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The more the better? A limited proportion of deep roots maximizes tree survival under drought in Mediterranean forest

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Abstract

Deep roots are assumed to enhance tree survival during drought by providing access to water stored at depth. However, the respective roles of deep soil water storage (SWC_{Deep}) and fine-root distribution ($FineRoot_{Distrib}$), which jointly determine access to deep water during drought, remain poorly understood. We assessed their relative importance during drought using the mechanistic hydraulic model SurEau-Ecos. The model was calibrated with leaf water potential and isotopic data collected in 2014 and 2015 for three species (*Quercus ilex* L., *Fagus sylvatica* L., and *Abies alba* Mill.) across two Mediterranean sites in France. Our results show trees predominantly rely on shallow water under non-limiting conditions, whereas SWC_{Deep} mobilisation becomes essential during drought, accounting for 11–36% of annual transpiration. Sensitivity analyses reveal a "rare-root strategy", whereby a limited proportion of deep roots maximizes survival by enabling access to deep water while preventing rapid depletion of deep reserves. These findings highlight that fine root distribution, through its control on the rate of SWC_{Deep} depletion, is a key driver of drought resistance, with an influence comparable to other major ecohydrological traits. Accounting for $FineRoot_{Distrib}$ is therefore essential when assessing vulnerability to drought.

Keywords:

Available water capacity; Groundwater resources; Tree physiology; Drought resistance; Mediterranean climate.

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1. Introduction

World ecosystems must cope with more frequent and intense droughts due to rising temperatures and changes in precipitation regimes (Dai, 2013; Samaniego et al., 2018; IPCC, WG II., 2023). These novel conditions are triggering widespread forest dieback events, particularly in water-limited regions (Hartmann et al. 2022).

Decades of ecophysiological research have established that hydraulic failure, defined as the loss of hydraulic conductance caused by xylem embolism and lethal tissue dehydration, is the primary mechanism underlying drought-induced mortality during extreme events (Choat et al., 2012; Schuldt et al., 2020; Mantova et al., 2022; Sanchez-Martinez et al., 2023). Risk of hydraulic failure is jointly driven by the plant-specific vulnerability to xylem embolism, defined as (i) the water potential threshold below which runway cavitation occurs, and (ii) the exposure to such threshold. Such exposure results from the dynamic balance between water demand, under the control of plant leaf area, stomatal regulation, and residual conductance (Martin-StPaul et al., 2017; Choat et al., 2018), and water supply (Nardini et al., 2024). However, how the abiotic environment –mediating the quantity of extractable water– and plant strategy –mediating the extraction rate by trees– interact to control total water supply as drought progresses remains difficult to disentangle.

On the one hand, the quantity of water in the soil and subsoil that is extractable by plants depends primarily on pedological, geological, and climatic factors (Cousin et al., 2022). Studies focusing on how those factors influence tree performance are longstanding and central (Granier et al., 2007; Nardini et al., 2021; 2024). For instance, using geophysical methods (Loiseau et al. 2023, Callahan et al. 2022) showed that bedrock properties strongly influence the amount of water available for trees and, consequently, the mortality rate of trees. Model sensitivity analyses have also demonstrated that soil holding capacities is a key driver of productivity (Hoff & Rambal, 2003) and hydraulic failure risk (Cochard et al., 2021). On the other hand, tree-available water depends on the trees' ability to mobilize the reservoir, which is physically driven by the variation in hydraulic resistivity at the soil-root interface across depth and time. This ultimately depends on the relative fine root density across soil layers (Affortit et al., 2024). What is the optimal fine root distribution to make the most of the soil reservoir across depth and minimize the hydraulic risk during droughts is unclear. Increasing root development enhances the amount of water that can be extracted from the soil (Preisler et al., 2019), and several studies have highlighted the importance of deep rooting for accessing enough water stored at depth (Ichii et al., 2007; McCormick et al., 2021). As a result, one might expect that the most advantageous strategy is to develop extensive roots within a large deep reservoir, enabling full exploitation of structurally available water resources. However, trees growing in the same environment vary in their rooting strategies (Chitra-Tarak et al., 2018; Carrière et al., 2020c; Laughlin et al., 2023). Chitra-Tarak et al. (2018) showed that trees with extensive deep rooting systems benefit during short droughts, but may

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experience severe dieback during prolonged drought, as deep reservoirs fail to recharge. This raises the question of whether an optimal rate of deep water mobilisation exists in environments experiencing extreme drought. The parsimonious use of deep roots has already been reported as a key factor for enhanced tree survival (Werner et al., 2021; Beyer et al., 2023), but the precise mechanisms and the relative contribution of this effect compared to other drivers (e.g., soil water capacity, vulnerability to cavitation, stomatal regulation) remain poorly understood. This phenomenon is particularly relevant in karstic Mediterranean ecosystems, where water resources are structured into two compartments: a shallow soil reservoir, that is easily accessible but often scarce, and a deeper rocky reservoir, that is more abundant but hardly accessible due to the rocky substrate (Carrière et al., 2020a).

While quantifying the distribution of absorptive roots across compartments is key for understanding and predicting tree survival under drought regimes, characterizing root profile in natural environments remains extremely challenging (Li et al., 2022) and often impossible below the first few decimetres of soil. To address this limitation, some studies have used isotopic tracers to estimate water uptake depths (Beyer et al., 2018; Kühnhammer et al., 2023). Others have relied on model inversions to infer root distribution profiles (Cabon et al., 2018; Ichii et al., 2007). Nevertheless, these approaches do not allow for simultaneous quantification of water volumes available and their effective use over time. Moreover, parameters governing deep water use are typically assessed independently of each other. They focus either solely on water volume in the soil (Carrière et al., 2020c; Nardini et al., 2021; 2024) or on the influence of root distribution on water uptake (Ichii et al., 2007; Cabon et al., 2018; Stocker et al., 2023). This results in a really simplified representation of interaction between vegetation and the underground part in vegetation models (Dukes et al., 2026). Because these two parameters are inherently interdependent, we propose a data–model approach to quantify deep plant-available water use and how root distribution controls it and shapes tree strategy to cope with extreme droughts. In particular, this study aims to (i) estimate the extent of the root system of trees within the deep reservoir across two karstic Mediterranean sites; (ii) develop and evaluate a method to quantify the volume of water used from the deep reservoir as drought progresses; (iii) investigate the effect of deep root development on tree survival under extreme drought conditions.

To address these objectives, we relied on isotopic tracing experiments and leaf water potential monitoring (Carrière et al., 2020a). The SurEau-Ecos (version 0.2.0) ecophysiological model (Cochard et al., 2021; Ruffault et al., 2022) was calibrated using these field data in order to estimate the proportion of the root system required in the deep reservoir to reproduce the observed patterns. Model sensitivity was then performed to explore how root distribution influences extracted water volumes and water stress.

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2. Material and methods

2.1. General framework

The methodology developed in this study consists in calibrating belowground parameters linked to root water uptake of a plant hydraulic model (the SurEau-Ecos model, Ruffault et al., 2022) for different tree species at the two different sites. To do so, we compared measured and simulated temporal dynamics of predawn leaf water potentials (Ψp) and relative fractions of deep water (f_{DW}) across a range of calibrated parameter values, and retained the ones minimizing errors between observations and simulations. Hydraulic trait data for the different species have been collected in literature, and the soil available water was constrained with our in-situ measurements. The main remaining adjustable variable used for calibration is the fine root profile, which drives the proportion of roots in the deep reservoir. In order to simplify the parametrization of the soil available water storage capacity, we used the Total Available Water for trees (*TAW; mm*) concept (Fig. **1**), which divide available water into a shallow compartment ($TAW_{Shallow}$) - representing the soil and rocky soil layers - and a deep compartment (TAW_{Deep}), representing the vadose zone and/or the saturated zone:

$$TAW = TAW_{Shallow} + TAW_{Deep}. \quad (1)$$

Using the calibrated model, we then explore the contribution of fine root distribution to the development of tree water stress and deep water use.

