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Combining root and soil hydraulics in macroscopic representations of root water uptake

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Abstract

Plant water uptake and plant and soil water status are important for the soil water balance and plant growth. They depend on atmospheric water demand and the accessibility of soil water to plant roots, which is in turn related to the hydraulic properties of the root system and the soil around root segments. We present a simulation model that describes water flow in the soil–plant system mechanistically considering both root and soil hydraulic properties. We developed an approach to upscale three-dimensional (3D) flow in the soil toward root segments of a 3D root architecture to a model that considers one-dimensional flow between horizontal soil layers and radial flow to root segments in that layer. The upscaled model couples upscaled linear flow equations in the root system with an analytical solution of the nonlinear radial flow equation between the soil and roots. The upscaled model avoids simplifying assumptions about root hydraulic properties and water potential drops near roots made in, respectively, soil- and root-centered models. Xylem water potentials and soil–root interface potentials are explicitly simulated and show, respectively, large variations with depth and large deviations from bulk soil water potentials under dry soil conditions. Accounting for hydraulic gradients in the soil around root segments led to an earlier but slower reduction of transpiration during a drought period and a better plant water status with higher nighttime plant water potentials.

1 | INTRODUCTION

Evaporation of water through the vegetation canopy or “transpiration” is an important component of the field soil water balance. Actual transpiration is a function of potential transpiration, which corresponds to the transpiration when stomatal

conductance is maximal (i.e., with fully opened stomata) and represents the atmospheric “demand” for water, and it is a function of the supply of water from the soil through the roots to the vegetation canopy. The supply is a function of the potential difference between the soil water in the root zone and the water in the leaves, and of the resistances (or their inverse, conductances) to flow in different parts of the soil–plant continuum. When the soil dries out, the water potentials decrease. To prevent plant water potentials from reaching lethal

Abbreviations: 1D, one-dimensional; 3D, three-dimensional; rld, root length density; SUF, standard uptake fraction.

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levels, stomata close and downregulate transpiration so that the supply does not satisfy the atmospheric demand or potential transpiration anymore. How the supply function depends on soil and root properties and on the distribution of water in the root zone needs to be understood to develop and parameterize models that simulate plant water uptake from the soil and plant water status.

Flow in the soil–plant system has been represented as a passive catenary process that can be represented as a flow driven by potential differences across a network of resistances (or their inverse, conductances) (van den Honert, 1948). First network models considered resistances to flow from the bulk soil to soil–root interfaces, to radial flow into root segments, and to axial flow along root segments toward the leaves (Cowan, 1965). The resistance to flow in the bulk soil to the soil root interface was derived from the radial flow equation in an unsaturated soil (Gardner, 1960) considering the dependence of the soil hydraulic conductivity on the soil water potential, which leads to nonlinear soil resistances. In these network models, the axial resistance to flow in the root xylem was neglected so that the root xylem water potential is uniform in the entire root system, which is an assumption still made in many root water uptake models currently used. A consequence of this assumption is that the absorptive capacity of root segments is independent of their location in the root network. Gardner (1965) observed that the absorptive capacity of roots in deeper soil layers was lower than those in shallower soil layer, which he attributed to axial flow resistance. Even though the intrinsic axial conductance of a root segment is up to eight orders of magnitude larger than its radial conductance, the distance over which water has to flow in the radial direction is only 0.01%–0.1% of the total distance between the soil–root interface and the leaves (Sperry et al., 2003). The role of the axial conductance for root water uptake along roots was evaluated using analytical solutions by Landsberg and Fowkes (1978) that were later refined to include lateral roots and nonuniform conductances along roots (Meunier, Couvreur, Draye, Vanderborght, et al., 2017; Meunier, Couvreur, Draye, Zarebanadkouki, et al., 2017; Roose & Fowler, 2004). Sensitivity analyses using three-dimensional (3D) root architecture models further confirmed and quantified the important role of axial conductances (Bouda et al., 2018; Boursiac et al., 2022). These studies focused on the role of root hydraulics and root hydraulic properties in root water uptake. They quantified how root absorptive capacity varies along the length of a root depending on the ratio of the axial to radial root conductance and on the variation of this ratio along a root. Maturation of root tissues alters conductances and their ratios, with younger roots having a higher radial-to-axial conductance ratio than older roots. Root hydraulic concepts were implemented in root water uptake modules of early soil water flow models in a simplified way. The resistance to flow along roots was included as a fitting parameter but without a direct link to axial root conductances (Hillel et al., 1976; Nimah & Hanks, 1973).

Core Ideas

- Root water uptake depends on root and soil hydraulic properties.
- Water uptake at root element scale was upscaled to the root system scale.
- The upscaled model can be implemented in one-dimensional soil water flow models.
- Low conductance of dry soil prevents low night-time plant water potentials.

The early resistance network models made a priori simplifications of the architecture of the root network. Network models that reconstruct the 3D hydraulic architecture of the root system have been developed and coupled to 3D soil water flow models (Doussan et al., 1998, 2006; Javaux et al., 2008). With these models, the effect of the root hydraulic architecture on water uptake is explicitly accounted for and can be used to identify traits of root systems that improve their water uptake capacity in different soils and climates (Leitner et al., 2014). Since they simulate 3D water flow, these simulation models are computationally expensive. This is even further aggravated by the need for very high spatial discretization to resolve the hydraulic gradients near soil–root interfaces (Khare et al., 2022). Therefore, approaches to upscale 3D root hydraulic models to one-dimensional (1D) root water uptake models (Couvreur, Vanderborght, Beff, et al., 2014; Vanderborght et al., 2021) were developed and implemented in models that simulate 1D soil water flow (Cai et al., 2018; Sulis et al., 2019) and crop growth (Nguyen et al., 2022, 2020). By an exact upscaling of the linear flow equations in the root system (i.e., conductances in the root system are independent of the water potentials), the root hydraulic architecture and properties are accounted for in a so-called bottom-up approach without making a priori simplifying assumptions about the network structure (Vanderborght et al., 2021). Besides simulating the interactive effect of root and soil water potential distributions on root water uptake in a mechanistic way, also the parameters of the upscaled model are derived in a direct way from the hydraulic properties of root segments and architecture of the root system so that parameter fitting is, in principle, not needed.

The upscaling approach and the root water uptake modules that focus on root hydraulics do not include the resistance to flow in the soil to the soil–root interface but assume that the water potentials at the soil–root interfaces are given. In wet soils, the soil hydraulic conductivity is not limiting and this assumption is appropriate (Draye et al., 2010), and root properties determine the water uptake distribution and plant water potentials. However, in dry soils, soil conductivity drops strongly with decreasing water content and limits the water

flow to the root system. The early root water uptake models developed in the 1960s, which were later further refined and implemented in soil water flow models (de Jong van Lier et al., 2006, 2013, 2008; de Willigen et al., 2012), focus on the soil hydraulic properties and small-scale flow processes around single-root segments but simplify the root hydraulics.

The zone around root segments where root water uptake induces radial flow and radial hydraulic gradients was often named the “perirhizal zone” (Tinklin & Weatherley, 1968). The volume of soil around roots that is modified by roots and that plays a pivotal role in exchange processes between plants and soils is also referred to as “the rhizosphere” (Hinsinger et al., 2009). Since there is a variety of soil processes and properties that are affected by the presence of plant roots, each with their own spatial scale, there is no unique definition of the extent of the rhizosphere. Furthermore, when “modified by roots” is interpreted as the zone where the water content and water fluxes are modified by the root water uptake, perirhizal zone and rhizosphere might be considered to be equivalent and would comprise the entire soil volume between individual root segments. However, “rhizosphere” is mostly interpreted as a narrow zone around roots where properties are influenced by roots, for example, by root exudates and compaction (Carminati, 2012; Carminati et al., 2016; Roose et al., 2016). To avoid confusion, we will use the term “perirhizal zone” for the zone around root segments where root water uptake generates radially symmetric flow and hydraulic gradient fields. Since this perirhizal zone comprises the total soil volume between roots, the bulk soil water contents and water potentials correspond with the average water contents and potentials in the perirhizal zone (and not with the water contents or potentials at the outer boundary of the zone as is often considered in rhizosphere models).

The upscaling of local processes in the perirhizal zone to the entire root system scale requires a coupling between the local flow toward root segments, the flow in the root system, and the flow in the soil that is driven by bulk soil hydraulic gradients that exist at a larger scale but average out local-scale radial hydraulic gradients around single-root segments (Schnepf et al., 2022). The objective of this work is to couple a root system hydraulic model with an upscaled 1D soil water flow model, which describes vertical soil water flow as a function of average or bulk soil water potentials in a horizontal plane, while accounting for perirhizal hydraulic gradients around root segments. The obtained upscaled 1D model should represent the interaction effects between root and soil water distributions and between root and soil hydraulic properties on root water uptake distributions and plant water potentials. Therefore, we will combine the upscaling approaches developed for root hydraulic architectures (Couvreur, Vanderborght, Beff, et al., 2014; Vanderborght et al., 2021) with approaches to simulate water flow from the bulk soil to soil–root interfaces. First, we

describe the development of the model and then demonstrate the model and evaluate the impact of some simplifications in three sets of simulation scenarios. Finally, we define water uptake properties at the root system scale and evaluate how they are influenced by perirhizal processes.

2 | MATERIALS AND METHODS

2.1 | Root system hydraulics

The 3D root system is represented by a network of N root segments that are connected at N root nodes, which represent the xylem tissue of the root segments, and one root system collar node. The flow through the xylem between the nodes is proportional to the difference in the xylem water potentials H_x [L] (expressed in head units, i.e., potential per unit weight) between the root/collar nodes and the axial conductance of the segment, K_x [$L^2 T^{-1}$], that connects two root nodes or a root node with the collar. Each root node is also connected to a node that represents the soil–root interface. The radial flow from the soil–root interface through the root cortex and the endodermis toward root xylem is proportional to the difference in water potential at the soil–root interface, $H_{\text{soil–root}}$ [L], and in the root xylem and to the radial conductance of the root segment, K_r [$L^2 T^{-1}$]. Note that soil water potentials refer to the total water potential that includes the pressure potential and the gravitation potential and in principle also the osmotic potential, which we do not consider in this study, but which is important in saline soils. Because of the typical architecture of a root system, each root node can be associated with a single proximal root segment that is connected to that node. The length (l_{root} [L]) and radius (r_{root} [L]) of this proximal root segment are used to calculate the axial and radial conductances from intrinsic conductances, k_x [$L^3 T^{-1}$] and k_r [T^{-1}], of the root tissues as

$$K_x = \frac{k_x}{l_{\text{root}}}, \quad (1)$$

$$K_r = 2\pi r_{\text{root}} l_{\text{root}} k_r. \quad (2)$$

Using the flow equations in this network and solving the mass balance equations for the root nodes, the flow from the soil–root interfaces to the associated root xylem nodes can be calculated directly from the water potentials at the soil–root interface, $H_{s,r}$ [L], and in the root collar, H_{collar} , using the following equation (Vanderborght et al., 2021):

