



Carbon accumulation in loblolly pine plantations is increased by fertilization across a soil moisture availability gradient



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ABSTRACT

Silvicultural practices, particularly fertilization, may counteract or accentuate the effects of climate change on carbon cycling in planted pine ecosystems, but few studies have empirically assessed the potential effects. In the southeastern United States, we established a factorial throughfall reduction (D) × fertilization (F) experiment in 2012 in four loblolly pine (*Pinus taeda* L.) plantations encompassing the climatic range of the species in Florida (FL), Georgia (GA), Oklahoma (OK), and Virginia (VA). Net primary productivity (NPP) was estimated from tree inventories for four consecutive years, and net ecosystem productivity (NEP) as NPP minus heterotrophic respiration (R_H). Soil respiration (R_S) was measured biweekly-monthly for at least one year at each site and simultaneous measurements of R_S & R_H were taken five to eight times through the year for at least one year during the experiment. Reducing throughfall by 30% decreased available soil water at the surface and for the 0–90 cm soil profile. Fertilization increased NPP at all sites and D decreased NPP (to a lesser extent) at the GA and OK sites. The F + D treatment did not affect NPP. Mean annual NPP under F ranged from 10.01 ± 0.21 MgC·ha⁻¹·yr⁻¹ at VA (mean ± SE) to 17.20 ± 0.50 MgC·ha⁻¹·yr⁻¹ at FL, while the lowest levels were under the D treatment, ranging from 8.63 ± 0.21 MgC·ha⁻¹·yr⁻¹ at VA to 14.97 ± 0.50 MgC·ha⁻¹·yr⁻¹ at FL. R_S and R_H were, in general, decreased by F and D with differential responses among sites, leading to NEP increases under F. Throughfall reduction increased NEP at FL and VA due to a negative effect on R_H and no effect on NPP. Mean annual NEP ranged from 1.63 ± 0.59 MgC·ha⁻¹·yr⁻¹ in the control at OK to 8.18 ± 0.82 MgC·ha⁻¹·yr⁻¹ under F + D at GA. These results suggest that fertilization will increase NEP under a wide range of climatic conditions including reduced precipitation, but either NPP or R_H could be the primary driver because F can increase stand growth, as well as suppress R_S and R_H . Moreover, D and F never significantly interacted for an annual C flux, potentially simplifying estimates of how fertilization and drought will affect C cycling in these ecosystems.

1. Introduction

Forests of the southeastern United States cover 99 million hectares,

almost one third of the forested lands in the contiguous U.S. (Oswalt et al., 2014). About 34% of southeastern forests are pine ecosystems, with 15% originating from natural regeneration and 19% from

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plantations (Wear and Greis, 2012). Loblolly pine (*Pinus taeda* L.) is the dominant planted species, and occupies more than 13 million hectares (69% of total planted pine) (Wear and Greis, 2012; Oswalt et al., 2014). Because of their extent and high productivity, southern pine plantations are important economic and ecological resources. For example, this region produces about 60% of the nation's timber (Prestemon and Abt, 2002), and generates more wood than any country (Wear and Greis, 2012). Southeastern forests annually sequestered 176 Tg C from 2000 to 2005, far more than any other forested region in the continental United States, an amount sufficient to offset 42% of the region's anthropogenic CO₂ emissions (Lu et al., 2015).

The implementation of coordinated, intensive silvicultural treatments across the region has substantially increased pine productivity. Southern pine plantations established in the 2000s can produce up to 16 Mg·ha⁻¹·yr⁻¹ of above ground biomass, four times more than forests planted in the 1950s and 1960s (Jokela et al., 2004; Fox et al., 2007), and up to six times more than extensively managed naturally-regenerated pine forests (Cubbage et al., 2007). Much of this increased productivity can be attributed to the alleviation of nutrient deficiency through fertilizer application (Fox et al., 2007; Jokela et al., 2010). The area of southern pine plantation fertilized annually increased from 1 × 10⁵ ha in the mid 1990s to more than 6 × 10⁵ ha in the early 2000s in the region (Albaugh et al., 2012), resulting in not only increased productivity, but also increased sequestered C (Markewitz, 2006; Vogel et al., 2011; Albaugh et al., 2012). For example, mid rotation fertilization increased stem C sequestration by 19.2 Mg CO_{2eq} in a loblolly pine plantation managed on a 25 year rotation (Albaugh et al., 2012).

During this and the next century, climate change may be an important factor affecting C cycling of pine plantations. Air temperatures are expected to increase between 2.5 °C and 4.0 °C across the region by the end of the 21st century (Collins et al., 2013; Walsh et al., 2014). Annual precipitation may slightly increase, but extreme rainfall events and more frequent drought periods during the growing season are expected within the next two decades (Christensen et al., 2007; Li et al., 2011; Dai, 2012). These expected climatic changes most likely will change plant species productivity and range (Noormets et al., 2010; Wear and Greis, 2012; Johnson et al., 2014; Gonzalez-Benecke et al., 2017) and survival (Berdanier and Clark, 2016). The southeastern United States has already experienced multiyear droughts in the last two decades (Crosby et al., 2015), that reduced productivity and C sequestration in planted pines (Bracho et al., 2012).

The positive effects of fertilization on the productivity of planted pines is well documented (Jokela and Martin, 2000; Jokela et al., 2004; Fox et al., 2007; Samuelson et al., 2008; Will et al., 2015), while results for the effect of water availability on productivity are mixed. Irrigation, when combined with fertilization in loblolly pine plantations, has caused relatively small increases in pine productivity above fertilization alone (Albaugh et al., 2004; Samuelson et al., 2008), no increases (Coyle et al., 2008), or relatively large increases (Campoe et al., 2013). Simulations have also indicated that net canopy assimilation is increased by 10% or less across the natural growth range of loblolly pine when the effects of water limitation are removed (Sampson and Allen, 1999). In contrast, natural drought has had a negative effect on loblolly pine stand growth (Ellsworth, 2000; Amateis et al., 2008; Domec et al., 2009). However, the interaction of fertilization and drought on loblolly pine has rarely been tested experimentally. The positive effects of nutrient amendments on pine productivity may be constrained by drought (Tang et al., 2004), or fertilization may enhance growth even under moderate drought (Samuelson et al., 2014; Maggard et al., 2016).

Productivity in loblolly pine is strongly related to leaf area index (LAI) (Sampson and Allen, 1999; Burkes et al., 2003; Jokela et al., 2004; Martin and Jokela, 2004). However, changes in growth in relation to LAI (growth efficiency) do occur and may reflect changes in stand development or response to environmental stress. For example, growth efficiency may be affected by stem density (Burkes et al., 2003) or age (Will et al., 2002), while for environmental factors, diverse results have

been found in relation to nutrient and water availability (Sampson and Allen, 1999; Samuelson et al., 2001, 2004; Albaugh et al., 2004). Others have found growth efficiency is maintained at low to intermediate LAI under a range of silvicultural treatments at different sites (Jokela et al., 2004), suggesting the potential of growth efficiency to change in planted loblolly pine in response to fertilization and water availability requires further clarification.

Net ecosystem productivity (NEP) is a measure of the amount of C potentially available for accumulation in an ecosystem during a given time (Lovett et al., 2006), reflecting the difference between NPP and R_H. Fertilization causes an increase in whole ecosystem C accumulation in pine plantations (Shan et al., 2001; Vogel and Jokela, 2011; Vogel et al., 2011), mostly because of increased tree biomass and forest floor pools. Less certain are fertilization effects on soil C (Vogel et al., 2011), which does not directly follow trends in aboveground productivity (Vogel et al., 2015). Autotrophic (R_A) and R_H are the primary C fluxes out of the soil. Both fluxes often decrease as nitrogen limitation is reduced (Ramirez et al., 2010; Kamble et al., 2013; Sun et al., 2014; Zhong et al., 2016), an effect previously observed in loblolly pine plantations (Maier and Kress, 2000; Butnor et al., 2003; Lee and Jose, 2003; Tyree et al., 2006; Zhang et al., 2016). These results could be associated with less belowground carbon allocation with fertilization (Haynes and Gower, 1995; Maier et al., 2004; Janssens and Luyssaert, 2009), resulting in lower fine root biomass (Giardina et al., 2003; Janssens et al., 2010), root exudates, and rhizosphere microbial biomass (Janssens et al., 2010). Increases in soil moisture by irrigation have increased soil respiration and microbial activity in loblolly pine plantations (Samuelson et al., 2009), and total below ground C allocation in a fire maintained longleaf pine (Ford et al., 2012). In contrast, reductions in soil moisture have reduced soil microbial and macro-invertebrates activity (Sardans and Penuelas, 2005; Zhang et al., 2016). We are not aware of any studies in southern pine that have examined the effects of reduced moisture availability and fertilization simultaneously with an explicit separation of plant productivity and soil respiration fluxes.

The objective of this study was to quantify the effects of fertilizer additions, decreased soil moisture due to throughfall reduction, and their interaction on productivity and C accumulation potential of loblolly pine plantations. Replicated experiments were installed in four locations spanning the natural climatic growing range of loblolly pine in the southeastern United States. We expected an increase in NPP from fertilization and a decrease with reduced soil water availability through changes in leaf area index. Consequently, growth efficiency was expected to be unchanged under different treatments but to change among sites because of differences in site characteristics or stand development. Total and heterotrophic soil respiration also were expected to decrease as a result of fertilization and soil water reduction. Testing these predictions allows for an estimate of NEP response to a key silvicultural and climatic variable in the region, while providing insights on the causes of variation in the primary drivers (NPP, R_s, and R_H) of the NEP response.

