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Reviews and syntheses: On the roles trees play in building and plumbing the Critical Zone

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Abstract. Trees, the most successful biological power plants on earth, build and plumb the critical zone (CZ) in ways that we do not yet understand. To encourage exploration of the character and implications of interactions between trees and soil in the CZ, we propose nine hypotheses that can be tested at diverse settings. Depending upon one's disciplinary background, many of the hypotheses may appear obviously true or obviously false. We infer from this lack of agreement that the following nine hypotheses are important and must be tested to advance critical zone science. 1) Tree roots can only physically penetrate and biogeochemically comminute the immobile substrate underlying mobile soil when that underlying substrate is fractured or pre-weathered. 2) In settings where the depth of weathered material, *H*, is large, trees primarily shape the CZ through biogeochemical reactions within the rooting zone. 3) In forested uplands, the thickness of mobile soil, *h*, can evolve toward a steady state because of feedbacks related to root disruption and tree throw. 4) In settings where $h << H$ and the rate of uplift and erosion are low, the uptake of phosphorus into trees is buffered by the fine-grained fraction of the soil, and the ultimate source of this phosphorus is dust. 5) In settings of limited water availability, trees maintain the highest density of functional roots at depths where water can be extracted over most of the growing season with the least amount of energy expenditure. 6) Trees grow the majority of their roots in the zone where the most growth-limiting resource is abundant, but they also grow roots at other depths to forage for other resources and to hydraulically redistribute those resources to depths where they can be taken up more efficiently. 7) Trees rely on matrix water in the unsaturated zone that at times may have an isotopic composition distinct from the gravity-drained water that transits from the hillslope to groundwater and streamflow. 8) Mycorrhizal fungi can use matrix water directly but trees can only use this water by accessing it indirectly through the fungi. 9) Even trees growing well above the valley floor of a catchment can directly affect stream chemistry where changes in permeability near the rooting zone promote intermittent zones of water saturation and downslope flow of water to the stream.

1 Introduction

Natural scientists have long known that soils affect biota and biota affect soils (e.g. Belt, 1874). The perspective most commonly invoked by soil scientists to study such phenomena emphasizes timescales from years to centuries and depths from centimeters to meters (e.g.Dokuchaev, 1883). By contrast, geologists commonly study soil and other altered material to depths as large as 1000s of meters over timeframes as long as millions of years (e.g. Becker, 1895;Ollier, 1984). Now, a new field of science bridges these spatial and temporal differences in perspective by targeting the entire weathering engine from vegetation canopy to deep bedrock and by developing quantitative models for the evolution and dynamics of the landscape. This zone has been named the “critical zone” (CZ), given its importance to life on this planet (U.S. National Research Council Committee on Basic Research Opportunities in the Earth Sciences, 2001). Implicit to CZ science is the idea that investigating both the abiotic and biotic CZ over all timescales will elucidate the form and function of the CZ itself and allow projections of its future forms and functions. One CZ focus is organismal. As such, a specific focus is on trees -- the most successful entities transforming solar energy into the chemical energy of biomass. In this paper, we highlight some puzzles about the nature of trees’ effect on the CZ and the CZ’s effect on trees.

Like industrial power plants, trees cycle large volumes of water as they transform the energy of the sun into chemical energy (Figure 1): more than two-thirds of the solar energy used by trees during growth moves water through vascular tissues from roots to leaves through transpiration (Jasechko et al., 2013). In addition to moving hydrogen and oxygen, trees move 16 essential micronutrients from the soil and rock into biomass along with 14 or so other less essential micronutrients (Sterner and Elser, 2002;Cornelis et al., 2009). At the same time, trees fix carbon from the atmosphere into carbohydrates which are moved in the tree’s phloem tissues. As biotic engines, trees thus strongly impact the energy, water, and element cycles in forested and savannah ecosystems, shaping and sculpting landscapes and soils over long timescales (van Breemen et al., 2000;Balogh-Brunstad et al., 2008a;Reneau and Dietrich, 1991). Soils and landscapes in turn affect plant species composition and size as well as above- and below-ground productivity and rooting depth (Hahm et al., 2014;Marshall and Roering, 2014;Clark et al., 2003;Bennie, 1996). Only by studying the entire CZ using concepts from hydrology, soil science, geomorphology, geochemistry, and ecology will a synthetic view of tree-soil-landscape co-evolution emerge. Here, we promote the emergence of this new understanding by posing nine hypotheses about trees as builders and plumbers of the CZ.

These hypotheses were crafted to target some of the key points that puzzle us and that warrant further research. Some holes in our understanding are obvious. For example, most numerical models that treat chemical weathering and erosion are based on the assumption that the largest effect of trees is to reduce the water flow through the soil as water is lost to evapotranspiration through leaves; at the same time; the models ignore or simplify the many other biotic processes (Minasny et al., 2008;Lichtner, 1988;Lebedeva et al., 2007;Maher et al., 2009). Likewise, where the impact of trees or biota have been incorporated into models of weathering or landscape development, the models typically focus on one aspect of tree's impact (Gabet and Mudd, 2010;Roering et al., 2010;Godderis and Brantley, 2014;Corenblit et al., 2011;Reinhardt et al., 2011). Many of our hypotheses target these holes in our understanding.

We also identified hypotheses that have arisen because we now can measure new phenomena, new hydrologic or chemical reservoirs, or new types of microbiota. For example, it is obvious that the water in many streams derives from rainfall. Yet other research suggests that the water that trees use might be different from water that flows into streams (Brooks et al., 2010;Evaristo et al., 2015). This documents that there is an uncharacterized heterogeneity of water resources in the CZ (Oshun et al., 2016;Bowling et al., 2016). These findings are now forcing researchers to develop new ways to investigate the parts of the CZ that trees access. In turn, this is driving a new re-calculation of the types, sizes, and residence times of water inventories that are available to plants in catchments (Oshun et al., 2016). We also know that nearly all tree species host mycorrhizal fungi in symbiotic association with their roots (Read, 1997). However, our understanding of the roles these fungi play in CZ processes is in its infancy. Some reports suggest that up to a third of the organic material formed during photosynthesis by trees is exchanged with mycorrhizal fungi for nutrients and water (Read, 1997;Leake et al., 2008). Since the surface area to volume ratio of fungal hyphae that absorb soil-borne resources far exceeds that same ratio for tree roots, mycorrhizal fungi are a key player in building and plumbing the CZ.

The paper begins with summary sections about evolution and distribution of tree roots and fungi, and a section on the structure of the CZ itself. The rest of the paper consists of two sections on building and plumbing the critical zone that respectively contain four and five hypotheses each. Trees *build* the CZ by altering the physical architecture and chemistry of the subsurface environment. Trees *plumb* the CZ because they impact the reservoirs and pathways of water in the subsurface. The two subsets of hypotheses that focus on building and plumbing the CZ each highlight processes with inherently different characteristic timescales. In the first section of the paper, we pose questions about how trees affect the CZ architecture and we thus focus on questions related to processes that steer solute and sediment production and erosion over timescales of decades to millenia. In the second part of the paper, we focus on how trees affect the movement of water at timescales of seconds to decades. This water passes through the architecture described in part 1, facilitating chemical, physical, and biological interactions.

We designed the paper to highlight areas of contradiction among disciplines and to clarify the new hypotheses that are emerging within the cross-disciplinary dialogue in CZ science. The paper thus provides a roadmap of puzzles to stimulate the research of the future.

1.1 Evolution of tree-fungi interactions

As noted above, most tree roots are associated with symbiotic mycorrhizal fungi (Read, 1997). The term "mycorrhiza" refers to the symbiotic association of a root ("rhiza") and a fungus ("myco"). The oldest type of such fungi, arbuscular mycorrhizal fungi (AMF), form associations with plants that are inside the cell and are thus known as endomycorrhizal. AMF were present when plants first colonized the land surface using modified stems before "true" roots evolved (Brundrett, 2002). As the first true roots of terrestrial vascular plants evolved, they were relatively thick and required AMF for the plant to survive (i.e., obligate association). Eventually, certain lineages of trees evolved thin roots and became facultatively associated with AM fungi: in other words, the trees could survive with or without the fungi.

These latter thin roots can readily proliferate into zones of high nutrient or water content (Eissenstat et al., 2015;Adams et al., 2013). These species can also readily allow these roots to die off if zones become barren. These late-to-evolve, thin-root species often depend less on mycorrhizas than the early-to-evolve, thick-root species. Thin roots presumably evolved to access environments unfavorable for thick roots, such as very dry soils (Chen et al., 2013). In addition to evolution of thin roots, a new type of mycorrhizal fungi known as ectomycorrhizal fungi (EMF) evolved and they do not colonize the inside of plant root cells. Specifically, in boreal and north temperate regions and other locations where nutrients often are retained in slowly decomposing organic matter, some lineages of higher fungi that were previously free-living saprotrophs (organisms utilizing non-living organic materials for food) evolved symbiotic associations with plants. These ectomycorrhizal fungi coevolved with and fine-tune their relationship with plants. EMF differ from AMF in that they can develop large mycelial networks that explore large volumes of soil for water and nutrients. Today, ectomycorrhizal trees often have short, numerous root tips that can aid in EMF colonization (Brundrett, 2002). In addition, EM fungi often have retained some of the enzymes associated with saprotrophs. Therefore, EM trees often are more adept than AM trees at utilizing nutrients that are organically-bound. It is also likely that the leaves of EM trees also co-evolved with the EM fungi. Specifically, EM trees tend to have chemically more recalcitrant leaves that decompose less readily than those of AM trees (Phillips et al., 2013;Lin et al., 2016).

