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Interactive effects of nocturnal transpiration and climate change on the root hydraulic redistribution and carbon and water budgets of southern United States pine plantations

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Deep root water uptake and hydraulic redistribution (HR) have been shown to play a major role in forest ecosystems during drought, but little is known about the impact of climate change, fertilization and soil characteristics on HR and its consequences on water and carbon fluxes. Using data from three mid-rotation loblolly pine plantations, and simulations with the process-based model MuSICA, this study indicated that HR can mitigate the effects of soil drying and had important implications for carbon uptake potential and net ecosystem exchange (NEE), especially when N fertilization is considered. At the coastal site (C), characterized by deep organic soil, HR increased dry season tree transpiration (T) by up to 40%, and such an increase affected NEE through major changes in gross primary productivity (GPP). Deep-rooted trees did not necessarily translate into a large volume of HR unless soil texture allowed large water potential gradients to occur, as was the case at the sandy site (S). At the Piedmont site (P) characterized by a shallow clay-loam soil, HR was low but not negligible, representing up to 10% of T . In the absence of HR, it was predicted that at the C, S and P sites, annual GPP would have been diminished by 19, 7 and 9%, respectively. Under future climate conditions HR was predicted to be reduced by up to 25% at the C site, reducing the resilience of trees to precipitation deficits. The effect of HR on T and GPP was predicted to diminish under future conditions by 12 and 6% at the C and P sites, respectively. Under future conditions, T was predicted to stay the same at the P site, but to be marginally reduced at the C site and slightly increased at the S site. Future conditions and N fertilization would decrease T by 25% at the C site, by 15% at the P site and by 8% at the S site. At the C and S sites, GPP was estimated to increase by 18% and by >70% under future conditions, respectively, with little effect of N fertilization. At the P site, future conditions would stimulate GPP by only 12%, but future conditions plus N fertilization would increase GPP by 24%. As a consequence, in all sites, water use efficiency was predicted to improve dramatically with future conditions. Modeling the effect of reduced annual precipitation indicated that limited water availability would decrease all carbon fluxes, including NEE and respiration. Our simulations highlight the interactive effects of nutrients and elevated CO₂, and showed that the effect of N fertilization would be greater under future climate conditions.

Keywords: carbon sequestration, Duke FACE, ecosystem respiration, hydraulic redistribution, loblolly pine (*Pinus taeda* L.), MuSICA, soil water content, transpiration.

Introduction

Although the functional consequences of root distributions have been inferred for decades (e.g., Weaver 1919, Walter 1963), it was only recently that the relative use of shallow water was shown, in some cases, to rely on deep water, regardless of surface water availability (Dawson 1993). When plant demand exceeds water supply, plants must find other sources of water or make more conservative use of available water to minimize water stress (Irvine et al. 2005). Since the 1920s it has been proposed (Weaver 1919), and later experimentally confirmed (Richards and Caldwell 1987), that during times of low transpiration plants can reduce water stress by extracting water from deeper and moisture soil layers through plant roots and storing it in the upper, drier rhizosphere, where it can be utilized when transpirational demand increases. This water loss by roots from deeper water layers and released in upper drier layers was termed hydraulic lift (Volk 1947, Caldwell and Richards 1989). However, as this process can be bidirectional (upward and downward) 'hydraulic redistribution' (HR) has been proposed as a more comprehensive term for the phenomenon (Burgess et al. 1998). This mechanism can partially prevent water stress during drought and can represent 20–40% of stand water use (Caldwell and Richards 1989, Jackson et al. 2000, Domec et al. 2010a). Although HR has been widely documented (Meinzer et al. 2004, Warren et al. 2008, Bleby et al. 2010, Prieto et al. 2010), its effect on whole ecosystem water use has received little attention (Brook et al. 2006, Warren et al. 2007; Scholz, et al. 2008) and few studies (Lee et al. 2005; Warren et al. 2007) have focused on the climatic and physiological factors controlling patterns of HR.

Conceptually, the exchange of water between the roots and the surrounding soil is driven by the soil (Ψ_s)-to-root (Ψ_r) water potential difference such that the flux of water into roots (Q_r) can be expressed as: $Q_r = (\Psi_s - \Psi_r) \times K_{\text{root}}$, where K_{root} is conductance for water transport through the rhizosphere and the roots. Under most natural conditions Ψ_s is less negative than Ψ_r , resulting in a positive Q_r . Conversely, a negative Q_r value can be observed when Ψ_s is more negative than Ψ_r , provided that K_{root} remains above zero. Such a situation will develop when roots remove water from a moist lower horizon and transport this water upward through a dry surface soil, which generates a larger gradient than the downstream xylem, a condition existing under low or zero transpiration. The magnitude of HR depends on a suite of environmental and biological variables, including the soil physical properties, the distribution and functioning of plant roots and the atmospheric water demand at night. Although plants are generally expected to close their stomata at night to conserve water when carbon gain is not occurring, there is growing evidence for a high nocturnal leaf stomatal conductance (g_{s_night}) and night-time transpiration (T_{night}) in many C_3 species (Oren and Pataki 2001,

Caird et al. 2007, Dawson et al. 2007, Kavanagh et al. 2007). In natural systems, increased vapor pressure deficit (VPD) has been strongly correlated with greater T_{night} of many tree species (Oren et al. 1999a, Daley and Phillips 2006). The level of stomatal control at night and T_{night} has significant implications for HR because these two processes compete for the same water (Hultine et al. 2003, Caird et al. 2007, Dawson et al. 2007). When T_{night} is high the water potential gradient between the soil and the leaves induces a flow of water from soil to plant to atmosphere instead of between soil layers through roots (Domec et al. 2006, Scholz et al. 2008). Given the observed sensitivity of T_{night} and g_{s_night} to VPD, it is important to determine how often environmental conditions cause night-time transpiration sufficiently large to reduce the magnitude of HR, and if this can be expected to change under future climatic conditions.

The first decade of the twenty-first century was the warmest on record and the most likely global average surface air temperature increase by 2040 lies between 2 and 4 °C, with larger increases projected in summer in most latitudes, and especially at night (IPCC WG II 2007). Because the water-holding capacity of the atmosphere increases with higher temperatures, and although relative humidity is not projected to change markedly (Trenberth et al. 2005, Yu and Weller 2007), this temperature increase will inevitably affect the movement of water through plants (Way and Oren 2010), and lead to higher VPD and transpiration rates at night that could potentially limit HR. In addition to the effect of temperature increase on g_s , future predictions must account for the effects of increased atmospheric carbon dioxide (CO_2) concentrations. Experimental results from the free-air CO_2 enrichment (FACE) experiments show that increased CO_2 concentrations reduce g_s in C_3 plants, although the effects vary considerably among species and depend on the water and nutrient status of the plants (Domec et al. 2009a, McCarthy et al. 2010, Warren et al. 2011, Ellsworth et al. 2012). Although elevated atmospheric CO_2 concentrations (e CO_2) can potentially stimulate tree growth, this effect may be limited by low nutrient and water supplies (Oren et al. 2001, Loustau et al. 2005, Norby et al. 2010). Overall, increased nutrient supply and e CO_2 have been shown to result in a lower fine root biomass but an increase in the dynamic fraction of the finest roots, i.e., the fraction of fine roots that varies seasonally in response to changes in environmental and growing conditions (King et al. 2002, Maier et al. 2004, Pritchard et al. 2008a, Bakker et al. 2009). These interactions between nutrient supply, e CO_2 and fine root biomass need to be accounted for in model parameterization.

In this study, we compared soil water uptake and HR in relation to soil water status among three contrasting loblolly pine stands. Although these stands were similar in age and genetic background, and experienced similar climatic conditions, their

tree hydraulic properties and photosynthetic capacities were different. Two of the sites (coastal plain and sandhills) had the requisite conditions for HR, namely a prolonged seasonal drought and deep well-drained soils that allow penetration of roots below 2 m. Published data on plant and soil characteristics, soil water and root profiles, cavitation resistance, plant hydraulic conductance and assimilation rate were used to parameterize a soil–plant–atmosphere model (MuSICA, Ogée et al. 2003). This model takes into account the measured plant and soil hydraulic properties to predict soil water extraction and redistribution, transpiration and carbon assimilation (Figure 1). We used MuSICA to (i) estimate how important the observed differences in water use between sites were for the maintenance of water uptake under reduced precipitation and increased temperature and $e\text{CO}_2$, (ii) test the hypothesis that under future higher evaporative demand, T_{night} will be enhanced and HR reduced, thus impacting on tree water use (T), gross primary productivity (GPP) and water use efficiency and (iii) stress the impact of climate change, $e\text{CO}_2$ and N fertilization on T , HR, GPP and water use efficiency.

