Ecohydrology Bearings - Invited Commentary

The ecohydrology of roots in rocks

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ABSTRACT

Large portions of the world are characterized by shallow soil underlain by weathered bedrock or cemented soil horizons. The implications of this substrate condition for ecohydrological processes have not been systematically explored, but misrepresentation in models could have profound consequences for climate prediction and global vegetation modelling. An issue of particular uncertainty is the characterization of water storage for these regions. A limited number of case studies have shown that plant water uptake is not restricted to shallow soils but can involve uptake from rock layers below. The mechanisms governing root–rock interactions are only beginning to be investigated. Research is needed to further characterize the dynamics of water recharge and depletion in weathered bedrock, to develop a better understanding of plant adaptations and rooting patterns required for effective use of bedrock-stored water, and to explore consequences for below-ground competition. Copyright © 2010 John Wiley & Sons, Ltd.

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INTRODUCTION

A quintessential topic in ecohydrology concerns the effective rooting depth of ecosystems. This variable plays a clearly defined role in hydrology by constraining the hydrological system's storage capacity for water (Seyfried and Wilcox, 2006). Rooting depth is an emergent property of ecohydrologic systems, arising from the interactions of infiltration and plant water uptake as affected by soil properties, climate, and plant adaptations (Schenk and Jackson, 2002b). The water balance equation demonstrates the hydrological role of water storage, the left-hand term in the following equation:

$$nZ_r \frac{ds}{dt} = I(s, t) - ET(s, t) - L(s, t) \qquad (1)$$

where s is the relative soil moisture content (scaled from 0 to 1 for water contents between the permanent wilting point and field capacity, the 'plant-available' fraction of soil water), n is soil porosity, Z_r is the rooting depth, $I(s, t)$ is the infiltration rate for precipitation, $ET(s, t)$ is the evapotranspiration rate including transpiration, soil evaporation, and interception, and $L(s, t)$ is the net rate of loss by overland flow and deep drainage (after Rodriguez-Iturbe, 2000). Changes in the amount of water stored in the root zone temporarily buffers any imbalance between ET and I, so that precipitation in excess of potential

ET (ET_0), due to seasonal or stochastic patterns of precipitation, can be stored locally and, instead of being immediately lost by runoff or drainage, can exit the system by evapotranspiration sometime later.

What makes the determination of rooting depth, and thus storage capacity, both interesting and challenging is the dynamic and variable nature of rooting depth. While porosity n is a relatively fixed characteristic of place, determined by long-term pedological and geological processes, rooting depth by contrast is a highly dynamic characteristic that varies by species (Schenk and Jackson, 2002a) and on shorter than geologic time scales with climate and vegetation (Viola *et al.*, 2008; Jackson *et al.*, 2009). Ecologists have long presumed that vertical root distributions of natural vegetation are optimized to local climate and soil texture, although opinions still vary regarding the most appropriate objective function to predict rooting depths (e.g. Kleidon and Heimann, 1998; van Wijk and Bouten, 2001; Laio *et al.*, 2006, Collins and Bras, 2007; Schenk, 2008b). Nonetheless, the range of predicted patterns is similar and fit observation, which Milly and Dunne (1994) and Milly (1994) summarized by saying that rooting depths (with some exceptions) are *almost* large enough to maximize ET, consistent with Schenk's (2008a) argument that plants favour shallow over deep root systems.

Although the conversion of theory and data for regions where root systems develop freely through deep soils is encouraging, it excludes from consideration large portions of terrestrial landscapes that are characterized by shallow soils overlaying substrates that impede

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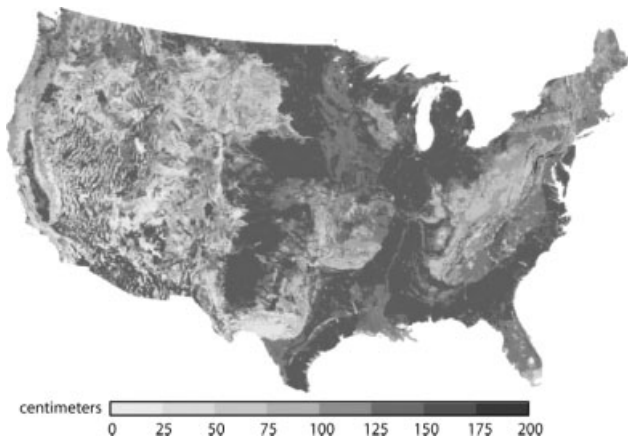E-mail: schwinn@txstate.edu