Given the evolutionary history, two predominant characteristics determine much about the strategies that trees use to forage for water and nutrients in the soil: the thickness of the roots and the type of fungi present (Cheng et al., 2016;Chen et al., 2016). First, thin-root tree species grow roots opportunistically to search for and take up nutrients, especially from organic-rich zones. In contrast, thick-root tree species do not show opportunistic root growth and thus rely more on their mycorrhizal fungal hyphae to explore and take up nutrients. Second, EM tree species favor foraging with their fungal hyphae rather than their roots. Thus, trees colonized by AM fungi generally forage for nutrients using their roots, especially if they have thin roots, but trees colonized by EM fungi forage more with their fungal hyphae, especially if they have thick roots.

Today, trees can have thick or thin roots and can be colonized by AM, EM, or no fungi at all. Examples of trees growing with these characteristics include elms and maples (thin roots colonized by AMF), magnolia, and tulip poplar (thick roots colonized by AMF), birches, hickories and oaks (thin roots colonized by EMF) and species in the pine family including spruce, pines and hemlock (thick roots colonized by EMF). Thick-root AM species generally can best compete in locations with more stable nutrient availability and higher moisture conditions. In contrast, thin-root AM species are generally better at taking advantage of temporally dynamic water and nutrient conditions (Chen et al., 2013). EM species are often found in conditions where nutrients are less available and more bound in organic matter. Valley floors in temperate forests may often have more AM trees, and this is the most common location of thick root species like tulip and poplar and magnolia (Smith et al., 2017 (in press)). In contrast, Smith et al. argue that ridgetops and steep midslopes with thin soils may be colonized by EM trees or AM trees with thin roots like maples.

1.2 Form, function, and distribution of tree roots

As discussed in the last section, much of the interplay between trees and earth materials is mediated by roots and their associated fungal hyphae. It is therefore important to understand where tree roots are found. In general, most tree roots, and a very high fraction of fine roots (i.e. < 2 mm), are observed in the upper 30 cm (Schenk and Jackson, 2005). Indeed, almost all roots are located within 2 m of land surface. However, the specific depths to which tree roots penetrate vary with precipitation, potential evapotranspiration, and tree species (Schenk and Jackson, 2002a, 2002b;Gale and Grigal, 1987). The depth of root penetration also varies with the thickness and properties of soil, and the characteristics of bedrock (Graham et al., 2010;Bornyasz et al., 2005b;Witty et al., 2003;Stone and Kalisz, 1991;Sternberg et al., 1996;Anderson et al., 1995;Hubbert et al., 2001a;Hubbert et al., 2001b;Kochenderfer, 1973;Nicoll et al., 2006).

For example, researchers generally have observed that most root mass is found in the disaggregated material above bedrock. However, where soils are shallow, the underlying substrate may contain roots, sometimes to many meters depth, especially in upland areas (Egerton-Warburton et al., 2003;Jackson et al., 1999;Graham et al., 2010;Hellmers et al., 1955;Scholl, 1976;Stone and Kalisz, 1991;Anderson et al., 1995;Canadell and Zedler, 1995;Hubbert et al., 2001a;Hubbert et al., 2001b;Rose et al., 2003;Witty et al., 2003;Bornyasz et al., 2005a;Estrada-Medina et al., 2013;Roering et al., 2010). Both fine roots and larger framework roots have been found at tens of meters depth beneath the land surface (Jackson et al., 1999;Canadell et al., 1996).

These different thicknesses of roots at depth point to the important fact that all roots are not the same, even at birth, and the type of root is important in terms of both plumbing and building the CZ. Most roots arise from the meristem (pericycle) of another root. However, another type of larger-diameter root -- commonly referred to as a pioneer root -- extends rapidly and undergoes woody secondary development within weeks (Zadworny and Eissenstat, 2011). These roots typically are not mycorrhizal and are chiefly used for transport and building the framework of the root system. Therefore, they are generally referred to as “framework” or “woody” roots upon maturation. While important in the root framework, such roots comprise only a very small fraction of total root length: most of the root length is derived from fine laterals that may branch two or three orders (McCormack et al., 2015). These laterals chiefly have an absorptive function and are characterized by a relatively high nitrogen concentration. They are colonized by mycorrhizal fungi and generally are ephemeral, living typically 0.5 to 2 years.

Most of our knowledge of deep root growth has arisen from studies in arid or semi-arid climates where water is a limiting resource. In those environments, trees must grow deep roots to harvest water in fractured or porous bedrock material (Graham et al., 2010;Egerton-Warburton et al., 2003;Lewis and Burgy, 1964;Zwieniecki and Newton, 1995;Hubbert et al., 2001a;Hubbert et al., 2001b;Rose et al., 2003;Witty et al., 2003;Bornyasz et al., 2005a;Schenk, 2008;Schwinning, 2010). In contrast, in temperate regions with higher rainfall (e.g. Gaines et al., 2016), trees have been observed to access water mostly from the upper soil even though their roots can still reach depths of several meters. In general, however, the extent of deep root penetration has not been systematically explored since most researchers have focused only on shallow depths (Maeght et al., 2013) and only a few lithologies: e.g., granite (Graham et al., 2010;Hubbert et al., 2001a;Hubbert et al., 2001b;Witty et al., 2003;Bornyasz et al., 2005a;Poot et al., 2012); shale (Hasenmueller et al., in review); or limestone (Hasselquist et al., 2010;Estrada-Medina et al., 2013). For example, Hasenmueller et al. (in review) identified deep roots that penetrate meters into bedrock in a temperate humid forest where trees generally are not water limited. In the same general region, however, roots at tens of meters depth are sometimes observed in karst lithologies. The utility of deep roots in such humid forests has not been established. It is possible that such deep roots allow water uptake late in the growing season when water has been depleted from shallow zones (Fimmen et al., 2007) or during drought episodes that may occur at decadal time scales.

In addition to providing water access, roots at depths deeper than 20 cm may also provide access to nutrients such as Ca that are low in abundance in shallower soils. For example, roots may pump Ca into shallow soil layers for easier uptake by surficial roots (Dijkstra and Smits, 2002). Deep roots also deposit organic reducing agents in the B or C horizons that allow extraction of nutrients through Fe-C cycling (Fimmen et al., 2007).

1.3 Architectural Layering of the CZ

A diverse array of observations implies that trees play a significant role in both building and plumbing the CZ architecture (Pawlik et al., 2016). For example, paleosols and sedimentary deposits have been used to argue that clay enrichment and chemical weathering was promoted by the proliferation of forest ecosystems during the Devonian, prompting the decline of atmospheric carbon dioxide and global cooling (e.g. Retallack, 1997). Other long-term studies that relate biogeochemistry to climate have also been used to argue that tree-CZ interactions may be central to our understanding of global change (Berner et al., 2004;Taylor et al., 2009). It is also well known that trees use many mechanisms that modulate CZ processes and development (Amundson, 2004;Brantley et al., 2012). To be specific, trees have the ability to alter bedrock chemically and physically as well as influence the style and pace of transport (Gabet et al., 2003;Kelly et al., 1998;Pawlik et al., 2016). In addition, trees limit the amount of water that flows to depth by taking up water in the rooting zone and evapotranspiring it back to the atmosphere before it has a chance to interact with deeper subsoil material (Keller et al., 2006;Moulton et al., 2000;Pavich et al., 1989).

Together, these fundamental processes govern the physical evolution of hillslope form and lead to important fingerprints of biota on the terrestrial landscape (Dietrich and Perron, 2006). On human timescales, trees are often associated with landscape stabilization because dense root systems create permeable soils bound together by the root network (Schmidt et al., 2001;Prosser et al., 1995). These two effects of roots – creating permeability and binding soils – can discourage surface runoff and associated erosion and decrease the likelihood of downslope soil movement, including via landslides. Over time, however, the insertion of root and hyphae networks in soil and bedrock results in a significant amount of mechanical and chemical work that breaks, dilates, and dissolves the near-surface material (Phillips, 2009;Schaetzl et al., 1990;Van Scholl et al., 2008;Bonneville et al., 2009). Trees have thus been characterized as engines of weathering and erosion (Gabet and Mudd, 2010;Roering et al., 2010). It is unclear whether trees are more important as hillslope and soil stabilizers or as catalysts of bedrock erosion and soil formation globally (Brantley et al., 2012).

If one considers eroding, upland, soil-mantled landscapes underlain at depth by bedrock, material at depth is moving up through the weathering zone over geomorphic timescales as material is removed near the earth’s surface. We adopt a simple conceptualization of this weathering zone that differentiates fresh bedrock at depth from overlying weathered material. The uppermost layer of weathered material can move and is thus referred to as mobile soil (Table 1). These zones are depicted in Figure 2 wherein h is the thickness of the mobile soil layer and H is the thickness of the entire weathered zone overlying bedrock. The relative values of h and H are thought to be set by the pace of erosion relative to the vigor of biotic and abiotic weathering processes. In regimes lacking substantial deep weathering, the thicknesses of h and H may be effectively equivalent. In this case, trees can influence the conversion of bedrock to mobile soil. By contrast, when $h << H$, trees’ direct influence on production of mobile soil has to be minimal. In these latter settings, weathered material may be sufficiently depleted and mechanically weakened as it moves up into the mobile soil layer that the contribution of tree root action is minimal compared to the sum total of reactions that produce the mobile soil material as it moves upward.

