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Long-term dynamics of loblolly pine crown structure and aboveground net primary production as affected by site quality, planting density and cultural intensity

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ABSTRACT

Crown attributes respond readily to silvicultural manipulations and mediate many aspects of stand structure, consequently they dynamically influence stand production. Numerous studies reported crown structure responses to intensive cultures or stand density and the relation between foliage quantity and growth efficiency at early stages of stand development. Long-term temporal patterns of crown structure and its relation to growth have been much less studied. With long-term remeasurement data from two loblolly pine culture-by-density studies, the roles of planting density, cultural intensity and site quality on crown structure, stand aboveground net primary production (ANPP), and growth efficiency were investigated using ANCOVA and linear mixed-effects modeling approaches. Using data from 480 destructively sampled trees, the Dirichlet regression modeling approach was used to analyze foliage and crown biomass allocations among the lower-, middle- and upper-third crown sections. Stands under different cultural intensities showed different temporal patterns of foliage biomass. Increased planting density or higher site quality enhanced wood production of loblolly pine. ANPP generally increased with increasing site quality, due to increased stand foliage biomass in the early stage of stand development, and mainly due to increased growth efficiency in the late stages of stand development. More intensive cultural treatments increased foliage biomass, thus increased ANPP at early ages; thereafter cultural intensity did not affect foliage biomass, ANPP, and growth efficiency. The trend of early age increases in both foliage biomass and ANPP resulting from increased planting density did not hold true with stand development. After correcting for the effects of tree size and dominance, cultural intensity still altered the vertical distribution of foliage biomass. More intensive culture resulted in an upward shift of foliage biomass.

1. Introduction

Loblolly pine (*Pinus taeda* L.) is the most common and commercially important species in the southeastern USA. Intensive silvicultural treatments including deployment of genetically improved seedlings, site preparation, competing vegetation control and fertilization are commonly used to enhance productivity and reduce rotation length of loblolly pine plantations (Martin and Jokela, 2004). Crown attributes responding readily to silvicultural manipulations are key physiological determinants of tree growth. Most silvicultural treatments that increase growth of pine stands are associated with increased crown and branch size as well as increased foliage biomass.

Several studies of southern pines have shown positive responses of foliage quantity (e.g., foliage biomass (FB), foliage density (FD), or leaf area index (LAI)) to intensive culture (Vose and Allen, 1988; Gholz et al., 1991; Dalla-Tea and Jokela, 1994; Albaugh et al., 1998; Will et al., 2002; Martin and Jokela, 2004) and planting density (Shelton, 1984; Dean and Baldwin, 1996; Will et al., 2005). Increased FB or LAI in turn increases intercepted photosynthetically active radiation (Dewar, 1996) and stem growth (Vose and Allen, 1988). Thus, a strong positive relation between foliage quantity and productivity has been reported in previous studies (e.g. Vose and Allen, 1988; Dalla-Tea and Jokela, 1991; Albaugh et al., 1998; Barron-Gafford et al., 2003; Burkes et al., 2003; Jokela et al., 2004, Will et al., 2005). Most of the previous research is short-term and has been conducted in young stands (i.e. before their FB, LAI or growth reaching their peaks). Foliage quantity,

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growth efficiency, and their responses to cultural treatments vary with stand age. Therefore, the previously reported responses and relationships for stands at early stages of stand development might not hold true in older stands. For example, the positive effect of planting density on young loblolly pine foliage biomass has been well documented (Will et al., 2005) and this effect diminished with stand age (Shelton, 1984; Vose and Allen, 1988). Martin and Jokela (2004) found that any combination of fertilizer and vegetation control treatments increased aboveground net primary production (ANPP) by 200–300% over the untreated controls at age 6–9 year, and the magnitude of these productivity increases declined with stand development. The increased ANPP at early ages by intensive treatments might be due to the increased foliage biomass. In mid-rotation loblolly pine stands, there was a small variation in foliage biomass (Zhao et al., 2019) but a high variation in ANPP (see below) between cultural intensities or among planting densities. Whether the declined or diminished ANPP response was due to the diminished FB response, reduced growth efficiency by age, increased mortality of older trees, or all remains unclear. In even-aged stands, growth and biomass accumulation decline after reaching a peak (Ryan et al., 1997). The amount and timing of the decline can vary with site quality and silvicultural inputs. Among several potential mechanisms, Ryan et al. (1997) believed that reduced leaf area and reduced photosynthetic capacity are most likely to be response for the age-related growth decline. To our best knowledge, however, these mechanisms have not been directly examined by experimental studies which especially involve multiple factors such as different cultural treatments, initial densities, and different quality sites. To fill this gap, long-term roles of intensive culture and stand density on foliage quantity, productivity, and their relationships especially in later stand development will be examined using two loblolly pine experimental studies.

Fertilization increased both tree- and stand-level foliage biomass, growth efficiency, and productivity of lodgepole pine (Blevins et al., 2005). Sword Sayer et al. (2004) found that fertilization increased foliage biomass (LAI) and stand productivity but had no effect on loblolly pine growth efficiency. Satoo (1967) reported that both stand-level foliage quantity and growth efficiency in *Cryptomeria japonica* D. Don increased with increasing site quality. DeRose and Seymour (2009) showed that growth efficiency increased significantly with site index for *Abies balsamea* but was unaffected by site quality for *Picea rubens*, and growth efficiency decreased with increasing leaf area for both species. It is still unclear whether the increased productivity was due to the increased foliage quantity, growth efficiency, or both. Reports examining the change of their relationships with stand development are limited.

In addition to foliage quantity, foliage distribution within the crown is also a primary element of crown structure. Silvicultural practices may impact both foliage quantity and distribution, which alter stand growth. Efforts were made to quantify foliage distributions of individual trees and their responses to silvicultural practices. For example, Gillespie et al. (1994) found that fertilization increased crown size and total tree foliage biomass but had no impact on foliage distribution. The vertical distribution of foliage in the crown depended on crown length, crown ratio, and crown foliage biomass (Maguire and Bennett, 1996; Weiskittel et al., 2009; William et al. (2018)), tree size (Gillespie et al., 1994), and tree dominance (Maguire and Bennett, 1996; Xu and Harrington, 1998). These crown attributes also depend on tree size. For example, total foliage and crown biomass was positively correlated with DBH and negatively correlated with tree height (Zhao et al., 2015; William et al., 2018). Therefore, the influences of stand density, cultural intensity and site quality on foliage distribution should be examined while correcting for the effects of tree size and dominance.

In 1995–96 and 1997–98, the Plantation Management Research Cooperative (PMRC) at the University of Georgia initiated two loblolly pine culture-by-density studies. These two studies with different levels of cultural intensity and a wide range of planting density were established across a variety of soil groups over the southeastern USA. Long-term remeasurement data from these two studies enable us to examine the effects of culture, stand density and site quality on stand-level crown structure, ANPP, and their relationships, focusing on mid- and past mid-rotation stands. With destructive sampling data from 480 trees sampled on plots of the culture-by-density studies at ages 12, 15, and 16, the distributions of tree foliage and crown biomass within the crown were modeled using the Dirichlet regression modeling approach. The specific objectives of the study were to

(i) explore temporal variation of stand-level average tree height, average crown length, average crown ratio, foliage biomass, foliage density, foliage/branch biomass ratio, stem/crown biomass ratio, and aboveground net primary production (ANPP) caused by different levels of planting density, cultural intensity and site quality;
(ii) analyze the relationship between stand foliage quantity and ANPP and test the hypotheses that this relationship was significantly affected by planting density, cultural intensity and site quality, resulting from their significant effects on foliage quantity, ANPP, and growth efficiency;
(iii) model the distribution of tree foliage and crown biomass within the crown and test the hypotheses that the distribution was still significantly influenced by cultural intensity and planting density after correcting for tree size and dominance effects.

2. Materials and methods

2.1. Study description

The CPCD96 study was established in 1995/1996 at 17 locations in the Lower Coastal Plain of Georgia (GA), Florida (FL) and South Carolina (SC), across five soil groups (Zhao et al., 2010). The UPCD98 study was established in 1997/1998 at 23 locations in the Upper Coastal Plain and Piedmont regions of GA, FL, SC, Alabama (AL) and Mississippi (MS), across seven broad soil classes (Zhao et al., 2010). Planting density treatments and experimental design were identical for these two studies. At each location, there were six levels of planting density (PLTPH: 741, 1483, 2224, 2965, 3706 and 4448 trees ha^{-1}) and two levels of cultural treatment (intensive and operational) (Table 1). A split-plot design with one replication was used in which cultural intensities were randomly assigned to main plots and within a cultural intensity level the planting densities were randomly assigned as subplots. There were some differences in the cultural treatments between these two studies. In the CPCD96 study, the operational treatment consisted of bedding in the spring followed by a fall banded chemical site preparation. The intensive treatment included bedding in the spring followed by a fall broadcast chemical site preparation, tip moth control through the first two growing seasons and repeated herbicide application to achieve complete vegetation control throughout the rotation. In the UPCD98 study, all tillage treatments included in site preparation were carried out on all treatment plots. Both the operational and intensive treatments included a broadcast chemical site preparation. The operational treatment included a first-year banded weed control, and the intensive cultural treatment included additional herbicide application for complete competing vegetation control throughout the rotation. The same level of fertilization was applied for the two studies in the operational and intensive treatments (Table 1).

2.2. Measurements

Treatment plots were comprised of an interior measurement plot that ranged from 80 to 184 trees per plot for the 741 to 4448 tree ha^{-1} densities, respectively, and a surrounding 7.3-m-wide buffer area. Each tree in measurement plots was tagged. Dormant-season tree measurements were collected at ages 2, 4, 6, 8, 10, 12, 15, 18 and 21 years. At each measurement, diameter at breast height (DBH) of each surviving

Table 1
Silvicultural treatments for two loblolly pine culture and density studies.

