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Tree water uptake patterns across the globe

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Summary

Plant water uptake from the soil is a crucial element of the global hydrological cycle and essential for vegetation drought resilience. Yet, knowledge of how the distribution of water uptake depth (WUD) varies across species, climates, and seasons is scarce relative to our knowledge of aboveground plant functions. With a global literature review, we found that average WUD varied more among biomes than plant functional types (i.e. deciduous/evergreen broadleaves and conifers), illustrating the importance of the hydroclimate, especially precipitation seasonality, on WUD. By combining records of rooting depth with WUD, we observed a

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consistently deeper maximum rooting depth than WUD with the largest differences in arid regions – indicating that deep taproots act as lifelines while not contributing to the majority of water uptake. The most ubiquitous observation across the literature was that woody plants switch water sources to soil layers with the highest water availability within short timescales. Hence, seasonal shifts to deep soil layers occur across the globe when shallow soils are drying out, allowing continued transpiration and hydraulic safety. While there are still significant gaps in our understanding of WUD, the consistency across global ecosystems allows integration of existing knowledge into the next generation of vegetation process models.

I. Introduction

Plant transpiration (E) represents on average 60% of terrestrial evapotranspiration (Wei *et al.*, 2017) and, therefore, significantly contributes to the global water cycle (Sellers *et al.*, 1997). Hence, understanding how plants acquire water has implications for predicting local and global hydrology, as well as mitigating climate change impacts on freshwater reserves. The amount of water plants transpire is limited by root water uptake (Kramer & Boyer, 1995). However, we have a better understanding of the aboveground processes involved in plant water use than those belowground due to the difficulty of accessing roots. This important knowledge gap has led to large predictive uncertainty in land surface and earth system models (Sulis *et al.*, 2019).

Tree roots have received increasing attention in recent years due to their importance for plant drought tolerance, avoidance, and mortality (Choat *et al.*, 2018; Nardini *et al.*, 2021). Multiple reviews and meta-studies have investigated root distribution and depth changes under drought (e.g. Weemstra *et al.*, 2016; Laliberté, 2017; Tumber-Dávila *et al.*, 2022). However, root distribution alone cannot be directly translated into the depth of water sources (Yang *et al.*, 2015; Bello *et al.*, 2019) as plants can rapidly shift the uptake depth as environmental conditions change. Plant water uptake is determined by the combined distribution of root surface area and soil water availability. Therefore, water uptake depth (WUD) is always a distribution of water fluxes over depth. The average WUD can be conceived as a flux-weighted mean depth. Since empirical studies of WUD effectively measure a flux-weighted mean (Box 1), we adopt this definition for this review. We still have little knowledge of how WUD varies among biomes, functional groups, and seasons, and of the link between WUD dynamics and aboveground drought responses. To better understand tree responses to drought, including E , growth and mortality risk, the dynamics of WUD have to be considered (Choat *et al.*, 2018; Carminati & Javaux, 2020).

Here, we provide the first global overview of woody plant WUD. Our review includes 120 studies worldwide that assessed WUD of trees and shrubs with isotopic tracers, soil water balance models, root and stem sap flow measurements, or a combination thereof (Box 1; Fig. 1; Supporting Information Table S1; Appendix A1). We focused on six questions: (1) What is our current understanding of the mechanisms of root water uptake? (2) How does WUD vary among biomes and plant functional groups, and (3) in relation to rooting depth across species? (4) What is the effect of seasonal soil water availability on WUD? (5) How does WUD affect E , productivity, and mortality? (6) What is the state and potential in simulating global WUD patterns in vegetation process models?

II. Mechanisms of root water uptake

Root water uptake is governed by how water and roots are distributed across the soil profile and, therefore, is spatially and temporally variable (Javaux *et al.*, 2008). It occurs mainly via the absorbent fine roots, which are thin, nonwoody tissues that are the most permeable portion of the root system and have the greatest capacity to absorb water (Kramer & Boyer, 1995; McCully, 1999; Comas *et al.*, 2013). By contrast, higher-order roots, coarse roots, and transport fine roots, serve other functions, such as anchorage, water transport, and storage (McCormack *et al.*, 2015). Additionally, root hairs and mycorrhizas associated with fine roots can increase absorptive surface area and, hence, enhance water uptake (Fig. 2; Weemstra *et al.*, 2016; Carminati *et al.*, 2017; Cai & Ahmed, 2022).

Mechanistically, water flow from the soil into the root is driven by the gradient in water potential between the soil (Ψ_{soil}) and the xylem of fine roots (Ψ_{root}) (MPa), and depends on the hydraulic conductance of the root-rhizosphere continuum (K_{s-r}) (MPa); Landsberg & Fowkes, 1978). Water uptake at a given depth and time $q(z, t)$ ($\text{m}^3 \text{s}^{-1}$) can be expressed as:

$$q(z, t) = K_{s-r}(z, t, \Psi_{\text{soil}}) \times (\Psi_{\text{soil}}(z, t) - \Psi_{\text{root}}(z, t)) \quad \text{Eqn 1}$$

Based on this equation, we can see that root water uptake is directly dependent on K_{s-r} , which is regulated by the hydraulic conductance of the roots (K_r) and soil (K_s), and is primarily limited by the lower of the two (Fig. 2; Carminati & Javaux, 2020). K_r and K_s both decrease when the respective water potential becomes more negative, due to cavitation in the xylem or displacement of water-filled soil pores with air, respectively (Sperry *et al.*, 1998). In wet soils, K_s is much larger than K_r and, therefore, not limiting to K_{s-r} (e.g. in the deep soil layer in Fig. 2). As the soil dries, K_s drops by several orders of magnitude and becomes a limiting element for K_{s-r} (e.g. in the shallow soil layer in Fig. 2), and hence for plant water uptake. The water potential at which the soil becomes limiting for K_{s-r} depends on soil texture, with less negative water potential in coarse-textured soils (Cai *et al.*, 2022). Water absorption by roots also depends on the root radial K_r , which plants can modify by suberization and Casparian bands (Steddele & Peterson, 1998), changing aquaporin activity (Maurel *et al.*, 2008), or altering the conductivity of the rhizosphere by growing new root hairs (Carminati *et al.*, 2017) and exuding mucilage (Carminati *et al.*, 2010). Roots with a high radial conductance (e.g. roots with low suberisation) function as porous pipes with low axial conductance, and thus a high water potential is needed along the

Box 1 Methods for estimating plant water sources.

The most effective and nondestructive measurement of water uptake depth (WUD) is provided via the use of natural abundance and tracer applications of the stable isotopes of oxygen ($\delta^{18}\text{O}$) and hydrogen ($\delta^2\text{H}$) in plant and soil water (Ehleringer & Dawson, 1992; Dawson & Ehleringer, 1998). Natural abundance applications make use of the evaporative enrichment of $\delta^{18}\text{O}$ and $\delta^2\text{H}$ near the soil surface, which leads to distinct isotopic compositions of water across the soil depth profile (von Freyberg *et al.*, 2020). Comparison of xylem water $\delta^{18}\text{O}$ and $\delta^2\text{H}$ with that of distinct water sources, such as rainwater, soil water from different depths, and groundwater is used to estimate changes in their contribution to E and thereby their seasonal dynamics (White *et al.*, 1985; Ehleringer & Dawson, 1992). Exact calculations of the relative contribution of all the soil layers at a specific moment in time rely on mixing models (e.g. IsoSource: Phillips & Gregg, 2003 and MixSIAR: Parnell *et al.*, 2010). These models were developed more recently, resulting in fewer studies providing absolute calculations of WUD compared to the large body of literature describing seasonal dynamics and species differences in the use of distinct water sources (Supporting Information Table S1).

