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Dubbert, M.

2023-01

Dubbert , M , Couvreur , V , Kübert , A & Werner , C 2023 , ' Plant water uptake modelling : added value of cross-disciplinary approaches ' , Plant Biology , vol. 25 , no. 1 , pp. 32-42 . <https://doi.org/10.1111/plb>

<http://hdl.handle.net/10138/356480>

<https://doi.org/10.1111/plb.13478>

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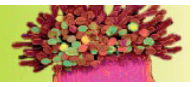
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REVIEW ARTICLE

Plant water uptake modelling: added value of cross-disciplinary approaches

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Keywords

Ecosystem water cycle; hydrological modelling; optimality; plant water uptake; root water uptake; transpiration.

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Editor

S. Wicke

Received: 28 July 2022;

Accepted: 10 October 2022

doi:10.1111/plb.13478

ABSTRACT

In recent years, research interest in plant water uptake strategies has rapidly increased in many disciplines, such as hydrology, plant ecology and ecophysiology. Quantitative modelling approaches to estimate plant water uptake and spatiotemporal dynamics have significantly advanced through different disciplines across scales. Despite this progress, major limitations, for example, predicting plant water uptake under drought or drought impact at large scales, remain. These are less attributed to limitations in process understanding, but rather to a lack of implementation of cross-disciplinary insights into plant water uptake model structure. The main goal of this review is to highlight how the four dominant model approaches, that is, Feddes approach, hydrodynamic approach, optimality and statistical approaches, can be and have been used to create interdisciplinary hybrid models enabling a holistic system understanding that, among other things, embeds plant water uptake plasticity into a broader conceptual view of soil–plant feedbacks of water, nutrient and carbon cycling, or reflects observed drought responses of plant–soil feedbacks and their dynamics under, that is, drought. Specifically, we provide examples of how integration of Bayesian and hydrodynamic approaches might overcome challenges in interpreting plant water uptake related to different travel and residence times of different plant water sources or trade-offs between root system optimization to forage for water and nutrients during different seasons and phenological stages.

INTRODUCTION

Analysing plant water uptake strategies, in particular the uptake of shallow *versus* deep soil water sources, has become a major research focus in hydrology as well as in plant and ecosystem ecology in recent years (McElrone *et al.* 2013; Míguez-Macho & Fan 2021). In hydrology, the central goal in understanding plant water uptake strategies includes improving water budget estimates and their partitioning (Ukkola *et al.* 2016), disentangling the impact of spatiotemporal water use dynamics (*i.e.* changes in water uptake depth distributions) for soil water budget components (groundwater recharge or infiltration; Zhang *et al.* 2019; Shi *et al.* 2021), water ages and transit times (Sprenger *et al.* 2019), and better informing water resource management (Dabach *et al.* 2015). In plant or ecosystem ecology, plant water use strategies are dominantly studied in the context of plant or ecosystem resilience to drought, with a focus on the interlinkage between water, carbon and nutrient uptake and use strategies (see *e.g.* Kong *et al.* 2014; Karlowsky *et al.* 2018; Cusack & Turner 2021). It is further worth noting that plant ecologists rather refer to plant water uptake (*i.e.* above- and belowground components of a plant as one hydrological unit), whereas in hydrological sub-disciplines the term ‘root water uptake’ is more common (emphasizing the soil–root interface). Here, we will use the term ‘plant water uptake’.

Physically, the uptake of water from the soil into the roots is essentially a passive process driven by the water potential gradient between the soil and the atmosphere (along the soil–plant–atmosphere continuum). In the soil, the redistribution of water is limited by soil hydraulic conductivity, which may vary by orders of magnitude within millimetres as the soil dries out (Javaux *et al.* 2013). Plants can actively regulate conductivity within the rhizosphere through, *e.g.* mucilage exudation (Carminati & Vetterlein 2012; Carminati *et al.* 2016). Moreover, it is still a matter of debate as to what extent root hairs and mycorrhizal hyphae contribute to the uptake of water and offer more than just physical bridges for water film–flow between soil particles and the root surface (Allen 2007; Le Pioufle *et al.* 2019; Vetterlein *et al.* 2022). Within the plant, water fluxes are regulated at three critical stages: (i) during its radial transport across root tissues; (ii) within plant vasculature for long-distance transport; and (iii) through stomatal pores, limiting exchange with the atmosphere. Mechanisms that control the hydraulic regulation of plant water transport from roots to leaves are generally complex, with components spanning environmental stimuli, hormones and genetic factors (Tardieu *et al.* 2011). For example, stomatal aperture is well studied and responds to both hydraulic and chemical signals from root to shoot, with osmotic adaptations to water deficit (Larcher 2003; Christmann *et al.* 2007; Dodd *et al.* 2010;

