Understanding plant rooting patterns in semi-arid systems: an integrated model analysis of climate, soil type and plant biomass

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ABSTRACT

Aim A consistent set of root characteristics for herbaceous plants growing in water-limited environments has been developed based on compilations of global root databases, but an overall analysis of why these characteristics occur is still missing. The central question in this study is whether an ecohydrological model which assumes that rooting strategies reflect maximization of transpiration can predict the variations in rooting strategies of plants in dry environments.

Location Arid ecosystems across the globe.

Methods A model was used to explore interactions between plant biomass, root–shoot allocation, root distribution, rainfall, soil type and water use by plants.

Results Model analyses showed that the predicted shifts in rooting depth and root–shoot allocation due to changes in rainfall, soil type and plant biomass were quite similar to observed shifts. The model predicted that soil type, annual rainfall and plant biomass each had strong effects on the rooting strategies that optimize transpiration, but also that these factors have strong interactive effects. The process by which plants compete for water availability (soil evaporation or drainage) especially affected the depth distribution of roots in the soil, whereas the availability of rainfall mainly affected the optimal root–shoot allocation strategy.

Main conclusions The empirically observed key patterns in rooting characteristics of herbaceous plant species in arid environments could be explained in this theoretical study by using the concept of hydrological optimality, represented here by the maximization of transpiration.

Keywords Arid, ecohydrology, growth strategy, model, optimization, root allocation, rooting depth, roots.

INTRODUCTION

Root systems play an important part in the global hydrological cycle by largely controlling the partitioning of water fluxes to the atmosphere and groundwater (Canadell et al., 1996). Roots determine the availability of water to individual plants, and in dry systems plant productivity often increases linearly with actual evapotranspiration (Rosenzweig, 1968; Chong et al., 1993). Actual water use by plants depends on local climate and edaphic factors, root strategies, plant vascular architecture and on the balance of above- and below-ground plant dimensions (West et al., 1999; Schenk & Jackson, 2002a). Despite a long history of study of the dynamics of root distributions, experimental knowledge of the determining processes remains inadequate.

Compilations of global root databases by Jackson et al. (1996) and Canadell et al. (1996), later updated by Schenk & Jackson (2002a,b, 2003), were used to establish relationships between climate, soil texture, vegetation type and vertical root distributions and maximum rooting depths. A consistent set of root characteristics for herbaceous plants growing in water-limited environments has been developed.

I. Herbaceous plants have larger root systems in dry climates than in wet climates (Schenk & Jackson, 2002a) and root–shoot
ratios increase with increasing aridity (Walter, 1963; Pallardy, 1981; Wilson, 1988; Chapin et al., 1993).

2. Root–shoot ratios decrease in soils richer in nutrients, i.e. where plants can attain higher productivity and higher biomass (e.g. Schenk & Jackson, 2002b).

3. In sandy soils a larger proportion of roots is present at greater depths than in loamy and clayey soils (Jackson et al., 1996; Schenk & Jackson, 2002b) and rather than shifting maximum rooting depths downwards as texture changes from fine to coarse, plants in water-limited environments may shift the zone of maximum root activity downwards in the profile.

4. With an increase in the wetness of the climate, plants produce deeper roots (Schenk & Jackson, 2002b).

These characteristics are quantified in Table 1 and Figure 1. The values are based on the ISLSCP II DAAC root database (http://daac.ornl.gov/; Schenk & Jackson, 2003) and the literature cited.

Recently, it has been proposed that vertical root distributions could be predicted from soil water infiltration and extraction patterns as a function of climatic variability, soil and vegetation characteristics. The central hypothesis in these analyses is that the observed consistent set of root characteristics in water-limited environments is a result of cost–benefit optimization by the plant. The goal that is maximized by the ‘optimal’ root distributions can be transpiration (van Wijk & Bouten, 2001; Collins & Bras, 2007) or carbon gain (Kleidon & Heimann, 1998; Schwinning & Ehleringer, 2001; Schymanski et al., 2009), or the goal to be achieved can be a minimization of energy expenditure for root construction and maintenance (Adiku et al., 1996, 2000).