LCP Culture Density Study (CPCD96)		UCP Culture Density Study (UPCD98)	
Operational	Intensive	Operational	Intensive
Bedding	Bedding	Tillage including subsoiling on some sites	Tillage including subsoiling on some sites
Fall banded chemical site preparation	Fall broadcast chemical site preparation	Broadcast chemical site preparation	Broadcast chemical site preparation
	Tip moth control		
Herbaceous weed control: 1st year banded	Repeated herbicide application to achieve complete vegetation control	Hardwood control: 1st year banded	Repeated herbicide application to achieve complete vegetation control
Fertilization: at planting, 561 kg ha^{-1} of 10–10–10 fertilizer (56 kg ha^{-1}N); before 8th, 12th, 16th, 20th growing seasons, 224 kg ha^{-1}N + 28 kg ha^{-1}P	Fertilization: at planting, 561 kg ha-1 of 10–10–10 fertilizer (56 kg ha^{-1}N); spring 3rd growing season, 673 kg ha^{-1} 10–10–10 + micronutrients + 131 kg ha^{-1}NH_4NO_3; spring 4th growing season, 131 kg ha^{-1}NH_4NO_3; spring 6th growing season, 336 kg ha^{-1}NH_4NO_3; spring 8th, 10th, 12th, 14th, 16th, 18th, 20th growing seasons, 224 kg ha^{-1}N + 28 kg ha^{-1}P	Fertilization: at planting, 561 kg ha^{-1} of 10–10–10 fertilizer (56 kg ha^{-1}N); before 8th, 12th, 16th, 20th growing seasons, 224 kg ha^{-1}N + 28 kg ha^{-1}P	Fertilization: at planting, 561 kg ha^{-1} of 10–10–10 fertilizer (56 kg ha^{-1}N); spring 3rd growing season, 673 kg ha^{-1} 10–10–10 + micronutrients + 131 kg ha^{-1}NH_4NO_3; spring 4th growing season, 131 kg ha-1NH_4NO_3; spring 6th growing season, 336 kg ha^{-1}NH_4NO_3; spring 8th, 10th, 12th, 14th , 16th, 18th, 20th growing seasons, 224 kg ha^{-1}N + 28 kg ha^{-1}P

tree was measured. After the fourth growing season, total height (*HT*) and height to live crown (*Hc*) were measured on every other tree. The live crown length (*CL*) is calculated as $CL = HT - Hc$, and live crown ratio (*CR*) is defined as the ratio of live crown length to tree height: $CR = CL/HT$. Stand average *CL* and *CR* were calculated based on the height measured trees. Total height of trees not measured for height was estimated from the model $\ln(HT) = b_0 + b_1 DBH^{-1}$ fitted separately for height measured trees in each plot at each measurement age.

The average dominant height (H_D) is defined as the average height of trees with diameter (*DBH*) larger than the average DBH of the stand. The base site index (*SI*) was estimated for each installation from the operational plot planted at 1483 tree ha^{-1} using the dominant height at age 21 years and the PMRC proprietary site index equation for loblolly pine plantations. The expressed SI for each plot was estimated using H_D of that plot at age 21 years. At age 21, there were a total of 15 viable installations that had not been thinned in these two studies (Fig. 1). Based on the base *SI*, 5 installations were grouped into a low-quality site class (L: $SI < 24.0$ m), 4 installation grouped into an intermediate-quality site class (M: $24.0 \le SI < 28.0$ m), and 6 installation grouped into a high-quality site class (H: $SI \ge 28.0$ m).

Stem wood biomass, stem bark biomass, branch biomass, foliage biomass, and total aboveground biomass were estimated for loblolly pine trees using the biomass equations of Zhao et al. (2015) that were updated in Zhao and Kane (2016). Stand-level stem wood, bark, branch and foliage biomass, total aboveground biomass, the ratio of foliage biomass to branch biomass (*RFB*), the ratio of stem biomass (stem wood + bark) to crown biomass (branch + foliage) (*RSCB*), and foliage density (*FD*, Mg ha^{-1} m^{-1}) defined as stand foliage biomass divided by average crown length, were estimated for each plot at each measurement age.

For each plot, aboveground net primary production (*ANPP*, Mg ha^{-1} yr^{-1}) at each measurement age was estimated using the following equation:

$$ANPP_{(T_1,\Delta T)} = \frac{ANPP_{(T_1,T_2)}}{\Delta T} = \frac{M_{T_2} - M_{T_1} + D_{(T_1,\,\Delta T)}}{\Delta T} = \frac{M_{T_2} - M_{Ns\cdot T_1}}{\Delta T} + \frac{1}{2\theta}(Mf_{T_1} + Mf_{T_2}) \qquad (1)$$

where M_{T_1} and M_{T_2} are total above-ground biomass of all living trees at measurement time T_1 and T_2, respectively; ΔT is the measurement period ($T_2 - T_1$); $D_{(T_1,\,\Delta T)}$ is the cumulative total biomass of mortality in the measurement period ΔT; Mf_{T_1} and Mf_{T_2} are foliage biomass of all living trees at measurement time T_1 and T_2, respectively; θ is needle longevity; $M_{Ns\cdot T_1}$ is the biomass of all trees at measurement time T_1 that survived at measurement time T_2.

Four installations at age 12 and three installations at age 15 from the UPCD98 and three installations at age 16 from CPCD96 were selected for destructive biomass sampling. The selected installations represent the range of site productivity across the region. Four trees per plot (one below-average DBH, one average tree, and two dominant/codominant trees) on these selected installations were chosen for destructive sampling in the dormant seasons, and their crown width was measured on two axes perpendicular to one another before cutting. For each felled tree, the crown length was measured, and the crown was divided into three equal length sections. The resultant dataset of the sampled trees included DBH, total tree height, taper measurements, green mass of cut bolts, green mass of branch with foliage in each crown section, green mass of disk, subsampled branch with foliage from each crown section, and dry masses of disk wood and bark, dry masses

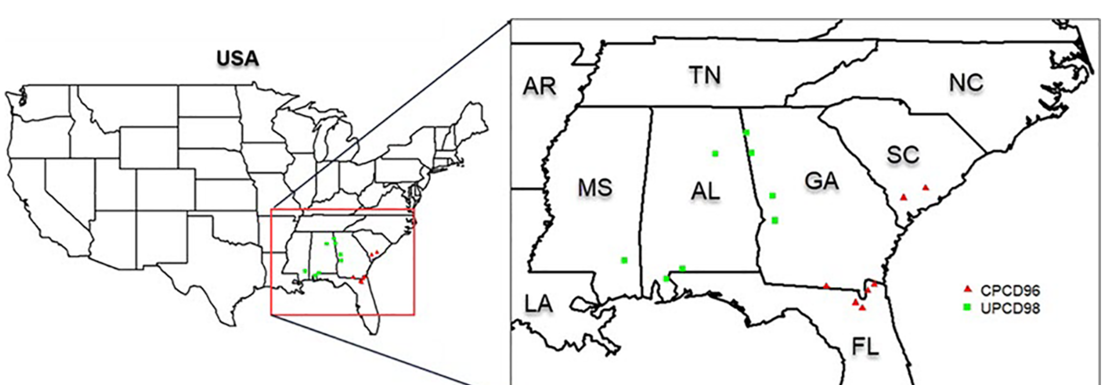

Fig. 1. Locations of 15 non-thinned installations at age 21 from two loblolly pine culture-by- density studies (CPCD96 and UPCD98).

of branch and foliage by crown section. The biomass sampling including field and laboratory measurements followed the protocols of Zhao et al. (2015). Proportions of foliage biomass in the lower-, middle- and upper-third crown sections were calculated as the ratio of crown-section foliage to total foliage biomass. Proportions of crown (branch and foliage) biomass allocated to the lower-, middle and upper-third crown sections were calculated in the same way.

2.3. Statistical analysis

For the analysis, we set five dummy variables to identify the six levels of planting density (PLTPH):

$$d_1 = \begin{cases} 1 & \text{PLTPH=1483} \\ 0 & \text{Other} \end{cases},\ d_2 = \begin{cases} 1 & \text{PLTPH=2224} \\ 0 & \text{Other} \end{cases},\ d_3 = \begin{cases} 1 & \text{PLTPH=2965} \\ 0 & \text{Other} \end{cases},$$
$$d_4 = \begin{cases} 1 & \text{PLTPH=3706} \\ 0 & \text{Other} \end{cases},\ \text{and}\ d_5 = \begin{cases} 1 & \text{PLTPH=4448} \\ 0 & \text{Other} \end{cases}.$$

Set one dummy variable to identify two levels of cultural intensity (M):

$$M = \begin{cases} 1 & \text{Intensive} \\ 0 & \text{Operational} \end{cases}$$

Set two dummy variables for three site classes (SI):

$$SI_1 = \begin{cases} 1 & \text{High-quality (H) sites} \\ 0 & \text{Other} \end{cases},\ \text{and}\ SI_2 = \begin{cases} 1 & \text{Mid-quality (M) sites} \\ 0 & \text{Other} \end{cases}.$$

And set two dummy variables for tree dominance in stands (S):

$$S_1 = \begin{cases} 1 & \text{Dominant/co-dominant trees} \\ 0 & \text{Others} \end{cases},\ \text{and}\ S_2 = \begin{cases} 1 & \text{Average trees} \\ 0 & \text{Others} \end{cases}.$$

Stand average height, average crown length, average crown ratio, foliage biomass, foliage density, foliage to branch biomass ratio, stem to crown biomass ratio, and ANPP were analyzed with a repeated-measures analysis of variance approach to evaluate effects of planting density, cultural intensity and site quality.

Based on the repeated measures from age 4–21 years, an analysis of covariance (ANCOVA) with a mixed-effects modeling approach was conducted for the relationship between ANPP and stand foliage biomass (FB) and the relationship between ANPP and foliage density (FD), respectively. Stand foliage biomass or density was the covariate; planting density, cultural intensity, site quality class, age and their interactions were treated as fixed effects; all factors containing installation were considered random effects.