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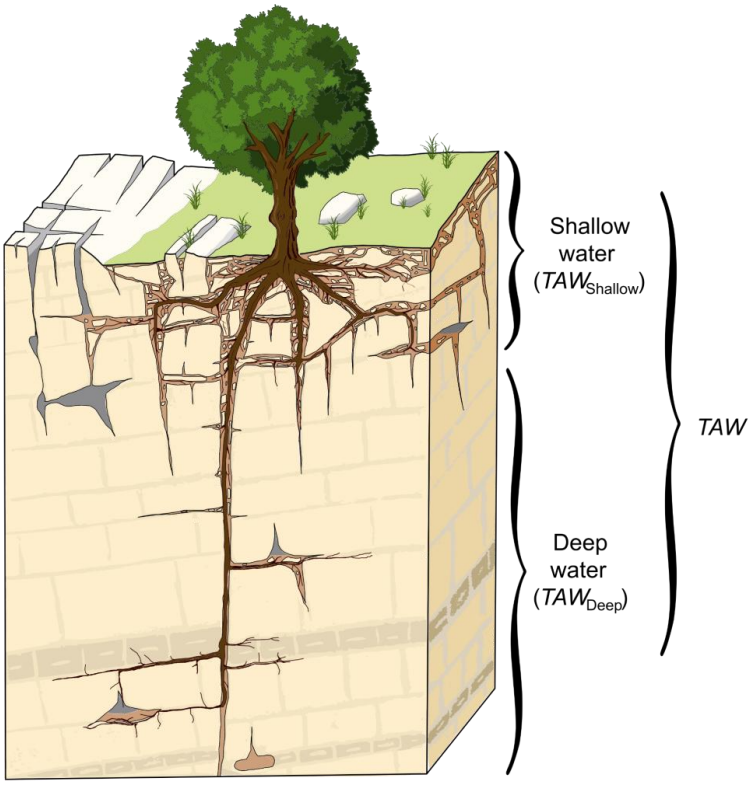

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123 ***Figure 1*** *: Representation of Total Available Water (TAW) in karst environments (modified from Carrière et al., 2020a).*

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2.2. SurEau-Ecos Model

The SurEau-Ecos model simulates the water transport along the soil–plant–atmosphere continuum with a detailed representation of the plant hydraulic architecture (Cochard et al., 2021). It is specifically designed to simulate the consequences of severe drought on plant hydraulic functioning, which includes the physiological processes that occur after the point of stomatal closure (Martin-StPaul et al., 2017; Cochard, 2021; Ruffault et al., 2022). SurEau-Ecos is a 1D model, simulating fluxes through only one individual without interaction with potential others. The version used here is an improved version of the R implementation presented in Ruffault et al. (2022), which is available on the Forge INRAe gitLab repository under the commit tag "https://forge.inrae.fr/urfm/sureau/-/tree/v2.2". The model is used to solve water potential and water content, as well as losses of conductivity and water storage resulting from cavitation. In practice, water fluxes between compartments are calculated using a succession of Darcy's relations, such as,

$$dq_{c1-c2} = dt\ K_{c1-c2}\ (P_{c1} - P_{c2}) + dS_{c1} \qquad (2)$$

where dq_{c1-c2} is the water flux between compartment 1 and compartment 2 (mmol.m^{-2}), dt is the time step (s), K_{c1-c2} is the conductance between compartments 1 and 2 (mmol.m^{-2}.s^{-1}.MPa^{-1}), $P_{c1}$and P_{c2} are the respective water potentials of compartments 1 and 2 (MPa) and $dS_{c1}$is the stock variation in compartment 1 (mmol.m^{-2}).

The model uses daily climatic data (temperature, radiation, relative humidity, wind speed) and interpolates them at hourly time steps to first calculate the vapor pressure deficit (VPD). The VPD drives the cuticular and stomatal transpiration. This initial flux induces a change in water potential in the leaves and triggers fluxes from adjacent compartments. This process is iteratively propagated from the leaves down to the soil at each time step, unless hydraulic failure occurs. In SurEau-Ecos, the tree is discretized into three organs (roots, stem, leaves), and the soil is divided into three layers. Each organ contains two compartments: the symplasm and the apoplasm. They are connected within an organ, but only the apoplasm connects different organs between them. The two compartments have different properties: the symplasm capacitance is dependent on water potential while the apoplasm capacitance is constant (Cochard et al., 2021). Likewise, apoplasm conductance depends on embolism levels, while the symplasm conductance is unaffected. Loss of stomatal conductance and loss of hydraulic conductivity are calculated with empirical sigmoid function based on species-specific traits. Each soil layer is connected in series to the stem via one idealized root. The conductance between a soil layer (j) and the apoplasm of the stem can be expressed as,

$$K_{soil_j - SApo} = \sum_j \frac{1}{\frac{1}{K_{R_j - SApo}} + \frac{1}{K_{soil_j - R_j}}}, \qquad (3)$$

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with $K_{R_j - SApo}$(mmol.m^{-2}.s^{-1}.MPa^{-1}) the conductance between the stem and the root at depth j and $K_{soil_j - R_j}$ (mmol.m^{-2}.s^{-1}.MPa^{-1}) the conductance between the soil and the root at depth j.

$K_{R_j - SApo}$ is defined as a constant fraction of the conductance between the entire root system and the stem (K_{R-SApo} , mmol.m^{-2}.s^{-1}.MPa^{-1}). Without cavitation occurring in the stem, this fraction is assumed proportional to the relative root biomass in layer j, computed using a power law parameterized following Jackson et al. (1996),

$$K_{R_j-SApo,max} = K_{R-SApo}\, RAI \left(\beta^{z_{h,j-1}\times 100} - \beta^{z_{h,j}\times 100}\right), \qquad (4)$$

where *RAI* is the total root area (supposed equal to *LAI*), β is a root distribution parameter, and $z_{h,j}$(m) is the depth from the soil surface to the top of layer (j). In this study, the only variable parameter was β.

The conductance between each soil layer and the roots ($K_{soil_j-R_j}$, mmol.m^{-2}.s^{-1}.MPa^{-1}) is calculated from the root density and the hydraulic conductivity in the layer (j) as:

$$K_{soil_j-R_j} = \frac{2\pi L_{a,j}}{ln(\frac{1}{r\sqrt{\pi L_{v,j}}})}\, k_{REW_j}\,, \qquad (4)$$

with $L_{a,j}$ and $L_{v,j}$ the root length per soil area and per soil volume of the layer (j), r the radius of absorbing roots and k_{REW_j} the soil hydraulic conductivity of layer (j) at a certain relative water content. $k_{REW_j}$is computed from Van Genuchten - Mualem parameters and the hydraulic conductivity at saturation.