For $h \approx H$ regimes, the relationship among h, topography, and trees may depend on hillslope position (i.e., crest, sideslope, toe). For example, near ridge crests and in valley bottoms, the stress fields vary markedly, affecting the distribution of fractures (St. Clair et al., 2015;Wyrick and Borchers, 1981). An increase in the sharpness of a ridge (increased convexity) or an increase in topographic relief and narrow valley spacing can generate stress concentrations sufficient to fracture bedrock along ridge crests and valley bottoms respectively (Miller and Dunne, 1996;St. Clair et al., 2015). Thus, topography affects fracture distributions, which in turn affect the efficiency of soil production. These hypothesized interactions integrate processes that occur on highly variable timescales, making them challenging to model.

The aforementioned mechanistic interdependence of tree root activity and fractures emphasizes the role of tectonics in regulating CZ architecture. In landscapes where the ratio of the regional horizontal compressive tectonic stresses to near-surface gravitational stresses is relatively large, these stresses may promote the opening of fractures at great depth under ridges (St. Clair et al., 2015). One might expect that trees in such locations will have a limited role in shaping the CZ architecture because of the prevalence of deep regolith with deep or widely spaced fractures. By contrast, in landscapes where the ratio of horizontal compressive tectonic stresses to near-surface gravitational stresses is relatively small, the opening of surface-parallel fractures in the near-surface might create a setting conducive to trees playing a critical role as near-surface opening-mode fractures are conducive to root growth. The roots can potentially extend fractures as well as detach and disaggregate bedrock, setting the thickness of the mobile soil layer (*h*) as formalized by empirical soil production models (Heimsath et al., 1997). Such models stipulate that root-bedrock interactions (and thus soil production rate) decrease with increasing soil thickness (Figure 3). Numerous soil production datasets that use cosmogenic nuclides to quantify bedrock-soil conversion support these concepts (Wilkinson and Humphreys, 2005;Heimsath et al., 2010).

The action of trees has frequently been implicated in controlling the dynamics of the mobile soil layer. For example, researchers have suggested that trees can set (1) the frequency with which soils are overturned and moved downslope by tree throw (Schaetzl et al., 1990;Norman et al., 1995;Lutz and Griswold, 1939;Schaetzl and Follmer, 1990); (2) the extent and magnitude of soil dilation through root network propagation (Brimhall et al., 1992;Hoffman and Anderson, 2013); and (3) the persistence of soil stabilizing root networks (Schaetzl and Follmer, 1990;Norman et al., 1995;Denny and Goodlett, 1956). In most erosional settings, the depth of mobile soil, *h*, coincides with the depth of physical or biological disturbance processes (Yoo et al., 2011;Roering et al., 2010). However, just because the depth of disturbances often correlates with soil thickness, this does not necessarily demonstrate causation.

The implications of the ideas in these opening sections are explored in the hypotheses formulated below to explain the formation of and movement of water within the CZ. Of particular interest are the widely held assumptions of each discipline that in some cases may be contradictory and may require more holistic understanding. While some of the hypotheses below may seem obviously true or obviously false to some practitioners in some disciplines, we argue that this just emphasizes the need for further research.

2 Hypotheses: How Trees Build the Critical Zone

2.1 Hypothesis 1: Tree roots can only physically penetrate and biogeochemically comminute the immobile substrate underlying mobile soil when that underlying substrate is fractured or pre-weathered.

Many authors have observed that roots can grow in close contact with weathered rock (Fig. 1). However, few studies have systematically addressed lithological controls on root penetration into unweathered or weathered rock (e.g. Marshall and Roering, 2014;Zwieniecki and Newton, 1994). Although such close coupling has been used to argue that root growth can fracture rock, this may not be the case. Plant roots can exert axial pressure sufficient to create accommodation space as the roots lengthen in a soil matrix, but the material properties of soil, even a stiff clay, are vastly different from rock. Specifically, the fracture toughness, tensile or compressive strength of rock must be overcome to lengthen or create fractures. Data summarized in the botany and agricultural literatures suggest that measured root pressures are unlikely to overcome the strength of all but the weakest bedrock: for example, laboratory experiments for peas indicate that the maximum measured axial and radial pressures of roots, 1.45 and 0.91 MPa respectively (e.g. Bennie, 1996), may only be large enough to break apart the weakest of sandstones. We therefore hypothesize, along with previous researchers (Zwieniecki and Newton, 1994), that tree roots can only grow into fresh bedrock and promote weathering when fractures are already present or when the underlying rock has already been weathered to some extent.

A large array of chemical and physical processes occur at the root-rock-regolith interface and some of these processes were recently reviewed, with an emphasis on the less direct (or obvious) process linkages (Pawlik et al., 2016). Although such processes have been studied to some extent, testing this hypothesis will require measuring root pressures for relevant species in natural settings in comparison to rock strength. Of course, laboratory experiments on root strength are poorly suited to real world bedrock settings both in terms of quantifying stresses over daily or annual time scales, and in replicating the fracture mechanics that result in actual root-fissure configurations (Gill and Bolt, 1955;Eavis et al., 1969;Misra et al., 1986;McCully, 1995;Gregory, 2006). Thus new techniques are needed to measure external root pressures *in situ*.

In addition to an incomplete understanding as to what controls the rates of root propagation into fractures or how the frequency of tree-driven processes may weaken rock, we also do not fully understand what controls the spatial distribution of roots within fractured material. Intriguingly, recent work suggests that this spatial distribution may be influenced by mycorrhizal fungal communities (Egerton-Warburton et al., 2003). These communities may serve as frontier scouts for water and nutrients, especially in thick-rooted tree species with EMF as described in a previous section, and may complement roots in acquisition of these resources. Such exploitation could in turn generate stresses that might be sufficient to deform bedrock. If true, this implies that the microbial community may affect the manner and degree to which trees are able to convert rock to soil. Of particular interest might be the possibility of phenomena such as stress corrosion – chemical weakening of material that promotes fracturing. For example, we need to understand how chemical exudates near roots or fungal hyphae may be related to fracturing (Bonneville et al., 2009).

Of course, this endeavor to understand root-generated fracturing strongly depends on our understanding of the mechanical properties of the material to be fractured. Under thin soils, the patterns of rock fracturing and weathering may be an important limit on the rate of bedrock detachment and on the size of detached fragments incorporated into the soil. In such cases, trees affect the efficiency of soil production (Jackson and Sheldon, 1949;Marshall and Roering, 2014). This contrasts with settings with thick regolith (Chadwick et al., 2013), whereby climate or slow erosion rates diminish the role of trees in the production of mobile soil thickness to the point that roots do not penetrate deeper than h (see Table 1 and Figure 2). The fracturing of bedrock has been well studied in structural geology and geomechanics. While the substantial literature generated by those fields is highly useful, the partially weathered status of immobile material in the CZ likely has a profound influence on mechanical properties, and we know less about the physical attributes of these weathered materials. This points toward the need for a systematic and comprehensive analysis of rock properties as a function of weathering state (Selby, 1993;Murphy et al., 2016).

2.2 Hypothesis 2: In settings where the depth of weathered material, *H*, is large, trees primarily shape the CZ through biogeochemical reactions within the rooting zone.

As argued in hypothesis 1, tree roots can affect material underlying the mobile soil when this underlying substrate is fractured or pre-weathered and $h \approx H$. The mobile soil layer contains the highest densities of roots and mycorrhizal fungal communities. Therefore, some of the effect of roots on bedrock when h approaches H is chemical in nature. Indeed, the chemical signature of trees is likely to be profound in the root- and hyphae-rich mobile soil layer. However, if the mobile soil is very thick, tree roots do not reach unweathered bedrock. In regions where $h << H$, therefore, we hypothesize that the most important role that living trees play in soil processes is not related to insertion of roots into fractures. Rather, the major effect is more likely biogeochemical in nature.

Of particular interest with respect to this hypothesis is soil associated with the rhizosphere (Hiltner, 1904;Hartmann et al., 2008). The rhizosphere is the most biologically and chemically active frontier of the soil (McNear, 2013) because this is where compounds are released which directly and indirectly affect soil minerals (Philippot et al., 2013). Specifically, roots provide carbon for the microbial and fungal communities (Berner et al., 2003;Calvaruso et al., 2009;Calvaruso et al., 2014;McGahan et al., 2014). In return, mycorrhizal fungi and associated bacteria generally increase the availability of nutrients to the trees (e.g. Berner et al., 2003;van Scholl et al., 2006a;van Scholl et al., 2006b;Balogh-Brunstad et al., 2008a;Calvaruso et al., 2009;Bonneville et al., 2011;Smits et al., 2012;Ahmed and Holmstrom, 2015).

