Forest Ecology and Management 380 (2016) 309–320

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Review and synthesis

A belowground perspective on the drought sensitivity of forests: Towards improved understanding and simulation ☆

Richard P. Phillips [a,*], Inés Ibáñez [b], Loïc D'Orangeville [a,c], Paul J. Hanson [d], Michael G. Ryan [e], Nathan G. McDowell [f]

[a] Department of Biology, Indiana University, Bloomington, IN 47405, United States
[b] School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI 48109, United States
[c] Centre d'Étude de la Forêt, Université du Québec à Montréal, Case Postale 8888, Succursale Centre-Ville, Montreal, Quebec H3C 3P8, Canada
[d] Climate Change Science Institute and Environmental Science Division, Oak Ridge National Lab, Oak Ridge, TN 37830, United States
[e] Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, United States
[f] Earth and Environmental Sciences Division, Los Alamos National Lab, Los Alamos, NM 87545, United States

ARTICLE INFO

Article history:
Received 15 July 2016
Received in revised form 23 August 2016
Accepted 24 August 2016
Available online 13 September 2016

Keywords:
Water stress
Ecosystem modeling
Drought resilience
Rooting strategies
Earth system models
Land surface models

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.

© 2016 Elsevier B.V. All rights reserved.

Contents

1. Introduction . . . 310
2. What is forest sensitivity to drought? . . . 310
3. Belowground strategies for dealing with drought . . . 311
   3.1. Root traits . . . 312
   3.2. Root dynamics . . . 312
   3.3. Root access to deep water . . . 312
   3.4. The role of soil microbes . . . 313
4. Soil factors that mediate drought . . . 314
   4.1. What water is available? . . . 314
   4.2. Groundwater availability to roots during drought . . . 314
5. Can models be improved with a belowground perspective? . . . 315
   5.1. Consideration of belowground strategies in process models . . . 316
   5.2. Consideration of available water in models . . . 316
6. Other interacting factors not considered . . . 316

☆ This article is part of a special section entitled "Drought and US Forests: Impacts and Potential Management Responses" published in Forest Ecology and Management 380, 2016.

* Corresponding author.
E-mail address: rpp6@indiana.edu (R.P. Phillips).

http://dx.doi.org/10.1016/j.foreco.2016.08.043
0378-1127/© 2016 Elsevier B.V. All rights reserved.

7. Implications for forest management . . . 316
8. Conclusions . . . 317
Acknowledgements . . . 317
References . . . 317

1. 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, 2015; Anderegg et al., 2012). 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 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 theses 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 1.5 m), 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). As such, 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, 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).

2. 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 draws a discinction between ecosystems where trees face water stress regularly (e.g., in semi-arid ecosystems) and ecosystems where severe water stress is uncommon, and emphasizes the differences between aridity and drought. We define sensitivity as short-term physiological

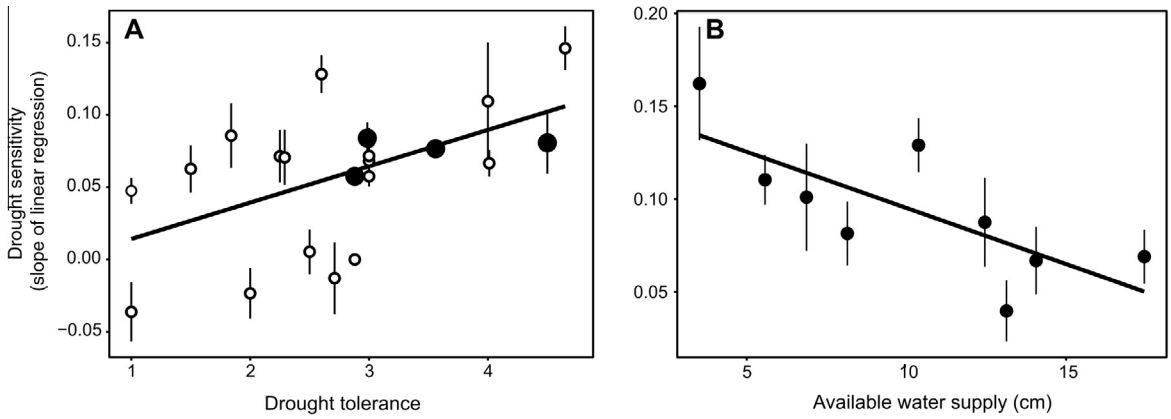

Fig. 1. The slope of the relationship between radial tree growth and a commonly used drought index provides an improved metric for determining tree species sensitivity to drought. Values on the y axis represent the relationship between tree growth and water balance anomaly during years drier than average (i.e., the slope of the linear regression). Water balance anomaly was determined by calculating the standardized precipitation-evapotranspiration Index (SPEI) at each site (for May to August). (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. Error bars represent standard errors for each slope estimate.

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 small 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 (Fig. 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 (Fig. 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.

3. 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.

3.1. 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, 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.

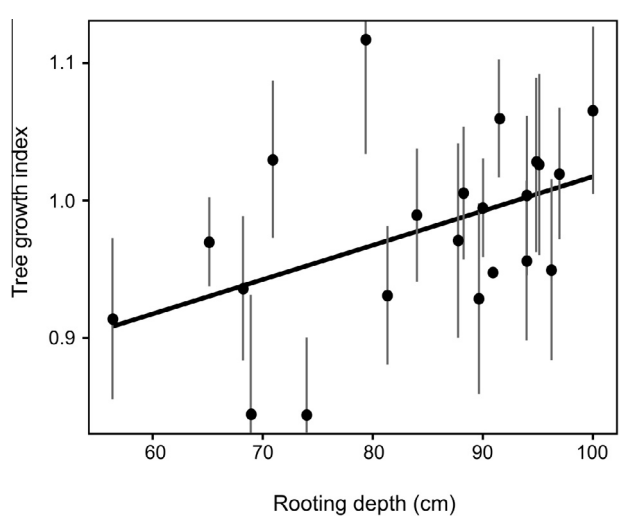

Fig. 2. Average annual growth response of 522 sugar maple trees to drought at twenty-two sites (individual points on the figure) across the Eastern US and Canada, plotted as a function of average rooting depth at each site ($R^2 = 0.17$, $P < 0.05$). The radial tree growth index (y axis) was calculated by quantifying tree growth 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 based on the SSURGO database. Error bars are 95% confidence intervals of the tree-ring growth index at each site during droughts.