$$\mathbf{Q} = K_{rs} \text{SUF} (H_{s,r \text{ eff}} - H_{\text{collar}}) + C_4 (\mathbf{H}_{s,r} - \mathbf{H}_{s,r \text{ eff}}), \quad (3)$$

where $\mathbf{Q}$ [$L^3 T^{-1}$] is the $N \times 1$ vector of flow rates to root nodes, K_{rs} [$L^2 T^{-1}$] is the root system conductance, SUF [–]

calculated from the root length density, rld [$L L^{-3}$], as

$$r_{prhiz} = \frac{1}{\sqrt{\pi rld}}. \quad (8)$$

Note that this definition of r_{prhiz} or the perirhizal radius corresponds with a typical halve distance between root segments. Other assumptions about the root segment distributions and sizes of the perirhizal cylinders around root segments could be made (Graefe et al., 2019) but model simulations by Schröder et al. (2009) showed that a uniform r_{prhiz} for all root segments was a good approximation. In the constructed perirhizal cylinders, the radial flow is described using a cylindrical coordinate system. Making the steady-rate assumption, that is, the water content change with time does not depend on the distance from the soil–root surface, an analytical solution of this equation can be derived (de Jong van Lier et al., 2006, 2008; Schröder et al., 2008). Based on this solution, the soil–root conductance of segment i , $K_{soil-root}[i]$ ($L^2 T^{-1}$) (Figure 1), which is defined as

$$K_{soil-root}[i] = \frac{Q[i]}{(H_{bs}[i] - H_x[i])}, \quad (9)$$

can be calculated from the conductances K_{prhiz} and K_r that are in series as

$$K_{soil-root}(h_{bs}, h_{s,r}) = \frac{K_{prhiz} K_r}{K_{prhiz} + K_r}. \quad (10)$$

K_r is defined in Equation (2) and K_{prhiz} is obtained from

$$K_{prhiz}(h_{bs}, h_{s,r}) = 2\pi l_{root} B \bar{k}_{prhiz}(h_{bs}, h_{s,r}), \quad (11)$$

$$\bar{k}_{prhiz}(h_{bs}, h_{s,r}) = \frac{\int_{-\infty}^{h_{bs}} K(h) dh - \int_{-\infty}^{h_{s,r}} K(h) dh}{h_{bs} - h_{s,r}}, \quad (12)$$

$$B = \frac{2(\rho^2 - 1)}{1 - (0.53\rho)^2 + 2\rho^2(\ln \rho + \ln(0.53))}, \quad (13)$$

$$\rho = \frac{r_{prhiz}}{r_{root}}, \quad (14)$$

where $\bar{k}_{prhiz}$ [$L T^{-1}$] is an “effective conductivity” of the perirhizal zone that corresponds with an average of the soil hydraulic conductivity K [$L T^{-1}$] in the perirhizal zone. $\bar{k}_{prhiz}$ represents the average of K when the pressure head varies

between the pressure head at the soil–root interface, $h_{s,r}$, and the pressure head in the bulk soil, h_{bs} . $\bar{k}_{prhiz}$ is calculated using integrals of the soil hydraulic conductivity–pressure head relationship, $K(h)$, also known as matrix flux potentials (Raats, 1970). Note that $\bar{k}_{prhiz}$ has other dimensions than the intrinsic radial root conductance, k_r , and can therefore not be compared directly to k_r .

B is a geometry factor that accounts for the radial flow and the variation of the soil conductivity with distance from the soil–root interface. The factor 0.53 is an approximation of the ratio to r_{prhiz} of the radial distance r where the pressure head $h(r)$ equals the bulk pressure head h_{bs} , which in turn corresponds with the pressure head for which the volumetric water content is equal to the average water content in the perirhizal zone (de Jong van Lier et al., 2008):

$$\frac{r(\theta(h_{bs}) = \bar{\theta})}{r_{prhiz}} \approx 0.53. \quad (15)$$

It must be noted that this factor was derived for flow from the soil to the root system. But, when $H_x > H_{bs}$, Q is negative and water flows from the root system to the soil. We use the same B geometry factor for these conditions but further testing the dependence of B on the flow direction is standing out.

Combining the above equations, we obtain for $K_{soil-root}$:

$$K_{soil-root}(h_{bs}, h_{s,r}) = \frac{2\pi l_{root} r_{root} B k_r \bar{k}_{prhiz}(h_{bs}, h_{s,r})}{r_{root} k_r + B \bar{k}_{prhiz}(h_{bs}, h_{s,r})}, \quad (16)$$

where $K_{soil-root}$ and $\bar{k}_{prhiz}$ are functions of the soil water pressure heads in the bulk soil, h_{bs} , and at the soil–root interface, $h_{s,r}$. Solving the flow and the water potentials in the network therefore requires solving a set of nonlinear equations, which cannot be done directly but requires an iterative solution. This solution is therefore more accurate than approaches speeding up calculation time by assuming $K_{soil-root}$ to be independent from radial water flow rates (Couvreur et al., 2020).

For a certain distribution of bulk soil water potential H_{bs} and a j^{th} estimate of $H_{s,r}^j$, we calculate the xylem water potentials using the linear root hydraulic model:

$$\begin{aligned} \mathbf{H}_x^j &= \mathbf{H}_{s,r}^j - \text{diag}(\mathbf{K}_r)^{-1} \left\{ K_{rs} \text{SUF} \left[H_{s,r}^j - H_{collar}^j \right] \right. \\ &\quad \left. + \mathbf{C}_4 \left[\mathbf{H}_{s,r}^j - \mathbf{H}_{s,r}^j \text{eff} \right] \right\} \end{aligned} \quad (17)$$

where $\text{diag}(\mathbf{K}_r)$ is an $N \times N$ diagonal matrix with the elements of the $N \times 1$ $\mathbf{K}_r$ vector on the diagonal. Then, we update the soil–root interface potential so that the water flow rate from the soil–root interface to the xylem equals the water flow rate from the bulk soil to the soil–root interface. For a certain root

segment i , we obtain (for readability, we leave out the index i referring to the root segment)

$$K_r \left(H_{s,r}^{j+1} - H_x^j \right) = K_{\text{prhiz}} \left(h_{\text{bs}}, h_{s,r}^{j+1} \right) \left(H_{\text{bs}} - H_{s,r}^{j+1} \right) \quad (18)$$

or

$$H_{s,r}^{j+1} = \frac{r_{\text{root}} k_r H_x^j + B \bar{k}_{\text{prhiz}} \left(h_{\text{bs}}, h_{s,r}^{j+1} \right) H_{\text{bs}}}{r_{\text{root}} k_r + B \bar{k}_{\text{prhiz}} \left(h_{\text{bs}}, h_{s,r}^{j+1} \right)}, \quad (19)$$

where h and H are related to each other according to Equation (7). Equation (19) is setup for each root segment and solved iteratively for $H_{s,r}^{j+1}$. Using $H_{s,r}^{j+1}$, a new iteration loop is started. To start the iteration, the initial estimate $\mathbf{H}_{s,r}^0$ could either be $\mathbf{H}_{\text{bs}}$ or $\mathbf{H}_{s,r}$ from the previous time step. A pseudo code of the different calculation steps is given in the [Appendix](#).

2.3 | Upscaling and simplifying

In a first step, it is assumed that H_{bs} does not vary in the horizontal direction so that the 3D soil water balance equation can be reduced to a 1D balance equation. This assumption implies that the bulk water potential in each perirhizal cylinder in a certain horizontal soil layer is the same. But the xylem and soil–root interface potentials may vary depending on the uptake and radial conductance of the root segment. The uptake, xylem, and soil–root interface water potentials must still be calculated iteratively for each single root segment of the root system. To reduce this computation cost, the flow equations in the root hydraulic architecture can be upscaled assuming that the soil–root interface water potentials are uniform in a certain soil layer. In wet soil layers, where the soil hydraulic conductivity is high and not limiting the radial flow toward the soil–root interface, the soil–root interface water potentials are close to the bulk soil water potentials and the assumption of uniform bulk soil water potentials can be translated to uniform soil–root interface water potentials. For dry soil layers, variations in root water uptake between different root segments with different xylem water potentials and different radial conductances lead to different water fluxes and hence different radial soil water potential gradients and different soil–root interface water potentials. Therefore, we tested to what extent this assumption is violated and what the effect of this violation is on the calculated uptake. The uptake from a soil layer, Q_{up} , for a constant $H_{s,r}$ in the layer is obtained from

$$Q_{\text{up}} = K_{\text{rs}} \text{SUF}_{\text{up}} \left(H_{s,r \text{ eff up}} - H_{\text{collar}} \right) + C_{4\text{up}} \left(\mathbf{H}_{s,r\text{up}} - \mathbf{H}_{s,r \text{ eff up}} \right), \quad (20)$$

where the subscript “up” refers to the upscaled vectors or matrices that have dimensions equal to the number of soil layers rather than the number of root segments. SUF_{up} is simply obtained from summing up the SUFs of root segments in a certain soil layer, whereas $C_{4\text{up}}$ is also obtained from summing up elements in blocks of the $\mathbf{C}_4$ matrix (Vanderborght et al., 2021). Since the root hydraulic model is linear (conductances do not depend on water potentials), the upscaled root hydraulic model is exact when the soil root interface potentials are uniform in a soil layer. We refer to Equation (20) as the “exact upscaled root hydraulic model” with “exact” referring to the upscaling of the root hydraulics, whereas the assumption of a uniform water potential at the soil–root interface in a soil layer is an approximation that was tested for a wet and a dry soil profile. Using the upscaled model, an upscaled xylem water potential, $H_{x,\text{up}}$, can be calculated for each soil layer with Equation (17) with a vector $\mathbf{K}_{\text{rup}}$ of radial conductances in the different soil layers. K_{rup} of layer i is the sum of the K_r values of all root elements in that layer and k_{rup} is K_{rup} divided by the total root surface area in layer i . $H_{x,\text{up}}$ can subsequently be used in Equation (19) with average values of r_{root} and B of the segments in the soil layer to calculate the upscaled soil–root interface water potential.

The upscaled water uptake equation has the same form as the original equation and for readability we will not further use the subscript “up.” Although the $\mathbf{C}_4$ matrix can be calculated directly from the root hydraulic architecture, it can also be approximated by $K_{\text{rs}} \mathbf{I}_N \text{SUF}$, where $\mathbf{I}_N$ is the $N \times N$ identity matrix, which simplifies the parameterization of the root hydraulic uptake model. This simplification comes down to representing the root system by a parallel root system in which all root segments in a certain soil layer are directly connected to the root collar. Vanderborght et al. (2021) showed that this approximation could reproduce the exact model accurately. A schematic overview of the concepts used to couple, upscale, and simplify the root and soil hydraulics is given in Figure 2.