2.3. Study sites and parameterization data

2.3.1. Sites and species

The study was conducted on two forest sites in the southeast of France, the Rustrel and Mont-Ventoux sites (Carrière et al. 2017; 2020a). Both sites are located on a Cretaceous limestone formation that forms the reservoir of the Fontaine-de-Vaucluse karst system. The saturated zones are inaccessible to trees, as they are located approximately 400 m and 1200 m below the surface at the Rustrel and Mont-Ventoux sites, respectively. However, part of the root systems of the trees are able to penetrate into the subsurface to access deep water resources within the weathered rock zone (Fig. **1**). Due to their different elevation and exposure, both sites experienced different climate conditions. Whereas the Mont-Ventoux site is characterized by mean annual temperature and precipitation of 7.5°C and 1258 mm (corresponding to temperate mountain forest); the Rustrel site is characterized by mean temperature and precipitation of 12.9°C and 909 mm (corresponding to temperate mediterranean forest). As a result, the vegetation differs between the two sites.

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The Rustrel forest plot

The Rustrel forest plot (43°56'12.15''N; 5°27'58.18''E; 530 m ASL) extend over 0.75 ha (150 m × 50 m) and is located at the southern boundary of the Fontaine-de-Vaucluse karst system. The plot is located right above an underground observatory system (the Fontaine-de-Vaucluse observatory), which is part of the French Critical Zone Observation Network (OZCAR, http://www.ozcar-ri.org/). The site is dominated (85% of the basal area) by a sparse population of Holm Oak (*Quercus ilex* L.), with dominant trees about 4 m tall and the remaining vegetation consisting of shrub layers (Carrière et al. 2017). This study focuses solely on the Holm Oak population.Numerous faults make the epikarst highly heterogeneous and complex (Carrière et al. 2013). A large amount of mobile water is stored within the vadose zone down to a depth of 90 m (Carrière et al. 2016). The Low Noise Underground Laboratory (http://lsbb.eu) located below the site allows the sampling of infiltration waters whose isotopic signal is representative of deep water. The soil thickness is highly variable ranging from 0 on bedrock outcrop to a maximum of about 60 cm. The soil is a silty to silty-clay rendisol with a variable proportion of coarse fragments, often exceeding 50% from a depth of just 15 cm. Therefore, the estimated $TAW_{Shallow}$ range from 0 mm to 65 mm using the protocol from Baize and Jabiol (2011). Climatic data were obtained from the Bonnieux station at approximately 4 km and have been gap-filled.

The Mont-Ventoux forest plot

The Mont-Ventoux forest plot (44°10'43.93''N; 5°14'36.85''E; 1340 m ASL) extends over 1ha and is located on the northern slope of Mont-Ventoux. The dominant tree species is Silver fir (*Abies alba* Mill.), accounting for 86.3% of the basal area. Beech (*Fagus sylvatica* L.) individuals are also present due to the natural regeneration of the forest (13.7% of basal area). The tallest trees reach an average height of about 17 m for both species.The site lies on calcareous scree deposits. Two nearby epikarstic springs (named Mont-Serein and Contrat) provide access to the isotopic signal of deep water. The soil is a silty rendisol with a high proportion of coarse fragments, reaching up to 80% within the first few centimeters. The total soil thickness is about 60 cm to 80 cm and the estimated $TAW_{Shallow}$ is about 80 mm (Hendrik and Maxime 2017). Climatic data were obtained from the Mont-Serein station at approximately 15 km from the study site.

2.3.2. Parameterization data

To operate, the model requires two sets of parameters:

Vegetation parameters – All vegetation parameters were kept constant throughout the simulations. The parameterization of vegetation was based on traits values obtained from previous literature or direct observation. The parameters of stomatal closure were derived from the Turgor Loss Point (TLP), following the approach of Copie et al. (2025). In addition, the leaf and stem parameters have been

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considered equal as in Copie et al. (2025). Among all parameters, fifteen parameters (**Table S1**) were species-specific. Previous sensitivity analyses have shown that seven of these parameters strongly influence the simulated Time to Hydraulic Failure (THF) (Ruffault et al., 2022). These parameters are linked to four types of processes: (i) water use regulation (i.e., before the point of stomatal closure); (ii) water losses beyond the point of stomatal closure; (iii) the vulnerability of the vascular system to cavitation; and (iv) water storage in shoots. The description, source and values of the vegetation parameters implemented are available in Table S1. The range of vegetation parameters are available in Table S2.

Soil parameters – The model includes three soil layers of varying stoniness based on field observations (Carrière et al., 2020a). Van Genuchten - Mualem parameters and saturated hydraulic conductivity are taken from empirical literature values (Carsel and Parrish, 1988; Ghanbarian-Alavijeh et al., 2010) and were assumed to be constant along the soil profile. The values of $TAW_{Shallow}$ retained are 50 mm in Rustrel and 90 mm in Mont-Ventoux. The rock fragment content (RFC) are drawn from field observations and have been adjusted in order to set the $TAW_{Shallow}$ measured in the first two layers. Overall, the two model application sites are distinguished by 10 parameter values. TAW_{Deep} represents the water available in the deepest layer. For the simulation investigating the root development of each species, TAW_{Deep} was set to a high value (150 mm) so that the simulation results depend solely on root system development. It appeared that all the simulation are equivalent as long as $TAW_{Deep} > 75$ mm (**Figures S1 – S3**). Above this value, de thickness of the deep compartment and the proportion of rock fragments are not sensitive. The description, source and values of the site-specific soil parameters implemented are available in Table S3. All the soil parameters are available in Table S4.

2.3.3. Calibration data

Predawn leaf water potential (Ψp)

Predawn leaf water potential (Ψp) is typically measured to estimate tree water availability since generally close to equilibrium with the soil water potential in the root zone (Limousin et al., 2009; Decarsin et al., 2024). Ψp was measured throughout the summer of 2014 and 2015 using a Scholander pressure chamber (Carrière et al., 2020a). At the Rustrel site, Ψp was measured on ten *Quercus ilex* individuals on eight different dates. At the Mont-Ventoux site, measurements were taken on 19 beech trees (*Fagus sylvatica*) on nine dates and on ten Silver firs (*Abies alba*) trees on eight dates. On each date and for each tree, at least three leaves were sampled between 04:00 and 05:00, immediately placed in a plastic bag saturated with water vapor, and stored in a cooler until measurement. Measurements were performed within one hour after sampling. Two of the three leaves were measured, and the third was only measured if the difference between the first two exceeded 0.2 MPa.

Isotopic tracing measurements and mixing model calculation

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Isotopic tracing is widely used to monitor water transfer within the soil–plant–atmosphere continuum (Sprenger et al., 2016). In this study, it was necessary to sample both shallow water and groundwater (deep water) (Fig. **1**). The "shallow water" pool includes understory precipitation and soil drainage water, which exhibit strong seasonal variation in the isotopic signal. The signal observed in these waters is considered representative of the signal from the first meter of subsoil, as it is nearly impossible to collect soil samples at depths of 1 or 2 metres in such a karst settings. Precipitation and soil drainage water were collected using a rain gauge and a mini-lysimeter respectively, as described in Carrière et al. (2020b). The "deep water" pool includes water collected at the LSBB for the Rustrel site and spring water for the Mont-Ventoux site.

The isotopic composition of xylem water reflects the contribution of water taken up by roots from different soil water sources (Barbeta et al., 2019; Seeger and Weiler, 2021). The sampling was conducted during the summer periods of 2014 and 2015. During each campaign, 3 to 4 branches were collected from each individual at solar noon. The bark and phloem were removed to avoid contamination by enriched water from the foliar system. The branches were then immediately wrapped in Parafilm and placed individually in sealed vials. These vials were stored in a freezer until extraction. Water extraction was performed by cryogenic distillation following the protocol of West et al. (2006). Analyses were carried out using mass spectrometry for xylem water and laser spectrometry for shallow and deep water samples.

