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Crown physiological responses of loblolly pine clones and families to silvicultural intensity: Assessing the effect of crown ideotype

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ABSTRACT

Clonal forestry must be linked with intensive silvicultural practices to increase forest productivity of loblolly pine (*Pinus taeda* L.) in the southern United States. Although the positive growth responses due to intensive silviculture have been reported extensively, much less is known about the physiological processes that drive these responses. This study assessed the responses of growth, leaf area, leaf-level gas exchange and foliage morphology of 4 year-old loblolly pine clones and families to changes in silvicultural intensity on the Virginia Piedmont (VA) and North Carolina Coastal Plain (NC). Four clones (differing in crown ideotype), 1 control-mass-pollinated (CMP) and 1 open-pollinated (OP) family were evaluated in two levels of silviculture (operational and intensive). The operational silvicultural treatment included only banded weed control, whereas the operational silvicultural treatment included broadcast weed control, fertilization and tip moth control. The effect of genotype and silvicultural intensity were site-specific, and expressed mostly at VA. The intensive silvicultural treatment increased stem volume by 68% and 36% relative to the operational silvicultural treatment at VA and NC, respectively. At VA, the differences in the leaf area responses to the silvicultural treatment among genotypes differed between 60 and 146%, which suggested great differences in growth efficiency among the genotypes. These responses were not linked to changes in leaf physiology and morphology. The seasonal variation of gas exchange parameters was similar between sites, but significant differences in leaf physiology and morphology were found among the genotypes. However, this variation was neither attributed to the genetic source (clonal versus non-clonal) nor the crown ideotype (broad- versus narrow-crown) as hypothesized. Understanding the differences in the crown physiological processes among loblolly pine genotypes may be required to optimize the gains expected from clonal forestry.

1. Introduction

Tree improvement and silvicultural management have increased the productivity of loblolly pine in the South almost 3-fold relative to natural stands (Fox et al., 2007a). Currently the majority of loblolly pine is planted as open-pollinated and control-mass-pollinated families (McKeand et al., 2008). Typical management practices include site preparation, weed control and fertilization (Fox et al., 2007a). Clonal forestry that includes more intensive silvicultural practices can further increase productivity (Wright and Dougherty, 2006; Fox et al., 2007a), with potential gains estimated between 27 and 70% (Isik et al., 2005; Bettinger et al., 2009; Whetten and Kellison, 2010).

Genotype by environment interactions have generally not been observed for OP and CMP families (McKeand et al., 2006). However, genotype by silvicultural treatment interactions have been reported more often for clonal varieties. For example, King et al. (2008), Stovall et al. (2011), Tyree et al. (2009) and Yáñez et al. (2015) reported different growth responses of loblolly pine clones to fertilization, which suggest that some genotypes are more sensitive to nutrient limitations, so they may have greater responses to fertilization. These studies were made in young stands, but there is a likelihood that this interaction would be greater once intraspecific competition for resources become more intense. In a 21-year-old loblolly pine, Adams and Roberts (2013) found no differences in stand-level volume when families are planted in pure- or mixed-family planting; however, some families exhibited unique characteristics to outperform under greater intraspecific competition. Hence, matching specific genotypes to specific sites and silvicultural regimes may be required to optimize gains from

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clonal forestry (Wright and Dougherty, 2007). Because the screening of a large number of candidate clones under a range of silvicultural treatments and sites may be inoperative, one approach to assess the growth responses to the environmental influences is by using the ideotype concept. Ideotype is an idealized biological model for the phenotype of a plant that is adapted to specific environmental conditions (Dickmann, 1985). In forestry, the concept of crown ideotype is typically used to recognize consistent patterns observed in tree crowns and their influence on intratree competition in forest stands. Cannell (1989) described 'crop' and 'isolation or competition' ideotypes as phenotypes that are weak and strong competitors with their neighbors, respectively. Narrow-crown phenotypes correspond to crop ideotypes and broad crown phenotypes are equivalent to competition ideotypes.

Although the positive growth responses due to more intensive silviculture treatments (e.g. weed control and fertilization) have been widely reported in loblolly pine (Albaugh et al., 1998; Samuelson, 1998; Vance and Sanchez, 2006; Roth et al., 2007; Zhao et al., 2009; Jones et al., 2010; Liechty and Fristoe, 2013), much less is known about how genotypes differing in crown ideotype may respond to silvicultural treatments. Overall, both the management of soil resources and genetics may affect leaf area development and phenology, photosynthesis, respiration, allocation patterns and growth efficiency (Kleb's concept). In a tree, net carbon gain may be expressed as a function of the photosynthetic and respiration rates of the photosynthetic tissue (i.e. leaf area), and of the respiration rate of the non-photosynthetic tissue (Teskey et al., 1987). Therefore, the size of the photosynthetic machinery explains why leaf area and light interception are well related to variations in productivity (Cannell, 1989). Hence, leaf area increases in response to silvicultural treatments leads to greater carbon assimilation and tree growth (Vose and Allen, 1988; Albaugh et al., 1998; Jokela and Martin, 2000; McGarvey et al., 2004; Will, 2005). In this context, many questions remain unanswered from the point of view of using crown ideotypes. For instance, are the physiological responses to silvicultural intensity of clones differing in crown ideotype similar? Are these responses consistent between clones within an ideotype? Might the growth response of clones over families be explained by differences in the crown physiology?

The productivity of loblolly pine across a broad gradient of environmental conditions appears to be better explained by differences in phenology and leaf area display than through changes in the leaf physiology (Lujan and Fernández, 2016; Vose et al., 1994). This is why the relationship between leaf-gas exchange measurements and growth has been generally poor (McGarvey et al., 2004; Chmura and Tjoelker, 2008). This may be attributed to a scaling problem (Martin et al., 2001), so the controversy still remains. Some studies have shown a significant effect of management treatments on instantaneous photosynthetic rates (Green and Mitchell, 1992; Teskey et al., 1994; Samuelson, 2000; King et al., 2008; Maier et al., 2008), while others have not (Samuelson, 1998; Maier et al., 2002; Munger et al., 2003; Gough et al., 2004a; Maggard et al., 2016), even when growth and foliar nitrogen (N) were affected (Gough et al., 2004a; Samuelson, 1998; Will et al., 2001; Munger et al., 2003). For instance, other studies have found a short term response in A_{sat} to fertilization. One of the mechanisms suggested by Gough et al. (2004b) is that the increase in A_{sat} after fertilization is only ephemeral, afterwards A_{sat} is down-regulated and the extra carbon gained is used to enlarge the canopy and consequently tree growth. Similarly, studying two contrasting crown ideotype clones of loblolly pine, Tyree et al. (2009) found some evidence of an increase in A_{sat} within the first six months after fertilization, accompanied with an increase of the foliar mass. Nonetheless, the results found by King et al. (2008) showed that some loblolly pine clones followed this pattern after fertilization, while others did not. Two clones had increases in A_{sat}, volume growth, and crown efficiency, and these clones maintained their superiority in A_{sat} during the growing season. Other clones exhibited higher response in volume growth to N fertilization, whereas the A_{sat} increased only moderately and the crown efficiency was low. The results reported by King et al. (2008) highlight that other mechanisms may be present (e.g. changes in carbon allocation) and differ among genotypes. Moreover, it has been reported that higher nutrient availability may have a greater impact on other gas exchange parameters than A_{sat} such as stomatal conductance and water use efficiency (Maggard et al., 2016).

