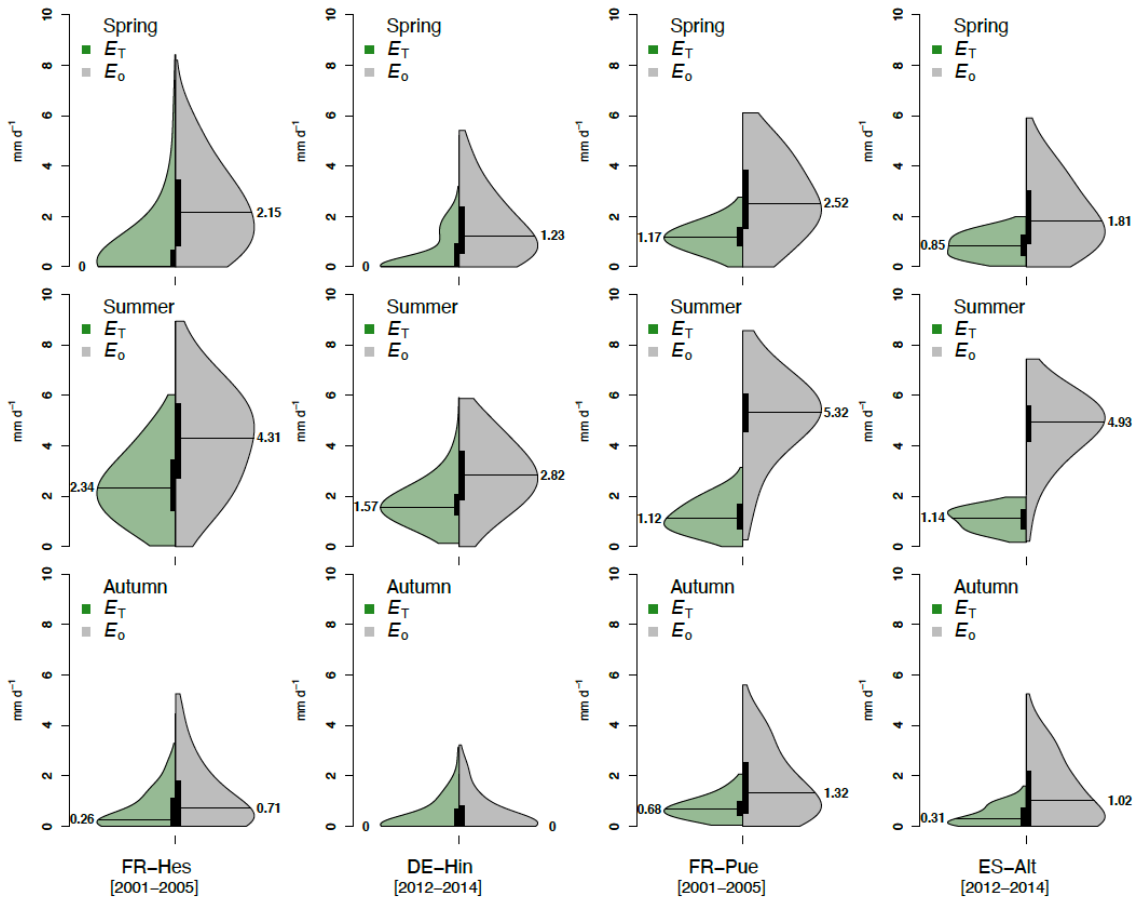

Figure 3. Seasonal variation of measured daily transpiration (E_T) and reference evaporation (E_o) of the four forested sites in Europe. The area of the violin plots represents the data density distribution. The horizontal line is the median of the data set with the respective value. The black box represents the first and third quartiles of the data set. The elongated tales outwards from the black boxes represent the data outliers.

3.2. Effects of Changing the Shape of the Vulnerability Curve

The experimental sites dominated by *Fagus sylvatica* have similar measured and modeled transpiration values (Figure 4), with minor differences during the summer and autumn seasons, but significant over-estimation of E_T in early spring. Note that for both deciduous sites, the sap

flow starts after the 105th day of the year, around the time of leaf flush, whereas the LAI values used in our simulations also include the understory of the forest, and therefore likely over-estimate early season tree LAI (see Figure S1). Figure 4 indicates that there are marginal differences at both sites (i.e., FR-Hes and DE-Hin) when representing a vulnerable (VC) and resistant (RC) shape of the vulnerability curve. As expected, the VC tends to produce, especially during the summer period, lower transpiration rates and higher water stress conditions represented by low β values. These stress conditions are mainly found at the stem-leaf level with the median of the PLC values going beyond 12% while those at the root-stem level remain close to zero. The comparison of the distribution of the PLC values at different plant levels (i.e., root-stem and stem-leaf) with those of the β stress factor provides some additional insights into the relative effect of stomata and plant hydraulics on the simulated transpiration response.

The effects of changing the shape of the vulnerability curve are remarkably different at the evergreen sites (i.e., FR-Pue and ES-Alt) populated with *Quercus ilex* species (Figure 4). At these sites, the default (DC) plant hydraulic model parameterization largely overestimates the transpiration response during spring/early summer (see Figure S1), which leads to a strong underestimation of E_T during prolonged dry conditions followed by a slow recovery in autumn. Counterintuitively, this tendency is amplified by the resistant configuration (RC) and is alleviated by the vulnerable configuration (VC) of plant hydraulics, with this latter simulating higher transpiration rates during most of the summer. The unexpected model response is confirmed by the distribution of the simulated water stress factor and PLC values, with the response of the RC reflecting a higher level of hydraulic failure compared to DC and VC during the summer.