2. Materials and methods

2.1. Sites description and experimental design

This project was executed within a regional integrated research network, known as PINEMAP (Pine Integrated Network: Education, Mitigation, Adaptation Project, www.pinemap.org), that focused on loblolly pine productivity in relation to changing climate. The effects of reduced soil water and increased nutrient availability on carbon dynamics were examined using a throughfall exclusion (D) x fertilization (F) network of experiments installed at four different sites: McCurtain County (34°01'47"N, 94°49'23"W), Oklahoma; Taylor County (30°12'22"N, 83°52'12"W), Florida; Taliaferro County (33°37'35"N, 82°47'54"W), Georgia; and Buckingham County (37°27'37"N,

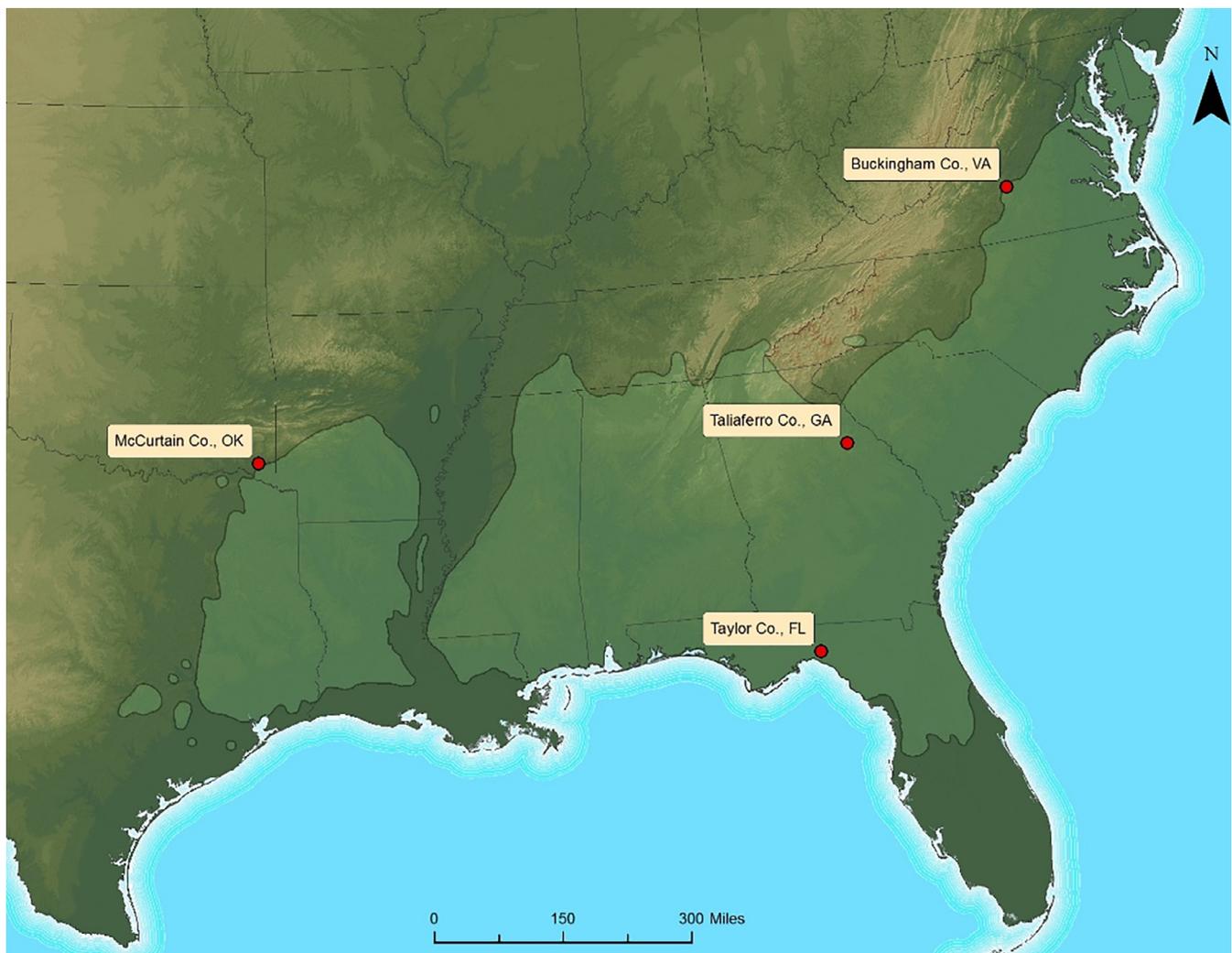


Fig. 1. Locations for loblolly pine experimental sites in Florida (FL), Georgia (GA), Oklahoma (OK), and Virginia (VA), United States. Shaded area correspond with the native range of loblolly pine. (Figure adapted from Will et al. (2015)).

78°39'50"W), Virginia (Fig. 1). These locations were chosen to include the wide variety of temperature and precipitation conditions found within the natural range of loblolly pine.

The 30 year mean annual precipitation (1982–2011, PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>) (Table 1, Fig. 2) ranges from 1100 mm at the GA and VA sites to 1400 mm at the FL site. The FL and VA sites had the highest and lowest

Table 1

Location, 30 year mean annual precipitation and mean annual temperature, and soil series for loblolly pine experimental sites in Florida (FL), Georgia (GA), Oklahoma (OK), and Virginia (VA), United States.

Site	Latitud/longitud	Mean annual precipitation (mm)	Mean annual temperature (°C)	Soil series
FL	30°12'22"N; 83°52'12 W"	1399	20.0	Melvina-Moriah-Lutteterloh
GA	33°37'35"N; 82°47'54 W"	1097	16.5	Lloyd
OK	34°01'47"N; 94°49'23"W	1270	16.8	Ruston
VA	37°27'37"N; 78°39'50"W	1105	13.6	Littlejoe

30 years (1982–2011) mean obtained from PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu/>.

(respectively) mean annual temperatures (20.0 °C and 13.6 °C), while the GA and OK sites experience a mean annual temperature around 16 °C. The OK site has the highest August daily temperatures and experiences the highest air vapor pressure deficit during the growing season (Supplements: Fig. 1). Soils at each site were described according to the California soil Resource Lab (<https://casoilresource.lawr.ucdavis.edu/soilweb-apps/>). At the FL site, the soils are Spodosols (Melvina-Moriah-Lutteterloh series), very deep, poorly drained; texture is fine sand (Table 2), with a spodic horizon between 71 cm and 114 cm depth, and an argillic horizon with very low permeability that extends below the 140–200 cm depth. At the GA site, soils are Ultisols (Lloyd Series), very deep, well drained, and moderately permeable; an argillic-kandic horizon extends from 20 cm to 155 cm depth. At the Oklahoma site, soils are Ultisols (Ruston series), very deep, well drained, moderate permeability, an argillic horizon extends from 25 cm to 216 cm depth. At the VA site soils are Ultisols (Littlejoe Series), an argillic horizon (silty clay loam), extends from 20 cm to 130 cm depth. Available water storage (AWS, cm) (Table 2), defined as the total volume of water at soil field capacity, is lower for FL soils and is higher below the 25 cm soil depth for each site.

In the spring of 2012, the experiments were established in commercial plantations that were planted between 2003 and 2008. Plantations were not thinned or fertilized prior to the study. A full description of initial stand characteristics and site conditions is found in Will et al. (2015), but briefly, stand density (trees ha⁻¹) was 786 in

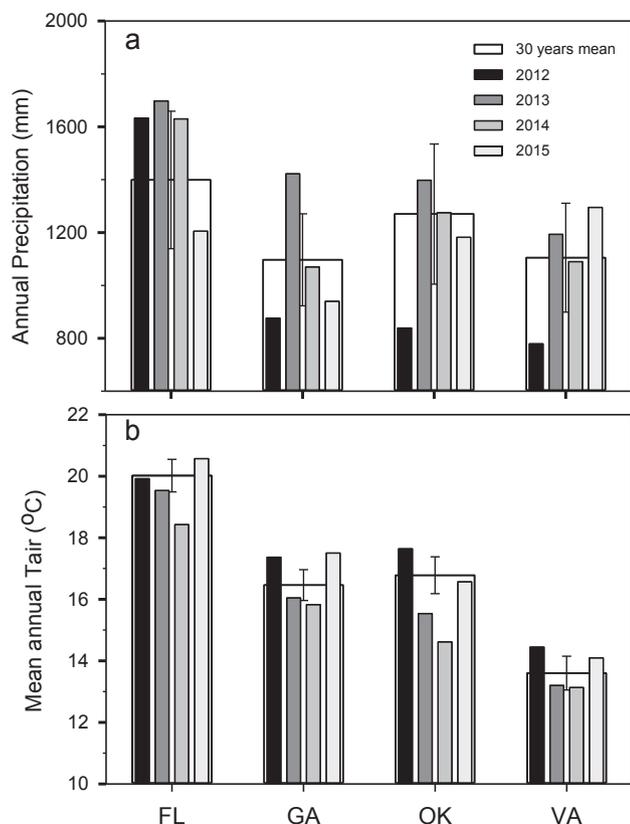


Fig. 2. Annual precipitation (a), mean annual temperature (Tair) (b) during four years for loblolly pine experimental sites in Florida (FL), Georgia (GA), Oklahoma (OK), and Virginia (VA), United States. Error bars are the standard deviation of 30 years means.