Gas exchange in loblolly pine have been mainly studied in stands with unknown genetic pedigree (Ellsworth, 2000; Munger et al., 2003; Tang et al., 2003), provenances (Boltz et al., 1986), and half- and full-sib families (Seiler and Johnson, 1988; Samuelson, 2000; Yang et al., 2002; McGarvey et al., 2004). The few studies on gas exchange on loblolly pine clones suggest some degree of variation among clones that may confer some advantage to those genotypes (Gebremedhin, 2003; King et al., 2008; Tyree et al., 2009). Others studies indicate that the variability in gas exchange may be as high within a clone as between clones or even OP and CMP families (Aspinwall et al., 2011). Yáñez et al. (2015) found that clones exhibiting different crown ideotypes did not differ in stem size after four years, but these had great differences in crown attributes. Overall, crown characteristics (e.g. crown diameter and height to the live crown HTLC)) of broad-crown clones were more responsive to the effect of site, silvicultural intensity and planting density than the narrow-crown clones. Moreover, they found great differences in branch mortality in the lower crown between broad-crown clones, which suggest potential differences in the crown physiology between the clones. Consequently, there is still a poor understanding whether gas exchange and foliage morphology and display could explain the differences in productivity among genotypes in a broad range of environmental conditions and silvicultural treatments.

The present study investigated the responses of loblolly pine leaf-level gas exchange and leaf morphological traits to changes in silvicultural intensity and genotypes at two sites. Two clones having broad crown (competition ideotype) and two clones having narrow crown (crop ideotypes) and one control mass pollinated (CMP) and one open pollinated (OP) family were examined. The experiments were located in two contrasting geographical regions, one on the Virginia Piedmont and one on the North Carolina Coastal Plain. We tested the following hypotheses: (1) improving soil resources by intensive silviculture will increase stem growth and foliage development of loblolly pine genotypes, but it will have no affect the leaf physiology, (2) the differences in growth among clonal and non-clonal stands are associated with differences in tree physiology and leaf deployment and (3) clones having a broad-crown (competition ideotype) will differ in leaf display and physiology from the narrow-crown clones (crop ideotype), which could be associated with differences in the demand for soil resources.

2. Materials and methods

2.1. Study sites and experimental design

Details of the experiments were presented by Yáñez et al. (2015). Briefly, trials were established in 2009 in the North Carolina Coastal Plain (NC), at the Bladen Lakes State Forest (34°49′49.63″N, 78°35′18.52″W), and at the Virginia Piedmont (VA) at the Reynolds Homestead Forest Resources Research Center (36°38′35.32″N, 80°09′18.84″W). The soil at the VA site was a well-drained Fairview Series (fine, kaolinitic, mesic Typic Kanhapludults). The soil at the NC site was a poorly drained Rains series (fine-loamy,

siliceous, semiactive, thermic Typic Paleaquults). The annual average temperature and precipitation at VA is 13 °C and 1159.3 mm, respectively. The annual average temperature and precipitation at NC are 16.9 °C and 1170.7 mm, respectively (from NOAA online weather data http://sercc.com/nowdata.html). The study was a split-split plot design with four replications at VA and three replications at NC. Two levels of silviculture (operational and intensive) were the whole plot treatments, six genotypes (4 clones, 1 OP family and 1 CMP family) were the split-plot treatments, and three initial planting densities (617, 1235 and 1852 trees/ha) were the split split-plot treatments.

Site preparation at VA included an aerial application of mixed solution of 9.3 L/ha of Accord XRTII plus (a.i. glyphosate) (Dow AgroSciences, Zionsvillle road, IN, USA), 9.3 L/ha of Milestone VM plus (a.i. aminopyralid) (Dow AgroSciences, Zionsvillle road, IN, USA), and 1.46 L/ha of Chopper (a.i. isopropylamine salt of imazapyr) (BASF Corporation, Florham Park, NJ, USA). The site was then burned. Site preparation at NC included a chemical application of 2.33 L/ha of Chopper, 11.6 L/ha of Krenite (a.i. ammonium salt of fosamine) (Bayer CropScience, Research Triangle Park, NC, USA), and 1.53 L/ha of Garlon (a.i. triclopyr) (Dow AgroSciences, Zionsville road, IN, USA), followed by V-blade bedding on 3.66 m centers using a Savannah bedding plow (Savannah Global Solutions, Savannah, GA).

At both sites, the operational silvicultural treatment was a banded weed control after planting, with a mix of 292 ml/ha of Arsenal AC and 146 ml/ha of Oust XP (a.i. sulfometuron methyl) (Bayer CropScience, Research Triangle Park, NC, USA). At VA, in the third growing season, a solution of 55 ml/ha of Escort (a.i. metsulfuron methyl) (Bayer CropScience, Research Triangle Park, NC, USA) was applied to control blackberry (*Rubus* spp.). The intensive silvicultural treatments at both sites consisted of a broadcast weed control with a mix of Arsenal AC (292 ml/ha), Oust XP (146 ml/ha) and Escort (18 ml/ha) in the first growing season; Arsenal AC (292 ml/ha) and Oust XP (146 ml/ha) in the second growing season; and Escort (55 ml/ha) in the third growing season. In the intensive treatment, tip moth control was applied after planting using PTM insecticide (a.i. fipronil) (BASF Corporation, Florham Park, NJ, USA) (1.5 ml/tree) and 93 g/tree of nitrogen and 10 g/tree of phosphorus in the form of Arborite coated urea fertilizer, which was spread around the base of each individual seedling.

The genetic entries included one open pollinated family (OP), one control-mass-pollinated family (CMP) and four clones (C1, C2, C3 and C4) produced through somatic embryogenesis by Arborgen Inc. (Ridgeville, SC). All the genotypes were coastal sources of loblolly pine. The parents of several of the genotypes were related (Table 1). The families were bare-root seedlings and the clones were containerized seedlings. Clones C1 and C3 were considered narrow-crown clones; whereas, clones C2 and C4 were considered broad-crown ideotype (Yáñez et al., 2015).

Three initial planting densities were the split split-plot treatments. Trees were planted at 617, 1235, and 1852 trees/ha. The spacing between rows in all the planting densities was held constant at 3.66 m with distance between trees within a row varying from 4.42, 2.21 and 1.47 m in low, medium and high density, respectively. Trees in each combination of silviculture, genotype and spacing were planted as block plots with 81 trees/plot in a 9 tree by 9 tree arrangement at VA and 63 trees/plot in a 7 tree by 9 tree arrangement at NC.

Table 1
Parents of the six genotypes assessed that were provided by Arborgen. Genotypes C1, C2, C3, and C4 correspond to clones; OP; open pollinated family; CMP; control mass pollinated family. A, B, C, D and E are arbitrary codes representing the pedigree of the parents.

		Mother		
		A	B	D
Father	A			C1
	B			C4
	C	C2	CMP	
	E			C3
	?	OP		

2.2. Tree selection

This study was conducted on a subsample of trees within the plots at planting density of 1235 trees per hectare. We assumed that at this planting density, the intraspecific competition for light was minimal. Three trees from each plot (within the 5 tree by 5 tree internal plot) were selected to represent the range in tree height present. In each site, the sampling was made in three replicates totalizing 108 trees per site. In each plot, trees were sorted by total height. A small tree from the 1st quintile, one medium height tree from the 3rd quintile, and a tall tree from the 5th quintile were selected. Trees with obvious problems such disease symptoms, mechanical damage, forking, and dieback were avoided.