Table 1

<table>
<thead>
<tr>
<th>Observed quantitative pattern</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>General observed rooting characteristics</td>
<td>• $D_{50}$ of herbs ranges from 0.20 m depth to a maximum depth of 0.78 m</td>
</tr>
<tr>
<td></td>
<td>• Root–shoot allocation varies between 0.1 and 0.5</td>
</tr>
<tr>
<td></td>
<td>• Rooting depth $D_{50}$ increases with 0.40 m</td>
</tr>
<tr>
<td></td>
<td>• $D_{50}$ increases from 0.20 m to up to 0.60 m</td>
</tr>
<tr>
<td></td>
<td>• Root–shoot allocation decreases from 0.5 to 0.3</td>
</tr>
<tr>
<td>Increase in precipitation from 200 to 500 mm</td>
<td>• Rooting depth $D_{50}$ increases up to 0.50 m when going from loam or clay soil to a sandy soil</td>
</tr>
<tr>
<td>Different soil types</td>
<td>• Root–shoot allocation in measured herbaceous species decreases from 0.5 to 0.2 with increasing nutrient availability</td>
</tr>
<tr>
<td>Nutrient availability</td>
<td>• Root–shoot allocation</td>
</tr>
</tbody>
</table>

Values and ranges based on the ISLSCP II DAAC root database (http://daac.ornl.gov/; Schenk & Jackson, 2003) and on literature cited. $D_{50}$ and $D_{95}$ are the soil depths above which, respectively, 50% and 95% of the root biomass is present.

Figure 1 Observed regression relationships between annual below-ground allocation of net primary production (BNNP) and annual rainfall for herbs in tropical savanna systems (a; Hui & Jackson, 2006) and rooting depth above which 95% of the root biomass is present ($D_{95}$) and annual rainfall (b; Schenk & Jackson, 2002b).
Each of the studies which tried to understand plant rooting characteristics by using models of the interactions between soil hydrology and rooting distributions focused on one or two of the four rooting patterns listed above (see Schwinning & Ehleringer, 2001; van Wijk & Bouten, 2001; Laio et al., 2006; Guswa, 2008; Himmelbauer et al., 2008; Schenk, 2008). However, a complete analysis of the interactions between productivity, root–shoot allocation, vertical root distribution, soil type and climate is still missing, while the list of key observations shows that there are strong interactions present: depending on soil type and climate, the observed root–shoot allocation and rooting patterns can change dramatically (Schenk & Jackson, 2002a,b, 2003).

In this study I present a model based on state-of-the-art soil hydrological concepts that can be used to explore interactions between plant biomass, root–shoot allocation, root distribution, rainfall, soil type and water use by plants. The focus in this study is on herbaceous plants to simplify the analysis of root–shoot allocation. In shrubs and trees the trunk plays a major structural role which is not linked to hydrology (e.g. competition for light or to prevent browsers eating the leaves) which would complicate this first analysis. The model was used to test whether the above-listed observations can be reproduced qualitatively and quantitatively using the hypothesis of hydrological optimality. Rooting characteristics were identified that maximized annual plant transpiration, which in an arid environment is a good proxy for plant productivity (Rosenzweig, 1968; Chong et al., 1993). Maximization of transpiration is furthermore assumed to be an important strategy for plants in arid environments as, in general, plants may maximize resource uptake, even if wasteful, to prevent these resources from becoming available to competitors (Cohen, 1970; Robinson et al., 1999). This is especially important for mobile resources like soil water, which are difficult for individual plants to monopolize (DeLucia & Schlesinger, 1991; Zea-Cabrera et al., 2006).

**MATERIALS AND METHODS**

**Model description**

A schematic representation of the model is given in Fig. 2 (e.g. Rodriguez-Iturbe & Porporato, 2004). The model is largely based on the model presented by Collins & Bras (2007), but has important additions in the description of the interactions between absolute root density and the effects of soil water stress on plant transpiration, thereby allowing a whole new type of analysis of the effects of root–shoot allocation, the results of which are presented in this study. The model is driven by rainfall and potential evapotranspiration (PET). For the description of the rainfall distribution we follow the approach of Collins & Bras (2007), in which the year is divided into two periods of 6 months, where one period is the dry season and one period is the rainy season. In this study 90% of the annual rainfall falls in the rainy season with a daily constant rainfall within a period. PET varies sinusoidally around the annual mean of 6 mm day\(^{-1}\) with an amplitude of 3 mm day\(^{-1}\). Rainfall is first intercepted by the plant canopy, in proportion to its leaf area index (LAI); the proportional factor used is 0.2 mm per unit of LAI. Rainfall that exceeds the canopy storage capacity continues as throughfall (TF). Settings are based on typical values for (semi)-arid environments (e.g. van Wijk & Rodriguez-Iturbe, 2002; Rodriguez-Iturbe & Porporato, 2004; Collins & Bras, 2007).