Table 2

Physical soil properties, available water storage (AWS, cm) and hydraulic conductivity at saturation (mm/h) for loblolly pine experimental sites in Florida (FL), Georgia (GA), Oklahoma (OK), and Virginia (VA), United States.

Site	Depth (cm)	% sand	%clay	Texture	AWS	K _{SAT}
FL	0–25	97.2	1.4	Sand	1.83	110.7
	25–50	97	0.6	Sand	3.50	109.9
	50–100	94.9	1.8	Sand	3.57	161.8
	100–150	89.8	7.6	Loamy sand	4.45	161.8
GA	0–25	37.6	27.2	Clay Loam	2.72	5.84
	25–50	26.1	45.0	Clay	4.2	1.02
	50–100	26.1	45.0	Clay	7.0	1.02
	100–150	30.2	36.6	Clay loam	7.0	1.78
OK	0–25	62.2	12.2	Sandy loam	3.36	26.2
	25–50	55.8	26.5	Sandy clay loam	3.82	6.9
	50–100	55.8	26.5	Sandy clay loam	7.64	6.9
	100–150	55.8	26.5	Sandy clay loam	7.63	10.7
VA	0–25	25.1	32.9	Clay loam	4.14	13.7
	25–50	23.3	47.5	Clay	3.75	1.02
	50–100	23.2	46.0	Clay	7.68	1.02
	100–150	21.9	23.0	Silt loam	8.82	4.06

Soil information was retrieved from: <https://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx>.

Virginia, 1610 in Oklahoma, 1383 in Georgia, and 1720 in Florida. We chose plantations established using a mixture of half-sib families obtained from local seed orchards, so that the inference for our experiments would be broader than if we had used single-family plantations.

Treatments at all sites consisted of four replications of a 2 × 2 factorial experimental design of throughfall reduction and fertilization, producing four treatments arranged within each randomized complete

block: Control (no treatment), throughfall exclusion (D), fertilization (F), and combined fertilizer plus throughfall exclusion (D + F). All understory competing vegetation was eliminated mechanically and with glyphosate herbicide applied at labelled rates at each plot. Treatments plots were square with a minimum of 0.08 ha and measurements were taken in an inner plot of at least 0.03 ha; adjacent plots were separated by at least 6 m. Throughfall exclusion was achieved by covering 30% of the plot surface with elevated plastic troughs installed in spring 2012 to capture and divert water away from the experimental plots (Will et al., 2015). Fertilization consisted of 224 kg·ha⁻¹ of nitrogen, 28 kg·ha⁻¹ of phosphorus applied in March 2012 (mix of 432 kg·ha⁻¹ of urea and 140 kg·ha⁻¹ ammonium diphosphate), elemental potassium applied at 56 kg·ha⁻¹ as KCl and a micronutrient mix (Oxysulfate, Southeast Mix, Cameron Chemicals, Inc., VA, USA) containing 6% sulfur, 5% boron, 2% copper, 6% manganese, and 5% zinc applied at 22.4 kg·ha⁻¹. The fertilizer rates were typical of operational nutrient applications for loblolly pine (Fox et al., 2007).

2.2. Measurements

2.2.1. Biomass, leaf area index (LAI) and net primary productivity (NPP)

Diameter at breast height (dbh, cm) and tree height (ht, m) of all trees from each treatment plot and site were measured during each dormant season from 2011 to 2015. Woody biomass (bark, stem wood, branches) and coarse (> 5 mm) root biomass were estimated using allometric equations (Gonzalez-Benecke et al., 2014, 2016). Foliage biomass production and annual leaf area index was estimated from litterfall (Gholz et al., 1991; Martin and Jokela, 2004). Litterfall was collected on a monthly basis starting during the summer of 2012 until the end of March of 2017 from 12 0.5 m² traps randomly located inside each measurement plot, and when needed, on top of troughs in the throughfall exclusion plots. Pine needles were separated from other litter, dried at 70 °C, and weighed. The dynamics of needle accretion and LAI were estimated from monthly needle fall collection using a logistic model (Kinerson et al., 1974; Dougherty et al., 1995); this model assumes that current-year needle accrual starts at the beginning of the phenological year, and that needles formed in a given year abscise by the end of the second phenological year, with a needle retention time of two years (Gholz et al., 1991). It follows that total needle fall for a specific year corresponded to needle production during the previous year (Dalla-Tea and Jokela, 1991; Gholz et al., 1991). Needles were corrected for C loss due to senescence and foliage biomass was converted to area using specific leaf area (Dalla-Tea and Jokela, 1991). Leaf area index was expressed on an all-sided basis (Liu et al., 1996).

Above-ground net primary productivity (NPP_A, Mg C·ha⁻¹·yr⁻¹) for each annual interval of measurements was calculated as the increment in woody biomass (I_w) plus foliage production estimated from litter fall collections. Total NPP (NPP_T, Mg C·ha⁻¹·yr⁻¹) was estimated as NPP_A plus coarse root (> 5 mm) biomass production. A 50% C content of biomass was assumed. Tree mortality was uncommon and thus was not included in either productivity estimate. Neither fine root growth nor herbivory were estimated. We considered fine root NPP to be a minor component, as previous studies report values ranging from 0.40 Mg C·ha⁻¹·yr⁻¹ to 0.72 Mg C·ha⁻¹·yr⁻¹ in loblolly pine plantations at similar tree densities as in this study (DeLucia et al., 1999; Matamala and Schlesinger, 2000; Lee and Jose, 2003; Pritchard et al., 2008).

2.2.2. Total soil respiration and partitioning (R_S & R_H)

Total soil respiration was measured in three randomly located surface soil collars placed inside each plot at each site. Collars were inserted about 2–5 cm into the mineral soil and R_S measured approximately every two weeks for at least one year. The heterotrophic component (R_H) of R_S was measured over a one-year period by installing three different root exclusion tubes within each plot at each site five to eight different times through the year, covering seasonal variability. At least 240 root exclusion tubes were installed at each site. In

the D and F + D plots, one tube was installed in a tree row, one directly under the plastic of the throughfall excluder and one in between the separations of the excluders. Tubes were between 32 and 35 cm long and 11–20 cm in diameter with a sharp beveled edge at the bottom. Live roots were cut as the tubes were inserted into the soil and the lateral growth of fine roots inside the soil core was stopped. More than 80% of fine roots are located in the first 30 cm of the soil profile (Mou et al., 1995), so this depth was considered sufficient to eliminate the root-associated signal from R_S . The clay-rich soils in Georgia resulted in water pooling inside the collars for extended periods; therefore a series of two 30 × 30 cm and 40 cm depth trenched subplots were installed at each plot during eight different times of the year. Thus, a total of 256 subplots were used to measure heterotrophic respiration (Yang, 2016). Simultaneous measurements of R_S and R_H were taken at different times after the root exclusions treatments were installed, allowing for depletion of root nonstructural carbohydrates (Heim et al., 2015). Ratios ($R_H:R_S$) were calculated for measurement periods between 40 and 80 days after each set of tubes were installed in FL and VA and 30 to 60 days in OK, when soil respiration measurements inside the excluded soil cores reached an asymptote and CO_2 fluxes were not different between the two sequential measurement periods (autotrophic respiration is assumed zero). Measurements from trenched subplots at the GA site were taken at 180 days after each trenched subplot was installed. All measurements were taken using closed loop gas exchange systems (LI-8100, LI-6400, LI-6200, LiCor Inc., Lincoln, Nebraska USA). Soil temperature (T_S) in the top 10 cm was measured simultaneously within 10 cm of the collar, with soil temperature probes attached to the gas exchange systems. Surface soil moisture also was measured in the top 15 cm using a hand held soil moisture probe (Hydrosense, Campbell Scientific, Logan, Utah, USA). All measurements were taken between 9 am and 2 pm. Annual R_S was estimated for each plot for the last three years of the experiment (2013–2015) from parameter estimates obtained by fitting measured R_S to T_S using an exponential function (proc nlin SAS 9.4, SAS Inc., Cary NC, USA):

$$R_S = a \cdot \exp^{bT_S} \quad (1)$$

where a and b are regression coefficients and T_S ($^{\circ}C$) is soil temperature. We do not have T_S measurements for the first part of 2012 when each experimental site was set up; however, R_S measurements during the latter part of 2012 (July–December) were used along with data from subsequent years to obtain parameter estimates used to scale up R_S . Annual R_H for each plot was estimated by multiplying the $R_H:R_S$ ratio to up scaled annual R_S . We acknowledge the limitations of the micro-trenching by deep soil tubes or the ‘trenching’ approach, as the disturbance created by the installation can affect soil water and soil temperature, and add decomposing roots to the inside the trenched area (Hanson et al., 2000; Kuzyakov, 2006b). However, if tubes are allowed to settle into the soil to overcome the initial soil disturbance, and sufficient time passes for the C associated with rhizo-microbial respiration, root non-structural C, to be depleted (Heim et al., 2015), then this method provides a direct measure of soil organic matter derived C flux (R_H) that is indistinguishable from the other methods used to separate R_H from R_S (Subke et al., 2006).

