Received: 21 December 2023 | Accepted: 7 March 2024

DOI: 10.1002/vzj2.20333

Vadose Zone Journal

ORIGINAL ARTICLE

Special Section: Tribute to Rien van Genuchten, Recipient of the 2023 Wolf Prize for Agriculture

Mechanistically derived macroscopic root water uptake functions: The α and ω of root water uptake functions

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Assigned to Associate Editor Binayak Mohanty.

Funding information
Fonds De La Recherche Scientifique—FNRS, Grant/Award Number: ValentinCouvreur; Deutsche Forschungsgemeinschaft, Grant/Award Numbers: 1502, EXC-2070 – 390732324, 2089-403670197-403641034; Bundesministerium für Bildung und Forschung, Grant/Award Number: 031BO910B; BonaRes, Grant/Award Number: 031B1066C; European Research Council, Grant/Award Number: 101043083

Abstract

Water uptake by plant roots is an important component of the soil water balance. Predicting to what extent potential transpiration from the canopy, that is, transpiration demand, can be met by supply of water from the soil through the root system is crucial to simulate the actual transpiration and assess vegetation water stress. In models that simulate the dynamics of vertical soil water content profiles as a function of water fluxes and soil water potential gradients, the root water uptake (RWU) distribution is represented by macroscopic sink terms. We present RWU functions that calculate sink terms based on a mechanistic model of water flow in the soil–root system. Based on soil–root hydraulics, we define α-supply functions representing the maximal uptake by the root system from a certain soil depth when the root collar water potential equals the wilting point, ω-supply factors representing the maximal supply from the entire root system, and a critical ω_c factor representing the potential transpiration demand. These functions and factors are subsequently used to calculate RWU distributions directly from potential transpiration or demand and the soil water potentials. Unlike currently used approaches, which define α-stress functions and ω factors representing ratios of actual uptake to uptake demand, the supply-based formulations can be derived directly from soil and root hydraulic properties and can represent processes like root hydraulic redistribution and hydraulic lift.

1 | INTRODUCTION

Root water uptake (RWU) is an important component of the soil water balance. Because evaporation of water is related to consumption of heat, soil water extracted by roots and transported to leaves where it is transpired plays an important role in the land surface energy balance. Because water leaves the plant via the same openings in the leaves as the ones through which CO_2 can enter, that is, stomata, RWU is also linked to assimilation of carbon by plants and plant growth. When water cannot be taken up at a sufficiently high rate by the roots from the soil to meet the evaporative demand, stomata close, reduce the water loss, and avoid plants to desiccate. The maximal supply rate of water from the soil to the plant can be defined as the flow of water from the soil toward the leaves when the leaf water potential reaches a critical minimal water potential at which stomata close. This maximal supply rate depends on the soil water potential, the hydraulic conductivity of the soil, hydraulic conductivities of root segments and the shoot, and

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Abbreviations: nrld, normalized root length density; rld, root length density; RWU, root water uptake; SUF, standard uptake fraction.

the architecture of the root system. Accurately predicting this maximal supply rate and its dependence on soil and root properties and the soil water content in the root zone is therefore important for predicting water, heat, and carbon fluxes in the soil–plant–atmosphere system.

The most complete models that simulate these relations consider the 3D architecture of the root system, the resistances or conductances of individual root segments (Doussan et al., 1998; Javaux et al., 2008), and the soil around the root segments, the perirhizal zone (Khare et al., 2022; Schröder et al., 2009). We upscaled these models to 1D models that calculate RWU from horizontal soil layers (Vanderborght et al., 2023). However, RWU rates need to be calculated iteratively since soil resistances depend nonlinearly on water potentials in the bulk soil and at the soil–root interface and since soil–root interface water potentials depend on RWU rates. When changes in soil water content and soil water potential over time are simulated using Richard's equation-based models, this calculation needs to be performed for each time step that the equation is solved numerically, requiring much computing time. An important challenge is thus to develop physically based or mechanistic functions that calculate actual transpiration and RWU directly from bulk soil water potentials and potential transpiration, avoiding iterative procedures.

A number of approaches have been developed to calculate RWU directly from soil water potentials and potential transpiration (Skaggs et al., 2006). These approaches do not explicitly consider water flow in the plant and plant water potentials and are called macroscopic soil water uptake functions. One of the approaches uses so-called α-stress functions that express the ratio of the actual RWU from a certain soil depth to the potential uptake as a function of the soil water matric potential at that depth and the potential transpiration (Feddes & Raats, 2004; Feddes et al., 1978). This approach has been implemented in several soil water balance models, for example, Hydrus (Šimůnek et al., 2016) and SWAP (Kroes et al., 2017; van Dam et al., 2008). The α-stress functions have been parameterized for different plants or crop types. However, under dry soil conditions, also the resistance to flow from the bulk soil to the soil root interface plays an important role and should be considered. Due to the nonlinearity of the relation between soil hydraulic conductivity and soil water matric potential, the α-stress functions are nonlinear functions of the soil water matric potential and depend on soil properties and potential transpiration (de Jong van Lier et al., 2013; Javaux et al., 2013).

However, stress functions that represent the reduction in RWU compared to the potential RWU or RWU demand at a certain depth can be calculated as a unique function of the soil water potential only when it is assumed that the soil water potential in the root zone is uniform. If water potentials vary with depth in the root zone, then the water potential within the root system at a certain depth depends on the water potentials in the soil at other depths since the root system connects these depths. The uptake from a certain soil depth therefore also depends on soil water potentials at other depths, which leads to so-called RWU compensation. To represent nonlocal effects and compensation on RWU in empirical models, it has been proposed to modulate the local water uptake by the root length density (rld) weighted average of the α-stress factor in the root zone, the so-called ω factor, and divide the local uptake that is calculated from the α-stress function by this root system scale stress factor ω (Jarvis, 1989; Simunek & Hopmans, 2009). As long as the root system stress factor is larger than a critical stress factor ω_c, the total uptake from the root system stays equal to the potential transpiration. When the root system scale stress factor ω is smaller than ω_c, the uptake calculated by the α-stress function is divided by ω_c and the root system uptake becomes smaller than the potential uptake. Since no explicit relation between flow in the root system and the modulation of the RWU is considered, there is considerable conceptual uncertainty about using this modulation approach to represent RWU compensation. First, the link of RWU modulation to the water stress functions implies that RWU compensation only occurs when somewhere in the root zone RWU demand cannot be met by the supply from the soil. However, also in wet soils there can be a considerable shift of RWU to parts of the root zone where water potentials are higher even when the uptake from parts where the water potentials are lower is not limited by the supply (Javaux et al., 2013). A second problem with RWU modulation using a root system stress factor ω is that ω is only defined when plants take up water. As a consequence, the approach cannot be used to simulate phenomena like hydraulic redistribution or hydraulic lift, which refer to water transfer via the root system from wetter to drier zones and occur especially at night when RWU is low or equal to zero.

The objective of this paper is to develop macroscopic RWU functions from mechanistic RWU models that describe water flow in the soil–root system mechanistically. By making links to physically based models, (i) parameters of the macroscopic functions can be inferred directly from root and soil

Core Ideas

- Functions to calculate root water uptake (RWU) from different soil depths were derived.
- RWU is calculated directly using soil water potentials and the potential transpiration rate.
- The functions are derived using soil and root hydraulic properties.
- Phenomena like RWU compensation, hydraulic redistribution, and hydraulic lift are reproduced.
- Similarities and differences with currently used uptake functions are discussed.

system properties, (ii) the conceptual basis of macroscopic functions to describe RWU when there is no water stress is improved, and (iii) mechanistic RWU models can be replaced by macroscopic RWU functions, which reduces computation time.

We start with presenting a mechanistic RWU model that is an upscaled version of a three-dimensional (3D) soil and root system flow model. Subsequently, we introduce empirical macroscopic RWU models that are implemented in models that simulate soil water flow in soil profiles using the Richard's equation. Finally, we derive macroscopic RWU functions directly from the mechanistic RWU models. We consider in first step systems in which the resistance to water flow in soils can be neglected compared with the resistance to flow in the root tissues. We extend the approach in a second step to conditions when also the resistance to water flow from the bulk soil to the root segments is important. To keep the focus on the derivation of mechanistic RWU functions from soil and root hydraulic properties, we do not analyze the sensitivity of simulation results to simplifications that were made to derive the upscaled mechanistic RWU model, to simplifications in the parameterization of the mechanistic RWU functions, or to simplifications or assumptions made in empirical RWU functions.

2 | MATERIALS AND METHODS

2.1 | Mechanistic RWU model

We use the parallel root system model as an upscaled model for the 3-D root hydraulic architecture. The structure of the model is illustrated in Figure 1. Flow is described as a function of total water potentials, H (L), which include gravitation, matric, osmotic, and turgor potentials and can be expressed in length units or heads representing the energy of water per unit weight. The RWU rate, Q (L T^{-1}), from the ith soil layer (the volume of water taken up per unit of time from the layer divided by the top surface area of the layer) can be described as:

$$Q_i = \frac{K_{r,i} K_{x,i}}{K_{r,i} + K_{x,i}} \left[H_{\mathrm{sr},i} - H_{\mathrm{collar}} \right] \tag{1}$$

where K_r (T^{-1}) and K_x (T^{-1}) are the effective radial and axial root conductances, H_{sr} (L) is the water potential at the soil root interface, and H_{collar} (L) is the water potential at the root collar. By dividing the RWU rate from layer i by the thickness of the layer, Δz_i, the sink term S_i (T^{-1}) is obtained. We can reformulate the RWU rate in terms of a root system conductance, K_{rs} (T^{-1}), and a standard uptake fraction for layer i, SUF$_i$ (−) as (Couvreur et al., 2014):

