



Growth responses of narrow or broad site adapted tree species to a range of resource availability treatments after a full harvest rotation



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ABSTRACT

Understanding the processes driving forest productivity is a critical element in our efforts to maximize production of biomass and wood products and more efficiently utilize resources required for plant growth. We examined above and belowground growth and productivity of four tree species – eastern cottonwood (*Populus deltoides*), American sycamore (*Platanus occidentalis*), sweetgum (*Liquidambar styraciflua*), and loblolly pine (*Pinus taeda*) – receiving irrigation and fertilization in the Upper Coastal Plain ecoregion of South Carolina, USA. Trees received treatments throughout an entire intensively-managed harvest rotation, which was nine years for cottonwood and sycamore, and 11 years for sweetgum and loblolly pine. Fertilization and irrigation positively affected growth and productivity of all tree species. Fertilization alone led to increases in stem volume index of up to 329% for cottonwood, 376% for sycamore, 261% for sweetgum, and 49% for loblolly pine. Loblolly pine grew the largest of all species tested, and sweetgum was the largest hardwood. Net primary productivity was driven by leaf and fine root tissue production. When accounting for the effect of tree size, belowground biomass decreased with increasing resource availability in sweetgum and loblolly pine, but not cottonwood or sycamore. These results help explain complex relationships between above and belowground tissues in woody species, and indicate that both ontogeny and resource availability can mediate allocation to belowground tissues.

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1. Introduction

The Earth's forest production capabilities are under constant pressure by the demands of an ever-increasing human population, increasing standards of living, and development of new wood-based products (FAO, 2013). Natural forests alone can no longer support the global demand for wood products and biofuel components, as the amount of forestland is declining worldwide (Hansen et al., 2010). In an effort to increase forest production, numerous forestry programs have dedicated resources to improving tree productivity through genetic selection and intensive silviculture (Fening and Gershenson, 2002; Rockwood et al., 2008; FAO, 2013; Mead, 2013). Intensive silviculture is similar to traditional agricultural systems, and includes mechanized planting and harvesting, pest control, and nutrient and water amendments. Reliance on these systems for wood and biomass products has increased over the last several decades (Nakada et al., 2014), and

woody biomass has the potential to provide 18% of the world's energy needs by 2050 (Lauri et al., 2014).

Despite the global importance of forest production and the worldwide prevalence of intensively-managed forests, we still lack understanding of how whole-tree productivity and biomass accumulation are affected by nutrient and water amendments. Fertilization can mitigate the effects of nutrient-poor soils and generally increases production of both hardwoods and conifers (Coyle and Coleman, 2005; Coyle et al., 2008; Trichet et al., 2009; da Silva et al., 2013). Irrigation is often a necessary component for wood product and biomass production in arid regions (Myers et al., 1996; Shock et al., 2002; Tomar et al., 2003) where soil moisture availability can be a major limiting factor for growth of both hardwoods (Bergante et al., 2010) and conifers (Brzostek et al., 2014). While increasing growth and production is a major focus of forestry worldwide, it remains crucial to understand how tree growth responds to resource availability so that appropriate silvicultural treatments can be administered.

Belowground tissues are critical components of tree physiological processes that can account for substantial (i.e., ~10–60%) portions of total net primary production (Cairns et al., 1997; Mokany

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et al., 2006) and nutrient dynamics (Saatchi et al., 2011; Aubrey et al., 2012; Smyth et al., 2013; Varik et al., 2013). Knowledge of belowground tissues is particularly lacking compared to aboveground tissues (e.g. Chave et al., 2014; Chojnacky et al., 2014; Gonzalez-Benecke et al., 2014; Warren et al., 2015), as detailed quantification of these components is difficult (Laclau et al., 2013). However, these data are needed for accurate landscape-scale estimation of vegetative biomass, net primary production, and carbon stocks (Clark et al., 2001; Ruiz-Peinado et al., 2012; Weiskittel et al., 2015). Particularly lacking from the literature are long-term data sets quantifying and comparing above- and belowground tree growth, productivity, and biomass of multiple species.

Here we compare comprehensive above- and belowground growth, productivity, and biomass accumulation for two soil moisture and nutrient availability levels in four intensively-managed commercial tree species over a full harvest rotation (hereafter referred to as simply “rotation”) – the basic study design of which was originally pioneered by Swedish researchers (e.g. Mead and Tamm, 1988; Linder, 1989; Bergh et al., 1999). Two of the species we studied were narrowly adapted to resource rich bottomland sites (eastern cottonwood, *Populus deltoides* Bartr.; American sycamore, *Platanus occidentalis* L.), and two were adapted to sites with a broader range of resource availability (sweetgum, *Liquidambar styraciflua* L.; and loblolly pine, *Pinus taeda* L.). These differences were reflected in nitrogen dynamics during early stand development (Aubrey et al., 2012), as loblolly pine and sweetgum were much less dependent upon water than were cottonwoods and sycamore. Cottonwoods and sycamore are typically found in moist nutrient rich environments such as floodplains and bottomland areas (Dickmann and Stuart, 1983; Wells and Schmidtting, 1990) and are more water- and nutrient-demanding than either loblolly pine or sweetgum. Prevailing consensus among many foresters in the southeastern U.S. is that these species may be useful for biomass production, but only in certain areas with high endemic soil resource availability (Kline and Coleman, 2010).

Several studies have used a chronosequence approach to gather growth and biomass data over a rotation (e.g. Chen, 1998; Laclau et al., 2000; King et al., 2007; Uri et al., 2012; Pacaldo et al., 2013). In contrast, we annually assessed ephemeral above- and belowground tissue pools and periodically sampled perennial root, stem and branch tissue pools over a rotation. This experiment allowed us to address several hypotheses regarding tree growth and productivity under different resource availability treatments. Our objective was to compare above- and belowground growth, productivity, and biomass accumulation among four tree species grown with or without irrigation, fertilization, or both. Early results from this project indicated that nutrient amendments were most critical to tree growth and biomass accumulation, and soil moisture availability was crucial to some, but not all, tree species tested (Coyle and Coleman, 2005; Coyle et al., 2008). Here we extend our findings beyond the early reports of stand establishment (Coleman et al., 2004a,b) and early growth (Coyle and Coleman, 2005; Coyle et al., 2008) to include the entire rotation with an emphasis on above and belowground tree growth and biomass responses to silvicultural amendments. We hypothesized that increased resource availability would positively influence above and belowground growth, productivity, and biomass accumulation of each species tested (e.g. Cobb et al., 2008; Brinks et al., 2011; Coyle et al., 2013). We also hypothesized that previously reported differences in growth, productivity, and biomass accumulation among species (Coyle and Coleman, 2005; Coyle et al., 2008) would be maintained throughout the rotation. Finally, we hypothesized that ontogenetic versus resource-dependent changes in belowground allocation observed in young trees (Coyle and Coleman, 2005; Coyle et al., 2008) is maintained throughout the rotation.

2. Materials and methods

Several previous publications detail most aspects of the study (Coleman et al., 2004a; Coyle and Coleman, 2005; Coyle et al., 2008; Aubrey et al., 2012). Following is a brief description of the study area, plant materials, experimental design, and sampling protocol.

2.1. Study area

We conducted the study at the U.S. Department of Energy Savannah River Site, a National Environmental Research Park, near Aiken, SC, USA (33°23'N, 81°40'E). This area lies in the Atlantic Coastal Plain physiographic region, and has primarily Blanton sand soils with a depth to argillic horizon exceeding 1 m (Rogers, 1990). The region has a humid subtropical climate, with warm, humid summers and mild winters. Annual rainfall ranged from 702 to 1264 mm and averaged 1045 mm yr⁻¹ (Supplemental Table A). Previous vegetation consisted of longleaf (*Pinus palustris* Mill.) and loblolly pine with an understory including oak (*Quercus* spp.), blackberry (*Rubus* spp.), and various non-woody plant species. The site was cleared in 1999 and soil was homogenized to a depth of 30 cm. We installed an automated drip irrigation system to supply water and nutrient treatments. Vertebrate, invertebrate, and pathogen control measures were used on all plots, and complete understory vegetation control was achieved through routine herbicide applications.

2.2. Plant material

We used five tree genotypes representing four species: two cottonwood clones (ST66 from Issaquena Co., MS; and S7C15 from Brazos Co., TX; Crown Vantage Corp., Fittler, MS, USA), sycamore (Westvaco orchard run; Westvaco Corp., Summerville, SC, USA), sweetgum (half-sib family WV340; Westvaco Corp., Summerville, SC, USA), and loblolly pine (half-sib family 7-56; International Paper Co., Lumberton, NC, USA). We soaked dormant cottonwood cuttings in water for at least 48 h prior to planting, and hand planted bare-root 1-0 sycamore, sweetgum, and pine seedlings. All cuttings and seedlings were planted in spring 2000.