Figure 1. Depth to bedrock based on the State Soil Geographic Database (STATSGO) developed by the US Department of Agriculture–Natural Resources Conservation Service (reprinted from Miller and White, 1998, courtesy of *Earth Interactions*).

water movement and root growth, typically bedrock, cemented horizons, or strongly developed argillic horizons (Figure 1). Furthermore, many of the areas with a potentially restrictive soil depth of <1 m are in water-limited climate regions with seasonally uneven precipitation where adequate storage capacity is critical for maximizing *ET* and primary productivity. The consequences of this surface condition for vegetation processes and hydrology are the focus of this commentary.

Although many studies have been conducted on landforms with shallow soil, they often took a geographically narrow focus, emphasizing either hydrological processes or ecological patterns, but seldom both. A notable exception to this generalization is the comprehensive body of work produced by Graham and coworkers on the granitic bedrocks of California (e.g. Graham *et al*.,1997; Hubbert *et al*., 2001; Rose *et al*., 2003; Bornyasz *et al*., 2005; Graham *et al*., 2010). I submit that the development of an integrated ecohydrological framework for regions with shallow soils underlain by substrates of uncertain water storage capacity is a fruitful new direction for ecohydrological research. It promises to achieve a more general understanding of the rules that govern plant development, form, and function, particularly of plant roots, and improve the way that increasingly accurate and extensive soil data can be incorporated in hydrological models.

Hydrologic effects of limited storage capacity

Hydrologists are well aware that soil saturation generates runoff and drainage at the expense of *ET*, per Equation (1). Soil saturation is common in wet climates, where annual precipitation P_a far exceeds annual potential evapotranspiration ET_{0a}, but runoff by saturation excess can also occur in dry climates if storage capacity is low. Dry climates typically alternate between wet and dry seasons, causing annual cycles in stored water that reach a maximum at the end of the wet season. When wet season precipitation exceeds storage capacity, less water will be available for dry season *ET*. Thus, storage capacity controls the partitioning of annual precipitation

P_a into ET_a and annual loss L_a: the smaller the storage capacity relative to P_a, the more often will cumulative precipitation exceed storage capacity, thus decrease ET_a and increase L_a (Milly, 1994).

The effect of storage capacity on the water budget is maximized in regions where $P_a \approx ET_a$ (Milly, 1994; Figure 2A) as factors other than storage capacity limit ET_a, both in wet regions (energy) and dry regions (P_a). However, the effect of storage capacity on the proportion of transpiration in evapotranspiration, T_a/ET_a, while it may also be small in the wettest regions, is likely to persist in dry regions (Figure 2B). In wet regions, root systems are shallow compared to infiltration depth (Schenk, 2008a), therefore reductions in storage capacity will have no effect on transpiration, unless layers that restrict the root development come within decimeters of the soil surface. However, dry regions, particularly if winter-wet and summer-dry, have some of the deepest root systems on earth (Schenk and Jackson, 2002b), probably approaching maximal infiltration depth to optimize water capture. In this case, a physical barrier to root development, even if several meters below the surface, could cause a noticeable reduction in transpiration and productivity, equivalent to a reduction in rain use
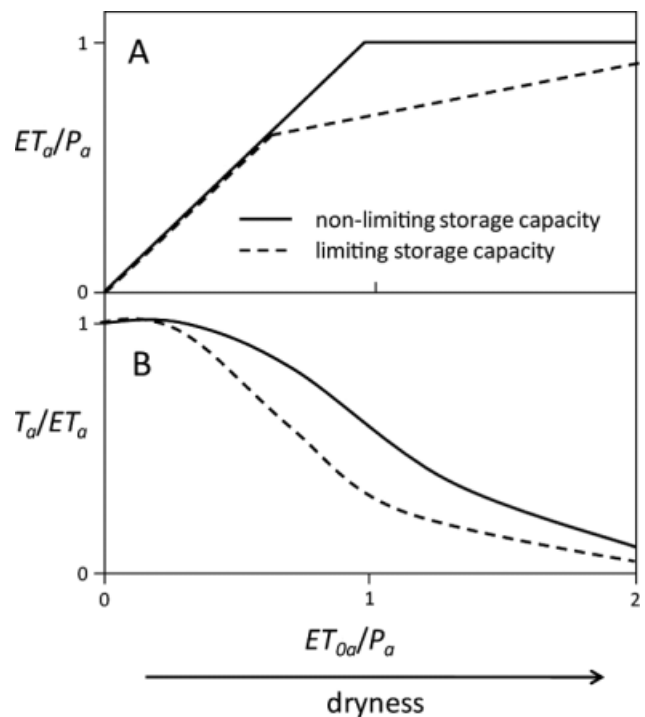