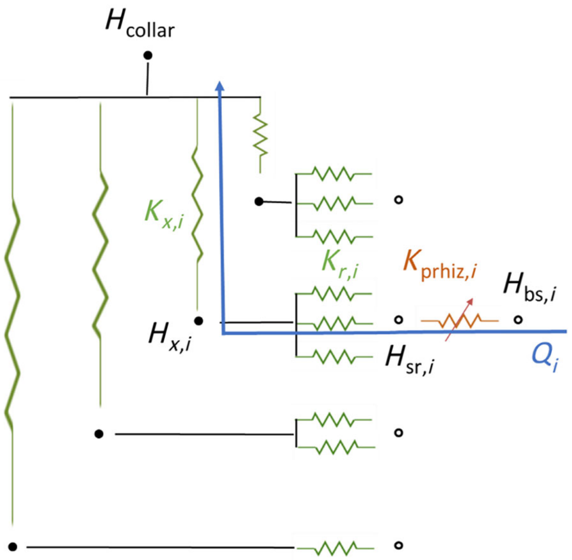

FIGURE 1 Parallel root system model. The green color refers to the root system, and the brown color refers to the perirhizal zone. The water that is taken up by the roots from ith soil layer, Q_i, flows to the root collar along a set of effective resistors: the resistance to flow in the perirhizal zone around the root segments, $K_{\mathrm{prhiz}}{}^{-1}$, the resistance to radial flow in the root segments, $K_r{}^{-1}$, and the resistance to axial flow in the root xylem, $K_x{}^{-1}$. (Instead of using resistances, we use their inverse, the conductance K.) Water flow along this path leads to a drop in water potentials from the water potential in the bulk soil, H_{bs}, at the soil–root interface, H_{sr}, in the root xylem, H_x, and at the root collar, H_{collar}.

$$Q_i = \mathrm{SUF}_i K_{\mathrm{rs}} \left[H_{\mathrm{sr},i} - H_{\mathrm{collar}} \right] \tag{2}$$

SUF$_i$ represents the fraction of the total RWU by the root system from the ith layer when the water potentials at the soil root interface are uniform in the root zone, that is, when there is a hydrostatic equilibrium in the root zone ($\mathrm{d}H_{\mathrm{sr}}/\mathrm{d}z = 0$). The root system conductance, K_{rs}, is a root system property that depends on the axial and radial conductances of the individual root segments and the root architecture. Since the axial and radial conductances of root segments are assumed to be independent of the water potential, K_{rs} is independent of the water potential. By summing up the uptake rate from all soil layers, it follows that K_{rs} represents the total RWU rate or transpiration, T (L T^{-1}), divided by the difference between the effective root zone water potential, H_{eff}, and H_{collar}:

$$K_{\mathrm{rs}} = \frac{T}{\left[H_{\mathrm{eff}} - H_{\mathrm{collar}} \right]} \tag{3}$$

$$H_{\mathrm{eff}} = \sum_i \mathrm{SUF}_i H_{\mathrm{sr},i} \tag{4}$$

Vanderborght et al. (2021) showed how K_{rs} and SUF can be derived directly from 3-D root hydraulic architectures. They found that also for non-uniform water potential distributions, the total RWU or transpiration that is calculated using the SUF-weighted local soil water potentials is exact. They also found that RWU distributions calculated with the parallel root model using SUF and K_{rs} derived from 3-D root hydraulic architectures approximate RWU distributions of the 3-D root system accurately.

When it is assumed that the resistance to water flow in the perirhizal zone, that is, the soil cylinder around a root segment in which water flows radially to the root segment, is small compared to the resistances to water flow in the root system, the soil water potential at the soil–root interface, H_{sr}, is close to the bulk soil water potential H_{bs} (L) and can be replaced by H_{bs} in the above equations.

When soil layers dry out, the soil hydraulic conductivity drops and the resistance to flow in the soil cannot be neglected. The soil hydraulic conductivity is a function of the soil water content, which in turn depends on the soil water matric potential, h (L). Therefore, soil water potential needs to be split up into its components. Assuming that the osmotic soil water potential can be neglected, the matric potential of the soil water, h, at a point at elevation z where the water potential equals H is:

$$h = H - z \tag{5}$$

The resistance to flow in the perirhizal zone, or its inverse, the perirhizal conductance, K_{prhiz} (T^{-1}), can be calculated from (de Jong van Lier et al., 2006, 2008; Schröder et al., 2008):

$$K_{\mathrm{prhiz}}\left(h_{\mathrm{bs}}, h_{s,r}\right) = 2\pi l_{\mathrm{root}} B \bar{k}_{\mathrm{prhiz}}\left(h_{\mathrm{bs}}, h_{s,r}\right) \tag{6}$$

$$\bar{k}_{\mathrm{prhiz}}\left(h_{bs}, h_{s,r}\right) = \frac{\int_{-\infty}^{h_{bs}} K(h)\,dh - \int_{-\infty}^{h_{s,r}} K(h)\,dh}{h_{bs} - h_{s,r}} \tag{7}$$

$$B = \frac{2\left(\rho^2 - 1\right)}{1 - (0.53\rho)^2 + 2\rho^2\left[\ln\rho + \ln(0.53)\right]} \tag{8}$$

$$\rho = \frac{r_{\mathrm{prhiz}}}{r_{\mathrm{root}}} \tag{9}$$

where l_{root} (L^{-1}) is total root length in a soil layer with thickness Δz divided by the horizontal surface area of the layer and which is calculated from the rld ($\mathrm{L\ L}^{-3}$) as $l_{\mathrm{root}} = \mathrm{rld}\ \Delta z$, $\bar{k}_{\mathrm{prhiz}}$ ($\mathrm{L\ T}^{-1}$) is an "effective conductivity" of the perirhizal zone, which is calculated from the soil hydraulic conductivity K ($\mathrm{L\ T}^{-1}$) in the perirhizal zone, h_{bs} (L) is the bulk soil matric potential, which corresponds to the matric potential at the average water content in the perirhizal cylinder, $h_{s,r}$ (L) is the matric potential at the soil–root interface, and r_{prhiz} (L) is the radius of the perirhizal cylinder and corresponds to the average distance between roots calculated from the root length as $r_{\mathrm{prhiz}} = (\pi\ \mathrm{rld})^{-0.5}$. B is a geometry factor that depends on the ratio of r_{prhiz} to the root radius, r_{root}. The perirhizal effective conductivity $\bar{k}_{\mathrm{prhiz}}$ is derived from the soil hydraulic conductivity curve, which is assumed to be identical to the hydraulic conductivity curve of the bulk soil.

Including the perirhizal conductance along the flow path from the bulk soil to the root collar, the RWU rate is obtained as:

$$Q_i = \frac{\mathrm{SUF}_i K_{\mathrm{rs}} K_{\mathrm{prhiz},i}}{\mathrm{SUF}_i K_{\mathrm{rs}} + K_{\mathrm{prhiz},i}}\left[H_{\mathrm{bs},i} - H_{\mathrm{collar}}\right] \tag{10}$$

As for the root system conductance (see Equations 2 and 3), we can formulate the RWU using the soil–root system conductance K_{srs} (T^{-1}):

$$Q_i = \mathrm{SUF}_i K_{\mathrm{srs},i}\left[H_{\mathrm{bs},i} - H_{\mathrm{collar}}\right] \tag{11}$$

with:

$$K_{srs,i} = \frac{K_{rs} K_{\mathrm{prhiz},i}}{\mathrm{SUF}_i K_{rs} + K_{\mathrm{prhiz},i}} \tag{12}$$

Unlike K_{rs} in Equation (2), the soil–root system conductance, K_{srs}, varies with depth in the soil profile since K_{prhiz} depends on the rld and bulk soil matric potential, h_{bs}, which both can vary with depth. K_{prhiz} also depends on the matric potential at the soil–root interface, h_{sr}, which is in turn related to the uptake rate and the collar water potential, H_{collar}, so that Equation (11) must be solved iteratively when either H_{collar} or the transpiration rate is known.

2.2 | Empirical macroscopic uptake functions

Empirical RWU functions are based on the demand for water by the atmosphere, the so-called potential transpiration, T_p, which can be calculated by solving an energy balance at the canopy surface (Allen et al., 1998). The demand is distributed over the root zone following the depth nrld (L^{-1}), and a potential RWU rate, Q_p ($\mathrm{L\ T}^{-1}$), from a certain soil layer can be defined as:

$$Q_{p,i} = \mathrm{nrld}_i \Delta z_i T_p \tag{13}$$

In a second step, an α-stress function is defined, which varies between 0 and 1 and is a function of soil water matric potential and the potential transpiration. Note that in empirical macroscopic RWU functions, the matric potential not the total hydraulic head or total water potential is used. Typically, the α-stress function is represented by a piecewise linear function with $\alpha = 1$ for $h > h_{\text{crit}}$, h_{crit} a function of T_p, and α decreasing linearly from $\alpha = 1$ for $h = h_{\text{crit}}$ to $\alpha = 0$ for $h = h_{\text{wilting}}$, where h_{wilting} is the "wilting point". As will be explained later, the physical meaning of the α-stress function is difficult to define. In order to describe uptake from a soil profile with variations in h in the root zone, a root system stress factor ω is defined as a rld weighted average of α-stress factors that are calculated with the α-stress function for different depths in the root zone:

$$\omega = \sum \text{nrld}_i \alpha \left(h_i\right) \Delta z_i \tag{14}$$

This stress factor represents an average stress level in the root system. When the stress factor is not smaller than a critical stress factor, ω_c, the root system uptake is equal to demand or the potential transpiration. The critical stress factor ω_c is an empirical factor that is assumed to depend on the crop type. When $\omega < \omega_c$, the total RWU is reduced so that the actual transpiration, T_{act}, is smaller than T_p:

$$T_{\text{act}} = \frac{\omega}{\omega_c} T_p \tag{15}$$

The local RWU rate is given by:

$$Q_i = \frac{\text{nrld}_i \alpha \left(h_i\right) \Delta z_i}{\max \left(\omega, \omega_c\right)} T_p \tag{16}$$

Equation (16) assures that the total RWU rate calculated from the sum of the local RWU rates is consistent with Equations (14) and (15) and with Equation (13) when $\alpha (h) = 1$ for all depths. By dividing the local uptake rate by ω or ω_c, the local uptake rate is modulated for every depth with the same factor. For $\omega > \omega_c$, the uptake increases more in regions where α is larger than in regions where α is lower compared to the case where $\omega = 1$ and the soil profile is sufficiently wet so that $\alpha = 1$ everywhere in the root zone. When the soil dries out nonuniformly and α becomes smaller than one in some regions, this leads to a shift in RWU from drier (where $\alpha < 1$) toward wetter soil layers (where $\alpha = 1$) where RWU rates even increase compared to the case when $\alpha = 1$ everywhere in the root zone. However, the relative RWU distribution, that is, the RWU rates divided by the total uptake, is not changed compared to the relative distribution that would be obtained using the α-stress factors. Equation (16) does not "shift" the relative RWU to wetter regions in the root zone more than the α-stress factors do. It changes the soil water matric potential (for a given T_p) at which the transpiration is reduced, which for $\omega_c < 1$ becomes more negative than the critical matric potential, h_{crit}, used in the α-stress function. As a consequence, the α-stress function used in Equation (16) does not represent the ratio of the actual to potential transpiration as a function of the soil water potential (Skaggs et al., 2006), which is the original interpretation of the α-stress function (Feddes & Raats, 2004). The original interpretation of the α-stress function corresponds with $\omega_c = 1$, so that actual transpiration is reduced when $h < h_{\text{crit}}$ in at least one layer of the soil profile. The original interpretation was used to determine the critical soil water matric potential at which α (h) becomes smaller than one, that is, $h_{\text{crit\_org}}$, empirically from experimental observations and assuming that the h is uniform in the root zone. This obviously leads to problems when $h_{\text{crit\_org}}$ is used in the α-stress function in Equations (14) and (16) in combination with $\omega_c < 1$, for which the interpretation of the α-stress function is different from the original one. The critical matric potential of the α-stress function used in Equations (14) and (16), h_{crit}, could be calculated from $h_{\text{crit\_org}}$ as:

$$h_{\text{crit}} = \frac{\left[h_{\text{crit\_org}} - \left(1 - \omega_c\right) h_{\text{wilting}}\right]}{\omega_c} \tag{17}$$

