REVIEW

Bedrock: the hidden water reservoir for trees challenged by drought

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Abstract

Key message **Bedrock can store appreciable amounts of available water, and some trees apparently use this resource to survive drought.**

Abstract Several forest ecosystems rely on only shallow soil layers overlying more or less compact bedrock. In such habitats, the largest water reservoir can be represented by rock moisture, rather than by soil water. Here, we review evidence for the presence of water available for root water uptake in some rock types, and show examples of the physiological and ecological roles of rock moisture, especially when trees are facing drought conditions. The possible magnitude of rock–root water exchanges is discussed in the frame of current knowledge of rock, soil, and root hydraulic properties. We highlight several areas of uncertainty regarding the role of rock moisture in preventing tree hydraulic failure under drought, the exact pathway(s) available for rock–root water exchange, and the relative efficiencies of water transport in the different compartments of the rock–soil–root continuum. Overall, available experimental evidence suggests that bedrock water should be incorporated into any model describing the forest seasonal water use and tree responses to drought.

Keywords Bedrock · Root · Available water content · Drought

Introduction: how climate change challenges tree survival?

Trees are long-living organisms exposed to variable, and sometimes harsh, environmental conditions. Water shortage, at least on a seasonal scale, is a common occurrence in several forest biomes and trees have evolved complex adaptations to manage and survive occasional or even prolonged drought stress, ranging from tight control of water loss (Klein [2014](#page-8-0); Roman et al. [2015\)](#page-9-0) to extreme resistance to xylem embolism and hydraulic failure (Maherali et al. [2004](#page-8-1); Nardini et al. [2013\)](#page-9-1), and to extensive and deep root systems accessing relatively reliable water stores (Canadell et al. [1996;](#page-7-0) Nardini et al. [2016\)](#page-9-2). Tree productivity, growth, reproduction, and survival depend on the maintenance of adequate water and carbon pools, which are essential to

assure plant hydration, active metabolism, and cell vitality. When these pools are depleted by stress factors, and related water and carbohydrate fuxes through the plant are reduced below critical levels, trees face the risk of decline and death (McDowell et al. [2022](#page-8-2)). In particular, trees exposed to water shortage close their stomata to reduce water loss to the atmosphere, with kinetics depending on the species-specifc hydraulic strategies (Klein [2014\)](#page-8-0) ranging from a 'safe' early prevention of water potential drop and xylem embolism formation to safeguard the integrity of the hydraulic system, to a 'risky' acceptance of some degree of embolism build-up to maximize carbon gain and delay eventual carbon starvation (Martínez-Vilalta and Garcia-Forner [2017](#page-8-3); Mirfenderesgi et al. [2019](#page-8-4)). Stomatal closure strongly reduces but does not eliminate plant water losses, as residual transpiration can occur through stomatal leaks or leaf cuticle, and even from the bark at stem level (Duursma et al. [2019;](#page-7-1) Wolfe [2020](#page-10-0)). After stomatal closure has occurred, the fate of the plant during a prolonged drought depends on the available carbohydrates reserves and on the water pools belowground (McLaughlin et al. [2020\)](#page-8-5) plus internal stores (Yu et al. [2019](#page-10-1); Preisler et al. [2022](#page-9-3)). Hence, the balance between residual water loss and uptake (from the soil) or release (from internal capacitors) becomes crucial to maintain the minimum

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hydration level required for cell survival (Abate et al. [2021](#page-7-2); Mantova et al. [2021](#page-8-6); Triflò et al. [2023\)](#page-10-2).