Methods

Plant material and study sites

Our modeling of water and carbon uptake was done on three contrasting loblolly pine sites, all located in North Carolina, in

the southeastern United States. The Coastal Plain (C) site ($35^{\circ}11'N$, $76^{\circ}11'W$) is located within the lower coastal plain mixed forest province of North Carolina (Noormets et al. 2010, Sun et al. 2010). This 100 ha mid-rotation loblolly pine stand (US-NC2 in the Ameriflux database) was established in 1992 after clear-cutting the previous mature pine plantation. The watershed is 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, improving site access (management) and tree productivity by reducing stresses caused by excessive soil water conditions during winter months. Water table at this site fluctuates between 20 cm in early spring to below 180 cm in late fall (Domec et al. 2012). The long-term (1945–2010) average annual precipitation was 1290 ± 199 mm (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 understory was primarily composed of young red maple (*Acer rubrum* L.), devil's walking stick (*Aralia spinosa* L.), beautyberry (*Callicarpa americana* L.), giant cane (*Arundinaria macrosperma* Michx.) and meadow grass (*Poa* spp.) (Domec et al. 2010a).

The upper coastal plain Sandhills (S) site ($34^{\circ}48'N$, $79^{\circ}12'W$) is part of the USDA Forest Service—North Carolina State University Southeastern Tree Research and Education Site (SETRES). The SETRES study site was established in 1992

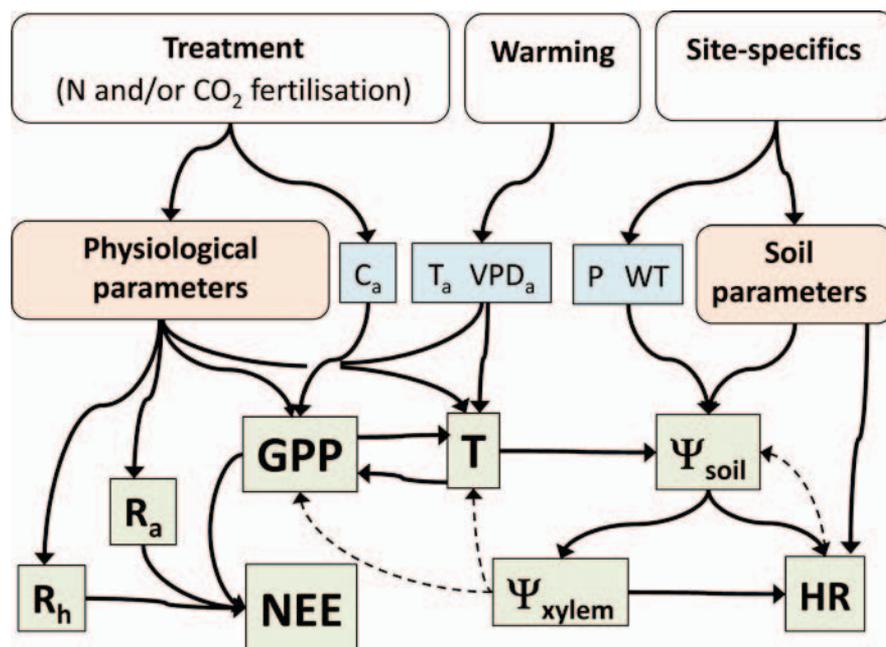


Figure 1. Flow chart describing how treatment (N and/or CO₂ fertilisation), warming and site-specific characteristics affect model parameters (pink, Table 1) and model forcing (blue), which, in turn, will affect model output (green). Solid arrows are direct effect while dotted arrows indicate feedback loops. C_a: atmospheric CO₂ mixing ratio; T_a: air temperature; VPD_a: air vapor pressure deficit; P: precipitation; WT: water table depth; R_h: heterotrophic respiration, R_a: autotrophic respiration; GPP: gross primary productivity; NEE: net ecosystem CO₂ exchange; T: transpiration; Ψ_{soil}: soil water potential, Ψ_{xylem}: xylem water potential; HR: hydraulic redistribution.

Table 1. Selected stand characteristics for the Coastal (US-NC2 in the Ameriflux database), Sandhills and the Piedmont sites, which are all located in North Carolina as well as main parameter values for the MuSICA model. Precipitation represents the mean annual precipitation between 1945 and 2010. Saturated soil hydraulic conductance (K_{soil}) is given for the first 30 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 P_{50} indicates the water potential at which 50% of the root conductance is lost due to cavitation. Reference stomatal conductance ($g_{s\text{-ref}}$) represents the stomatal conductance at a vapor pressure deficit (VPD) of 1 kPa (Oren et al. 1999b), analyzed based on $g_s = g_{s\text{-ref}} - m \times \ln \text{VPD}$, where m is the sensitivity of g_s to VPD ($-dg_s/d\ln D$). Nocturnal stomatal conductance ($g_{s\text{-night}}$) was determined from the relationship between sapflow-based canopy g_s and VPD at night. Values of foliar nitrogen, $V_{\text{cmax}25}$, $J_{\text{max}25}$ and foliage dark respiration rates (R_d) are the mean values between both needle age classes taken for the upper mid-canopy. R_{25} represents the soil respiration rate at 25 °C. Note that although LAI represents projected leaf area index, all photosynthetic and hydraulic parameters are expressed on an all-sided leaf area reflecting the fact that loblolly pine needles have stomata on all surfaces (using a total surface-to-projected leaf area ratio of 2.36).

	Coastal (C)-	Sandhills (S)—SETRES			Piedmont (P)—Duke FACE		
	Control	Control	Fert.	Fert.-eCO ₂	Control	Fert.	Fert.-eCO ₂
Precipitation (mm year ⁻¹)	1290	1210	1150	1150	1145	1145	1145
Tree density (tree ha ⁻¹)	635	1160	1160	1160	720	720	720
Mean tree height (m)	17	11	14	14	20	22	23
Stand age (years)	18	19	19	19	26	26	26
Clay (%)	8	5	5	5	12	11	11
Sand (%)	45	90	90	90	42	42	42
Soil organic matter (%)	25	2	2	2	5	5	5
Soil bulk density (g m ⁻³)	1.2	1.2	1.2	1.2	1.3	1.3	1.3
Saturated K_{soil} (mol s ⁻¹ m ⁻¹ MPa ⁻¹)	415 ¹	108 ^{2,3}	108 ^{2,3}	108 ^{2,3}	19 ⁴	19 ⁴	19 ⁴
Saturated K_{tree} (mmol m ⁻² s ⁻¹)	0.85 ⁵	1.10 ^{2,3}	0.55 ^{2,3}	0.90 ^{2,3}	0.75 ⁶	0.65 ⁶	0.49 ⁶
Percent K_{tree} in roots	56 ⁵	50 ^{2,3}	50 ^{2,3}	50 ^{2,3}	53 ⁶	48 ⁶	45 ⁶
Root P_{50} (MPa)	-0.85 ⁷	-1.0 ^{2,3}	-1.2 ^{2,3}	N/A*	-1.1 ⁷	-0.6 ⁷	-0.5 ⁷
$g_{s\text{-ref}}$ (mmol m ⁻² s ⁻¹)	62 ⁵	85 ²	39 ²	N/A*	55 ⁶	45 ⁶	43 ⁶
m (mmol m ⁻² s ⁻¹ lnkPa ⁻¹)	33 ⁵	46 ²	20 ²	N/A*	36 ⁶	26 ⁶	25 ⁶
$g_{s\text{-night}}$ (mmol m ⁻² s ⁻¹)	18 ⁷						
Leaf area index (projected)	3.0–4.2 ⁵	1.5–2.1 ⁸	2.4–3.2 ⁸	2.4–3.2 ⁸	3.0–4.2 ⁹	3.3–4.8 ⁹	3.5–5.1 ⁹
Root area index (all-sided)	8.9 ¹⁰	14.2 ^{2,3}	12.5 ^{2,3}	N/A*	5.5 ^{11,12}	6.3 ^{11,12}	6.9 ^{11,12}
Foliar nitrogen (g m ⁻²)	2.4 ⁷	2.1 ⁸	2.5 ⁸	2.5 ⁸	2.3 ¹³	2.8 ¹³	2.3 ¹³
$V_{\text{cmax}25}$ (μmol m ⁻² s ⁻¹)	41 ⁷	34 ⁸	37 ⁸	38 ⁸	33 ^{13,14}	28 ^{13,14}	27 ^{13,14}
$J_{\text{max}25}$ (μmol m ⁻² s ⁻¹)	52 ⁷	56 ⁸	62 ⁸	58 ⁸	38 ^{13,14}	32 ^{13,14}	44 ^{13,14}
R_d (μmol m ⁻² s ⁻¹)	0.35 ⁷	0.34 ⁸	0.33 ⁸	0.33 ⁸	0.36 ^{13,14}	0.32 ^{13,14}	0.36 ^{13,14}
Q_{10} soil	2.9 ⁷	2.4 ¹⁵	2.3 ¹⁵	N/A*	1.6 ¹⁶	1.8 ¹⁶	N/A*
R_{25} soil (μmol m ⁻² s ⁻¹)	13.6 ⁷	5.9 ¹⁵	5.1 ¹⁵	N/A*	8.5 ¹⁶	9.6 ¹⁶	N/A*