Instead of relating the α-stress function and ω to the ratio of actual uptake to the transpiration demand (Equation 15), Jarvis (2011) defined them as ratios of the maximal possible RWU rate to the maximal RWU rate when the soil is completely wet. The maximal RWU rates are defined as the maximal flow that is possible from the soil to the root collar when the water potential in the root collar, H_{collar}, is equal to the wilting water potential, H_{wilting}. This flow rate corresponds with the maximal flow rate that can be "supplied" by the soil and the root system to the root collar and is independent of the atmospheric "demand" or T_p, which corresponds with the maximal amount of water that can be transferred from the leaves to the atmosphere with the available energy for evaporation. By redefining α, Jarvis (2011) showed that (i) under plant water stress, the empirical model (i.e., Equations 14–16) gives identical water uptake distributions in the soil profile as the physics-based model derived by de Jong van Lier et al. (2008), which explicitly considers perirhizal resistances but not plant resistances, but that (ii) the water uptake distributions in the soil profile predicted by the empirical model do differ from the physically based model when the plants are unstressed, that is, when actual transpiration equals the potential transpiration. However, neglecting the root resistance led to the simulation of spurious redistribution of water in wet soils. In the following, we first derive uptake functions using supply ratios for the case that resistances in the soil–root system are dominated by the root system. Subsequently, we add the perirhizal resistances in the analyses.

2.3 | Macroscopic uptake functions when perirhizal resistances, $K_{\mathrm{prhiz}}{}^{-1}$, are negligible

We define α as the maximal uptake from a soil layer for a certain soil water potential H_{bs} in that layer, $Q_{i,\max}$, to the maximal uptake from that layer when the soil is completely wet $Q_{i,\max,\mathrm{wet}}$. It must be noted that we do not consider a reduction in RWU when the soil is wet and roots experience oxygen stress. ω represents the ratio of the maximal uptake by the root system from the entire soil profile, $T_{\max}$, for a certain effective soil water potential, to the maximal uptake when the soil profile is wet, $T_{\max,\mathrm{wet}}$. When defining $z = 0$ at the root collar, a completely wet soil profile corresponds with an effective soil water potential $H_{\mathrm{eff}} = 0$, so that α and ω can be derived using the parallel root system model as:

$$\alpha\left(H_{\mathrm{bs},i}\right) = \frac{Q_{i,\max}}{Q_{\mathrm{i},\max,\mathrm{wet}}} = \frac{\mathrm{SUF}_i K_{\mathrm{rs}}\left[H_{\mathrm{bs},i} - H_{\mathrm{wilting}}\right]}{\mathrm{SUF}_i K_{\mathrm{rs}}\left[-H_{\mathrm{wilting}}\right]} = \frac{\left[H_{\mathrm{bs},i} - H_{\mathrm{wilting}}\right]}{\left[-H_{\mathrm{wilting}}\right]} = 1 - \frac{H_{\mathrm{bs},i}}{H_{\mathrm{wilting}}} \tag{18}$$

$$\omega = \frac{T_{\max}}{T_{\max,\mathrm{wet}}} = \frac{\sum \mathrm{SUF}_i K_{\mathrm{rs}}\left[H_{\mathrm{bs},i} - H_{\mathrm{wilting}}\right]}{\sum \mathrm{SUF}_i K_{\mathrm{rs}}\left[-H_{\mathrm{wilting}}\right]} = \frac{\sum \mathrm{SUF}_i\left[H_{\mathrm{bs},i} - H_{\mathrm{wilting}}\right]}{\left[-H_{\mathrm{wilting}}\right]} = 1 - \frac{H_{\mathrm{eff}}}{H_{\mathrm{wilting}}} \tag{19}$$

Observe that the root system conductance is no longer in the definitions of α and ω. α only depends on the wilting water potential and is a linear function of H_{bs} and ranges from $\alpha = 0$ for $H_{\mathrm{bs}} = H_{\mathrm{wilting}}$ to $\alpha = 1$ for $H_{\mathrm{bs}} = 0$. Unlike currently used α-stress functions (see, for instance, Simunek and Hopmans [2009]), the redefined α -supply ratio function is defined in terms of the soil water potential or hydraulic head, H_{bs}, no longer depends on the potential transpiration T_p, and does not reach 1 for H_{bs} values smaller than 0. As a consequence, α varies with depth as soon as H_{bs} varies with depth. When using nrld Δz as a proxy for SUF, the same relation between α and ω is obtained as in the empirical macroscopic RWU function (see Equation 14):

$$\omega = \sum \mathrm{SUF}_i \alpha\left(H_{\mathrm{bs},i}\right) \tag{20}$$

According to Jarvis (2011), we define the critical supply ratio ω_c as the ratio of the potential transpiration or the transpiration demand to the maximal supply by the root system when the soil is completely wet:

$$\omega_c = \frac{T_p}{T_{\max,\mathrm{wet}}} = \frac{T_p}{\sum \mathrm{SUF}_i K_{\mathrm{rs}}\left[-H_{\mathrm{wilting}}\right]} = \frac{T_p}{\left[-H_{\mathrm{wilting}}\right] K_{\mathrm{rs}}} \tag{21}$$

When the actual supply ratio ω is smaller than the critical supply ratio ω_c, then the transpiration demand cannot be met. When ω is defined as a supply ratio instead of a stress factor, the critical supply ratio, ω_c, is proportional to the transpiration demand. That implies that for higher transpiration demands, water stress, that is, the transpiration demand cannot be met by the RWU, occurs for higher ω factors, which correspond to wetter soil conditions or higher H_{bs}.

When $\omega \le \omega_c$, the actual water uptake equals the maximal supply with $H_{\mathrm{collar}} = H_{\mathrm{wilting}}$, and the uptake distributions can be written in terms of the α and ω_c supply ratios as:

$$\begin{aligned} Q_i = Q_{,i,\max} = {} & \left[\frac{Q_{,i,\max}}{Q_{i,\max,\mathrm{wet}}}\right]\left[\frac{Q_{,i,\max,\mathrm{wet}}}{T_{\max,\mathrm{wet}}}\right]\left[\frac{T_{\max,\mathrm{wet}}}{T_p}\right] T_p \\ = {} & \quad \alpha\left(H_{\mathrm{bs},i}\right) \qquad \mathrm{SUF}_i \qquad \frac{1}{\omega_c} \qquad T_p \end{aligned} \tag{22}$$

When $\omega > \omega_c$, the maximal RWU or maximal supply, $T_{\max}$, is larger than the transpiration demand T_p, so that the actual RWU rate, T_{act}, is equal to T_p, and $H_{\mathrm{collar}} > H_{\mathrm{wilt}}$. To describe the uptake distribution for $\omega > \omega_c$ as a function of the α and ω factors, the SUF and the potential transpiration, we use Equation (3) to relate H_{collar} to the effective soil water potential, H_{eff}, K_{rs}, and T_p, and plug it into Equation (2):

$$Q_i = \mathrm{SUF}_i K_{\mathrm{rs}}\left[H_{\mathrm{bs},i} - H_{\mathrm{eff}} + \frac{T_p}{K_{\mathrm{rs}}}\right] \tag{23}$$

which corresponds to:

$$Q_i = \mathrm{SUF}_i K_{\mathrm{rs}}\left[H_{\mathrm{bs},i} - H_{\mathrm{wilting}}\right] - \mathrm{SUF}_i K_{\mathrm{rs}}\left[H_{T,\mathrm{eff}} - H_{\mathrm{wilting}} - \frac{T_p}{K_{\mathrm{rs}}}\right] \tag{24}$$

The first term of Equation (24) corresponds to the maximal supply rate, $Q_{i,\max}$ (Equation 22), while the second term is a correction term that accounts for the difference between the actual and wilting collar water potential. After rearranging the second term, we obtain using Equations (18), (19), and (21):

$$Q_i = \alpha\left(H_{\mathrm{bs},i}\right) \mathrm{SUF}_i \frac{T_p}{\omega_c} - \mathrm{SUF}_{\mathrm{i}}\left[\frac{\omega}{\omega_c} - 1\right] T_p \tag{25}$$

According to Equation (18), when the soil water potential H_{bs} is not uniform and smaller than 0, α is larger in regions where H_{bs} is larger, so that following Equation (25), Q will be larger from soil layers with higher H_{bs} and smaller from layers with lower H_{bs} compared to the situation when the soil water potential is uniform and equal to H_{eff}. This implies that Equation (25) simulates the redistribution of water uptake toward regions in the root zone where the water potentials are higher. This is different from the empirical approach that does not simulate redistribution of uptake when the demand can be met by the supply at each depth in the root zone and the α-stress function equals one everywhere in the root zone.

According to Equation (21), $\omega_c = 0$ when $T_p = 0$. Since the limit of T_p/ω_c when T_p tends to zero is defined as $-H_{\text{wilting}} K_{\text{rs}}$, Equation (25) can also be used at night when $T_p = 0$. Since the total uptake rate at night is zero, it follows that Equation (25) will simulate uptake from some layers and release in others, that is, hydraulic redistribution, depending on H_{bs}.