2.3. Experimental design

Each genotype was arranged in a randomized block design, with four 0.22 ha treatment plots in each of three blocks. Each plot had a central 0.04 ha measurement plot consisting of 54 trees, and large end borders with additional trees to accommodate selected destructive sampling. Two border rows were included in each plot. Trees were planted at 2.5 × 3 m spacing (1333 trees ha⁻¹).

Our study consisted of four treatments along an increasing resource availability gradient: an untreated control (C), irrigation (I), fertilization at 120 kg N ha⁻¹ yr⁻¹ (F), and irrigation + fertilization (IF). Irrigation was applied daily to meet projected evaporative demand (NOAA, 1993, 1997) and ranged up to 5 mm d⁻¹. Fertilization treatments were applied via drip irrigation lines, and were split among 26 weekly applications from April through October each year. Fertilizer applications supplied an additional 5 mm of water per week; that amount of water was also applied to non-fertilized plots to maintain experimental consistency. Therefore, trees in the I and IF treatments received 780 mm of water annually in addition to rainfall, while those in the C and F treatments received 130 mm of additional water annually. To correspond with demand made by growing trees, fertilizer application rates increased during stand establishment (van Miegroet et al., 1994). Cottonwood and sycamore received 40 kg N ha⁻¹ in year one,

80 kg N ha⁻¹ in year two, and 120 kg N ha⁻¹ yr⁻¹ through year nine. Sweetgum and loblolly pine received 40 kg N ha⁻¹ in years one and two, 80 kg N ha⁻¹ in years three and four, and 120 kg N ha⁻¹ yr⁻¹ through year eleven. Other macro- and micro-nutrients were applied in balance with N (Coleman et al., 2004a; Coyle and Coleman, 2005; Coyle et al., 2008; Aubrey et al., 2012).

2.4. Growth and biomass determination

We recorded height and diameter at breast height (DBH, 1.37 m) on every live tree in the measurement plot annually in mid-winter. We stratified the diameter range within each treatment and randomly selected trees for destructive harvest from among available trees in each stratum by choosing 1–2 trees per plot from extended border rows for a total of five trees per treatment. Trees were felled at the base and the aboveground portion was separated into branch and stem components. Subsections of stems were further dissected to measure the proportion of bark and wood. We used an allometric approach to estimate pine foliage. Briefly, we separated the crown into three strata. For a single branch within each strata, we recorded the fresh mass in the field and then removed all foliage and determined the fresh mass of just the branch. The proportion of mass attributed to foliage was then applied to the fresh weights of total branch mass within each strata. We then summed foliage across strata and added the mass of foliage removed from the stem to calculate a whole-tree foliage mass. Branch, stem, and leaf fresh mass was recorded in the field and representative subsamples were dried to constant mass at 60 °C to determine dry weight.

Leaf litter was collected in three baskets (56 cm wide × 41 cm long × 27 cm deep) installed in each plot and hardwood litter was removed monthly from June to December. Loblolly pine litter continued to be collected monthly during winter. Samples were pooled within a plot, oven dried to 60 °C, and weighed. Leaf biomass and leaf litter were kept separate for pine, whereas leaf biomass for hardwoods was estimated from leaf litter.

We measured perennial belowground biomass by excavating the stump and attached lateral roots with a mechanical tree spade (model TS34C, Bobcat Co., West Fargo, ND, USA). The total volume of the soil cone removed by the tree spade was 0.18 m³ (1 m diam. × 0.69 m deep). The stump and attached lateral roots collected during stump excavation were washed and separated. Fresh mass was determined, and representative subsamples were dried as described above to determine dry weight. We estimated coarse root mass by excavating three randomly selected pits (0.19 m² × 0.3 m deep) within each plot (Coleman, 2007). No roots with diameter >5 mm were observed below the 0.3 m depth. The stump and lateral biomass collected from within the excavated tree's 1 m diameter growing space was used to parameterize predictive allometric relationships at the individual tree level (see below), whereas the additional excavated pits provided an estimate of perennial belowground biomass at the plot-level. We estimated belowground ephemeral biomass (i.e., fine root <5 mm diam.) at the plot-level by sampling five locations per plot using a 4.9 cm diam. corer, removing fine roots via root elutriation (Gillison's Variety Fabrication, Inc., Benzonia, MI, USA), separating live roots from other organic matter, and drying roots to a constant weight of 60 °C (Coleman, 2007).

We used fine root turnover data collected from cottonwood ST66 and loblolly pine from 2000 through 2005 (Coleman and Aubrey, unpublished data). Roots observed with minirhizotrons were monitored through the first six years of the study. Fine root turnover was predicted from survival functions calculated via Cox regression in PROC PHREG (SAS, Version 9.1.3, SAS Inc., Cary, NC, USA). We assumed turnover was the inverse of median root lifespan (Majdi and Andersson, 2005). We used separate estimates

for each treatment × year combination, and assumed that cottonwood S7C15, sycamore, and sweetgum had the same turnover rates as cottonwood ST66; the average for all treatment × year combinations was 0.87 g fine root mass g⁻¹ soil volume year⁻¹. For loblolly pine, the average turnover rate for all treatment × year combinations was 1.10 g fine root mass g⁻¹ soil volume year⁻¹. Although fine root turnover likely differs among hardwood species, turnover estimates derived on site from a hardwood are expected to yield better approximations for sycamore and sweetgum than would estimates derived from pine or from other studies had they been available. In a species intercomparison study, the representative *Populus* species (*P. tremuloides* Michx.) had the highest turnover rate (McCormack et al., 2014), so our approach likely overestimated fine root turnover for sweetgum and sycamore. We further assumed that fine root turnover stabilized with plantation development, as demonstrated by a model fit to the data (Coleman and Aubrey, unpublished), and therefore applied turnover estimates from the sixth year of the study as a constant for the remaining years.

2.5. Biomass calculations and statistical analyses

Growth and biomass were reported previously (Coyle and Coleman, 2005; Coyle et al., 2008); a brief recount of methodology is presented here. Tree height and diameter were recorded annually. Whole tree destructive biomass harvests were conducted during December or January after the 2000–2002, 2006, and 2008 growing seasons for cottonwood and sycamore, and after the 2001, 2003, 2006, and 2010 growing seasons for sweetgum and loblolly pine. In addition, sycamore was also harvested after the 2004 growing season, and cottonwood ST66 was harvested after the 2005 growing season. We generated two sets of allometric regressions – one based on groundline diameter (2000, 2001, and 2002) and one based on diameter at breast height (2002 and later) – for each species × treatment combination using destructive biomass harvest data from multiple years. We estimated branch, bark, wood, leaf, stump, and coarse root biomass fractions (y) from measurements of individual tree diameters of harvested trees using

$$y = ax^b + \varepsilon \quad (1)$$

where x is DBH (cm), a and b are regression parameters, and ε is a random normally distributed additive error term with zero mean and constant variance (Parresol, 1999; Coyle and Coleman, 2005; Coyle et al., 2008). Model parameters were estimated using PROC NLIN in SAS. Parameter values (Supplemental Table B) were then applied to estimate branch, bark, wood, leaf (pine only), stump, and coarse root biomass for all live trees in each plot as a function of DBH. Individual tree biomass values were scaled up to obtain plot-level biomass values. Aboveground biomass components (branch, bark, and wood) were summed to obtain plot-level shoot biomass. Belowground biomass components (stump and associated lateral roots collected during stump excavation) were scaled to the plot level and then summed with plot-level coarse and fine root biomass to yield plot-level estimates of total root biomass. Total biomass was calculated as the sum of shoot and root biomass. To maintain equivalent comparisons among genotypes, only standing woody biomass was analyzed; leaf and litter biomass values are presented but were not included in total biomass analyses.

Annual NPP (NPP) was calculated as the difference between total dormant season biomass from one year to the next plus root turnover and leaf litter within that annual period. For the first year, NPP was calculated simply as total biomass plus root turnover and leaf litter within that initial year. Aboveground NPP (ANPP) and belowground NPP (BNPP) were calculated the same as NPP, but using only shoot or root tissues, respectively. Stem volume index was calculated as the square of dbh multiplied by the height. Mean annual

increment (MAI) for each genotype \times treatment was calculated as the average stem growth per year on a volume index basis. Root mass fraction (RMF) was calculated as the proportion of root to total mass.

We analyzed age, genotype, and treatment effects using a multi-factorial repeated measures split-plot arranged in a randomized complete block. Species was treated as the fixed whole-plot factor, year was treated as the fixed repeated factor, block was treated as the random subject factor, and irrigation and fertilization were treated as fixed sub-plot factors. We used plot means to analyze biomass components, an approach that adequately accounts for between plot variation, but eliminates variance among sample trees used to develop regression equations (Parresol, 1999). Therefore, the total variance in our models may have been less than what actually existed among sample trees. However, the central limit theorem suggests that individual tree variance equilibrates because we had a large number of trees per plot ($n = 54$). All analyses were performed using a mixed model procedure (PROC MIXED in SAS) with a type-I error rate of 0.05.