However, the natural abundance technique cannot identify WUD when the isotopic profile of soil water is homogenous due to low atmospheric evaporative demand, high rainfall, or snowmelt. In these cases, labelling studies with isotope tracers of hydrogen, oxygen, and lithium allow measurement of WUD, as their signatures have a distinct vertical gradient in the soil (reviewed in von Freyberg *et al.*, 2020). However, both the natural abundance and tracer approaches are challenging due to spatial and temporal sampling limitations. Both approaches require labour-intensive sampling across soil depths that inherently limits the number of samples that can be collected, which is further exacerbated by the effort and cost of processing and measuring the samples in the laboratory. Additionally, both approaches are difficult or impossible to employ in soils with a high rock content that precludes digging holes. The limited temporal resolution can be addressed via continuous *in situ* monitoring of tree and soil water isotopic composition using laser spectroscopy (Volkman *et al.*, 2016; Seeger & Weiler, 2021; Gessler *et al.*, 2022). However, this approach requires regular monitoring and intensive installations in the field and, thus, is still limited in spatial replication.

In addition to the stable isotope approaches, water balance models can estimate WUD based on measurements of soil water potential from different depths, often in combination with tree sap flux data (Table S1, for example Markewitz *et al.*, 2010; Pinto *et al.*, 2014). While this approach has been successfully used to assess ecosystem-level water source dynamics, it does not allow identification of individual tree WUD, as water use cannot be attributed to specific individuals. The latter is possible with sap flow measurements on roots at different soil depths to quantify their contribution to E (e.g. Nadezhkina *et al.*, 2008; Bleby *et al.*, 2010), or with combined measurements of stem sap flow, predawn foliar water potentials, and vertical profiles of soil water potentials (Binks *et al.*, 2022).

root to drive axial water flow (Zwieniecki *et al.*, 2003; Comas *et al.*, 2013). Conversely, roots with high axial conductance (i.e. high suberization), have a low radial conductance, highlighting a trade-off in the effective utilisation of root length for water absorption and the root axial water transport. This trade-off can constrain water uptake from deep soils by long roots, but this trade-off in water uptake capacity and root length has rarely been assessed (but see, for example Zwieniecki *et al.*, 2003; Clément *et al.*, 2022 for corn, wheatgrass and alfalfa).

Root water uptake will further depend on Ψ_{root} that declines with greater E due to the higher water flux through the vascular system, thus creating a greater water potential gradient from the soil to the root and higher water uptake. Typically, Ψ_{root} is more negative than Ψ_{soil} when E occurs, which provides the driving force for water uptake. However, when E is minimal, Ψ_{root} can be less negative than Ψ_{soil} , driving water flux from the root to the soil (i.e. hydraulic redistribution; Fig. 2; Burgess *et al.*, 1998; Jackson *et al.*, 2000). In ecosystems with woody plants with a dimorphic root system, hydraulic redistribution seems to occur frequently, resulting in soil rewetting during dry periods (Bleby *et al.*, 2010; Neumann & Cardon, 2012). During periods when the topsoil dries out, access to soil nutrients can be limited, as soil nutrients are usually concentrated in the topsoil, and soil moisture is the main means for nutrient uptake (Ryel *et al.*, 2008). Therefore, hydraulic redistribution of humidity to the topsoil can increase nutrient uptake, water availability for neighbouring shallow-rooted plants, and can mitigate drought effects on mycorrhizal fungi (Querejeta *et al.*, 2003; Ryel *et al.*, 2008).

Ψ_{root} also varies significantly along the root system (Zarebanadkouki *et al.*, 2013), with the least negative values near the root tips. Under drought stress, a highly negative Ψ_{root} can reduce K_{s-r} via embolism (Fig. 2) and mechanical failure of the cortex that causes lacunae formation and root shrinkage (Cuneo *et al.*, 2016). Fine roots are more susceptible to cavitation than coarse roots (Sperry & Ikeda, 1997); therefore, root embolism during droughts is usually greatest at the tip of the rooting system (Cuneo *et al.*, 2016). Root embolism may be partly reversible following a rain event, but can be irreversible after severe droughts (Domec *et al.*, 2004), and thus lead to root mortality (Cuneo *et al.*, 2016). Considering Ψ_{root} to be only a function of depth and time implicitly assumes that all roots at a given depth have the same water potential, which is more an exception rather than the general case (Pierret *et al.*, 2007). Treating this complexity requires solving water flow in the 3D root architecture (Javaux *et al.*, 2008).

Finally, Ψ_{soil} is composed of the matric potential, which is the negative work to extract a unit of volume of water from the porous soil matrix, the gravitational potential, that is proportional to soil depth, and the osmotic potential (Hillel, 2003). The matric potential has a prominent effect on root water uptake during soil drying. While the hydrostatic pressure necessary to lift water by 1 m is *c.* -0.01 MPa, the matric potential can drop below -1 MPa as the soil dries, thus having a major impact on the pressure necessary to extract water from the soil (Eqn 1). As the soil dries, the matric potential decreases nonlinearly, which is described by a soil texture specific water retention curve (Karup *et al.*, 2017). Typical values of matric potential range from *c.* -0.01 MPa at field capacity to values below -1.5 MPa at permanent wilting point (values are approximations and soil texture specific; de Melo *et al.*, 2023). However, a permanent wilting point of -1.5 MPa has been defined for crops, while natural vegetation in arid regions can tolerate more negative soil matric potentials.

Although the theory above and Eqn 1 are well established, their use is challenged by the lack of information on K_{s-r} and the difficulty in measuring Ψ_{root} . As a first approximation, K_{s-r} can be assumed to scale with the fraction of roots absorbing water, thus