Vandeleur *et al.* 2014). Similarly, the dynamics of root hydraulic conductivity show short-term responses to the availability of water (Hachez *et al.* 2012) through circadian rhythms (Caldeira *et al.* 2014), but also soluble nutrient concentration, such as nitrate (Gorska *et al.* 2008; Ishikawa-Sakurai *et al.* 2014), possibly *via* aquaporin regulation (Javot & Maurel 2002; Pou *et al.* 2022). Last, but not least, plant hydraulic properties are spatially heterogeneous and dynamic in leaves (Tardieu *et al.* 2015; Earles *et al.* 2018) and stems (Bohrer *et al.* 2005; Couvreur *et al.* 2018). Several of these small-scale features may have substantial impacts on water fluxes, which are integrated at larger scales (*e.g.* stand or ecosystem scales). Besides variations in plant hydraulic properties, there is also plasticity allowing exploration of their environment to access resources. When water is limited, trees can decrease the shoot–root ratio (for a global overview, see Ledo *et al.* 2018) *via* increased carbon allocation to roots. Root architecture can adapt to the co-limitation of water and nutrients (Ho *et al.* 2005). Such plastic responses have genetic origins, as found in *Arabidopsis thaliana* for hydrotropism (Dietrich *et al.* 2017), ‘hydropatterning’ of lateral roots (Bao *et al.* 2014) and the absence of laterals in air gaps (Orman-Ligeza *et al.* 2018). The level of spatiotemporal plasticity of plant roots is impressive (Jackson *et al.* 1996). However, despite these discoveries and a recent surge in studies describing root traits, plant roots are still underrepresented in modelling frameworks, in particular their dynamic nature (Guerrero-Ramirez *et al.* 2021).

Plant water uptake modelling approaches have evolved from various disciplines over past decades, some assessing the complex processes described above, others considering the idea that ‘simplicity is the ultimate sophistication’, quoting Leonardo Da Vinci, with clear trade-offs involving computing time and data availability (water isotopic ratios, water potentials and hydraulic properties). Reminiscent of a diverse colour palette, these approaches occupy niches determined by compromises between [model] specificity and [desired] simplicity (De Swaef *et al.* 2022). In the context of inaccurate large-scale predictions of plant water uptake under drought, Hrachowitz *et al.* (2013) and De Kauwe *et al.* (2015) stated clearly that the major limitation is less a lack of understanding of the underlying physiological processes than their implementation in catchment-scale hydrological model structures. This is equally true for links between water, carbon and nutrient cycling, and the trade-offs plants face in terms of their root traits to optimize productivity (Cusack & Turner 2021). Therefore, interdisciplinary approaches are needed to create cross-disciplinary hybrid models (Cocozza & Penna 2021). Models related to each niche have been extensively reviewed (*e.g.* for isotopic approaches: Rothfuss & Javaux 2017; Beyer *et al.* 2020; for hydrodynamic and conceptual approaches: Raats 2007; De Swaef *et al.* 2022).

Here, we highlight how four dominant plant water uptake model approaches (the Feddes approach, Bayesian approaches, Optimality approaches and Hydrodynamic approach) have recently been used to create hybrid models and draw inferences, highlighting new ways forward to overcome current limitations of plant water uptake modelling. We (i) provide a brief overview of the *modus operandi* and state-of-the-art for these four predominantly used plant water uptake modelling approaches; (ii) highlight the inter-relations between plant water uptake and other physiological processes; and (iii) propose examples of interdisciplinary approaches that might be

key to advance our ability to predict plant water uptake dynamics.

MODELLING PLANT WATER UPTAKE FROM A HYDROLOGICAL PERSPECTIVE

A quantitative assessment of the regulation of plant water uptake depth plasticity of plants (*e.g.* in response to increasing droughts) is essential to understand vegetation contributions to ecosystem–/catchment-scale water cycling and to close water budgets on larger scales (Fan *et al.* 2017; Werner *et al.* 2021). Hydrological models are highly sensitive to plant water uptake depth, which has a large impact on, for example, modelled plant productivity (Chenu *et al.* 2011; Lynch 2013) and hydrological cycling (Feddes *et al.* 2001; Li *et al.* 2021). Recently, there has been significant progress in hydrological modelling of plant water uptake, improving representations of plant hydraulic parameters and their dynamic nature, or the coupling of tracer-based statistical models with process-based plant water uptake approaches (Javaux *et al.* 2013; Rothfuss & Javaux 2017; Couvreur *et al.* 2020; Nguyen *et al.* 2020). Currently, we can distinguish four major approaches to describe plant water uptake (see Fig. 1; Table 1).

