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Crown characteristics of juvenile loblolly pine 6 years after application of thinning and fertilization

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Abstract

Total foliage dry mass and leaf area at the canopy hierarchical level of needle, shoot, branch and crown were measured in 48 trees harvested from a 14-year-old loblolly pine (*Pinus taeda* L.) plantation, six growing seasons after thinning and fertilization treatments.

In the unthinned treatment, upper crown needles were heavier and had more leaf area than lower crown needles. Branch- and crown-level leaf area of the thinned trees increased 91 and 109%, respectively, and whole-crown foliage biomass doubled. The increased crown leaf area was a result of more live branches and foliated shoots and larger branch sizes in the thinned treatment. Branch leaf area increased with increasing crown depth from the top to the mid-crown and decreased towards the base of the crown. Thinning stimulated foliage growth chiefly in the lower crown. At the same crown depth in the lower crown, branch leaf area was greater in the thinned treatment than in the unthinned treatment. Maximum leaf area per branch was located nearly 3–4 m below the top of the crown in the unthinned treatment and 4–5 m in the thinned treatment. Leaf area of the thinned-treatment trees increased 70% in the upper crown and 130% in the lower crown. Fertilization enhanced needle size and leaf area in the upper crown, but had no effect on leaf area and other variables at the shoot, branch and crown level. We conclude that the thinning-induced increase in light penetration within the canopy leads to increased branch size and crown leaf area. However, the branch and crown attributes have little response to fertilization and its interaction with thinning.
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Keywords: Branch size; Crown section; Cultural treatments; Foliage biomass; Leaf area; Vertical distribution; *Pinus taeda*

1. Introduction

Foliage biomass, leaf area expansion, and crown structure are important factors influencing tree growth and stand productivity (Brix, 1983; Vose and Allen, 1988; Shelburne et al., 1993; Dean and Baldwin, 1996). The primary productivity of a stand depends on the quantity and spatial distribution of foliage in the canopy and environmental factors for crown expansion and carbon dynamics. Foliage quantity and distribution in different hierarchical levels of canopy determine the amount of intercepted solar radiation and affect other microclimate factors such as temperature, vapor pressure deficit and wind speed in the canopy (Kellomaki and Oker-Blom, 1983; Gholz et al., 1991; Tang et al.,

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1999). Norman and Jarvis (1974) emphasized that detailed measurements of leaf area at the needle, shoot and branch level within the canopy were important in predicting light interception and photosynthetic production. Jordan and Smith (1993) reported that in coniferous stands, variation in intercepted solar radiation associated with needle geometry was responsible for variation in net photosynthetic rates.

Tree growth is related to crown leaf area, carbon gain and environment (Brix, 1981; Binkley and Reid, 1984; Teskey et al., 1987; Albaugh et al., 1998). Short-term responses in foliage growth of loblolly pine (*Pinus taeda* L.) relative to thinning or fertilization have been studied by Dalla-Tea and Jokela (1991), Albaugh et al. (1998) and Jokela and Martin (2000). Vose and Allen (1988) pointed out that leaf area index of juvenile pine trees positively responded to nitrogen fertilization, but remained unaffected by phosphorus addition 2–3 years after treatment. Gillespie et al. (1994) found that thinning or fertilization increased crown size during the first two post-treatment years. Detailed information on crown hierarchical characteristics (needle, shoot, branch and whorl) as affected by cultural treatments has also been reported for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Brix, 1981) and Scots pine (*Pinus sylvestris* L.) (Kellomaki and Oker-Blom, 1983). However, our knowledge of long-term thinning and fertilization effects on crown hierarchical characteristics of field-grown trees is rather limited. The objectives of the current paper are to (1) quantify the impacts of thinning and fertilization on needle, shoot, branch and crown characteristics of 14-year-old loblolly pine trees six growing seasons after application, and (2) identify the effects of thinning and fertilization on foliage quantity and distribution within the canopy. We hypothesized that 6 years following thinning and fertilization treatments, foliage dry weight and leaf area at each level of needle, shoot, branch and crown has increased, and that foliage distribution throughout the canopy has been altered in response to the silvicultural treatments.