Figure 2. Effects of reducing storage capacity to a fraction of maximal infiltration depth. Abbreviations as follows: ET_a, annual evapotranspiration; ET_{0a}, potential annual evapotranspiration; P_a, annual precipitation; T_a, annual transpiration; *LAI*, leaf area index. (A) The effect of storage capacity limitation on ET_a/P_a is maximal in regions where $ET_{0a}/P_a \approx 1$ (after Milly, 1994). In wet regions, ET_a is energetically constrained and $ET_a = ET_{0a}$. In dry regions, ET_a is constrained by P_a and $ET_a \rightarrow P_a$. (B) The effect of storage capacity limitation on T_a/ET_a also becomes maximal where $ET_{0a}/P_a \approx 1$, but persists in dry regions. In wet regions, $T_a \approx ET_a$ since a high *LAI* minimizes soil evaporation. In dry regions, ET_a is increasingly dominated by soil evaporation as *LAI* declines and bare soil becomes exposed (Huxman *et al*., 2005).

efficiency (RUE; annual productivity divided by annual precipitation; Le Houérou, 1984).

Limitations of rooting depth and storage capacity have effects far beyond regional water partitioning. In one spectacular example of climate sensitivity to storage capacity, Kleidon and Lorenz (2001) showed in a model that assumptions of rooting depth for trees of the Amazon rainforest have profound consequences for forest persistence through a colder, drier glacial period. When roots in the model were 1–2 m deep, the rainforest was replaced by savanna, as the rate of moisture return to the atmosphere declined and the tropical climate turned drier. When roots were 5–10 m deep, the rainforest persisted, and climate in the tropics remained comparatively cooler and wetter.

Misrepresentations of storage capacity may have similarly dramatic effects on predictions of future climate and global biome distributions (Milly and Dunne, 1994; Feddes et al., 2001; Pitman, 2003). Uncertainties regarding rooting depths and storage capacities have been addressed in part by using increasingly accurate and detailed soil maps in models. However, this approach still overlooks the potentially important storage component of plant-extractable water below the soil horizon.

Water storage beyond soils
Since the earliest scientific investigations of plant roots in natural environments, it has been known that the roots of woody perennials grow through fractured rock, or breaks in caliche or other hardpan layers, presumably to access water (Cannon, 1911; Phillips, 1963). Recent technological advances have made it possible to estimate in some cases the contribution of rock-stored water to plant transpiration (Table I). However, on the whole, as Sternberg et al. (1996) pointed out, water capture from below the soil horizon is still mostly overlooked as an ecosystem component. The hand full of studies that attempted to quantify water use from weathered bedrock, not coincidentally all from seasonally dry regions, show substantial use of bedrock water, which is maximized during the dry season when soil water has become depleted beyond the plant extraction limit (Table I).

Several studies have now shown quite clearly that non-soil substrates can and do store large amounts of water, including weathered granite (Graham et al., 1997), epikarst (Klimchouk, 2004; Bonacci et al., 2009; Jacob et al., 2009), and petrocalcic horizons (Hennessy et al., 1983; Duniway et al., 2007). All these substrates have water storage capacities typically in the range of $0.1–0.2$ m^3 m^{-3}, comparable to coarse-textured soils, but with much smaller pore sizes that resist root penetration and confine root growth to macroscopic fractures. It is the rigidity of the porous matrix in weathered bedrock rather than pore size *per se* which prohibits root growth, as cell expansion in growing root tips does not have enough force to enlarge pores, which it does in pliable soils. By contrast, some highly weathered limestone products (clays, marl, sascab) have exceptionally high water storage capacities of $0.35–0.50$ m^3 m^{-3} (Querejeta et al., 2006) and do permit fine root penetration, thus are arguably proper soils, although they may be sandwiched between layers of impervious limestone.