2.3. Growth measurements, leaf-level gas exchange, leaf morphology

Each selected tree was repeatedly measured for all the variables during the third growing season from October 2011 to November 2012. Measurements of leaf-level gas exchange were made every 6–8 weeks (a total of 8 dates at each site in the months of October 2011 and January, March, May, June, August, October, and November 2012). Both sites were measured with a difference of 1–2 weeks between them. Diameter at the root collar (D) (using a digital caliper) and total height (HT) (using a Philadelphia rod) were also measured. Volume index (VOL) was calculated by multiplying HT by D squared and expressed in cubic centimeters (cm^3). Additionally, We measured light-saturated photosynthetic rate (A_{sat} at 1600 μmol m^{-2} s^{-1}), stomatal conductance (g_s, mmol m^{-2} s^{-1}), transpiration (E, mmol m^{-2} s^{-1}), and the derived intrinsic water use efficiency ($WUE_{int} = A_{sat}/g_s$) and instantaneous water use efficiency ($WUE_{ins} = A_{sat}/E$), between 9 am and 3 pm with a portable photosynthesis system (LI-6400, LiCor Inc., Lincoln, NE, USA). Fully sun-exposed fascicles collected from the upper, medium and lower third of the crown were combined and placed in the chamber immediately after detachment (<30 s). The chamber air temperature and relative humidity was held near to ambient conditions. Thus, during the study period, this implied varying the block temperature in the chamber from 5 to 32 °C at VA and from 9 to 34 °C at NC. Carbon dioxide concentration was set to 385 μmol mol^{-1}. Additional measurement of leaf morphology (fascicle diameter and number of needles per fascicle) were used to calculate leaf area according to the formula used by Ginn et al. (1991): Leaf area per fascicle = 3.14159(d)(l) + (n)(d)(l), where d = fascicle diameter, l = needle length, and n = number of needles in the fascicle. The fascicle metrics of all the foliage collected per each tree during the entire measurement period were treated as a sample for further analyses of foliage morphology.

2.4. Carbon isotope discrimination

During the last measurement date (November 2012), the same fascicles used for needle physiology were used for further determination of carbon isotope discrimination at NC and VA. The foliage was dried at 65 °C, and finely ground in a ball mill. The ratio of ^{13}C and ^{12}C was determined in 1.8 mg foliage subsample through a stable isotope ratio mass spectrometer (IsoPrime100, Isoprime Ltd., UK). The Δ^{13} values were expressed relative to the Pee Dee Belemnite international standards (Farquhar et al., 1989) as:

$$\Delta^{13} = \frac{\delta_a - \delta_p}{1 + \delta_p}$$

where Δ^{13} is the carbon isotope discrimination (‰), and $\delta_a$and δ_p are the stable carbon isotope ratio for the plant material and air (−8‰), respectively.

2.5. Leaf area determination

At the end of the fourth growing season, in addition to growth and physiological traits, the diameter, length and position from the ground was measured for each branch of the selected trees. Parallel, a destructive sampling was carried out for leaf area determination. Fifteen branches per treatment combination of silvicultural treatment and genotype were sampled at each site (5 branches per block-plot × 3 blocks). The branches were collected on two buffer trees at each block-plot and on different crown positions. In the laboratory, the foliage was detached from the branches, and a subsample was scanned in a leaf area meter (LI-3100, LiCor Inc., Lincoln, NE, USA) to determine projected leaf area. Then, the foliage was oven-dried to a constant weight. Specific leaf area (SLA) in the subsample was estimated as the leaf area by dry weight ratio. Branch leaf area was obtained by multiplying SLA by the total foliage weight and then regressed on DBH and relative height position. The final allometric equations were genotype-specific, and then were scaled to the selected trees. Tree leaf area was obtained as the sum of leaf area of each individual branch.

2.6. Statistical analysis

Plot means for each trait were calculated and analysis of variance (ANOVA) was carried out at each site. All the explanatory variables (silvicultural intensity, genotype and the interactions among these factors) were considered fixed effects, whereas except the effects of the replication were considered random. This model was applied on carbon isotope discrimination, leaf area and leaf-morphological traits. For stem growth and leaf-gas exchange parameters, the model was expanded to repeated measures analysis. For leaf-gas exchange parameters, a second-order polynomial containing the variables temperature (T), vapor pressure deficit (VPD) and VPD^2 was used as covariates in the analysis of variance. To account for some possible temporal correlation among different measurement dates, we contrasted the AR(1) variance-covariance structures against the independent and identical distributed error structure (IDD). For the analysis of variance under the AR(1) structure, we assumed that the gap between measurements dates was constant, and that small variations among measurement dates did not affect the biological interpretation of the data. The model selection was based on the Akaike (AIC) and Bayesian (BIC) information criteria. The analyses of variances and regressions were performed using PROC MIXED of SAS version 9.3 (SAS Institute, Cary, North Carolina, USA), respectively. Post-hoc comparison of main effects was based in the Tukey's means comparisons method, and contrast analyses to test for differences between genetic source (clonal versus non-clonal) and crown ideotype (broad- versus narrow-crown). Significant differences were considered at an alpha level of 0.05.

3. Results

3.1. Variability in stem volume, leaf area, and leaf morphology parameters

During the study period, the trees in the intensive silvicultural treatment were significantly larger than in the operational silvicultural treatment only at VA, and that effect increased over time (Table 2 and Fig. 1A and B). At the end of the study period, the intensive silvicultural treatment at VA increased stem volume 68% relative to the operational treatment, whereas the effect of the silvicultural treatment was not significant at NC. At NC, average tree volume did not differ among the genotypes over the study period ($P > 0.05$) (Fig. 1C). At VA, there were significant ($P = 0.03$) differences among the genotypes at the end of the study (Fig. 1D), which was explained by the higher stem volume of the clones over the CMP and OP families (on average clones had 28% higher stem volume than the families).

Similarly, the effect of the intensive silvicultural treatment and genotype on leaf area was significant only at VA ($P < 0.05$), although there was a trend of the effect of the silvicultural treatment at NC ($P = 0.06$) (Table 2 and Fig. 2). At VA, the differences in leaf area among the genotypes were significant only in the intensive silvicultural treatment (Fig. 2), where the broadest crown variety C4 had the highest leaf area. Although, the variety C2 was classified as having broad crown, it exhibited similar leaf area than the narrow crown variety C1 and the CMP family (Variety C4 had 65% higher leaf area to these genotypes). Both stem growth and leaf area were similar at the two sites in the operational silvicultural treatment (Fig. 2).

At NC, the intensive silvicultural treatment significantly increased both the fascicle diameter and the number of needles per fascicle relative to the operational silvicultural treatment (4% and 7%, respectively), whereas no effect was detected at VA (Table 2). Moreover, there were significant differences in the leaf morphology parameters among the genotypes (Table 2). At NC, the increase of fascicle diameter due to the intensive silvicultural treatment varied from 2% to 12% for the different genotypes, which explained the silvicultural treatment by genotype interaction (Table 2). In this site, variety C4 had significantly lower fascicle diameter than variety C1 and the OP family (Fig. 3). At VA, variety C3 and C4 had significantly lower fascicle diameter than variety C1 and the OP family. When comparing only the clones, at both sites, variety C4 consistently had lower fascicle diameter than variety C1. Variety C1 had a higher number of needles per fascicle than the other clones, whereas the families had middle values for this variable. At both sites, the broad-crown clones C2 and C4 showed the lowest number of needles per fascicle.