2. Materials and methods

2.1. Study site

The study was conducted in a 14-year-old loblolly pine plantation located on the Palustris Experimental Forest in central Louisiana (31°07′N, 93°17′W). The soil is a Beauregard silt loam (fine-silty, siliceous, thermic, Plinthaquic Paleudults) and low in nitrogen and phosphorus. Soil drainage is moderate and slope is sufficient to prevent water from standing on the site (Haywood, 1994).

In May 1981, the 0.93 ha plantation was established by USDA Forest Service SRS-4111 for a long-term assessment on loblolly pine growth response to silvicultural practices. Fourteen-week-old seedlings were planted at 1.82 m × 1.82 m (approximately 2990 trees ha^{-1}). Twelve research plots, uniform in tree size and spacing, were established in the plantation in the fall of 1988. Each plot (0.06 ha) was 23.8 m × 23.8 m and consisted of 13 rows of 13 trees (including three rows of border trees). Two levels each of thinning and fertilization treatments were applied to the 12 plots in a 2 × 2 factorial completely random design with three replications. Each treatment replication had four combined treatment plots (thinned-fertilized, thinned-unfertilized, unthinned-fertilized and unthinned-unfertilized). In the thinned-treatment plots, 75% of the trees were removed in November 1988 by harvesting every other row of trees and every other tree in the remaining rows to leave a density of 731 trees ha^{-1}. In the fertilized treatments, diammonium phosphate at 744 kg ha^{-1} (134 kg N ha^{-1} + 150 kg P ha^{-1}) was broadcast in April 1989. The fertilizing rate was recommended for juvenile loblolly pine trees growing on the nitrogen- and phosphorus-deficient soil at the site (Shoulders and Tiarks, 1983).

2.2. Sampling and measurements

In March 1995, 48 trees (four per plot, based on the mean crown size in each plot) were harvested. The harvested trees were chosen from the interior of the plots (three and seven rows of trees in the thinned and unthinned plots, respectively). Immediately after felling, total height, diameter at breast height (DBH), live crown length, height to the base of live crown, and height to mid-crown were measured on each tree. The middle of the crown was marked to divide the entire crown into the upper and lower crown sections. Number of whorls and branches per whorl within each crown section were counted. The distance (nearest 0.01 m) from the top of the crown to individual whorls

was measured. Eight first-order branches (four from the upper and lower crown, respectively, hereafter referred to as branch) were randomly chosen on each tree and cut at the base of branch. A total of 384 sample branches were collected. The base diameter and length of each sample branch were recorded. Number of shoots (the second order or higher order branches, hereafter referred to as shoot) on the sample branch were counted and all shoots were cut, kept by branch, and placed in a cold storage room for further analyses.

Twelve sample trees (one per plot, representing the mean plot basal area) were selected from the 48 harvested trees for detailed branch and shoot and needle measurements. For each selected tree, three shoots were randomly chosen from each of the eight branches sampled earlier. Base diameter (nearest 0.01 mm) and length (nearest 0.1 cm) of the foliated shoot were measured. Total number of needles per shoot was recorded. Needle density (number of needles per cm of the foliated shoot) was calculated by dividing number of needles per shoot by foliated shoot length. Ten needle fascicles per shoot were randomly taken and needle length (nearest 0.1 cm) of each fascicle was measured. Then, all needles were removed from the sample shoot and total green weight (nearest 0.01 g) of the needles was determined. The needles were oven dried at 60 °C to a constant mass and their dry weights (nearest 0.01 g) were measured. When the measurements were completed for each of the three sample shoots per branch, needles on the remaining shoots of the branch were measured for foliage green and dry weights.

The remaining 36 harvested trees (three per plot) were used for subsampling. Needles were collected and measured for green weights by each whorl and crown section to estimate crown-level foliage dry weights. Needle green and dry weights of the branches from all 48 trees were used to estimate branch-level foliage dry weights. One hundred and twenty needle fascicles were randomly taken from each of the upper and lower crown sections and used to determine the ratio of total surface leaf area to needle dry weight. Leaf area was calculated from needle volume measured (Johnson, 1984). Total leaf area per branch and per crown section was calculated based on the relationship between leaf area and dry weight of the sample needles.