To determine the proportion of deep water in the total water resources used by trees, it was assumed that the isotopic signal of xylem water represents a mixture of deep water and shallow water (Fig. **1**). We used an approach based solely on oxygen isotopes due to the isotopic fractionation of deuterium (Barbeta et al., 2019). Without isotopic fractionation, the contribution of each source can be obtained using a simple mixing equation (Dawson, 1993; Rothfuss and Javaux, 2017),

$$\delta^{18}O_{xyl} = f_{SW}\delta^{18}O_{SW} + f_{DW}\delta^{18}O_{DW}\,, \quad (5)$$

with $\delta^{18}O_{xyl}$ the isotopic signature of xylem water as presented in Section S1, $\delta^{18}O_{SW}$ the isotopic signature of shallow water (average of understory precipitation and soil drainage water), $\delta^{18}O_{DW}$ the isotopic signature of deep water, and f_{SW} and f_{DW} their respective fractions in the water used by the tree. The contribution of deep water in the xylem can be calculated as,

$$f_{DW} = 1 - f_{SW}\,, \quad (6)$$

then,

$$f_{DW} = \frac{\delta^{18}O_{xyl} - \delta^{18}O_{SW}}{\delta^{18}O_{DW} - \delta^{18}O_{SW}}. \quad (7)$$

The results of the mixing models are presented and discussed in Carrière et al. (2020a).

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1.4. Application of the SurEau-Ecos model

1.4.1. Calibration

Nineteen simulations were run for the years 2014 and 2015, varying parameter β from 0.905 to 0.98, corresponding to 0.3 to 25% of the root system in the deep reservoir (assumed constant across years). For each simulation, the simulated leaf predawn water potential (Ψp) were extracted, and the proportion of deep layer use (f_{DW}) was calculated using

$$f_{DW} = \frac{dq_{soil_3-stem}}{dq_{soil-stem}}, \qquad (8)$$

with dq_{soil_3-stem} and $dq_{soil-stem}$ representing the simulated sap fluxes from the deepest soil layer and from all soil layers combined (mm.d^{-1}), respectively. A 5-day moving average of f_{DW} was applied. This averaging accounts for the root-to-leaf transfer time (Marc and Robinson, 2004).

The simulated values were compared to field measurements, and the β parameter value retained was the one minimizing the Root Mean Square Error (RMSE). To identify the β value optimizing both model outputs, a combined RMSE was calculated from the Normalised Root Mean Square Error (NRMSE) of each simulation:

$$Combined\ RMSE\ = \sqrt{NRMSE_{\Psi_p}^2 + NRMSE_{f_{dw}}^2}, \qquad (9)$$

and,

$$NRMSE_X = \frac{RMSE_X}{max(RMSE_X)}, \qquad (10)$$

where $NRMSE_{\Psi_p}$ is the NRMSE calculated from the simulated predawn leaf water potentials, $NRMSE_{f_{dw}}$ is the NRMSE calculated from the simulated contribution of the third soil layer to total water use, and $RMSE_X$ is the RMSE of the modeled values (i.e., Ψp or f_{DW}).

2.4.2. Model sensitivity analysis

The sensitivity of the model to root distribution and to the TAW_{Deep} was investigated using theoretical scenarios for each species. Trees were subjected to a constant mean summer climate in Rustrel with no precipitation, and the soil reservoir was initialized at field capacity. Soil parameters, climate and LAI were kept identical across species (those of Rustrel) to clearly highlight interspecific differences. Beeches trees were able to defoliate in order to represent the reduction of transpiration. This exercise aimed to analyze the tree response to drought examining (1) leaf water potential, (2) Percentage Loss of Conductivity (*PLC*) and (3) stomatal conductance (g_s) until the tree's death by hydraulic failure. The hydraulic failure is defined as 90% of cavitation.

We first analysed the effect of the proportion of roots located in the deep soil layer (f_{DR}) by simulating trees with 0.2%, 3%, and 30% of their roots in the deep layer (β = 0.90, 0.943, and 0.98, respectively),

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while keeping TAW_{Deep} fixed at 65 mm. This relatively low value of TAW_{Deep} was selected because our objective was to assess the influence of β on mortality. Using a larger TAW_{Deep} would not have altered the relative differences among the three simulations. We then investigated the effect of deep water availability by varying TAW_{Deep} across 10, 45, and 65 mm while keeping f_{DR} constant at 3%. The aim of this theoretical study was not to develop a fully validated model of drought-induced mortality, but rather to explore, through sensitivity analyses, the relative influence of root distribution and deep water availability on drought responses. Finally, we examined interspecific differences by analysing how THF varied as a function of f_{DR}.

3. Results

3.1. Simulating tree water use at two Mediterranean ecosystems

3.1.1. Calibration of the proportion of deep roots

The proportion of deep roots minimizing the errors between observed and simulated Ψp and f_{DW} varied among species, with 1.5% of the root system located in the deep reservoir for oaks (Fig. **2a**), 2.6% for firs (Fig. **2b**), and 11.9% (Fig. **2c**) for beeches. For firs and beeches, model calibration was less constrained due to less field measurement available.

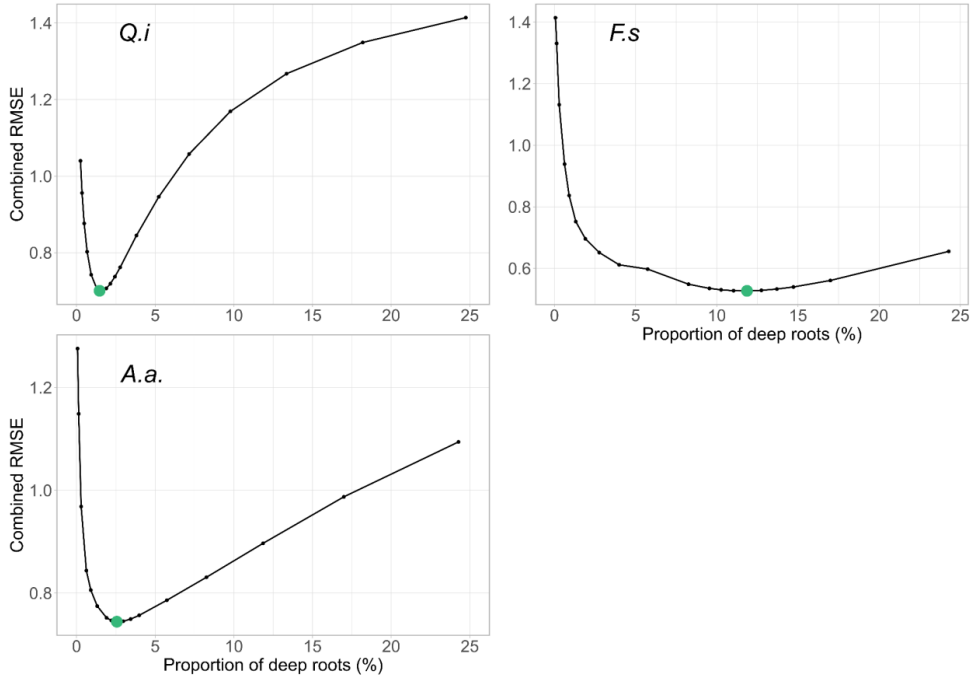

***Figure 2**: Changes in combined RMSE as a function of the proportion of the root system located in the deep reservoir. a. Changes for Holm oaks at Rustrel (Q.i); b. Changes for beeches at Mont Ventoux (F.s); c. Changes for firs at Mont Ventoux (A.a).*

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3.1.2. Description of temporal dynamics

Simulated water stress was noticeably more intense during summer 2015. At Rustrel, Ψp remained below -2.5 MPa throughout July and August 2015, whereas it only briefly reached this value in 2014 (Fig. **3b**). Simulated f_{DW} reached a maximum of 92% in 2014 and 96% in 2015 (Fig. **3a**).