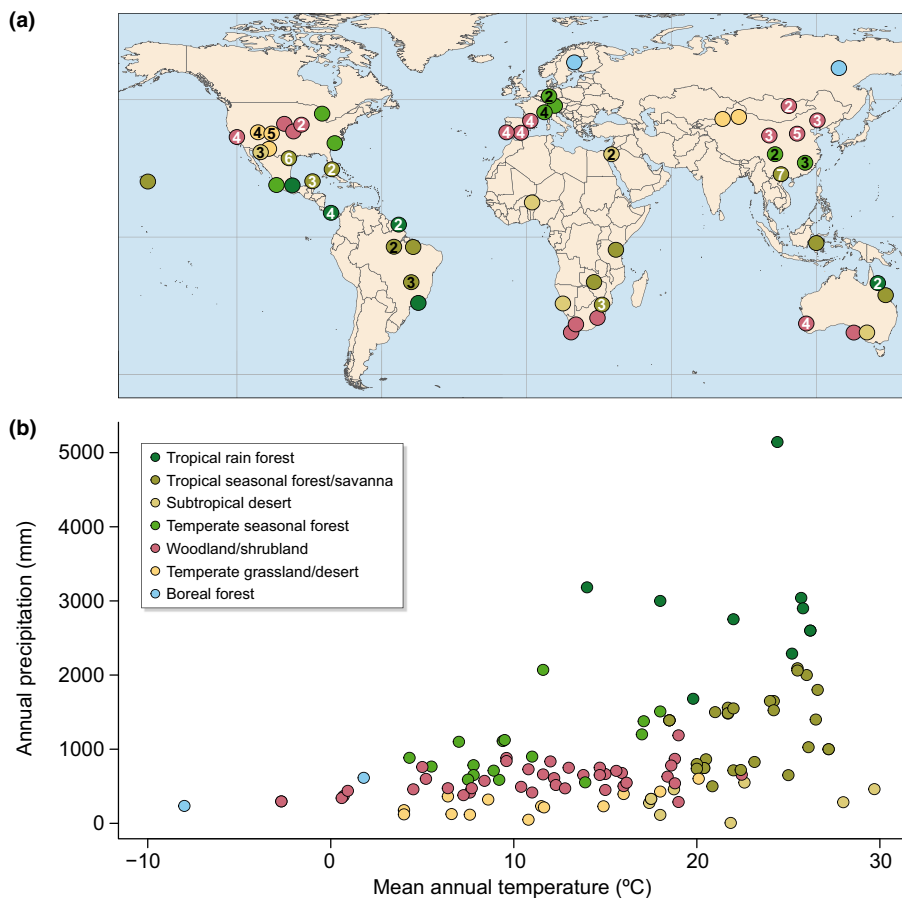


Fig. 1 This review includes 120 studies worldwide that assessed water uptake depth (WUD) of trees and shrubs with isotopic tracers, soil water balance models, root and stem sap flow measurements, or a combination there of (Box 1). (a) Global distribution of the studies on WUD included in this work (Supporting Information Table S1; Appendix A1). Numbers indicate multiple studies in locations that could not be individually represented on the map. (b) Mean annual temperature and precipitation of the 120 studies. Colours indicate the biome type.

scaling with the root length density. The root surface area, which decreases exponentially with soil depth (Schenk, 2008; Fig. 2), is thus an important factor controlling K_{s-r} and WUD. However, simplifying K_{s-r} with root length density without considering the distribution of water potential along the root system oversimplifies the important hydraulic aspects discussed above, with important consequences for modelling of WUD (see Section VIII).

III. Global variation of water uptake depth with biomes and plant functional groups

WUD of woody plants has been studied in a wide variety of ecosystems from tropical rainforests with high annual precipitation to arid deserts with very little rainfall (Fig. 1). Most studies of WUD focus on seasonally water-limited systems, such as subtropical forests with a pronounced monsoonal climate (i.e. dry and wet seasons, for example Yang *et al.*, 2015; Antunes *et al.*, 2019), semiarid, Mediterranean, and savanna-type woodlands with extended droughts (e.g. Kulmatiski & Beard, 2013; Case *et al.*, 2020) or trees growing on limestone karst with a very low water retention capacity (e.g. Swaffer *et al.*, 2014; Wenping *et al.*, 2021). By contrast, temperate forests are somewhat underrepresented (but see Bello *et al.*, 2019; Brinkmann *et al.*, 2019 for recent exceptions) and boreal forests comprise only two studies, one on larch and pine WUD in permafrost soils (Sugimoto *et al.*, 2002), and a drought experiment on boreal Scots

pine (Plamboeck *et al.*, 1999). A better understanding of WUD dynamics in boreal ecosystems is, therefore, critically needed, because large-scale vegetation changes in boreal forests are driven by their ability to acquire water from different soil depths (Sugimoto *et al.*, 2002).

We searched the literature for WUD records of trees and shrubs that were quantified with isotopic tracers, soil water balance models, or sap flow measurements (Box 1). From the 120 studies on water uptake depth that we found, 49 studies (147 records of 125 species at 46 sites) calculated WUD numerically either with Bayesian mixing models or direct inference (Tables S1, S2; Appendix A1). WUD was most frequently reported as relative contributions of the soil depths from which water was extracted and analysed at a given date (exceptions: see Notes S1). To summarise WUD across studies, we first harmonised the vertical distributions by linearly interpolating relative contributions of WUD to a 1 cm interval. We then calculated for each species at each site the average WUD as the weighted mean of the soil depths during either the dry or the wet season, as reported by the studies. As weights, we used the relative contribution of each soil depth. The result corresponds to the average depth of water uptake (average WUD). From the average WUD of each species at each site, we calculated means for each biome and plant functional type.

We found that across seasons, temperate forests and humid tropical forests show the shallowest WUD (mean of 42 and 46 cm, respectively; Fig. 3b). Woodland and shrublands (comprising

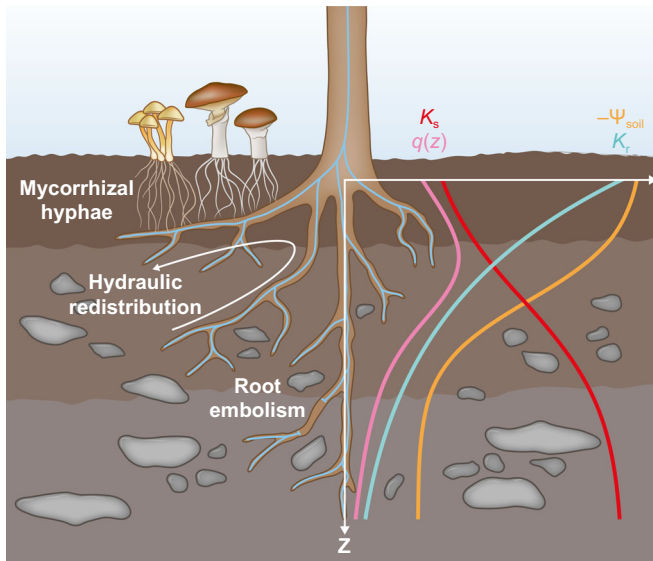


Fig. 2 Illustration of the key mechanisms of root water uptake, including association with mycorrhizal fungi, hydraulic redistribution, and root embolism. On the right side, root water uptake as a function of depth ($q(z)$) is shown for a soil profile with a dry upper layer (leading to more negative soil water potential (Ψ_{soil}) and low soil hydraulic conductivity (K_s)) and a deeper soil layer with higher water content (leading to less negative Ψ_{soil} and higher K_s). At the whole-plant scale, root conductivity (K_r) is correlated with the root surface area, which decreases exponentially with depth. As a result, $q(z)$ typically has its maximum at superficial to intermediate soil depth, where there is sufficient soil water and root surface. All variables increase from left to right.

many Mediterranean sites) exhibit a wide range of WUD but are generally deeper than temperate and humid tropical forests (mean of 55 cm). Trees from seasonal tropical forests and savannas show similar WUD as temperate seasonal forests (55 cm), whereas subtropical deserts and arid grasslands show the deepest water uptake (mean of 144 and 166 cm, respectively). The deepest WUD was found in the hyper-arid Gurbantunggut desert (Xinjiang, China), where two *Haloxylon* species take up to 96% of their water

from groundwater sources at *c.* 4 m during the dry season (Dai *et al.*, 2015), and in the hyper-arid subtropical Namib desert, where Schachtschneider & February (2010) found up to 82% of tree water uptake from groundwater table at 8 m depth during the dry season. Hence, global WUD variation seems to be driven by differences in regional climate.