2.4 | Macroscopic uptake functions including perirhizal resistances, $K_{\text{prhiz}}{}^{-1}$

When we account for perirhizal resistance, α_i as the ratio of the maximal RWU rate from the ith soil layer to the maximal RWU rate from that layer when the soil is wet becomes:

$$\alpha_i\left(H_{bs,i}\right) = \frac{\text{SUF}_i K_{\text{srs},i}\left[H_{\text{bs},i} - H_{\text{wilting}}\right]}{\text{SUF}_i K_{\text{rs}}\left[-H_{\text{wilting}}\right]} = \frac{K_{\text{srs},i}\left[H_{\text{bs},i} - H_{\text{wilting}}\right]}{K_{\text{rs}}\left[-H_{\text{wilting}}\right]} \tag{26}$$

where $K_{srs,i}$ is the soil–root system conductance in the ith soil layer and for a collar water potential equal to H_{wilting} (Equation 12). Since the soil root system conductance, K_{srs}, is a nonlinear function of the bulk soil water potential and a function that varies with depth due to variations in rld and SUF with depth (Figure 2d), (in a layered soil profile, K_{srs} also varies with depth due to varying soil hydraulic properties), α is a nonlinear function of H_{bs} that varies with depth. When H_{bs} approaches zero (wet soil conditions), the perirhizal resistance can be neglected compared to the root resistance, and K_{srs} tends to K_{rs}. For each depth, a set of $K_{\text{srs},i}$ values can be derived for a set of H_{bs} values and for $H_{\text{collar}} = H_{\text{wilting}}$ by iteratively solving Equation (11). With this set of $K_{\text{srs},i}$ values, a set of α_i values is obtained (Equation 26), which can be used in an interpolation function to calculate α_i values directly for a given H_{bs}.

Analogous to the case where perirhizal resistances can be neglected (Equation 20), the ω factor is equal to the SUF-weighted α-supply ratios:

$$\omega = \frac{T_{\max}}{T_{\max,\text{wet}}} = \frac{\sum \text{SUF}_i K_{\text{srs},i}\left[H_{\text{bs},i} - H_{\text{wilting}}\right]}{\sum \text{SUF}_i K_{\text{rs}}\left[-H_{\text{wilting}}\right]} = \sum \text{SUF}_i \alpha_i\left(H_{\text{bs},i}\right) \tag{27}$$

The difference between Equations (27) and (20) is that in the former, the α–supply ratio function varies with depth.

Since K_{srs} is smaller than K_{rs} and decreases with decreasing H_{bs}, the ω factor is smaller when perirhizal conductances are considered. However, the ω_c factor, which is defined as the ratio of the potential transpiration to the maximal uptake when the soil is wet, hardly depends on the perirhizal conductances since the saturated soil hydraulic conductance is generally much larger than the root hydraulic conductance so that $K_{\text{srs}}(H_{\text{bs}} = 0) \approx K_{\text{rs}}$. Considering perirhizal conductance or resistance therefore leads to a reduction in transpiration rate at less negative H_{bs} than in case perirhizal conductance or resistance is not considered.

The RWU rate when $\omega \leq \omega_c$ is calculated in the same way as for the case where perirhizal conductances are not considered, with the only difference that the α functions are depth dependent and nonlinearly dependent on the soil water potential:

$$Q_i = \alpha_i\left(H_{\text{bs},i}\right) \text{SUF}_i \frac{T_p}{\omega_c} \tag{28}$$

Plugging Equations. (21) and (26) in Equation (28) leads exactly to Equation (11), so that the RWU rate calculated with the macroscopic uptake function (Equation 28) is exactly the same as the uptake calculated with the soil–root hydraulic model (Equation 11).

When $\omega > \omega_c$, the uptake is smaller than the maximal RWU rate and corresponds to the transpiration demand, T_p. Under these conditions, $H_{\text{collar}} > H_{\text{wilting}}$. The perirhizal conductance K_{prhiz} (Equation 6) and the soil–root system conductance K_{srs} are both functions of the bulk soil water potential and the collar water potential. When the flux at the root collar is set to T_p, the water potentials at the soil root interfaces at the different depths and the root collar water potential have to be found by solving the set of nonlinear uptake equations for each soil layer (Equation 11), which are coupled by one additional equation: $T_p = \sum Q_i$, iteratively. To avoid these iterations so that the uptake rates can be calculated directly from H_{bs} and T_p, we assume that K_{srs} calculated for $H_{\text{collar}} = H_{\text{wilting}}$ can also be applied for other collar water potentials. Unlike for the previous case with $\omega < \omega_c$ where the soil–root hydraulics could be represented exactly using the α and ω functions, this assumption leads to an approximation. Using Equation (11), with K_{srs} approximated by K_{srs} for $H_{\text{collar}} = H_{\text{wilting}}$, H_{collar} is calculated from:

$$H_{\text{collar}} \approx \frac{\sum \text{SUF}_i K_{\text{srs},i} H_{\text{bs},i}}{\sum \text{SUF}_i K_{\text{srs},i}} - \frac{T_p}{\sum \text{SUF}_i K_{\text{srs},i}} \tag{29}$$

The first term could be interpreted as an effective root zone water potential. However, unlike the case when perirhizal resistance can be neglected, the weights used to calculate the effective root zone water potential depend on soil water potentials and their distribution, since K_{srs} depends on the bulk soil water potential.

Substituting H_{collar} in Equation (11) gives:

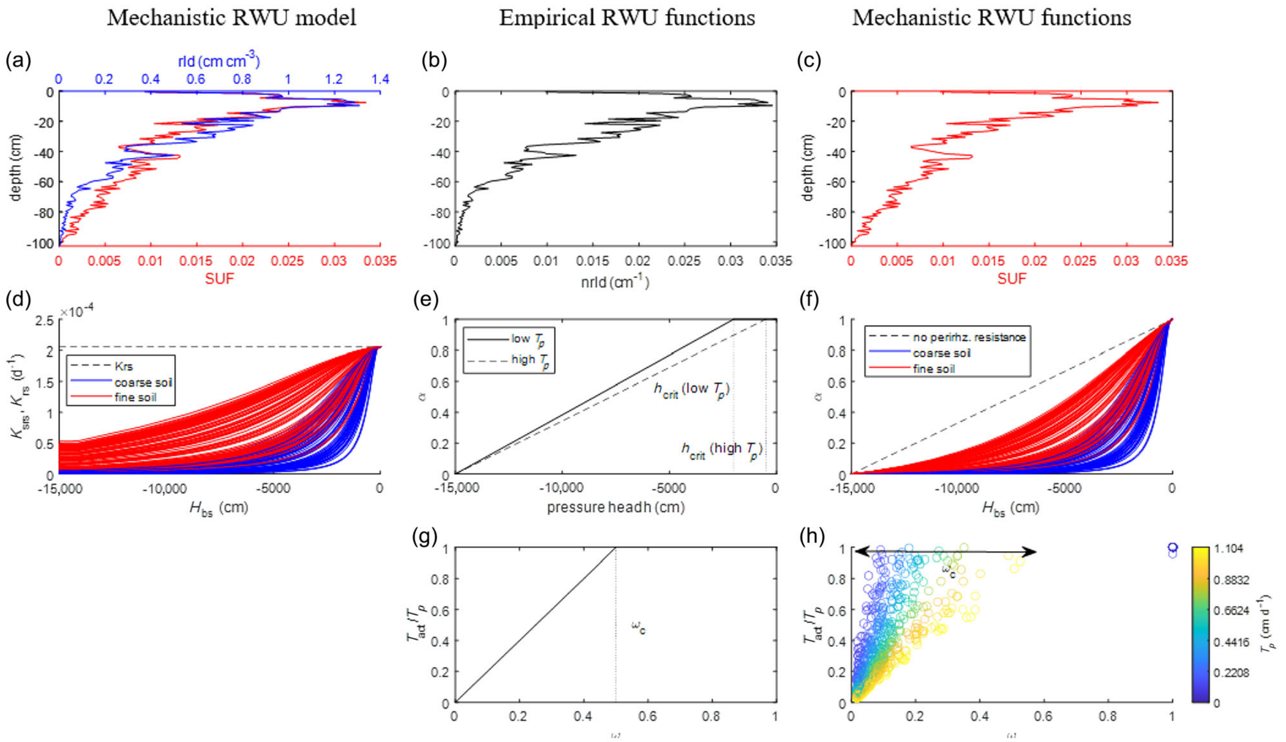

FIGURE 2 Functions used in the mechanistic root water uptake (RWU) model (a, d), empirical RWU functions (b, e, and g), and mechanistic RWU functions (c, f, and h). The top row represents: the root length density (a), normalized root length density (b), and standard uptake fraction (SUF) fractions (a, c) that are used to distribute RWU over the root zone. The middle row shows functions that relate the uptake to the bulk soil water potentials or soil water matric potentials: the soil root system conductances, K_{srs}, for a root collar water potential $H_{collar} = H_{wilting}$ and for different soil depths in the fine- and coarse-textured soil (the black dashed line represents the root system conductance, K_{rs}) (d); the α-stress functions for a high and a low potential transpiration (e); and the α-supply ratio functions in a fine- and coarse-textured soil for different depths (the dashed black line is for the case the soil resistance is not included) (f). The bottom row represents the relation between the ratio of actual to potential transpiration rate T_{act}/T_p and the root zone weighted stress factor ω (g); and the root zone weighted supply ratio factor ω (h); together with the critical stress factor ω_c (g); and the critical supply ratio factor ω_c, which depends on T_p (h).

$$Q_i \approx \mathrm{SUF}_i K_{\mathrm{srs},i}\left[H_{\mathrm{bs},i} - \frac{\sum \mathrm{SUF}_i K_{\mathrm{srs},i} H_{\mathrm{bs},i}}{\sum \mathrm{SUF}_i K_{\mathrm{srs},i}} - \frac{T_p}{\sum \mathrm{SUF}_i K_{\mathrm{srs},i}}\right] \tag{30}$$

Equation (30) is an approximation of Equation (11) since K_{srs} in Equation (30) is calculated for a collar water potential $H_{collar} = H_{wilting}$. Equation (30) can be written in terms of α and ω_c as:

$$\begin{aligned} Q_i &\approx \alpha_i\left(H_{\mathrm{bs},i}\right)\mathrm{SUF}_i\frac{T_p}{\omega_c} - \mathrm{SUF}_i\frac{K_{\mathrm{srs},i}}{\sum \mathrm{SUF}_i K_{\mathrm{srs},i}}\left[\frac{\omega}{\omega_c}-1\right]T_p \\ &\approx \alpha_i\left(H_{\mathrm{bs},i}\right)\mathrm{SUF}_{\mathrm{i}}\frac{T_p}{\omega_c} - \mathrm{SUF}_i\frac{K_{\mathrm{srs},i}}{\overline{K}_{\mathrm{srs}}}\left[\frac{\omega}{\omega_c}-1\right]T_p \\ &\approx \alpha_i\left(H_{\mathrm{bs},i}\right)\mathrm{SUF}_i\frac{T_p}{\omega_c} - \frac{\alpha_i\left(H_{\mathrm{bs},i}\right)\mathrm{SUF}_i}{\left[H_{\mathrm{bs},i}-H_{\mathrm{wilting}}\right]\left[\sum\frac{\alpha_i\left(H_{\mathrm{bs},i}\right)\mathrm{SUF}_i}{H_{\mathrm{bs},i}-H_{\mathrm{wilting}}}\right]}\left[\frac{\omega}{\omega_c}-1\right]T_p \end{aligned} \tag{31}$$

This equation is similar to the equation for the case that perirhizal resistance can be neglected (Equation 25), but the weighting factor of the second term is not equal to SUF.

