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The Shallowest Possible Water Extraction Profile: A Null Model for Global Root Distributions

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The factors that shape vertical root distributions in different soils and under different climates and vegetation are poorly understood. This makes it difficult to parameterize root profiles in vegetation-, hydrology, biogeochemistry-, or global circulation models. Recently, it has been proposed that vertical root distributions in the vadose zone could be predicted from soil water infiltration and extraction patterns as a function of climatic variability, soil, and vegetation characteristics. A number of ecological factors favor shallow over deep roots, suggesting that root profiles of plant communities may tend to be as shallow as possible and as deep as needed to fulfill evapotranspirational demands. To test this hypothesis, a stochastic, one-dimensional soil water infiltration and extraction model (SWIEM) was developed that simulates soil water infiltration through 600 discrete soil layers to a depth of 6 m. Water input is simulated in Monte Carlo fashion based on site-specific long-term precipitation data. Water extraction proceeds from the top down, with extraction depths determined by potential evapotranspiration (PET) and the vertical distribution of soil water. The resulting shallowest possible water extraction profile was tested against nine measured root profiles from long-term ecological research sites in different biomes. Two other approaches, based on mean root distributions for biomes and an empirical regression model, were also compared to the observed root distributions. Soil water extraction patterns predicted by the SWIEM model matched observed vertical root distributions better than the other two approaches. These findings show that vertical root distributions in different biomes tend to approach the shallowest possible shape, thereby creating a useful null model for future research on root distributions and a promising tool for parameterization of global models.

Abbreviations: $FC_{\%}$, percentage volumetric water content at field capacity; ISLSCP2, International Satellite Land-Surface Climatology Project 2; $P_{m1/2}$, semimonthly precipitation; $PAW_{\%}$, plant-available water in volume percent; PET, potential evapotranspiration; $PET_{m1/2}$, semimonthly potential evapotranspiration; $PWP_{\%}$,. percentage volumetric water content at the permanent wilting point.

Differences in rooting depth of vegetation can have pronounced effects on ecosystem fluxes of water and carbon and thereby directly affect climate (Jackson 1999; Kleidon and Heimann 2000; Feddes et al., 2001; Lee et al., 2005). Biogeochemistry, hydrology, and global circulation models parameterized to use unrealistically shallow or deep root distributions may seriously under- or overestimate transpiration and thereby cause under- or overestimates of net primary productivity, the major process by which carbon is removed from the atmosphere. The problem until recently was that plant biologists lacked the understanding to allow quantitative predictions of vertical root distributions from abiotic and/or biotic factors for a given combination of climate, soil, and vegetation. Without the ability to realistically parameterize root distributions, modelers had to rely on highly simplified depictions of belowground structure and function of global vegetation (Jackson et al., 2000).

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Compilations of global root databases by Jackson et al. (1996) and Canadell et al. (1996), later updated by Schenk and Jackson (2002a,b, 2003a), resulted in information on mean vertical root distributions and maximum rooting depths for biomes that could be used in global models. At the same time, these databases allowed analyses of relationships between climate, soil texture, vegetation type, and vertical root distributions or maximum rooting depths (Schenk and Jackson, 2002a,b). These analyses resulted in empirical models and maps of predicted rooting depths for global vegetation (Schenk and Jackson, 2003b, 2005).

The most obvious conclusion from these studies was that globally the vast majority of root profiles show exponential declines of root density with increasing depth (Fig. 1). Out of 564 root profiles compiled in a global database, 93% had the highest root density, on average, 60% of fine roots, in the upper 20 cm of the soil profile, including organic layers (Schenk and Jackson, 2002a, 2003a). This distribution does not match the vertical distribution of the major plant nutrients nitrogen, phosphorus, and potassium, as only 10 to 30% of these nutrients tend to be concentrated in the upper 20 cm of the soil profile (Fig. 1; Jobbágy and Jackson, 2001). Clearly, the more shallow distribution of roots must be at least partly the result of other factors besides nutrient availability.