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).

3.2. 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. Given the variable rooting strategies of species, a multidimensional view that considers root traits, root trait plasticity and root-shoot allocation tradeoffs may be needed to make predictions about belowground responses to drought (Weemstra et al., 2016).

3.3. 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.,

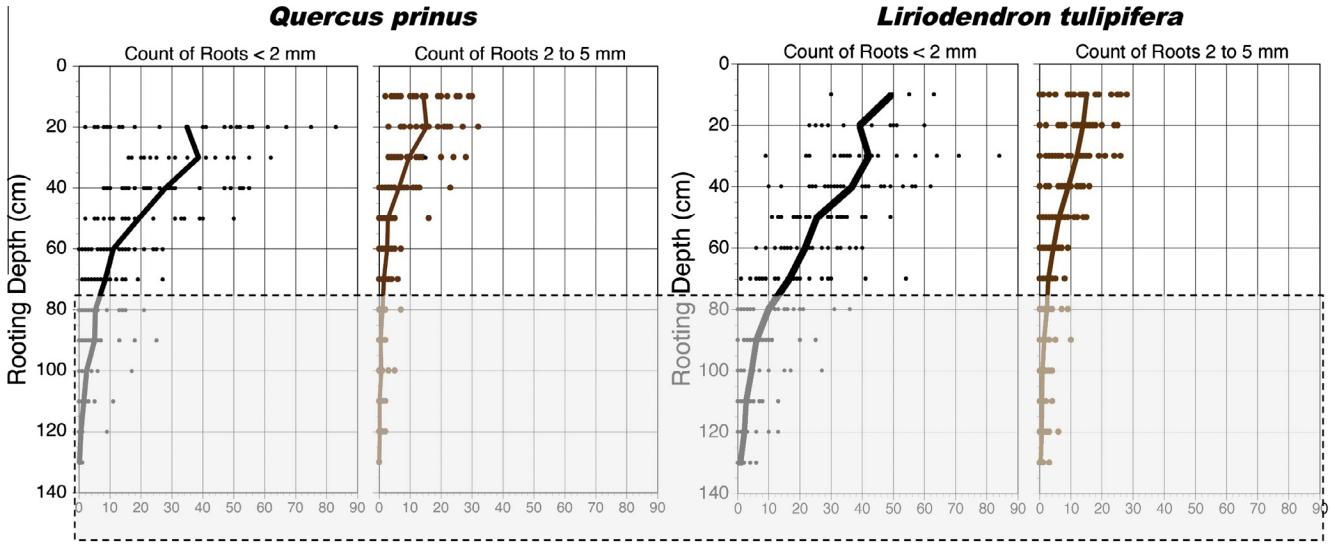

Fig. 3. Post-treatment assessment of root presence below the soil surface to a depth of 140 cm for *Quercus prinus* and *Liriodendron tulipifera* canopy trees following years of acute drought manipulations (Hanson et al., 2007).

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 accessible to the trees. 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 et al., 2008). Although there is still some debate about the quantitative significance of hydraulic redistribution of water (Neumann and Cardon, 2012; Prieto et al., 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 to tap into (Brzostek et al., 2014).

3.4. 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 that 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, submitted for publication), 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. Root rot pathogens such as *Armillaria* spp. and *Heterobasidion* spp. often 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., 2016). 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, submitted for publication).

4. Soil factors that mediate drought

Interspecific variation in tree species responses to drought (Orwig and Abrams, 1997) 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.

4.1. 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).

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 (Fig. 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; Fig. 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.