Nowadays, the survival of several tree species in different forest ecosystems is challenged by ongoing climate change (Choat et al. [2012;](#page-7-3) Neumann et al. [2017\)](#page-9-4), leading to increased frequency and severity of drought coupled to extreme heat waves that increase atmospheric evaporative demand (Teskey et al. [2015](#page-9-5); Grossiord et al. [2020\)](#page-8-7). Over recent decades, background tree mortality rates have apparently spiked in several biomes (Peng et al. [2011](#page-9-6); Hember et al. [2017\)](#page-8-8) and some extreme 'hot' droughts have produced sudden and massive mortality events (Moore et al. [2016](#page-8-9); Hammond et al. [2022](#page-8-10)), raising consciousness on the increasing risk of difuse forest decline over the next future (Hartmann et al. [2022](#page-8-11)). Tree decline and death are caused by complex and interrelated processes and mechanisms (de la Serrana et al. [2015;](#page-7-4) Yi et al. [2022](#page-10-3)), but most available evidence supports the crucial role of 'plant hydraulic failure' in tree mortality (Nardini et al. [2013;](#page-9-1) Nolan et al. [2021](#page-9-7)), while proofs for the occurrence of death induced by sole carbon starvation are more elusive (McDowell et al. [2022](#page-8-2)). Hence, a better understanding of the performance of trees typically thriving in arid habitats or occasionally exposed to severe/prolonged drought calls for a thorough description and quantifcation of the nature of water pools available to root systems (Dawson et al. [2020;](#page-7-5) Phelan et al. [2022\)](#page-9-8), and how roots interact with diferent water stores at diferent water contents (Carminati and Javaux [2020](#page-7-6); Duddek et al. [2022](#page-7-7)) to maintain the minimal vital hydration of the plant.

Water stores belowground: not only soil and groundwater

The most important reservoirs sustaining tree water uptake are soil moisture and groundwater (Lobet et al. [2014](#page-8-12); Fan et al. [2017\)](#page-7-8), with foliar uptake of rain and dew contributing to water balance in some species and under some environmental conditions (Berry et al. [2019\)](#page-7-9). While soil water is potentially available to all tree species, only some of them can exploit groundwater, when this is relatively shallow and/ or when roots are deep enough to target this more reliable source (see Evaristo and McDonnell [2017](#page-7-10)). Extensive literature has described changes in soil water availability to plants as a function of soil texture, water content, and water potential (Kramer [1944;](#page-8-13) Gardner [1965](#page-7-11); Saxton and Rawls [2006](#page-9-9); Cousin et al. [2022\)](#page-7-12), and most basic and advanced textbooks of plant physiology and ecophysiology focus on the crucial importance of soil as a water (and nutrient) source for plants. This view is partly infuenced by the fact that the most productive agricultural areas are characterized by relatively deep soils (e.g., Tautges et al. [2019](#page-9-10)), and that most root biomass is found in shallow horizons (Jackson et al. [1996\)](#page-8-14) making soil water the most obvious and important reservoir for crop functioning and productivity. Yet, it is very interesting to note that several natural ecosystems, including forests, cannot rely on thick and well-developed soils, but thrive on relatively thin substrates overlying more or less compact bedrock (Shangguan et al. [2017;](#page-9-11) Dawson et al. [2020](#page-7-5); McCormick et al. [2021\)](#page-8-15). This situation becomes very apparent for non-woody plants colonizing volcanic or desert areas, where rocks are often the only water reservoirs (Bashan et al. [2002](#page-7-13); Puente et al. [2004;](#page-9-12) Lopez et al. [2009](#page-8-16)). Yet, even trees often face situations where a large share of belowground water sources is stored in rocks and not in soil, which is the case of forest ecosystems occupying karstic areas (Fig. [1\)](#page-1-0) (Estrada-Medina et al. [2013](#page-7-14); Nardini et al. [2016;](#page-9-2) Geekiyanage et al. [2019\)](#page-7-15). Karstic substrates are characterized by dissolution features like cracks, fissures, and caves where soil can accumulate even at substantial depths (Peng et al. [2020\)](#page-9-13). Thus, weathered limestone offers some opportunities for plants to access relatively deep soil pockets that can store rainfall water and protect it from direct evaporation to the atmosphere (Jackson et al. [1999](#page-8-17); Hahm et al. [2020](#page-8-18)). Still, compact bedrock frequently occupies by far most of the volume belowground (Nardini et al. [2021](#page-9-14)). The chemical and physical features of bedrock can be very diferent and so its