The soil water part of the overall model follows the Richards–Darcy type of soil hydrology model (e.g. Tikta & Bouten, 1992; Collins & Bras, 2007). Water enters the soil through infiltration. The infiltration rate is described as the minimum of three factors

\[
I = \min\left\{K_{sat}(\theta, -\theta_{top}) \frac{\Delta \theta}{\Delta t}, TF\right\}
\]

where \(I\) is the infiltration rate (m day\(^{-1}\)), \(K_{sat}\) is the saturated hydraulic conductivity (m day\(^{-1}\)), \(\theta\), is the saturated volumetric soil water content (m\(^3\) m\(^{-3}\)), \(\theta_{top}\) is the near-surface volumetric soil water content (m\(^3\) m\(^{-3}\)), \(\Delta z\) is the thickness of the layer (m; the value used in this study is 0.05 m), \(\Delta t\) is time (days) and TF is the throughfall rate (m day\(^{-1}\)). The fraction of TF not entering the soil is considered to be runoff, and leaves the system.

Once in the soil column, water is redistributed vertically through the Richards–Darcy equation

\[
\frac{d\theta}{dt} = -\frac{d}{dz}\left[K(h)\left(\frac{dh}{dz} + 1\right)\right]
\]

where \(\theta\) is the volumetric soil–water content (m\(^3\) m\(^{-3}\)), \(t\) is time (days), \(z\) is soil depth (m), \(h\) is the water pressure head (m) and \(K(h)\) is the hydraulic conductivity (m day\(^{-1}\)).

The \(K–\theta–h\) relations are described by the van Genuchten (1980) equations.
The variable $\alpha_1(\theta)$ represents the maximum efficiency when soil moisture availability is not limiting water uptake, and accounts for both local and non-local uptake efficiency limits. The maximum need not be unity even though the plant experiences no water stress. The non-local limit (the second term in equation 10) allows the more efficient deeper roots to preferentially take up water if soil moisture is roughly uniform (see Lai & Katul, 2000). The local limit (the first term) accounts for the ability of shallow roots to become more efficient during times of abundant near-surface moisture (for example, in the event of rapid soil wetting following a precipitation event), irrespective of deeper conditions (Collins & Bras, 2007).

The parameters that represent the soil water content below which soil water stress occurs ($\theta^*$) and the soil water content at wilting point ($\theta_w$; below this value of soil water content plants can no longer extract water from the soil) vary from soil layer to soil layer and depend on the absolute root density in a certain soil layer (de Jong van Lier et al., 2006). In the study of de Jong van Lier et al. (2006) numerical simulations of a detailed soil hydrology model were used to construct relationships between $\theta^*$, root density and PT. In recent research they applied this approach to $\theta_w$ as well (K. Metselaar, pers. comm.). A look-up table was constructed based on this recent work and the results presented in de Jong van Lier et al. (2006), adapted for the arid systems analysed in this study and the root densities that are observed in these systems. In the table absolute root density and PT determine $\theta^*$ and $\theta_w$; with increasing root density and increasing PT, the values of $\theta^*$ and $\theta_w$ decrease. In Fig. 3 the relationships between $\theta^*$ and $\theta_w$ and the root length density in a certain layer are given for a PET of 6 mm day$^{-1}$. The complete look-up table is given in Appendix S1 in Supporting Information.

The root length density in each layer is determined by the vertical root distribution function, the specific root length and the total root biomass. Total root biomass (in kg C m$^{-2}$) is calculated by multiplying total plant biomass by 1 minus the shoot–root allocation factor. We will use two values for total plant biomass, 0.75 and 1.25 kg C m$^{-2}$, to represent two levels of soil fertility and therefore plant productivity. The relative vertical distribution of the roots follows the approach of Schenk & Jackson (2002b):

$$Y(z) = \frac{1}{1 + \left(\frac{z}{D_{30}}\right)^c}$$

where $Y$ is the cumulative fraction of total root biomass between the soil surface and depth $z$, $D_{30}$ is the depth above which 50% of the root biomass is located and $c$ is a shape parameter, which is determined by

$$c = \frac{2.94}{\ln(D_{30}/D_0)}$$

where

$$\alpha_1(\theta(z)) = \frac{\theta(z) - \theta_w}{\theta^* - \theta_w} \quad \text{if} \quad \theta_w \leq \theta(z) \leq \theta^*$$

and

$$\alpha_1(\theta(z)) = 1 \quad \text{if} \quad \theta^* < \theta(z).$$
where $D_{95}$ is a parameter, with $Y = 0.95$ if $D_{95} = z$. By combining the total root biomass, equations 12 and 13 and a specific root length value of 2.0 cm kg$^{-1}$ (van Wijk et al., 2003) the root density per soil layer can be calculated. Soil layers with a thickness of 5 cm were used in the model.

