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2 A belowground perspective on the drought sensitivity of forests: Towards
3 improved understanding and simulation.

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Abstract

Predicted increases in the frequency and intensity of droughts across the temperate biome have highlighted the need to examine the extent to which forests may differ in their sensitivity to water stress. At present, a rich body of literature exists on how leaf- and stem-level physiology influence tree drought responses; however, less is known regarding the dynamic interactions that occur belowground between roots and soil physical and biological factors. Hence, there is a need to better understand how and why processes occurring belowground influence forest sensitivity to drought. Here, we review what is known about tree species' belowground strategies for dealing with drought, and how physical and biological characteristics of soils interact with rooting strategies to influence forest sensitivity to drought. Then, we highlight how a belowground perspective of drought can be used in models to reduce uncertainty in predicting the ecosystem consequences of droughts in forests. Finally, we describe the challenges and opportunities associated with managing forests under conditions of increasing drought frequency and intensity, and explain how a belowground perspective on drought may facilitate improved forest management.

Keywords

Water stress, ecosystem modeling, drought resilience, rooting strategies, earth system models, land surface models

Introduction

Climate change is projected to increase the frequency of droughts across much of the temperate zone (Wuebbles and Hayhoe, 2004; Huntington, 2006; O'Gorman and Schneider, 2009; Dai, 2011), with some regions predicted to experience droughts on par with the driest periods of the Medieval Climate Anomaly (Cook *et al.*, 2015). While there is much uncertainty about the ecological impacts of these changes, increases in the frequency and intensity of droughts are likely to be particularly consequential for forests, one of the largest sinks for carbon (C) globally. In the conterminous US, forests dominate the land C sink (>75%; (Xiao *et al.*, 2011)), removing from the atmosphere the C equivalent of 10% of annual US fossil fuel emissions (Wear and Coulston, 2015). Given that nearly one fifth of the land area in the US may be vulnerable to drought stress in the coming decades (Lienard *et al.*, 2016), there is a critical need to understand how and why forests differ in their sensitivity to drought, if at all.

Drought has long been viewed as an important factor regulating the survival of trees (Running *et al.*, 2004), and numerous investigations have focused on drought effects on forest mortality (Mueller *et al.*, 2005; McDowell *et al.*, 2008; Allen *et al.*, 2010; Anderegg *et al.*, 2012; Allen *et al.*, 2015). However, in many regions, the vast majority of trees do not die during drought unless other factors (e.g., insect attacks and fire) occur in combination with drought (Allen *et al.*, 2015; Millar and Stephenson, 2015). More commonly, droughts impact forest function by reducing C assimilation by trees - a process that can have large consequences for regional-scale C cycling (Breda *et al.*, 2006; Brzostek *et al.*, 2014; Roman *et al.*, 2015). Such impacts may persist for years following

the drought (Anderegg *et al.*, 2015) and impact tree species sensitivities to future environmental conditions (Peltier *et al.*, 2016). Consequently, there is a need for an improved understanding of the physiological mechanisms that underlie forest responses to (and recovery from) drought that goes beyond assessing forest susceptibility to mortality.

A rich body of literature exists on the structural and physiological adaptations of trees for avoiding, tolerating and resisting drought (Henckel, 1964; Kramer and Boyer, 1995; Breda *et al.*, 2006; McDowell *et al.*, 2008; Manzoni *et al.*, 2011; Martinez-Vilalta *et al.*, 2014). Nevertheless, we still lack a fundamental understanding of why tree species of similar age and exposure (to water stress) differ in their drought sensitivity (Weltzin *et al.*, 2003). One possible reason for this relates to a “surface bias”; specifically, most investigations of tree species and drought have focused on the hydraulic properties of leaves and stems (Ryan *et al.*, 2006; Meinzer *et al.*, 2009), with limited consideration of belowground traits and processes and their consequences for whole-tree water relations. Trees possess myriad belowground strategies for dealing with drought (Sperry *et al.*, 1998; Breda *et al.*, 2006), and these strategies likely interact with soil properties (e.g., soil texture, gravel content and effective rooting depth) and soil biota (e.g., mycorrhizal fungi) to determine forest sensitivity to drought. For these reasons, classifying tree species based on their aboveground sensitivity alone – without consideration of belowground traits and site conditions – may lead to incorrect projections of the consequences of drought on C cycling.

Large-scale models reflect the scientific community's best understanding of how environmental conditions shape species distributions and ecosystem functioning. Two types of models are commonly used to project the impacts of drought on forests. Species distribution models, also known as niche or climate envelope models, link observed spatial variations in tree species abundances to underlying environmental gradients in order to project potential suitable habitat for species under future climates. While these models typically include soil characteristics (e.g., percent clay, organic matter content, slope, depth to bedrock, total available water holding capacity to 1.5m), the models are not mechanistic, so there is no consideration of how rooting strategies of dominant trees interact with soil factors to influence tree growth under drought (Iverson *et al.*, 2008). Process models, in contrast, are mechanistic, and based on a theoretical understanding of relevant ecological processes. These models explore how climate change will affect forest community composition and ecosystem function. Process models vary widely in the spatial scales at which they operate (e.g., ranging from forest gaps to the earth's land surface) and as such, there is substantial variation among models in how belowground processes are treated. However, a common feature of most process models is that root allocation is a fixed proportion of shoot biomass or photosynthesis, and associations between root traits and soil factors are sparse or non-existent (Warren *et al.*, 2015). Consequently, process models often perform poorly under drought conditions (Hanson *et al.*, 2004), a factor that has been attributed to the lack of belowground drought response mechanisms in the models (McDowell *et al.*, 2013).