Fig. 1 Roots protruding through a stalactite in a Karstic cave (**a**) or penetrating a rock fssure and spreading over the rock surface (**b**). Photograph (a) courtesy of Prof. L. Zini, Department of Mathematics, Informatics and Geosciences, University of Trieste, Italy

primary porosity, raising questions on the possible role of this matrix as a water source for plants. Some studies have explored this possibility, and most evidence supports the view that rocks can store signifcant amounts of available water in their pores, depending on rock material density and fragment size. Highly weathered bedrock can have saturated water contents comparable to those of coarse-textured soils (Graham et al. [1997;](#page-8-19) Querejeta et al. [2006\)](#page-9-15), but experimental evidence suggests that also compact and unweathered bedrock can store signifcant amounts of extractable water. To cite a few examples, Zwieniecki and Newton ([1996\)](#page-10-4) reported an available water content (AWC) of about $0.15 \text{ m}^3/\text{m}^3$ in a metasedimentary rock formation in Southern Oregon. Robertson et al. [\(2021](#page-9-16)) reported water contents between 0.03 and $0.07 \text{ m}^3/\text{m}^3$ for rock fragments from a hard sandstone alluvium. Schoeman et al. ([1997\)](#page-9-17) showed that 2–40% of total water content of diferent rock types (ranging from 0.05 to $(0.3 \text{ m}^3/\text{m}^3)$ was released at water potential values between 0 and – 1.5 MPa, i.e., the range conventionally considered as water extractable by plant roots (Ritchie [1981](#page-9-18); Cousin et al. [2022](#page-7-12)). In a granitic rock in southern California, Jones and Graham ([1993](#page-8-20)) found AWC ranging from 0.01 to 0.07 m³/m³. More recently, Korboulewsky et al. [\(2020](#page-8-21)) reported AWC of $0.08 \text{ m}^3/\text{m}^3$ for limestone pebbles collected from a Calcaric Cambisol in the Beauce region (central France) and Nardini et al. [\(2021](#page-9-14)) found similar AWC values (about $0.03 \text{ m}^3/\text{m}^3$) for a Breccia limestone from the Classical Karst formations at the border between Italy and Slovenia.

All these data suggest that rocks commonly store water in their pores and that an appreciable amount of this water reservoir is potentially available to plants. The absolute values of rock AWC might appear relatively low at frst sight, but it should be noted that they overlap with the bottom end of AWC reported for soils, which typically ranges from $0.03 \text{ m}^3/\text{m}^3$ for sands, and up to $0.30 \text{ m}^3/\text{m}^3$ for heavy clays (Kirkham [2005\)](#page-8-22). Indeed, in rocky habitats like karstic ones, where the bedrock dominates the belowground volume, the largest share of water storage in the critical zone is due to the rock matrix and not to the soil. As an example, Nardini et al. [\(2021](#page-9-14)) calculated the total available water content of a soil bedrock system in a Karst area dominated by Breccia limestone, taking into account a total depth of 5 m, which is easily explored by roots of several woody species in the area (Nardini et al. [2016;](#page-9-2) Savi et al. [2018](#page-9-19)). Soil occupied only the frst 70 cm of the profle, and the remaining 4.3 m were dominated by compact bedrock, as detected by ground penetrating radar analysis (Jayawickreme et al. [2014\)](#page-8-23). Based on AWC values of soil and rock, and taking into account their relative volumes, the total amount of water stored in the system and potentially absorbable by plant roots was 190 mm, of which only 60 mm were attributable to the soil layer, while the remaining 130 mm were stored in the primary pores of bedrock.

Hence, available experimental evidence suggests that rocks can store appreciable amounts of water that can be released in a water potential interval compatible with physiological ranges of root water uptake. The relative belowground volumes occupied by soil and rock in some ecosystems are such that rocks can become the primary site for storage of water available to sustain plant hydration and transpiration. Thus, rocks have the potential to be primary water pools sustaining forest productivity and survival under drought, provided trees can actually exploit this reservoir. An important diference between soil and rocks is that pore size in the former allows root penetration and growth, while rock pores largely exclude roots (Schwinning [2020\)](#page-9-20). Hence, water stored in the soils is promptly available to a relatively large root surface area, while the same does not hold true for rocks, especially when the surface-to-volume ratio is unfavorable like in the case of large rock fragments or compact bedrock. So, is there any evidence that trees can actually use rock water for their physiological needs?

Is bedrock water important for tree water relations?