2.3. Statistical analyses

Data of the measured characteristics were evaluated by the two-way analysis of variance using a 2×2 factorial completely random design. The whole plot was thinning and fertilization treatments. Crown section was considered as the subplot. Effects of cultural treatments and crown sections were tested for statistical significance at the 0.10 probability level, because large variability was expected for the branch and crown attributes under the natural environment. Treatment means of thinning or fertilization or thinning × fertilization interaction were separated using an adjusted Tukey test (Stehman and Meledith, 1995). SAS software package (SAS Institute Inc., Cary, NC, USA) was used for all statistical analyses.

3. Results

3.1. Needle-level characteristics

Foliage dry weight (DW_{100}) and leaf area per 100 needles (LA_{100}) were significantly different with respect to crown section (Table 1). Across all treatment plots, mean DW_{100} was 4.5 and 3.2 g for the upper and lower crown, respectively. The upper crown needles had 23% more LA_{100} than the lower crown needles (531 vs. 433 cm^2). Fertilization significantly increased LA_{100} in the upper crown section (Fig. 1A). Needle length (L_N) was also greater in the upper crown than in the lower crown of the fertilized-treatment trees. Additionally, the interaction of thinning by crown section on LA_{100} was significant. In the unthinned treatment plot, the upper crown needles had more LA_{100} than the lower crown needles. In the thinned treatment, however, LA_{100} was similar between the upper and lower crown sections (Fig. 1B), indicating that leaf area of lower crown fascicles increased in response to thinning.

3.2. Shoot- and branch-level characteristics

Shoot length (L_S) and base diameter of the foliated shoot portion (D_S), and leaf area per shoot (LA_S) differed significantly between the two crown sections (Table 1). Over all treatments, LA_S, L_S and D_S were 124, 70 and 43%, respectively, greater in the upper

Table 1
Analysis of variance for the morphological characteristics measured in the upper and lower crown section (C) of 14-year-old loblolly pine trees, 6 years after thinning (T) and fertilization (F)[a]

Source	d.f.	L_N	DW_{100}	LA_{100}	L_S	D_S	LA_S	L_B	D_B	LA_B	NS_B	DW_C	LA_C	NB_C	NW_C
T	1	ns[b]	ns	ns	ns	ns	ns	*	*	*	*	*	*	*	*
F	1	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
T × F	1	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
C	1	ns	*	*	*	*	*	*	*	*	*	*	*	*	*
C × T	1	ns	ns	*	ns	ns	ns	*	*	*	*	ns	ns	ns	ns
C × F	1	*	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
C × T × F	1	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

[a] d.f.: degree of freedom; L_N: needle length; DW_{100}: dry weight per 100 needles; LA_{100}: leaf area per 100 needles; L_S: shoot length; D_S: base diameter of shoot; LA_S: leaf area per shoot; L_B: branch length; D_B: base diameter of branch; LA_B: leaf area per branch; NS_B: number of shoots per branch; DW_C: foliage biomass per crown; LA_C: leaf area per crown; NB_C: number of branches per crown; NW_C: number of whorls per crown.

[b] Not significant.

* Significant at $P = 0.10$.