Bayesian-isotopic or statistical approach

This compares water stable isotope ratios ($\delta^{2}\text{H}$ and $\delta^{18}\text{O}$) in plant tissues (δ_{plant}) to those of the water sources in the soil (δ_{source}) and estimates the likelihood of water uptake of each water source by randomly combining water isotope ratios from sources and selecting combinations that match the plant water isotope ratios (*e.g.* $\delta_{\text{plant}} - \sum_{\text{sources}} \delta_{\text{source}} f_{\text{source}} < \epsilon_{\delta}$, where f_{source} is the fraction of water uptake in a source, and ϵ_{δ} is the error tolerance; Erhardt & Bedrick 2013). An important prerequisite of this method is that δ_{plant} only reflects the combination of potential soil water sources and is not subjected to isotopic fractionation: *e.g.* either xylem isotope signatures (generally δ_{xylem}) or transpired water vapour in an isotopic steady state (δ_{T} ; used in non-woody species where xylem sampling is not an option). This statistical method, which is more broadly termed ‘end-member mixing analysis’ (EMMA), requires either significant differences in natural abundance soil water isotopic ratios along the soil profile (mostly found in dry ecosystems) or the use of isotopically labelled water to artificially enhance the isotopic gradient along the soil profile (Beyer *et al.* 2018; Couvreur *et al.* 2020). Recent advances in *in-situ* water stable isotope monitoring techniques that enable continuous observation of soil and plant xylem water isotope ratios have boosted the spatiotemporal resolution of this method (Rothfuss *et al.* 2013; Volkmann & Weiler 2014; Volkmann *et al.* 2016; Kuehnhammer *et al.* 2019; Kübert *et al.* 2020; Marshall *et al.* 2020). Their combination with stable isotope mixing models currently provides the only *in-situ* and high-resolution method to quantify the water uptake depth probabilities of individual plants or communities. While their use was once limited to the classification of plant species’ reliance on rainwater *versus* groundwater (Evaristo & McDonnell 2017), such techniques are now routinely used in hydrology and ecophysiology (Parnell *et al.* 2010; Dubbert & Werner 2018; Dubbert *et al.* 2019; Kuehnhammer *et al.* 2019; Popp *et al.* 2019). Nevertheless, if not combined with

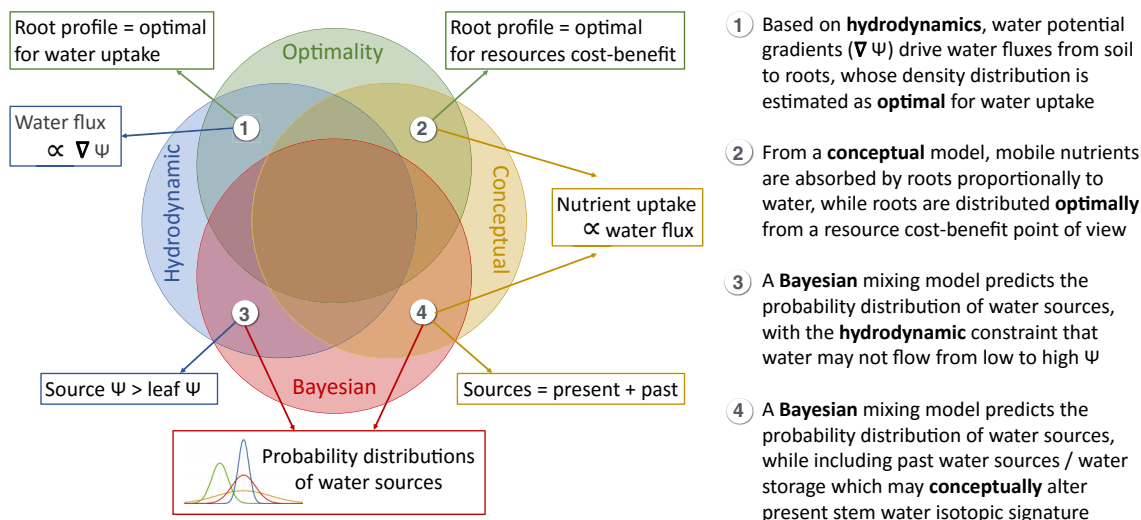


Fig. 1. How different approaches to water uptake by plants may complement each other through four examples.

additional constraints (e.g. spatial boundaries of the root system, water potential in each soil layer combined with plant water potential), this statistical method is prone to predict contributions to plant water uptake by sources that are physiologically not, or currently not, available for plant water uptake.

