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Conversion of natural forests to managed forest plantations decreases tree resistance to prolonged droughts ☆

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ABSTRACT

Throughout the southern US, past forest management practices have replaced large areas of native forests with loblolly pine plantations and have resulted in changes in forest response to extreme weather conditions. However, uncertainty remains about the response of planted versus natural species to drought across the geographical range of these forests. Taking advantage of a cluster of unmanaged stands (85–130 year-old hardwoods) and managed plantations (17–20 year-old loblolly pine) in coastal and Piedmont areas of North Carolina, tree water use, cavitation resistance, whole-tree hydraulic (K_{tree}) and stomatal (G_s) conductances were measured in four sites covering representative forests growing in the region. We also used a hydraulic model to predict the resilience of those sites to extreme soil drying. Our objectives were to determine: (1) if K_{tree} and stomatal regulation in response to atmospheric and soil droughts differ between species and sites; (2) how ecosystem type, through tree water use, resistance to cavitation and rooting profiles, affects the water uptake limit that can be reached under drought; and (3) the influence of stand species composition on critical transpiration that sets a functional water uptake limit under drought conditions. The results show that across sites, water stress affected the coordination between K_{tree} and G_s. As soil water content dropped below 20% relative extractable water, K_{tree} declined faster and thus explained the decrease in G_s and in its sensitivity to vapor pressure deficit. Compared to branches, the capability of roots to resist high xylem tension has a great impact on tree-level water use and ultimately had important implications for pine plantations resistance to future summer droughts. Model simulations revealed that the decline in K_{tree} due to xylem cavitation aggravated the effects of soil drying on tree transpiration. The critical transpiration rate (E_{crit}), which corresponds to the maximum rate at which transpiration begins to level off to prevent irreversible hydraulic failure, was higher in managed forest plantations than in their unmanaged counterparts. However, even with this higher E_{crit}, the pine plantations operated very close to their critical leaf water potentials (i.e. to their permissible water potentials without total hydraulic failure), suggesting that intensively managed plantations are more drought-sensitive and can withstand less severe drought than natural forests.

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1. Introduction

In the southern US, the most common land conversion by area was from native mixed hardwood forests to pine plantations. It is estimated that more than 10 million ha of forests were harvested or cleared between 1973 and 2000 (Drummond and Loveland, 2010). Additionally, wetlands cover around 8% percent of the 20 eastern US ecoregions and plantations caused a loss of more than 500,000 ha of wetland since 1980, including a large proportion of forested wetland (Loveland et al., 2002). In the Southern Coastal and the Middle Atlantic Coastal Plains alone, 2.4–5.0% loss of wetlands occurred during the past 25 years (Daniel and Dahlen, 2002; Drummond and Loveland, 2010). While forest conversion to intensively managed plantations is driven by the need for wood- and fiber-based products, forest conversion provides fewer ecosystem services (Franklin and Johnson, 2004; Burger, 2009; Puettmann, 2011). In the southern US the 14 million hectares of loblolly pine (*Pinus taeda*) trees planted accounts for nearly one-half of the world's industrial forest plantation and is known as the "wood basket of the world" (Brown and Sheffield, 2003; Fox et al., 2007; Wear et al., 2013). The future of the plantation-based forest industry in this region will depend, in part, on how these managed systems will adapt to changing climate (Fox et al., 2004; McNulty et al., 2014).