Relatively few studies have been relating WUD to plant functional type (but see, for example Hasselquist *et al.*, 2010; Nie *et al.*, 2011; Knighton *et al.*, 2021). In our literature analysis, all major plant functional groups and growth forms of woody plants were represented, but broadleaved species were better represented with 111 species (58 deciduous or semi-deciduous, 53 evergreen) than conifers with 14 species, of which one was deciduous (*Larix sibirica*, Li *et al.*, 2007). We observed a wide range of WUD within groups but there were some notable trends across plant functional types. Shrubs of both evergreen and deciduous broadleaves had slightly shallower WUD (mean of 40 and 36 cm, respectively) compared to trees of evergreen and deciduous broadleaves (62 and 57 cm, respectively). Furthermore, conifers had on average a less deep WUD (47 cm) compared to broadleaved trees. The trees and shrubs with the deepest WUD are deciduous and evergreen broadleaved species from hyper-arid deserts (Schachtschneider & February, 2010; Dai *et al.*, 2015) and encroaching conifers from semiarid grasslands (Eggemeyer *et al.*, 2009). However, WUD of conifers might be underestimated, because most conifers were represented in Mediterranean woodlands, for which many studies reported shallow soils (e.g. Barbeta *et al.*, 2015; Voltas *et al.*, 2015). Sampling these rocky soils can be very challenging and deep soil contribution to WUD could, therefore, be underestimated (Carrière *et al.*, 2020; Nardini *et al.*, 2021). At the other side of the WUD spectrum are deciduous broadleaved trees from temperate forests that show consistently shallow water uptake depth (e.g. Bello *et al.*, 2019; Brinkmann *et al.*, 2019; Gessler *et al.*, 2022). Overall, our study confirms that WUD varies across plant functional types, but the variation within functional types and between biomes are much larger, emphasising the role of the local environment for WUD (Figs 3, S1).

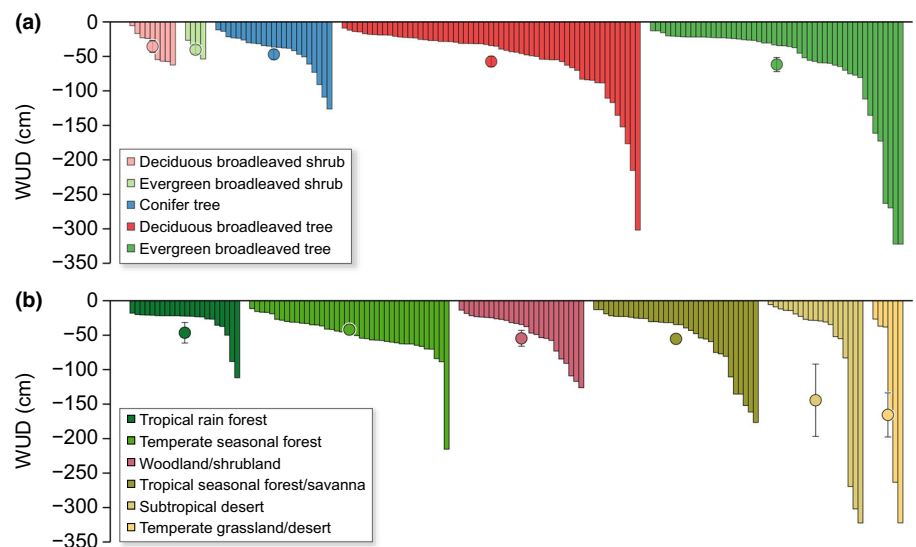


Fig. 3 Averaged water uptake depth (WUD) of each species at all the sites retrieved from all the 49 studies that numerically calculated WUD (Table S2). (a) ordered by plant functional types and (b) ordered by biome. Colours indicate the plant functional type and the biome type. Circles show averages (mean \pm SE) per plant functional type and biome.

IV. Relationship between rooting depth and water uptake depth

Rooting depth is the primary metric used to estimate the vertical space occupancy of a root system, and has, therefore, been used to infer the depth of soil and weathered bedrock from which a plant can uptake water (Schenk & Jackson, 2005). In many ecosystems, tree rooting depth is closely related to the depth of the water table (Fan *et al.*, 2017; but see: Pierret & Lacombe, 2018). Deeper roots generally allow for greater plasticity in the depths through which water can be acquired (Markewitz *et al.*, 2010; Choat *et al.*, 2018; Nardini *et al.*, 2021). WUD is a function of the vertical gradient of Ψ_{root} , Ψ_{soil} , and root surface area (Fig. 2). The vertical distribution of the root surface area, while relatively sparsely documented (Schenk, 2008), can be highly plastic, driven by the availability of soil resources (Zanetti *et al.*, 2015; Weemstra *et al.*, 2017). As root systems deepen, their capacity to take up and transport significant amounts of water at the whole-tree scale is limited by a decline in root biomass density (e.g. Fig. 2; Schenk, 2008; Nippert & Holdo, 2015), increased root suberization, and higher fraction of woody roots (Kramer & Boyer, 1995). A larger root xylem diameter and higher hydraulic conductivity of deeper roots may partly compensate this effect (Pate *et al.*, 1995; McElrone *et al.*, 2004). However, the presence of deep roots does not always equate to deeper water uptake depths, such as when surface water is abundant (Ehleringer & Dawson, 1992; Yang *et al.*, 2015; Bello *et al.*, 2019), but may be reflective of the longer term hydroclimate and water deficit (Stocker *et al.*, 2023).

Maximum rooting depth varies widely among woody plants, from a few centimetres to more than 68 m, (Canadell *et al.*, 1996). Observations of maximum rooting depths can be subject to large observer-expectancy bias, as root excavations are often being limited to an arbitrary depth, and as a result deepest roots undersampled (Fan *et al.*, 2017). Despite these limitations, large-scale patterns can be observed, such as large variation within species (Canadell *et al.*, 1996; Jackson *et al.*, 1996; Tumber-Dávila *et al.*, 2022), and with topography, climate, and edaphic conditions (Fan *et al.*, 2017). Multiple factors limit the maximum rooting depth of plants, including the penetrability of the soil (Case *et al.*, 2020), inability of roots to survive hypoxic conditions (Fan *et al.*, 2017), and the carbon cost to maintain and build larger root systems (Da Silva *et al.*, 2011). The deepest roots are found in large woody plants in seasonally dry climates with deep penetrable soils (Canadell *et al.*, 1996).

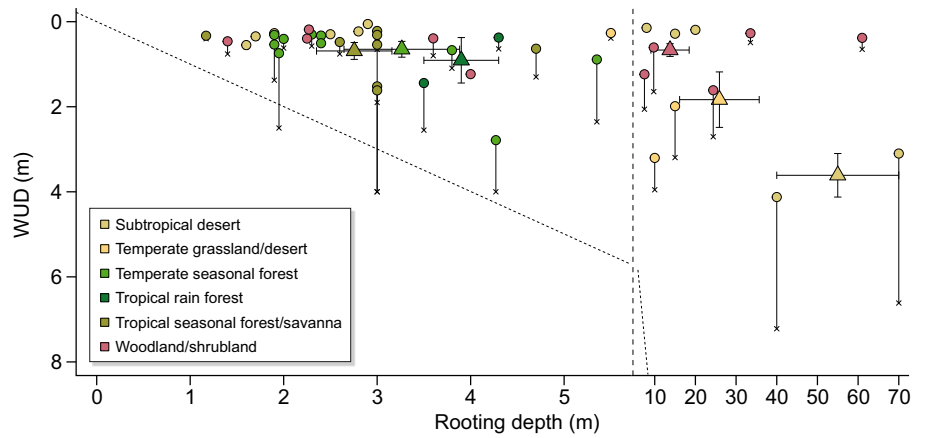
To understand the functional relationship between rooting depth and WUD across species and biomes, we extracted maximum rooting depth observations from the Root Systems of Individual Plants (RSIP; Tumber-Dávila *et al.*, 2022) database (157 observations, Appendix A2) along with WUD data for the same species (60 observations) from publications. In total, 44 species were present in both datasets and could be directly compared (Table S3; Notes S1). As the maximum WUD is determined by the depth of soil water analyses (Box 1), it might be underestimated by sampling limitations, similarly as maximum rooting depths. To avoid this bias, we calculated both the average WUD (see Section III) and with the same approach the 90%