Stand ANPP-FB and ANPP-FD relationships after age 15 years were further analyzed with a multiple regression model:

$$ANPP = \left(\alpha_0 + \sum_{i=1}^{5} \alpha_{0i} d_i + \alpha_{06} SI_1 + \alpha_{07} SI_2 + \alpha_{08} M\right) + \left(\beta_0 + \sum_{i=1}^{5} \beta_{0i} d_i + \beta_{06} SI_1 + \beta_{07} SI_2 + \beta_{08} M\right) FB \text{ (or } FD) \tag{2}$$

where d_i ($i = 1, 2, \ldots, 5$) are dummy variables for planting densities, SI_j ($j = 1, 2$) are dummy variables for site class, M is a dummy variable for cultural intensity, α and β are parameters to be estimated.

With data from destructively sampled trees, the relationship between tree crown width (CW) and tree crown length (CL) was explored using the following multiple regression model:

$$CW = \left(\alpha_0 + \sum_{i=1}^{5} \alpha_{0i} d_i + \alpha_{06} S_1 + \alpha_{07} S_2\right) + \left(\beta_0 + \sum_{i=1}^{5} \beta_{0i} d_i + \beta_{06} S_1 + \beta_{07} S_2\right) CL \tag{3}$$

where d_i ($i = 1, 2, \ldots, 5$) are dummy variables for planting densities; S_j ($j = 1, 2$) are dummy variables for tree dominance; α and β are parameters to be estimated.

Foliage biomass proportions and crown biomass proportions in the lower-third, mid-third, and upper-third potions of the crown were modeled, respectively, using the Dirichlet regression method (DRM). Assuming the foliage or crown biomass proportions $\mathbf{p} = (p_1, p_2, p_3)'$ follow the Dirichlet distribution with parameters $\alpha_1, \alpha_2, \alpha_3 > 0$:

$$\text{Dir}(3, \alpha) = f(\mathbf{p}|\alpha) = \frac{\Gamma(\alpha_1 + \alpha_2 + \alpha_3)}{\Gamma(\alpha_1)\Gamma(\alpha_2)\Gamma(\alpha_3)} p_1^{\alpha_1 - 1} p_2^{\alpha_2 - 1} p_3^{\alpha_3 - 1}. \tag{4}$$

The log link functions for the shape parameter (α) of each third portion can be related to tree size (DBH, HT), cultural intensity, planting density, and tree dominance in a stand as

$$\log(\alpha_m) = g_m(\mathbf{X}_m, \beta_m)\ (m = 1, 2, 3). \tag{5}$$

The maximum likelihood estimates of β parameters are obtained with the full log-likelihood of the Dirichlet distribution:

$$l(\mathbf{p}|\alpha) = \log\Gamma\left(\sum_{m=1}^{3} \alpha_m\right) - \sum_{m=1}^{3} \log\Gamma(\alpha_m) + \sum_{m=1}^{3} (\alpha_m - 1)\log(p_m). \tag{6}$$

Then $\hat{\alpha}_m = \exp\{g_m(\mathbf{X}_m, \hat{\beta}_m)\}$, and $\hat{p}_m = \hat{\alpha}_m/\hat{\alpha}_0$, where $\hat{\alpha}_0 = \hat{\alpha}_1 + \hat{\alpha}_2 + \hat{\alpha}_3$.

The following log link function was used for foliage biomass or crown biomass proportions:

$$\log(\alpha_m) = \left(\beta_{00m} + \sum_{i=1} \beta_{0im} d_i + \beta_{06m} S_1 + \beta_{07m} S_2 + \beta_{08m} M\right) + \left(\beta_{10m} + \sum_{i=1} \beta_{1im} d_i + \beta_{16m} S_1 + \beta_{17m} S_2 + \beta_{18m} M\right) \log(DBH) + \left(\beta_{20m} + \sum_{i=1} \beta_{2im} d_i + \beta_{26m} S_1 + \beta_{27m} S_2 + \beta_{28m} M\right) \log(HT)\ (m = 1, 2, 3) \tag{7}$$

where d_i ($i = 1, 2, \ldots, 5$) are dummy variables for planting densities, S_1 and S_2 are dummy variables for tree dominance, and M is a dummy variable for cultural intensity. The parameters whose estimates were not statistically significantly different from zero ($p > 0.05$) were excluded from the models.

3. Results

3.1. Stand average tree height, average crown length (CL) and crown ratio (CR)

More intensive silvicultural treatments generally increased average height and stands on higher quality sites had larger average height (Fig. 2). At early ages (< 8 years), planting density did not significantly affect stand average height. After age 10 years, stand average height decreased with increasing planting density. Operationally managed stands or stands on low-quality sites had a greater response to planting density.

The more intensive cultural treatment increased average CL and stands planted at the lower density or on higher quality sites had significantly longer CL (Fig. 3). Both cultural intensity and site quality did not affect average CR (Fig. 4). Planting density significantly affected average CR, the CR declined over time and the rate of decrease increased with increasing initial density.

3.2. Foliage to branch biomass ratio (RFB) and stem to crown biomass ratio (RSCB)

There was no significant effect of cultural intensity or planting density on RFB, but site quality significantly affected RFB (Fig. 5). Stands on higher quality sites had smaller RFB. RSCB was significantly affected by site quality and planting density, but not by cultural intensity (Fig. 6). Stands planted at higher densities or stands on higher quality sites had greater RSCB. RFB declined and RSCB increased significantly with increasing stand age, suggesting stands allocated more

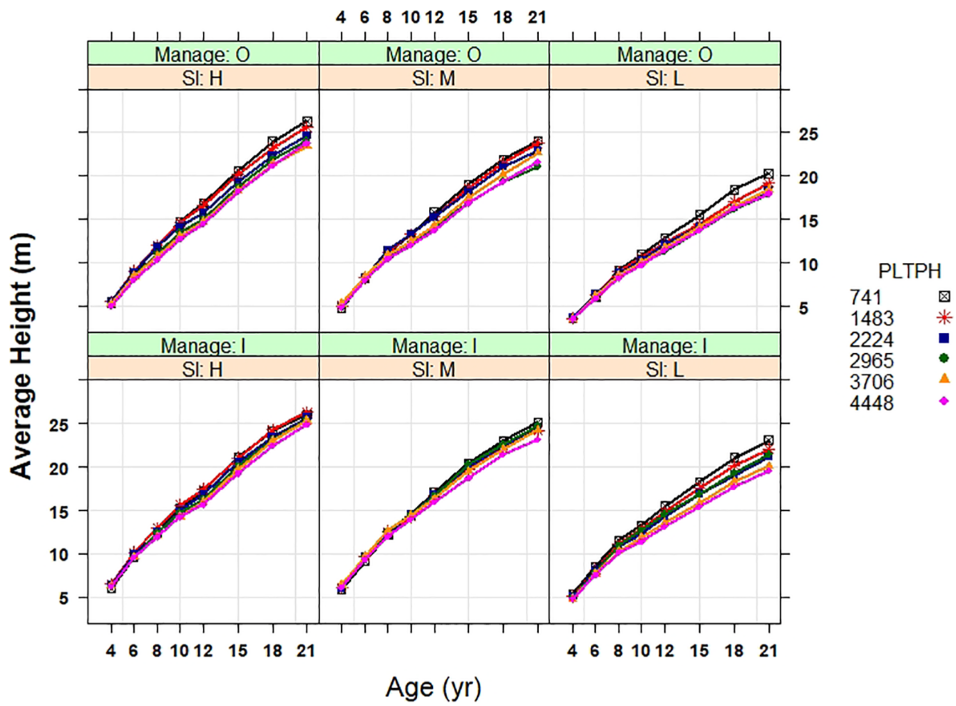

Fig. 2. Stand average height by planting density (PLTPH), cultural intensity (O: operational; I: intensive), and site class (H: high-quality; M: mid-quality; L: low-quality).

aboveground biomass to wood (stem plus branch) as stands age.

3.3. Stand foliage biomass (FB) and foliage density (FD)

Planting density significantly affected stand FB at early ages, then at later ages this effect was not significant in operational stands or stands on low-quality sites. The general temporal patterns of stand FB were mainly determined by cultural intensity and site quality (Fig. 7). Given planting density and cultural intensity, stands on higher-quality sites had more foliage biomass at early ages (< 6 years). More intensive culture stands or stands on high quality sites reached smaller maximum FB earlier and then flattened. The intensively managed stands on high-quality sites had higher level of foliage biomass at very early ages, increased to a smaller maximum FB quickly, then decreased to over a period, then maintained a constant level. However, foliage biomass in the operational stands on low-quality sites increased from lower levels

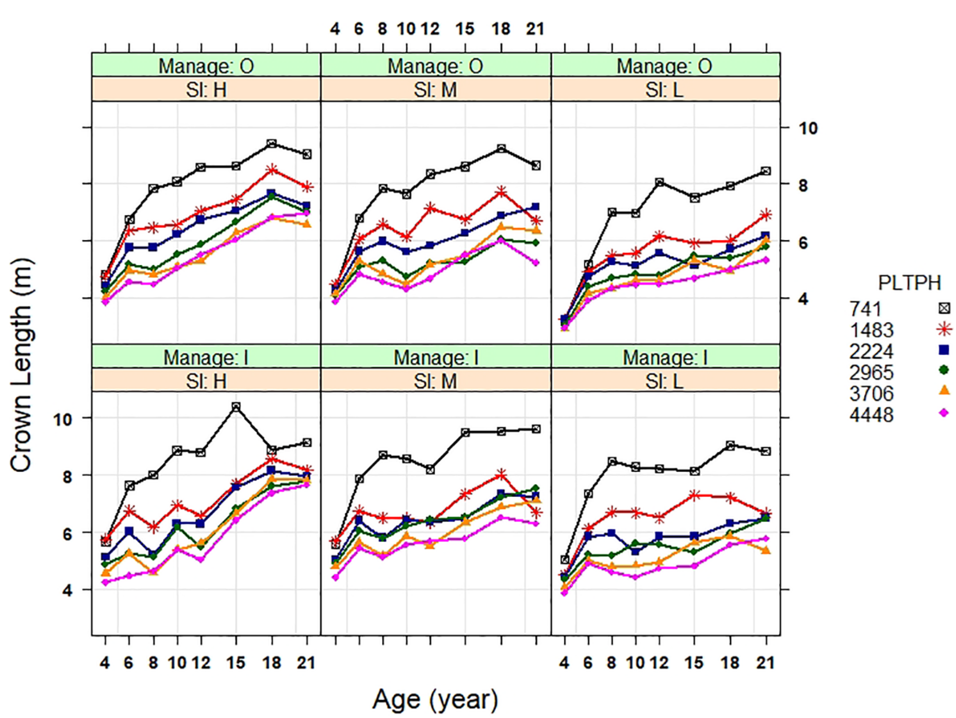

Fig. 3. Stand average crown length by planting density (PLTPH), cultural intensity (O: operational; I: intensive), and site class (H: high-quality; M: mid-quality; L: low-quality).

