



A critical question for the critical zone: how do plants use rock water?

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Abstract

Background The paper by Korboulewsky and co-authors in this issue of *Plant and Soil* address some of the central questions of critical zone ecohydrology: how do plants interact with rocks that exclude roots but hold plant-available water?

Scope I compare plant water uptake from stony soils and fractured bedrock in the critical zone, suggesting that the two cases may represent endpoints of a continuum along which the proportion of available space for root growth changes.

Conclusions Rhizosphere models could be improved and generalized by structuring the layers of the critical zone into volume fractions that can be rooted and fractions from which roots are excluded. I hypothesize that plant-available water capacity of the rooted fraction governs productivity, while plant-available water in the unrooted fraction governs drought resilience.

Keywords Fractured bedrock · Model · Mycorrhizae · Plant-water uptake · Rhizosphere · Rock water · Stony soil

Plant roots and rocks have a complex relationship. Roots enhance the chemical weathering of rock by

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transporting assimilated carbon underground, where plants and microbes release CO₂ and organic acids. Acidic water dissolves minerals in rocks, opening pore space in the rock matrix (Hasenmueller et al. 2017; Koele et al. 2014). In time, as pores become increasingly connected, the tortuosity of the flow path for water declines and decreases the resistance to flow in and out of the rock. At this stage, weathered rock, while still having the rigidity of rock, can readily take up, store and release water (Graham et al. 2010; Jones and Graham 1993). Meanwhile, the cell pressures of living roots expand flow paths through weathered materials and physical forces drive the weathering front further into fresh bedrock (Phillips et al. 2019). In this way, through the relentless activities of innumerable roots, their associations with other biota and interaction with physical processes, Earth's critical zone is created; the thin reactive transition zone between the land surface and bedrock, within which water circulates and fresh rock is continually exposed to chemical weathering (Grant and Dietrich 2017).

Processes that happen deep in the critical zone are difficult to observe, but some of the interactions between roots, rocks and water are also observable in shallow, stony soils. There are similar knowledge gaps in the ecohydrology of stony soils and of the deep critical zone (Dawson et al. 2020; Zhang et al. 2016), both grappling with the fact that there are two pore domains that contain water for plants. In one domain, pores are sufficiently wide, connected and/or pliable enough for growing root tips to navigate and populate strategically, presumably to shorten the transport

pathway between roots and their water (and nutrient) sources (Dunbabin et al. 2013). This pore domain, by definition, is soil (SSSA 2020). The other pore domain physically excludes roots (= ‘rock’), which alters the dynamics of water extraction by plants in ways that are not well understood (Tetegan et al. 2011). *How much water do plants draw from rocks and under what climatic circumstances? What are the pathways through which water moves from rock to the root surface? Does rock water contribute significantly to site productivity or does it mainly help to keep plants hydrated during drought? And related, how should the rock fraction of plant-available water capacity (PAWC) be represented in models?*

The paper by Korboulewsky and co-authors in this issue of *Plant and Soil* (Korboulewsky et al. 2020) and its companion article (Tetegan et al. 2015) address some of these questions by way of a greenhouse experiment. Poplar saplings (*Populus euramericana*) were raised in 3 L pots from cuttings. Pots were filled with fine earth and 0, 20 or 40% rock fragments by volume (Fig. 1). The rock fragments were composed either of limestone pebbles with a plant-available water capacity of $0.07 \text{ cm}^3 \text{ cm}^{-3}$ or inert quartz pebbles. The fine earth fraction had a PAWC of $0.17 \text{ cm}^3 \text{ cm}^{-3}$. Thus, the combined PAWC per 3 L was approximately 510, 450, 408, 390 and 306 cm^3 for the 100% soil, 20% limestone, 20% quartz, 40% limestone and 40% quartz treatments, respectively.

Plants were grown for 60 days under conditions of moderate water-limitation (40% of PAWC), then briefly brought to field capacity by capillary rise, then not watered for 13 days. During this first desiccation interval, pots were sampled repeatedly to track the depletion of soil and rock water content (Tetegan et al. 2015). After another brief interval at field capacity, watering was halted for another 15 days, after which all plants were harvested. Leaf conductance was tracked over both the first and second desiccation intervals.

