

REVIEW PAPER

Model-assisted integration of physiological and environmental constraints affecting the dynamic and spatial patterns of root water uptake from soils

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Abstract

Due in part to recent progress in root genetics and genomics, increasing attention is being devoted to root system architecture (RSA) for the improvement of drought tolerance. The focus is generally set on deep roots, expected to improve access to soil water resources during water deficit episodes. Surprisingly, our quantitative understanding of the role of RSA in the uptake of soil water remains extremely limited, which is mainly due to the inherent complexity of the soil–plant continuum. Evidently, there is a need for plant biologists and hydrologists to develop together their understanding of water movement in the soil–plant system. Using recent quantitative models coupling the hydraulic behaviour of soil and roots in an explicit 3D framework, this paper illustrates that the contribution of RSA to root water uptake is hardly separable from the hydraulic properties of the roots and of the soil. It is also argued that the traditional view that either the plant or the soil should be dominating the patterns of water extraction is not generally appropriate for crops growing with a sub-optimal water supply. Hopefully, *in silico* experiments using this type of model will help explore how water fluxes driven by soil and plant processes affect soil water availability and uptake throughout a growth cycle and will embed the study of RSA within the domains of root hydraulic architecture and sub-surface hydrology.

Key words: Drought, hydraulics, hydrology, modelling root system architecture.

Introduction

Plant water deficit occurs when the availability of resources cannot match water demand for growth and transpiration. Breeding strategies often hinge on a clever capture and use of water, helping crops to maintain a better internal water status and avoid, or at least delay the onset of drought. Such strategies rely on traits which contribute to (i) adjust the rate of water uptake to climatic and environmental conditions, through appropriate phenology, reduced transpiration or growth cessation, or (ii) increase water capture via carefully designed root architecture and hydraulics (Boyer, 1982; King *et al.*, 2003; Parent *et al.*, 2009; Nord and Lynch, 2009).

The last decade has seen an increasing awareness that root system architecture (RSA) and root hydraulics play an

important quantitative role in water capture in drought-prone environments (Tuberosa *et al.*, 2002a; Zhao *et al.*, 2005; de Dorlodot *et al.*, 2007; Lynch, 2007). In rice and maize, testing of introgression lines (ILs) under laboratory and field conditions suggest that deep roots can improve drought tolerance (Shen *et al.*, 2001; Tuberosa *et al.*, 2002b; Steele *et al.*, 2007). In lettuce, QTLs for taproot length were shown to improve deep water extraction (Johnson *et al.*, 2000). Interestingly, it was recently shown that a slight improvement in water uptake (7%), thought to result from a 30% increase of deep root length at constant total root length and maximum rooting depth, can be sufficient to generate a significant increase of grain yield under drought (Bernier *et al.*, 2009).

During the same period, enormous progress has been achieved in our understanding of the molecular and genomic bases of RSA and of some aspects of root hydraulic conductivity (Stedule, 2000a; Sperry et al., 2002; De Smet et al., 2006; Hachez et al., 2006; de Dorlodot et al., 2007; Maurel et al., 2008; Hodge et al., 2009; Peret et al., 2009). This progress promises new opportunities to manipulate the morphological and hydraulic architecture of plants in a carefully designed manner, i.e. by targeting very specific aspects of RSA and hydraulics. However, to take full advantage of these opportunities, our knowledge of the quantitative role of root system architecture and root hydraulics in water uptake behaviour and drought resistance has to be improved.

During the last years, 3D mathematical models of soil water dynamics have been extended to embrace the soil-plant system (Doussan et al., 2006; Javaux et al., 2008). Although these novel tools respond to the definition of 3D functional structural plant models (FSPM; Godin and Sinoquet, 2005), they seem to remain within the soil science community and have not attracted much attention from plant scientists. The objective of this paper is to illustrate how these novel FSP models of water dynamics extended to the soil compartment may provide insights on the dynamics of water capture under water-limiting conditions.

Constraints to water flow and the distribution of uptake

It is generally believed that the plant is setting the limits to the flow of uptake in most conditions, except in very dry

soils (Hopmans and Bristow, 2002). Under wet conditions, soil hydraulic conductivity tends to be higher than most root radial conductivity values and the water uptake tends to be proportional to root length density (RLD) (Gardner, 1965). In such circumstances, superficial root systems with little investment in root axes and large investment in branches are believed to be sufficient. In contrast, in drought-prone environments, the likelihood that the soil would limit the flow at some location or time increases. When the soil is limiting, the influence of RLD is lower and the availability of water depends more on the volume of soil explored, on the pathway of water from the soil to the root surface, and on the local driving force (i.e. water potential gradients at the soil/root interface). Therefore, long vertical roots with branching in deep soil layers are generally believed to improve water capture and yield under drought (King et al., 2003). What happens in intermediate conditions is less clear, and Passioura (1980) summarized the discussion as follows: ‘When the soil is wet it has little influence on the uptake of water from it by the plant. When it is dry it has a large influence. When it is neither wet nor dry, the extent of influence is a matter of controversy.’