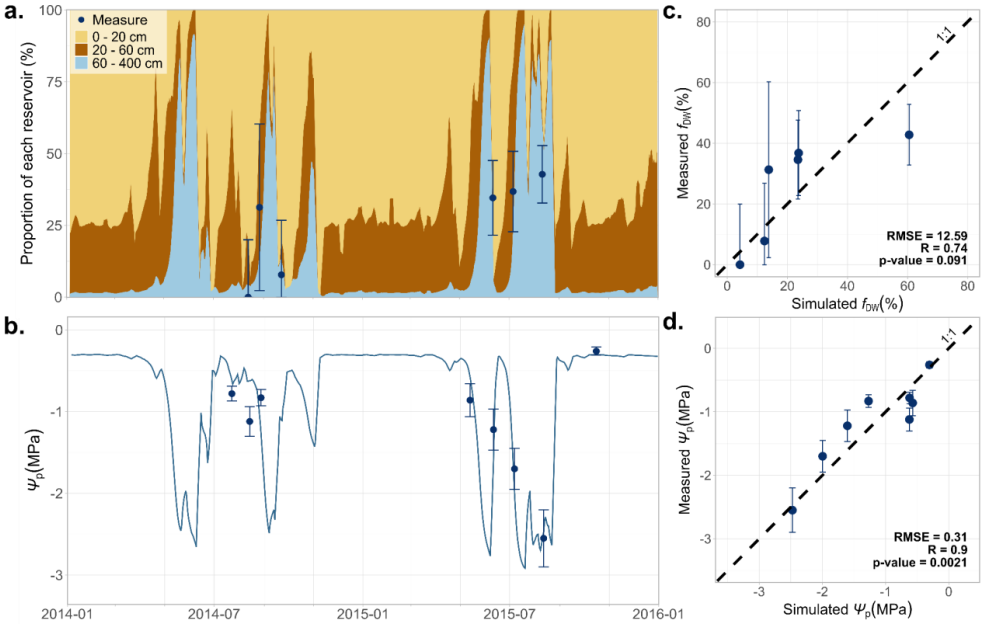

***Figure 3**: Results of the calibrated model simulations for the Holm oaks of Rustrel (Fig. **2**). a. Time series of deep reservoir use relative to evapotranspired volumes (f_{DW}); b. Time series of predawn water potential (Ψp); c. and d. Correlation between observed and simulated values.*

Differences in water stress and deep-water use between 2014 and 2015 were even more pronounced at the Mont Ventoux site (**Figures S4 & S5**). Beech trees experienced almost no water stress in 2014, with minimum Ψp of -0.5 MPa, whereas Ψp values in July–August 2015 were much lower (-2 MPa). Similarly, a maximum of 41% of the daily root uptake came from the deep layers in 2014, compared to 97% during the drought peak in 2015 (**Figure S4**). During summer 2014, firs Ψp drops to -1.5 MPa, compared with -2 MPa in 2015 (**Figure S5**). Up to 97% of root uptake originates from deep layers in July 2015, compared with 52% at the peak of the 2014 drought (**Figure S5**).

These 2014/2015 dynamics were consistent with the field measurements and are in agreement with observed meteorological conditions (**Figures S6 – S8**). However, the simulated values deviate strongly from the final measurement on 08/11/2015. Simulated Ψp values are really lower than measured (-0.7

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MPa vs -1.2 MPa for beech and -0.9 MPa vs -1.8 MPa for Fir) and simulated f_{DW} are really higher (65% vs 86% MPa for beech and 55% vs 79% for Fir).

3.1.3. Quantification of deep water use

Figures 3a, G1 and G8 illustrate the proportion of deep water uptake, but they do not allow estimation of the actual quantities used. The SurEau-Ecos model enables computing the amount of deep-water uptake and total transpiration (Table **1**).

Table 1. *Precipitation observed and Potential EvapoTranspiration (PET), Transpiration, and Deep-water uptake simulated for studied species during the 2014 and 2015 summer periods (21 June to 21 September).*

	2014					2015				
	Rainfall (mm)	PET (mm)	Transpiration (mm)	Deep uptake (mm)	Deep uptake (%)	Rainfall (mm)	PET (mm)	Transpiration (mm)	Deep uptake (mm)	Deep uptake (%)
Quercus ilex	191	523	128	12	9.4	154	589	96	21	22
Fagus silvatica	218	557	152	35	23	171	608	210	96	46
Abies alba			137	16	12			132	33	25

At Rustrel, summer transpiration of oaks decreased by 25% in 2015 compared to 2014. This reduction can be attributed to a stronger regulation of water fluxes due to higher water stress conditions in 2015. Indeed, the simulated Ψp reached the oak's TLP in 2015, which was not the case in 2014. At the same time, oaks relied more heavily on the deep-water reservoir in 2015 (Table **1**). At Mont Ventoux, summer transpiration of firs remained relatively stable between the two years and increased a lot for beeches (+38%). These results reflect the less arid climatic climate and more favorable edaphic conditions at Mont Ventoux compared to those in Rustrel. Consequently, the level of water stress experienced by firs and beeches was insufficient to induce complete stomatal closure. In both species, Ψp did not reach the TLP, and in beeches it also remained above P12_gs. Nevertheless, both species made more intensive use of deep water in response to the more severe conditions, with deep-water uptake increasing by 174 % for beeches and by 107 % for firs. The stronger mobilisation of the deep reservoir in 2015 enabled the trees to respond to a higher evaporative demand. The interspecific differences at this site can be explained by the greater development of the deep root system of beeches compared to firs (Fig. **3**). These observations were expected and are consistent with previous studies (Nourtier et al., 2014; Zelíková et al., 2025). The simulated evapotranspiration values are consistent with those reported in the literature for similar contexts. In 2015, trees transpired 454 mm for oaks (468 mm in Limousin et al., 2024), 319

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mm for firs (260 mm in Davi & Cailleret, 2017), and 450 mm for beeches (427 mm in Zelíková et al., 2025).

3.2. Analysis of the influence of TAW_{Deep} and f_{DR} on tree survival

When TAW_{Deep} was kept constant (Fig. **4**), increasing f_{DR} from 0.2% initially increased but then decreased the survival time under drought. During the first weeks of the drought, a larger proportion of deep roots allows trees to exploit the deep reservoir more extensively and to delay the initial decline of g_s and Ψp, which started 7, 10 and 25 days after the drought started when f_{DR} = 0.2%, 3%, and 30%, respectively. However, once the water stress starts, g_s and Ψp decreased almost linearly until tree death when f_{DR} = 30%. This is because trees with a high density of deep roots rapidly depleted the deep reservoir, while the shallow reservoir is already wildly depleted. In contrast, simulations with f_{DR} = 3% showed an earlier decline of g_s and Ψp followed by a sharp drop until Ψp reached about -2.5 MPa, corresponding to 75% stomatal closure ($\Psi_{gs,75}$), to then plateaued for several weeks. In this simulation, the lower deep root development enabled a lent withdrawal of deep reservoirs, stabilising the water status. Conversely, this plateau does not occur when the deep root system is not developed (f_{DR} = 0.2%) because they are not able to fully exploit the deep reservoir. This value of f_{DR} = 3% is of the same order as those obtained by calibration in the real-case scenario (1.5%-11.9%, see section 2.1).