The Feddes approach

This is also termed *conceptual approach*, where the water uptake profile is assumed to be proportional to the relative root length density profile when water is equally available throughout the rooting zone. When water availability is limited, water uptake is reduced independently in each soil layer according to a ‘soil water stress’ function of local soil matric potentials (Feddes & Zaradny 1978). Over time, this approach has been updated with a ‘compensation factor’ to account for the fact that a local reduction in water uptake does not necessarily result in a reduction in transpiration (Jarvis 1989; Simunek & Hopmans 2009). Overall, in addition to vertical profiles of soil matric potential and root length density, this approach requires as input data the plant potential transpiration rate and parameters of soil water stress and compensation functions, which have commonly been parameterized to reproduce the overall plant transpiration response to an index of average soil water potential (Wesseling 1991; Novak & Havrila 2006). The Feddes approach has been termed ‘conceptual’ as it was built on relatively simple and intuitive ideas that do not emerge from a process-based description of hydrodynamics in the soil–plant system. As summarized by Feddes *et al.* (1976): “Because of the amount of fieldwork and experimental difficulties involved in determining [soil and plant hydraulic properties], an attempt was made to describe the [profile of root water uptake] with a more simple expression (...) of the soil water content”, a compromise that has been a major driver for its widespread success. Despite its conceptual nature, this approach has been widely used in land surface models (Feddes *et al.* 2001; Oleson *et al.* 2008) and crop models (Wolf *et al.* 2011; Kroes *et al.* 2018).

The hydrodynamic approach

This assumes that water flows passively along downhill gradients of water potentials between soil and plant xylem, at a rate limited by hydraulic resistances on the paths of the water (Van Den Honert 1948; Doussan *et al.* 1998; Couvreur *et al.* 2012). Such process-based plant water uptake models require as input the variables transpiration rate, soil water potentials and root length densities, although complementary measurements can be used to better constrain the model, e.g. stem water potential or root hydraulic properties. These hydraulic parameters can either be estimated by inverse modelling, as in the Feddes approach (Cai *et al.* 2017), be measured directly (Jerszurki *et al.* 2017), inferred from hydraulic and geometric observations at different scales (Passot *et al.* 2018) or translated from libraries of parameter values from the Feddes model (Couvreur *et al.* 2014). Recent advances have allowed further improvements in estimations of plant water uptake profiles by mechanistically modelling the transport of water isotopologues, measured either destructively in the soil and plant tissues (Meunier *et al.* 2017; Couvreur *et al.* 2020) or *in situ* (Zarebanadkouki *et al.* 2016, 2019; Pascut *et al.* 2021). Specific advantages of the process-based framework are the physical consistency of its predictions with the second law of thermodynamics and a more descriptive nature that allows drawing new insights into processes involved in water transport in the soil–plant system when compared to direct measurements. This approach is very frequently used in functional–structural plant models (Javaux *et al.* 2008; Postma *et al.* 2017; Braghieri *et al.* 2020; De Swaef *et al.* 2022) and has started to make its way into land surface models (Kennedy *et al.* 2019; Sulis *et al.* 2019; Agee *et al.* 2021) and crop models (Mboh *et al.* 2019; Nguyen *et al.* 2020) in simple upscaled forms.

The optimality approach

This assumes that natural systems are optimized to fulfil goals (related to entropy, net carbon gain or access to multiple

Table 1. Overview of current plant water uptake modelling approaches and necessary input parameters, proposed future advancements (in bold) and recommended literature.