2.4 | Setup of simulation scenarios

To demonstrate the model, evaluate the effect of some simplifications, and show the impact of the perirhizal conductance on root water uptake, we setup three different simulation scenarios. In all scenarios, we considered a root hydraulic architecture that was used in Vanderborght et al. (2021) and represents a fibrous root system, for example, maize. The root system was generated using the CRootBox shiny app (<https://plantmodelling.shinyapps.io/shinyRootBox/>) (Schnepf et al., 2018). The intrinsic radial, k_r , and axial root segment conductances, k_x , depended on the root order and varied with age (Figure 3). The plant density was assumed to be $0.00356 \text{ plants}\cdot\text{cm}^{-2}$ to generate a homogeneous lateral distribution of root density.

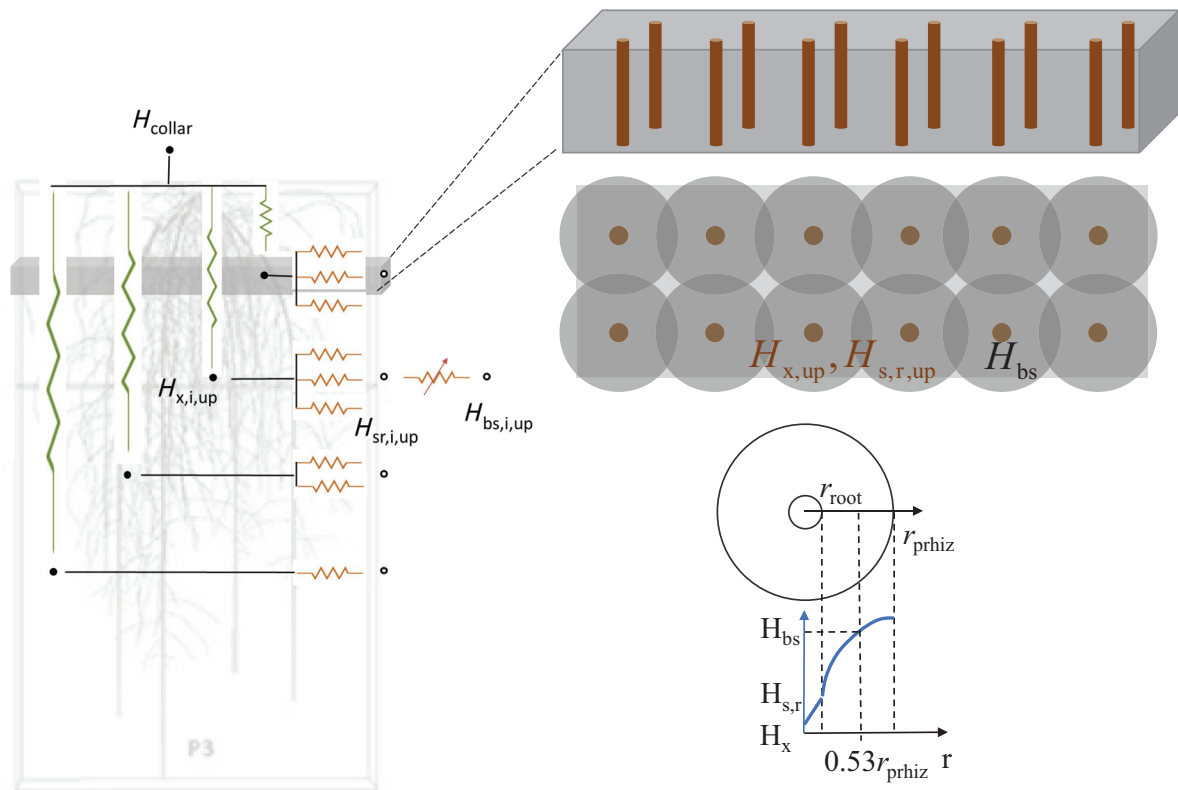


FIGURE 2 Upscaling concept. Left image: three-dimensional root system and its simplification to a parallel root system and estimates of an upscaled xylem water potential $H_{x,up}$, soil–root interface potential $H_{s,r,up}$, and bulk soil water potential $H_{bs,up}$ of root elements in a certain soil layer. Right images: simplification of uniformly distributed and parallel root segments in a soil layer and concept of perirhizal cylinders with a radius r_{prhiz} . In the perirhizal cylinders, flow is assumed to be radially symmetric and the bulk soil water potential H_{bs} corresponds with the water potential in the perirhizal cylinder at $r = 0.53 r_{prhiz}$.

TABLE 1 Parameters of the van Genuchten–Mualem hydraulic functions 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 root length density and SUF vertical profiles of the crop stand are shown in Figure 4. Of note is that the SUF does not decline so strongly with depth as the rld. This is explained by the younger roots with a larger radial conductance, k_r (Figure 3), deeper in the soil profile. The derived root system characteristics should not be interpreted as the characteristics of a specific maize crop but were chosen to be representative of generic root hydraulic properties and root length densities. Two soils with different hydraulic properties were considered: a soil with a coarse texture and one with a fine texture. The water retention curve and hydraulic conductivity curve were described by the van Genuchten–Mualem functions (Mualem, 1976; van Genuchten, 1980) and the parameters of these functions are given in Table 1. We assumed that the soil hydraulic

properties in the perirhizal zone are uniform and equal to those of the bulk soil, meaning that we did not consider the impact of roots on soil hydraulic properties in the rhizosphere. Only the effect of root water uptake on water potential gradients in the perirhizal zone was considered. An overview of the simulation setups and the assumptions or simplifications that are tested in the simulations is given in Table 2.

In a first set of simulations, we evaluated the effect of perirhizal conductances on root water uptake for two distributions of soil water potentials—one representing a wet soil profile and one representing a soil profile that is dry near the soil surface and wet at the bottom of the root zone. In these simulations, we also tested the assumption of uniform soil water potentials at soil–root interfaces in horizontal soil layers

TABLE 2 Simulation setups and tested processes and approximations.

	Effect of perirhizal conductance on...	3D versus upscaled 1D root systems	Exact upscaled 1D root hydraulic model versus parallel root system
Simulation 1	root water uptake for given soil water potential distribution representing wet and dry soil.	Effect of assuming uniform water potentials at soil root interfaces in 1D upscaled root models	Only parallel root model.
Simulation 2	root water uptake and plant water potentials during monotonic drying.	Only 1D	Effect of approximation of upscaled 1D root hydraulic model by parallel root model.
Simulation 3	root water uptake and plant water potentials during a cropping season with a long drought period in two soils.	Only 1D	Only parallel root model

Abbreviations: 1D, one-dimensional; 3D, three-dimensional.

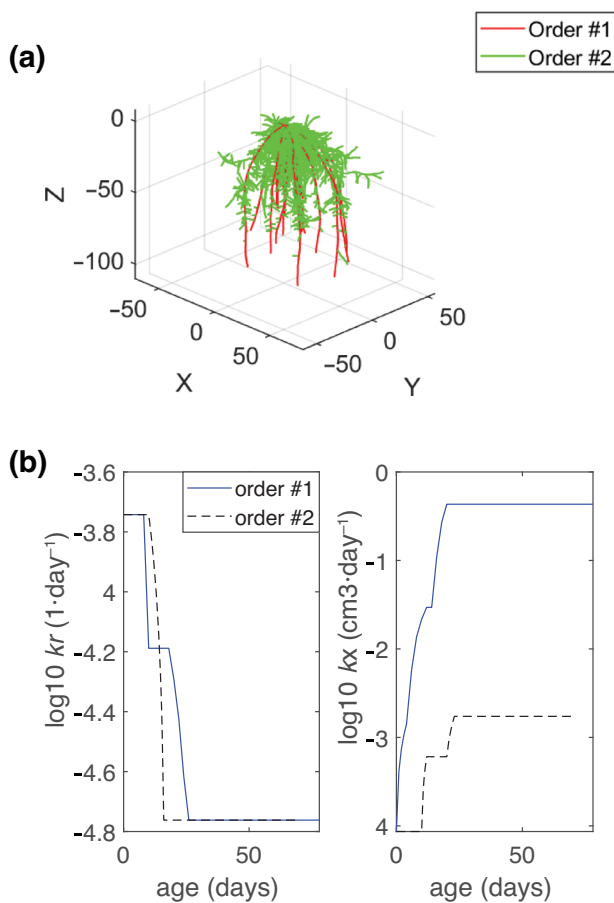


FIGURE 3 “Maize” root system (a) and radial and axial conductances of primary and secondary root segments as a function of root age (b). From Vanderborght et al. (2021).

in upscaled models. Therefore, we compared simulations for a 3D root architecture, with variable xylem and hence variable soil–root interface water potential of different root segments in a soil layer, with simulations for its upscaled 1D version

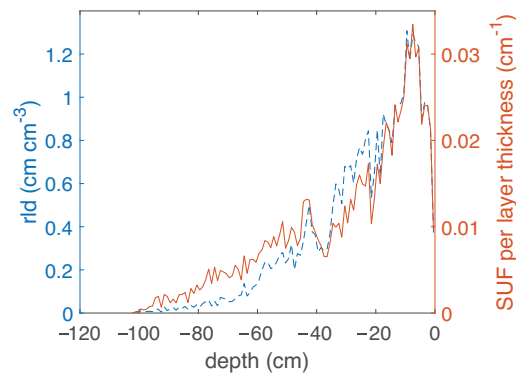


FIGURE 4 Root length density (rld) and standard uptake fraction by the root system (SUF) that represents the fraction of uptake by root segments from a soil layer to the total uptake when the soil water potential is uniform in the root zone. SUF is normalized by the thickness of the soil layer in cm-units, so that the integral of SUF over depth equals 1.

that assumes one single xylem water potential and hence a uniform soil–root interface water potential in a soil layer. We assumed that the water potential in the root collar, which is placed at the soil surface where we put the reference height $z = 0$, equals -8000 cm. For the wet soil case, we consider a linear water potential profile that decreases from $H_{bs} = -300$ cm at the soil surface to $H_{bs} = -200$ cm at the bottom of the root zone at $z = -103$ cm depth so that the pressure head h_{bs} increases from -97 cm at the bottom of the root zone to -300 cm near the soil surface. For the dry scenario, H_{bs} is equal to -5000 cm at $z = 0$ and -200 cm at the bottom of the root zone generating a strong gradient of water potentials and pressure heads in the root zone. For both scenarios, we considered the coarse soil. The effect of the perirhizal conductance on the root water uptake profiles was evaluated by comparing simulations using water potentials at the soil root interface equal to the bulk soil water potentials at the same depth, that is,

gradients in water potentials around the root segments in the perirhizal zone were not considered (case “no-prhiz”), with simulations that considered perirhizal conductances. For the evaluation of the upscaling from the 3D root system to the 1D parallel root hydraulic model ($C_4 = \text{diag}(K_{rs}) \text{SUF}$), we assumed that the bulk soil pressure heads in the perirhizal cylinders around all root segments at the same depth in the 3D model were the same.

