



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



Jean-Christophe Domec ^{a,b,*}, John S. King ^b, Eric Ward ^b, A. Christopher Oishi ^c, Sari Palmroth ^d, Andrew Radecki ^b, Dave M. Bell ^e, Guofang Miao ^b, Michael Gavazzi ^f, Daniel M. Johnson ^g, Steve G. McNulty ^f, Ge Sun ^f, Asko Noormets ^b

^a Bordeaux Sciences AGRO, UMR 1391 ISPA INRA, 1 Cours du général de Gaulle 33175, Gradignan Cedex, France

^b Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27606, USA

^c Southern Research Station USDA Forest Service, Coweeta, NC 28763, USA

^d Nicholas School of the Environment and Earth Sciences, Duke University, Durham, NC 27708, USA

^e Pacific Northwest Research Station, USDA Forest Service, Corvallis, OR 97331, USA

^f Eastern Forest Environmental Threat Assessment Center, USDA Forest Service, Raleigh, NC 27606, USA

^g Department of Forest, Rangeland and Fire Sciences, University of Idaho, Moscow, ID 83844, USA

ARTICLE INFO

Article history:

Received 14 February 2015

Received in revised form 13 April 2015

Accepted 15 April 2015

Available online 27 April 2015

Keywords:

Cavitation

Drought

Natural stands

Pine

Roots

Transpiration

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.

© 2015 Published by Elsevier B.V.

[☆] This article is part of a special issue entitled "Carbon, water and nutrient cycling in managed forests".

* Corresponding author at: Bordeaux Sciences AGRO, UMR 1391 ISPA INRA, 1 Cours du général de Gaulle 33175, Gradignan Cedex, France.

E-mail addresses: jdomec@ncsu.edu, jc.domec@agro-bordeaux.fr (J.-C. Domec).

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

Table 1

Selected stand characteristics for the coastal and Piedmont sites, which are all located in North Carolina as well as key parameter values for the hydraulic model (Sperry et al., 1998). Precipitation represents the mean annual precipitation between 1945 and 2010. Saturated soil hydraulic conductance (K_{soil}), the soil texture coefficient (c , Eq. (3)), θ_s and θ_w are given for the first 50 cm of soil. Saturated whole tree hydraulic conductance (K_{tree}) corresponds to the tree hydraulic capacity at full saturation i.e. in the absence of xylem cavitation. Root and branch P_{50} indicates the water potential at which 50% of the root or branch conductance is lost due to cavitation. Reference stomatal conductance (G_{s-ref}) represents the stomatal conductance at a vapor pressure deficit (VPD) of 1 kPa (Oren et al., 1999), analyzed based on $G_s = G_{s-ref} - m \times \ln VPD$, where m is the sensitivity of G_s to VPD. Root to leaf area index (RAI/LAI) represents the ratio of all-sided fine root area to effective leaf area index. Note that although LAI represents projected leaf area index, RAI/LAI, K_{tree} and G_{s-ref} are expressed on an all sided-leaf-area for the plantations reflecting the fact that loblolly pine needles have stomata on all surfaces.

	Coastal		Piedmont	
	Natural	Plantation	Natural	Plantation
Precipitations (mm yr ⁻¹)	1380	1290	1145	1145
Tree density (tree ha ⁻¹)	3949	645	850	1013
Stand age (years)	90–145	18	85–105	26
Tree height (m)	29–36	17–19	25–35	19–21
Leaf area index (projected)	0.9–4.0	3.0–4.4	0.3–6.0	2.0–3.5
RAI/LAI	3.8	1.6	2.7	1.3
Clay (%)	7–9	4–5.5	13–16	12.5–13.4
Sand (%)	46–53	59–68	44–49	52–57
Soil bulk density (g cm ⁻³)	0.5–0.7	0.91–0.99	1.14–1.19	1.17–1.24
Saturated K_{soil} (mol s ⁻¹ m ⁻¹ MPa ⁻¹)	751–856	396–436	33–42	16–24
c	4.0	3.7	3.8	4.5
Saturated soil water content (θ_s , m ³ m ⁻³)	0.59	0.52	0.55	0.53
Permanent wilting point (θ_w , m ³ m ⁻³)	0.07	0.08	0.10	0.13
Saturated K_{tree} (mmol s ⁻¹ m ⁻² MPa ⁻¹)	0.31–0.84	0.87	0.36–1.36	0.75
Root P_{50} (–MPa)	0.2–0.75	0.85	0.5–1.0	1.1
Branch P_{50} (–MPa)	1.9–3.7	4.1	2.5–4.8	4.5
G_{s-ref} (mmol m ⁻² s ⁻¹)	30–85	63	22–115	54
G_s sensitivity to VPD (mmol m ⁻² s ⁻¹ ln kPa ⁻¹)	10–62	35	15–80	36

Peninsula of North Carolina, USA (35°47'N, 75°54'W). This research site was established in November 2008, and includes a 35-m instrumented tower for eddy covariance flux measurements, a micrometeorological station, and 13 vegetation plots spread over a 4 km² area (Miao et al., 2013). The mean annual temperature and precipitation from climate records of an adjacent meteorological station (Manteo AP, 35°55'N, 75°42'W) for the period 1981–2010, are 16.9 °C and 1270 mm, respectively (Table 1). The forest type is mixed hardwood swamp forest; the overstory is predominantly composed of black gum (*Nyssa sylvatica*) that represents 39% of the basal area and an even mix of red maple (*Acer rubrum*), bald cypress (*Taxodium distichum*) and loblolly pine. We occasionally found swamp tupelo (*Nyssa biflora*) and white cedar (*Chamaecyparis thyoides*) that represents less than 18% of the total tree basal area (Radecki, 2014). The understorey is predominantly fetterbush (*Lyonia lucida*), bitter gallberry (*Ilex glabra*), and red bay (*Persea borbonia*). The canopy of this site is fairly uniform with heights ranging from 16 m to 21 m, and with leaf area index peaking at 4.0 ± 0.3 in early July from a minimum of 1.3 ± 0.3 during the non-growing season (from early November to late March). The major soil series are poorly drained Pungo and Belhaven mucks. Dry soil bulk density was estimated at 0.07–0.10 g cm⁻³ when soil samples were taken during unflooded conditions (Table 1).

The Coastal Plain plantation site (35°11'N, 76°11'W) is located within the lower coastal plain mixed forest province of North Carolina (Noormets et al., 2010, 2012; Sun et al., 2010). This 100-ha mid-rotation loblolly pine stand (US-NC2 in the Ameriflux database) was established in 1992 with 2-year-old half

sibling seedlings after clear-cutting the previous mature pine plantation. The pine plantation watersheds are drained with a network of parallel ditches (90–130 cm deep; 90 m spacing) and more widely spaced roadside canals. Drainage lowers the height of the water table, improves site access and tree productivity by reducing stresses caused by excessive soil water conditions, especially during winter months. The long-term (1945–2010) average annual precipitation was 1290 ± 199 mm, and was evenly distributed throughout the year (Table 1). Long term mean annual temperature averaged 15.5 °C, with a monthly high temperature occurring in July (26.6 °C), and a monthly low occurring in January (6.4 °C). The histic-mineral soil at this site is classified as Belhaven series. The understorey was primarily composed of young red maple (*A. rubrum*) and other non-woody plants such as devil's walking stick (*Aralia spinosa*), pokeweed (*Phytolacca americana*), beautyberry (*Callicarpa americana*), giant cane (*Arundinaria macrosperma*) and meadow grass (*Poa* spp.) (Domec et al., 2010a).

2.2. Piedmont sites

The Piedmont natural study site (35°97'N, 79°08'W) is the Duke Hardwood Ameriflux site (US-Dk2 in the Ameriflux database) located in the Blackwood Division of Duke Forest, NC. This natural forest stand is comprised of mixed hardwood species with a maximum age near 110 years (Pataki and Oren, 2003; Palmroth et al., 2005; Oishi et al., 2008). Mean canopy height is 27 m with emergent crown tops extending above 38 m. This 25-ha stand is dominated by hickories (*Carya tomentosa* and *Carya glabra*), yellow poplar (*Liriodendron tulipifera*), sweetgum (*Liquidambar styraciflua*), and oaks (*Quercus alba*, *Q. michauxii* and *Q. phellos*). Species in the mid- and under-story extend to 12 and 7 m, respectively, and include *Carpinus caroliniana*, *Ulmus alata*, *A. rubrum*, *Cercis canadensis* and *Cornus florida*, while coniferous species (including *P. taeda* and *Juniperus virginiana*) make up a minor component of the over- and understorey, respectively. Long-term (1945–2010) mean annual precipitation for the area is 1149 ± 166 mm, with 630 ± 133 mm falling between April and September (www.ncdd.noaa.gov). Annual mean temperatures range from 21.9 °C to 9.1 °C during the growing and non-growing seasons, respectively. The soil is a gravelly loam of the Iredell series and the topography is relatively flat with <4% slope. Although bedrock can be as shallow as 2 m (D. Richter, personal communication), a clay pan with low hydraulic conductivity limits the majority of the rooting zone to ~45–65 cm (Stoy et al., 2005).

The adjacent Piedmont loblolly pine plantation site was part of the Duke FACE Project (<http://face.env.duke.edu>). The experimental site was clear-cut in 1982 to remove a 50-year-old mixed pine forest, and replanted in 1983. This 32-ha experimental forest of loblolly pine was derived from 3-year-old, half-sibling seedlings planted in 2.4 m × 2.4 m spacing. The mean annual temperature is 15.8 ± 0.7 °C and the growing season mean temperature is 22.1 ± 0.12 °C. The long-term (1945–2010) average annual precipitation was 1145 ± 112 mm, and was evenly distributed throughout the year (Table 1). Moderate and severe droughts are not infrequent in those Piedmont sites, with at least three in the past ten years. However, even during relatively wet growing seasons, warm temperatures, high atmospheric demand for water, and intermittent precipitation can lower extractable soil water into a range that limits transpiration for approximately 14 days (Oishi et al., 2010).