3.2. Variability in leaf-level physiological parameters

Significant differences among the genotypes were found for all the physiological parameters only at VA, while no effect was detected at NC (Table 3). Table 4 shows the post hoc contrast analyses to test for differences in all the traits between clonal versus control-mass and open pollinated families, and for broad- versus narrow-crown. At VA, the analysis indicates that on average A_{sat}, g_s and E of the clones was significantly higher than the non-clonal sources (CMP and OP family) ($P < 0.01$), while no differences were found for the parameters associated with water use efficiency (WUEs and Δ^{13}). Moreover, the contrast analysis showed that none of the physiological parameters differed when compared the broad- versus narrow-crown clones. Nonetheless, genotypes ranked differently for each physiological parameter (Fig. 4). Overall, the narrow-crown clones exhibited similar leaf-level physiology, but when compared to the broad-crown clones, E in variety C2 was similar to the narrow-crown clones, and had significantly higher WUE_{int} and WUE_{ins} than variety C4. Variety C2 also had similar WUE_{int} and WUE_{ins} than the CMP family (Fig. 4). Δ^{13} was significantly higher in variety C4 relative to the OP family, but it did not differ among clones.

The effect of the silvicultural treatment on A_{sat}, g_s and E differed by date at NC, whereas it did not showed any affect at VA (Table 3 and Fig. 5). During the study period, the ranges for A_{sat}, g_s and E

Table 2
P-values from the analysis of variance per site for stem volume, leaf area, number of needles per fascicle and fascicle diameter.

SITE	EFFECT	Stem volume	Leaf area	Needles per fascicle	Fascicle diameter
NC	SILV	0.2776	0.0605	**0.0276**	**0.0223**
	GEN	0.7753	0.2723	**<0.0001**	**0.0001**
	SILV × GEN	0.7269	0.9059	0.1496	**0.0221**
	DATE	**<0.0001**			
	SILV × DATE	0.4610			
	GEN × DATE	0.6152			
	SILV × GEN × DATE	0.8237			
VA	SILV	**0.0143**	**0.0071**	0.2706	0.1665
	GEN	**0.0045**	**0.0002**	**0.0025**	**0.0158**
	SILV × GEN	0.6127	**0.0438**	0.3770	0.5944
	DATE	**<0.0001**			
	SILV × DATE	**<0.0001**			
	GEN × DATE	**<0.0001**			
	SILV × GEN × DATE	0.6600			

Note: Significant effects are shown in bold type. The effects are silvicultural intensity (SILV), genetic entry (GEN) and DATE.

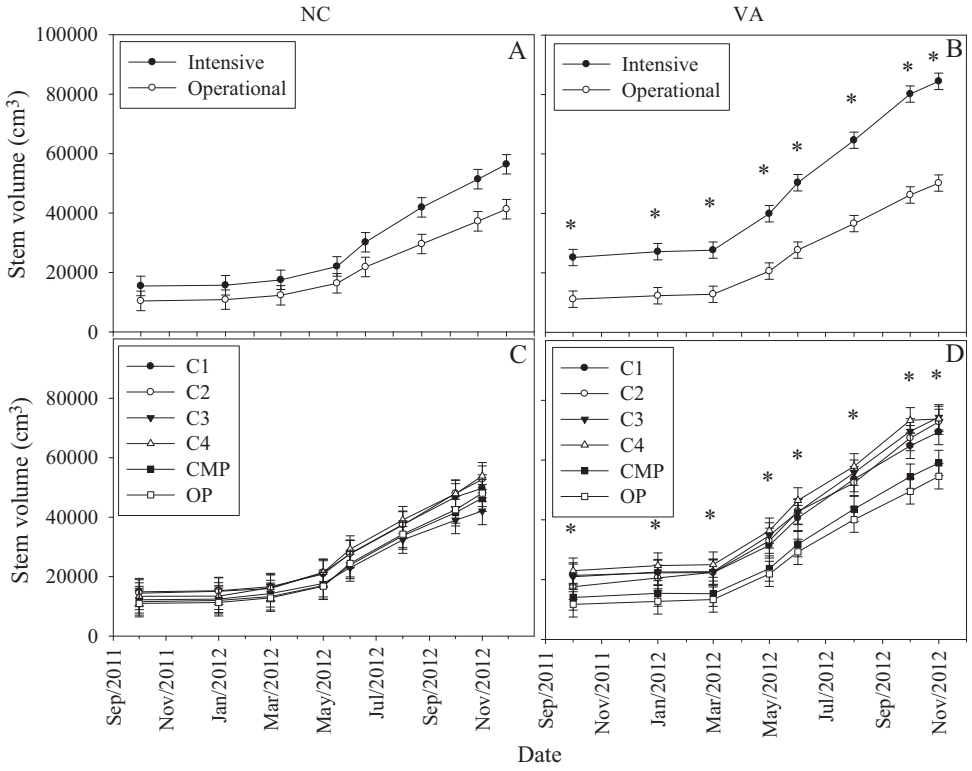

Fig. 1. Least-square means (±standard error) for loblolly pine stem volume for each site as influenced by silvicultural treatment (upper panel), and genotype (lower panel) (NC = North Carolina Coastal Plain, VA = Virginia Piedmont; C1, C2, C3, C4 = clones, CMP = controlled mass pollinated, OP = open pollinated). * indicate significant differences at an alpha level of 0.05.

were similar at both sites (values from 0.13 to 8.6 μmol/m^2 s^{-1}, and 12 to 217 mmol m^2 s^{-1} and 0.01 to 3.6 mmol m^2 s^{-1}, respectively), and also exhibited similar seasonal patterns. These parameters peaked in the summer dates and then decreased toward the autumn months (Fig. 5). At NC, A_{sat}, g_s and E were higher in the operational silvicultural treatment than the intensive silvicultural treatment in the most productive months. The results for WUE_{ins} and WUE_{int} were less conclusive than for the parameters of which these were derived. The effect of the silvicultutal treatments on WUEs differed between site and date (Table 2 and Fig. 6). At both sites, significant differences in WUEs between silvicultural treatments occurred only in the winter measurements. At these months, the effect of intensive silviculture was an increase in WUEs at VA, and a decrease at NC. At NC, WUE_{int} peaked in the winter month, and decreased toward the summer dates. At VA, WUE_{int} and WUE_{ins} were lower at May 2012 and fluctuate during the study period in both silvicultural treatments (Fig. 6). Δ^{13} was lower at VA (22.1 ‰) than NC (22.6 ‰), suggesting that across all the treatments the water use efficiency was higher at VA.

4. Discussion

The use of loblolly pine clones has the potential to further increase productivity as traditional silviculture moves to precision forestry systems. However, forest management may become more complex when genotype by silviculture treatment interactions are present. The use of crown ideotypes provides a framework to design ideotype-based silvicultural prescriptions (Martin et al., 2001; Yáñez et al., 2015). This study investigated the growth and

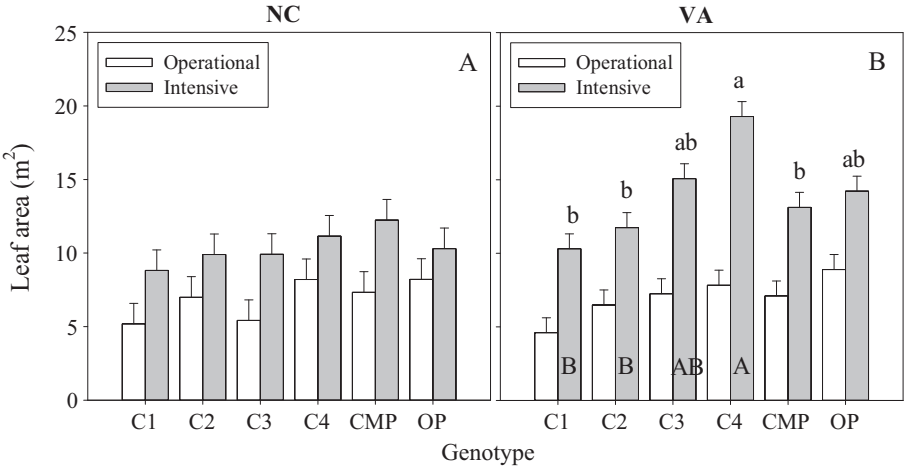

Fig. 2. Least-square means (±standard error) for loblolly pine leaf area for each site as influenced by silvicultural treatment. NC = North Carolina Coastal Plain, VA = Virginia Piedmont; C1, C2, C3, C4 = clones, CMP = controlled mass pollinated, OP = open pollinated. Lowercase and uppercase letters indicate significant differences (*P*-value < 0.05) regarding first all the genotypes and second only the clones, respectively.