Having the quartz control was an excellent experimental design feature, since it allowed the separation of effects stemming from the reduction in soil volume and rooting space, which was the same at a given rock fraction, and PAWC, which was higher for mixtures with limestone than with quartz. Across experiments examined by the Poorter et al. (2012) meta-analysis, past a threshold of ca. 2 g of biomass per L of soil volume, a 50% reduction in soil volume decreases plant biomass by about 30% on average. This threshold was exceeded in some of the treatments in Korboulewsky et al.’s experiment (Korboulewsky et al. 2020: Table 3). Plant growth was clearly reduced in pots containing rocks relative to the all-soil control, but plants growing with limestone instead of quartz at equal soil volume had some advantages.

Plants that grew with 20% limestone were larger at the end of the experiment than plants that grew with 20% quartz. Presumably, much of this size difference

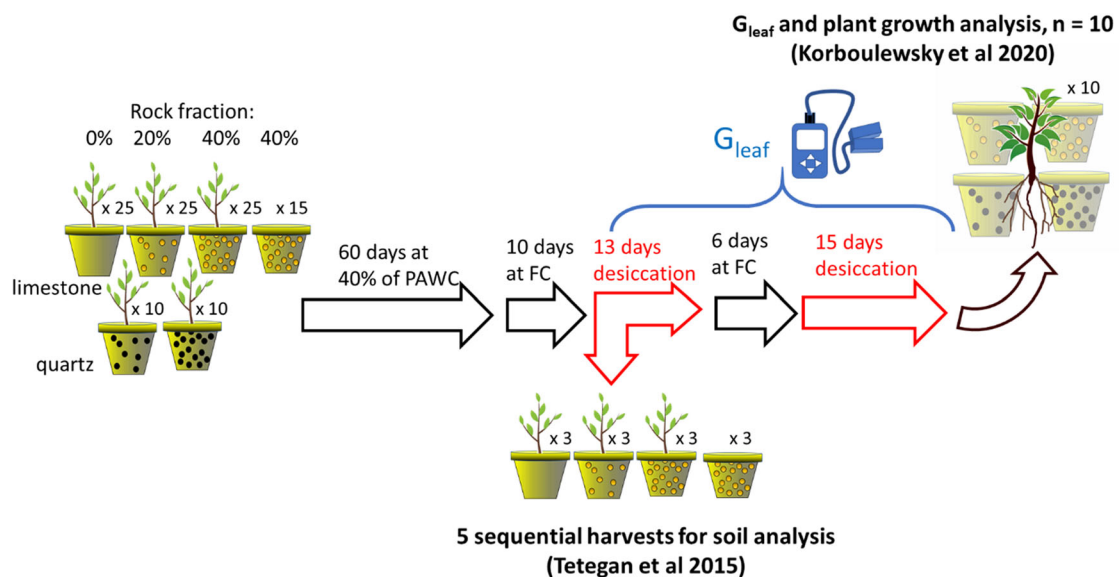


Fig. 1 Design overview of Tetegan et al. (2015) and Korboulewsky et al. (2020) experiment. PAWC = plant-available water capacity, FC = field capacity, G_{leaf} = leaf conductivity. The numbers next to the pot symbols represent replication numbers

would have developed during the 60-day runup to the first desiccation interval, in which plants were watered every other day to a set point equivalent to 40% PAWC (180 or 163 cm³ for limestone and quartz, respectively). At a rock fraction of 40%, plants had similar size at the end of the experiment. Here I focus on the 40% rock fraction to avoid the complication of potentially unequal sapling transpiration rates with limestone or quartz.

During the first desiccation interval, plants growing with limestone maintained higher leaf conductance (G_{leaf}) for longer than plants growing with quartz, demonstrating that water stored in limestone became available to plants.

Tetegan et al. (2015) give a detailed account of water depletion in the soil and limestone fractions during the first desiccation interval. I combined it with G_{leaf} values reported by (Korboulewsky et al. 2020) in Fig. 2. Initially, water was overwhelmingly lost from the soil fraction and about half by evaporation as suggested by comparison with unplanted containers. Daily soil water loss declined in both planted and unplanted containers, as did water loss from limestone fragments in unplanted containers. However, water loss from limestone in planted containers increased over time, indicating that plant roots established conditions that facilitated the depletion of water in limestone.

According to the estimates by Tetegan et al. (2015), the soil fraction reached permanent wilting point on day 6 or 7, and most rock fragments by day 9 or 10, with only rocks of lowest porosity (and presumably lowest hydraulic conductivities) maintaining PAW after day 10. If this is correct, plants could have drawn water from both soil and limestone before day 7, but after day 7 soil water would have been unavailable to plants. These estimates may not be quite accurate, since on day 8, G_{leaf} was still the same for plants growing with limestone or quartz. Nevertheless, G_{leaf} in the two treatments did diverge shortly after and on day 10, when the limestone fraction lost water about as fast as the soil fraction, plants growing with limestone were able to maintain G_{leaf} values (thus transpiration rates) 2–3 x higher than plants growing with quartz. By day 11, soil water loss was nearly zero and limestone may well have been the only source of transpiration water for the remaining days of the desiccation interval.