When f_{DR} was kept constant at 3% (Fig. **5**), increasing TAW_{Deep} prolonged tree survival under drought. Until 25 days, TAW_{Deep} did not affect the tree response because individuals predominantly used $TAW_{Shallow}$ (which is set constant across all 3 simulations). During this initial phase, g_s and Ψp decrease slowly and then suddenly drops until reaching $\Psi_{gs,75}$. The stabilization of water stress described above (Fig. **5**) only occurred when TAW_{Deep} = 45 mm or 65 mm, while water stress kept increasing when TAW_{Deep} = 10 mm because the reservoir is not big enough to supply water. The duration of this stabilisation was bigger for the highest TAW_{Deep}. When the Relative Extractable Water content (REW) is below 25%, g_s = 0 mmol.m^{-2}.s^{-1} and the rate of decrease in Ψp and increase in *PLC* becomes constant because all cases are now equivalent (at 25 days when TAW_{Deep} = 10 mm; 61 days when TAW_{Deep} = 45 mm; 80 days when TAW_{Deep} = 65 mm). At this time, trees have reached their maximum level of stomatal closure and water is lost only through the residual conductance. Additional simulations with finer increments of f_{DR} are presented in Figure S9.

The most drought-resistant configuration therefore combines existing deep roots, but in limited proportion, combined with the largest possible deep reservoir (f_{DR} = 3%; TAW_{Deep} = 65 mm; Fig. **4, 5**). However, the optimal f_{DR} varies according to the species (0.4% for holm oak, 2.6% for beech and 1.2% for fir; Fig. **6**). The impact of this strategy on drought resistance is comparable in magnitude to that of species-specific hydraulic traits, as firs or beeches under optimal conditions exhibit drought resistance similar to that of Holm oaks growing under unfavourable conditions (Fig. **6**). In such a case, a beech can

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even be more drought resistant than an oak (when f_{DR} = 2.6%). Overall, silver fir appeared to be the least drought-resistant even at the optimal root development (Fig. **6**). This finding helps explain the current decline of the species in its natural environment (Cailleret et al., 2013) and highlights the need to reconsider the use of silver fir in silvicultural plantations under future climatic conditions.

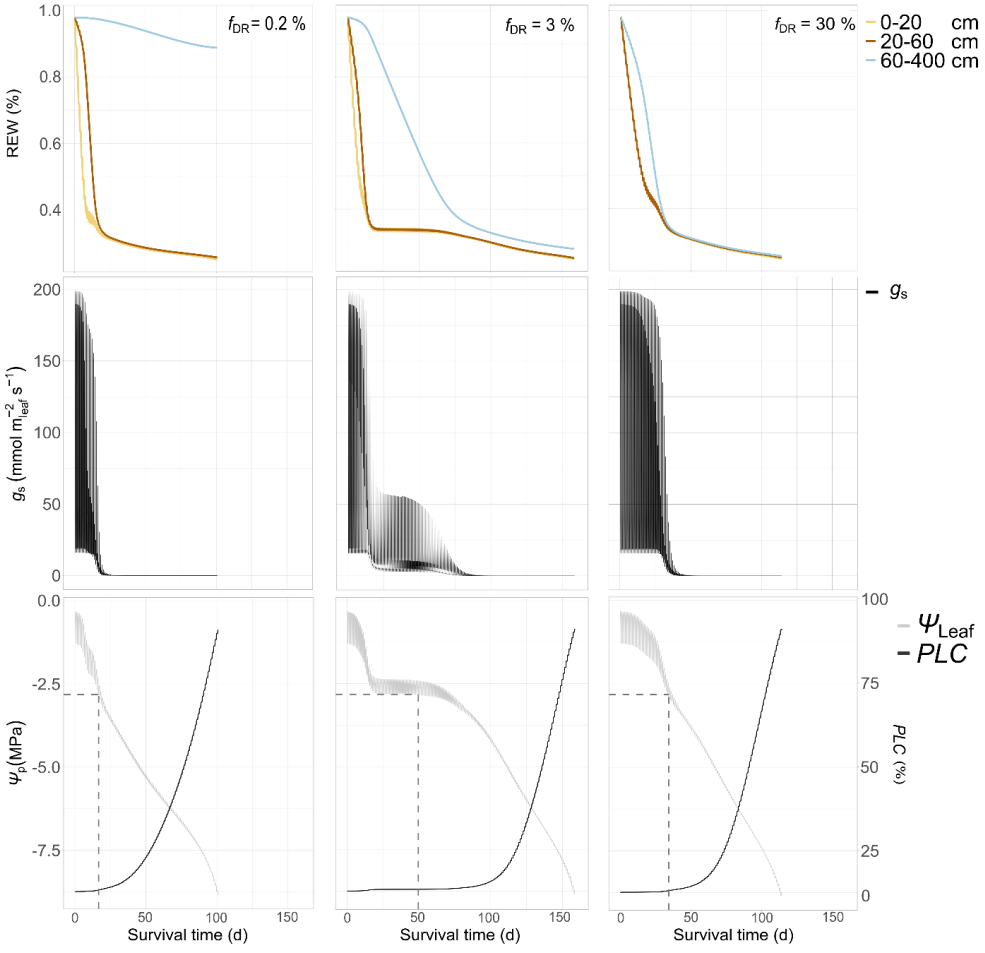

***Figure 4**: Dynamics of Relative Water Content (REW), stomatal conductance (g_s), Percentage Loss of Conductivity (PLC) and base potentials (Ψp) of a Holm oak during a theoretical continuous drought, with different proportions of the root system in the deep layer (f_{DR}) and TAW_{Deep} = 65 mm. The dashed line corresponds to the oak TLP and the time it is reached.*

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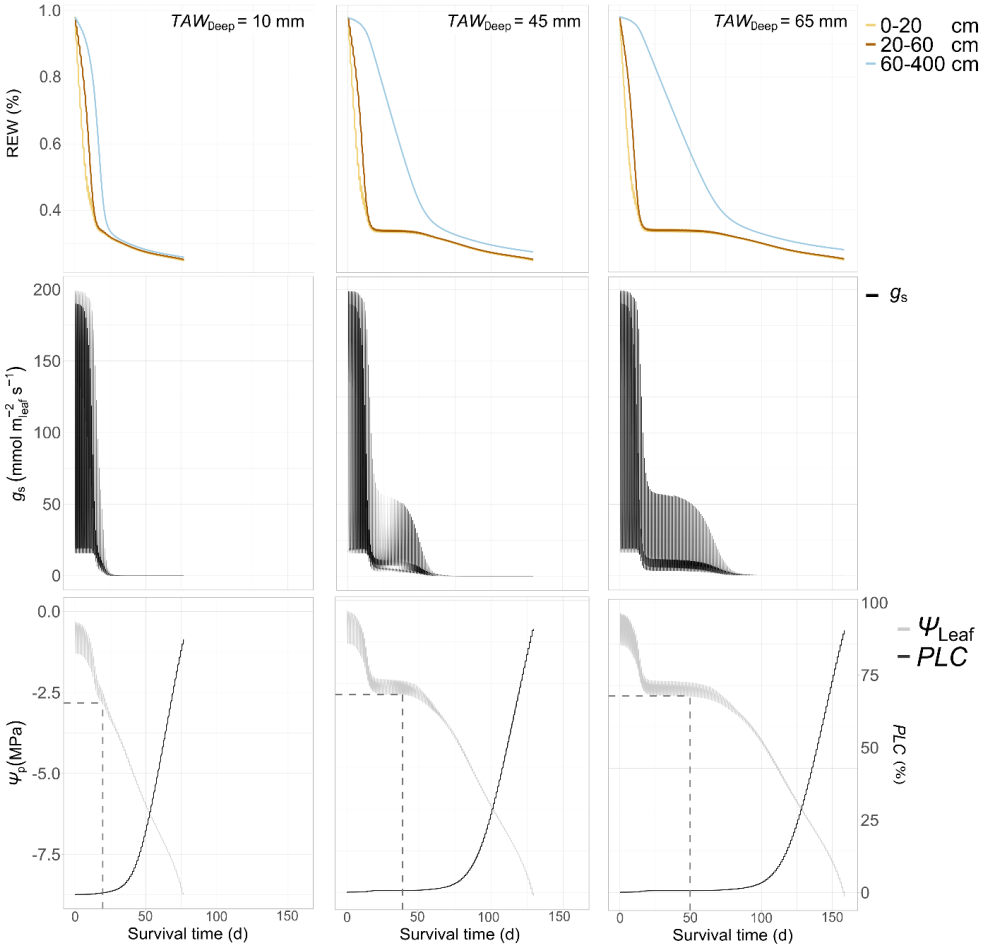