Water-storing layers of regolith, epikarst, and cemented soil horizons can be several tens of meters thick, and have the potential to hold at least as much water as a meter of soil. The critical question from the viewpoint of water balance (Equation 1) is how much of this water is available to plants. For soils, Equation 1 implies that all soil water between the surface and the maximal rooting depth, and between field capacity and the permanent wilting point, is plant-available. Without physical barriers to root growth in the soil, root systems can reach anywhere and adjust root length densities to swiftly and uniformly deplete soil water content, or at least nearly so (Breshears et al., 2009a). This assumption may not be valid for impervious substrates where pathways for root growth proliferation are few and far between (Figure 3). Although roots have seemingly limitless capacity to grow along vertical cracks—in one famous example, mesquite roots were found nearly 60 m below the original surface in an open pit mine near Tucson, Arizona (Phillips, 1963)—the amount of water accessed by a deep root may nevertheless be small, except in situations where the root meets up with the capillary zone of a shallow

Table I. Estimated proportional water uptake of shrubs or trees from regolith.

System	Climate zone	AAP (mm)	Soil depth (m)	Regolith water use (%)	Citation
Chaparall, southern CA, USA	Mediterranean	550	0·35	91	Sternberg et al., 1996
Ponderosa pine forest, Sierra Nevada, CA, USA	Mediterranean	750	0·4–1·2	70	Witty et al., 2003
Jeffrey pine plantation, Sierra Nevada, CA, USA	Mediterranean	760	0·75	70–100	Hubbert et al., 2001; Rose et al., 2003
Oak-juniper woodlands, Central Texas, USA	Sub-humid	800	0·15–0·50	up to 100	McCole and Stern, 2007; Schwinning, 2008
Tropical deciduous forest, Yucatan, Mexico	Sub-humid	1000	0·15	13–97	Querejeta et al., 2007
Tropical deciduous forest, southern India	Sub-humid	1120	1–2	11	Ruiz et al., 2010

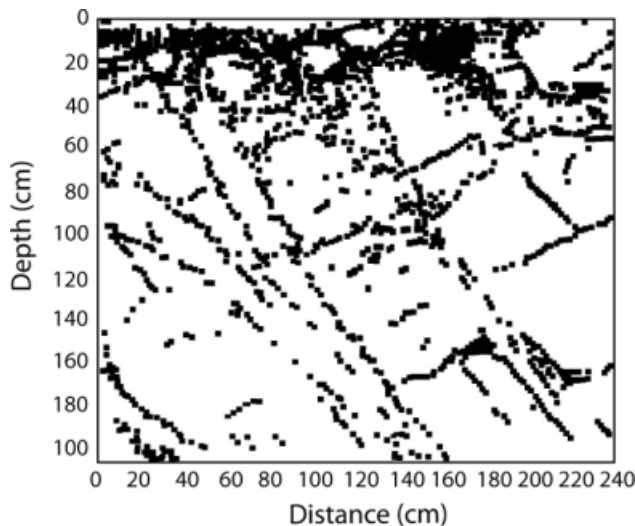Estimates describe dry season conditions. AAP, average annual precipitation.

Figure 3. Map of chaparral root distribution in weathered granitic bedrock. The soil–bedrock boundary is within the 20–40 cm depth. Each point represents a single root intersecting the trench wall. Roots are concentrated in planar fractures typically separated by several decimeters. Redrawn from Sternberg *et al.* (1996), with permission.

groundwater or perched water table (Jackson *et al.*, 1999; McElrone *et al.*, 2007; Querejeta *et al.*, 2007). Thus, the assumption implicit in Equation 1 that storage capacity is proportional to rooting depth, probably does not hold for roots in rock. To understand plant use of rock water, we need to develop a comprehensive theory of root–rock interactions.