In fact, several factors favor shallow root distributions under most conditions (Schenk and Jackson, 2002a; Schenk, 2005): (i) energy costs for construction, maintenance, and resource uptake are lower for shallow roots; (ii) soil strength is typically lowest near the soil surface; (iii) water in most soils enters the profile predominantly from above; (iv) nutrient concentrations are typically

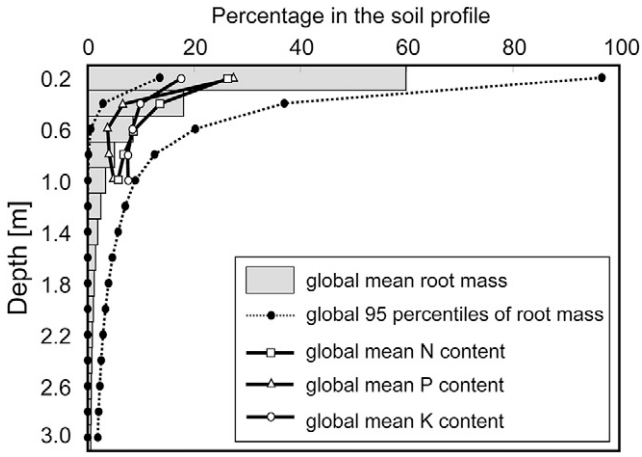

FIG. 1. Global average vertical root distribution and 95 percentiles calculated from 564 soil profiles from many global vegetation types (Schenk and Jackson, 2002a). The data are available at http://www.daac.ornl.gov (Schenk and Jackson, 2003a). Also depicted are global averages for plant nutrient profiles in percent of the total within a standard 1 m profile taken from Jobbágy and Jackson (2001).

highest in the upper soil layers; (v) shallow soil layers are usually less likely to be oxygen deficient; (vi) deep roots in dry soil can potentially be a drain for downward hydraulic redistribution; and (vi) because of the first six reasons, shallow roots generally have competitive advantages over deeper roots (Schenk, 2006). On the basis of these considerations, Schenk and Jackson (2002a) proposed a conceptual model that predicts that root distributions generally will be as shallow as possible to fulfill transpirational demand.

This simple prediction, which was the conceptual basis for a recent model by Laio et al. (2006), provides a convenient framework for predicting vertical root distributions from patterns of soil water infiltration and evapotranspirational demand. This is a much simpler approach than cost–benefit optimization models that calculate "optimal" root distributions that maximize transpiration (van Wijk and Bouten, 2001; Collins and Bras, 2007) or carbon gain (Kleidon and Heimann, 1998; Schwinning and Ehleringer, 2001) or that minimize energy expenditure for root construction and maintenance (Adiku et al., 1996, 2000). The model described here is a simple stochastic soil water infiltration and extraction model (SWIEM) designed to calculate the shallowest possible profile of soil water extraction based on climate, soil, and vegetation data. Predicted extraction profiles are compared to observed vertical distributions of fine roots in nine ecosystems ranging from boreal and cool-temperate forests to grassland, tropical savanna, and tropical forest. I also compare SWIEM predictions to two other methods for predicting vertical root distributions, mean rooting depths for biomes (Schenk and Jackson, 2002a) and an empirical regression model developed for NASA's International Satellite Land-Surface Climatology Project 2 (ISLSCP2) global data initiative (Schenk and Jackson, 2003b).

Materials and Methods

The SWIEM Model

The SWIEM model is a one-dimensional stochastic model consisting of a water input module, a water infiltration module, and a water extraction module, all implemented in Excel spreadsheet software (Microsoft, Redmont, WA). The model is run on a semimonthly time-step. It has no inherent assumptions about vertical root distributions; instead, extraction always proceeds from the top of the profile downward to create the shallowest possible extraction profile. The water infiltration and extraction modules divide the vadose zone, including organic layers, into 1-cm-deep layers down to a maximum depth, which was set to 6 m for all model runs presented here. Each 1-cm layer is assigned an individual water holding capacity for plant-available water ($PAW_{\%}$, Table 1), and during model runs layers are assumed to be either full or empty of plant-available water. At a given field site, $PAW_{\%}$ for vadose zone layers were determined either from the literature about that site or calculated as percentage volumetric water content at field capacity ($FC_{\%}$) minus percentage volumetric water content at the permanent wilting point ($PWP_{\%}$), assumed to be −1.5 MPa for humid environments and −5 MPa for arid to subhumid environments. Soil water holding capacities at $FC_{\%}$ and $PWP_{\%}$ were calculated from soil texture after Saxton et al. (1986).