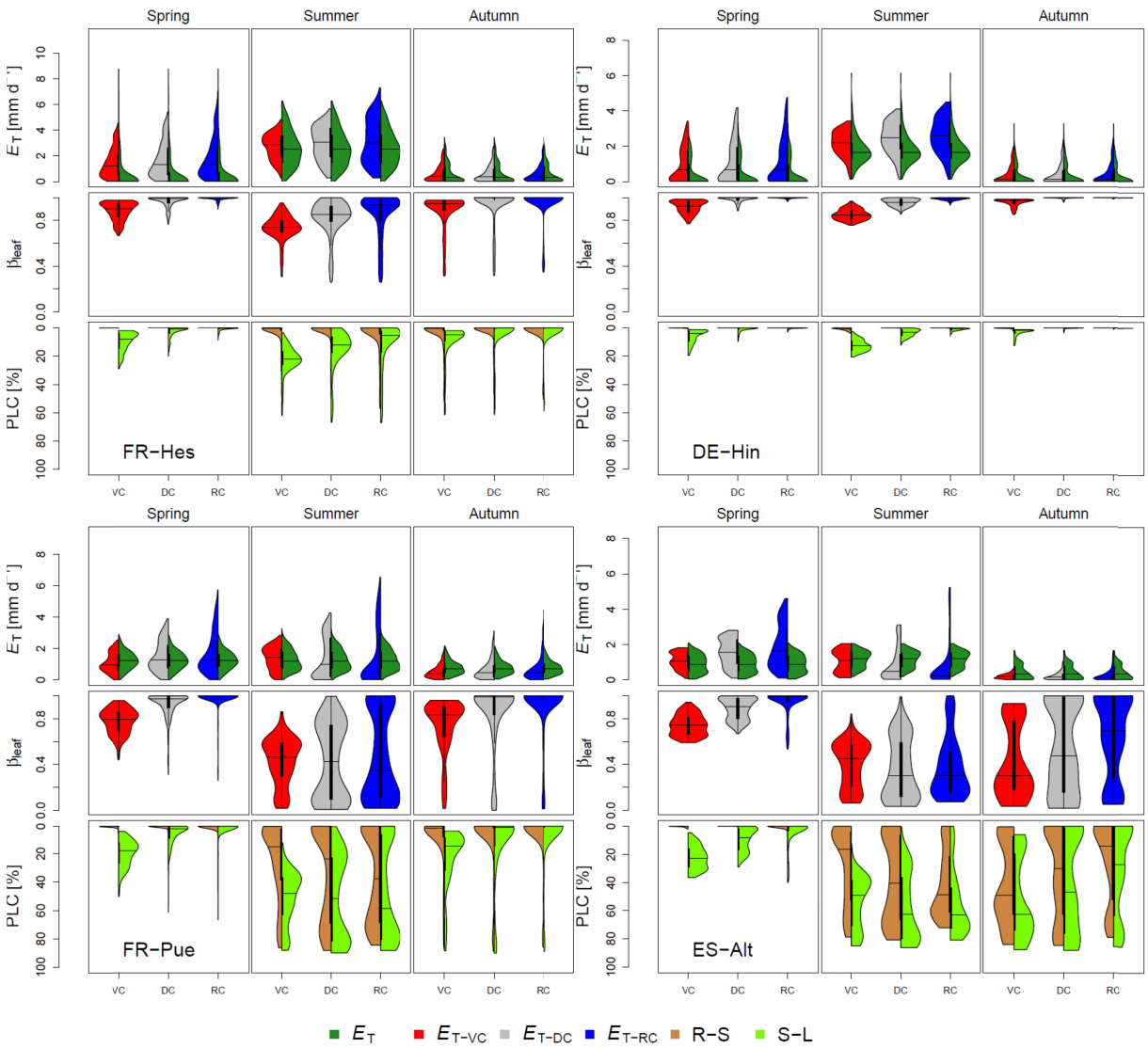

Figure 4. Seasonal distribution of daily transpiration (E_T), leaf water stress factor (β) and percent loss of conductance (PLC) for each experimental site showing the responses to changes in the shape parameters (i.e., Ψ_{p50} and c_k) of the plant vulnerability curve. Each violin plot contains the multiannual data for each site and season. The distribution of E_T is contained in the upper plot of each site (solid dark green). The vulnerable (VC), default (DC), and resistant (RC) configurations are represented by red, grey, and blue solid colors, respectively.

3.3. The Regulating Effects of Xylem Conductance

The second set of numerical experiments investigated the extent to which the water use strategy can be modified in the model through gradual changes over a wide spectrum of k_{max} values. The 'optimal' k_{max} was selected based on the minimum mean absolute error (MAE) with respect to the upscaled E_T values. Figure 5 illustrates that moving from high k_{max} (Hk_{max}) towards the low k_{max} (Lk_{max}) configuration, the simulated transpiration can be 'adjusted' to capture the differences in transpiration seasonality at the four selected sites. The Hk_{max} and intermediate high

k_{max} (IHk_{max}) did not show differences in the simulated E_T for the selected sites, as within this range of k_{max} values transpiration rates are limited by the atmospheric water demand. Most effective changes in the simulated E_T values occur in the range between the default k_{max} (DCk_{max}) and low k_{max} (Lk_{max}), with the best correspondence between observed sap flow and simulated transpiration rates achieved by the DCk_{max} at FR-Hes, and the ILk_{max} for the other sites. Here it is interesting to note that at ES-Alt, the model performances can be further improved by increasing the sampled k_{max} values between ILk_{max} and Lk_{max} (see Figure S4), with an 'optimal' k_{max} value of 6.5 x 10^{-8} mm_{H2O} $mm_{H2O}^{-1}s^{-1}$.

We found that gradual changes in k_{max} systematically affected soil evaporation across all sites, where soil evaporation increased from Hk_{max} towards Lk_{max} (Figure 5). These effects are visible at the top 12 cm of soil (first three layers), where the model allocates 34 % of the root biomass. This tendency shows the impact of transpiration on the soil water reservoir by increasing the plant water acquisition. Higher k_{max} values allow extracting more water from the soil and hence reducing the soil moisture. In contrast, reduced k_{max} compared to the default value result in a reduced water transport capacity and diminishing soil water acquisition. As a result, when k_{max} is smaller than DC, soil evaporation increases considerably at all sites (Figure 5). The Lk_{max} configuration restricts the plant water transport at all sites to a point where the soil matric potential is close to 0 all year round (Figure S3), allowing the soil to evaporate more water while transpiration rates are reduced. For the evergreen sites (i.e., FR-Pue and ES-Alt), the Lk_{max} configuration makes soil water to evaporate at high rates, even matching the transpiration measured in summer at FR-Pue and similar values all year round at ES-Alt.