In the second and third sets of simulations, dynamic boundary conditions at the root collar were assumed. To reduce the computational costs, only simulations with 1D upscaled models were considered. A root water uptake module that simulates root water uptake using the 1D upscaled root-soil hydraulic network was implemented in a Matlab code using the algorithm of the SWAP model (van Dam & Feddes, 2000) that solves the 1D Richards equation with an implicit finite difference scheme. But, the sink term during a time step is calculated explicitly and iteratively using the water potential distribution at the start of the time step. In a 1D soil water balance model, vertical water fluxes and transpiration fluxes correspond with flow rates per unit surface area. To match the units of the root hydraulic model, which calculates flow rates or uptake rates per plant, the flow rates were multiplied by the plant density. The conductances in 1D field plot, stand, or crop scale models, K_{rs} , K_{prhiz} , $K_{soil-root}$, and K_r have units T^{-1} . K_{prhiz} , $K_{soil-root}$, and K_r refer to the uptake by the root system from a soil layer of a certain thickness dz and the values of these conductances depend on the amount of root segments and their radial conductances in that layer.

In the second set of simulations, a drying out period of 20 days was simulated. In these simulations, the effect of perirhizal conductances on the dynamics of the root water uptake and plant water potentials during a drought period with a monotonous drying of the soil was evaluated. The effect of representing the root system by a parallel root system was evaluated and simulations with the exact upscaled root hydraulic model were compared with simulations that use the parallel root model. The daily transpiration demand was constant and equal to 6 mm-day^{-1} . Diurnal variation in transpiration demand were simulated using a halve sine function assuming that transpiration was zero during night (from 6:00 p.m. until 6:00 a.m.) resulting in a peak transpiration at midday of 19 mm-day^{-1} . If the collar water potential was above the isohydric water potential threshold, $H_{collar,lim} = -15,000 \text{ cm}$, the flux at the collar was equal to the transpiration demand. When the collar water potential reached $-15,000 \text{ cm}$, the collar water potential was kept constant, and the transpiration flux was equal to the supply from the soil. The depth of the simulation domain was 150 cm and a spatial discretization of 1 cm was used. A zero-flow and a free drainage boundary condition were applied at the top and bottom boundaries of the simulation domain, respectively. As initial conditions, a uniform pressure head $h_{bs} = -330 \text{ cm}$ was used. Simulations were

carried out for the coarse soil: (i) using the exact upscaled 1D root hydraulic model and (ii) using the 1D parallel root hydraulic model, both coupled with the perirhizal conductance, and (iii) using the 1D parallel root hydraulic model that did not consider water potential drops in the perirhizal cylinders.

In the third set of simulations, a time series of 157 days starting on April 24, 2019 with hourly potential evapotranspiration calculated with the Penman Monteith equation (Allen et al., 1998) and precipitation at the Bad Läuchstadt field site (Jorda et al., 2022) were used as boundary conditions. In these simulations, the effect of perirhizal conductances on root water uptake and plant water potentials under natural boundary conditions were evaluated. Cumulative precipitation and evapotranspiration are given in Figure 5. The precipitation deficit was around 400 mm over the simulation period. Simulations were done using the same root system as in the other simulations (assuming that it did not grow over time) for the coarse and fine soils and using the 1D parallel root hydraulic model either coupled or not coupled with the perirhizal conductance.

3 | RESULTS

3.1 | Uptake for the linear water potential profiles: Effect of perirhizal conductance and upscaling 3D to 1D root hydraulics

For the wet soil profile, the perirhizal conductances did not influence the root water uptake profile (Figure 6a) since the perirhizal conductance of the wet soil was much larger than the radial root conductance. For the soil profile that is dry near the soil surface, the lower soil water potentials near the soil surface led, for the same collar water potential, to a smaller simulated uptake than in the wet soil profile, especially near the soil surface (compare Figure 6a with Figure 6b). The reduction in uptake near the soil surface where the soil was drier was even stronger when perirhizal conductance was considered (compare no-prhiz vs. the other two models in Figure 6b), illustrating that the perirhizal conductance becomes limiting under dry soil conditions.

Due to the nonlinear dependence of the perirhizal conductance on the soil–root interface potential and its associated xylem water potential, the total uptake from a soil layer calculated with the 3D root hydraulic model, which represents the variability of xylem water potentials in root segments, could not be reproduced exactly by the upscaled 1D root hydraulic model, which uses one effective xylem water potential and one soil–root interface water potential in a soil layer (compare 3D with upscaled 1D in Figure 6b). Figure 7a,b and Figure 7c,d show, respectively, the xylem and soil–root interface water potentials in the segments of the maize root system and the

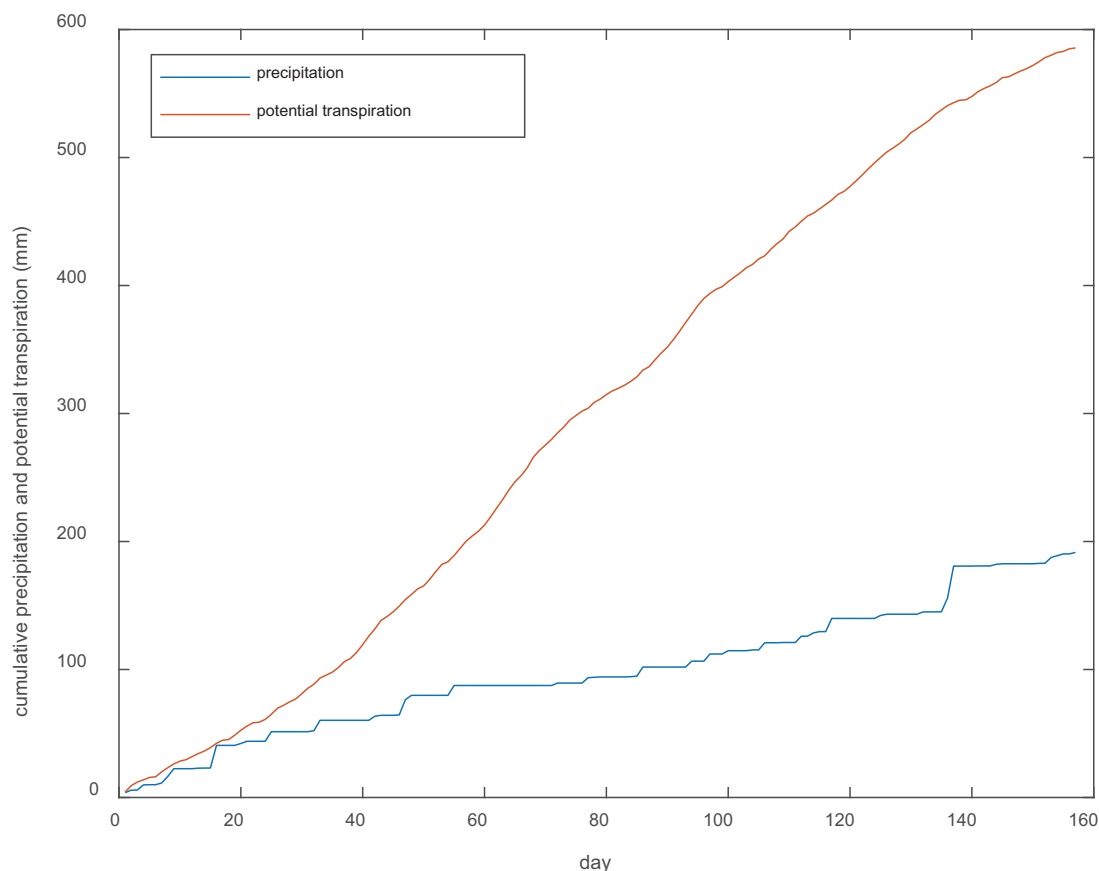


FIGURE 5 Cumulative precipitation and potential transpiration at the Bad Lauchstädt site during the summer of 2019 (day 0 corresponds to April 24, 2019).

effective xylem and soil–root interface water potentials in the different soil layers that are simulated with the upscaled 1D parallel root hydraulic model. The water fluxes at the soil root interfaces of individual root segments simulated with the 3D model and the effective water fluxes derived from the upscaled 1D model are shown in Figure 7e,f. Under wet conditions, both xylem water potentials and water fluxes varied a lot within a soil layer (Figure 7a,e). But this variability was totally determined by the root hydraulic properties since the soil–root interface water potentials did not vary much between root segments (Figure 7c) and were close to the bulk soil water implying that perirhizal conductances were not limiting under wet conditions. Since the root hydraulic properties did not depend on the water potentials and since the soil–root interface potentials did not vary much between root elements in a single soil layer, the water uptake could be upscaled nearly exactly regardless of the variability of the xylem water potentials and water fluxes, which is demonstrated by the perfect match between the sink term distributions that are calculated using 1D and 3D root hydraulic models (Figure 6a). In the “dry” soil profile, the soil–root interface water potentials show much more variation among root segments and are closer to the xylem water potentials (Figure 7b,d) than in the wet pro-

file. This demonstrates that except for the deeper wetter part (below -80 cm) of the “dry” soil profile, the perirhizal conductances were lower than the radial root conductances and limiting the flux toward root segments. The flux to individual root segments decreased toward the soil surface in the dry soil profile (Figure 7f), and the variability of the fluxes toward individual root segments decreased drastically compared to the variability in the wet soil profile (compare (Figure 7e with Figure 7f). The water uptake is more homogeneously distributed over the different root segments in the dry soil layers than in the wet soil layers. The limiting perirhizal conductance seems to uniformize fluxes toward soil–root interfaces and lower the impact of variations in xylem water potentials on these fluxes. This may explain the relatively good performance of the upscaled model that does not account for these variations in xylem and root–soil interface water potentials. Another result is that xylem water potentials were in both wet and dry soils considerably higher than the collar water potential (-8000 cm) and were not constant with depth. The latter is a consequence of the xylem conductance of the considered root system that limited the flow in the root system and shows that water flow in the root system needs to be considered when root water uptake is simulated.