Plants, however, are often likely to be in intermediate situations, for soil water content is spatially and temporally variable as a result of climate, root water uptake, and other drivers. The extent to which the soil may control the uptake rate is illustrated in Fig. 1, where the envelope of hydraulic conductivities of the main soil types (Van Genuchten, 1980) is compared with the range of experimental root hydraulic conductivity values from different species, root types, and growing conditions. The comparison suggests that, in a sandy soil, the highest observed root conductivity values

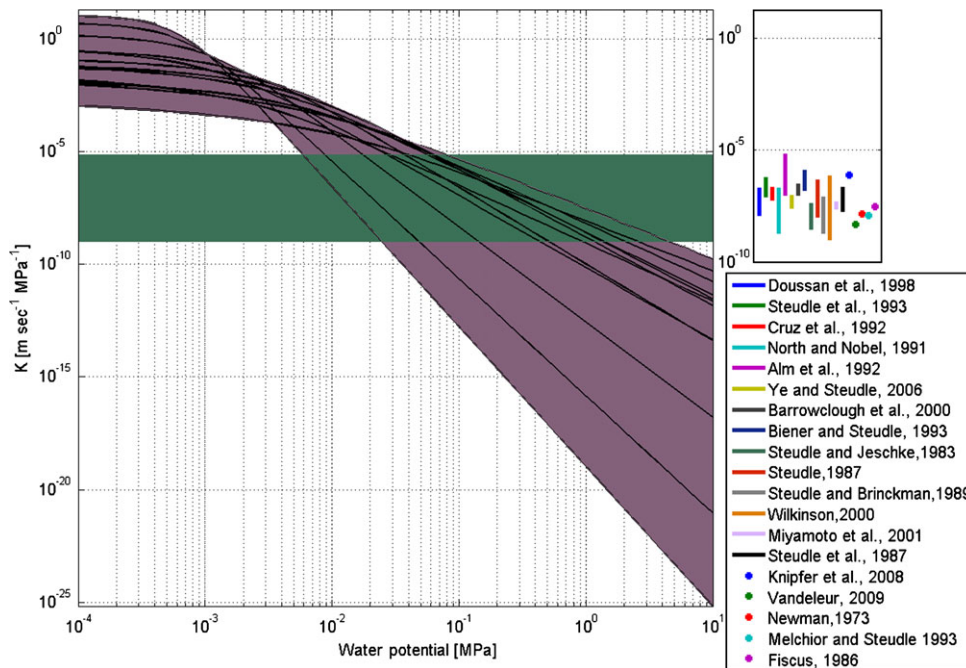


Fig. 1. Envelopes of typical soil conductivity curves (blue area) and apparent root conductivity values (green area) redrawn from the literature. The upper right plot represents root conductivity values from 19 studies (see Supplementary data S1 at *JXB* online for additional information).

may locally affect the root water uptake at soil water potentials as high as -0.01 MPa. For an average soil, the threshold would occur around -0.1 MPa and the soil always controls the uptake under -1.5 MPa, even for the lowest observed root conductivity values.

As the water transfer between soil and root xylem is a passive process driven by the water potential difference (catenary hypothesis; Cowan, 1965), the spatial distribution and the magnitude of the uptake in intermediate conditions will depend on the spatial distribution of the ratio between root radial and soil conductivity and on xylem conductivity. This principle is greatly complicated for soil conductivity is a highly non-linear function of the water content and as the radial and axial root conductivities vary along roots and among root types (Hose *et al.*, 2001). These combined effects of RSA and root and soil hydraulics will thus enhance the spatial heterogeneity of soil water content which, in a feedback effect, may affect root conductivity (Vandeleur *et al.*, 2005) and the subsequent development of the root system (North and Nobel, 2000). Not surprisingly, even under relatively wet conditions, the soil may affect the spatial distribution of the uptake before affecting its magnitude (Dodd *et al.*, 2008).

Although soil and roots consist of very different media, the principles underlying water flow in the soil–root system rest basically on a unique theory. Understanding the distribution of water uptake is then a matter of quantifying resistances and gradients of water potential in a common spatial and highly dynamic framework. There are therefore several reasons to adopt a fine-grained 3D modelling approach to explore how the interplay between RSA, root and soil hydraulics determines water uptake patterns.

Towards a functional root model: R-SWMS

A series of models addressing water transport in the soil–plant system have arisen from soil physics (see, for example, Somma *et al.*, 1998; Dunbabin *et al.*, 2002). These models are based on the so-called 3D Richards equation in which a root uptake function has been added (Vrugt *et al.*, 2001):

$$\frac{\partial \theta}{\partial t} = \nabla \cdot [\mathbf{K} \nabla (h - z)] - S \quad (1)$$

where θ is the volumetric water content ($\text{m}^3 \text{m}^{-3}$), t is the time [s], \mathbf{K} the hydraulic conductivity tensor (m s^{-1}), h the water potential on weight basis or matric head (m), and z the vertical coordinate (m). Both θ and \mathbf{K} are non-linear functions of the matric head which are called the unsaturated hydraulic soil properties. The sink term S represents root water uptake in terms of volume of extracted water by volume of soil per day (d^{-1}). Basically, this equation states that the temporal evolution of soil water content in a given soil element (e.g. 1 cm^3) follows the mass balance between (i) the exchange of water with the surrounding soil elements, driven by the spatial gradient of water potential in the soil and constrained by the soil

hydraulic conductivity, and (ii) the uptake of water by roots contained within this soil element.

