

RELATION OF STEM DIAMETER, BRANCH BASAL AREA, AND LEAF BIOMASS IN RAPIDLY GROWING LOBLOLLY PINE

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Abstract—Twenty loblolly pines, growing in International Paper's maximum growth experiment at Bainbridge GA, were destructively sampled at the end of the sixth growing season. Ten trees in the control and 10 in the maximum treatment were sampled. All trees were planted at a 2.4- by 3.6-m spacing and grown with complete competition control. The maximum trees also received irrigation, fertilization, and pest control. Tree measures were basal diameter, d.b.h., height of live crown, diameter at base of live crown, and total height. Each tree was sectioned at 1-m intervals and stem diameter determined at each end. Branches were removed and height, basal diameter, and length were measured on each branch. Branches were separated into foliated and unfoliated segments and weighed green. One branch from each meter was returned to the lab to determine dry weight and foliated branch to foliage ratios. The maximum treatment trees were considerably larger (17.2 cm-d.b.h., 9.57 m tall, 0.118 m³ stem volume to 5-cm top) than the controls (13.5 cm- d.b.h., 7.72 m tall, 0.58 m³ stem volume), but crown lengths were similar (6.7 m maximum, 6.6 m control). In the upper 5 m of crown, leaf biomass was highly correlated with branch basal area ($r^2 = 0.697$ to 0.947), and there was a constant ratio of leaf biomass to branch basal area (50.4 gm per cm² for maximum, 50.2 gm per cm² for control). In general, we found a constant ratio of bole basal area to cumulative branch basal area throughout the crowns (0.94 for controls, 1.06 for maximum).

INTRODUCTION

Growth and productivity of loblolly pine (*Pinus taeda* L.) have been studied for several decades. There has been a series of principles that have been formulated to explain growth of forest trees. Carl Olaf Tamm proposed that conifer growth in Sweden was controlled by the supply rate of nitrogen. Ågren (1983) presented a formal differential equation suggesting the instantaneous growth rate was determined by the soil supply rate of nitrogen. The equation was found to be accurate for small seedlings and foliage (Ågren 1985). Vose and Allen (1988) tied foliage production to stem wood volume, showing that subsequent stand growth is highly correlated to present leaf area index. Waring and others (1982) found a predictable relation between sapwood basal area and foliar biomass, suggesting wide applicability of the pipe model of Shinozaki and others (1964). The pipe model described a tree as a collection of pipes that conduct water from roots to leaves. New foliage requires a simultaneous increase in branch, bole, and root cross section to carry water to the new foliage.

Branches are the connection of stem and foliage. Spurgel and others (1991) examined literature on the degree of branch autonomy. They concluded that older branches are essentially autonomous with regard to carbon. That is, if respiration exceeds photosynthesis in an older branch, it does not import photosynthate from the stem. They generally found that this was true for old branches and, with respect to carbon, older branches were completely autonomous. If respiration exceeded photosynthesis over a sustained period, older branches died rather than withdraw carbon from the stem. Their conclusions on water tended to support the pipe model in that individual branches were hydraulically separated, and stress on one branch was not transmitted to others.

In addition to providing conductive material, the stem also provides support for the tree. Long and others (1981) examined form of 45-year-old Douglas fir [*Pseudotsuga menziesii* (Mirb.)Franco] and found that stem form fit the cubic equation first proposed by Metzger (1893). He estimated bole diameter distribution required to produce uniform resistance to wind acting on the crown. They found that the cubic power equation of Metzger could explain the stem form of Douglas-fir.

In this paper we will examine growth and tree morphology of loblolly pine grown with only light, temperature, and intra-specific competition limitation. These trees are part of an International Paper study at Bainbridge, GA, on which there have been several previous reports (Gresham and Williams 2002, McLemore and others 1999, Samuelson 1998, Williams 1999, Williams and Gresham 2002). We compared loblolly pine grown in the most and least intensive treatments after six growing seasons. Growth and morphology were examined in relation to the above principles.

METHODS

The study is located on International Paper's Silver Lake Farm, Southlands Experimental Forest in Bainbridge, GA (30°51' N, 80°45' W). The study examines addition of irrigation, fertilization with irrigation (fertigation), and pest control to superior loblolly that were planted on an abandoned agricultural field and that have been maintained competition free. Trees were planted in the spring of 1995 on 12-foot subsoiled rows on a 10-foot spacing within rows. Design was randomized complete block with three reps of four treatments. Plots were 144 feet by 180 feet or 12 rows and 18 trees per row. The inner 8 rows and 10 trees were used as a measurement plot. In addition to the three measurement replications, a destructive sampling partial

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replication was planted with only maximum and minimum treatments.