	statistical approach	conceptual approach	hydrodynamic approach	optimality/game-theoretic approach	future advances statistical approach	thermodynamic approach
Basic principle to derive RWU	Comparison of isotope ratios in soil and plant	Soil pressure head limits for plant water uptake	Potential gradient between soil and plant, limit for plant water uptake	Potential gradient between soil and inside of the roots, limit for plant water uptake optimize root related costs versus water demand	Add physiological and/or optimality criteria	Iterative methods (e.g. Markov Chain Monte Carlo simulation): posterior probability functions for input
Input for approach						
Aboveground information shoot-atmosphere interface						
Shoot	Isotope ratios of plant/xylem water (usually $\delta^2\text{H}$ and $\delta^{18}\text{O}$, but also He values)	Potential plant transpiration	Actual transpiration rate or leaf/stem water potential Leaf/stem water potential or actual transpiration rate	Plant water content	Isotope ratios of plant/xylem water Nutrient demand	Isotope ratios of plant/xylem water
Additional information						
Belowground information root-soil interface						
Root	Root biomass per depth or root length density per depth	Root biomass per depth or root length density per depth	Root biomass per depth or root length density per depth		Root biomass per depth or root length density per depth Derive root profiles from optimality approaches if not available Maximum possible water uptake by roots Space-time-dimension of water sources: transport time to plant stem	Root biomass per depth or root length density per depth
Soil	Isotope ratios of soil water per depth (usually $\delta^2\text{H}$ and $\delta^{18}\text{O}$ but also He values)	Soil water potential per depth (or soil water content to derive using retention curve)	Soil water potential per depth (or soil water content to derive using retention curve)	Soil water potential per depth (or soil water content to derive using retention curve)	Isotope ratios of soil water per depth Nutrient availability per soil depth Soil water potential per depths (i.e. physiological limits)	Soil water potential per depth (or soil water content to derive using retention curve) Isotope ratios of soil water per depth

Table 1. (Continued)

	statistical approach	conceptual approach	hydrodynamic approach	optimality/game-theoretic approach	future advances statistical approach	thermodynamic approach
Additional information	Soil water potential per depths (i.e. exclude dry soil layers due to plant physiological limits)		Root hydraulic properties modelling transport of plant/soil water isotopologues			
Literature recommendations	Parnell <i>et al.</i> (2010), Erhardt & Bedrick (2013), Popp <i>et al.</i> (2019)	Feddes <i>et al.</i> (1976), Simunek & Hopmans (2009)	Couvreur <i>et al.</i> (2012), Zarebanadkouki <i>et al.</i> (2016), Meunier <i>et al.</i> (2017)	Schymanski <i>et al.</i> (2008), Drewniak (2019), Ledder <i>et al.</i> (2020)	Seeger & Weiler (2021), Knighton <i>et al.</i> (2020)	Brooks (1998), De Deurwaerder <i>et al.</i> (2021)

resources) under environmental and/or physiological constraints (irradiance, water balance, carbon cost of plant organs). From a mathematical perspective, hypothesizing optimal behaviour provides equations that allow solving of expressions for unknown variables. Several researchers have used this approach to derive shapes of rooting profiles for optimal access to water resources (van Wijk & Bouten 2001; Laio *et al.* 2006; Schymanski *et al.* 2008), which strongly affect predicted water uptake depths. Interestingly, to better constrain plant water uptake depth predictions, some studies combine the optimality and hydrodynamic approaches (Schymanski *et al.* 2008) (example 1 in Fig. 1), while others combine optimality and Feddes approaches (van Wijk & Bouten 2001; Laio *et al.* 2006). Hence, approaches are not necessarily exclusive (see Fig. 1), although they may work independently, for instance using simple mass balance principles in the case of the optimality approach (Kleidon 2004; Guderle & Hildebrandt 2015). An advantage of the optimality approach is that the rules can be relatively simple, with few parameters, while still yielding relatively good predictions, possibly because ecosystems have been selected to respond in the best way possible. In other words, any ensemble of complex physiological processes might simply be trained at providing the ‘optimal’ response that can be captured as a simple rule. A good example is the isohydric regulation of stomatal opening. Complex modelling of guard cell turgidity regulation *via* specific osmolytes might reproduce the response of isohydricity, which is well captured by a simple rule to maintain leaf water potentials above a defined threshold, e.g. “ $\psi_{\text{leaf}} > \psi_{\text{threshold}}$ ”. Another important aspect of the optimality approach is its potential to predict trends of vegetation responses to new environmental conditions (e.g. water uptake under elevated atmospheric CO₂) without the necessity of parametrization (Schymanski *et al.* 2015). Moreover, distinct constraints to root growth and water uptake depth distribution, such as water *versus* nutrient uptake can be optimized (Drewniak 2019; Hildebrandt 2020), which is a very important trade-off, yet not routinely included in plant water uptake modelling.

