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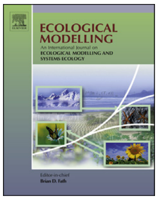

# Can diversity in root architecture explain plant water use efficiency? A modeling study

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ABSTRACT

Drought stress is a dominant constraint to crop production. Breeding crops with adapted root systems for effective uptake of water represents a novel strategy to increase crop drought resistance. Due to complex interaction between root traits and high diversity of hydrological conditions, modeling provides important information for trait based selection. In this work we use a root architecture model combined with a soil-hydrological model to analyze whether there is a root system ideotype of general adaptation to drought or water uptake efficiency of root systems is a function of specific hydrological conditions. This was done by modeling transpiration of 48 root architectures in 16 drought scenarios with distinct soil textures, rainfall distributions, and initial soil moisture availability. We find that the efficiency in water uptake of root architecture is strictly dependent on the hydrological scenario. Even dense and deep root systems are not superior in water uptake under all hydrological scenarios. Our results demonstrate that mere architectural description is insufficient to find root systems of optimum functionality. We find that in environments with sufficient rainfall before the growing season, root depth represents the key trait for the exploration of stored water, especially in fine soils. Root density, instead, especially near the soil surface, becomes the most relevant trait for exploiting soil moisture when plant water supply is mainly provided by rainfall events during the root system development. We therefore concluded that trait based root breeding has to consider root systems with specific adaptation to the hydrology of the target environment.

## 1. Introduction

Water scarcity is considered a serious threat for the 21st century (UNESCO, 2012). Currently 36% of the world population lives in regions where water is a limited resource (Safriel et al., 2005). Climatic changes may potentially vary the water resource availability for agriculture, which is the dominant user of fresh water (Vörösmarty et al., 2000; Hoekstra and Mekonnen, 2012). The productivity of both irrigated and rainfed agriculture can be expected to change (Howell, 2001; Turral et al., 2011). Sposito (2013) pointed out the need of new approaches based on plant–soil feedbacks to enhance crop productivity.

Breeding of water efficient crops contributes to the goal of a sustainable crop production intensification (FAO, 2011; Raza et al., 2012). Recently, attention to the plant root system as a promising target for breeding crops more resistant to drought is increasing. Root breeding may be crucial for selecting water efficient crops as (i) root dynamics are still largely unexploited, (ii) a high natural diversity in root systems is expected, and (iii) roots can lead to dehydration avoidance via efficient uptake compatible with high yields (Blum, 2009; Gewin, 2010; Kell, 2011; Palta et al., 2011).

However, root breeding still has major constraints due to the lack of high throughput measurement systems and uncertainty on the key root traits to be targeted. Tardieu (2011) stated that any plant trait may confer drought resistance to a crop, it is just a matter of designing the right drought scenario. This also applies for the root system. E.g. it is commonly sustained that the depth of a root system is the key trait for optimizing water uptake: deeper root systems are able to take up more water (e.g. Kage and Ehlers, 1996; Lynch, 2013). This hypothesis is due to the common assumption that root density does not constrain water uptake due to the relatively quick convective transport of water between bulk soil and root surface (see also Carminati et al. (2010) for a different view on the traditional assumption of water depletion zones around single

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root axes). Conversely, Czyz and Dexter (2013) have demonstrated that interruption of capillary continuity in a drying soil may become a major resistance for plant water uptake long before the permanent wilting point. Thus, in dry soils, root density may play a critical role to avoid water stress.

Also some ecohydrological studies have shown that, in semiarid ecosystems, shallow root systems may be the most efficient in water uptake. The optimal depth of these root systems is strictly related to the mean depth of the infiltrating soil water, which mainly depends on the temporal rainfall distribution in the given area (Laio et al., 2006; Schenk and Jackson, 2005; Schwinning and Ehleringer, 2001).

Therefore, we suppose that there is no a general root ideotype for a dynamic water stress in semiarid ecosystems, but only specific root traits adaptation to specific hydrological conditions. This implies that root breeding efforts can only be successful when based on a sound understanding of root–hydrology interactions.

Root system models are appropriate tools to deal with such a challenge. They allow to identify the key distinctive traits among a continuity of different root architectures (see Bodner et al., 2013). When coupled to a water transport model, they can infer on the expected implication of root structural diversity on plant water supply under different hydrological conditions. Therefore, such coupled models are indispensable tools for pre-breeding *in silico* experiments that allow to define root ideotypes with specific adaptation to the hydrology of a target environment.

In this paper, we use a newly developed model coupling root growth and soil water transport to analyze plant water uptake efficiency resulting from the interaction between root system and site hydrology. While root water uptake is simulated in 1D to allow for a high number of experimental scenarios, the 1D sink term is the scaling result of a 3D root architecture model that preserves the main features of architectural diversity. Using this model, we will verify two main hypotheses: (i) structural similarity of root systems is an adequate proxy to infer on root functional similarity in water uptake and (ii) the importance of root depth for a water efficient root system decreases in favor of root density when passing from a storage driven to a supply driven hydrology. The overall aim of the study is to obtain a more appropriate understanding of root system ideotypes via an innovative model analysis of diversity in root–hydrology interactions.