4.2. 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

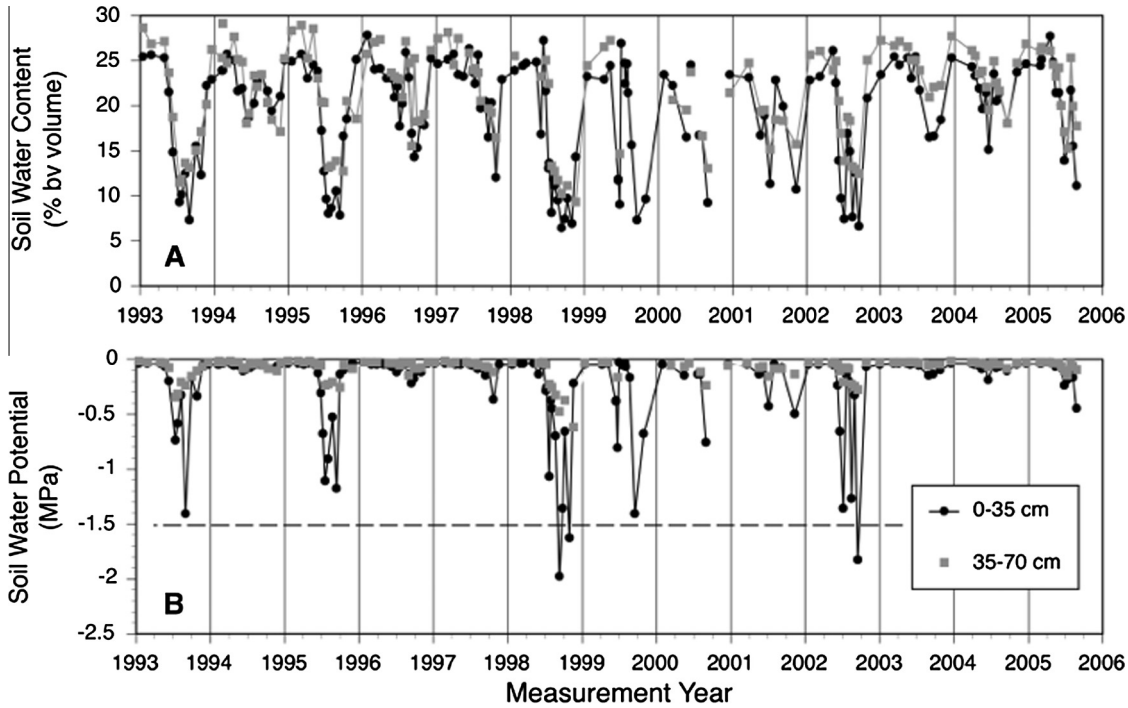

Fig. 4. A 13-year record of soil water content (A) or soil water potential (B) at two measurement depths (0–35, or 35–70 cm) for the Walker Branch Watershed in Tennessee (modified from data in Hanson et al. (2004)). The dashed line in B represents the threshold at which water is unavailable to plants (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.

low water availability (David et al., 2013). The depth to groundwater across much of the US is ~5 m (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.), the impacts of droughts may be minor. 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 (<2 m) but variable groundwater table, intraannual and interannual variation in groundwater depth had no 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 trichocarpa*) 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.

5. 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.

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

5.1. Consideration of belowground strategies in process models

Ecosystem models vary considerably in how they incorporate belowground processes in their representations of forests. These range from high-detail temporally dynamic models 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 (TBMs), 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, the land surface is separated into 5–15 plant functional types (PFTs), each with their own unique paramterizations. 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).

5.2. 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 by parameterized with soil databases (e.g., the USDA's Soil Survey Geographic database), and available water can them 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.

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

Future assessments of drought effects on forests and the modeling of such effects should strive to employ soil water potential for various soil depths and new model structures to account for variation in rooting depth and variation in belowground hydraulic conductance as a function of embolism (Mackay et al., 2015). Rather than requiring model parameters for each belowground component, these models could use an optimality approach – allowing the model to "select" the optimal rooting strategy (greater allocation to fine roots, deeper roots, mycorrhizal fungi) depending on the site conditions and nature of the drought (Fisher et al., 2014). An integrated sum of daily water potential 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.

6. 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 CO_2 and increasing temperature) represents a critical area for future research. Higher atmospheric CO_2 increases the diffusion of CO_2 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 CO_2 uptake to water loss) with increases in CO_2, and elevated CO_2 generally increases root growth and rooting depth (Iversen, 2010), which may help deep-rooted species overcome water stress. This short-term benefit of elevated CO_2 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-CO_2 fertilized stand when and if a drought strikes (Warren et al., 2011). Such a situation could occur if elevated CO_2 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 CO_2). This mechanism has been invoked as a primary driver of *Quercus robur* mortality in response to drought in Europe (Levanič et al., 2011).

7. Implications for forest management

Improved representations in the models of plant-available water, root functionality and belowground dynamics should lead

to significant improvements in how drought impacts in forests are predicted. By identifying drought impacts across communities and areas in the landscape, these improved predictions will facilitate management practices targeting resilience and/or restoration of forest ecosystems. Models are valuable tools for guiding decisions by land managers about how to manage forests before, during and after drought; nevertheless, they should be used more as tools to inform strategic management decisions or land-use planning, as opposed to specific decisions about stand management.

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

8. 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 over parameterization of the models. 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.

Acknowledgements

All authors would like to thank Kim Novick, Eddie Brzostek, Anthony O'Grady and two anonymous reviewers for their constructive feedback on an earlier version of the manuscript. This review is a modified version of a comprehensive synthesis developed by the authors for the USDA Forest Service Report "Effects of Drought on Forests and Rangelands in the United States: A Comprehensive Science Synthesis", a part of the National Climate Assessment. RPP acknowledges support from the Department of Energy (DOE), Office of Biological and Environmental Research (via the Ameriflux Management Project). RPP wishes to acknowledge the National Science Foundation (NSF) for its support of the Research Coordination Network "Drought-Net". PJH was supported by the DOE Office of Biological and Environmental Research. Oak Ridge National Laboratory is managed by UT-Battelle, LLC, for the DOE under contract DE-AC05-00OR22725. NGM was supported by the DOE, Office of Science, Survival-Mortality and Next Generation Ecosystem Experiment-Tropics projects. II was partially supported by NSF-DEB (award # 1252664).

References

Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684.

Anderegg, L.D.L., HilleRisLambers, J., 2016. Drought stress limits the geographic ranges of two tree species via different physiological mechanisms. Glob. Change Biol. 22, 1029–1045.

Anderegg, W.R., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., Ogle, K., Shaw, J.D., Shevliakova, E., Williams, A.P., Wolf, A., Ziaco, E., Pacala, S., 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349, 528–532.

Anderegg, W.R.L., Berry, J.A., Smith, D.D., Sperry, J.S., Anderegg, L.D.L., Field, C.B., 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. Proc. Natl. Acad. Sci. USA 109, 233–237.

Bakker, M.R., Jolicoeur, E., Trichet, P., Augusto, L., Plassard, C., Guinberteau, J., Loustau, D., 2009. Adaptation of fine roots to annual fertilization and irrigation in a 13-year-old Pinus pinaster stand. Tree Physiol. 29, 229–238.