Thus, limestone fragments slowed the onset of more acute water stress in poplar, as plants switched from taking up soil water to limestone water (Korboulewsky et al. 2020). The switch may have been gradual, starting before the divergence of G_{leaf} values between the limestone and quartz treatments, but the physiological effect became observable after day 8.

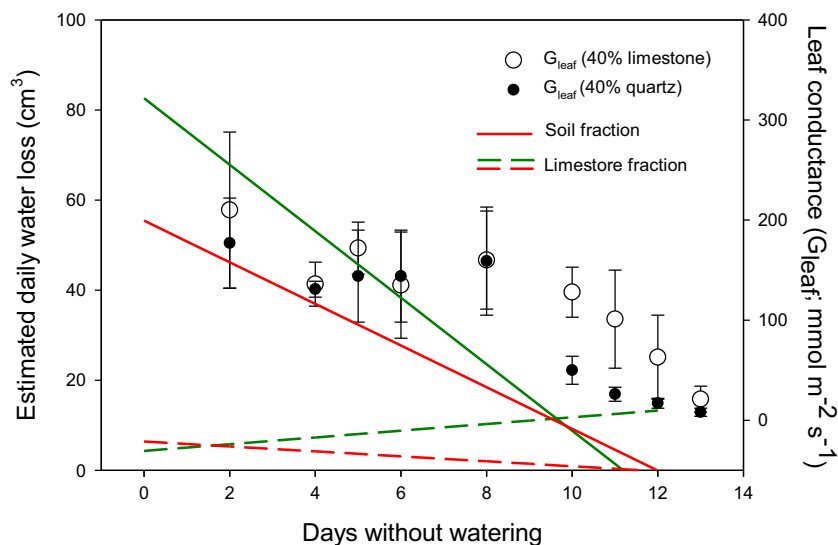


Fig. 2 Estimated daily water loss of soil and rock fractions and leaf conductance in the 40% limestone treatment. The solid lines represent water loss from soil, the broken lines from limestone. Containers into which poplar saplings were planted are shown in dark green, the unplanted control is drawn in red. Water loss values are based on Table 1 in Tetegan et al. (2015) and for G_{leaf}

on Table 4 in Korboulewsky et al. (2020). Daily water loss was estimated by fitting a second order polynomial function to water content data reported for days 2, 4, 6, 9 and 13, assuming an initial water content at field capacity. Volumetric water content was converted to water volume by multiplying the soil and rock fractions with the total pot volume (3000 cm³)

Water transport pathways between rock and root

While (Korboulewsky et al. 2020) and (Tetegan et al. 2015) demonstrated convincingly *that* plants take up rock water, nobody knows exactly *how* water passes from rocks to plant roots. There are four potential pathways (Fig. 3). Water could simply flow out of the rock matrix into the soil following water potential gradients (Fig. 3a). In this case, recharged rock fragments simply delay soil water depletion and plant water uptake remains controlled by soil water potential. The equivalent process in bedrock would be water leaking or dripping from rock walls into soil-filled cavities. Second, as observed by Korboulewsky et al. (2020), roots could wrap around rock fragments to establish direct contact with the rock phase (Fig. 3b). In bedrock, one can observe fine root mats filling fracture planes (Hasenmueller et al. 2017). This would bypass the soil pathway and potentially increase the driving force for

rock water release. Rock-bound roots could still take up water from soil they are in contact with, albeit with reduced effective conductivity per root length since their cylindrical soil depletion zone would be cut in half (de Willigen et al. 2018). Root crowding on the surface of rocks might further reduce effective soil-to-root conductance per root length (Campbell 1991). This could translate into a potential tradeoff in the function of ‘free’ roots embedded in soil and roots that cling to rock surfaces. If so, the development of free versus rock-bound roots may be part of a broader root allocation strategy that could depend on climate and plant functional type.