An overview of the functions and their meaning is given in Table 1. It is interesting that the RWU functions, considering only root resistances, relate the α-supply ratios exactly in the same way to RWU rates as the RWU functions that were derived by Jarvis (2011) (compare Equations 12 and 13 in Jarvis (2011) with Equations 22 and 25), but the shape of the α-supply ratio functions and the weighting factors (SUF in our paper versus R in Jarvis [2011]) are different when either root or perirhizal conductances are considered. However, when considering both root and perirhizal conductances (Equations 28 and 31), we obtained slightly different relations of the non-stressed RWU equation (Equation 31), with a different weighting of its second term. We found that this term should be weighted by the SUF-weighted soil–root system conductance, K_{srs}.

2.5 | Simulation setups

To illustrate and evaluate the mechanistically derived macroscopic uptake functions that consider perirhizal resistances (Equations 28 and 31), we carried out simulations of water flow and RWU in drying soil profiles during a summer crop growing season with a large precipitation deficit of 400 mm. Two soil profiles, one with a coarse texture and one with a

TABLE 1 Overview of the α functions and ω factors used in the empirical and mechanistic root water uptake (RWU) functions to calculate RWU rates, Q.

		α	ω	ω_c	Q
Empirical	Meaning	$\frac{\text{Actual uptake from depth } z}{\text{Water demand from depth } z}$ (when soil water matric potential is uniform)	Root system averaged stress factor	Critical stress factor	
	Functions	$\begin{cases} \alpha = \frac{h - h_{\text{wilting}}}{h_{\text{crit}}(T_p) - h_{\text{wilting}}} & \text{for } h < h_{\text{crit}}(T_p) \\ \alpha = 1 & \text{for } h \geq h_{\text{crit}}(T_p) \end{cases}$	$\omega = \sum \text{nrld}_i \alpha(h_i) \Delta z_i$	Fixed parameter	$Q_i = \frac{\text{nrld}_i \alpha(h_i) \Delta z_i}{\max(\omega, \omega_c)} T_p$
Mechanistic	Meaning	$\frac{\text{Maximal supply from depth } z}{\text{Maximal supply from depth } z \text{ when soil is wet}}$ (when $H_{\text{collar}} = H_{\text{wilting}}$)	$\frac{\text{Maximal supply by the root system}}{\text{Maximal supply when soil is wet}}$	$\frac{\text{Transpiration demand}}{\text{Maximal supply when the soil is wet}}$	
	Functions	$\alpha_i = \frac{K_{\text{srs},i}[H_{\text{bs},i} - H_{\text{wilting}}]}{K_{\text{rs}}[-H_{\text{wilting}}]}$	$\omega = \sum \text{SUF}_i \alpha_i$	$\omega_c = \frac{T_p}{[-H_{\text{wilting}}]K_{\text{rs}}}$	For $\omega < \omega_c$ $Q_i = \alpha_i (H_{\text{bs},i}) \text{SUF}_i \frac{T_p}{\omega_c}$ For $\omega \geq \omega_c$ $Q_i \approx \alpha_i \text{SUF}_i \frac{T_p}{\omega_c} - \frac{\alpha_i \text{SUF}_i}{[H_{\text{bs},i} - H_{\text{wilting}}][\sum \frac{\alpha_i \text{SUF}_i}{H_{\text{bs},i} - H_{\text{wilting}}}]} [\frac{\omega}{\omega_c} - 1] T_p$

fine texture, of 150-cm depth and with uniform soil hydraulic properties, were simulated. The hydraulic properties of the soils are given in Table 2. The initial condition was a uniform matric potential profile with $h = -330$ cm. Hourly reference potential transpiration rates were calculated from meteorological data using the FAO Penman equation (Allen et al., 1998). At times without precipitation, a no-flow boundary condition (no evaporation) was used at the soil surface, and a free drainage boundary condition was applied at the bottom of the simulation domain. The root system conductance K_{rs} of a generic crop was 2.05×10^{-4} day^{-1}. Its rld and SUF are given in Figure 2a–c and the SUF was close to the nrld. The similarity between the SUF and rld profile suggests that rld may be a good proxy of SUF for the considered root system. A more detailed analysis of the analogy or difference between SUF and rld and of the root hydraulic properties that influence this difference is given by Javaux et al. (2008) and Javaux et al. (2013). For further details of the simulation setup, we refer to Vanderborght et al. (2023).

We compared the simulation using macroscopic uptake functions with a simulation using the upscaled mechanistic model (Equation 11). We focus on the setup that considers perirhizal resistances since their impact on the simulated uptake and the plant water potentials, compared with the case where they were neglected, was discussed in Vanderborght et al. (2023). Furthermore, our analyses above showed that the approach considering only linear root system hydraulics and neglecting perirhizal resistances can be represented exactly by macroscopic RWU functions (Equations 22 and 25).

3 | RESULTS

Figure 2 gives an overview of the functions and properties used in the different approaches to simulate RWU: the mechanistic RWU model, the empirical RWU functions, and the mechanistically derived RWU functions. In Figure 2d, K_{srs} of the generic crop with a root collar potential H_{collar} of −15,000 cm is plotted versus the bulk soil water potential, H_{bs}, for a soil with a coarse texture (blue lines) and a soil with a fine texture (red lines). Each line corresponds to a K_{srs} at a specific depth. Figure 2d illustrates that for high H_{bs}, K_{srs} converges at all soil depths to the root system conductance, K_{rs}, and that, due to a decrease in soil hydraulic conductivity, K_{srs} decreases when H_{bs} drops. The change of K_{srs} with H_{bs} therefore depends on the soil hydraulic properties. In the soil with a fine texture, K_{srs} does not decrease so strongly with decreasing H_{bs} than in the soil with a fine texture.

The variation in K_{srs} versus H_{bs} curves with depth can be explained by the variation in perirhizal conductance, K_{prhiz}, with depth. K_{prhiz} depends on the radii of the roots and of the perirhizal cylinders, which depend on the rld. A lower rld deeper in the soil corresponds to a larger distance between

TABLE 2 Parameters of the van Genuchten-Mualem hydraulic functions (van Genuchten, 1980) estimated with ROSETTA (Schaap et al., 2001).

Soil texture	θ_s	θ_r	α (cm^{-1})	N	K$_s$ (cm day^{-1})	l
Coarse	0.403	0.025	0.0383	1.3774	60	0.5
Fine	0.43	0.01	0.0083	1.2539	2.272	0.5

the bulk soil and the root surface, a lower K_{prhiz}, and a lower K_{srs}. The decrease in K_{srs} with depth, for a given H_{bs}, due to a decrease in root density may be partly compensated by an increase in soil matric potential, h, with depth. Considering that the root system is around 100 cm deep, the soil water matric potential, h, increases, for a given H_{bs}, with 100 cm from the top to the bottom of the root system. Especially in the coarse-textured soil and for larger H_{bs} (>-1000 cm), this variation in h with depth may generate a substantial increase in effective perirhizal conductivity $\bar{k}_{\text{prhiz}}$ with depth.

The relative variation in K_{srs} with depth for a given H_{bs} increases when H_{bs} decreases. This implies that the RWU distribution in a soil profile with a uniform H_{bs} may differ between dry and wet soils. In wet soils, the relative variation in K_{srs} is small, and the uptake distribution depends on the root hydraulic properties and is represented by the root system property SUF. In dry soils, the resistance to flow in the perirhizal zone, which depends on the soil hydraulic properties and the rld, defines K_{srs}, its variation with depth, and the RWU distribution.

Figure 2f shows the α-supply ratio (Equation 26) versus H_{bs} for different depths in the soil profile. The variation in the α-supply ratio versus H_{bs} curves between different soil textures and with depth, which is mainly due to variations in root length density, reflects the corresponding variation in the soil–root system conductance K_{srs} versus H_{bs} curves. The deviation of the α curves from a straight line between $\alpha = 0$ at $H_{\text{bs}} = H_{\text{wilting}}$ and $\alpha = 1$ at $H_{\text{bs}} = 0$, reflects the impact of the perirhizal conductance, K_{prhiz}, which depends on the soil hydraulic conductivity and the radii of the roots and perirhizal cylinders around the roots. The concave shape of the α-supply ratio functions and their dependency on root density and soil hydraulic properties are qualitatively similar to the shape and dependency of α-stress functions (which represent the ratio of actual to potential transpiration) that were derived by Metselaar and de Jong van Lier (2007) and de Jong van Lier et al. (2008).

The ω-supply ratio factors that were derived from the soil and root system properties and from the bulk soil water potential distributions that were simulated using the mechanistic soil–root model in the coarse-textured soil during the crop growing season are plotted in Figure 2h) versus simulated T_{act}/T_p ratios. The plot shows that for a given T_p, the relation between T_{act}/T_p and ω can be represented by a linear relation and that the slope of this line decreases with increasing T_p.

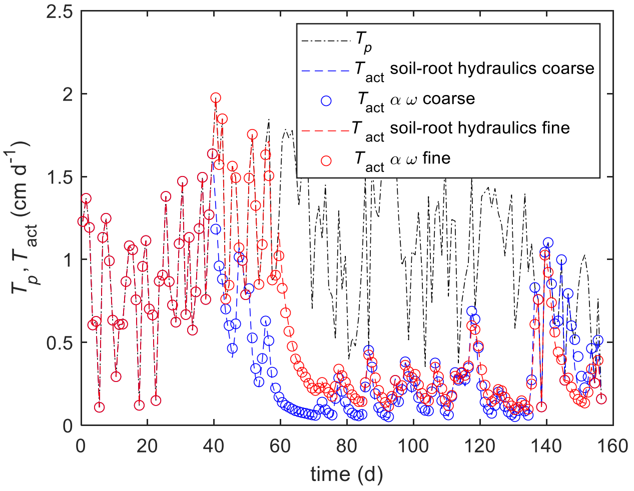

FIGURE 3 Potential (T_p) and simulated actual transpiration rates (T_{act}) at midday in the coarse- (blue) and fine-texture (red) soil using the soil root hydraulic model (dashed lines) and the model with mechanistically derived α-ω macroscopic uptake functions (open circles).