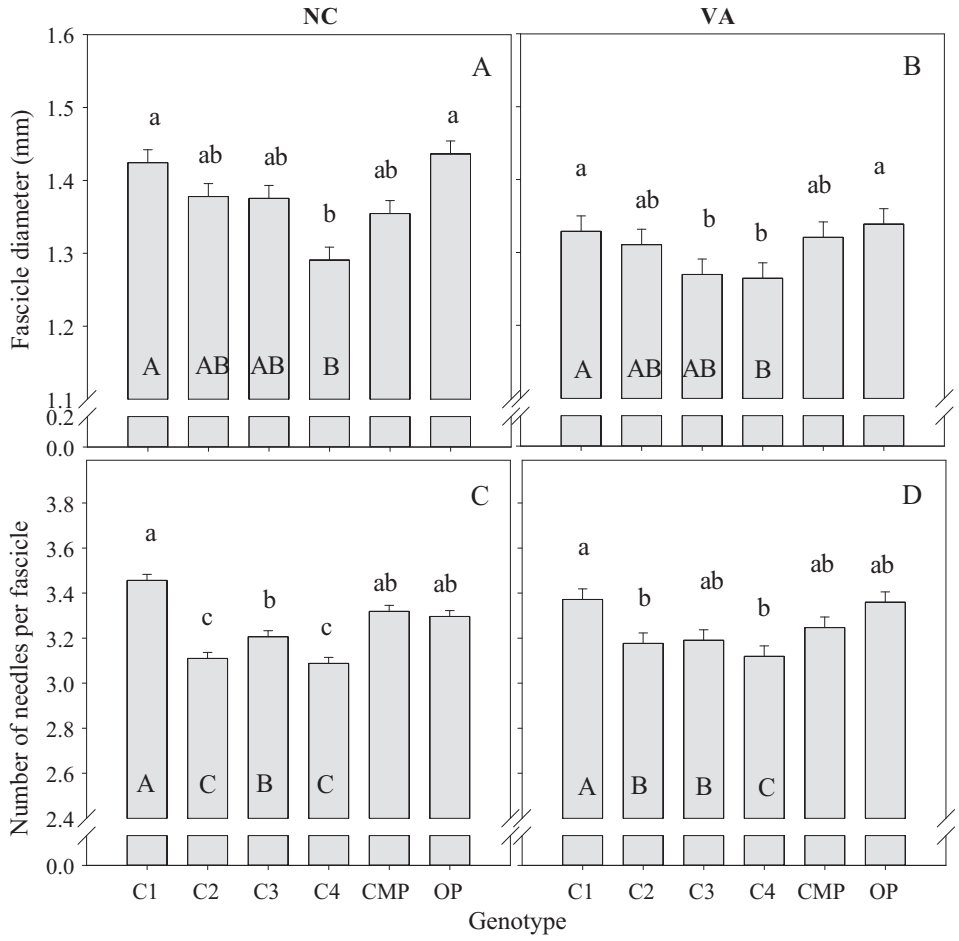

Fig. 3. Least-square means (±standard error) for loblolly pine fascicle diameter (upper panel) and number of needles per fascicle for each site as influenced by genotype. NC = North Carolina Coastal Plain, VA = Virginia Piedmont; C1, C2, C3, C4 = clones, CMP = controlled mass pollinated, OP = open pollinated. Lowercase and uppercase letters indicate significant differences (*P*-value < 0.05) regarding first all the genotypes and second only the clones, respectively.

leaf physiology of clones, differing in crown ideotypes, along with a CMP and OP family under different silvicultural treatments and sites. Our results indicate that the gains in productivity using both intensive silviculture and clones were site specific and not expressed in the poorly drained site in NC. The results are consistent with the first hypothesis; hence, improving soil resources by intensive silviculture increased stem growth and foliage display, but not through a detectable effect on leaf physiology. However, we reject the second and third hypotheses as the genotypes responses in leaf area deployment, foliage morphology and

Table 3
P-values from the analysis of variance per site for light-saturated photosynthetic rate (A_{sat}), stomatal conductance (g_s), transpiration (E), intrinsic water use efficiency (WUE_{int}), instantaneous water use efficiency (WUE_{ins}) and carbon isotope discrimination (Δ^{13}).

SITE	EFFECT	A_{sat}	g_s	E	WUE_{int}	WUE_{ins}	Δ^{13}
NC	SILV	**0.0068**	0.1736	**0.0251**	0.4536	0.4532	0.2943
	GEN	0.6650	0.4160	0.6124	0.0924	0.0511	0.7200
	SILV × GEN	0.5985	0.4564	0.6539	0.9512	0.8355	0.4297
	DATE	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	
	SILV × DATE	**0.0093**	**0.0012**	**0.0002**	**0.0231**	**0.0259**	
	GEN × DATE	0.6778	0.3818	0.408	0.1365	0.2979	
	SILV × GEN × DATE	0.9634	0.8726	0.8606	0.9473	0.9545	
VA	SILV	0.5753	0.2745	0.4255	0.0519	0.0622	0.1946
	GEN	**0.0023**	**0.0065**	**0.0009**	**0.0094**	**0.0143**	**0.0493**
	SILV × GEN	0.1300	0.4116	0.5355	0.5359	0.3696	0.0848
	DATE	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	
	SILV × DATE	0.9788	0.9852	0.8384	**0.0095**	**0.0056**	
	GEN × DATE	0.9903	0.9722	0.9607	0.6336	0.7351	
	SILV × GEN × DATE	0.9949	0.9912	0.9834	0.9918	0.9922	

Note: Significant effects are shown in bold type. The effects are silvicultural intensity (SILV), genetic entry (GEN) and DATE.

Table 4
Summary of statistical contrasts testing the effect of the crown ideotype (broad- versus narrow-crown) and genetic source (clonal versus non-clonal) loblolly pine stem volume, leaf area, and fascicle morphological and physiological traits by site (NC = North Carolina Coastal Plain, VA = Virginia Piedmont). Values for a specific trait within a row followed by different letters differ significantly (*P*-value < 0.05) between crown ideotype and genetic source, respectively.