Bauerle, T.L., Richards, J.H., Smart, D.R., Eissenstat, D.M., 2008. Importance of internal hydraulic redistribution for prolonging the lifespan of roots in dry soil. Plant Cell Environ. 31, 177–186.

Bleby, T.M., Mcelrone, A.J., Jackson, R.B., 2010. Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. Plant Cell Environ. 33, 2132–2148.

Bloom, A.J., Chapin, F.S., Mooney, H.A., 1985. Resource limitation in plants - an economic analogy. Annu. Rev. Ecol. Syst. 16, 363–392.

Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320, 1444–1449.

Breda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann. For. Sci. 63, 625–644.

Brooks, J.R., Meinzer, F.C., Coulombe, R., Gregg, J., 2002. Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. Tree Physiol. 22, 1107–1117.

Brunner, I., Herzog, C., Dawes, M.A., Arend, M., Sperisen, C., 2015. How tree roots respond to drought. Front. Plant Sci. 6.

Brzostek, E., Dragoni, D., Schmid, H.P., Rahman, A.F., Sims, D., Wayson, C.A., Johnson, D.J., Phillips, R.P., 2014. Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests. Glob. Change Biol. http://dx.doi.org/10.1111/gcb.12528.

Canadell, J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. Maximum rooting depth of vegetation types at the global scale. Oecologia 108, 583–595.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martinez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R. B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012. Global convergence in the vulnerability of forests to drought. Nature 491, 752.

Christoffersen, B.O., Restrepo-Coupe, N., Arain, M.A., Baker, I.T., Cestaro, B.P., Ciais, P., Fisher, J.B., Galbraith, D., Guan, X.D., Gulden, L., van den Hurk, B., Ichii, K., Imbuzeiro, H., Jain, A., Levine, N., Miguez-Machor, G., Poulter, B., Roberti, D.R., Sakaguchi, K., Sahoo, A., Schaefer, K., Shi, M.J., Verbeeck, H., Yang, Z.L., Araujo, A. C., Kruijt, B., Manzi, A.O., da Rocha, H.R., von Randow, C., Muza, M.N., Borak, J., Costa, M.H., de Goncalves, L.G.G., Zeng, X.B., Saleska, S.R., 2014. Mechanisms of water supply and vegetation demand govern the seasonality and magnitude of evapotranspiration in Amazonia and Cerrado. Agric. For. Meteorol. 191, 33–50.

Clapp, R.B., Hornberger, G.M., 1978. Empirical equations for some soil hydraulic-properties. Water Resour. Res. 14, 601–604.

Clark, J.S., Bell, D.M., Hersh, M.H., Nichols, L., 2011. Climate change vulnerability of forest biodiversity: climate and competition tracking of demographic rates. Glob. Change Biol. 17, 1834–1849.

Clinton, B.D., Boring, L.R., Swank, W.T., 1993. Canopy gap characteristics and drought influences in oak forests of the Coweeta Basin. Ecology 74, 1551–1558.

Comas, L.H., Becker, S.R., Cruz, V.V., Byrne, P.F., Dierig, D.A., 2013. Root traits contributing to plant productivity under drought. Front. Plant Sci. 4.

Cook, B.I., Ault, T.R., Smerdon, J.E., 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Sci. Adv. 1, e1400082.

Cudlin, P., Kieliszewska-Rojucka, B., Rudawska, M., Grebenc, T., Alberton, O., Lehto, T., Bakker, M.R., Borja, I., Konopka, B., Leski, T., Kraigher, H., Kuyper, T.W., 2007. Fine roots and ectomycorrhizas as indicators of environmental change. Plant Biosyst. 141, 406–425.

Dai, A.G., 2011. Drought under global warming: a review. WIREs Clim. Change 2, 45–65.

David, T.S., Pinto, C.A., Nadezhdina, N., Kurz-Besson, C., Henriques, M.O., Quilho, T., Cermak, J., Chaves, M.M., Pereira, J.S., David, J.S., 2013. Root functioning, tree water use and hydraulic redistribution in *Quercus suber* trees: a modeling approach based on root sap flow. For. Ecol. Manage. 307, 136–146.

Dawson, T.E., 1993. Hydraulic lift and water-use by plants - implications for water-balance, performance and plant-plant interactions. Oecologia 95, 565–574.

De Kauwe, M.G., Medlyn, B.E., Zaehle, S., Walker, A.P., Dietze, M.C., Hickler, T., Jain, A.K., Luo, Y.Q., Parton, W.J., Prentice, I.C., Smith, B., Thornton, P.E., Wang, S.S., Wang, Y.P., Warlind, D., Weng, E.S., Crous, K.Y., Ellsworth, D.S., Hanson, P.J., Kim, H. Seok, Warren, J.M., Oren, R., Norby, R.J., 2013. Forest water use and water use efficiency at elevated CO_2: a model-data intercomparison at two contrasting temperate forest FACE sites. Glob. Change Biol. 19, 1759–1779.

Dietze, M.C., Serbin, S.P., Davidson, C., Desai, A.R., Feng, X.H., Kelly, R., Kooper, R., LeBauer, D., Mantooth, J., McHenry, K., Wang, D., 2014. A quantitative assessment of a terrestrial biosphere model's data needs across North American biomes. J. Geophys. Res.-Biogeosci. 119, 286–300.

Domec, J.C., King, J.S., Noormets, A., Treasure, E., Gavazzi, M.J., Sun, G., McNulty, S.G., 2010. Hydraulic redistribution of soil water by roots affects whole-stand evapotranspiration and net ecosystem carbon exchange. New Phytol. 187, 171–183.

Dracup, J.A., Lee, K.S., Paulson, E.G., 1980. On the definition of droughts. Water Resour. Res. 16, 297–302.