In these models, the S function is based on various estimates of root length density (RLD), thereby assuming a prominent role of RLD. The R-SWMS model (Doussan *et al.*, 2006; Javaux *et al.*, 2008) introduces a novel, FSPM-like approach, in which the sink function $S(x, y, z, t)$ derives from a root water flow model, which simulates explicitly the water flow through the cortex (from the root–soil interface to the xylem vessels) and in the xylem (Doussan *et al.*, 1998a). Radial flow across the cortex is based on the gradient of water potential between the soil/root interface and the xylem, while flow in the xylem is based on longitudinal water potential gradients, xylem hydraulic conductivity, and boundary conditions at the root/shoot collar.

The merging of equation 1 and Doussan's model requires the movement of water to be considered as being driven by the water potential gradient through the whole soil–plant system. The model essentially computes the water potential at any position in the xylem and in the soil, as well as its evolution in time under fixed or variable boundary conditions. The solution given by the model corresponds to the spatial distribution of the water uptake that satisfies the equations of flux driven by water potential gradients in the whole system. This solution maximizes the (signed) water potential at the root collar while satisfying the boundary conditions limits.

In the following sections, different simulations have been run in which three attributes of the soil/plant system thought to influence water uptake and its spatial distribution have been varied separately: the soil hydraulic conductivity (K_s), the root hydraulic conductivities (K_r and K_x , respectively, radial and axial) and the root architecture. For the sake of clarity, the scenarios have been deliberately oversimplified. In particular, root conductivities are uniform along and among roots and growth has been neglected (in accordance with the short duration of the simulations). The examples provided should thus not be taken other than as an illustration.

Soil hydraulic properties and the movement of water in soils

As mentioned above, the various climatic (evapotranspiration and rainfall), biological (water uptake, hydraulic lift), and hydrological (drainage) disturbances acting on soils generates spatial and temporal heterogeneity of the soil–root water potential gradient and affects the distribution of water uptake. In fact, a local decrease of water potential also leads to a drop in soil conductivity which restrains the mobility of water and further amplifies the heterogeneity of root water uptake (Schroder *et al.*, 2008). Within the rhizosphere, such local conductivity drops are predicted to occur very quickly (depending on the soil type and the volumetric flow) and could generate short-term local hydraulic near-isolation of soil and roots (Schroder *et al.*, 2009). In the soil, the conductivity drop should arise on

longer time-scales and will negatively affect the rate at which water moves into the rhizosphere. It follows that the distribution of the soil hydraulic resistances around the root system continuously evolves, which affects the uptake distribution, even in uniform soils and well before the wilting point is reached.

The hydraulic conductivity curve is highly variable in space and is soil dependent and this can be exploited to illustrate the effect of soil conductivity on the distribution of root water uptake. To this end, a root system subjected to a constant transpiration demand for 7 d in three uniform soils with different hydraulic conductivity curves (clay, clay-loam, and loam) has been simulated with the R-SWMS model. The root system was characterized by a fixed 3D architecture and uniform root hydraulic properties and the initial soil was initially set at equilibrium with an aquifer level located 3 m below the soil surface (see Supplementary data S2 at *JXB* online for parameter values).

The simulations indicate that even at water potentials higher than -0.1 MPa, soil hydraulic properties impact the spatial distribution of the sink term and therefore the soil hydraulic gradient distribution (Fig. 2). The soil with a loam texture displays strong gradients around the upper central roots, while the clay texture leads to a much smoother and vertical distribution of water potential. This reflects the unsaturated conductivity values of these soils: at these potential levels, the clay-loam soil has a higher unsaturated conductivity which tends to redistribute water throughout the soil profile efficiently. Part of this also relates to the larger water content range of the clay-loam soil before the soil conductivity becomes limiting (see Supplementary data S3 at *JXB* online). On the other hand, the resistance of the loam soil is so high when it dries out that the water gradient

cannot be compensated anymore. The simulation also illustrates the impact of the relationship between soil water potential and soil water content, which strongly differs between the three soil types. With the same amount of water uptake in the three scenarios (imposed by the constant potential transpiration flux), the water potential of the clay soil reaches much lower values compared with the other soils.

The depletion of water in soil elements containing roots (Fig. 2) is the difference between the rate of uptake by roots and the rate of water supply from the soil. The latter is affected not only by the mobility of water in the soil (soil hydraulic conductivity), but also by the rate of water uptake in surrounding regions. For example, the recharge of water in a 1 cm^3 soil element (with a RLD of 1) from the surrounding soil will be restrained if the surrounding soil elements also contains roots. It is therefore difficult to analyse the effect of soil hydraulic conductivity without taking into account the geometric configuration of bulk and rhizospheric soil compartments, which is primarily set by RSA. The location of roots in the soil may therefore influence the evolution of water potential at the soil-root interface, and also contribute to the spatial variability of water uptake.