The water input module simulates semimonthly precipitation ($P_{m1/2}$) based on long-term monthly precipitation records for each field site, which are used to parameterize a stochastic precipitation simulator using the software Crystall Ball Pro (version 4.0 g, Decisioneering, Denver, CO), an add-in to the Excel spreadsheet software. The Crystall Ball Pro program allows analysis of the long-term variability of monthly precipitation, which is used to determine the statistical distribution that best fits the data, in most cases, a Weibull distribution. These fitted distributions in turn are used to simulate semimonthly precipitation for the water-input module. Rainfall interception (Table 1) by vegetation and surface runoff is deducted as a percentage from precipitation, and runon is added. Because all field sites used for testing this model are relatively flat, runoff and runon were assumed to be zero.

The water infiltration module moves water downward, depending on the $PAW_{\%}$ of each individual 1-cm layer and depending on whether the layer was left full or empty after the previous semimonthly time interval. Water that infiltrates beyond the maximum depth (here 6 m) is assumed to be unavailable to plants.

The soil water extraction module is driven by data on mean semimonthly potential evapotranspiration ($PET_{m1/2}$), calculated from monthly PET data that were available for several of the field sites (Table 1) used to test the model. In some cases, monthly PET values, as calculated by the Penman–Monteith method, were taken from a global database (Choudhury, 1997; Choudhury and DiGirolamo, 1998). Semimonthly PET does not vary in the model; instead, the variability of the difference between $P_{m1/2}$ and PET is driven by stochastic variation of $P_{m1/2}$ alone. During the growing season, all water extraction is assumed to be the result of plant water uptake (no soil evaporation). During a cold season, water extraction is assumed to result from soil evaporation alone, as plants are assumed to be dormant. Extraction always proceeds from the top downward, and because the 1-cm layers can be only either full or empty of plant-available water, the instantaneous extraction rate is not dependent on soil moisture content. However, long-term mean extraction from each layer will be a linear function of its mean $PAW_{\%}$.

At each semimonthly time-step, water inputs are calculated first, followed by infiltration into the profile, followed

Table 1. Long-term research sites used in this study. Sources for root, site, and climatic data are listed in the footnotes for each site.

Site	Lat, long	Vegetation	MAP_a†	PET_a†	$I_{\%}$†	Length of warm growing season	Soil texture†	$PAW_{\%}$† at surface	$PAW_{\%}$ at 2 m
					%	mo		%	
Jädraås Ih V SWECON, Sweden‡	60.82 N, 16.50 E	boreal pine forest	607	494	19	7	O+S	37	12
Solling International Biological Program, Germany§	51.77, N 9.55 E	cool-temperate broadleaved forest	1060	637	Winter: 15.3; Summer: 28.4	8	lU	37	17
Shortgrass Steppe Long-Term Ecological Research, Colorado¶	40.82 N, 104.77 W	shortgrass-steppe	321	1248	2.5	8	sL	12.7	12.7
Jornada Long-Term Ecological Research, New Mexico#	32.50 N, 106.80 W	desert grassland	264	1420	2.5	10	sL	11.5	11.5
La Copita Research Area, Texas††	27.65 N, 98.22 W	warm-temperate savanna	716	1123	20	10	sL	13.5	13.5
Rock Valley International Biological Program, Nevada‡‡	36.67 N, 116.12 W	desert shrubland	100	1413	2.5	8	lS	4.05	4.05
Nyslvley Nature Reserve, S. Africa§§	24.65 S, 28.75 E	dry tropical savanna	630	1256	6	11	lS	11	11
HAPEX-Sahel, Niger¶¶	13.25 N, 2.25 E	dry tropical savanna	585	2264	10	12	sL	18	18
Paragominas, Brazil##	2.98 S, 47.52 E	seasonally dry evergreen tropical forest	1750	1313	11	12	C	19	12.5

† MAP_a, mean annual precipitation; PET_a, mean annual potential evapotranspiration; $I_{\%}$, mean percentage of precipitation intercepted by plant canopies; O, organic; s, sandy; l, loamy; S, sand; L, loam; U, silt; C, clay; $PAW_{\%}$, plant available water in volume percent.
‡ Persson (1982), Axelsson and Bråkenhielm (1980), Jansson and Halldin (1979), Bringfelt and Lindroth (1987).
§ Ellenberg et al. (1986), Benecke (1984).
¶ Lee and Lauenroth (1994), http://sgs.cnr.colostate.edu/.
# Jackson et al. (2002), McCulley et al. (2004), http://jornada-www.nmsu.edu/.
†† Midwood et al. (1998).
‡‡ Wallace et al. (1980), Lane et al. (1984).
§§ Scholes and Walker (1993).
¶¶ Gaze et al. (1998).
Nepstad et al. (1994), Jipp et al. (1998), Sternberg et al. (1998).