2.3. Root sampling

Root biomass profiles at both plantations were taken from Pritchard et al. (2008), Jackson et al. (2009) for the Piedmont site and from Domec et al. (2010a) for the coastal site. Published data

for the Piedmont plantation site were only collected for the top 40 cm of the soil profile, and at that site no information on maximum rooting depth was available. A linear regression applied to the data of Pritchard et al. (2008) was used to predict that the depth at which root biomass decreased to zero was approximately 62 cm. This estimated maximum rooting depth was in agreement with previous assessment of root biomass at the same site when the trees were seven years younger (Matamala and Schlesinger, 2000). In addition, visual assessment of root biomass was done in October 2010 by digging two 1.0-m-deep, 0.5 × 1.5 m soil pits with a mechanical back-hoe. These pits revealed that although the tap roots stopped at 80 cm, very few fine roots were present between 60 cm and that depth. At the coastal wetland site, roots were sampled on four dates in June 2009 using a circular soil corer with a 10-cm inside diameter to extract one 40-cm-deep core from four random locations. Although this method to estimate root biomass differ from the one used at the other stands, in well mixed soils with no rocks and shallow root layers like those from this wetland site, soil cores have been shown to estimate accurately soil properties and biomass (Ellert et al., 2008; Harrison et al., 2003). To further improve the representativeness of the roots sampled, we collected soil cores on tree mounds and between the trees because it is important to comprehensively sample microtopography when coring wetland soils (Iversen et al., 2011). The intact humus and soil cores were divided into four layers by depth: 0–10 cm (humus layer), 10–20 cm, 20–30 cm, 30–40 cm. A previous visual assessment revealed that there was no visible roots below 45 cm. Soil samples were transported from the stand to the laboratory and stored at –15 °C until analysis. After thawing, the whole sample was sieved under water through mesh with 1 mm size. Fine roots with diameter less than 2 mm were manually picked out and separated into dead and live fine roots according to the color of the cortex (Hertel and Leuschner, 2006). Finally, roots were dried at 60 °C for 48 h and weighted. The fine root biomass was expressed as the oven dry weight per soil volume (g dm^{-3}). At the Piedmont mixed hardwood site, to determine change in root distribution and biomass we excavated four 1 × 1.5 × 1.4-m-deep, pits in August–September 2012 and sampled roots every 10 cm to a depth of 1.0 m and then every 20 cm to a depth of 1.6 m. We sorted roots by diameter into three classes (<1, 1–2, >2 mm) and determined the total dry mass of each size class. At both natural stands, root area was calculated from the total dry mass and from a linear relationship ($R^2 = 0.78$, $P < 0.01$) between dry mass and root area (specific root area) calculated from 80 randomly selected roots.

2.4. Canopy conductance and its response to vapor pressure deficit

Canopy conductance derived from sapflow measurements comprises the total water vapor transfer conductance from the 'average' stomata of the tree canopy to the measurement height of vapor pressure deficit (VPD), which includes both surface boundary-layer and stomatal components. At the four sites, sapflow was measured at breast height using 20 mm length, thermal dissipation probes. The sensor signal was converted to sap flux density (J_s , $\text{g m}^{-2} \text{s}^{-1}$) according to Granier (1987) assuming that natural temperature gradients between sensors are small and accounted for the effects of non-zero night-time fluxes on the signal baseline (Oishi et al., 2008). Probes were installed at 20 mm depth intervals to the maximum depth of active sapwood (up to 60 mm in some species) to account for radial variability in flow rates. While sensors were not replaced systematically on a regular interval, sensor breakages led to frequent replacements and the average sensor longevity was about 12 months.

At both managed stands, sapflow measurements were made on a minimum of seven pine trees (Domec et al., 2009a; Oishi et al.,

2008). At the forested wetland, 24 trees representing four different species (*N. sylvatica*, *T. distichum*, *A. rubra* and *P. taeda*) were measured. Those species accounted for more than 78% of the total basal area (Radecki, 2014). At the Piedmont site five trees each of *C. tomentosa*, *Q. alba*, *Q. michauxii*, *Q. phellos*, *L. tulipifera* and *L. styraciflua* were measured for a total of 42 sensors deployed in the thirty sample trees. All *Carya* species were assumed to behave like *C. tomentosa*. Those six species represented 82% of the stand basal area (Oishi et al., 2010). Thirty-minute averages of temperature difference data were computed and stored in data loggers (Campbell Scientific Inc., Logan, UT, USA). Using tree sapwood area, stand LAI and stand tree density (Table 1), J_s was scaled and converted to a tree-scale average transpiration per unit leaf area (E , in $\text{mmol m}^{-2} \text{s}^{-1}$). At the Piedmont natural site, stand characteristics, including LAI and sapwood area per unit ground area were taken in a 6.25 ha area surrounding the eddy covariance tower (Oishi et al., 2010). At the Piedmont loblolly pine plantation LAI and sapwood area were determined from four 30-m diameter plots (control plots of the Duke FACE Project). At both Coastal sites, LAI and sapwood area were determined from 13 vegetation survey plots (14 m in diameter) centered on the eddy covariance towers. The total sapwood area of the trees equipped with sapflow probes was estimated from the relationship between sapwood area (from increment cores) and diameter at breast height. Sapwood depth was determined by visual inspection of the core and converted to sapwood area based on the area of a circle, subtracting the areas represented by the heartwood and bark. Methods for generating half-hourly estimates of E at the Piedmont sites are described in Oishi et al. (2008, 2010), and at the Coastal wetland and plantation sites in Radecki (2014) and Domec et al. (2010a), respectively.

Canopy stomatal conductance (G_s) was calculated from E and VPD, using the simplification of the inversion of Penman–Monteith model (Ewers et al., 2000):

$$G_s = (RT_a \rho E) / \text{VPD} \quad (1)$$

where R is the universal gas constant adjusted for water vapor ($0.46 \text{ m}^3 \text{ kPa K}^{-1} \text{ kg}^{-1}$), T_a is air temperature in degrees K and ρ is density of water (998 kg m^{-3}). This simplified calculation was sufficient because in all treatments VPD was close to the leaf-to-air vapor pressure deficit due to high boundary-layer conductance (Oishi et al., 2008; Ward et al., 2013; Domec et al., 2009a).

Oren et al. (1999) showed that under saturated light, the decrease in G_s with increasing VPD is proportional to G_s at low VPD. Therefore, the sensitivity of the stomatal response to VPD when the photosynthetically active radiation was above $800 \text{ mmol m}^{-2} \text{ s}^{-1}$ (light-saturated G_s) was determined by fitting the data to the functional form:

$$G_s = b - m \times \ln(\text{VPD}) \quad (2)$$

where b is G_s at VPD = 1 kPa (hereafter designated as reference canopy stomatal conductance, $G_{s\text{-ref}}$), and m is the rate of stomatal closure and reflects the sensitivity of G_s to D ($-dG_s/d\ln \text{VPD}$, in $\text{mmol m}^{-2} \text{ s}^{-1} \ln(\text{kPa})^{-1}$). The slope, $-dG_s/d\ln \text{VPD}$ is proportional to $G_{s\text{-ref}}$ with the proportionality averaging 0.60 across a wide range of species, and varying predictably depending on the range of VPD used in the analysis (Oren et al., 1999; Ward et al., 2013). The stomatal sensitivity to VPD does not vary whether g_s (leaf-based) or G_s (canopy-based) is used (Kim et al., 2008; Domec et al., 2009a).

2.5. Hydraulic parameters

To analyze the effect of the whole tree hydraulic conductance (K_{tree}) on stomatal conductance, K_{tree} was calculated from the slope of the relationship between diurnal variation in leaf water potential and tree transpiration (Loustau and Granier, 1993). Changes in leaf water potentials (Ψ_l) from dawn to mid-afternoon were

quantified with a pressure chamber (PMS, Albany, OR, USA) on six to eight leaves collected from each tree equipped with sapflow sensors.

Cavitation vulnerability curves were determined using the air injection technique (Cochard et al., 1992) on six roots (2.5–4.0 mm in diameter) and five to six branches (8–12 mm in diameter) collected in February–March 2010 at the Piedmont natural forest site and in February–March 2013 at coastal natural forest site. Cavitation parameters for *Q. alba* (white oak) and *Quercus velutina* (black oak) were taken from Maherali et al. (2004). At both managed forest plantations, plant vulnerability curves were taken from Domec et al. (2010a, 2012b).

2.6. Model application to estimate water use under extreme drought

We used the hydraulic transport model developed by Sperry et al. (1998) to estimate values of maximum tree transpiration (E) that would have occurred under soil drying. This model has previously been parameterized and performed well for estimating water use for the coastal (Domec et al., 2010a) and the Piedmont plantations (Hacke et al., 2000). The model also calculates the upper boundary for steady-state water transport as a function of soil water potential (Ψ_s) that represents the plant's 'water use envelope' (termed critical transpiration). Once E exceeds the critical transpiration, water uptake terminates due to irreversible hydraulic dysfunction caused by embolism in the soil-leaf hydraulic pathway (Sperry et al., 2002). From the hydraulic properties of soil and xylem, the model solves the relationship between steady state E and the driving force in the soil plant continuum ($E = K_{\text{tree}}(\Psi_s - \Psi_l)$), where $\Psi_s - \Psi_l$ represents the water potential difference between soil and leaf. The drop in water potential in the continuum is used to calculate the reduction in K_{tree} from the rhizosphere drying, root and stem cavitation, and to determine E . The root components were assumed to comprise 50% of K_{tree} and shoots and leaves were assumed to represent the other 50% (Sperry et al., 1998; Domec et al., 2009a). We used the same fitting parameters for axial and lateral components within the root and shoot systems. We parameterized the model to simulate K_{tree} and transpiration rates using Ψ_s predicted during drought. The water-potential-dependent decrease in rhizosphere conductance was calculated from soil conductivity (K_s), soil texture and Ψ_s assuming a cylindrical rhizosphere sheath of 5-mm thickness from bulk soil to root surface (for details, see Sperry et al., 1998). The initial saturated K_{tree} and K_s values as well as the main input parameters of the model are presented in Table 1. For the coastal natural site, soil parameters were taken from Caldwell (2005) and Caldwell et al. (2007). For the coastal plantation soil data were taken from Domec et al. (2010a). For the Piedmont sites, data were taken from Oren et al. (1998), Hacke et al. (2000) and Thompson et al. (2010). Rhizosphere conductance was converted to a ground area basis using the measured all-sided fine root area index (RAI). Soil water potential was calculated from Campbell (1985) as:

$$\Psi_s = \Psi_e(\theta/\theta_s)^{-c} \quad (3)$$

where Ψ_e is the soil water potential at air entry, θ_s is the saturated volumetric water content and the exponent c is related to soil texture (Table 1). We started our simulation with a soil at θ_s and each day θ was reduced in response to tree water use. Simulation stopped when soil water content reached the permanent minimum wilting point (θ_w). Physiological input parameters for the natural forests were calculated as the mean value of each tree species weighted according to their proportion of the stand leaf area as determined by Oishi et al. (2008) and Radecki (2014) for the piedmont and coastal site, respectively. To compare across sites and to erase the influence of soil texture on θ , drought intensity is best

quantified in the form of relative extractable soil water (REW dimensionless), and therefore θ was converted to REW as defined by Granier et al. (2000):

$$\text{REW} = \frac{\theta - \theta_w}{\theta_s - \theta_w} \quad (4)$$

2.7. Statistical analyses

Variance estimates of E and G_s were computed according to Oren et al. (1998) to include the variances of J_s and LAI and their mutual dependency. Similarly, variance estimates of K_{tree} were also computed using the variance estimate of E , and mean variance of Ψ_l . Variations in θ , E and $G_{s\text{-ref}}$ over the measurements period were analyzed by repeated measures ANOVA. To assess the difference in $G_{s\text{-ref}}$ at each date within each site or between sites from the same region, we used a two-way ANOVA with one repeated measure factor. For between-species comparisons of $G_{s\text{-ref}}$, $-dG_s/d\ln\text{VPD}$, K_{tree} and hydraulic parameters from the vulnerability curves, ANOVAs with post hoc Holm-Sidak comparisons were performed. Additionally, linear regressions were performed to test for significant relationships between G_s and $\ln\text{VPD}$. An ANCOVA was performed to test for equal slopes for these relationships. The water-potential-dependent decrease in xylem hydraulic conductance was calculated from a Weibull function fit to the root or branch vulnerability curve data. Statistical analyses were performed using SAS (Version 9.3, Cary, NC, USA) and curve fits were performed using Sigmaplot (version 12.3, SPSS Inc. San Rafael, CA, USA).