The spatial variability of soil water potential seen in Fig. 2 stresses the contrasting soil water potentials experienced simultaneously by roots of the same plant. This situation may seem similar to partial root zone drying (PRD) which occurs under partial irrigation. The principle of PRD is that drought sensed by part of the root system leads, via root-shoot ABA signalling, to partial closure of stomata and a reduction of crop water demand, without necessarily affecting C assimilation (Dodd, 2007). It would be

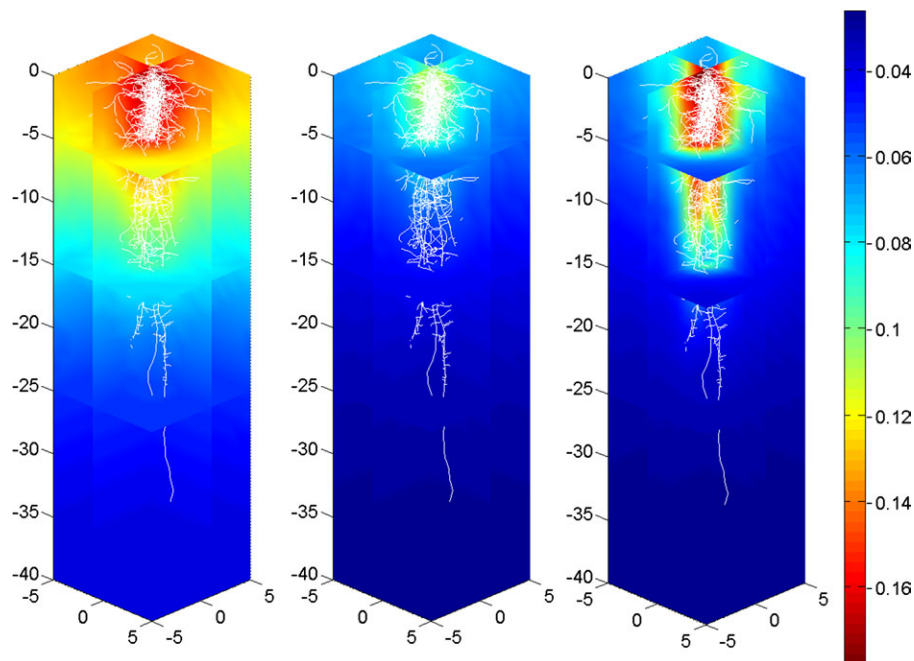


Fig. 2. Soil water potential (MPa) in clay (left), clay loam (mid), and loam soils (right) after 3 d without water supply. The same amount of water has been absorbed by the root system in the three soils.

extremely interesting to see to what extent local drying patterns are normally occurring in soils before the occurrence of water deficit.

To explore this, the previous simulation was continued until 50 d, under the same potential flux of $10 \text{ cm}^3 \text{ d}^{-1}$ at the root collar. During this extended period, the number of 'stressed' root segments, defined as segments whose radial conductivity is larger than the conductivity of the surrounding soil voxel, increased progressively. Taking as a simple hypothesis that stressed segments release ABA at a flow rate proportional to their water uptake rate (Dodd *et al.*, 2008) and that the transfer time in the xylem is negligible (compared to the soil dynamics), a relative evolution of the xylem ABA concentration at the collar could be computed. Figure 3 traces this evolution for the three soil types, as a function of the total soil water content, the relative soil water content, and the xylem and soil water potentials. The simulation indicates that, even under this simple hypothesis, none of the explanatory variables lead to a common ABA dynamics in the xylem for the three soil types, which stresses how sensitive ABA signalling could be to soil types and conditions.

Root hydraulic properties and the propagation of transpiration-driven negative tension to the root surface

Root systems consists of dynamic populations of roots of different types and age, to which correspond contrasting

values of radial and axial (xylem) hydraulic conductivities (Eshel and Waisel, 1996; Doussan *et al.*, 1998b; Pierret *et al.*, 2006). The same observation applies along roots, which should be viewed as a series of segments of increasing age (from the tip to the base) and developmental stage (Frensch and Steudle, 1989; Hachez *et al.*, 2006).

Variation in the radial hydraulic conductivity, on the one hand, is explained in terms of a composite transport model where water crosses the root tissues using inter-connected apoplastic and cell-to-cell pathways (Steudle, 2000a, b). The apoplastic flow can be altered irreversibly by anatomical changes, including the deposition of apoplastic barriers (Steudle and Peterson, 1998) while the cell-to-cell flow can be largely determined by the activity of aquaporins, which allow rapid and reversible changes in conductivity (Maurel *et al.*, 2008).

Variations in the axial hydraulic conductivity of roots, on the other hand, rest on the principles of fluid dynamics into a network of narrow pipes. From a structural point of view, the axial conductivity of a root segment is set by the number, diameter, and wall decorations of its xylem vessels. It is therefore dependent on the type and developmental stage of the root segment. The xylem structure also affects the susceptibility of the root segment to cavitation, which generates transient drops of axial conductivity (Sperry *et al.*, 2003). These effects essentially affect the long-distance propagation of the transpiration-driven negative xylem tension through successive segments until the root surface,

