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Short-term impacts of nutrient manipulations on leaf gas exchange and biomass partitioning in contrasting 2-year-old *Pinus taeda* clones during seedling establishment

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ABSTRACT

We conducted a 1-year greenhouse experiment to assess the impact of nutrient manipulations on seedling growth, biomass partitioning, and leaf gas exchange between two fast growing *Pinus taeda* clones that differed in growth efficiency. After 1 year we observed significant treatment and treatment by clone effects on growth, biomass partitioning, and gas exchange parameters. Fertilization increased total seedling biomass 18% primarily through an increase in foliage and coarse-roots. Clones did not differ in total seedling biomass, however, clone 85 produced more stem than clone 93 leading to 37% greater stem:leaf, while clone 93 maintained more branch biomass. The logging residue treatment increased stem:leaf by 30%, but had no effect on total biomass or partitioning. Differences in leaf morphology resulted in significantly greater canopy leaf area in clone 93 than clone 85. Increased foliar N concentration from fertilization had only minor effects on specific photosynthesis under saturating light (A_{Sat}), but lowered stomatal conductance (g_s), transpiration (E), and internal to external CO_2 concentration ratio (C_i/C_a) as well as improved water use efficiency (*WUE*) independently of genotype. When gas exchange data was scaled to the canopy level both genotypes achieved similar canopy level CO_2 assimilation rates, but our data suggests they did this by different means. Although we did see a small effect of nutrient limitations in total canopy photosynthesis under saturating light (A_{Canopy}), A_{Sat}, and total leaf area (*TLA*), our foliar N concentration ([N]) indicated that our level of logging residue incorporation did not cause [N] to decrease below sufficiency limits. From a practical standpoint, a better understanding of strategies for capturing and partition C may lead to better selection of clonal material, thereby, optimizing productivity.

1. Introduction

Differences in nutrient availability can influence the short-term capacity of conifer seedlings to collect and utilize light energy from photosynthesis as well as the distribution of that photosynthate between plant tissues. Nitrogen and phosphorus are usually the most limiting nutrients to plant growth and have been shown to exert a strong influence on leaf area (Zhang et al., 1997a; Albaugh et al., 1998; King et al., 1999), leaf morphology (Niinemets et al., 2001; Maier et al., 2002; Will, 2005) and chemistry, as well as leaf-level physiology in *Pinus* spp. (Tissue et al., 1993; Gough et al., 2004b; Samuelson et al., 2004; Bown et al., 2007; King et al., 2008). Nitrogen is a major component of most of the proteins and pigments involved in photosynthesis, therefore, it is not surprising that increases in specific net CO_2 assimilation under saturating light (A_{Sat}; Table 1) have been commonly observed following N fertilization (Green and Mitchell, 1992; Tissue et al., 1993; Murthy et al., 1996, 1997; Samuelson, 2000; Gough et al., 2004b). Increases in foliar N concentration ($[N]_f$) have been shown to correspond with increased chlorophyll content (Chandler and Dale, 1995; Ripullone et al., 2003; Bauer et al., 2004; Chmura and Tjoelker, 2008), Rubisco content, or both (Tissue et al., 1993; Warren et al., 2004; Manter et al., 2005) in conifer species.

However, some studies have found no change or even a decrease in A_{Sat} following fertilization in both young (Zhang et al., 1997b; Samuelson et al., 2001; Warren and Adams, 2002) and mature trees (Tang et al., 1999; Maier et al., 2002; Bauer et al., 2004; Gough et al., 2004a). In most of these instances measurements were taken after continuous or in some cases chronic N additions. One hypothesis proposed by Gough et al. (2004b) and

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Table 1
List of abbreviations.

Abbreviation	Description	Units
A_{Canopy}	Canopy level net CO_2 assimilation	μmol CO_2 s^{-1}
A_{Sat}	Instantaneous specific net CO_2 assimilation under light and CO_2 saturation	μmol CO_2 m^{-2} s^{-1}
C_i/C_a	Internal CO_2 to ambient CO_2 ratio	Unitless
CSA	Canopy silhouette area	cm^2
E	Transpiration	mmol H_2O m^{-2} s^{-1}
g_s	Stomatal conductance	mol m^{-2} s^{-1}
LR	Logging residue	Treatment
$[N]_a$	Nitrogen concentration per unit leaf area	g N m^{-2} leaf
$[N]_f$	Foliar nitrogen concentration	Unitless
$[N]_m$	Nitrogen concentration per unit leaf mass	mg N g^{-1} leaf
PNUE	Instantaneous photosynthetic N use efficiency	μmol CO_2 g^{-1} N s^{-1}
SLA	Specific leaf area	cm^2 g^{-1}
TLA	Total leaf area calculated from *SLA* and leaf mass	m^2
WUE	Instantaneous water use efficiency	μmol CO_2 mmol H_2O^{-1}

later supported by King et al. (2008) is that increases in A_{Sat} rates immediately following fertilization allow for increased photo-assimilates, which then can be used to produce greater leaf area for light interception, and lead to an eventual down regulation of A_{Sat}. Therefore, timing of fertilization and measurements is a contributing factor hypothesized by both Gough et al. (2004b) and King et al. (2008) that may help explain these discrepancies.

