



Tansley insight

Digging deeper: what the critical zone perspective adds to the study of plant ecophysiology

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Summary

The emergence of critical zone (CZ) science has provided an integrative platform for investigating plant ecophysiology in the context of landscape evolution, weathering and hydrology. The CZ lies between the top of the vegetation canopy and fresh, chemically unaltered bedrock and plays a pivotal role in sustaining life. We consider what the CZ perspective has recently brought to the study of plant ecophysiology. We specifically highlight novel research demonstrating the importance of the deeper subsurface for plant water and nutrient relations. We also point to knowledge gaps and research opportunities, emphasising, in particular, greater focus on the roles of deep, nonsoil resources and how those resources influence and coevolve with plants as a frontier of plant ecophysiological research.

I. Introduction

Plants link the solid Earth to its atmosphere (Nadkarni, 2008). Through the process of transpiration, plants move water from within and across the Earth's surface into the atmosphere, thereby regulating the terrestrial hydrological cycle. Through the process of photosynthesis, plants fix atmospheric carbon dioxide to form the majority of the Earth's food and macroscopic life. Plants also drive the Earth's nutrient cycles through the acquisition and translocation of elements between the land surface and deep subsurface. These remarkable characteristics of plants control the fate of critical resources (water, carbon, chemicals and energy) that both limit and

drive the global biogeochemical cycles that sustain the Earth's biophysical systems. Hence, we cannot fully understand, nor predict, the trajectory of the Earth's system processes without also understanding the role of plants within those systems. Progress in understanding the role of terrestrial plants in the Earth's system requires research focused on how and where plants impact the balance between the pools and the fluxes of key growth-limiting resources, and how, in turn, the Earth's near-surface environment impacts plant function and distribution. In recent years, the near-surface environment has come to be known as the 'critical zone' (CZ) (National Research Council, 2001; Anderson *et al.*, 2004), which, in a broad sense, is a set of biophysical layers on and in the

Earth, extending from the canopy downwards through the soil and into weathered bedrock (Fig. 1). The recognition of the CZ as an integrated biophysical layer (Richter & Billings, 2015) has set the stage for advancing the field of plant ecophysiology and our understanding of the Earth's system processes as a whole.

Our goal in this *Tansley Insight* is to consider what the critical zone (CZ) perspective has brought to the field of plant ecophysiology and the roles it will play in furthering the science. By presenting recent advances in the field of CZ science, we explore how CZ properties impact the distribution, function and sensitivity of plants to the Earth's system. Our focus is on the resources that plants require and that limit their performance (see also Brandley *et al.* (2017) for additional insights on the role of trees in CZ

science). Specifically, we highlight very recent research on water and nutrient resources that plants acquire from the deep subsurface and mobilise throughout the entire profile of the CZ. Ultimately, we advocate for a purposeful integration of the CZ perspective – which considers the joint function of the Earth's biophysical layers – into plant ecophysiological research.

Digging deeper

A suite of transdisciplinary findings has emerged from CZ field sites (<https://www.czen.org/>) that suggests that the CZ perspective is necessary for a holistic understanding of plant ecophysiology, defined here as the interaction between plants and their biotic and

