



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.

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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; Turrall 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 semi-arid 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

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

where θ 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:

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

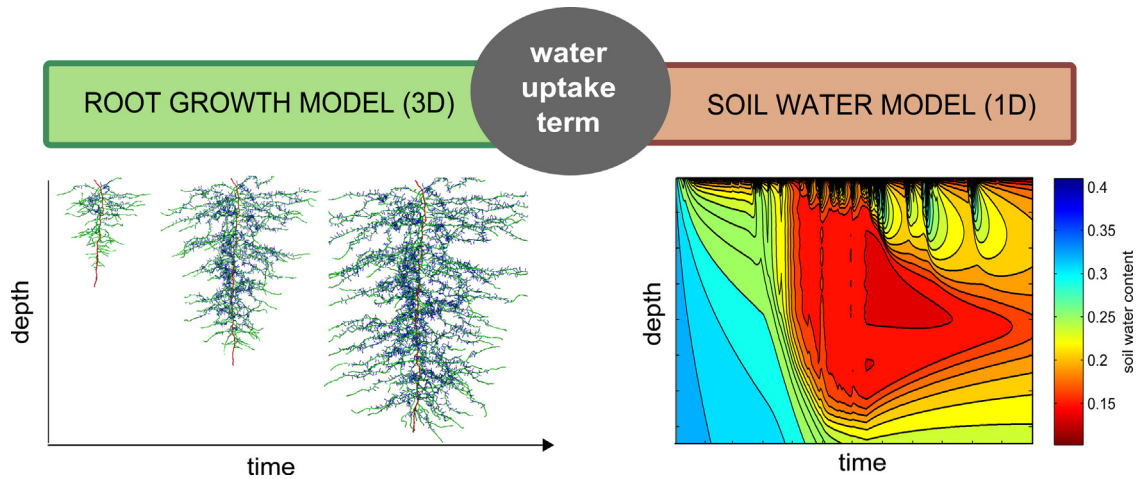


Fig. 1. Synthetic representation of the model coupling. An example of growing root system is shown on the left, while on the right a graphic shows the soil moisture dynamics over a year due to infiltration, evaporation, and root water uptake.

This condition assures that in case of evaporation the actual water flux q out of the soil would correspond to the potential evaporation rate only if that does not exceed the maximum flux allowed by the actual soil water conditions, given by the right hand side of the equation, with $h = h_{atm}$ at $z = 0$. Similarly, the actual flux q into the soil, would be equal to the rainfall rate only if it is lower than the r.h.s. of Eq. (2), with $h = 0$ at $z = 0$.

2.3. Coupling of the models

The link between root and soil water models is the 1D sink term $S(h)$ in Eq. (1). This term represents root water uptake for each horizontal soil layer. A schematic representation of the connection between the two models is shown in Fig. 1. The water uptake term mainly depends on two factors: the amount of roots and the availability of water in each soil layer. When pressure head in soil, due to water depletion, decreases under a certain threshold, the plant senses water stress and starts to gradually close its leaf stomata thereby reducing water uptake.

In order to integrate both vertical distribution and density information from a 3D root architecture to a 1D water uptake term, we use the function proposed by de Jong van Lier et al. (2008), which includes microscopic single root processes into a macroscopic 1D sink term. The sink term is given as

$$S(h) = \rho(M(h) - M_0), \quad (3)$$

where $M(h)$ is the matric flux potential [L^2T^{-1}] in a discrete soil layer and is defined as the integral of unsaturated conductivity, $M(h) = \int_{h_w}^h K(h) dh$, where h_w [L] is the water potential at wilting point. The parameter M_0 [L^2T^{-1}] is the matric flux potential at the root surface. The factor ρ [L^{-2}] is related to the root system structure and is equal to

$$\rho = 4 \cdot \left[r^2 - \frac{a^2}{\pi R} + 2 \left(\frac{1}{\pi R} + r^2 \right) \ln \left(\frac{a}{r\sqrt{\pi R}} \right) \right]^{-1}, \quad (4)$$

where a is a constant equal to 0.53, and R [LL^{-3}] and r [L] are root length density and mean root radius, respectively. The value of ρ increases with increasing R and r , but the sensitivity to root length density is much higher than to root radius. Both of these root traits vary with depth and time and are obtained from the root architecture simulations. Thus, they are not merely empirical distributions, but scaling results from biologically meaningful architectural parameters driving the 3D root system development. This scaling from a 3D evolving root architecture allows one to

maintain the essential structural properties of the root system within the 1D sink term.

Total transpiration is given by the integral of the sink term (Eq. (3)) $T = \int_0^{z_{max}} S(z) dz$, where z_{max} is the maximum root depth. Transpiration T cannot be higher than the potential transpiration T_p [LT^{-1}] of the plant. The matric flux potential M_0 is initially considered equal to zero, i.e., $h = h_w$ at the root surface, but if the obtained transpiration is larger than potential transpiration, no water stress occurs and thus M_0 is larger than zero and its value is obtained by setting $T = T_p$.

2.4. Simulation scenarios

2.4.1. Parameters of the root growth model

Root systems are created from architectural parameters obtained from literature and based on a previous root classification analysis realized by Bodner et al. (2013). The parameter values are listed in Table 1 with the respective references. Bodner et al. (2013) initially analyzed the structural similarity of 288 different root system types. The 48 root architectures produced by the parameter set given in Table 1 represent a subsample of these root systems that still captures the entire diversity reported by these authors. The other parameters of the root model are kept constant for all root systems. Both primary and lateral roots have a basal zone of 4 cm and an apical zone of 7 cm. The root system has a maximum of 120 lateral branches along primary roots and 50 along root axes of second order, while the distance between branching is set equal to 1 cm for secondary roots (Arredondo and Johnson, 2011;

Table 1
Parameter values used for generating 48 different root architectures.

| Parameter | Values | References |
|---------------------------------------|---------------------------------------|---|
| Number of primary roots | 1, 4 | Kutschera et al. (2009) |
| Growth rate of primary roots | 1.5, 3 cm/d | Shelden et al. (2013) and Schmidt et al. (2013) |
| Interbranch distance at primary roots | 0.4, 0.8 cm | Arredondo and Johnson (2011) and Pages (2014) |
| Tropism of primary roots | Gravitropism, exotropism ^a | Pages et al. (2004) |
| Growth rate of secondary roots | 0.5, 1.5 cm/d | Shelden et al. (2013) and Schmidt et al. (2013) |
| Tropism of secondary roots | Gravitropism, exotropism | Pages et al. (2004) |

^a The exotropism is applied only in the cases with 4 zero-order roots.