Eamus, D., 2003. How does ecosystem water balance affect net primary productivity of woody ecosystems? Funct. Plant Biol. 30, 187–205.

Egerton-Warburton, L.M., Querejeta, J.I., Allen, M.F., 2008. Efflux of hydraulically lifted water from mycorrhizal fungal hyphae during imposed drought. Plant Signal. Behav. 3, 68–71.

Ehleringer, J.R., Dawson, T.E., 1992. Water uptake by plants: perspectives from stable isotope composition. Plant Cell Environ. 15, 1073–1082.

Fatichi, S., Pappas, C., Ulvanov, V.Y., 2015. Modeling plant–water interactions: an ecohydrological overview from the cell to the global scale. Wiley Interdisciplinary Rev.: Water. http://dx.doi.org/10.1002/wat2.1125.

Fisher, J.B., Huntzinger, D.N., Schwalm, C.R., Sitch, S., 2014. Modeling the terrestrial biosphere. Annu. Rev. Environ. Resour. 39, 91.

Ford, C.R., Hubbard, R.M., Vose, J.M., 2011. Quantifying structural and physiological controls on variation in canopy transpiration among planted pine and hardwood species in the southern Appalachians. Ecohydrology 4, 183–195.

Grant, G.E., Tague, C.L., Allen, C.D., 2013. Watering the forest for the trees: an emerging priority for managing water in forest landscapes. Front. Ecol. Environ. 11, 314–321.

Grant, R.F., 1998. Simulation in ecosys of root growth response to contrasting soil water and nitrogen. Ecol. Model. 107, 237–264.

Gu, L., Pallardy, S.G., Hosman, K.P., Sun, Y., 2015. Drought-influenced mortality of tree species with different predawn leaf water dynamics in a decade-long study of a central US forest. Biogeosciences 12, 2831–2845.

Gustafson, E.J., Sturtevant, B.R., 2013. Modeling forest mortality caused by drought stress: implications for climate change. Ecosystems 16, 60–74.

Hanson, P.J., Amthor, J.S., Wullschleger, S.D., Wilson, K.B., Grant, R.F., Hartley, A., Hui, D., Hunt, E.R., Johnson, D.W., Kimball, J.S., King, A.W., Luo, Y., McNulty, S. G., Sun, G., Thornton, P.E., Wang, S., Williams, M., Baldocchi, D.D., Cushman, R.M., 2004. Oak forest carbon and water simulations: model intercomparisons and evaluations against independent data. Ecol. Monogr. 74, 443–489.

Hanson, P.J., Todd, D.E., Amthor, J.S., 2001. A six-year study of sapling and large-tree growth and mortality responses to natural and induced variability in precipitation and throughfall. Tree Physiol. 21, 345–358.

Hanson, P.J., Tschaplinski, T.J., Wullschleger, S.D., Todd Jr., D.E., Augé, R.M. (Eds.), 2007. The Resilience of Upland-Oak Forest Canopy Trees to Chronic and Acute Precipitation Manipulations.

Hanson, P.J., Weltzin, J.F., 2000. Drought disturbance from climate change: response of United States forests. Sci. Total Environ. 262 (3), 205–220.

Henckel, P.A., 1964. Physiology of plants under drought. Annu. Rev. Plant Physiol. 15, 363.

Hendrick, R.L., Pregitzer, K.S., 1996. Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. J. Ecol. 48, 167–176.

Huntington, T.G., 2006. Evidence for intensification of the global water cycle: review and synthesis. J. Hydrol. 319, 83–95.

Ibáñez, I., McCarthy-Neumann, S., 2016. Effects of mycorrhizal fungi on tree seedling growth: quantifying the parasitism-mutualism transition along a light gradient. Can. J. For. Res. 46, 48–57.

Iversen, C.M., 2010. Digging deeper: fine-root responses to rising atmospheric CO_2 concentration in forested ecosystems. New Phytol. 186, 346–357.

Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M., 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. For. Ecol. Manage. 254, 390–406.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108, 389–411.

Jany, J.L., Martin, F., Garbaye, J., 2003. Respiration activity of ectomycorrhizas from *Cenococcum geophilum* and *Lactarius* sp. in relation to soil water potential in five beech forests. Plant Soil 255, 487–494.

Joslin, J.D., Wolfe, M.H., Hanson, P.J., 2000. Effects of altered water regimes on forest root systems. New Phytol. 147, 117–129.

Kannenberg, S.A., Phillips, R.P., 2016. Native soil microbial communities buffer tree physiological parameters from drought stress without altering carbon dynamics. Oecologia (submitted for publication).

Klein, T., Yakir, D., Buchmann, N., Grunzweig, J.M., 2014. Towards an advanced assessment of the hydrological vulnerability of forests to climate change-induced drought. New Phytol. 201, 712–716.

Kolb, T.E., Fettig, C.J., Ayres, M.P., Bentz, B.J., Hicke, J.A., Mathiasen, R., Stewart, J.E., Weed, A.S., 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. For. Ecol. Manage. 380, 321–334.

Kozlowski, T.T., Kramer, P.J., Pallardy, S.G., 1991. The Physiological Ecology of Woody Plants. Academic Press, San Diego.

Kramer, P.J., Boyer, J.S., 1995. Water Relations of Plants and Soils. Academic Press, San Diego.

Kramer-Walter, K.R., Bellingham, P.J., Millar, T.R., Smissen, R.D., Richardson, S.J., Laughlin, D.C., 2016. Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. J. Ecol. http://dx.doi.org/10.1111/1365-2745.12562.

Larson, J.E., Funk, J.L., 2016. Seedling root responses to soil moisture and the identification of a belowground trait spectrum across three growth forms. New Phytol. 210, 827–838.