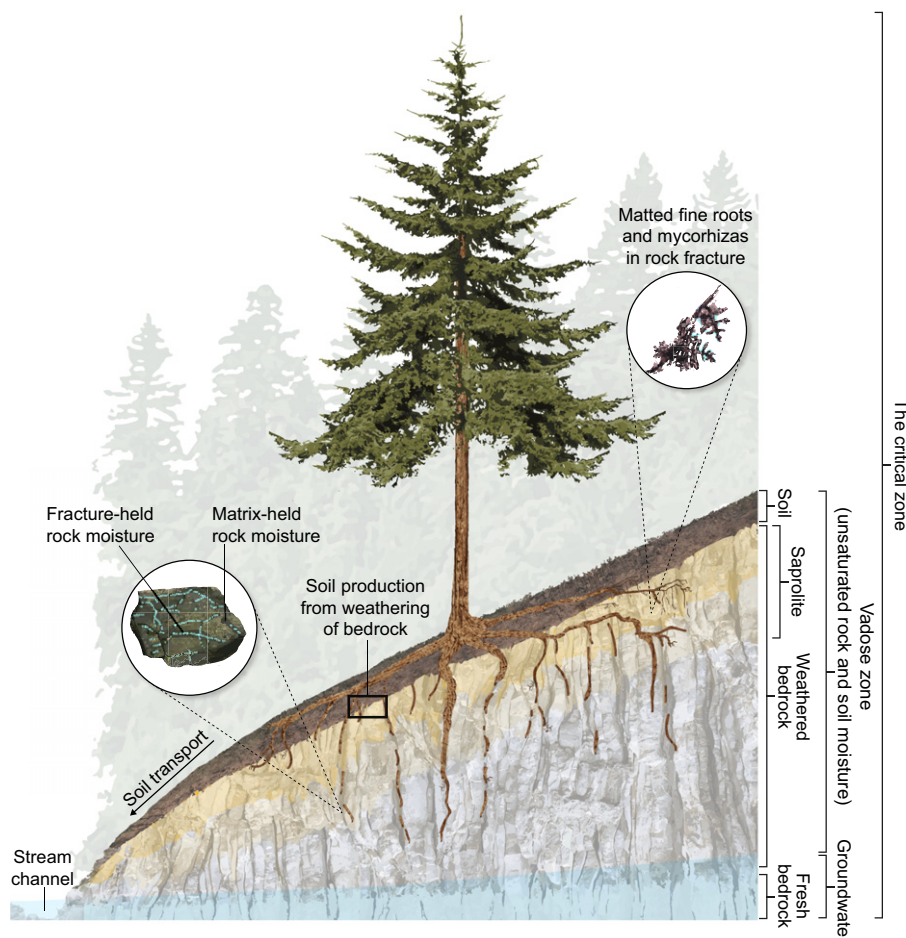


Fig. 1 A cross-sectional look into a critical zone (CZ), with commonly observed layers defined along the right-hand margin. The CZ extends from the top of the vegetation canopy to the base of weathered bedrock or actively circulating groundwater. While the relative thicknesses of each layer will vary with tectonic history, lithology, vegetation types and climate, these layers of CZ structure are generally emergent and widespread. The aboveground CZ consists of the microclimate from the soil surface to the top of the canopy and the plants themselves. The belowground CZ is composed of layers that vary in their physical and biogeochemical properties as well as in their water storage capacity and nutrient supply. We highlight the soil, which lacks any bedrock structure, and is often physically detached and highly weathered; underlying saprolite that is also highly weathered but remains *in situ*, retaining relict bedrock structure; and weathered bedrock, which becomes increasingly less fractured and chemically weathered with depth and can extend many metres deep to the top of fresh bedrock. Groundwater (light blue zone at the base of the figure) fluctuates within the CZ. At some depth, weathered bedrock grades into fresh, chemically unaltered bedrock that is typically perennially saturated with equilibrated pore fluids. Both large, structural roots and fine, absorptive roots permeate soil and weathered saprolite and bedrock layers, acquiring essential life-supporting resources from both fracture and matrix-held water. Roots drive weathering deep in the unsaturated vadose zone where dynamic rock moisture is held. Plants cycle water and elements between the subsurface and the land surface and mediate hillslope and Earth system processes such as erosion, evapotranspiration, biogeochemical transformations and runoff. Thus, the vegetation integrates and mediates biogeophysical functions across and within the critical zone, and is in turn shaped by CZ processes, emphasising the importance of the CZ to plant science as a whole and ecophysiology in particular.

physical environments. This perspective has yielded new insights gained through a widening of the focus of plant ecophysiological studies by digging deeper and looking higher at the boundary conditions responsible for the function and distribution of plants.

The belowground physical environment traditionally considered in studies of plant ecophysiology consists of the soil (consider prevailing terminology such as the 'soil–plant–atmosphere–continuum' and 'soil moisture'). Within the context of the CZ, *soil* (Box 1) is the often physically mobile material that mantles hillslopes and moves downslope under gravity due to physical and biological perturbations. Such soils are typically thin (<0.5 m) in upland, eroding environments where forests are common (Amundson *et al.*, 2015).

One of the key aspects of the CZ is that it includes not only soil, but also the chemically and physically weathered bedrock that lies beneath, where the rhizosphere commonly extends. As originally defined, the CZ extends at depth to the base of the groundwater zone (National Research Council, 2001), which may be kilometres below the surface; it is also common to define the lower extent of the CZ, as we do here, as the transition between bedrock that has been altered or weathered due to surface processes and unaltered fresh