Table 2

Van Genuchten soil parameters taken from Wösten et al. (1999). θ_r and θ_s are the residual and saturated water content [L^3L^{-3}], respectively. α and n are the Van Genuchten parameters and K_s is the saturated hydraulic conductivity [LT^{-1}].

| | θ_r | θ_s | α (1/cm) | n | K_s (cm/d) |
|------------------|------------|------------|-----------------|--------|--------------|
| Coarse soil | 0.025 | 0.403 | 0.0383 | 1.3774 | 60 |
| Medium-fine soil | 0.010 | 0.430 | 0.0083 | 1.2539 | 2.272 |

Pages, 2014). The root diameter is 1.6 mm, 0.8 mm, and 0.4 mm for primary, secondary, and tertiary roots, respectively (Pages, 2014).

Root water uptake is analyzed for a typical growing season of spring crops from March to mid July. Root growth is assumed to stop at flowering after 92 days (beginning of June). Water uptake simulation ends at mid-July, at the harvest time. We do not consider here the effect of water dynamics on the root growth, i.e., hydrotropism. In this way, we have exactly the same growing root system in the different hydrological scenarios and we can easily compare the results.

2.4.2. Parameters of the soil water model

The water uptake efficiency of each root system is tested in 16 distinct hydrological scenarios, i.e., two soils with different water holding capacity (coarse vs. medium-fine textured), four initial soil moisture conditions, and two rainfall distributions (768 simulation runs). The adopted soils, characterized by different water holding capacities, are a coarse textured soil and a medium-fine one. The parameters of the Van Genuchten model used to simulate the hydraulic behavior of the two soil types are shown in Table 2.

At the beginning of the growing season we impose four different soil moisture conditions. These initial conditions approximate diverse soil moisture vertical distributions due to rainfall and evaporation before the growing season, i.e., during previous fall and winter seasons. In case of a wet initial soil, winter rainfall was sufficient to refill the entire soil profile to field capacity, i.e., the initial condition is $h = -330$ cm (equal to 1.69 mm of water per cm of coarse soil and 3.25 mm per cm of fine soil). Conversely, scarce winter rainfalls and/or a strong depletion of soil moisture due to relatively high temperatures in the previous autumn may result in low water storage at the beginning of the growing season with a dry ($h = -5000$ cm) or only partially wet soil profile. In the latter case we assume pressure head to linearly increase or decrease with depth. In one case $h = -5000$ cm at the soil surface and increases till

$h = -330$ cm at 1 m depth, while the inverse occurs in the other case (from $h = -330$ cm till -5000 cm).

2.4.3. Boundary conditions of the soil water model

The boundary conditions at the soil surface, i.e., potential evapotranspiration and rainfall rates during the growing season, simulate two climates, continental and Mediterranean, respectively. For a straightforward comparison of the simulation results, we use the same potential evapotranspiration ET_p in both climates, but opposite rainfall distributions (shown in Fig. 2). The frequency of rainfall is higher during summer in the continental climate and during winter in the Mediterranean one. Both evapotranspiration and rainfall series are generated in order to obtain semiarid climates characterized by an aridity index equal to 0.5 (climate classification by UNEP (1992)). The total annual potential evapotranspiration is set to 1000 mm, twice the total rainfall.

The rainfall series are realized using a stochastic model which produces random rectangular daily pulses of rainfall (Tron et al., 2013). In order to have a seasonality effect on precipitation distributions, mean rainfall rate and intensity are multiplied by a sine function that reaches its maximum value in summer or winter (Viglione et al., 2012). The rainfall series are scaled in order to have a total annual amount of rainfall equal to 500 mm.

The daily time series of potential evapotranspiration is obtained by using a sinusoidal function. The sine function has a period of 365 days and a mean value of 2.74 mm/d (total annual ET_p divided by 365 days). The maximum values of ET_p are reached during summer. The daily variability of ET_p is obtained by adding to the sine function values randomly extracted from a normal distribution with a standard deviation equal to 0.15 mm/d. The obtained potential evapotranspiration is divided into evaporation E_p and transpiration T_p during the growing season. Following Ritchie (1972), we assume that potential transpiration increases likewise the increase of the plant leaf area index, which can be described by a Pearl-Verhulst logistic process. The partition into evaporation and transpiration is shown in Fig. 3.

