



# Fertilization and irrigation effects on tree level aboveground net primary production, light interception and light use efficiency in a loblolly pine plantation

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## ABSTRACT

Fertilization and irrigation may substantially increase productivity of forests by increasing stand leaf area index and the efficiency of converting intercepted light into wood biomass. This stand-level growth response is the summation of individual tree responses, and these tree-level responses are often non-linear, resulting from shifting in the intensity of competition and dominance. We examined tree-level responses of aboveground net primary production (ANPP), absorbed photosynthetically active radiation (APAR) and (light use efficiency) LUE in relation to tree size class to explore how stand-level outcomes depend on shifting patterns among trees. We evaluated the production ecology of a nine-year-old loblolly pine (*Pinus taeda* L.) plantation, 2 years after the initiation of treatments: control, irrigation, fertilization and irrigation + fertilization. We measured tree level ANPP, simulated APAR for individual tree crowns using the MAESTRA process-based model and calculated LUE (ANPP/APAR) in relation to tree size to explore the influence of tree dominance on both light capture and light use efficiency. Fertilization and irrigation + fertilization strongly increased both APAR and LUE, in contrast to little effect of irrigation alone. Tree size had a strong influence on APAR and LUE across all treatments; the largest 20% trees showed 3.4 times greater ANPP when compared to the smallest 20% trees, with 66% resulting from higher APAR, and 34% from higher LUE, than the smallest 20% of trees. Fertilization increased the growth of the largest 20% trees 2-fold (8.6 kg tree<sup>-1</sup> year<sup>-1</sup>), with 29% of the increase resulting from higher APAR (13.7 GJ tree<sup>-1</sup> year<sup>-1</sup>), and 71% from higher LUE (0.63 g MJ<sup>-1</sup>), relative to the largest trees in the control treatment (4.3 kg tree<sup>-1</sup> year<sup>-1</sup>, 11 GJ tree<sup>-1</sup> year<sup>-1</sup> and 0.39 g MJ<sup>-1</sup>, respectively). Irrigation and fertilization tripled production (13.2 kg tree<sup>-1</sup> year<sup>-1</sup>) of the largest trees with an even greater proportional contribution from increased LUE (15.1 GJ tree<sup>-1</sup> year<sup>-1</sup>, 85% response contribution; APAR 0.87 g MJ<sup>-1</sup>, 15% response contribution). Overall, large trees grow faster than smaller trees because of greater light capture, whereas the greater response of large trees to treatments resulted more from increased efficiency of using light.

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## 1. Introduction

The productivity of loblolly pine (*Pinus taeda* L.) plantations has increased over the past few decades as a result of the intensification of silvicultural practices (including soil preparation, fertilization, weed and pest control) and selection and breeding of more productive genotypes (Fox, 2000; Samuelson et al., 2004; Aspinwall et al., 2011). The production ecology of these plantations typically shows that high rates of growth (particularly in response to intensive

silviculture) develop when stands have high leaf area, high light absorption, and particularly high rates of stem growth per unit of light absorption (Albaugh et al., 2004; Binkley et al., 2004; Pangle et al., 2009).

Recent work on *Eucalyptus* plantations has shown that stand-level productivity results from non-linear production ecology among individual trees. For example, across four different clonal genotypes and climatic regions in Brazil, dominant trees at the end of the rotation (6–7 years after planting) grew four-times faster than non-dominant trees, as a result of 2.1-fold greater light absorption, and 1.8-fold greater stem growth per unit of light absorption (Binkley et al., 2010). The individual tree dominance pattern is particularly important for understanding stand-level productivity because variance of tree size within stands increases

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the gap in light use efficiency (LUE) among trees and lowers stand yields by 5–20% compared with highly uniform stands (Stape et al., 2010).

The importance of dominance and resource use efficiency at the level of individual trees for *Eucalyptus* may or may not be as important for pine plantations. After canopy closure, *Eucalyptus* plantations develop a strong growth dominance that lasts throughout the rotation (Doi et al., 2010), but growth dominance is typically less pronounced or even absent in pine forests (Martin and Jokela, 2004; Binkley et al., 2006; Fernández and Gyenge, 2009; Bradford et al., 2010).

We used the Southeast Tree Research and Education Site (SETRES) experiment to determine how tree size classes differ in response to fertilization and irrigation, and how the responses depend on changes in light use and LUE. We hypothesized: (1) both APAR and LUE contribute substantially to higher growth rates of dominant trees; and (2) increasing resource availability (fertilization and irrigation) will increase the LUE of dominant trees more than non-dominant trees, further accentuating dominance and decreasing stand uniformity.

## 2. Material and methods

### 2.1. Study site

The study was established in the Sandhills of Scotland County, North Carolina, USA (35°N latitude, 79°W longitude) on a flat (<1% slope), infertile, excessively drained, sandy, siliceous, thermic Psammentic Hapludult soil (USDA Soil Classification System). Precipitation averages 1210 mm year<sup>-1</sup> and mean annual temperature is 17 °C (30-year averages). In 1985, the site was hand planted on an approximate 3 × 2 m spacing with loblolly pine after felling of the previous natural longleaf pine (*P. palustris* Mill.) stand and application of 17 kg ha<sup>-1</sup> of Velpar™ herbicide (active ingredient hexazinone).