Interactions between roots and rocks

Rock substrates are of mixed value to roots. On the one hand, the mechanical impedances of rocks and hardpans severely restrict available rooting space. On the other hand, water stored in or below rock layers is relatively safe from evaporative loss, thus can await slow rates of extraction by root systems. Rooting space in rock is limited by the frequency of fissures that are wide enough to permit root growth. Wide fissures are usually filled with a mixture of coarse grains and organic materials with hydraulic properties much like soil and support correspondingly high root densities (Bornyasz *et al.*, 2005). But most fissures are narrow, forcing root systems to develop into nearly two-dimensional root fans or mats (Figure 4). Zwieniecki and Newton (1994) determined a minimal fissure width for root exploration, which corresponded to the minimal fine root diameter of a species. Interestingly, the two conifers in the study required widths of at least 500 μm, while two angiosperms required fissures of only 100 μm width. Unlike the two conifers, the two angiosperms were able to distort the shape of the root cortex into a flat wing-like shape, which maximized the contact between the root epidermis and the rock (Figure 5). Thus, in the angiosperms, minimal fissure width was determined by the width of the fine root stele, and in the conifers by whole fine root width. Differences in the ability of fine roots to invade fractures may produce species differences

in the efficiency of water extraction from rock, as well as differences in maximal rooting depth, as weathering decreases and fissures become smaller with depth in bedrock.

As mentioned earlier, a number of studies done on the granitic bedrocks of California have shown that the root–rock interface may not be the main pathway for plant water uptake. It was noticed that the rate and uniformity of water loss from the rock matrix was incompatible with a mechanism of passive diffusion from the rock matrix towards root-occupied fissures, as the unsaturated hydraulic conductivity of matrix rock is very low, on the order of 10^{-3} cm h^{-1} (Hubbert *et al.*, 2001; Graham *et al.*, 2010). At this rate, water would take more than a year to travel a 10 cm distance, and it would presumably take much longer to deplete a typical block of matrix rock to a water potential corresponding to the plant extraction limit. Egerton-Warburton *et al.* (2003)
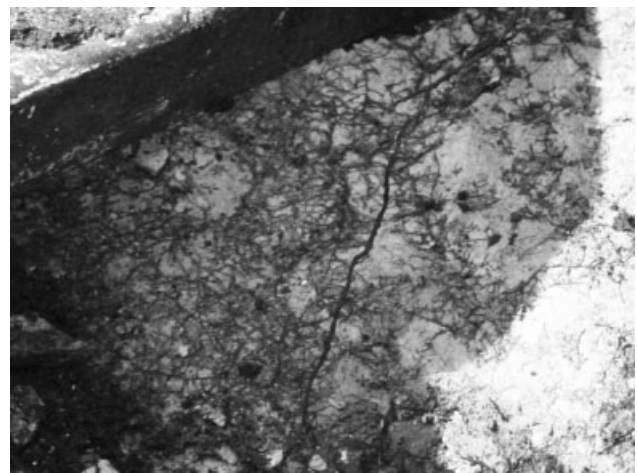

Figure 4. Root mat of Ashe juniper (*Juniperus ashei*) in the Edwards Plateau of central Texas exposed after lifting a large limestone block. Photo by S. Schwinning.
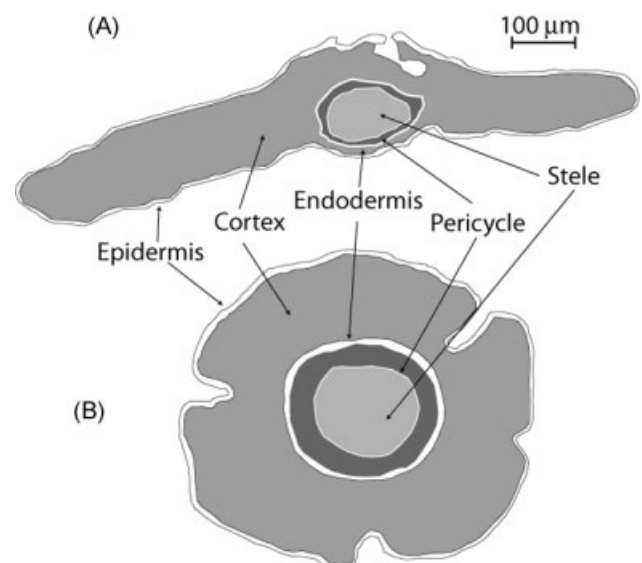