Sites covered with *Fagus sylvatica* do not experience extreme transpiration stress ($\beta<0.5$) even when the E_T is overestimated as in the Hk_{max}, IHk_{max}, and DC configurations. The increment of leaf water stress with the Lk_{max} configuration at these two sites (i.e., FR-Hes and DE-Hin) does not go beyond 0.5. This is the consequence of the limited water transport within the plant, impacting the stomatal conductance used to determine the β values. The sites with *Quercus ilex* (i.e., FR-Pue and ES-Alt) experience a more significant leaf water stress in summer when the k_{max} overestimates the transpiration in spring (Hk_{max}, IHk_{max}, and DC). The use of smaller k_{max} values at these drier sites triggers a more restricted vegetation water use under wet conditions (i.e., spring and early summer). Using a smaller k_{max} at sites with stronger dry seasons enables the vegetation to not use all the water in spring, allowing the soil water reservoir to supply the moisture needed in summer. The most suitable k_{max} at FR-Hes corresponds to the DC. DE-Hin, which has the same tree species as FR-Hes, shared with FR-Pue the ILk_{max} as the best performing $k_{max.}$ This is despite the differences between the two sites in tree species, tree size, and stand age (Table 1). The fact that a similar k_{max} does not characterize the same species points out that xylem conductance can be influenced by factors other than genetics (e.g., environmental conditions, growth history).

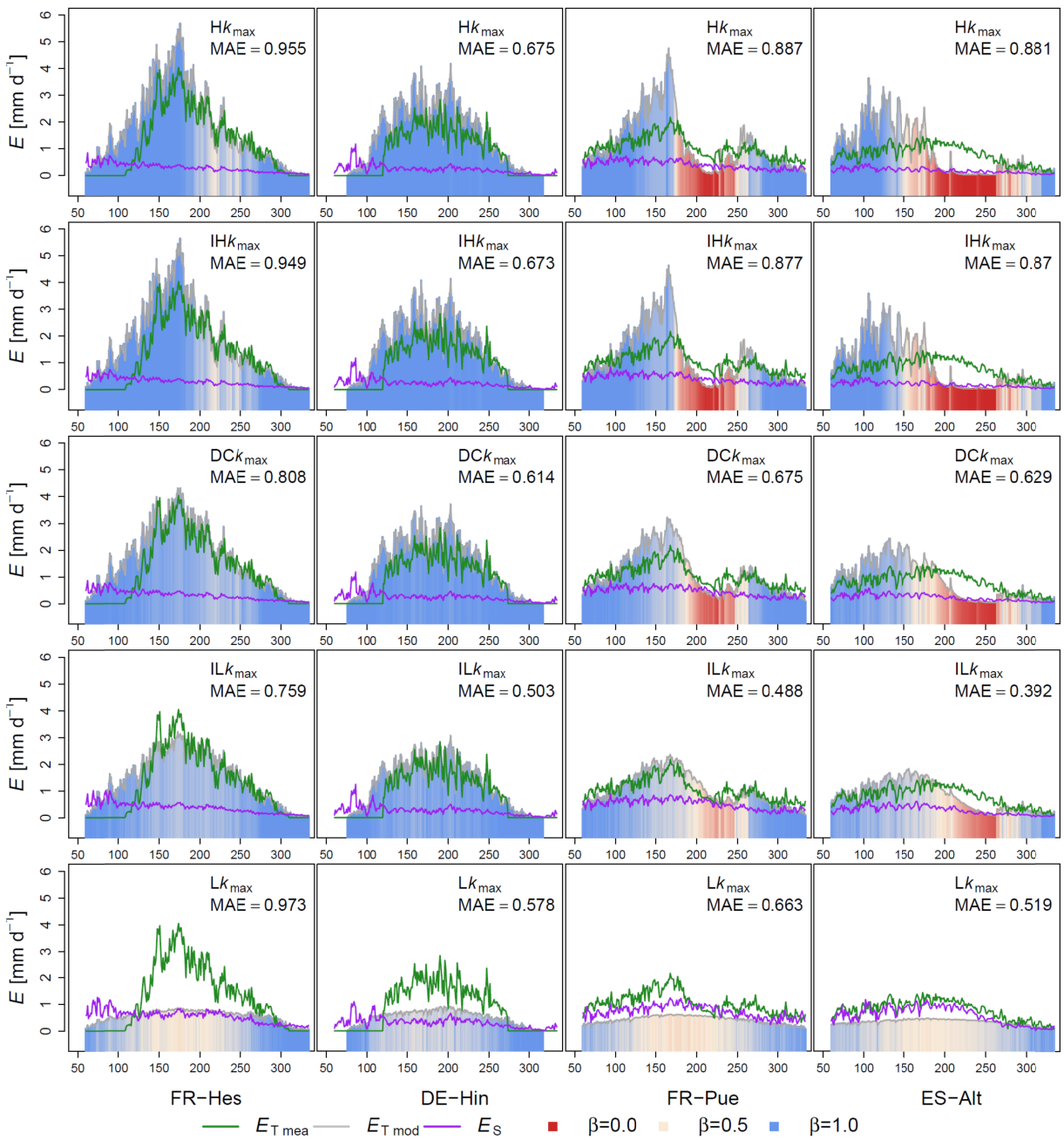

Figure 5. Temporal variation of transpiration (E_T), soil evaporation (E_S), and leaf water stress factor (β) to gradual changes of maximum xylem conductance (k_{max}) at each experimental site. The plots for each site represent a decrease of maximum xylem conductance from top (larger k_{max}) to bottom (low k_{max}). The leaf water stress (β) in each plot tends towards reddish colors when β falls below 0.5 (extreme stress), while the blueish colors represent unstressed leaf conditions. The MAE is the mean absolute error of the modelled vs. the measured E_T for each configuration per site.