A change in species composition and/or density following conversion of natural lands to plantations will not be sustainable if the planted trees consume more water than the previous vegetation (Swank et al., 1988; Oishi et al., 2008; O'Hara and Ramage, 2013), or if they are less resilient to drought compared to the previous forest type. Increased productivity per land area of planted forests is usually associated with increased evapotranspiration (Samuelson et al., 2008) and effectively yielding less stream outflow (McNulty et al., 1996; Oishi et al., 2010). Although annual precipitation is not necessarily predicted to decrease in the southern US as a consequence of global warming, an increase in the frequency and duration of summer droughts and temperature-driven evaporative demand are expected (IPCC, 2013). There is potential for these climatic changes to decrease plant available soil water and to increase the risk of drought-induced mortality, possibly more so in plantations compared to natural forests. While studies comparing stand water balance or watershed properties between hardwood stands and pine plantations exist (Stoy et al., 2005; Palmroth et al., 2010), species-specific drought responses and contribution on overall ecosystem function are still largely unknown. Furthermore, as forest management is increasingly used as a tool for ecosystem restoration, a mechanistic understanding of natural and managed forest climatic sensitivity is needed. For example, in mixed stands, tree species may interact to complementarily use the different soil profiles (Krämer and Hölscher, 2010; Forrester, 2014). Moreover, water use and tolerance to drought in natural stands are non-uniform due to specific responses of each co-existing tree to variation in climatic variables (Granier et al., 2000; Pataki and Oren, 2003). More diverse communities thus have potential to better resist future drought (Yachi and Loreau, 1999; Jactel et al., 2009). Hence, productivity and resilience of future pine plantations may be hard to predict due to changing climate if gaps in current physiological understanding are not improved (Gessler et al., 2004; Samuelson et al., 2008). The conversion of unmanaged to intensively managed forest lands in eastern North Carolina was historically widespread, and yet the consequences on plant functioning and in turn on plant resilience to extreme drought have not been well determined.

Water flow in the soil–plant-atmosphere continuum is determined by the whole-tree hydraulic conductance (K_{tree}) of soil and plant tissues that characterize the structural capacity of the whole plant to move water (Wullschleger et al., 1998). Trees undergo dynamic structural and physiological adjustments to preserve the integrity of their hydraulic system, and to maximize carbon uptake during summer droughts (Bréda et al., 2006). For example, short term acclimation to drought is achieved by stomatal closure to limit water loss and the drop in leaf water potential (Loustau and Granier, 1993; Sperry et al., 2002). Long-term, plastic responses to drought include biomass allocation strategies such as changing the ratio of root area to transpiring leaf area and by exploring deeper soil horizons and the production of a more resistant xylem to drought-induced cavitation (Sperry et al., 2002). Measures of xylem resistance to cavitation are particularly good estimators of a species tolerance to drought in vascular plants (Maherali et al., 2004). However, values of P_{50} (the water potential at which 50% of hydraulic conductivity is lost) vary enormously across species. Regardless of climate or soil type, many plants have a small safety margin when the observed xylem tensions are compared with tensions needed to induce loss of hydraulic capacity (Sperry et al., 2002; Choat et al., 2012). In this sense, it is necessary to characterize in detail the ecophysiology of intensively managed plantations relative to more natural hardwood forests, particularly regarding water relations, in order to help define the most adequate management criteria for the future.

At the interface between atmosphere and soils, the rooting zone plays a major role in regulating forest water fluxes (Domec et al., 2012a; Manoli et al., 2014). Root profiles are strongly influenced by soil properties and species composition. Complex natural systems with a fully developed understory may have the capacity to explore a greater soil volume than single species, which could potentially increase drought tolerance. These traits may be crucial when forests are exposed to increased summer drought, favoring communities that are better adapted to tolerate water shortage and possibly inducing alterations in tree species composition and rooting profile (Warren et al., 2015). The study of how water stress interacts with local environmental conditions to affect managed conifer productivity compared to natural forests is essential to understanding the impact of climate change on ecosystem services provisioning of both forest types (Anchukaitis et al., 2006).

We studied water use of natural forests and plantations in Southeast US to better understand how tree responses to soil drying are altered following the conversion of mixed hardwood forest to managed pine. During prolonged wet and dry periods, nearly continuous tree sapflow measurements as well as plant and soil moisture were monitored in two mid-rotation loblolly pine plantations and two natural stands. These data along with direct estimates of tree resistance to drought-induced cavitation were used to examine the temporal variability of soil water content and canopy conductance. The field data were also used to parameterize a hydraulic model to compare tree transpiration rates and the resilience of natural versus plantation stands to extreme soil drying. Specifically, our objectives were to determine (1) the relationship between K_{tree} and stomatal regulations and if it differs among species and sites; (2) if stand type, through differential resistance to cavitation, water use and rooting profiles affects whole stand resilience to summer droughts; (3) if the influence of stand species composition on critical transpiration sets a functional water uptake limit under drought conditions (Kolb and Sperry, 1999).

2. Setting and material

2.1. Coastal sites

The forested wetland study site is located at the Alligator River National Wildlife Refuge (ARNWR), on the Albemarle–Pamlico