



Plant rooting strategies in water-limited ecosystems

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[1] Root depth and distribution are vital components of a plant's strategy for growth and survival in water-limited ecosystems and play significant roles in hydrologic and biogeochemical cycling. Knowledge of root profiles is invaluable in measuring and predicting ecosystem dynamics, yet data on root profiles are difficult to obtain. We developed an ecohydrological model of environmental forcing, soil moisture dynamics, and transpiration to explore dependencies of optimal rooting on edaphic, climatic, and physiological factors in water-limited ecosystems. The analysis considers individual plants with fixed biomass. Results of the optimization approach are consistent with profiles observed in nature. Optimal rooting was progressively deeper, moving from clay to loam, silt and then sand, and in wetter and cooler environments. Climates with the majority of the rainfall in winter produced deeper roots than if the rain fell in summer. Long and infrequent storms also favored deeper rooting. Plants that exhibit water stress at slight soil moisture deficiencies consistently showed deeper optimal root profiles. Silt generated the greatest sensitivity to differences in climatic and physiological parameters. The depth of rooting is governed by the depth to which water infiltrates, as influenced by soil properties and the timing and magnitude of water input and evaporative demand. These results provide a mechanistic illustration of the diversity of rooting strategies in nature.

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1. Introduction

[2] Plants rely on soil moisture as their primary source of water. Growth, reproduction, and survival depend on plants' abilities to absorb sufficient water through their root systems [Lee and Lauenroth, 1994; Lynch, 1995], which is of paramount importance in water-limited ecosystems [Nobel, 2002]. What constitutes an adequate root system depends on the spatial and temporal variability of the soil moisture resource, which is driven by climatic forcing and regulated by the soil. Depth and distribution of plant roots varies greatly among biomes and life-forms [Jackson *et al.*, 1996]. Among water-limited ecosystems, roots tend to be deeper in coarser soils [Kramer, 1983] and in climates that are cooler, wetter, or whose wet season occurs during winter [Schenk and Jackson, 2002a]. However, the deepest roots are found in arid environments and those with a long dry season [Canadell *et al.*, 1996]. Where water is limiting, root penetration has been related to the depth of infiltration and intensity of evaporative demand [Noy-Meir, 1973; Schenk and Jackson, 2005; Weaver, 1920].

[3] Roots play a critical role in the hydrologic cycle, nutrient cycling, and carbon sequestration. Rooting depth is an important parameter in general circulation models [Desborough, 1997; Zeng, 2001], regulating evapotranspi-

ration. Roots are also the intermediaries between transpiration demand and the supply of groundwater and stream flow. Soil nutrients and microorganisms are intimately tied to the physical and biochemical environment provided by roots [Farrar *et al.*, 2003; Holden and Fierer, 2005; Jobbágy and Jackson, 2001]. Root distributions are susceptible to land use and climate change, as well as being a key component in associated ecosystem changes [Jobbágy and Jackson, 2004; Schenk and Jackson, 2002b].

[4] Understanding and predicting ecosystem roles in current and changing hydrologic and biogeochemical cycles requires detailed knowledge of rooting distributions, including how they may change in the future. This study offers mechanical insight into the nature of root distributions in water-limited ecosystems using a physically based model to explore the interaction of plants and their environment, expanding on the work of Collins and Bras [2005]. A simpler but similar analytical model was recently presented by Laio *et al.* [2006]. Models offer a means to test our assumptions, to conduct controlled experiments at a detail impossible to achieve in nature, and to generate new hypotheses. This study emphasizes the ecohydrological facets of the soil-plant-atmosphere system rather than the physiological, paying attention to the influence climate and soil have on the development of root systems. Because root distributions may be seen as a reflection of plants' survival strategies, optimization concepts are used to infer how climatic and edaphic factors contribute to the proliferation of rooting strategies.

2. Model Description

[5] A one-dimensional ecohydrological model of the coupled soil-plant system was developed (Figure 1) [Collins,

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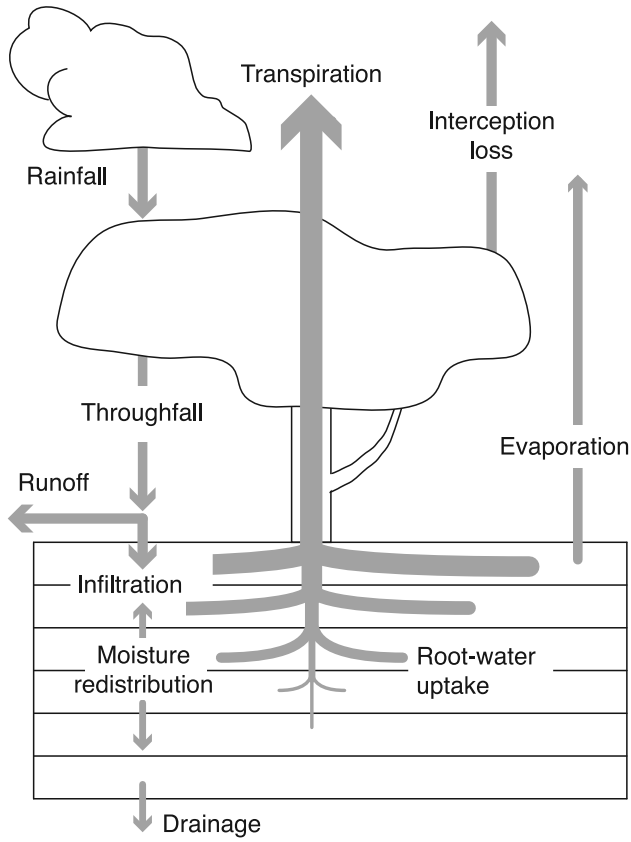


Figure 1. Schematic representation of the one-dimensional model's hydrological fluxes. Stochastic rainfall is partitioned between interception and throughfall. Throughfall is partitioned between runoff and infiltration, and soil moisture is redistributed with Richards equation. Gravity drainage occurs across the bottom of the soil column. Evaporation from the soil surface and plant-water uptake are functions of soil moisture, evaporative demand, and root distribution.