¹Diggs (2004), ²Ewers et al. (2000), ³Hacke et al. (2000); ⁴Oren et al. 1998; ⁵Domec et al. (2009a); ⁶Domec et al. (2009b); ⁷this study; ⁸Maier et al. (2002); ⁹McCarthy et al. 2007; ¹⁰Domec et al. (2010a); ¹¹Pritchard et al. (2008a); ¹²Jackson et al. (2009); ¹³Maier et al. (2008); ¹⁴Ellsworth et al. (2012); ¹⁵Maier and Kress (2000); ¹⁶Bernhardt et al. (2006).

*N/A indicates that no published values were available.

and includes a 2 × 2 factorial combination of nutrient (no addition and optimum nutrition) and water (no addition and well-watered) treatments imposed on large plots within what was

then a 7-year-old loblolly pine stand (Albaugh et al. 1998, 2004). Nitrogen (N) fertilizer (ammonium nitrate) was applied as needed to maintain optimum nutrition (corresponding to a

N fertilization of 42.5 g N m⁻²), defined by a foliar N concentration of 1.3% with other macro- and micro-nutrients in balance; foliar N concentration of control trees was ~0.9%. The soil is very infertile and excessively drained. It is classified as a sandy, siliceous, thermic psammentic hapludult (Wakulla series, USDA Soil Classification System). The site receives an average annual precipitation (1945–2010) of 1150 mm (Table 1) with the winter water table being close to the soil surface. Temperatures average 17 °C annually, with seasonal averages of 26 °C in summer. Details on the study design, site and treatments are provided by [Albaugh et al. \(1998, 2004\)](#).

The Piedmont (P) site (35°58'N, 79°08'W) is part of the Duke FACE site located in a loblolly pine plantation established in 1983 on low fertility, acidic clay-loam of the Enon series, in the Blackwood Division of Duke Forest. 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 is derived from 3-year-old, half-sibling seedlings planted in 2.4 m × 2.4 m spacing. The study is represented by four plots exposed to ambient CO₂ and four plots targeted at +200 μmol mol⁻¹ CO₂ above ambient, implemented according to the Brookhaven National Laboratory FACE protocol (<http://face.env.duke.edu>). In 1998, the prototype plot and its reference plot were halved using a ditch and a barrier, and one-half of each has received annual ammonium nitrate corresponding to an N fertilization of 11.2 g N m⁻² to meet optimal values based on the optimal nutrition management approach similar to that used at the S site ([Oren et al. 2001](#)). The same design was implemented in the rest of the plots in 2005. The mean annual temperature is 15.8 °C and the growing season mean temperature is 22.1 °C. The long-term (1945–2010) average annual precipitation was 1145 ± 112 mm, evenly distributed throughout the year (Table 1).

Ecosystem model MuSICA

The multilayer, multi-leaf process-based biosphere–atmosphere gas exchange model MuSICA used here was primarily developed to simulate the exchanges of mass (water, CO₂) and energy in the soil–vegetation–atmosphere continuum and is particularly well designed for studies on conifer trees because it deals with needle clumping of various needle cohorts ([Ogée et al. 2003](#)). It assumes the terrain to be relatively flat and the vegetation horizontally homogeneous. Several species can share a common soil and the mixed canopy is partitioned into several vegetation layers (typically 10–15) where several leaf types (sunlit/shaded, wet/dry) for each cohort and species (up to three annual cohorts per species) are distinguished. The version 2.0.x of MuSICA used in this study has been upgraded compared with the versions 1.x.x used in previous publications (e.g., [Ogée et al. 2003, 2009](#)). In this new version, all routines are now organized in independent modules according to the Fortran 90 standards. In particular, the so-called force-restore

scheme used previously to describe the water and energy transfer in soils and litter ([Ogée and Brunet 2002](#)) has been replaced by a multilayer coupled heat and water transport scheme ([Braud et al. 1995](#)) that explicitly accounts for root water uptake for each species using the quasi-steady-state, radially symmetrical formulation developed by [Cowan \(1965\)](#) and reformulated by [Federer \(1979\)](#). The model also accounts for water storage in the plants with a single water storage capacity for each species that scales with leaf area ([Williams et al. 2001](#)). The turbulent transfer scheme is unchanged ([Raupach 1989](#)) but some more generic parameterizations have been introduced ([Massman and Weil 1999](#)). Leaf-to-air energy, water and CO₂ exchange are described in a similar fashion as in the original version and consist of a photosynthesis model ([Farquhar et al. 1980](#)), a stomatal conductance model ([Leuning 1995](#)), a leaf boundary-layer model ([Grant 1984, Nikolov et al. 1995](#)) and a leaf energy budget equation. Rain interception, leaf wetness duration and evaporation are computed for each species and vegetation layer using the concept of maximum storage capacity ([Rutter et al. 1971](#)). The MuSICA model allows the computation of scalar vertical profiles (e.g., air temperature and CO₂) and the different component fluxes of the carbon, water and energy budget. Notably, it gives separate estimates of not only tree water use (T), gross primary productivity (GPP) and net ecosystem exchange (NEE), but also soil moisture profile and root water uptake for each modeled soil layer (Figure 1). Specifically for this study, we incorporated a root cavitation function ([Sperry et al. 1998](#)) and a stomatal conductance response to VPD at night ([Kavanagh et al. 2007](#)).

Unlike other approaches ([Amenu and Kumar 2008](#)), our model neglects pressure losses within the root xylem, but this has been shown to be negligible, especially under dry conditions where water potential gradients occur radially through the root endodermis ([Katul and Siqueira 2010](#)). Our model also assumes that root absorption is driven by pressure differences between root–soil interface and root xylem tissue, which is also a fair assumption except when the soil is near saturation ([Siqueira et al. 2008](#)). From the soil and xylem hydraulic properties, the model then solves the relationship between water loss through T and total soil–root exchange (Q_r):

$$C_{\Psi} \frac{d\Psi_l}{dt} = Q_r - T \quad (1)$$

where C_{Ψ} is the total water storage capacity of the trees and Ψ_l is leaf water potential. The soil–root exchange can be further expressed as $Q_r = \langle \Psi_s \rangle - \Psi_l \times K_{tree}$, where K_{tree} is the total tree and rhizosphere hydraulic conductance, and $\langle \Psi_s \rangle$ is the average soil water potential perceived by the plants and depends on the root length density and water status of the soil in the different soil layers. Root cavitation (and thus tree

hydraulic conductance) and tree transpiration (through stomatal conductance) are also functions of Ψ_i , while the rhizosphere conductance depends on root length density, soil hydraulic conductivity (K_s), soil texture and Ψ_s in the different soil layers (Cowan 1965, Braud et al. 1995). Soil conductivities in each soil layer at each time step were obtained as a function of the soil saturation degree, K_s at saturation (Table 1) and from the water retention model formulated by van Genuchten (1980).

For each site, root components were split into 10 soil layers. Water uptake can continue as long as hydraulic continuity is maintained from the soil through the xylem, which is a function of the physical limits on plant water uptake and transport (Tyree and Zimmermann 2002). In the root extraction module of the model, roots can be allowed to leak and redistribute water into the soil if a hydraulic gradient exists between the roots and the soil. For the C site, modeled HR from root leakage was compared with values of HR (Domec et al. 2010a) that were determined directly from soil moisture recharge at night (Brooks et al. 2006, Warren et al. 2005). Root hydraulic failure can occur as a result of xylem cavitation (characterized by the xylem pressure at which 50% of the root conductivity is lost: P_{50} in Table 1), or if K_s at the root–soil interface falls to zero due to high rates of plant water extraction or desiccation (Sperry et al. 1998).