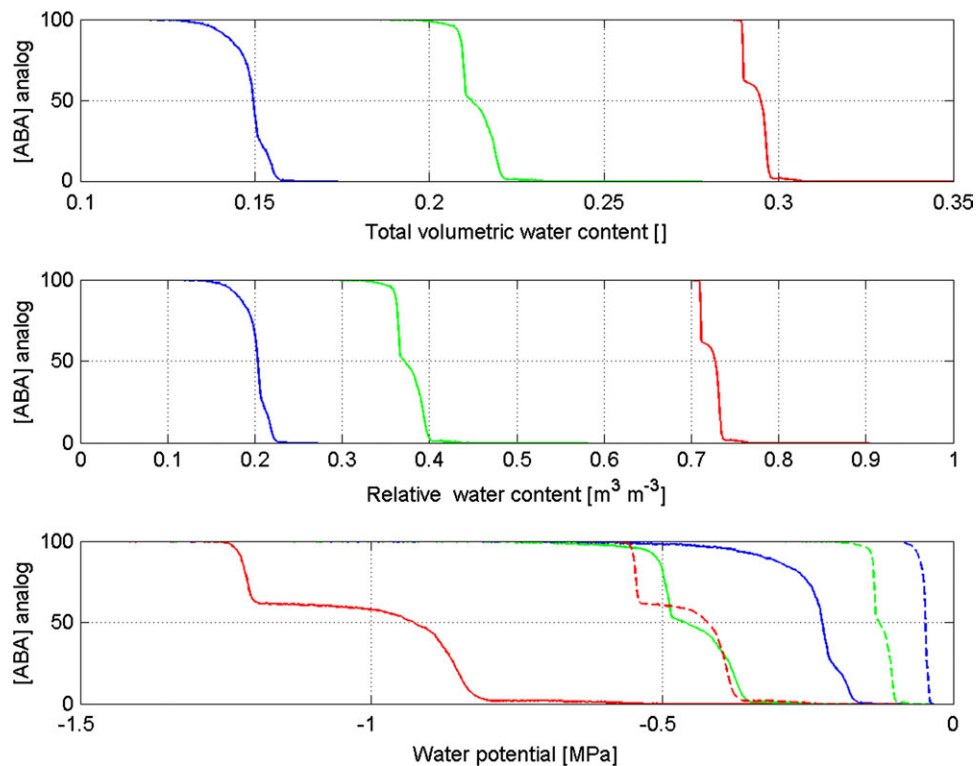


Fig. 3. Evolution of the ABA concentration analogue (see text) for clay (red lines), clay-loam (green lines), and loam soils (blue lines), as a function of the total volumetric water content (top plot), of the relative water content (middle plot), of the average soil water potential (bottom plot, dashed lines), and of the root collar water potential (bottom plot, continuous lines).

i.e. the plant contribution to the uptake driving force at the root–soil interface.

These extended interrelationships between RSA and hydraulic behaviour have given rise to the concept of hydraulic architecture, in which RSA is merged with the radial and axial hydraulic properties of every root segment (Doussan *et al.*, 1998a). The concept is most valuable when soil–plant relationships are taken into account, as it aggregates the complexity of root physiology (e.g. radial versus axial, constitutive versus inducible, short versus long time-scale) into a unifying theoretical framework that allows a systems dynamics approach at the whole plant scale. At this stage, however, data on many aspects of hydraulic architecture of plants in field conditions is lacking. Hydraulic parameters are usually estimated either on isolated roots from hydro- or aeroponically grown plants or, on whole root systems in solid substrates. Very little is known on the hydraulic behaviour of the whole root system at the level of individual roots.

Simulations illustrating the role of the root hydraulic properties in the spatial distribution of water uptake are given in Fig. 4. The same root architecture was used with different ratios of cortex to xylem conductivity, with a large constant and uniform radial conductivity and low to high xylem conductivity values. Soil properties were imposed as constant and uniform, and transpiration followed day–night cycles (see Supplementary data S4 at *JXB* online for parameter values).

Under the small ratio (Fig. 4, left), the water potential gradient in the xylem is expected to be very small (Fig. 4,

bottom-left) and water tends to be taken up everywhere in the profile (Fig. 4, top-left). Since the radial conductivity is larger than the soil conductivity (for all three scenarios), water is taken up as a function of the water distribution rather than depending on the root architecture.

Under the high ratio (Fig. 4, right), the xylem limits the water flow through the root system and important water potential gradient builds in the xylem (Fig. 4, bottom-right). In this case, the water is preferably extracted from the upper layers where large gradients between soil and roots develop and where root xylem conductance is high enough to transfer water to the collar (Fig. 4, top-right). This results fits well within the work of Passioura and coworkers who manipulated the root hydraulic architecture of wheat by selecting for narrow xylem vessels, thereby increasing the cortex-to-xylem conductivity ratio. As suggested, this turned out to reduce the rate of water uptake, preserve subsoil water until anthesis and, ultimately, achieve a significant yield gain (Passioura, 1972; Richards and Passioura, 1989). Root hydraulic architecture therefore appears to have a potential impact on the distribution of water uptake, which adds to the soil effects discussed above.

