Amount and vertical distribution of foliage of young loblolly pine trees as affected by canopy position and silvicultural treatment[1]

ANDREW R. GILLESPIE[2]
Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907-1159, U.S.A.
H. LEE ALLEN
Department of Forestry, North Carolina State University, Raleigh, NC 27695-8008, U.S.A.
AND
JAMES M. VOSE
USDA Forest Service, Coweeta Hydrologic Laboratory, Otto, NC 28763, U.S.A.

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Silvicultural practices such as thinning and fertilization can affect both canopy foliage quantity and distribution, altering stand growth. The objectives of this research were to quantify the effects of tree size and silvicultural treatment on the vertical distribution of foliage of individual trees of loblolly pine (*Pinus taeda* L.) and to estimate foliage quantity and distribution using easily measured tree data. In three stands sampled in North and South Carolina, fertilization and (or) thinning treatments had been applied 2 years prior to sampling. A fourth stand was untreated. Nonlinear and linear regression models were developed to test the effects of silvicultural treatment on individual branch foliage biomass and whole tree foliage biomass. Vertical distributions of foliage and branches were modelled using a Weibull probability density function. Analyses indicated that individual branch foliage biomass was positively related to branch size but negatively related to distance from the top of the tree. Fertilization with nitrogen and phosphorus, or thinning, increased the foliage biomass carried by a given sized branch. Silvicultural treatment effects on individual branches translated into whole-tree foliage biomass with thinning and fertilization increasing the crown size of individual trees. Though treatment affected crown size, the distribution of foliage (and branches) remained unaffected. Because silvicultural treatments change the size of crowns for trees of given dimensions, any estimation of loblolly pine crown biomass must be site and treatment specific.

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Les pratiques sylvicoles telles l'éclaircie et la fertilisation peuvent affecter la distribution et la quantité de feuillage dans le couvert entraînant ainsi une modification dans la croissance du peuplement. Les objectifs de cette étude consistaient à quantifier les effets de la dimension des arbres et des traitements sylvicoles sur la distribution verticale du feuillage chez des pins à encens (*Pinus taeda* L.) pris individuellement et à estimer la quantité et la distribution du feuillage à l'aide de données dendrométriques facilement mesurables. Des traitements d'éclaircie et (ou) de fertilisation ont été appliqués 2 ans avant l'échantillonnage dans les trois peuplements étudiés en Caroline du Nord et du Sud. Un quatrième peuplement n'a pas été traité. Les effets des traitements sylvicoles sur la biomasse du feuillage des branches prises individuellement et de l'arbre dans son ensemble ont été testés à l'aide de modèles de régression non linéaire et linéaire. La distribution verticale des branches et du feuillage a été modélisée à l'aide d'une fonction de probabilité de densités de Weibull. Les analyses ont montré que la biomasse du feuillage des branches individuelles était positivement reliée à la dimension des branches mais négativement reliée à la distance du sommet de l'arbre. La fertilisation avec de l'azote et du phosphore ou l'éclaircie ont augmenté la biomasse pour une dimension donnée de branches. Les effets des traitements sylvicoles sur les branches prises individuellement se sont répercutés sur la biomasse du feuillage de l'arbre dans son ensemble de telle sorte que l'éclaircie et la fertilisation ont entraîné une augmentation de la dimension de la cime des arbres pris individuellement. Même si les traitements ont affecté la dimension de la cime, la distribution du feuillage et des branches n'a pas été affectée. Comme les traitements sylvicoles modifient la dimension des cimes pour des arbres d'une dimension donnée, toute estimation de la biomasse de la cime du pin à encens doit être spécifique pour un site et un traitement donné.

[Traduit par la rédaction]

Introduction

Foliage quantity and distribution within the canopy play an important role in the ability of a forest to assimilate carbon (Russell et al. 1989). Profiles of light interception, O_2, CO_2, water vapor, temperature, and wind speed are all important properties of forest canopies affecting carbon assimilation. Recognition of the importance of these profiles has led to the inclusion of foliage distribution in detailed models of crown carbon gain (e.g., MAESTRO; Wang and Jarvis 1990).

The influence of silvicultural practices such as thinning and fertilization may impact both foliage quantity and distribution. Increases in leaf area following amelioration of nutrient limitations, with associated increases in stemwood production, have been reported (e.g., Linder and Axelsson 1982; Vose and Allen 1988; Colbert et al. 1990). However, reports examining the effects of silvicultural practices on the vertical distribution of foliage are much more limited (e.g., Vose 1988).