The focus of this review is to describe how the belowground responses of tree species to drought can interact with site characteristics (e.g., soils and hydrology) to determine forest sensitivity to drought. Given that previous reviews have focused primarily on drought-induced physiological mechanisms leading to tree mortality (McDowell *et al.*, 2008; McDowell *et al.*, 2011; Martinez-Vilalta *et al.*, 2012; Wang *et al.*, 2012; Zeppel *et al.*, 2013), we focus here mostly on belowground responses to sub-lethal droughts. Additionally, we highlight how a belowground perspective of drought may be used to reduce uncertainty in model predictions of drought impacts on forests, as well as a predictive tool for understanding what combinations of tree species and site characteristics are most likely to experience reduced physiological function under drought. Finally, we describe the challenges and opportunities associated with managing forests under conditions of increasing drought frequency and intensity, and explain how a belowground perspective on drought may facilitate improved management and conservation of forests (Grant *et al.*, 2013).

What is forest sensitivity to drought?

Numerous functional definitions have been proposed for droughts, with most focusing on the duration and biological/hydrological impact of the drought condition (Dracup *et al.*, 1980; Wilhite and Glantz, 1985; Paulo and Pereira, 2006). For this review, we define drought as *sustained periods of anomalously low water availability (i.e., at levels rarely experienced at the site based on historical records)*. Hence, this definition excludes regions where trees face water stress regularly (e.g., in semi-arid ecosystems) and emphasizes the distinction between aridity and drought. We define sensitivity as short-

term physiological responsiveness to drought, and distinguish this term from ‘susceptibility’, which is used to denote risk of drought-induced injuries that can lead to mortality.

Trait-based frameworks are commonly used to predict how plants use resources and respond to shifts in resource availability, including water stress (Reich, 2014). Most of these traits relate to aboveground tissues. Short plant height, low ratios of leaf area to sapwood area and median leaf size are aboveground traits that reduce plant sensitivity to drought, and are therefore considered drought avoidance traits. In contrast, low specific leaf area, low xylem vulnerability to embolism and high safety margins reduce the plant susceptibility to drought rather than its sensitivity, thus increasing plant drought tolerance (Anderegg and HilleRisLambers, 2016). Another aboveground-centric framework for assessing plant sensitivity to water stress is to classify tree species along an isohydric and anisohydric spectrum (Tardieu and Simonneau, 1998; McDowell *et al.*, 2008; Manzoni *et al.*, 2011; Choat *et al.*, 2012; Klein *et al.*, 2014; Martinez-Vilalta *et al.*, 2014). Tree species with relatively anisohydric behavior maintain photosynthesis during drought by keeping stomata open, but they do this at the risk of xylem embolism and hydraulic failure; alternatively, trees with isohydric behavior close stomata in response to even mild water stress – at a cost to C assimilation – but in doing so, minimize embolism risk (McDowell *et al.*, 2008). While both frameworks – tolerators vs. avoiders and isohydric vs. aniohydric – have greatly improved our conceptual understanding of the tradeoffs that underlie the drought-sensitivity of plants – theory that is critical for models –, neither framework has been extended to consider the belowground traits and processes that link

the subsurface and surface environments. Thus, a goal of this review is to ask the question what belowground traits, if any, might map onto aboveground hydraulic strategies of plants, and how does the soil environment shape the coordination of these responses.

The drought tolerance of tree species is often established according to where a species occurs on the landscape (e.g. top of ridges, south-facing slopes) rather than its physiological responses to drought (Niinemets and Valladares, 2006). Most oak (*Quercus*) spp. in Eastern and Midwestern forests are considered drought tolerant – especially when compared to other co-occurring hardwoods (Hanson *et al.*, 2001; Gustafson and Sturtevant, 2013; Brzostek *et al.*, 2014; Roman *et al.*, 2015; Levesque *et al.*, 2016), owing to their high abundances on xeric sites. However, the sensitivity of oaks to drought can differ on xeric vs. mesic sites (Orwig and Abrams, 1997; Maxwell *et al.*, 2015), and many oak species demonstrate some of the highest sensitivity to drought (in terms of reduced growth relative to other hardwoods) across the Eastern and Midwestern US (Figure 1a), despite being classified as a drought tolerant species in one of the most commonly used ranking systems (Niinemets and Valladares, 2006). This suggests that while oaks may be more drought tolerant in a physiological sense based on experimental studies or tree census data, they may actually be more drought sensitive than co-occurring species (in terms of growth) owing to their occupation of xeric sites. This is because low water availability, which defines the xeric sites that oak occupies, translates into more severe droughts (in terms of absolute water content) than on mesic sites. Gu et al. (2015)

demonstrate this with data from a site at the prairie/forest ecotone in Missouri, and place oak responses in the context of other upland hardwood species.

A similar response has also been documented for *Pinus* spp. (Clark *et al.*, 2011). In the case of white pine (*Pinus strobus*), which tend to occupy dry sites, radial growth increments during drought indicate that this species is more drought sensitive on xeric sites than mesic sites (Figure 1b). Conversely, the opposite pattern – greater drought sensitivity on mesic sites relative to dry sites – has been reported for *P. virginia* (Orwig and Abrams, 1997). This raises the point that trait-based frameworks, even ones including belowground traits, may have limited predictive ability if environmental context is not considered.