2.5. Statistical analyses

The structural and functional similarities among root systems are investigated using cluster analyses following Bodner et al. (2013). Cluster analysis provides a multivariate method to group similar root systems based on different descriptors. The number

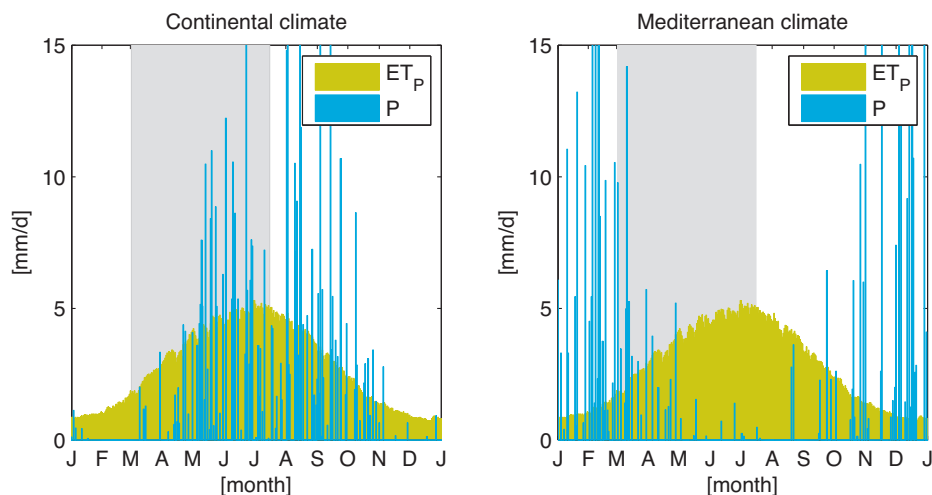


Fig. 2. The two panels show a representative year of a continental climate and a Mediterranean one, to the left and to the right, respectively. The distribution of the rainfall P has its maximum in summer for the continental climate, and in winter for the Mediterranean one, while the potential evapotranspiration ET_p is the same in both the climates with a maximum during summer. The total annual ET_p is 1000 mm, while the total rainfall is 500 mm. The gray areas indicate the growing season.

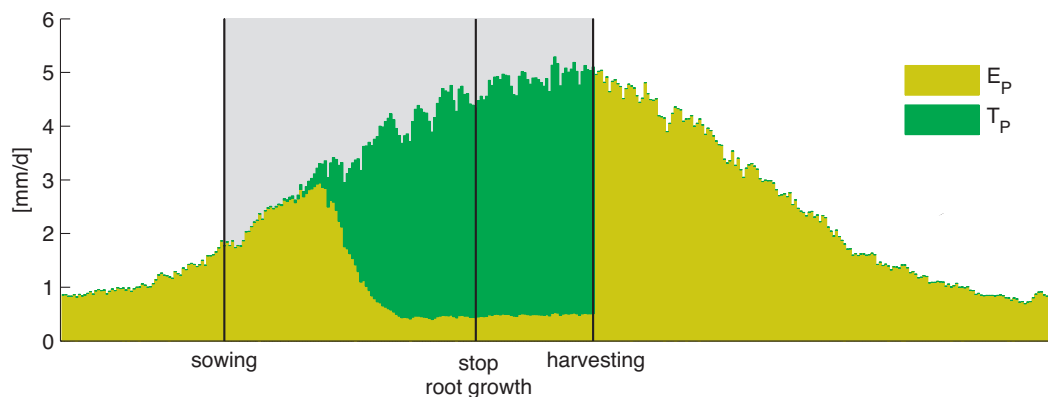


Fig. 3. Potential evapotranspiration is divided into potential evaporation E_P and potential transpiration T_P . In gray the growing season is represented.

of clusters to be considered for meaningful interpretation is determined by the cubic clustering criterium. We calculate structural clusters from root morphological traits and functional clusters from root water uptake under different hydrological conditions. Thereafter, we compare the number of root systems sharing the same cluster when using structural and functional descriptors, respectively, to reveal the predictability of root functioning from root morphology. Then, we use univariate regression analysis to infer the key structural root trait determinant for root functionality. Finally, joint regression is used to test for cross over interactions between root system under different hydrological scenarios. This provides insight into root systems with general vs. site specific adaptation.

3. Results

Root functionality of the different architectures under 16 hydrological scenarios is analyzed in terms of cumulative root water uptake, i.e., total transpiration, during the growing season. The main constraint to plant water uptake is rainfall water availability. The two analyzed climates differ substantially in average total transpiration (continental: 204 mm; Mediterranean: 55 mm). This is mainly due to the difference amount of rainfall during the growing season: 218 and 73 mm, for the continental and Mediterranean climate, respectively. Within each climate, the diverse root systems explain about 14% of the variance in cumulative water uptake, while soil water holding capacity contributes between 10 and 13%. The strongest contribution to variance of water uptake is due to the initial soil wetness (the percent contributions are shown in Table 3), which constitutes, together with the in-season rainfall, the overall potentially available water for crop transpiration.

Hereafter we present the finding obtained with cluster analyses based on architectural and functional root traits. Then, we analyze the correlations between transpirations and maximum depth (and total root length density) of the root systems, and finally we observe the performance of some representative root architectures in two very different hydrological scenario.

Table 3
Percent contribution of different factors to the total variance of transpiration in two different climates.

| | Continental climate | Mediterranean climate |
|-----------------------|---------------------|-----------------------|
| Soil | 10.0 | 13.0 |
| Root system | 14.0 | 14.6 |
| Initial soil moisture | 66.0 | 61.5 |

3.1. Root system similarity structure vs. functionality

To find out if the structural description of a root system is able to capture its functionality in terms of water uptake, we first divide the analyzed root systems in groups characterized by an architectural affinity. The structural clustering is based on descriptors of the root architecture. From a set of 20 initial structural descriptors we select nine descriptors using principal component analysis and using the following criteria: (i) no descriptors with high mutual correlation among each other should be selected, (ii) the weight of the single descriptors on the principal components should be higher than 0.4, and (iii) each descriptor should relate to one of the principal components only to obtain clearly interpretable principal components. The selected root descriptors are: maximum root depth, vertical distribution shape, homogeneity and skewness of the vertical root profile, vertical root growth rate, total root length density, local maximum root density, rate of the root density increase, and mean root radius. Clusters of similar root systems based on structural descriptors are shown in Fig. 4. Statistical indicators suggested seven main clusters to be retained. The strongest structural distinction is due to root traits determining depth, while the second main differentiation is from root density related traits. For root systems with intermediate depth and high density, growth velocity provides an additional relevant distinctive trait.