Lehto, T., Zwiazek, J.J., 2011. Ectomycorrhizas and water relations of trees: a review. Mycorrhiza 21, 71–90.

Levesque, M., Walthert, L., Weber, P., 2016. Soil nutrients influence growth response of temperate tree species to drought. J. Ecol. 104, 377–387.

Lienard, J., Harrison, J., Strigul, N., 2016. US forest response to projected climate-related stress: a tolerance perspective. Global Change Biol. 22, 2875–2886.

Loewenstein, N.J., Pallardy, S.G., 1998. Drought tolerance, xylem sap abscisic acid and stomatal conductance during soil drying: a comparison of canopy trees of three temperate deciduous angiosperms. Tree Physiol. 18, 431–439.
Lowry, C.S., Loheide, S.P., 2010. Groundwater-dependent vegetation: quantifying the groundwater subsidy. Water Resour. Res. 46.
Mackay, D.S., Roberts, D.E., Ewers, B.E., Sperry, J.S., McDowell, N.G., Pockman, W.T., 2015. Interdependence of chronic hydraulic dysfunction and canopy processes can improve integrated models of tree response to drought. Water Resour. Res. 51, 6156–6176.
Manzoni, S., Vico, G., Katul, G., Fay, P.A., Polley, W., Palmroth, S., Porporato, A., 2011. Optimizing stomatal conductance for maximum carbon gain under water stress: a meta-analysis across plant functional types and climates. Funct. Ecol. 25, 456–467.
Martinez-Vilalta, J., Lloret, F., Breshears, D.D., 2012. Drought-induced forest decline: causes, scope and implications. Biol. Lett. 8, 689–691.
Martinez-Vilalta, J., Poyatos, R., Aguade, D., Retana, J., Mencuccini, M., 2014. A new look at water transport regulation in plants. New Phytol. 204, 105–115.
Maxwell, J.T., Harley, G.L., Matheus, T.J., 2015. Dendroclimatic reconstructions from multiple co-occurring species: a case study from an old-growth deciduous forest in Indiana, USA. Int. J. Climatol. 35, 860–870.
Maxwell, R.M., Kollet, S.J., 2008. Interdependence of groundwater dynamics and land-energy feedbacks under climate change. Nat. Geosci. 1, 665–669.
McCormack, M.L., Adams, T.S., Smithwick, E.A.H., Eissenstat, D.M., 2012. Predicting fine root lifespan from plant functional traits in temperate trees. New Phytol. 195, 823–831.
McCulley, R.L., Jobbagy, E.G., Pockman, W.T., Jackson, R.B., 2004. Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. Oecologia 141, 620–628.
McDowell, N.G., Allen, C.D., 2015. Darcy's law predicts widespread forest mortality under climate warming. Nat. Clim. Change 5 (7), 669–672.
McDowell, N., Brooks, J.R., Fitzgerald, S.A., Bond, B.J., 2003. Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. Plant Cell Environ. 26, 631–644.
McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol. 178, 719–739.
McDowell, N.G., Adams, H.D., Bailey, J.D., Hess, M., Kolb, T.E., 2006. Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. Ecol. Appl. 16, 1164–1182.
McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F., Stitt, M., 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. TREE 26, 523–532.
McDowell, N.G., Fisher, R.A., Xu, C.G., Domec, J.C., Holtta, T., Mackay, D.S., Sperry, J.S., Boutz, A., Dickman, L., Gehres, N., Limousin, J.M., Macalady, A., Martinez-Vilalta, J., Mencuccini, M., Plaut, J.A., Ogee, J., Pangle, R.E., Rasse, D.P., Ryan, M.G., Sevanto, S., Waring, R.H., Williams, A.P., Yepez, E.A., Pockman, W.T., 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. New Phytol. 200, 304–321.
Meinzer, F.C., Johnson, D.M., Lachenbruch, B., McCulloh, K.A., Woodruff, D.R., 2009. Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. Funct. Ecol. 23, 922–930.
Millar, C.I., Stephenson, N.L., 2015. Temperate forest health in an era of emerging megadisturbance. Science 349, 823–826.
Mohan, J.E., Cowden, C.C., Baas, P., Dawadi, A., Frankson, P.T., Helmick, K., Hughes, E., Khan, S., Lang, A., Machmuller, M., Taylor, M., Witt, C.A., 2014. Mycorrhizal fungi mediation of terrestrial ecosystem responses to global change: mini-review. Fungal Ecol. 10, 3–19.
Mueller, R.C., Scudder, C.M., Porter, M.E., Trotter, R.T., Gehring, C.A., Whitham, T.G., 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. J. Ecol. 93, 1085–1093.
Neumann, R.B., Cardon, Z.G., 2012. The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. New Phytol. 194, 337–352.
Niinemets, U., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547.
O'Gorman, P.A., Schneider, T., 2009. The physical basis for increases in precipitation extremes in simulations of 21st-century climate change. Proc. Natl. Acad. Sci. USA 106, 14773–14777.
Oleson, K.W., Niu, G.Y., Yang, Z.L., Lawrence, D.M., Thornton, P.E., Lawrence, P.J., Stockli, R., Dickinson, R.E., Bonan, G.B., Levis, S., Dai, A., Qian, T., 2008. Improvements to the Community Land Model and their impact on the hydrological cycle. J. Geophys. Res.-Biogeosci. 113.
Orwig, D.A., Abrams, M.D., 1997. Variation in radial growth responses to drought among species, site, and canopy strata. Trees-Struct. Funct. 11, 474–484.
Parolari, A.J., Katul, G.G., Porporato, A., 2014. An ecohydrological perspective on drought-induced forest mortality. J. Geophys. Res.-Biogeosci. 119, 965–981.
Paulo, A.A., Pereira, L.S., 2006. Drought concepts and characterization: comparing drought indices applied at local and regional scales. Water Int. 31, 37–49.
Peltier, D.M.P., Fell, M., Ogle, K., 2016. Altered climatic sensitivity of tree growth after drought: multi-species synthesis of tree-rings in the southwestern US. Ecol. Monogr. http://dx.doi.org/10.1002/ecm.1219.
Phillips, R.P., Fahey, T.J., 2007. Fertilization effects on fine root biomass, rhizosphere microbes and respiratory fluxes in hardwood forest soils. New Phytol. 176, 655–664.
Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P., Mommer, L., 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol. 193, 30–50.
Powell, T.L., Galbraith, D.R., Christoffersen, B.O., Harper, A., Imbuzeiro, H.M.A., Rowland, L., Almeida, S., Brando, P.M., da Costa, A.C.L., Costa, M.H., Levine, N.M., Malhi, Y., Saleska, S.R., Sotta, E., Williams, M., Meir, P., Moorcroft, P.R., 2013. Confronting model predictions of carbon fluxes with measurements of Amazon forests subjected to experimental drought. New Phytol. 200, 350–364.
Pregitzer, K.S., Burton, A.J., King, J.S., Zak, D.R., 2008. Soil respiration, root biomass, and root turnover following long-term exposure of northern forests to elevated atmospheric CO_2 and tropospheric O_3. New Phytol. 180, 153–161.
Pregitzer, K.S., DeForest, J.L., Burton, A.J., Allen, M.F., Ruess, R.W., Hendrick, R.L., 2002. Fine root architecture of nine North American trees. Ecol. Monogr. 72, 293.
Prieto, I., Armas, C., Pugnaire, F.I., 2012. Water release through plant roots: new insights into its consequences at the plant and ecosystem level. New Phytol. 193, 830–841.
Querejeta, J.I., Egerton-Warburton, L.M., Allen, M.F., 2007. Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California Oak savanna. Soil Biol. Biochem. 39, 409–417.
Querejeta, J.I., Egerton-Warburton, L.M., Allen, M.F., 2009. Topographic position modulates the mycorrhizal response of oak trees to interannual rainfall variability. Ecology 90, 649–662.
Raich, J.W., Rastetter, E.B., Melillo, J.M., Kicklighter, D.W., Steudler, P.A., Peterson, B. J., Grace, A.L., Moore, B., Vorosmarty, C.J., 1991. Potential net primary productivity in South America - application of a global-model. Ecol. Appl. 1, 399–429.
Rapparini, F., Peñuelas, J., 2014. Mycorrhizal fungi to alleviate drought stress on plant growth. In: Miransari, M. (Ed.), Use of Microbes for the Alleviation of Soil Stresses, vol. 1. Springer, New York, pp. 21–42.
Reich, P.B., 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. J. Ecol. 102, 275–301.
Rincon, A., Valladares, F., Gimeno, T.E., Pueyo, J.J., 2008. Water stress responses of two Mediterranean tree species influenced by native soil microorganisms and inoculation with a plant growth promoting rhizobacterium. Tree Physiol. 28, 1693–1701.
Roman, D.T., Novick, K.A., Brzostek, E.R., Dragoni, D., Rahman, F., Phillips, R.P., 2015. The role of isohydric and anisohydric species in determining ecosystem-scale response to severe drought. Oecologia 179, 641–654.
Running, S.W., Nemani, R.R., Heinsch, F.A., Zhao, M.S., Reeves, M., Hashimoto, H., 2004. A continuous satellite-derived measure of global terrestrial primary production. Bioscience 54, 547–560.
Ryan, M.G., Phillips, N., Bond, B.J., 2006. The hydraulic limitation hypothesis revisited. Plant Cell Environ. 29, 367–381.
Saxton, K.E., Rawls, W.J., 2006. Soil water characteristic estimates by texture and organic matter for hydrologic solutions. Soil Sci. Soc. Am. J. 70, 1569–1578.
Schaefer, K., Schwalm, C.R., Williams, C., Arain, M.A., Barr, A., Chen, J.M., Davis, K.J., Dimitrov, D., Hilton, T.W., Hollinger, D.Y., Humphreys, E., Poulter, B., Raczka, B. M., Richardson, A.D., Sahoo, A., Thornton, P., Vargas, R., Verbeeck, H., Anderson, R., Baker, I., Black, T.A., Bolstad, P., Chen, J.Q., Curtis, P.S., Desai, A.R., Dietze, M., Dragoni, D., Gough, C., Grant, R.F., Gu, L.H., Jain, A., Kucharik, C., Law, B., Liu, S.G., Lokipitiya, E., Margolis, H.A., Matamala, R., McCaughey, J.H., Monson, R., Munger, J.W., Oechel, W., Peng, C.H., Price, D.T., Ricciuto, D., Riley, W.J., Roulet, N., Tian, H.Q., Tonitto, C., Torn, M., Weng, E.S., Zhou, X.L., 2012. A model-data comparison of gross primary productivity: results from the North American Carbon Program site synthesis. J. Geophys. Res.-Biogeosci. 117.
Schenk, H.J., Jackson, R.B., 2002a. The global biogeography of roots. Ecol. Monogr. 72, 311–328.
Schenk, H.J., Jackson, R.B., 2002b. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. J. Ecol. 90, 480–494.
Smithwick, E.A.H., Lucash, M.S., McCormack, M.L., Sivandran, G., 2014. Improving the representation of roots in terrestrial models. Ecol. Model. 291, 193–204.
Soylu, M.E., Kucharik, C.J., Loheide, S.P., 2014. Influence of groundwater on plant water use and productivity: development of an integrated ecosystem - variably saturated soil water flow model. Agric. For. Meteorol. 189, 198–210.
Sperry, J.S., Adler, F.R., Campbell, G.S., Comstock, J.P., 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. Plant Cell Environ. 21, 347–359.
Sturrock, R.N., Frankel, S.J., Brown, A.V., Hennon, P.E., Kliejunas, J.T., Lewis, K.J., Worrall, J.J., Woods, A.J., 2011. Climate change and forest diseases. Plant. Pathol. 60, 133–149.
Tardieu, F., Simonneau, T., 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. J. Exp. Bot. 49, 419–432.
Treseder, K.K., 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. New Phytol. 164, 347–355.
Vicca, S., Luyssaert, S., Penuelas, J., Campioli, M., Chapin, F.S., Ciais, P., Heinemeyer, A., Hogberg, P., Kutsch, W.L., Law, B.E., Malhi, Y., Papale, D., Piao, S.L., Reichstein, M., Schulze, E.D., Janssens, I.A., 2012. Fertile forests produce biomass more efficiently. Ecol. Lett. 15, 520–526.
Volkmann, T.H.M., Haberer, K., Gessler, A., Weiler, M., 2016. High-resolution isotope measurements resolve rapid ecohydrological dynamics at the soil-plant interface. New Phytol. 210, 839–849.