Belowground strategies for dealing with drought

Roots provide many functions for plants, but our focus here is on water acquisition in relation to drought. Trees have evolved numerous root traits and rooting strategies to avoid and tolerate drought. These include morphological traits that are relatively fixed for a given species e.g., root architecture, anatomy, and depth, type of mycorrhizal fungi association, as well as more plastic physiological responses e.g., shifts in belowground carbon allocation, increased rhizodeposition, etc. that depend on both species and site (Brunner *et al.*, 2015). An additional factor that may limit the utility of using root traits to predict drought sensitivity of trees is that root traits can be plastic for trees growing at a single site and highly variable among trees across sites (see section below on root dynamics). Here, we review what is known and unknown about tree species'

belowground responses to drought in forests, focusing on root traits, root dynamics, and root interactions with soil microbes.

Root traits

Several morphological root traits are known to influence plant responses to water stress. Plants that produce small diameter absorptive roots i.e., roots with high mass-specific length or mass-specific surface area, increase the amount of root surface area in contact with soil water, and thus minimize the impacts of drought by exploring a greater volume of soil (Comas *et al.*, 2013). Among the absorptive roots, those with small xylem diameters may be more tolerant of drought due to their reduced risk of cavitation and embolism, which is generally greater in roots relative to shoots (Jackson *et al.*, 1996). In general, tree species with an abundance of small diameter absorptive roots should be better able to sustain physiological function during periods of water stress than species with larger diameter fine roots. While this is generally true across temperate tree species (Pregitzer *et al.*, 2002; McCormack *et al.*, 2012)), studies of woody shrubs in semi-arid environments show the opposite pattern: drought induces plants to increase root diameter and decrease specific root length (i.e., reducing the number of absorptive roots), possibly as a mechanism for increasing root longevity (Larson and Funk, 2016). This suggests that there are likely multiple belowground strategies for dealing with drought, and that root traits that relate to drought may depend on the whole plant response or environmental context.

A critical question then is whether there is whole plant coordination between a tree species' aboveground and belowground traits related to drought tolerance or avoidance. If so, this would provide an opportunity to incorporate root traits into a whole-plant drought classification framework. In a study of 66 tree species grown under identical conditions, Kramer-Walter et al. (2016) reported that while root diameters generally tracked a soil fertility gradient, there was little relationship between root diameter, or any other measured root trait, and aboveground (e.g., leaf and stem) traits. Thus, despite the growing interest in using trait-based approaches to predict ecosystem responsiveness to changes in resource availability, more work is needed to identify which root traits, if any, may be linked to the leaf and stem hydraulic attributes that underlie forest sensitivity to drought.

Root architecture and root depth distribution e.g., dimorphic distribution or presence of a tap root, influence variability in stand sensitivity to water stress if some species have access to water that other species do not. However, site conditions can be critical modifiers of rooting strategies. Consider tulip poplar, often described as an extremely drought sensitive species owing to its relatively shallow root system and high water use (Wullschleger *et al.*, 2001; Ford *et al.*, 2011). While many tulip trees show growth reductions during drought, these species recover rapidly following drought owing to their greater allocation to shoots than roots, particularly on mesic sites (Orwig and Abrams, 1997). Whether some of the variation in site sensitivity for tulip trees relates to soil depth is unknown, though in other co-occurring species like sugar maple (*Acer saccharum*), physical barriers to effective rooting depth may constrain growth during dry conditions

(Fig. 2). This suggests that putative drought-sensitive tree species growing on mesic sites with deep soils may be less affected by drought than putative drought-tolerant tree species growing on drier sites with shallower soils (e.g., ridge tops).

Root dynamics

Optimal allocation (or partitioning) theory suggests that plants should increase C allocation to fine roots as soils dry down and water and nutrient limitation is exacerbated (Bloom *et al.*, 1985). While there is some evidence of this at the biome scale (Kozlowski *et al.*, 1991; Schenk and Jackson, 2002b), demonstrations of increases in fine root allocation during drought (either absolute or relative) in forest trees are inconsistent (Eamus, 2003; Cudlin *et al.*, 2007), and changes in root allocation are often apparent for intense droughts only (Poorter *et al.*, 2012). Root production may increase during the early stages of drought (Hendrick and Pregitzer, 1996), often resulting in increases in root proliferation at depth. However, the presence of roots at a given depth may not always correspond to the activity of the roots. Volkmann *et al.* (2016) reported that sessile oak (*Quercus petraea*) responded to drought by acquiring water from deeper in the soil, but this strategy potentially came at a cost to acquiring water from surface soils once the drought subsided. In contrast, European beech (*Fagus sylvatica*) showed little shift in the location of water uptake regardless of drought condition. Such variation in plasticity suggests that predictions of root dynamics at the onset, during, and after a drought may require a multidimensional view that considers root traits, root trait plasticity and root-shoot allocation tradeoffs (Weemstra *et al.*, 2016).

Root access to deep water

In a multi-year throughfall displacement study, Joslin et al. (2000) found that 33% reductions in water input induced no changes in fine root biomass, fine root turnover or root to shoot ratio. While this result suggests that tree species allocation patterns are more static than dynamic, it's important to note that the trees in this experiment showed few signs of drought stress in their aboveground tissues too – a factor that has been attributed to the tree's exploitation of deep water sources at this site (Hanson et al. 2001). It is well-established that water-stressed plants deploy a greater fraction of their roots deep in the soil profile (Canadell *et al.*, 1996; Schenk and Jackson, 2002a; Breda *et al.*, 2006). However, there is limited evidence that tree roots dynamically respond to drought by proliferating roots into the saturated zone of soil (see section below on root accessible groundwater); nevertheless, trees with deep tap roots can delay the onset of drought impacts. In most forests, deeper soils are wetter than shallower soils owing to the greater evaporative loss of water at the soil surface.