Model analysis

In this study the effects of different plant rooting strategies on the total annual transpiration were quantified, and strategies were identified that maximized this annual transpiration. The model parameters that represent different rooting strategies are the shoot–root allocation parameter (which determines how many roots are present given a certain amount of biomass) and the parameters $D_{50}$ and $D_{95}$ that determine the root distribution in the soil. The effects of soil type, rainfall and plant biomass on transpiration and the optimal values of the rooting strategy parameters were quantified. In this study increased plant biomass is used as a proxy for the effect of increased nutrient richness under the same hydrological conditions. Three different soil types were analysed: a clay soil, a loamy soil and a sandy soil. The standard parameter values capturing the physical characteristics of these soils are presented in Table 2 (e.g. Collins & Bras, 2007). In the analysis the model was run for 10 years for a range of values for annual rainfall (200, 300, 400 and 500 mm) and for different values for plant biomass (0.75 and 1.25 kg C m$^{-2}$), the shoot–root allocation factor and the parameters $D_{50}$ and $D_{95}$. The first 5 years were not used for the analysis in order to remove any initialization effects and average annual values of transpiration, evaporation and drainage were calculated for the last 5 years of each model run.

RESULTS

Components of the water balance

The different components of the water balance after optimization of the rooting strategy showed strong differences between soil types and for different values of annual rainfall (Table 3). At low rainfall, drainage was small in all soil types. In the sandy soil in particular drainage increased strongly with increasing rainfall. In absolute amounts soil evaporation increased equally for all three soil types, but in relative terms this increase was largest for the clay soil. Transpiration increased for all soils with increasing rainfall, but transpiration in the clay and loamy soils was always higher than in the sandy soil. These results showed that with increasing rainfall the relative distribution of the rainfall over the different components of the water balance differed strongly between soil types (Table 3). Y early transpiration values presented in Table 3, obtained by identifying the parameter settings of root–shoot allocation, $D_{50}$ and $D_{95}$, are in general about 30 mm higher than would have been obtained with an overall average setting, using a root–shoot allocation value of 0.5, a $D_{50}$ of 0.3 m and $D_{95}$ of 0.7 m. The sensitivity of the simulated transpiration to changes in the different parameter settings is further explored in Figures 4–7.

Shoot–root allocation

The amount of transpiration achieved by the plant was strongly affected by the shoot–root allocation (Fig. 4). Plant transpiration increased with increasing plant biomass and was lowest for a sandy soil and highest for a clay soil. The shoot–root allocation value that resulted in the maximum annual amount of transpiration depended on total plant biomass and type of soil for a given amount of rainfall (300 mm for Fig. 4). The optimal value for shoot–root allocation increased with plant biomass and was highest for a clay soil and lowest for a sandy soil. The simulated values of the optimal shoot–root allocation are similar to what has been observed in reality: for herbaceous plant species in arid environments allocation to shoot is normally substantially

Figure 3 Relationships used in the model between root length density and the water uptake parameters $\theta^*$ (a; the soil water content below which water stress occurs) and $\theta_*$ (b; the soil water content below which transpiration is zero) for a sandy soil, a loamy soil and a clay soil.
larger than allocation to root (Table 1). Also the range of the
response of shoot–root allocation to an increase in productivity
is similar to what has been observed in the field: the observed
value was a change in root–shoot ratio of 0.3 (from around 0.5
to 0.2), whereas the model at low productivity predicts a change
of about 0.25. The results of the model showed that this change
is strongly dependent on soil type, which is a feature that can be
tested in more detail with the appropriate field measurements.