2006]. The model is similar to that used in the work of *Small* [2005]; the major difference is the degrees of freedom granted the vertical root profile. The model is driven by stochastic rainfall [Eagleson, 1978], which is either aseasonal or biseasonal, and potential evapotranspiration (PET). If the latter, mean annual precipitation (P_a) is divided between the two seasons as follows: f denotes the fraction that falls in the wet season, Δt_w is the duration of the wet season, and T_w marks the start of the wet season (Figure 2); PET varies sinusoidally about the annual mean with an amplitude of 3 mm/day. Rainfall is first intercepted by the plant foliage, in proportion to the leaf area index (LAI), which is fixed in time. One millimeter of canopy water storage is used, along with an LAI of 1 as a central value for the environments considered [Breuer et al., 2003]. Rainfall that exceeds the foliage storage capacity continues as throughfall to be partitioned at the ground surface between runoff and infiltration. Runoff is lost from the system.

[6] Infiltration rate is expressed as the minimum of three factors as follows:

$$I = \min \left\{ K_s, (n - \theta_{top}) \frac{\Delta z}{\Delta t}, TF \right\} \quad (1)$$

where K_s is the saturated hydraulic conductivity, n is soil porosity, θ_{top} is the near-surface volumetric soil water content, Δz is the thickness of the layer, and TF is the throughfall rate.

[7] Once in the soil column, water is redistributed vertically following Richards equation as follows:

$$\frac{d\theta}{dt} = \frac{\partial}{\partial z} \left[K(\psi) \frac{\partial \psi}{\partial z} - K(\psi) \right] \quad (2)$$

where θ is the volumetric soil-water content, t is time, z is the soil depth, ψ is the matric potential, and $K(\psi)$ is the hydraulic conductivity. The solution follows an explicit, finite difference method over the 3.5-m soil column, divided into 5-cm layers. Water retention and hydraulic conductivity are specified by the model of *van Genuchten* [1980], with parameters from the work of *Leij et al.* [1999], as follows:

$$S_e = \frac{\theta - \theta_r}{n - \theta_r} = (1 + [\alpha_{vg} h]^\nu)^\mu \quad (3)$$

$$K(\theta) = K_{sat} \sqrt{S_e} \left(1 - [1 - S_e^{1/\mu}]^\mu \right)^2 \quad (4)$$

where θ_r is the residual volumetric soil water content, n is porosity, α_{vg} , ν , and μ are parameters in the van Genuchten model, h is the soil water pressure head in centimeters, and K_{sat} is the saturated hydraulic conductivity. Gravity drainage occurs across the lower boundary. No groundwater table is considered in these simulations, though, when present, it has quite significant effects on plant behavior [e.g., *Nepstad et al.*, 1994; *Oliveira et al.*, 2005].

[8] Between storms, Richards equation is coupled to evapotranspiration. The instantaneous PET is partitioned between canopy and soil [Ritchie, 1972] as follows:

$$PET_{canopy} = PET (1 - e^{-\sigma LAI}) \quad (5)$$

$$PET_{soil} = PET - PET_{canopy} \quad (6)$$

where σ is 0.4. The fraction applied to the foliage first acts to evaporate any intercepted water, the remainder to trans-

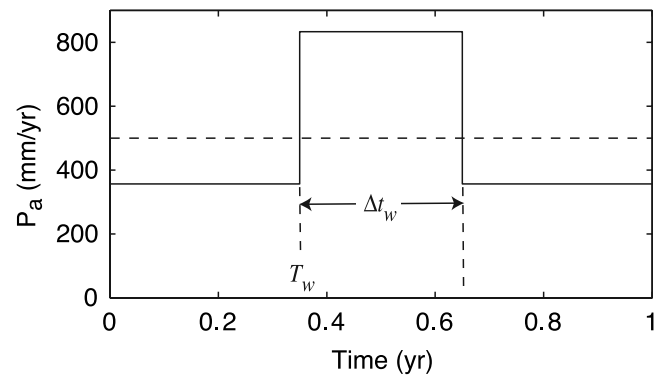


Figure 2. Instantaneous rainfall rates for nonseasonal and seasonal climates. $P_a = 500$ mm/year, $\Delta t_w = 0.3$, $f_w = 0.5$, and $T_w = 0.35$.

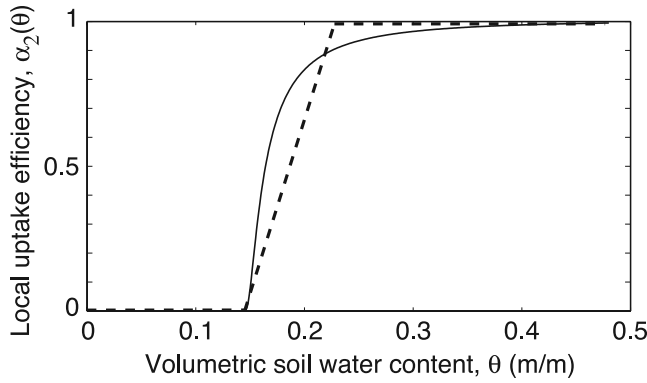


Figure 3. Comparison of the local root water uptake efficiency models ($\alpha_2(\theta)$) of *Lai and Katul* [2000] (continuous) and *Rodriguez-Iturbe et al.* [2001a] (dashed) for silt, ψ_w of -4 MPa, ψ^* of -170 MPa, and γ of 0.05 . From the work of *Lai and Katul* [2000], $\alpha_2(\theta) = \left(\frac{\theta}{n - \theta_w}\right)^{\gamma/(\theta - \theta_w)}$.

piration. The fraction of PET applied to the soil acts to drive evaporation from the uppermost soil layer [*Kurc and Small*, 2004]. Timesteps vary to optimize numerical calculations, but are always a day or less.