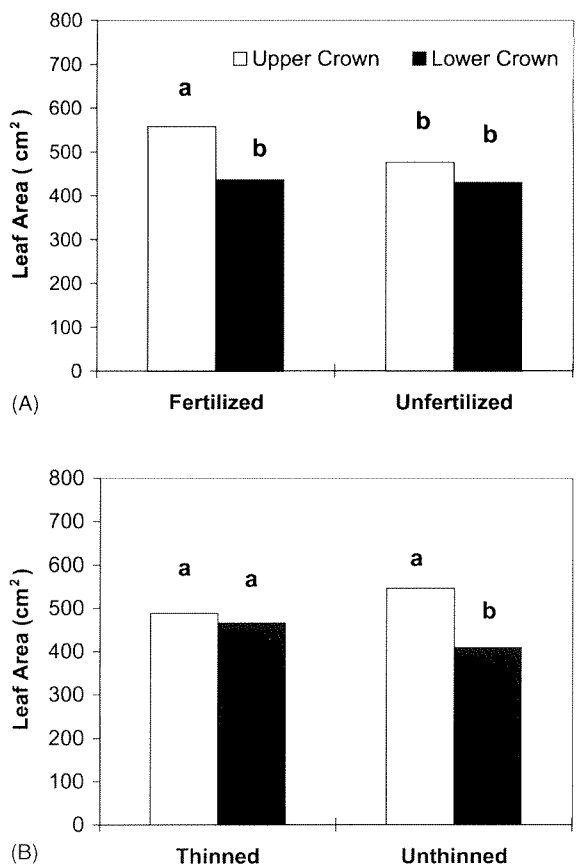

Fig. 1. Mean leaf area per 100 needles in the upper and lower crown section of 14-year-old loblolly pine trees 6 years after thinning and fertilization treatments. Bars with different letters differ significantly at $P \leq 0.10$.

crown shoot than in the lower crown shoot. The shoot variables did not exhibit any response to thinning or fertilization or their interaction.

Branch characteristics were significantly affected by thinning (Table 1). Six growing seasons after thinning, the thinned-treatment trees produced more branches (NB_C), greater branch length (L_B) and base diameter (D_B), more shoots per branch (NS_B) and total leaf area per branch (LA_B) than the trees in the unthinned treatment (Table 2). In the thinned treatment, NS_B in the lower crown section rose 140% compared with the value of the unthinned treatment (35 vs. 15), but NS_B in the upper crown was not statistically different between the thinned and unthinned treatments. Fertilization had no effect on the measured branch characteristics.

There was a significant difference in branch characteristics with respect to crown section (Table 1). NB_C, L_B and D_B were smaller in the upper crown than in the

Table 2
Mean branch length, base diameter, leaf area and number of shoots per branch of 14-year-old loblolly pine, 6 years after thinning[a]

Characteristics	Thinned treatment	Unthinned treatment
Branch length (m)	1.98 (±0.08) a	1.45 (±0.06) b
Branch base diameter (mm)	24.89 (±0.85) a	18.05 (±0.59) b
Leaf area per branch (m^2)	2.04 (±0.15) a	1.07 (±0.09) b
Number of shoots per branch	21.7 (±1.46) a	10.90 (±0.77) b

[a] Means not followed by the same letters for each variable in each row differ significantly at $P = 0.10$.

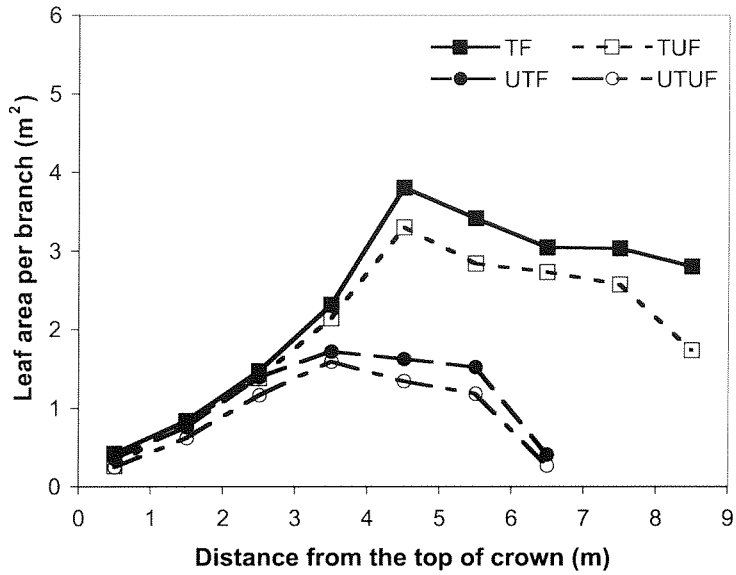

Fig. 2. Distribution of mean branch leaf area vertically within the crown of 14-year-old loblolly pine trees 6 years after thinning and fertilization treatments (TF: thinned-fertilized; TUF: thinned-unfertilized; UTF: unthinned-fertilized; UTUF: unthinned-unfertilized).

