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COMMENTARY

Do we need new rhizosphere models for rock-dominated landscapes?

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Abstract
Background In this issue, Estrada-Medina and co-workers described the diversity of materials in the rhizosphere of the Yucatán karst, México, and quantified the distribution of roots across karst features.
Scope This commentary explores the implications of their work for below-ground competition and the dynamics of plant-available water on seasonal to inter-annual timescales. Though details differ, seasonal dynamics of water use were consistent with a two-layer model, characterized by water uptake from shallow soil and rock layers during the wet season and deeper soil pockets and rock layers during the dry season. Soil pockets were more densely rooted than rock and experienced large fluctuations in soil moisture, suggesting intense below-ground competition. Total water storage capacity in the rhizosphere was far greater than actual storage in the year of the study. This raises the question whether some storage components in the karst rhizosphere fluctuate on time scales exceeding 1 year.
Conclusions Despite the significant global extent of karst and their larger than proportional contribution to global biodiversity, vegetation models have ignored their unique rhizosphere structure. Differences in water storage could affect the responses of karst ecosystems and communities to climate change.

Keywords Below-ground competition · Drought karst · Ecohydrology · Root distributions · Water

William Austin Cannon (1870–1958) and John Ernest Weaver (1884–1956) were among the first to recognize the central role of root distributions for the adaptive strategies of plants and the function of communities and ecosystems. The remark by Weaver (1915) at the end of his first major work on the roots of prairie plants is still an accurate description of today's research agenda: "A knowledge of the distribution and extent of root-systems helps us to more correctly interpret the present structure of vegetation as well as to analyze the causes which have led up to and are constantly active in modifying these conditions".

In the past century, our understanding of root form and function has advanced in numerous ways. Through detailed 3D modeling of root structure, we have come to better understand the implications of root architecture for water and nutrient uptake (Danjon and Reubens 2008; Draye et al. 2010). Root architecture is the hybrid product of genetically programmed branching rules that give root systems a characteristic appearance, and local environmental effects on root development that allow plants to grow strategically

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and opportunistically in heterogeneous soil (Ingram and Malamy 2010; Malamy 2005; Mulia et al. 2010). While earlier research focused on root-soil interactions, today numerous biotic interactions of roots with other roots, bacteria, fungi and nematodes through chemical signals are being investigated (Bais et al. 2006). At the scale of ecosystems, the representation of root systems is far less detailed, but this field of research has benefited from the identification of predictable root system geometries associated with plant functional type, climate and soil texture (Schenk and Jackson 2002a, b, 2005). Root and rhizosphere effects in ecosystem models include largely unresolved contributions of root respiration, fine root turn-over, exudation and mycorrhizal interactions to soil respiration (Chapin et al. 2009) and hydrologic effects. Within the framework of structurally uniform soil, ecosystem rooting depth sets the water storage capacity of the rhizosphere (Caylor et al. 2009) which in turn controls the amount of precipitation that is cycled back into the atmosphere. Error in the attribution of the water storage capacity of the rhizosphere can modify global climate predictions on a grand scale (Kleidon and Lorenz 2001; Milly and Dunne 1994). Put simply, a world in which root growth is physically constrained is drier and warmer than a world in which roots have free reign.

In this issue, the study by Estrada-Medina and coworkers on root distributions in a seasonally deciduous forest of Yucatán, México, is challenging many models of root system form and function. The team examined root distributions in an environment not usually the focus of below-ground studies, the rocky subsoil of the limestone karst that pervades the Yucatán peninsula. They did so by examining the freshly exposed rock faces of a limestone quarry over the course of 1 year and painstakingly quantified the abundance of various karst features, their capacities for water storage, accessibility to roots and seasonal changes in water content. They also quantified the abundance of excised root tips across karst features. The study provided a rare glimpse into rhizosphere organization in a setting where root systems have highly reduced capacity for spatial self-organization.