Site	Variable	Crown Ideotype			Genetic Source		
		Narrow-crown	Broad-crown	*P*-value	Clonal	CMP and OP	*P*-value
NC	Stem volume (cm^3)	45,907 a	53,323 a	0.3556	49,615 a	47,285 a	0.4778
	Leaf area (m^2)	7.33 a	9.06 a	0.0887	8.19 a	9.52 a	0.1288
	Needles per fascicle	3.41 a	3.04 b	0.0001	3.21 a	3.30 b	0.0004
	Fascicle diameter (mm)	1.47 a	1.37 b	0.0013	1.36 a	1.39 a	0.0764
	A_{sat} (μmol m^{-2} s^{-1})	3.79 a	4.11 a	0.4823	4.95 a	4.90 a	0.8811
	g_s (mmol m^{-2} s^{-1})	69.1 a	67.1 a	0.8338	101.6 a	101.4 a	0.6914
	E (mmol m^{-2} s^{-1})	0.55 a	0.60 a	0.9315	1.50 a	1.49 a	0.7104
	WUE_{int} (μmol $mmol^{-1}$)	0.055 a	0.066 a	0.0685	0.052 a	0.054 a	0.3824
	WUE_{ins} (μmol $mmol^{-1}$)	7.10 a	7.51 b	0.0336	4.51 a	4.73 a	0.4430
	Δ^{13} (‰)	22.03 a	22.44 a	0.1351	22.63 a	22.72 a	0.6898
VA	Stem volume (cm^3)	71,851 a	73,271 a	0.8848	72,561 a	56,811 b	0.0001
	Leaf area (m^2)	9.3 a	11.3 b	0.0144	10.3 a	10.8 a	0.4181
	Needles per fascicle	3.38 a	3.08 b	0.0065	3.21 a	3.31 b	0.0305
	Fascicle diameter (mm)	1.40 a	1.33 a	0.4781	1.29 a	1.32 b	0.0179
	A_{sat} (μmol m^{-2} s^{-1})	3.77 a	4.15 a	0.1647	4.79 a	4.53 b	0.0002
	g_s (mmol m^{-2} s^{-1})	66.0 a	69.8 a	0.3356	83.6 a	79.5 b	0.0025
	E (mmol m^{-2} s^{-1})	0.59 a	0.63 a	0.8912	1.14 a	1.09 b	0.0114
	WUE_{int} (μmol $mmol^{-1}$)	0.058 a	0.062 a	0.5995	0.065 a	0.067 a	0.1721
	WUE_{ins} (μmol $mmol^{-1}$)	7.77 a	7.86 a	0.5713	6.14 a	6.32 a	0.1350
	Δ^{13} (‰)	22.09 a	22.41 a	0.0983	22.25 a	21.99 a	0.1163

physiology differed indistinctly and are not associated with the genetic source (clonal versus non-clonal) or the crown ideotype (broad- versus narrow-crown), respectively.

Fertilization and weed control in the intensive silviculture treatment had a positive and significant effect on tree size only at VA (68% higher stem volume than the operational silvicultural treatment), while there was a similar trend at NC. These results suggest that there was some type of resource limitation (i.e. nutrient and water) that was corrected at VA. These responses are also consistent with the results reported previously by Yáñez et al. (2015) in these trials. They indicated that the poor growth response at NC is likely due to the high water table at this site, whose negative effect on growth was not entirely ameliorated by bedding. Similarly, at VA the intensive silvicultural treatment increased leaf area in all the genotypes, with responses varying from 60% to 146% relative to the operational silvicultural treatment, while there was some slight increase in leaf area appearing at NC. The large impact of silvicultural intensity on growth and leaf area typically occurs in loblolly pine and has been reported in numerous studies (Albaugh et al., 1998; Vose and Allen, 1988; Jokela and Martin, 2000; McGarvey et al., 2004). The large increase in leaf area by the intensive silvicultural treatment at VA was associated with a greater foliage display and canopy size than to an effect on the foliage morphology. Contrarily to what was expected, both the fascicle diameter and number of needles per fascicle were increased by the intensive treatment at NC, but not at VA where the growth responses to silviculture intensity were higher. These results partially agree with the findings by Will (2005). He found that loblolly pine foliage morphology is responsive to fertilization (increasing the fascicle size), but this accounted for a small change (<10%) in the increase in total leaf biomass, which doubled in some stands. In our study the small but significant increase in fascicle size due to the intensive silvicultural treatment would not explain the increase in the total leaf area as the genotypes exhibited great differences in leaf area deployment. Moreover, although it was not assessed in this study, fertilization may also have increased the number of flushes, size of the fascicles, and number of fascicles per flush (Maier et al., 2002). In this study, the trials were purposely located to span a wide range of environmental conditions where loblolly pine is planted. The VA Piedmont site represents the northern limit of the species distribution. Soils are well drained, but have poor fertility and growth responses to intensive