bedrock, whose pore spaces are filled with chemically equilibrated fluids (Riebe *et al.*, 2017). Regardless of the precise definition of the lower boundary of the CZ, the weathered bedrock zone can be tens of metres thick. Weathered bedrock retains relict structures from its original state such as sedimentary bedding or magmatic fabrics, but has experienced mineralogical alteration and strain, resulting in the liberation of nutrients and the production of porosity for plant-available water storage (Fig. 1). Importantly, from the perspective of plant ecophysiology, weathered bedrock can extend deep below the lower boundary of existing soil maps (e.g. the US Natural Resources Conservation Service soil surveys stop at 200 cm depth) and the lower limit of most field investigations. Pioneers in the study of root–rock interactions such as Sternberg *et al.* (1996) and Schwinning (2010) provided needed inspiration for some of the recent CZ-focused work we review below. As we discuss, one of the more exciting and novel aspects of the CZ science approach is that it asks, by virtue of its multidisciplinary origins, not only how the extant subsurface structure matters to plants but also why the subsurface is structured in the way it is. Seeking such a process origin understanding is essential for predicting the CZ structure across the Earth's terrestrial surface, modelling its evolution through geologic time, and ultimately understanding its impact on plant ecophysiology. Below, we highlight examples that underscore the necessity of going deeper in considerations of plants' physical environments.

Box 1 A critical zone lexicon for plant ecophysicologists

This glossary includes common definitions used by critical zone scientists that plant ecophysicologists could use to guide and contextualise future research in the critical zone.

Erosion: mass removal in either solution or the solid phase.

Fresh bedrock: chemically unweathered and generally physically intact bedrock, typically of relatively low hydraulic conductivity and perennially saturated with chemically equilibrated pore fluids.

Groundwater: water in the saturated zone, where all pore spaces are filled with water, generally experiencing greater than atmospheric pressure.

Regolith: altered material overlying intact bedrock, which may be either *in situ* or mobile; 'mobile regolith' is often used to refer to soil.

Rock moisture: exchangeable water that resides within the weathered bedrock unsaturated (vadose) zone, below the soil and (usually) above groundwater.

Saprolite: extensively chemically weathered and decomposed bedrock that nonetheless remains physically *in situ*, retaining relict bedrock structures like bedding.

Soil: the layer of mineral and/or organic material at the Earth's surface that is detached from the underlying bedrock and altered by physical, chemical and/or biological processes.

Soil moisture: unsaturated (vadose zone) water that resides within the soil (mineral/organic) layer at the surface of the Earth.

Vadose zone: the portion of the subsurface where pore spaces are not completely filled with water (= unsaturated); water in this zone is held under variable tensions (but less than atmospheric pressure).

Water table: the surface of water with pressure equal to atmospheric pressure; top of the groundwater.

Weathered bedrock: *in situ* bedrock that has experienced chemical and physical alteration, including mineral dissolution and alteration and fracturing.

Weathering: alteration of parent material in the Earth's near-surface environment, manifested both chemically, by dissolution and alteration of minerals to secondary forms, and physically, by fracturing, dilation and compaction.

II. Water resources in weathered bedrock determine plant distribution and sensitivity to drought

Where fog and dew water supply are negligible (McLaughlin *et al.*, 2017), plants must acquire moisture from belowground, where it is replenished by rainfall or snowmelt. The high density of roots in the near surface and their exponential decline with depth has resulted in the common wisdom that *soil moisture* (Box 1) is the primary supplier of water for plant transpiration. However, the shallow extent of soils relative to underlying weathered bedrock and the tendency for near-surface soils to dry out between precipitation events have led investigators for decades to propose that water stored in the fractures and matrix of weathered bedrock can constitute a significant plant water source, particularly in seasonally dry climates (Klos *et al.*, 2018). Recent CZ studies have extended these ideas by demonstrating that plant use of moisture from weathered bedrock fundamentally impacts the hydrologic cycle, dictates plant community distribution and regulates plant sensitivity to drought. Rempe & Dietrich (2018) demonstrated the importance of *rock moisture* (Box 1) across an entire hillslope via multi-year observations of down-borehole neutron logging. They found that this weathered bedrock unsaturated zone moisture supplied about four times more water than the soils in an old growth forest in the Northern California Coast Ranges in the summer Mediterranean dry season and mediated the partitioning of rainfall into runoff and evapotranspiration. Thus, deep unsaturated zone water storage can sustain transpiration for any plants rooting into weathered bedrock long after shallow soils have dried, 'regardless of where the bulk of the roots occur', as Szutu & Papuga

(2019) put it, and is being more thoroughly integrated into conceptual views of the hydrological cycle.