Figure 5. Comparison of roots growing in a narrow fissure (A) and in an unconstrained soil space (B). Redrawn from Zwieniecki and Newton (1994), with permission.

and Bornyasz *et al.* (2005) then found evidence that oaks and chaparral shrubs harness the support of mycorrhizal fungi to extract rock water. Ectomycorrhizal hyphae are much narrower than fine roots (2–10 μm) and can grow up to a meter in length (Allen, 2007). They are therefore able to do what roots themselves cannot: grow deep into the rock matrix and establish numerous pathways for water to travel from the bulk of the rock towards plant roots. According to Allen (2007), the main contribution of mycorrhizal associations in rock is not to decrease path conductivity, as long-distance symplastic transport is still slow, but to decrease the tortuousity of the path, thus decreasing the effective length of the transport pathway.

The ecophysiological implications of mycorrhizal associations on plant–water relations is still controversial (Augé, 2001) and awaits full integration into the theory of water transport (Allen, 2007). Owing to the lack of case studies from other geographical regions, it is also not known how general this mechanism might be for water uptake from other parent materials or from hardpan layers.

Questions for research

How general is the contribution of weathered rock to storage capacity? Detailed case studies on granitic regolith in California (Graham *et al.*, 1997) and petrocalcic horizons in New Mexico (Duniway *et al.*, 2007) have demonstrated the large contribution of non-soil substrates to storage capacity. Data are needed for other lithologies, other cemented soil horizons, and in other geographic locations. Whether or not weathered bedrock fully substitutes for the storage capacity of missing deep soils remains an open question, even in regions where this phenomenon has been well studied.

Given enough time for weathering processes to unfold, the storage capacity of bedrock may be self-organizing to some extent, owing to the role of roots and mycorrhizae in facilitating the weathering process (Bornyasz *et al.*, 2005; Dasgupta *et al.*, 2006). To develop this aspect of ecohydrology further, the contribution of scientists trained in weathering and pedogenic processes would be particularly valuable. In the meantime, existing data sets could be scrutinized for the existence of a 'bedrock signal', for example in any discrepancy between available soil water and *ET*.

What are the dynamics of infiltration and depletion?. Bedrock has at least two components of recharge dynamics, (1) fast infiltration along wide fissures and solution channels that can rapidly transport moisture deep into the bedrock, and (2) slow diffuse transport at the surface and from saturated fissures into the rock matrix (Frazier *et al.*, 2002; Cassiani *et al.*, 2009). The complex structures of epikarst add threshold phenomena where more flow paths become active during higher intensity inputs (Dasgupta *et al.*, 2006). Similarly, there may be multiple components to plant water uptake, with rapid depletion of water from fissures, soil lenses, saturated clay layers or perched

water tables, and a much slower rate of depletion from the rock matrix. Slow depletion of a potentially large storage of bedrock water can create long time lags between recharge and depletion, which would effectively uncouple annual precipitation from annual losses by evaporation and leakage, as seen most recently by Ruiz *et al.* (2010).

What adaptations are needed for water uptake from rock?. The development of plant ecophysiology has been deeply influenced by its historic focus on the soil–plant–atmosphere continuum. The relatively simple spatial and temporal patterns created by the processes of infiltration, evaporation, and plant water uptake in soils have dominated our understanding of plant functional types, for example, the functional dichotomy between deep-rooted, slow-growing drought-tolerators and shallow-rooted drought-avoiders that maximize the use of resource pulses (e.g. Schwinning and Ehleringer, 2001). The ecohydrology of bedrock may challenge some of these stereotypes, by considering critical differences in the mechanisms of recharge and depletion as described above. For one, the division of functional types by rooting depth may not have much meaning in this context, as pathways for root growth are similarly constrained for many woody plant species and depth *per se* may be indicative neither of water availability nor of moisture dynamics.

Several lines of evidence suggest that plants require specific adaptations to grow well on shallow soils over bedrock. Thin and deformable fine roots may be required to effectively extract water from narrow fissures (Zwieniecki and Newton, 1995). The ability to form mycorrhizal associations may be critical as well (Bornyasz *et al.*, 2005). Successful establishment on a thin soil may also require a comparatively high investment in deep root growth to search the soil–rock interface for entryways into the bedrock (Poot and Lambers, 2008; Schenk, 2008a).

