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Discussions

Parameterizing complex root water uptake models – the arrangement of root hydraulic properties within the root architecture affects dynamics and efficiency of root water uptake

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Abstract

Detailed three-dimensional models of root water uptake have become increasingly popular for investigating the process of root water uptake. However they suffer from a lack of information in important parameters, especially distribution of root hydraulic properties. In this paper we explore the role that arrangement of root hydraulic properties and root system topology play for modelled uptake dynamics. We apply microscopic models of single root structures to investigate the mechanisms shaping uptake dynamics and demonstrate the effects in a complex three dimensional root water uptake model. We introduce two efficiency indices, for (a) overall plant resistance and (b) water stress and show that an appropriate arrangement of root hydraulic properties can increase modelled efficiency of root water uptake in single roots, branched roots and entire root systems.

The average uptake depth of the complete root system was not influenced by parameterization. However, other factors such as evolution of collar potential, which is related to the plant resistance, root bleeding and redistribution patterns were strongly affected by the parameterization. Root systems are more efficient when they are assembled of different root types, allowing for separation of root function in uptake (short young) roots and transport (longer mature) roots. Results become similar, as soon as this composition is accounted for to some degree (between 40 and 80 % of young uptake roots). Overall resistance to root water uptake was decreased up to 40 % and total transpiration was increased up to 25 % in these composed root systems, compared to homogenous root systems. Also, one parameterization (homogenous young root system) was characterized by excessive bleeding (hydraulic lift), which was accompanied by lowest efficiency. We conclude that heterogeneity of root hydraulic properties is a critical component of complex three dimensional uptake models. Efficiency measures together with information on critical xylem potentials may be useful in parameterizing root property distribution.

1 Introduction

Soil-plant interactions are important factors in hydrological and ecological processes. By using soil water for transpiration, plants are the essential link in the mass and energy transfer at the soil-vegetation-atmosphere-interface (Shukla and Mintz, 1982). Much of this interaction hinges upon the ability of plants to gain flexible access to soil water (Churkina and Running, 1998; Kleidon and Heimann, 2000; Feddes et al., 2001; Hildebrandt and Eltahir, 2007; Collins and Bras, 2007; Katul et al., 2012). Inversely changes in soil water content reflect on energy partitioning and carbon fluxes at the soil surface (Kleidon and Heimann, 1998; El Maayar et al., 2009; Seneviratne et al., 2010). Furthermore, access to soil water is an important prerequisite for biomass production, including crops (Blum, 1996; Huszár et al., 1998; Cai et al., 2009).

The ubiquitous influence of root water uptake on soil as well as ecological and atmospheric processes necessitates the prediction of root water uptake (Shukla and Mintz, 1982; Jackson et al., 2000). For this, together with observations, models have become vital tools that are used both in order to gain local process understanding as well as to predict macroscopic root water uptake characteristics.

Water uptake is driven by gradients in water potential, whereby water is pulled up from the soil into the root and up to the leaf (Steudle, 2001; Angeles et al., 2004). Besides soil hydraulic resistance tissue and vessel resistances determine the actual values of water uptake and water transport (Van Den Honert, 1948): radial resistance of soil and roots for the flow path along the soil-root-interface and roots axial resistivity for the flow path within the root xylem. The ratio between radial and axial resistance is of substantial importance. It dominantly shapes the distribution of xylem water potential along the root and thus influences root water uptake (Landsberg and Fowkes, 1978). Moreover, Zwieniecki et al. (2003) modeled a tradeoff between hydraulically active root length and the corresponding water uptake in unlimited water reservoirs. The term “hydraulically active” corresponds to the portion of the root that considerably contributes to root water uptake. The proposed tradeoff hinges upon the ratio of radial and axial root hydraulic resistance: When radial resistance increases, the active root length increases whereas water uptake decreases.

For process studies of root water uptake, models that compute microscopic three-dimensional root water uptake with respect to gradients in water potential and hydraulic resistances have become more and more popular (Clausnitzer and Hopmans, 1994; Tuzet et al., 2003; Doussan et al., 2006; Javaux et al., 2008; Schneider et al., 2010). Most of these models resolve the root geometry and water flow in detail. They account for the microscopic soil water flow towards individual roots, radial flow into the root xylem and the axial xylem flow within the root system. The modelling scale of these small-scale approaches comes close to the scale at which root water uptake takes place. Thus, they promise an important contribution to process understanding. Indeed, they capture well observed processes such as compensation of local water stress and resulting redistribution patterns, including moving uptake fronts (Garrigues et al., 2006; Javaux et al., 2008; Schneider et al., 2010) and also hydraulic lift (Dunbabin et al., 2013). Such processes could not be reproduced with earlier one-dimensional models, which related uptake directly to rooting density and soil moisture and lead to early water stress when upper densely rooted layers dry out (Feddes et al., 1978).

However, parameterization of small-scale models still poses a substantial challenge, since it requires detailed information that are difficult to obtain: (a) on root geometry and even more challenging (b) on distribution of root hydraulic properties. Some progress on point (a) has already been made. Recent improvements in imaging (Oswald et al., 2008; Mooney et al., 2012) and image analysis (Leitner and Schnepf, 2012) have improved information on root system geometry like position, orientation, branching order and root diameter. However, information on root hydraulic properties (point (b)) is still extremely sparse, because the necessary measurements are tedious (Knipfer et al., 2007). Thus, an important input to three-dimensional root water uptake models, that is the exact arrangement of root hydraulic properties within the root system, remains largely unknown.

Modelling results suggest that the lack of knowledge on root hydraulic properties may be a substantial hindrance. As stated above, the distribution of water potential and root water uptake along the root system depends dominantly on the ratio between root axial and root radial resistance (Landsberg and Fowkes, 1978; Zwieniecki et al., 2003; Levin et al., 2007). For what is more, during root maturation individual root hydraulic properties change with time (Steudle, 2000). Older suberized roots with more and mature xylem vessels have lower axial and higher radial resistance compared to younger roots. A root system contains both mature and young roots and observations show that conductivities along the radial and axial pathways vary within several orders of magnitude along root networks (Frensch and Steudle, 1989; Doussan et al., 2006). Hence a root system is a network of elements with contrasting hydraulic properties. Modellers account for this heterogeneity differently. Doussan et al. (2006) distributed hydraulic properties stepwise according to root length in tap roots and root age in lateral roots. Schneider et al. (2010) translated a root developmental stage (obtained with a root generator from Pagés et al. (2004)) into five hydraulic classes with distinct root hydraulic properties. However, as stated earlier, the actual arrangement of hydraulic properties within the root system is most of the time unknown and parameterization has to be based on intuition. To our knowledge, there exists no systematic investigation on whether and how strongly the spatial arrangement of root hydraulic properties affects model results, although such an analysis would greatly help in making decisions on model parameterization.

Root hydraulic properties do not only shape root water uptake profiles (Landsberg and Fowkes, 1978) and active root length (Zwieniecki et al., 2003), but may also be important for the water relations of a plant, because they reflect on total plant resistance and hence on evolution of xylem potential during the uptake process. Strongly negative xylem water potentials increase the danger of embolism and cavitation of xylem vessels, resulting in a progressive loss of axial hydraulic conductivity (Pockman and Sperry 2000; McDowell et al., 2008). Research suggests that plants operate with little safety margin with regard to danger of embolism across climates (Choat, 2013; Manzoni et al., 2013). As a consequence, plants probably apply strategies to minimize their vulnerability to cavitation, which includes efficient distribution of resistances within their water uptake apparatus. Therefore, xylem water potential recommends itself as a tool for distinguishing efficient from less efficient root parameterizations. On the other hand, if modelled xylem potentials are meaningful they can serve as a valuable model output for example for coupling root water uptake to stomatal control (Tuzet et al., 2003).

Within this research we investigate how heterogeneity of root hydraulic properties influences root water uptake dynamics and evolution of xylem water potential. We also investigate the role of branching topology. Our results show that both the heterogeneity of root hydraulic properties and branching strongly influence the modelled evolution of xylem water potential, microscopic and macroscopic location of root water uptake as well as hydraulic lift.