[9] Plant transpiration (T) is the sum of water taken up by roots throughout the soil column. The uptake from each layer is the product of two root efficiency terms, $\alpha_1(\theta)$ and $\alpha_2(\theta)$, the fraction of total root mass present in the layer, $g(z)$ ($\int_0^L g(z) dz = 1$), and the PET available to drive transpiration [*Lai and Katul*, 2000; *Rodriguez-Iturbe et al.*, 2001a] as follows:

$$T(t) = \int_0^L \alpha_1(\theta(z)) \alpha_2(\theta(z)) g(z) PET_{canopy} dz \quad (7)$$

$$\alpha_1(\theta(z)) = \max \left\{ \frac{\theta(z)}{n - \theta_w}, \frac{\int_0^z \theta(z') dz'}{\int_0^L \theta(z') dz'} \right\} \quad (8)$$

$$\alpha_2(\theta(z)) = \begin{cases} 0 & \theta(z) \leq \theta_w \\ \frac{\theta(z) - \theta_w}{\theta^* - \theta_w} & \theta_w < \theta(z) \leq \theta^* \\ 1 & \theta^* < \theta(z) \end{cases} \quad (9)$$

where L is the depth of the entire soil column and z is the depth of an individual soil layer. The compound representation of uptake efficiency is derived from the work of *Lai and Katul* [2000], though we replace their model of α_2 by the expression from the work of *Rodriguez-Iturbe et al.* [2001a], which is more widely used and accepted, and explicitly treats the two plant physiological parameters ψ_w and ψ^* corresponding to the volumetric water contents of θ_w and θ^* , respectively. The replacement is unlikely to produce substantial differences because the two models have similar forms (Figure 3).

[10] The parameter $\alpha_1(\theta(z))$ represents the maximum efficiency when soil moisture availability is not limiting water uptake and accounts for both local and nonlocal uptake efficiency limits. The maximum need not be unity even though the plant experiences no water stress. The

nonlocal limit [the second term in equation (8)] allows the more efficient deeper roots to preferentially take up water if soil moisture is roughly uniform. The local limit (the first term) accounts for the ability of shallow roots to become more efficient during times of abundant near-surface moisture, irrespective of deeper conditions. Whether to model these compensatory effects, and in what manner, is controversial [e.g., *Guswa*, 2005; *Laio et al.*, 2006], but it is important to recognize their role in altering soil moisture dynamics [*Teuling et al.*, 2006].

[11] $\alpha_2(\theta(z))$ represents root “shut down” as a function of soil moisture. θ_w is the wilting point or water content for 100% cavitation. As the soil dries, the onset of water stress occurs at θ^* . Plant stress ξ is modeled after the work of *Porporato et al.* [2001] as

$$\xi = \int_0^L [1 - \alpha_2(\theta(z))] g(z) dz \quad (10)$$

[12] A final constraint is placed on uptake efficiency ensuring $\int_0^L \alpha_1(\theta(z')) \alpha_2(\theta(z')) dz' \leq 1$. In the unlikely case where the model produces such an outcome, the product at each soil layer is scaled by the same amount so that the constraint is met.

[13] To visualize the relationships between soil moisture and both transpiration and plant stress, Figure 4 illustrates

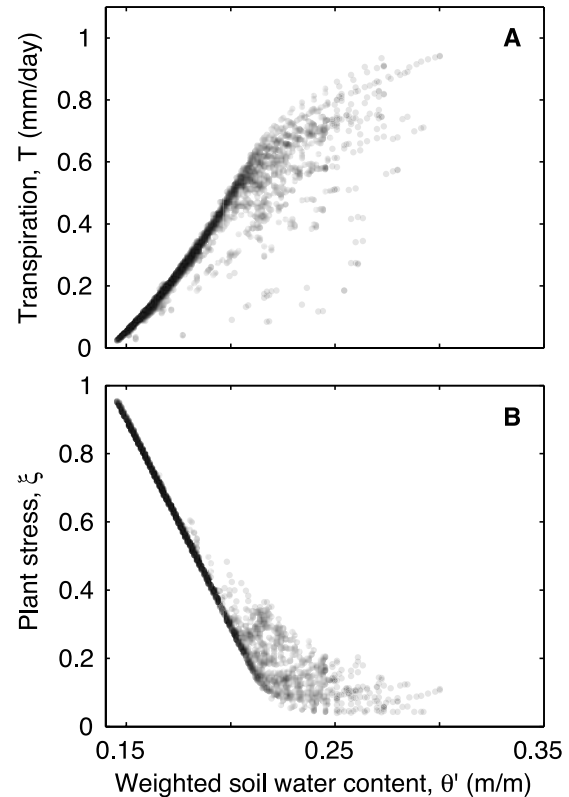


Figure 4. (a) Total transpiration and (b) Total plant stress for different soil water contents weighted by local root density ($\theta' = \int_0^L g(z) \theta(z) dz$). The data span 5 years of a nonseasonal simulation with silt soil: P_a of 500 mm/year, PET of 4 mm/day, ψ_w of -4 MPa (θ_w of 0.14), ψ^* of -170 MPa (θ^* of 0.23), D_{50} of 15 cm, and D_{95} of 40 cm. Darker regions indicate more frequent occurrence.

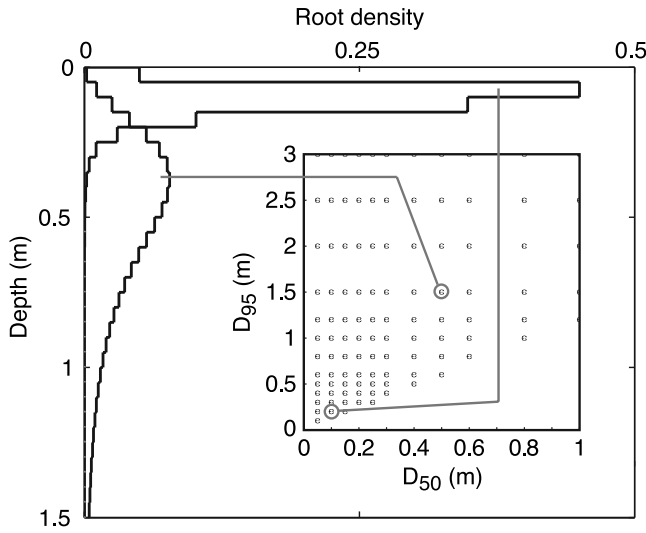


Figure 5. Two vertical root profiles showing the fraction of total roots in each 5-cm soil layer, following the LDR model [Schenk and Jackson, 2002b] sampled from the D_{50} - D_{95} state-space explored by the simulations (inset).