2.2.3. Meteorological conditions and soil moisture

Meteorological sensors at each site were mounted above the canopy on a triangular tower. Air temperature and relative humidity were measured using air temperature and relative humidity probes (CS215, or HMP155A, Campbell Scientific, Inc, Logan Utah, USA); precipitation was measured using a rain gage (TE-525 Campbell Scientific Inc, Logan Utah, USA), and the data were recorded using a datalogger (CR1000, Campbell Scientific Inc, Logan Utah, USA). Total soil moisture (volumetric water content, θ $m^3 m^{-3}$), was measured in the center of each plot and site, except Virginia where the sensor type was unavailable, every two to six weeks by time domain reflectometry (TDR), using a 1502C metallic cable tester (Tektronix, Inc., Beaverton, OR, USA) (Topp

et al., 1988). At least two permanent pairs of rods were installed within the tree rows (all plots) and under the throughfall exclusion structures (D and D + F treatments) at different depth increments in the soil profile (0–30 cm, 0–60 cm and 0–90 cm) at the OK, FL and GA sites. Soil moisture at intermediate depths (30–60 cm and 60–90 cm) was estimated by difference. Surface soil moisture was also measured in the top 15 cm each time R_S was measured using a hand held soil moisture probe (Hydrosense, Campbell Scientific, Logan, Utah, USA). All volumetric soil moisture measurements were converted to soil matric potential (ψ_m), a metric of the thermodynamic state of soil water, using a function from (Campbell and Norman, 1998):

$$\psi_m = -\psi_e \left(\frac{\theta}{\theta_s} \right)^{-b} \quad (2)$$

where ψ_e is the air entry water potential, θ_s is the volumetric soil water content at saturation ($m^3 m^{-3}$), and b is the exponent of the moisture release equation; ψ_e and b were obtained by fitting ψ_m to soil moisture (proc nlin SAS 9.4, SAS Inc., Cary NC, USA) from soil water retention curves estimated from soil characteristics for each depth and site using the SPAW model (Saxton and Rawls, 2006). For the purposes of discussion, we defined soil matric potential at saturation as 0 kPa, –1500 kPa as the permanent wilting point, and –33 kPa as field capacity.

Long term means (30 years 1982–2011) for total annual precipitation and annual temperature were estimated from the PRISM Climate Group, Oregon State University (<http://prism.oregonstate.edu>).

2.2.4. Net ecosystem productivity (NEP)

NEP represents the difference between carbon uptake through gross primary production (GPP) and C losses through respiration (autotrophic R_a and heterotrophic R_H):

$$NEP = (GPP - R_a) - R_H \quad (3)$$

where $(GPP - R_a)$ equals net primary productivity (NPP).

NEP was estimated for all treatment and control plots as the difference between NPP and heterotrophic respiration as:

$$NEP = NPP - R_H \quad (4)$$

2.3. Statistical analysis

For each of the response variables, a repeated measures analysis was performed across years for each of the sites. The fitted linear mixed models had the main fixed effects of F, D, year, and all two-way and three-way interactions. Sites were initially included as main effects but all sites became significantly different and we decided to test them individually. In addition, the random effects of block and plot were considered. Measurements from the same plot were modelled using a homogeneous and heterogeneous autoregressive of order 1 error structure. The best structure was selected based on the AIC value. Models were fit using SAS v. 9.4 (SAS Inc., Cary NC, USA), with the procedure MIXED and Kenward–Rogers correction was used to adjust the degrees of freedom. Differences among treatment means were assessed by using the Tukey adjustment, and a 5% significance levels was considered for all tests. Variables were transformed when needed and residuals checked for normality and heterogeneity of variance. Summary statistics for precipitation and air temperature were obtained for each of the sites.

3. Results

3.1. Environmental and soil moisture

Annual precipitation during the year when the experiments were established (2012) was below the 30 years average (mean \pm SD) for GA, OK and VA but within one standard deviation (1SD) of the 30 years

Table 3

P values for treatments effects on soil matric potential (ψ_m) for different soil depths at loblolly pine experimental sites in Florida (FL), Georgia (GA), Oklahoma (OK), and Virginia (VA), United States. Main effects are throughfall exclusion (D), fertilization (F), and day of year (DOY). NA = Data not available. Bold = p-values < 0.05.

Site	Effect	(surface) ψ_m	(0–30 cm) ψ_m	(30–60 cm) ψ_m	(60–90 cm) ψ_m	(0–90 cm) ψ_m
FL	D	< 0.0001	< 0.001	0.029	0.127	0.009
	F	0.205	0.528	0.694	0.893	0.867
	F × D	0.393	0.747	0.919	0.816	0.808
	DOY	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
	D × DOY	< 0.0001	< 0.0001	0.024	< 0.001	< 0.0001
	F × DOY	0.509	0.957	0.774	0.179	0.825
	F × D × DOY	0.991	0.935	0.142	0.447	0.975
GA	D	0.018	0.246	0.372	0.688	0.576
	F	0.797	0.771	0.376	0.433	0.245
	F × D	0.177	0.197	0.798	0.441	0.336
	DOY	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
	D × DOY	< 0.0001	0.047	0.009	0.467	0.003
	F × DOY	0.015	1.000	< 0.001	0.408	0.687
	F × D × DOY	< 0.0001	0.985	0.895	0.820	0.454
OK	D	0.002	0.133	0.020	0.001	< 0.001
	F	0.412	0.108	0.320	0.323	0.182
	F × D	0.112	0.097	0.132	0.034	0.009
	DOY	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
	D × DOY	0.096	0.476	0.873	0.245	0.001
	F × DOY	0.231	0.809	1.000	0.303	0.194
	F × D × DOY	< 0.001	0.932	1.000	0.912	0.622
VA	D	< 0.001	NA	NA	NA	NA
	F	0.452	NA	NA	NA	NA
	F × D	0.618	NA	NA	NA	NA
	DOY	< 0.0001	NA	NA	NA	NA
	D × DOY	< 0.0001	NA	NA	NA	NA
	F × DOY	0.756	NA	NA	NA	NA
	F × D × DOY	0.096	NA	NA	NA	NA

Surface ψ_m : From soil moisture measurements at 0–15 cm depth using a Campbell Hydrosense probe.

ψ_m : From soil moisture measured at the other depths performed using time domain reflectometry. NA = data not available.

at the FL site. Mean annual air temperatures were above the 30 years averages for these same three sites for the same year (Fig. 2). Annual precipitation was within 1SD of the 30 years average for all sites except 2013 for GA, which had precipitation in 2013 > 1SD above the 30 years average. Average monthly maximum and minimum air temperature and maximum air vapor pressure deficit (VPD) during the four years of experiments are shown in Supplemental Fig. 1. Notable was that the OK site had monthly maximum VPD > 3 kPa from June to September in 2012, and August–September in 2013 and 2015, while the other three sites mostly had monthly maximum VPD < 3 kPa from May to September during the four years of study. The only exception was 2012, when GA and VA sites had monthly maximum VPD > 3 kPa in July.

Soil matric potential (ψ_m), at the soil surface (0–15 cm) was significantly reduced (became more negative) by the D treatment at all sites (Table 3). For the three sites where ψ_m was measured (OK, GA, and FL) through the 0–90 cm profile, the ψ_m was also significantly reduced by the D treatment. In general, the negative D effect depended on the day of year (DOY), as indicated by the significant D × DOY interaction through all depths at the FL site, the 0–30 cm and 30–60 cm at the GA site, and in the 0–90 cm soil profiles. The D × DOY interaction resulted from an increasing difference between D and non-D treatments for ψ_m as soil moisture decreased, e.g., at the GA site, ψ_m in the 0–30 cm depth was 621 kPa lower under the D treatment when mean ψ_m under non drought treatment was –706 kPa (26% of available water), and the largest differences were recorded during the growing seasons. Similar results were seen in the 0–90 cm soil profile at the OK site, where differences in ψ_m due to the D treatment increased as soil moisture decreased, reaching a difference of 270 kPa when mean ψ_m under non drought was –300 kPa (48% of available water), similar to the GA site, the largest differences were recorded during the growing season. At the FL site, although a significant D × DOY interaction was found through all depths, a difference of 267 kPa was recorded when mean ψ_m under

non drought was –273 kPa (67% of available water). Mean ψ_m for the 60–90 cm layer at the FL site generally remained above field capacity. The mean lowest ψ_m were recorded under the D treatment in the 30–60 cm depth at all sites, with the lowest mean at the OK site (–1133, 95% CI = –1271, –995 kPa), mean ψ_m of –1045 (95% CI = –1167, –923 kPa) for the GA site and –227 (95% CI = –271, –184 kPa) for the FL site. Lowest mean ψ_m in the 90 cm soil profile was recorded at the GA site (–496, 95% CI = –572, –420 kPa), followed by the OK site (–261, 95% CI = –308, –215) and the FL site (–11, 95% CI = –19, –4 kPa). A significant D × F × DOY in the surface soil at the Oklahoma site reflected that the F treatment counteracted the D treatment on some days during the growing season, causing some increases in ψ_m .

3.2. NPP, LAI and biomass

At all sites, NPP_T increased under F (Table 4, Fig. 3); however, at the OK site, the positive F effect depended on the year (F × YEAR), e.g. NPP_T was higher under the F than the unfertilized treatment (p = 0.0074) in 2013. NPP_T decreased under the D treatment at GA and in some years at OK (D × YEAR) (Table 4), e.g., at the OK site NPP_T was lower under D than the non D treated plots in 2013 (p = 0.004) and 2014 (p = 0.018) (Fig. 3). The GA site had on average the highest increase in NPP_T (20.2%) due to fertilization, followed by the VA site with 11.5%, OK site with 8.1% and FL site with 6%; the D effect reduced NPP at the GA site by 11.6% and 6.8% at the OK site. After four years of treatments, the main effects on accumulated NPP_T was a significant (p < 0.05) positive effect for F at all sites, and lower under D treatment at the GA and OK sites relative to the control plots (Supplements: Table 1). The cumulative NPP_T was significantly higher at the D + F than at the D treated plots at the VA site (p = 0.003), marginally significant at the GA site (p = 0.058), and although not significant, tended

Table 4

P values for treatment effects on all sided leaf area index (LAI), above ground biomass (AGB), above ground net primary productivity (NPP_A), total NPP (NPP_T) and net ecosystem productivity (NEP) for loblolly pine experimental sites in Florida (FL), Georgia (GA), Oklahoma (OK), and Virginia (VA), United States. Main effects are throughfall exclusion (D), fertilization (F), and year. Bold = p-value < 0.05.