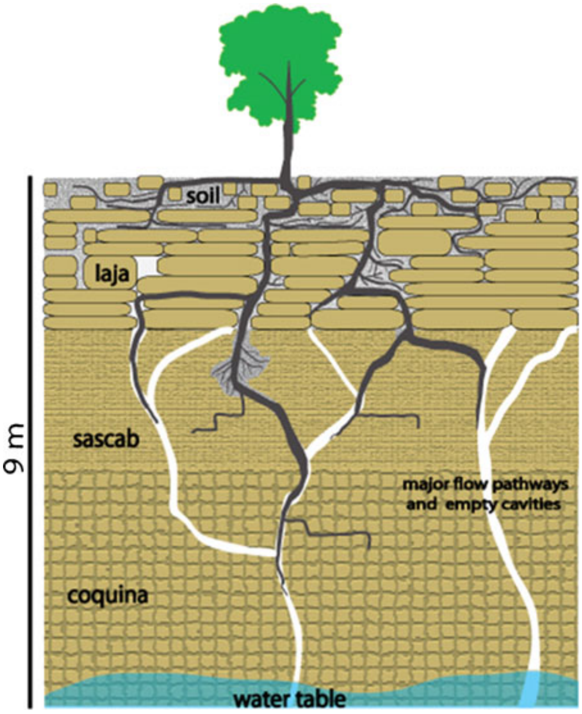

Fig. 1 Schematic representation of the rhizosphere in the Yucatán karst

The study portrayed a belowground environment with a surprising diversity of materials beneath a 30 cm soil horizon (Fig. 1). This included a 2.5-m thick layer of hard, highly fractured rock (laja) just below the soil, followed by a 2.5-m thick layer of porous, soft rock with high storage capacity for water and fragile enough to permit root growth through the matrix (sascab), and another 4-m thick layer of porous rock with less storage capacity due the presence of larger, freely draining pores (coquina) that was at times continuous with the water table. In addition, solution-enhanced cavities of various sizes were strewn throughout all three rock layers and were either empty or, most often, soil filled. The authors' research question was well taken: how do roots utilize this heterogeneous matrix of materials?

As several other studies have also shown (reviewed by Schwinning (2010)), the storage capacity of subsoil materials was substantial, 296 mm at a minimum over 9.3 m depth, of which only 36 mm (12 %) was contributed by the thin and rocky soil cover. Twice as much, 72 mm (24 %) was contributed by soil pockets enclosed at various depths in the limestone rock, while the largest capacity for storage, about 40 %, was located in the intermediate sascab layer.

Roots were strongly associated with soil pockets. Only 40 % of the 1,320 examined rectangular segments on the rock face were classified as containing cavities, but they contained 80 % of all 1,394 counted root tips. I estimated that root tips inside cavities could have been 11–26 times more concentrated than in rock, and that root tips became progressively more concentrated in soil pockets, relative to the root density in rock with each successive limestone layer (Table 1). The reason for this strong inequality in root distribution between soil pockets and the surrounding rock is almost surely related to the relative inaccessibility of the rock matrix for roots (Bornyasz et al. 2005) but may also reflect a local growth response to the higher nutrient concentration in soil compared to rock (Estrada-Medina et al. 2012). Soil also had much higher plant-available storage capacity for water on a volume basis (i.e. the difference between water content at field capacity and at the permanent wilting point).

On average, 55 % of all roots were found in the shallow laja layer, 38 % in the sascab layer below, and 7 % in the deep coquina layer, combining roots in both rock and soil pockets. Although root densities in the 30 cm soil layer were not assessed, roots appeared to be more evenly distributed by depth than the logistic-dose response curve that describes their distributions in soil (Schenk and Jackson 2002a). Even though the forest in this study was only 15 years old, its rooting depth already far exceeded that reported for tropical deciduous forests in deep soils, which have on average 95 % of all root biomass in the top 1 m. It is likely that given more time, roots could grow to even greater depth, even into the aquifer below (Estrada-Medina, personal communication), supporting Schenk's (2008) generalization that roots in rock go deeper.

In soil-dominated systems, the distinct dynamics of shallow and deep soil moisture, and differences in the physiological and morphological investments necessary to exploit one or the other, enables species to differentiate into distinct hydrological niches (e.g. Schwinning and Ehleringer 2001). One may ask if the more complex structure of the subsoil and its diversity of materials allows species to evolve more diverse niches in rock-dominated ecosystems. Among all 45 possible pair-wise comparisons between the 10 species for which Estrada-Medina reported root counts, I found 27 significantly different root distributions (based on Chi-square analysis, $\alpha=0.05$). Most species differed primarily in root allocation between the shallow laja and intermediate sascab layer. However, two species (*Neomillspaughia emarginata* and *Bursera simaruba*) had proportionally more roots in the deep coquina layer than the other eight species and this pattern was statistically significant. While future studies will have to settle whether species have more diverse root distributions in rock substrates than in soil, the study by Estrada-Medina and coworkers points to some intriguing possibilities.