There is substantial experimental and anecdotal evidence for tight physical association between roots and rocks. More than a century ago, Cannon ([1911\)](#page-7-16) highlighted the close contact between roots of a succulent plant and the rocky substrate, and it was also already suggested that rock moisture might represent an important water source to maintain a minimum level of plant hydration during dry periods (Cooper [1922](#page-7-17)). Hellmers et al. [\(1955\)](#page-8-24) described how several woody plants of California Chaparral displayed roots penetrating by more than 50 cm into cracks of unweathered rock material, or showed a layer of roots growing over the soil–bedrock interface. Similar observations were later reported by other studies for diferent vegetation types, climates, and geological contexts (Zwieniecki and Newton [1994;](#page-10-5) Matthes-Sears and Larson [1995;](#page-8-25) Sternberg et al. [1996](#page-9-21)). Zwieniecki and Newton [\(1995\)](#page-10-6) also described the peculiar morphology of roots of two species growing in rock fssures as small as 100 µm, in a site characterized by sedimentary rock layers and a Mediterranean-like climate. There are also several observations of root layers growing over the rock surface in caves, or protruding inside the cave from even very narrow fssures in rocks (e.g., Lamont and Lange [1976](#page-8-26); Maeght et al. [2013](#page-8-27); Nardini et al. [2016](#page-9-2); Adams et al. [2020\)](#page-7-18) (Fig. [1](#page-1-0)).

The visual evidence of root–rock contact does not necessarily prove that plants use rock moisture to sustain transpiration or to maintain hydration after full stomatal closure. In fact, rocks also represent a potential source of nutrients, and roots growing inside rock fssures or over rock surface might be mainly involved in mining for P, K, Ca, Mg, Mn,

Fe, and other elements (Burghelea et al. [2015\)](#page-7-19), indeed contributing to a signifcant extent to rock weathering (Raven and Edwards [2001](#page-9-22)). However, several studies suggest that rock moisture signifcantly contributes to plant water use (Schwinning [2010](#page-9-23)), and we will provide some examples of such experimental evidence.

Based on a mix of measurements of plant water status, isotopic composition of plant/soil/rock water, and direct measurements of annual trends in bedrock moisture, Hahm et al. [\(2020](#page-8-18)) showed that plants of *Quercus garryana* growing in Northern California use soil moisture pools during spring, but then shift to exploiting residual moisture in the underlying bedrock. Notably, neutron probe measurements revealed a decline of rock moisture in late summer but only under the oaks, while rock moisture levels remained constant under areas covered by grasses. Similarly, Montaldo et al. ([2021\)](#page-8-28) investigated trees of *Olea europaea* and *Quercus suber* growing in a Mediterranean site with shallow soil $(< 50 \text{ cm})$ overlying fractured basalt, and showed that plants absorbed all the available rock moisture during summer drought. The dynamics of rock moisture in the deep vadose zone were also monitored in a catchment of the Rocky Mountains with a set of tools and methods (water isotope analysis, nuclear magnetic resonance, neutron probes, soil moisture and sapfow sensors), showing that during the growing season rock water depletion occurred from 0.3 to 5 m depth, with a magnitude that mirrored vegetation water consumption (Burns et al. [2023](#page-7-20)). In another isotope-based study, Querejeta et al. ([2006](#page-9-15)) showed that plants of *Brosimum alicastrum* growing on shallow soil atop limestone in Yucatán were able to absorb bedrock water from a depth of 0–5-2.5 m, improving plant water status during the peak of summer drought. Using a similar approach, Rose et al. [\(2003\)](#page-9-24) detected a progressive shift of water use from surface soil to bedrock at several meters depth for plants of *Pinus jefreyi* and *Arctostaphylos patula* in southern Sierra Nevada. Isotopic evidence for the use of crystallization water in gypsum substrates by *Helianthemum squamatum* was also provided by Palacio et al. ([2014](#page-9-25)). In a controlled experiment, Korboulewsky et al. ([2020](#page-8-21)) analyzed the water status of cuttings of *Populus euramericana* growing in a mix of soil and either quartz or limestone pebbles, showing that limestone contained water that was used by plants to buffer water stress under a drought treatment. Similarly, Savi et al. [\(2019](#page-9-26)) reported that young grapevine plants growing in a soil mixed with crushed limestone rocks had a better water status during summer drought compared to plants growing in plots with only soil. Wang et al. ([2023\)](#page-10-7) showed that rock moisture contributed by about 20% to total root water uptake over the growing season in an apple orchard in the hinterland of Shandong Peninsula, China. Nardini et al. ([2021\)](#page-9-14) investigated seasonal water relations of *Fraxinus ornus* trees growing on shallow soil overlying compact