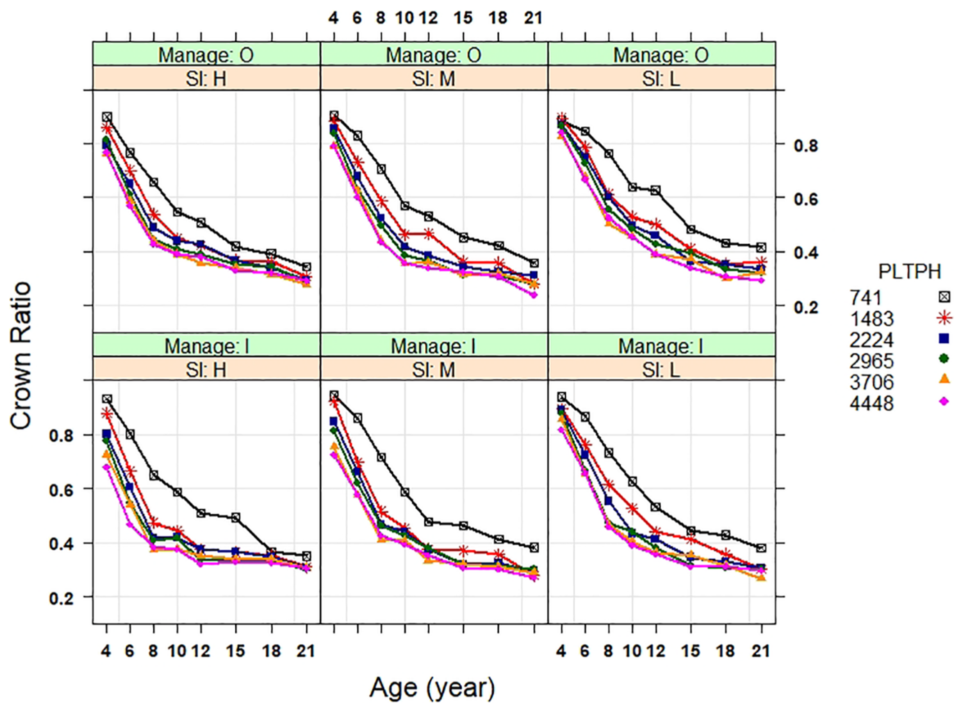

Fig. 4. Stand average crown ratio by planting density (PLTPH), cultural intensity (O: operational; I: intensive), and site class (H: high-quality; M: mid-quality; L: low-quality).

in early ages to higher maximum levels and then maintained FB. After age 12, there were no significant effects of cultural intensity or site quality on stand FB, while planting density effect on FB was significant but with no consistent trend.

Planting density significantly affected FD in early stages of stand development, but this effect was no longer significant after 15 years on high and mid-quality sites (Fig. 8). More intensive stands or stands on high-quality sites achieved a maximum foliage density (FD) at earlier ages, then decreased and then flattened to a lower FD. After age 12, there was significant differences in FD between low- and high-quality sites and among some planting densities, and no significant effect of cultural intensity on FD.

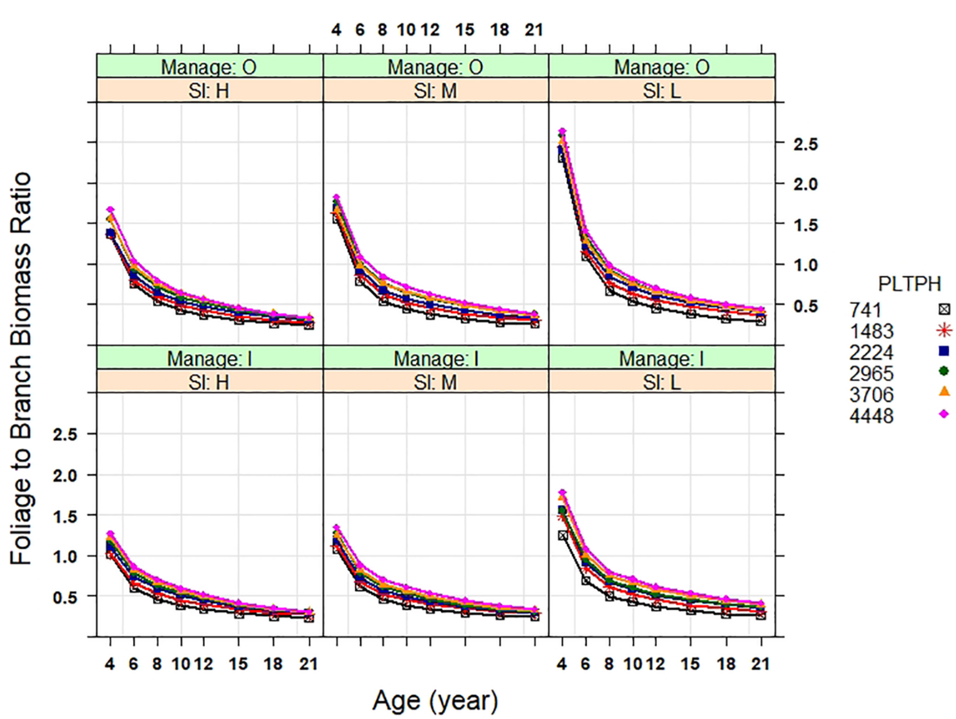

Fig. 5. The ratio of foliage to living-branch biomass by cultural intensity (O: operational; I: intensive), planting density (PLTPH), and site class (H: high-quality; M: mid-quality; L: low-quality).

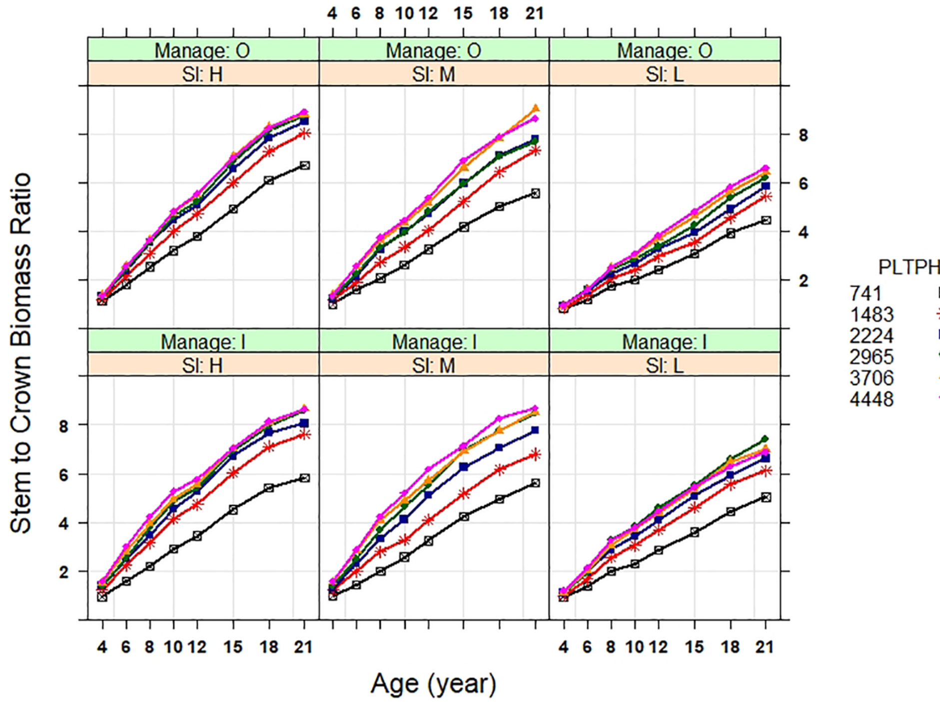

Fig. 6. Stem to crown biomass ratio affected by age, cultural intensity (O: operational; I: intensive), planting density (PLTPH), and site class (H: high-quality; M: mid-quality; L: low-quality).

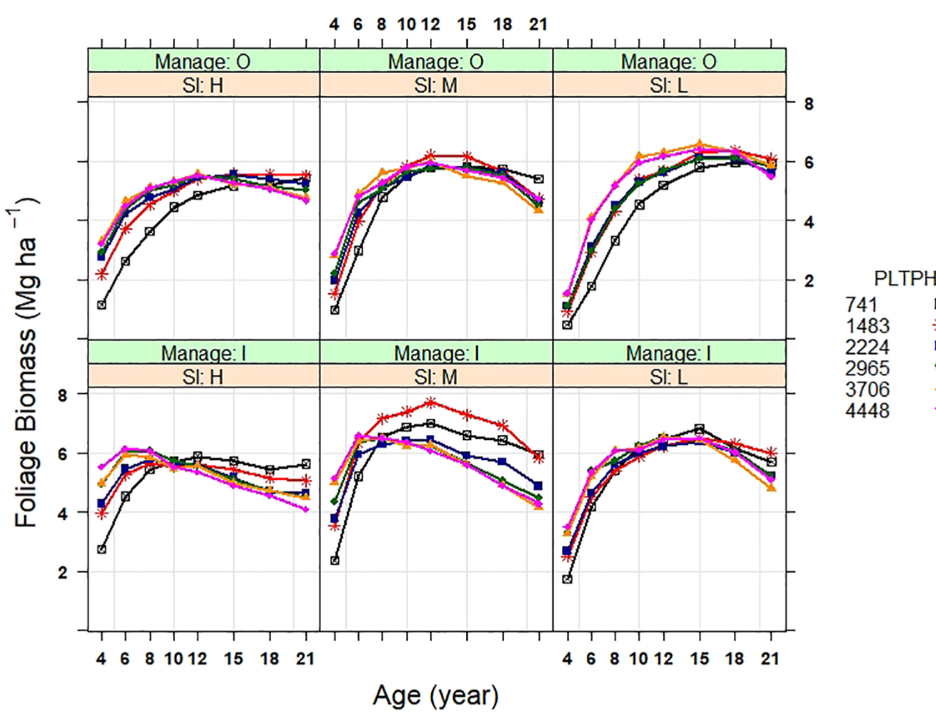

Fig. 7. Stand foliage biomass by planting density (PLTPH), cultural intensity (O: operational; I: intensive), and site class (H: high-quality; M: mid-quality; L: low-quality).