TRADE-OFFS AND CONFLICTING DEMANDS – PLANT WATER UPTAKE IS TIGHTLY LINKED TO NUTRIENT AND CARBON CYCLING

From a plant ecological viewpoint, water uptake from the soil is one of many functions of a plant’s root system, which include nutrient uptake, physical stabilization and interactions with mycorrhizal networks and other life forms (Larcher 2003; Freschet *et al.* 2021). In plant ecology, root traits and their functionality have recently received increased attention, as well as the coupling between above- and belowground controls of plant water use and the trade-off between water (and nutrient) uptake, on the one hand, and carbon investment, on the other hand (Cusack & Turner 2021). A critical component of root water acquisition is the spatial exploration of soils by roots. Many root traits, such as (fine) root biomass distribution, root elongation rate or root branching density, are decisive to overcome water limitation, but they are not static (as still often represented in plant water uptake models; Cusack & Turner 2021). Despite their impact and a recent surge in studies describing root traits, they are still underrepresented in modelling frameworks, in particular their dynamic nature (Guerrero-Ramirez *et al.* 2021; but see Agee *et al.* 2021). Root traits are not only highly variable in time and space, but

species-specific and can not only be adjusted to forage for water, but also for various nutrients (Kong *et al.* 2014; Addo-Danso *et al.* 2020; Cusack & Turner 2021). Naturally, this creates the need for trade-offs in their spatiotemporal adjustment when different resource availabilities (*e.g.* water *versus* nutrients) are separated in time and space. In many ecosystems, nutrient concentrations decline exponentially with depth, whereas water becomes limited particularly in the upper soil horizon upon drought (see example I below). Regulating fine root growth in response to such shifts in dominance of nutrient *versus* water limitation on growth demands a significant investment in carbon allocation belowground. However, aboveground drought responses, such as increased stomatal control, not only reduce plant water loss but also limit photosynthesis and thereby carbon availability for belowground organs (Karlowisky *et al.* 2018).

In summary, plant water uptake is highly linked with nutrient uptake and carbon allocation, controlled by complex regulation of both below- and aboveground processes and traits. These traits are highly variable in space and time. On larger scales (community or stand scale), they involve further processes, such as resource niche differentiation (Comas *et al.* 2013; Guderle *et al.* 2017; Chitra-Tarak *et al.* 2018) and competition (Craine & Dybzinski 2013; Grossiord *et al.* 2014). Consequently, to quantify plant water uptake depth distribution and its dynamics requires an understanding of such trade-offs between nutritional demands, carbon allocation strategy and species-specific water use strategies and their integration in quantitative modelling approaches that are neither excessively complex nor lacking in accuracy. Before addressing potential ways forward (for a summary, see Fig. 1; Table 1), we highlight these challenges with two examples:

I Root traits (*e.g.* root biomass depth distribution) are often optimized to maximize nutrient uptake from surface soils (Cornejo *et al.* 1994; Cusack & Turner 2021). During times of ample water supply, plant water uptake predominantly takes place from shallow soil layers, hence, nutrient and water uptake are constrained (*e.g.* Carvalho & Foulkes 2018). During dry periods, however, nutrient-rich upper soil layers become increasingly dry and inaccessible for plant water uptake. Root responses include a shift in water uptake from shallow (already dry) to deeper (wetter) soil layers within the rooting zone, and impaired uptake of mobile nutrients, such as nitrogen, in dry layers (Henriksson *et al.* 2021). Consequently, water uptake from deeper and wetter soil layers under drought will likely be a compromise between: (i) current demand for nutrients and changes over the growing period, (ii) vertical nutrient profile, (iii) type of nutrient (mobile or immobile), (iv) drought severity, timing and duration, and (v) species-specific water use adaptations and abilities to extract water from dry soils (hydraulic resistance, stomatal control, hydraulic redistribution). Furthermore, geomorphology and general distribution pattern of water and nutrient availability play a major role: ecosystems with pronounced dry periods generally suffer more from a spatiotemporal separation of water and nutrient availability compared to temperate ecosystems (Carvalho & Foulkes 2018; Cusack & Turner 2021).

II Another example is grassland or agricultural systems, where a common drought mitigation strategy of many species is to trigger early completion of the life cycle in response to drought. An equally intense and long drought during spring might be compensated by shifts in plant water uptake depths, among other mitigation strategies. During later stages of the growing period, however, especially grasses and crops induce early flowering and grain production, accompanied by die-back of transpiring leaf biomass, instead of mitigating drought effects through physiological responses focused on preserving productivity (Kottmann *et al.* 2016; Shavrukos *et al.* 2017; Kübert *et al.* 2019, 2020). This might lead to a lack of plasticity in plant water uptake depth distribution that cannot be predicted using current plant water uptake models. Moreover, in diverse ecosystems like grasslands or mixed forests that comprise plant species varying in rooting vertical and horizontal extent and water use strategies, community-scale drought responses can involve: (i) niche differentiation and complementarity regarding plant water uptake depth during drought (Guderle *et al.* 2017; Brum *et al.* 2019; Dubbert *et al.* 2019; Kahmen *et al.* 2022), or (ii) competition between species for shallow water sources (Dubbert *et al.* 2014; Kübert *et al.* 2019; Magh *et al.* 2020). Importantly, such community-scale interactions require an understanding not only of the vertical but also the horizontal extent of the root system and plant water uptake (see Schwärzel *et al.* 2009; Henriksson *et al.* 2021).