Some of the adaptations required for tolerating shallow soils and/or exploiting bedrock water may be maladaptive in deep soils, and conversely, adaptations associated with the exploration of deep soils may be maladaptive in shallow soils (Schenk, 2008a). For example, mesquite (*Prosopis sp.*) is among the species more sensitive to restrictions of soil depth, owing to the inability to develop sufficiently deep root systems, even where weathered bedrock is present (Eggemeyer and Schwinning, 2009). Strongly expressed gravitropism in the taproots of this facultative phreatophyte (Smith *et al.*, 1997) may hamper its chances of finding pathways into the bedrock as suggested by Schenk (2008a). In the Chihuahuan Desert, soil depth determines the balance between mesquite and grass cover, with mesquite excluded from soils that are less than 15 cm deep, and mesquite cover increasing linearly with soil depth above the 15 cm threshold (Molinar *et al.*, 2002; Khumalo *et al.*, 2008).

As we examine the global importance of storage in bedrock, ecophysiologists are called upon to re-evaluate and perhaps expand the characterization of plant

functional types to include traits related to the ability to either cope with limitations of soil depth or else root in bedrock.

Do the rules of optimal root allocation change for roots in rocks?. Predictions of root distribution have drawn considerable research interest in recent years (van Wijk and Bouten, 2001; Laio *et al.*, 2006; Collins and Bras, 2007; Guswa, 2008; Schenk, 2008b), not the least for their application in global vegetation and climate modelling. However, all predictions have been formulated on the assumption of unlimited soil depth. It is not clear if or how root development in weathered bedrock changes the outcome of the underlying cost-benefit analysis, but some considerations suggest they may: (1) Root growth through deep fissures may meet much less mechanical resistance than root growth through deep soils, because comparable open void space for root growth is generally not available in soil material. (2) Roots in deep fissures may be longer-lived because of the absence of many root consumers and burrowers. (3) Deep roots may have higher water uptake per biomass investment since water infiltration is funnelled along the same narrow spaces as are occupied by roots. (4) Root xylem may have to be more cavitation resistant, since low unsaturated hydraulic conductivities of the rock matrix call for the establishment of steep water potential gradients, except where (5) Deep roots tap into perched water tables and should maximize transport efficiency instead (McElrone *et al.*, 2007). Integrating these changed constraints and trade-offs into a more general theory of optimal root allocation may require a different kind of modelling paradigm, one that departs from associating rooting depth with preconceived patterns of water availability and moisture dynamics (e.g. shallow roots → high amplitude pulse dynamics, deep roots → low amplitude seasonal dynamics).

The new approach may divide the total available storage volume into weakly linked dynamically distinct storage classes (e.g. soil cover, fracture space, rock matrix, water table, etc), each characterized by total storage capacity, a characteristics frequency of water input as a function of climate, and an effective hydraulic conductivity function for the relevant root interface, keeping in mind that water transport systems are always bidirectional (Caldwell *et al.*, 1998; Allen, 2009). A step in this direction was recently taken by Brooks *et al.* (2010) after recognizing isotopically separate pools of water with distinct and complex recharge and depletion dynamics. The division of total storage into storage classes can avoid the implicit link between rooting depth and moisture dynamics without excluding the possibility of attaching distinct cost factors (to account for rooting depth or mycorrhizal involvement) to the exploitation of specific storage classes.