419
420 ***Figure 5**: Dynamics of Relative Water Content (REW), stomatal conductance (g_s), Percentage Loss of Conductivity (PLC) and*
421 *base potentials (Ψp) of a Holm oak during a theoretical continuous drought, with different total water available to trees in the*
422 *deep layer (TAW_{Deep}) and f_{DR}= 3%. The dashed line corresponds to the oak TLP and the time it is reached.*

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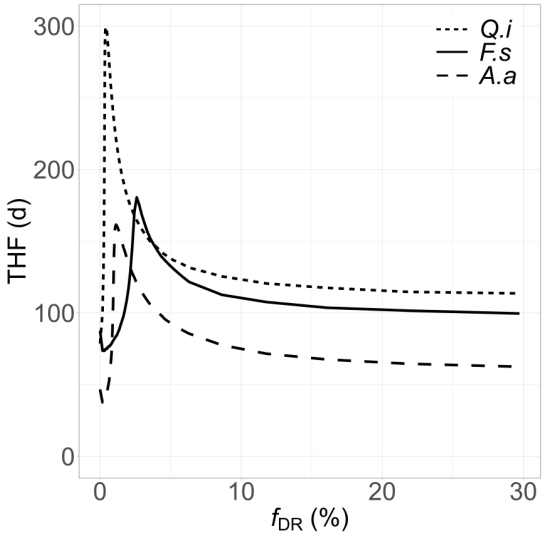

***Figure 6**: Interspecific comparison of Time to Hydraulic Failure (THF) according to the proportion of the root system in the deep layer (f_{DR}) for Holm oak (Q.i), silver fir (A.a) and beech (F.s), with TAW_{Deep}= 65 mm.*

4. Discussion

4.1. A rare-root strategy

Werner et al. (2021) showed that contrasting drought-response strategies among tree functional groups led to different patterns of water use during drought. In particular, drought-sensitive trees rapidly reduced their water use, whereas more drought-tolerant trees maintained ecosystem water fluxes for longer. In our study, we tested the hypothesis that a strongly asymmetric fine-root distribution, with only a small fraction of fine roots at depth, could explain the conservative use of deep water and thereby increase survival time under extreme drought. This represents a good compromise between a water-saving strategy and sufficient access to deep resources to meet the residual evaporative demand with partly closed stomata. We propose to name this compromise the “rare root strategy” since this effect implies a density of roots that is sufficiently high to allow accessing deep wet layers and maintaining water uptake, but sufficiently low to avoid over-exploiting the deep water resources and rapidly reaching catastrophic hydraulic failure. Our sensitivity tests indeed evidenced that trees can experience strong hydric stress either early in the drought when the proportion of deep roots is not enough to meet the evaporative demand (f_{DR} = 0.2% in Fig. **4**), or later when deep root development is so important that deep water reserves are quickly depleted after shallow reserves are (f_{DR} = 30% in Fig. **4**). The rare-root strategy emerges as an intermediate strategy between these two extremes to maximize survival under prolonged drought.

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In this configuration, a limited proportion of deep roots allows trees to access deep water while preventing rapid depletion of the deep reservoir by regulating transpiration. Several mechanisms controlling transpiration operate at different time scales to regulate water stress (e.g. stomatal closure, residual transpiration, adjustments of the leaf area). Among these mechanisms, stomatal closure is a key regulator of water stress and hydraulic failure avoidance (Brodribb et al., 2003; Martin-StPaul et al., 2017). Physiologically, the optimum proportion of deep roots is low enough to trigger early stomatal closure, but still sufficient to withdraw water from the deep reservoir. As drought progresses, leaf water potential and stomatal closure declines until a threshold. At this point, water loss through transpiration matches the maximum water flux that the deep root system can sustain, leading to a stabilisation of plant water status (Oren et al., 1999; Martin-StPaul et al., 2017). In our sensitivity tests, this optimum corresponds to f_{DR} = 0.4 to 2.6% according to the species. These findings are consistent with recent large-scale evidence further highlighting the functional importance of root profile structure (Lu et al., 2025). Vertical root distributions often show a dominant concentration near the soil surface and a secondary peak in deeper soil layers, facilitating complementary acquisition of water and nutrients (Lu et al., 2025). Such structuring enables trees to access deep water and important nutrients, without neglecting shallow development. These observations are also consistent with the concepts of root system "plasticity" proposed by Fan et al. (2017

Our study use a timely restricted set of data (2014–2015). Mediterranean climates are characterized by strong climatic interannual variability and a two-year window may not capture the full range of conditions. Nevertheless, 2014 and 2015 differed markedly in their climatic conditions and the calibrated f_{DR} values fall within the range reported by studies using different methods (Jackson et al., 1996; Cabon et al., 2018; Tumber-Davila et al., 2022). All the three studied species also developed a proportion of their root system in the deep soil of the same order as the optimal f_{DR} in the sensibility test (1.5% to 11.9%; Fig. **2**). Our results also indicate that f_{DR} is species-dependent, varying from 2.6% for firs to 11.9% for beeches at the same site (Fig. **2**). Tumber-Davila et al. (2022) also reported that conifers often develop shallower root systems than broadleaf species. Then, although direct empirical evidence of the rare-root strategy at the ecosystem scale remains limited, our work and several observational and modelling studies provide indirect support.

Higher f_{DR} of beeches and fires (Fig. **2**) can be explained by the more favorable edaphic conditions at Mont Ventoux compared to those in Rustrel. However, both calibrated f_{DR} (Fig. **2**) and theoretical optimal f_{DR} (Fig. **6**) exhibited the same ranking in species, from the most developed fine root system in depth (beech) to the less developed (oak). Accordingly, the optimal proportion of deep fine roots predicted by the rare-root strategy depends on both species' hydraulics traits (as P50 or TLP, explaining the difference in Fig. **6**) and environmental conditions. For instance, when the deep water reservoir is very small, a very low f_{DR} may be optimal as it allows the tree to conserve deep water resources and

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delay their total depletion. On the contrary, Carrière et al. (2020c) demonstrated, using isotopic tracing combined with geophysical methods, that individuals growing on shallow soils tend to develop more extensive deep root systems penetrating karstified and fractured bedrock. Laughlin et al. (2023) showed through modelling that the observed variability on mortality rates can be partly explained by differences in root system development. Further field measurements or controlled experiments would help to test the rare-root strategy explicitly. Extending the calibration to additional years or validating the approach against independent datasets (e.g. sap flow, stable water isotopes, or geophysical root detection as in Carrière et al., 2020c) would also help further confirm the temporal robustness of the estimated deep root proportions.