In an experimental test of *L. tulipifera* and *Quercus prinus* sensitivity to acute drought, Hanson et al. (2007) used understory tarps to remove 100% of the growing-season throughfall and stem flow, and trenches to minimize water uptake of lateral roots outside the tarped area. Remarkably, three years of acute water stress had little affect on either species' growth, non-structural carbohydrates, sap flux, and leaf-level gas exchange, indicating that water supplies deep in the soil were the likely explanation for this unexpected response. Post-treatment excavations of the soil profile verified a surprisingly high density of roots between 70 and 140 cm depth for both species (Fig. 3) and ample

soil water storage at these same depths, despite being well above the groundwater table, which was greater than 10 m below the soil surface. These results indicate that tree species growing in deep soils may be able to avoid acute drought conditions - even when their deepest roots are isolated from groundwater.

Deep rooting can also be used by some tree species to transfer water from the surface through hydraulic lift (Schenk and Jackson, 2002a) – a process that would ameliorate some of the impacts of drought (Brooks *et al.*, 2002; Egerton-Warburton L.M. *et al.*, 2008). Although there is still some debate about the quantitative significance of such hydraulic redistribution of water (Neumann and Cardon, 2012; Prieto *et al.*, 2012) (Neumann and Cardon, 2012), the phenomenon appears to be widespread for trees, occurring in plantation forests (Brooks *et al.*, 2002; Domec *et al.*, 2010), old growth forests (Brooks *et al.*, 2002; Warren *et al.*, 2007), and in savannahs (Bleby *et al.*, 2010). Hydraulic redistribution is likely to be consequential for shallow-rooted tree seedlings and saplings in the forest understory (Domec *et al.*, 2010). Water lifted by trees and released to surface soils allow understory trees to avoid drops in water potential that would otherwise cause embolism, while providing indirect benefits such as enhancing nutrient availability (McCulley *et al.*, 2004), increasing root longevity (Bauerle *et al.*, 2008), and maintaining plant associations with mycorrhizal fungi (Querejeta *et al.*, 2007).

Given that the cohort of understory trees that survive the drought will eventually become overstory trees in the stand, the amelioration of drought by mature trees lifting water can have critical impacts on the future forest composition and its drought sensitivity. Of

course, whether trees hydraulically lift water at all depends not only on the belowground traits of the trees, but on the presence of water potential gradient driven by soil type and underlying geology (e.g., soil texture, depth to water table, etc.). Thus, tree species that have the capacity to lift large quantities of subsurface water (e.g., *Acer saccharum*; Dawson (1993)) may still show strong growth declines in response to moderate water stress, if there are no deep pools of available water (Brzostek *et al.*, 2014).

The role of soil microbes

Mycorrhizal fungi, which form symbiotic associations with all trees, represent an additional strategy that trees deploy in the wake of water stress. All trees are colonized to some degree by one of two types of mycorrhizal fungi: arbuscular mycorrhizal (AM) fungi or ectomycorrhizal (ECM) fungi. AM fungi promote drought resistance by synthesizing metabolites that act as osmolytes, thereby lowering the plant's water potential (Rapparini and Peñuelas, 2014). ECM fungi may increase or decrease a tree's susceptibility to drought (Lehto and Zwiazek, 2011) depending on the exploration type of the fungi and the ability of the fungi to produce aquaporins, or actively regulated water transport channels (Breda *et al.*, 2006; Lehto and Zwiazek, 2011). Both types of fungi produce thin filamentous structures in soil (i.e., hyphae) that increase water uptake and transport by increasing absorptive surface area and by exploiting water in soil micropores that are not accessible to plants. As such, the root colonization by AM or ECM can mitigate the negative impacts of drought on tree growth (Mohan *et al.*, 2014). However, given that mycorrhizal fungi vary in the degree to which they harm or help their hosts, some fungi under certain conditions may actually reduce drought tolerance if they utilize

C (i.e., enhance C starvation) but provide few resources (e.g., water or nutrients) in exchange (Ibáñez and McCarthy-Neumann, 2016).

Studies of dual colonists (i.e., tree species that can associate with both AM or ECM) suggest that AM-colonized roots are more drought-tolerant than ECM-colonized roots (Querejeta *et al.*, 2009), however an analysis of the drought tolerance of the 20 most common deciduous tree species (>300,000 trees) in the eastern and midwestern US suggests that ECM trees, on average, may be more tolerant of water stress than AM trees (Brzostek *et al.*, 2014). Moreover, interspecific differences in fungal physiology (aquaporin expression) or morphology (e.g., degree of cell wall melanization) within each fungal group may affect the drought tolerance of fungi and trees. Jany *et al.*, (2003) reported that beech trees (*Fagus grandifolia*) colonized by the ECM fungi *Cenococcum geophilum* were far less sensitive to water stress than those colonized by another ECM fungi *Lactarius* spp. Such trends indicate the need for more research to better understand the role of AM and ECM taxa in facilitating water uptake and enhancing drought tolerance. Additionally, more research is needed to understand whether the impacts of AM and ECM fungi on drought tolerance depend on site conditions such as soil depth (e.g., if the fungi are maintained by hydraulically lifted water).