To model the correlation within experimental units over time, we analyzed each response using common covariance structures appropriate for data collected at equal temporal spacing within and among experimental units (i.e., first-order autoregressive, Toeplitz, unstructured, compound symmetry, and variance component) and used AICC (Burnham and Anderson, 1998) to determine which structure best fit each model. Denominator degrees of freedom were estimated according to the Kenward–Roger method (Kenward and Roger, 1997). Treatment means were compared using Fisher's Least Significant Difference (LSD) test. When interactions occurred, we performed tests of simple main effects in SAS using the SLICE option in the LSMEANS statement (Schabenberger et al., 2000; Littell et al., 2006).

It was necessary to account for ontogenetic effects on biomass allocation while testing for treatment effects (Poorter et al., 2012). To do this, we examined k , the allometric constant, which is the slope of the line relating two biomass fractions (Coyle and Coleman, 2005; Coyle et al., 2008). With log of root mass arranged on the y-axis and log of shoot on the x-axis, a lower k indicates lower root allocation relative to shoot.

3. Results

3.1. Growth and production

3.1.1. Resource availability

Fertilization and irrigation significantly affected growth and biomass production of all genotypes after nine years (Table 1, Supplemental Table C), but after 11 years only fertilization consistently impacted growth and biomass production of sweetgum and loblolly pine (Table 1, Supplemental Table D). Increasing resource availability resulted in significant growth and biomass production increases among treatments within a genotype (Table 1). Trees receiving IF or F were consistently larger than trees that received I or C. For instance, stem volume index was >735% larger in cottonwoods, 597% larger in sycamore, 321% larger in sweetgum, and 81% larger in loblolly pine receiving IF compared to C after nine growing seasons (Table 1). Production was similarly affected, but not as consistently, as only loblolly pine and cottonwood ST66 showed significantly greater total NPP in the IF treatment compared to all other treatments (Table 1). MAI index generally followed the pattern IF > F > I > C, although F and IF were not different in sweetgum or loblolly pine (Fig. 1).

The relative contribution of different tissues to NPP was influenced by fertilization and irrigation. As resource amendment levels increased, stem production increased and coarse root production decreased in all hardwoods, but this trend was not evident with loblolly pine (Fig. 2). Production of some tissues, such as branch

and bark, was consistent among treatments, while others were influenced by treatment (e.g. fertilized treatments in ST66 had at least 82% more wood biomass production than non-fertilized treatments) (Fig. 2). Relative tissue biomass production in sweetgum and loblolly pine was similar after nine and 11 growing seasons.

3.1.2. Genotype differences

Loblolly pine exhibited increased growth and higher productivity rates than any hardwood genotype we tested (Table 1). Across all treatments, loblolly pine dbh was 36% greater, basal area was 75% greater, and stem volume index was 85% greater than any hardwood genotype after nine growing seasons, and these differences were maintained after 11 growing seasons when loblolly pine was compared to sweetgum (Table 1). Among hardwood genotypes, sweetgum and sycamore growth and biomass production was generally greater than both cottonwood genotypes, although these differences were not always significant (Supplemental Table C). Total NPP and ANPP were always highest in loblolly pine, and BNPP was highest in sweetgum and loblolly pine (Table 1). Loblolly pine total NPP was 42% higher than sweetgum and >141% higher than any other genotype after nine years (Table 1). Loblolly pine ANPP was 77% higher than sweetgum after nine and 43% higher after 11 years. Loblolly pine ANPP was 200% higher than sycamore or cottonwood genotypes after nine years. Loblolly pine and sweetgum BNPP was 60 and 53% higher, respectively, than other hardwood genotypes after nine years (Table 1). Mean annual increment among hardwoods was greatest in sweetgum, and similar among cottonwoods and sycamore; loblolly pine MAI index was nearly twice that of sweetgum (Fig. 1).

The relative contribution of different tissues to NPP was similar among hardwood genotypes, with increases in wood and decreases in leaf and fine root production as resource availability increased. Leaf production was relatively consistent in sweetgum, and production of most tissues was affected little by resources in loblolly pine (Fig. 2). An exception is loblolly pine fine root production, which was 64% greater in non-fertilized treatments. Coarse root production was at nearly 41% greater in sweetgum than in any other genotype (Fig. 2). At the end of the rotation loblolly pine had the greatest proportion of wood production, while S7C15 had the greatest proportion of leaf tissue production.

3.2. Biomass accumulation and allocation

3.2.1. Resource availability

Increased resource availability resulted in greater biomass accumulation. Total biomass accumulation followed the order IF > F > I > C for all genotypes after nine growing seasons, although trees receiving F and IF did not always differ significantly, just as C and I did not always differ (Fig. 3). Tree biomass increases in IF compared to C were substantial, ranging from 47% in loblolly pine to 288% in ST66 (Fig. 3). Stem biomass followed a similar overall pattern; however, stem biomass in hardwood genotypes responded much more strongly to IF compared with C as increases ranged from 313% greater in sweetgum to 575% greater in ST66 (Fig. 4). Loblolly pine stem biomass was 62% greater when grown with IF compared to C (Fig. 4). Aboveground biomass followed the IF > F > I > C pattern for most genotypes, but belowground biomass was more variable. Individual biomass components were not consistently affected by resource treatments over time, although fertilization and irrigation generally increased biomass accumulation of most tissue components after nine years with only a few exceptions (Supplemental Table E). Significant effects of higher order interactions (e.g. year \times fertilization \times irrigation) were present but showed few patterns. For instance, after nine growing seasons the genotype \times irrigation and year \times genotype \times fertilization \times irrigation interactions affected root biomass but not shoot

Table 1

Mean growth and productivity of five tree genotypes grown in South Carolina, USA after nine (2008) and 11 (2010) growing seasons. Within a genotype \times year, treatment means followed by the same letter are not significantly different from other treatments within that genotype (Fisher's LSD, $\alpha = 0.05$). Among genotype means across treatments (shown below the 2008 and 2010 data) genotype means followed by the same letter are not significantly different from other genotypes (Fisher's LSD, $\alpha = 0.05$).