bedrock in two sites with contrasting lithology. Trees growing over compact dolostone, with low rock AWC, displayed a critical water status during the peak of summer drought. On the contrary, trees growing over highly porous breccia with relatively higher AWC showed higher water content and water potential. The important contribution of rock moisture to tree performance under drought was also confrmed in saplings grown under controlled conditions in diferent mixtures of soil and either dolostone or breccia pebbles. During an experimental drought, critical and lethal water potential values were reached earlier in plants growing with the compact dolostone, and were delayed for plants growing with the porous breccia (Nardini et al. [2021\)](#page-9-14). Considering all the above data, it is not surprising that a recent study by McCormick et al. [\(2021\)](#page-8-15), based on a meta-analysis of studies in diferent sites across the continental USA, came to the conclusion that woody plants extensively and routinely access bedrock water, and not only during extreme drought conditions. In particular, the study identifed several sites where soil water-storage capacity was insufficient to explain annual evapotranspiration, and bedrock was apparently the actual additional source supplying plants with water.

Possible ecological consequences of plant– rock water relations

Considering the evidence for widespread use of bedrock water by plants, especially in sites with limited soil depth, it is interesting to consider the possible functional and ecological consequences of this phenomenon, as well as pointing out the current gaps in our understanding of plant-rock water relations. A first important question is whether tree growth and productivity are infuenced by the nature of bedrock, especially in areas characterized by shallow soil cover. Indeed, higher availability of rock moisture in such areas might sustain tree transpiration, thus enhancing photosynthesis, carbon gain, and growth. Unfortunately, answering this question is quite complex because in natural settings, it is very difficult to disentangle the impact of bedrock moisture from that of nutrient availability, which is also afected by the geological nature of the substrate and can signifcantly impact plant productivity. Indeed, an analysis of available literature on this topic yields contrasting results. Jiang et al. ([2020\)](#page-8-29) reported that bedrock nature was an important determinant of vegetation productivity in a karst region in Southwest China, and Callahan et al. [\(2022\)](#page-7-21) showed that site-to-site diferences in forest cover across diferent sites in California are driven by differences in belowground water-storage capacity, that are in turn regulated by mineral composition and porosity of bedrock. On the other hand, Nardini et al. [\(2021](#page-9-14)) reported that two sites both dominated by *Fraxinus ornus* trees but overlying bedrock of diferent nature and porosity showed overlapping seasonal trends of above-ground biomass productivity, as revealed by changes of remotely sensed NDVI (Marusig et al. [2020](#page-8-30)), despite spatial diferences in water status at the peak of summer drought (see above).

Although the impact of bedrock moisture on vegetation productivity is unclear, there are several lines of evidence supporting the view that bedrock nature can impact tree water relations and forest responses under drought. As an example, Liu et al. [\(2014\)](#page-8-31) showed that bedrock water was fundamental to sustain transpiration and hydration of adult *Celtis wightii* trees over the seasonal drought in a tropical rainforest characterized by karst-like soils. Similar fndings for diferent species and settings were reported by Hubbert et al. [\(2001](#page-8-32)), Rose et al. ([2003](#page-9-24)), Eliades et al. [\(2018](#page-7-22)), Rempe and Dietrich [\(2018](#page-9-27)), Crouchet et al. [\(2019](#page-7-23)), McDowell et al. [\(2022\)](#page-8-2), Hahm et al. ([2022\)](#page-8-33), Ding et al. ([2021\)](#page-7-24), and Nardini et al. [\(2021\)](#page-9-14).