In addition to symbiotic root-associated microbes, free-living microbes can also affect plant sensitivity to drought. Soil microbes can minimize drought stress by inducing stomatal closure via abscisic acid production (Loewenstein and Pallardy, 1998; Yang *et al.*, 2009). While microbial effects on drought sensitivity have been reported for both

anisohydric (Ríncon *et al.*, 2008) and isohydric tree species (Kannenberg and Phillips, In Revision), few studies have explored the effects of microbial communities on plant hydraulics and leaf-level gas exchange. Likewise, soil microbes can also exacerbate drought stress by inducing secondary compound synthesis, by decreasing nutrient availability to plants or by directly consuming poorly-defended plant tissue (ref). Root rot pathogens such as *Armillaria* spp. and *Heterobasidion* spp. have been reported to colonize drought-stressed trees (Sturrock *et al.*, 2011), leading to significant mortality in the southeastern US, intermountain west in the US, as well as in Europe (Kolb *et al.*). Additionally, interactions between drought and root pathogens were considered the primary cause of mortality in many species of oak trees in the Midwestern US (Clinton *et al.*, 1993). Collectively, these studies indicate that the net effects of soil microbes on the drought sensitivity of trees may be difficult to determine unless the specific root-associated microbes – both beneficial and pathogenic – are known for a given species at a given site. To the extent that soil microbes have the potential to alter key hydraulic parameters that are used to diagnose drought sensitivity, future studies are needed to better understand their effects on the physiological sensitivity of tree species to drought (Kannenberg and Phillips, In Revision).

Soil factors that mediate drought

Interspecific variation in tree species responses to drought (Orwig and Abrams 2001) suggests that soil factors must also influence forest sensitivity. Two main soil factors mediate this sensitivity: the size of the pool of available water in the unsaturated zone, and the accessibility (or inaccessibility) of groundwater in the saturated zone. Notably,

both factors interact with the rooting strategies of trees, as species that have roots with high absorptive area and a high degree of colonization by mycorrhizal fungi, or coarse roots that can store non-structural carbohydrates or reach saturated zones of soil will strongly impact their drought sensitivity.

What water is available?

At the most basic level, drought for a plant can be defined as a deficit in the amount of water available for transpiration relative to plant and atmospheric demand. Quantifying this imbalance requires understanding how much water is available to plants from surface and subsurface reservoirs, the evaporative demand of the atmosphere (which depends on temperature and humidity), and the plant's uptake and storage capacity, and hydraulic conducting system. Thus, mechanistic measures of plant physiological responses to drought require an expression of "available water" which is based on soil and tree factors, and cannot be attained by measurements of precipitation or bulk soil water content alone.

Plant available water is a function of the difference between the soil water potential (Ψ_{soil}) - the sum of gravimetric, osmotic and matric potentials - and leaf water potential (Ψ_{leaf}), and a multiplier based on plant hydraulic conductance (i.e., Darcy's Law; McDowell and Allen, 2015). Most of the variation in Ψ_{soil} within and among forest soils comes from the matric potential, which is determined by soil texture, soil organic matter and gravel content (Saxton and Rawls, 2006). Given that all three of these factors often vary both horizontally and vertically within a stand, estimating the total amount of water available requires measurements of Ψ_{soil} (or simply matric potential) throughout the

rooting zone and across the landscape. Direct assessments of the development of plant water potential directly are possible, but seldom measured in the context of seasonal drought developments (see Gu et al. 2015 for an exception).

Unfortunately, direct measures of Ψ_{soil} in forests are relatively sparse owing to the difficulty of obtaining these measurements, especially in deep soils (Vicca *et al.*, 2012). And while it is possible to convert gravimetric measurements of soil moisture to matric potential, the nonlinear functions needed to correct these data are not readily available for all sites, and may vary considerably across sites and with soil depth at a given site (Clapp and Hornberger, 1978; Saxton and Rawls, 2006). For these reasons, soil water content (determined by gravimetric or volumetric methods) is often used as a proxy for Ψ_{soil} , and the amount of available water in an ecosystem is expressed relative to the soil's maximum saturated state or water-holding capacity. Critical to this approach, is an assessment of the water content of soils at field capacity and at the wilting point – both of which are needed to calculate relative extractable water (Vicca *et al.*, 2012) – integrated over the depth of the rooting zone.

A consequence of defining water availability based on soil water content is that it can impact how a drought is characterized. Consider the interannual variability in water content at the Walker Branch Watershed in Tennessee from 1993 to 2005. If soil water content deficits alone were chosen as the metric of water deficit (Figure 4a), one could conclude that drought occurred in ~11 out of 13 of the years. However, if Ψ_m is derived from soil water content using soil moisture release characteristics, a different picture

emerges. The Ψ_m data show reduced water availability approaching limits of plant accessibility or the wilting point (-1.5 MPa; Figure 4b) in the surface soils for only 5 of 13 years for shallow soil, and perhaps for no more than 3 of 13 years when deep soil water supplies are evaluated. Thus, Ψ_m or Ψ_{soil} (depending on which expression most influences plant water status), provide a different view of soil water availability than measurements of soil water content. As explained above, a common misrepresentation of drought as reduced soil water content can be aggravated when estimates of soil water availability are extrapolated across the landscape.