Do the rules of below-ground competition change?. Root competition for soil water and nutrients has been well studied and some robust principles have emerged. When plants compete for soil water they do so either (1) directly by depleting the availability of soil moisture to their neighbours, or (2) indirectly by exuding chemicals that suppress the growth of non-self roots in their vicinity (Mahall and Callaway, 1992). Plants can also (3) avoid or reduce competition for soil water by outgrowing the root system of some competitors as usually happens between shallow-rooted herbaceous and deeper-rooted woody species (Walter, 1954). More generally, and in the language of game theory, plants can make strategic decisions to avoid, confront, or tolerate competitors (Novoplansky, 2009). Resource competition occurs where zones of influence overlap (Casper *et al.*, 2003) and the species that can draw down resources faster or to lower levels wins a greater portion of the resources in a zone of overlap (Schwinning and Weiner, 1998), or wins the competition outright where zones of influence overlap widely (Tilman, 1982). More than a decade ago, Casper and Jackson (1997) commented on the uncertain role of mycorrhizal associations for competition below ground; we know little more now than we knew then. The net worth of symbiotic relationships tends to depend on a fine balance between resource deficiency and carbon excess in the host plant, so consequences for competition may be varied and case specific (de Mazancourt and Schwartz, 2010). However, where networks of fungal hyphae create connections between individuals, including between different species, one might expect competition not necessarily reduced but rather homogenized among a larger number of individuals.

Competition in a physically constrained below-ground environment can be quite a different game. Although the spatial separation between the root systems of short-lived herbaceous plants (which tend to remain confined to soils) and longer-lived woody perennials (which can grow into bedrock) still holds, among woody perennials with roots in rock, competition may play out very differently. First, zones of influence are much less under the control of the plant but dictated by the frequency of suitable fissures. This may constrain the ability of woody species to realize niche differentiation based on differences in the geometry and architecture of root systems, as discussed by Casper *et al.* (2003) and Novoplansky (2009). However, to possibly balance this effect, spatial constraints may often separate individual root systems entirely, thereby increasing the effect of self-limitation and decreasing the effect of interspecific competition. This could promote alpha diversity (Huston and Deangelis, 1994) and offers one additional explanation for the persistence of competitively inferior species in communities with minimal soil (Poot and Lambers, 2003; 2008). However, competitive isolation would be minimized by the actions of mycorrhizal fungi which can extend effective zones of influence beyond average plant distances and across large blocks of bedrock.

Limits to woody plant cover may be set by the availability of gaps in the bedrock, rather than by resource levels, making competition less about rates of resource capture and more about space preemption.

Thus, successful establishment may depend on a seed germinating close to a major unoccupied gap through the bedrock, and less on protracted resource competition. Once a gap is occupied, subsequent arrivals may simply not establish. This may suggest a stronger role for seed numbers and dispersal in deciding competitive outcomes within the context of the lottery model of competition (Chesson, 2000).

CONCLUSIONS

Is the water storage capacity of semi-arid regions limited by the presence of shallow soils? A cursory glance at the soil depth map for the United States (Figure 1) might suggest significant reductions, if not for ET_a, then for T_a/ET_a over large portions of the western half of the United States. However, the map does not account for the storage capacity of rock strata below the soil. Limited evidence to date suggests that trees and shrubs take up substantial amounts of water from weathered bedrock after soil water has become unavailable (Table I). Thus, Milly's (1994) insight that 'the rooting depths of plants (a crucial determinant of plant-available water-holding capacity) reflect ecologically optimized responses to the relative timing and magnitude of water and energy supplies' still rings true. It suggests that plant-available water-holding capacity is a strong self-organized attribute of ecological systems, and that plants lacking in soil moisture keep expanding their root systems in the rock layers below, widening gaps by exposing more rock surfaces to solution weathering, until water demands are met or water simply runs out.

The set of ecosystems genuinely limited by storage capacity may thus be much smaller than Figure 1 suggests and include hilltops, hill slopes, barrens, glades, rehabilitated open mine sites, where for whatever reasons (topography, parent material, time) bedrock weathering has been minimal. Though perhaps limited in extent, these regions are intrinsically interesting places for research on plant–rock interactions. Recently 'rehabilitated' open mine sites could be used as natural laboratories for studying the evolution plant–rock interactions in real time.

There remains one aspect of water storage in bedrock that may yet turn out to be globally important and different from soil water storage. Since bedrock water stores can be at once large and slow to recharge and deplete, they may exhibit long response lag times. Groundwater hydrologists are very familiar with lag times exceeding 1 year, but they have been largely ignored by surface hydrologists (Seyfried and Wilcox, 2006). Multi-year lag times in surface hydrological processes, if real, would provide a simple hydrological mechanism for explaining increasingly severe effects of successive drought years on vegetation, including on tree mortality (Breshears *et al.*, 2009b).

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