A third way in which water may pass from rocks to roots is via mycorrhizal hyphae, which would establish a cell connection between rock water and roots, which could be either at a distance from rock surfaces (Fig. 3c) or sitting on the rock surface (Fig. 3d). Fungal hyphae are small enough to grow through the narrower pore

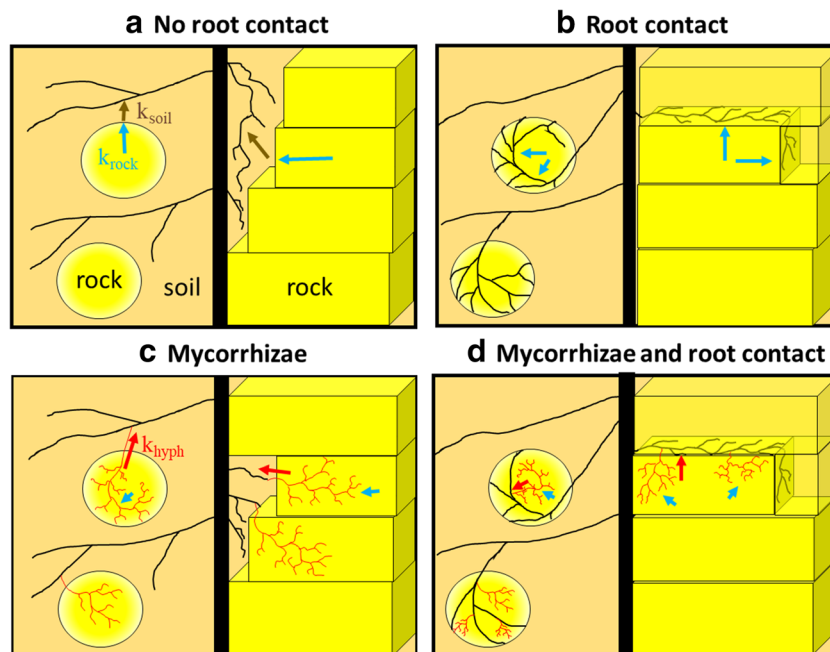


Fig. 3 Potential transport pathways for rock water uptake by plants. The two panels in each figure illustrate the equivalent cases for stony soils (left) and fractured bedrock (right). Plant roots are represented by black lines, mycorrhizal hyphae by thin red lines. Three distinct hydraulic conductivities (k) are potentially involved in plant water extraction from rock: the hydraulic conductivity of

the soil k_{soil} (brown), the rock matrix k_{rock} (light blue) and along or within hyphae of mycorrhizal fungi k_{hyph} (red). Transport pathways through rock are longest if roots are not in contact with rock surfaces and there are no mycorrhizae. They are shortest if mycorrhizae proliferate within the pores and microfissures of the rock

spaces of weathered rock matrix, including microfissures (Bornyasz et al. 2005; Witty et al. 2003). Whether or not they facilitate plant water extraction has not been conclusively settled (Lehto and Zwiazek 2011), but it seems likely, especially when water is transported over longer distances through rock matrix (Bornyasz et al. 2005). Korboulewsky et al. (2020) did not mention fungal infection, but poplar (*Populus euramericana*) is associated with ectomycorrhizae (Jabeen et al. 2012) and roots can become spontaneously infected in unsterilized soil (Baum et al. 2002).

Under what conditions do plants use rock water?

Weathered limestone is among the rock types that have significant PAWC (Parajuli et al. 2017; Tetegan et al. 2011), but water transfer from rocks to plants probably meets greater pathway resistance compared to soil. One reason is the generally longer flow path from source to sink (Fig. 3). Secondly, hydraulic conductivity along the flow path may be lower (Freeze and Cherry 1979; Katsura et al. 2009). Since water follows the path of least resistance, rock water should become a significant plant water source only after soil water uptake slows down due to partial depletion. The transition to rock water should therefore be associated with a drop in plant water potential, a reduction in transpiration, or a mixture of both responses, as the Korboulewsky et al. (2020) study indicated.

A further requirement is for rock fractions to be near field capacity. Lack of sufficient recharge may have foiled the establishment of a treatment effect on G_{leaf} during the second desiccation interval in the Korboulewsky et al. (2020) experiment. Under field conditions, the rock fragments in stony soils may likewise not always have maximal water content at the beginning of a dry-down period, which would diminish their average effect on G_{leaf} and site productivity.

Recharge conditions for the rock matrix in the deep critical zone may be different, however, potentially producing a more reliable water reserve for deep-rooted species. During the wet season, water flows into the bedrock through large fractures. Eventually, narrowing fracture aperture or fracture-fill halts the downward flow, water accumulates and infiltrates into weathered rock walls (Frazier et al. 2002; Hasenmueller et al. 2017; Hubbert et al. 2001a, b), potentially over a period of months to some distances away from the fracture-rock

interface (Bornyasz et al. 2005; Peng et al. 2019). In weathered granites, the rock matrix can indeed contain more PAW than the rooted fracture space (Bornyasz et al. 2005).