3.4. The Combined Effects of Changing the Shape of the Vulnerability Curve and the Maximum Xylem Conductance

The third set of experiments was designed to evaluate the sensitivity of E_T to the plant vulnerability curve (PVC) parameters with the modified k_{max}. We expect that the use of best-fitted k_{max} values obtained in the second set of experiments allows a better evaluation of the impacts of the coordinated changes between c_k and $\Psi_{p50.}$ As compared to Figure 1, the simulated E_T is much closer to the observed at all sites for DC, also avoiding extreme stress at xylem level (PLC < 50%) for extended periods (Figure 6). Furthermore, the coordinated changes of the shape parameters with the k_{max} enable the simulation of a more realistic hydraulic response of the root-stem and stem-leaf segment to dry season conditions across the four selected sites (Figure 6). The results indicate that in sites populated by *Fagus sylvatica*, the severe hydraulic failure events (PLC > 50%) simulated by the model are much less frequent at FR-Hes and are completely absent at DE-Hin. Meanwhile, the Mediterranean sites (i.e., FR-Pue and ES-Alt) are characterized by low PLC values (<20 %) for the root-stem plant segment, while more severe PLC values are simulated at the stem-leaf level. Only the RC of these evergreen sites shows a more severe stress response in summer, where the root-stem compartment experiences PLC values larger than 20% for half of the time (second half of the violin plot of Figure 6). At the same time, the xylem-leaf compartment also shows a strong reduction of conductance (PLC > 50%). The impact of the RC also affects the xylem-leaf compartment, where the bimodal distribution depicts the problem of the reduced provision of water for vegetation during summer due to a more aggressive soil water extraction in late spring or early summer.

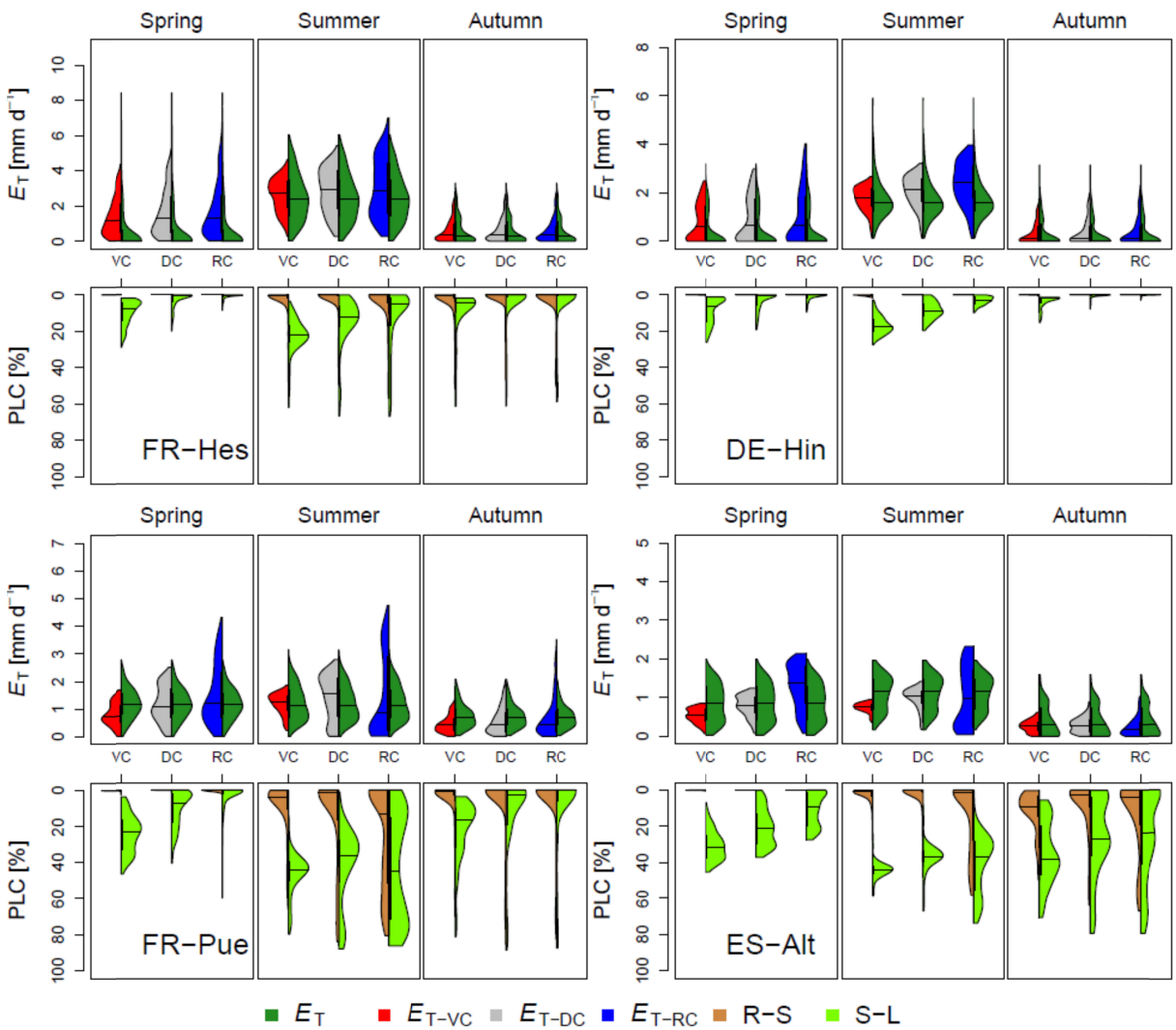

Figure 6. Seasonal response of daily transpiration and loss of hydraulic conductivity to changes in the shape parameters (i.e., Ψ_{p50} and c_k) of the vulnerability curve to hydraulic failure with the best fitted k_{max} at four forested sites in Europe. The distribution of daily transpiration (E_T) and percent loss of conductance (PLC) are represented by seasonal violin plots. The distribution of E_T is contained in the upper plot of each site (solid dark green). The vulnerable (VC), default (DC), and resistant (RC) configurations are represented by red, grey, and blue solid colors, respectively.