For each site, most MuSICA parameters were taken from published measurements of soil physical parameters (profiles of soil porosity, soil matric potential and K_s at saturation), rooting profiles (Figure 2), leaf area index (LAI), hydraulic and photosynthetic parameters and soil respiration functions (Table 1). Input variables determined specifically for this study such as root cavitation, g_{s_night} and leaf photosynthetic parameters are highlighted below and detailed in Table 1.

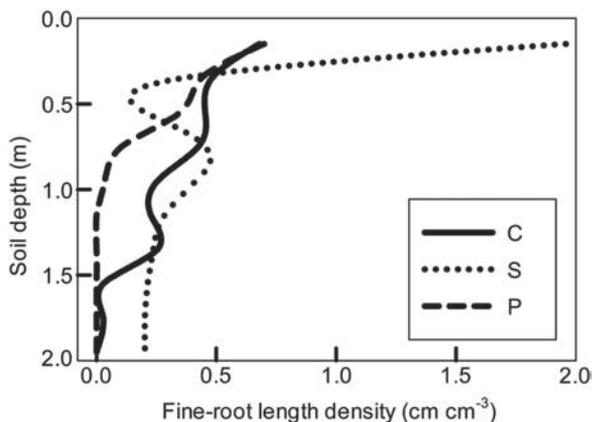


Figure 2. Fine-root length density versus depth at the three North Carolina sites (C = coastal site, S = SETRES site and P = Piedmont site). The corresponding total fine-root area index at each site is indicated in Table 2. Data are redrawn after Domec et al. (2010a) (C site), Ewers et al. (2000) and Hacke et al. (2000) (S site) and Pritchard et al. (2008a) and Jackson et al. (2009) (P site).

Nocturnal stomatal conductance (g_{s_night}) was determined at the P site from the relationship between sap flow-based canopy g_s and VPD at night (Domec et al. 2009b). Our measured values of g_{s_night} at the P site represented 28% of the g_s (Table 1). This ratio agreed well with published ratios of g_{s_night} to g_s for several conifer species (Kavanagh et al. 2007) and was therefore applied to the other two sites under current and future conditions. For comparisons with published values of T , GPP and NEE we forced the MuSICA model with meteorological values collected at each site from 1998 to 2009 depending on the years the published data were available. At the ecosystem level, NEE of carbon is defined as the difference between GPP, the amount of carbon assimilated in photosynthesis and ecosystem respiration, the amount of carbon released to the atmosphere from autotrophic and heterotrophic respiration. Model outputs were compared with published data of T from Lai et al. (2002), Schäfer et al. (2002), Stoy et al. (2006a), Domec et al. (2009b) and of GPP and NEE from Schäfer et al. (2003), Stoy et al. (2006b), McCarthy et al. (2010), Noormets et al. (unpublished), Maier et al. (2004) and Gough et al. (2004). Net ecosystem exchange estimates at the P site under eCO_2 and $eCO_2 \times N$ fertilization were calculated from published values of net primary productivity (McCarthy et al. 2010) and from estimates of heterotrophic respiration measured at the same site (Drake et al. 2011).

The effect of decreasing annual precipitation on T , GPP and NEE was modeled at each site using meteorological data typical to central North Carolina collected at the C site. An increase in temperature of 3 °C to mimic future climatic conditions (IPCC 2007) and a value of 600 $\mu\text{mol mol}^{-1}$ for atmospheric CO_2 concentration (i.e., around 200 $\mu\text{mol mol}^{-1}$ above current conditions) was applied to the baseline reference meteorological data.

Rooting profile

Fine root biomass and root length at the C and S sites were taken from Domec et al. (2010a) and Hacke et al. (2000), respectively (Figure 2, Table 1). At the P site, root profile and fine root biomass was taken from Pritchard et al. (2008a) and Jackson et al. (2009). Under future conditions, at the C and S sites, we increased root area by 20% in all the soil layers, following recent FACE studies (P site) indicating that eCO_2 increases belowground carbon allocation by stimulating fine root production and root turnover (Pritchard et al. 2008a; Jackson et al. 2009).

Leaf area index

Loblolly pine displays two cohorts of foliage during the growing season, with the development of current-year foliage beginning in early spring, peak LAI occurring in late summer (two fully expanded cohorts), followed by senescence of the

previous-year foliage occurring in the autumn. As a consequence, loblolly pine LAI varies by ~50% over the year (Table 1). Forest LAI at the C site was measured using an LAI-2000 Plant Canopy Analyzer (Licor Inc., Lincoln, NE, USA). To confirm that most of the seasonal variations in LAI were related to loblolly pine trees and to calibrate the LAI-2000, we also measured the seasonal change in leaf needle loss from 30 litter traps (0.18-m² wide laundry baskets suspended on polyvinyl chloride tubes). The litter was collected every 60 days during spring and summer, and every 2 weeks during fall and early winter. More details on LAI measurements at this site are given in Domec et al. (2009b) and Noormets et al. (2010). At the S and P sites LAI dynamic was taken from Flores et al. (2006) and McCarthy et al. (2007), respectively (Table 1). Fertilization and eCO₂ typically increase LAI with an additive effect of 20% (McCarthy et al. 2006, 2007). Under future conditions at the C site, we therefore applied this 20% increase in LAI reported at the P site between control and fertilization × eCO₂ conditions. Because loblolly pine has three-needled fascicles with stomata on all surfaces, all gas exchange and related photosynthetic parameters are expressed on an all-sided leaf area basis (using a total surface to projected leaf area ratio of 2.36, Rundel and Yoder 1998).

Hydraulic and photosynthetic model parameters

Photosynthetic capacity of loblolly pine foliage is affected by both age and position within the canopy with generally a decline in photosynthetic capacity with needle age (Maier et al. 2002, Crous and Ellsworth 2004). MuSICA was therefore parameterized with different photosynthetic parameters for each needle class. At the C site, the biochemical parameters of photosynthesis were calculated from A–C_i curves developed on detached shoots (Maier et al. 2002) from May to October 2007 using an LI-COR 6400XT (Licor). Measurements were completed by early afternoon to avoid stomatal closure. Measurements were made over eight external CO₂ concentrations (100, 180, 280, 370, 570, 800, 1500 and 2000 μmol mol⁻¹) and required ~20 min to be completed. Maximum rates of carboxylation (V_{cmax}), rate of photosynthetic electron transport (J_{max}) and mesophyll conductance were determined for each shoot with the Farquhar–von Caemmerer–Berry biochemical model of photosynthesis (Farquhar et al. 1980) as described by Sharkey et al. (2007). Several studies have looked at the effect of eCO₂ and N fertilization at the S and P site. The effect of eCO₂ on the photosynthetic parameters were taken from Maier et al. (2002) for the S site and from Maier et al. (2008) and Ellsworth et al. (2012) for the P site (Table 1). Analysis of A–C_i curves indicates that in general V_{cmax} and J_{max} are reduced by 15% in response to eCO₂ (Crous and Ellsworth 2004; Maier et al. 2008), so we applied this down-regulation for the C site. Although fertilization results in significant increases in foliar nitrogen concentration, its impact on photosynthetic parameters in loblolly pine is low

(Teskey et al. 1994, Samuelson et al. 2001, Gough et al. 2004). Therefore, a stimulation of only 10% was added for fertilized trees growing under future climate conditions.

Cavitation vulnerability curves were determined using the air injection technique (Sperry and Saliendra 1994) on six roots (1.5–2.5 mm in diameter) collected in February–March 2008 at the C site and at the P site. At the S site, vulnerability curves were taken from Ewers et al. (2000). Because of the lack of data at the C and S sites, the effect of eCO₂ on the hydraulic input parameters (K_{tree}, percent K_{tree} in roots, P₅₀) measured at the P site (Domec et al. 2009a, 2010b) was applied to the other two sites (in Table 1).