Not surprisingly, an increase in annual rainfall resulted in an
increase in annual transpiration (Fig. 5). Annual rainfall also
strongly affected the optimal shoot–root allocation: an increase
in annual rainfall led to an increase of the shoot–root allocation
value that maximized transpiration, independent of soil type.
The predicted change of about 0.2 in shoot–root allocation for a
sandy soil is roughly similar to what has been observed in the
field (Table 1, Fig. 2), but the absolute values of the shoot–root
allocation are higher than has been observed for herbs in dry
savanna systems as reported by Hui & Jackson (2006). Their
below-ground annual allocation values range from 0.6 to 0.4,
whereas the model predicts for sandy soils a below-ground
steady-state allocation between 0.45 and 0.2. As shown earlier in
Fig. 4, and also in the results presented in Fig. 5 for a given plant
biomass, soil type strongly influenced the optimal shoot–root
allocation, with the lowest optimal shoot–root allocation occur-
ing in sandy soils and the highest in clay soils.

**Vertical root distribution**

Annual plant transpiration was not only affected by annual rain-
fall, plant biomass and soil type, but also by the vertical distri-

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**Table 2** Parameter description and the values used in the study.

<table>
<thead>
<tr>
<th>Parameter Name</th>
<th>Description</th>
<th>Clay soil</th>
<th>Loamy soil</th>
<th>Sandy soil</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \theta_r ) (m(^3) m(^{-3}))</td>
<td>Residual soil water content</td>
<td>0.01</td>
<td>0.01</td>
<td>0.02</td>
</tr>
<tr>
<td>( \theta_s ) (m(^3) m(^{-3}))</td>
<td>Saturated soil water content</td>
<td>0.59</td>
<td>0.42</td>
<td>0.46</td>
</tr>
<tr>
<td>( K_{sat} ) (m day(^{-1}))</td>
<td>Saturated hydraulic conductivity</td>
<td>0.05</td>
<td>0.13</td>
<td>0.15</td>
</tr>
<tr>
<td>( \pi ) (–)</td>
<td>Porosity</td>
<td>1.11</td>
<td>1.44</td>
<td>1.53</td>
</tr>
<tr>
<td>( \alpha ) (m(^{-1}))</td>
<td>Scaling parameter in equation 4</td>
<td>1.95</td>
<td>0.84</td>
<td>1.44</td>
</tr>
<tr>
<td>( \lambda ) (–)</td>
<td>Scaling parameter in equation 5</td>
<td>−5.90</td>
<td>−1.50</td>
<td>−0.22</td>
</tr>
<tr>
<td>( \theta_h ) (m(^3) m(^{-3}))</td>
<td>Hygroscopic soil water content</td>
<td>0.42</td>
<td>0.15</td>
<td>0.10</td>
</tr>
<tr>
<td>( \theta_s ) (m(^3) m(^{-3}))</td>
<td>Soil water content at field capacity</td>
<td>0.45</td>
<td>0.25</td>
<td>0.25</td>
</tr>
<tr>
<td>( \theta_{w,min} ) (m(^3) m(^{-3}))</td>
<td>Minimum value of wilting point soil water content</td>
<td>0.22</td>
<td>0.08</td>
<td>0.06</td>
</tr>
<tr>
<td>( \theta_{w,max} ) (m(^3) m(^{-3}))</td>
<td>Maximum value of wilting point soil water content</td>
<td>0.30</td>
<td>0.13</td>
<td>0.09</td>
</tr>
<tr>
<td>( \theta^{*}_{min} ) (m(^3) m(^{-3}))</td>
<td>Minimum value of soil water content at which water stress starts</td>
<td>0.38</td>
<td>0.10</td>
<td>0.06</td>
</tr>
<tr>
<td>( \theta^{*}_{max} ) (m(^3) m(^{-3}))</td>
<td>Maximum value of soil water content at which water stress starts</td>
<td>0.45</td>
<td>0.15</td>
<td>0.15</td>
</tr>
</tbody>
</table>

**Table 3** Most important components of annual water balance for different amounts of rainfall and soil types using values for shoot–root allocation, \( D_{50} \) and \( D_{95} \) that maximize transpiration and a plant biomass of 1.25 kg m\(^{-2}\).