3. Results

3.1. Canopy conductance and its response to VPD

The two study periods with soil moisture and sapflow data included wet growing seasons (e.g., 2003–2004 and 2009–2010 for the Piedmont and coastal sites, respectively) as well as dry growing seasons (e.g., 2002 and 2008). The Piedmont sites experienced an extreme drought during the 2002 growing season, with a mean annual precipitation of only 945 mm, which was 71% of the 30-year mean for the area (Fig. 1). Consequently, at these sites, soil water content of the top soil (0–45 cm) reached $0.12 \text{ m}^3 \text{ m}^{-3}$ for several months and mean daily VPD ranged from 0.6 to 0.8 kPa. At the coastal sites, 2008 was also a very dry year with 890 mm of rainfall representing 65% of the 30-year mean. Seasonal fluctuations in transpiration per unit leaf area (E) and reference canopy-averaged stomatal conductance (at $\text{VPD} = 1 \text{ kPa}$, $G_{s\text{-ref}}$) were different in years with wet versus dry growing seasons. The general trend for both *P. taeda* plantations was a sharp decrease in E and $G_{s\text{-ref}}$ during drought ($P < 0.016$). At both sites, $G_{s\text{-ref}}$ was higher when soil water content was not limiting and decreased by more than 35% (from 51 to 32 $\text{mmol m}^{-2} \text{ s}^{-1}$ at the Piedmont site and from 62 to 40 $\text{mmol m}^{-2} \text{ s}^{-1}$ at the coastal site) when minimum soil water content was reached (Fig. 1). For the unmanaged stands, primarily composed of deciduous species, little transpiration occurred in the first quarter of each year, so we omitted the $G_{s\text{-ref}}$ values from further analyses. At the Piedmont natural stand, $G_{s\text{-ref}}$ did not decline by more than 20% during the dry periods. However, at the coastal site, changes in water table strongly affected $G_{s\text{-ref}}$ with declines ranging from 45% for *N. sylvatica* to only 14% for *P. taeda*.

The sensitivity of G_s to VPD ($-dG_s/d\ln\text{VPD}$) was linearly related to $G_{s\text{-ref}}$ ($P < 0.001$; Fig. 2). Stomatal conductance declined in response to increasing VPD, and the magnitude of the reduction varied over the measurement period as shown by the decline in

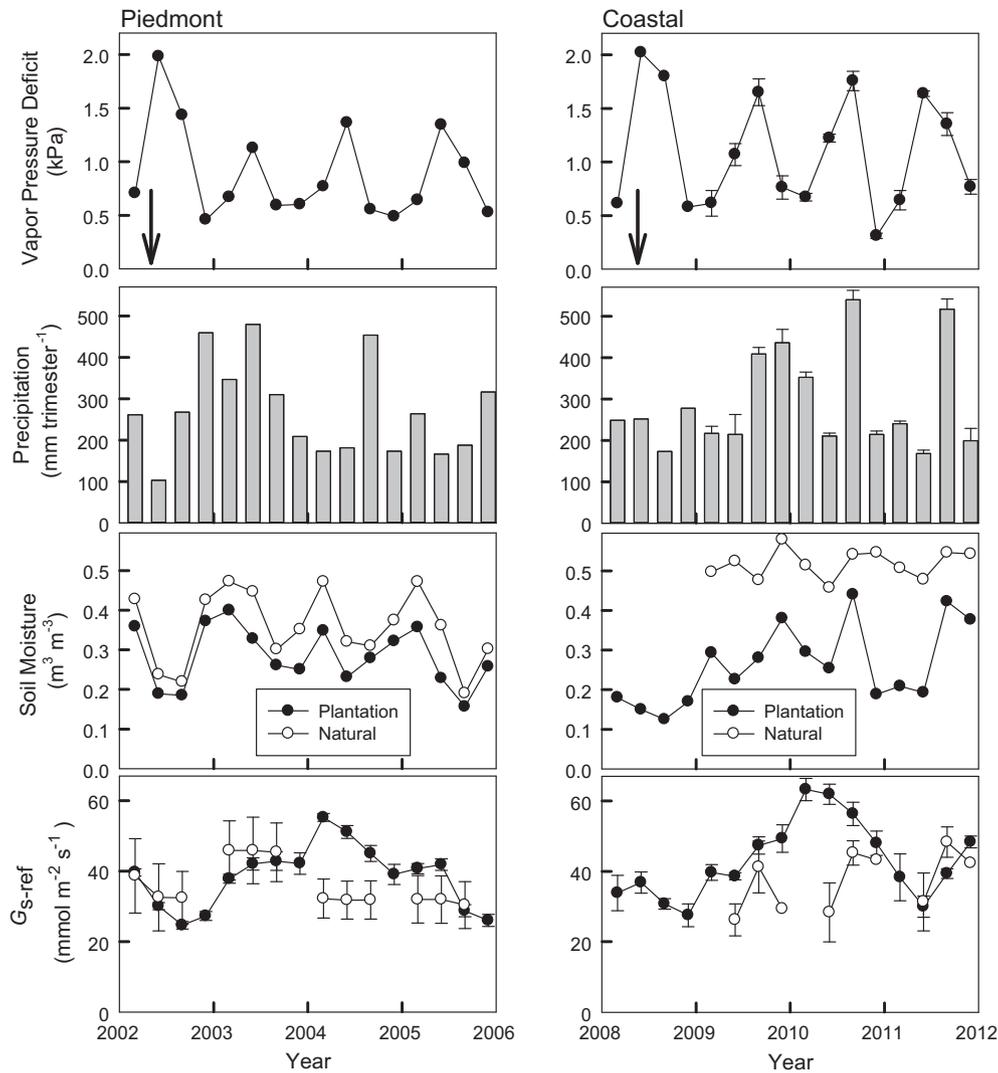


Fig. 1. Piedmont and coastal forests seasonal patterns (3-month average except for precipitation that represents a 3-month sum) in daylength-normalized vapor pressure deficit (i.e. mean daily vapor pressure deficit times the proportion of hours when photosynthetically active radiation >0), precipitation, soil moisture content of the upper soil profile (0–45 cm) and reference canopy stomatal conductance (G_{s-ref}). Down arrows in top panels represent the onset of the 2002 and 2008 droughts, respectively. Error bars for vapor pressure deficit and precipitation represent the standard errors associated with the mean values between stands.

G_{s-ref} . The slope of the relationship between G_s and the sensitivity of the G_s to VPD (-0.57 ± 0.08) was not significantly different ($P=0.29$) than the previously reported generic value of -0.60 based on a hydraulic model that assumes tight stomatal regulation of leaf water potential (Oren et al., 1999). Across species, G_{s-ref} and the sensitivity of G_s to VPD were very responsive to K_{tree} , and showed a general pattern between sites and management practices (i.e., natural versus plantation). The G_{s-ref} of all species at all locations and both measurement periods increased proportionally with K_{tree} (Fig. 2). There was no difference in the relationship between G_{s-ref} and K_{tree} for trees growing in the natural stands ($P=0.56$) and in the plantations. Overall, as K_{tree} increased by 50% from minimum, G_{s-ref} increased by 42% to 47% (Fig. 2). Species differences were apparent in K_{tree} , with higher values in *N. sylvatica* at the coastal site and in *L. tulipifera* and *Carya tomentosa* at the Piedmont site.

Based on P_{50} values (the water potential at which 50% of hydraulic conductance is lost), branches from almost all species growing in the natural stands were more vulnerable ($P=0.03$) to cavitation than the branches from the pine plantations at both locations (Fig. 3). This was opposite for roots, where roots from

the plantations were more vulnerable ($P < 0.01$) than roots from natural stands. For branches, values of P_{50} at the coastal site ranged from -1.4 MPa in *N. sylvatica* to -3.0 MPa in *P. taeda*. Conversely, root P_{50} ranged from -0.70 MPa for *P. taeda* to -1.30 MPa in *N. sylvatica*. At the Piedmont sites, P_{50} of branches varied from -1.5 MPa in *Q. velutina* to -3.8 MPa in *P. taeda* and *L. tulipifera*. For roots, *L. styraciflua* and *P. taeda* have the least negative P_{50} values of around -0.95 MPa and *L. tulipifera* the most negative at -2.1 MPa.

3.2. Root biomass and root to leaf area index

Root biomass decreased exponentially in the plantations at both coastal and Piedmont locations (Fig. 4). At the coastal natural forest, we observed a dense network of shallow lateral roots growing at 10–40 cm depth connected to sinker roots. At the Piedmont natural hardwood forest, a dimorphic root profile was evident represented by a shallow and a deep system of lateral roots. Total fine root biomass at the managed Piedmont and coastal sites was 25–30% lower than at the natural forests. Root to leaf area index was lower at both pine plantations with on average 1.45 m² of root area for each square meter of transpiring leaf surface (Table 1). Trees in

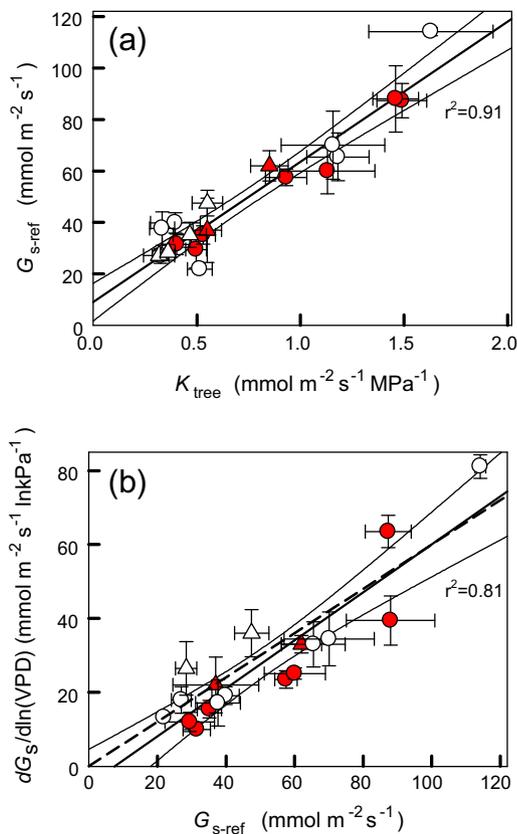


Fig. 2. (a) Linear relationship between G_s at VPD = 1 kPa (G_{s-ref}) and b) tree hydraulic conductance (K_{tree}) and between the sensitivity of canopy conductance to vapor pressure deficit ($-dG_s/d\ln \text{VPD}$) and G_{s-ref} . Circles represent natural forests and triangles loblolly pine plantations. Red and white symbols represent coastal and Piedmont regions, respectively. In (b), the dashed line (slope = 0.6) indicates the theoretical slope between stomatal conductance at VPD = 1 kPa and stomatal sensitivity to VPD that is consistent with the role of stomata in regulating minimum leaf water potential (Oren et al., 1999). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the natural sites required more than twice as much root area per unit leaf area compared to the plantation sites. For each stand type, root to leaf area index was $\sim 30\%$ higher at the coastal location than the Piedmont one.