by extraction from the top downward. Water stored in layers below the extraction depth remains in the profile until the next time interval, when it may infiltrate further downward as additional water infiltrating from above pushes it down, or it can be extracted. Model simulations are run for a thousand years to create an average extraction profile that matches the natural variability of infiltration and extraction patterns. The predicted extraction profile for vegetation is calculated for the warm season alone and is determined by the proportion of extraction occurring on average from each individual layer of the vadose zone down to the maximum depth. For illustration purposes and comparisons with measured vertical root distributions, extraction profiles were compiled into 0.1-m depth increments.

Vertical Root Distributions

Vertical fine-root distributions for each of the nine field sites were taken from the literature listed in Table 1. For consistent comparisons with the predicted soil water extraction profiles, all root profiles were interpolated into 0.1-m depth intervals, measured from the top of the profile, including any organic horizons. The proportion of fine roots in each 0.1-m layer was calculated by setting the total amount of fine roots to the sampled depth equal to 1. In some cases, roots may have occurred below the sample depth.

Comparisons of Vertical Root Distributions to Model Predictions

Predicted root profiles generated by the SWIEM model were compared to two other model predictions that could be used to parameterize vertical root distributions in global model. One of these predictions used an empirical regression model developed by Schenk and Jackson (2003b) for the ISLCP2 initiative (Hall et al., 2006), which is based on vegetation-type-specific relationships between rooting depths, mean monthly PET, and mean monthly precipitation. The regression model predicts two rooting depths: D_{95}, the depth above which 95% of all roots are located, and D_{50}, the depth above which 50% of all roots are located. These two depths, D_{95} and D_{50}, are then used to calculate a vertical root distribution using the logistic dose response equation described by Schenk and Jackson (2002a, 2003b). The other prediction uses mean vertical root distributions predicted for global biomes, calculated as above from mean D_{95} and D_{50} depths for biomes (Schenk and Jackson, 2002a), which is the approach currently used in many global models. All three predicted profiles were compared to the measured root profiles using Bray–Curtis indices of dissimilarity (Faith et al., 1987) calculated using Systat (version 12, Systat Software Inc., San Jose, CA). Bray–Curtis indices for all nine field sites were compared between the three predictive methods using three Bonferroni-corrected paired *t* tests to determine the overall best approach.

Results

The shallowest possible soil water extraction profiles calculated by the SWIEM model matched observed fine root distributions in the soil profiles at all nine field sites very well (Fig. 2). Because of the surprising degree of this match in all cases, it bears repeating that the SWIEM model does not make any inherent assumptions about root distributions. Instead, it appears that fine root distributions closely match soil water extraction profiles that are as shallow as possible and as deep as needed to fulfill evapotranspirational demands. The largest deviation between observed fine root profiles and predicted extraction profile was observed for the boreal pine forest in Jädraås, Sweden, where the extraction profile was significantly deeper than the observed root distribution. Deviations between observed root profiles and predicted extraction profiles in the other eight field sites were minor and may have been caused in part by limited root sampling depths (Fig. 2). The mean Bray–Curtis index of dissimilarity between root profiles and soil water extraction profiles predicted by the SWIEM model was very low (0.101 ± 0.013; Table 2), indicating a high degree of similarity. The other two predictors for vertical root distributions did not perform as well as the SWIEM model. Biome means were slightly better predictors of observed root distributions than the SWIEM model in two out of the nine sites (Jädraås, Sweden, and HAPEX-Sahel, Niger), but the mean Bray–Curtis index for biome means was significantly lower (0.211 ± 0.035) than for the SWIEM model. The empirical ISLSCP2 regression model resulted in predicted root distributions that were about as good as those using biome means (mean Bray–Curtis index 0.166 ± 0.024). In summary, the SWIEM model performed significantly better than any other method previously available to global modelers.