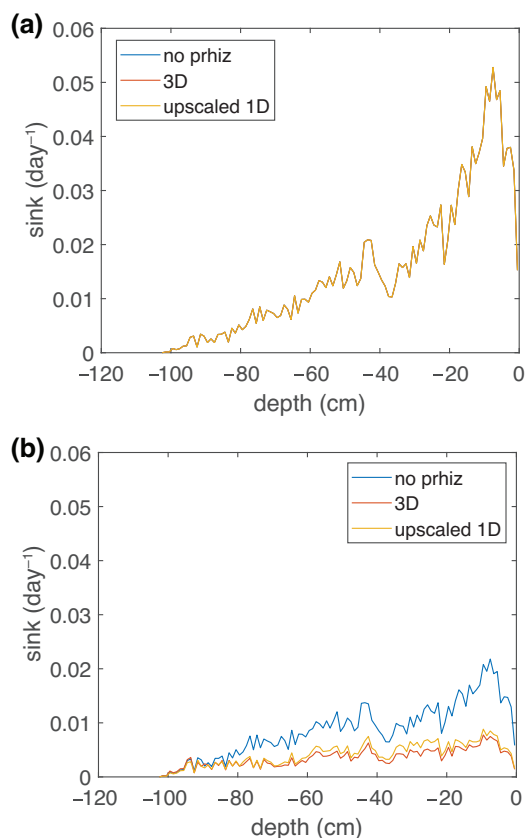


FIGURE 6 Simulated water uptake profiles in the coarse soil by the maize root system with a collar water potential of -8000 cm for a wet ($h_{bs} = -300$ cm at soil surface and -97 cm at bottom of the root zone) (a) and a dry ($h_{bs} = -5000$ cm at the soil surface and -97 cm at bottom of the root zone) (b) soil profile, using a three-dimensional (3D) root hydraulic model that considers nonlinear perirhizal conductances (3D), an upscaled one-dimensional (1D) parallel root hydraulic model that considers nonlinear perirhizal conductances (upscaled 1D), and a root hydraulic model that does not consider perirhizal conductance (no prhiz.). Lines in plot (a) overlap.

3.2 | Simulation of water uptake, and soil and plant water potentials during a dry out period: Effect of perirhizal conductances and the approximation of the exact upscaled 1D root hydraulic model by the 1D parallel root hydraulic model

The drop in perirhizal conductance when the soil dries out led to an earlier simulated drop in root water uptake, that is, after 8 (1D parallel root model) or 9 days (exact upscaled root model), compared to the scenario where perirhizal conductance is not considered (i.e., after 12 days) (Figure 8). Consequently, resistance to flow in the perirhizal zone reduced the amount of water that can be extracted by the plant to meet the demand. In the model simulations, the uptake switched from potential transpiration to supply-limited transpiration when the collar water potential reached $-15,000$ cm.

The 1D parallel root model and exact upscaled root hydraulic model simulated nearly the same collar water potentials (Figure 9) and reached the threshold collar water potential earlier than the root water uptake model that did not consider perirhizal conductances. When perirhizal conductances were not considered, the bulk soil water potentials were equal to the soil–root interface water potentials. In accordance with the larger transpiration simulated by the model that does not consider perirhizal conductances, the effective bulk soil water potential simulated by this model ($H_{bs,eff}$ no prhiz) dropped earlier than the effective bulk soil water potential ($H_{bs,eff}$ exact) but later than the effective soil–root interface water potential ($H_{sr,eff}$) simulated by the models that consider perirhizal conductance.

During daytime, the water potential drop from the bulk soil to the soil–root interface is related to the perirhizal conductance, and this drop increased when the soil dried out. Due to the decrease in transpiration when the soil dried out and the constant axial and radial root conductances, the drop in water potential from the soil–root interface to the collar decreased. The simulated redistribution of water via the root system at night with uptake deeper in the soil profile where soil water potentials were higher and release in the upper part with lower soil water potentials is shown in Figure 10. The model that does not consider perirhizal conductances simulated higher redistribution of water at night, whereas the drier perirhizal zone with a lower perirhizal conductance reduced this redistribution. Note that redistribution or exudation by the root system may also be simulated during the day when the collar water potential is higher than the lowest soil water potential occurring in the root zone, which may occur when the transpiration rate is low or after a long dry period when only the upper soil layers are wetted up by rain or irrigation, whereas the deeper layers remain dry (Jorda et al., 2022). Also, for these cases, the model that does not consider perirhizal conductances simulates higher exudation rates.

The approximation made in the 1D parallel root model, which requires considerably less parameters than the exact upscaled hydraulic root model, had no major impact neither on the simulated root water uptake (Figure 8) nor on the simulated collar water potentials, soil–root interface potentials, and bulk soil water potentials (Figure 9). The 1D parallel root model can hence be applied as a parsimonious approximation of the exact upscaled root hydraulic model. It should be noted that the computational cost was very similar when compared with the 3D model since both models solve the same number of equations iteratively.

3.3 | Simulations for the Badlauchstädt site for two different soil types

Potential transpiration and actual root water uptake simulated by the upscaled 1D parallel root model with and without

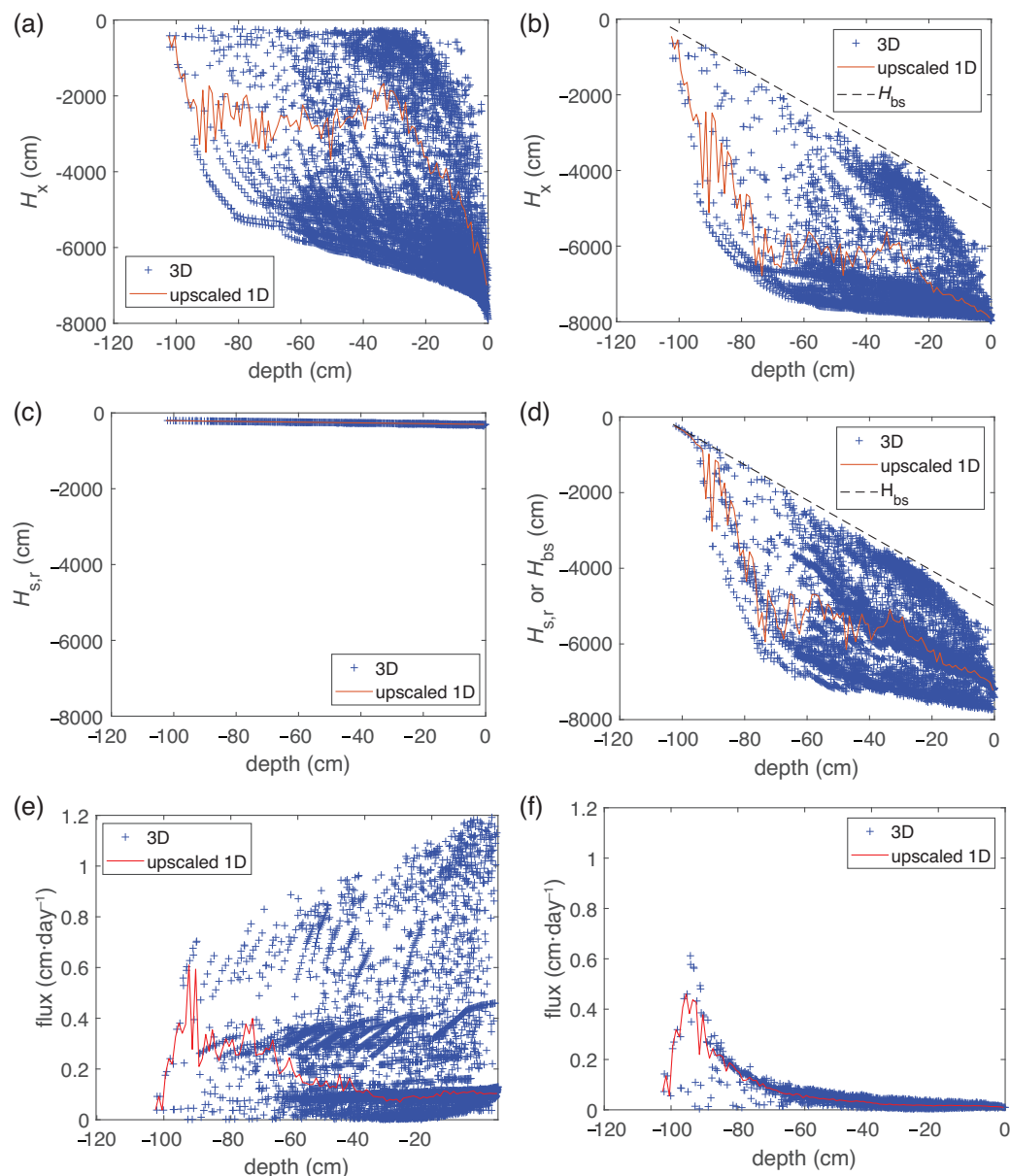


FIGURE 7 Xylem water potentials (a, b) and soil–root interface potentials (c, d) in root segments of the maize root system with a collar water potential of -8000 cm, and fluxes at soil–root interfaces of individual root segments (e, f) for the “wet” soil profile (a, c, e) and the “dry” (b, d, f) soil profile. Red lines refer to effective xylem water potentials (a–d) or fluxes (e, f) simulated with the one-dimensional parallel root hydraulic model. Black dashed line refers to the bulk soil water potentials in the dry soil profile.

perirhizal conductances are shown in Figure 11 for the fine and coarse soil. Due to the large precipitation deficit, transpiration decreased and became supply limited when the readily plant-available water that was stored in the soil profile at the start of the simulation was depleted. For both soils, including perirhizal conductance led to an earlier reduction in transpiration, whereas transpiration was maintained at a slightly higher level during the drought period.

When perirhizal conductances were considered, cumulative transpiration was smaller: 352 versus 372 mm in the fine soil, and 291 versus 308 mm in the coarse soil than in case they were not considered, and the soil profile did not dry out

so strongly (Figure 12). The drop in perirhizal conductance when the soil dries out had an important impact on the simulated collar water potentials and bulk soil water potentials. When perirhizal conductances were considered, the collar water potentials at midday reached the water potential threshold ($-15,000$ cm) faster and since the soil remained a bit wetter, the bulk soil water potentials remained higher during the drought period. Because the perirhizal hydraulic conductances decrease strongly with decreasing soil water potentials at less negative soil water potentials in the coarse soil than in the fine soil, bulk soil water potentials remained higher in the coarse than in the fine soil (Figure 13). The most striking

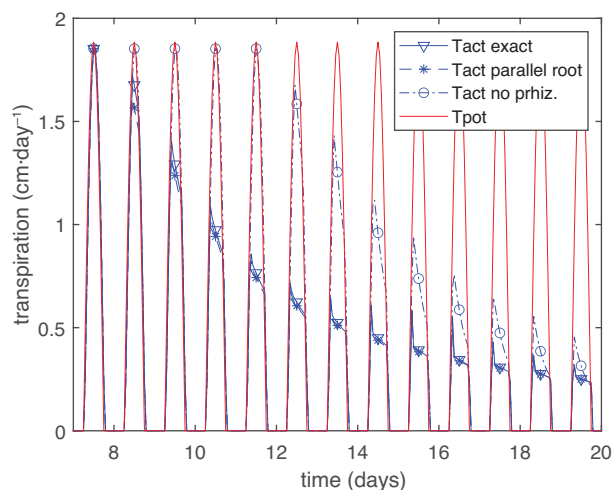


FIGURE 8 Potential transpiration (red line) and root water uptake (blue lines) simulated during a dry-out period in the coarse soil using the exact upscaled root hydraulic model (full line, crosses), the upscaled one-dimensional parallel root hydraulic model (dashed line, asterisks), and the upscaled root hydraulic model that does not consider perirhizal conductance (dotted-dashed line, open circles).