3.3. Effects of soil drying on tree transpiration and tree resistance to soil drying

The hydraulic model yielded reasonable estimates of canopy-scale transpiration (Fig. A1). Reflecting substantial embolism of roots under drought, K_{tree} decreased with decreasing soil water potential (Fig. 5). The largest modeled change of K_{tree} occurred in *L. styraciflua* and in *T. distichum* at the Piedmont and coastal sites, respectively (data not shown). The decrease in daily E was mainly explained by the change in K_{tree} , which followed a non-linear response. However, in both natural forests, K_{tree} remained at its maximum value for soil water potentials above -0.3 MPa, corresponding to a REW ranging from 1 to less than 0.2 (filled arrows in Figs. 5 and 6). The decline in K_{tree} was greater in both pine plantations with trees experiencing more than 50% loss of tree conductance over the range of field water potentials (dashed arrows in Fig. 5). Natural forests did not start losing K_{tree} before 0.2 REW (Fig. 6). As a consequence, averaged over all species, transpiration of trees growing in both natural forests declined by 40–50% at soil REW = 0.05 and by 60–75% in both pine plantations (Figs. 5 and 6). There was a sharp linear decrease in

transpiration and whole-tree hydraulic conductance below 0.25 REW for both plantations and below 0.15 REW for the natural forests (Figs. 6 and A2). Consequently, at the onset of drought (REW = 0.2), transpiration was predicted to decrease by less than 10% in both natural stands and by more than 20% in both plantations (Fig. 6).

Our modelling outputs suggested that at the coastal sites, maximum E could be maintained for 60–80 days without any rain events (Fig. 7), and that it would take about 100–105 days to deplete the soil water storage enough to reach 0.2 REW, and to start having a significant negative impacts on E (up arrows in Fig. 7). In the Piedmont region, there was a large difference between stand types on the impact of continuous soil drying on the number of days required to see a significant drop in E . For the plantation, it would take only 50 days to the start of a decline in E and 90 days to deplete the soil enough to reach 0.2 REW, inducing a significant (more than 20%) reduction effect in E (Fig. 7). The unmanaged stand, on the other hand, is expected to hold its maximum E for more than 100 days, and no significant decrease in E would be noticeable before 150 days, or when REW would reach 0.2.

The critical transpiration rate (E_{crit}), which corresponds to the maximum rate at which transpiration begins to level off or even decline to prevent irreversible hydraulic failure, was higher in pine plantations than their unmanaged counterparts (Fig. 8). However, even with this higher E_{crit} , the pine plantations operated with a smaller safety margin between soil water potential and critical transpiration rates, suggesting that pine plantations can withstand less severe drought than natural stands. There were large differences between E/E_{crit} ratios in natural and plantation forests at the onset of drought (0.2 REW) at both locations, with ratios of 0.65–0.7 for the natural stands and ratios of 0.80–0.85 for the pine plantations, respectively. This smaller difference between E and E_{crit} in plantations indicated that *P. taeda* functioned very close to their critical leaf water potentials corresponding to their permissible water potentials without total hydraulic failure.

4. Discussion

4.1. Plant resistance to soil drying

As ecosystem management in some regions is attempting to restore specific forest services, the need for an understanding of how previous species shifts may have changed tree response to future climate is vital. Although we have to be careful with generalizing the findings from the two regions studied, which represent only one natural site in the coastal and Piedmont regions, we demonstrated that the influence of stand species composition on critical transpiration sets a functional water uptake limit that can be reached under drought conditions. Our results showed that plantations operated with a small safety margin from total hydraulic failure, suggesting that pine plantations are more drought-sensitive and can withstand less severe drought than natural forests.

The latest climate change scenario projections for US southeast predict that by 2100, total rainfall is expected to increase by up to 15% of current annual precipitation (IPCC, 2013). However, and more importantly, it is also projected that summer precipitation will be slightly reduced (5–10%) and above all, the maximum number of consecutive dry summer days is predicted to increase because of an increase in the frequency of heavy spring precipitation (IPCC, 2013). Such patterns are already evident during the last 15 years, where the very dry periods (e.g., 2002–2003 and 2007–2008) did not correspond to the lowest total rainfalls, but mid-summer and early fall drought was prolonged (Karl et al.,

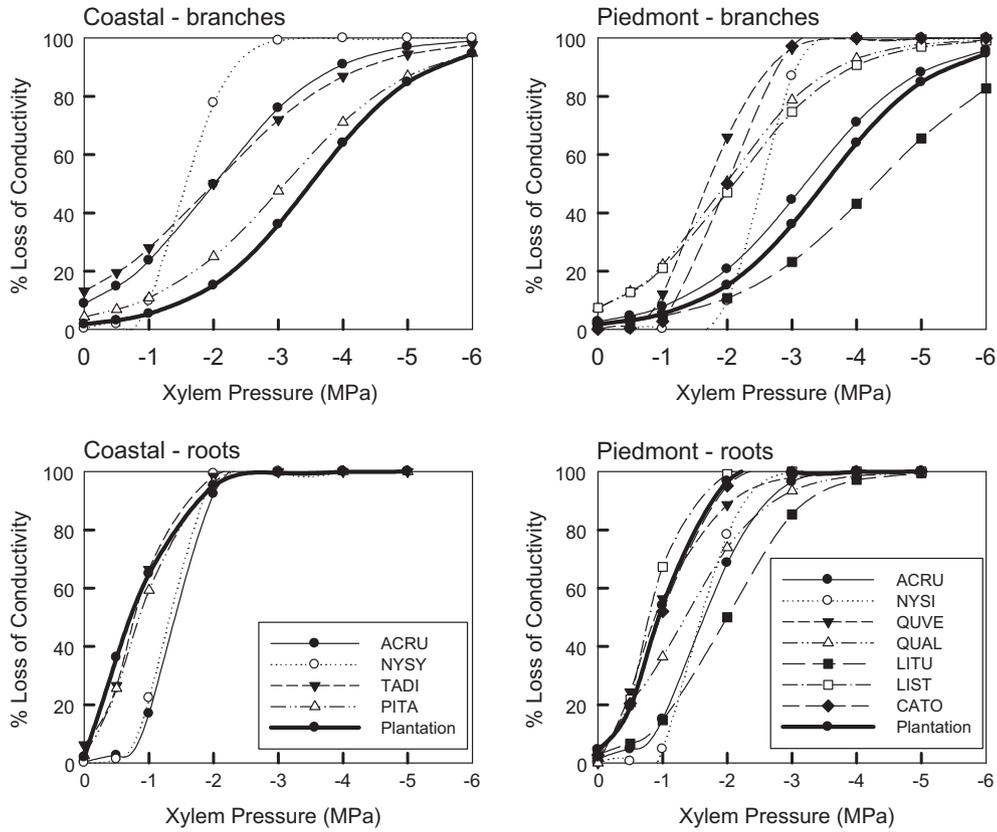


Fig. 3. Vulnerability curves showing the percentage loss of hydraulic conductivity with decreasing xylem pressure of roots or branches from species from the natural hardwood forests or from the loblolly pine plantations growing either in the coastal or the Piedmont region of North Carolina, USA. The first and the last two letters of the tree names represent the first two letters of the genus and species names, respectively. These curves were used to parameterize the model (see Section 2.6).

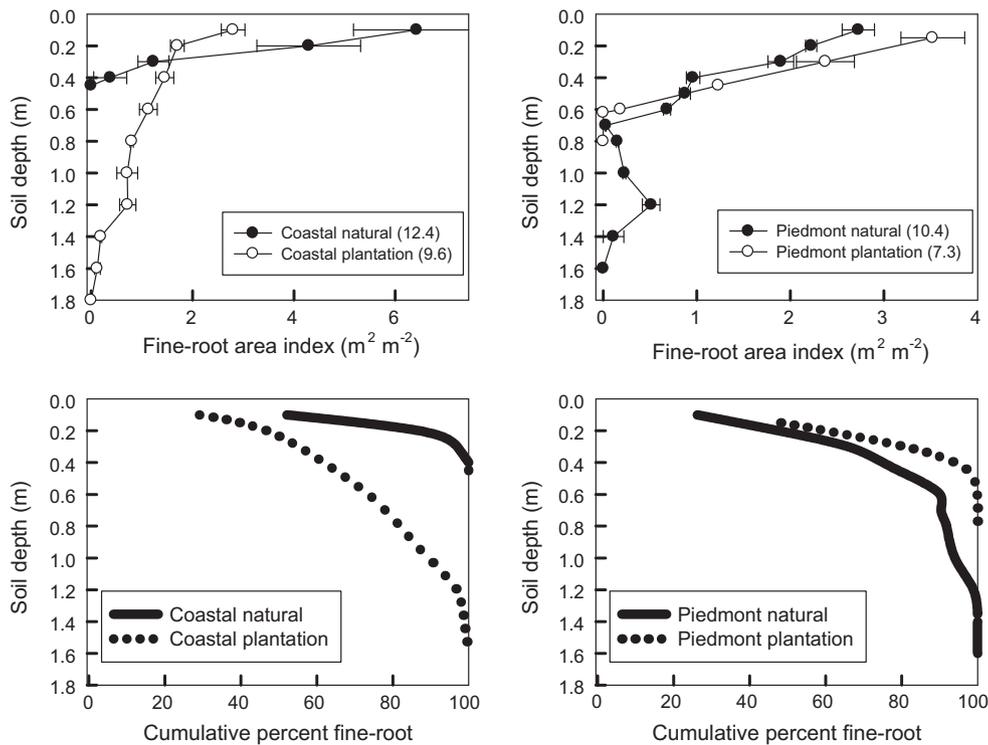


Fig. 4. Fine-root area and cumulative fine root (% of total fine roots) versus depth at the four sites. The corresponding total fine-root area index at each site is indicated in parentheses.