3.4. Stand aboveground net primary production (ANPP) and its relationships with FB and FD

In general, ANPP in operational stands increased over age 4–18 years, thereafter decreased (Fig. 9). ANPP in intensively managed stands flattened before age 12 years on high-quality sites, while it increased until age 12 then decreased on low-quality sites. After age 12, the effect of cultural intensity on ANPP was no longer significant, and significant differences in ANPP were found only between high-quality level and other quality levels of sites and among some planting densities. In general, ANPP increased with increasing site quality, but the trend of increasing ANPP with increased planting density observed at early stages of stand development did not hold true anymore.

The ANCOVA was conducted for ANPP using a mixed-effects model approach, in which planting density, cultural intensity, site quality class, foliage biomass (or foliage density), age and some interactions

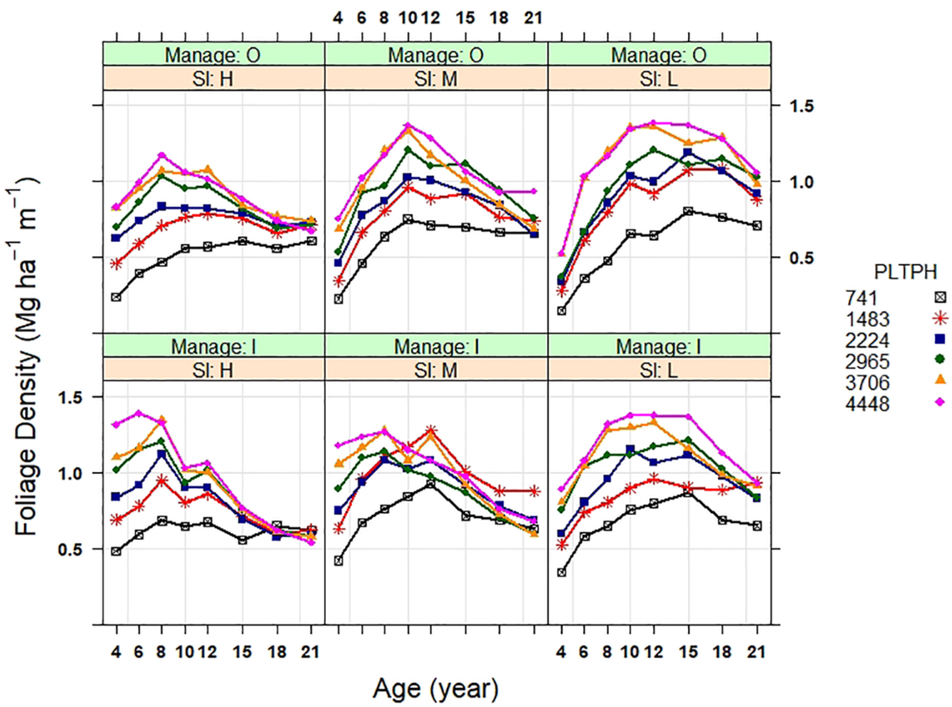

Fig. 8. Stand foliage density by planting density (PLTPH), cultural intensity (O: operational; I: intensive), and site class (H: high-quality; M: mid-quality; L: low-quality).

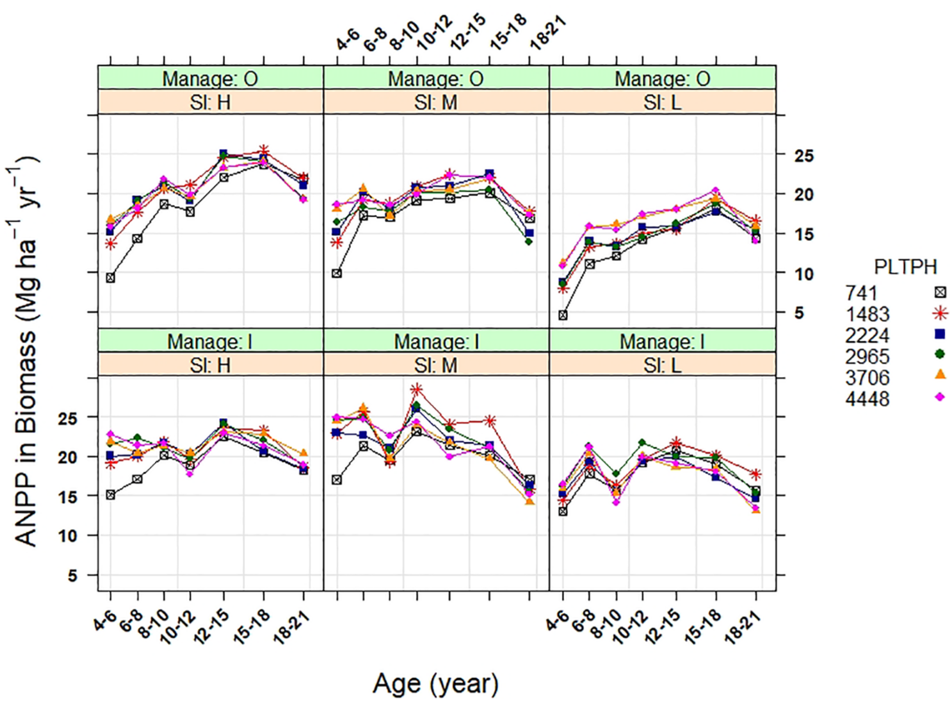

Fig. 9. Temporal patterns of stand aboveground net primary production (ANNP) affected by cultural intensity (O: operational; I: intensive), planting density (PLTPH), and site class (H: high-quality; M: mid-quality; L: low-quality).

were treated as fixed effects. The results of ANCOVA (Table S1) indicated that planting density, site quality and age significantly affected the relationship between ANPP and FB, but cultural intensity did not. However, all cultural intensity, planting density, site quality and age significantly affected the relationship between ANPP and FD. Regardless of initial density, cultural intensity and site quality, further analysis between ANPP and FB suggested a very strong relationship before age 8 years, moderately strong relationship over age 8–15 years, and very weak linear relationship after age 15 years (Fig. S1). The ANPP and FD relationship was moderately strong before age 8 years, weak over ages 8–12 years, and very weak or nonexistent after 12 years (Fig. S2).

For stand ANPP-FB and ANPP-FD relationships after age 15 years, parameter estimates for model (2) are given in Table 2. Variables whose associated parameter estimates were not statistically significant were excluded from the model. The ANPP-FB relationship after age 15 years

Table 2
The estimated parameters, standard errors, and p-values for aboveground net primary production (ANPP) and foliage biomass (FB) or foliage density (FD) regression model (2) including dummy variables for planting density (d_i) and site quality (SI_i).

Variable	Parameter estimate	Standard error	p-value	R^2
Relationship between ANPP and foliage biomass (FB)				
Intercept	2.6280	1.3360	0.0500	0.4138
SI_2	2.8781	0.5173	$<$ 0.0001	
FB	2.2981	0.2102	$<$ 0.0001	
$SI_1 \times$ FB	1.3177	0.0953	$<$ 0.0001	
Relationship between ANPP and foliage density (FD)				
Intercept	10.0794	1.0023	$<$ 0.0001	0.3366
FD	8.3609	1.1388	$<$ 0.0001	
$(d_2 + d_3 + d_4) \times$ FD	−2.4883	0.5787	$<$ 0.0001	
$d_5 \times$ FD	−3.1241	0.7139	$<$ 0.0001	
$SI_1 \times$ FD	9.6927	0.7652	$<$ 0.0001	
$SI_2 \times$ FD	3.5246	0.6005	$<$ 0.0001	

was significantly affected by site quality, but not by culture or planting density (Fig. 10 and Table 2). The ANPP-FB relationship after age 15 years is described by:

$$ANPP = 2.628 + 2.878SI_2 + (2.298 + 1.318SI_1)FB. \quad (8)$$

The ANPP-FD relationship after age 15 years was significantly affected by site quality and planting density, but not by culture (Fig. 11 and Table 2). The relationship was expressed as:

$$ANPP = 10.079 + [8.361 + 9.693SI_1 + 3.525SI_2 - 2.488(d_2 + d_3 + d_4) - 3.124d_5]FD. \quad (9)$$

3.5. Individual tree CW-CL relationship

Using data from destructively sampled trees, tree crown width (CW) was regressed over tree crown length (CL), stand planting density, and tree dominance in the stand. The individual tree CW-CL relationship was significantly affected by planting density and tree dominance (Fig. 12 and Table 3). This relationship was described by the following model (10):

$$CW = 1.347 + 0.928d_1 + [0.297 - 0.219d_1 - 0.132d_2 - 0.163(d_3 + d_4) - 0.199d_5 + 0.117S_1 + 0.049S_2]CL \quad (10)$$

All dummy variables for planting densities (d_1, ...,d_5) had significant and negative estimates of the slope, suggesting crown narrowing with increasing planting density. Dominant/codominant trees had relatively wider crowns than average trees, and the latter had little wider crowns than below-average trees (Fig. 12).