Year	Genotype	Treatment	Ht (m)	DBH (cm)	BA (m ² ha ⁻¹)	Vol. index (m ³ ha ⁻¹)	ANPP (Mg ha ⁻¹ yr ⁻¹)	BNPP (Mg ha ⁻¹ yr ⁻¹)	NPP (Mg ha ⁻¹ yr ⁻¹)
2008	Cottonwood ST66	C	6.2 ^d	6.3 ^d	4.3 ^c	41.2 ^c	2.6 ^b	4.8 ^b	7.4 ^b
		I	7.8 ^c	7.9 ^c	6.7 ^c	76.5 ^c	3.3 ^b	6.3 ^{ab}	9.6 ^b
		F	11.0 ^b	10.2 ^b	11.3 ^b	176.8 ^b	4.8 ^{ab}	4.8 ^b	9.6 ^b
		IF	13.6 ^a	12.4 ^a	17.4 ^a	343.8 ^a	7.2 ^a	8.1 ^a	15.3 ^a
	Cottonwood S7C15	C	6.5 ^d	6.2 ^d	4.1 ^c	40.8 ^c	2.2 ^b	2.5 ^b	4.7 ^c
		I	8.1 ^c	8.1 ^c	7.0 ^c	87.5 ^c	2.5 ^b	3.5 ^{ab}	6.0 ^{bc}
		F	11.2 ^b	10.6 ^b	11.8 ^b	194.3 ^b	4.7 ^{ab}	5.4 ^a	10.1 ^{ab}
		IF	13.5 ^a	12.2 ^a	17.2 ^a	343.7 ^a	6.4 ^a	3.8 ^{ab}	10.2 ^a
	Sycamore	C	7.8 ^d	6.9 ^c	5.2 ^c	52.7 ^d	2.7 ^c	6.0	8.7 ^b
		I	11.2 ^c	10.0 ^b	10.4 ^b	156.3 ^c	5.5 ^{bc}	6.0	11.5 ^{ab}
		F	14.1 ^b	12.3 ^a	15.6 ^a	285.9 ^b	6.8 ^{ab}	6.1	12.9 ^a
		IF	16.1 ^a	13.6 ^a	17.4 ^a	367.4 ^a	8.6 ^a	3.7	12.3 ^{ab}
	Sweetgum	C	8.8 ^b	9.1 ^b	8.8 ^d	99.7 ^c	4.0 ^d	10.8 ^a	14.7 ^c
		I	10.0 ^b	10.4 ^b	12.2 ^c	167.9 ^c	7.7 ^c	10.5 ^a	18.3 ^{bc}
		F	12.9 ^a	13.4 ^a	19.4 ^b	319.7 ^b	11.8 ^b	8.6 ^{ab}	20.4 ^{ab}
		IF	14.1 ^a	14.6 ^a	23.1 ^a	420.3 ^a	16.5 ^a	6.9 ^b	23.4 ^a
	Loblolly Pine	C	11.9 ^b	15.1 ^b	23.6 ^c	370.4 ^c	14.3 ^c	9.8	24.1 ^b
		I	11.5 ^b	14.2 ^b	20.9 ^c	315.6 ^c	14.9 ^c	9.5	24.4 ^b
		F	12.3 ^b	17.2 ^a	32.0 ^b	508.4 ^b	19.1 ^b	8.7	27.8 ^b
		IF	14.6 ^a	18.3 ^a	35.1 ^a	671.9 ^a	22.4 ^a	10.5	32.9 ^a
	Genotype mean across treatment	ST66	9.7 ^b	9.2 ^c	10.0 ^c	159.9 ^b	4.5 ^c	6.0 ^b	10.5 ^c
		S7C15	9.8 ^b	9.3 ^c	10.0 ^c	166.6 ^b	4.0 ^c	3.8 ^c	7.7 ^d
		Sycamore	12.3 ^a	10.7 ^b	12.2 ^b	215.6 ^b	5.9 ^c	5.4 ^b	11.3 ^c
		Sweetgum	11.5 ^a	11.9 ^b	15.9 ^b	251.9 ^b	10.0 ^b	9.2 ^a	19.2 ^b
		Loblolly Pine	12.6 ^a	16.2 ^a	27.9 ^a	466.6 ^a	17.7 ^a	9.6 ^a	27.3 ^a
2010	Sweetgum	C	9.5 ^d	9.7 ^b	10.1 ^c	123.3 ^c	4.8 ^c	13.6 ^a	18.4 ^b
		I	11.1 ^c	11.2 ^b	14.3 ^b	220.6 ^c	7.4 ^c	13.7 ^a	21.1 ^b
		F	14.4 ^b	14.9 ^a	24.1 ^a	445.1 ^b	16.4 ^b	10.8 ^b	27.2 ^a
		IF	15.8 ^a	16.1 ^a	28.0 ^a	574.5 ^a	21.3 ^a	7.4 ^c	28.7 ^a
	Loblolly Pine	C	13.7 ^b	16.6 ^b	28.7 ^b	518.0 ^c	13.8 ^b	12.1	25.0 ^b
		I	13.2 ^b	15.8 ^b	25.7 ^b	443.1 ^c	15.3 ^b	10.7	26.0 ^b
		F	15.4 ^a	19.4 ^a	39.2 ^a	772.2 ^b	21.2 ^a	10.2	31.4 ^a
		IF	16.7 ^a	20.7 ^a	41.8 ^a	895.6 ^a	21.4 ^a	10.4	31.8 ^a
	Genotype mean across treatment	Sweetgum	12.7 ^b	13.0 ^b	19.1 ^b	340.9 ^b	12.5 ^b	11.4	23.9 ^b
		Loblolly Pine	14.8 ^a	18.2 ^a	33.9 ^a	657.2 ^a	17.9 ^a	10.9	28.8 ^a

or total biomass. Stem biomass was affected by the year \times fertilization \times irrigation interaction. These higher order interactions generally resulted from differences in tissue components appearing in most – but not all – years.

Fertilization affected every individual and composite biomass component of sweetgum and loblolly pine after the 2010 growing season (Fig. 5, Supplemental Table F). Conversely, irrigation had minimal impact as only branch, leaf, and leaf litter biomass increased with irrigation (Supplemental Table F).

Belowground biomass allocation typically declined over the course of tree development (i.e. ontogenetic drift) and was influenced by both fertilization and irrigation (Supplemental Table G). The decline in RMF was most rapid during establishment years in sycamore, higher resource treatments of ST66, and sweetgum (Fig. 6). Lower RMFs always occurred in treatments receiving increased resource amendments, and irrigated or control trees always had the highest RMFs (Fig. 6). As expected, there were strong relationships between total root and total shoot biomass fractions (all $R^2 > 0.81$, all $P < 0.001$, Fig. 7). For both cottonwood genotypes and sycamore, ontogeny explained all of the variation in belowground biomass allocation; that is, k did not differ among treatments within a genotype (Supplemental Table H). However, resource availability treatments altered biomass allocation for sweetgum and loblolly pine. Sweetgum exhibited the lowest k in both F and IF treatments, while k was lower in the I, F, and IF compared to the C treatment for loblolly pine (Supplemental Table H).

3.2.2. Genotype differences

Loblolly pine accumulated the greatest amount of total biomass compared with the other genotypes. After nine years loblolly pine total biomass was 218% greater than S7C15, 207% greater than ST66, and 88% greater than sycamore (Fig. 3). Loblolly pine total biomass was 33% greater than sweetgum after nine (Fig. 3) or 11 years (Fig. 4). Total aboveground biomass followed the same pattern, but total belowground biomass did not differ significantly between loblolly pine and sweetgum. Pine stem biomass was 261% greater than S7C15, 251% greater than ST66, 91% greater than sycamore, and 55% greater than sweetgum after nine years (Fig. 4).

Perennial belowground tissues comprised 57–81% of belowground biomass in cottonwood genotypes, 71–91% in sycamore or sweetgum, and 85–95% in loblolly pine after 9 or 11 years. After the fourth growing season (2003) RMFs had generally stabilized (Fig. 6). Hardwood genotypes had a much larger range of RMF values among amendment treatments compared to loblolly pine. Loblolly pine had a higher k value compared with all hardwood genotypes, while ST66 and sycamore had lower k values than S7C15 and sweetgum (Supplemental Table H).

4. Discussion

Our first hypothesis – that increased resource availability would positively influence above and belowground growth, productivity, and biomass accumulation of each species tested – was confirmed

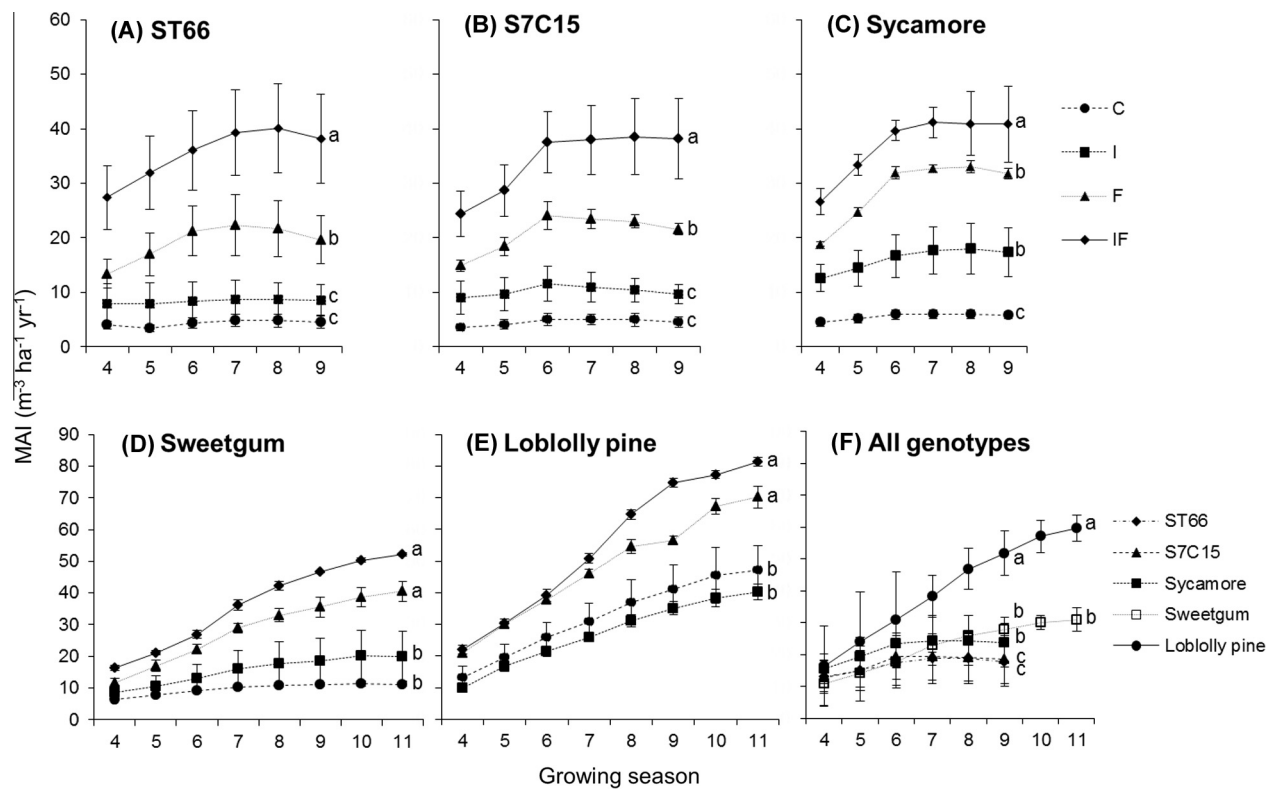


Fig. 1. Mean annual volume index increment (MAI) (\pm SE) for five tree genotypes that received control (C), irrigation (I), fertilization (F), or irrigation + fertilization (IF) treatments in South Carolina, USA. We calculated volume increment based on a height by diameter squared volume index. A rotation was nine years for cottonwood genotypes ST66 and S7C15 and sycamore, and 11 years for sweetgum and loblolly pine. Within a species, means sharing a letter are not significantly different (Fisher's LSD, $\alpha = 0.05$).