quantile of WUD, that is the depth at which 90% of the water is taken up. As could be expected, we found higher WUD in woody plants with deeper roots, but the maximum rooting depth was consistently deeper than the average WUD and, with very few exceptions, the 90% quantile of WUD (Fig. 4). The difference between the maximum rooting depth and WUD was most pronounced in arid regions (Figs 4, S2). For instance, woody species in semiarid woodlands can have maximum rooting depths up to 13 m (Tierney & Foxx, 1987; Fan *et al.*, 2017), whereas most of their water uptake happens within the top 40 cm (West *et al.*, 2007; Grossiord *et al.*, 2017). Similarly, in hyper-arid deserts, extremely deep roots down to 47 m were observed, whereas most WUD took place within 3–4 m (Schachtschneider & February, 2010). Hence, the majority of water taken up by trees comes from much shallower soil layers than reached by the roots (Miguez-Macho & Fan, 2021). Calculations of WUD are often weighted means of stable isotope measurements (Box 1, Section III, Notes S1) and, therefore, do not represent the maximum WUD but rather the average depths from which most of the water was acquired. The maximum WUD, where usually very little water uptake occurs, corresponds in most studies to the maximum depth of the soil from which stable isotopes were analysed, which is dependent on the feasibility of extracting deep soil cores. The difference between WUD and rooting depth can, therefore, be explained by the advantage of having a deep rooting system that, while not contributing to the majority of water uptake, allows trees in dry regions to maintain *E* during extended droughts and avoid extreme desiccation (Schenk & Jackson, 2005; Davidson *et al.*, 2011; Stahl *et al.*, 2013; Mackay *et al.*, 2020; Laughlin *et al.*, 2023). In contrast to arid ecosystems, maximum rooting depth was closer to both the average and the 90% quantile of WUD in more humid climates (Figs 4, S2; Schmid & Kazda, 2005; Brinkmann *et al.*, 2019). Trees growing at wetter locations showed less reliance on deep roots as expected by the greater availability of soil water at shallower depths. Hence, our analysis is consistent with findings that rooting depth alone should not be used as a proxy for plant WUD (Nippert & Holdo, 2015); however, plants with deeper roots do generally have deeper water uptake depths and occur at more arid locations (Fig. 4).

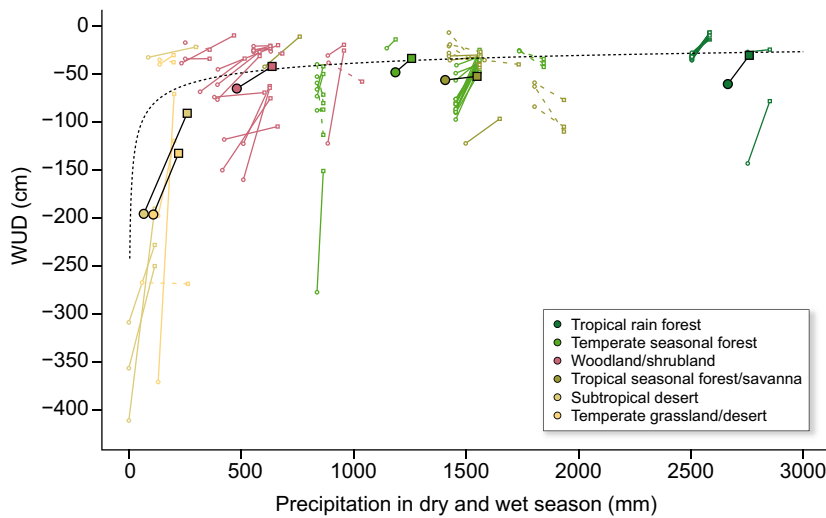
V. Water uptake depth under seasonal soil moisture variation

WUD is highly dynamic within local areas, changing within a few days in response to drying or wetting soils (e.g. Gessler *et al.*, 2022). Seasonal changes in WUD in response to naturally changing soil water availability are the most ubiquitous observation in the literature with 74 out of the 120 reviewed studies reporting seasonal WUD shifts (Figs 5, S3; Table S1). Experiments testing drought effects on WUD through precipitation exclusion set-ups are less common (e.g. Barbeta *et al.*, 2015; Grossiord *et al.*, 2017; Chen *et al.*, 2021). Nevertheless, both observational and experimental studies agree that WUD tracks the depth of the soil with the least negative water potential by taking up water from the shallow layers during moist conditions and switching to deeper layers when the shallow layers become dry (e.g. Brinkmann *et al.*, 2019; Grellier

Fig. 4 Mean water uptake depth (WUD, circles) and the 90% quantile of WUD (crosses) in relation to the maximum rooting depth for all the 44 species for which records of both measurements were available, and mean water uptake depth averaged by biomes (triangles; means \pm SE; Supporting Information Table S3). The dotted diagonal line shows the 1 : 1 relationship. Colours indicate the biome type ranging from tropical rainforests to arid deserts. Note that the scale of maximum rooting depth changes above 6 m.



(a)



(b)

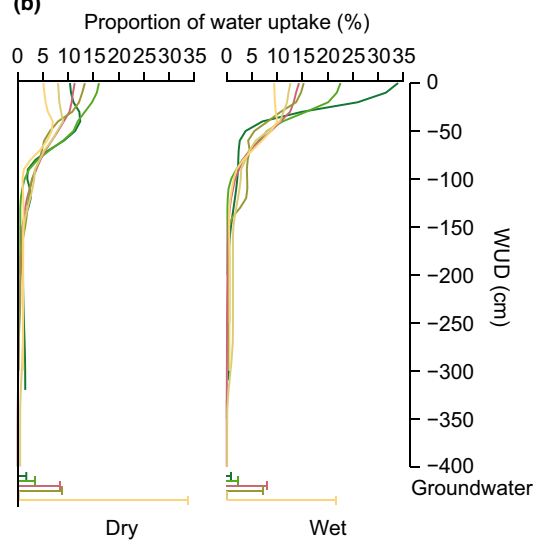


Fig. 5 Differences in water uptake depth between wet and dry season across biomes for all the 49 studies that numerically calculated it (Table S2). (a) Seasonal changes in averaged water uptake depth (WUD) from wet (squares) to dry (circles) season in relation to the precipitation in the dry vs wet seasons for all the 49 studies that numerically calculated WUD (Supporting Information Table S2). Small open symbols show species- and site-specific values and large filled symbols show averages of all the sites per biome. Solid lines indicate studies that found deeper WUD during the dry than the wet season, whereas dashed lines indicate studies that found less deep WUD during the dry than the wet season. The dotted line shows the significant relationship between WUD and precipitation across species and sites ($P < 0.001$, $R^2 = 0.142$). (b) Proportional WUD interpolated at 10 cm interval. Values were aggregated by biome for wet and dry seasons. Several studies indicated groundwater source use without explicit depth of the groundwater table for which the proportion of groundwater use was averaged.

et al., 2021; Wenping *et al.*, 2021). In some cases, woody plants switched their WUD from deep to more shallow sources from the wet to the dry season (Fig. 5). Such seemingly contradictory WUD dynamics were explained by the depletion of groundwater sources during extreme droughts (Barbeta *et al.*, 2015) and the replenishment of superficial soils during the dry season by recent rainfall events (e.g. Grellier *et al.*, 2021; Liu *et al.*, 2021). Thus, even deeply rooted plants preferentially uptake water from shallow soil layers when soil moisture becomes higher (Schenk, 2008; Feldman *et al.*, 2023).