The direct importance of variations in bedrock weathering to plants was recently highlighted by Hahm *et al.* (2018, 2019b), who explained the origin of a sharp ecotone that runs for hundreds of kilometres and separates a dense mixed coniferous-broadleaf evergreen forest from a sparsely canopied oak savanna. These radically different plant communities coexist under a similar climate and soil thickness due to geologically mediated controls on the extent of weathering and seasonal water storage capacity in the underlying bedrock. Similarly, Liu *et al.* (2019), working in a karst CZ in China, found that higher fracture densities in limestone explained increased woody plant cover. These studies point to the importance of understanding the spatial distribution and extent of weathering of bedrock, which is not included in most Earth system models and remains largely unmapped. One of the most exciting research frontiers in CZ science is the development of models that predict the evolution and architecture of the deep subsurface CZ (Riebe *et al.*, 2017), due to processes including fracture opening in evolving topographical and regional stress fields, fluid flow paths and chemical weathering, the penetration of frost cracking, and the slow drainage of equilibrated pore fluids. New methodological advances, particularly using geophysical methods (such as seismic refraction and nuclear magnetic resonance) can be used to test these models and characterise the resulting subsurface porosity structure that determines the water-holding capacity of weathered bedrock (e.g. Flinchum *et al.*, 2018; Rempe *et al.*, 2018).

Widespread plant die-back associated with recent droughts has resulted in concentrated research into the physiological mechanisms underlying hydraulic failure and carbon starvation that may accompany water deficits and heat stress. In spite of important progress, the biogeography of recent large mortality events is not entirely explained by the interactions between physiology, competition, pests and climatic drivers. This fact hints at the understudied but crucial role of the subsurface, which mediates how arriving precipitation is stored and released to plants. McLaughlin *et al.* (2017) proposed that areas of relatively high water availability (mesic microenvironments) might persist due to a variety of subsurface hydrologic mechanisms such as deep groundwater flow paths that are decoupled from interannual rainfall variability and therefore provide hydrologic refugia for plants in a changing climate. McDowell *et al.* (2019) argued that the supply of moisture from deeply weathered bedrock enabled a piñon pine-juniper woodland to survive an experimental heat and drought manipulation experiment in New Mexico, USA. Goulden & Bales (2019), working in the granitic southern Sierra Nevada, attributed widespread conifer mortality to recent extreme drought in California that prompted multiyear depletion and eventual exhaustion of deep water supplies (to 15 m depth). Perhaps counterintuitively, Hahm *et al.* (2019a) proposed that relatively low water storage capacity in weathered bedrock can decouple plants that experience Mediterranean climates from year-to-year swings in winter rainfall. This is because a small subsurface water storage capacity relative to typical annual rainfall totals can be replenished in both wet and dry years, resulting in a consistent dry season water supply to plants. They attributed the survival of

diverse plant communities in northwestern California to this 'storage capacity limitation' mechanism. Collectively, these studies pointed to the importance of deep subsurface water storage dynamics in weathered bedrock, which – although out of sight – can play a key role in determining when and where precipitation shortages become water supply shortages to plants.

Our understanding of subsurface plant water-sourcing dynamics has relied heavily on direct observations of gains and losses of water as well as the extensive use of natural abundance stable isotope analysis of water to trace the subsurface water pools used by plants. Recent exploration of the deep CZ has revealed a new, heterogeneous structure of water stable isotope profiles within weathered bedrock (e.g. Oshun *et al.*, 2016), in which variable inputs and evaporative enrichment in shallow soils are not the only potential mechanisms for creating isotopically distinct subsurface reservoirs (mineral-mediated and pore space-mediated fractionation are also likely at play; see discussion in Oshun *et al.* (2016)). These types of observations are spurring efforts into understanding the distribution of the stable isotopic composition of water across subsurface pores in the vadose zone (Box 1), with particular emphasis on understanding how water is held at varying tension (Sprenger *et al.*, 2018). Advances are being made through new observational techniques, including *in situ* vapour phase monitoring (Oerter & Bowen, 2019) and unique vadose zone sampling capabilities to obtain vertically infiltrating unsaturated zone moisture to >10 m depth within weathered bedrock (Druhan *et al.*, 2017). Higher frequency and resolution sampling and the use of cosmogenic radioisotopes are also enabling researchers to address previously intractable problems, such as the age distribution of water that supplies transpiration (e.g. Sprenger *et al.*, 2019; Visser *et al.*, 2019)).