The high concentration of roots in soil pockets suggests that roots are competing for occupancy of this relatively rare but obviously important karst feature (Table 1). Poot and Lambers (2008) recently presented evidence of specialized rooting patterns in species endemic to rocky outcrops, involving more vigorous root growth above rock surfaces presumably to enhance the ability to locate fractures. But some of

Table 1 Measured and estimated root distributions across karst features based on information given in Figure 2 and Table 5 (Estrada-Medina et al. 2012)

	Laja	Sascab	Coquina
Number of sections classified as containing EC/SP (%)	56.5	50.8	9.0
Area photographically estimated as being EC/SP (%)	12.6	14.4	2.0
Estimated fraction of actual EC/SP area in sections classified as containing EC/SP (%)[a]	22.3	28.3	22.2
Root tip density in sections classified as containing only rock (# m^{-2})	0.62	0.36	0.09
Root tip density in sections classified as containing EC/SP (# m^{-2})	2.03	1.60	0.58
Estimated root tip density in EC/SP area (# m^{-2}) [b]. In brackets: as multiples of root densities in rock for that layer.	6.94 (×11)	4.74 (×13)	2.30 (×26)

EC/SP empty cavities and/or soil pockets

[a] This value is calculated by determining what the % area of EC/SP in sections classified as containing EC/SP would have to be to match the EC/SP fraction determined by image analysis (e.g. for column 1: 22.3 % of 56.5 is 12.6)

[b] This value is calculated by assuming that the rock fraction of sections classified as containing EC/SP has the same root density as sections classified as containing only rock (e.g. in column 1: (1–0.223)*0.62+0.223*6.94=2.03)

the species found by Estrada-Medina and coworkers are broadly distributed, among them, *B. simaruba*. It would be fascinating to determine whether broadly distributed species have karst-ecotypes with distinct adaptations of root growth similar to those exhibited by karst endemics.

We can only speculate how the complex belowground structure of karst landscapes might change the nature of competition for water and nutrients. It is possible that the pathways for roots through rock are so scarce that roots of different individuals rarely come into close contact, except in the soil horizon. If so, random effects, related to the chance encounter of soil pockets could dominate the competitive hierarchies of trees, comparable to drawing the winning ticket in a lottery. An alternative model is that fractures actually channel the roots of neighboring trees towards the same soil pockets. Pathways for water flow and root growth through rock are largely identical, and the formation of cavities by dissolution requires a high degree of connectivity between cavities and surface water. If soil pockets frequently contain the roots of several species, belowground competition could be very intense, as competitor "avoidance" ceases to be a viable strategy (Novoplansky 2009). Instead, competitive interactions below ground could be dominated by pre-emptive resource competition, which rewards those individuals that consume limiting resources at a faster rate (Schwinning and Weiner 1998).

The distribution of root systems across materials of different water content invites speculation about the importance of hydraulic redistribution in these systems. For example, it would be very useful for plants to redistribute rock-stored water into soil pockets to keep alive mycorrhizal hyphae (Querejeta et al. 2007) and facilitate nutrient uptake (Scholz et al. 2008). Models show that the efficacy of hydraulic redistribution depends on low pathway resistance, as well as water potential gradients (Doussan et al. 2006; Ryel et al. 2002). Thus, unsaturated rock matrix is an unlikely source of water for hydraulic lift, since the hydraulic conductivity from the rock matrix to the root is quite low (Hubbert et al. 2001). On the other hand, where deep roots meet with a water table, water uptake has been shown to be enhanced through lowered axial hydraulic resistance and the participation of aquaporins in water uptake (McElrone et al. 2004, 2007).

The patterns of water availability and use in seasonally dry, soil dominated systems without groundwater access have been reasonably well approximated by two-layer models with shallow soil layers that are rapidly recharged and depleted, and deeper soil layers, which due to lower root density and less frequent recharge, tend to be governed by seasonal fluctuations (Neilson 1995; Noy-Meir 1985; Walter 1971). In the transition from the wet to the dry season, ecosystem water use shifts from shallow to deeper soil moisture (Chimner and Cooper 2004; Davidson et al. 2011; Giambelluca et al. 2009; Nippert et al. 2010), and in the absence of disturbance, vegetation density adjusts so that soil water reaches the same minimum at the end of the dry season, corresponding to the extraction limit of the community (Neilson 1995; Seyfried et al. 2005). If water does drain out of the deep layer, it is assumed forever beyond the reach of roots. The study by Estrada-Medina and coworkers allows us to examine how well this model may apply to rock-dominated landscapes, despite the structural differences.