Two direct pathways by which nutrients are extracted from soil minerals are (1) dissolution driven by protons released into the rhizosphere in exchange for other cations; and (2) chelation with organic compounds released into the rhizosphere by fungi (Leake et al., 2008;Smith and Read, 2008;Ahmed and Holmstrom, 2015;Finzi et al., 2015). Other more indirect pathways also are hypothesized to be important, including exudation of reductive compounds (Fimmen et al., 2007), pumping of water up and down within the soil to access different minerals (Dijkstra and Smits, 2002), exudation of siderophores to take up iron (Liermann et al., 2000), effects on temperature and water throughput (Keller et al., 2006;Moulton et al., 2000), and the increase in chemical affinity that results from uptake and sequestration of reaction products.

In addition, plants can also indirectly promote weathering by secreting bio-signaling molecules to activate their mycorrhizal networks and associated micro-organisms (Deveau et al., 2012;Venkateshwaran et al., 2013). Such secretions initiate a cascade of reactions that then allows them to take up weathering products. Mycorrhizal fungi also are able to actively decompose organic matter to acquire nitrogen and phosphorus (Marschner, 2011;Reed et al., 2011). In fact, at the watershed scale, many studies have shown that trees can increase mineral dissolution rates (Berner et al., 2003;Calvaruso et al., 2009;Calvaruso et al., 2014;Augustin et al., 2015) compared to rates observed for rock areas that are bare or lichen- or moss-covered (Berner et al., 2003).

A big unknown in regard to the chemical effects of biota is the mycorrhizal fungal community (Grantham et al., 1997;Balogh-Brunstad et al., 2008b;Graham et al., 2010). Studies of such fungi below the mobile soil are limited but numerous experimental studies have shown that roots and their symbiotic fungi constantly forage and biosense nutrient sources (Leake et al., 2008;McNear, 2013), perhaps even at some depth. These studies support the idea that there is a large potential for mycorrhizal fungi to weather the immobile substrate at depth in locations where hyphae penetrate downward. Since roots are sometimes observed to reach the immobile weathered material even in humid forested regions (Hasenmueller et al., in review), mycorrhizal fungi undoubtedly also reach this zone and may explore and contact the immobile material (Rosling et al., 2003;Callesen et al., 2015). To understand such phenomena will require exploration of how and when secondary phases such as clays, organo-amorphous phases and oxides seal the surfaces of soil minerals from further dissolution (Kleber et al., 2007;Zhu et al., 2014). The fungal contribution -- and more broadly, the soil microbial contribution -- to weathering remains a largely unexplored research area in CZ science.

2.3 Hypothesis 3: In forested uplands, the thickness of mobile soil, *h*, can evolve toward a steady state because of feedbacks related to root disruption and tree throw.

Geomorphic and geochemical process models imply critical zone properties will tend toward a time-independent depth of mobile soil, *h*, if tectonic forcing (e.g. uplift rate) and climate forcings (e.g. rainfall, temperature, and seasonality) are constant. In this hypothesis, we posit that the thickness, *h*, of the mobile soil under a forest is maintained mainly by soil churning and disturbance of the underlying immobile substrate via root-wedging and tree-throw. We also implicitly argue based on the previous two hypotheses that such a steady state is only likely for the endmember case when $h \approx H$. Under these conditions, we hypothesize that trees act as the main feedback that maintains a steady-state value of h/H by coupling erosion and weathering. Steady state is most likely when tectonic or topographic stresses promote near-surface fracturing and weathering (see hypothesis 1) and when transport processes are sufficiently fast such that erosion is not rate-limiting. Instead detachment of mobile material from underlying material limits denudation.

When $h \approx H$, trees have access to the immobile weathered substrate at depths greater than *h* because of fragmentation of this underlying substrate and subsequent uplift by roots (Figure 2A). In detachment-limited settings, the ability of tree root networks to disturb shallow weathered rock material likely depends on the material properties, which may affect whether the soil production rates (represented by bedrock erosion rate) exhibits a humped relationship with soil thickness as exemplified in Figure 3 (Cox, 1980;Furbish and Fagherazzi, 2001). Empirical data (Heimsath et al., 2001;Gabet and Mudd, 2010) from the heavily forested Oregon Coast Range are generally consistent with the humped model predictions of increasing and then decreasing soil production rate with increasing soil thickness. However, an exponential soil production function may equally well fit the data (e.g. Heimsath et al., 2005), suggesting that either tree density or bedrock thickness disturbed by tree throw may not exponentially vary with soil thickness.

The nature of the feedbacks that explain how a steady state thickness might develop are not well understood. Numerical simulations have been used in the geological literature to explore tree-driven soil production: these models are consistent with a ‘humped’ soil production function (Figure 3). Such a function predicts maximum production rates at values of mobile soil thickness that are non-zero (Gabet and Mudd, 2010). This leads to the idea that a complex relationship likely exists between soil thickness and tree density. One explanation for this functional relationship emerges from the *a priori* stipulation that tree density increases with soil thickness. As mobile soils become sufficiently thick, however, Gabet and Mudd (2010) have argued that a negative feedback must exist. Specifically, as h increases, tree density continues to increase but the frequency of root-bedrock interaction decreases, resulting in a reduction in the rate of mobile soil production. In fact, however, in landscapes with maturing forests and where soils are not extremely thin or very infertile, tree density becomes independent of soil thickness because tree density becomes dictated mostly by canopy closure and differential mortality of smaller, light-limited individuals (“self-thinning” (Lonsdale, 1990)). Thus, as forests mature, tree density is affected more by tree age and size than by soil thickness. The negative feedback that slows down soil production (Figure 3) as soil thickness increases must therefore be related to phenomena other than tree density. Some have argued that porewater chemistry might provide such a negative feedback such that thicker soil produces less corrosive fluids at depth that could slow down the rate of soil production (Fletcher et al., 2006). Additionally, the model is based on the assumption that all bedrock is amenable to disruption by tree roots, which may not be the case if tectonics and rock properties are a first-order control on root penetration into bedrock as suggested by hypothesis 1.

This hypothesis implicitly assumes that trees can contribute chemically to altering minerals when $h << H$, but cannot physically or chemically set the rate of formation of mobile soil from underlying material because the subsurface injection of carbon into weathering rock is minimal. When $h << H$, solute fluxes, transmissivity, grain size distribution and other near-surface attributes of the mobile layer may vary significantly with time and therefore are not expected to reach a steady state. If a steady state is reached under these conditions, other attributes of erosion and weathering unrelated to trees presumably maintain the stable value of h.

In the two end-member cases of $h \approx H$ and $h << H$ (Figure 2), roots and rhizospheric microbiota may function in two different ways. When $h \approx H$ (Figure 2A), roots and associated microbial communities interact significantly with both the mobile soil and the upper immobile substrate layers, actively weathering primary minerals containing many macronutrients (e.g. P, K, Mg, Fe, and Ca). Uptake of these nutrients into hyphae and roots nourish the plants. In fact, if P is present at a low concentration, some root-associated fungi can "biosense" P hotspots and proliferate into those locations (Leake et al., 2004). This has not been shown for other elements (Wallander and Ekblad, 2015) although upward pumping of elements such as Ca has been hypothesized (Dijkstra and Smits, 2002). We expect that water availability in the soil most likely influences all these processes that are mediated by mycorrhizal fungi (see Figure 4 and hypothesis 4).

In contrast, when $h << H$, roots and associated mycorrhizal fungi have little to no contact with the underlying bedrock (Figure 2B). In this end-member, roots and associated microbes are not likely to access nutrients in the bedrock itself and therefore must recycle nutrients by decomposing organic matter and capturing nutrients from water infiltrating downward in the soil profile (Smith and Read, 2008;Marschner, 2011). In addition, the degree to which tree species rely on their mycorrhizal fungi depends on the thickness of their roots and the type of mycorrhizal fungi (Brundrett, 2002;Cheng et al., 2016;Chen et al., 2016). Roots and associated microbiota may be able to shift between actively weathering primary mineral phases to purely recycling nutrients from organic matter and soil surfaces depending upon the relative magnitude of h with respect to H in different climatic, lithologic, and tectonic settings.

In forested steeplands, trees may impart a distinctive topographic signature that results from these process interactions. For example, analysis of airborne lidar for western Oregon hillslopes shows that pit-mound features generated by tree turnover dominate landscape morphology at length scales less than 8 m while hillslope-valley landforms characterize landscape form at longer length scales (Roering et al., 2010). Ground-penetrating radar reveals a similar pattern along the soil-bedrock interface, which results in highly variable soil thickness (Heimsath et al., 2001). On these closed-canopy coniferous slopes with typical soil thickness values of 0.5 to 1.0 m, large roots (>10 cm diameter) are observed to utilize shallow bedrock fractures to reach depths of 2-3 m in the column of shallow bedrock immediately below tree stems. In these below-stem zones, root penetration results in the disaggregation of bedrock. Although at any given time the basal area of stems only occupies <5% of the forest floor, the regional average erosion rate (~0.1 mm/yr) and recurrence interval of stand-resetting fires (250 to 400 yrs) imply that virtually all parcels of bedrock and soil are impacted by below-stem large root penetration during their exhumation to the land surface. In other words, when erosion rates are not overly fast, tree roots interact with or ‘touch’ the vast majority of shallow bedrock (as well as soil) that eventually erodes from the hillslope and is delivered to stream networks (Roering et al., 2010). This suggests that trees influence not just their near-surface terrestrial environment but likely contribute to the grain size distribution that participates in stream incision or that supports aquatic ecosystems (Sklar, 2016).