Background

We first use a thought experiment to illustrate that root properties inevitably shape active root length, but more importantly how this root length reflects an optimization of the total resistance of the root. To demonstrate this, we use the common description of root water uptake as being composed of two pathways: first water flows from the soil across the root cortex into the root xylem (radial pathway) and along the root xylem towards the collar (axial pathway). We can now formulate the total resistance to root water uptake as two resistors acting in series

$$R_{\text{Total}} = R_{\text{Rad}} + R_{\text{Ax}}.$$

Radial resistance to root water uptake can be calculated from a root radial resistivity ρ_{Rad} and scales inversely with the surface area of the root, A_{surf} (see also Sect. “Materials and methods”). Thus, the radial resistance can always be reduced by prolonging the root:

$$R_{\mathrm{Rad}} = R_{\mathrm{Rad}}(l) = \frac{\rho_{\mathrm{Rad}}}{A_{\mathrm{Surf}}} = \frac{\rho_{\mathrm{Rad}}}{2 \cdot \pi \cdot r \cdot l}$$
$$\lim_{l \to \infty} R_{\mathrm{Rad}}(l) = 0.$$

The root axial resistance on the other hand integrates xylem resistivity (ζ_{Ax}) over the path towards the collar. Let us consider a single unbranched root strand of length l with water uptake distributed evenly along its length. Then the mean distance of water transport equals $l/2$. The mean axial resistance to root water uptake can be expressed by $\zeta_{\mathrm{Ax}} \cdot l/2$, and increases with greater values of l:

$$R_{\mathrm{Ax}} = R_{\mathrm{Ax}}(l) = \zeta_{\mathrm{Ax}} \cdot l/2$$
$$\lim_{l \to \infty} R_{\mathrm{Ax}}(l) = \infty.$$

Thus, a differential increase in root length at the same time reduces radial resistance and increases axial resistance. This suggests the existence of an optimal root length (l_{opt}) that minimizes the total resistance:

$$\frac{\mathrm{d}R_{\mathrm{Total}}(l)}{\mathrm{d}l} = \frac{\mathrm{d}R_{\mathrm{Rad}}(l)}{\mathrm{d}l} + \frac{\mathrm{d}R_{\mathrm{Ax}}(l)}{\mathrm{d}l} \propto -\frac{\rho_{\mathrm{Rad}}}{l^2} + \zeta_{\mathrm{Ax}} \overset{!}{=} 0$$
$$\frac{\rho_{\mathrm{Rad}}}{\zeta_{\mathrm{Ax}}} \propto l_{\mathrm{opt}}^2$$

Note that this optimal length depends only on the ratio $\rho_{\mathrm{Rad}}/\zeta_{\mathrm{Ax}}$, and not their absolute values, and that $\sqrt{\rho_{\mathrm{Rad}}/\zeta_{\mathrm{Ax}}}$ indeed has units of m.

When root length is shorter than its optimum, an increase in root length decreases total resistance by increasing the uptake area. We will refer to this case as “radial limitation”. On the other hand an increase of l beyond its optimal value increases total resistance, because in this case the axial resistance term dominates. This situation will be referred to as “axial limitation” in this paper.

That the active root length depends on the ratio of $\rho_{\mathrm{Rad}}/\zeta^{i}_{\mathrm{Ax}}$ is consistent with previous studies (Zwieniecki et al., 2003; Javaux et al., 2008), but our emphasis is different: The ratio $\rho_{\mathrm{Rad}}/\zeta_{\mathrm{Ax}}$ defines the optimal root length with minimal total resistance. From a physical point of view, it is inefficient to extend roots of a given ratio $\rho_{\mathrm{Rad}}/\zeta^{i}_{\mathrm{Ax}}$ beyond their optimal length, since this effectively increases their total resistance. Typically, $\rho_{\mathrm{Rad}}/\zeta_{\mathrm{Ax}}$ ratios for young roots (with low radial and high axial resistance) are much lower than those for mature and suberized roots (with high radial and low axial resistance). Young roots therefore have much smaller efficient uptake length (in the order of some centimetres) than mature roots, although observations show that total fine root length in root systems is substantial. In the following we show that this is no contradiction because the active fine root length can be enhanced in branched root systems that are composed of root segments of different $\rho_{\mathrm{Rad}}/\zeta_{\mathrm{Ax}}$ ratios.

Moreover, radial and axial limitation may occur in model applications and increase modelled total resistance. In the following we show that these effects dominate model results in some parameterizations and can be avoided with others.

2 Materials and methods

In this study we investigate the combined influence of heterogeneity of root hydraulic properties and root system topology (branching structure) on spatiotemporal root water uptake dynamics by the help of a simple and a complex root water uptake model. The simple model serves to describe processes of root water uptake qualitatively that are hard to detect at higher levels of model complexity. Within this section we first describe the two models of root water uptake that we used. Second, we explain how heterogeneity of root hydraulic properties was systematically altered along the different root systems. Finally, we introduce two indices of root water uptake that are used to quantify water stress and overall resistance to root water uptake: "Water yield" and "effort". All comparisons of the efficiency of root water uptake are made according to these two criteria.

2.1 Simple root water uptake model for root modules

Root water uptake along single branched and un-branched roots was calculated with the help of a simple root water uptake model (see Fig. 1 for the considered root structures). It treats the root as a short network of porous pipes. Each root segment is considered to have a cylindrical shape of radius r and length l. Water is taken up from a soil cylinder with radius r_{soil} surrounding the root. We assumed that water was distributed initially uniformly along the soil profile. Furthermore water redistribution between the soil layers was neglected. Since the soil is also considered to be homogeneous, changes in soil matric potential reflect changes in soil water content. Water transport within the root follows an axial pathway, while water uptake (flow from the surrounding soil into the root) occurs along the radial pathway only. Water flow along each pathway is governed by gradients in hydraulic potential and resistances, similar to Ohm's law. In either direction, the water flow for a given root segment i is given as:

$$Q^i_{\text{Rad}} = \frac{\psi^i_x - \psi^i_{\text{Soil}}}{R^i_{\text{Rad}}} \tag{1a}$$

$$Q^i_{\text{Ax}} = \frac{\psi^{i+1}_x - \psi^i_x}{R^i_{\text{Ax}}} \tag{1b}$$

where Q^i_{Ax} and Q^i_{Rad} are the volumetric rates of water flow along the axial and radial pathway in $\text{m}^3\,\text{s}^{-1}$; ψ^i_x, ψ^{i+1}_x and ψ^i_{Soil} are the xylem potential within the root segment i, the xylem potential within the directly connected root segment $i+1$, and the bulk soil water potential within the soil surrounding the root segment i, given in terms of a negative hydraulic head in m; and where R^i_{Ax} and R^i_{Rad} are the axial and radial root resistance within segment i. The resistances are derived from material properties and scale with geometric dimensions as follows:

$$R^i_{\text{Ax}} = \zeta^i_{\text{Ax}} \cdot l^i \tag{2a}$$

$$R^i_{\mathrm{Rad}} = \frac{\rho^i_{\mathrm{Rad}}}{A^i_{\mathrm{Surf}}} = \frac{\rho^i_{\mathrm{Rad}}}{2 \cdot \pi \cdot r^i \cdot l^i} \tag{2b}$$

The factors ζ^i_{Ax} and ρ^i_{Rad} are the axial and radial resistivity, given in $\mathrm{s\,m^{-3}}$ and s respectively; geometric inputs l^i and r^i are the length and radius of the root segment i. Although the resistances R_{Ax} and R_{Rad} determine water flow along potential gradients in both models, the underlying axial and radial root resistivities ζ^i_{Ax} and ρ^i_{Rad} define root hydraulic properties and can be obtained via measurements. Each root segment obtains root hydraulic resistivities corresponding to two discrete hydraulic classes taken from Schneider et al. (2010) (see Sect. 2.3, and Table 1). Heterogeneity of root hydraulic properties is introduced in roots by associating these different hydraulic classes with different regions of the root system.

As a consequence of mass conservation and the absence of storage capacities within the root, the water mass balance holds for each segment i:

$$Q^i_{\mathrm{Ax}} + Q^i_{\mathrm{Rad}} = Q^{i+1}_{\mathrm{Ax}}. \tag{3}$$

By substituting the axial and radial flow rates by Eqs. (1a) and (1b) for all n root segments and by defining Q^0_{Ax} as the unknown total outflow at the root collar, we obtain n equations for the $n+1$ unknown xylem water potentials (including the xylem water potential at the root collar). Closure of this underdetermined system of equations is achieved in terms of a boundary condition. In our model, this can either be a prescribed flux rate Q^0_{Ax} or a constant xylem potential ψ^0_x at the root collar. The former represents a constant transpirational demand of a plant at a given time; the latter is used to simulate a plant under water stress. At the onset of water stress transpiration reduces, as collar potential does not further decrease. All simulations are started with a flux boundary condition, until collar potential drops to a critical threshold, here taken as a typical value of the permanent wilting point $\psi^0_{\mathrm{Crit}} = -150\,\mathrm{m}$ ($-1.53\,\mathrm{MPa}$) upon which the boundary condition switches to a potential boundary.

The bulk soil water potential ψ^i_{Soil} is derived from relative soil water content θ^i_{Soil} with a van Genuchten parameterization of the soil $\theta^i_{\mathrm{Soil}} = f(\psi^i_{\mathrm{Soil}})$. Parameters are taken from Schneider et al. (2010) and were originally obtained for a sandy soil (see Table 2 for details). Within the simple model, each root segment is surrounded by an individual reservoir of soil, and different reservoirs are assumed to be hydraulically disconnected. It follows that no redistribution of water along gravitational and hydraulic gradients occurs in the soil. This assumption is made for reasons of simplicity and is suitable, while root water uptake velocity dominates soil water dynamics. Furthermore the results are in good agreement with the ones obtained with the complex root water uptake model which explicitly accounts for soil water redistribution (see Sect. 3).

After all soil and xylem water potentials have been calculated, root water uptake rates can be deduced using Eq. (1a) and are regarded as sink terms in the soil water balance. After deriving the water uptake rates at time t, soil water status is updated using a steady state approach for a sufficiently short interval of time Δt,

$$\theta^i_{\mathrm{Soil;\,new}} = \theta^i_{\mathrm{Soil;\,old}} - \frac{Q^i_{\mathrm{Rad}} \cdot \Delta t}{V^i_{\mathrm{Soil}}} \tag{4}$$

where V^i_{Soil} is the total volume of the soil surrounding the root segment i. After calculating the water uptake, soil water status is reset with respect to Eq. (4) and the soil water potential decreases correspondingly.