As a consequence, the critical ω factor at which the maximal supply becomes smaller than the demand, ω_c, increases with increasing potential transpiration. Since ω_c and its relation with the potential transpiration depends only on the root system conductance but not on the soil properties (Equation 21), the relation between T_{act}/T_p and ω is independent of the soil properties. However, the relation between ω and the soil water potentials and their distribution depends, through the α-supply ratios, on the soil properties (see Figure 2f).

The transpiration rates that were simulated with the mechanistic soil–root system model (Equation 11) are plotted together with the transpiration rates that were calculated directly from the mechanistic macroscopic RWU functions (Equations 28 and 31) in Figure 3.

The approximation of the soil–root system conductance by assuming that the collar water potential is always equal to H_{wilting} did not affect the simulated transpiration rates notably. The root mean square deviation (RMSD) between the simulated transpiration rates by the two models was 0.03 and 0.01 cm day^{-1} for the coarse- and fine-textured soils, respectively.

Also, the RWU distributions that were simulated by the soil–root hydraulic model were well reproduced by the model that uses the mechanistically derived macroscopic α-ω uptake

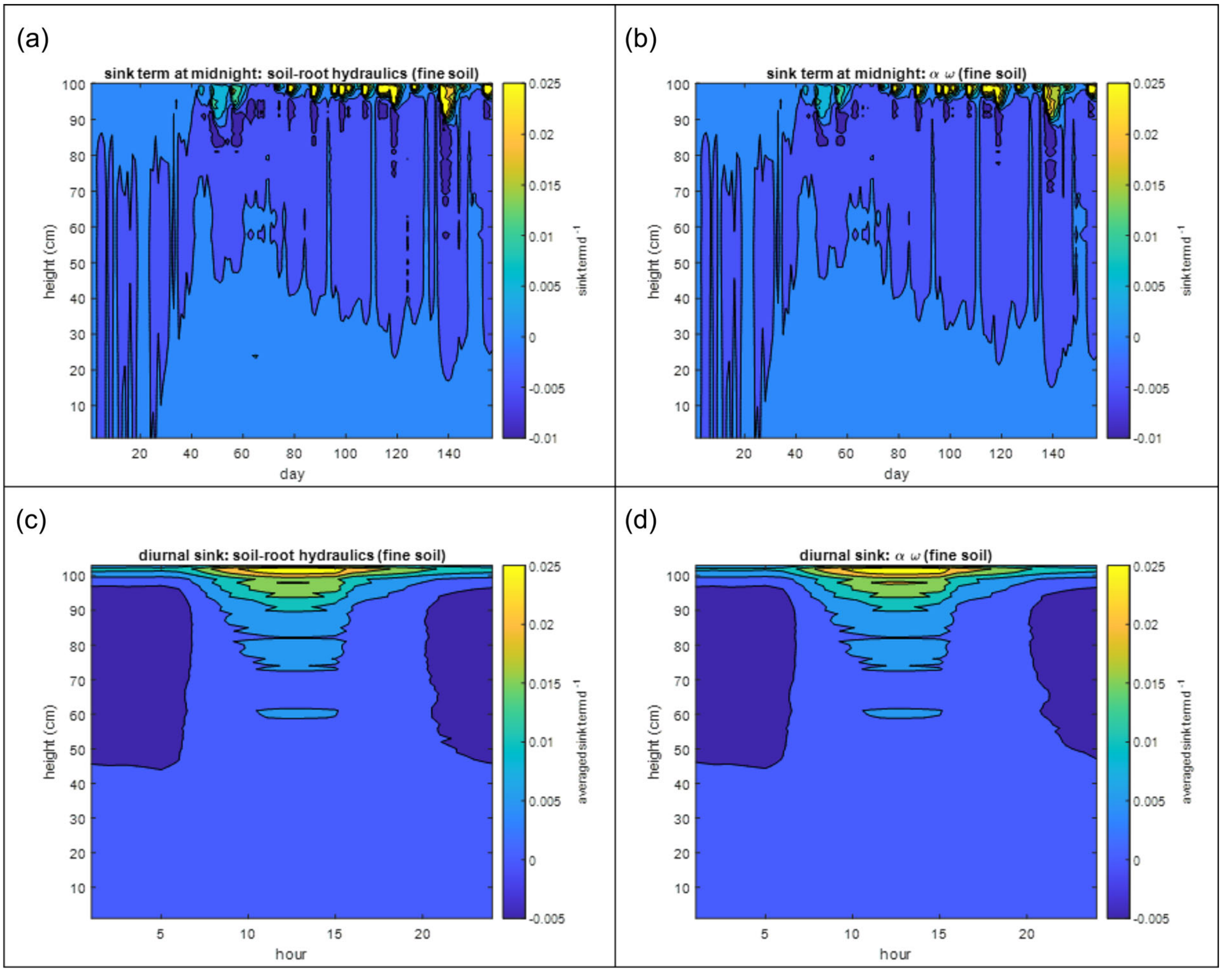

FIGURE 4 Simulated sink term distributions at midnight when the $T_p = 0$ in the fine-textured soil using the mechanistic soil–root hydraulic model (a), the mechanistically derived α-ω macroscopic uptake functions (b), the average diurnal course of the sink terms simulated by the mechanistic soil root hydraulic model (c), and the mechanistically derived α-ω macroscopic uptake functions (d).

functions (Figure 4). Hydraulic redistribution at night could be reproduced using the specific root water uptake functions for conditions when the maximal supply is larger than the demand (Equation 31). Figure 4 illustrates that at midnight, in part of the root zone, water is exuded by the root system, which is taken up in other parts. Interestingly, approximately 60 days after the soil profiles dried out and the actual transpiration in the fine-textured soil cannot meet the demand anymore (Figure 3), hydraulic redistribution at night occurred from the topsoil layer, which was sporadically rewetted by rain, toward the deeper layers. Figure 4 illustrates that the mechanistically derived α-ω uptake functions reproduce this redistribution as well as the average diurnal course of the RWU. In Figure 5, profiles of the average sink term at midnight and midday that are simulated in the two soils (coarse- and fine-textured) are shown for the two model approaches. The α-ω uptake functions can reproduce the uptake profiles and how they differ between the two soil textures quite well, but especially for the coarse-textured soil from 20- to 60-cm depth, there are slight deviations at midnight between the two approaches. Integrating all the negative sink terms over depth, the total simulated hydraulic redistribution during the simulation period was calculated for the two different soils and the two model approaches. In the sandy soil, the averaged water exudation rates by the whole root system and over the entire simulation period that were simulated by the soil–root hydraulic model and by the mechanistically derived α-ω uptake functions amounted to −0.012 and −0.0055 cm day^{-1}, respectively, which are relatively small compared to the simulated average uptake rates which are 0.197 and 0.192 cm day^{-1} respectively. In the fine-textured soil, the simulated exudation rates were −0.017 and −0.016 cm day^{-1} for the soil–root hydraulic model and the α-ω uptake functions, respectively, and the uptake rates were 0.245 and 0.243 cm day^{-1}, respectively. The larger perirhizal conductance of the fine than of the coarse-textured soil led to more hydraulic redistribution.

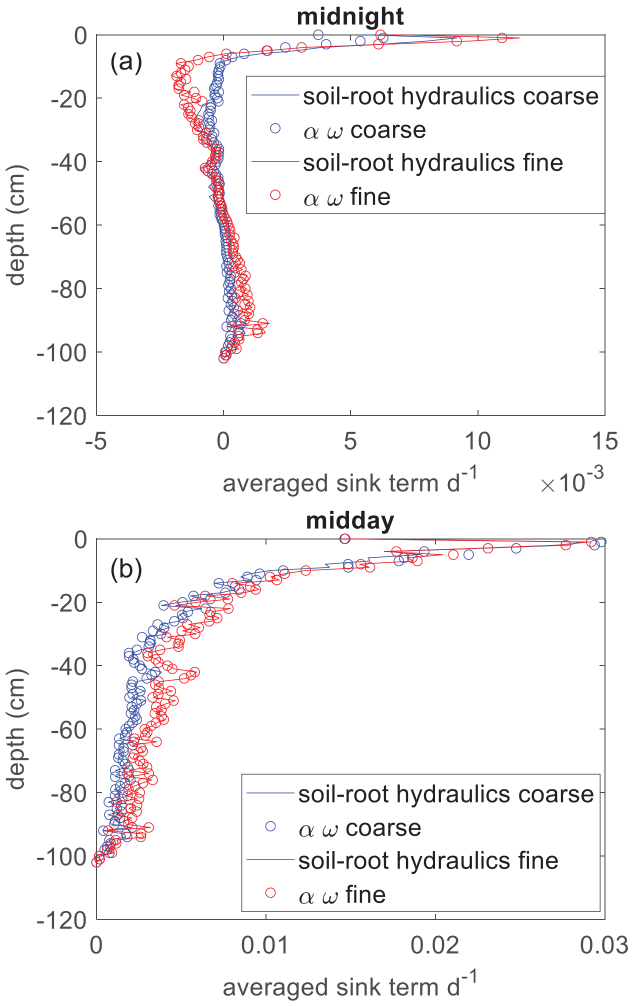

FIGURE 5 Sink term profile at midnight (a) and at midday (b) averaged over the entire simulation period in the coarse- (blue) and fine-textured (red) soil simulated by the soil–root hydraulic model (lines) and the mechanistically derived α-ω uptake function (open circles).