In contrast, in a relatively moist, mixed temperate forest in a catchment developed on grey shale with more gentle slopes of ~40% and erosion rates of approximately 0.03 mm/y (West et al., 2013), only very fine roots are observed penetrating deeper than 1 meter into the soil and they are typically only observed when they penetrate fractures in the bedrock (Hasenmueller et al., in review). The lack of a high density of roots at depth is not due to a lack of fractures in the shale because the upper 5 to

8 m of the rock is highly fractured, a characteristic attributed to the periglacial climate during the Last Glacial maximum (Jin et al., 2010). Although these deep roots are present, their density is very low compared to the roots in the upper 30 cm of soil where the trees get most of their water (Gaines et al., 2016). Generally, rooting depth is not only controlled by the availability of fractures in the rock, but also by the demand for deeper sources of water (Schenk 2008). This demand is not high for most of the year in this humid, shale catchment because frequent showers during the summer wet the surface soil layers and transpiration is tempered by relatively low winds, high humidity and modest temperatures. Rooting depth may thus be considerably shallower in more mesic environments than in more arid environments.

Clearly, the systematic feedbacks between roots and rocks remain to be investigated. Open research questions abound: how do trees set and maintain steady-state values of *h* within the global range of tectonic, lithologic, and climate conditions? What are the implications of our two end-member scenarios ($h \sim H$ and $h << H$) in terms of how trees plumb the Critical Zone (see next section)? How do disturbances on the local to landscape scale affect the role of trees in building, maintaining, and plumbing the Critical Zone? How can this framework of trees creating and maintaining their CZ resources be extended to depositional settings, glaciated landscapes, etc.? Furthermore, how does the ecological functioning of trees differ, including their access to nutrient resources such as phosphorus, under the global range of conditions?

2.4 Hypothesis 4: In settings where $h << H$ and the rate of uplift and erosion are low, the uptake of phosphorus into trees is buffered by the fine-grained fraction of the soil, and the ultimate source of this phosphorus is dust.

Since phosphorus (P) is a rock-derived nutrient, its availability to an ecosystem is usually controlled by the concentration of the phosphorus-containing mineral apatite in rock, which is in turn controlled by lithology. P availability is also affected by the rate that apatite is inserted into the weathering zone by the erosion rate, which in a steady-state system is ultimately set by the uplift rate (Vitousek et al., 2010). Some rocks are naturally low in P content, in which case the limiting lithogenic source requires that P is strongly recycled within the soil and that leakage of P is replenished by inputs of dust. However, as suggested by other researchers (Porder et al., 2007), we hypothesize that even for lithologies with abundant P, the main source of this macronutrient can still be dust. We expect dust to be the predominant source especially in systems where the thickness of the mobile soil *(h)* << thickness of the total mobile soil + immobile subsoil substrate *(H)*, and slow rates of uplift and erosion lead to long mineral residence times within the weathering zone. These long time periods can magnify slow losses of P. Once P is released from primary minerals, it can be strongly sorbed onto clay, organic matter, and iron oxide surfaces. Thus weathering produces available P but also produces the high surface-area phases (clays and organic matter) that remove P from soil solutions. Together, these phases, known by soil scientists as "plasma" to contrast them from the larger mineral grains ("skeleton"), buffer the P availability.

We thus hypothesize that for rocks that produce soils with high plasma : skeleton ratios such as basalt and shale, the absolute control on P availability to trees will be governed by uplift and net primary production. This latter parameter governs the physical and chemical properties enabled by existing vegetation. This hypothesis posits that the proximal control on P availability is controlled by P sorption onto plasma surfaces and that this sorption can lead to both reduced plant availability on the one hand and reduced losses of P by leaching on the other. By contrast, for rocks that produce low plasma : skeleton ratios such as granite and sandstone, we expect that uplift (erosion) will impose an absolute constraint on P availability that is far less buffered by proximal controls such as plasma sorption.

3 Hypotheses: How Trees Plumb the Critical Zone

3.1 Hypothesis 5: In settings of limited water availability, trees maintain the highest density of functional roots at depths where water can be extracted over most of the growing season with the least amount of energy expenditure.

Water potential is defined as the potential energy per unit volume of water within a soil-plant system relative to pure water at sea level (Kramer and Boyer, 1995). Generally, water in the soil-plant system is at a negative potential, i.e., the plant is “sucking” water out of its environment under tension. Water potential is affected by the gravitational, turgor, osmotic, and matric potential of water in the system (Kramer and Boyer, 1995). Briefly, these terms refer to the hydrostatic head, the pressure associated with cell expansion in growing tissues, the tension related to the solute content of the water in different reservoirs, and the surface tension that arises between water and solids.

A water molecule will move to the root if the water potential in the soil is higher than the water potential in the root. Of particular importance for plants is the matric potential of soil water. At some times of year or in some environments, the matric potential can be more negative than the lowest potential from which plants can access appreciable water, i.e., the so-called wilting point (Figure 4). However, this concept may be inappropriate for trees because it is based on the concept of a “standard [herbaceous] crop plant”. Within the soil matrix, a plot of matric potential versus the volume of water can be conceptualized as delineating different water reservoirs ranging from water that drains freely due to gravity to so-called hygroscopic water which may not be accessible directly to roots except under certain conditions (Figure 4). Field capacity is operationally defined as the water potential associated with the moisture remaining after a soil has been fully wetted and any excess water has been drained away. Between the wilting point and field capacity is the potential of capillary water: this water is held by surface tension in the soil matrix and is readily accessible by plants.

If water in the upper 10 cm of soil is of equal water potential to that at 1 m depth, then trees will use the surface water first, both because it requires less energy to move the water to the leaves and because there is typically much greater root length near the soil surface (Green and Clothier, 1999). Higher root length density means that the distance from bulk soil to root is shorter, on average, and this shorter distance of transport enables the plant to take up water quicker. However, if soil water potentials are low (more negative) in the surface layers but high at depth, some trees may instead acquire a substantial portion of water at depth instead of from the surface (Jackson et al., 1999).

Some studies have identified circumstances where despite groundwater being readily available within 0.5 m of the surface, tree species instead use rainfall at shallower depths (Busch et al., 1992;Snyder and Williams, 2000). For example, after one rainfall event, as much as 40 – 50% of tree sap water in one system was shown to be derived from rain water (White et al., 1985). Such opportunistic use of water is a strategy consistent with the expectation that new, shallow, sources of water from a rainfall event are energetically less costly to obtain because they are present at a higher water potential and are present in the zone of greater root length density (and we also know that more of the nutrients that plants require are generally present in surface soils). Strategically, the tree takes up shallow water instead of deeper groundwater at least partly because the root length density is generally lower at depth.

Similarly, trees growing alongside perennial streams in arid regions do not necessarily use what seems to be the most easily accessible stream water. Instead trees may access soil water from either deeper layers (Dawson and Ehleringer, 1991) or from deeper saturated soils where a high fraction of roots reside (Bowling et al., 2016). In those locations, it is possible that the root density is larger at depth than near the surface, allowing water to be taken up from depth even during the parts of the year when plentiful water is available in the stream. This idea has led to the view that plants may partition their hydrological niches (Silvertown et al., 2015) into different layers (e.g., *Walter's Two-Layer Hypothesis*). Specifically, Walter's hypothesis states, in part, that shallow and deeply rooted plants do not compete for the same water resources (Walter, 1939;Ward et al., 2013;Ehleringer et al., 1991;Schwinning, 2008;Weltzin and McPherson, 1997;Holdo, 2013;Schenk and Jackson, 2002a).

From these observations emerges our hypothesis, namely that trees grow high root densities at depths where water is most easily extracted for the largest portion of the growing season. Thus, during time periods of the year where water is available at depths that generally do not have water, trees will continue to extract water from other depths where they have more dependably found readily available water. A corollary to this hypothesis is that the root length density is a map of where water is most likely to be present for much of the growing season when trees need water. Such corollaries can be tested by measurement of root length densities and water usage by trees in soils in different landscape positions, on different lithologies, and on soils developed in different climates.

3.2 Hypothesis 6: Trees grow the majority of their roots in the zone where the most growth-limiting resource is abundant, but they also grow roots at other depths to forage for other resources and to hydraulically redistribute those resources to depths where they can be taken up more efficiently.

This hypothesis is a corollary of hypothesis 5 where we hypothesized that the depth where trees in water-limited environments grow roots is intimately linked to where they are able to acquire water while conserving the most energy over most of the growing season. However, uptake of water and nutrients need not be tightly coupled (Pate et al., 1998). While some plant species rely mainly on deep soil moisture for transpiration (Cavanaugh et al., 2011;Kurc and Benton, 2010;Kurc and Small, 2007), their nutrient uptake may be uncoupled from this water uptake if the nutrients are only present in shallow soil or near decomposing leaf litter. On the other hand, significant pools of some nutrients may be found in deeper soil layers closer to the protolith (Maeght et al., 2013;McCulley et al., 2004). Such deep nutrient access might provide an explanation for observations of some low-density root growth in deep soils even when most of the roots grow in the shallow, wetter layers (e.g. Hasenmueller et al., in review). In fact, some trees in more arid environments have so-called “dimorphic root systems”. These trees produce abundant fine roots in the surficial soil to recover nutrients from fallen leaves, and, at the same time that they grow abundant deep roots with highly efficient transport anatomies to acquire sufficient water from deeper reservoirs (Pate et al., 1998).