4. Discussion

4.1. What is known about the tree species selected?

Fagus sylvatica and *Quercus ilex* are two tree species with contrasting responses to dry periods. These responses depend on physiological adaptations and the cumulative exposure to specific environmental conditions that shape the WUS of each species. *Fagus sylvatica* relies on a small water reservoir because of its shallow root system (Houston Durrant et al., 2016; Kirchen et al., 2017; Leuschner, 2020). This has been documented at FR-Hes and DE-Hin (Granier et al.,

2000; Heinrich et al., 2018), where the species were found to be more susceptible to reductions of soil water availability due to dry spells and droughts. This tree species prefers to grow under favorable climatic conditions with abundant precipitation and no water stagnation or prolonged dry periods (Houston Durrant et al., 2016; von Wuehlisch, 2008). This could be why *Fagus sylvatica,* keeps significant transpiration rates as leaf water potentials decline, but it is also frequently observed to shed leaves prematurely under extreme drought, which could be to reduce water loss and hydraulic failure or due to hydraulic failure (Leuschner, 2020).

Quercus ilex can grow deep roots, increasing the accessible water reservoir and allowing the trees to withstand long dry periods (Peñuelas & Filella, 2003; Zapater et al., 2011), as has been shown at FR-Pue and ES-Alt (Baldocchi et al., 2010; Forner et al., 2018). Its evergreen character is maintained during summer thanks to its physiological adaptations such as sclerophyllous leaves, summer growth reduction, and strong stomatal control (Barbeta & Peñuelas, 2016; Terradas & Savé, 1992). The high wood density of oak is linked to its reduced porosity, allowing it to resist lower matric potentials during summer, reducing its susceptibility to hydraulic failure (Terradas & Savé, 1992). The strong stomatal control of this species classifies it as the most isohydric species of the *Quercus* genus (Barbeta & Peñuelas, 2016). This process is clearly visible in summer at FR-Pue and ES-Alt, where precipitation is scarce, and the trees reduce transpiration rates by closing their stomata. Overall, the difference between the two selected species relies on the degree of vulnerability to hydraulic failure and the WUS, with *Fagus sylvatica* showing a vulnerable response and aggressive WUS, while *Quercus ilex* is more resistant to hydraulic failure with a conservative WUS.

4.2. Some unexpected effects of the vulnerability curve shape parameters

The pant vulnerability curve (PVC) is widely used to model the plant water use response to water stress from single trees up to the ecosystem scales (Kennedy et al., 2019; Li et al., 2021; Mackay et al., 2015; Mencuccini et al., 2019; Sloan et al., 2021). To our knowledge, the impact of characterizing the shape parameters of the curve (Ψ_{p50} and c_k) for the different species or plant functional types (PFTs) has not been investigated in detail for the current implementations of the PVC in land surface models (LSMs). In CLM5, the default parameterization of the plant hydraulic traits is the same for the PFTs under analysis at the four experimental sites. This provided the opportunity to evaluate the effect of the environmental conditions, namely the dynamics of atmospheric water demand and soil water availability, on the simulated plant hydraulic response. FR-Hes and DE-Hin are sites with a continuous water supply during summer due to the low intra-seasonal variability of precipitation (Blume et al., 2022; Granier et al., 2008). Regular precipitation prevents the drying out of the soil water reservoir during summer, allowing the vegetation to operate at low to moderate levels of water stress throughout the year. The default plant hydraulic parameterization of CLM5 reproduces an aggressive water use strategy (WUS) of *Fagus sylvatica* at FR-Hes, allowing the vegetation to transpire at rates close to the atmospheric water demand. However, the use of the same plant hydraulic parameterization across the selected PFTs (Table 2) does not reflect the conservative WUS expected at Mediterranean sites, such as FR-Pue and ES-Alt, which are inhabited by *Quercus ilex*. These two sites have a strong atmospheric water demand but receive very little precipitation in summer (Allard et al., 2008; Lorenzo-Lacruz et al., 2010), resulting in extremely negative soil water potentials and severe plant water stress in the default model simulations (Jiménez-Rodríguez et al., 2022). Although inclusion of water uptake from deeper soil reservoirs can reduce the severity of simulated water stress and under-estimation of transpiration rates in the model (Jiménez-

Rodríguez et al., 2022), here we found that reducing the plant hydraulic conductance can improve both, the over-estimation of transpiration in the early growing season and the under-estimation in late summer, due to more carry-over soil resources from the early to the late season.

The limitations underscored by the default plant hydraulic parameterization of CLM5 in reproducing the aggressive and conservative WUS persist when changes are applied only to the Ψ_{p50} and c_k parameters. That is, the model response is dominated by the instantaneous atmospheric water demand and restricted by the soil water availability. Therefore, at sites where water supply is continuous throughout the year (e.g., FR-Hes and DE-Hin) the decrease of Ψ_{p50} with the resistant configuration (RC) allows more water to be extracted under given meteorological conditions while reducing plant water stress (PLC and β) as expected (Knüver et al., 2022; Walthert et al., 2021). However, the RC overestimates transpiration rates (E_T) for both sites (Figure 4 and Figure S1). This pattern of the model response illustrates the dominant role of plant hydraulics over stomatal control of E_T. Under seasonally limited soil water supply, as is the case at FR-Pue and ES-Alt during summer, the model simulates a counter-intuitive response when changing the shape parameters of the PVC, with the resistant configuration (RC) suffering more water stress and a reduced E_T than the default or vulnerable configurations (DC and VC, respectively) (Figure 4). The entire intraspecific variability in PVC shape parameters for *Quercus ilex* does not reproduce the conservative WUS in the model that would be expected of a tree species able to withstand significant water shortage conditions (Barbeta & Peñuelas, 2016; Terradas & Savé, 1992). In the contrary, the choice of more resistance PVC shape parameters diminished soil water availability simulated at FR-Pue and ES-Alt during summer due to over-use of water in spring, magnifying the overall vegetation water stress.