Overall, these studies suggest that bedrock moisture might behave like a water pool relatively protected from evaporation that remains hydrated even when the soil has been depleted by evaporation or by root water uptake, and can, thus, release some water that is important to maintain some minimal hydration levels of plants under prolonged drought. It is tempting to speculate that this process might be at least partly responsible for the well know, but still partly unexplained phenomenon of patchy tree mortality under extreme drought. In fact, anomalous drought events frequently cause episodes of tree dieback and mortality, but quite often the extension of these events is highly variable on even narrow spatial scales (Fensham and Fairfax [1997;](#page-7-25) Schwantes et al. [2018](#page-9-28); Flake and Weisberg [2019](#page-7-26)). We speculate that in some ecosystems, such spatial variability in drought impacts might be partly correlated to belowground heterogeneity of bedrock and root/bedrock interactions, so that in some patches, trees might have access to a residual water sources stored in rocks and made available under critical conditions, allowing some plants to maintain minimum vital hydration levels and, thus, survive the drought (McDowell et al. [2022\)](#page-8-2). A recent study by Crouchet et al. ([2019](#page-7-23)) provides support to this view, by showing that trees of *Juniperus ashei* and *Quercus fusiformis* experiencing a severe drought displayed better crown conditions when growing in closer contact with bedrock. Based on data analysis, Crouchet et al. ([2019\)](#page-7-23) argued that excess precipitation falling on the year preceding the drought was stored in the bedrock below the soil horizon, especially on sites characterized by thin soil layers. This rock-stored water apparently rescued plants from crown death, and these fndings might explain other cases of spatial heterogeneity of drought impacts on forest ecosystems. The spatial heterogeneity of bedrock properties might also explain the smallto medium-scale variability in crop water status in karstic area otherwise characterized by very similar pedo-climatic conditions, as shown by Petruzzellis et al. ([2022\)](#page-9-29) for diferent vineyards experiencing summer drought.

The need for a mechanistic understanding of rock–root water relations

The picture emerging from the studies reviewed in the previous section supports the view that rock moisture can signifcantly contribute to plant water use, especially under drought conditions. Despite experimental evidence for rock water use by trees, the mechanistic relationships between roots and rocks remain still largely unexplored. Stating that plants use rock moisture implies that water can move from rock pores to the roots and then to leaf cells, but how this can be achieved is not clear. Schwinning [\(2020\)](#page-9-20) has listed some possible pathways allowing exchange of water between rocks and roots (see Fig. [2](#page-5-0)). In the simplest scenario, the close association between roots and rock surface might allow direct water transfer from the rock matrix to the root cells. In a second scenario, water could be released from the hydrated porous matrix to the dehydrated surrounding soil, which would be frst depleted by root water uptake; water potential gradients between soil–rock interface and the rock pores might then favor water release from bedrock and local 'rehydration' of soil volumes explored by the roots. In a third scenario, mycorrhizal hyphae could be directly involved in exploring the narrow rock pores, thus promoting a more direct contact between plant roots and the water-flled rock matrix. Indeed, in several angiosperm and gymnosperm trees, arbuscular and ectomycorrhizal hyphae, responsible for enhancing rock weathering, can grow directly over the surface of carbonate rocks or are able to pit them (Thorley et al. [2015](#page-9-30)).

An important question, and a very relevant one for each of the above scenarios, is how rock hydraulic conductivity compares to soil and root hydraulic conductivity. Clearly, water transfer between rock, soil, and roots can occur at physiologically relevant rates only when hydraulic conductivities and or water potential gradients between these three compartments allow water flows comparable to residual leaf- and bark-level water losses under drought conditions (see scheme in Fig. [3\)](#page-6-0). Rock hydraulic conductivities are generally measured at spatial scales and with methods that are only partially relevant for the analysis of rock–root physiological interaction and its role in plant water relations, but some data from existing literature can provide interesting insights into this under-investigated topic. Root hydraulic conductivity per unit root/leaf surface area ranges from about 10^{-1} to 10^{-6} kg s⁻¹ m⁻¹ MPa⁻¹ (Nardini and Tyree [1999](#page-9-31); Nardini et al. [2000;](#page-9-32) Atkinson et al. [2003](#page-7-27); Li et al. [2018](#page-8-34)) according to species, water status, aquaporin expression level and other factors regulating **Fig. 2** Factors infuencing potential rock moisture contribution to plant water use in soil-limited sites, and possible pathways for rock-to-root water transfer