In January 1992, sixteen 50 × 50 m (0.25 ha) treatment plots separated by 10 m untreated buffers with 30 × 30 m measurement plots centered in each treatment plot were established in the eight-year-old stand. Plot selection and thinning ensured initial similarity among plots in mean tree height, diameter, stand basal area, volume, leaf area index (LAI), and density (1260 stems ha<sup>-1</sup>) prior to treatment imposition. Complete, sustained control of non-pine vegetation in the treatment plots was initiated in 1992 and utilized a combination of mechanical and chemical (glyphosate) methods. The experimental design was a 2 × 2 factorial combination of nutrition and water additions (control (C) with no additions, irrigated (I), fertilized (F), and irrigated and fertilized (I + F)) replicated four times. The nutritional treatments, which began in March 1992 were (1) optimum nutrition through fertilization or (2) no fertilization. The fertilizer treatment goal was to maintain a nitrogen concentration of 1.3% in upper canopy foliage of co-dominant or dominant trees with other nutrients (phosphorus, potassium, calcium, magnesium, and sulfur) balanced with nitrogen (Allen, 1987; Jokela, 2004). Boron levels were maintained at greater than 12 mg kg<sup>-1</sup>. Foliar nutrient status was monitored and fertilizer was applied annually to meet targets (Table 1). Fertilizers applied included urea,

boron coated urea, ammonium sulfate, diammonium phosphate, triple super phosphate, potassium chloride, dolomitic lime, Epsom salts, Sulphomag (potassium, sulfur and magnesium), and borax. The water treatments, which began in April, 1993, were (1) natural precipitation and (2) natural precipitation with an additional 650 mm year<sup>-1</sup> applied by irrigation during the growing season (March 1 to October 31). In 1993, 668 mm of irrigation water were added to the irrigated plots (Table 1).

### 2.2. Biomass estimation

Stand-level biomass (dry mass) estimates for needles, branch wood and stem wood components were calculated from age and treatment-specific whole tree regression equations, applied to all trees and then scaled to an area basis for each plot. Whole tree regression equations were developed following the methods presented in Albaugh et al. (1998, 2004, 2006) and were based on destructive harvests. Work at this site carried on through 2009 and data collected in biomass harvests performed after 1993 were used to provide the best estimates of biomass in 1993. Dormant season harvests occurred in 1992, 1994, 1996, 1998 (16 trees each year, one tree in each plot), and 2003 and 2009 (four trees each year, one in each treatment). Aboveground net primary production (ANPP) was estimated as the sum of biomass production of each aboveground tree compartment.

### 2.3. Leaf area estimation

We estimated individual tree leaf area (m<sup>2</sup> tree<sup>-1</sup>) for the end of 1992 and the end of 1993. We used site and treatment specific leaf area estimates from Maier et al. (2002) and foliage duration estimates from Sampson et al. (2003) to convert our individual tree foliage mass estimates to individual tree leaf area. Projected stand scale leaf area index was measured monthly in 1993 in each of the 16 treatment plots using a Li-Cor LAI2000 plant canopy analyzer (Li-Cor, 1991). For each month in each plot, 20 LAI measurements along a transect on the south side of the plot were made at a height of 60 cm between 0700 and 1000 EST using a 180° view cap. Simultaneously, above canopy light measurements were collected in an open field adjacent to the study site where the light sensor had an unobstructed view of the sky.

### 2.4. MAESTRA model parameterization

The simulation of radiation absorption at individual tree level was performed using MAESTRA (Wang and Jarvis, 1990; Bauerle et al., 2004; Medlyn et al. 2005), a three-dimensional ecophysiological model developed to estimate radiation absorption, photosynthesis and transpiration at the individual tree level, considering the influence of self-shading from needles within a crown and neighboring tree crowns. Our study focused on tree level light absorption, therefore leaf-level photosynthesis and stomatal conductance parameters remained constant during simulations.

Tree crown structural characteristics for MAESTRA parameterization were determined during field campaigns in 1993. For assessments during the year, we measured eighty trees, five trees

**Table 1**  
Nutrient and water additions to treatment plots from 1992 to 1993.

Year	Age	Nutrient additions							Water additions <sup>a</sup>	
		N (kg ha <sup>-1</sup> )	P (kg ha <sup>-1</sup> )	K (kg ha <sup>-1</sup> )	Ca (kg ha <sup>-1</sup> )	Mg (kg ha <sup>-1</sup> )	S (kg ha <sup>-1</sup> )	B (kg ha <sup>-1</sup> )	Non-irrigated (mm)	Irrigated (mm)
1992	8	224	56	112	134	56	0	1.7	866	866
1993	9	82	50	113	0	56	120	0.0	735	1403

<sup>a</sup> Water additions from March 1 to October 31. No irrigation in 1992.

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