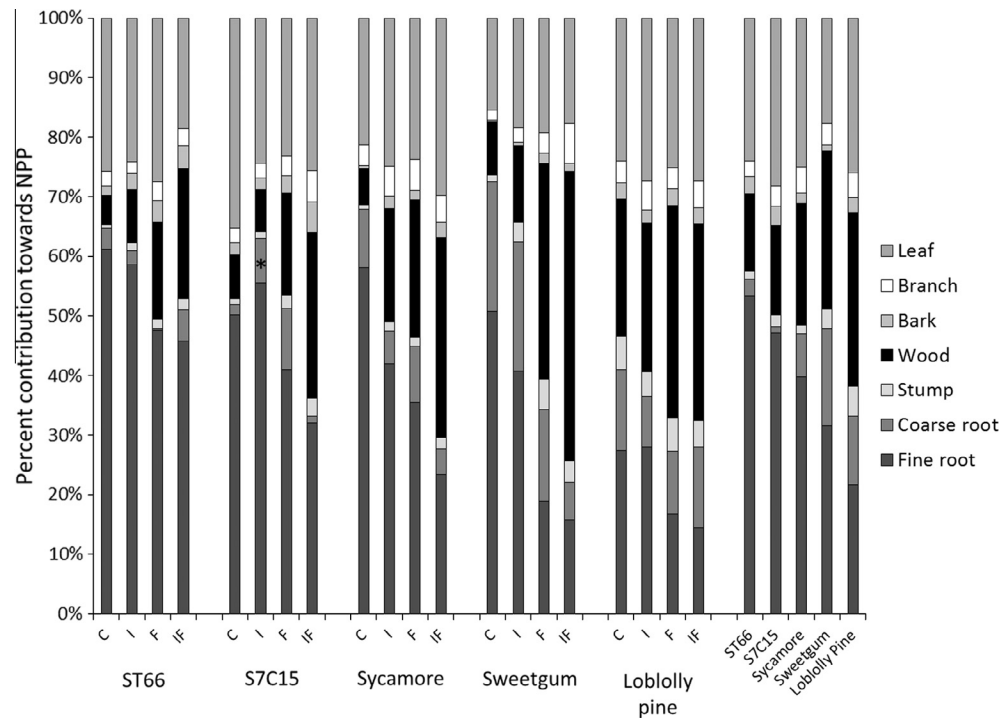


Fig. 2. Relative contribution of different tissues to total NPP of five tree genotypes that received control (C), irrigation (I), fertilization (F), or irrigation + fertilization (IF) treatments after nine (cottonwood clones ST66 and S7C15, and sycamore) or 11 (sweetgum and loblolly pine) growing seasons in South Carolina, USA. Fine root production includes turnover. To estimate current year foliage we used leaf litter production for hardwood genotypes; leaf production was used for loblolly pine. The asterisk in S7C15 coarse root signifies that this production was negative at the end of the rotation, indicating a relative cessation of additional tissue production.

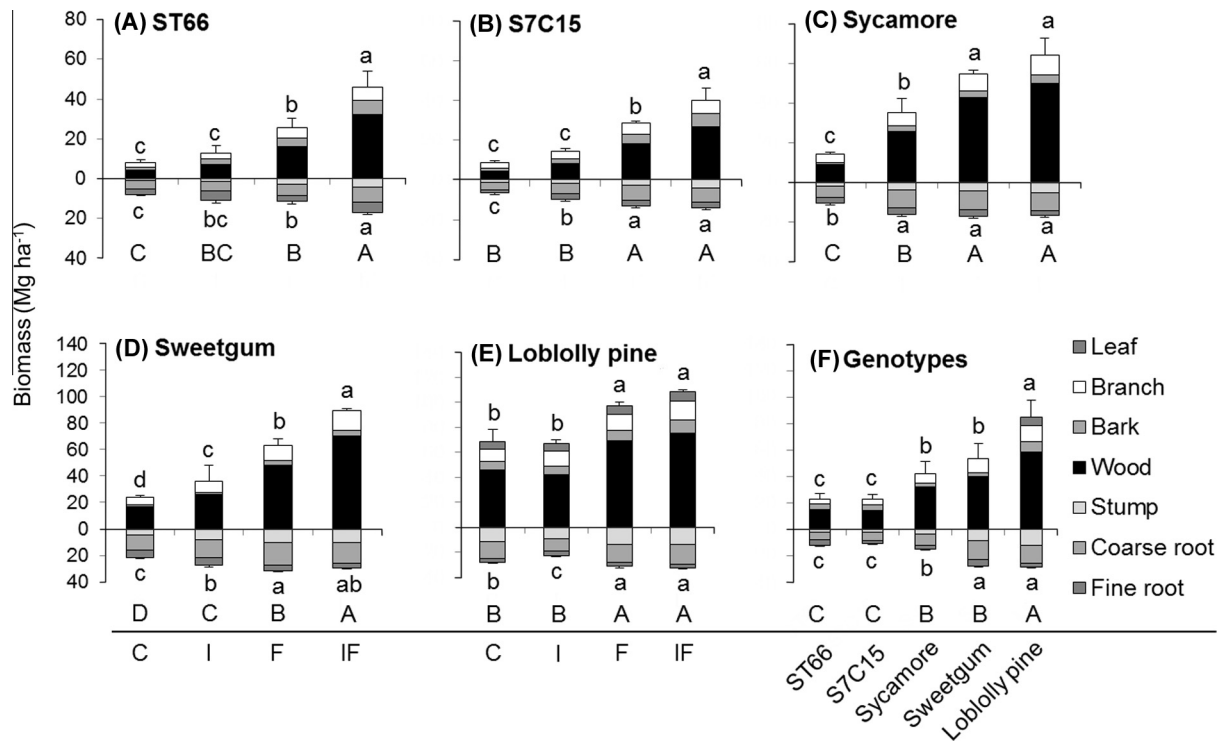


Fig. 3. Above and belowground biomass of five tree genotypes after nine growing seasons in South Carolina, USA. Treatments consisted of control (C), irrigation (I), fertilization (F), and irrigation + fertilization (IF). Zero on the y-axis represents the groundline. Error bars are standard error. Lowercase letters and error bars above the columns are for total aboveground biomass; those below the columns are for total belowground biomass. Capital letters above the x-axis refer to total biomass. Within a species, aboveground, belowground, or total biomass means with the same letter are not significantly different (Fisher's LSD, $\alpha = 0.05$). Leaf biomass is presented for loblolly pine, but was not included in the analysis in order to maintain a valid statistical comparison with hardwood genotypes.

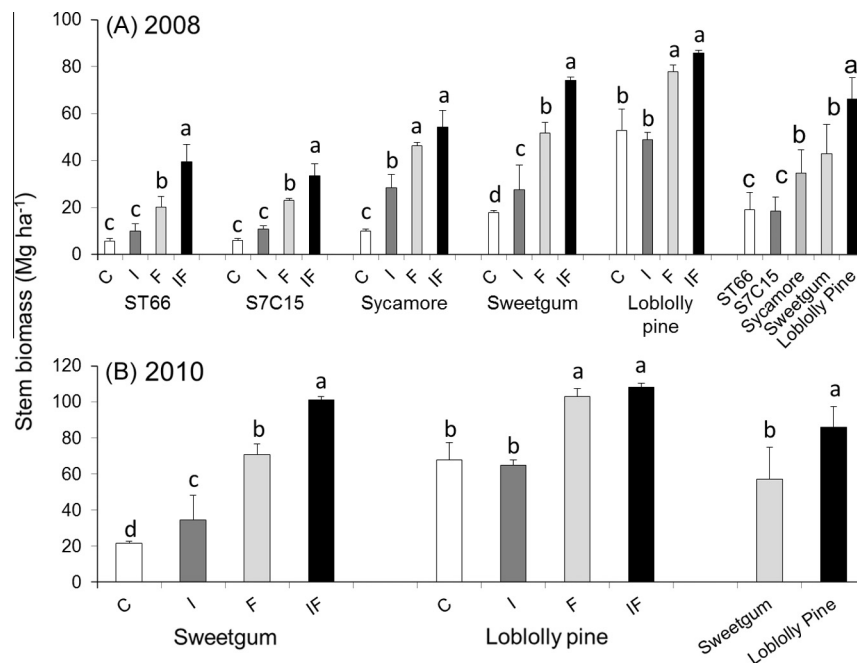


Fig. 4. Stem biomass (mean \pm SE) after nine (A) or 11 (B) growing seasons for five tree genotypes that received control (C), irrigation (I), fertilization (F), or irrigation + fertilization (IF) treatments in South Carolina, USA. A rotation was nine years for cottonwood genotypes ST66 and S7C15 and sycamore, and 11 years for sweetgum and loblolly pine.