Assuming analogous processes of water uptake in the deep critical zone and in stony soils, we may expect plants to preferentially take up mobile water inside wider, rooted fractures, with or without soil (Hasenmueller et al. 2017). As this source becomes depleted and plant water potentials decline, water would be drawn from the walls of the fracture continuum. Alternatively, water could continue to flow out of connected microfissure and -fracture spaces, too narrow to host roots, but allowing faster movement of water compared to the unbroken rock matrix. Rocks contain different fractional volumes of such micro-voids and in different spatial arrangements, which affect their macroscopic physical properties including permeability (Anders et al. 2014).

Processes at the microscopic scale of rock water extraction by roots are speculative, but we can observe the macroscopic consequences in annual fluctuations of bedrock bulk water content (Hubbert et al. 2001a, b; Rempe and Dietrich 2018; Sternberg et al. 1996). Water uptake from rock layers at water potentials below -2.2 MPa (the presumed permanent wilting point for native trees) suggests that mobile water in rooted fissures is depleted early in the growing season, leaving only the more distant water sources available to plants for the rest of the growing season (Hubbert et al. 2001a, b).

Does rock water facilitate growth or lower drought stress?

Water taken up under moderate to severe water stress conditions is typically not used for growth but for biomass maintenance, to avoid or delay the loss of leaf area, fine roots and mycorrhizal associations. Ryel et al. (2009) originally introduced this intriguing idea of a functional dichotomy between two water pools; a ‘growth pool’, which supports gas exchange and primary production and a ‘maintenance pool’, which allows plants to better tolerate drought. The key difference between these pools is one of plant access: growth pools are densely rooted and are the main source of water during the growing season. Maintenance pools are less densely rooted and extraction rates are therefore lower.

For the same reason they retain water for longer and become the main water source only when more accessible water pools have become depleted. Ryel et al. (2009) envisioned deep soil to be the maintenance pool, but rock fragments and bedrock clearly belong to this category as well, whereas macro-voids and -conduits in the bedrock, so far as they contain roots, could be counted in the growth pool. Therefore, both growth and maintenance pools could be distributed throughout the critical zone from the top to the bottom of the root zone.

There is a perception that that all water extracted from bedrock is a source of last resort for plants (e.g., Crouchet et al. 2019; Duniway et al. 2010; Grant and Dietrich 2017; McDowell et al. 2019). However, studies from Mediterranean climate zones showed that water extracted from weathered bedrock can make substantial contributions to annual transpiration and site productivity (Liu et al. 2019; Rempe and Dietrich 2018; Sehhati et al. 2015; Zwieniecki and Newton 1996). In an influential paper, (Hahm et al. 2019) recently showed that some sites in the Mediterranean climate zone of California have limiting subsoil storage capacity relative to the amount of winter precipitation they receive. This limitation capped productivity in years with high winter precipitation. But the same sites also had greater drought resilience with much lower mortality compared to more productive sites. A link between low productivity in high-rainfall years and low mortality in low-rainfall years can have several underlying causes, but the influence of subsoil structure resulting in a relatively small growth pool (rooted fissure space) and a relatively large maintenance pool (unrooted rock matrix) is among the plausible explanations.

Implications for modeling the root zone

The general insight that can be taken from the study by Korboulewsky et al. (2020) is that the rhizosphere is composed of two water-bearing pore domains or phases, one that can be rooted and one that cannot. This structure influences the dynamics of plant water uptake, productivity and drought response (Parajuli et al. 2019). Given a fixed rooting depth, more volume for root exploration increases the growth potential but more root-excluding volume delays acute water stress during drought. This tradeoff potentially explains why a site can be storage limited and at the same time more

resilient to drought, as discussed by (Hahm et al. 2019). Assuming that plant productivity is more strongly tied to the amount of readily available water in the rooted volume, the amount of water available in the unrooted volume determines how long plants can persist under drought conditions.

The appeal of this two-phase model is that it might have greater flexibility in representing complex, climate-vegetation interactions in the hydrological cycle. It can also unify the representation of the entire critical zone, from the soil-dominated top to the rock-dominated weathering front and all transition zones between (Fig. 3).