3.6. Tree foliage biomass or crown biomass allocation among crown sections

The proportions of individual tree foliage biomass allocated in the lower-, middle- and upper-third sections of the crown were fitted to the DRM. Both DBH and HT were significantly related to α_1 and α_2, and DBH was significantly related to α_3. Cultural intensity (i.e., dummy variable M) was significantly related to α_1 and α_3 through DBH, and one dummy variable for tree dominance (S_1) was significantly related to α_2 through HT (Table 4). Foliage biomass allocation among the lower-, middle- and upper-third crown sections were estimated by the following models (11):

$$\begin{aligned} \hat{\alpha}_1 &= 9.5554DBH^{1.2171-0.0626M}HT^{-1.5196} \\ \hat{\alpha}_2 &= 28.4344DBH^{0.7821}HT^{-1.2781+0.0596S_1} \\ \hat{\alpha}_3 &= 3.4301DBH^{0.0382M} \\ \hat{\alpha}_0 &= \hat{\alpha}_1 + \hat{\alpha}_2 + \hat{\alpha}_3 \\ \hat{p}_{Lf} &= \hat{\alpha}_1/\hat{\alpha}_0 \\ \hat{p}_{Mf} &= \hat{\alpha}_2/\hat{\alpha}_0 \\ \hat{p}_{Uf} &= \hat{\alpha}_3/\hat{\alpha}_0 \end{aligned} \quad (11)$$

Trees allocated more foliage biomass in the middle-third section than in the lower- or upper-third crown sections (Fig. 13). The proportion of foliage biomass in the middle-third section was relatively stable (about 50%). The proportion of foliage biomass in the lower-third section increased and the proportion of foliage biomass in the upper-third section decreased with increasing tree size. In general,

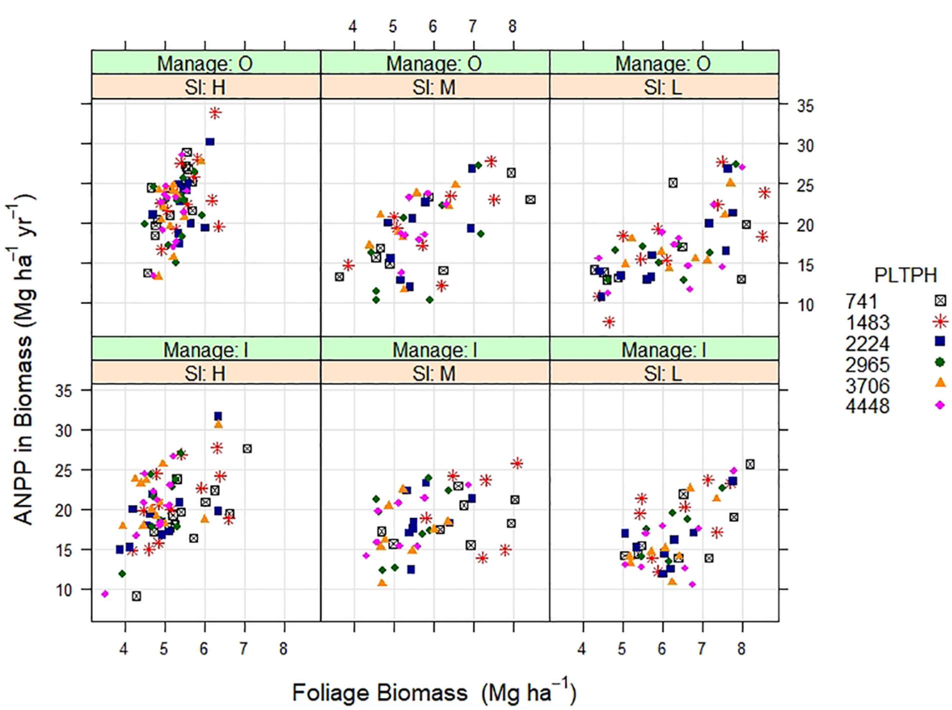

Fig. 10. Relationship between stand aboveground net primary production (ANPP) and foliage biomass when stand age ≥ 15 years by planting density (PLTPH), cultural intensity (O: operational; I: intensive) and site quality class (H: high-quality; M: mid-quality; L: low-quality).

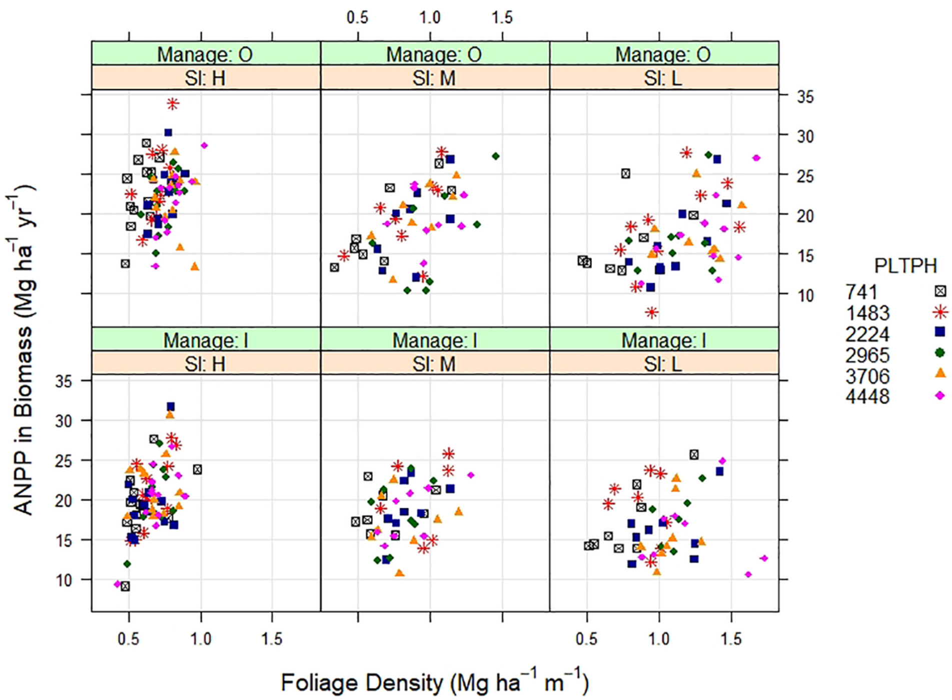

Fig. 11. The relationship between stand aboveground net primary production (ANPP) and foliage density when stand age ≥ 15 years by planting density (PLTPH), cultural intensity (O: operational; I: intensive) and site quality class (H: high-quality; M: mid-quality; L: low-quality).

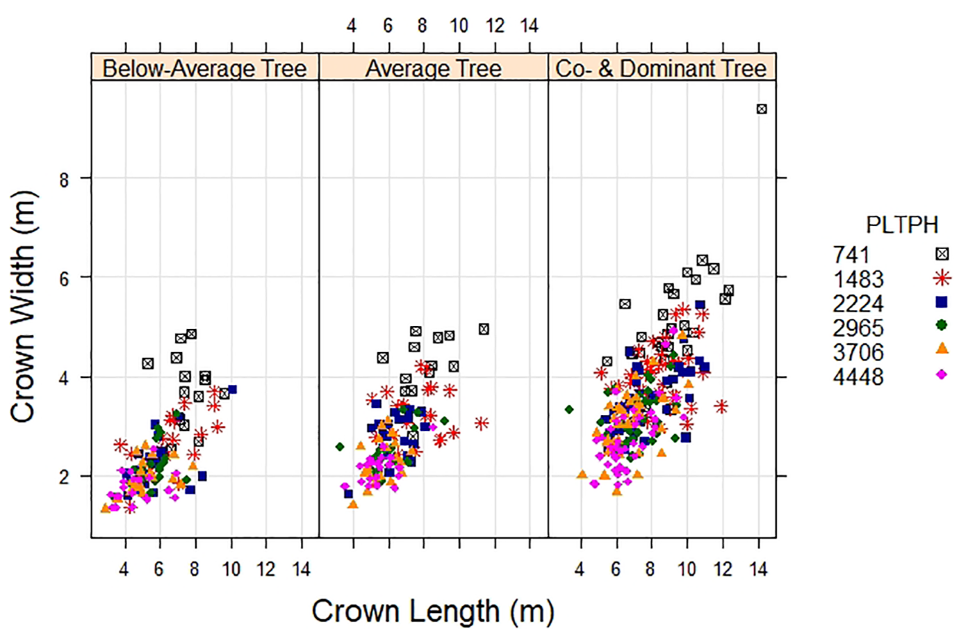

Fig. 12. Relationship between tree crown width and crown length affected by planting density (PLTPH) and tree position in terms of dominance.

more foliage biomass was allocated in the lower-third section than in the upper-third section.

Besides DBH and HT, both dummy variables for tree dominance (S_1 and S_2) were significantly related to all crown biomass allocation parameters (Table 4). However, the dummy variable for cultural intensity was not significant in any crown biomass allocation parameter. The proportion of crown biomass allocated in the lower-, middle- and upper-third crown sections were estimated by the following models (12):

$$\hat{\alpha}_1 = 20.5837 \times 34.4669^{S_2} DBH^{1.3137-1.4239S_1-1.3009S_2} HT^{1.5431+1.5133S_1}$$
$$\hat{\alpha}_2 = 33.8656 \times 18.0041^{S_2} DBH^{0.7432-1.1685S_1-1.0528S_2} HT^{1.1685+1.2109S_1}$$
$$\hat{\alpha}_3 = 3.6441 \times 11.4799^{S_2} DBH^{-0.8958S_1-0.8878S_2} HT^{0.9618S_1}$$
$$\hat{\alpha}_0 = \hat{\alpha}_1 + \hat{\alpha}_2 + \hat{\alpha}_3$$
$$\hat{p}_{Lc} = \hat{\alpha}_1/\hat{\alpha}_0$$
$$\hat{p}_{Mc} = \hat{\alpha}_2/\hat{\alpha}_0$$
$$\hat{p}_{Uc} = \hat{\alpha}_3/\hat{\alpha}_0 \quad (12)$$

The proportion of crown biomass in the upper-third crown section was relatively stable (< 20%) (Fig. 14). The highest proportion of crown biomass allocated in the lower-third section.

Table 3
The estimated parameters, standard errors and p-values for the crown width (CW) and crown length (CL) regression model (3) including dummy variables for planting density (d_i) and tree dominance (S_i).