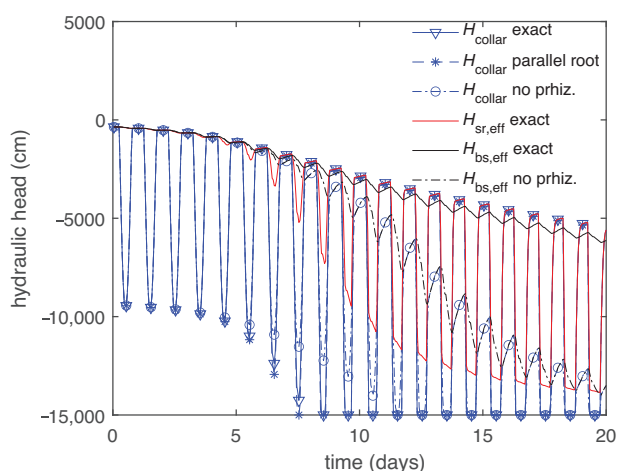


FIGURE 9 Simulated root collar water potentials (blue lines) and SUF-weighted average water potentials at the soil–root interface (red lines) and in the bulk soil (black lines) during a dry-out period in the coarse soil using the exact upscaled one-dimensional (1D) root hydraulic model (full line), the upscaled 1D parallel root hydraulic model (dashed line), and the upscaled 1D root hydraulic model that does not consider perirhizal conductance (dotted-dashed line).

impact of perirhizal conductances is on the collar water potentials at midnight. At night, the collar water potentials bounced back and even exceeded bulk soil water potentials, which were considerably higher when perirhizal conductances were considered. The perirhizal zone prevented roots from extracting all plant-available water from the bulk soil and prevented the water potential in the bulk soil from reaching the isohydric water potential threshold ($-15,000$ cm).

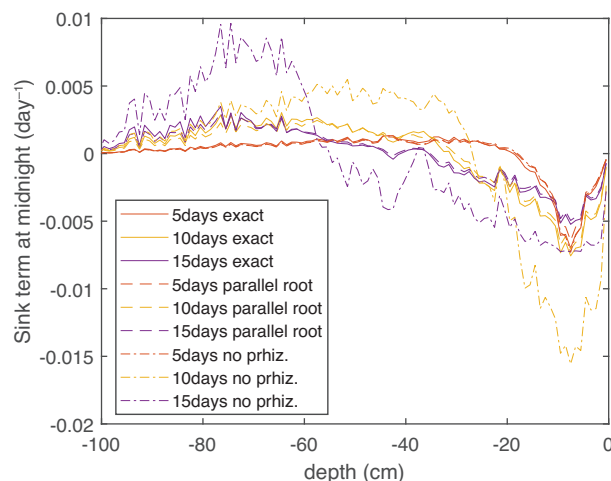


FIGURE 10 Water uptake and redistribution by the root system at night simulated using the exact upscaled root hydraulic model (full line), the upscaled one-dimensional parallel root hydraulic model (dashed line), and the upscaled root hydraulic model that does not consider the perirhizal conductance (dotted-dashed line). Different colors refer to different days after the start of the dry out period.

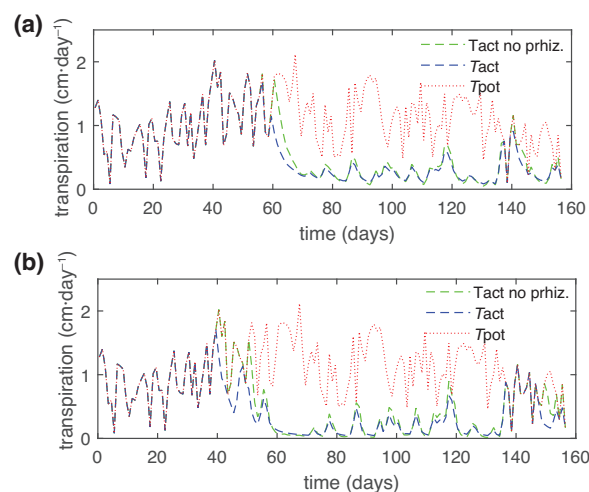


FIGURE 11 Potential transpiration (red dotted lines) and root water uptake at midday simulated by the upscaled one-dimensional parallel root model that considers perirhizal conductance (dashed blue line) and that does not consider perirhizal conductance (dashed green line) at the Bad Lauchstädt site for a soil with a fine (a) and coarse (b) texture.

3.4 | Effect of perirhizal conductances on root system scale uptake properties

We refer to root system properties as the characteristics of the entire root system that determine the total water uptake from the root zone without describing the uptake distribution within the root zone. The first set of functions expresses the uptake as a function of the bulk soil water pressure head, h_{bs} , in the root zone while assuming that h_{bs} does not

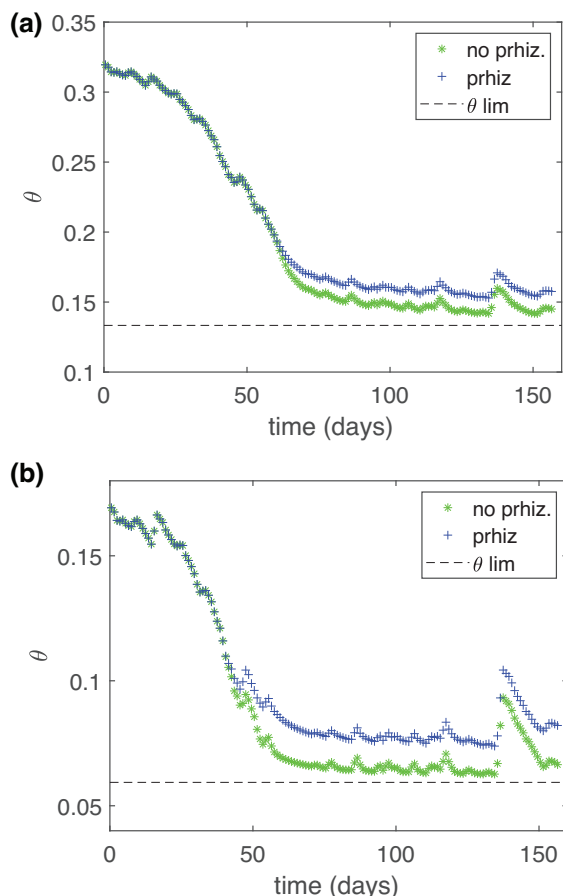


FIGURE 12 Average water content in the root zone in the soil with fine (a), and coarse texture (b) simulated with the upscaled one-dimensional parallel root model considering (blue) or not considering (green) perirhizal conductances. Horizontal dashed line represents the water content at the isohydric water potential threshold ($-15,000$ cm).

change with depth in the root zone. The total maximal uptake or maximal supply by the maize root system, $\max T$, corresponds with the uptake that is simulated when the collar water potential equals the isohydric water potential threshold ($H_{\text{collar,lim}} = -15,000$ cm), and $\max T$ in the coarse and fine soil was calculated for a range of bulk soil water potentials in the root zone. When no perirhizal conductance was considered, the supply increased linearly with the bulk soil water potential and the slope corresponds with the root system conductance K_{rs} (multiplied by the plant density). The perirhizal conductance generated a nonlinearity in the supply function with a stronger decrease of the supply with decreasing h_{bs} in the coarse than in the fine soil (Figure 14). Based on the supply functions, α -stress functions that describe the ratio of the supply (actual transpiration T_{act}) to the demand (potential transpiration T_{pot}) as a function of h_{bs} can be derived for different T_{pot} values. As for the supply functions, the perirhizal conductances induce a nonlinearity in the α -stress functions and the shape of the functions we obtained

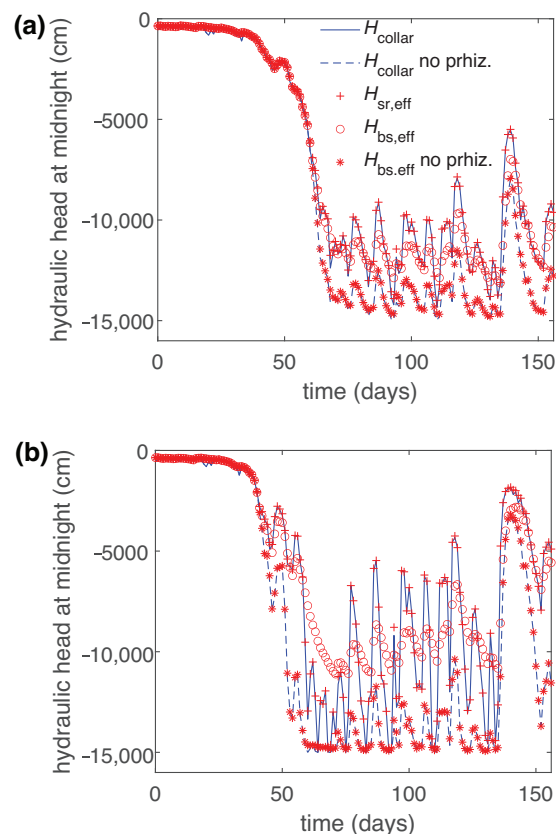


FIGURE 13 Collar water potentials (blue lines) considering (full line) or not considering (dashed) perirhizal conductances, SUF-weighted average water potentials at the soil–root interface (red crosses) and in the bulk soil (open circles), and SUF-weighted soil water potentials when perirhizal conductances are not considered (red asterix), at midnight and in the fine (a) and coarse (b) soil.

is similar to the shape obtained by a model that that did not consider variations of xylem water potential with depth in the root system (de Jong van Lier et al., 2013). When perirhizal conductances are not considered, the α function is a piecewise linear function that is similar to the stress function proposed by Feddes (Feddes & Raats, 2004; Feddes et al., 1978) and determined by K_{rs} and T_{pot} but independent of the soil hydraulic properties. However, the threshold values of h_{bs} below which the demand cannot be satisfied by the supply are much more negative than threshold values above -1000 cm for $T_{\text{pot}} = 5 \text{ mm} \cdot \text{day}^{-1}$ reported by Wesseling (1991) and threshold values that are used in soil water balance models, for example, Hydrus (Šimůnek et al., 2016). Including perirhizal conductances shifted the threshold values to less negative values but still more negative than values reported by Wesseling (1991). Since the perirhizal conductance depends on the soil hydraulic conductivity, α -stress functions depend, next to the root system properties related to a specific crop, also on soil hydraulic properties.