In regions where there is little variability in soil moisture, water sources tend to stay constant during the year. For instance, trees growing on constantly dry soils will persistently take up water from deep WUD (Kray *et al.*, 2012; Kukowski *et al.*, 2013), whereas trees

growing on permanently water-saturated soils will show consistent shallow water uptake (Goldsmith *et al.*, 2012). Moreover, in some instances, trees growing in arid regions may not reach the deep groundwater level with their roots and, therefore, rely on recent precipitation as their main water source and consistently take up water from shallow soil layers (February *et al.*, 2007; West *et al.*, 2007; Fan, 2015). Furthermore, savannas trees often rely consistently on relatively deep water sources, despite considerable seasonal changes in soil moisture, which can be attributed to the avoidance of competition with herbaceous species at shallow layers (Kulmatiski & Beard, 2013; Case *et al.*, 2020) and thus a niche complementarity strategy (Le Roux *et al.*, 1995; Grellier *et al.*, 2021). Thus, despite an overall positive effect of aridity on WUD (Fig. 5), there is large variation driven by edaphic

conditions, such as the depth of the groundwater table, water holding capacities of soil horizons, and competition for soil water.

By comparing dry and wet season WUD from 147 records of 125 species at 46 sites (see Section III, Notes S1), we observed marked differences in the extent of the seasonal shifts in WUD across biomes. Subtropical deserts and arid grasslands show the largest seasonal changes (92 vs 197 cm and 134 vs 198 cm, respectively, Fig. 5). Tropical rain forests and woodland and shrublands (comprising many Mediterranean sites) also consistently shift to deeper soil layers in the dry season, resulting in large shifts in WUD (31 vs 61 cm in tropical forests and 43 vs 66 cm in woodland and shrublands). In temperate forests, changes in WUD were less pronounced (35 vs 49 cm), and trees from seasonal tropical forests and savannas had the smallest changes between wet and dry season (53 vs 57 cm). Across the entire range of study sites, WUD was significantly related to the seasonal precipitation ($P < 0.001$, Fig. 5). A common hypothesis is that precipitation variability (i.e. the frequency and intensity of rainfall events) may be an important driver of long-term patterns of tree WUD. This is because small regular rainfall events that infiltrate shallow soil layers favour plants with shallow water uptake, whereas when more irregular and intense rainfall events replenish deep soil layers, it favours plants with access to deep water sources (Sala & Lauenroth, 1982; Schwinning *et al.*, 2003). By relating the 147 records of WUD from the published literature to the precipitation variability (intra-annual variability of precipitation as a percentage of the average annual precipitation) at the respective sites, we found some evidence supporting this hypothesis ($P < 0.001$, $R^2 = 0.21$, Fig. S4). Hence, WUD changes in response to seasonal and short-term soil water availability, but is also influenced by long-term climatic conditions, such as annual precipitation sum and variability across the year.

VI. The role of water uptake depth for tree water and carbon exchange, and mortality

WUD has significant implications for whole-tree responses to climate, including water and carbon exchange and vulnerability to drought-induced mortality. Soil drought typically drives more negative plant water potentials (Ψ_p) and induces WUD shifts to deeper sources (Eggemeyer *et al.*, 2009; Yang *et al.*, 2011), resulting in lower E and CO_2 assimilation (Grossiord *et al.*, 2017), indicating that shifting to deeper plant water sources is insufficient to compensate for reduced water availability (Mas *et al.*, 2024). Nevertheless, in cross-species comparisons within a given location, trees with deeper WUD can maintain less negative Ψ_p during dry seasons than co-occurring species that rely on shallow soil water (e.g. Stahl *et al.*, 2013; Brum *et al.*, 2019; Liu *et al.*, 2021, but see Jiang *et al.*, 2020). Species that maximise water acquisition by switching WUD to deeper, wetter sources during dry periods can maintain higher E and CO_2 assimilation compared to species that cannot reach deep water sources (e.g. Moreno-Gutiérrez *et al.*, 2012; Schwendenmann *et al.*, 2015). As a consequence, water use efficiency (WUE, that is the ratio between carbon assimilation and water loss) is lower in species and individuals that have deeper WUD compared to those with shallower WUD

(Hasselquist *et al.*, 2010; Moreno-Gutiérrez *et al.*, 2012, but see Jiang *et al.*, 2020). While WUD was correlated with Ψ_p across several woody plant species (Ding *et al.*, 2021), differences in Ψ_p may not always be reliably used to infer differences in WUD between co-occurring species (Kukowski *et al.*, 2013). The relationship between WUD and Ψ_p varies depending on the plant's hydraulic sensitivity to decreasing Ψ_p , that is whether they rapidly close their stomata (relatively isohydric species) or maintain higher stomatal conductance at decreasing Ψ_p (relatively anisohydric species). The limited studies that have investigated this relationship come to inconsistent conclusions and find either a deeper (West *et al.*, 2007; Moreno-Gutiérrez *et al.*, 2012; Ding *et al.*, 2021) or shallower (Grossiord *et al.*, 2017) WUD of more isohydric compared to more anisohydric species. Nevertheless, relatively anisohydric species with deep roots have shown a higher capacity to switch from shallow to deep water sources compared to relatively isohydric ones (West *et al.*, 2007; Grossiord *et al.*, 2017; Tang *et al.*, 2018). While this shows a link between aboveground water use strategy and WUD, we are still lacking empirical evidence for the relationship between the plant's hydraulic sensitivity to Ψ_p and WUD and its impact on E and photosynthesis.

Access to reliable water sources through deep water uptake should also enable to survive long dry spells (Nepstad *et al.*, 1994; Stahl *et al.*, 2013). During droughts, reduced water uptake leads to a decline in hydraulic conductance and stomatal closure (Cuneo *et al.*, 2016). Due to the continued water loss by evaporation from plant surfaces (i.e. the minimum stomatal conductance), the risk of xylem embolism increases (Cochard, 2021). Under continued soil drought, xylem cavitation spreads throughout the xylem network, increasing the risk of mortality via hydraulic failure (Choat *et al.*, 2018; Mantova *et al.*, 2021). Having roots at great depths where soil water is available during drought can mitigate the risk of hydraulic failure during periods of severe water limitations (Stahl *et al.*, 2013; McDowell *et al.*, 2019; Chitra-Tarak *et al.*, 2021; Laughlin *et al.*, 2023). Indeed, rooting depth has been positively related to drought survival at the local scale (Padilla & Pugnaire, 2007; Nardini *et al.*, 2016). However, in regions with seasonal recharge of deep soil layer, greater WUD does not guarantee long-term survival, and can even increase mortality due to delayed recharge of deep soil layers (Chitra-Tarak *et al.*, 2018). By contrast, in locations where the soil layer is thin and rooting depth is restricted, access to fissures within the rock that concentrate water can prevent tree mortality (McDowell *et al.*, 2019; Preisler *et al.*, 2019; Nardini *et al.*, 2021, 2024). Thus, WUD may play a fundamental role in tree mortality, but more empirical work is needed to understand the mechanisms, especially as very few studies have directly linked tree mortality and WUD *in situ* (but see crown defoliation effects in, for example West *et al.*, 2012; Barbeta *et al.*, 2015; Ding *et al.*, 2021), highlighting an important research gap.