In late February 2002, we sampled 10 trees from each maximum and minimum treatment. Trees were systematically sampled from the destructive replication to assure that each sampled tree would have four surrounding trees at the same spacing as trees on the measurement replications. Trees were cut at ground line and measures of basal diameter, d.b.h., height and diameter at base of live crown, and total height were taken. Each tree was then cut into 1-m sections. Diameter at each end of the meter was recorded, total green weight determined, and a disk removed and weighed green and dry. Dead branches were combined and weighed green and a sub sample weighed dry. Each branch was removed, and height along stem, basal diameter, and length were measured. Foliated and unfoliated sections were separated and weighed green. One branch per m was returned to the laboratory. The dried foliated branch and needles were separated and weighed in addition to weighing the dried unfoliated branch.

For bole sections, the diameters at each end were calculated and dry weight determined from the disk weights. Bole section volume and total bole volume were calculated as truncated cones for each meter. Bole volume was calculated to a 5-cm top. Branch basal area and volume were calculated as a cone; biomass of unfoliated branch, foliated branch, and foliage were calculated from the ratio of the branch collected on that tree and that meter. This proved to

be unnecessary since ratios were very similar in the upper crowns of all trees.

All new growth above the last meter was called top and treated as a single branch. This will be evident in the variation in the following tables. On some, such as cumulative foliar mass or stem basal areas, the entire tree was included, and there was a meter 9 on maximum treatment and 7 on minimum. On data such as number or length of branches, the top was excluded, and the upper meter was 6 or 8.

RESULTS

There has been a highly significant response to intensity of culture with the maximum treatment trees having nearly doubled the minimum treatment trees in bole volume and biomass (table 1). The maximum trees are both larger in diameter and height, resulting in highly significant increases in bole size. There were no significant differences in crown biomass with the exception of dead branches, which were highly significantly different. Dead branches accounted for 28 percent of the crown biomass on the maximum treatment but only 6.6 percent on the minimum. Height of live crown explained the big difference in dead branches. The height of live crown was 2.5 m on the maximum treatment but only 0.5 m on the minimum.

Most branches were in the upper crown, and there was a definite die off of branches in lowest m of each crown (table 2). Branch length showed a strong conical form on

Table 1—Comparison of average tree sizes on 10 trees sampled from maximum and minimum treatments

	Maximum	Minimum	Significance
Bole volume (m^3)	0.121	0.056	0.001
Height (m)	9.67	7.82	0.001
D.b.h. (cm)	17.16	13.62	0.01
Bole biomass (kg)	39.81	22.08	0.001
Dead branch biomass (kg)	9.36	1.51	0.001
Unfoliated branch biomass (kg)	12.79	9.62	NS
Foliated branch biomass (kg)	3.41	2.90	NS
Foliage biomass (kg)	8.01	8.26	NS

NS = no significance.

Bole volume is to a 5-cm top.

Table 2—Comparisons of tree morphology of maximum and minimum treatments

Meter	Ave. bole diameter		Ave. number of branches		Ave. length of branches		Sum of branch basal area		Foliage biomass	
	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min
	--- cm ---				--- cm ---		--- cm^2 ---		---- gm ----	
1	23.5	18.9	0	1.5	—	149	—	8.1	—	127
2	18.9	14.1	0	5.4	—	220	—	28.9	—	806
3	16.4	13.4	1.1	6.2	354	211	27.5	32.5	201	1,476
4	15.2	10.0	3.4	8.6	287	194	31.1	43.8	611	2,412
5	12.8	8.8	4.3	7.6	276	172	30.7	33.8	905	1,909
6	11.0	8.4	8.7	7.8	226	131	63.4	33.0	2,995	1,121
7	8.4	3.9	5.4	—	181	—	32.1	11.5	1,038	478
8	6.7		7.7	—	148	—	34.4	—	1,795	
9	4.5						16.0	—	782	

Bole diameter is at base of meter, other measures are along the indicated meter. The upper meter of bole diameter, branch basal area, and foliage biomass represents the top.

the maximum treatment with a more oval form for the minimum treatment. The diagonal spacing of a 10- by 12-foot planting is 238 cm, indicating that the lower branches of the maximum treatment had considerable vertical growth. There was strong light competition in the lower 3 m of the maximum treatment. The minimum crowns had just closed during the sixth season, with longest branches at the diagonal spacing.

Foliar biomass was large in both treatments. It was distributed very symmetrically in the minimum treatment but with less regularity and a slight upward skew in the maximum treatment. Branch basal area was distributed similarly to foliar biomass in the upper crown but not in the lower crown of the maximum treatment.

In the upper 4 m, there was a high correlation of branch basal area to foliar biomass on an individual branch basis ($r^2 = 0.7-0.9$). Accumulating from the top downward, branch basal area explained 97 percent of the change in foliar biomass (fig. 1). At the bottom of the crown the relation became curvilinear. In the upper crown, each cm^2 of branch basal area supported roughly 50 g of foliage. At the bottom of the crown, the value fell to about 20 g per cm^2 .