4 | DISCUSSION AND CONCLUSION

Macroscopic RWU functions calculate RWU rates and their distribution in the soil profile directly from soil water potentials and the transpiration demand without solving the flow equations in the soil–root system. By deriving macroscopic RWU functions using soil and root hydraulics (Equations 28 and 31), the conceptual basis of the RWU functions is put on solid grounds, which leads to consistent descriptions of RWU compensation and hydraulic redistribution via the root system when soil water potentials vary in the root zone. By linking RWU functions with root and soil hydraulic properties, these functions can be derived directly from the physical properties of the system, which can be determined directly using specific experiments not requiring the fitting of empirical parameters. An at first sight contradictory result is that mechanistically derived α-ω RWU functions (Equations 28 and 31), with α-supply ratio functions that vary with depth, have less degrees of freedom than the empirical α-ω RWU function (Equation 16) with an α-stress function that does not vary with depth. The soil and root hydraulic properties and root density distributions define the α-supply ratio functions at different depths, SUF relates the α-supply ratio functions at different depths with ω, and K_{rs} and T_p define ω_c. When, for instance, the soil hydraulic properties and rld distributions are known and when it is assumed that the SUF distribution is equal to the rld distribution, the only parameter that still needs to be fitted is the root system conductance, K_{rs}. However, certain root system properties, which are more difficult to measure, could be estimated by inverse modeling. The same could apply to the hydraulic properties of the perirhizal zone, which we assumed to be identical to those of the bulk soil. However, roots could alter the properties, including the hydraulic properties of the zone just around roots, that is, the rhizosphere. In addition, the soil-to-root contact could be lost (Faiz & Weatherley, 1977, 1982; Herkelrath et al., 1977) when roots (Carminati et al., 2009) or root hairs (Duddek et al., 2022) shrink. The impact of changing soil hydraulic properties (Landl et al., 2021) or changing root (de Willigen et al., 2018), or root hair contact (Duddek et al., 2023) on RWU can be simulated and evaluated using single root segment scale models. Simulations with these small-scale root segment models could be used to parameterize effective perirhizal conductivities, which could subsequently be used in the macroscale mechanistic RWU functions. This could be an example of the multiscale modeling approach that was proposed by Schnepf et al. (2022) to link rhizosphere processes across scales. In an alternative approach, simultaneous measurements of the diurnal course of plant and soil water potentials and transpiration (measured, for instance, with sapflow sensors), which were found to be sensitive to the effective perirhizal conductivity (Vanderborght et al., 2023), could be used to infer perirhizal conductivities independently from the bulk soil hydraulic conductivity by inverse modeling.

To link macroscopic RWU functions to soil and root hydraulics, we had to redefine the commonly used empirical α-stress function, which relates the reduction of RWU when the soil dries out to the bulk soil water potential and the transpiration demand. A conceptual problem with the α-stress function, which represents the ratio of the RWU rate from a soil layer to the uptake demand from that layer when the transpiration is equal to the potential transpiration, is the definition of the uptake demand from a certain layer. The uptake demand from a certain layer is defined as the potential transpiration multiplied by the nrld and the layer thickness (Equation 13), which could be interpreted as a proxy of the SUF. However, this definition of demand only applies when the soil water potential is uniform in the entire root zone. When soil water potentials vary in the root zone, the demand from a certain soil layer depends on the water potentials in other soil layers, so that the α-stress function is not a mathematical function of the water potential in the soil layer but should depend on the water potentials in all root zone soil layers. Therefore, describing RWU distributions when soil water potentials are not uniform using a stress function that is defined assuming a uniform soil water potential is contradictory. This problem is avoided when using supply ratios since the supply ratio in a soil layer can be defined as a function of the soil water potential in that layer without making assumptions about the water potentials in other layers. It must be noted that this property of supply ratios hinges on the approximation of the upscaled root system architecture by the parallel root model. Although the parallel root model was shown to represent a few exemplary root hydraulic architectures with realistic root hydraulic parameters accurately (Vanderborght et al., 2021), a more general testing of this model is still standing out.

Another problem with the α-stress function is that they relate to water stress and do not provide information on how RWU should be redistributed over the root zone when there is no stress. When there are no dry layers in the soil profile, $\alpha = 1$ in all soil layers, and the RWU distribution is proportional to the SUF distribution or its proxy the nrld. This implies that it is not possible to link the RWU distribution using the α-stress function with the flow between the soil and the root system and within the root system when the soil water potentials vary with depth and when the soil is wet or transpiration demand is very low or zero.

Following Jarvis (2011), we redefined α-functions as the ratio of the maximal possible RWU for the given soil water potential to the maximal possible uptake when the soil is saturated. By redefining the α-stress functions as supply ratio functions, redistribution of water uptake is also simulated in cases when there is no supply limitation anywhere in the root zone. Since the newly defined α functions are not directly related to the occurrence of water stress, they are not dependent on the transpiration demand. This implies that critical supply ratio factor ω_c is now a function of the transpiration demand. By including the root hydraulic properties in the definition of α and ω functions, spurious redistribution of RWU under wet soil conditions, which were observed by Jarvis (2011), who considered only perirhizal conductances (see figs. 2 and 3 in Jarvis (2011)), are no longer simulated.

When the perirhizal resistance can be neglected, the macroscopic functions represent the root hydraulics exactly. Since the root hydraulic properties are assumed not to depend on the water potentials, the macroscopic uptake functions are linear functions of the water potentials at the soil–root interfaces. When perirhizal conductances are considered, the obtained relations represent the soil and root hydraulics exactly when the transpiration demand cannot be met by the uptake and the water potential at the root collar is equal to the wilting water potential. The nonlinear soil hydraulic properties lead to nonlinear relations between the macroscopic functions and the bulk soil water potential. When transpiration demand can be met by the RWU and the root collar water potential is higher than the wilting water potential, an approximation is needed to calculate the uptake distribution directly from bulk soil water potentials and the potential transpiration. A comparison with simulations by a mechanistic soil–root hydraulic model showed that the approximations did not lead to large differences in simulated transpiration rates or RWU profiles.

When accounting for the root hydraulic properties and neglecting perirhizal zone resistances, the maximal supply rate when the soil is wet can be calculated without making assumptions about the variation of soil hydraulic properties with depth. Jarvis (2011) had to assume uniform soil hydraulic properties with depth when defining the maximal supply rate when the soil is wet, so that RWU uptake functions could only be derived for vertically uniform soil profiles but not for soil profiles that consist of layers with different hydraulic properties. This limitation is now overcome, and supply ratios can be calculated for each soil layer with different soil properties, soil water potentials, and root properties.

The mechanistic RWU model that we used to derive the mechanistic RWU functions is analogous to the RWU model introduced by de Jong van Lier et al. (2013). One difference between the two models is the parameterization of root resistances. de Jong van Lier et al. (2013) attribute the resistance to flow in the root system solely to radial flow in the roots from the soil–root surface to the xylem tissue, whereas the resistance to the axial flow in the root xylem, which is considered in our approach, is neglected. However, since we use a parallel root system model, the effective root resistance only depends on the sum of the axial and radial root resistances but not on how the radial and axial resistances compare to each other. As a consequence, this difference can be resolved by a reparameterization of radial root resistances that are used in the de Jong van Lier et al. (2013) model so that they include a depth-dependent additional axial flow resistance. Vanderborght et al. (2021) illustrated that a parameterization of the parallel root model based on root hydraulics leads to a more accurate prediction of the RWU distribution than a parameterization that only considers radial root resistances. Another difference between the two model approaches is that we do not consider a root-to-shoot resistance and use the water potential at the root collar to evaluate whether transpiration reduces compared to the potential transpiration. This difference is more fundamental, and we are currently evaluating how it influences supply ratios and mechanistic RWU functions.

Using α, ω, and ω_c, the uptake can be derived directly from the bulk soil water potential and the potential transpiration without calculating the collar water potential, so that iterative solutions are avoided. This speeded up the simulations considerably. Interpolation tables with pairs of H_{bs} and α values were calculated for each numerical soil layer before the start of a simulation, and α values were derived for simulated H_{bs} values by interpolation. When root systems develop over time, the interpolation tables must be adapted over time. When root system development is not dependent on the simulated RWU or plant stress, a time series of interpolation tables can be calculated before the start of the simulation. If feedback between root system development and plant water stress is considered, the interpolation tables must be calculated during the simulation.

Considering root system properties and how they change in response to water stress was found to be important to assess the sensitivity of crops to drought stress using crop growth models (Nguyen et al., 2022, 2020). Water flow in the soil–plant systems and the relationship between crop water stress and soil water content in the root zone are simulated in many crop models using empirical functions. Jarvis et al. (2022) argued that these empirical models have as many, if not more, parameters than macroscopic physics-based models. Furthermore, since these empirical functions and parameters are not linked directly to observable or measurable soil and root properties, information about these properties cannot be used to parameterize these functions. Empirical RWU and soil water flow modules used in crop models have been coined the elephant in the room by Jarvis et al. (2022), standing in the way of badly needed model improvements that would enhance the reliability of model predictions for future climates, new and improved crop varieties, and changes in management practices. In our view, the simple mechanistic RWU function described in this paper can help pave the way for the elephant to leave the room.

AUTHOR CONTRIBUTIONS

Jan Vanderborght: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; software; validation; visualization; writing—original draft; writing—review and editing. **Valentin Couvreur**: Formal analysis; methodology; validation; writing—review and editing. **Mathieu Javaux**: Formal analysis; methodology; validation; writing—review and editing. **Daniel Leitner**: Formal analysis; methodology; validation; writing—review & editing. **Andrea Schnepf**: Formal analysis; methodology; validation; writing—review and editing. **Harry Vereecken**: Formal analysis; investigation; validation; writing—review and editing.

ACKNOWLEDGMENTS

We would like to thank two anonymous reviewers for their thoughtful and constructive comments. This work has partially been funded by the German Research Foundation (DFG) under Germany's Excellence Strategy, EXC-2070–390732324–PhenoRob, by projects P3 (403670197) and P24 (403641034) of the DFG priority programme 2089 "Rhizosphere spatiotemporal organization–a key to rhizosphere functions", by project C02 of the DFG Collaborative Research Centre 1502 DETECT, the project BonaRes (Module A): Sustainable Subsoil Management—Soil3; subproject 3 (grant 031B1066C) in the framework of the funding initiative Soil as a Sustainable Resource for the Bioeconomy BonaRes of the German Federal Ministry of Education and Research (BMBF), and the project "RhizoWheat" (grant 031BO910B) in the framework of the funding initiative "Rhizo4Bio" of the German Federal Ministry of Education and Research (BMBF). Valentin Couvreur is a Research Associate of the Belgian Fonds de la Recherche Scientifique (FNRS), co-funded by the European Union (ERC grant 101043083).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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REFERENCES

Allen, R. G., Pereira, L. S., Raes, D., & Smith, M. (1998). *Crop evapotranspiration: Guidelines for computing crop water requirements*. FAO.