But some problems remain to be solved: First, even though the soil and highly weathered bedrock features can admit roots, not all do contain roots. For example, the extraction of water from soil regions of low root density may be similarly constrained by long transport pathways as the extraction of water from rocks (e.g., Schwinning et al. 2020). The only difference is that over the course of time, dynamic root systems probably will occupy all accessible soil volumes, so long as this serves the overall plant carbon strategy (Bloom et al. 1985). Conversely, even though solid rocks generally exclude roots, fine roots and mycorrhizal hyphae are present in microscopic rock fissures (Bornyasz et al. 2005). Structuring the root zone into just two domains based on root occupancy is clearly a simplification compared to the true heterogeneity of the root zone, which would require pragmatic approaches to model parameterization.

Nevertheless, forcing soil/rock mixtures into the parameterization scheme of a pure soil model introduces predictable and potentially larger errors (Cousin et al. 2014). In the case of stony soils, if models classify the rock fraction as inert, they underestimate total PAWC by ignoring the PAWC of the rock phase. Conversely, if the rock fraction is simply ignored, they overestimate total PAWC and the potential productivity of a site. A similar conundrum exists in the characterization of the entire critical zone. Models either assume that the root zone is limited to the soil horizon (e.g., Brunke et al. 2016), which might underestimate their drought resilience, or that deep roots interact with regolith and fractured rock in the same way as with soil (e.g., Fan et al. 2017), which might overestimate the productivity of a site. The assumption of two pore domains in the rhizosphere may be a simple and general solution to modeling plant-water relations at global scales.