## 2. Materials and methods

### 2.1. Root growth model

Root systems of diverse architecture are generated using the model developed by Leitner et al. (2010). This model simulates 3D root growth using L-systems (Prusinkiewicz, 1990). Basic production rules are applied for simulating root growth, branching, and different types of tropisms, e.g. gravitropism, exotropism, etc. Root elongation follows a negative exponential function of elongation velocity till maximum length is reached. Each root axis is composed of an unbranched basal and apical zone. In between these two zones branching of lateral roots takes place. The model parameters for generating diverse root architectures are root radius, length of basal and apical zones, interbranching distance between roots of successive order, maximum number of branching, initial root growth velocity, tropism type, and its degree of influence on root tip deflection. Each parameter includes a standard deviation that allows for a certain degree of randomness in root system development. The number of primary roots determines whether a tap (one primary axis) or a fibrous root system (several primary axes) is created. The parameter values for simulating diverse root architectures used in the study are given in Section 2.4.1.

### 2.2. Soil water model

Root water uptake is simulated by coupling the root model to a model that simulates soil water fluxes. The fluxes are modeled only in the vertical direction because (i) main water dynamics occur in this direction and (ii) the focus of simulations is the diversity of root–hydrology interactions beyond the details of single root water fluxes of functional–structural models. Moreover, a simulation with a 1D soil hydraulic model is significantly less time consuming with respect to a 3D model, and therefore, a 1D model allows to execute a larger number of simulations.

Water movement in unsaturated soil is described using Richards equation. In the vertical dimension this equation can be written as

$$\frac{\partial \theta(h)}{\partial t} = \frac{\partial}{\partial z}\left[K(h)\left(\frac{\partial h}{\partial z}+1\right)\right] - S(h), \tag{1}$$

where $\theta$ is the water content [$L^3L^{-3}$], $h$ is the soil water pressure head [L], $t$ is the time [T], $K$ is the unsaturated hydraulic conductivity [$LT^{-1}$], $z$ is the vertical coordinate [L] taken positive upward, and $S$ is the sink term for root water uptake [$L^3L^{-3}T^{-1}$]. Soil hydraulic functions $\theta(h)$ and $K(h)$ in Eq. (1) are described by the Mualem-Van Genuchten model (van Genuchten, 1980).

Due to the strong non-linearity of soil hydraulic functions $\theta(h)$ and $K(h)$ the Richards equation is difficult to solve also numerically. In this work we implement the implicit, backward, finite difference scheme proposed by van Dam and Feddes (2000), after Celia et al. (1990). This numerical approach solves Eq. (1) in a mass conservative way (Celia et al., 1990). In order to minimize simulation time we use a variable time step dependent on the number of iterations needed to reach convergence in the former time step.

The initial condition is imposed through the specification of the pressure head $h$ along the depth $z$ at time $t = 0$. Following Feddes et al. (1978), the boundary conditions can be of two types, Dirichlet condition, i.e., specification of the pressure head $h$, or Neumann condition, i.e., specification of a flux $q$ through the boundaries.

At the lower boundary we assume that the water table is deep enough to not influence soil water dynamics and the gradient of water pressure head $\partial h/\partial z$ is equal to zero. Thus, the flux is solely driven by gravity and is equal to the unsaturated hydraulic conductivity calculated at this boundary.

At the top boundary, i.e., the soil surface, water flux depends on both meteorological and soil conditions. The soil can lose water by evaporation or gain water by infiltration. In case of evaporation, the potential water flux from the soil surface only depends on atmospheric conditions, but the actual flux would be conditioned by availability of water in upper soil layers. If these soil layers dry out, the boundary condition will switch from flux-controlled, with $q$ equal to the potential evaporation $E_P$ [$LT^{-1}$], to head-controlled, with $h = h_{atm}$. The parameter $h_{atm}$ is the water pressure head at the soil surface in equilibrium with the pressure head of the atmosphere.

Similarly, the potential infiltration is equal to the rainfall rate $P$ [$LT^{-1}$], but the actual flux can be limited by the absorption capacity of soil: if the upper soil layers are saturated, rain can no longer infiltrate into the soil and water flows away as surface runoff. In this case the boundary condition will shift from flux-controlled, with $q$ equals to the rainfall rate, to head-controlled, with $h = 0$ at the soil surface (we assume that no ponding occurs and all the water that do not infiltrate runs off).

In both cases the following condition must be respected:

$$|q| \le \left|-K(h)\left(\frac{\partial h}{\partial z}+1\right)\right| \tag{2}$$