WAYS FORWARD TOWARDS INTEGRATIVE INTERDISCIPLINARY MODELLING OF PLANT WATER UPTAKE

Summarizing the previous paragraphs, current approaches to plant water uptake depth prediction may integrate and possibly combine multiple factors, such as water potentials and water isotopic signatures (in soil and/or plant), simple to more complex root traits (rooting depth, root length density distribution, root hydraulic properties) and optimality criteria. However, these approaches are not exhaustive: root traits can adapt at various temporal scales, as can aboveground controls for plant water uptake dynamics. Moreover, demands that conflict with plant water use strategies, *e.g.* nutrient uptake strategies or limits to below-ground carbon investment, are rarely considered. In particular, predictions of water uptake in current land surface models, as well as the Bayesian approach (without adding further constraints) remain largely unsatisfactory under drought conditions (Ukkola *et al.* 2016; Rothfuss & Javaux 2017). Therefore, multiple publications have called for the integration of more mechanistic yet parsimonious functions of plant water uptake into ecohydrological models (Bonan *et al.* 2014; Sperry *et al.* 2016; Li *et al.* 2021). Key advances for such an integration will require inclusion of interdisciplinary model modules. In the following, we briefly address two potential ways forward, with examples of recent pioneering studies:

Integrating novel criteria into statistical approaches

In the original isotope-based Bayesian plant water uptake approach, large numbers of virtual sets of water sources are

randomly sampled then pooled, and the sets that yield the same pooled water isotope signature as found in the plant stem constitute the posterior probability distribution of water sources. While the nature of this approach is purely statistical, constraints can be relatively easily added to its random search domain. Existing examples of criteria include restrictions to the spatial dimension of the search domain, excluding soil water sources where no roots are present or where water extraction is thermodynamically impossible (*i.e.* soil layers whose water potential is lower than plant water potential, a typical ‘hydrodynamic’ consideration in plant water uptake modelling; see example 3 in Fig. 1; Kuehnhammer *et al.* 2019; Magh *et al.* 2020; Gessler *et al.* 2021). From the same perspective, one could consider that the finite hydraulic conductivity of a root (below $10^{-5} \text{ m s}^{-1} \text{ MPa}^{-1}$; Meunier *et al.* 2018) implies that there is only a restricted amount of water that the root can absorb at a time. Hence, if a profile of root length density is available, one may set further constraints to how much water can be absorbed at a time in each soil layer relative to other layers, given a maximum water potential difference between soil and stem of *e.g.* 1.0 MPa.

Moreover, recent studies show that water travel and residence times may vary widely in space (Sprenger *et al.* 2019) and time (Werner *et al.* 2021), so that water from some sources would reach plant stems faster than from other sources (Henriksson *et al.* 2021). A solution would be to ‘distort’ the Bayesian search domain in both space and time to account for the diversity of water velocities along the soil–plant continuum. To this end, instead of analysing individual spatial snapshots of water signatures in the soil and plant, one could delineate regions in space and time from where and when water has the same ‘arrival time’ in the plant. An adjusted EMMA approach could then, for instance, pool shallow water located near a plant at day D-1, to deep water that is further away at day D-15, if these ‘waters’ are estimated to have the same arrival time in the plant at day D (example 4 in Fig. 1). A similar (although non-statistical) approach was recently proposed by Seeger & Weiler (2021), aiming to ‘deconvolute’ the stem water isotopic signature based on a time series of root-zone water signatures and estimated water travel times, combined with the conceptual Feddes & Zaradny (1978) plant water uptake model. Interestingly, Knighton *et al.* (2020) also challenged the idea of whether the xylem water signature results from soil water sources sampled at similar times, through the prism of plant water storage. They considered that the sampled plant water is not necessarily entirely constituted of soil water with the same arrival time in the plant. With their integrative experimental and process-based modelling approach, their results suggest that newly absorbed water mixes with older water stored in the stem, although mixing is not perfect, and part of the newly absorbed water only slowly progress along the stem (‘piston flow’ hypothesis). This process could become particularly important in plants with large water storage capacities and fluctuations in stem water content, such as trees (Werner *et al.* 2021). Implementing this in an EMMA framework would imply an enlargement of the search domain to include not just the signatures of water sources at the right ‘departure times’ (*i.e.* that yield the same arrival time in the plant), but also prior times that contributed to the reserve of older plant water, inherently sampled. While meaningful, such evolutions of statistical approaches also raise questions regarding the increasing