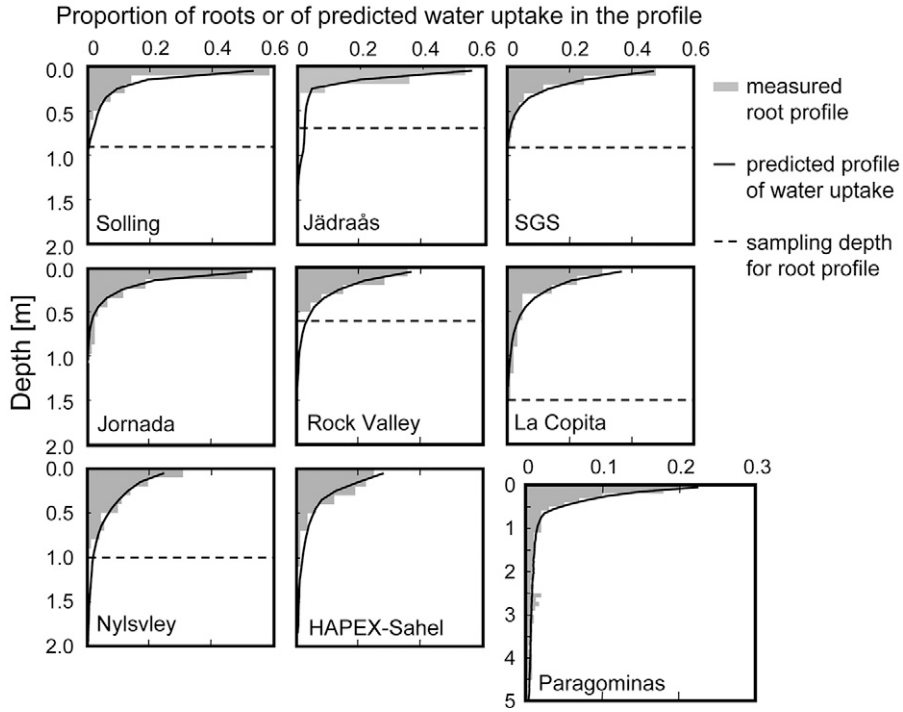

FIG. 2. Comparisons of soil water extraction profiles predicted for nine soil profiles using the SWIEM model compared with observed root distributions to the sampling depth indicated by dashed lines. The Jornada (New Mexico), HAPEX-Sahel (Niger), and Paragominas (Brazil) sites had sampling depths of 5 m or more. Details about the nine field sites and references for the root data are found in Table 1. SGS, Shortgrass Steppe Long-Term Ecological Research.

TABLE 2. Bray–Curtis indices of dissimilarity for comparisons between predicted and measured root profiles for the SWIEM model (this study), biome means of Schenk and Jackson (2002a), and the empirical regression model of the International Satellite Land-Surface Climatology Project 2 (ISLSCP2) initiative (Schenk and Jackson 2003b). The lowest Bray–Curtis index for each site, indicating highest similarity, is given in italics for each comparison.

Site	SWIEM model	Biome mean	ISLSCP2 model
Jädraås SWECON, Sweden	0.164	*0.157*	0.180
Solling International Biological Program, Germany	*0.089*	0.357	0.265
Shortgrass Steppe Long-Term Ecological Research, Colorado	*0.036*	0.110	0.037
Jornada Long-Term Ecological Research, New Mexico	*0.062*	0.176	0.140
La Copita Research Area, Texas	*0.114*	0.131	0.122
Rock Valley International Biological Program, Nevada	*0.080*	0.283	0.171
Nyslvley Nature Reserve, S. Africa	*0.095*	0.169	0.126
HAPEX-Sahel, Niger	0.133	*0.123*	0.193
Paragominas, Brazil	0.136	0.389	0.263
Mean ± SE	*0.101*a ± 0.013†	0.211b ± 0.035	0.166b ± 0.024

† Different letters after the means denote results that are significantly different at $p < 0.05$.

Discussion

The findings of this study provide very strong support for the hypothesis that vertical root distributions at the vegetation scale tend to be as shallow as possible and as deep as needed to fulfill evapotranspirational demands. The SWIEM approach was significantly better in predicting vertical root distributions than the two other methods that were tested, even though SWIEM makes no assumptions about root distributions or root function except to consistently favor the most shallow extraction profile. These findings beg the question why root distributions should so closely reflect the shallowest possible extraction profile.