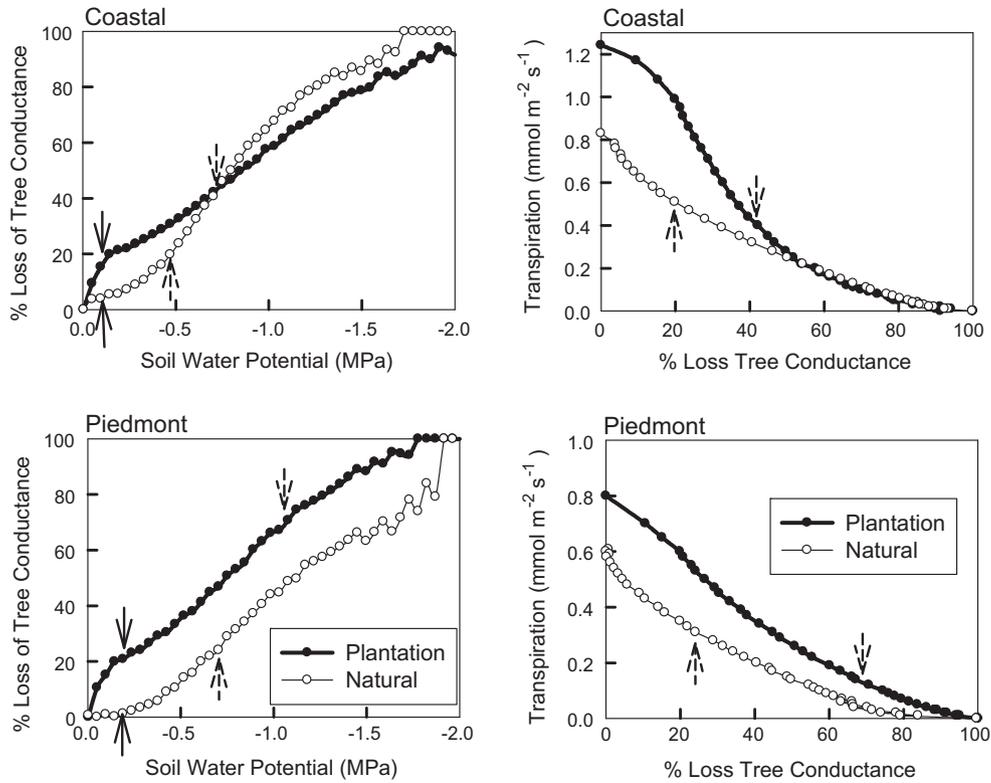


Fig. 5. Whole-tree loss of hydraulic conductance versus the integrated soil water potentials (left panels) and transpiration rates at the full canopy stage versus whole-tree loss of hydraulic conductance (right panels) of a natural hardwood forest or a pine plantation growing either in the coastal or the Piedmont region of North Carolina, USA. Simulations started with soil moisture being at full saturation. Filled and dashed arrows represent 20% and 5% REW, respectively.

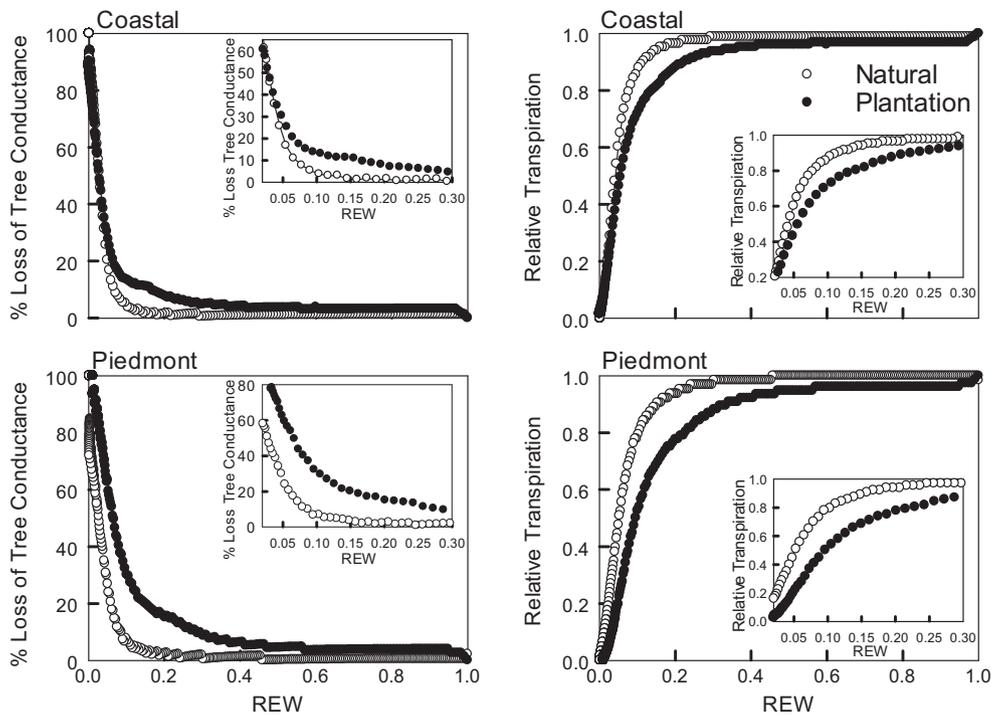


Fig. 6. Whole-tree loss of hydraulic conductance (left panels) and relative transpiration (right panels) at the full canopy stage versus relative extractable water (REW) for both a natural hardwood forest (open circles) or a pine plantation (filled circles) growing either in the coastal or the Piedmont region of North Carolina, USA. The inserts magnify the loss in tree conductance and relative transpiration between 0.02 and 0.3 REW.

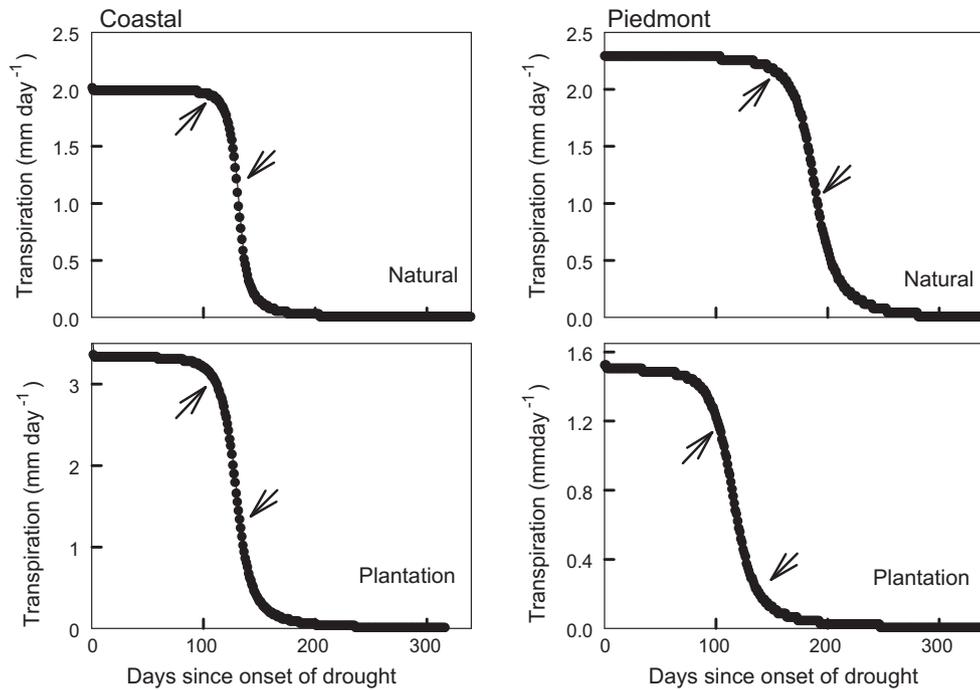


Fig. 7. Daily transpiration rates at the full canopy stage versus the number of days without any rain events in a natural hardwood forest or a pine plantation growing either in the coastal or the Piedmont region of North Carolina, USA. Simulations started with soil moisture being at full saturation (Table 1). Up and down arrows represent 20% and 5% REW, respectively.

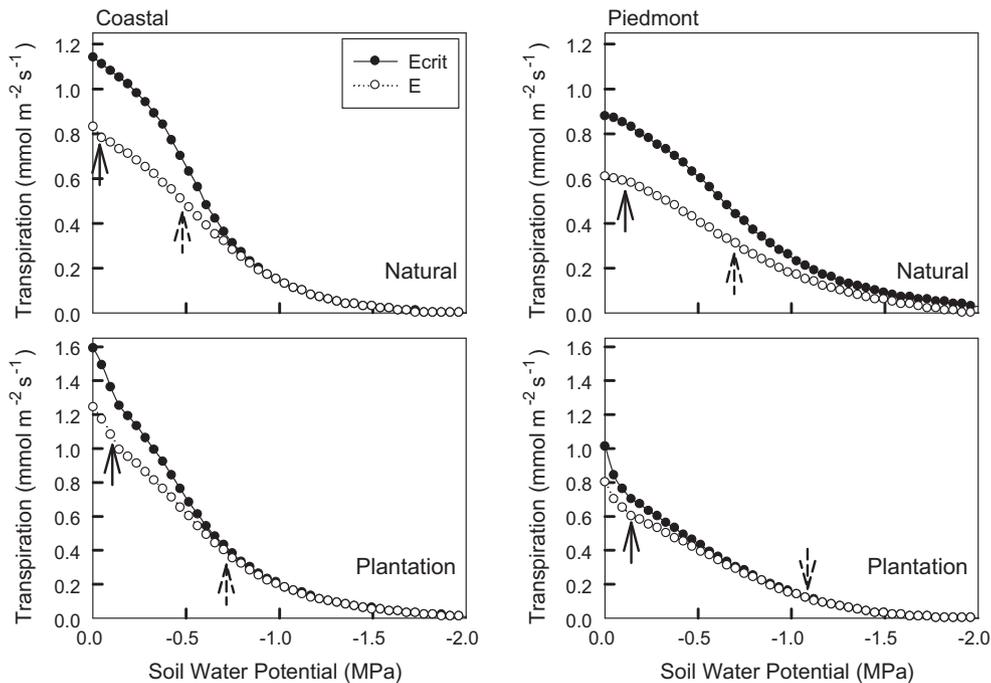


Fig. 8. Transpiration rates (E) and critical transpiration rates (E_{crit}), which corresponds to the maximum rate at which transpiration begins to level off or even decline to prevent irreversible hydraulic failure versus the integrated soil water potentials of the whole rooting zone of a natural hardwood forest or a pine plantation growing either in the coastal or the Piedmont region of North Carolina, USA. Simulations started with soil moisture being at full saturation. Filled and dashed arrows represent 20% and 5% REW, respectively.