Results

Measured versus modeled water and carbon fluxes

For clarity, we only present in detail here the results related to the effects of future climatic conditions with and without N fertilization on the water and carbon fluxes (see Table S1 available as Supplementary Data at *Tree Physiology Online*). Briefly, across sites, N fertilization under current climatic conditions marginally increased *T* per ground area (<15%) because the sharp increase in LAI was compensated by a decrease in *T*_{leaf} (*T* per unit leaf area) by 25–40%. The increase in *T* on fertilization was only significant at the S and C sites. However, fertilization stimulated GPP by 13–27% with the highest effect at the S and C sites. Fertilization only had a minor effect on *T* and GPP at the P site. Measured and modeled 30-min water and carbon fluxes are displayed in Figure 3a for four sunny days followed by two cloudy days. The model reproduced reasonably well the daily variations in *T*, GPP and NEE. Under hot days, however, the model over-predicted *T* by 5–8%. On dry days when soil moisture content was <15%, NEE was also underestimated by 7–12%. Root leakage at night simulated by MuSICA underestimated HR by up to 40% at the C site where direct measurements of HR were available (Figure 3b). Modeled HR was also calculated as the difference between the minimum soil moisture content of 1 day and the maximum soil moisture content of the next day. Although this nightly increase in soil moisture agreed well with root leakage, it also underestimated measured HR during the peak of the growing season (Figure 3b).

The annual *T* and GPP under current conditions as well as under eCO₂ estimated by MuSICA for the unfertilized and fertilized stands agreed within 9% of the empirical data (Figure 4). Excluding the amount of water released into the soil through root leakage from the modeling reduced annual *T* prediction by 14% at the C site and by 5–6% at the other two sites (Table 2, dashed lines in Figure 4). As a consequence, the absence of HR was predicted to diminish annual GPP and NEE by 16–20% at the C site and by 5–12% at the S and P sites (Table 2, dashed lines in Figure 4). The effect of HR on *T* and GPP was

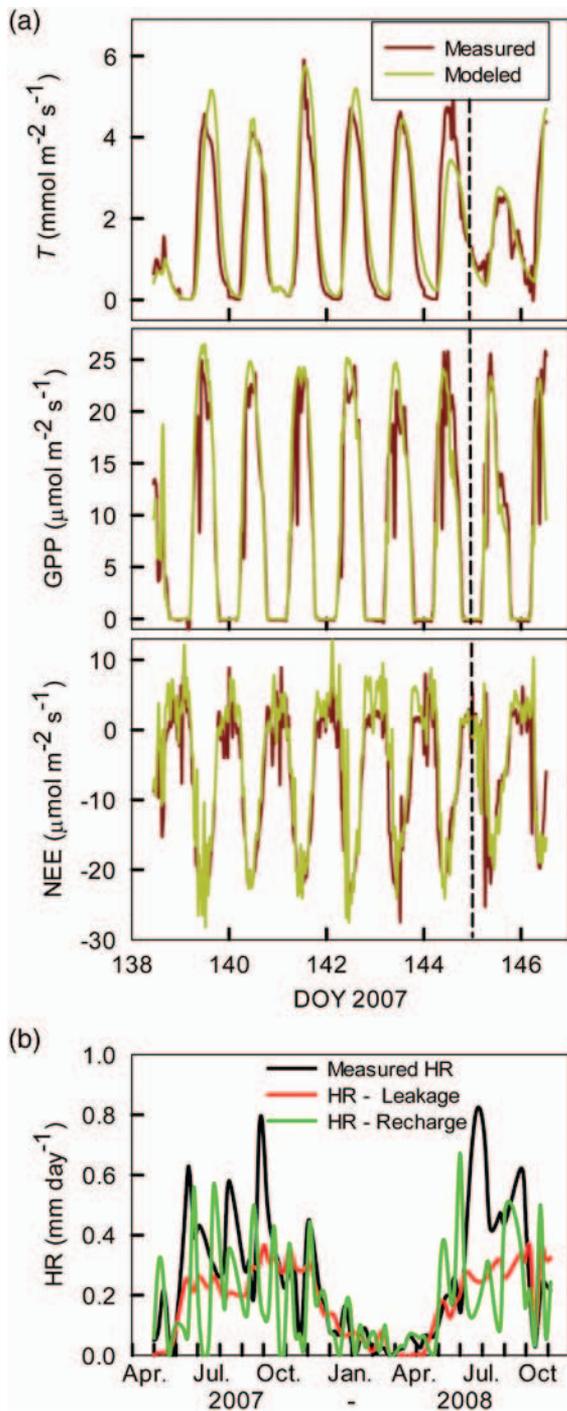


Figure 3. (a) Modeled from MuSICA versus measured tree transpiration (T) derived from sap-flow (Domec et al. 2010a), gross ecosystem productivity (GPP) and net ecosystem exchange (NEE) both derived from eddy-covariance measurements (Noormets et al. 2010) at the coastal site (C site). (b) Comparisons of measured hydraulic redistribution (HR, Domec et al. 2010a) and modeled hydraulic redistribution from root leakage, and from soil moisture recharge at night over two growing seasons at the C site. The vertical dash lines in (a) represent the transition between sunny and cloudy days.

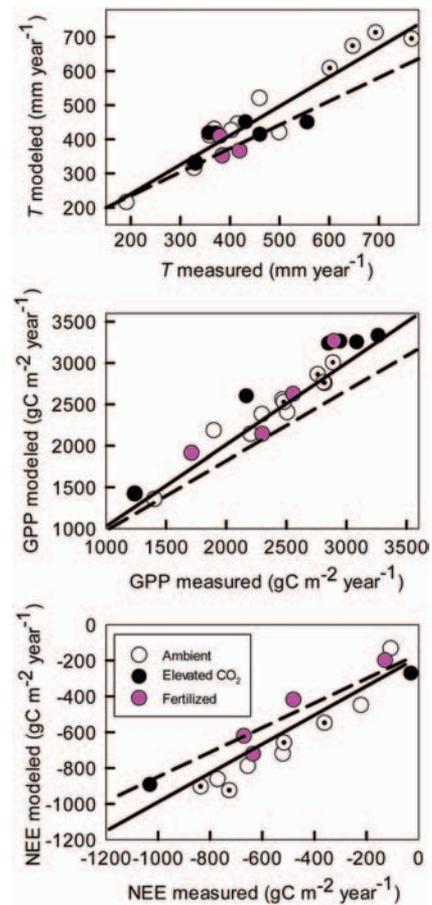


Figure 4. Relationships between modeled versus measured tree transpiration (T), gross ecosystem productivity (GPP) and net ecosystem exchange (NEE) at three North Carolina loblolly pine sites. White symbols are for current climatic conditions, black symbols are for elevated CO₂ (eCO₂) conditions and pink symbols are for N fertilization or for eCO₂ × N fertilization conditions. Dotted white symbols represent the coastal site (C site) where a large amount of root water leakage (HR) was present. The full lines represent the linear fit to the data points ($r^2 > 0.87$, $P < 0.001$). The dashed lines represent the linear fit by assuming that no root leakage occurred. Excluding the amount of water release into the soil though root leakage reduced the overall T prediction by 17%, GPP by 10% and NEE by 14%. The number of points are different in the three panels because some published results did not report all the parameters modeled (T , GPP and NEE) in the same study.

predicted to decline under future conditions by 10–13% and 4–7% at the C and P sites, respectively (Table 2). As a consequence of this reduction in HR under future conditions NEE was also predicted to reduce by 9–14% (Table 2, dashed lines in Figure 4).

Effect of night transpiration on HR

Vapor pressure deficit at night was >0.5 kPa for 20% of night-time hours at the P site, versus 34% at the C and S sites. At the C site, T_{night} never exceeded 8% of T , whereas at the other two sites, T_{night} increased water loss by 14–18%. As a consequence, the effect of T_{night} on HR was larger at the P site, reducing direct root leakage by more than a third, compared

Table 2. Root water that was predicted to leak at night (hydraulic redistribution; HR) presented as a percentage of the total root water uptake (% Root leakage), modeled effect of HR on annual gross primary productivity (GPP) and net ecosystem exchange (NEE), and modeled effect of night transpiration (T_{night}) and root cavitation on the amount of water redistributed by the roots in the top soil layers for the three sites studied. Values are presented assuming 900 mm of annual precipitation under current conditions (CO_2 concentration = $400 \mu\text{mol mol}^{-1}$) as well as under future conditions (temperature = $+3 \text{ }^\circ\text{C}$; CO_2 concentration = $600 \mu\text{mol mol}^{-1}$).