Site	Effect	LAI	AGB	NPP _A	NPP _T	NEP
FL	D	0.542	0.624	0.768	0.798	0.616
	F	< 0.001	0.025	0.005	0.005	0.079
	D × F	0.942	0.501	0.587	0.574	0.135
	YEAR	< 0.001	< 0.0001	< 0.0001	< 0.0001	0.962
	D × YEAR	0.923	0.836	0.764	0.809	0.980
	F × YEAR	0.051	0.018	0.800	0.771	0.882
	D × F × Year	0.419	0.463	0.559	0.543	0.423
GA	D	< 0.0001	0.195	0.004	0.005	0.436
	F	< 0.0001	0.004	< 0.0001	< 0.0001	0.002
	D × F	0.567	0.971	0.375	0.380	0.291
	YEAR	< 0.0001				
	D × YEAR	0.194	0.037	0.319	0.304	0.300
	F × YEAR	0.025	< 0.0001	0.308	0.303	0.251
	D × F × Year	0.815	0.903	0.720	0.706	0.755
OK	D	0.659	0.012	0.010	0.005	0.329
	F	0.052	0.091	0.001	0.001	< 0.001
	D × F	0.238	0.087	0.604	0.448	0.261
	YEAR	< 0.0001				
	D × YEAR	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.008
	F × YEAR	0.0001	0.038	0.024	0.044	0.312
	D × F × YEAR	0.776	0.012	0.100	0.089	0.407
VA	D	0.496	0.614	0.259	0.221	< 0.001
	F	0.001	0.005	< 0.0001	< 0.001	< 0.001
	D × F	0.116	0.636	0.238	0.272	0.436
	YEAR	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.002
	D × YEAR	0.295	0.099	0.078	0.076	0.172
	F × YEAR	0.046	0.0001	0.334	0.346	0.382
	D × F × YEAR	0.425	0.926	0.942	0.946	0.846

to be higher at the FL and OK sites. Florida reached the highest NPP_T at the F treated plots (68.8 Mg C·ha⁻¹), followed in order by the GA, OK, and VA sites. The greatest differences between control and the F treatment (11.4 Mg C·ha⁻¹) or control and D treatments (5.5 Mg C·ha⁻¹) was found at the GA site.

At all sites, LAI increased under the F treatment (Fig. 4, Table 4). However, the degree of enhancement of LAI by F varied by year for the GA, OK and VA sites, as indicated by the F × YEAR interactions. LAI was greater due to F from 2012 to 2014 at the GA site, in 2013 at the OK site and from 2013 to 2015 at the VA site (p < 0.05). LAI was consistently reduced under the D treatment at the GA site, and the negative D effect on LAI depended on the year at OK (Table 2) (e.g., 2014, Fig. 4). No D effect on LAI was detected at the FL and VA sites, and no significant D × F effects were observed at any site. Maximum LAI for the FL site fluctuated around 10 m²·m⁻² for the fertilized plots and LAI increased on average 11.6% due to fertilization. Maximum LAI for the GA site was reached under the F treatment, reaching values greater than 8 m²·m⁻², and the GA site had an average increase in LAI of 20% due to F. At the OK site, LAI increased from around 3 m²·m⁻² during the first year of treatments, to a maximum LAI of 8 m²·m⁻² four years later for all treatments. The average increase due to F was 8.1% at this site. This was the youngest site at the experiment set up (4 years old), and it was still accruing LAI, at least during the first two years of the experiment (Fig. 4). At the VA site, LAI increased from around 5 m²·m⁻² to maximum LAI of 10 m²·m⁻² in the fertilized plots, average increase in LAI due to F was 11.5% for VA site.

Carbon in total aboveground biomass (AGB) differed between sites and was significantly affected by treatments (Table 4, Supplements: Fig. 2). AGB increased under the F treatment at all the sites but the effect was year dependent as indicated by the F × YEAR interactions. AGB decreased under the D treatment at the GA and OK sites only, but this effect was year dependent. The Florida site was the oldest in the study and its AGB was twofold greater than other sites reaching values > 75 MgC·ha⁻¹ in the F treated plots after four years the

experiment was initiated. The Oklahoma site was the youngest plantation at site installation and had the lowest average AGB in the F treated plots (≈ 25 MgC·ha⁻¹) over the course of the experiment. Georgia and Virginia sites reached up to 40 MgC·ha⁻¹ in F treated plots.

Woody growth efficiency was calculated as the slope of the linear regression between woody biomass increment (I_W) and maximum LAI (Fig. 5). At all sites, I_W increased with LAI (p < 0.0001). No treatment effect on woody growth efficiency (p > 0.05) was detected; however, slopes differed among sites (p < 0.05). Woody growth efficiency for FL (0.79 ± 0.16) was similar to GA (0.98 ± 0.11) (p = 0.14), but, higher than OK (0.42 ± 0.04) (p = 0.01) and VA (0.27 ± 0.04) (p < 0.01). Growth efficiency at GA was higher than OK and VA (p < 0.001), and the OK site tended to be higher than VA (p = 0.052).

3.3. Soil respiration

Measured soil respiration (R_S) fluctuated with day of year and differences were mainly associated with seasonal soil temperature (data not shown), e.g., greater R_S with higher soil temperatures (Supplements: Table 2). Across all sites, whenever the effect was significant, both the F and D main effects decreased R_S (Table 5). F had a significant effect at the GA, OK, and VA sites. The effects of D on R_S at the FL and VA sites depended on the day of year, as indicated by D × DOY interactions. R_H was reduced by F at the OK and VA sites. The D effect on R_H was time dependent at the FL and VA sites (Table 5). Ratios of R_H:R_S were not statistically different among treatments, and any potential treatment effects on the ratios were difficult to identify due to large within-treatment variance compared to across-treatment variance (data not shown). However, mean ratios per plot within each treatment were used to estimate R_H. Mean R_H:R_S values (mean, 95% (CL)) per site were: 0.81 (0.79, 0.83) for the FL site, 0.77 (0.73, 0.81) for the GA site, 0.71 (0.66, 0.75) for the OK site, and 0.75 (0.72, 0.78) for the VA site.

Treatment effects on parameter estimates, slopes (temperature

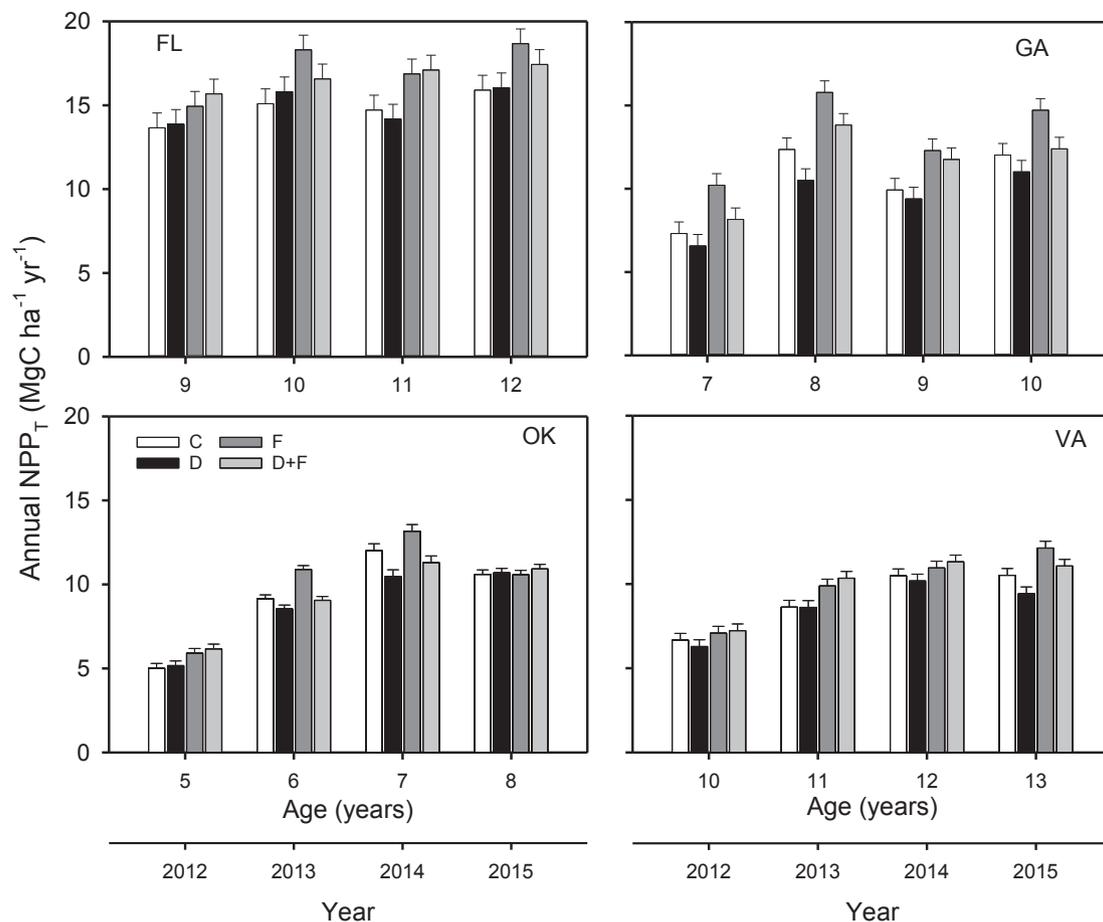


Fig. 3. Annual total net primary productivity (NPP_T) (mean \pm SE) for loblolly pine experimental sites in Florida (FL), Georgia (GA), Oklahoma (OK), and Virginia (VA), United States. Treatments are C = Control, D = throughfall exclusion, F = fertilizer, D + F combination of F and D.

sensitivity) and intercepts obtained by fitting measured R_S to soil temperature were tested for treatment effect by site (Supplements: Table 3). Results indicated that temperature sensitivity was reduced by D at FL ($p = 0.009$) and F at OK ($p = 0.041$). Intercepts did not differ from one another for any treatment at any site.