<table>
<thead>
<tr>
<th>Rainfall (mm year(^{-1}))</th>
<th>Soil type</th>
<th>Transpiration (mm year(^{-1}))</th>
<th>Evaporation (mm year(^{-1}))</th>
<th>Drainage (mm year(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>200</td>
<td>Sand</td>
<td>106</td>
<td>24</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Loam</td>
<td>139</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Clay</td>
<td>146</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>300</td>
<td>Sand</td>
<td>144</td>
<td>39</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Loam</td>
<td>202</td>
<td>12</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Clay</td>
<td>203</td>
<td>17</td>
<td>1</td>
</tr>
<tr>
<td>400</td>
<td>Sand</td>
<td>181</td>
<td>52</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>Loam</td>
<td>264</td>
<td>20</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Clay</td>
<td>265</td>
<td>27</td>
<td>1</td>
</tr>
<tr>
<td>500</td>
<td>Sand</td>
<td>223</td>
<td>69</td>
<td>69</td>
</tr>
<tr>
<td></td>
<td>Loam</td>
<td>337</td>
<td>28</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Clay</td>
<td>352</td>
<td>37</td>
<td>1</td>
</tr>
</tbody>
</table>

Values presented are average values of the last 5 years of a 10-year simulation. The difference between rainfall and the sum of the components shown disappears from the system through interception and run off. \( D_{50} \) and \( D_{95} \) are the soil depths above which, respectively, 50% and 95% of the root biomass is present.


The distribution of the roots. The two root shape parameters ($D_{50}$ and $D_{95}$) have a clear effect on transpiration, with soil type again being a strong interacting factor (Fig. 6). For a given amount of rainfall (300 mm in Fig. 6) the value of the $D_{50}$ parameter (representing the depth of the most active roots in terms of water uptake) that maximized transpiration increased with increasing plant biomass for the sandy soil and increased slightly for the loamy soil. No effect of plant biomass was visible for the clay soil. The optimal $D_{50}$ value was larger for sandy and loamy soils than for the clay soil.

**Figure 4** Annual plant transpiration for different shoot–root allocation values and two different plant biomasses in a sandy soil (a), a loamy soil (b), and a clay soil (c). Rainfall was 300 mm in these simulations and optimal values for $D_{50}$ and $D_{95}$ (the depths above which 50 and 95%, respectively, of the root biomass is located) were used (see Figs 6 & 7).

**Figure 5** Annual plant transpiration for different shoot–root allocation values and amounts of annual rainfall in a sandy soil (a), a loamy soil (b), and a clay soil (c). Plant biomass in these simulations was 0.75 kg C m$^{-2}$ and optimal values for $D_{50}$ and $D_{95}$ (the depths above which 50 and 95%, respectively, of the root biomass is located) were used (see Figs 6 & 7).
The optimal value of $D_{50}$ is also strongly influenced by rainfall: increasing amounts of rainfall resulted in an increase in $D_{50}$ for the sandy soil (Fig. 7), together with an increase in $D_{95}$ representing an increase in rooting depth. The $D_{50}$ parameter showed the strongest response to annual rainfall in the sandy soil, but for the loamy soil the optimal $D_{50}$ value also increased with rainfall. In the clay soil rainfall did not affect the optimal value of $D_{50}$ in the clay soil the model predicted that a shallow rooting pattern would maximize transpiration in a clay soil. The model results for the sandy soil roughly coincide with the observed ranges of $D_{50}$ and $D_{95}$ (Table 1). The observed changes in $D_{50}$ due to increasing rainfall (between 200 and 500 mm of rain) $D_{50}$ increases from 0.35 to 0.7 m according to the regression relationship found by Schenk & Jackson, 2002b is similar to the predictions of the model for sandy soils (Fig. 7): an increase from 0.3 to 0.7 m with rainfall ranging from 200 to 500 mm.
DISCUSSION

The results showed that soil type, annual rainfall and plant biomass have strong effects on the rooting strategies that optimize transpiration and that the interactions between these factors are key to understanding the observed variations in rooting patterns. The model system presented in this study, in combination with the hypothesis of maximization of transpiration, could explain the observed key patterns in rooting characteristics of herbaceous plant species. The model predicted shifts in the rooting characteristics due to a gradient in environmental conditions which were roughly similar to the observed general shifts. With the model, the effects of soil type, soil fertility and rainfall on rooting characteristics could be disentangled, and using these model results targeted measurements can be collected for specific sites for which the model and the optimality approach can be tested in more detail. This is essential to be able to assess more clearly under which conditions the optimality approach will or will not work.

Earlier studies focused on one or two of the four observed patterns, but no study has been published until now in which all four patterns have been explained using one integrated analysis. This Discussion is structured around the four observed rooting patterns mentioned in the Introduction and each will be considered. This is then followed by an overall assessment of the approach and the insights that came out of the analyses.