	Coastal (C)		Sandhills (S)—SETRES		Piedmont (P)—Duke FACE	
	Current	Future	Current	Future	Current	Future
% Root leakage (HR)						
Annual	14	4	5	2	6	1
Growing season	20–45	8–15	8–10	3–5	7–11	2–4
Effect of root leakage on GPP	19%	7%	7%	4%	9%	3%
Effect of root leakage on NEE	16%	9%	5%	<2%	7%	<2%
Effect of T_{night} on root leakage (HR)	–25%	–41%	–31%	–52%	–36%	–56%
Effect of root cavitation on HR	–17%	–11%	–4%	–9%	–22%	–24%

with just 25% at the C site (Table 2). The water potential gradient existing between deep soil and the plant became greater than the gradient between different soil layers, which decreased HR in upper soil layers. Furthermore, T_{night} was larger under future conditions since an increase in temperature by $4 \text{ }^\circ\text{C}$ was predicted to increase VPD at night by at least 0.1 kPa . Using this prediction, the modeling outputs from MuSICA showed that the negative effect of T_{night} on root leakage would be larger under future conditions (Table 2).

Root water uptake and root water loss at night

Root mass was larger at greater soil depth at the S site than at the P and C (Figure 2) sites where deeper rooting depths were found in sandy soils relative to clay or loam soils. While roots were observed in the deepest measured soils, they were <5% of the total found in the profile. The maintenance of relatively low (more negative) soil water potentials at depth depended upon the range of water potentials over which trees were taking up water. At the C site, during summers the depth of maximum water uptake simulated by MuSICA shifted below 1 m, towards regions of higher soil water potential (Figure 5a and c). This trend in root uptake was maintained until the end of the growing season. At the S site, simulated root water uptake was quite deep but was mostly concentrated in the top 50 cm (Figure 6a) where almost 50% of root biomass was found (Figure 2). At the P site, characterized by shallow roots, root water uptake was localized in the upper 40 cm in spring, when soil water potentials were above -0.6 MPa , but switched rapidly to deeper layers as soil dried (Figure 7a and c). Large differences in simulated root leakage existed between sites and deep roots at the S site did not necessarily translate into a large amount of water released by the roots at night (Figure 6b). At the C site root leakage accounted for 14% of the growing season water use,

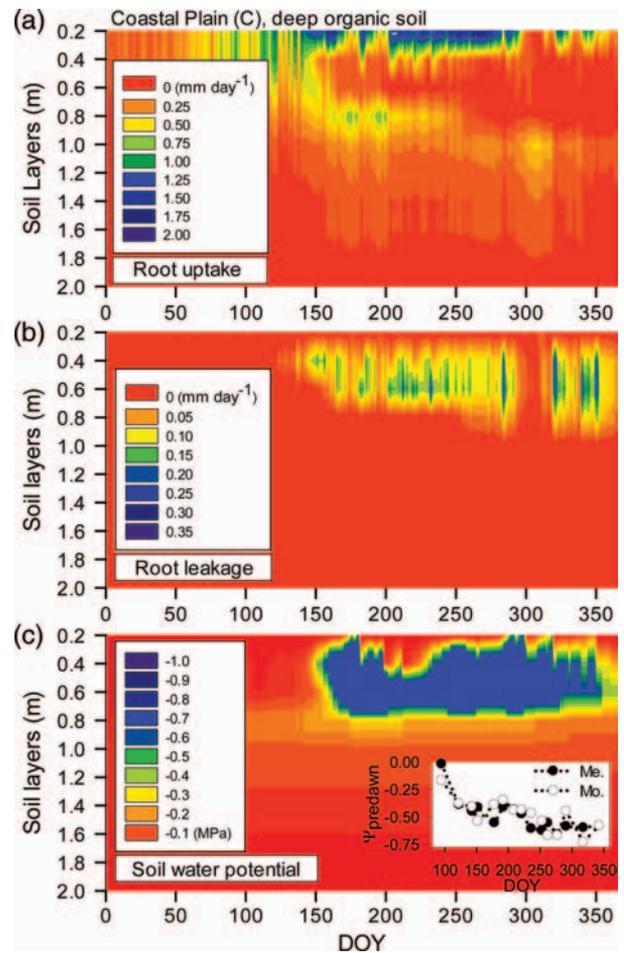


Figure 5. Modeled root water uptake (a) and root leakage (b) by loblolly pine trees from the coastal plain of North Carolina. The insert in (c) shows the comparisons of measured (Me.) predawn water potential (Ψ_{predawn}) (Domec et al. 2009b) and modeled (Mo.) Ψ_{predawn} for the year 2007.

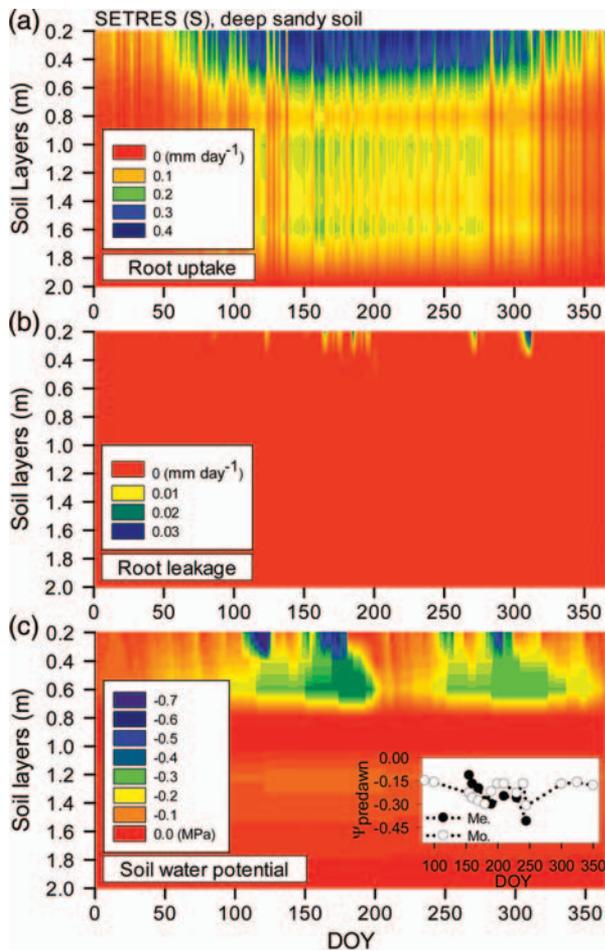


Figure 6. Modeled root water uptake (a), root leakage (b) and soil water potential (c) by loblolly pine trees from the Sandhills of North Carolina. The inset in (c) shows the comparisons of measured (Me.) predawn water potential (Ψ_{predawn}) (Hacke et al. 2000) and modeled (Mo.) Ψ_{predawn} for the year 1998.

with a peak of 35% in early fall (Table 2, Figure 5b). Towards the end of a drought cycle (DOY 275), night-time root leakage replaced 0.3–0.5 mm day⁻¹ in the upper soil at this site, representing 25–35% of the daily water extracted from that layer. At the S and P sites, root leakage did not account for >10% of the growing season water uptake (Table 2; Figures 6b and 7b). However, at the P site, root leakage increased as soil dried to reach almost 0.10 mm day⁻¹ in late fall (Figure 7b).

In all sites, modeled predawn water potentials (Ψ_{predawn}) compared very well with measured Ψ_{predawn} (inset in Figures 5c, 6c and 7c). The main differences between measured and predicted Ψ_{predawn} occurred at the C site at the beginning of the growing season when soil water potentials were close to zero, or when soils were at full water holding capacity (Figure 5a and c).