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[2]Author to whom all correspondence should be addressed.

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TABLE 1. Summary of stand characteristics and applied treatments for four sampled loblolly pine plantations in the lower coastal plain of North and South Carolina

Stand	Location	Stems (no./ha)	Basal area (m^2/ha)	SI (m)	Age (years)	Treatments*	No. of trees sampled per treatment
1	Craven County North Carolina	1504	8	18	9	Nontreated with various size classes sampled	4
2	Craven County North Carolina	1092	22	23	11	Nitrogen (0 and 336 kg/ha) in factorial combination with phosphorus (0 and 56 kg/ha)	4
3	Colleton County, South Carolina	1230	28	23	14	Nitrogen (0 and 336 kg/ha) in factorial combination with phosphorus (0 and 56 kg/ha)	4
4	Beaufort County, North Carolina			20	9	Nitrogen (0 and 168 kg/ha) in factorial combination with thinning (none and 70% stocking)	3
	Nonthinned	1991	29				
	Thinned	1107	20				

*Treatments were applied 2 years prior to assessment.

The objectives of this research were to (*i*) quantify the effects of tree size and silvicultural treatment on the vertical distribution of foliage of individual trees of loblolly pine (*Pinus taeda* L.) in young stands, and (*ii*) estimate foliage quantity and distribution using easily measured tree data.

Methods

Field sampling

Branches were sampled from the crowns of 55 trees from four loblolly plantations located in the lower coastal plain of North and South Carolina (Table 1). Stands 2–4 were very productive, fully stocked stands that ranged in age from 9 to 14 years old. Stand 1, which was untreated, was less productive and had not achieved canopy closure at time of sampling. In stands 2, 3, and 4, fertilization and (or) thinning treatments had been applied to approximately 0.1 ha or larger plots 2 years prior to the time when sampling was undertaken. Treatments were replicated four, two, and three times, respectively, for stands 2, 3, and 4. In addition to the imposed midrotation treatments, all stands (except stand 1) were fertilized with phosphorus (P) at time of planting. Stands 2, 3, and 4 were dense enough for competition-induced mortality to have occurred.

One or two representative trees were felled in each plot within each stand. For stand 1, 11 trees were selected from a range of sizes, four small, four medium, and three large trees reflecting the nonuniform stand. For stands 2, 3, and 4, trees selected were of average height and diameter (codominants). Crown class, total height, crown length, diameter at breast height (DBH), diameter at the base of the live crown (DLC), diameter at the base of each live branch, and distance of each live branch from the top of the tree were measured. Ten to 15 branches were randomly subsampled from the crown of each tree for foliage biomass determinations. Foliage was separated from woody branch material and oven-dried at 65°C.

Statistical analyses

Using data from destructively sampled branches, nonlinear regression equations of the form $FOLWT = BRDIA^{B1}DFT^{B2}$ were computed (SAS Institute Inc. 1988). FOLWT, BRDIA, and DFT represent individual branch foliage biomass (grams), branch diameter (millimeters), and distance from the top of the tree (centimeters), respectively. Initial regression analyses indicated stand and treatment effects on the foliage biomass regressions. Thus, individual treatment equations were developed for each stand. These equations were used to estimate foliage biomass for each branch using measured branch diameter and distance from the top.

Whole tree branch numbers and average branch diameters were calculated for individual trees. Similarly, whole tree foliage biomass was calculated by summing estimates of individual branch foliage biomass for individual trees. Treatment differences for tree height, DBH, crown length, crown ratios, average branch size, branch number, and foliage biomass within each stand were examined using a factorial analysis of variance with a randomized block design.

Vertical profiles of predicted foliage weight and measured branch diameter for each tree were characterized by a two-parameter cumulative Weibull distribution function using nonlinear regression (SAS Institute Inc. 1988). This probability density function has been shown to adequately describe pine foliage distribution (Schreuder and Swank 1974; Vose 1988). The cumulative distribution takes the form

$$[1] \quad \frac{FB}{TRFOLWT} = 1 - \exp\left(\frac{RDFT}{\beta}\right)^{\alpha}$$

where FB is the cumulative foliage biomass (grams) at a specified position within the canopy, TRFOLWT is the whole tree foliage weight (grams), RDFT is the relativized distance from the top of the tree (0–1), and α and β are the shape and scale parameters of the Weibull distribution function.