Within this simple model several assumptions are made some of which seem to be oversimplifying and unrealistic. These assumptions allow for a qualitative description of root water uptake dynamics, which would be hard to detect at a higher level of complexity. Indeed, our assumptions are justified subsequently as the qualitative results are reproduced within the complex root water uptake model at a full level of complexity (see Sect. 3).

2.2 Root water uptake model for complete root systems

We modelled root water uptake in complete root systems of a single plant individual with the three dimensional root water uptake model “aRoot”, developed by Schneider et al. (2010). “aRoot” mimics a pot experiment where a complete root system is embedded in one block of soil. Within this block, water redistribution is gradient driven and calculated by explicitly solving the 3-D Richards equation (Kolditz et al., 2012). Furthermore, “aRoot” accounts for gradients in soil hydraulic conductivity in the immediate vicinity of individual roots. The model of water flow within the root system is equivalent to the simple model described above. For detailed information about the features of “aRoot”, please refer to Schneider et al. (2010). Both the van Genuchten parameters of the soil and the root hydraulic properties are the same as in the simple model (Tables 1 and 2).

2.3 Heterogeneous root hydraulic properties in roots

The complex process of root maturation is simplified by introducing two discrete hydraulic classes, which possess both different axial and radial resistivities ζ_{Ax}^{i} and ρ_{Rad}^{i}, as well as ratios of radial and axial resistivity $\rho_{\mathrm{Rad}}^{i} \big/ \zeta_{\mathrm{Ax}}^{i}$. Values for the two classes are taken from Schneider et al. (2010). They refer to young and mature roots of a 28 d old sorghum plant. For reasons of simplicity root radius is set evenly to 1 mm within all roots. This simplification is supposed to have minor influence on root resistance, since changes in root radius are small compared to changes in root length (see Eqs. 2a and 2b).

In order to assess the influence of the degree of heterogeneity of root hydraulic properties, the distribution of the two hydraulic classes along the roots is varied systematically. We assume that mature roots do always constitute the basal parts and young roots the apical parts in all roots. Figure 1 illustrates the assignment of hydraulic classes along single roots in the simple model. In un-branched single roots the mature root is located in the basal, the young root in the apical part of the root strand. We modelled un-branched roots with a total length between 1 and 800 cm, containing between 0 and 100 % of mature roots. We also considered branched roots with one, two, three, four or six young root branches (*n*). All of those branches are assumed to be equally long and to be distributed evenly along the central mature root strand, resulting in fishbone-like structures. Besides the number of branches we vary total root length of branched root structures between 5 and 400 cm. We only modelled branched structures with one central mature as well as *n* apical young root branches. Therefore, relative amounts of mature roots vary between 10 and 90 %. We are aware that un-branched roots of great length are unrealistic. However, un-branched roots serve as a default to assess the efficiency of root water uptake depending on the branching structure.

We used “aRoot” to calculate spatiotemporal root water uptake for one exemplary root system with respect to the degree of heterogeneity of root hydraulic properties. The geometry of the root system was obtained with the root generator “RootTyp” by Pagés et al. (2004) and the location of the roots within the soil was kept the same for all simulations (see Fig. 7). The parameters used for “RootTyp” are taken from Schneider et al. (2010) and correspond to a 28 d sorghum plant. Resulting total root length was 9.93 m. In order to investigate the influence of heterogeneous hydraulic properties on spatiotemporal root water uptake and its efficiency, we varied the proportions of young and mature roots in steps of 20 % between 0 and 100 %. Branching points were only classified as young roots, if all associated branches have already been classified as young roots. By this we ensure that mature roots are never preceded by young roots and therefore constitute the basal and apical root part respectively. Particularly, this also ensures that all root tips are young roots, which is physiologically sensible.

2.4 Measuring the efficiency of root water uptake

In order to compare efficiency of root water uptake with respect to root topology and the degree of heterogeneity of root hydraulic properties we define two indices: water yield and effort. Water yield measures the amount of water extracted from the soil until the onset of water stress, effort estimates overall resistance to root water uptake. Figure 2 illustrates how these two indices can be deduced from the temporal evolution of xylem water potential at the root collar.

Water yield is related to the amount of water that can be taken up by the root until the onset of water stress. In our simulations water stress occurs when xylem water potential at the collar reaches the permanent wilting point $\psi^0_{\mathrm{Crit}} = -150\,\mathrm{m}$ ($-1.53\,\mathrm{MPa}$). As plants explore soils by extending their root system via root growth, total amount of extracted water is additionally normalized by the total length of the root and thus has units of $\mathrm{dm}^3\,\mathrm{m}^{-1}$. Denoting with $Q(t) = Q$ the time constant transpiration under unstressed conditions we calculate water yield $\tilde{V}$ as

$$\tilde{V} = \frac{V_{\mathrm{Total}}(\tilde{t})}{l_{\mathrm{Total}}} = \frac{\int\limits_{\tau=0}^{\tilde{t}} Q(\tau)d\tau}{l_{\mathrm{Total}}} = \frac{Q\cdot\tilde{t}}{l_{\mathrm{Total}}}, \tag{5}$$

where $\tilde{t}$ is the time of reaching $\psi^0_{\mathrm{Crit}} = -150\,\mathrm{m}$ and hence entering water stress. Since the water yield $\tilde{V}$ is directly proportional to time at which water stress occurs, both water yield $\tilde{V}$ and $\tilde{t}$ can be used equivalently when the roots to be compared are equally long.

Effort uses xylem water potential at the root collar to estimate the efficiency of root water uptake. It is beneficial for plants to take up water at small negative xylem water potentials in order to avoid xylem cavitation under conditions of sustained water demand. As the soil reservoir is emptied in the course of root water uptake, xylem water potentials have to follow decreasing soil water potentials to meet the transpirational demand. As will be seen later, assignment of root hydraulic properties may cause substantial additions to modelled overall resistances, however. Accordingly, we define a second efficiency criterion $\tilde{\psi}$ called effort. It can be shown (see Appendix A) that under a time constant flux boundary condition, the average work $w(t)$ necessary to take up water until time t corresponds to the time average xylem water potential at the root collar and thus is related to the plants overall resistance to water uptake. Hence we relate effort to the average work necessary to take up water before entering water stress at time $\tilde{t}$:

$$\tilde{\psi} = w(\tilde{t}) = \frac{\int\limits_{\tau=0}^{\tilde{t}} \psi_x^0(\tau)\mathrm{d}\tau}{\tilde{t}} \tag{6}$$

According to the xylem water potential at the root collar the effort has units of a negative hydraulic head in m.

Figure 2 illustrates water yield and effort for one branched (green) and one unbranched (red) single root, both sharing the same total length. It can be seen that in this case water yield $\tilde{V}$ is directly proportional to the time $\tilde{t}$ at which the plant enters water stress. Effort $\tilde{\psi}$ corresponds to the area below the two curves, divided by the respective values of $\tilde{t}$. The green area is much smaller than the red area and consequently lower effort for maintaining root water uptake in the branched root. This indicates overall lower resistance of the branched compared to the unbranched root. In this particular case, the differences in effort are induced by branching (see Sect. 3), and Fig. 2 illustrates that the two efficiency measures actually convey different information. Water yield gives the total volume of water that could be extracted per unit root length before water stress occurred. The effort relates to the time evolution of water potential and gives a measure of the total resistance to root water uptake of a root system, integrating all soil and root hydraulic properties. Since research suggests that plants operate with little safety margin with regard to danger for embolism across climates, plants should apply strategies to avoid very negative xylem water potentials. As lower effort is tantamount for lower xylem water potentials over the course of time, effort recommends itself as a tool for distinguishing efficient from less efficient parameterizations.

3 Results

We will present how the distribution of hydraulic properties along roots influenced the two model efficiency measures water yield and effort as well as root water uptake dynamics in different root topologies. We investigate single un-branched and branched roots (Sects. 3.1–3.3) as well as entire root systems (Sects. 3.4 and 3.5).

3.1 Effort and water yield in un-branched root strands

Figure 3 shows effort and water yield in un-branched homogenous (top) and heterogeneous (bottom) root strands. All heterogeneous root strands consist of basal mature and apical young roots, the length of both regions was varied independently (see Fig. 1). We can by this means find optimal proportions for the given hydraulic classes, based on each criterion.

For homogenous root strands (top) effort and water yield propose similar optimal root length, but different ones for young and mature roots: Young roots have to be short in order to achieve low effort and high water yield, whereas mature roots have to be long. Interestingly, the actual values at the respective optima are not much different – it is (almost) as efficient to be a short young root as it is to be a long mature root. Water yield is by far the lesser sensitive of the both measures with regard to changes in root length. Also, mature roots exhibit less pronounced differential changes in effort and water yield than young roots.