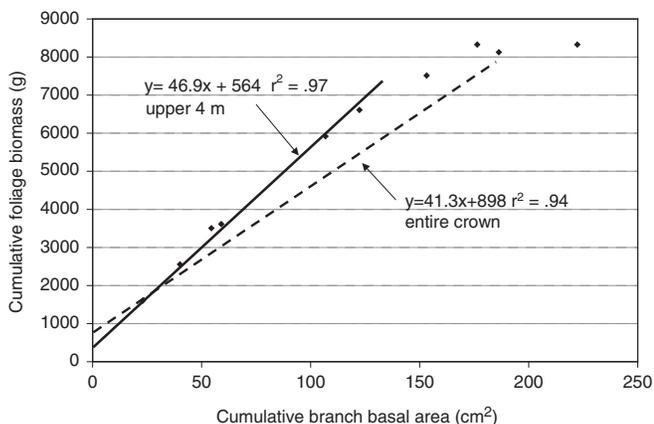


Figure 1—Comparison of branch basal area and foliar biomass. Data are average values for each meter for both maximum and minimum treatments.

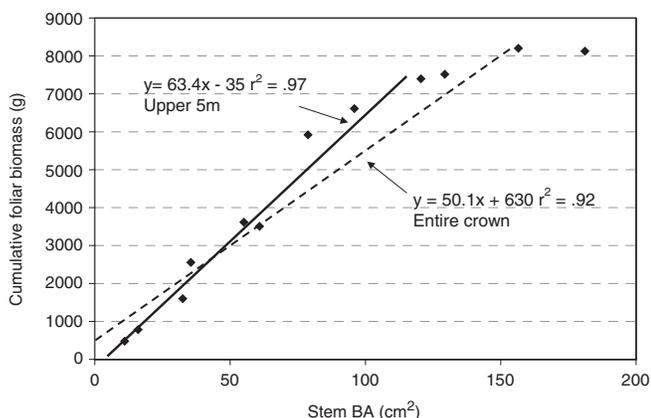


Figure 2—Increase of stem basal area with cumulative biomass from the top of the tree. Data are a composite of both maximum and minimum averages.

The relationship of stem basal area to foliar biomass was very similar to that of branch basal area (fig. 2). This was because stem basal area was nearly equal to cumulative branch basal area, also with an r^2 of 0.96. The relation of stem basal area to foliar biomass had a flat area near the bottom of the tree. Metzger (1893) suggested a relation of stem diameter of the form: $\text{Height} = a - b (\text{diameter}^3)$, where b is a slope dependent on wood strength and a is the center of the crown mass. The data for both treatment trees fit this relation very well (fig. 3). The intercept of the equation of the maximum treatment was very near the center of the crown as predicted. The minimum treatment equation indicated slightly stronger wood but also estimated the center of the crown above where it actually occurred.

CONCLUSIONS

These data tend to support many of the principles that were outlined in the introduction. Evidence was most convincing that these loblolly pine were growing in accordance with the pipe model of Shinozaki and others (1964). Throughout the upper crown there was a constant ratio of foliar biomass to cumulative branch basal area and stem basal area. Only in the lower crown did this relation break down. The data suggested that each g of needle required 0.02 cm^2 of vascular system to support evapotranspiration.

The data also supported the branch autonomy of Spurgel and others (1991). Below the layer where branches were longer than the diagonal spacing the ratio of foliar biomass to basal area declined. In this zone it was probable that light limits the ability of the branch to maintain leaf replacement. The ratio of foliar biomass to branch basal area dropped to about 20g per cm^2 in the lowest living branches.

Finally there was a very good agreement with Metzger's (1893) relation. He developed the relation assuming that the tree bole should be uniformly resistant to wind on the crown. The relation fits the stem shape of both treatments well and also predicts perfectly the center of the maximum treatment crowns.

It has been difficult to identify any nitrogen relations in this experiment. However, data on leaching of nitrate to the

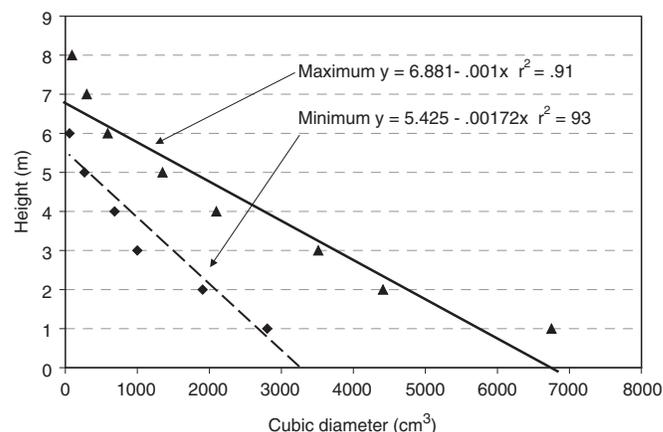


Figure 3—Comparison of stem diameter distribution to cubic distribution described by Metzger (1893).

groundwater suggest that the field had an abundant supply of nitrogen (Williams 1999).

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