as greater growth and biomass accumulation was associated with increasing resource availability across all genotypes. Differences in total biomass accumulation among treatments were similar to those reported at age three for ST66 (Coyle and Coleman, 2005)

and at age four for loblolly pine (Coyle et al., 2008). S7C15 and sycamore showed a greater growth response to fertilization after nine growing seasons compared to age three (Coyle and Coleman, 2005). Sweetgum growth and biomass accumulation

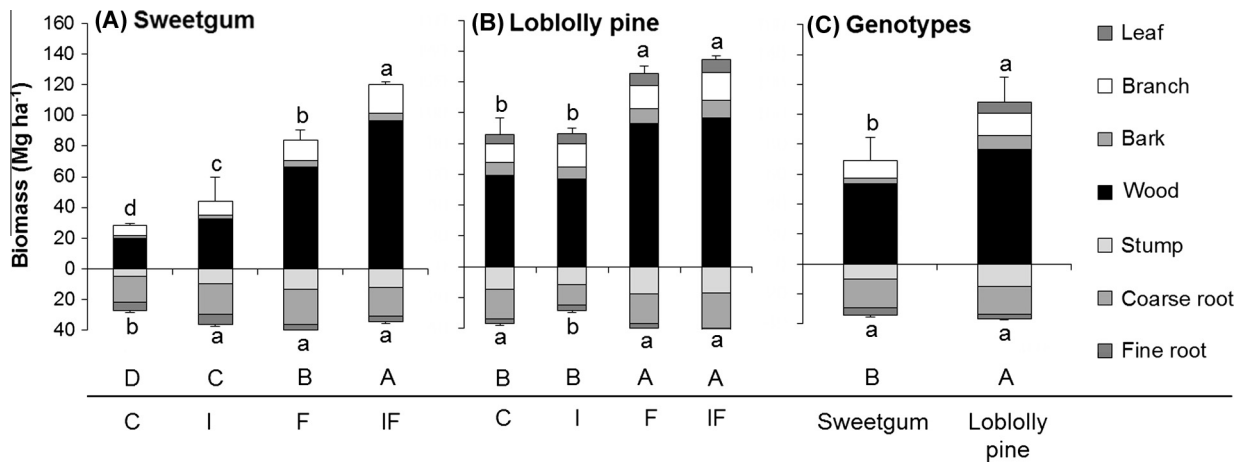


Fig. 5. Above and belowground standing biomass of sweetgum and loblolly pine after 11 growing seasons in South Carolina, USA. Treatments consisted of control (C), irrigation (I), fertilization (F), and irrigation + fertilization (IF). Zero on the y-axis represents the groundline. Error bars are SEs. Lowercase letters and error bars above the columns are for total aboveground biomass; those below the columns are for total belowground biomass. Capital letters above the x-axis refer to total biomass. Within a species, aboveground, belowground, or total biomass means with the same letter are not significantly different (Fisher's LSD, $\alpha = 0.05$). Leaf biomass is presented for loblolly pine, but was not included in the analysis in order to maintain a valid statistical comparison with sweetgum.

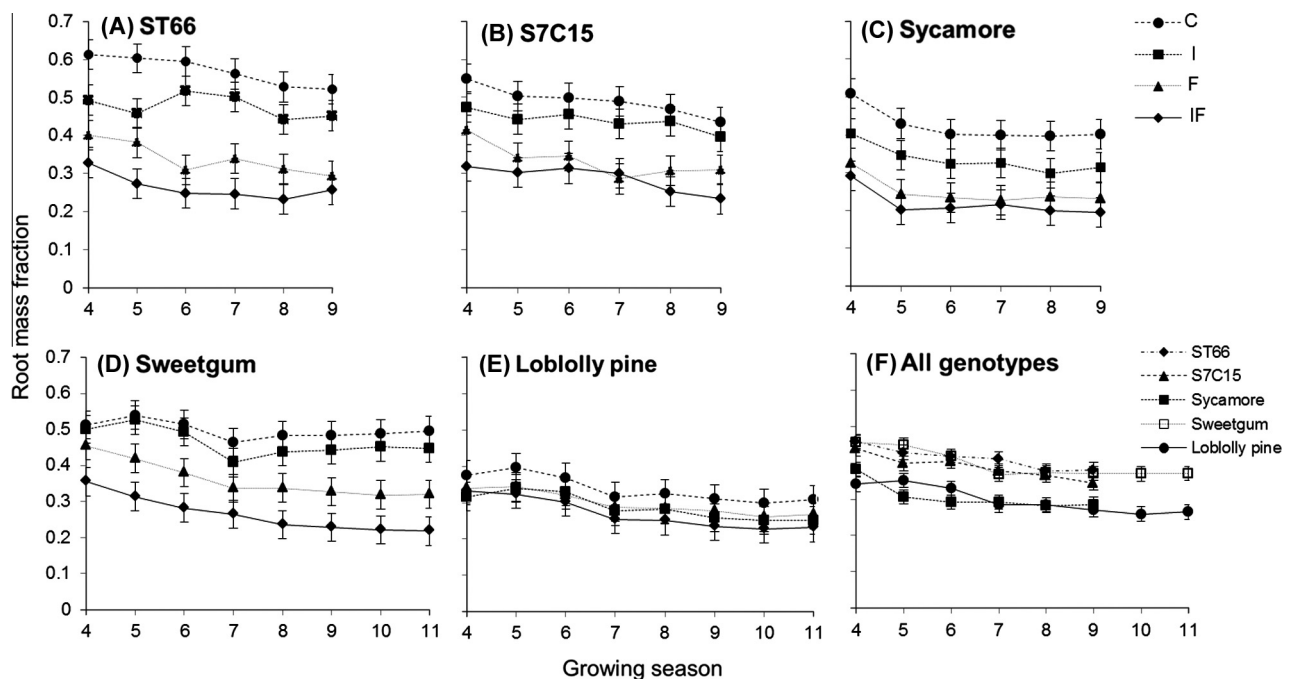


Fig. 6. Root mass fraction (\pm average SE) of five tree genotypes that received control (C), irrigation (I), fertilization (F), or irrigation + fertilization (IF) treatments (A–E) and all genotypes (F) in South Carolina, USA. ST66, S7C15, and sycamore were harvested after nine growing seasons.

was affected by fertilization at age four (Coyle et al., 2008), but by age 11 it was affected by irrigation, fertilization, and their combination. Aboveground and belowground biomass showed similar patterns among genotypes, although belowground biomass increased in sycamore and sweetgum receiving irrigation at the end of the rotation compared to early stand development (Coyle and Coleman, 2005; Coyle et al., 2008).

Our study is unique in that we followed multiple genotypes, each receiving four different silvicultural treatments, over a rotation, and found that after early stand development (years 1–4) there was little or no change in how each genotype responded to resource amendments at the end of the rotation – thus confirming our second hypothesis that previously reported differences in

growth, productivity, and biomass accumulation among species would be maintained throughout the rotation. Correlations between young and older tree growth and biomass production are common, but there are exceptions. For instance, about 70% of several *Populus* spp. clones grown in Argentina showed the same growth rankings at age 3 and ages 9 or 10 (Ares, 2002), yet few *Populus* genotypes in the Midwestern U.S. maintained growth and disease rankings from age 7 to 12 (Netzer et al., 2002). In Belgium, several *Populus* genotypes showed significant correlations between annual biomass production during the first 3-yr coppice rotation, but these correlations occurred less frequently in subsequent rotations (Afes et al., 2008). Four years was shown to be the economically optimum age to select loblolly pine for