Subsequently, we analyze similarity among different root architectures based on their root functionality, i.e., using total transpiration as clustering criterion. Again we performed this analysis separately for each climate due to the obvious strong distinction in transpiration between the continental (Fig. 5) and the Mediterranean (Fig. 6) scenario. Within each climate, the clustering reveals similar root architectures based on the total transpiration under eight hydrological conditions, ranging from stressful (low storage soil with low initial moisture) to low stress (high storage soil with high initial moisture).

Root architectures first differentiate into four (very high, high, intermediate and low) and three (high, intermediate and low) main groups of transpiration capacity in the continental and Mediterranean climate, respectively. Generally, the change in mean transpiration among groups with different functionality is higher in the drier Mediterranean climate. This points out a more marked difference in the performance of root systems in more stressful conditions.

Root systems having on average a low or very high transpiration under continental conditions and high transpiration under Mediterranean conditions never change their rank, i.e., these root systems show a superior or inferior water efficiency under all hydrological conditions. Conversely, root systems with intermediate and high transpiration in a continental climate as well as

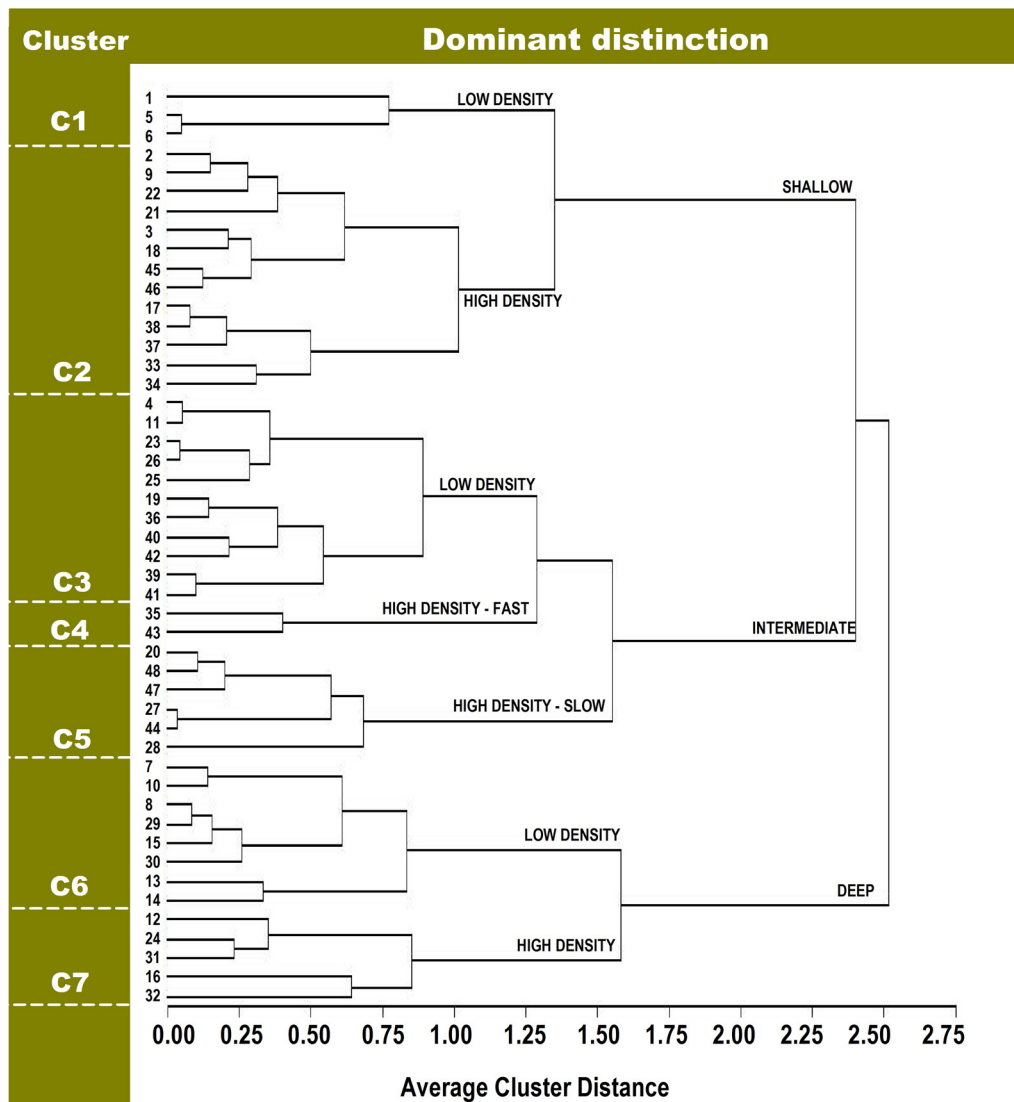


Fig. 4. Cluster analysis of the root systems based on nine structural descriptors: maximum root depth, vertical distribution shape, homogeneity and skewness of the vertical root profile, vertical root growth rate, total root length density, local maximum root density, rate of the root density increase, and mean root radius.

those with low and intermediate transpiration in a Mediterranean climate change their rank according to the specific hydrological scenario. That means they perform differently under different stress conditions, e.g. change of soil type or initial water content. Thus, most root systems do not show a general adaptation to all hydrological scenarios, but rather specific adaptation to a given environmental water regime.

On the left panels of Figs. 5 and 6 the structural clusters to which root systems of each functional cluster belong to are shown. If all the root systems of a functional cluster were within a unique structural cluster, this would indicate a perfect correspondence between root architecture and functionality, i.e., root systems with similar architecture are characterized by a similar water efficiency in different hydrological environments. However, in both climates, there are only two functional clusters where all root systems are identified entirely by a defined structural cluster. Nevertheless, in most cases, the root systems of a functional group belong to close structural clusters, which are characterized by some basic similarities. In both climates the lowest transpiration values are produced by the shallowest root systems, which are part of the structural clusters C1 and C2, while the largest transpiration values are obtained by

the deepest ones, contained in clusters C6 and C7. However, there are a lot of intermediate cases with root structural types changing their efficiency according to the hydrological environment. Thus, it is not possible to obtain a clear and univocal indication of root functionality when just relying on structural features.