the state variables across 5 years. Volumetric water content is weighted by root density and is denoted θ . Most of the data lie between θ_w and θ^* , tracing the upper bound of transpiration or the lower bound of plant stress. Higher stress arises because some soil layers have $\theta > \theta^*$ while others have $\theta < \theta^*$. Lower transpiration arises because of the same reason, in addition to $\theta(z)$ being distributed vertically in such a way that $\alpha_1(\theta(z))$ is low where $\alpha_2(\theta(z))$ is high.

[14] Evaporation from the upmost soil layer follows a similar form as α_2 as follows:

$$E = \frac{\theta(\text{top}) - \theta_h}{n - \theta_h} PET_{\text{soil}} \quad (11)$$

where θ_h is the hygroscopic point below which soil water is so tightly bound and further evaporation is not feasible. Kurc and Small [2004] showed that evaporative fraction is predicted well by the water content in the upmost 5 cm in both a semi-arid grassland and shrubland, implying that a finer resolution is not necessary in this model.

[15] The vertical root profile is prescribed by the linear dose response (LDR) model [Schenk and Jackson, 2002b] as follows:

$$Y(z) = \frac{1}{1 + (z/D_{50})^c} \quad (12)$$

where Y is the cumulative fraction of total root mass between the soil surface and depth z ; D_{50} is the depth above which 50% of the root mass is located (or z such that $Y = 0.5$); and c is a shape parameter as related to D_{50} and D_{95} (where $D_{95} = z$ such that $Y = 0.95$) as follows:

$$c = \frac{2.94}{\ln(D_{50}/D_{95})} \quad (13)$$

The minor fraction of the root mass located below the soil column is redistributed within the existing layers in

proportion to their existing density. Root distributions are fixed during the simulations and are used to weight the water uptake function. Figure 5 illustrates two root profiles for a given pair of D_{50} and D_{95} , as sampled from the state-space to be explored by the simulations.

[16] The objective of the simulations is not to reproduce the root profiles of specific sites, but rather to identify the functional dependencies that affect root distributions in general. In so doing, the model must overlook a number of influential factors as follows: lateral surface and subsurface flow, phreatophytes and a groundwater table, preferential flowpaths, soil heterogeneity, plant competition, nutrient availability, and temperature effects. Furthermore, because LAI is fixed, we are interested in rooting depths relative to aboveground biomass rather than absolute rooting depths.

3. Simulations

[17] Experiments consist of 200-year simulations of the ecohydrological model with prescribed parameter values. The first 100 years are a spin-up period; the second 100 are used in the analysis. The experiments are designed to isolate the effects of individual edaphic, climatic, and physiological factors on optimal root profiles. The edaphic factor considered is soil texture. The climatic factors considered are mean annual precipitation P_a , annual PET , the timing and intensity of the wet season, and the timing and duration of storms. The physiological factors considered are ψ_w and ψ^* . In this work we define the optimal vertical root profile, with corresponding D_{50} and D_{95} , as that which maximizes mean annual transpiration subject to prescribed model and imposed environmental and physiological conditions [Mäkelä et al., 2002]. Alternatively, the optimum could be defined as that profile that minimizes plant stress, a proxy for maximizing survivorship. There is no explicit cost in the optimization approach, just a limitation on the transpirational demand which is distributed across the rooting profile proportional to local root density. The optimization procedure identifies where best in the soil column the roots should be distributed. Kleidon [2004] used an equivalent optimization assumption to infer global hydrologically active rooting depths based on inverse modeling. His results corresponded well with rooting depths derived from observations. A. Hildebrandt and E. A. B. Eltahir (Ecohydrology of a seasonal cloud forest in Dhofar: II. Role of clouds, soil type, and rooting depth in tree-grass competition, submitted to *Water Resources Research*, 2007, doi:10.1029/2006WR005262, hereinafter referred to as Hildebrandt and Eltahir, submitted manuscript, 2007) used an optimization approach to understand tree-grass coexistence in a cloud forest in Oman. van Wijk and Bouten [2001] used a genetic algorithm to identify the optimal root profiles at four sites in the Netherlands, and rooting depths were one of many parameters explored by the genetic algorithm employed by Schwinning and Ehleringer [2001]. Protopapas and Bras [1987] used a similar concept to model root development.

4. Identifying the Optimal Profile

[18] For each fixed set of environmental and physiological parameters, 104 simulations are run covering the specified D_{50} - D_{95} state-space (Figure 5). Hydrological fluxes and plant stress may be plotted as a function of D_{50} and D_{95} , producing