Estimated annual R_S reflected site differences and treatments effects on measured instantaneous R_S (Fig. 6). The FL site had the highest annual R_S for all sites and treatments with values higher than $14 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$; a flux more than two fold greater than annual R_S at the GA and VA sites, while the OK site had intermediate values. Annual R_S decreased by 8% in the D treated plots at the FL site, 23% and 28% in the F treated plots at the GA and OK sites, and 27% in the combined plots (D + F) at the VA site. Annual R_H ranged from around $5 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ to $14 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ and, in general, C lost by R_H at the FL site was double the amount lost at GA and VA, and about 1.5 times higher than at OK. Average annual R_H decreased by 9% in D treated plots at the FL site, 13% in the combined treated plots at the GA site, 23% for F and D + F plots at the OK site and 29% and 39% in the D and D + F treated plots respectively at the VA site.

3.4. Net ecosystem productivity (NEP)

NEP increased under the F treatment at all sites (Table 4). NEP also increased under the D treatment at the VA site, while for the OK site, a $D \times \text{YEAR}$ interaction on NEP indicated suppressed NEP in one year (Table 4). Maximum annual NEP for the FL site ($5.35 \pm 1.10 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) and the GA site ($9.71 \pm 1.07 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) was reached under the F treatment in 2013, the year immediately after fertilization (Fig. 7). The control and D treatments at the OK site were

carbon neutral in 2013 when the plantation was six years old (Fig. 7); however, NEP under the F treatment reached $3.91 \pm 0.68 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ the same year, and peaked at $6.65 \pm 0.64 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ the following year. At the VA site, maximum annual NEP ($6.54 \pm 0.54 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) was reached under the combined treatment (D + F) in 2014 (Fig. 7).

The accumulated NEP differences for the last three years of treatment (Supplements: Table 4) reflected the main effects on NEP. Cumulative NEP was always higher under the F treatment, where the FL site registered the highest difference between control and F treatment ($9.2 \text{ Mg C}\cdot\text{ha}^{-1}$). Notably, F increased NEP at the D treated plots (D + F) at all sites except the FL site; e.g., NEP increased by 28% at the GA site, 53% at the OK site and 39% at the VA site at the combined treatment plots (D + F), relative to the D treatment plots alone.

4. Discussion

We used a replicated, multi-site experimental approach to determine how reduced water availability (30% throughfall reduction) across the natural climatic range of loblolly pine interacts with fertilization to influence tree biomass, NPP, R_S , R_H , and NEP. Throughfall diversion significantly reduced available soil moisture at all sites, inducing potentially stressful levels of soil matric potential at sites that were at average or in the lower range of the long term annual precipitation. Fertilization and throughfall effects were independent and fertilization did not exacerbate throughfall treatment effects. Our hypothesis regarding increased NPP in response to F treatment was supported for all sites, while the expected decrease in NPP by decreased available soil moisture was only found for the GA and OK sites. Support

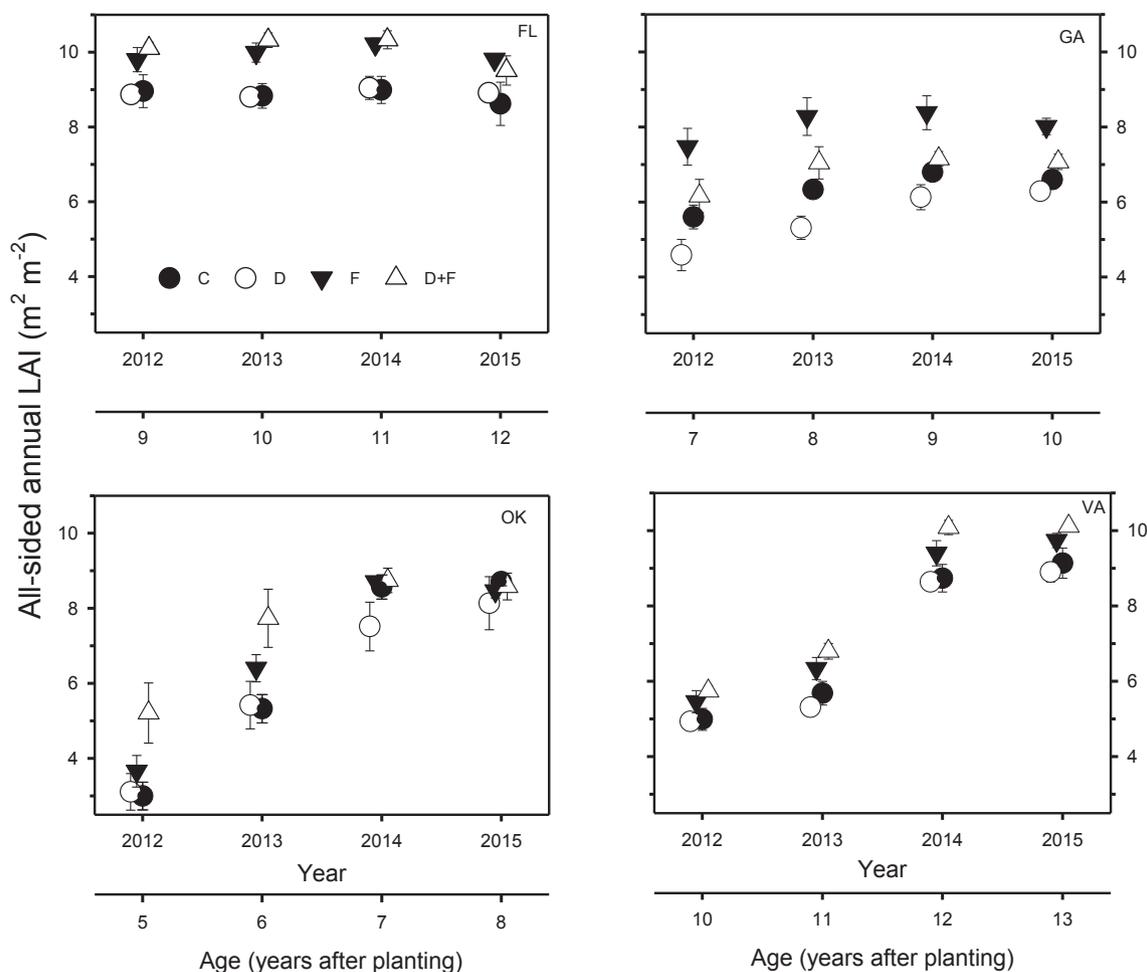


Fig. 4. All-sided annual leaf area index (LAI) (mean \pm SE) for loblolly pine experimental sites in Florida (FL), Georgia (GA), Oklahoma (OK), and Virginia (VA), United States. Treatments are C = Control, D = throughfall exclusion, F = fertilizer, D + F combination of F and D.

was sometimes found for predictions regarding decreased R_s and R_H to both F and D; however, differential responses of R_s and R_H were often recorded at the same site across years and this carried over to NEP trends. This result highlights the importance of understanding how water availability and fertilization affect both NPP and R_H over multiple years.

4.1. NPP_T

NPP_T at the four study sites, spanning the climate range of native loblolly pine ranged from 5 to 12 $Mg\ C\ ha^{-1}\ yr^{-1}$ for controls in GA, OK and VA sites, and 16 $Mg\ C\ ha^{-1}\ yr^{-1}$ at the FL site. Fertilizer amendment (F) increased NPP_T at all sites by 6–20%, whereas 30% throughfall exclusion (D) suppressed NPP_T by 0–12%, depending on site. Increases in loblolly pine productivity with fertilization have been well documented, and pine plantation fertilization is a common practice in the southeastern United States (Borders et al., 2004; Jokela et al., 2004; Fox et al., 2007; Samuelson et al., 2008). Fertilization is associated with increased leaf area (Jokela et al., 2004; Martin and Jokela, 2004; Sayer et al., 2004; Samuelson et al., 2008) and increased water use efficiency (Samuelson et al., 2014; Ward et al., 2015; Maggard et al., 2016, 2017).

In the current study, reduced water availability significantly reduced NPP at the GA and OK sites, although an interaction $D \times YEAR$ was marginally significant at the VA site ($p = 0.07$). Although throughfall diversion affected surface available soil moisture at the plot level at the FL and VA sites, deep soils (60–90 cm) at the FL site provided water to the plants as indicated by continuous high average

matrix potential ($-4.96\ kPa$) at this depth. The FL site was located in an area with a high water table, and for three out of the four study years was wetter than or within the 30-years average precipitation. Although deep soil moisture at VA was not measured, this site's soils had the highest water storage capacity among sites (Table 2), which, combined with average precipitation and a lower evaporative demand (lowest mean VPD of the four study sites), suggests an adequate water supply was present for the trees. In contrast, the GA and OK had high evaporative demand and the water supply in the soil profile at the GA and OK sites was significantly reduced by the throughfall reduction at the plot level.