3.2. Structural traits for root functionality depth vs. density

Cluster analysis reveals that the functional response of a root system cannot be a priori predicted from a general structural description of root architecture. Using regression analysis we further investigate whether maximum root depth or total root length density, calculated as total length of the root systems divided by a fixed soil volume, are the key determinants for superior functioning in different hydrological environments. These traits are two basic uncorrelated root descriptors which strongly shape the architectural appearance of different root systems (cf. Fig. 4). In almost all scenarios the maximum root depth is highly correlated with transpiration, as shown in Fig. 7 by the large values of the coefficient of determination: deeper root systems are able to take up more water and thus to transpire more.

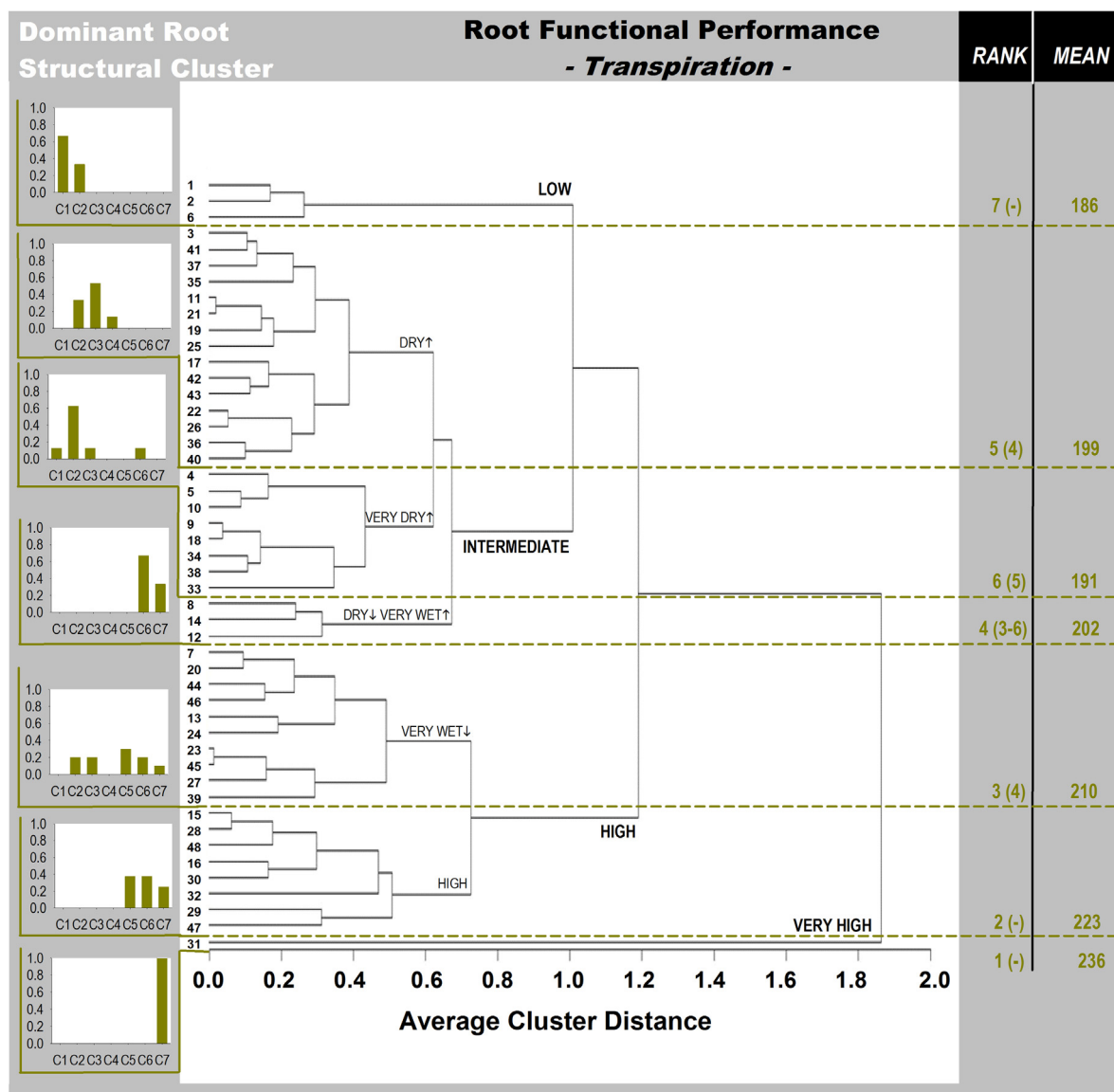


Fig. 5. Cluster analysis of the root systems based on functional traits in a *continental climate*, i.e., transpiration values obtained in eight scenarios (combination of two soil types and four initial soil moisture conditions). The transpiration rank and the mean transpiration value [mm] for each cluster are reported on the right. On the left, the small graphics show the structural clusters to which belong the root systems of each functional cluster. The arrows in the labels indicate in which scenarios the root systems perform better (↑) or worse (↓). 'Very dry' indicates the scenarios with coarse soils totally dry or dry at the top at the beginning of the growing season, 'dry' includes also the fine soils, and 'very wet' denotes the scenarios characterized by fine soils and initial wet conditions.

The correlation is strongest in soils initially totally wet *W* or wet at the bottom *WB*. In these scenarios the ability of root systems to grow in depth ensures a larger exploration of the wet soil layers. Thus, in most hydrological scenarios root depth is a key trait to assure water uptake efficiency.