root hydraulic properties (Aroca et al. [2012](#page-7-28); Miniussi et al. [2015](#page-8-35)). A similar range of variation is observed in irrigated soils, with typical values ranging between 10 and 10^{-4} kg s⁻¹ m⁻¹ MPa⁻¹ (Adamcova et al. [2005](#page-7-29)). Interestingly, some rock types display relatively high hydraulic conductivities ranging from 10^{-3} to 10^{-7} kg s⁻¹ m⁻¹ MPa⁻¹ (Boving and Grathwohl [2001;](#page-7-30) Pulido-Bosch et al. [2017;](#page-9-33) Pirastru et al. [2017](#page-9-34)). The overlap between values of hydraulic conductivities of rocks and those in the lower range for roots suggests that water movement from the rock to the root interior might be moderately efficient, at least under stress conditions limiting root hydraulics (Lo Gullo et al. [1998;](#page-8-36) Nardini et al. [1998](#page-9-35)). This scenario would agree with the putative role of rock moisture as a water reservoir that can be slowly released to the roots when transpiration is reduced, thus helping some tree species to maintain a minimum level of hydration and allowing survival under drought. Yet, as mentioned above, the size of rock pores largely excludes root penetration, unlike soil pores. Hence, the length of the water transport pathway in large-volume rocks might increase the overall hydraulic resistance to values incompatible with signifcant water

supply to the plant. Clearly, these and other considerations highlight a number of questions that still remain open: is rock-root contact direct, or is it mediated by thin soil layers and/or mucilage (Carminati and Vetterlien [2013](#page-7-31); Schwartz et al. [2016\)](#page-9-36)? Is the rock–root hydraulic contact maintained under drought, or does root shrinkage prevent water uptake from the rock reservoir (Triflò et al. [2004](#page-10-8); Carminati et al. [2009\)](#page-7-32)? Do mycorrhizae warrant the hydraulic connection between roots and rock interior, and what are typical hyphal hydraulic conductivities compared to rock hydraulics (Nardini et al. [2000;](#page-9-32) Muhsin and Zwiazek [2002\)](#page-9-37)?

We highlight some areas of research and possible techniques that might help to advance our understanding of the complex nature of rock-soil-root water transfer.

1. Quantifcation of the hydraulic conductivity of diferent rock types among those known to be colonized/explored by roots: hydraulic techniques used to measure the hydraulic properties of plant samples (e.g., High Pressure Flow Meter; Tyree et al. [1995](#page-10-9); Nardini and Tyree [1999\)](#page-9-31) might be adapted to quantify water fow under different water pressure diferences in cylindrical rock sam-

Fig. 3 Conceptual scheme of water fuxes and hydraulic resistances (jagged lines) potentially determining plant productivity (when belowground water sources are abundant) and drought survival (when belowground water sources are limited). Plant productivity is likely dominated by soil water pools in a scenario of low hydraulic resistances of soil, root and shoot. Under drought conditions, the strong reduction of soil water pools coupled to increased hydraulic resistances of both roots and shoots make rock moisture a water source

ples, thus allowing to compare rock and root hydraulic properties when measured with similar instrumentation.

- 2. Visualization and quantifcation of root-rock contact using X-Ray microcomputed tomography in small-sized plants grown in diferent soil-rock mixtures, to assess the potentially available area for direct water transfer from rocks to roots (Hou et al. [2022](#page-8-37)).
- 3. Implementation of neutron tomography techniques to quantify water flow from different rock types to soil and/ or directly to roots in vivo (Tötzke et al. [2017\)](#page-9-38).
- 4. Generation of a global dataset of rock coverage to improve our understanding of the infuence of bedrock on plant drought resilience; such a dataset, when integrated into large-scale ecological and hydrological models and combined with advanced remote sensing analysis, might signifcantly enhance our insights into how geological formations impact vegetation under drought conditions (Ernst et al. [2003](#page-7-33); Marusig et al. [2020\)](#page-8-30).

exploitable by the plant to keep cells hydrated. R_{Soil} , R_{rock} , R_{root} , and R_{short} indicate soil, rock, root, and shoot resistances, respectively. The green part of the circuit indicates the dominating water transport pathway in the two scenarios, whereas the red one indicates the limited one. Blue circles indicate belowground water pools. The size of the circles and resistances represents the relative magnitude of water pools and hydraulic resistances, respectively

Closer interdisciplinary cooperation between scientists with expertise in plant physiology, ecology, geology, mineralogy and hydrology, aimed at harmonizing hydraulic concepts and techniques, might fnally provide numerical solutions to the basic question: how rock water can be used by plants under drought?

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Declarations

Conflict of interest The authors declare that they have no confict of interest.

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