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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

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A B S T R A C T

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.

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

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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

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