References

- Anders MH, Laubach SE, Scholz CH (2014) Microfractures: A review. *J Struct Geol* 69:377–394. <https://doi.org/10.1016/j.jsg.2014.05.011>
- Baum C, Stetter U, Makeschin F (2002) Growth response of *Populus trichocarpa* to inoculation by the ectomycorrhizal fungus *Laccaria laccata* in a pot and a field experiment. *For Ecol Manag* 163:1–8. [https://doi.org/10.1016/s0378-1127\(01\)00534-5](https://doi.org/10.1016/s0378-1127(01)00534-5)
- Bloom AJ, Chapin FS, Mooney HA (1985) Resource limitation in plants - An economic analogy. *Annu Rev Ecol Syst* 16:363–392. <https://doi.org/10.1146/annurev.es.16.110185.002051>
- Bornyas MA, Graham RC, Allen MF (2005) Ectomycorrhizae in a soil-weathered granitic bedrock regolith: Linking matrix resources to plants. *Geoderma* 126:141–160. <https://doi.org/10.1016/j.geoderma.2004.11.023>
- Brunke MA, Broxton P, Pelletier J, Gochis D, Hazenberg P, Lawrence DM, Leung LR, Niu GY, Troch PA, Zeng XB (2016) Implementing and evaluating variable soil thickness in the community land model, version 4.5 (CLM4.5). *J Clim* 29:3441–3461. <https://doi.org/10.1175/jcli-d-15-0307.1>
- Campbell GS (1991) Simulation of water uptake by plant roots. In: Hanks J, Ritchie JT (eds) *Modeling plant and soil systems*. Agronomical Monographs. ASA, CSSA, and SSSA, I, Madison
- Cousin I, Nicoulaud B, Tetegan M, de Forges ACR, Arrouays D, Bouthier A (2014) Estimating the Available water Content of highly heterogeneous soils including stony soils at the regional scale
- Couchet SE, Jensen J, Schwartz BF, Schwinning S (2019) Tree mortality after a hot drought: Distinguishing density-dependent and -independent drivers and why it matters. *Front For Glob Chang* 2:21
- Dawson T, Hahm W, Crutchfield-Peters K (2020) Digging deeper: what the critical zone perspective adds to the study of plant ecophysiology. *New Phytol* 226(3):666–671
- Dunbabin VM, Postma JA, Schnepf A, Pages L, Javaux M, Wu LH, Leitner D, Chen YL, Rengel Z, Diggel AJ (2013) Modelling root-soil interactions using three-dimensional models of root growth, architecture and function. *Plant Soil* 372:93–124. <https://doi.org/10.1007/s11104-013-1769-y>
- Duniway MC, Herrick JE, Monger HC (2010) Spatial and temporal variability of plant-available water in calcium carbonate-cemented soils and consequences for arid ecosystem resilience. *Oecologia* 163:215–226. <https://doi.org/10.1007/s00442-009-1530-7>
- Fan Y, Miguez-Macho G, Jobbagy EG, Jackson RB, Otero-Casal C (2017) Hydrologic regulation of plant rooting depth. *Proc Natl Acad Sci USA* 114:10572–10577. <https://doi.org/10.1073/pnas.1712381114>
- Frazier CS, Graham RC, Shouse PJ, Yates MV, Anderson MA (2002) A field study of water flow and virus transport in weathered granitic bedrock. *Vadose Zone J* 1:113–124. <https://doi.org/10.2136/vzj2002.1130>
- Freeze RA, Cherry JA (1979) *Groundwater*. Prentice-Hall, Inc., Englewood Cliffs
- Graham RC, Rossi AM, Hubbert KR (2010) Rock to regolith conversion: Producing hospitable substrates for terrestrial ecosystems. *GSA Today* 20:4–9. <https://doi.org/10.1130/GSAT57A.1>
- Grant GE, Dietrich WE (2017) The frontier beneath our feet. *Water Resour Res* 53:2605–2609. <https://doi.org/10.1002/2017wr020835>
- Hahm WJ, Dralle DN, Rempe DM, Bryk AB, Thompson SE, Dawson TE, Dietrich WE (2019) Low subsurface water storage capacity relative to annual rainfall decouples mediterranean plant productivity and water use from rainfall variability. *Geophys Res Lett* 46:6544–6553. <https://doi.org/10.1029/2019gl083294>
- Hasenmueller EA, Gu X, Weitzman JN, Adams TS, Stinchcomb GE, Eissenstat DM, Drohan PJ, Brantley SL, Kaye JP (2017) Weathering of rock to regolith: The activity of deep roots in bedrock fractures. *Geoderma* 300:11–31. <https://doi.org/10.1016/j.geoderma.2017.03.020>
- Hubbert KR, Beyers JL, Graham RC (2001) Roles of weathered bedrock and soil in seasonal water relations of *Pinus jeffreyi* and *Arctostaphylos patula*. *Can J For Res-Revue Canadienne De Recherche Forestiere* 31:1947–1957. <https://doi.org/10.1139/cjfr-31-11-1947>
- Hubbert KR, Graham RC, Anderson MA (2001) Soil and weathered bedrock: Components of a Jeffrey pine plantation substrate. *Soil Sci Soc Am J* 65:1255–1262. <https://doi.org/10.2136/sssaj2001.6541255x>
- Jabeen S, Ilyas S, Niazi ARK, Khalid AN (2012) Diversity of ectomycorrhizae associated with *Populus* Spp. Growing in two different ecological zones of Pakistan. *Int J Agric Biol* 14:681–688
- Jones DP, Graham RC (1993) Water-holding characteristics of weathered granitic rock in chaparral forest ecosystems. *Soil Sci Soc Am J* 57:256–261. <https://doi.org/10.2136/sssaj1993.03615995005700010044x>
- Katsura S, Kosugi K, Mizutani T, Mizuyama T (2009) Hydraulic properties of variously weathered granitic bedrock in headwater catchments. *Vadose Zone J* 8:557–573. <https://doi.org/10.2136/vzj2008.0142>
- Koele N, Dickie IA, Blum JD, Gleason JD, de Graaf L (2014) Ecological significance of mineral weathering in ectomycorrhizal and arbuscular mycorrhizal ecosystems from a field-based comparison. *Soil Biol Biochem* 69:63–70. <https://doi.org/10.1016/j.soilbio.2013.10.041>
- Korboulewsky N, Tétégan M, Samouelian E, Cousin I (2020) Plants use water in the pores of rock 1 fragments during drought. *Plant Soil X*:xxx-xxx
- Lehto T, Zwiazek JJ (2011) Ectomycorrhizas and water relations of trees: a review. *Mycorrhiza* 21:71–90. <https://doi.org/10.1007/s00572-010-0348-9>
- Liu HY, Jiang ZH, Dai JX, Wu XC, Peng J, Wang HY, Meersmans J, Green SM, Quine TA (2019) Rock crevices determine woody and herbaceous plant cover in the karst critical zone. *Sci China-Earth Sci* 62:1756–1763. <https://doi.org/10.1007/s11430-018-9328-3>
- McDowell NG, Grossiord C, Adams HD, Pinzon-Navarro S, Mackay DS, Breshears DD, Allen CD, Borrego I, Dickman LT, Collins A, Gaylord M, McBranch N, Pockman WT, Vilagrosa A, Aukema B, Goodsman D, Xu CG (2019) Mechanisms of a coniferous woodland persistence under drought and heat. *Environ Res Lett* 14:14. <https://doi.org/10.1088/1748-9326/ab0921>