VII. Model representation of WUD across scales

Vegetation process models (VMs; Trugman, 2022) spanning tree-to-Earth scales play a key role on bridging between observations of WUD and making predictions about woody plant

mortality, understanding ecosystem resilience, and quantifying primary production. Designed around soil–vegetation–atmosphere transfer theory, models quantify how atmospheric demand for water and E , translates into water uptake from the soil. They typically simulate WUD as a function of soil water content in different layers and can account for structural and functional root traits (McCormack *et al.*, 2015; Warren *et al.*, 2015). Most VM's partition the soil into two or more layers and simulate water uptake from each layer in proportion to the root surface area and hydraulic pressure gradients that depend on relative soil water content in each soil layer. They thus have the necessary functionality for simulating known WUD mechanisms (Eqn 1, Section II) in accordance with empirical evidence of WUD (Sections III–VI). Most models describe water uptake with a flux equation that includes a sink term, as:

$$\frac{\partial s(z, t)}{\partial t} = \frac{\partial q(s, z, t)}{\partial z} - F(s, z) \quad \text{Eqn 2}$$

where s is the soil water content, z is the depth below the land surface, t is time, q is the water flux via infiltration, vertical or lateral flux. $F(s, z)$ is a water flux term, that is often used to represent plant water uptake (after Feddes *et al.*, 2001) following:

$$F(s, z) = f_{r,z} \frac{\beta_{r,z}}{\beta_r} \frac{E(\beta_r)}{\Delta z} \quad \text{Eqn 3}$$

where $f_{r,z}$ is the fraction of root area at depth z , $\beta_{r,z}$ and β_r are, respectively, the relative soil water content for depth z and for the whole root, and E is transpiration. $\beta_{r,z}$ can be a function of the soil matric potential (Jarvis, 2011) rather than soil water content, to account for the nonlinear response of water flow to potential gradients. Some models distribute roots with depth using an exponential function (de Rosnay & Polcher, 1998) parameterized using information from global databases (e.g. Schenk & Jackson, 2005).

Commonly used WUD modelling frameworks allow for the adjustments to the proportion of water uptake by depth (commonly called WUD compensation by modellers; Fig. 6). In most models, WUD compensation is a passive process, driven only by hydraulic pressure gradients without changing the depth distribution of roots. However, a small number of models include an active process that require either root growth, changes to root permeability (e.g. Casparian band or aquaporin changes), or both (Knighton *et al.*, 2021). Model simulations support empirical evidence that suggests WUD compensation is an important trait for tree survival during drought (Markewitz *et al.*, 2010; Christina *et al.*, 2017). For models that do not have WUD compensation (e.g. Ivanov *et al.*, 2012), water uptake is calculated as a function of the proportion of the root surface at a given depth ($f_{r,z}$, see Eqn 3) and the response of E to β_r for each root zone or layer independently. Without compensation, the simulation of WUD is increasingly inaccurate as soils dry (Li *et al.*, 2012). Consequently, these models overestimate the mean WUD when soil water content is uniformly high because they acquire water via deep roots when they need only water from shallow ones. Conversely, as soil water content drops

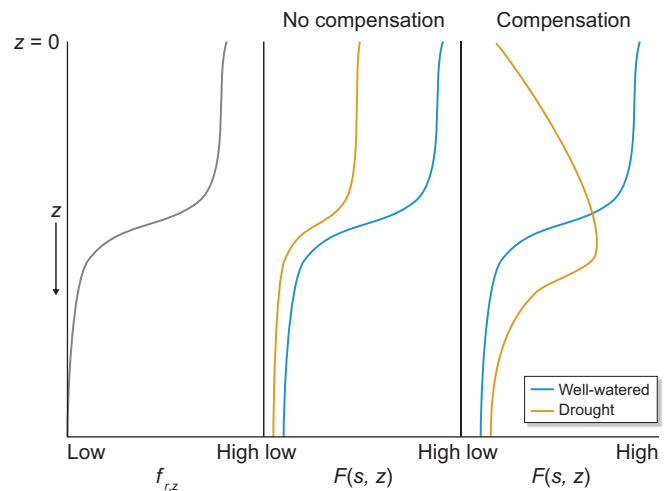


Fig. 6 Model representations of the effect of compensation on WUD dynamics, with $f_{r,z}$ representing relative root fraction with depth z and $F(s, z)$ representing the relative water uptake by roots by depth and soil water content (drought vs well-watered conditions).

the mean WUD is static and thus underestimated, and total water uptake is also underestimated (Kuhlmann *et al.*, 2012). Moreover, WUD compensation can explain tree survival in both natural (Johnson *et al.*, 2018) and experimental extreme droughts (Mackay *et al.*, 2020). Similarly, simulating WUD compensation via the Sperry *et al.* (2017) model has proven valuable for understanding tree responses to drought in aspen (Love *et al.*, 2019) and tropical forests (Pivovarov *et al.*, 2021). An important finding in these studies is that E is sustained through extreme droughts by water uptake from $< 5\%$ of their total root area (i.e. small values of $f_{r,z}$) at depths exceeding 0.6 m.

Two approaches with a different representation of soil and root hydraulics are commonly used to calculate root water uptake and its support for E : macroscopic and hydraulic models (Fig. 7). In both, the belowground soil–plant system is represented using soil–root layers with each layer accounting for its respective bulk water uptake. However, hydraulic VMs simulate water flow through the soil and xylem separately (hydraulic approach, Fig. 7), whereas macroscopic VMs use the physics of water flow through the soil as a proxy for plant water uptake (macroscopic approach; Clark *et al.*, 2015). In the macroscopic approach, water uptake is calculated as a function of local soil water content (Fig. 7) following Feddes *et al.* (2001). Data accuracy trade-offs have led to the use of simplified soil–xylem hydraulics in larger scale models (Vanderborght *et al.*, 2021), and yet Earth Systems models are moving towards implementing xylem hydraulics (e.g. Kennedy *et al.*, 2019; Li *et al.*, 2021). The hydraulic approach (Clark *et al.*, 2015; Vogel *et al.*, 2016) implements a full description of soil–xylem hydraulics that considers the effects of both lateral and axial pressure gradients on E by using soil matric potential to account for the radial soil–root pressure gradient. This approach is used by some VMs to account for the role of plant hydraulic architecture on WUD (e.g. Mackay *et al.*, 2015; Huang *et al.*, 2017; Silva *et al.*, 2022). The hydraulic approach builds on the electric circuit analogy of resistances and capacitances. A representative way to solve for water

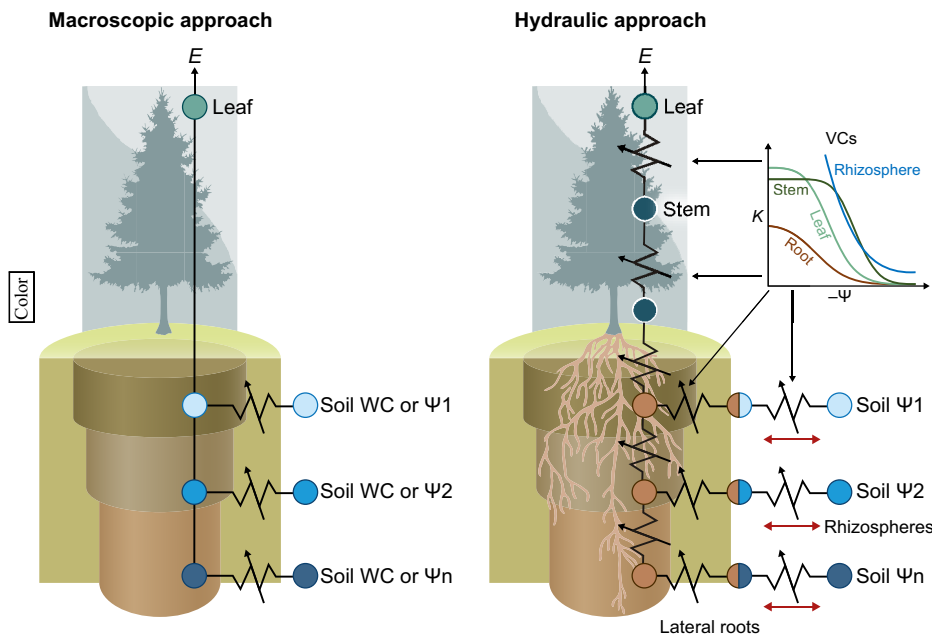


Fig. 7 Conceptual frameworks for macroscopic and hydraulic models for computing water uptake to support transpiration (E). Macroscopic models ignore the soil–root water potential gradient (c. Eqn 1) while considering soil water content (WC) or soil water potential (Ψ). Hydraulic models consider pressure (Ψ) and hydraulic conductance (K) in both soils and xylem using vulnerability curves (VCs). Some models allow for hydraulic redistribution (red two-headed arrows).