4.3. Uncovering the role of maximum xylem conductance

The results of the second set of numerical experiments highlight the role of the maximum xylem conductance (k_{max}) in determining the transpiration rates under ample water supply and therefore shaping the seasonal water use strategy. The presented results illustrate the effective role of k_{max} in constraining the water use at sites with seasonal water limitations (i.e., FR-Pue and ES-Alt). The maximum specific hydraulic conductance is a parameter highly influenced by local environmental conditions rather than genetics (Hochberg et al., 2018; Lu et al., 2022). This characteristic is represented by the range of k_{max} values observed for the same species (Figure S5). The observed k_{max} values vary by two orders of magnitude for *Fagus sylvatica* (BDT) and five orders of magnitude for *Quercus ilex* (BET), with similar maximum values for both. The primary role of k_{max} for the plant hydraulic system of CLM5 is in constraining the water transport during unstressed conditions and thereby determining the magnitude of plant water use and how much water is left in the ground, some of which might be available later. At FR-Hes, larger k_{max} values compared to the default value increase the water transport in the model, allowing to match the atmospheric water demand and observations. In contrast, smaller k_{max} values are needed at ES-Alt and FR-Pue to prevent the vegetation from depleting the soil water reservoir in spring and therefore enable continued plant water use under moderate stress during the dry summer. A lower k_{max} depicts a transport limitation allowing to reduce the water stress on the plant in the model, while a larger k_{max} allows the model to transpire at higher rates, mimicking an aggressive WUS. CLM5 differs from other numerical models that rely on stomatal conductance to control or mimic the WUS (Sloan et al., 2021). Therefore, in CLM5, an adequate selection of k_{max} plays the role of restraining the vegetation from transpiring excessively in spring and at the beginning

of summer to ensure an adequate water supply as summer progresses in a Mediterranean (summer-dry) climate. Note that in the Darcy's law equation used in the plant hydraulics system of CLM5 a certain sensitivity in the simulated transpiration fluxes could be expected by changing also the cross-sectional area of the different plant segments (e.g., SAI). However, there is not a direct correspondence between the prescribed SAI values in the model (defined as the sum of all non-photosynthetic vegetation, including stems, branches, and dead leaves (P. J. Lawrence & Chase, 2007)) and the basal area reported from the selected sites (Table 1), which adds uncertainty in the simulated transpiration fluxes.

Most models describe the plant vascular factor by lumping the entire system into a single term (Fatichi et al., 2016), omitting the large variability of the forest ecosystems related to tree species and age (Weithmann et al., 2022). This is the case for k_{max} within the plant hydraulic system of CLM5, where the default k_{max} value is commonly used, disregarding the variability of different tree species and stand density within the PFT classification. Previous studies argue that k_{max} expresses the maximum xylem specific conductance of vegetation under the most favorable environmental conditions (Sabot et al., 2020) and its determination depends on the measurements of specific xylem conductance (k_s), which is a key plant hydraulic trait contributing to the control of the water transport capacity of vegetation (Eamus et al., 2016). This plant hydraulic trait (PHT) varies accordingly with the plant species, environmental conditions, and tree size (Anfodillo & Olson, 2021; Domec et al., 2012; Domec Jean-Christophe et al., 2008; Hochberg et al., 2018; Willigen et al., 2000).

The use of plant hydraulics in land surface modelling provides a framework to connect the environmental conditions with the stomatal response (Venturas et al., 2017), allowing a better control on the simulated plant water use strategies. However, we found that the site-specific character of k_{max} has largely been ignored by the modelling community. The default value for k_{max} is the same for all PFTs, and an order of magnitude lower than the lowest reported specific xylem conductance (k_s) for *Fagus sylvatica*, whereas the reported values for *Quercus ilex* have two outliers, one and three orders of magnitude below the default value (see Figure S5 for more details). The k_s values of *Fagus sylvatica* do not match the range of k_{max} used in the second experiment, where the high xylem conductance (Hk_{max}) is close to the lowest k_s value found for this tree species. However, we found little difference in the simulations between the highest values of k_{max}, so exploring the range of values where most observations lie would not improve the model simulations. The differences between the reported k_s and model-default k_{max} highlights the complexity of defining the k_{max} value for different plant functional types (PFTs) based on experimental data with a larger number of species. Here we show how important is the correct parametrization of k_{max} in CLM5 for capturing the water use by vegetation in summer-dry climates. To progress, we need a better understanding of how k_{max} is controlled by a complex set of growing conditions and co-ordination between the root system and leaf area index (Aranda et al., 2015; Lemoine et al., 2002).

4.4. Understanding the impact of coordinated changes of plant hydraulic traits in CLM5

We found that the adjustment of the hydraulic vulnerability curve shape parameters (Ψ_{p50} and c_k) alone did not enable the reproduction of the observed water use dynamics (Figure 4), as choosing a parameterization that is more resistant to hydraulic failure (RC) resulted in even more reduced dry season water use, if the maximum hydraulic conductance (k_{max}) was too high.

Indeed, the drastic effect caused by the more negative Ψ_{p50} of the RC is diminished by using a smaller k_{max}, reducing the water extraction in spring, and letting the vegetation experience lower PLC values in summer (Figure 6). Also, the fact that the VC of *Fagus sylvatica* results in low PLC for the root-stem and more severe PLC for stem-leaf shows the model's ability to reproduce important physiological processes along the PLC curve (Huber et al., 2019). These processes may trigger different drought survival strategies depending on the species. For *Fagus sylvatica*, water stress and loss in conductance may result in premature shedding of leaves during dry conditions (Arend et al., 2022) or stomatal closure (Schuldt et al., 2016). The sites populated by *Quercus ilex* are better simulated using low k_{max} values (Figures 5 and S4), which allow to better reproduce the WUS of species adapted to water scarce environments (Terradas & Savé, 1992). Nonetheless, extremely low Ψ_{p50} still trigger an excessive water uptake during the driest part of the summer at Mediterranean sites (Figure 6), demonstrating the lack of stomatal regulation in the model and its strong dependency on hydraulic limitations and soil water availability to control the magnitude of E_T. Note that in our study, k_{max} was selected based on the default vulnerability curve shape parameters, whereas the latter were adjusted in a second step, using the previously selected k_{max}. The results could likely be improved by choosing an optimal combination of k_{max}, Ψ_{p50} and c_k, but model calibration is not the goal of the present study.