Groundwater availability to roots during drought

In cases where tree roots can reach the groundwater, forests are likely to be buffered from the adverse consequences of droughts (Ehleringer and Dawson, 1992). This is especially true in riparian forests that rely on groundwater primarily but also may occur in forests that rely on seasonal (e.g., summer) groundwater during low water availability (David *et al.*, 2013). The depth to groundwater across much of the US is ~5m (Maxwell and Kollet, 2008; Lowry and Loheide, 2010; Soylu *et al.*, 2014). While this depth is typically below the rooting depth of most tree species (Schenk and Jackson, 2002b), there are many areas on the landscape where groundwater is closer to the surface. Provided that these sites are occupied by deep-rooted species (e.g., *Populus* spp. and *Salix* spp.), these sites may be less prone to experiencing drought. However, even the presence of shallow groundwater may not necessarily be predictive of the drought sensitivity of tree species at a given site. In a study of 10 tree species growing on a common soil with a shallow (< 2m) groundwater table, intraannual and interannual variation in groundwater depth had no

significant impact on the radial growth of six of the 10 species (Weemstra *et al.*, 2013). That shade intolerant species (e.g., *Betula pendula*, *Salix alba*, and *Populus tricarpa*) were more sensitive to changes in water table depth than in variation in precipitation or potential evapotranspiration suggests that traits related to the rooting strategies of tree species likely combine with soil factors to determine forest sensitivity to drought.

Can models be improved with a belowground perspective?

Models reflect the scientific community's best understanding of how environmental conditions influence species distributions and ecosystem functioning. Two types of models are commonly used to project the impacts of drought on forests: species distribution (niche) models and process models. Species distribution models rely on observed correlations between contemporary species abundances and site/environmental conditions to predict which species will increase or decrease under future climates. For example, the DISTRIB model, uses tree, soil and environmental data from the US Forest Service's Forest Inventory and Analysis (FIA) plots. This network of 100,000 forest plots consists of ~3 million tree records for 134 tree species, and includes 13 soil-based predictor variables, including several properties (e.g., total available soil water, soil slope, depth to bedrock) related to water stress (Iverson *et al.*, 2008). However, like all other species distribution models, DISTRIB is based on purely on correlations between species' abundances and environmental conditions; as such, these models say little about tree species' drought sensitivities. So while useful for understanding how future climates may impact future habitat suitability, such models are inappropriate for considering tree species' drought sensitivity in a physiological context.

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481 Process models, in contrast, are better suited for understanding the mechanisms that
482 determine forest sensitivity to climate changes. These models are typically used to
483 integrate small-scale, process-level phenomena into comprehensive characterizations of
484 stand- and ecosystem-scale dynamics, including vegetation-climate feedbacks (Bonan,
485 2008). However, these models often perform poorly under drought conditions (e.g.,
486 Hanson et al. 2004). This is particularly true in mesic ecosystems (e.g., eastern forests of
487 the US; Hanson and Weltzin 2000, Hanson et al. 2004) where models are frequently
488 ‘tuned’ to non-drought conditions. Model intercomparison projects have reported that
489 model errors are often highest under drought conditions (Schaefer *et al.*, 2012), owing in
490 large part to how the models represent plant-water relations (De Kauwe *et al.*, 2013;
491 Dietze *et al.*, 2014). Moreover, many models represent drought indirectly (e.g., using a
492 simple scalar to downregulate photosynthesis or respiration, (Powell *et al.*, 2013) e.g.
493 Powell et al. 2013), or do not explicitly consider belowground processes and interactions
494 (Christoffersen *et al.*, 2014). The lack of known drought response mechanisms in models
495 – particularly for belowground dynamics – can produce model results that underestimate
496 the sensitivity of forests during drought (McDowell *et al.*, 2013) and limit their capacity
497 for predicting ecosystem responses to future droughts (McDowell *et al.*, 2011).

498

499 *Consideration of belowground strategies in process models*

500 Ecosystem models vary considerably in how they incorporate belowground processes in
501 their representations of forests. These range from high-detail temporally dynamic models
502 that run on hourly timesteps and include root and mycorrhizal hyphae that acquire water

based on radial and axial distances (Grant, 1998) to those that run on monthly timesteps, and model water uptake almost exclusively as a function of soil water holding capacity and maximum rooting depth (Raich *et al.*, 1991). In terrestrial biosphere models, root and mycorrhizal fungal representations are rare (Warren *et al.*, 2015), and most contain limited representations of rhizosphere and mycorrhizal dynamics, if at all. In a review of 26 terrestrial biosphere models, only a single model contained representations of rhizosphere (JSBACH) or mycorrhizal (Ecosys) dynamics, and no model included model structures for both (Fatichi *et al.*, 2015). In the absence of such a mechanism, simulated trees cannot modify or adjust their total belowground allocation or the depth distribution of their roots to increase water uptake. Consequently, the models often do a poor job of capturing forest responses to drought (Schaefer *et al.*, 2012; Powell *et al.*, 2013), emphasizing the need to move towards including these factors in forecasting models.

Given that far more is known about interspecific and intraspecific differences in leaf-level responses to water stress (Breda *et al.*, 2006; Brunner *et al.*, 2015), simulating belowground traits has become a major modeling focus (McDowell *et al.*, 2013; Powell *et al.*, 2013). Trait-based approaches are increasingly being used to refine our understanding of how plant form and function represent coordinated strategies for dealing with environmental variation and global environmental change (Reich, 2014). Given that plant functional traits represent the way in which process models consider biological diversity, there is great interest in determining whether a trait-based approach can be used to better predict plant sensitivity to drought. In terrestrial biosphere models (TBMs), the land surface is separated into 5-15 plant functional types (PFTs), each with their own

unique parameterizations. But most have few root parameters (e.g., root C:N is 42 for all PFTs). A clear improvement could come from parameterizing belowground attributes to the different PFTs such as maximum rooting depth, root distribution vertically, water uptake rates and belowground hydraulic failure resulting from embolism in the root-soil continuum (Sperry *et al.*, 1998; McDowell *et al.*, 2013).

