



## 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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### ARTICLE INFO

#### Article history:

Received 2 September 2015

Received in revised form 24 November 2015

Accepted 27 November 2015

Available online 14 December 2015

#### Keywords:

Fertilization

Irrigation

*Liquidambar styraciflua*

*Pinus taeda*

*Platanus occidentalis*

*Populus deltoides*

### 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 Schmidtling, 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<sup>-1</sup> (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., Fidler, 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<sup>-1</sup>).

Our study consisted of four treatments along an increasing resource availability gradient: an untreated control (C), irrigation (I), fertilization at 120 kg N ha<sup>-1</sup> yr<sup>-1</sup> (F), and irrigation + fertilization (IF). Irrigation was applied daily to meet projected evaporative demand (NOAA, 1993, 1997) and ranged up to 5 mm d<sup>-1</sup>. 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<sup>-1</sup> in year one,

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