The results of our study also demonstrate that generalizing the use of k_{max} as a homogeneous parameter across PFTs in CLM5 prevents an adequate reproduction of the magnitude and timing of E_T at sites in different climates. Also, the independence between stomatal control and hydraulic conductance in the model is contradictory to what the existing evidence suggests (Franks, 2004). These aspects magnify the effect that more negative Ψ_{p50} has on the water extraction when we change only the curve shape parameters, something that was overlooked in previous studies (e.g., Bai et al. (2021), Song et al. (2020)). The results of the coordinated changes in safety (i.e., the shape parameters Ψ_{p50} and c_k) and efficiency (i.e., k_{max}) hydraulic traits underline how k_{max} rules the WUS in the model, while Ψ_{p50} and c_k modulate the level of the hydraulic stress experienced. An adequate parameterization of k_{max}, Ψ_{p50} and c_k in combination is critical for obtaining a simulated plant hydraulic response that conforms with the plant water supply theory and the expected physiological response of vegetation subjected to dry conditions.

4.5. Addressing the plant hydraulic traits: homogeneity versus diversity

The plant functional type (PFT) classification system has been a valuable tool for understanding drought resilience from an ecosystem perspective (Sturm et al., 2022). However, the large variation in ecosystem functional properties related to the water cycle is insufficiently explained by this classification system (Reichstein et al., 2014). Skelton et al. (2015) stressed the need to characterize the plant response to drought by merging the current knowledge of the water use strategies (WUS) with the xylem vulnerability. To fulfill this need, this classification system requires the characterization of the physiological traits per vegetation type and growing stage. Nonetheless, these aspects are heavily homogenized using the current PFT classification system, affecting the capacity to correctly predict the ecosystem water use (Konings & Gentine, 2017) and leading to a poor predictive skill of the vulnerability to hydraulic failure.

Fagus sylvatica and *Quercus ilex* represent part of the variability of the plant hydraulic traits (PHT) within the broadleaf deciduous (BDT) and broadleaf evergreen (BET) PFT classes. Aiming to provide a broader context of the role of homogeneity versus diversity in plant

hydraulic trait studies, we sampled the XFT database (Choat et al., 2012) for a preselected set of species per PFT in Europe (Buras & Menzel, 2019; Fyllas et al., 2020; Leuschner & Meier, 2018) with the emphasis placed on the temperate BDT, BET, and adding the needleleaf evergreen (NET) PFT to enrich the analysis (see Table S2 for details of the sampled species). Figure 7 illustrates that the Ψ_{p50} used by default in CLM5 fails to capture the values of Ψ_{p50} for NET and BDT in Europe, as the default values are not even close to the median values of the distributions. The Ψ_{p50} of NET in CLM5 is way beyond the Ψ_{p88} for this PFT, representing an extremely resistant tree with respect to the published data, while the Ψ_{p50} of BDT depicts a more vulnerable tree closer to the reported median of Ψ_{p12}. The default Ψ_{p50} of BET in CLM5 matches the median of the published data, but the large range showed by this PFT (-0.5 MPa to -9 MPa) raises the question of how much of this variability is driven by geography or environmental conditions. An even more important aspect to be considered is an adequate selection of k_{max} for the PFTs, where the large variability showed for individual species does not agree with the best fitted k_{max} of the model. This finding depicts the issue of considering k_{max} as constant among PFTs when the variability of the species describing these PFTs is large (see Figure S5).

Liu et al. (2020) showed the benefit of considering the plant hydraulics in LSMs, where the overestimation of vegetation water use is a common issue. They also recognize the ability of plant hydraulics to predict vulnerability to droughts. In this regard, Kennedy et al. (2019) introduced the plant water stress routine in CLM5 that compartmentalized the PHT according to PFT type. From an ecosystem perspective, simplifying hydraulic traits into single plant functional types has additional repercussions. Matheny (2021) highlighted the importance of incorporating flexible traits based on prevalent environmental stressors since tree species' sensitivity to water stress is determined by their plasticity to the environment (Haberstroh & Werner, 2022). This plasticity is exemplified by the different k_{max} values in *Fagus sylvatica* and *Quercus ilex* in this manuscript, and the reported variability of xylem specific conductance reported across many orders of magnitude for each species (e.g., Bär et al., 2018; Carevic et al., 2014; Charra-Vaskou et al., 2012; Choat et al., 2012; David et al., 2007; Limousin et al., 2010; Lübbe et al., 2022; Martínez-Vilalta et al., 2002; Tomasella et al., 2019). Flexible traits based on the environmental stressors in CLM5 can be used by the spectrum of PVCs per PFT and exploiting the role of k_{max} in regulating the WUS in the model. By adjusting the k_{max} to better represent the transpiration response we may be able to identify the timing of important physiological processes (e.g., leaf shedding) that differ between the VC and RC. In this way, we may be able to better understand the significant changes in different ecosystem processes triggered by intense dry periods (Oddi et al., 2022).