Variable	Parameter estimate	Standard error	p-value	R^2
Intercept	1.3466	0.1377	< 0.0001	0.7883
d_1	0.9284	0.3031	0.0023	
CL	0.2968	0.0215	< 0.0001	
$d_1 \times$ CL	−0.2190	0.0383	< 0.0001	
$d_2 \times$ CL	−0.1316	0.0121	< 0.0001	
$(d_3 + d_4) \times$ CL	−0.1631	0.0117	< 0.0001	
$d_5 \times$ CL	−0.1987	0.0143	< 0.0001	
$S_1 \times$ CL	0.1165	0.0105	< 0.0001	
$S_2 \times$ CL	0.0493	0.0113	< 0.0001	

Table 4
Parameter estimates, standard errors (SE) and p-values for foliage and crown biomass allocation among three crown portions fitted to the Dirichlet regression model.

Component	Parameter	Estimate	SE	*p* value
Foliage biomass allocation among lower-, middle- and upper-third crown portions				
Lower: $\log(\alpha_1)$	Intercept	2.2571	0.4829	< 0.0001
	log(DBH)	1.2171	0.1389	< 0.0001
	log(HT)	−1.5196	0.2139	< 0.0001
	M × log(DBH)	−0.0626	0.0185	0.0007
Middle: $\log(\alpha_2)$	Intercept	3.3476	0.4514	< 0.0001
	log(DBH)	0.7821	0.1428	< 0.0001
	log(HT)	−1.2781	0.1823	< 0.0001
	S_1 × log(HT)	0.0596	0.0196	0.0024
Upper: $\log(\alpha_3)$	Intercept	1.2326	0.0554	< 0.0001
	M × log(DBH)	0.0382	0.0193	0.0476
Crown biomass allocation among lower-, middle- and upper-third crown portions				
Lower: $\log(\alpha_1)$	Intercept	3.0245	0.4648	< 0.0001
	S_2	3.5400	1.3263	0.0076
	log(DBH)	1.3137	0.2311	< 0.0001
	log(HT)	−1.5431	0.2301	< 0.0001
	S_1 × log(DBH)	−1.4239	0.4643	< 0.0001
	S_2 × log(DBH)	−1.3009	0.4829	0.0071
	S_1 × log(HT)	1.5133	0.4804	0.0016
Middle: $\log(\alpha_2)$	Intercept	3.5224	0.4760	< 0.0001
	S_2	2.8906	1.3528	0.0326
	log(DBH)	0.7432	0.2247	0.0009
	log(HT)	−1.1685	0.2209	< 0.0001
	S_1 × log(DBH)	−1.0770	0.4569	0.0184
	S_2 × log(DBH)	−1.0528	0.4922	0.0324
	S_1 × log(HT)	1.2109	0.4742	0.0107
Upper: $\log(\alpha_3)$	Intercept	1.2931	0.0954	< 0.0001
	S_2	2.4406	1.1841	0.0393
	S_1 × log(DBH)	−0.8958	0.3805	0.0186
	S_2 × log(DBH)	−0.8876	0.4264	0.0374
	S_1 × log(HT)	0.9618	0.4017	0.0167

4. Discussion and conclusions

4.1. Stand average height, crown length and crown ratio

In applying the site index concept, one typically assumes that height development is not affected by stand density. Our results showed that planting density significantly affected average height after age 10 years, with a general trend of height decreasing with increasing initial density. The wide range of planting density (741–4448 trees ha^{-1}) in the study makes possible detecting this effect. While the significant difference in average height came from the extremely low density (741 trees ha^{-1}) and very high planting densities (> 3700 trees ha^{-1}), there was no significant difference among the commonly used planting densities (1480–2224 trees ha^{-1}). A strong, highly significant negative correlation between average or dominant height and initial planting densities for loblolly pine stands has been reported by MacFariane et al. (2000) and Antón-Fernández et al. (2011). We also found that average height increased with increasing cultural intensity. The magnitude of height responses to cultural intensity and planting density varied with site quality, more response on the low-quality sites than on the high-quality sites (Fig. 2). As a result, the plots receiving more intensive treatment had a somewhat higher expressed SI than its counterpart plot with operational treatments and the SI response to more intensive treatments decreased with increasing the base SI (Fig. S3; Zhao et al., 2016). Given intensive or operational treatment, SI response (i.e. height response) to planting density was more varied on the lower quality sites than on the higher quality sites. This finding means that plots might express different SI values even at the same location depending on the planting density and cultural treatments. The installations used in the current analysis were classified into three site groups based on the base SI (rather than the expressed SI), helping us identify the effects of cultural intensity, planting density, and site quality.

Stand average height and stand average crown length were proportionally affected by both cultural intensity and site quality. Thus, stand average crown ratio was not significantly affected by cultural intensity or site quality. When planted at higher densities, loblolly pine tended to have smaller trees with shorter and narrower crowns.

4.2. Foliage biomass, foliage density, and biomass allocations

With stand development, foliage biomass and foliage density increased to some maxima and then maintained, or fell to relative stable levels, or followed by a gradual decrease. The magnitude and timing of maxima were strongly related to planting density, cultural intensity, and site quality. Our results are consistent with the findings of earlier research that a positive relationship between stand density and stand foliage production at early stages of stand development (Dean and Baldwin, 1996; Will et al., 2005), but also confirmed that this effect diminished through time (Shelton, 1984; Vose and Allen, 1988). More intensive culture or high site quality were associated with more foliage biomass and higher foliage density at early ages. Thereafter the relationship became more complex due to strong interaction of cultural intensity or site quality stand on stand foliage biomass. Intensively managed loblolly pine on high-quality sites quickly reached a smaller maximum foliar biomass and then fell to the more sustainable level of foliage (Vose et al., 1994). Intensively managed loblolly pine on low-quality sites or operationally managed stands slowly reached a larger maximum foliage biomass and then maintained or gradually decreased from it. As a result, mid- or past mid-rotation loblolly pine stands under operational treatments or on low-quality sites might maintain more foliage biomass than under more intensive treatments or on high-quality sites. This could be explained by the difference in mortality rates. High site quality and more intensive cultural treatments that increase early growth of pine stands are usually associated with increased mortality rates with stand development.

On higher quality sites, loblolly pine stands had more foliage biomass at early ages, maintained less foliage biomass during the mid-rotation stage, and allocated more aboveground biomass to wood. More intensive treatments enhanced site quality, and thus improved site productivity (Zhao et al., 2009). Unlike the effect of site quality, however, there was not significant effect of cultural intensity on loblolly pine biomass allocation. This finding is consistent with prior research (Zhao et al., 2012) showing that a more intensive management increased stand-level aboveground biomass but did not affect aboveground biomass allocation. One reason for this is that the SI response to more intensive treatments largely depends on the base site quality, as mentioned above.

Mensah et al. (2016) reported that tree-level foliage/wood mass ratio declined significantly with increasing tree diameter. Our results demonstrated that stand-level foliage/wood mass ratio also declined with stand development. We also found that the increased planting density generally enhanced stem biomass. The effects of planting density on stand aboveground biomass accumulation and partitioning were

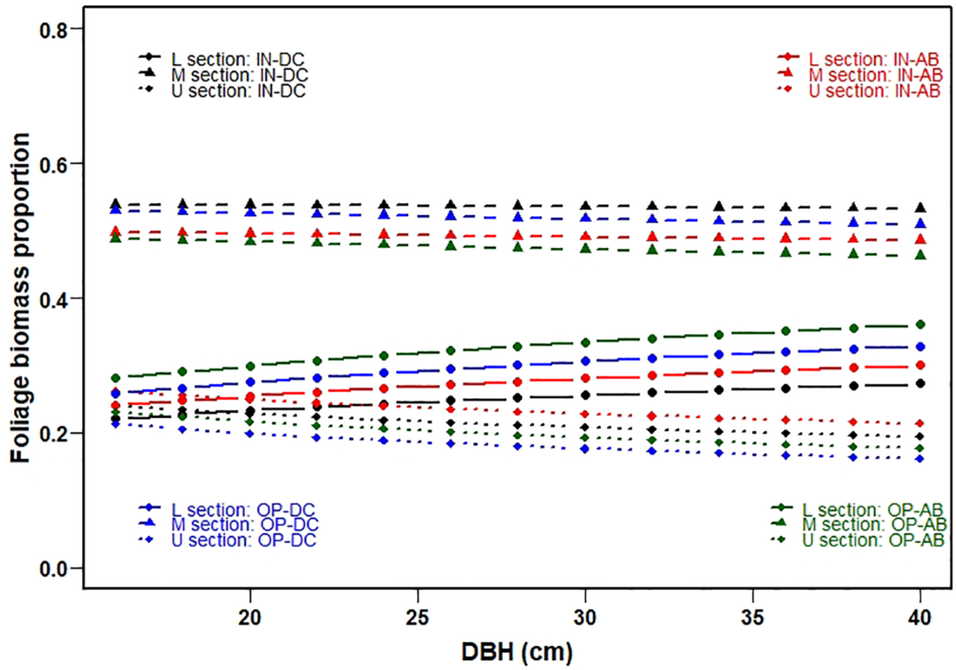

Fig. 13. Tree foliage biomass allocation among lower-, middle- and upper-third crown sections influenced by tree size, cultural intensity (OP: operational; IN: intensive) and tree position (DC: dominant/codominant trees; AB: average and below-average trees).

no longer significant among higher planting densities (≥2965 trees ha^{-1}), as found in Zhao et al. (2012).