Limits to the influence of root system architecture

The previous sections illustrate that RSA interacts closely with soil and root hydraulic properties to influence the distribution of the sink term. In the next example, five

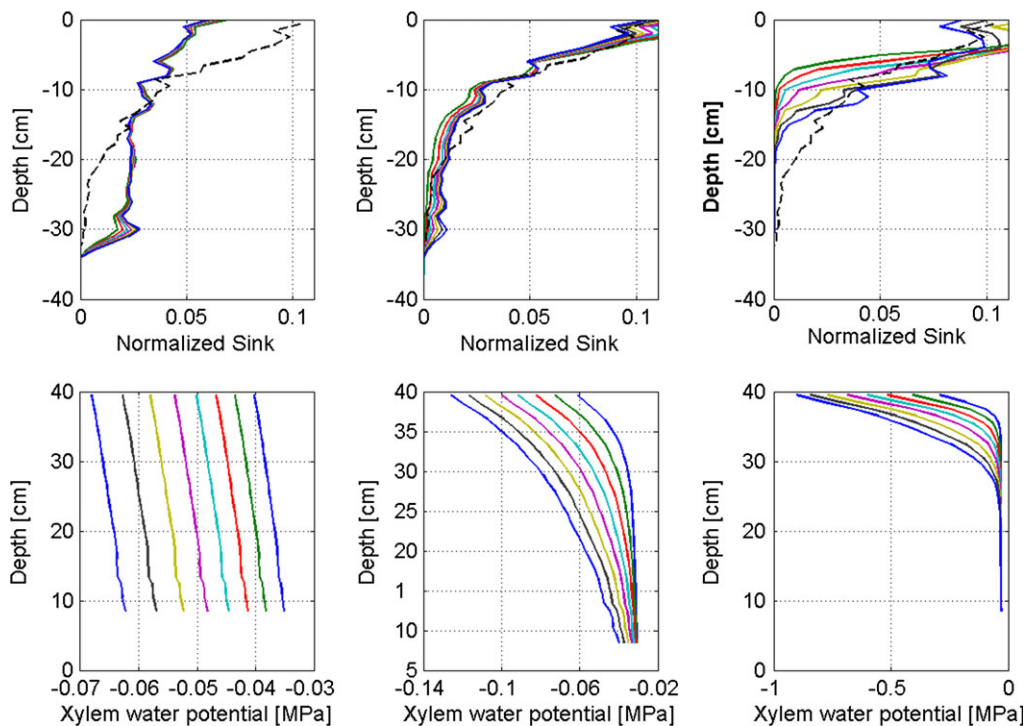


Fig. 4. Distribution of sink term (top) and xylem water potential (bottom) summarized from 3D simulations. The dashed line is the normalized root length density profile. Colours represent successive days. Left: low ratio radial to xylem conductivity ratio. Right: high radial to xylem conductivity ratio.

ryegrass (*Lolium multiflorum*) and maize (*Zea mays*) root systems have been simulated using the RootTyp model (Pagès *et al.*, 2004) using parameter values (kindly provided by L. Pagès) adjusted to fit drawings of ryegrass and maize root systems (Kutschera, 1960). The 10 simulated root systems are shown in Fig. 5, along with their RLD profiles which are similar among replicates.

These 10 root systems were used in simulations with the R-SWMS model, with the same soil, constant transpiration, and the same uniform root hydraulic properties for 10 d (Fig. 6, red and blue curves; see Supplementary data S5 at *JXB* online for parameter values). The sink terms tend to follow the RLD of the two species. Near the soil surface, however, the greater RLD of ryegrass does not give rise to a greater water uptake. This could be an effect of the topology of the root system, which favours root uptake deep in the profile, or could result from the RLD not necessarily matching soil water availability. This redistribution of water uptake in drying soil may be typical of the adventitious root system of monocots, as shown for maize plants where a small proportion of roots in the moist deep soil took up most of the water (Sharp and Davies, 1985).

In a further scenario, the same root systems and conditions were used but the root conductivity (axial and radial) was increased by a factor 100 (Fig. 6, cyan and pink curves). It appears clearly that the heterogeneity (between species and replicates) is masked when the root exceeds certain conductivity values and water is taken relatively homogeneously from the soil profile. It must, however, be noticed that this occurs before stress is reached (taken here

as the time when xylem water potential at the collar falls below -1.5 MPa), when the soil profile is still wet.

On the other hand, it is interesting to observe that despite a relative similarity in uptake profiles (Fig. 6) the horizontal distribution of the sink and the water content arising from these two architectures are quite distinct (Fig. 7).

Concluding remarks

Novel 3D models developed by the soil physics community provide new opportunities to explore how spatial and temporal heterogeneity of soil and root hydraulic properties arises within the soil–plant continuum and affects water uptake in situations where it is not clear whether the soil or the plant is the main controller of water flow. Soil limitations arise wherever the water potential gradient in the soil is more important than the water potential gradient through the plant tissues. If this situation propagates to a significant part of the root system, the transpiration demand will not be met and the plant will start experiencing water deficit. Simulations with the R-SWMS model such as those presented here pinpoints that, in the controversy zone mentioned by Passioura (1980), it is the interplay between root hydraulic architecture and soil water distribution which controls extraction patterns. In this context, it is therefore important to consider where and when the largest resistance occurs: in the soil, due to the low soil hydraulic conductivity (Schroder *et al.*, 2008), at the soil–root interface (Sperry *et al.*, 2002; Schroder *et al.*, 2009), in the