lower crown. Total leaf area per branch (LA_B) also varied with crown depth (Fig. 2). As crown depth progressed from the top to the mid-crown, LA_B increased. Below the mid-crown point, LA_B decreased towards the base of the crown. This pattern was consistent for all treatment combinations. Maximum LA_B was approximately 3–4 m below the top of the crown in the unthinned treatment and 4–5 m in the thinned treatment. There was a large difference in lower crown LA_B between the two thinning treatments. In the thinned treatment, lower crown LA_B was 2.8 m^2, compared to 1.3 m^2 in the unthinned treatment.

3.3. Crown-level characteristics

Across all treatments, the lower crown section had greater foliage dry mass (DW_C) and leaf area (LA_C) than the upper crown. Six years after thinning, foliage dry mass and total leaf area per tree of the thinned treatment was twice as much of the unthinned treatment (Table 1). The difference in total leaf area between the two treatments (82 vs. 40 m^2) resulted from a 130% increase in lower-crown leaf area in the thinned treatment (60 vs. 26 m^2).

Live crown length and ratio were significantly greater in the thinned treatment compared with the unthinned treatment (7.3 vs. 5.5 m and 50 vs. 36%, respectively) (Table 1). The thinned-treatment trees retained more branches and whorls than the unthinned-treatment trees. Number of branches and whorls per tree were 23 and 9, respectively, in the thinned treatment and 16 and 5 in the unthinned treatment. However, fertilization did not show a significant effect on crown leaf area and other crown variables. There was no two- or three-way interaction between fertilization, thinning and crown section on the measured variables.

4. Discussion

Shoot geometry, needle physiology and crown structure determine the utilization of intercepted light and photosynthetic efficiency within the canopy of conifers (Brix, 1981; Teskey et al., 1987; McCrady and Jokela, 1996; Sprugel et al., 1996). Leverenz and Hinckley (1990), investigating the productivity of 12 coniferous species, found that shoot geometry was closely correlated with maximum leaf area index and annual volume increment (R^2 = 0.84 and 0.93, respectively). We observed that large variation in shoot morphology and branch structure exists vertically

within the crown. Shoots in the upper crown section were larger and had more leaf area than lower crown shoots, but there were more live branches bearing shoots and larger branch sizes in the lower crown. As a result, the number of shoots and total leaf area in the lower crown section were 3.6 and 2.3 times, respectively, greater than the values in the upper crown section. Our findings imply that in the upper crown, the amount of intercepted light increases with increasing shoot size and leaf area, whereas in the lower crown more light is intercepted by a greater number of shoots and needles. The lower crown shoots and needles may make a large contribution to whole-crown carbon fixation and tree growth (Leverenz, 1996).

Previous studies have found that the branch retention of pine trees increases during the first 4–5 years after thinning as a result of increasing light penetration within the canopy (Ginn et al., 1991; Gillespie et al., 1994; Peterson et al., 1997). However, little information is known about how much longer the thinning effects on branch retention and crown structure last 5 years after stand density manipulation. Data from our study demonstrates that after 6 years, thinning still had a residual impact on branch and crown characteristics. The thinned-treatment trees maintained more branches and shoots, larger branch size, and leaf area per branch in the lower crown than the unthinned-treatment trees. Consequently, total leaf area per tree in the thinned treatment doubled that in the unthinned treatment. From the physiological measurements related to this study, Gravatt et al. (1997) and Tang et al. (1999) observed that needle photosynthesis and carbon exchange index of lower crown foliage were greater in the thinned treatments than in unthinned treatments during the fifth and sixth post-thinning years. The thinning-induced increase in whole-crown leaf area and photosynthetic rate (per unit leaf area) leads to an increase in carbon fixation and ultimately tree productivity (Teskey et al., 1987; Peterson et al., 1997).