Gillespie at al. (1994) reported that silvicultural treatments have no impact on foliage distribution for young loblolly pine trees. After correction for tree size and dominance effects in our study, we still detected a significant effect of cultural intensity on foliage biomass distribution for loblolly pine trees in later stand development. More intensive treatments increased proportions of foliage biomass in both middle- and upper-third sections of the crown, regardless of the tree dominance. This suggested that more intensive treatments resulted in an upward shift of foliage biomass. No additional effect of either planting density or cultural intensity was detected on crown biomass distribution. Xu and Harrington (1998) reported that less dominant trees shifted their foliage to the top of the crown and the vertical distribution of foliage biomass was more even for more dominant trees. Given a cultural intensity, we found that dominant/codominant trees had larger proportion of tree foliage biomass in the middle-third section and smaller proportions in both lower- and upper third sections than average/ below-average trees. This finding is inconsistent with previous observations (Maguire and Bennett, 1996; Xu and Harrington, 1998) that foliage biomass of more dominant trees tended to shift downward. Crown biomass proportion in the upper-third section was relative stable (about 15%), while dominant/codominant trees allocated more crown biomass in the middle-third section and below-average trees allocated

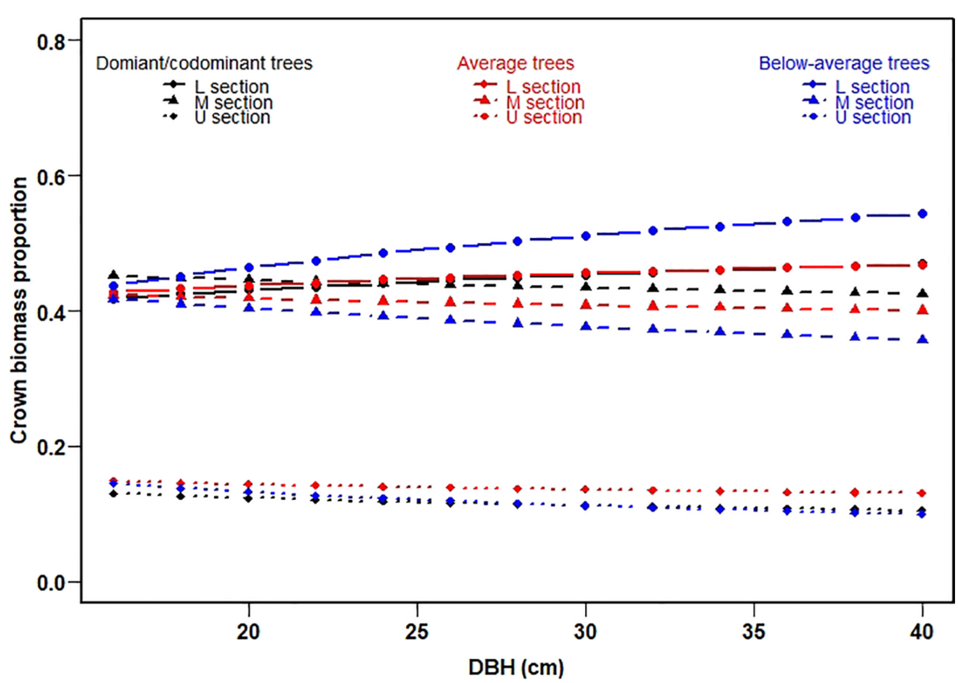

Fig. 14. Tree crown biomass allocation among lower-, middle- and upper-third crown sections influenced by tree size and tree position.

relatively more crown biomass in the lower-third section. Compared with dominant/codominant trees or average trees, below-average trees allocated higher proportion of foliage and crown biomass in the lower-third section. But foliage there would contribute little to production because of lowered photosynthetic rates (caused by an increase in self-shading) and increased branch maintenance.

4.3. Stand ANPP and growth efficiency

Intensively managed loblolly pine stands or stands on more productive sites had higher ANPP at very early ages (before 6 or 8 years) than operationally managed stands or stands on low quality sites. This is because higher foliage production was associated with more intensive culture and high site quality in earlier stage of stand development. During that period, ANPP also increased with increasing planting density because of an increased foliage biomass. In general, the ANPP of operational stands slowly reached a peak, which increased with increasing site quality, at about age 18, then declined. In intensively managed stands, ANPP rapidly reached a peak at an age before 12 years, depending on site quality, then leveled off over a longer period before slowly declining.

It should be noted that the ANPP in intensively managed stands suddenly dropped to almost the same level of corresponding operational stands in ages 10–12 on high-quality sites, or ages 8–10 on middle- and low-quality sites, then recovered. In the growing season of these intervals, most plots used in the study underwent extreme drought (PDSI ≤ -4.0). Extreme drought was associated with highly reduced ANPP in more intensive stands than operational stands, suggesting that more intensively managed loblolly pine stands are more drought sensitive. The ANPP gain due to more intensive cultures was substantially reduced by extreme drought, and then returned to normal levels the following measurement without extreme drought conditions (Zhao, unpublished, presented at IUFRO-AO 2016).

Under operational treatments, ANPP of loblolly pine stands generally reached a peak about the same time as stand foliage biomass, but this might not hold under more intensive treatments. ANPP declined sooner and more strikingly than foliage biomass, especially in the last interval (18–21 years). All these findings suggested growth efficiency (expressed as the slope of ANPP-FB linear regression) changed with the development of stands.

Without considering the influences of other factors, a strong positive relationship between ANPP and FB or FD was observed in young stands (before age 8). This is consistent with previous findings in southern pine studies (e.g., Vose and Allen, 1988; Dalla-Tea and Jokela, 1991; Albaugh et al., 1998; Barron-Gafford et al., 2003; Burkes et al., 2003; Jokela et al., 2004; Will et al., 2005). Planting density, cultural intensity and site quality significantly affected both foliage quantity and ANPP at early ages in the same direction, thus the variance for ANPP during that period could be mostly explained by stand foliage biomass only ($R^2 = 0.69$). After age 12, however, site quality did not significantly affect FB but still affected ANPP, and cultural intensity effects on both FB and ANPP were no longer significant. Planting density effect on ANPP was no longer significant, while its effect on FB was still significant but with no consistent trend. As a result, there seemed to be a weak or negligible linear relationship between ANPP and FB or FD in mid- or past mid-rotation loblolly pine stands, but ANPP still varied greatly with site quality and planting density. These results agree with the finding of Sword Sayer et al. (2004) that a static linear relationship between foliage quantity and loblolly pine productivity did not universally occur at all ages and all sites. Therefore, it is necessary to explore the ANPP-FB or ANPP-FD relationship integrating the effects of site quality, cultural intensity, and planting density. Our analysis showed site quality significantly influenced the ANPP-FB relationship after age 15. Including two site-quality dummy variables in the ANPP-FB model increased R^2 from 0.067 to 0.414, and including two site-quality dummy variables and four planting-density dummy variables in the ANPP-FD model increased R^2 from 0.000 to 0.337. An increase in the ANPP-FB and ANPP-FD slopes causes by increased site quality and a decrease in the ANPP-FD slope caused by increased planting density suggested that mid- or past mid-rotation loblolly pine stands still had higher growth efficiency on higher quality sites or when planted at lower densities. Satoo (1967) found that both stand-level foliage quantity and efficiency in *Cryptomerica japonica* Don increased with increasing site quality (Satoo, 1967). DeRose and Seymour (2009) reported that tree-level growth efficiency increased significantly increased with site quality for *Abies balsamea* but was unaffected by site quality for *Picea rubens*. The positive relationship between stand growth efficiency and site quality was supported by our results. The positive relationship between stand foliage biomass and site quality held in the early ages but did not always hold true in or past mid-rotation stages in our study. Our results also suggested that loblolly pine growth efficiency was not affected by cultural intensity and partially confirmed the finding of McDowell et al. (2007) that growth efficiency declined with increasing stand density.

Loblolly pine productivity is a function of foliage quantity (Vose and Allen, 1988; Albaugh et al., 1998; Jokela and Martin, 2000; Sword Sayer et al., 2004), the changed growth efficiency with stand development or caused by silvicultural practices or natural site variability should also be taken into consideration for describing the relationship. After age 15, for example, operationally managed loblolly pine stands on low-quality sites maintained considerably more foliage biomass but still had lower ANPP than intensively managed stands on high-quality sites, because of lower growth efficiency on low-quality sites. More intensive treatments increased foliage biomass, thus increased ANPP at early ages (i.e., before age 10), thereafter did not affect foliage biomass, ANPP, and growth efficiency. This early "push" effect, especially on higher quality sites did not guarantee higher yields, because site quality and most silvicultural treatments that increase early growth of pine stands are associated with increased mortality rates. It should be emphasized that all analyses in this study were based on data from unthinned plots. But the results suggested that it is necessary to increase foliar efficiency and foliage production through various silvicultural treatments, such as pruning lower branches, thinning from below, and thinning plus fertilizing.

Previous research on LAI or FB of loblolly pine has focused on peak growing season values derived from needlefall or branch samples (Vose and Allen, 1988; Dalla-Tea and Jokela 1991; McCrady and Jokela, 1996), or indirectly measured using canopy analyzer (Xu and Harrington, 1998; Harrington et al., 2002). In this study, the destructive sampling was conducted during dormant seasons. Thus, the estimated values of FB and FD based on the destructive sampling data were smaller than the values measured on peak growing season. This might not invalidate our conclusions, because differences in foliage quantity (e.g., FB, FD, LAI) and foliage biomass allocation due to cultural treatments and site quality should be maintained throughout the year, and not just during periods of active shoot growth (Harrington et al., 2002).

In summary, loblolly pine ANPP increased with increasing site quality. This increase was due to increased foliage biomass at early ages and thereafter due primarily to an increase in growth efficiency. More intensive treatments increased foliage biomass and thus increased ANPP at early ages. Thereafter more intensive treatments did not alter stand foliage quantity, ANPP and growth efficiency, but resulted in an upward shift of tree foliage biomass within the crown. Both foliage biomass and ANPP increased with increasing planting density at early ages, and thereafter density-induced differences in foliage biomass, ANPP, and growth efficiency were less pronounced. The relative vertical distribution of foliage biomass within the crown was not affected by planting density.

CRediT authorship contribution statement

Dehai Zhao: Conceptualization, Investigation, Methodology, Formal analysis, Writing - original draft. **Bronson P. Bullock:** Project administration, Writing - review & editing. **Cristian R. Montes:** Project administration, Writing - review & editing. **Mingliang Wang:** Data management. **James Westfall:** Funding acquisition, Writing - review & editing. **John W. Coulston:** Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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