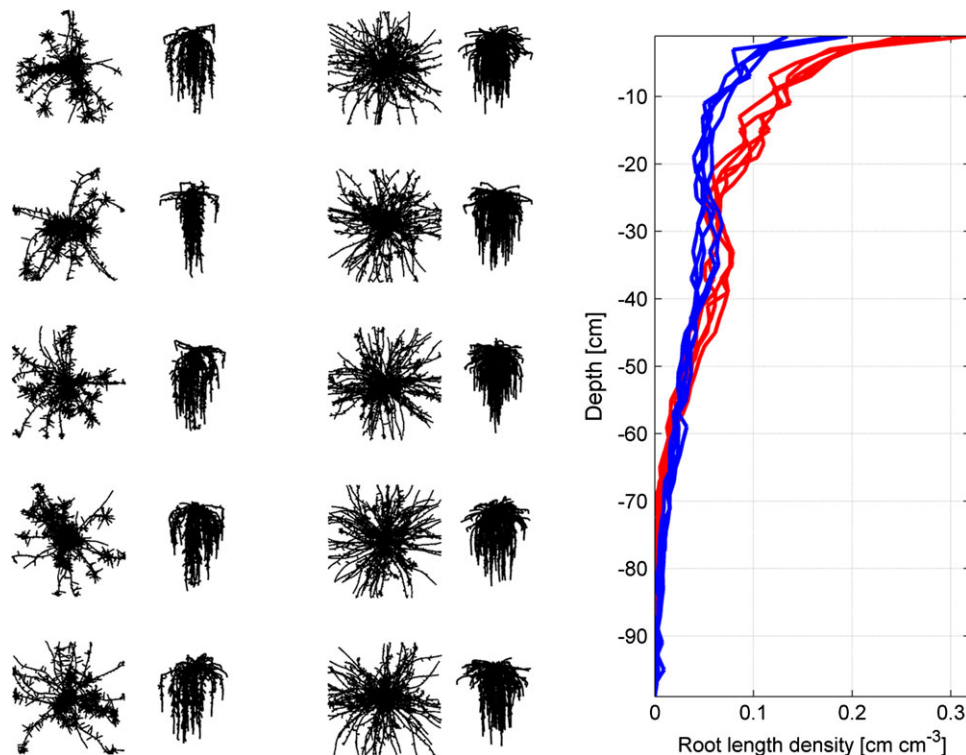


Fig. 5. Left panel: lateral and upper view of maize (left) and ryegrass (right) root systems. Right panel: root length density profiles of the five replicates for maize (blue) and ryegrass (red) root systems.

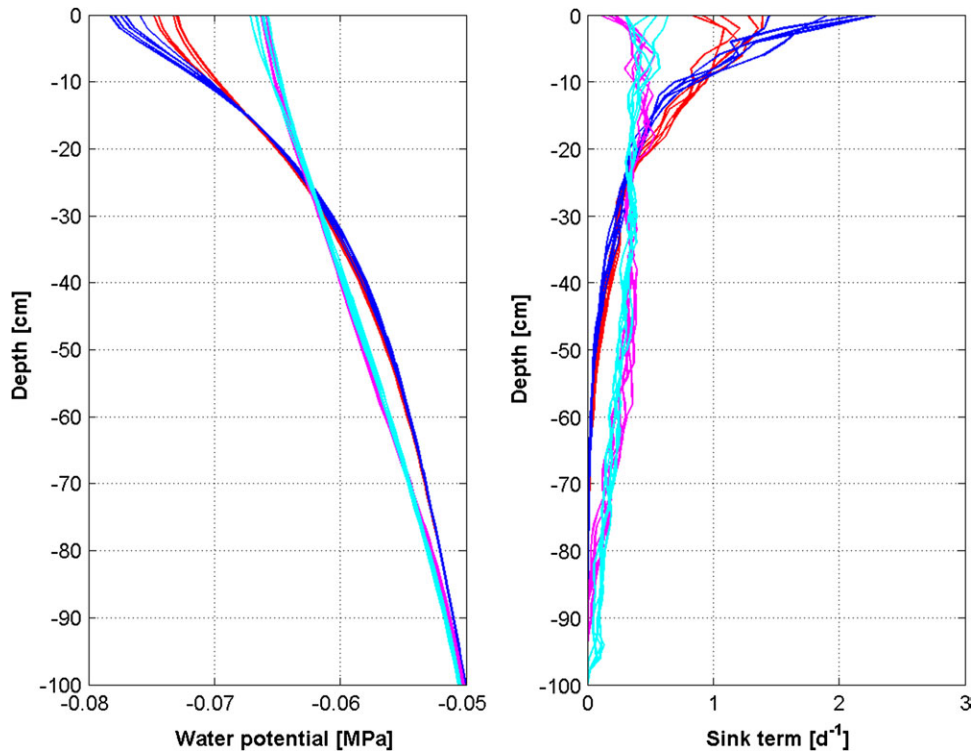


Fig. 6. Soil water potential and sink term profiles for simulated maize (blue) and ryegrass (red) architecture using reference and enhanced ($\times 100$) radial and axial conductivity values. Blue: maize, reference conductivity values. Red: ryegrass, reference conductivity values. Cyan: maize, conductivity values $\times 100$. Pink: rye grass, conductivity values $\times 100$.