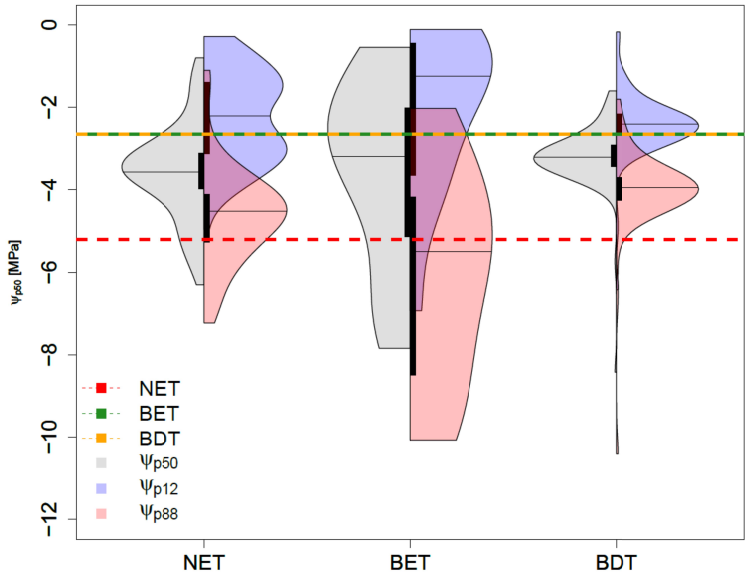

Figure 7. Violin plots describing the variability of the plant hydraulic traits (Ψp12, Ψp50, and Ψp88) within broadleaf evergreen (BET), broadleaf deciduous (BDT), and needleleaf evergreen (NET) trees plant functional types (PFTs) representative of European forests (see Table S2 for the list of pre-selected tree species per PFT). The red, green, and yellow dashed lines represent the NET, BET, and BDT default values of Ψp50 used by CLM5, respectively.

5 Conclusions

The intraspecific variability of the plant hydraulic traits of individual plant functional types (PFT) allows to describe the spectrum of vulnerability to hydraulic failure from vulnerable to resistant responses of different tree species. Understanding the importance of the right selection of k_{max}, Ψ_{p50} and c_k from their large within-species variation requires a detailed understanding of the role played within the model. This information is crucial for the modelling community, where the parameter selection may induce considerable bias when assuming that all tree species within the same PFT behave equally in different environmental conditions. The adequate identification of dominant tree species per experimental site allows to narrow down the variability of multiple species or by weighing the tree species contribution within the PFT, but given the large variability in hydraulic traits even within a single species, a large uncertainty prevails. Adjustments of the shape parameters of the hydraulic vulnerability curve (Ψ_{p50} and c_k) alone do not enable the model to reproduce E_T during spring and summertime at sites with seasonal water deficits. The seasonal differences between measured and modelled transpiration illustrate the importance of the maximum plant hydraulic conductance (k_{max}) for controlling the magnitude and timing of E_T, i.e. the general water use strategy (WUS). A larger k_{max} allows the trees to transpire larger amounts of water during favorable water conditions, quickly depleting the soil water reservoir. In contrast, smaller k_{max} values limit the water transport and hence soil water extraction rates, pushing the vegetation towards a more conservative WUS. Consequently, k_{max} is a significant player in controlling the transpiration in CLM5 and allowing to mimic the WUS of different species by limiting or enhancing the water transport. However, given the large within-species variability in k_{max}, more research is needed to enable adequate parameterization of the site-specific k_{max}. This work reveals the potential of plant hydraulic traits to mimic aggressive

or conservative WUS in CLM5, crucial for adequate reproduction of plant water use dynamics in different climates. Given the large intra-specific variation in plant hydraulic traits and the importance of the stand characteristics (e.g., tree height, stem area index) for limiting transpiration rates in the model, a more fundamental understanding of the drivers for adjustments in these parameters is needed.

Acknowledgments

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Open Research

The SAPFLUXNET data used for atmospheric forcing and transpiration estimates in the study are available at ZENODO repository via https://doi.org/10.5281/zenodo.3971689 with a Creative Commons Attribution 4.0 International license for the files. The COSMO-REA6 data used to complete the missing data for the atmospheric forcing in the study are available from the opendata-FTP server at DWD (https://opendata.dwd.de/climate_environment/REA/COSMO_REA6/).

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Table 1. Summary of the environmental characteristics of each experimental site. All data is based on Poyatos et al. (2021) except those explicitly mentioning the source.

	DE-Hin	ES-Alt	FR-Hes	FR-Pue
Country	Germany	Spain	France	France
Site Name	Hinnensee	Alto Tajo	Hesse	Puechabon
Latitude (°)	53.33	40.802	48.674	43.741
Longitude (°)	13.192	-2.230	7.065	3.596
Elevation (m a.s.l.)	90	981	300	270
Mean Annual Precipitation (mm yr^{-1})	606.40	566.90	1003.48	1022.97
Mean Annual Temperature (°C)	8.68	11.74	9.97	13.80
Köppen-Geiger Climate Classification (Beck et al., 2018)	Cfb	Csb	Cfb	Csa
Slope (%)	2-5	5-10	0-2	0-2
Soil Texture	Sandy	n.a.	Silty	Clay-Loam
Soil Depth (cm)	n.a.	n.a.	120	52.5
Species under analysis	*Fagus sylvatica*	*Quercus ilex*	*Fagus sylvatica*	*Quercus ilex*
Stand Age (yr)	~200	59	34	58
Stand Basal Area (m^2 ha^{-1})	n.a.	13.1	19.7	28.1
Stand Height (m)	24.0	4.9	13.0	5.0
Period of Analysis	2012-2014	2012-2014	2001-2005	2001-2005

Table 2. Plant hydraulic traits describing the vulnerable and resistant curves of the two selected tree species.

	Parameter	Units	*Fagus sylvatica*	*Quercus ilex*
Default Model Configuration	k_{max}	mm_{H2O} $mm_{H2O}^{-1}s^{-1}$	2 x 10^{-8}	2 x 10^{-8}
	c_k	-	3.95	3.95
	Ψ_{p50}	MPa	-2.70	-2.70
Vulnerable Tree Configuration	k_{max}	mm_{H2O} $mm_{H2O}^{-1}s^{-1}$	2 x 10^{-8}	2 x 10^{-8}
	c_k	-	1.73	1.70
	Ψ_{p50}	MPa	-1.90	-1.23
Resistant Tree Configuration	k_{max}	mm_{H2O} $mm_{H2O}^{-1}s^{-1}$	2 x 10^{-8}	2 x 10^{-8}
	c_k	-	3.33	8.04
	Ψ_{p50}	MPa	-4.7	-5.72