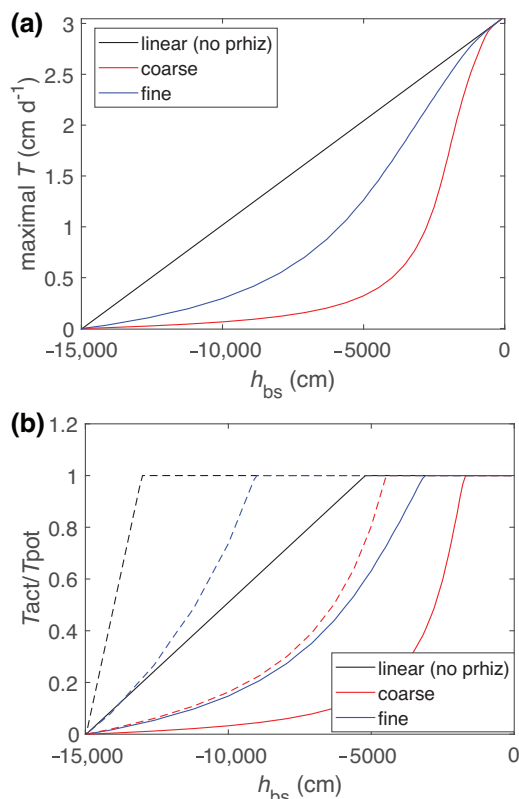


FIGURE 14 Supply functions (maximal root water uptake when the collar water potential equals the isohydric water potential threshold) versus the bulk soil water pressure head (a) and α -stress functions for a potential transpiration at midday of 2 cm day⁻¹ (corresponding with a daily averaged transpiration of 5 mm day⁻¹) (full lines) and of 0.4 cm day⁻¹ (corresponding with a daily averaged transpiration of 1 mm day⁻¹) (dashed lines) (b) for the maize root system in the fine (blue line) and coarse (red line) soil and for the case of not considering perirhizal conductance (black line).

To obtain further insight in the role of different conductances and their dependence on h_{bs} at the root system scale, root system scale perirhizal, radial, and axial conductances were defined. Since all radial root segment conductances are in parallel to each other, the root system scale total radial conductance, $K_{r,tot}$, is the sum of all root segment radial conductances:

$$K_{r,tot} = \sum K_r [i]. \quad (21)$$

Considering that the total radial and axial conductances are in series, the root system total axial conductance is derived from

$$K_{x,tot} = \frac{K_{r,tot} K_{rs}}{K_{r,tot} + K_{rs}}. \quad (22)$$

A total soil–root system conductance, $K_{rs,nonlin}$, that includes both the conductances of the root system, K_{rs} , and the

nonlinear conductance of the perirhizal zone can be defined based on the maximal supply for a certain bulk soil water pressure head as

$$K_{rs,nonlin}(h_{bs}) = \frac{\max T_{nonlin}(h_{bs})}{h_{bs} + \bar{z}_{root} - H_{collar,lim}} = \frac{\max T_{nonlin}(h_{bs})}{\max T_{lin}(h_{bs})} K_{rs}, \quad (23)$$

where $\bar{z}_{root}$ is the mean elevation of the root system that corresponds with the SUF-weighted depths in the root profile ($\bar{z}_{root} = \text{SUF}^T z$), and $\max T_{nonlin}$ and $\max T_{lin}$ are the maximal uptake when perirhizal conductances are and are not considered, respectively. Since the perirhizal and root system are connected in series, the total perirhizal conductance, $K_{prhiz,tot}$, is obtained as

$$K_{prhiz,tot} = \frac{K_{rs,nonlin} K_{rs}}{(K_{rs} - K_{rs,nonlin})} = \frac{K_{rs}}{\left(\frac{\max T_{lin}}{\max T_{nonlin}} - 1\right)}. \quad (24)$$

Alternatively, $K_{prhiz,tot}$ may be calculated approximately by assuming the same soil–root interface water potential in the entire root zone and assuming a vertically uniform root density distribution:

$$K_{prhiz,tot}(h_{bs}, \bar{h}_{s,r}) \approx 2\pi l_{root,tot} \bar{B} k_{prhiz}(h_{bs}, \bar{h}_{s,r}), \quad (25)$$

where $l_{root,tot}$ is the total root length, $\bar{B}$ is the average of the geometry factor over all soil depths, and $\bar{h}_{s,r}$ is the average soil–root interface pressure head over the entire root system. $\bar{h}_{s,r}$ is calculated from

$$\bar{h}_{s,r} = \frac{\max T_{nonlin}}{K_{rs}} + H_{collar,wilt} - \bar{z}_{root}. \quad (26)$$

The root system scale conductances are shown in Figure 15. The axial conductance of the root system was smaller than the radial conductance, which demonstrates that resistance to flow in the axial direction should not be neglected, which is consistent with previous calculations and simulations (Dousan et al., 1998, 2006; Landsberg & Fowkes, 1978) and recent anatomical observations (Clement et al., 2022). The root xylem water potential and soil root interface water potential therefore varied with depth (Figure 7). The perirhizal conductance of the fine soil is, except for very wet conditions, larger than the perirhizal conductance of the coarse soil. As expected, the perirhizal conductances are larger than the root conductances in wet soil and lower in dry soil. Perirhizal conductances calculated using an averaged soil–root interface water pressure head in the root zone approximate the root system perirhizal conductances well, except for the coarse soil under dry conditions where they underestimate the conductances.

To illustrate the effect of a nonuniform bulk soil water pressure head in the root zone, we compared total soil root

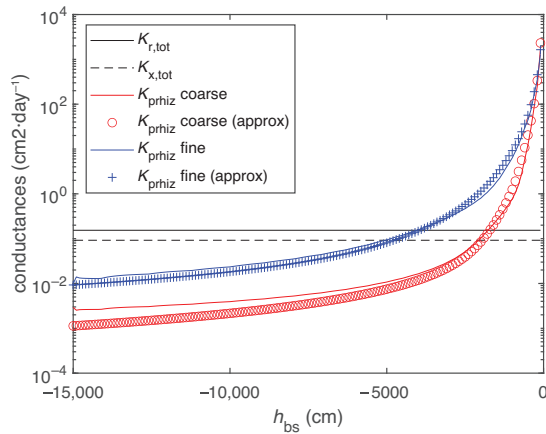


FIGURE 15 Root system scale radial ($K_{r,tot}$; full black line), axial ($K_{x,tot}$; dashed black line), and perirhizal ($K_{prhiz,tot}$) conductances in the coarse (red) and fine soil (blue) as a function of the bulk soil water pressure head, h_{bs} . K_{prhiz} is calculated from the supply functions and the root system conductance (full lines) and approximately assuming a uniform root soil–interface water potential in the root zone (symbols). (conductances are given here for a single plant).

system conductances $K_{rs,nonlin}$ that were calculated assuming a uniform h_{bs} using Equation (23), with $K_{rs,nonlin}$ that were calculated for nonuniform distributions of the bulk soil water pressure head. From the Badlauchstädt simulations, we used the simulated transpiration rates, the SUF-weighted bulk soil water potentials $H_{bs,eff}$, and the collar water potentials H_{collar} at midday to calculate $K_{rs,nonlin}$ for a set of nonuniform soil water potential distributions:

$$K_{rs,nonlin} = \frac{T}{H_{bs,eff} - H_{collar}}. \quad (27)$$

The uniform h_{bs} used to calculate $K_{rs,nonlin}$ with Equation (23) were translated to $H_{bs,eff}$ using $H_{bs,eff} = h_{bs} + \bar{z}_{root}$. Figure 16 illustrates how $K_{rs,nonlin}$ decreased depending on the soil hydraulic properties due to decreasing perirhizal conductances when the soil dries out and how it approximated the linear conductance of the root system when the soil is wet. It also demonstrates that when the soil water pressures are not uniform in the root zone, $K_{rs,nonlin}$ estimated from the simulated actual uptake and collar water potentials was mostly larger than $K_{rs,nonlin}$ estimated assuming a uniform soil water pressure head in the root zone. Variations in bulk soil water pressure in the root zone generated variations in perirhizal conductance and due to the strong nonlinear relation between perirhizal conductance and h_{bs} (see Figure 15), the average perirhizal conductance was larger than the perirhizal conductance calculated for the average bulk soil water potential. This is especially true when variations in h_{bs} in the root zone are large, for example, after rainfall events on a dried-out soil profile that generated hysteresis loops in the $K_{rs,nonlin}$ – $H_{bs,eff}$

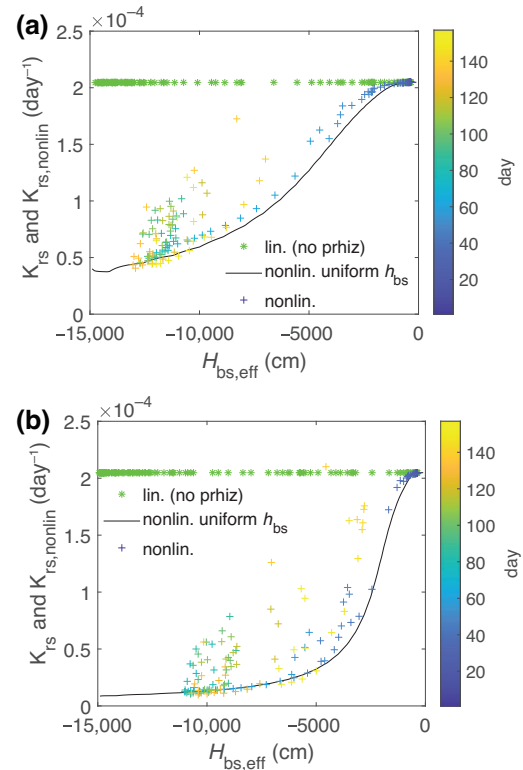


FIGURE 16 Linear, K_{rs} , and nonlinear soil–root system conductance, $K_{rs,nonlin}$, that includes the nonlinear perirhizal conductance versus the effective bulk soil water potential in the root zone, $H_{bs,eff}$, in the fine (a) and coarse (b) soil. $K_{rs,nonlin}$ is calculated either from the simulated transpiration and the difference between $H_{bs,eff}$ and H_{collar} at midday in the Badlauchstädt simulations (crosses) or from supply functions assuming a uniform bulk soil water pressure head in the root zone (black line). Color bar represents the day of the simulation.

relation. Under wet soil conditions, the total uptake can be calculated exactly using an SUF-weighted average of the bulk soil water potentials. The SUF is higher in a soil layer where the conductance of the root segments and of their connections to the root collar is higher. When perirhizal conductances are included, these conductances depend also on the bulk soil water pressure head so that the weights used to calculate an effective mean root zone water potential should depend on the pressure head distribution in the root zone.