2009; Seager et al., 2009). Thus, the impact of drought on the forest was greatest toward the end of the growing season when VPD was at its highest, and soil water content was at its lowest. Future precipitation variability could be particularly important because extended droughts have much more drastic consequences on tree performance and survival than gradual changes in climate conditions (Loustau et al., 2005; Martínez-Vilalta et al., 2008).

4.2. Root and leaf areas

Fine roots were more abundant at shallow depths (0–30 cm) for all sites, especially in the coastal forested wetland site, where more than half of the total root biomass lied in the top 10 cm of soil. There are few published root area values for forested wetland ecosystems for comparison, but root biomass reported here are

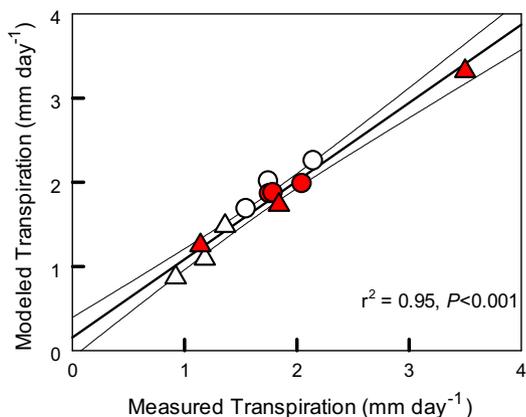


Fig. A1. modeled versus measured daily tree water use during wet and dry conditions. Circles represent natural stands and triangles loblolly pine plantations. Red and white symbols represent coastal and Piedmont regions, respectively. Note the largest effect of drought on the pine plantations (difference in transpiration between either both red or both white triangles as opposed to the differences between circles). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

within the range of values reported within a South Carolina floodplain forest (Baker et al., 2001; Rodgers et al., 2004)). Root system sensitivity to anoxic soil environments is a commonly cited reason for shallow root systems in saturated soil conditions. At the Piedmont sites, the soil profile is dominated by a clay pan at a depth of ca. 50–60 cm that is almost impenetrable by the *P. taeda* fine roots (Oren et al., 1998; Stoy et al., 2005). As a consequence of their shallow rooting depth, the Piedmont pine plantation reduced stomatal conductance and transpiration rates to a third of their maximum just after 90 days without precipitation (Fig. 7). Trees in the natural forests produced twice as much root area per unit transpiring leaf area (RAI/LAI) compared to the plantations with RAI contributing to about one-third of this difference

(Fig. 4; Table 1). Higher RAI/LAI in the natural forests had important implications for root water uptake since it affected the relative importance of soil versus plant limitations on water uptake by limiting the drop in conductance at the soil-root interface and maintaining proportionally higher transpiration rates as soils dried (Hacke et al., 2000; Ewers et al., 2000). Due to the creation of large soil-to-root water potential gradients, low RAI/LAI in both plantations caused a rapid loss of rhizosphere hydraulic conductance, which impacted negatively the sensitivity of whole-tree conductance to soil drying (Figs. 5 and A2).

In conifer plantations that maintain leaves for multiple growing seasons, long-term water stress could also impose further challenges if leaf area was reduced during the drought event (Bréda et al., 2006), because of the increased carbon allocation required to replace lost leaf area. In natural forests, drought-induced decreases in leaf area will increase the proportion of water transport tissues relative to leaves, which will improve tree water uptake (Pataki et al., 1998). However at the extreme end and if the drought will not be sufficiently long for the trees to adjust, then leaf area may become too low and reduce carbon assimilation (McNulty et al., 2014).

4.3. The role of root versus branches cavitation resistance

The roots emerged as potentially the most vulnerable component of the xylem reflected in the higher predicted rate of hydraulic conductivity loss in field conditions (Fig. 3; Sperry et al., 1998; Domec et al., 2009b, 2010b). Unlike the branches, the capability of roots to resist xylem pressure have an important impact on tree-level water use and ultimately on tree resistance to drought. In general, distal organs such as roots and leaves may be more vulnerable to embolism than trunks (Domec and Pruyn, 2008; Johnson et al., 2011; McCulloh et al., 2014) and this may be an adaptation to protect the bole of the tree from hydraulic failure.

Not surprisingly, the broadleaved deciduous species of the Piedmont stand had the highest resistance to embolism.

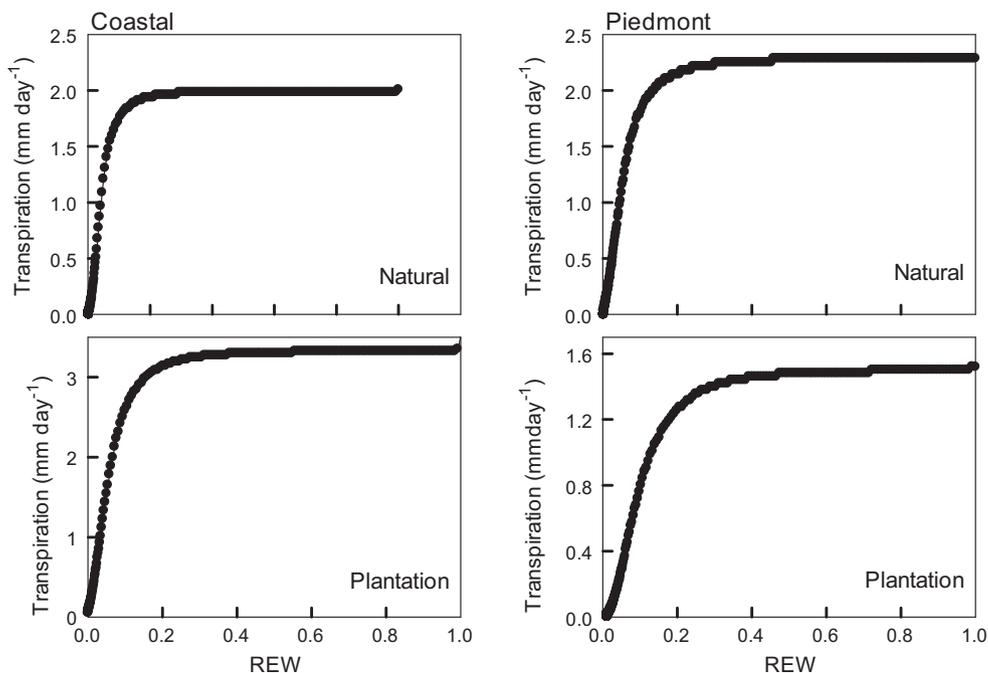


Fig. A2. Daily transpiration versus REW at the full canopy stage for both either a natural hardwood stand or a pine plantation growing either in the coastal or the Piedmont region of North Carolina, USA.

However, we did not expect *P. taeda* to bear roots less resistant to embolism than almost any of the deciduous species. Root vulnerability curves of *Acer rubrum* and *N. sylvatica* growing at the coastal site did not support the hypothesis that species occurring on wetter sites would exhibit higher vulnerability to xylem cavitation. Although this result is not unprecedented (Cochard and Tyree, 1990; Cavender-Bares and Holbrook, 2001), it emphasizes that the current understanding of species cavitation resistance along a soil moisture gradient is still limited.

4.4. Stomatal regulation and transpiration in response to soil water availability

The results of this study also showed that across the contrasting systems, species with large reference stomatal conductance (G_{s-ref}) possessed an efficient plant hydraulic system, and the decline in G_{s-ref} was strongly related to the decline in K_{tree} indicative of a hydraulic effect on stomata regulation. Thus, K_{tree} acted in concert with stomata to limit water loss under conditions of low soil water content (Cochard et al., 2002; Meinzer, 2002). This stomatal closure would prevent Ψ_l from declining to values that could provoke embolism formation in stems where embolism reversal may not be as efficient as in roots (Meinzer and McCulloh, 2013). Many studies have examined the changes in tree resistance related to drought and variation in gas exchange and transpiration relationships between K_{tree} and G_s (e.g., Hubbard et al., 2001; Meinzer, 2002; Domec et al., 2009a), yet the causes of variation in K_{tree} are rarely studied. Here we show that drought-induced differences in the whole hydraulic apparatus of the soil plant system of all species were largely a reflection of the loss of root conductivity over a wide range of soil water potentials. Root cavitation limited wet season tree water uptake (when REW was above 0.2%) by almost 50% in both plantations. At all sites, the dependence of K_{tree} on root hydraulic failure reflects that the short portion of the pathway through the root constitutes 50–60% of whole plant hydraulic resistance to water flow, and that root hydraulic conductance greatly declines with soil water content (Hacke et al., 2000; Domec et al., 2009a). On average, trees from both natural forests had roots less vulnerable to cavitation and had larger RAI/LAI compared to the planted trees, which explained their initial lower sensitivity of transpiration to soil drying and allowed them to extract a higher proportion of water as soil dried. When soil was drier, below 0.2 REW, soil resistance became a larger component of resistance, and the cavitation-induced decrease in root conductivity had a smaller impact on whole tree resistance and transpiration at all sites.

Our modelling results demonstrate a mechanism by which natural stands can withstand more severe drought than pine plantations, based on greater safety margins between soil water potential and critical transpiration rates (Fig. 8). Regardless of the soil type, plantations had a marginal safety factor suggesting that they operated at xylem tensions closed to xylem tensions capable of inducing total hydraulic dysfunction. This result is in disagreement with recent studies looking at inter-species resistance to drought that predicted higher rates of hydraulic dysfunctions in angiosperms as opposed to conifers (Choat et al., 2012) but is consistent with others showing that pines can be very vulnerable to drought (Hacke et al., 2000; McDowell et al., 2013). Differences in E and E_{crit} between managed and natural stands can also be explained by RAI/LAI and by differences in the species xylem structure. Ring porous species such as *Quercus* spp. and *Carya* spp. stop earlywood growth earlier than pine and the diffuse porous species such as *L. styraciflua* and *L. tulipifera*. In those species, the need for higher safety margins could be related to the fact that K_{tree} is determined in a few weeks, and therefore cannot be modified before the next growing season.

4.5. Management issues

Shifting from monoculture to mixed-species stands has been viewed as increasing the forest's ability to deal with disturbances (Forrester et al., 2005; Puettmann, 2011). Traditionally, the species choice is typically driven by growth compatibility, e.g., a shade-intolerant species that will overtop a shade-tolerant species (Krämer and Hölscher, 2010). In Piedmont sites, the need to modify current practices such as an increase in thinning activities to reduce stand density and increase water and other resources available to the residual trees (Newton, 2009; Zhao et al., 2010) is advisable. This, in turn, will result in more vigorous trees and thus higher ability to resist and recover from drought (McDowell et al., 2009; Komatsu et al., 2014) and probably of damage or mortality from insects, diseases, and other agents (Desprez-Loustau et al., 2006; Jactel et al., 2009). Additionally, the management of tree density in natural systems relies on the balance between the facilitation and competition processes necessary to provide optimal conditions for tree growth. If climate change results in lower water availability, then it can be suggested to manage for lower overstorey densities to decrease competition for water, although higher mature tree densities may be necessary to protect seedlings from temperature extremes. Managing forests as more diverse systems (rather than monocultures) to increase ecosystem resilience would add other criteria to these decisions (Linares et al., 2010). One such criterion is whether or not the “added” species responds differentially to drought and can decrease the forest's vulnerability to projected inter-annual variability in precipitations (McNulty et al., 2014).