The first observed characteristic was that herbaceous plants have larger root systems in dry climates than in wet climates and root–shoot ratios increase with increasing aridity. The model analyses showed that the concept of transpiration maximization can be used to explain this pattern (Fig. 4) and the model produced similar relative changes in root–shoot ratios to those that have been observed in reality (Hui & Jackson, 2006). The study of Hui & Jackson (2006) is the only one that gives a quantitative relationship between carbon root–shoot allocation and rainfall, but it is difficult to link observed annual below-ground allocation of net primary production directly to the steady state root–shoot allocation values produced in that study, because root turnover can be different from shoot turnover, with strong consequences for observed root and shoot biomass. It is certainly encouraging for the current study that the relative change in predicted below-ground allocation is similar, as has been observed for herbs in tropical savanna systems. The explanation of the shift in root–shoot allocation with increasing rainfall links up with the basic theory that plants optimize their allocation of biomass in such a way that capture of the most limiting resource is maximized: typically plants respond to a decrease in above-ground resources with increased allocation to shoots (leaves) or to a decrease in below-ground resources with increased allocation to roots (Mäkelä & Sievänen, 1987; Thornley, 1995). As rainfall becomes available to the plants by its infiltration into the soil, it also represents a below-ground resource and therefore the observed characteristics agree with this theory. In this study the same pattern was produced by our modelling system only looking at the hydrological component of the system. Until now this pattern had received little attention in traditional hydrological models because in these models root distributions are only presented as relative distributions in depth, and absolute root densities are not taken into account (e.g. van Wijk & Bouten, 2001; Laio et al., 2006; Collins & Bras, 2007; Schenk, 2008). Only recently have relationships been established between the widely used soil water stress parameters $\theta^*$ (the soil water content below which soil water stress starts occurring) and $\theta_w$ (the soil water content below which soil water can be taken up by the plants) and absolute rooting densities (de Jong van Lier et al., 2006). By incorporating these results in the model presented in this study (see Fig. 3) a new type of analysis could be performed and the effects of the interactions between plant biomass, climate and soil type on rooting strategies could be explored more comprehensively than could be done before.

The second observed characteristic was that root–shoot ratios decrease in richer soils, i.e. where plants can attain higher productivity and higher biomass. The results of Fig. 4 clearly showed this pattern. This characteristic has been studied in detail in the past (e.g. Poorter & Nagel, 2000) and a range of modelling approaches have reproduced the observed pattern (Thornley, 1972, 1995, 1998; Mäkelä & Sievänen, 1987; Cannell & Dewar, 1994; van Wijk et al., 2003). The results of this study showed that both increased productivity (resulting in higher plant biomass) and increased rainfall, independently of each other, result in lower root–shoot allocation, although in the field increased rainfall and productivity will often be correlated. With higher plant biomass and lower root allocation values there is already no further positive effect on root water uptake with increasing the number of roots. In that case it is more efficient for the goal of maximizing transpiration to increase above-ground biomass allocation to increase transpiration demand.

The third observation was that in sandy soils a larger proportion of roots is present at deeper depths than in loamy and clayey soils, and rather than shifting maximum rooting depths downwards as texture changes from fine to coarse, plants in water-limited environments may shift the zone of maximum root activity downwards in the profile. This study showed that in soils with a relatively high hydraulic conductivity (like sandy soils) plant transpiration competes especially with drainage, whereas in soils with a relatively low conductivity (like clay soils) plant transpiration competes especially with soil evaporation. To maximize transpiration it is preferable in a fine soil to have a relatively high proportion of the roots in the upper soil layers, whereas in coarser soils the roots shift downwards as water moves more quickly downwards through the profile. This was observed in earlier hydrological studies (e.g. Collins & Bras, 2007) but not in a study in which the number of roots was varied as well. With increasing coarseness of the soil both root–shoot allocation and the depth of root allocation increase (see Figs 4 & 6).

The fourth observation was that with an increase in the wetness of the climate plants produce deeper roots. This was shown for a sandy soil in Fig. 7, and the simulated changes in rooting depth with an increase in annual rainfall coincide well with observed values (Figs 2 & 7). The pattern of deeper roots with increased rainfall can be explained by the shift in the importance of water losses from the system through either evaporation or
drainage (see Table 3). With low amounts of rainfall drainage is less important than evaporation, and plants allocate their roots in the upper soil layers to be able to best compete with this process. With increasing rainfall, drainage increases more rapidly than evaporation (Table 3), and in order to capture as much of the water as possible as it moves through the soil column it is optimal for the plant to redistribute its roots to deeper soil layers. This response of root distribution to increases in rainfall is similar to the response to increasing coarseness of the soil, as the competition between the different systems via which water is lost from the system (transpiration, evaporation and drainage) changes in a similar manner.