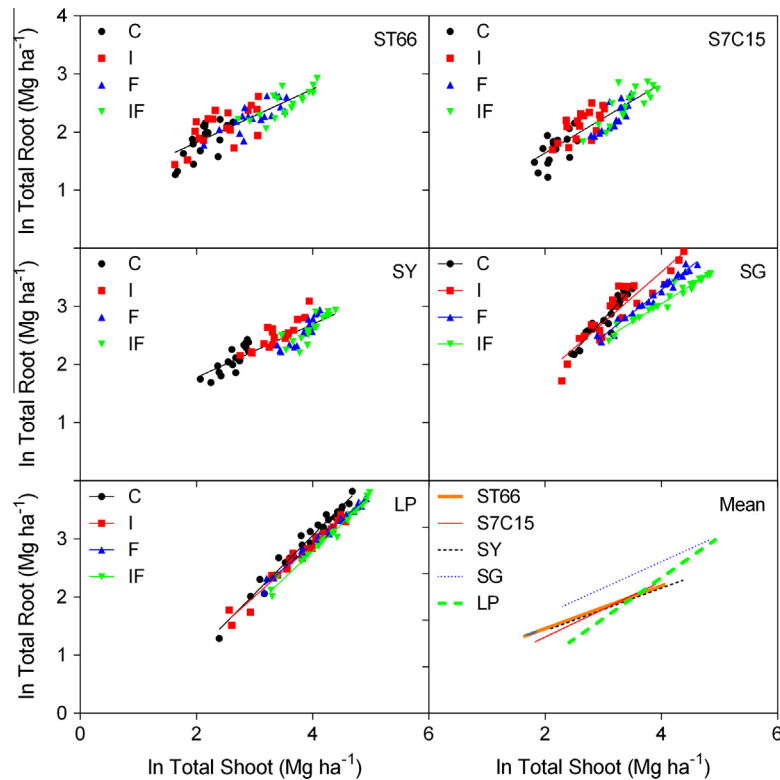


Fig. 7. Allometric relationships for total biomass in ST66, S7C15, sycamore (SY), sweetgum (SG), loblolly pine (LP), and all genotypes together (Mean) in response to control (C), irrigation (I), fertilization (F), and irrigation + fertilization (IF) treatments. All tissue fractions are natural log transformed plot means. Data are included from growing seasons four (2003) through final harvest (growing season nine for ST66, S7C15, and sycamore; growing season 11 for sweetgum and loblolly pine). The slope of each line (i.e. allometric coefficient, k') is listed in [Supplemental Table H](#). Where no significant difference occurs among slopes (i.e. ST66, S7C15, and sycamore) only one line, encompassing all points, is shown.

late-rotation (39–75 yr) growth characteristics (McKeand, 1988), and Lambeth et al. (1983) found strong correlations in several growth parameters between 5- and 20-year old loblolly pine.

Trees in this study experienced several abiotic and biotic disturbances that may have impacted overall growth and productivity. For instance, loblolly pine in this study experienced a severe ice storm after the fourth growing season (Aubrey et al., 2007). Irrigation and fertilization influenced the amount of tree bending and breakage, but the proportion of undamaged trees did not differ among treatments, and recovery of most stems occurred within 6–7 months. Loblolly pine also recovered from Nantucket pine tip moth, *Rhyacionia frustrana* Comstock, damage early in the rotation (Coyle et al., 2003). Fusiform rust, *Cronartium quercuum* f. sp. *fusiforme* Hedg. & Hunt ex Cum., was also present, though occurrence did not differ among treatments (Coleman, unpublished data). Sycamore experienced varying levels of damage from sycamore anthracnose, *Apiognomonia veneta* (Sacc. & Speg.) Höhn. This fungus thrives in humid conditions (Ammon, 1990), and repeated defoliations can reduce tree vigor. Sycamore lace bug, *Corythucha ciliata* (Say), and a leafhopper, *Erythroneura lawsoni* Robinson, populations were also present, especially on non-fertilized trees (Coyle et al., 2010). Cottonwood genotypes in our study were impacted by cottonwood leafcurl mites, *Aculops lobuliferus* (Keifer) (Coyle, 2002), and various ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) (Coyle et al., 2005) early in the rotation. Sweetgum, on the other hand, did not experience any noticeable abiotic or biotic maladies. The abiotic and biotic factors observed in this study had the capacity to negatively impact stand productivity, yet even with these factors – none of which were out of the ordinary for these tree genotypes in this region – relative growth differences

among treatments within a genotype remained largely unchanged over the course of the rotation.

Cottonwood and sycamore genotypes showed a strong positive response to irrigation in our study, while sweetgum showed a weak (but positive in some cases) response, and loblolly pine was not affected by irrigation. Our study was conducted in a humid environment, and it is not uncommon for conifers to show no response to irrigation in this type of environment (Table 2). In fact, only one study that evaluated conifer growth in a humid climate showed an irrigation response, while those in drier climates generally responded to irrigation (Table 2). Further, rainfall was relatively consistent throughout our study (Supplemental Table A), and this may have negated any potential positive effects of irrigation in loblolly pine. This also occurs with other commercial hardwoods when planted in humid environments, such as *Eucalyptus* spp. (Cromer et al., 1993). However, eucalyptus does show significant growth increases when grown with irrigation under more arid conditions (Minhas et al., 2015). Had our study been conducted on a more arid site, in finer-textured soil, or used a different water delivery method, we may have seen a positive response to irrigation in loblolly pine. While we did not record maximum root depth, it is possible that sweetgum and loblolly pine may have reached water along the argillic soil horizon, thus reducing the importance of the applied irrigation. We observed benefits of irrigation on cottonwood and sycamore growth and production both early (e.g. Coyle and Coleman, 2005) and late in the rotation. Hardwood species are known to exhibit greater growth responses to irrigation (e.g. Harrington and DeBell, 1984; Lockaby et al., 1997; Henderson and Jose, 2010) than are pine species (e.g. Albaugh et al., 1998, 2004; Jokela et al., 2004) (Table 2). In the southeastern

Table 2

Young (<20 year old) commercial tree species' response to irrigation and fertilization in varying climates and soil conditions. Studies were conducted in the field (i.e. no potted plant studies) and contained at least the following treatments: control, irrigation, fertilization, and irrigation \times fertilization.

Tree species	Location	Climate	Soils	Tree age during study	+Irr response	+Fert response	+IF response	Reference
<i>Pinus taeda</i> L.	NC, USA	Humid subtropical	Sandy	8–12	Diameter, height, BA, stem vol. (only in three drought years)	Diameter, height, basal area, stem volume, peak LAI	Height (1 of 4 years)	Albaugh et al. (1998)
<i>Pinus taeda</i>	NC, USA	Humid subtropical	Sandy	8–17	Height, LAI, crown length, stem mass, stem mass increment, total biomass	Height, basal area, LAI, crown length, stem mass, stem mass increment, foliar N, total biomass	None	Albaugh et al. (2004)
<i>Pinus taeda</i>	FL, USA	Humid subtropical	Sandy	2	None	Biomass, leaf area	None	Johnson (1990)
<i>Pinus taeda</i>	SC, USA	Humid subtropical	Sandy	1–11	None	Height, diameter, basal area, above, below, total biomass	None	This study
<i>Pinus taeda</i>	NC, USA	Humid subtropical	Sandy	8–9	None	Aboveground biomass, leaf area index	Aboveground biomass, leaf area index	Campoe et al. (2013)
<i>Pinus taeda</i>	FL, USA	Humid subtropical	Sandy	1–4	None	Height, diameter, stem volume	None	Neary et al. (1990)
<i>Pinus elliottii</i> Engelm.	FL, USA	Humid subtropical	Sandy	1–4	None	Height, diameter, stem volume	None	Neary et al. (1990)
<i>Pinus elliottii</i>	FL, USA	Humid subtropical	Sandy	2	None	None	Biomass, leaf area	Johnson (1990)
<i>Pinus pinaster</i> Aiton	Bordeaux, France	Oceanic (but arid)	Sandy	4–9	None	Diameter, stem volume, aboveground biomass	Height, diameter, stem volume, aboveground biomass	Tritchett et al. (2008)
<i>Pinus radiata</i> D. Don	Canberra, Australia	Oceanic (but arid)	Sandy	10–15	Height, diameter, basal area, volume, needle, stem, and total biomass	Diameter, basal area, needle, branch, and total biomass	Diameter, basal area, volume, needle, branch, stem, and total biomass	Snowdon and Benson (1992)
<i>Eucalyptus grandis</i> \times <i>urophylla</i>	Entre-Rios, Brazil	Tropical savanna	Sandy	3–5.5	Gross primary production, belowground C allocation, aboveground woody biomass	None	None	Stape et al. (2008)
<i>Pinus sylvestris</i> L.	Stora Strasan, Sweden	Humid continental	Loamy	9–20	None	Total, aboveground, belowground biomass	None	Axelsson and Axelsson (1986)
<i>Quercus ilex</i> L. subsp. <i>ballota</i>	Teruel, Spain	Oceanic	Loamy	6–8	None	Height, diameter	Height, diameter	Pardos et al. (2005)
<i>Liquidambar styraciflua</i>	SC, USA	Humid subtropical	Sandy	1–11	Basal area, above, below, total biomass	Basal area, above, below, total biomass	Basal area, above, total biomass	This study
<i>Liquidambar styraciflua</i>	AL, USA	Humid subtropical	Sandy	1–4	None	Height, diameter	None	Lockaby et al. (1997)
<i>Platanus occidentalis</i>	SC, USA	Humid subtropical	Sandy	1–9	Above, below, total biomass	Above, below, total biomass	Basal area	This study
<i>Platanus occidentalis</i>	AL, USA	Humid subtropical	Sandy	1–4	Height, diameter	Height, diameter	Height, diameter	Lockaby et al. (1997)
<i>Populus deltoides</i>	NY, USA	Humid continental	Rocky, loamy	2	Diameter	Diameter	Diameter	Funk et al. (2007)
<i>Populus deltoides</i>	SC, USA	Humid subtropical	Sandy	1–9	Diameter, height, above, below, total biomass	Diameter, height, above, below, total biomass, basal area	Diameter, height, above, below, total biomass, basal area	This study
<i>Populus deltoides</i>	AL, USA	Humid subtropical	Sandy	1–4	Diameter	None	Height	Lockaby et al. (1997)
<i>Populus tremuloides</i> Michx.	Alberta, Canada	Humid continental	Loamy	1–3	None	Stem volume	Height, diameter, stem volume	van den Driessche et al. (2003)
<i>Populus maximowiczii</i> \times <i>trichocarpa</i>	PA, USA	Humid continental	Loamy	1–4	Height and diameter in some years/locations	Height, diameter	None	Bowersox et al. (1991)
<i>Salix miyabeana</i> Seemen	Quebec, Canada	Humid continental	Loamy	1–2	Aboveground biomass	Aboveground biomass	Aboveground biomass	Jerbi et al. (2015)