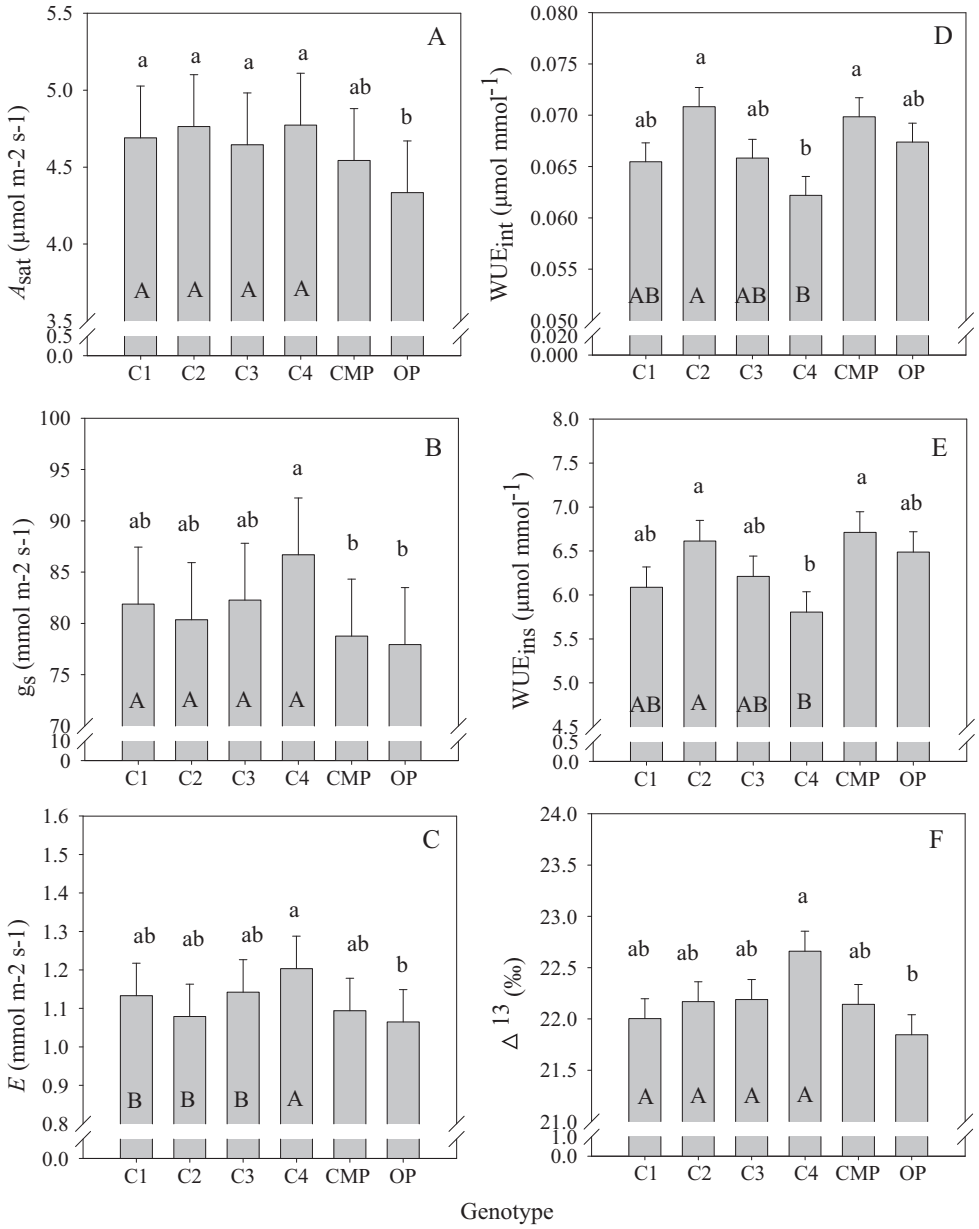

Fig. 4. Least-square means (±standard error) for loblolly pine light-saturated photosynthetic rate (A_{sat}), stomatal conductance (g_s), transpiration (E), intrinsic water use efficiency (WUE_{int}), instantaneous water use efficiency (WUE_{ins}) and carbon isotope discrimination (Δ^{13}) for each site as influenced by genotype. NC = North Carolina Coastal Plain, VA = Virginia Piedmont; C1, C2, C3, C4 = clones, CMP = controlled mass pollinated, OP = open pollinated. Lowercase and uppercase letters indicate significant differences (P-value < 0.05) regarding first all the genotypes and second only the clones, respectively.

silviculture have been found for the same area by Amishev and Fox (2006) and Stovall et al. (2011). The site at NC represents some of the typical poorly drained soils in the Coastal Plain, and growth responses to intensive silviculture have been previously reported in these types of sites (McKee and White, 1986; Nilsson and Allen, 2003; Tyree et al., 2009).

In addition, the differences among the genotypes in stem growth, foliage development and physiology were expressed only at VA. At this site, the clones had higher productivity than the CMP and OP family. Moreover, although no differences in stem growth were found between clones, their differences in leaf area display indicate that the clones greatly differ in growth efficiency (understood as the stem growth to leaf area ratio). For instance, at VA one of the narrow-crown clones (C1) and one of the broad-crown clones (C2) had higher growth but similar leaf area than the CMP family. Otherwise, comparing the broad-crown clones, variety C4 had similar stem growth but 68% higher leaf area than variety C2. This suggests that great differences in growth efficiency among genotypes can be found, even within the same crown ideotype. Differences in growth efficiency and crown development in clonal loblolly pine have also been reported in previous studies (Emhart, 2005; King et al., 2008; Tyree et al., 2009; Stovall et al., 2011). From the point of view of forest management, these large differences in leaf area display and canopy development may represent large differences in the demand of soil resources and consequently in the future intra-specific competition within the stands.

During the study period, the seasonal variation of gas exchange parameters was similar between the two sites and was in the range previously reported for loblolly pine; for A_{sat} (0.13–8.6 µmol m^2 s^{-1}) (Ellsworth, 2000; Munger et al., 2003; Tang et al., 2003; Gough et al., 2004a), WUE_{int} (0.027–0.14 µmol mmol^{-1}) (Aspinwall et al., 2011), and Δ^{13} (20–24 ‰) (Gebremedhin,

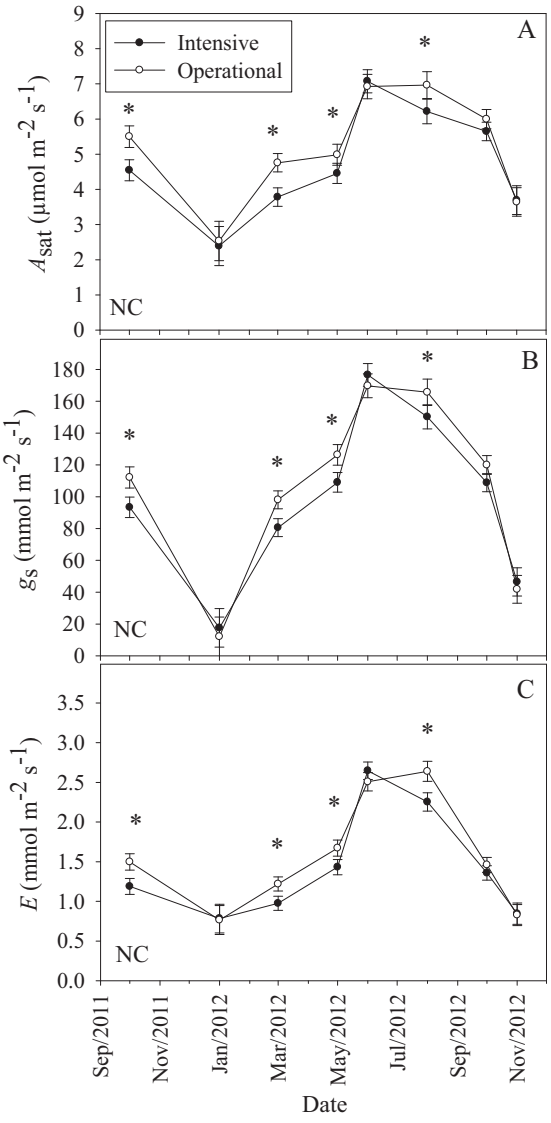

Fig. 5. Least-square means (±standard error) for loblolly pine light-saturated photosynthetic rate (A_{sat}, upper panel), stomatal conductance (g_s, middle panel), transpiration (E, lower panel) at NC (North Carolina Coastal Plain) as influenced by silvicultural treatment (upper panel). * indicate significant differences at an alpha level of 0.05.

2003). In our study, we hypothesized that the differences in growth among clonal and non-clonal stand were associated to differences in leaf deployment and physiology. Additionally, we hypothesized that genotypes differing in the crown ideotype will differ in foliar display and consequently in leaf physiology. Overall, although the contrast analysis partially supports the differences in leaf physiology among the genetic sources, it did not support the differences between crown ideotypes. However, we rejected both hypotheses as the leaf display and physiology of the genotypes indistinctly differed and there was no association to either the genetic source (clonal versus non-clonal) or to the crown ideotype (broad- versus narrow-crown), respectively. For instance, A_{sat} was similar among clones, whose values significantly differed only from the OP family. Narrow-crown clones exhibited similar leaf physiology, but great differences were found between the broad-crown clones. The broad-crown variety C2 had low transpiration rates compared to the narrow-crown clones, but it had higher instantaneous water use efficiency than the crown ideotype for C4. Based on process-based-models, McMurtrie et al. (1990) found that the annual canopy net photosynthesis in radiata pine was 111% higher in fertilized/irrigated stands than control stands, and that the increased photosynthetic rate due to N nutrition explained only 10% of the total carbon gain.

In our study, we argue that although leaf-level physiology had little variation within the species, small differences may confer some advantage when clonal material is planted. The few studies comparing genetic differences in A_{sat} in loblolly pine have shown contrasting results. Some studies did not find differences in A_{sat} among half-sib families (Seiler and Johnson, 1988; Samuelson, 2000), even when different sources were compared (half- and full-sib families versus clones) (Aspinwall et al., 2011); while others have found differences in A_{sat} in clonal studies (Gebremedhin, 2003; King et al., 2008; Tyree et al., 2009). A_{sat} appears to be conservative within the species; these studies consistently showed differences in other gas exchange parameters related with the water-plant relationship such as g_s, E and photosynthetic water use efficiency, which agree with the results found in our study. In addition, Ingwers et al. (2016) found that on a per-fascicle basis, loblolly pine gas exchange is higher in four-needle fascicles than three-needle fascicles. They also found that at the canopy level different clones may differ in the proportion of these types of fascicles as was found in our study. However, the mechanisms of how this may affect growth efficiency needs further research. Small variation in needle gas exchange and morphological parameters among genotypes might have a great impact in the stand-water use and consequently in the ecosystem sustainability (Aspinwall et al., 2011). For instance, if the higher E and lower WUE in variety C4 is scaled with its large leaf area relative to variety C2, it could be that these two broad-crown genotypes (competition ideotype) will differ significantly in the water use at the stand level. Besides, broad-crown ideotypes might demand more nutrients and water than the narrow ones, implying that narrow crown clones might tolerate drought to nutrient limitation better than a broad type (Tyree et al., 2009). Our study indicates little similarity in the leaf physiological processes and morphology among clones classified in the same ideotype.