Soil pockets became recharged well into the wet season. In this, they were dynamically similar to deeper layers on a uniform soil column, which become recharged only after shallower layers have been saturated. However, unlike deeper soil layers, water in soil pockets was also rapidly depleted, probably due to the high root concentration. This generated pulse-like dynamics in soil pockets, but different from pulses of shallow soil moisture, pulses in soil pockets lagged months behind the beginning of the rainy season. The shallow laja layer recharged immediately after rainfall, consistent with being recharged by macro-pore flow, but depletion was more gradual, likely due to root confinement to fractures. The intermediate sascab layer had relatively little water stored during the entire study period, and there was no strong seasonal signal in moisture fluctuations. This and the fact that root density was far more dynamic in the shallow laja layer makes it likely that plants took up water chiefly from the top soil and the laja layer during rainy periods, shifting briefly to deeper soil pockets at the end of the rainy season, and possibly back to the laja layer before entering the dormant stage.

Though the data collected by Estrada-Medina and coworkers do not offer much temporal resolution due to high sample variance, it is clear that woody plants used shallow, dynamic water sources distributed between the top soil and shallow rock layers during the rainy season, and deeper sources during the dry season, also composed of a mixture of soil and rock sources. Switching between shallow and deeper water sources has also been reported in other karst studies (Nie et al. 2011; Querejeta et al. 2007). Thus, while recharge and storage in karst is certainly more complex than in soil-dominated ecosystems, the generalization that shallow sources are recharged and taken up first, and deeper sources only when shallow sources have become sufficiently depleted, seems to hold just the same, and is essentially in agreement with the two-layer model.

However, the enigma of Estrada-Medina's data set is the sascab rock, which held far less water during the study period than it was capable of holding. The water content for rock in this layer was between 0 and 20 %, almost always below the reported extraction limit of ca. 19 % (the permanent wilting point) for this material. The sascab layer probably contributed little to tree transpiration in the year of the observation, but this could have been different in another year. Recharge of the entire rock profile happens when hurricanes pass over the region, about once every 10 years (Estrada-Medina, personal communication). It is unknown how long water is retained in the sascab after such recharge events.

Ruiz et al. (2010) concluded through modeling the water balance of a monsoonal, seasonally dry deciduous forest in India, that the water content of regolith, deep below the soil layer but still accessible by deep roots, could fluctuate with periods in excess of a decade. If this model applies to the Yucatán karst, there could be extended wet periods during which the forest is well buffered in the dry season and extended dry periods during which the dry season may have more detrimental effects on woody plant survivorship and recruitment. For predicting the future of tropical and subtropical karst ecosystem under novel climate conditions, it would seem very important to determine how the potentially large water reservoirs in the subsoil become recharged, how long they hold on to water, and how much they give up to plant roots in a given year to subsidize transpiration (Jarvis 2011).

For hydrological modeling, we must consider that the storage capacity of all materials in the rhizosphere may overestimate the amount of water a community can realistically extract in 1 year, not for lack of evaporative demand but for lack of hydraulic conductance between rock and root. Rock-dominated landscapes could have unexpectedly long memories for antecedent precipitation. This would be a significant departure from the two-layer model, which assumes that precipitation, evapotranspiration and drainage approximately balance to zero on an annual basis.

Karst and other landscapes in which plant transpiration is in part supported by weathered bedrock are surprisingly common globally (Schwinning 2010). Karst, barrens, and rocky outcrops of various geologic origins contain unique communities of high diversity and endemism, the Yucatán peninsula being one of many examples. What is the future of these communities in the warmer, drier or hydrologically more extreme environment that climate models predict? Will their response be qualitatively different from that of soil-dominated systems? The usually more drought-adapted vegetation of karst, together with a potentially large but slow to exchange reservoir of plant-available water, may buffer rock-dominated systems better against drought episodes under some circumstances, but they may also be more devastated by extreme or multiyear drought conditions. In the karst system of the Edwards Plateau, Texas, USA, intermittent drought conditions that began in 2000 had unremarkable effects on woody vegetation—up until the summer of 2011, when tree die-off was sudden, vast and did not spare the most drought-tolerant species (Nielsen-Gammon 2011; Edgar and Carraway 2011). To predict the vulnerabilities of these ecosystems to climate change, we need more information of the type collected by Estrada-Medina et al. (2012), as a basis for developing vegetation models that more adequately represent the subsoil rhizosphere.

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