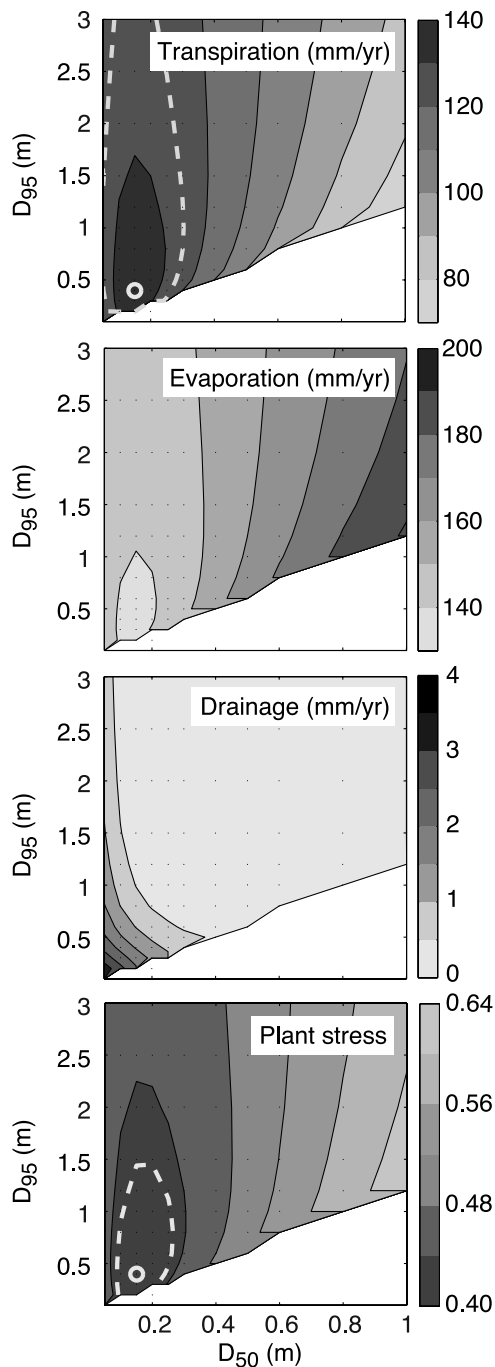


Figure 6. Transpiration, evaporation, drainage, and plant stress across the D_{50} - D_{95} state-space for silty soil with P_a of 500 mm/year and PET of 4 mm/day. Circles identify the optimum; dashed line denotes the optimal region.

the surfaces seen in Figure 6. This allows us to identify the maximum transpiration rate and corresponding root profile parameters, as well as examine the physical drivers for such a profile.

[19] For the case of a nonseasonal, average semi-arid environment with silt soil, the maximum transpiration (T_{\max}) is 134 mm/year and corresponds to the root profile of 0.15 m D_{50} and 0.4 m D_{95} (Figure 6). This is precisely coincident with the point of minimum evaporation (E_{\min}). As transpiration decreases away from the optimum, evapo-

ration increases in a reciprocal manner, indicating that the optimum is that which minimizes evaporation. The drainage flux is too small to be a valuable source of water, so the only flux with which transpiration competes is evaporation. The drainage surface does show, however, that as roots get deeper less water infiltrates past the plant's zone of influence. As T_{\max} is also coincident with the minimum stress (ξ_{\min}), there may be no confusion as to the location of the optimum if we alternatively define it by maximizing survivability rather than maximizing productivity.

[20] Because simulations are stochastic, there is uncertainty in the estimate of transpiration, and hence also in the location of the optimum. To identify the approximate optimal region we compare the transpiration time series of each profile in the D_{50} - D_{95} state-space to those of the absolute optimum using the Kolmogorov-Smirnov test ($\alpha = 5\%$). The resulting region represents a set of root profiles within which plants may not perceive any significant environmental difference, and thus are equivalently fit. The same procedure is applied to plant stress. In Figure 6 these regions cover a large area of the state-space and shows greater sensitivity to D_{50} than to D_{95} . The size and location of this region differs among experiments.

5. Soil Texture

[21] Soil texture is a key variable controlling soil moisture dynamics and distributions, and thus optimal root profiles. In the simulated moderate semi-arid climate, the coarser the soil, the deeper the roots (Table 1). This is also seen by *Laio et al.* [2006] and Hildebrandt and Eltahir (submitted manuscript, 2007). The high hydraulic conductivity of sand provides infiltrating water the greatest opportunity to penetrate to depth, so much so that root-water uptake cannot keep up and significant drainage occurs. To catch as much of this water as possible, optimized root profiles are as deep as possible. Evaporation is very low, so transpiration is effectively competing only with drainage. As soils become finer, from silt to loam to clay, optimal rooting depths become shallower, reflecting the restricted infiltration depths due to lower hydraulic conductivities. Loam produces only slightly deeper roots than does clay. Roots have little chance competing directly with evaporation [Noy-Meir, 1973], so roots are not the shallowest they can be. It must be noted that the optimum identified for sand occurs at the boundary of the state-space explored; the true optimum is likely deeper. Furthermore, of the four textures studied, sand is the only one in which ξ_{\min} is not coincident with T_{\max} . For all finer textures in this set of experiments, transpiration, stress, and evaporation extrema are all coincident.

Table 1. Optimal Root Profiles and Corresponding Mean Annual Fluxes and Plant Stress for Four Soil Textures^a

	Sand	Silt	Loam	Clay
D_{50} (m)	1	0.15	0.1	0.05
D_{95} (m)	3	0.4	0.3	0.2
Transpiration (mm/year)	145	134	132	125
Evaporation (mm/year)	41	137	140	139
Drainage (mm/year)	82	1.5	1.0×10^{-4}	1.6×10^{-5}
Plant Stress	0.04	0.41	0.41	0.62

^a $P_a = 500$ mm/year and $PET = 4$ mm/day.