4.2. Ecological implication of the rare-root strategy

The rare-root strategy has strong ecological implications. In our simulations, it allows a fir tree with an optimal proportion of deep roots to be as drought-resistant as a Holm oak possessing either too many or too few deep roots. Indeed, in the sensitivity test, the f_{DR} has an impact on survival comparable to that of other key drought resistance traits such as stomatal regulation (Martin-StPaul et al., 2017), leaf deciduousness (Ruffault et al., 2023), xylem vulnerability to embolism (Cochard et al., 2021) or residual conductance (Duursma et al., 2018; Burlett et al., 2025). However, under the rare-root strategy, maximum survival time is achieved through a drastic reduction of stomatal conductance and transpiration. This comes at the cost of sustained carbon assimilation through photosynthesis (Oren et al., 1999; Ruffault et al., 2022). In this case, increasing survival probability under prolonged drought comes at the cost of under-exploiting available water resources at the beginning of the drought, in contrast to individuals that extensively exploit deep water. There is therefore a balance between drought resistance and continuing photosynthesis.

Chitra-Tarak et al. (2018) highlighted these two contrasting strategies among species. Species extracting limited amounts of deep water (i.e., following a rare-root strategy) enter dormancy rapidly and may exhibit higher mortality during short, intense droughts. Conversely, during prolonged or repeated droughts, individuals relying heavily on deep water become disadvantaged: deep reservoirs are rapidly depleted, and recharge may take several years. Importantly, our simulations considered individual trees and did not explicitly account for stand-level interactions. In a competitive and water-limited context, neighboring trees may simultaneously access the same deep water reservoir. In such a case, the benefits of the rare-root strategy observed at the individual level may differ depending on the rooting strategies of surrounding trees. For instance, a tree adopting a rare-root strategy may conserve deep water through reduced uptake, but this conserved resource could subsequently be exploited by neighboring individuals with more extensive deep root systems. These strategies ultimately depend on the size of the deep reservoir and its recharge capacity. There is therefore no universally optimal rooting strategy, which notably depends on the neighborhood composition, the local edaphic properties, and the drought

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frequency and intensity. If climate change leads to progressive drying of deep water reserves (IPCC, WGII., 2023), individuals currently relying most heavily on deep water reserves may become the most vulnerable. However, under prolonged drought conditions, even trees with only 3% of deep roots may completely deplete deep water reservoirs if recharge becomes insufficient.

This central role of root development enhances the conclusions of Dukes et al. (2026). Climate and vegetation models still represent plant water stress in an overly simplified manner. In particular, the belowground compartment remains poorly constrained and often underdeveloped. This limitation likely contributes to substantial uncertainties in projections of drought impacts. Our results further emphasize that a mechanistic understanding of root functioning and its variability are essential. Future modelling approaches should explicitly account for multiple interacting trees sharing finite and spatially heterogeneous deep water reservoirs to determine whether the rare-root strategy remains advantageous, or whether its effects emerge differently, at the community level. It could be further improved by accounting for interspecific variability in root morphological traits as well as the role of mycorrhizal associations (Pietig et al., 2026).

4.3. Impact of deep water uptake on subsurface water reserves

It is well known that trees mobilize deep water reservoirs during water-limited periods (Breda et al., 2006; Carrière et al., 2020a; Kühnhammer et al., 2023) in order to better withstand intense water stress. In our study, deep water uptake by firs and beeches was higher in 2015 than in 2014, up to account for 97% of daily transpiration during the summer period. The importance of deep reservoirs in Mediterranean climates was previously highlighted by McCormick et al. (2021) in the United States, but the reported values were proportions of deep water use. In the present study, we go further by quantifying both transpired volumes and the size of deep reservoirs (Table **2**). Our results show that, although trees rely heavily on deep water at the daily time step during summer, the annual cumulative volumes extracted from depth remain limited (26 mm to 107 mm) compared with annual transpiration volumes. This contrast between daily and annual time scales is consistent with values reported in the literature (Table **2**).

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***Table 2**. Summary of the proportions of deep and shallow water used by trees reported in the literature. When studies covered multiple climate types, only data from Mediterranean climates are shown.*

	Maximum contribution of deep water to daily transpiration (%)	Contribution of deep water to annual transpiration (%)
Present study	90 – 97[1]	11 – 36[1]
Beyer et al. 2018	/	11
Miguez-Macho and Fan 2021	68 – 89[2]	30
Kühnhammer et al. 2023	21 – 90[1]	/

[1] Interspecific differences

[2] Differences among methods

Our study shows that deep water uptake represents at most 5% and 15% of annual precipitation at Rustrel and Mont Ventoux, respectively. Although annual water uptake occurs mainly from shallow layers (Table **2**), root water uptake from deep reservoirs is substantial (26–107 $mm.y^{-1}$; Table **2**). This depletion of the vadose zone necessarily affects groundwater recharge. Even if deep reservoir mobilization mainly occurs outside recharge periods, the water deficit created by trees in shallow layers delays the deep recharge during wetter periods. However, some authors suggest that an optimal forest canopy and trunk density can maximize infiltration and groundwater recharge by slowing runoff (Ilstedt et al. 2016; Vicente et al. 2018). In cases where root systems reach the groundwater fluctuation zone, the development of phreatophytic trees could lead to a generalized lowering of piezometric levels in particular hydrogeological and climatic settings (Dresel et al., 2018, Li et al., 2024). Characterizing the impact of forests on groundwater recharge therefore remains challenging and strongly dependent on the eco-hydro-(geo)logical context.

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5. Conclusion

The methodology developed in this study enabled us to estimate the extent of deep root systems and assess their role in tree drought resistance under prolonged droughts. Our results show that trees predominantly rely on shallow water sources under non-limiting conditions. However, during summer drought, a substantial proportion of transpired water originates from deep reservoirs. Access to deep water is a key determinant of tree functioning in water-limited ecosystems. However, an excessive proportion of deep roots may lead to rapid depletion of deep reservoirs and compromise long-term survival. We identified the existence of an optimal proportion of deep roots (on the order of a few percent of the root system located below a depth 70 cm), at which trees maintain limited but sufficient access to deep water to sustain reduced transpiration under stomatal closure.

The approach developed in this study will be tested in the near future across other forest sites, located under various climate and geological contexts. Overall, our results demonstrate that deep water uptake by vegetation is a critical process, comparable in importance to other key plant traits. This highlights the need to integrate plant hydraulic functioning, deep rooting strategies and bedrock water storage to improve predictions of forest responses to drought and for refining estimates of groundwater recharge.

Data availability

Water potential and isotopic data are available on Carrière et al. 2020 (DOI: 10.17632/mvfvpmnxgs.3). The model is available on the Forge INRAe gitLab repository under the commit tag "https://forge.inrae.fr/urfm/sureau/-/tree/v2.2"

Author contributions

Conceptualisation: NM, SC. Investigation: LM, NM, SC. Methodology: LM, GR, NM, SC. Software: LM, GR, NM, AD**.** Supervision: NM, SC, DJ, MP, IO. Visualisation: LM, NM, SC. Writing (original draft preparation): LM, NM, SC. Writing (review and editing): IM, AD, QC, DJ, ND, MP, IO, HC.

Competing interests

Authors declares no competing interests.

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