The D treatment had the strongest negative effect on LAI and NPP in GA; unlike the other sites, the GA site was drier than the 30 years average precipitation for two of the four years of treatment. Combined with throughfall reduction, the GA site reflected severe drought conditions at the plot level with the longest period of soil matrix potential below the wilting point of any site, affecting LAI the first two years of the experiment. Limited photosynthesis (Tang et al., 2004; Samuelson et al., 2014; Maggard et al., 2016), needle growth and canopy development (Hennessey et al., 1992; Raison et al., 1992) are common responses to drought that directly affect tree productivity (Domec et al., 2009). Loblolly pine holds two cohorts of needles formed in consecutive years (Dalla-Tea and Jokela, 1991; Gholz et al., 1991); thus, the effect of drought can carry over multiple years. Notably for this site, fertilization resulted in higher LAI, even during the drought conditions.

Woody growth efficiency in this study was maintained, as expected, at every site across treatments, emphasizing the importance of leaf area

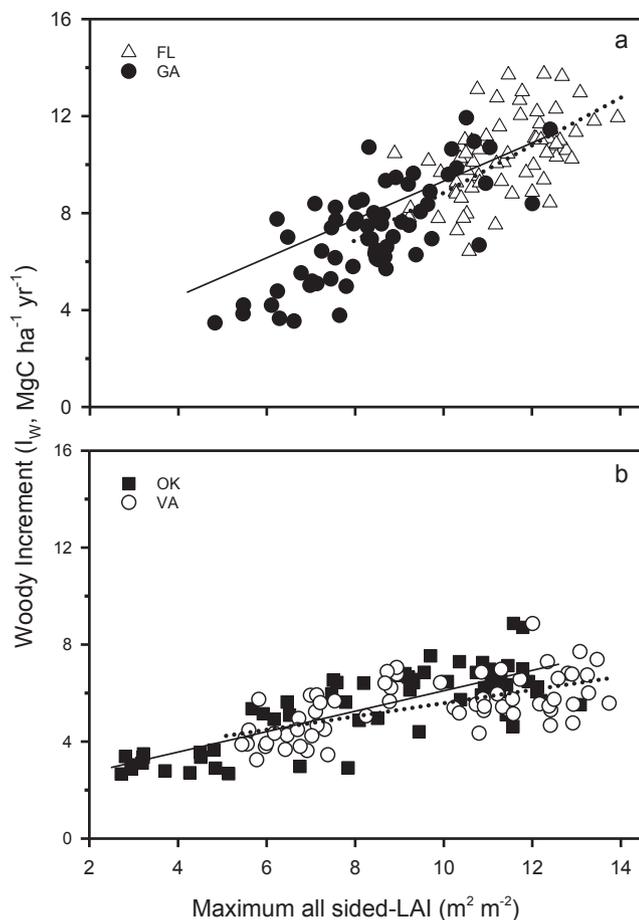


Fig. 5. Woody increment (I_w) related to maximum all sided leaf area index (LAI) for loblolly pine experimental sites in Florida (FL), Georgia (GA), Oklahoma (OK), and Virginia (VA), United States. (a) Solid line = regression for Florida, dotted line = regression for Georgia. (b) Solid line = regression for Oklahoma, dotted line = regression for Virginia.

management and development to loblolly pine productivity (Sampson and Allen, 1999; Jokela et al., 2004). This result concurs with model results showing loblolly pine productivity across the Southeastern United States is dependent on LAI (Sampson and Allen, 1999). Our results indicate that across a range of soil water availability and storage capacity (as seen for the GA and OK soils with high water holding capacity but not FL) significant decreases in water supply have a strong negative effect on leaf area growth and consequent pine productivity. However, woody growth efficiency did differ among sites, with the similar growth efficiencies for FL and GA contrasting with the OK and VA sites. These groupings could be related to the climatic differences and similarities among sites. The VA site has the lowest mean annual temperature, and the OK site experiences low winter season temperatures. In contrast, the FL and GA sites experience both higher precipitation and higher mean annual temperature. Also, the trees at each site reflect the genetic material within each region (Will et al. 2015), and inherited lower growth efficiencies may have been associated with the more northerly, cold resistant seed sources at the OK and VA sites relative to the FL and GA sites. If this site variation in growth efficiency reflects a genetic influence, then climatic warming may not increase a region's productivity without a concurrent change in genetic material. However, regional simulations of loblolly pine productivity under future climate scenarios indicate that NPP is likely to increase across most of the species' range, with the greatest proportional increases happening in the cooler portions of the range where CO_2 fertilization and increased temperature act together to increase potential productivity (Gonzalez-

Table 5

P values for treatment effects on measured soil respiration (R_S) and heterotrophic respiration (R_H) for loblolly pine experimental sites in Florida (FL), Georgia (GA), Oklahoma (OK), and Virginia (VA), United States. Main effects are throughfall exclusion (D), fertilization (F), and day of year (DOY). Bold = p-value < 0.05.

Site	Effect	R_S	Df	R_H	Df
FL	D	0.883	1, 11	0.478	1, 48
	F	0.487	1, 13	0.902	1, 48
	D × F	0.219	1, 13	0.788	1, 40
	DOY	< 0.001	29, 575	< 0.001	5, 92
	D × DOY	< 0.001	29, 576	0.009	5, 92
	F × DOY	0.077	29, 568	0.255	5, 92
GA	D	0.654	1, 64	0.503	1, 29
	F	0.045	1, 64	0.494	1, 29
	D × F	0.213	1, 59	0.926	1, 27
	DOY	< 0.001	16, 394	< 0.001	8, 73
	D × DOY	0.341	16, 394	0.751	8, 73
	F × DOY	0.051	16, 395	0.375	8, 73
OK	D	0.589	1, 98	0.357	1, 56
	F	0.007	1, 98	0.019	1, 56
	D × F	0.003	1, 87	0.610	1, 42
	DOY	< 0.001	8, 169	< 0.001	5, 102
	D × DOY	0.275	8, 169	0.134	5, 102
	F × DOY	0.940	8, 169	0.290	5, 103
VA	D	< 0.001	1, 46	< 0.001	1, 79
	F	0.005	1, 46	0.009	1, 79
	D × F	0.916	1, 42	0.483	1, 103
	DOY	0.001	23, 405	< 0.001	9, 172
	D × DOY	< 0.001	23, 404	0.005	9, 172
	F × DOY	0.058	23, 405	0.809	9, 172

Benecke et al., 2017).

4.2. NEP and soil respiration

Net ecosystem productivity in this study, similar to NPP, most often increased in response to fertilization. However, given that NEP is a composite metric, its magnitude depends on the direction and relative size of responses of NPP and R_H to fertilizer additions and soil moisture availability. The NEP increase in response to fertilizer additions originates from two mechanisms acting in opposing directions, as NPP increases with fertilization, while R_S and R_H often decrease (Maier et al., 2004; Sampson et al., 2006; Janssens et al., 2010). This decrease in soil carbon fluxes under fertilization may originate from altered carbon allocation patterns with plants producing fewer fine roots (Haynes and Gower, 1995; Maier and Kress, 2000; Lee and Jose, 2003), lower microbial biomass, and shifts in microbial community composition (Wallenstein et al., 2006; Blazier et al., 2008; Janssens et al., 2010; Hay et al., 2015), and changes in soil enzymes (Allison and Vitousek, 2005), with consequent reductions in heterotrophic activity (Maier et al., 2004; Ramirez et al., 2010). Our results indicate that both R_S and R_H often decreased under fertilization but the general difficulty of making these measurements poses a limitation to making generalizable predictions about how each will respond to silvicultural treatments and climate change in the region.

Under low soil moisture, microbial activity is mediated by direct water limitation and substrate gaseous diffusivity (Davidson et al., 1998; Fang and Moncrieff, 1999; Palmroth et al., 2005). The largest increase in NEP was under the combined treatment (D + F) at the VA site (Fig. 7), again reflecting that the drivers of NPP and R_H moved in opposite directions. LAI increasing factors (deep water availability and fertilization) allowed for continued assimilation at the site while low surface soil moisture and fertilization decreased R_H . However, wherever water supplies declines below plant needs at the whole soil profile, both NPP and NEP are reduced because of significant reductions in LAI (Noormets et al., 2010; Bracho et al., 2012).