Results for mixed root strands are shown at the bottom of Fig. 3 with green colour indicating high and red colour indicating low efficiency. Efficiency in heterogeneous strands has only slightly increased compared to those in homogeneous root strands with regard to both effort and water yield. However, the optimal total root lengths differ from expectation, in that the optimal mixed root strand is not a composition of an optimal mature root strand and an optimal young root strand. In composed roots some of the water is taken up by the basal mature root part and less water has to be transported through the apical young roots. Therefore drops in xylem potential are smaller, axial limitation is less severe and hydraulically active young root region is extended in composed root structures. For this reason, in optimal composed root modules the young roots are longer and the mature roots are shorter in comparison with the respective homogenous root strands. This leads to overall shorter composite roots.

3.2 Effort and water yield in single branched roots

Figure 4 shows the effort in mixed root strands (Fig. 4a) and branched single roots with two, four and six tips respectively (Fig. 4b–d). The root composition is now given by the total root length of the respective root (*y* axis) and the proportion of mature roots (*x* axis). Colours are the same as in Fig. 3. As above, an optimal branched root is neither a composition of the optimal mature root strand, connected to *n* branches of optimal young root strands nor the optimal mixed root strand, which contains *n* instead of one branches of young roots (the latter one is indicated with a cross in Fig. 4b–d). While the proportion of mature roots in optimal branched roots decreases disproportionally, the total length of all young roots is almost proportional to the number of tips *n*. The overall total root length is only reduced up to a point. When four or six branches of young roots are contained in the branched root individual young root tips can become a little shorter, allowing for the total root length to increase without resulting in increased effort. In this way, branching favours soil exploration, without compromising efficiency. Notably, the effort surface becomes flatter, and hence the domain of nearly efficient hydraulic parameterizations expands with the number of tips.

Similar results are obtained for water yield but results are far less sensitive. Figure 5 shows water yield for mixed un-branched roots (Fig. 5a, equivalent to Fig. 3b, but axis denote for total root length and mature root proportion as in Fig. 4) and a branched root with two tips (Fig. 5b). For the branched root water yield is nearly constant (little sensitive) within the domain of modelled root compositions and did increase only very little compared to the optimal unbranched strand. This result was observed for all branched root structures (see top of Table 3 for optimal values of water yield and effort).

3.3 Water uptake dynamics and redistribution in single roots

The proportions of root hydraulic properties within a branched or un-branched single root do not only affect the efficiency of root water uptake, but also its location and dynamics. This may even be the case, if the efficiency is similar between parameterizations. Figure 6 depicts root water uptake rates along three exemplarily chosen un-branched root strands of equal length ($l_{\text{total}} = 0.42\,\text{cm}$), which all share very similar values of water yield and effort. The strands consist of young roots only (red), mature roots only (blue) or are an optimal composition of young and mature roots in terms of effort (green). The latter root strand contains 0.14 m of basal mature roots and 0.28 m of apical young roots. Root water uptake along the root strand is shown from the collar (left) towards the tip (right) for different simulation times, namely $t = 0\,\text{d}$ (top), $t = 4\,\text{d}$ (middle) and $t = 8\,\text{d}$ (bottom).

At the initial stage, the young root strand shows an exponential decrease in root water uptake rate towards the tip. In contrast, root water uptake is distributed almost equally along the mature root strand. The uptake of the mixed root is a combination: an almost homogeneous uptake rate in the basal mature root part is followed by an increased rate of root water uptake in the young root part, which decays exponentially. After some time (four days in the model), a moving uptake front (MUF) has developed both in the pure young and in the mixed root strand, reaching the root tip after 8 days. Additionally, water uptake rate in the basal mature root part increases in the mixed root strand in the course of time. Root water uptake in the pure mature root strand remains almost constant during the entire simulation period. Although the occurrence of moving uptake fronts is accentuated by the neglect of soil water flow within the simple root water uptake model, qualitatively the same results are obtained within the complex "aRoot" model, in which soil water redistribution is explicitly considered (see Sect. 3.5 and Fig. 7).

3.4 Effort and water yield in entire root systems

In order to quantify what influence the above mentioned small scale processes have at the scale of an individual plant and taking soil water flow into account, we used the detailed three dimensional root water uptake model "aRoot". We calculated effort, water yield and local root water uptake for one exemplary entire root system, which was kept the same for all simulations (see Fig. 7 for geometry). We varied only the proportions of young and mature roots in steps of 20 % between 0 and 100 % (see Sect. 2.3).

Table 4 shows water yield and effort for these six different hydraulic parameterizations. Both criteria showed lowest efficiency in the homogeneous young root system, followed by the homogeneous mature root system. Heterogeneous root systems (containing between 20 and 60 % of mature roots) generally had an increased water yield of up to 25 % and decreased their effort substantially by a factor of 2. Root systems containing more mature roots (80 and 100 %) showed less increased efficiency.

3.5 Water uptake dynamics and redistribution in entire root systems

As mentioned above, single young and mature roots possess different optimal lengths with respect to both water yield and effort. Efficiency of root water uptake in entire root systems is substantially decreased whenever heterogeneity in root hydraulic properties is neglected. In this section we will investigate to what extend heterogeneity of root hydraulic properties also influences spatiotemporal root water uptake at the single plant scale.

Figure 7 shows the spatial distribution of root water uptake characteristics in a root system containing young roots only (left) and a combination of 40 % mature and 60 % young roots (right). These root systems showed lowest and highest efficiency with regard to water yield and effort respectively.

In the top most part of Fig. 7, time averaged root water uptake rate is depicted along the root system. Regions with negative net uptake (bleeding) are depicted in red, independent of the actual amount of bleeded water. Mean root water uptake rates vary much less in the homogeneous compared to the heterogeneous root system (spanning one order of magnitude compared to three orders of magnitude). This indicates the separation of root function in the heterogeneous root system between uptake roots and transport roots, and is in agreement with the earlier observations in the simple model. Apical young roots have a higher mean uptake rate than inner young roots in both hydraulic parameterizations, which is due to higher root density in the central parts of the root system. The domain of hydraulic lift is noticeably larger in the homogenous compared to the heterogeneous root system. The total length of bleeding roots decreases with increasing proportion of mature roots, being smallest in the homogeneous mature root system (see also Fig. 9).

The lower part of Fig. 7 shows the magnitude (centre) and timing (bottom) of the maximum uptake at each location of the root system. This allows tracking of moving uptake fronts. In the homogenous root system (left) maximum uptake is distributed rather homogenously, compared to the heterogeneous system (right). The timing of the maximum shows how uptake moves evenly away from the collar in the young root system as expected from the simple model (see Fig. 6). The overall maximum uptake rates occur at the outer ends of the root system here. The latter appears counterintuitive, because the uptake at root tips should suffer from axial limitation. The reason is the higher root density at the centre, which limits maximum uptake rates there. Axial limitation becomes apparent however in the overall higher resistances which lead to the increased effort of root water uptake in the homogeneous young root system (see Table 4).

In heterogeneous root systems the uptake pattern is more complex than in the homogeneous root system. Maximum uptake rates occur in the young roots, which are located anywhere within the root system. The timing of the maximum uptake shows that uptake fronts move not only outwards but also inwards (see the blue roots in the centre of the root system depicted in Fig. 7, bottom right). Uptake in inner mature roots is activated late and only if the surrounding soil was not previously dried out by young roots. Together with distant young roots, mature roots contribute the majority to total water uptake after 8 days (see Figs. 7 and 9). This redistribution pattern corresponds to the one observed with the simple model in heterogeneous single roots (Sect. 3.3 and Fig. 6). In the simple model root water uptake was redistributed in two ways: along young roots towards the root tips by moving uptake fronts; and the backward redistribution away from distal young roots to inner mature roots. In the complex “aRoot” model, which considers root length density and soil water redistribution, a third redistribution pattern is added: redistribution between different root branches. Root water uptake is distributed away from (inner) branches of young and mature roots as they fall dry in the course of soil drying; and is redistributed towards roots in wetter soils. Altogether, compensation for local water stress is more efficient in heterogeneous root systems compared to homogeneous root systems, resulting in higher efficiency (Table 4).

Regardless of the complex uptake dynamics, heterogeneous root systems show overall deeper uptake compared to homogenous ones. Figure 8 shows evolution of the depth above which half of the root water uptake occurred (z_{50}) with time. The water uptake of the homogeneous young root system is most shallow, followed by the homogeneous mature root system and all heterogeneous root systems. Over the course of time, z_{50} moves downwards in all hydraulic parameterizations and equilibrates at the onset of water stress, with the homogeneous young root system being most dynamical.

Figure 9 integrates the contribution of mature roots to total root water uptake (Fig 9a) as well as the relative amount of bleeding (Fig. 9b) along the root systems, showing the temporal evolution for the different hydraulic parameterizations. Results for homogeneous and heterogeneous root systems are shown in solid and dashed lines, respectively. For the homogeneous root systems, mature root water uptake is either 0 % in the young root system or 100 % in the mature root system. Within all heterogeneous root systems, water uptake of mature roots is at any time smaller than the mature root proportion of total root length, indicating that they function as transport roots. At the beginning of the simulation mature root water uptake decreases: Because of their location in the centre of the root system, some mature roots fall dry due to high water uptake from neighbouring young roots. Later, mature roots contribute more water to total uptake, because of the backward redistribution already observed in the simple model (Fig. 6). The maximum contribution of mature roots to total uptake is reached at the onset of water stress when critical xylem water potential is reached.