An important aspect of this hypothesis is the potential for hydraulic redistribution. Such redistribution may provide another mechanism for plants to solve the problem of different spatial distributions for water versus nutrients (Caldwell et al., 1998). Hydraulic redistribution is the process by which plants redistribute water in the soil profile from moist to dry regions using their root systems (e.g. Caldwell et al., 1998;Oliveira et al., 2005). Specifically, hydraulic redistribution can bring water (and perhaps nutrients) in some soils from depth to the dry surface, so that at night, the rhizosphere is moistened, allowing for nutrient solubilization as well as decomposition of organic matter (Armas et al., 2012). Although not proven, Ca redistribution from deep to shallow has been hypothesized in at least one soil system (Dijkstra and Smits, 2002).

To explore this hypothesis will require careful studies that determine the distribution of root length density, water isotopes, nutrient distributions and fluxes, and hydraulic redistribution. For example, some stable isotope studies (e.g. Phillips and Ehleringer, 1995) and sap flow measurements linked with soil moisture measurements at depth (e.g. Cavanaugh et al., 2011) have identified cases in which plants with roots mostly near the surface still rely mainly on deep soil moisture for transpiration. For those systems, we infer that the shallow roots are grown densely to provide growth-limiting nutrients; however, such an inference should be tested. Similar studies have also identified cases in which plants which have grown a high density of roots at depth actually seem to prefer taking water up from shallow reservoirs (e.g. Nippert and Knapp, 2007). For those cases, plants may be growing deep roots as a competitive strategy to limit uptake of water and nutrients by neighbors (McNickle and Dybzinski, 2013).

3.3 Hypothesis 7: Trees rely on matrix water in the unsaturated zone that at times may have an isotopic composition distinct from the gravity-drained water that transits from the hillslope to groundwater and streamflow.

Given the importance of tree roots in affecting soil permeability, trees play a significant role in routing water within the critical zone. Ecohydrological separation -- defined as trees using water of a character different from the gravity-drained water found in soils, in saprolite or in groundwater and streams -- has been hypothesized to be common based on a recent meta-analysis of isotope ecology literature (Evaristo et al., 2015) and global remote-sensing data based on the deuterium composition of atmospheric vapor (Good et al., 2015). These and related studies (e.g., Brooks et al. 2010) suggest that trees rely on water present in the unsaturated zone and this water may have an isotopic composition distinct from the gravity-drained water that transits the hillslope to become groundwater recharge and streamflow.

This “two-water-world” hypothesis (McDonnell, 2014) could be at odds with the existence of subsurface reservoirs such as layers of saprolite and fractured bedrock that hold water that is accessed by trees (Oshun et al., 2016). For example, in seasonally dry climates, trees may derive a significant portion of their moisture from weathered bedrock sources well below the soil (Nie et al., 2012;Zwieniecki and Newton, 1996;Graham et al., 2010). In arid or hyperarid systems, the fraction of use of deep water increases as annual rainfall decreases (Dawson and Pate, 1996;Dawson et al., 2002). Such deep water resources link deep unsaturated zone moisture to the atmosphere and hydrologic cycle through root uptake and transpiration. Yet, the evidence for ecohydrological separation suggests that trees may not always use gravity-drained water if other, more energetically available sources are present.

The evidence for ecohydrological separation (Good et al., 2015;Evaristo et al., 2015;McDonnell, 2014) suggests that plants are sometimes using water from unknown depths and that the water potentials are different from what might be considered the “crop plant” wilting point (e.g., <-1.5 MPa). Furthermore, in some cases, Evaristo et al. showed that gravity-drained and transpired waters were not isotopically distinct. These observations document that our understanding of how water is obtained by roots in the deeper subsurface is lacking. Some of the paucity of knowledge is related to questions of physiology and some to subsurface structure and character (Hiscock et al., 2011;Walker and Richardson, 1991;Washburn and Smth, 1934).

Methods to extract and measure tree water sources are currently being refined and improved to test the generality of hypothesis 7 more thoroughly. For example, an additional intriguing observation is that many trees with mycorrhizal fungal associations appear to have a mechanism for tapping water even below the agronomically-defined soil wilting point of cultivated plants (also see hypothesis 8). This should not surprise us since we have known that the wilting point of a crop plant and a tree are rarely, if ever, the same (tree values can be much, much lower (Meinzer et al., 2016). So the “two-water world” hypothesis must now be thoroughly tested in the context of water potential measurements and theory (see hypothesis 5 and Bowling et al. (2016)) for how plants are known to take up water. Research is also needed to investigate the physical and chemical effects on the isotope composition of water in the subsurface (Oshun et al. 2016) and new observations about fungal access to water as described below in hypothesis 8.

3.4 Hypothesis 8: Mycorrhizal fungi can use matrix water directly but trees can only use this water by accessing it indirectly through the fungi.

Mycorrhizal fungi may play an important role in water acquisition (Duddridge et al., 1980;Augé, 2001;Plamboeck et al., 2007;Bárzana et al., 2012). Hyphae, fungal threads emanating from the root, may allow a plant to access water from water-filled pores that are too small for the roots. Arbuscular mycorrhizal (AM) fungi, for example, have hyphae with diameters between 2-20 μm, which is typically an order of magnitude or more smaller than roots. Hyphal length density can vary between 1 and >100 m per gram of soil (Smith et al., 2010). Thus, mycorrhizal hyphae may access water not available to plant roots, presumably because fungal hyphae can penetrate small water-filled pores to a greater extent than the larger roots (Allen, 2007;Lehto and Zwiazek, 2011). Thus, mycorrhizae may be a factor that facilitates plant access to rock moisture and matrix waters that would otherwise be inaccessible to roots. Although water in the rock matrix may not actually be held at tensions higher than the permanent wilting point, the pore network may be so small that only hyphae can penetrate. These hyphae-pore interactions also have the potential to affect *h/H* through mineral plucking, and changes in pH or redox status (see hypothesis 3).

Although it makes physical sense that hyphae may penetrate smaller pores in rock matrix than roots can penetrate, many researchers are not convinced that mycorrhizal fungi play an important role in acquiring water at water potentials beyond the wilting point (Kothari et al., 1990;George et al., 1992;Koide, 1993;Bryla and Duniway, 1997). For example, one counterargument is that the hyphae have high axial resistance to water flow because of their small diameters and their lack of vessel-like structures: this observation might lead one to argue that flow rates in hyphae simply are too slow to appreciably contribute to transpiration directly (Koide, 1993). Most improvements in plant growth or survival related to mycorrhizal fungi are considered to result not from water uptake but rather from the indirect effects of fungal-mediated nutrient acquisition and improved plant nutrition (Kothari et al., 1990;Bryla and Duniway, 1997). In this regard, EM and AM fungi may differ significantly. Unlike AM, EM fungi are capable of forming relatively large-diameter rhizomorphs made of fused hyphae where hydraulic conductance is high enough to contribute significant water to plants (Brownlee et al., 1983;Warren et al., 2008). Of course, these larger hyphae may be unable to access the finest matrix pores. Clearly, to explore hypothesis 7 requires not only assessing the size and distribution of small pores in bedrock and regolith (Bazilevskaya et al., 2014), but also which pores allow hyphal access and water and nutrient uptake (Graham et al., 2010).

3.5 Hypothesis 9: Even trees growing well above the valley floor of a catchment can directly affect stream chemistry where changes in permeability near the rooting zone promote intermittent zones of water saturation and downslope flow of water to the stream.

One of the outstanding research questions concerning small catchments is how to predict the relationship of solute chemistry and discharge as a function of variations in precipitation (Godsey et al., 2009). In many catchments, most of the nutrients and other solutes added to rain water as it transits through hillslopes to the bounding streams are added from weathering reactions in the soil. These reactions largely occur in the matrix, where the surface area wetted by porewater is high. However, as discussed in hypothesis 7, this water does not drain by gravity. In fact, pore waters in gravity-draining pores in regolith may mix with matrix pore waters only under water-saturated conditions. Under these conditions, nutrients and other solutes in matrix waters mix with the gravity-drained waters and then move to the stream. Therefore, the matrix will only deliver water to the stream if the hillslopes are hydrologically connected to the stream.

Given these observations, it is difficult to imagine how trees growing high on hillslopes might affect stream chemistry (Figure 5). For example, hillslopes are mostly disconnected from streams during baseflow, and stream chemistry is not strongly influenced by trees during those time periods. We hypothesize that during hydrologically connected periods, trees on hillslopes can impact stream chemistry detectably. The impact of trees on stream chemistry therefore depends on the degree of connection between the hillslope and the stream (Herndon et al., 2015). According to this hypothesis, biogeochemical processes such as cation exchange occurring in matrix waters can influence ecological responses in streams under conditions of high connectivity (e.g. Green et al., 2013).

Hydrologic connectivity can be quantified in multiple ways (Larsen et al., 2012;Spence and Phillips, 2015). However, metrics of connectivity that work well in some settings are not always transferable to different locales (James and Roulet, 2007). We hypothesize that changes in connectivity are dictated by the extent of water saturation and the nature of the architecture of the critical zone in any given catchment. For example, we assume that there is usually a sharp decrease in vertical hydraulic conductivity at the base of the mobile soil layer (Figure 2). At this interface, water may pond and create a transiently saturated layer that can drain via macropores laterally and vertically, allowing matrix waters to preferentially mix along the mobile soil -immobile material contact. If the perched water zone connects all the way down the hillslope, water can flow downslope to the stream. A hypothetical geometry for this is shown for the connected gravity-drained water in Figure 5. Spatial heterogeneity in the contact between the mobile and immobile layers will greatly influence the subsurface drainage to the stream. Specifically, the subsurface topography in many locations is characterized by depressions that “fill and spill” depending upon the extent of saturation (Tromp-van Meerveld and McDonnell, 2006).