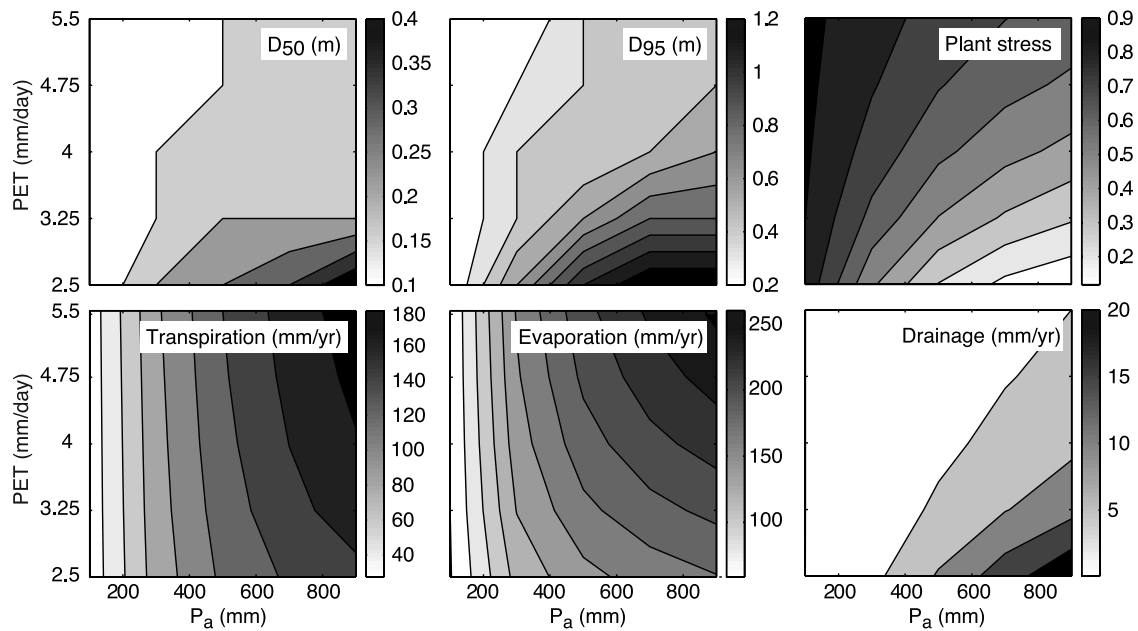


Figure 7. Rooting depths, fluxes, and plant stress for optimal profiles across P_a - PET state-space.

[22] Field data show that the probability of deep roots is higher in coarse and fine soil textures than in medium textures [Schenk and Jackson, 2005]. They explained this by noting that medium textures have ample moisture in shallow layers, so deep rooting is not necessary. Coarse soils do not have ample moisture at shallow depths but do have moisture at depth. Fine textures are less likely to have ample moisture anyway, in which case the plants are likely to exploit what macropores exist to reach deeper groundwater, if present. The present model, lacking both macropores and groundwater, does not produce deep roots for fine textures.

6. Climate

[23] When P_a and PET are covaried (100 to 900 mm/year and 2.5 to 5.5 mm/day, respectively, selected to reflect the data used by Schenk and Jackson [2002a]), without rainfall seasonality and again in silty soil, wetter and cooler climates

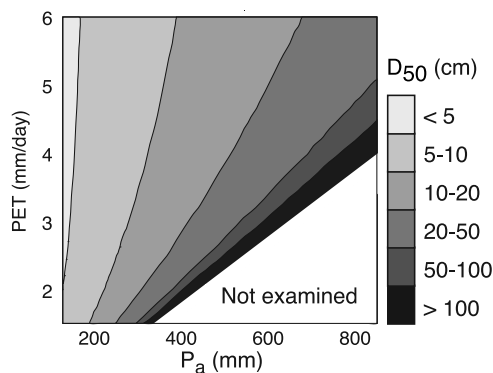


Figure 8. Optimal average rooting depths in sandy loam across the P_a - PET state-space after the work of Laio *et al.* [2006]. Trends and values are both similar to the results presented in Figure 7 for silt.

foster deeper roots (Figure 7), as shown also by Laio *et al.* [2006] (Figure 8). This arises because more water is infiltrating into the soil and draining from the soil column. As drainage increases, it becomes a more intense competitor for moisture. The optimum profile responds by extending its roots deeper (0.4 m D_{50} and 1.2 m D_{95} for $P_a = 900$ mm/year and $PET = 2.5$ mm/day; 0.1 m D_{50} and 0.2 m D_{95} for $P_a = 100$ mm/year and $PET = 5.5$ mm/day). ξ_{min} is coincident with T_{max} , though in this instance E_{min} remains very shallow while only slightly deepening in wetter climates. These results illustrate that, when drainage becomes substantial, transpiration begins to compete for moisture with both evaporation and drainage, but minimizes neither of the two fluxes. The results also confirm that the greater probability of deep roots in less arid regions can arise simply from trade-offs between infiltration and evaporative demand [Noy-Meir, 1973; Schenk and Jackson, 2005]. The trend along the P_a gradient agrees with the relative rooting depths of woody plants as reported by Schenk and Jackson [2002a], but not with forbs and grasses; the trend along the PET gradient is in agreement for all of the reported life-forms. For loam and clay the optimal depths are shallow and quite insensitive to changes in climatic variables. The

Table 2. Optimal Root Profiles and Corresponding Mean Annual Fluxes and Plant Stress for Different Seasonalities, for Silty Soil, P_a of 500 mm, and PET of 4mm/day^a

	Nonseasonal	Summer		Winter	
		(0.4)	(0.1)	(0.4)	(0.1)
D_{50} (m)	0.15	0.15	0.15	0.2	0.15
D_{95} (m)	0.4	0.6	0.5	1.0	0.8
Transpiration (mm/year)	134	136	108	134	107
Evaporation (mm/year)	137	132	107	127	103
Drainage (mm/year)	1.5	2.2	0.9	1.8	1.4
Plant Stress	0.41	0.35	0.46	0.35	0.43

^aValues in parentheses are Δt_w .

Table 3. Optimal Root Profiles and Corresponding Mean Annual Fluxes and Plant Stress for Different Storm T_r and Interstorm T_b Durations (in Hours), for Silty Soil, P_a of 500 mm/year, and PET of 4 mm/day^a

	$T_r = 5$		$T_r = 20$	
	(100)	(400)	(100)	(400)
D_{50} (m)	0.15	0.15	0.15	0.15
D_{95} (m)	0.5	0.4	0.6	0.4
Transpiration (mm/year)	151	94	151	93
Evaporation (mm/year)	168	89	161	85
Drainage (mm/year)	2.1	0.3	2.8	0.4
Plant Stress	0.34	0.62	0.27	0.58

^aValues in parentheses are T_b .

optimum in sand remains outside the D_{50} - D_{95} state-space explored.