Hydraulic lift occurred in all root parameterizations. However, the amount of outflow depends on the hydraulic parameterization, with by far highest values modelled for the homogeneous young root system (up to 10 % of total root water uptake). The amount of bleeding decreases along with decreasing young root proportion, which is in accordance with the decrease in total root length contributing to bleeding (Fig. 7). It must be stated that bleeding usually occurs at night and may hence not be well captured with the time constant flux boundary condition used here. However, simulations with a sinusoidal day/night cycle of transpiration showed qualitatively the same results (data not shown).

4 Discussion

We used two models in order to examine to what extent heterogeneity of root hydraulic properties influences root water uptake at two spatial scales. Particularly we introduced two measures to compare the efficiency of root water uptake: water yield as a proxy for the plants ability to extract soil water before entering water stress; and effort as a proxy for overall resistance to water uptake under unstressed conditions. By this we were able to derive optimal lengths of single roots with contrasting hydraulic properties and different ratios of radial and axial resistivities. Finally we outlined how the heterogeneous distribution of these two hydraulic properties along entire root systems increases efficiency of root water uptake by allowing more efficient compensation of local water stress and avoiding both axial and radial limitation.

At the single root scale a simple model is used to describe principal mechanisms of root water uptake dynamics qualitatively rather than to predict actual values of root water uptake. Although the simple model is comparatively conceptual, our results suggest that descriptions of root water uptake dynamics can be transferred to the single plant scale. The latter results are obtained by the “aRoot” model (Schneider et al., 2010), which accounts for complex processes such as soil water redistribution, root length density or unsaturated flow in the vicinity of roots.

In order to disentangle different processes of root water uptake redistribution acting at the same time, we applied several simplifications. First we presuppose soil to have homogenous hydraulic properties and to be homogeneously wetted at the initial stage. These assumptions emphasize the effects originating from root hydraulic properties as they relate differences in soil hydraulic conductivity to soil water content. Second, soil water redistribution was only considered in the complex “aRoot” model. This rather strong simplification in the simple model proved to be sufficient as similar results were obtained both in the simple and in the complex model. Third the presented results were obtained assuming an idealized drying scenario with a time constant flux boundary condition. We do this mainly to facilitate interpretation of the results. In order to validate that our results do not depend on this assumption, the same analysis was also performed with a sinusoidal transpiration function in which results remained qualitatively the same. Especially the ranking of the six hydraulic parameterizations of the complete root system remained the same with regard to the duration of water stress, the temporal evolution of collar potential or the amount of simulated hydraulic lift (bleeding).

We combine two approaches from Schneider et al. (2010) and Doussan et al. (2006) to generate heterogeneity of root hydraulic properties in roots: first we use two classes of roots with both distinct radial and axial resistivities (young and mature roots). Second, we systematically change the degree of heterogeneity within the respective root by altering the proportions of these two root classes a priori, and by subsequently neglecting both root growth and maturation during the modelling period. Although roots are reported to alter their hydraulic properties according to parameters like topology, diameter and age (Frensch and Steudle, 1989; Steudle and Peterson, 1998; Doussan et al., 2006), we assume that this will not affect our results at the model time scale. Furthermore, these idealizations allow us to neglect processes (which themselves demand for detailed but mainly unknown information and parameters) and facilitate both the description of root water uptake mechanisms and the detection of axial and radial limitation. Generally, considering for root maturation by incremental changes of hydraulic properties within each class as in Doussan et al. (2006) or the further addition of classes as in Schneider et al. (2010) would further enhance the complex redistribution patterns described in this paper. Our results should therefore be validated in an extensive modelling study on a larger sample of different root systems, root hydraulic classes and soil types. Taken together, we believe our model idealizations serve the purpose of discovering drivers that shape root water uptake patterns which are difficult to discover in more comprehensive simulations. They nevertheless capture the essential features to yield process insight.

The two criteria used to compare efficiency of root water uptake, water yield and effort, relate to different aspects of plant physiology and hydrology. Water yield measures the ability of plants to deplete soil water before transpiration is reduced because of water stress (much according to the Feddes (1976) model). Due to the importance in soil vegetation interactions, and the fact that it is relatively easy to measure in experiments, water yield appears in different forms in many modelling studies of root water uptake (Doussan et al., 2006; Javaux et al., 2008; Schneider et al., 2010). In contrast, temporal evolution of xylem water potential at the root collar is usually not discussed in detail, although it includes information at which average cost the root water uptake was achieved. Large negative xylem potentials may lead to cavitation, i.e. the sudden change of water from liquid to vapour phase in root conduits (Tyree and Sperry 1989; Pockman and Sperry 2000). As cavitation is strongly connected to losses of hydraulic conductivity in root xylem via interruptions of water transport, effort may be related to a plants ability to exploit soil water and to sustain droughts (McDowell et al., 2008). We observe that water yield and effort behave differently with effort being more sensitive to changes in parameterization than water yield. Thus effort suggests itself as an efficiency criterion which may even be more meaningful to plants than water yield. Especially effort was a useful and sensitive tool for assessing efficient root length proportions. Thus together with simulators for root architecture (Pagès et al., 2004; Leitner et al., 2010), and given knowledge of critical xylem pressures it may be helpful for parameterizing root hydraulic properties of given species.

Both water yield and effort give similar results for optimal root composition in all root topologies investigated, with effort being far more sensitive. Particularly, efficiency of optimal (short) young and (long) mature root strands was nearly the same, both in terms of water yield and effort. We found that unbranched young root strands possess optimal lengths in the range of some centimetres, whereas optimal length of mature root strands may be in the range of meters. Optimal root length of young root strands already includes the redistribution of root water uptake from dry soils to wetter soils by moving uptake fronts. This compensation of local water stress in young roots extends hydraulically active root length and agrees with other models and observations (Roose and Fowler, 2004; Levin et al., 2007). However, young root strands suffer from axial limitation when they are too long. Thus, maturation on the one hand is meaningful from a hydraulic point of view, as it keeps young roots short. On the other hand overall root water uptake would be much more efficient, if the active length of young roots could be increased, despite axial limitation. As we will discuss immediately, this can be achieved by the use of heterogeneous hydraulic properties in branched roots.

All optimal heterogeneous hydraulic parameterizations were more efficient than the corresponding homogenous ones, which is intuitive and consistent with observations showing that roots differentiate with maturation (Frensch and Steudle, 1989; Doussan et al., 2006). Our results prove that efficiency increases by a division of root water uptake and transport, whereby active young root length is maximized. Mature roots with higher axial conductivity act as a transport system for uptake delivered from many individual short young roots with high radial conductivity. In other words, conducting the xylem potential effectively to the young root branches is preferably done by mature transport roots in central parts of the heterogeneous root system. This rather intuitive result needs to be considered when parameterizing models for hydrological applications as it also impacts root water uptake dynamics.

In the realistic and efficient heterogeneous root systems, uptake behaviour becomes more complex. As long as the soil is moist, water uptake is achieved through young roots with uptake starting near the branching points, as it was already pointed out by Roose and Fowler (2004) and agrees with experimental results from Zarebanadkouki et al. (2013) on lupines. As the soil around the branching points dries out, water uptake is redistributed to the apical ends of the central young roots by moving uptake fronts. Over the course of time xylem water potential drops to a point where water uptake in mature roots becomes possible and water uptake is redistributed "backward" from young roots to mature roots. At the single plant scale we additionally observe re-distribution of water uptake between different root branches as inner short branches fall dry. Thus, particularly in the heterogeneous root systems, the temporal evolution of water uptake is the result of several interacting re-distribution patterns, which do not only move vertically, but also horizontally, and not only from top to down, but also from bottom up. By this, plants with heterogeneous root hydraulic properties have more possibilities to compensate for local water stress in distinct regions of the root system leading to increased water yield at decreased effort. Therefore heterogeneity of hydraulic properties should be considered at least up to the single plant scale. Surprisingly, changing the proportion of mature roots between 20 and 60 % resulted in similar, nearly optimal values of both water yield and effort, suggesting that a precise consideration of heterogeneity may not be necessary.

Heterogeneity of hydraulic properties does also influence other root water uptake characteristics, primarily bleeding. Simulated bleeding of water from roots to soil can be associated with hydraulic redistribution of soil water through plant roots as described in Prieto et al. (2012). This redistribution of water into dry soils equilibrates soil water potential and may facilitate less negative xylem water potentials, thus inhibiting cavitation (Domec et al., 2006). Several studies report positive effects of hydraulic redistribution on life span of young roots (Caldwell et al., 1998; Bauerle et al., 2008), the accessibility to nutrients (Ryel et al., 2002) and to water relations in plants and ecosystems (Siqueira et al., 2008; Domec et al., 2010; Brooksbank et al., 2011; Prieto et al., 2012).