The α-parameter describes the shape of the distribution. This shape can be used to examine canopy leaf area distribution and assess pattern change due to silvicultural treatment (cf. Schreuder and Swank 1974; Vose 1988). The β-parameter describes the scale or variability of the distribution. Its interpretation is that of foliage density or foliage weight per unit height. The greater the β-parameter, the greater the foliage weight found at a specific position within the canopy. The α- and β-parameters together describe the amount (or density) and distribution of foliage within a single tree crown.

Our final objective was to estimate whole tree foliage biomass and parameters of the foliage distribution using more easily measured tree dimensional characteristics. Linear and nonlinear regression models were developed to predict foliage biomass and Weibull parameters using combinations of diameters at breast height and at the base of the live crown, total height, and live crown length.

Results and discussion

Individual branches

Individual branch foliage biomass is strongly and positively related to branch size, and negatively related to distance from the top of the tree (Table 2). That is, foliage quantity increases greatly with increasing branch size. The effect of increasing distance from the top of the tree is a reduction in the quantity of foliage on a branch of a given size, hence the negative coefficient. Similar patterns of foliage display

TABLE 2. Summary of parameters and statistics for nonlinear regression equations estimating individual loblolly pine branch foliage weight as a function of branch diameter and distance from the top of the crown of the form FOLWT = $BRDIA^{B1}DFT^{B2}$

	$B1$	$B2$	n	R^2
Stand 1				
Large *	1.805 (1.322–2.289)	−0.169 (−0.429 – −0.090)	28	0.75
Medium	2.995 (2.495–3.496)	−0.780 (−1.051 – −0.509)	46	0.78
Small	2.646 (1.924–3.368)	−0.630 (−1.000 – −0.261)	39	0.67
Stand 2				
C	4.546 (3.847–5.246)	−1.846 (−2.299 – −1.395)	30	0.87
N	1.818 (1.136–2.500)	−0.132 (−0.535 – −0.272)	39	0.72
P	2.906 (2.631–3.180)	−0.761 (−0.930 – −0.592)	34	0.96
N+P	3.081 (2.478–3.684)	−0.863 (−1.239 – −0.486)	22	0.93
Stand 3				
C	2.878 (2.493–3.263)	−0.778 (−0.997 – −0.560)	41	0.86
N	2.357 (1.997–2.717)	−0.438 (−0.646 – −0.231)	46	0.89
P	2.365 (1.693–3.035)	−0.485 (−0.843 – −0.127)	42	0.57
N+P	2.318 (1.786–2.850)	−0.419 (−0.719 – −0.119)	42	0.77
Stand 4				
C	3.639 (3.252–4.026)	−1.157 (−1.378 – −0.936)	82	0.81
N	2.947 (2.558–3.340)	−0.755 (−0.983 – −0.529)	94	0.78
Thin	2.300 (2.011–2.589)	−0.388 (−0.554 – −0.222)	102	0.87
N + Thin	2.574 (2.297–2.851)	−0.566 (−0.731 – −0.401)	99	0.88

NOTE: Values are parameter estimates with 95% confidence intervals given in parentheses.
*Stand characteristics separate tree size (stand 1) and silvicultural treatment (stands 2, 3, and 4) including control (C), nitrogen (N) and phosphorus (P) fertilization, and thinning (Thin). Treatments are defined in Table 1.