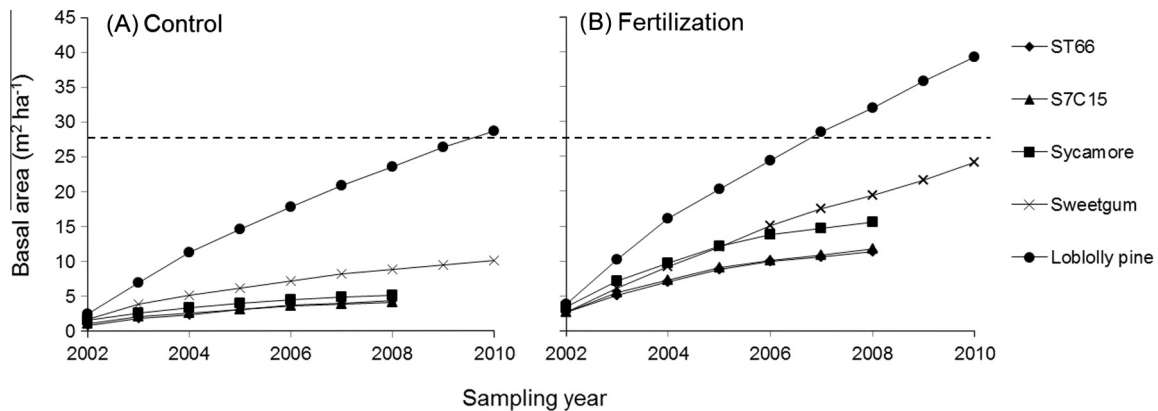


Fig. 8. Basal area in trees receiving control (A) and fertilization (B) treatments in an intensively-managed forest in South Carolina, USA. The dashed line represents the basal area ($27.5 \text{ m}^2 \text{ ha}^{-1}$) at which thinning is recommended for pine in the southeastern USA (Dickens et al., 2004).

U.S. irrigating forest plantations incurs a substantial financial cost (Gallagher et al., 2006), and is not economically feasible for any tree genotype in this study (Coyle et al., 2013). If hardwood genotypes are grown in this region, they will perform best in areas with greater access to water (e.g. lowlands). As others have suggested, a focus on nutrient use and management is recommended for pine production (Haywood and Tiarks, 1990; Fox et al., 2007; Antony et al., 2009; Jokela et al., 2010).

Many plantation forests in the southeastern U.S. are fertilized (Fox et al., 2007) because fertilization can improve growth and yield throughout the rotation (Williams and Farrish, 2000; Carlson et al., 2014). In our study, trees in the C treatment (i.e. neither irrigated nor fertilized) were managed similar to how much pine in the southeastern U.S. is grown, although the frequency of herbicide application was atypical. Typical pine management recommends thinning when basal area exceeds $27.5 \text{ m}^2 \text{ ha}^{-1}$ ($120 \text{ ft}^2 \text{ ac}^{-1}$) (Dickens et al., 2004). Trees in C treatments reached this basal area at age 10 (Fig. 8), which is typical for loblolly pine in the southeastern U.S. However, fertilization increased growth and these plots reached $27.5 \text{ m}^2 \text{ ha}^{-1}$ basal area at age 7 (Fig. 8). Thus, the landowner could accelerate thinning (and revenue generation) by three years – though many factors, including the cost of fertilizer, would have to be considered. Further, growth of loblolly pine in our study would be acceptable for use in short rotation biomass plantations, provided minimum stumpage prices were met (Kantavichai et al., 2014).

Understanding belowground production and allocation in forest stands is hindered by several factors, including logistic difficulties of adequately sampling roots and the perennial nature of trees. Capturing changes in woody plant biomass allocation in response to nutrient and water amendments requires repeated harvests to account for ontogenetic changes in both growth and allocation. Studies that employ a single harvest (e.g. Gower et al., 1992; Stoval et al., 2013; Tripathi and Raghubanshi, 2014; Lim et al., 2015) may fail to capture ontogenetic changes in biomass allocation. We found that ontogeny explained all of the differences in biomass allocation among resource availability treatments early in plantation development (Coyle and Coleman, 2005; Coyle et al., 2008), but resource availability did influence belowground allocation in some species at the completion of the rotation. After accounting for ontogeny, belowground allocation decreased 14% for sweetgum in response to the two fertilization treatments compared with non-fertilized treatments, which accounts for a significant portion of the variation observed in RMF (Fig. 6). Drip irrigation is known to influence root distribution (Coleman, 2007), but proper sampling protocols can alleviate this concern. Further, increasing resource availability resulted in a decrease of biomass partitioning to roots (Fig. 3). The overall decline in loblolly

pine RMF was small, and k was significantly lower for all resource amendment treatments compared to the control (Supplemental Table H), which suggests that both irrigation and fertilization affected the decline. These results differ from those early in this stand's rotation, when k values did not differ among resource amendment treatments (Coyle et al., 2008), and also from a study in Florida, USA, where fertilization – but not irrigation or the irrigation \times fertilization interaction – increased biomass allocation to root tissues of young loblolly pines (Johnson, 1990).

That ontogeny explained the shifts in allocation observed among resource availability treatments for two cottonwood genotypes and for sycamore refutes the initial hypothesis motivating the establishment of this study that growth increases of intensively managed tree plantation are due to shifts in allocation from root to stem growth (Coleman et al., 2004b). For sweetgum, our data support the hypothesis that belowground allocation is altered by resource amendment treatments, and this relationship is maintained throughout the rotation. For ST66 and loblolly pine, belowground allocation patterns changed during the rotation, and were opposite those found in younger trees (Coyle and Coleman, 2005; Coyle et al., 2008). These findings further emphasize the importance of long-term sampling as opposed to a more short-term approach when investigating questions pertaining to growth and physiology of long-lived plant species. Further, belowground allocation patterns mirrored those of nitrogen cycling and use (Aubrey et al., 2012) in that allocation to belowground tissue in narrow-site adapted genotypes (i.e. cottonwoods and sycamore) was driven by ontogeny, while resource availability mediated belowground allocation in the broad site-adapted genotypes (i.e. sweetgum and loblolly pine).

5. Conclusions

Despite rapid early growth in hardwood genotypes, loblolly pine was the most productive tree genotype in our study at the conclusion of the rotation. Our results support conventional wisdom, as loblolly pine is the most widely-grown tree species in the southeastern USA. Fertilization led to increases in productivity in all genotypes, while irrigation had positive but inconsistent impacts on tree growth and biomass accumulation. Additional water and nutrient resources expedited tree development, and developmental rate was the primary driver of above and belowground biomass allocation patterns. This study provides the first above and belowground biomass account for four tree species over a rotation, and highlights the importance of belowground tissues. Belowground tissues accounted for a substantial proportion of total biomass, and these data highlight the need for increased

attention to the role of roots in ecosystem biomass and carbon dynamics. Relationships between above and belowground tissues were generally stable after the fourth growing season, and our data indicate that both tree growth rate and resource availability can impact on root:shoot relationships, and these relationships seem to be genotype-dependent. Studies that focus on aboveground growth and biomass only may be missing a critical component with respect to landscape scale ecological and physiological processes.

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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.2015.11.047>.

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