Conversely, the correlation with depth is quite low when the soil has low retention capacity, the water content is initially low, and most of the water absorbed by roots comes from in season-rainfall (continental climate with a coarse soil and dry initial soil conditions *D* or solely wet at the top *WT*). In these cases, a deep root system does not provide an advantage to the plant. Root systems able to transpire more are those characterized by a larger root density, as shown by the R^2 values referred to the total root length density in Fig. 7. In these scenarios, the total length density of a root system plays a key role in water uptake by catching most of the infiltrating water before this is lost as leakage. As in this work total root length density and total root surface are highly correlated

($R^2 = 0.99$), the results in terms of root length density are analogous to the one obtained with the root surface (not shown here). From the regression analyses, we infer the root system target traits for superior drought resistance clearly change with soil hydrological conditions.

3.3. Supply vs. storage driven hydrologies require specific root systems

The inexistence of a general root ideotype is demonstrated by the lack of correlation among the transpiration values obtained by root systems in contrasting hydrological scenarios. E.g. the correlation coefficient between transpiration values in a continental climate with a coarse and initially dry soil and a Mediterranean climate with a fine and initially wet soil is as low as 0.06. Thus, efficient root systems in one scenario are not the most efficient in the other one.

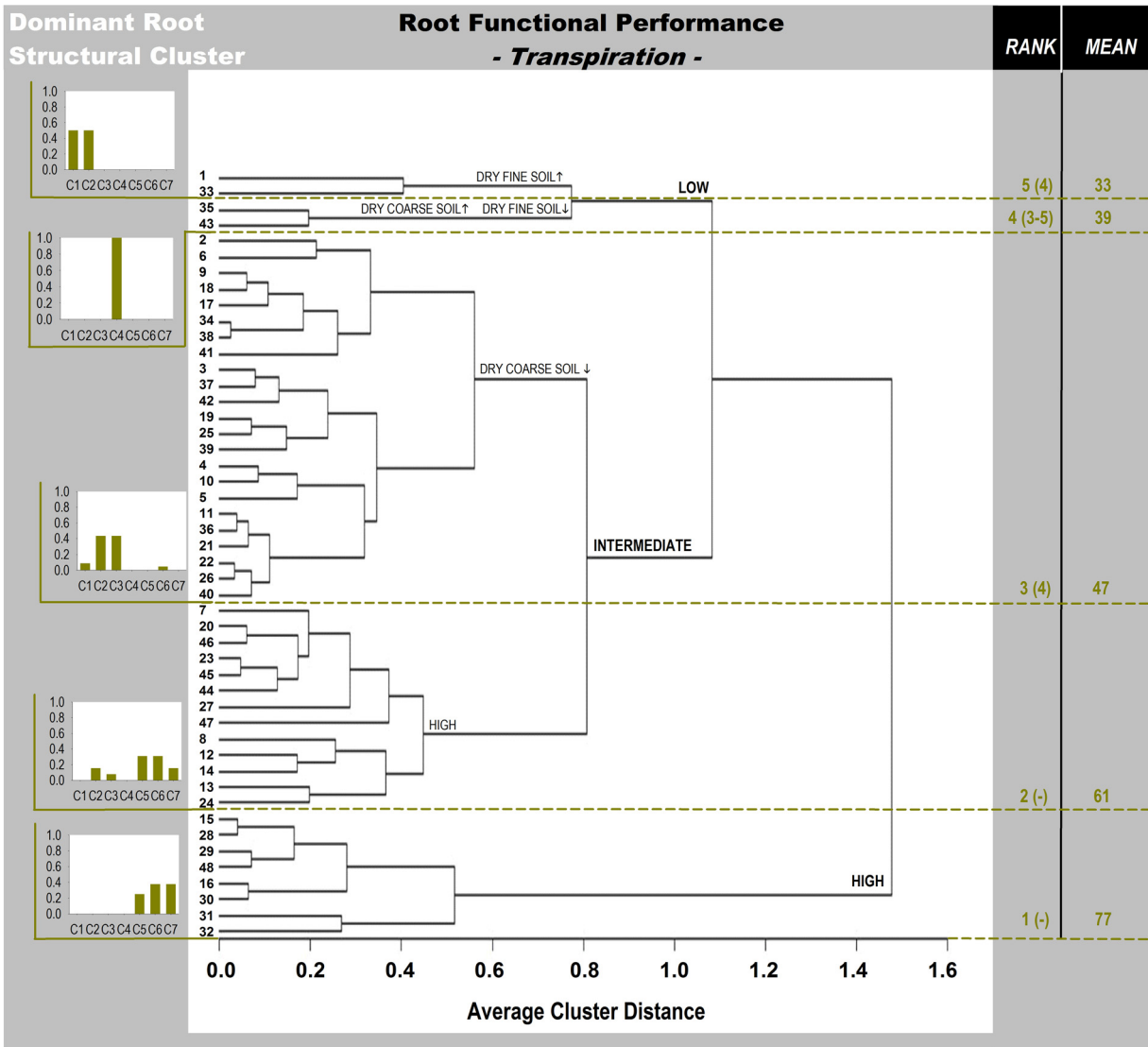


Fig. 6. Cluster analysis of the root systems based on functional traits in a *Mediterranean climate* (transpirations values obtained in eight scenarios). Mean transpiration value [mm] and correspondent rank of each cluster are listed on the right columns. The graphics on the left show the structural clusters of the root systems of each functional cluster. The arrows ↑ and ↓ in the labels show improvement or worsening of the transpiration, respectively. The labels 'dry-fine soil' and 'dry-coarse soil' denote the scenarios with dry initial conditions (totally and at the top).