Based on hypothesis 1, it is furthermore possible that the location and depth of the depressions at the base of the mobile layer that “fill and spill” and control hillslope-stream connectivity are related to the penetration of tree roots into the immobile soil layer and the effects of tree throw. Such penetrating roots (see hypothesis 1) can have a strong influence by plucking rock material and creating the rough undulations at the interface between the overlying permeable layer and the underlying more impermeable layer (Figure 2). Rooting depths in systems where $h \approx H$ are deep enough to interact with the bedrock or the underlying immobile weathered material, and can draw up water from below (hypothesis 2) as well as enhance physical and chemical weathering (hypothesis 1). Furthermore, fracture density and development both affect the tension under which water is held in rock and soil, potentially affecting timescales of movement of water and solutes, as well as chemical weathering. These feedbacks are likely to affect the spatial pattern of roots and mycorrhizal hyphae at various depths and create a subsurface mosaic of hydrological connectivity. In addition, a recent hypothesis suggests that the shallow lateral flowpaths underlying hillslopes in catchments may be co-located at depth intervals marking biogeochemical reactions: in other words, the zones of lateral flow may be caused by or may mark the position of reaction fronts in catchments (Brantley et al., 2016).

4 Conclusions and a Vision for Moving Forward

The role of trees in building and plumbing the critical zone is poorly understood because the topic must be addressed by scientists of multiple disciplines trained to think in very disparate ways. Yet, understanding how soils form and are sustained is an important focus as the human population grows toward 10 billion in the next century. Soils also act as natural filters of water but our understanding of the flowpaths and residence times of pore waters in forested soils are rudimentary. This paper has explored the role of trees as builders and plumbers of the critical zone and trees in the context of movement of water. Trees are the most important architects and plumbers of the CZ in many landscapes.

Much work needs to be done to understand the distribution of water content in the soil and the characteristic timescales of water movement. Similarly, research is needed to address how trees affect chemical, physical, and biological subsurface processes. Trees affect subsurface mixing and the movement of water in ecosystems, especially where the water that passes through a soil into a stream may be isotopically very different than the water that is held in that soil and taken up into the tree itself during transpiration. Such ecohydrological separation has implications for how we conceptualize and parameterize water storage and release in our models but a thorough understanding of these ideas requires understanding both the architecture of trees and the architecture of the critical zone.

Observatory networks (Anderson et al., 2008;Banwart et al., 2012;Weathers et al., 2016) may provide the only way to investigate all the chemical, physical and biological processes in the environment that are affected by trees. The hypotheses stated here should be tested across the growing network of critical zone observatories. Only with scientists crossing disciplines and studying the same sites together, will we be able to answer questions about how trees have plumbed and built the CZ. For example, the long timescale focus on the architecture of the CZ as investigated by geologists will elucidate the nature of short timescale water movements as studied by hydrologists and ecologists. Likewise, the interpretation of short timescale water movements is necessary to understand the nature of slow geological change at earth's surface. As humans impact the CZ more extensively and at more rapid rates, we will continue to need fundamental knowledge of both the long and short timescale phenomena that couple trees and the CZ.

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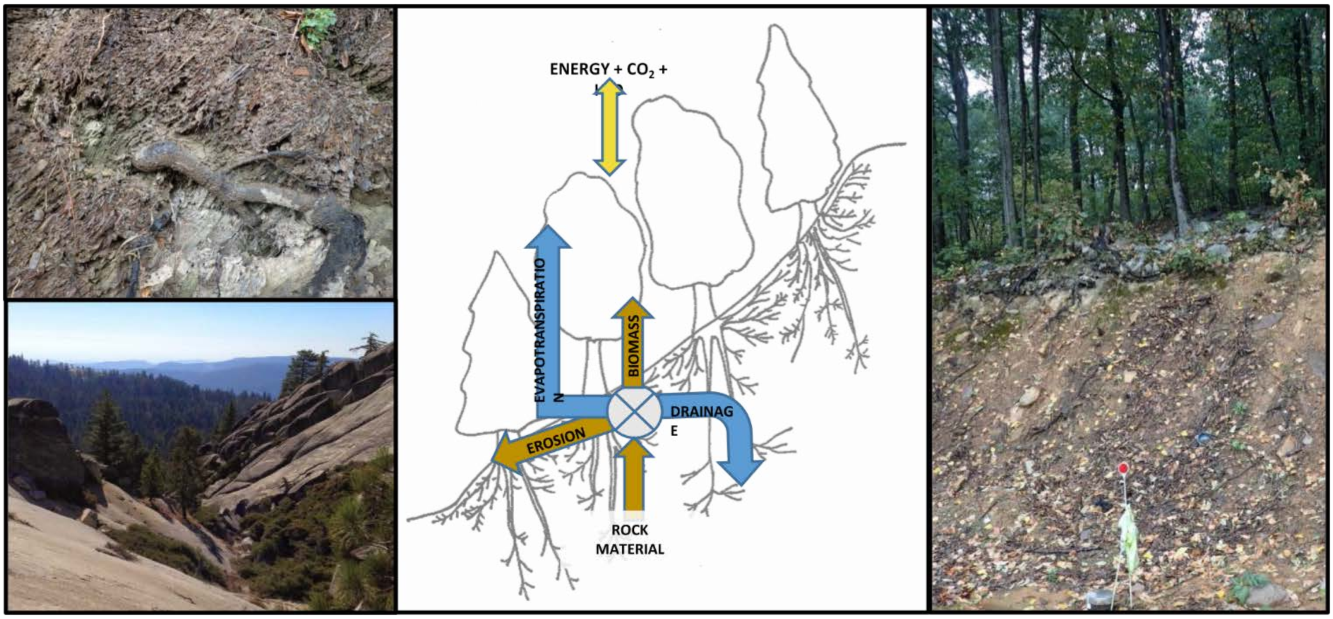

Figure 1: Trees transform energy + CO_2 + H_2O to biomass at the same time that they affect erosion, weathering, hillslopes, soil microbiota, water fluxes, and climate. Energy from the sun radiates on to the earth at about 800 watts m^{-2}. Each day, one tree transpires on the order of 100 kg water day^{-1}. As tree roots embed themselves in the soil, they stabilize its structure while simultaneously removing water and injecting acids into the soil. Nutrient material is then returned to the soil as leaves fall or the tree dies. After decay, the nutrients return to the soil. Trees thus act as chemical stirring agents that remove nutrients from the rooting depth and return them to the top of the soil. Likewise, after dying, tree fall can lift the rock material in the root wad, moving it toward the earth's surface and then downhill. Such bioturbation over millenial timeframes contributes to soil creep downslope.

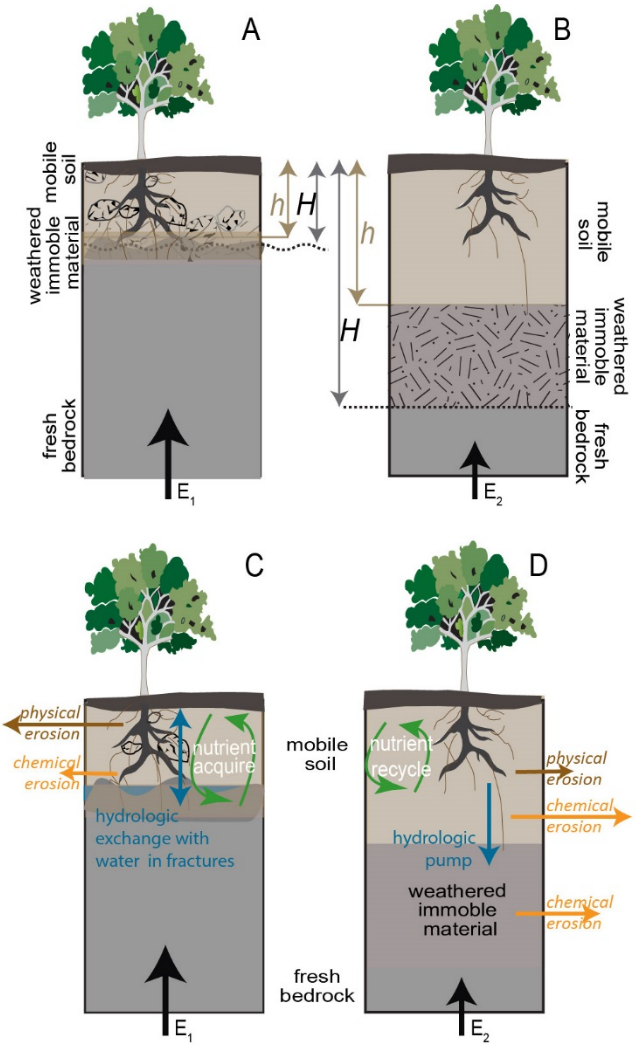

Figure 2: Here, conceptual models are shown that describe the architecture of the critical zone and emphasize tree roots in a setting where the rate of movement of material through the system equals the erosion rate, *E*. Removal of material occurs by both chemical and physical mechanisms. Sizes of the arrows convey the relative fluxes. A) When tree roots cross the boundary between the mobile and immobile layers (when $h \approx H$), both solute and solid material are transferred across the mobile and immobile material boundary by roots and fungi because they can penetrate fractures and can bio-sense and acquire nutrients from rock material. In this end-member case, root processes can set the thickness of *h* and impart a non-uniform undulating boundary between mobile and immobile material. These processes include plucking of rock fragments during tree throw. B) When the *h/H* ratio is small, chemical erosion is generally larger than physical erosion. In this case, nutrients are primarily recycled, especially by fungi, from organic material and water in the mobile layer.