Effect of precipitation water use and carbon assimilation and HR

Under future climatic conditions (eCO₂ plus elevated temperature) and for precipitations within 20% of current precipitations

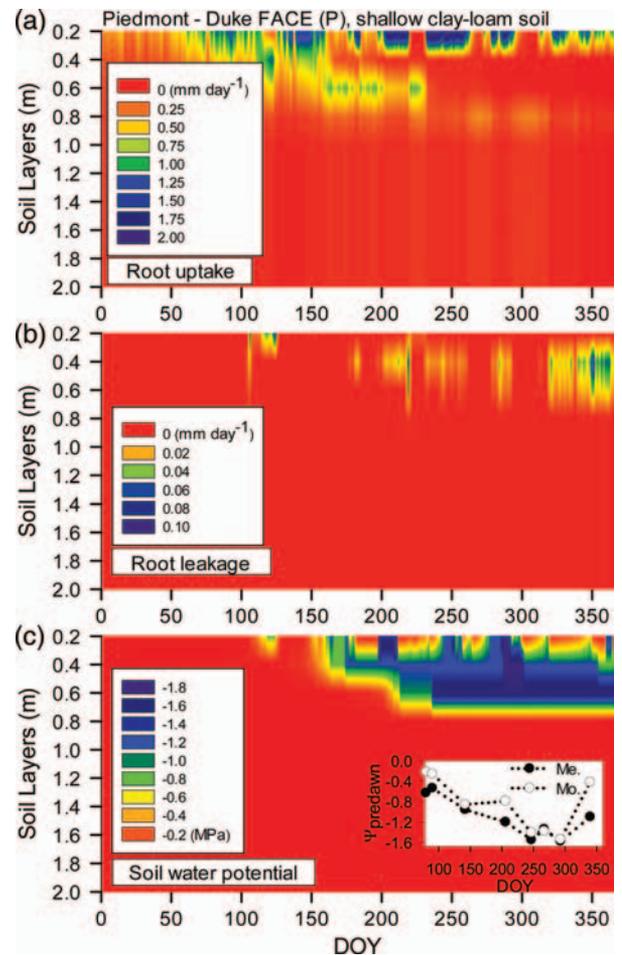


Figure 7. Modeled root water uptake (a), root leakage (b) and soil water potential (c) by loblolly pine trees from the North Carolina Piedmont. The inset in (c) shows the comparisons of measured (Me.) predawn water potential (Ψ_{predawn}) (Domec et al. 2009a) and modeled (Mo.) Ψ_{predawn} for the year 2007.

(800–1200 mm year⁻¹), T was predicted to be marginally reduced at the C site and slightly increased at the S site (Figure 8, see Table S1 available as Supplementary Data at *Tree Physiology Online*). Future climatic conditions were predicted to have no significant effect on T at the P site. However, under future conditions and N fertilization, T would decrease by 25%, or 150 mm year⁻¹, at the C site, by 15%, or 75 mm year⁻¹, at the P site, and by 8% or 16 mm year⁻¹ at the S site. Those trends were largely due to the negative effect of fertilization on K_{tree} (Table 1) and the effect of eCO₂ on stomatal conductance. Below 700 mm of precipitation per year, T started to drop significantly at the C and P sites. Under future conditions at the P site, the drop in T caused by partial rain exclusion was predicted to be faster, reflecting the reduction in HR (root leakage). This was the consequence of the negative effect of larger VPD-induced T_{night} on the magnitude of HR (Table 2). There was no effect of precipitation on T at the S site.

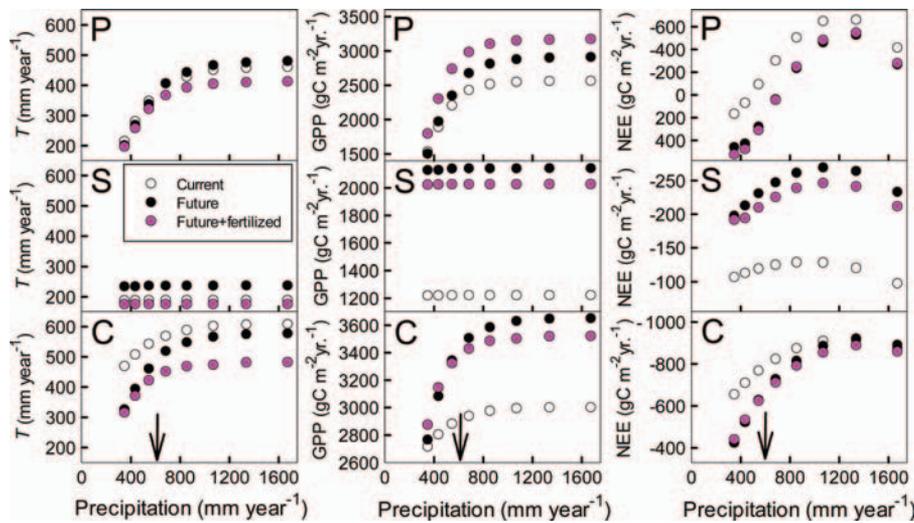


Figure 8. Modeled (MuSICA) tree transpiration (T), gross ecosystem productivity (GPP) and net ecosystem exchange (NEE) at the three north Carolina sites (C = coastal site, S = SETRES site and P = Piedmont site) as a function of precipitation. Simulations are given under current conditions as well as under future conditions (temperature = +3 °C; CO₂ concentration = 600 $\mu\text{mol mol}^{-1}$), and under future conditions plus N fertilization. The arrows represent the minimum precipitation ever recorded for these sites (i.e., 590–640 mm).

As predicted, the three sites had greater GPP under future climatic conditions (Figure 8) with an average increase of >500 $\text{g C m}^{-2} \text{ year}^{-1}$ (Figure 8). At the site with rich organic soil (C site), the GPP estimated by MuSICA was ~ 2800 and $3200 \text{ g C m}^{-2} \text{ year}^{-1}$ under the control and fertilized conditions, respectively, and increased by 18% more under future conditions. However, at this site, the effect of N fertilization on GPP under future conditions was negligible (Figure 8), indicating that N limitation at this site would not impose a constraint on future productivity. At the S site, fertilization was predicted to increase GPP under current conditions by 40% (data not shown) and by >70% under future conditions (Figure 8). At this site, GPP was not affected by changes in precipitation and NEE increased with high precipitation, which was exacerbated under future and fertilized conditions. At the P site, we found that future conditions would stimulate GPP by only 12%, but that future conditions plus N fertilization would increase GPP by almost 24%. As a consequence of a steeper decrease in T than in GPP with reduced precipitation, water use efficiency was predicted to increase with decreasing precipitation (see Figure S1 available as Supplementary Data at *Tree Physiology* Online). Water use efficiency was also predicted to increase by 40–60% under future conditions (see Figure S1 available as Supplementary Data at *Tree Physiology* Online). At all the sites, as yearly precipitation decreased <700 mm, the effects of future conditions and N fertilization were reduced.

Because of the reduced root leakage (HR) under future conditions at the C site (Table 2), the reduction in T , GPP and NEE was predicted to be more sensitive to reduced precipitation under future conditions. For example, a reduction in annual rainfall from 900 to 450 mm would reduce T by 19% under current conditions and by 36% under future conditions

(Figure 8). At the other two sites, since root leakage represented <11% of T , the reduction in root leakage had minor effect on the response of T and GPP to precipitations. As opposed to the C site, the rates of decline in T and GPP with decreasing precipitation at the P and S sites were similar under current and future conditions (Figure 8).

Discussion

The MuSICA model reproduced reasonably well the daily variations in water and carbon fluxes and predicted that N fertilization alone would decrease T but would stimulate GPP with the strongest effect at the S site (Albaugh et al. 1998) and at the C site (McCarthy et al. 2010). The over-prediction of T on hot days, however, was probably because stomatal sensitivity to VPD for this species has been shown to decrease with decreasing water availability (Domec et al. 2009b). The under-estimation of NEE on dry days was likely due to an over-estimation of soil respiration under dry conditions (Palmroth et al. 2005, Noormets et al. 2008). Soil respiration includes various complex processes such as root growth, microbial activities and CO₂ dissolution in soil water (Pangle and Seiler 2002, Bernhardt et al. 2006) that are not explicitly included in the model, and the down-regulation of heterotrophic respiration during drought is captured only empirically and might explain the higher predicted rates of respiration.

Root mass at all sites decreased with soil depth similar to other studies (Schenk and Jackson 2002, Pritchard et al. 2008a). However, root mass was larger at greater soil depth at the S site than at the P and C sites (Figure 2), in agreement with the root biogeography analysis of Schenk and Jackson (2002) that shows that deeper rooting depths are more likely

found in sandy soils than in clay or loam soils. The observations that root water uptake varied significantly by soil type, and that deeper rooting provides access to more available nutrients (Laclau et al. 2004, da Silva et al. 2011) especially under eCO₂ (Pritchard et al. 2008b, Iversen et al. 2011), highlight the need for models to incorporate soil depth when estimating N availability. Moreover, since coniferous species have been shown to respond to annual fertilization by reducing fine root biomass (Albaugh et al. 1998, Achat et al. 2008, Bakker et al. 2009), models should also take into account that fertilized trees can meet their nutrient demands with a smaller fine root uptake system than unfertilized trees.