Pinus taeda is planted over a large geographic range within the southeastern United States, exposing it to a wide range of site conditions (e.g., climate and resource availability). Natural within species plasticity allows for tolerance of resource limitations while still achieving adequate growth, and has led to the widespread planting of *P. taeda* throughout the southeast (Wear and Greis, 2002). Breeding programs have exploited this large genetic variation resulting in superior planting stock in terms of growth, disease resistance, and form. The widespread use of superior planting stock, and to a lesser extent clonal material, has increased wood volume gains 10–30% in southern pines. Further, it has been estimated that by combining clones and appropriate silvicultural prescriptions volume gains as high as 50% to over 60% could be achieved (Allen et al., 2005; Martin et al., 2005; McKeand et al., 2006).

With increased emphasis being placed on site-specific management there is a need to determine how specific genotypes will vary across environments (Fox, 2000). There are conflicting opinions on the importance of genetic by environment interactions (G × E). McKeand et al. (2006) in a summary of the current literature suggested that G × E are of little practical importance for open-pollinated, half-sib, and full-sib families, but more long-term studies are needed before the importance of G × E of clones are known. In contrast, Roth et al. (2007) found large G × E for stem volume and basal area between full-sib genotypes when planted at different locations or managed with varying silvicultural prescriptions. Further, the authors concluded that matching the best genotype to site conditions might be necessary in the future to maximize productivity. Some studies have found significant family by fertilization interactions in stem growth (Li et al., 1991c), C allocation (Li et al., 1991b; Retzlaff et al., 2001), and nitrogen use efficiency (Li et al., 1991a) in *P. taeda*, but the effects of G × E have been less stable for leaf-level gas exchange measurements. For example, researchers have found strong fertilizer effects on leaf photosynthesis and conductance, but no genotype by fertilizer interactions (Samuelson, 2000; Bown et al., 2007; Chmura and Tjoelker, 2008), while others have found differences in specific leaf photosynthesis between full-sib clones when fertilized (King et al., 2008).

The use of contrasting genotypes in physiological research has implications beyond matching specific genotypes to site conditions. For example, improved ability to detect treatment differences by eliminating genetic variability, or the use of contrasting clones combined with resource manipulations may allow for improved understanding of the mechanism involved in C capture and partitioning. Additionally, their use in research may provide insight into the stability of these mechanisms within *P. taeda* under a range of resource availability. We conducted a greenhouse experiment with a factorial combination of fertilization and high C:N logging residue (LR) incorporation (applied to modify nutrient availability) to assess the impact of nutrient manipulations on leaf gas exchange and biomass partitioning between 2-year-old *P. taeda* clones believed to maintain different growth efficiencies (stem produced per unit leaf area). We ask if seedling growth response to nutrient availability is a function of increased A_{Sat} or a result of changes in leaf area due to reallocation of C, and is this response consistent across clones. We hypothesize that A_{Sat} in both clones will increase immediately following fertilization, but to different degrees. We expected that one clone would invest more C to increasing leaf area and the other in photosynthetic machinery per unit leaf area leading to no overall difference in canopy level net CO_2 assimilation (A_{Canopy}) between genotypes. Similarly, we anticipated clones to respond differently to LR incorporation due to differences in biomass partitioning and photosynthetic N use efficiency (*PNUE*). We hypothesize that the clone that maintains more leaf area will show greater declines in overall productivity (growth) relative to the clone which maintains less leaf area.

2. Materials and methods

2.1. Experimental design

In April 2006, 1-year-old *P. taeda* clones were planted in 170-L plastic containers (93 cm × 53 cm × 50 cm) and grown in a greenhouse through July 2007. The greenhouse vents and climate settings were adjusted to provide a summer and winter temperature regime representative of the southeastern United States. The study design was a randomized complete block design replicated six times. Treatments were arranged in a full 2 by 2 by 2 factorial with two levels of LR incorporated into the soil (none, present), two levels of fertilization (none, present), and two clones (CL93, CL85). Forty-eight plastic containers were fitted with a single brass spigot for collecting water, and each was filled with approximately 0.17 m^3 of Eunola series (fine-loamy, siliceous, semiactive, thermic Aquic Hapludults) soil 2 months prior to planting. Soil was collected from the Virginia Tech Tidewater Agricultural Research and Extension Center located in Holland, VA on February 2006 to a depth of approximately one meter, which included a mixture of the Ap, BE, and Bt horizons.

2.2. Treatments

Logging residue (LR; C:N = 128 ± 14; *n* = 4) was collected from residue piles near the logging deck of a *P. taeda* stand in South Carolina that had been harvested 6 months prior to collection. The residue consisted mainly of bark, needles, and small branches that remained following an onsite processing of merchantable timber. The LR was passed through a 5 cm × 10 cm screen and was mixed uniformly into the soil during pot filling at a rate of 4.92 kg LR o.d. container^{-1} (equivalent to 25 Mg o.d. ha^{-1}). Fertilizer was applied on two separate dates. Due to slow initial growth of the clones, the first application was not applied until July 28, 2006. Fertilizer was in the form of diammonium phosphate (DAP) and ammonium nitrate (AN)