In contrast, our results show the highest amount of bleeding in the most inefficient root hydraulic parameterization, namely in the homogeneous young root system. This result remained unaltered when a sinusoidal transpirational demand was used instead of a fixed flux boundary condition (data not shown). This indicates that bleeding in this case did not act to improve the overall water status of the plant. Thus although hydraulic redistribution is frequently observed in the real world (Neumann and Cardon, 2012) its occurrence in models does not necessarily imply efficient parameterization. A transition from the single plant to the small community scale therefore promises valuable insights on niche partitioning and potential redistribution of soil water in ecosystems (Nippert and Knapp, 2007; Ward et al., 2013). Although recent development of the “aRoot” model allows for these simulations (Kalbacher et al., 2011), large computational demand and the complexity of the expected results both prevented us from treating this issue in this paper.

5 Conclusions

In this modeling study we show that root hydraulic properties, in particular the ratio of root radial and axial resistivity, determines optimal root length. We investigate this with two different indices of root water uptake: water yield and effort. Both are suitable to detect efficient lengths of young and mature roots, with effort being more sensitive than water yield. Optimal lengths of un-branched young roots are some centimeters, compared to several meters for mature roots. Efficiency of simulated root water uptake increases, when more young root length can be activated. This necessitates branched systems with heterogeneous root hydraulic properties, which allow for a division of function between water uptake and transport. This is supported by simulations in complex three dimensional root systems, where mature roots contribute disproportionally less to overall root water uptake compared to young roots, suggesting that they act as transport roots. Overall root resistance to root water uptake is reduced substantially by conducting the xylem water potential through mature roots efficiently to a large number of apical young roots, which are sufficiently short to take up water efficiently.

As heterogeneity in root hydraulic properties leads to lower effort, increased water yield and altered root water uptake dynamics, heterogeneity should be addressed in root water uptake models. Overall, parameterization of the root system has a great effect on modeled processes that are of interest for the hydrological and ecological community, such as root water uptake profiles, moving uptake fronts, evolution of collar potential over time, and hydraulic re-distribution. As the exploration of these processes is one of the main purposes for using complex three dimensional models, we believe that parameterization of root properties warrants more attention. Some root water uptake features are similar within a broad range of efficient heterogeneous parameterizations. Therefore the actual degree of heterogeneity may play a subordinate role for root water uptake simulations, as long as hydraulic heterogeneity is accounted for in a principal way.

Appendix A

Effort as a time average xylem water potential at the root collar

In this section we will show that under a time constant flux boundary condition the effort $\tilde{\psi}$ can be understood as an average collar potential $\bar{\psi}$. Effort is assumed to be proportional to the water-normalized work $w(t)$, which is given as the fraction of cumulative energy $E(t)$ and cumulative uptake $V(t)$ until time t. Following an analogy to electric circuits, $E(t)$ can be expressed as

$$E(t) = \int_{\tau=0}^{t} P(\tau)\mathrm{d}\tau \qquad \text{(A1)}$$

where $P(t)$ is the (hydraulic) power necessary to meet the transpirational demand $Q(t)$ at a given time t. If we follow the same analogy, the power $P(t)$ can be calculated by associating root water uptake rate $Q(t)$ with the electric current $I(t)$ and collar xylem water potential $\psi_x^0(t)$ with electric voltage $U(t)$, via

$$P(t) = Q(t) \cdot \psi_x^0(t) \tag{A2}$$

Using Eqs. (A1), (A2) and the flux boundary condition $Q(t) = Q$ under unstressed conditions the work $w(t)$ becomes

$$w(t) = \frac{E(t)}{V(t)} = \frac{\int\limits_{\tau=0}^{t} P(\tau)\mathrm{d}\tau}{\int\limits_{\tau=0}^{t} Q(\tau)\mathrm{d}\tau} = \frac{\int\limits_{\tau=0}^{t} Q(\tau)\cdot\psi_x^0(\tau)\mathrm{d}\tau}{\int\limits_{\tau=0}^{t} Q(\tau)\mathrm{d}\tau} = \frac{Q\cdot\int\limits_{\tau=0}^{t} \psi_x^0(\tau)\mathrm{d}\tau}{Q\cdot t} = \frac{\int\limits_{\tau=0}^{t} \psi_x^0(\tau)\mathrm{d}\tau}{t} = \bar{\psi}_t \tag{A3}$$

Thus we obtain (under a fixed flux boundary) a temporal average of the collar potential at each time t. The average collar potential $\bar{\psi}_{\tilde{t}}$ at the onset of water stress is equal to the effort necessary $\tilde{\psi}$ for the root water uptake:

$$\tilde{\psi} = w(\tilde{t}) = \bar{\psi}_{\tilde{t}} \tag{A4}$$

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Table 1. Root hydraulic properties used within both the simple and the "aRoot" model.

	Root radius r[mm]	Axial resistivity ζ_{Ax} [s m^{-3}]	Radial resistivity ρ_{Rad} [s]
Mature root	1.0	8×10^{10}	5×10^{8}
Young root	1.0	1×10^{12}	1×10^{8}

Table 2. Parameters and important features of the simple and the “aRoot” model.

	Simple model	“aRoot” model
Soil properties		
Limited water reservoir	Yes	
Gravitation	No	Yes
Redistribution of soil water	No	Yes (3-D Richards)
Gradients in soil hydraulic conductivity	No	Yes
Soil porosity	0.46	
Saturated soil water conductivity	$1.785\,\mu\mathrm{m\,s^{-1}}$	
n_{VG}	1.534	
α_{VG}	$1.44\,\mathrm{m^{-1}}$	
λ_{VG}	−0.215	
Root properties		
Heterogeneous root hydraulic properties	Yes	
Critical collar potential	−150 m	
Flux boundary condition $Q(t)$	$5 \times 10^{-11}\,\mathrm{m^3\,s^{-1}}$	$3 \times 10^{-9}\,\mathrm{m^3\,s^{-1}}$
Total root length l_{total}	0.01–8 m	9.93 m
Branching Order	≤ 1	$>> 1$
Account for root length density	No	Yes

Table 3. Optimal compositions of single roots referring to effort (top) and water yield (bottom). Results are obtained with the simple model for different root topologies.

Structure	l_{total}	l_{mature}	l_{young}	l_{young} per branch	$\tilde{\Psi}$ [m]
Young root strand	0.20 m	–	0.20 m/100 %	0.20 m	−18.01
Mature root strand	1.60 m	1.60 m/100 %	–	–	−15.27
Mixed root strand	1.50 m	1.20 m/80 %	0.30 m/20 %	0.30 m	−15.05
Branched structure, 2 tips	1.30 m	0.65 m/50 %	0.65 m/50 %	0.325 m	−14.36
Branched structure, 3 tips	0.90 m	0.09 m/10 %	0.81 m/90 %	0.27 m	−13.45
Branched structure, 4 tips	1.20 m	0.12 m/10 %	1.08 m/90 %	0.27 m	−12.84
Branched structure, 6 tips	1.60 m	0.16 m/10 %	1.44 m/90 %	0.24 m	−12.26

Structure	l_{total}	l_{mature}	l_{young}	l_{young} per branch	$\tilde{V}$ [cm^3 m^{-1}]
Young root strand	0.15 m	–	0.15 m/100 %	0.15 m	153.07
Mature root strand	1.80 m	1.80 m/100 %	–	–	153.21
Mixed root strand	1.60 m	1.28 m/80 %	0.32 m/20 %	0.32 m	153.21
Branched structure, 2 tips	0.90 m	0.27 m/30 %	0.63 m/70 %	0.315 m	153.24
Branched structure, 3 tips	0.90 m	0.18 m/20 %	0.72 m/80 %	0.24 m	153.28
Branched structure, 4 tips	1.20 m	0.12 m/10 %	1.08 m/90 %	0.27 m	153.30
Branched structure, 6 tips	2.00 m	0.20 m/10 %	1.80 m/90 %	0.30 m	153.32

Table 4. Initial collar potential ψ_x^0, effort $\tilde{\psi}$, water yield $\tilde{V}$ and mean uptake depth z_{50} for one fixed root geometry with a total length of $l_{\text{total}} = 9.93\,\text{m}$, depending on hydraulic parameterization. Data was obtained with the "aRoot" model for roots containing between 0 and 100 % of mature roots.

l_{mature}	Ψ_x^0 [m]	$\tilde{\Psi}$ [m]	$\tilde{V}$ [cm^3 m^{-1}]	z_{50} [cm]
0.00 m (0 %)	−67.03	−105.18	162.13	−6.55
1.99 m (20 %)	−15.72	−44.06	205.43	−6.78
3.97 m (40 %)	−16.75	−42.70	207.45	−6.87
5.96 m (60 %)	−19.09	−46.39	203.42	−6.90
7.94 m (80 %)	−23.55	−54.22	196.37	−6.86
9.93 m (100 %)	−34.72	−77.84	174.22	−6.74

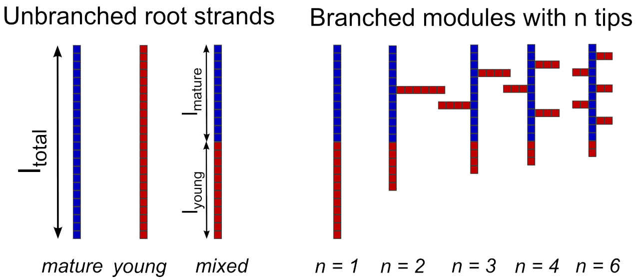

Fig. 1. Schematic representation of the root topologies and parameters that were investigated with the simple root water uptake model. Young (l_{young}) and mature root length (l_{mature}) can be varied independently both in unbranched and branched root structures, resulting in varying total length (l_{total}). In all cases mature roots constitute the basal part of the root and are succeeded by apical young roots. Within branched roots, total young root length is evenly divided into n parts, which are attached to the central mature root at equal distances. A mixed root strand can equivalently be regarded as a branched root with $n = 1$.