[24] Differences in seasonality have less pronounced effects on the optimal root profile than texture, P_a or PET (Table 2). Optimal root profiles are deeper in winter-rainfall than in summer-rainfall environments; 0.2 m D_{50} and 1.0 m D_{95} for winter compared with 0.15 m D_{50} and 0.6 m D_{95} for summer for the slightly seasonal case. Water that infiltrates in the winter is subject to lower evapotranspirational demand than in the summer and is more likely to infiltrate to depth. As the wet season becomes more intense, with half the annual rainfall falling in ever fewer months, runoff increases at the drainage's expense and optimal D_{50} and D_{95} become slightly shallower. Asynchrony of evaporational and transpirational fluxes plays a significant role in generating heterogeneity in the landscape and hence diversity of plant functional types [Paruelo *et al.*, 2000; Hildebrandt and Eltahir, submitted manuscript, 2007]. These results are consistent with the observations by Schenk and Jackson [2005] that the probability of deep roots is higher in seasonal climates, and with those of Schenk and Jackson [2002a] regarding shrubs, though both sets of observations consider absolute depth rather than relative.

[25] When we isolate the effects of storm duration and timing, drainage becomes appreciable in the silt experiments provided that storms are short and frequent (Table 3). As drainage increases, transpiration starts to compete for moisture with both evaporation and drainage, and thus the optimal profile is slightly deeper; D_{95} increases from 0.4 to 0.8 m. No change in the optimal profile is observed for the coarser or finer soil textures because either drainage always overwhelms evaporation, or vice versa. Altered rainfall regimes have been shown to change net primary productivity [Fay *et al.*, 2003]. Our numerical experiments suggest that altered rainfall regimes may also affect root profile preference; the parameter space explored indicates this would more likely occur in silt.

7. Plant Physiology

[26] The two physiological parameters studied define the soil moisture bounds within which the plant is stressed but still able to transpire. The lowest ψ^* used (-10 kPa) yields a substantial increase in drainage compared with higher values (up to -1.8 MPa) (Table 4). As with the P_a - PET experiments, this drives the optimal profile deeper. The D_{95} of the absolute optimum changes little, though the optimal region changes substantially. The sooner ψ^* is surpassed as

the soil dries, the less moisture is taken up by the plant and the more remains to infiltrate. ψ_w has little effect on the location of the optimal profile (varied from -2 to -8 MPa). ψ^* is more influential because soil pressures are more often more negative compared to ψ^* than they are to ψ_w . Our results correspond to more drought-tolerant species having shallower roots, not because they can tolerate a more stressful environment in the surface layers, but because that is where water is more abundant. This is consistent with observations that cavitation resistance is negatively correlated with rooting depth [Sperry and Hacke, 2002], a strategy suiting both intensive and extensive soil moisture use [Rodriguez-Iturbe *et al.*, 2001b].

8. Discussion

[27] Because a similar work has been presented by Laio *et al.* [2006], it is valuable to compare and contrast the two approaches. Laio *et al.* [2006] developed a steady state analytical representation of vertical root profiles in water-limited ecosystems. Its simplicity provides a distinct advantage over the present optimization modeling by more readily demonstrating the connections between environmental factors and rooting depths. Their model results on the effects of soil texture and climate compare well with our results (Figure 8). Their results go further by showing that the form of the rainfall probability distribution is important and by comparing the derived root profile to the observation from a semi-arid shortgrass steppe in Colorado, USA. However, the same simplicity constrains the model's applicability and potential ecohydrological insight.

[28] Where the work of Laio *et al.* [2006] substantially diverge from the present model is in the absence or simplification of hydrological fluxes. By omitting evaporation and leakage losses, Laio *et al.* [2006] gave plants a competition-free environment in which rooting strategies respond to infiltration depth alone. The lack of evaporation leads to an analytical representation of root density that decreases monotonically with depth. In water-limited environments, evaporation cannot be overlooked, as it plays a significant role in near-surface moisture dynamics and thus plant rooting strategies. Furthermore, leakage losses cannot be assumed negligible in all water-limited environments [Small, 2005]. Different root profiles are also likely to develop by discounting the potential of roots to take up water preferentially from different depths. Simplifications that merely limit the scope of the model are the absence of seasonality in climatic

Table 4. Optimal Root Profiles and Corresponding Mean Annual Fluxes and Plant Stress for Different Wilting Points ψ_w and Stomatal Closure Pressures ψ^* (in MPa), for Silty Soil, P_a of 500 mm/year, and PET of 4 mm/day^a

	$\psi_w = -2$		$\psi_w = -8$	
	(-0.01)	(-1.8)	(-0.01)	(-1.8)
D_{50} (m)	0.3	0.1	0.3	0.1
D_{95} (m)	0.6	0.6	0.6	0.6
Transpiration (mm/year)	56	173	64	177
Evaporation (mm/year)	198	104	195	101
Drainage (mm/year)	5.7	0.07	5.2	0.08
Plant Stress	0.74	0.23	0.71	0.17

^aValues in parentheses are ψ^* .

forcings and a transpiration model whose only physiological parameter is ψ_w .

[29] Returning to the current study, the $\psi^* - \psi_w$ experiments demonstrate that plants themselves alter the soil environment with feedbacks that affect rooting preference. In these experiments we considered only solitary plants or populations of equivalent plants, but the inclusion of competition for water among plants will have a pronounced effect on realized rooting preferences in mixed communities. As a corollary, the genetic algorithms used by *van Wijk and Bouten* [2001] produced very different profiles depending on whether or not competition was included. Furthermore, as PET affects optimal rooting depths, so too would LAI , and therefore also biomass and phenophase. As a plant reaches more or less water, the carbon balance would shift, leading to more or fewer roots. This begs the questions as follows: What would happen if the optimization approach searched over LAI as well as D_{50} and D_{95} ; or how deep would roots delve if they had to meet their own carbon needs?