4 | DISCUSSION AND CONCLUSIONS

We developed a model that links root system hydraulics with perirhizal hydraulics and used it to develop an upscaled root water uptake model that was implemented in a 1D soil water flow model. For the upscaling, we make use of the linear properties of the root system hydraulics to calculate an effective xylem water potential for each depth. This is a step

forward compared to previous approaches where xylem water potentials were either assumed to be constant in the root zone or where xylem water potentials were derived based on approximate estimates of axial root segment conductance without representing the root architecture. In the upscaled model, all root segments in a certain layer are represented by a set of identical root segments with the same effective xylem water potential, soil root interface potential, and radial root conductance. The nonlinear uptake equation has to be solved only once per soil layer in the upscaled model, which reduces the computation time considerably compared to the 3D model, where it must be solved for all root segments. Despite the nonlinear soil–root hydraulic conductance, the upscaling approach was robust against variations in xylem water potentials and flow rates to individual root segments within a soil layer. The upscaling approach is based on the assumption that the bulk soil water potential is uniform in a certain soil volume and we assumed that this was the case for a thin horizontal soil layer. We did not test this assumption and testing it requires full 3D simulations of water flow in the soil, around roots and in the 3D root system, which we are currently carrying out (Leitner et al. in preparation). For row crops like maize, there can be considerable lateral variability in root density, root water uptake, and bulk soil water potentials (Hupet & Vanclooster, 2005). Couvreur, Vanderborght, Beff, et al. (2014) showed that neglecting this lateral variation in root density and bulk soil water potentials leads to an overestimation of the simulated collar water potentials. Therefore, our 1D simulations are representative for a crop with uniform lateral root distributions. However, a uniform root distribution at a ‘macroscopic scale’ is not equivalent to equally distant parallel root segments as we assumed in the current approach. Random distributions of roots correspond with random distributions of perirhizal zone radii. Approaches to consider these distributions have been proposed by Graefe et al. (2019) who found that random distributions led to an earlier decrease in root water uptake and onset of stress compared to cases where roots are equally distant distributed. These approaches, as well as the numerical simulations that were used to test them, were also based on assumptions (uniform water potential at soil–root interfaces, and uptake is proportional to the volume of the perirhizal zone) and would require further testing against 3D simulations with a coupled soil–root model.

To reduce the number of parameters of the upscaled root hydraulic model, we considered a simplification of the root hydraulic architecture by a parallel root system, which is fully defined by K_{rs} and SUF. Vanderborght et al. (2021) tested this approximation for a few root systems with different architectures but for a given distribution of water potentials at the soil–root interface. We have now extended this test to dynamic simulations, including perirhizal conductances, and found that the small deviations in root water uptake distributions simulated by the two approaches did not propagate over

time so that simulated collar water potentials and transpiration rates hardly differed between the two approaches. This further confirms that parallel root models that are used in some land surface models such as Community Land Model (CLM) (Fu et al., 2016; Tang et al., 2015; Yan & Dickinson, 2014) are appropriate representations of root hydraulics.

Including the perirhizal conductance in the root water uptake model resulted in an earlier reduction of root water uptake during a drought period. This earlier reduction saved water that could be extracted by the plants later during the drought period so that the total simulated water uptake over a prolonged drought did not differ much between simulations that did or did not consider perirhizal conductances. The decrease in perirhizal conductance in dry soil prevented the soil to dry out completely so that simulated bulk soil water potentials remained considerably higher than that in simulations that did not consider perirhizal conductances. Perirhizal zone processes and properties seem to be more important for the plant water status at night than for the daytime water fluxes in the soil–plant system. The collar and plant water potentials at night, when the plants do not transpire, equilibrate back to bulk soil water potentials, which were higher when perirhizal conductances were considered. Because of the strong nonlinearity of the soil water retention and hydraulic conductivity curves in dry soils, a small difference in simulated water content has a large effect on the water potential. Furthermore, the “plant-felt” water potentials at night were higher than the weighted average of bulk soil water potentials using SUF weights that are based on linear root hydraulics and that represent the root water uptake distribution when the soil is uniformly wet. The low perirhizal conductances in drier layers and higher conductances in wetter layers raise the weights of wet soil layers in the root zone and decrease those of dry layers. The reduced perirhizal conductance in dry soil layers quasi disconnected the root system and the plant from the highly negative potentials present in these dry layers. Similar observations were made by Couvreur, Vanderborght, Draye, et al. (2014) using a simplified representation of the perirhizal conductance. The recovery of the plant water potential at night may have important physiological consequences. Since perirhizal conductances differ with soil type (texture and structure), the adaptation of plants to dry conditions also depends on soil properties. Some desert species develop xylem tissue that is more resistant to low water potentials in soils with a fine texture than in sandy soils so that they can extract water from small pores in these fine soils that is withheld by strong capillary forces (Sperry & Hacke, 2002). Roots can dry out fine soils to lower soil water potentials so that nighttime water potentials are lower than that in coarse soils, which could be another reason for adaptation of plants to lower plant water potentials in fine soils. The effective disconnection due to low perirhizal conductances between roots and dry bulk soil also reduces the redistribution of water

from wet to dry soils considerably. This needs to be considered when interpreting tracer studies (e.g., using stable water isotopes) to evaluate root water redistribution and derive root hydraulic parameters by inverse modeling (Meunier et al., 2018).

We illustrated that it is important to consider both root and perirhizal hydraulics and that root system-scale root water uptake properties or functions such as the supply function or the α -stress functions depend on both the root and perirhizal hydraulic properties, which reconfirms the results from de Jong van Lier et al. (2006) and de Jong van Lier et al. (2013). We demonstrated that including perirhizal hydraulic properties leads to α -stress functions that are nonlinear with threshold pressure head values that are less negative and closer to threshold values currently used in soil water flow models. But, the obtained threshold values are still more negative. One reason could be that we assumed that the perirhizal hydraulic properties were identical to the bulk soil hydraulic properties. Landl et al. (2021) showed in a simulation study that lower bulk soil densities around roots and the impact of root mucilage on rhizosphere hydraulic properties result in an earlier onset of drought stress compared to cases where uniform bulk soil properties were used in the perirhizal. Another reason could be the loss of soil–root contact in dry soils (Faiz & Weatherley, 1977, 1982; Herkelrath et al., 1977) due to root (Carminati et al., 2009) or root hair (Duddek et al., 2022) shrinkage.

By comparing the perirhizal conductances with the radial and axial root system conductances, we observed that the perirhizal conductances become limiting at pressure heads above -5000 cm. This is higher than limiting pressure heads at which xylem conductivity decreases due to cavitation and illustrates that rhizosphere properties induce nonlinearities in the relation between bulk soil water potential and plant water potential (Carminati & Javaux, 2020; Carminati et al., 2020).

The total soil–root system conductance and the supply function from which it is deduced are nonlinear functions of the bulk soil water potential. However, to use the supply or total conductance functions to calculate the total root water uptake, an effective or average bulk soil water potential for the root zone must be defined. For a linear supply function or a constant root system conductance, which does not depend on the perirhizal conductance and the bulk soil water potential, the SUF-weighted average of the bulk soil water potential in the root zone can be used. When nonlinear perirhizal conductances are limiting in parts of the root zone, the averaging weights that are used to calculate an effective bulk soil water potential depend on the bulk soil water potential distribution in the entire root zone. Not considering this dependence but calculating an effective bulk soil water potential using the SUF distribution generally leads to an underestimation

of the effective bulk soil water potential and the soil–root system conductances. This within root zone variability generates a hysteretic behavior of the relation between the soil–root system conductance and the SUF-weighted average pressure head. After a wetting event that generates a nonuniform bulk soil water potential distribution in the root zone, the conductance of the system increases more than what would be expected assuming a uniform water distribution. Interestingly, this hysteretic behavior due to nonhomogeneous water distribution at the root system scale is opposite to the hysteretic behavior of the rhizosphere and the bulk soil, which remain for the same water potential drier and less conductive after wetting (Carminati et al., 2010, 2016). To what extent opposing hysteretic behavior at the small and larger scales compensate each other requires further research.

The hysteretic or nonunique relation between soil–root system conductance and the SUF-weighted average pressure head in the root zone also leads to hysteretic supply (relation between the average soil pressure head and the maximal supply) and α -stress relations (relation between the average soil pressure head and the supply to demand ratio). The loss in accuracy of models that estimate root water uptake using non-hysteretic supply or α -stress functions also requires further investigation.

It must be noticed that we considered the drying out of a soil profile by a nongrowing root system. A root system that grows into deeper and wetter soil layers may observe a more heterogeneous water distribution in its root zone and consequently a higher soil–root system conductance than a static root system that dries out the root zone more homogeneously. The upscaled root water uptake model that considers perirhizal conductances can be coupled to a dynamic crop growth model as was done for the linear root water uptake model by Nguyen et al. (2020) and Nguyen et al. (2022). Using such a coupling, relations and feedbacks between root water uptake, root development, and crop growth, and how they are influenced by the perirhizal zone, can be investigated.

AUTHOR CONTRIBUTIONS

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

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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APPENDIX: PSEUDO CODE OF THE ROOT WATER UPTAKE FUNCTION

1. Start with the j th estimate of the soil–root interface water potential vector $\mathbf{H}_{s,r}^j$ and calculate H_{collar} , $\mathbf{Q}$, and $\mathbf{H}_x$. The initial estimate of $\mathbf{H}_{s,r}^0$ can be either the bulk soil water potential or the $\mathbf{H}_{s,r}$ from the previous time step.

$$H_{s,r \text{ eff}}^j = \text{SUF}^T \times \mathbf{H}_{s,r}^j,$$

$$H_{\text{collar}}^j = \max \left(H_{\text{collar,lim}}, H_{s,r \text{ eff}}^j - \frac{T_p}{K_{rs}} \right),$$

$$\mathbf{Q}^j = K_{rs} \times \left(H_{s,r \text{ eff}}^j - H_{\text{collar}}^j \right) \times \text{SUF} + \mathbf{C}_4 \\ \times \left(\mathbf{H}_{s,r}^j - \mathbf{H}_{s,r \text{ eff}}^j \right),$$

$$\mathbf{H}_x^j = \mathbf{H}_{s,r}^j - \text{diag}(\mathbf{K}_r)^{-1} \times \left\{ K_{rs} \times \left(H_{s,r \text{ eff}}^j - H_{\text{collar}}^j \right) \right. \\ \left. \times \text{SUF} + \mathbf{C}_4 \times \left(\mathbf{H}_{s,r}^j - \mathbf{H}_{s,r \text{ eff}}^j \right) \right\}. \quad (28)$$

2. Update $\mathbf{H}_{s,r}^j$ and obtain $\mathbf{H}_{s,r}^{j+1}$:

for $i = 1$ to $i = \text{length } \mathbf{H}_{s,r}$

$$\text{solve} \left[\frac{r_{\text{root}}[i] \times k_r[i] \times H_x^j[i] + B[i] \times H_{bs}[i] \times \bar{k}_{\text{prhiz}}(h_{bs}[i], H_{s,r}^{j+1}[i] - z[i])}{r_{\text{root}}[i] \times k_r[i] + B[i] \times \bar{k}_{\text{prhiz}}(h_{bs}[i], H_{s,r}^{j+1}[i] - z[i])} - H_{s,r}^{j+1}[i] = 0 \right] \quad (29)$$

(“solve” can be any nonlinear solver that solves the above equation for $H_{s,r}^{j+1}[i]$)

1. Update H_{collar} , $\mathbf{Q}$, and $\mathbf{H}_x$ in Equation (28).
2. Check for convergence and repeat, if necessary, the iteration loop.