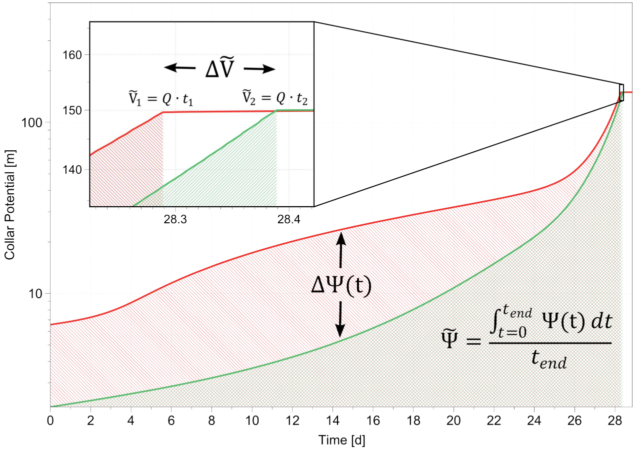

Fig. 2. Evolution of collar xylem water potential over the course of time for two exemplary chosen single roots: an unbranched homogeneous young root strand (red) and a branched structure with six tips (green) of equal length (0.8 m). The two characteristics that are used to assess efficiency of root water uptake, water yield and effort, can be deduced as follows: Water yield is proportional to the occurrence time of water stress, the later collar potential reaches the critical value $\psi^0_{\mathrm{Crit}} = -150$ m (-1.53 MPa) the higher water yield is. Thus, it measures the total amount of water that could be extracted before reaching critical xylem water potential. Effort is a time averaged collar potential and is proportional to the area below the graph. Lower effort corresponds to less negative collar potentials in the course of root water uptake and overall decreased total resistance to root water uptake. Both measures convey different information: Although water yield is very similar between the two root structures in this case, effort is different.

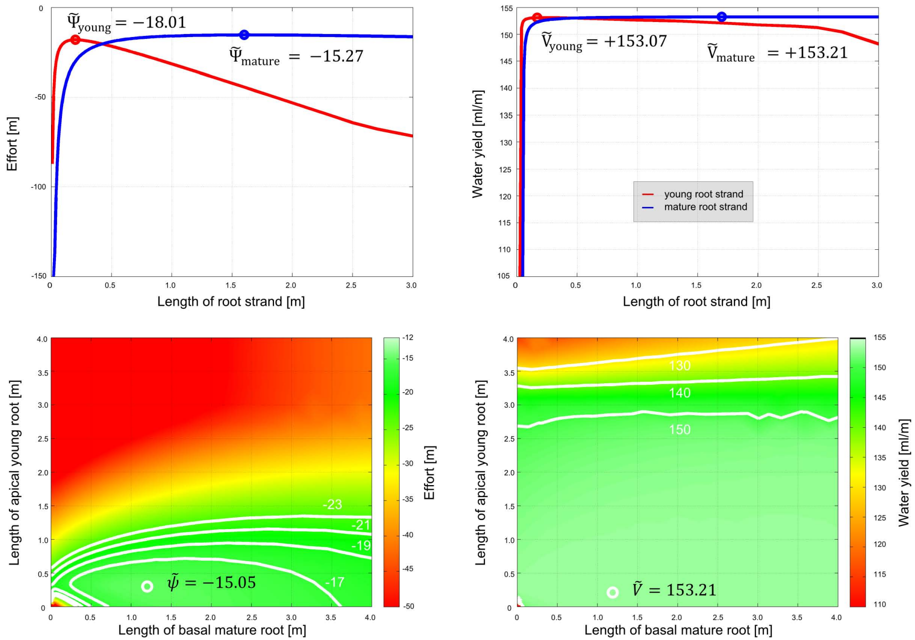

Fig. 3. Effort $\tilde{\Psi}$ (left) and water yield $\tilde{V}$ (right) in unbranched root strands, depending on their composition of young and mature roots. On top effort and water yield are depicted for homogeneous young (red) and mature (blue) root strands, depicted over total root length. Below effort and water yield are shown for mixed root strands depending both on mature (x axis) and young root length (y axis). Values of effort and water yield are indicated by colors, optimal values are additionally indicated with circles. More negative effort and lower water yield are depicted in red whereas green and light green are indicating higher water yield and less negative effort. Isolines show root compositions that resulted in equal effort and water yield.

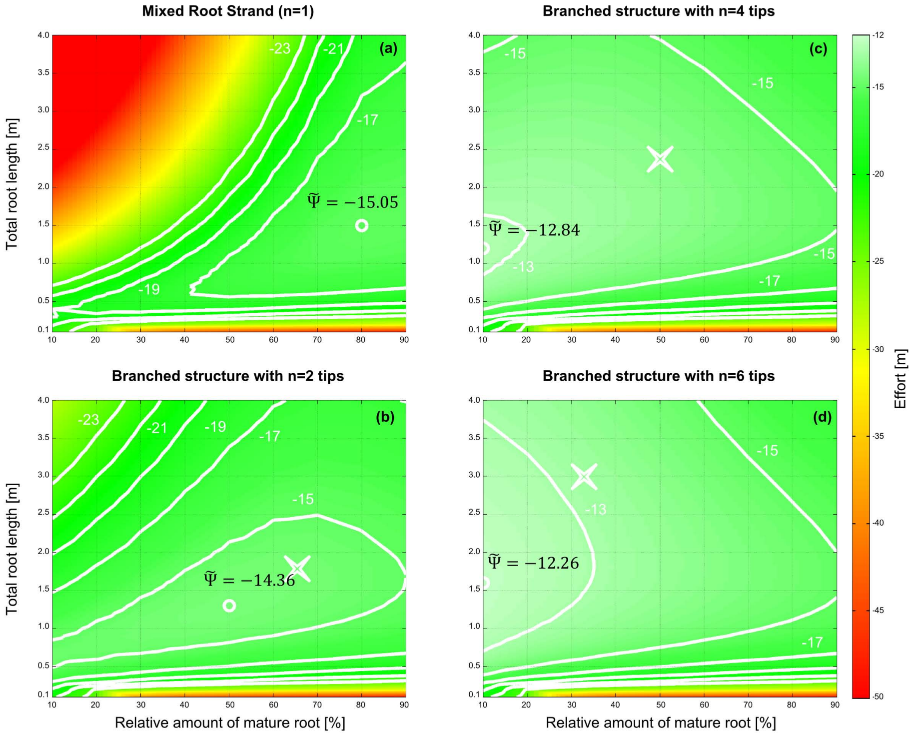

Fig. 4. Effort $\tilde{\Psi}$ depending on topology and composition of single roots. Results are shown for **(a)** unbranched root strands and single branched roots (fishbone structures) with **(b)** two, **(c)** four and **(d)** six tips. Root composition is given by total root length (y axis) and the proportion of mature roots (x axis). Colors are the same as in Fig 3. Data was obtained with the simple model. Optimal values of effort are denoted by white circles, isolines show root compositions that resulted in equal effort. The crosses in **(b)**–**(d)** indicate effort for a root that is the same as the optimal unbranched mixed strand from **(a)** except for containing one, three and five more equal young root tips respectively.

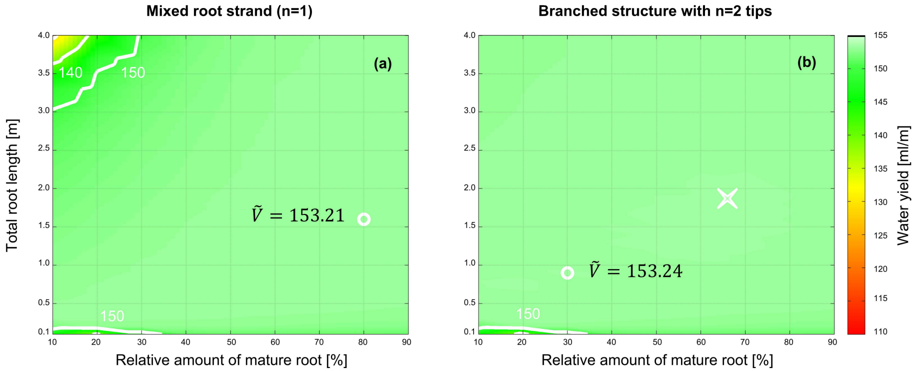

Fig. 5. Water yield $\tilde{V}$ depending on topology and composition of single roots. Results are shown for **(a)** unbranched root strands and single branched roots (fishbone structures) with **(b)** two tips. Root composition is given by total root length (y axis) and the proportion of mature roots (x axis). Colors are the same as in Fig 3. Data was obtained with the simple model. Optimal values of water yield are denoted by white circles, isolines show root compositions that resulted in equal water yield. The cross in **(b)** indicates water yield for a root that is the same as the optimal unbranched mixed strand from **(a)** except for containing one more equal young root tip.