We observed that there was no residual thinning effect on shoot characteristics 6 years after treatment. Shoot length and diameter and leaf area in the thinned treatment were similar to those in the unthinned treatment, suggesting that shoot growth in the lower crown of the thinned-treatment trees may be light limited. Early physiological data indicated that a large difference in light intensity and foliar gas exchange re-occurred between the upper and lower crown in the thinned treatments during the fifth and sixth post-thinning year (Gravatt et al., 1997; Tang et al., 1999). Later, Yu et al. (1999) found that tree annual ring width and volume increment did not differ between the thinned and unthinned treatments six growing seasons following thinning. These findings demonstrate that canopy closure had started to take place again in the thinned treatments. A second thinning in the thinned treatments is needed to optimize shoot expansion, foliar net photosynthesis and stem growth.

Available nitrogen and phosphorus are inherently deficient in the Beauregard silt loam on this site (Shoulders and Tiarks, 1983). Field measurements have shown that nitrogen and phosphorus fertilization improved soil fertility and substantially increased tree height, diameter and stem volume during the first four post-treatment years (Haywood, 1994; Yu et al., 1999). Other studies have also found that nutrient addition increased growth efficiency and productivity (Albaugh et al., 1998; Jokela and Martin, 2000). In a study of 24-year-old Douglas-fir, Brix (1981) reported that maximum leaf area per tree occurred 7 years after thinning and fertilization treatments, but the impact of fertilization (224 and 448 kg N ha^{-1}) alone on foliage area and branch growth persisted for 4–5 years. On a North Carolina site, Albaugh et al. (1998) observed that nitrogen fertilization enhanced leaf area index and stem growth in an 8-year-old loblolly pine plantation during the first 4 years. On our study site, Yu et al. (1999) also found that tree volume growth in the fertilized treatments increased for the first three to four post-fertilizing years and began to decline during the fifth year when the difference in volume increment no longer existed between the fertilized and unfertilized treatments. The results from the present study showed that nutrient supply had little impact on total leaf area at the shoot, branch and crown level 6 years after fertilizer application. This may explain in part why stem volume growth in the fertilized treatment decreased during the fifth growing season following fertilization.

In a study at this site, Gravatt (1994) found that as tree size continued to rise during the fifth post-fertilizing year, foliar nitrogen concentration averaged 11.1 and 12.6 g kg^{-1} in the fertilized and unfertilized treatments, respectively. Foliar phosphorus concentration

averaged 0.90 and 0.58 g kg^{-1} in the fertilized and unfertilized treatments. The concentrations of foliar nitrogen and phosphorus that denote the onset of deficiency in plantation loblolly pine are 11.0 and 1.0 g kg^{-1}, respectively (Allen, 1987). Additionally, during the sixth post-fertilizing year, light intensity in the canopy of fertilized treatments declined as a result of increased mutual shading associated with rapid foliage growth (Tang et al., 1999). Therefore, the lack of fertilization effects on crown leaf area on this site is likely due to a combination of decreased light level and low nutrient availability in the fertilized treatments.

5. Conclusions

Six growing seasons after application of thinning and fertilization, thinning still had a positive residual effect on branch morphology and crown characteristics. Trees in the thinned treatment produced more foliage biomass and total leaf area, especially in the lower crown section. The increased foliage biomass and leaf area were attributed to more live branches and shoots and larger branch size. However, needle size, shoot length and leaf area per shoot and needle density all were no longer affected by thinning. Fertilization stimulated needle size and leaf area of individual needles in the upper crown, but had little residual effect on leaf area at the shoot, branch and crown level. Thinning and fertilization combined had no interaction on the crown hierarchical characteristics.

The effects of thinning and fertilization appear to be relatively long, but the thinning-induced effect may remain longer than five growing seasons. The intensity of silvicultural practices may have a large impact on the response level of crown morphology and the period of treatment effect persistence. Future studies of repeated cultural manipulations are needed to thoroughly understand the effects of continuing forest management practices on crown development, foliage growth and tree productivity.

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