Model simulations in this study allowed a better understanding of the interaction between climate and HR for contrasted soil textures. Although HR has been shown to occur in a wide range of ecosystems (Burgess et al. 1998, Hultine et al. 2003, Meinzer et al. 2004, Oliveira et al. 2005, Bleby et al. 2010, Domec et al. 2010a), most studies have focused on the tree level without scaling up this effect to the whole ecosystem. At the sandy site (S), simulated root water uptake was quite deep but was mostly concentrated in the top 50 cm where most nutrients are found (Albaugh et al. 1998; King et al. 2002). Although the sandy soil at the S site allowed for deep roots, root biomass <50 cm was evenly distributed (Laclau et al. 2001), which prevented significant root leakage because water potential gradients could not be large enough between soil and roots (Irvine et al. 2005, Katul and Siqueira 2010, Markewitz et al. 2010). Root leakage at night simulated by MuSICA (Figures 5b, 6b and 7b) represents the passive part of the water hydraulically lifted by the deep roots. Although HR could be seen as a passive process, which depends on the soil suction head and the root distribution within the soil column (Burgess et al. 2001, Meinzer et al. 2004), there is also evidence suggesting that root aquaporins may play an active role in regulating root water uptake (McElrone et al. 2007), and possibly in influencing HR. This hypothesis could explain in part why the modeled root leakage was 30–40% lower than the measured HR at the C site (Domec et al. 2010a) and 20% lower than the estimated HR based on stand water balance determined at the P site (Oishi et al. 2010). At the C site, our model prediction confirmed that water leakage by roots can be important and that deep roots can facilitate water transfer between deep and shallow soil layers (Domec et al. 2010a). Even when root leakage only represents a relatively small amount of ecosystem water use (<0.2 mm day⁻¹) and just a fraction (5–10%) of total water use during spring and early summer (Figure 5b), the daily partial recharge of upper soil water by shallow roots is enough to slow the decline in soil water content and thus maintain upper soil water availability (Lee et al. 2005, Warren et al. 2007). This influx of soil water maintains soil water potential above -0.8 MPa (Figure 5c), and thus limits root cavitation to <50% (P_{50} , Table 1). Previous work has shown that water supplied by HR can help keep fine roots hydrated for

longer periods during drought (Domec et al. 2004), and delay the drying of top soil layers (Brooks et al. 2006; Domec et al. 2006), therefore sustaining water uptake from the nutrient-rich horizons (Jobbagy and Jackson 2004; Prieto et al. 2010; Armas et al. 2011).

Our model simulations highlighted also the interactive effects of nutrients and eCO₂ on water use by predicting that at all sites, T would be slightly increased when fertilization is applied. This was the direct consequence of the negative effect of N fertilization on tree water transport capacity (Table 1) and the effect of eCO₂ on stomatal conductance (Warren et al. 2011). As directly measured at the C and P sites using sap flow techniques, T was sensitive to precipitation (Schäfer et al. 2002, Domec et al. 2009b), but not at the S site (Ewers et al. 1999, 2000). At the S site, soil is extremely nutrient poor, and most physiological responses have been limited by nutrient rather than by water (Albaugh et al. 1998, 2004). The very deep, coarse sandy soils allow roots to penetrate very deep, resulting in deep soil water uptake (Albaugh et al. 1998). This rooting pattern can explain why T was not as responsive to precipitations, because when trees have access to deep water they may not be as responsive to rapid changes in soil moisture content of the shallow soil layers following precipitations.

MuSICA predicted that the three sites would have greater GPP under future climatic conditions and N fertilization. At the S site, this gain in production was the consequence of a large increase in leaf area (Linder et al. 1987, Teskey et al. 1994, Maier et al. 2004) rather than by the enhancement of photosynthesis rates per unit leaf area (Table 1, Maier et al. 2004). Gross primary productivity at the S site was similar to that estimated by Law et al. (1999) for a *Pinus ponderosa* Laws. pine forest growing on a sandy site and with a similar LAI (1.5–2). The outputs of MuSICA for the fertilized conditions were also similar to GPP estimated from another process-based model (Lai et al. 2002). Consistent with published studies, our modeling exercise suggested that the loblolly pine stands exposed to eCO₂ will exhibit enhanced carbon gain if fertilization is applied (Oren et al. 2001, McCarthy et al. 2010). However, under rich organic soil (C site), the effect of N fertilization under future conditions was negligible (Figure 8), indicating that N limitation may not impose a constraint on future productivity or that the trees were not N limited. At all the sites, the reduced effect of future conditions and N fertilization when precipitation dropped below 700 mm provided limited support for the early prediction that the response of productivity to eCO₂ would be greater in drier ecosystems (Strain and Bazzaz, 1983, Nowak et al. 2004). At the S site, there seemed to be an optimal level of soil moisture with excesses and deficiencies having negative effects on soil respiration rates (Noormets et al. 2008). Since GPP was not affected by changes in precipitation at this site, as a consequence NEE increased with high precipitation (Maier and Kress 2000, Pangle and Seiler 2002).

Vapor pressure deficit at night was sufficient to drive significant T_{night} at all sites (Oishi et al. 2008, Novick et al. 2009), which reduced root leakage (Table 2), because the plant and the atmosphere become a sink for hydraulically redistributed water pools. This is consistent with previous studies that have shown that HR can be artificially reduced when T_{night} is experimentally increased (Caldwell and Manwaring 1994, Bleby et al. 2010). Under current conditions, with relatively low T_{night} , HR at the C site maintained steady soil water availability despite seasonality in rainfall, facilitating greater carbon fixation, where transpiration rates can increase by 30–50% (Lee et al. 2005, Domec et al. 2010a). However, at the C site, the reduction of root leakage under future conditions was predicted to influence the sensitivity of T to precipitation, thus limiting the effect of HR on water and carbon fluxes (Table 2). At the other two sites, T_{night} increased water loss by 10–14%, which reduced water use efficiency (see Figure S1 available as Supplementary Data at *Tree Physiology* Online) since water loss at night is not accompanied by a carbon gain (Caird et al. 2007). In the model simulation, we assumed that $g_{s,\text{night}}$ and its sensitivity to VPD was similar under eCO₂ and N fertilization. The next step will be to determine whether future conditions affect $g_{s,\text{night}}$ and T_{night} and thus the sensitivity to VPD at night.

Conclusions

The predicted reductions in HR under future climate conditions are expected to play an important regulatory role in the land–atmosphere interaction by affecting the whole ecosystem water balance and thus the partitioning of net radiation between sensible and latent heat fluxes (Feddes et al. 2001, Siqueira et al. 2009). The role of afforestation in carbon sequestration has been acknowledged in the Kyoto protocol. Thus, a basic understanding of how water availability interacts with prevailing water demand is required for quantifying the potential of forest plantations to store carbon in an economically and environmentally sustainable manner (Law et al. 2000, Johnsen et al. 2001). Knowledge on how water use by plant and carbon sequestration could be affected by HR is therefore a relevant issue, especially in forests where water availability is predicted to decrease with climate change. Our work enhances our confidence in accurately predicting how HR impacts on forest carbon balance by establishing a direct link between plant root functioning and carbon fluxes. Our modeling study showed that deep roots do not necessarily translate into large volume of HR if soil texture, as was the case at the S site, does not allow a large water potential gradient to occur (Markewitz et al. 2010). In addition, we showed that future climate conditions would increase night-time transpiration, thus limiting the effect of HR on water and carbon fluxes. Future soil–vegetation–atmosphere transfer models should therefore account for HR and the interactions between

rooting depth and soil texture should treat root distribution dynamically in response to climate change and N fertilization levels. Hydraulic redistribution has not been widely implemented in weather forecasting or climate studies (Lee et al. 2005), and current land surface models do not use proper root distribution, root water uptake and HR in their simulations (Dirmeyer 2001, Feddes et al. 2001). Consequently, these oversimplified model simulations likely contain errors in the computation of dry-season evapotranspiration and the associated heat fluxes, and thus in the possible feedbacks between soil moisture and climate. We acknowledge that it is often impossible, and probably unnecessary, to incorporate all the details of complicated physical and biological processes into a large-scale model. Yet, as with MuSICA, incorporating simplified physical mechanisms may be necessary to improve coarse scale modeling. Such an analysis is important for several reasons. First, HR is found in most biomes, especially water-limited ones (Jackson et al. 2000, Meinzer et al. 2004). Second, the current importance of HR on plant water use is increasing with reduced global precipitation rates (Howard et al. 2009), but HR is expected to decline due to predicted increase in T_{night} .

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Conflict of interest

None declared.

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