non-unicity of sets of water sources, past and present, which possibly yield the right stem water signature, besides the large uncertainties on the estimated water travel times and mixing rates. Could statistical approaches only become more meaningful at the cost of becoming too complex? Clearly, further empirical and process-based studies on the velocity and mixing rates of water pools within plant tissues are essential to improve our understanding of the relevance of past water sources in present plant water isotopic signatures (Sprenger *et al.* 2019; De Deurwaerder *et al.* 2020; Pascut *et al.* 2021).

Indeed, better constraints to statistical problems of determining sources of plant water might arise from non-hydrological disciplines. Organic and inorganic nitrogen compounds are highly mobile and move with water towards roots. Hence, if plant transpiration and a concentration profile of one or more mobile nutrients are available, the tentative vertical partitioning of water uptake could be evaluated in respect to the sufficient accumulation of nutrients over large temporal periods. Plant water uptake relying solely on water sources with too low mobile nutrient contents could be considered as unlikely in an isotope-based Bayesian framework (see example 4 in Fig. 1). Finally, vertical rooting profiles should serve multiple purposes which should be included in the isotope-based Bayesian approach (*e.g.* to exclude water sources below the rooting zone; to derive the prior distribution of plant water uptake; to evaluate the hydrodynamic limit to local water uptake, as proposed above), but are not always available (particularly at species level and under field conditions). To counter this issue, multiple studies have used the optimality approach to evaluate likely rooting profiles based on trade-offs between carbon costs and needs for water and nutrients (Schymansky *et al.* 2015; Drewniak 2019; Ledder *et al.* 2020). Combining optimality and Bayesian isotopic approaches could open avenues for the investigation of season-dependent resource allocation and acquisition. Accounting for different phenological stages and distinct seasonal responses of the vegetation to environmental changes (*e.g.* drought intensity and duration) could be in sight.

Integrating Bayesian elements into the hydrodynamic approach

Regardless of their level of complexity, ranging from ‘big root’ (Bisht & Riley 2019) to 3D root ‘hydraulic architecture’ resolution at a very fine scale (Meunier *et al.* 2019), soil–plant hydrodynamic models tend to be deterministic and have commonly been used to solve inverse problems in a framework aimed at minimizing differences from observed variables, even when simulating the mixing of water isotopologues (Meunier *et al.* 2017; Couvreur *et al.* 2020; Knighton *et al.* 2020). Elements of stochasticity are, however, not new to models of root architecture (Pages *et al.* 2004) and soil hydrodynamics (Scharnagl *et al.* 2011), which share the same level of complexity as soil–plant hydrodynamic models. The most relevant example, to our knowledge, is that of De Deurwaerder *et al.* (2021), who fully coupled a physically-based soil–plant hydrodynamic model including water isotopologues advection–diffusion and Bayesian statistics to retrieve the probability density of soil water sources. Therefore, the inverse problem of reproducing target plant water isotope ratios with the hydrodynamic approach is posed in a probabilistic framework. While simple linear models allow the use of analytical equations to directly

express water sources probability functions, the non-linearity of soil and plant hydraulic functions (see *e.g.* Van Genuchten 1980) requires the use of iterative methods to find back probability densities, like an EMMA analysis. The most common iterative method is the Markov Chain Monte Carlo simulation (Brooks 1998), which repeatedly runs the (here, hydrodynamic) times with different sets of parameter values and compares the simulated and measured target outputs (stem water isotopic signature). Hence, while the search domain of the EMMA approach consists of water sources (possibly their past and present signatures), the search domain of the combined hydrodynamic–Bayesian approach determines the hydrodynamic model parametric space (*i.e.* the relative uptake from water sources is indirectly affected by the model parameter values). In the latter case, posterior probability densities concern parameter values, and indirectly other model outputs like the probability distribution of water sources. As such, iterative methods require a very large number of simulations before reaching convergence, where using simple models both in terms of number of parameters and computational requirements will be critical. Therefore, we envision that soil–plant hydrodynamic models with simple big-root or parallel-root geometries (Amenu & Kumar 2008; Kennedy *et al.* 2019) or upscaled forms (Sulis *et al.* 2019; Vanderborgh *et al.* 2021) will be favoured over models with very descriptive geometries (Javaux *et al.* 2008; Postma *et al.* 2017) when using Bayesian elements to estimate the probability function of plant water uptake profiles.

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