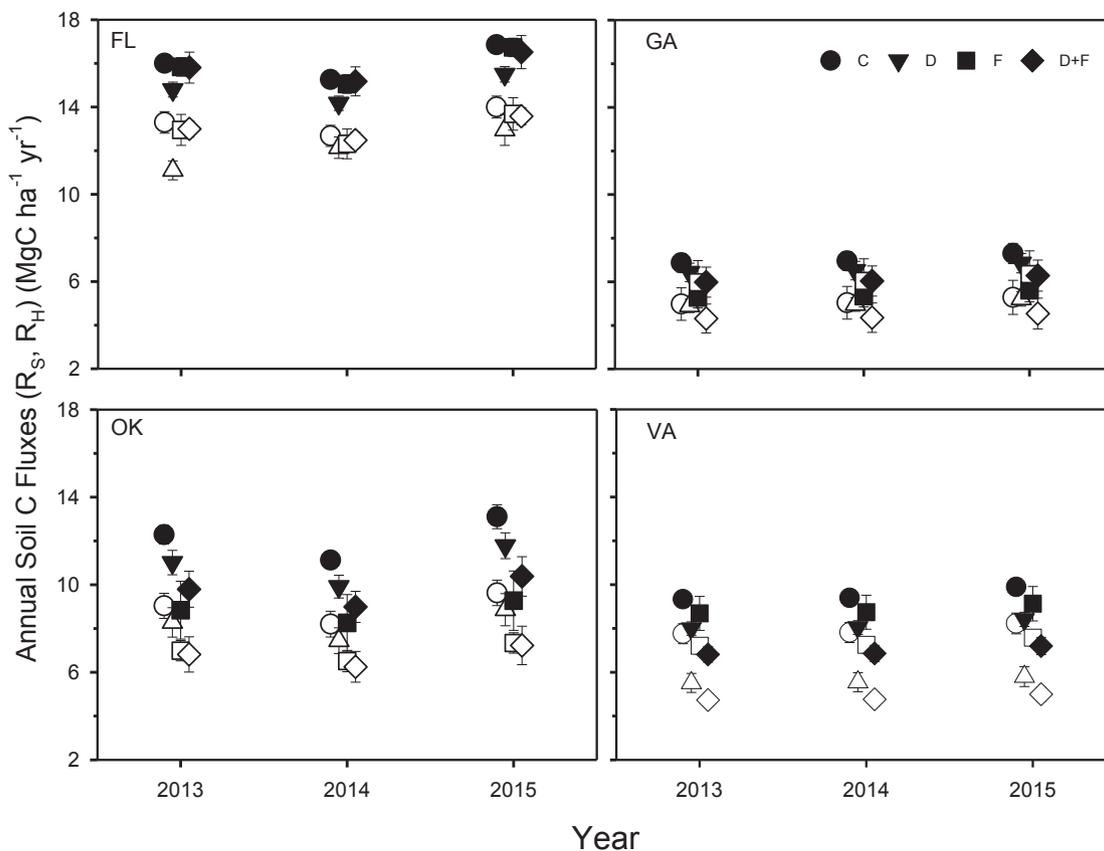


Fig. 6. Annual soil respiration (R_S) and heterotrophic Respiration (R_H , open symbols) for loblolly pine experimental sites in Florida (FL), Georgia (GA), Oklahoma (OK), and Virginia (VA), United States. Treatments are C = Control, D = throughfall exclusion, F = fertilizer, D + F combination of F and D.

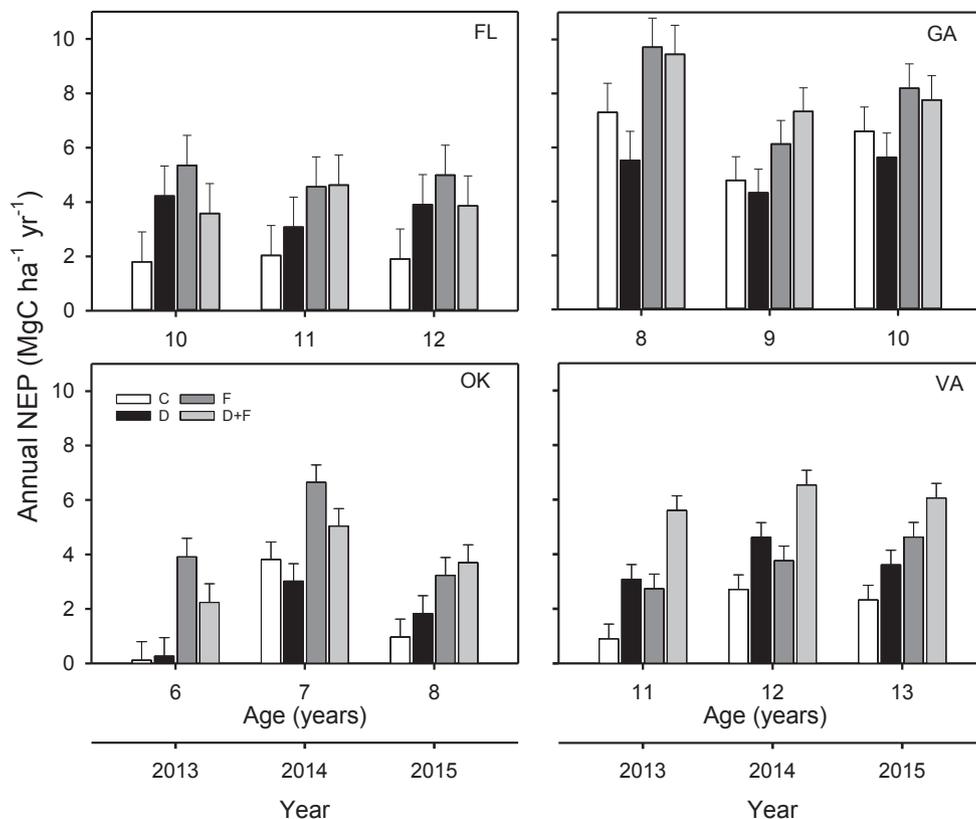


Fig. 7. Annual net ecosystem productivity (NEP) for loblolly pine experimental sites in Florida (FL), Georgia (GA), Oklahoma (OK), and Virginia (VA), United States. Treatments are C = Control, D = throughfall exclusion, F = fertilizer, D + F combination of F and D.

NEP values in this study were within the range reported for previous studies conducted in pine plantations in the southeastern United States (Maier and Kress, 2000; Maier et al., 2004; Noormets et al., 2010, 2012; Bracho et al., 2012), and other 11–30 year-old forests in temperate regions (Pregitzer and Euskirchen, 2004). In contrast, the NPP and R_H values were relatively high compared with other temperate forests of similar age (Pregitzer and Euskirchen, 2004). High R_H could be attributed to the harvest-related soil disturbance and the pulse of detritus inputs in plantation forests. The relatively high $R_H:R_S$ ratio observed across the current study sites reflects the intermediate ages of the plantations, recent disturbance and the decomposition of residuals from the previous forest harvest. A post-disturbance pulse in R_H may last 7–10 years (Bracho et al., 2012; Noormets et al., 2012), and then it generally declines with age. In a recent chronosequence study across pine plantations, the $R_H:R_S$ ratio decreased from 0.8 at an intermediate age to 0.5 by age 20 (McElligott et al., 2016). A similar $R_H:R_S$ ratio of 0.5 has been reported for many mature forests (Hogberg et al., 2001).

An important question to address is to what extent changing NPP and R_H individually contributed to the variability in NEP. In other studies, NEP measured independently with micrometeorological and biometric approaches were correlated with one another (Pregitzer and Euskirchen, 2004; Bracho et al., 2012). In our study, NEP was derived from the NPP and R_H measurements and, thus the relationships linking NEP to NPP or R_H were not explanatory, but rather illustrate how the primary drivers differed among sites (Supplements: Fig. 3). The FL site had the highest NPP_T but its NEP estimates were similar to OK and VA because of high R_H . The sandy Spodosols in FL would likely offer less protection to detrital litter than the Ultisols found at the GA, OK and VA sites, where the higher clay contents in the soil may have protected detritus from microbial decomposition (Kuzyakov, 2006a). Indeed, soils at the GA site had the highest clay content (Will et al. 2015), and the lowest R_H , resulting in this site having the highest NEP among all sites. At the OK site, NEP followed trends in both NPP_T and R_H but VA more closely followed R_H . These two sites were probably still decomposing harvest residues at the time of this study; VA was the oldest site in the study but it had the lowest mean annual temperature, and the OK site was the youngest. As these two sites age, the relationship between NEP vs R_H may weaken or disappear and the data cluster as seen for the FL and GA sites. These results highlight that understanding the controls on R_H is central to predicting how NEP may respond to changing environmental conditions.

The trenching and micro-trenching approach used in this study to separate R_H from R_S creates a disturbance with installation and can affect soil moisture and temperature regimes (Hanson et al., 2000; Kuzyakov, 2006b; Bond-Lamberty et al., 2011). The approach also adds severed fine and coarse roots in the trenched area that can lead to an overestimation of R_H . However, in a meta-analysis review of methods used to separate R_H from R_S , Subke et al. (2006) found trenching approaches returned similar results to other methods. The possible overestimation of R_H may have led to an underestimation of annual NEP. However, the comparisons among treatments within a site would likely have suffered only a minimal differential effect of elevated R_H from root decomposition as all exclusion collars were installed at the same time. Moreover, the annual NEP values reported here for the four study sites are within the range of reported NEP for pine plantations growing in the Southeastern United States (Bracho et al., 2012). Improvement in the R_H estimates could be had by estimating C loss from severed roots (Subke et al., 2006), nonetheless, the NEP values used here are likely capturing the direction and magnitude of differences among treatments within a site.

5. Conclusions

The experimental treatments across the climate gradient in this regional study for loblolly pine plantations provided key insights into how these ecosystems might respond to climate change and highlighted

some areas for future research. The increase in NPP in response to fertilization under the wide range of climate conditions suggests that fertilization is likely to remain effective even under mild to moderate drought conditions, and is unlikely to exacerbate the negative impacts of water limitation on productivity. A key area for future research is to assess whether the suppression in total and heterotrophic soil carbon fluxes that occur with fertilizer applications is maintained, if that suppression results in increased soil C pools and with lower decomposability through the end of the rotation cycle, and if those pools are stabilized against future changes in climate (e.g., warming), management, and stand development.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.04.029>.

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