One possible answer is that root densities within soil layers may be closely correlated with long-term mean water uptake from that layer. Root densities will obviously be high in layers in which most water uptake occurs, but why should there be living roots in deeper layers from which significant water uptake may only occur during dry periods? McCulley et al. (2004) suggested that such deep roots may play an important role for nutrient uptake in water-limited ecosystems, an idea supported by the observation that significant amounts of nutrients tend to occur below 20 cm depth (Fig. 1; Jobbágy and Jackson, 2001; McCulley et al., 2004). Moreover, plants

may benefit from having living roots at depth that can be quickly activated to grow when upper soil layers begin to dry. There are indications that deep roots may be inactive as long as resources are available at shallower depths (Fernandez and Caldwell, 1975; Andraski, 1991; Scanlon et al., 1999; Seyfried et al., 2001). In fact, roots can survive dry conditions in a dormant state for some time by protecting their root cap cells with cork layers, a process known as metacutization (Müller, 1906; Leshem, 1970).

The other answer as to why vertical root distributions at the vegetation scale should match the shallowest possible extraction profile lies in the six factors listed in the introduction that favor shallow roots over deep roots. Individual plants and species may differ greatly in their rooting architecture and may specialize in shallow or deep roots or both. It is not to be expected that the SWIEM approach could predict root distributions for individual plants. However, at the plant community scale, plants that take advantage of the factors that favor shallow root distributions on average may have higher fitness and be better competitors (Schenk 2006). As pointed out in Schenk (2005), light and soil water are both directional resources that plants compete for. Only the tallest plants can compete successfully for the maximum amount of light, but all plants potentially can compete for water that enters the soil surface from above and the nutrients that accumulate near the surface. This means that plant competition may tend to create the shallowest possible root distribution, and because root competition is ubiquitous (Casper and Jackson, 1997; de Kroon et al., 2003; Schenk, 2006), most plant communities will tend to have the shallowest possible root profiles. If most root water uptake for transpiration occurs in shallow soil layers, then less water can be taken up from lower layers, because transpiration of vegetation is limited by the physics of evapotranspiration. Actual evapotranspiration from plant communities increases somewhat as canopy height and roughness increase, but this is at least partly the result of increased canopy interception, not transpiration (Calder, 1990; Rey, 1999).

In essence, then, some plant species may take advantage of the niche of soil resources at depth that other plants do not compete for, but the majority of plant roots will be close to the surface (Fig. 1), thereby tending to create the "shallowest possible" root profile at the vegetation scale. This simple explanation for vertical root distributions could be seen as the null model that was lacking in previous research on root distributions until the publication of the model by Laio et al. (2006). Using this null model, researchers can identify those sites or plant communities that deviate from the model, which would open up new avenues of research on the causes of deeper- or shallower-than-expected rooting depths. Until now, there were no specific expectations about root distributions other than empirical ones. For example, McCulley et al. (2004) discussed the possible reasons for deep roots in water-limited ecosystems without a reference model that could tell them what rooting depths to expect. In fact, one of their research sites, the desert grassland at the Jornada Long Term Ecological Research site, has root distributions that almost exactly match the null model of the shallowest possible profile (Fig. 2, Table 2). To take another example, in this study, the predicted extraction profile for the boreal pine forest in Jädraås, Sweden, was significantly deeper than the observed root distribution (Fig. 2). This raises the question whether rooting depths at that site may be restricted by highly acidic soil horizons or low soil temperatures.

Most field sites used for testing the SWIEM model were from water-limited ecosystems because detailed soil and climate data to parameterize field sites in very humid forests were not available. However, the model by design will predict very shallow soil water extraction curves for moist ecosystems, such as perhumid tropical rainforests, where shallow root distributions are the norm (Odum, 1970; Sanford, 1989; Pavlis and Jeník, 2000). The model's validity for such ecosystems remains to be tested, but there is no reason to expect a priori that the approach is valid only for water-limited systems.

In summary, the success of the SWIEM approach or the related approach of Laio et al. (2006) to predict realistic vertical root distributions provides a way for modelers to parameterize vegetation, hydrology, biogeochemistry, or global circulation models by simply calculating the shallowest possible root profile, given soil conditions and the predicted long-term variability of climate. These findings also open up new avenues of research into the causes of root distributions by offering a simple null model that can be compared to observed root distributions.

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