- Parajuli K, Sadeghi M, Jones SB (2017) A binary mixing model for characterizing stony-soil water retention. *Agric For Meteorol* 244:1–8. <https://doi.org/10.1016/j.agrformet.2017.05.013>
- Parajuli K, Jones SB, Tarboton DG, Flerchinger GN, Hipps LE, Allen LN, Seyfried MS (2019) Estimating actual evapotranspiration from stony-soils in montane ecosystems. *Agric For Meteorol* 265:183–194. <https://doi.org/10.1016/j.agrformet.2018.11.019>
- Peng XD, Dai QH, Ding GJ, Shi DM, Li CL (2019) The role of soil water retention functions of near-surface fissures with different vegetation types in a rocky desertification area. *Plant Soil* 441:587–599. <https://doi.org/10.1007/s11104-019-04147-1>
- Phillips JD, Pawlik L, Samonil P (2019) Weathering fronts. *Earth-Sci Rev* 198. <https://doi.org/10.1016/j.earscirev.2019.102925>
- Poorter H, Buhler J, van Dusschoten D, Climent J, Postma JA (2012) Pot size matters: a meta-analysis of the effects of rooting volume on plant growth. *Funct Plant Biol* 39:839–850. <https://doi.org/10.1071/fp12049>
- Rempe DM, Dietrich WE (2018) Direct observations of rock moisture, a hidden component of the hydrologic cycle. *Proc Natl Acad Sci USA* 115:2664–2669. <https://doi.org/10.1073/pnas.1800141115>
- Ryel R, Ivans C, Peek M, Leffler A (2009) Functional differences in soil water pools: a new perspective on plant water use in water-limited ecosystems. *Progress Bot*. Springer-Verlag, Berlin
- Schwinnig S, Litvak ME, Pockman WT, Pangle RE, Fox AM, Huang C-W, McIntire CD (2020) A 3-dimensional model of *Pinus edulis* and *Juniperus monosperma* root distributions in New Mexico: implications for soil water dynamics. *Plant Soil* 450:337–355
- Sehhati MT, Sepehr A, Ekhtesasi MR, Goudie A (2015) The geomorphological roles of rocky deep crevices for water supply on arid zone mountain slopes (case study: Mehriz-Yazd, Iran). *Environ Earth Sci* 74:493–504. <https://doi.org/10.1007/s12665-015-4056-9>
- SSSA (Soil Science Society of America) (2020) Glossary of soil science terms. <https://www.soils.org/publications/soils-glossary>. Accessed 28/6/2020
- Stenberg PD, Anderson MA, Graham RC, Beyers JL, Tice KR (1996) Root distribution and seasonal water status in weathered granitic bedrock under chaparral. *Geoderma* 72:89–98. [https://doi.org/10.1016/0016-7061\(96\)00019-5](https://doi.org/10.1016/0016-7061(96)00019-5)
- Tetegan M, Nicoulaud B, Baize D, Bouthier A, Cousin I (2011) The contribution of rock fragments to the available water content of stony soils: Proposition of new pedotransfer functions. *Geoderma* 165:40–49. <https://doi.org/10.1016/j.geoderma.2011.07.001>
- Tetegan M, Korboulewsky N, Bouthier A, Samouelian A, Cousin I (2015) The role of pebbles in the water dynamics of a stony soil cultivated with young poplars. *Plant Soil* 391:307–320. <https://doi.org/10.1007/s11104-015-2429-1>
- Willigen P, Heinen M, van Noordwijk M (2018) Roots partially in contact with soil: Analytical solutions and approximation in models of nutrient and water uptake. *Vadose Zone J* 17:16. <https://doi.org/10.2136/vzj2017.03.0060>
- Witty JH, Graham RC, Hubbert KR, Doolittle JA, Wald JA (2003) Contributions of water supply from the weathered bedrock zone to forest soil quality. *Geoderma* 114:389–400. [https://doi.org/10.1016/s0016-7061\(03\)00051-x](https://doi.org/10.1016/s0016-7061(03)00051-x)
- Zhang YH, Zhang MX, Niu JZ, Li HL, Xiao R, Zheng HJ, Bech J (2016) Rock fragments and soil hydrological processes: Significance and progress. *Catena* 147:153–166. <https://doi.org/10.1016/j.catena.2016.07.012>
- Zwieniecki MA, Newton M (1996) Water-holding characteristics of metasedimentary rock in selected forest ecosystems in southwestern Oregon. *Soil Sci Soc Am J* 60:1578–1582. <https://doi.org/10.2136/sssaj1996.03615995006000050042x>

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