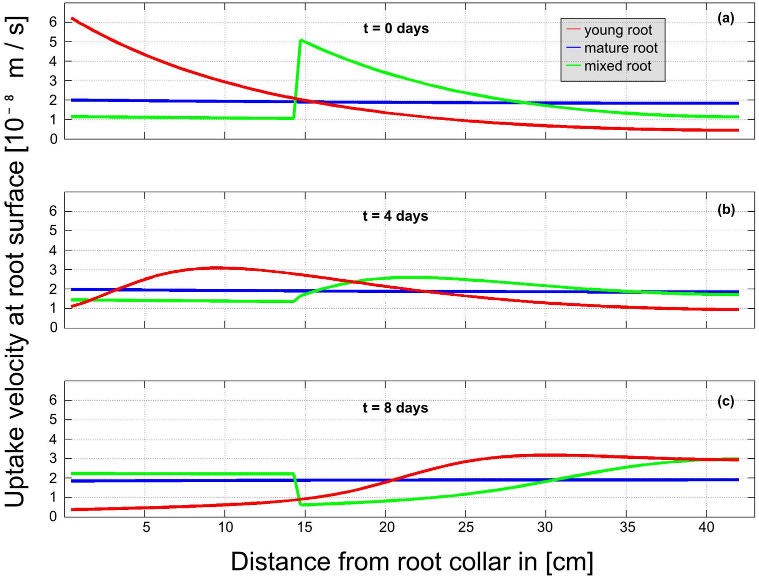

Fig. 6. Velocity of radial inflow (uptake velocity) at the root surface along three root strands with equal length ($l_{\text{total}} = 0.42\,\text{m}$) but different composition. Values are obtained with the simple model for strands containing young roots only (red), mature roots only (blue) or an optimal mixture with respect to water yield (green; $l_{\text{mature}} = 0.14\,\text{m}$, $l_{\text{young}} = 0.28\,\text{m}$). Results are depicted for **(a)** initial stage, **(b)** 4 days and **(c)** 8 days of simulation time.

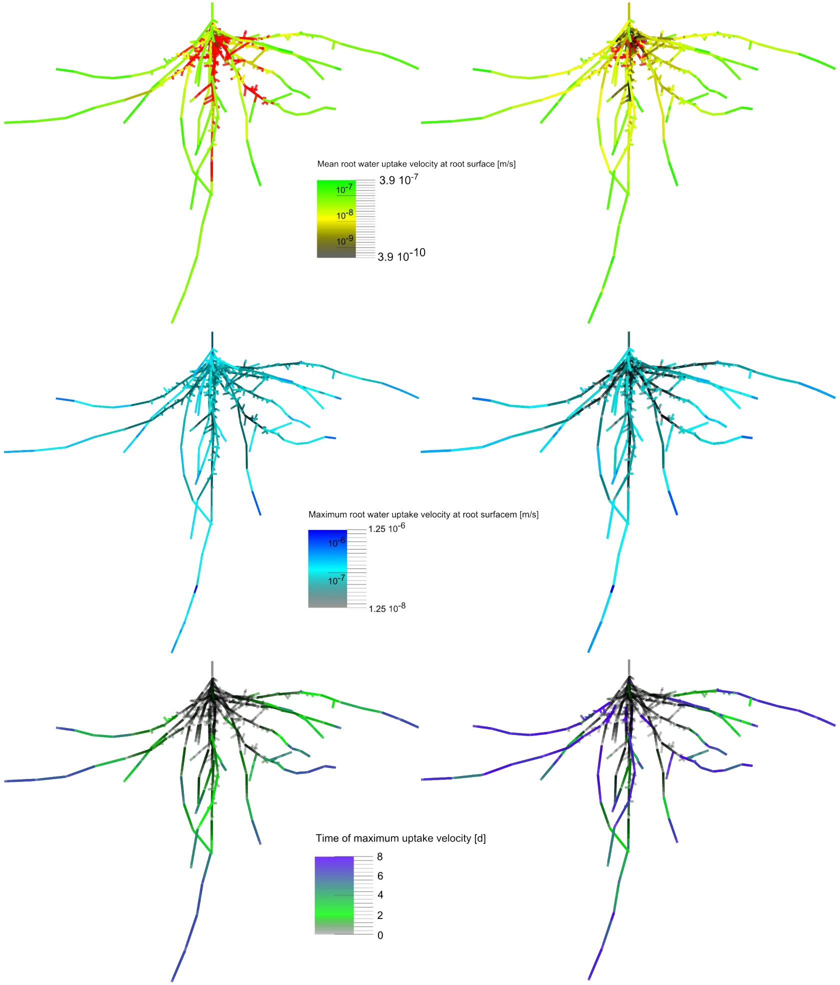
Mean root water uptake velocity at root surface [m/s]
3.9 10^{-7}
10^{-7}
10^{-8}
10^{-9}
3.9 10^{-10}
Maximum root water uptake velocity at root surfacem [m/s]
1.25 10^{-6}
10^{-6}
10^{-7}
1.25 10^{-8}
Time of maximum uptake velocity [d]
8
6
4
2
0

Fig. 7. Root water uptake dynamics in a fixed root geometry under two different hydraulic parameterizations. Data was obtained with the "aRoot" model for one root system containing young roots only (left) and a mixture of 40 % of basal mature and 60 % of apical young roots (right). Time averaged root water uptake rate along the root system is depicted on top. Values cover three orders of magnitude, ranging from black (low values) over yellow to green (high values) on a log scale. Regions with negative net uptake (hydraulic lift or bleeding) are depicted in red, independent of the actual amount of bleeded water. The lower part of the figure shows the magnitude (center) and timing (bottom) of maximum uptake velocity along the root system. Magnitude of maximum root water uptake ranges over two orders of magnitude and is depicted from black (low values) to blue (high values) on a log scale, whereas timing is given on a linear scale ranging from black (representing initial stages of the simulation) over green to blue (maximum uptake after 8 days).

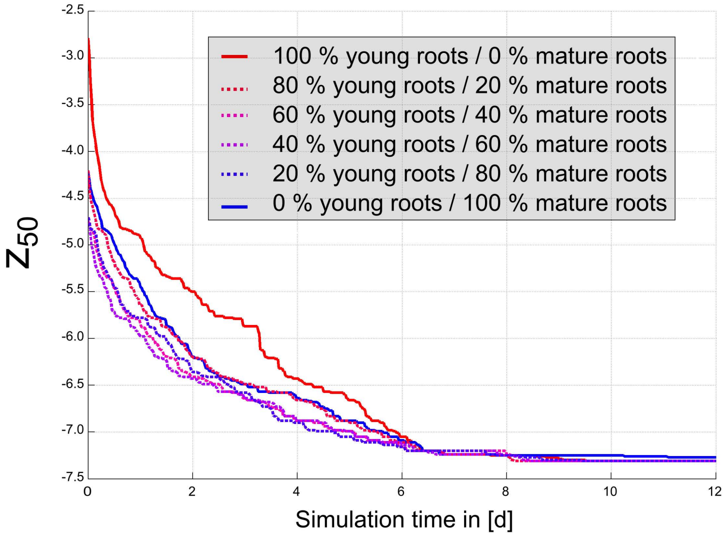

Fig. 8. Evolution of mean uptake depth z_{50} over time in one fixed root geometry under six different hydraulic parameterizations. Results are obtained with the "aRoot" model for one fixed root geometry containing between 0 and 100 % of apical young roots. Root systems consisting of young or mature roots only are depicted in solid lines; heterogeneous root systems are depicted with dashed lines.

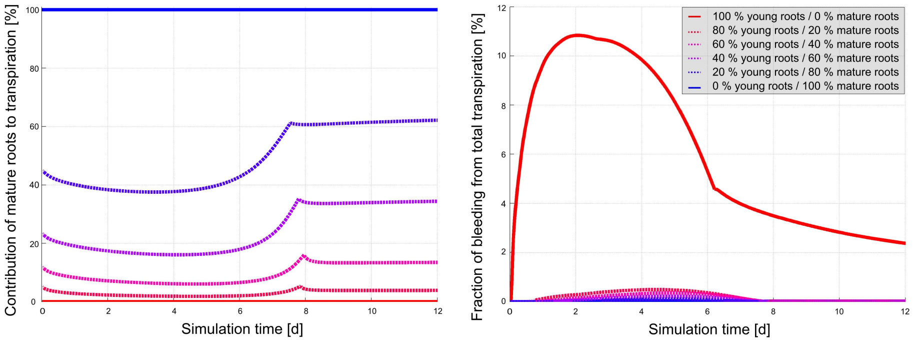

Fig. 9. Evolution of mature root contribution to overall transpiration (left) and the fraction of bleeding (right) over time in one fixed root geometry under six different hydraulic parameterizations. Results are obtained with the "aRoot" model for one fixed root geometry containing between 0 and 100 % of apical young roots. Root systems consisting of young or mature roots only are depicted in solid lines; heterogeneous root systems are depicted with dashed lines.