Wang, W.F., Peng, C.H., Kneeshaw, D.D., Larocque, G.R., Luo, Z.B., 2012. Drought-induced tree mortality: ecological consequences, causes, and modeling. Environ. Rev. 20, 109–121.

Ward, E.J., Domec, J.C., Laviner, M.A., Fox, T.R., Sun, G., McNulty, S., King, J., Noormets, A., 2015. Fertilization intensifies drought stress: water use and stomatal conductance of *Pinus taeda* in a midrotation fertilization and throughfall reduction experiment. For. Ecol. Manage. 355, 72–82.

Warren, C.R., McGrath, J.F., Adams, M.A., 2001. Water availability and carbon isotope discrimination in conifers. Oecologia 127, 476–486.

Warren, J.M., Hanson, P.J., Iversen, C.M., Kumar, J., Walker, A.P., Wullschleger, S.D., 2015. Root structural and functional dynamics in terrestrial biosphere models - evaluation and recommendations. New Phytol. 205, 59–78.

Warren, J.M., Meinzer, F.C., Brooks, J.R., Domec, J.C., Coulombe, R., 2007. Hydraulic redistribution of soil water in two old-growth coniferous forests: quantifying patterns and controls. New Phytol. 173, 753–765.

Warren, J.M., Norby, R.J., Wullschleger, S.D., 2011. Elevated CO_2 enhances leaf senescence during extreme drought in a temperate forest. Tree Physiol. 31, 117–130.

Wear, D.N., Coulston, J.W., 2015. From sink to source: regional variation in US forest carbon futures. Sci. Rep.-UK 5.

Weemstra, M., Eilmann, B., Sass-Klaassen, U.G.W., Sterck, F.J., 2013. Summer droughts limit tree growth across 10 temperate species on a productive forest site. For. Ecol. Manage. 306, 142–149.

Weemstra, M., Mommer, L., Visser, E.J.W., van Ruijven, J., Kuyper, T.W., Mohren, G. M.J., Sterck, F.J., 2016. Towards a multidimensional root trait framework: a tree root review. New Phytol. http://dx.doi.org/10.1111/nph.14003.

Weltzin, J.F., Loik, M.E., Schwinning, S., Williams, D.G., Fay, P.A., Haddad, B.M., Harte, J., Huxman, T.E., Knapp, A.K., Lin, G.H., Pockman, W.T., Shaw, M.R., Small, E.E., Smith, M.D., Smith, S.D., Tissue, D.T., Zak, J.C., 2003. Assessing the response of terrestrial ecosystems to potential changes in precipitation. Bioscience 53, 941–952.

Wilhite, D.A., Glantz, M.H., 1985. Understanding the drought phenomenon: the role of definitions. Water Int. 10, 111–120.

Wuebbles, D.J., Hayhoe, K., 2004. Climate change projections for the United States Midwest. Mitig. Adapt. Strat. Glob. Change 9, 335–363.

Wullschleger, S.D., Hanson, P.J., Todd, D.E., 2001. Transpiration from a multi-species deciduous forest as estimated by xylem sap flow techniques. For. Ecol. Manage. 143, 205–213.

Xiao, J.F., Zhuang, Q.L., Law, B.E., Baldocchi, D.D., Chen, J.Q., Richardson, A.D., Melillo, J.M., Davis, K.J., Hollinger, D.Y., Wharton, S., Oren, R., Noormets, A., Fischer, M.L., Verma, S.B., Cook, D.R., Sun, G., McNulty, S., Wofsy, S.C., Bolstad, P.V., Burns, S.P., Curtis, P.S., Drake, B.G., Falk, M., Foster, D.R., Gu, L.H., Hadley, J.L., Katulk, G.G., Litvak, M., Ma, S.Y., Martinz, T.A., Matamala, R., Meyers, T.P., Monson, R.K., Munger, J.W., Oechel, W.C., Paw, U.K.T., Schmid, H.P., Scott, R.L., Starr, G., Suyker, A.E., Torn, M.S., 2011. Assessing net ecosystem carbon exchange of U.S. terrestrial ecosystems by integrating eddy covariance flux measurements and satellite observations. Agric. For. Meteorol. 151, 60–69.

Yang, J., Kloepper, J.W., Ryu, C.M., 2009. Rhizosphere bacteria help plants tolerate abiotic stress. Trends Plant Sci. 14, 1–4.

Zeppel, M.J.B., Anderegg, W.R.L., Adams, H.D., 2013. Forest mortality due to drought: latest insights, evidence and unresolved questions on physiological pathways and consequences of tree death. New Phytol. 197, 372–374.