flow is the Kirchhoff integral transform of the Richards equation used to calculate water flux (Sperry *et al.*, 1998):

$$F(\varphi_i, \varphi_{i+1}, \varphi_{i-1}) = (\varphi_i - \varphi_{i-1}) - (\varphi_{i+1} - \varphi_i) - \left(\frac{\Delta W_i}{\Delta t} \right) \quad \text{Eqn 4}$$

where Φ_i is the matric flux potential for soil or xylem element, i , which is the integral hydraulic conductance over water potential for soil hydraulic conductivity (e.g. VanGenuchten, 1980) or vulnerability curves for xylem (e.g. Neufeld *et al.*, 1992), and W_i is the water content. Depth-specific soil–xylem hydraulics can compute both water uptake and export depths associated with hydraulic redistribution (see Fig. 2, for example Gou & Miller, 2014; Huang *et al.*, 2017). Such models have successfully demonstrated hydraulic redistribution, which calls for it to be included in large-scale models (Warren *et al.*, 2015).

Overall, while many mechanisms and empirically observed processes can be successfully simulated, the biggest frontier for WUD modelling is the representation of active water uptake. To account for active water uptake, the role played by fine roots needs to be better quantified (McCormack *et al.*, 2015), the modification of hydraulic conductivity via changes in aquaporin expression better understood (Ding *et al.*, 2023), and plant hydraulic status must be integrated with a carbon-limited growth strategy in which roots explore the soil with both benefits (i.e. water uptake) and costs (i.e. carbon allocated to root growth; Mackay *et al.*, 2020). Although there are models that include root growth for stand-to-ecosystem scales (see table 1 in Potkay *et al.*, 2021) and regional-to-global scales (see table 1 in Wang *et al.*, 2021), they generally rely on stochastic precipitation inputs or use empirical functions for root distribution. To understand tree and shrub responses to transient environmental conditions, models should be evaluated whether root water uptake depth is sufficiently flexible

when shallow layers are dry (e.g. Fan *et al.*, 2017), grow roots based on carbon allocation and xylem–phloem hydraulics (e.g. Mackay *et al.*, 2020; Potkay *et al.*, 2021), and account for cessation of root growth during extreme drought (Mackay *et al.*, 2020). Based on Eqn 1, soil water potential represents half the resistance to plant water uptake, and so vegetation model developers should strive to improve their soil water hydrology routines to account for deep soils, rock-to-root water transfer (Korboulewsky *et al.*, 2020; Nardini *et al.*, 2021), and accurate representations of storage limitation capacity of the subsurface (Hahm *et al.*, 2019; Tai *et al.*, 2021). Including active water uptake by root growth and the limit thereof by root access to water during extreme drought might be critically needed to predict WUD (and by extension E) under climate change scenarios across biomes and seasons. Furthermore, models with such capability will no doubt aid in understanding why WUD is related to plant functional type, but also in revealing the underlying physiological explanations for the large interspecific variations in WUD (see Section V).

VIII. Conclusions and perspectives

Water uptake by woody plants is a dynamic process driven by the plant's transpirational demand and changes in soil water availability and root hydraulic conductivity (Fig. 2). WUD varies across biomes, with woody plants in arid grasslands and deserts using water sources four times as deep as trees from humid temperate forests across the year (Fig. 3). By contrast, differences between plant functional types are less pronounced, whereas they show a large within-group variability. Globally, biome differences in WUD are thus much more pronounced than differences in plant functional types. Although deep roots are a prerequisite for water uptake from deep soils, average WUD can deviate considerably from maximum rooting depth, particularly in arid locations (Fig. 4). In those locations, deep taproots, while contributing little to the bulk of transpired water, play

an important role in ensuring survival during dry seasons by providing sufficient water to sustain *E*. During dry seasons, woody plants across all biomes and plant functional types shift water uptake to soil layers with higher moisture, which usually results in deeper WUD (Fig. 5). We can thus observe dynamic responses in WUD around the globe and WUD changes seem mainly limited by soil and rooting depth, and the avoidance of interspecific competition. This consistent pattern opens the opportunity to modelling woody plant WUD as a passive process driven by water potentials at a large scale (e.g. Stocker *et al.*, 2023), but it relies on knowledge of the vertical profiles of soil moisture and root surface area. A framework linking WUD to the vertical profile in soil water potential and the vertical distribution of roots (Figs 6, 7) is thus a promising approach for vegetation modelling.

To better understand WUD at the global scale, we need measurements from underrepresented locations, notably boreal forests, temperate seasonal forests, and rainforests (Fig. 1). In these ecosystems, measurements of WUD are technically challenging, often due to the absence of a gradient in water isotopic composition, which can be partly overcome using isotopic labelling. Moreover, to know how rooting depth limits WUD we need to understand whether roots can grow opportunistically upon soil drought, as suggested in Li *et al.* (2019), or whether they have to be grown in advance (Mackay *et al.*, 2020). Furthermore, we need more knowledge of how WUD dynamics influence aboveground responses, such as *E* and xylem embolism to understand the impact of WUD on tree mortality. WUD dynamics could be related to species-specific sensitivity of hydraulic conductance to drought and VPD, but the low number of studies directly relating above- and belowground dynamics restricts generalisations. Such improvements could be used in next-generation vegetation process models that should include carbon- and water-limited soil exploration by roots and its effect on regional and global scale models.

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Competing interests



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Author contributions

CB and CG conceived and planned the research, CB collected and analysed the data, CB, SJT-D, DSM, NGMD, AC, TK, BDS, MM and CG all contributed equally to manuscript writing.

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Appendix A2

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Proportional and averaged water uptake depth (WUD) aggregated by plant functional type during the wet and dry seasons.

Fig. S2 Difference between the maximum rooting depth and water uptake depth (WUD) in relation to the mean annual precipitation sum.

Fig. S3 Summary of the experimental approaches, measurement techniques and core findings of the 120 studies on water uptake depth dynamics.

Fig. S4 Averaged water uptake depth (WUD) during the wet and dry seasons in relation to precipitation seasonality, and precipitation seasonality of the sites in each biome.

Table S1 Summary of the findings from the 120 studies on water uptake depth dynamics, their measurement approach and experimental settings.

Table S2 Reviewed studies calculating depth of water uptake using natural ^{18}O and D isotopes or isotopic tracers in combination with mixing models or direct inference.

Table S3 Species for which both water uptake depth (WUD) and rooting depth are provided and the respective studies.

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