Consideration of available water in models

To capture the concept of available water, ecosystem process models rely on parameterizations for soil texture, as well as other relevant parameters such as maximum rooting depth and coarse fragments. In cases where soils data is not available for specific sites, these models can be parameterized with soil databases (e.g, the USDA's Soil Survey Geographic database), and available water can then be estimated as a function of soil texture, bulk density and landscape position. Given that the ease with which water can be extracted from soil depends on soil texture and the topographic features of a site (Sperry *et al.*, 1998), many models use relative extractable water to express water availability – an expression of soil water content relative to the maximum (field capacity) and minimum (wilting point) values for the soil (Hanson *et al.*, 2004). However, relative extractable water does not account for the nonlinear relationship between water content and water potential as soils become dry. As soils dry, the water used first is the most easily accessible to plants. With drying it takes larger driving gradients to pull a similar amount of water from a defined soil layer. Thus, models that pool available water into a single available pool may overestimate plant accessible water as soil water deficits develop.

549

550 TBMs such as the Community Land Model generally include hydrology submodels to
551 predict available water based on soil texture (Oleson *et al.*, 2008). Notably, drought stress
552 for plants is determined by a characterization of rooting distribution and a stomatal
553 closure factor based on soil water availability (Powell *et al.*, 2013). A major limitation in
554 this representation of drought is the coarse resolution of the model and of its hydraulic
555 mechanisms. Currently, the water stress at which stomatal closure is initiated is fixed for
556 each plant functional type (PFT; e.g., deciduous broadleaf temperate vs. evergreen
557 broadleaf tropical), despite evidence suggesting substantial within PFT variability in the
558 magnitude of this critical value (Choat *et al.*, 2012; Roman *et al.*, 2015). Moreover, the
559 depth distribution of roots is also fixed for each PFT (Smithwick *et al.*, 2014; Warren *et*
560 *al.*, 2015) which may be a primary reason current model structures cannot reproduce
561 observed differences in drought sensitivity among forests within the same PFT.

562

563 Future assessments of drought effects on forests and the modeling of such effects should
564 strive to employ soil water potential for various soil depths and new model structures to
565 account for variation in rooting depth and variation in belowground hydraulic
566 conductance as a function of embolism (Mackay *et al.*, 2015). Rather than requiring
567 model parameters for each belowground component, these models could use an
568 optimality approach – allowing the model to “select” the optimal rooting strategy (greater
569 allocation to fine roots, deeper roots, mycorrhizal fungi) depending on the site conditions
570 and nature of the drought (Fisher *et al.*, 2014). An integrated sum of daily water potential
571 values (becoming more negative with drought severity) has been suggested as a metric

for comparing droughts across different sites (Hanson *et al.*, 2004). Alternatively, when water potential data are unavailable, a metric such as the sum of soil-water deficit days (Brzostek *et al.*, 2014) may do an effective job of characterizing the severity of drought from the perspective of plants.

Other interacting factors not considered

Given that processes occurring in soil do not operate in isolation of other environmental changes and drivers, an improved understanding of how drought sensitivity is mediated by other global change factors (e.g., elevated CO₂ and increasing temperature) represents a critical area for future research. Higher atmospheric CO₂ increases the diffusion of CO₂ into leaves through the stomata, effectively increasing the availability of this critical resource to the plants. Most plants have been observed to increase their water-use efficiency (the ratio of CO₂ uptake to water loss) with increases in CO₂, and elevated CO₂ generally increases root growth and rooting depth (Iversen, 2010), which may help deep-rooted species overcome water stress. This short-term benefit of elevated CO₂ can yield sustained and significant increases in the growth of forests. However, increased growth results in higher leaf area of individual trees, which predisposes them to even greater drought stress compared to a non-CO₂ fertilized stand when and if a drought strikes (Warren *et al.*, 2011). Such a situation could occur if elevated CO₂ increased transpiring leaf area, and thus water consumption and hydraulic function, to a greater extent than root length (which also tends to increase under elevated CO₂). This mechanism has been invoked as a primary driver of *Quercus robur* mortality in response to drought in Europe (Levanič *et al.*, 2011).

595

596 **Implications for forest management**

597 Improved representations in the models of plant-available water, root functionality and
598 belowground dynamics should lead to significant improvements in how drought impacts
599 in forests are predicted. By identifying drought impacts across communities and areas in
600 the landscape, these improved predictions will facilitate management practices targeting
601 resilience and/or restoration of forest ecosystems. Models are valuable tools for guiding
602 decisions by land managers about how to manage forests before, during and after
603 drought; nevertheless, they should be used more as tools to inform strategic management
604 decisions or land-use planning, as opposed to specific decisions about stand management.

605

606 Thinning of forests is arguably the most practical short-term management strategy, as
607 thinning can enhance growth rates during droughts (Warren *et al.*, 2001; McDowell *et al.*,
608 2003; McDowell *et al.*, 2006). While this is frequently associated with greater water
609 availability, refined predictions of forest survival and growth after thinning could perhaps
610 be obtained by the model improvements on belowground water acquisition we
611 highlighted above. Fertilization of forests may have the opposite effect, increasing a
612 stand's sensitivity to drought. Belowground allocation often depends on nutrient
613 availability, and fertilization can reduce tree species' allocation to roots and mycorrhizal
614 fungi (Treseder, 2004; Phillips and Fahey, 2007; Pregitzer *et al.*, 2008) and lead to a
615 shallower root system (Bakker *et al.*, 2009). Both factors would predispose trees to
616 greater drought impacts. This idea is supported by the findings of Ward *et al.* (2015), who
617 reported that loblolly pine sensitivity to drought was greatest in fertilized plots owing to

fertilizer-induced changes in root activity.