[30] Allowing LAI (or biomass) to vary with the availability of resources is certainly more realistic than keeping it fixed. However, to model this additional degree of freedom within this optimization framework would substantially change the nature of the study, as we argue as follows. If the optimal root density profile were that which maximizes transpiration, and because transpiration depends positively on LAI , then the optimum LAI would grow until the reduced throughfall no longer supplies the soil with sufficient plant-available water, or increased water stress critically limits the plant from taking up and transpiring water. Plant stress would play a role in either case, and yet our ability to model the relevant processes is so limited that it would become the fulcrum on which the results would rest. By allowing LAI to vary in this manner we would become less clear about the roles of evaporation, drainage, and moisture redistribution in fostering different rooting strategies. It is possible to examine fixed values of LAI other than 1. We did so for 2 (results not shown), and while the magnitudes of rooting depths changed, trends across the climatic gradients did not. In fixing LAI we restrict the analysis to studies of relative rather than absolute rooting depth.

[31] Instead of considering root density, we could explicitly consider the biomass of the root system. This would allow us to identify the root distribution in which roots only develop so that the rate of carbon fixation meets the maintenance costs of the existing biomass. This is again a more realistic expectation, yet to model it would require an assessment of the carbon requirements of the plant, again shifting the balance of insight from hydrology to physiology. There is ample to learn without the additional complexities of varying biomass and carbon accounting, though they are necessary progressions as we seek to understand the origins of rooting strategies.

[32] Looking at what rooting strategies were identified, it is noteworthy that by far the majority of experiments produce D_{50} in the vicinity of 20 cm or shallower, which is the global mean reported by *Jackson et al.* [1996]. The drive to send roots deeper when appreciable drainage exists reflects the greater likelihood of finding deep roots in water-limited systems. However, we presume the majority of truly deeply rooted plants are phreatophytes [*Nobel*, 2002] and thus not considered within this model. The drive to diminish drainage is also

consistent with observations from the US southwest [*Scanlon et al.*, 2005], where plants have essentially eliminated groundwater recharge for the last 10,000 years.

[33] Where our results differ from observed trends is when considering the relative rooting depths of forbs and grasses along a gradient of precipitation. *Schenk and Jackson* [2002a] observed that in wetter climates relative root depths of these life-forms become ever shallower, even though their absolute depth increases. Because our model reflects the trends of woody plants, it is likely that there is an important physiological process omitted from the model. Resolving this discrepancy is an important step in connecting ecohydrology to rooting strategies.

[34] Combining the results for the P_a - PET and texture experiments offers insight on the inverse texture effect that the same type of vegetation may occur in coarse soil under dry climates and in fine soil in wetter climates [*Noy-Meir*, 1973]. The optimal root profile is deeper in coarser soils and in wetter climates. If soils coarsen at the same time as the climate dries, it is conceivable that the optimal rooting depth may remain the same. Because rooting strategies are species-specific [*Gale and Grigal*, 1987; *Poot and Lambers*, 2003; *Yamada et al.*, 2005], the reciprocal changes in soil and climate, in some cases, may indeed provide conditions for a single species.

[35] Changing the root profile often has a significant effect on hydrologic fluxes and plant stress [*Rodriguez-Iturbe et al.*, 2001b]. This further highlights the need to properly account for root profiles when modeling land-atmosphere interactions, groundwater recharge, and habitat suitability. Land use changes often lead to altered groundwater recharge and streamflow. If the changes are associated with a shift in the preferred root profile by plants, a component of the hydrologic response would arise from the vertical shifts in the belowground biomass.

[36] If differences in rooting preference exist among climates, we can expect climate changes to foster changes in belowground biomass. This may entail the modification of the existing species' roots to the new depths, or replacement by fitter species. A substantial increase in winter precipitation in the last quarter of last century in the US southwest caused a threefold increase in woody shrub density [*Brown et al.*, 1997]. Cast in the light of the simulations herein, greater winter precipitation favors deeper rooted plants, such as shrubs, over more shallow-rooted herbaceous life-forms. Resultant changes in community structure and composition following climate changes would further affect ecosystem processes and services [*Chapin et al.*, 1997]. Potential impacts include changes in water, carbon, and other nutrient fluxes, as well as the distribution of soil fauna [*Holden and Fierer*, 2005; *Jackson et al.*, 2000; *Jobbágy and Jackson*, 2001; *Johnston et al.*, 2004].

[37] Our results reproduce many of the trends related to root profiles in water-limited ecosystems, supporting the contention that infiltration and evaporative demand are indeed the mechanisms behind these profiles. However, roots are not static. Plant growth entails changes both above and below ground, and plasticity is vitally important in resource acquisition [*Grime et al.*, 1986], though to varying degrees [*Wraith and Wright*, 1998]. What is optimal in the long term may thus be suboptimal on shorter timescales. The root profiles we employ are best interpreted as gener-

alist strategies or static approximations to a dynamic system, providing mechanistic insight on the root profile snapshots that comprise belowground surveys with which we are making our comparisons.

9. Conclusions

[38] The numerical ecohydrological modeling study employed in this paper provides a window into the ecological relationships that give rise to the diversity of rooting strategies observed in nature. Root depth and distribution are vital components of a plant's strategy for growth and survival in water-limited ecosystems and play significant roles in hydrologic and biogeochemical cycling. Knowledge of root profiles is invaluable in measuring and predicting ecosystem dynamics, yet data on root profiles are difficult to obtain. Using an optimization approach, model simulations thus offer a means to explore the mechanistic relationships among climate, soil, and plant systems in water-limited ecosystems. It should be noted that noninvasive techniques using isotopes have recently been developed [Ogle *et al.*, 2004].

[39] Results of the optimization approach were consistent with profiles observed in nature. Optimal relative rooting depths were progressively deeper moving from clay to loam, silt and then sand, and in wetter and cooler environments. Climates with the majority of the rainfall in winter produced deeper roots than if the rain fell in summer. Short and frequent storms also favored deeper rooting. Plants that exhibit water stress at slight soil moisture deficiencies consistently showed deeper optimal root profiles. Of the four soil textures examined, silt generated the greatest sensitivity to differences in climatic and physiological parameters. Thus, in the absence of groundwater and assuming obtaining water is the only purpose of the roots, the depth of rooting is driven by the depth to which water infiltrates, as influenced by soil properties and the timing and magnitude of water input and evaporative demand.

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