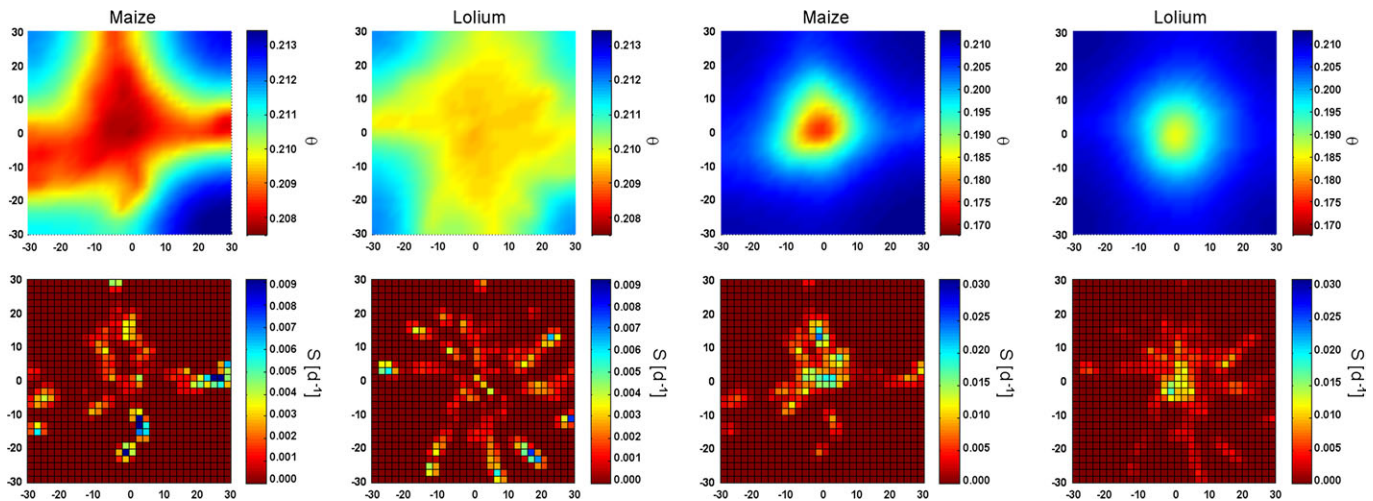


Fig. 7. Horizontal cross-sections of the soil water content (first line) and the sink term distributions at 5 cm depth (second line) for reference (left panel) and enhanced root conductivity values (right panel).

root cortex (Stedde and Peterson, 1998) or in the xylem (Sperry et al., 2003). Being able to separate the contributions of these resistances during crop evolution will be especially important in predicting the water availability to plants with promising traits.

The relevance of models considering the flow of water to individual rootlets of a complete root system has long been questioned in soil physics, primarily because the precise geometry of the root system is impossible to capture (Molz and Remson, 1970; King et al., 2003). As exploration tools,

however, such models have great potential since they enable visual, intuitive, and quantitative appreciation of the hydraulic behaviour of root systems in their soil environment. Similar modelling strategies have been used for the capture of phosphorus and nitrogen, where the overlap of depletion zones seems to be the consequence of RSA (Ge et al., 2000). In addition, models which include an explicit 3D formulation of the root system (FSPM) offer the required mathematical framework to integrate available molecular, physiological, biophysical, and hydrological data

which relate to different parts of the system and pertain to different scales (Godin and Sinoquet, 2005).

Many important aspects of plant water dynamics have not been addressed here. The following is a short list of priority issues to be dealt with to unleash the potential of FSPM such as R-SWMS.

(i) The daily evolution of transpiration demand impacts the soil–root interplay and will thereby affect the distribution of water uptake and subsequent availability of water to roots. Different scenarios of transpiration demand can be set in R-SWMS, under the form of boundary conditions at the root collar. These conditions can be expressed in terms of water flow or water potential, which may well fit the contrasting anisohydric or isohydric behaviour, respectively (Tardieu and Simonneau, 1998).

(ii) If simulations extend over a few days, root growth should be taken into account, especially the growth responses to water deficit which contribute to plant adaptations to drought. Earlier models simulated changes of root tropism as a function of the direction of water potential gradients in soil (Somma *et al.*, 1998). The R-SWMS model allows for root growth and plasticity, but a sound and quantitative view of these responses is still lacking.

(iii) If longer time-scales are considered, the seasonal variability in water availability becomes significant and a consideration of phenology is required, through its effect on the synchrony of availability, acquisition capacity, and transpiration demand (Nord and Lynch, 2009). Not surprisingly, optimal distribution of roots may not be the same depending on phenology (King *et al.*, 2003).

(iv) In principle, this type of model could be used to estimate a few hidden parameters by fitting the model output to experimental data. This type of strategy, referred to as inverse modelling, is currently being tested in our laboratory to estimate root hydraulic conductivities, exploiting recent non-invasive techniques to establish real-time maps of soil water content (Pierret *et al.*, 2003; Garrigues *et al.*, 2006; Van As, 2007; Pohlmeier *et al.*, 2008).

Supplementary data

Supplementary data are available at *JXB* online.

Supplementary data S1. Description of the method used to generate Fig. 1.

Supplementary data S2. Parameters values for simulations represented on Figs 2 and 3.

Supplementary data S3. Simulated hydraulic behavior of the three soil types.

Supplementary data S4. Parameters values for simulations represented on Fig. 4.

Supplementary data S5. Parameters values for simulations represented on Figs 5 to 7.

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