Carminati, A., Vetterlein, D., Weller, U., Vogel, H. J., & Oswald, S. E. (2009). When roots lose contact. *Vadose Zone Journal*, *8*(3), 805–809. https://doi.org/10.2136/vzj2008.0147

Couvreur, V., Vanderborght, J., Draye, X., & Javaux, M. (2014). Dynamic aspects of soil water availability for isohydric plants: Focus on root hydraulic resistances. *Water Resources Research*, *50*(11), 8891–8906. https://doi.org/10.1002/2014wr015608

de Jong van Lier, Q., Metselaar, K., & van Dam, J. C. (2006). Root water extraction and limiting soil hydraulic conditions estimated by numerical simulation. *Vadose Zone Journal*, *5*(4), 1264–1277. https://doi.org/10.2136/vzj2006.0056

de Jong van Lier, Q., van Dam, J. C., Durigon, A., dos Santos, M. A., & Metselaar, K. (2013). Modeling water potentials and flows in the soil–plant system comparing hydraulic resistances and transpiration reduction functions. *Vadose Zone Journal*, *12*(3), 1–20. https://doi.org/10.2136/vzj2013.02.0039

de Jong van Lier, Q. D., van Dam, J. C., Metselaar, K., de Jong, R., & Duijnisveld, W. H. M. (2008). Macroscopic root water uptake distribution using a matric flux potential approach. *Vadose Zone Journal*, *7*(3), 1065–1078. https://doi.org/10.2136/vzj2007.0083

de Willigen, P., Heinen, M., & van Noordwijk, M. (2018). Roots partially in contact with soil: Analytical solutions and approximation in models of nutrient and water uptake. *Vadose Zone Journal*, *17*(1), 1–16. https://doi.org/10.2136/vzj2017.03.0060

Doussan, C., Pages, L., & Vercambre, G. (1998). Modelling of the hydraulic architecture of root systems: An integrated approach to water absorption—Model description. *Annals of Botany*, *81*(2), 213–223. https://doi.org/10.1006/anbo.1997.0540

Duddek, P., Ahmed, M. A., Javaux, M., Vanderborght, J., Lovric, G., King, A., & Carminati, A. (2023). The effect of root hairs on root water uptake is determined by root–soil contact and root hair shrinkage. *New Phytologist*, *240*(6), 2484–2497. https://doi.org/10.1111/nph.19144

Duddek, P., Carminati, A., Koebernick, N., Ohmann, L., Lovric, G., Delzon, S., Rodriguez-Dominguez, C. M., King, A., & Ahmed, M. A. (2022). The impact of drought-induced root and root hair shrinkage on root-soil contact. *Plant Physiology*, *189*, 1232–1236. https://doi.org/10.1093/plphys/kiac144

Faiz, S. M. A., & Weatherley, P. E. (1977). The location of the resistance to water movement in the soil supplying the roots of transpiring plants. *New Phytologist*, *78*(2), 337–347. https://doi.org/10.1111/j.1469-8137.1977.tb04837.x

Faiz, S. M. A., & Weatherley, P. E. (1982). Root contraction in transpiring plants. *New Phytologist*, *92*(3), 333–343. https://doi.org/10.1111/j.1469-8137.1982.tb03391.x

Feddes, R. A., Kowalik, P. J., & Zaradny, H. (1978). Simulation of field water use and crop yield. In F. W. T. Penning de Vries & H. H. van Laar (Eds.), *Simulation of plant growth and crop production* (pp. 194–209). Simulation monographs. Pudoc.

Feddes, R. A., & Raats, P. A. C. (2004). Parameterizing the soil-water-plant root system. In R. A. Feddes, G. H. De Rooij, & J. C. Van Dam (Eds.), *Unsaturated-zone modeling* (pp. 95–141). Kluwer Academic Publishers.

Herkelrath, W. N., Miller, E. E., & Gardner, W. R. (1977). Water-uptake by plants: 2. Root contact model. *Soil Science Society of America Journal*, *41*(6), 1039–1043. https://doi.org/10.2136/sssaj1977.03615995004100060004x

Jarvis, N., Larsbo, M., Lewan, E., & Garré, S. (2022). Improved descriptions of soil hydrology in crop models: The elephant in the room? *Agricultural Systems*, *202*, 103477. https://doi.org/10.1016/j.agsy.2022.103477

Jarvis, N. J. (1989). A simple empirical-model of root water-uptake. *Journal of Hydrology*, *107*(1-4), 57–72. https://doi.org/10.1016/0022-1694(89)90050-4

Jarvis, N. J. (2011). Simple physics-based models of compensatory plant water uptake: Concepts and eco-hydrological consequences. *Hydrology and Earth System Sciences*, *15*(11), 3431–3446. https://doi.org/10.5194/hess-15-3431-2011

Javaux, M., Couvreur, V., Vanderborght, J., & Vereecken, H. (2013). Root water uptake: From three-dimensional biophysical processes to macroscopic modeling approaches. *Vadose Zone Journal*, *12*(4), 1–16. https://doi.org/10.2136/vzj2013.02.0042

Javaux, M., Schröder, T., Vanderborght, J., & Vereecken, H. (2008). Use of a three-dimensional detailed modeling approach for predicting root water uptake. *Vadose Zone Journal*, *7*(3), 1079–1088. https://doi.org/10.2136/vzj2007.0115

Khare, D., Selzner, T., Leitner, D., Vanderborght, J., Vereecken, H., & Schnepf, A. (2022). Root system scale models significantly overestimate root water uptake at drying soil conditions. *Frontiers in Plant Science*, *13*, 798741. https://doi.org/10.3389/fpls.2022.798741

Kroes, J. G., van Dam, J. C., Bartholomeus, R. P., Groenendijk, P., Heinen, M., Hendriks, R. F. A., Mulder, H. M., Supit, I., & van Walsum, P. E. V. (2017). *SWAP version 4, Theory description and user manual* (Report No. 2780). Wageningen Environmental Research. https://doi.org/10.18174/416321

Landl, M., Phalempin, M., Schlüter, S., Vetterlein, D., Vanderborght, J., Kroener, E., & Schnepf, A. (2021). Modeling the impact of rhizosphere bulk density and mucilage gradients on root water uptake [Original Research]. *Frontiers in Agronomy*, *3*, 622367. https://doi.org/10.3389/fagro.2021.622367

Metselaar, K., & de Jong van Lier, Q. (2007). The shape of the transpiration reduction function under plant water stress. *Vadose Zone Journal*, *6*(1), 124–139. https://doi.org/10.2136/vzj2006.0086

Nguyen, T. H., Langensiepen, M., Hueging, H., Gaiser, T., Seidel, S. J., & Ewert, F. (2022). Expansion and evaluation of two coupled root–shoot models in simulating CO2 and H2O fluxes and growth of maize. *Vadose Zone Journal*, *21*(3), e20181. https://doi.org/10.1002/vzj2.20181

Nguyen, T. H., Langensiepen, M., Vanderborght, J., Hüging, H., Mboh, C. M., & Ewert, F. (2020). Comparison of root water uptake models in simulating CO2 and H2O fluxes and growth of wheat. *Hydrology and Earth System Sciences*, *24*(10), 4943–4969. https://doi.org/10.5194/hess-24-4943-2020

Schaap, M. G., Leij, F. J., & van Genuchten, M. T. (2001). ROSETTA: A computer program for estimating soil hydraulic parameters with hierarchical pedotransfer functions. *Journal of Hydrology*, *251*(3–4), 163–176. https://doi.org/10.1016/s0022-1694(01)00466-8

Schnepf, A., Carminati, A., Ahmed, M. A., Ani, M., Benard, P., Bentz, J., Bonkowski, M., Knott, M., Diehl, D., Duddek, P., Kroner, E., Javaux, M., Landl, M., Lehndorff, E., Lippold, E., Lieu, A., Mueller, C. W., Oburger, E., Otten, W., … Vetterlein, D. (2022). Linking rhizosphere processes across scales: Opinion. *Plant and Soil*, *478*, 5–42. https://doi.org/10.1007/s11104-022-05306-7

Schröder, T., Javaux, M., Vanderborght, J., Korfgen, B., & Vereecken, H. (2008). Effect of local soil hydraulic conductivity drop using a three-dimensional root water uptake model. *Vadose Zone Journal*, *7*(3), 1089–1098. https://doi.org/10.2136/vzj2007.0114

Schröder, T., Javaux, M., Vanderborght, J., Körfgen, B., & Vereecken, H. (2009). Implementation of a microscopic soil-root hydraulic conductivity drop function in a three-dimensional soil-root architecture water transfer model. *Vadose Zone Journal*, *8*(3), 783–792. https://doi.org/10.2136/vzj2008.0116

Simunek, J., & Hopmans, J. W. (2009). Modeling compensated root water and nutrient uptake. *Ecological Modelling*, *220*(4), 505–521. https://doi.org/10.1016/j.ecolmodel.2008.11.004

Šimůnek, J., van Genuchten, M. T., & Šejna, M. (2016). Recent developments and applications of the HYDRUS computer software packages. *Vadose Zone Journal*, *15*(7), 1–25. https://doi.org/10.2136/vzj2016.04.0033

Skaggs, T. H., van Genuchten, M. T., Shouse, P. J., & Poss, J. A. (2006). Macroscopic approaches to root water uptake as a function of water and salinity stress. *Agricultural Water Management*, *86*(1), 140–149. https://doi.org/10.1016/j.agwat.2006.06.005

van Dam, J. C., Groenendijk, P., Hendriks, R. F. A., & Kroes, J. G. (2008). Advances of modeling water flow in variably saturated soils with SWAP. *Vadose Zone Journal*, *7*(2), 640–653. https://doi.org/10.2136/vzj2007.0060

Vanderborght, J., Couvreur, V., Meunier, F., Schnepf, A., Vereecken, H., Bouda, M., & Javaux, M. (2021). From hydraulic root architecture models to macroscopic representations of root hydraulics in soil water flow and land surface models. *Hydrology and Earth System Sciences*, *25*(9), 4835–4860. https://doi.org/10.5194/hess-25-4835-2021

Vanderborght, J., Leitner, D., Schnepf, A., Couvreur, V., Vereecken, H., & Javaux, M. (2023). Combining root and soil hydraulics in macroscopic representations of root water uptake. *Vadose Zone Journal*, e20273. https://doi.org/10.1002/vzj2.20273

van Genuchten, M. T. (1980). A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. *Soil Science Society of America Journal*, *44*(5), 892–898. https://doi.org/10.2136/sssaj1980.03615995004400050002x

How to cite this article: Vanderborght, J., Couvreur, V., Javaux, M., Leitner, D., Schnepf, A., & Vereecken, H. (2024). Mechanistically derived macroscopic root water uptake functions: The α and ω of root water uptake functions. *Vadose Zone Journal*, e20333. https://doi.org/10.1002/vzj2.20333