III. Elements sourced from weathered bedrock and dust determine ecosystem nutritional status

Recent research has also expanded our understanding of nutrient delivery and cycling mechanisms within terrestrial ecosystems in the CZ context. For instance, Houlton *et al.* (2018) presented multiple lines of evidence that rock-derived N – by contrast to atmospherically fixed N – is a significant source of N to terrestrial ecosystems globally, with as much as 6–17% of modern-day N inputs into ecosystems derived from weathering of the underlying N-bearing bedrock. Chadwick & Asner (2018) explicitly coupled channel incision to nutrient rejuvenation at depth and foliar nutrient composition in the canopy of *terra firma* forests of the Amazon Basin. Aciego *et al.* (2017) and Arvin *et al.* (2017) challenged the assumption that P delivery to upland environments is dominated by underlying bedrock weathering by demonstrating that atmospheric dust, not rock, can be the primary source of P to ecosystems, even when they are actively undergoing physical erosion (Box 1).

Alongside a focus on nutrient inputs to terrestrial ecosystems, CZ research is beginning to reveal deep subsurface elemental cycling driven by plants, within bedrock fractures. Through an innovative application of Mg stable isotopes and elemental mass balance, Uhlig *et al.* (2017) demonstrated that nutrients (P, K, Mg, Ca and Si) are directly incorporated into plant biomass from weathering of parent material within the rock moisture zone,

providing evidence of plant acquisition of nutrients at depth. Taking a different approach, Hasenmueller *et al.* (2017) described the physical and biogeochemical environment of tree roots extending from surface soils into fractured bedrock using a series of pits to assess plant–rock interactions and the potential of plant-mediated weathering of rock to regolith. Their findings imply that plant roots facilitate rock weathering and production of ‘fracture fill’ (i.e. loose, soil-like material in fractures) at depth, and lend support to the findings of Uhlig *et al.* (2017) that plant roots also take up nutrients from fracture environments (Fig. 1). In a complementary but distinct discovery, Teodoro *et al.* (2019) documented direct weathering and acquisition of nutrients from quartzite rock by specialised roots of the Velloziaceae family in the P-impooverished *campos rupestres* ecosystem in Brazil.

In recognition of its essential role in plant resource acquisition and biogeochemical cycling, the deep subsurface root-associated microbiome has also lately received increased attention. Brantley *et al.* (2017) summarised recent work that hypothesises mycorrhizas facilitate not only nutrient uptake, but water uptake in the weathered rock zone. However, the role of mycorrhizas in acquiring essential resources from depth, particularly water in meaningful quantities, is still uncertain. Some work has demonstrated that rhizosphere microbes facilitate mineral weathering and, as a result, nutrient uptake (Balogh-Brunstad *et al.*, 2017), but more research is needed that to directly quantify the functional diversity of root-associated microbes at depth and their role in plant nutrient acquisition. Oeser *et al.* (2018) offered a step in that direction, by quantifying the abundance – but not the functional roles – of bacterial and archaeal communities in weathered rock across several sites along a climatic gradient in the Chilean cordillera. Taken together, these studies on deep subsurface roots and their associated microbiome demonstrate how the CZ perspective can push the field forward and provide new insights on plant nutrient ecophysiology in the deep CZ.

IV. Future directions

Attention paid to biologically mediated impacts of plants (and microbes) on the water and element cycles below the soil and their feedbacks should continue to open up new avenues for understanding the development and evolution of plant resource acquisition strategies within the context of larger Earth system processes. While the deep subsurface CZ is increasingly recognised as an essential reservoir for life-sustaining resources to plants, the CZ also includes a complex and dynamic aboveground environment in which leaf-mediated gas exchange occurs, nutrient and water deposition take place and where climatic conditions directly affect plant function and distribution. For example, topographically induced microclimate impacts plant physiology, yet its attendant impacts on subsurface CZ development and function are poorly understood. CZ-related research on radiation and its interactions with topography has explored the role that hillslope aspect (e.g. Pelletier *et al.*, 2018; Fan *et al.*, 2019) plays on plant distribution and energy delivery. There is also evidence that couplings exist between plant life cycles and productivity, hillslope aspect, bedrock weathering, soil production, sediment delivery to

channels, and channel incision and migration (Sklar *et al.*, 2017); together, these processes interact to drive the coevolution of the CZ's topographic form, land-surface energy balance, and ultimately plant ecophysiology (Ackerly *et al.*, In press). These processes should be fully integrated into our current understanding of topographic impacts on nutrient deposition and subsurface moisture balance resulting from variation in land-surface inputs (e.g. rainfall, cloud or fog water interception) and losses (e.g. runoff, infiltration, latent and sensible heat flux) in ecophysiological investigations. Research that successfully links deep subsurface structure to water and nutrient availability for the vegetation and integrates land-surface processes and feedbacks to better understand how plant communities and the CZ coevolve – both in the short term, in response to immediate climate impacts, and over geological timescales – will provide the most novel contributions at the interface between plant ecophysiology and Earth system science.

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