At the end of the fourth growing season, the trees had not yet reached the start of canopy closure. Thus, we ensured that the foliage collected for gas exchange measurements was fully-sun exposed. Hence, only a deficiency in soil resources might limit gas exchange. However, the effect of the silvicultural intensity on the gas exchange parameters was less conclusive than for the genetic component. At VA, the higher responses in growth and leaf area display due to the intensive silvicultural treatment were not linked to an effect on gas exchange parameters. Moreover, although some effect of the silvicultural intensity was found on WUE_{ins} and WUE_{int}, it occurred in the months with lower growth rate, so its impact on productivity should be minor. In contrast, at NC, A_{sat}, E, and WUEs tended to be lower across the growing season in the intensive than in the operational silvicultural treatment. The mechanism involved in this trend cannot be elusive by this study. Regarding the poor above-ground growth response to intensive silviculture at this site, we speculate that some soil resource is limiting the growth and physiology of trees at this early state. Some studies in loblolly pine showed that water table greatly constrained root development, which alters the resource uptake and the balance between aerobic and anaerobic respiration (De Bell et al., 1984). Nonetheless, at this point the soil resources in both silvicultural treatments were likely sufficient to maintain the levels of gas exchange. These results corroborate the lack of effect of management intensity on gas exchange in loblolly pine, even when growth and foliar nitrogen (N) was affected (Gough et al., 2004a; Samuelson, 1998; Will et al., 2001; Munger et al., 2003). Some studies indicate that there is a short term response in A_{sat} to fertil-

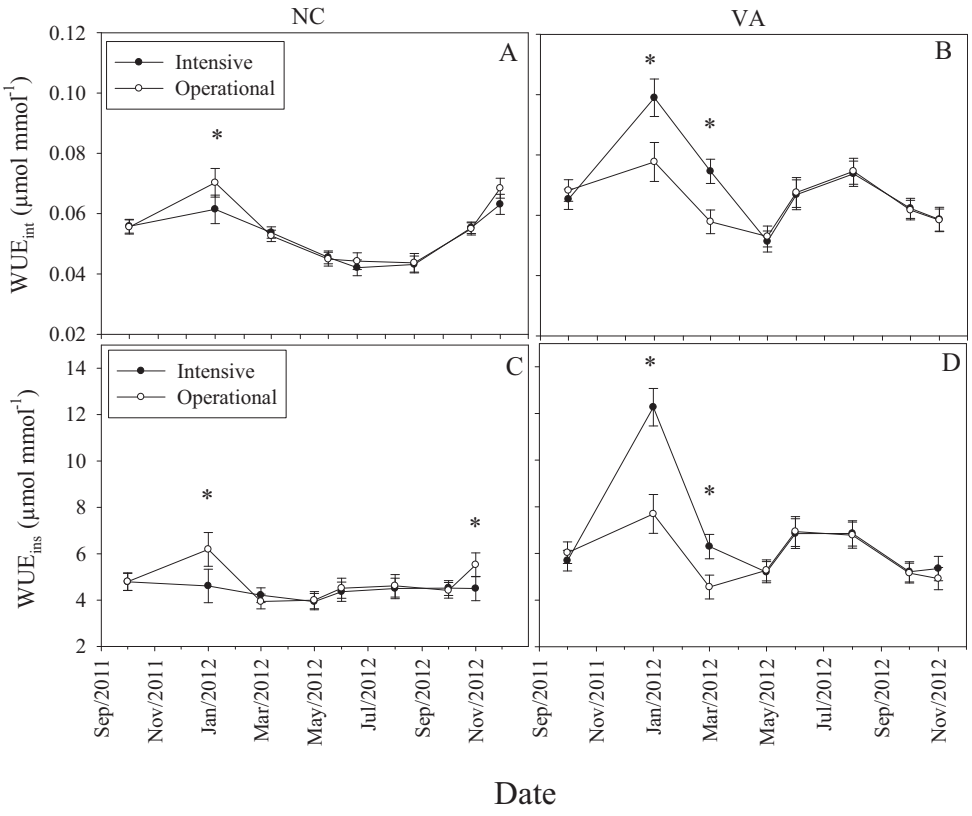

Fig. 6. Least-square means (±standard error) for loblolly pine intrinsic water use efficiency (WUE_{int}, upper panel), instantaneous water use efficiency (WUE_{ins}, lower panel) at NC (North Carolina Coastal Plain) as influenced by silvicultural treatment (upper panel). * indicate significant differences at an alpha level of 0.05.

ization, in which the increase in A_{sat} after fertilization is only ephemeral and the extra carbon gained is used to enlarge the canopy and consequently tree growth (Gough et al., 2004b; King et al., 2008). Studying two contrasting crown-ideotype clones of loblolly pine, Tyree et al. (2009) found some evidence of an increase in A_{sat} within the first six month after fertilization, accompanied with an increase of the foliar mass. The results found by King et al. (2008) showed that the pattern after fertilization may be clone-specific. These finding may explain the results in our study, where physiological measurements were made in field trials between the 3rd and 4th growing season, and started 1.5 year after the fertilization. Fertilization in the south is most commonly used to correct N and Phosphorous (P) deficiencies (Fox et al., 2007b), and both elements were present in the fertilization in the intensive silvicultural treatment. We also did measure nitrogen concentration in the same foliage collected for A_{sat} determination on August 2012 (end of summer), where the peak in leaf area occurs (Albaugh et al., 1998). At NC, the N concentration ranged from 1 to 1.9%; whereas at VA it ranged from 1.1 to 1.7%, with no significant differences among the silvicultural treatments within the sites. Almost all the trees (98 and 100% NC and VA, respectively) had N concentration above the critical level of 1.1% reported for loblolly pine (Allen, 1987); therefore, foliar N deficiency was not likely a limiting factor in our study at this time. We speculate that the assart effect from the previous harvested stands at the sites was still providing a sufficient level of N (Fox et al., 2007b). Therefore, the effects of site and intensive silviculture on growth suggests that other mechanisms than gas exchange could be affected such as the changes in the above- and below-grown carbon partitioning (Albaugh et al., 1998; King et al., 1999; Litton et al., 2007), light use efficiency (LUE) (Campoe et al., 2013), or carbon use efficiency (Ryan et al., 1996).

5. Conclusions

Our findings indicate that the growth responses due to the effects of silvicultural intensity and genotype were site specific and not explained through an effect on leaf level gas exchange or needle morphology. There was not great variation in gas exchange among sites, and so far the differences in productivity are probably associated with favorable soils conditions. We found small, but significant differences in gas exchange and foliage morphology among the genotypes, and that variation was genotype-specific and not associated neither to the genetic source nor the crown ideotype. As was described, broad crown ideotypes allocate more C to branch and foliage development, but they did not necessarily allocate more C in the stem. This study highlights the complex genotype by environmental interaction that may arise when clonal material is deployed.

Conflict of interest

None declared.

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