The integrated analysis showed that for understanding plant root strategies a combined hydrological and plant response analysis was helpful. The focus of this study was on explaining general rooting patterns rather than on exact prediction of observed root distributions in a certain location, and the model system used was capable of that. The model analyses quantified the interactions between soil type and amount of rainfall, and showed that these determine the process with which plants have to compete in terms of water use, i.e. soil evaporation or drainage. This competition strongly affected which vertical root distribution in the soil was optimal in terms of maximization of transpiration. The interaction between amount of rainfall and soil type also explained differences in root–shoot allocation between soil types, whereas changes in the amount of rainfall caused shifts in these root–shoot allocation patterns: increases in rainfall resulted in a decrease in root–shoot allocation. This study showed that the concept of hydrological optimality, represented here by maximization of transpiration, can help to explain differences in observed rooting characteristics, although other factors like nutrients and plant stability should not be ignored and can be determining factors, even in arid systems (e.g. van Wijk & Bouten, 2001; van Wijk et al., 2003). Furthermore, in this study competition between plants was only taken into account implicitly in the assumption of maximization of transpiration. No direct effects of root competition on the availability of soil water for a plant with a specific rooting strategy in the presence of a species with another rooting strategy was taken into account, although it was shown in earlier studies that it can be a key factor as well (e.g. van Wijk & Bouten, 2001; van Wijk & Rodriguez-Iturbe, 2002; Schenk, 2006; van Wijk, 2007; Novoplansky, 2009). The focus in this study was on herbaceous plants to simplify the analysis of root–shoot allocation, and the analysis showed that the concept of maximization of transpiration can be used successfully to explain observed characteristics. In follow-up studies shrubs and trees can now also be analysed, although the model set-up needs to be more complex to be able to take into account the role of the trunk and of branches. A potentially interesting approach for doing this is the pipe theory, which states that sapwood area is proportional to foliage area and also to root characteristics like root length or biomass (e.g. Shinozaki et al., 1964a,b; Mäkelä, 2002). By playing with the factor that determines the proportionality of leaf area and root length with sapwood area, optimal tree or shrub dimensionalities in different hydrological settings can be explored.

One element in the current model is under discussion, and that is the assumption that deeper roots take up water more efficiently than shallow roots. In this model study I followed the description of Lai & Katul (2000), who based their approach on the study of Taylor & Klepper (1973), but the debate is ongoing as to whether this difference in efficiency is really present or not, or whether the reverse is actually the case, i.e. that shallow roots are more efficient in taking up water that deeper roots. This is an important issue for studying root water uptake in (semi-)arid systems because the depth uptake pattern when water is freely available will affect the depth distribution of water availability under dry conditions, and therefore the optimality of certain root distributions. Some studies indicate that roots preferentially take up water from shallow layers if water is available there (Green & Clothier, 1995; Huang et al., 1997; Nippert & Knapp, 2007), although other studies suggest higher hydraulic conductivities in deeper roots, thereby resulting in more efficient deep roots (Wan et al., 1994; McElrone et al., 2004). This debate is typically a research area where modelling and field measurements can be complementary: in measurements it is difficult to disentangle the effects of differences in water distribution and rooting density on the depth distribution of root water uptake. When measurements are combined with an ecohydrological model it should be possible to identify when and where there are differences in root water uptake efficiencies, and what the effects of these differences are on water use in the whole plant.

By incorporating the consequences of changes in root density (see Fig. 3) on key plant/soil hydrological parameters, a whole new range of analyses is possible in which current theories of soil water movement and plant growth are combined and the consequences of certain rooting strategies during plant growth can be explored. In similar ecohydrological studies, the focus until now has been on explaining relative root distributions, which is a powerful way of representing rooting patterns but has the limitation of being in principle a static description of the system. Representation of a growing plant is difficult in such a model system. In the model system described in this study such a representation is easy, and the effects on the soil water ‘harvesting’ capacity of a plant of increasing root densities during plant growth can be studied. Modelling the competition for water between individual plants (of, for example, different plant types) is also an interesting topic for studying the trade-offs between plant growth strategies in a harsh, water-driven, environment (e.g. van Wijk & Bouten, 2001; Violle et al., 2009).

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REFERENCES


**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Look-up table used for quantifying the effect of the rooting length density on $q^*$.

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**BIOSKETCH**

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