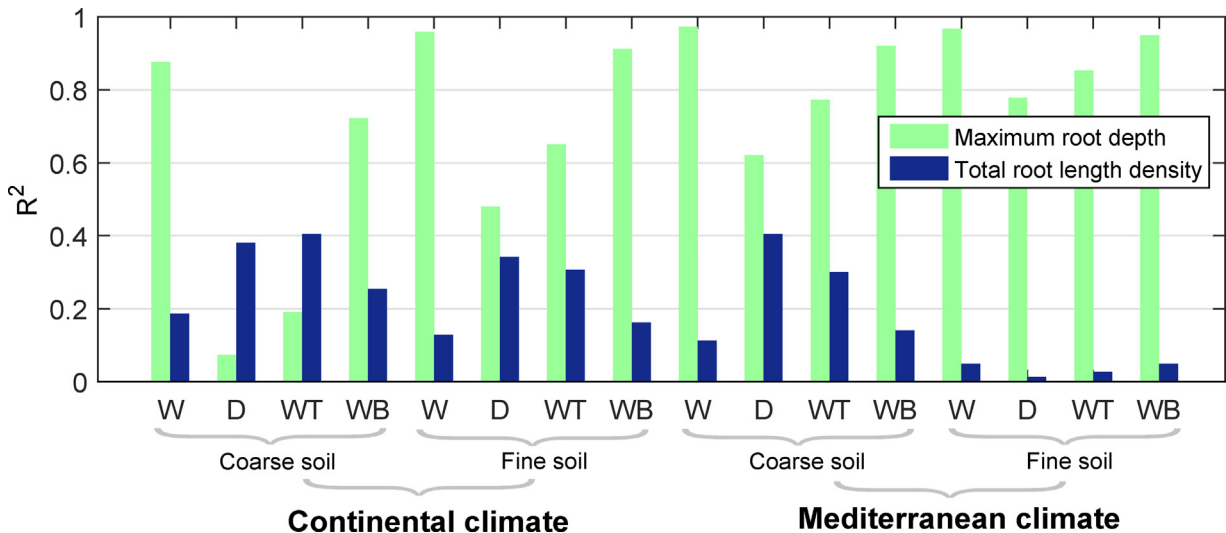


Fig. 7. Coefficient of determination R^2 of the linear regression between transpiration and root trait values in the 16 scenarios. The labels 'W', 'D', 'WT', 'WB' denotes the initial soil moisture conditions: wet, dry, wet at the top, and wet at the bottom, respectively.

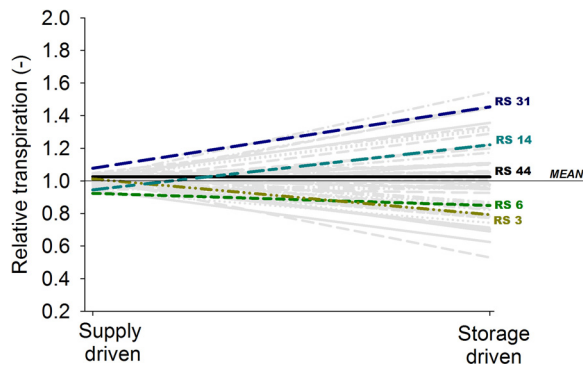


Fig. 8. Relative transpirations, i.e., transpiration obtained by the root systems divided by the mean transpiration of all the root systems in a specific scenario. The relative transpiration values are shown for two scenarios: the supply driven and the storage driven. The first corresponds to a continental climate, with a coarse soil, and initially dry conditions, while the second indicates a Mediterranean climate, with a fine soil, and initially wet conditions.

These two cases represent two opposite hydrological conditions: the first case can be considered a supply driven environment, as soil is initially dry and water supply to the plant comes predominantly from in-season rainfall. In the second case, rainfall during growing season is very scarce: the water used by the plant is stored in soil before sowing time. This latter can be considered a storage driven environment. Fig. 8 shows in gray the relative transpiration of the root systems in the two scenarios, i.e., the transpiration of each root system divided by the mean transpiration under the given hydrological condition. Generally, there is higher scattering of relative transpiration under storage driven conditions. This indicates the increasing importance of root system diversity for plant adaptation where plant water uptake mainly depends on stored soil water resources.

The performances of some representative root systems (shown in Fig. 9) are highlighted in Fig. 8 with different colors. A deep and dense root system (RS 31) shows a general good adaptation with transpiration rates above the mean in both scenarios, with a particular advantage under storage driven conditions. However, the construction and maintenance of such a root system could also represent a high carbon cost for the plant. Root system 6, instead, has transpiration below the mean in both scenarios. In this case, low root carbon investment cannot ensure a sufficient uptake for high stomata conductance. Root system 44, quite dense but not very deep, shows a total transpiration slightly above the mean in both the hydrological conditions. A plant with such a root system is thus widely adaptable to different climate and pedologic conditions.

The root systems 14 and 3, instead, show opposite performances in the two scenarios. In the storage driven environment root system 14 is more efficient than 3 and vice versa. Root system 14 reaches larger soil depths, thereby making better use of deep soil water. In these hydrological conditions, root density is not a limiting constraint. Conversely, in the supply driven environment, where most

of water arrives from rainfall during the growing season, root system 3 is able to absorb more water with respect to 14. In this case, sufficient density in surficial soil layers is important to absorb water before this evaporates.

4. Discussion

4.1. Root modeling for ecohydrological analysis

The increase of the crop yield requires plants with root systems capable to use most of the available soil water for transpiration (Passioura, 2006). However, plant traits associated with drought tolerance, such as a specific root architecture, may have positive effects in a hydrological environment and negative effects in another one (Tardieu, 2011). The modeling approach allows to identify specific root traits that provide a better plant adaptation to a well defined target environment.

In this work, for the first time, the growth and water uptake of a large number of root systems is simulated in several hydrological environments during a prolonged period correspondent to the growing season. A 1D model allows to simulate the performance of this number of root architectures. Possibly, a 3D water uptake model (as the one of Javaux et al. (2008)) could represent more in detail the resistance in the water flow from soil to roots. However, with this scale of detail and with such a time scale it would not be possible to realize this number of simulations (see e.g., the work of Leitner et al. (2014)). Moreover, the scaling from 3D root architecture and the use of the reduction function of de Jong van Lier et al. (2008) allows to have a dynamic 1D sink term that conserves the main structural characteristics of the growing root system. Thus, root uptake modeling can progress both toward detailed modeling of physiological processes in the plant hydraulic architecture (e.g. Couvreur et al. (2014)) and toward better ecohydrological understanding of the diversity of interactions between root systems and environment as presented in this study.