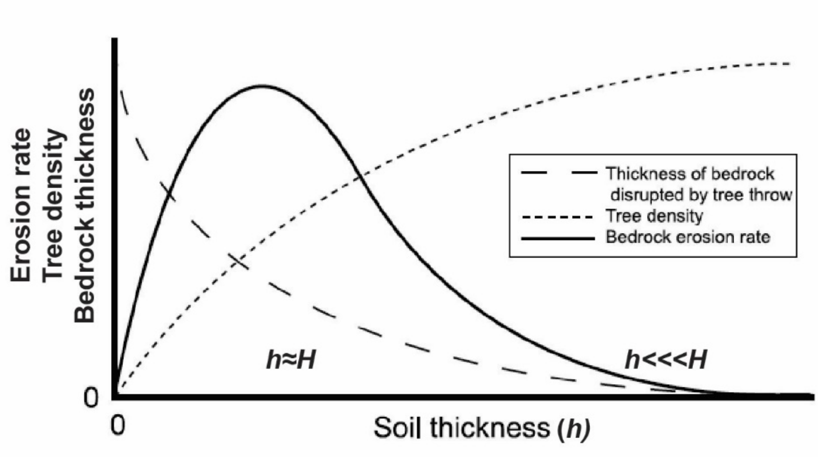

Figure 3: Conceptual relationship (as proposed by Gabet and Mudd, 2010) showing the production rate of mobile soil (here called the bedrock erosion rate) as a function of the soil thickness. As shown, the tree density and the thickness of bedrock disrupted by a tree throw event are thought to vary with thickness of the mobile soil. According to these ideas, the tree density increases from settings with bare bedrock (i.e., zero soil thickness) to settings with mobile soil present. In contrast, the thickness of immobile material ('bedrock') disturbed during tree turnover declines with soil thickness. By multiplying the tree density times the thickness of bedrock disrupted by each tree throw and an assumed tree throw frequency (not shown), we infer that the mobile soil production rate (sometimes called the bedrock erosion rate) over geomorphic timescales is humped as shown in the solid black line. The mobile soil production rate first increases and then decreases because thin soils support too few trees to realize significant production but thick soils buffer (or insulate) underlying bedrock from significant root disturbance.

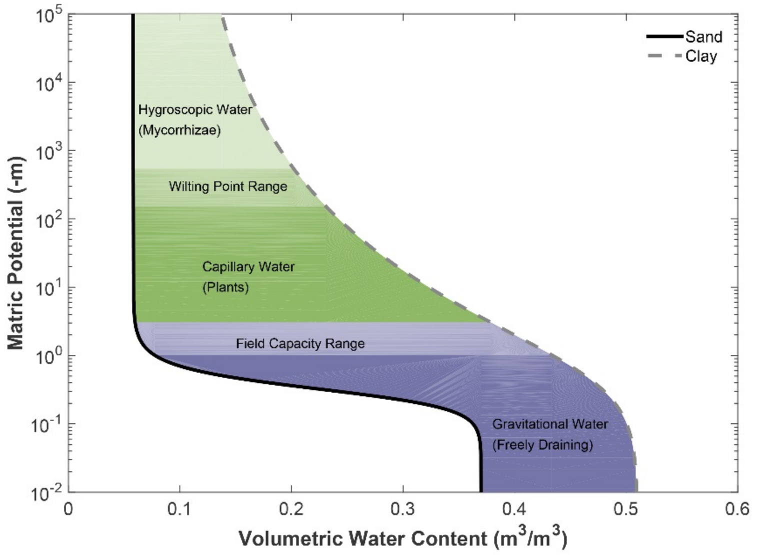

Figure 4: Water available to streams, trees, and mycorrhizae may come from pores that drain under different tensions. Only water that is freely draining will contribute to streamflow whereas matrix waters, held at tension in soils or rock, will not. Matrix waters include capillary waters available to plants, and hygroscopic waters that are held at tensions beyond the wilting point (and thus unavailable to) agronomic plants. Such waters may be available to mycorrhizal fungi (hypothesis 5). More energy is required to acquire water that is held under higher tensions, so we hypothesize that plants will use water that is most energetically favorable (hypothesis 4) and the nutrients available with it.

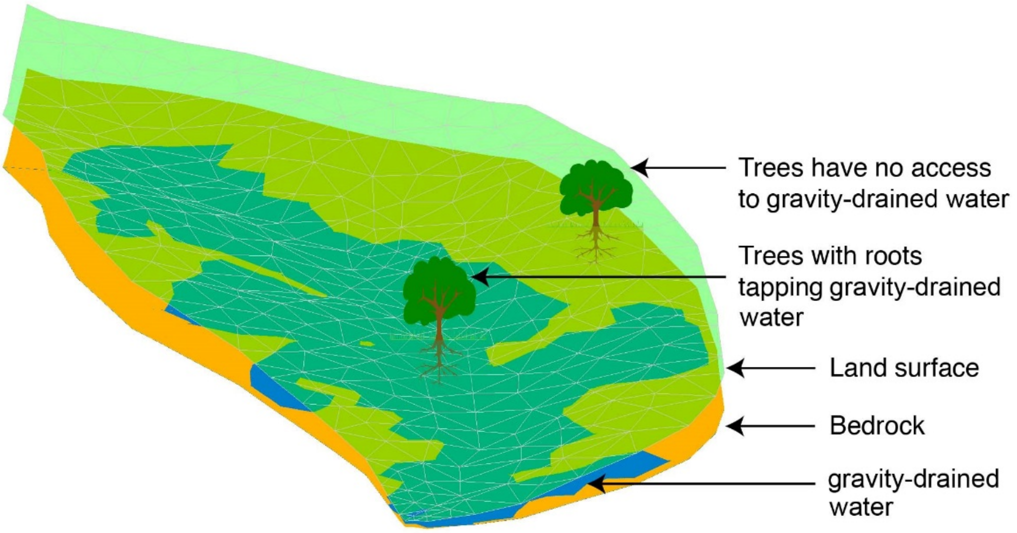

Figure 5: A schematic diagram showing how connectivity of a landscape affects the distribution of water that is drained by gravity or held in the matrix. Gravity-drained water enters as rainfall, drains through soil to the stream, and leaves the watershed. Roots of trees high in the catchment do not access this water (except ephemerally during drainage), and instead may rely predominantly on matrix water. These trees may not have roots that reach the bedrock because of the thickness of the soil and weathered material high in the landscape. By contrast, roots of trees in the channel or swales may access gravity-drained water as well as the bedrock interface, at least in watersheds with in-channel bedrock exposures.

Table I. Nomenclature. For related conceptual diagrams, see Figures 2 and 4.

Name of layer	*Description of earth material in layer*	*Description of trees in the layer*
Fresh bedrock	Parent material that has not been affected by surface processes (commonly denoted as R layer in soil sciences or protolith in geology). Fresh bedrock is unweathered and typically underlies weathered immobile material.	No tree material present
Weathered immobile material (thickness = H-h)	Rock or soil-like material (commonly denoted as C layer in the soil sciences) which has been chemically altered but still manifests the fabric of the fresh bedrock. The degree and distribution of weathering is highly influenced by fractures and other structural properties of bedrock. This zone can contain weathered rock, saprolite, and/or saprock. Overlies fresh bedrock.	This zone can contain tree roots, which may enhance physical and chemical weathering through root expansion, mineral acquisition including that of mycorrhizal fungi and uptake or release of water
Mobile soil or colluvium (layer defined to have thickness h)	Mixed, disrupted or churned material which contains mineral and organic constituents. Mobile soil reflects displacement from the original bedrock fabric (but not necessarily significant transport) via detachment, mixing, or larger-scale transport (e.g. via ice lens growth, gopher burrowing or tree throw) such that the fabric of the original bedrock is no longer intact, and the material is available for transport. This contrasts with H, which is the depth that encompasses both immobile and mobile weathered material.	This zone, which contains most of the tree roots, is the zone most chemically influenced by trees. Woody roots (including tap roots when present) typically can reach below this zone.
Type of water	***Description of water***	***Other terms used***
Gravity-drained water	Water that flows freely under the force of gravity.	Also referred to as "mobile" water or "freely drained" water
Matrix water	Water that does not flow freely under the force of gravity and is comprised of hygroscopic and capillary water. Capillary water consists of water held at tensions greater than the agronomically-defined wilting point, and water between the "wilting point" and field capacity. Hygroscopic water consists of water that forms thin films around soil particles, held at tensions beyond the wilting point of agronomic plants	Also commonly referred to as "immobile", "bound" or "tightly bound" water. "Matrix water" is preferred here because tightly bound water may not be immobile over timescales relevant to CZ researchers