Forest managers are being compelled to follow practices that accommodate for the impact of future droughts on the ecosystems they manage. However, the lack of specific predictions about how particular sites and species combinations will respond to drought makes it difficult to define set management practices. Management of forests for mitigating drought impacts could be readily improved once appropriate databases of relevant traits and soil properties are gathered, and expressed within models in accordance with the mechanistic equations already developed. While major advances have been made in the representation of mortality (Parolari *et al.*, 2014) and ecophysiological traits and their sensitivity to water stress (McDowell *et al.*, 2013), most models still do a poor job of predicting forest sensitivity to drought (Fatichi *et al.*, 2015).

Valuable forest management practices require plans tailored to the specific forest type, landscape features and other attributes (e.g., plantation vs. natural, main disturbance agent) characteristic of the site of interest. Currently, outputs from ecosystem process models and TBMs are too broad to be effectively used in management as they miss the site-specific nuances critical to generating information meaningful for management, i.e. productivity and likelihood of particular stands. For example, as drought resilience varies with depth to the water table and nutrient content, optimal thinning densities will vary depending on soil and topographic features of the stand; particular species assemblages, and the relative abundance of each species, will determine niche partitioning of soil resources, and thus the stand's response to drought; plasticity in tree species responses to

annual-to-decadal water scarcity should also inform about the most effective management practices, e.g., species most competitive in favorable stands may fair better during short drought periods than those relegated to drier areas, but under prolonged droughts it will be these second group that would persist in the area.

Conclusions

Here we address a critical knowledge gap in determining the sensitivity of forest ecosystems to drought: subsurface interactions between roots and soils. If we aim to generate predictions that facilitate management and conservation of forests (Grant *et al.*, 2013), we need to be able to predict not only which species are most sensitive to drought, but also which particular areas of the landscape, and under which conditions, could be most affected by future droughts. One way to achieve this is to bring together datasets from tree rings (e.g., the International Tree Ring Data Bank), soils (e.g., the Harmonized World Soil Database) and plant traits (e.g., the TRY database, the Fine Root Ecology Database), to look at which soil and root factors determine forest sensitivity to drought.

A second approach would be to add additional structures to process models that allow the model to be used as tool to test hypotheses about the importance of rooting strategies. A key challenge for all large-scale models is to strike the balance between generality (e.g., by including representations of ecosystem, processes based on first principles) and specificity (e.g., by capturing the unique biotic and abiotic attributes of a given site). Thus, the decision to improve model performance by including new structures must be weighed against the cost of adding to model complexity and increasing potential sources

of error due to the over parameterization. Consequently, details about root traits and soil factors for which too little is known, may inappropriate for inclusion in these models. However, since models are tools for testing hypotheses, including new model structures – even if poorly parameterized – should lead to improved understanding. And to the extent that explicit representations of belowground processes lead to a better understanding of drought impacts, they should also help land managers reduce uncertainty in projecting forest sensitivity to drought.

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Figures

Figure 1. The slope of the relationship between radial tree growth and a commonly used drought index provides an improved metric for tree species sensitivity to drought. The slope on the y axis represents significant linear regression slopes ($P < 0.05$) between negative values (i.e., drier than average years) from the summer Standardized Precipitation-Evapotranspiration Index (May to August) and the corresponding radial growth index. A) With slopes averaged per tree species, species with the highest drought sensitivity (as defined by the highest slopes) are paradoxically ranked as the species with the highest drought tolerance ($R^2 = 0.25$, $P < 0.05$; based on Niinemets and Valladares 2006). Filled circles are oak species, error bars are standard error of the mean. B) The sensitivity of white pine stands to drought depends on the total amount of available water (AWS; data from the SSURGO database), and decreases from xeric to mesic sites ($R^2 = 0.60$, $P < 0.05$). AWS is calculated as the available water capacity times the thickness of each soil horizon to a 1-m depth and accounts for soil depth and rock fragments.

Figure 2. Average annual growth response of 522 sugar maple trees to drought at twenty-two sites (individual points on the figure) across the Eastern US and Canada, plotted as a function of average rooting depth at each site ($R^2 = 0.17$, $P < 0.05$). The tree growth index (y axis) was calculated by quantifying tree growth only during periods of summer drought, defined here as times when the standard precipitation-evaporation index (SPEI)

during the May to August interval was -1.5 or less. Growth responses were calculated by averaging standardized individual tree-ring widths (i.e., dendrochronological reconstructions) and matched to soil depth maps.

Figure 3. Post-treatment assessment of root presence below the soil surface to a depth of 140 cm for *Quercus prinus* and *Liriodendron tulipifera* canopy trees following years of acute drought manipulations (Hanson et al. 2007).

Figure 4. A 13-year record of soil water content (A) or soil water potential (B) at two measurement depths (0-35, or 35-70 cm) for the Walker Branch Watershed in Tennessee (modified from data in Hanson et al. 2003). The dashed line in B represents the threshold at which water is unavailable to plants (i.e., the wilting point), and water stress occurs. It is clear that similar surface (0-35 cm depth) water potentials are approaching critical drought thresholds while somewhat deeper soils (35-70 cm depth) retain ample soil water for plant function.

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Figure 2

Figure 3

Quercus prinus

Liriodendron tulipifera