More advanced sink term calculations including explicit modeling of the hydraulic conductivities within the root architecture have been developed (Roose and Fowler, 2004; Javaux et al., 2008; Couvreur et al., 2012). These structural–functional root models account for the physiological complexity of plant water regulation under drought. Still they imply a major challenge for parameterization: particularly for herbaceous plant root systems data availability is restricted (Sperry et al., 2003). Therefore, the definition of root hydraulic parameter sets to approximate natural diversity within meaningful constraints is still difficult.

4.2. Root classification: predicting functioning from structural similarity?

Different classification systems for rooting types have been suggested, e.g. based on root topology (Fitter, 1987) or developmental origin (Zobel and Waisel, 2010). The objective of root classification is rather functional than taxonomical, i.e., to identify plants with similar behavior under given environmental conditions. Therefore,

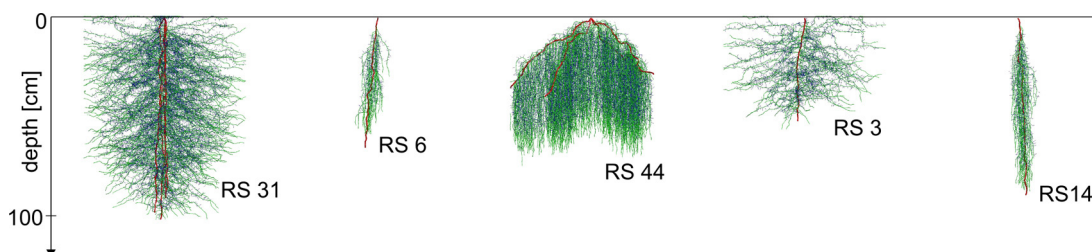


Fig. 9. Root system architectures whose performances are highlighted in Fig. 8.

Bodner et al. (2013), using a statistical classification method, raised the question whether structural similarity of rooting types are sufficient to capture such a functional similarity. The obtained results show that a mere structural classification from root architecture is not enough to identify root functional similarity. We observe from cluster analysis that most of the root systems perform differently in distinct hydrological scenarios, also within the same climate. An exception is represented by very dense and deep root systems which are able to guarantee large transpiration values in almost all hydrological conditions: the widespread presence of roots into the soil would assure an effective exploitation of both infiltrating rain water and stored soil water. However, such a root system requires high building costs in terms of carbon use and may be challenging for the plant to maintain it (Guswa, 2008).

4.3. Explorative vs. exploitative root systems

Most root systems show specific adaptation to water stress scenarios with transpiration values varying between 57% and 76% around their mean. Thus, in water limited conditions there is not a unique ideotype except for a root system with high assimilate investment into a both deep and dense rooting which could probably imply negative trade off in terms of crop yield production. When water is already stored within the entire soil profile due to previous rainfall events, then, a suitable root system is a deep one, and also a low root density is sufficient to guarantee an adequate water uptake. This root system ensures extensive soil exploration to extract the water accumulated before the growing season (Rodríguez-Iturbe et al., 2001). Thus, deep roots are necessary to improve drought resistance in plants (Kato et al., 2006; Lynch, 2013) in environments mainly characterized by storage driven conditions.

However, when soil is shallow with poor retention capacity and plant water supply is mainly driven by in-season rainfall, dense root systems can even become superior in water use compared to deep root systems. Here, intensive exploitation enables a quick response to intermittent and unpredictable rainfall during the growing season (Rodríguez-Iturbe et al., 2001; Schwinning and Ehleringer, 2001; Nakhforoosh et al., 2014). Also Palta et al. (2011) sustained that a root system with larger length density is more suitable in environments where crops largely rely on seasonal rainfall.

Thus, root breeding ideotypes are primarily a function of site hydrology, which is determined by rainfall amount and distribution, as well as soil storage capacity. This is in agreement with results from Schenk and Jackson (2005) who demonstrated that root depth of different vegetation types is strongly related to the mean infiltration depth of rainfall. Also Preti et al. (2010) showed that roots are closer to the surface when climate and soil result in higher plant water availability in the upper soil layers.

Although we consider only water dynamics in this simulation study, an effective crop improvement requires other factors to be taken into account. Root systems have to be adapted to multiple stresses in natural environment. E.g. beyond water shortage, also the availability of non-mobile nutrients, which are mainly located in the surficial soil layers, is an important factor (Tardieu, 2011; Johnson et al., 2000).

5. Conclusions

Root uptake efficiency is a trait of specific plant adaptation involving distinct root structural features. There is no unique root ideotype for semiarid ecosystems, except for the extreme case of very dense and deep root systems. These are able to exploit all available soil water assuring high transpiration rates, but require a massive use of biomass that could affect the yield. A breeding

rule that can be achieved from our modeling study is that with increasing storage dependence of a target environment, there is an increasing importance of achieving deep rooted crops. Instead, an exploitative root system with sufficient density in the surficial soil layers, optimal as well for non-mobile nutrient uptake, fits better in a supply driven environment, where plant water supply is mainly driven by in-season rainfalls.

Scaling of root architectures toward dynamic 1D sink terms allows to infer on relevant root structural traits required for drought resistant crops, while conserving modeling efficiency necessary to perform multi-location and multi-genotype analyses. Such ecohydrological application of root architecture models is therefore an important path to increase our understanding of plant–environment interactions and has to go along with the strengthening of physiological process representation in the current models. Beyond site hydrology and hydraulic root architecture, further model development for the assessment of plant water uptake efficiency should also take into account the dynamic and complex soil pore system.

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