Acknowledgments

This work was supported by DOE BER-TES (#7090112 and DE-FG02-11ER65189). This work was also funded by NSF IOS (#1146746) and NSF EAR (#1344703), and a Grant from USDA-AFRI (#2012-00857). We also gratefully acknowledge financial support of this research the Pine Integrated Network: Education, Mitigation, and Adaptation Project (PINEMAP), which is funded by the USDA NIFA (#2011-68002-30185). Further support was provided by the USDA Forest Service Eastern Forest Environmental Threat Assessment Center (# 08-JV-11330147), and USDA NIFA (#2014-67003-22068). The USFWS Alligator River National Wildlife Refuge provided the forested wetland research site, and in-kind support of field operations.

References

- Anchukaitis, K.J., Evans, M.N., Kaplan, A., Vaganov, E.A., Hughes, M.K., Grissino-Mayer, H.D., Cane, M.A., 2006. Forward modeling of regional scale tree-ring patterns in the southeastern United States and the recent influence of summer drought. *Geophys. Res. Lett.* 33, L04705.
- Baker, T.T., Conner, W.H., Lockaby, B.G., Stanturf, J., Burke, M.K., 2001. Fine root productivity and dynamics on a forested floodplain in South Carolina. *Soil Sci. Soc. Am. J.* 65, 545–556.
- Bréda, 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. Forest Sci.* 63, 625–644.
- Brown, M.J., Sheffield, R.M., 2003. Forest Statistics for the Piedmont of North Carolina, 2002. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, Resource Bulletin SRS 86.
- Burger, J.A., 2009. Management effects on growth, production and sustainability of managed forest ecosystems: past trends and future directions. *Forest Ecol. Manage.* 258, 2335–2346.
- Caldwell, P.V., 2005. Characterization of the hydrologic regime of four Carolina Bay plant communities. PhD Dissertation, North Carolina State University, 279p.
- Caldwell, P.V., Vepraskas, M.J., Skaggs, R.W., Gregory, J.D., 2007. Simulating the water budgets of natural Carolina bay. *Wetlands* 27, 112–1123.
- Campbell, G.S., 1985. Soil Physics with BASIC: Transport Models for Soil-Plant Systems. Elsevier, Amsterdam, the Netherlands, p. 236.

- Cavender-Bares, J., Holbrook, N.M., 2001. Hydraulic properties and freezing-induced cavitation in sympatric evergreen and deciduous oaks with contrasting habitats. *Plant Cell Environ.* 24, 1243–1256.
- Choat, B., Jansen, S., Cochard, H., Delzon, S., 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491, 752–755.
- Cochard, H., Tyree, M.T., 1990. Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiol.* 6, 393–407.
- Cochard, H., Cruziat, P., Tyree, M.T., 1992. Use of positive pressures to establish vulnerability curves. Further support for the air-seeding hypothesis and implications for pressure–volume analysis. *Plant Physiol.* 100, 205–209.
- Cochard, H., Coll, L., Le Roux, X., Améglio, T., 2002. Unraveling the effects of plant hydraulics on stomatal closure during water stress in walnut. *Plant Physiol.* 128, 282–290.
- Daniel III, C.C., Dahlen, P.R., 2002. Preliminary hydrogeologic assessment and study plan for a regional ground water resource investigation of the Blue Ridge and Piedmont Provinces of North Carolina. U.S.G.S. Water-Resources Investigations Report 02-4105, 60 p.
- Desprez-Loustau, M.-L., Marçais, B., Nageleisen, L.-M., Piou, D., Vannini, A., 2006. Interactive effects of drought and pathogens in forest trees. *Ann. Forest Sci.* 63, 597–612.
- Domec, J.-C., Prunty, M.L., 2008. Bole girdling affects metabolic properties and root, trunk and branch hydraulics of young ponderosa pine trees. *Tree Physiol.* 28, 1493–1504.
- Domec, J.-C., Noormets, A., King, J.S., Sun, G., McNulty, S.G., Gavazzi, M.J., Boggs, J.L., Treasure, E.A., 2009a. Decoupling the influence of leaf and root hydraulic conductances on stomatal conductance and its sensitivity to vapor pressure deficit as soil dries in a drained loblolly pine plantation. *Plant Cell Environ.* 32, 980–991.
- Domec, J.-C., Warren, J.M., Meinzer, F.C., Lachenbruch, B., 2009b. Safety factors for xylem failure by implosion and air-seeding within roots, trunks and branches of young and old conifer trees. *IAWA J.* 30, 100–120.
- Domec, J.-C., King, J.S., Noormets, A., Treasure, E., Gavazzi, M., Sun, G., McNulty, S.G., 2010a. Hydraulic redistribution of soil water by roots affects whole-stand evapotranspiration and net ecosystem carbon exchange. *New Phytol.* 187, 171–183.
- Domec, J.-C., Schafer, K., Oren, R., Kim, H., McCarthy, H., 2010b. Variable conductivity and embolism in roots and branches of four contrasting tree species and their impacts on whole-plant hydraulic performance under future atmospheric CO₂ concentration. *Tree Physiol.* 30, 1001–1015.
- Domec, J.-C., Sun, G., Noormets, A., Gavazzi, M.J., Treasure, E.C., Swenson, J.J., McNulty, S.G., King, J.S., 2012a. A comparison of three methods to estimate evapotranspiration in two contrasting loblolly pine plantations: age related changes in water use and drought sensitivity of evapotranspiration components. *Forest Sci.* 58, 497–512.
- Domec, J.-C., Ogée, J., Noormets, A., Jouany, J., Gavazzi, M., Treasure, E., Sun, G., McNulty, S.G., King, J.S., 2012b. Interactive effects of nocturnal transpiration and climate change on the root hydraulic redistribution and carbon and water budgets of southern United States pine plantations. *Tree Physiol.* 32, 707–723.
- Drummond, M.A., Loveland, T.R., 2010. Land-use pressure and a transition to forest-cover loss in the Eastern United States. *BioScience* 60, 286–298.
- Ellert, B.H., Janzen, H.H., VandenBygaart, A.J., Bremer, E., 2008. Measuring change in soil organic carbon storage. In: Carter, M.R., Gregorich, E.G. (Eds.), *Soil Sampling and Methods of Analysis*, second ed. CRC Press, Boca Raton, FL, pp. 25–38.
- Ewers, B.E., Oren, R., Sperry, J.S., 2000. Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*. *Plant Cell Environ.* 23, 1055–1066.
- Forrester, D.I., Auhus, J.B., Cowie, A.L., 2005. On the success and failure of mixed-species tree plantations: lessons learned from a model system of *Eucalyptus globules* and *Acacia mearnsii*. *Forest Ecol. Manage.* 209, 147–155.
- Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. *Forest Ecol. Manage.* 312, 282–292.
- Franklin, J.F., Johnson, K.N., 2004. Forests face new threat: global market changes. *Issues Sci. Technol.* 20, 41–48.
- Fox, T.R., Jokela, E.J., Allen, H.L., 2004. The evolution of pine plantation silviculture in the Southern United States. In: Rauscher, H.M., Johnsen, K. (Eds.), *Southern Forest Science: Past, Present, and Future*. Gen. Tech. Rep. SRS-75. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, pp. 63–82 (Chapter 8).
- Fox, T.R., Jokela, E.J., Allen, H.L., 2007. The development of pine plantation silviculture in the southern United States. *J. Forest.* 105, 337–348.
- Gessler, A., Keitel, C., Nahm, M., Rennenberg, H., 2004. Water shortage affects the water and nitrogen balance in central European beech forests. *Plant Biol.* 6, 289–298.
- Granier, A., 1987. Sap flow measurement in Douglas fir stems using a new thermal method. *Ann. Sci. Forest* 44, 1–14.
- Granier, A., Loustau, D., Bréda, N., 2000. A generic model of forest canopy conductance dependent on climate, soil water availability and leaf area index. *Ann. Sci. Forest* 57, 755–765.
- Hacke, U.G., Sperry, J.S., Ewers, B.E., Ellsworth, D.S., Schäfer, K.V.R., Oren, R., 2000. Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* 124, 495–505.
- Harrison, R.B., Adams, A.B., Licata, C., Flaming, B., Wagoner, G.L., Carpenter, P., Vance, E.D., 2003. Quantifying deep soil and coarse-soil fractions: avoiding sampling bias. *Soil Sci. Soc. Am. J.* 67, 1602–1606.
- Hertel, D., Leuschner, C., 2006. The in situ root chamber: a novel tool for the experimental analysis of root competition in forest soils. *Pedobiologia* 50, 217–224.
- Hubbard, R.M., Ryan, M.G., Stiller, V., Sperry, J.S., 2001. Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant Cell Environ.* 24, 113–121.
- Iversen, C.M., Murphy, M.T., Allen, M.F., Childs, J., Eissenstat, D.M., Lilleskov, E.A., 2011. Advancing the use of minirhizotrons in wetlands. *Plant Soil* 352, 23–39.
- IPCC, 2013. Summary for policymakers. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1–30.
- Jackson, R.B., Cook, C.W., Phippen, J.S., Palmer, S.M., 2009. Increased belowground biomass and soil CO₂ fluxes after a decade of carbon dioxide enrichment in a warm-temperate forest. *Ecology* 90, 3352–3366.
- Jactel, H., Nicol, B.C., Branco, M., Gonzalez-Olabarria, J.R., Grodzki, W., Långström, B., 2009. The influences of forest stand management on biotic and abiotic risks of damage. *Ann. Forest Sci.* 66, 701–705.
- Johnson, D.M., McCulloh, K.A., Meinzer, F.C., Woodruff, D.R., Eissenstat, D.M., 2011. Hydraulic patterns and safety margins, from stem to stomata, in three eastern US tree species. *Tree Physiol.* 31, 659–668.
- Karl, T.R., Melillo, J.M., Peterson, T.C., 2009. *Global Change Impacts in the United States*. Cambridge University Press, Cambridge, UK.
- Kim, H.-S., Oren, R., Hinckley, T.M., 2008. Actual and potential transpiration and carbon assimilation in an irrigated poplar plantation. *Tree Physiol.* 28, 559–577.
- Kolb, K.J., Sperry, J.S., 1999. Differences in drought adaptation between subspecies of sagebrush (*Artemisia tridentata*). *Ecology* 80, 2373–2384.
- Komatsu, H., Shinohara, Y., Kumagai, T., Kume, T., Tsuruta, K., Xiang, Y., Ichihashi, R., Tateishi, M., Shimizu, T., Miyazawa, Y., Nogata, M., Laplace, S., Han, T., Chiu, C.-W., Ogura, A., Saito, T., Otsuki, K.A., 2014. Model relating transpiration for Japanese cedar and cypress plantations with stand structure. *Forest Ecol. Manage.* 334, 301–312.
- Krämer, I., Hölscher, D., 2010. Soil water dynamics along a tree diversity gradient in a deciduous forest in Central Germany. *Ecohydrol. Hydrobiol.* 3, 262–270.
- Linares, J.C., Camarero, J.J., Carreira, J.A., 2010. Competition modulates the adaptation capacity of forests to climatic stress: insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. *J. Ecol.* 98, 592–603.
- Loustau, D., Granier, A., 1993. Environmental control of water flux through Maritime pine (*Pinus pinaster* Ait.). In: Borghetti, J., Grace, J., Raschi, A. (Eds.), *Water Transport in Plants under Climatic Stress*. Cambridge University Press, Cambridge, pp. 205–218.
- Loustau, D., Bosc, A., Colin, A., Davi, H., François, C., Dufrene, E., Déqué, M., Cloppet, E., Arrouays, D., le Bas, C., 2005. Modelling the climate change effects on the potential production of French plains forests at the sub regional level. *Tree Physiol.* 25, 813–823.
- Loveland, T.R., Sohl, T.L., Stehman, S.V., Gallant, A.L., Saylor, K.L., Napton, D.E., 2002. A strategy for estimating the rates of recent United States land-cover changes. *Photogramm. Eng. Remote Sens.* 68, 1091–1099.
- Maherali, H., Pockman, W.T., Jackson, R.B., 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* 85, 2184–2199.
- Manoli, G., Bonetti, S., Domec, J.-C., Putti, M., Katul, G., Marani, M., 2014. Tree root systems competing for soil moisture in a 3D soil-plant model. *Adv. Water Resour.* 66, 32–42.
- Martínez-Vilalta, J., López, B.C., Adell, N., Badiella, L., Ninyerola, M., 2008. Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. *Glob. Change Biol.* 14, 2868–2881.
- Matamala, R., Schlesinger, W.H., 2000. Effects of atmospheric CO₂ enrichment on fine root production and activity in an intact temperate forest ecosystem. *Glob. Change Biol.* 6, 967–980.
- McCulloh, K.A., Johnson, D.M., Meinzer, F.C., Woodruff, D.R., 2014. The dynamic pipeline: hydraulic capacitance and xylem hydraulic safety in four tall conifer species. *Plant Cell Environ.* 37, 1171–1183.
- McDowell, N.G., Allen, C.D., Marshall, L., 2009. Growth, carbon isotope discrimination, and climate-induced mortality across a *Pinus ponderosa* elevation transect. *Glob. Change Biol.* 16, 399–405.
- McDowell, N.G., Fisher, R.A., Xu, C., Domec, J.C., Holtta, T., Mackay, S., Sperry, J.S., Boutz, A., Dickman, L., Gehres, N., et al., 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel–experiment framework. *New Phytol.* 200, 304–321.
- McNulty, S.G., Vose, J.M., Swank, W.T., 1996. Loblolly pine hydrology and productivity across the Southern United States. *Forest Ecol. Manage.* 86, 241–251.
- McNulty, S.G., Boggs, J.L., Sun, G., 2014. The rise of the mediocre forest: why chronically stressed trees may better survive extreme episodic climate variability. *New Forests* 45, 403–415.
- Meinzer, F.C., 2002. Co-ordination of vapour and liquid phase water transport properties in plants. *Plant Cell Environ.* 25, 265–274.
- Meinzer, F.C., McCulloh, K.A., 2013. Xylem recovery from drought-induced embolism: where is the hydraulic point of no return? *Tree Physiol.* 33, 331–334.
- Miao, G., Noormets, A., Domec, J.-C., Trettin, C.C., McNulty, S.G., Sun, G., King, J.S., 2013. The effect of water table fluctuation on soil respiration in a lower coastal plain forested wetland in the southeastern US. *J. Geophys. Res.: Biogeosci.* 118, 1748–1762.

- Newton, P.F., 2009. Development of an integrated decision-support model for density management within jack pine stand-types. *Ecol. Modell.* 220, 3301–3324.
- Noormets, A., Gavazzi, M.J., McNulty, S.G., Domec, J.-C., Sun, G., King, J.S., Chen, J.Q., 2010. Response of carbon fluxes to drought in a coastal plain loblolly pine forest. *Glob. Change Biol.* 16, 272–287.
- Noormets, A., McNulty, S.G., Domec, J.-C., Gavazzi, M., Sun, G., King, J.S., 2012. The role of harvest residue in rotation cycle carbon balance in loblolly pine plantations. Respiration partitioning approach. *Glob. Change Biol.* 18, 3186–3201.
- O'Hara, K.L., Ramage, B.S., 2013. Silviculture in an uncertain world: utilizing multi-aged management to integrate disturbance. *Forestry* 86, 401–410.
- Oishi, A.C., Oren, R., Stoy, P.C., 2008. Estimating components of forest evapotranspiration: a footprint approach for scaling sapflux measurements. *Agric. Forest Meteorol.* 148, 719–732.
- Oishi, A.C., Oren, R., Novick, K., Palmroth, S., Katul, G.G., 2010. Interannual invariability of forest evapotranspiration and its consequence to water flow downstream. *Ecosystems* 13, 421–436.
- Oren, R., Phillips, N., Katul, G.G., Ewers, B.E., Pataki, D.E., 1998. Scaling xylem sap flux and soil water balance and calculating variance. *Ann. Sci. Forest.* 55, 191–216.
- Oren, R., Sperry, J.S., Katul, G.G., Pataki, D.E., Ewers, B.E., Phillips, N., Schäfer, K.V.R., 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant Cell Environ.* 22, 1515–1526.
- Pataki, D.E., Oren, R., Phillips, N., 1998. Responses of sap flux and stomatal conductance of *Pinus taeda* L. trees to stepwise reductions in leaf area. *J. Exp. Bot.* 49, 871–878.
- Pataki, D.E., Oren, R., 2003. Species differences in stomatal control of water loss at the canopy scale in a mature bottomland deciduous forest. *Adv. Water Res.* 26, 1267–1278.
- Palmroth, S., Maier, C.A., McCarthy, H.R., Oishi, A.C., Kim, H.S., Johnsen, K.H., Katul, G.G., Oren, R., 2005. Contrasting responses to drought of forest floor CO₂ efflux in a loblolly pine plantation and a nearby oak-hickory forest. *Glob. Change Biol.* 11, 421–434.
- Palmroth, S., Katul, G.G., Hui, D., McCarthy, H.R., Jackson, R.B., Oren, R., 2010. Estimation of long-term basin scale evapotranspiration from streamflow time series. *Water Resour. Res.* 46, W10512.
- Pritchard, S.G., Strand, A.E., Cormack, M.L., Davis, M.A., Finzi, A.C., Jackson, R.B., Matamala, R., Rogers, H.H., Oren, R., 2008. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO₂-enrichment: a six year-minirhizotron study. *Glob. Change Biol.* 14, 588–602.
- Puettmann, K.J., 2011. Silvicultural challenges and options in the context of Global Change: 'simple' fixes and opportunities for new management approaches. *J. Forest.* 109, 321–331.
- Radecki, A., 2014. Why eco-hydrologically based management plans are an important tool to address both the ecological and economic concerns of terrestrial ecosystem management in the coming decades. Master Thesis, North Carolina State University, 118p.
- Rodgers, H.L., Day, F.P., Atkinson, R., 2004. Root dynamics in restored and naturally regenerated Atlantic white cedar wetlands. *Restorat. Ecol.* 16, 401–411.
- Samuelson, L.J., Butnor, J., Maier, C., Stokes, T.A., Johnsen, K., Kane, M., 2008. Growth and physiology of loblolly pine in response to long-term resource management: defining growth potential in the southern United States. *Can. J. Forest Res.* 38, 721–732.
- Seager, R. et al., 2009. Drought in the southeastern United States: causes, variability over the last millennium, and the potential for future hydroclimate change. *J. Climate* 22, 5021–5045.
- 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.
- Sperry, J.S., Hacke, U.G., Oren, R., Comstock, J.P., 2002. Water deficits and hydraulic limits to leaf water supply. *Plant Cell Environ.* 25, 251–263.
- Sun, G., Noormets, A., Gavazzi, M.J., McNulty, S.G., Chen, J., Domec, J.C., King, J.S., Amaty, D.M., Skaggs, R.W., 2010. Energy and water balance of two contrasting loblolly pine plantations on the lower coastal plain of North Carolina, USA. *Forest Ecol. Manage.* 259, 1299–1310.
- Swank, W.T., Swift Jr, L.W., Douglass, J.E., 1988. Streamflow changes associated with forest cutting, species conversions, and natural disturbances. In: Swank, W.T., Crossley, D.A. (Eds.), *Forest Hydrology and Ecology at Coweeta, Ecological Studies*, vol. 66. Springer-Verlag, New York, pp. 297–312.
- Stoy, P.C., Katul, G.G., Siqueira, M.B.S., Juang, J.Y., McCarthy, H.R., Kim, H.S., Oishi, A.C., Oren, R., 2005. Variability in net ecosystem exchange from hourly to inter-annual time scales at adjacent pine and hardwood forests: A wavelet analysis. *Tree Physiol.* 25, 887–902.
- Thompson, S.E., Harman, C.J., Heine, P., Katul, G.G., 2010. Vegetation-infiltration relationships across climatic and soil type gradients. *J. Geophys. Res.* 115, G02023.
- Ward, E.J., Oren, R., Bell, D.M., Clark, J.S., McCarthy, H.R., Seok-Kim, H., Domec, J.-C., 2013. The effects of elevated CO₂ and nitrogen fertilization on stomatal conductance estimated from scaled sapflux measurements at Duke FACE. *Tree Physiol.* 33, 135–151.
- Warren, J.M., Hanson, P.J., Iversen, C.M., Kumar, J., Walker, A.P., Wullschlegel, S.D., 2015. Root structural and functional dynamics in terrestrial biosphere models evaluation and recommendations. *New Phytol.* 205, 9–78.
- Wear, D.N., Prestemon, J., Huggett, R., Carter D., 2013. Markets. In: Wear, David N., Greis, John G. (Eds.), *The Southern Forest Futures Project: Technical Report*. Gen. Tech. Rep. SRS-178. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, 542 p.
- Wullschlegel, S.D., Meinzer, F.C., Vertessy, R.A., 1998. A review of whole-plant water use studies in trees. *Tree Physiol.* 18, 499–512.
- Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment, the insurance hypothesis. *Proc. Natl. Acad. Sci. U.S.A.* 96, 57–64.
- Zhao, D., Kane, M., Borders, E.B., 2010. Development and applications of the relative spacing model for loblolly pine plantations. *Forest Ecol. Manage.* 259, 1922–1929.