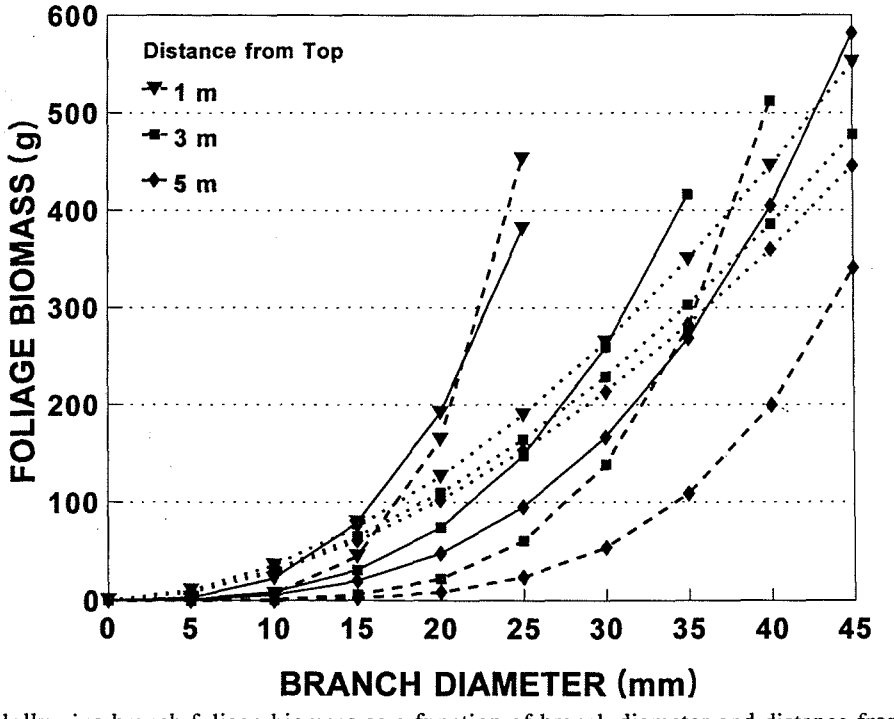

FIG. 1. Individual loblolly pine branch foliage biomass as a function of branch diameter and distance from the top (DFT) of the tree for fertilization treatments in stand 2. Solid lines represent untreated trees, dotted lines represent trees fertilized with nitrogen, and broken lines represent trees fertilized with both nitrogen and phosphorus.

have been previously reported for loblolly pine (Hepp and Brister 1982; Kinerson et al. 1974).

The negative effect of increasing canopy depth is of particular interest because the magnitude of its effect is strongly affected by treatment. If the model form is examined for treatment effects, the parameter estimates for BRDIA and DFT shift with treatment. For branches from nontreated trees in stand 2, foliage weight increases with branch size (Fig. 1). The effect of increasing branch depth within the crown reduces the foliage weight per unit branch size considerably. A simple explanation is that increased shading lower in the crown reduces the ability of the foliage to fix carbon and thus less foliage is carried (e.g., Perry 1985). However, nitrogen fertilization alters this relationship, dramatically increasing the amount of foliage on a branch of a given size at all canopy depths for these young trees. In

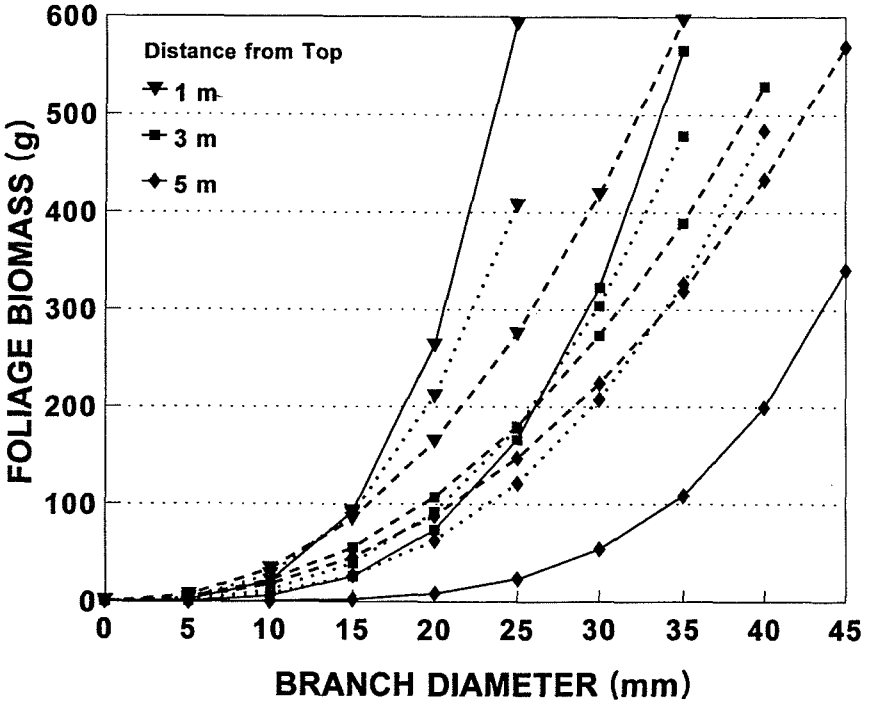

FIG. 2. Individual loblolly pine branch foliage biomass as a function of branch diameter and distance from the top (DFT) of the tree for fertilization treatments in stand 4. Solid lines represent untreated trees, dotted lines represent trees fertilized with nitrogen, and broken lines represent trees fertilized with nitrogen and thinned.

fact, branch depth within the canopy has very little effect in nitrogen-fertilized trees (Fig. 1), suggesting that lower branches may be nitrogen limited rather than light limited, or at least a combination of the two. This is in agreement with the observation that leaf areas in fully stocked stands of loblolly pine are well below the optimum across the region (Allen and Gillespie 1991). Fertilization may increase light-use efficiency for lower canopy needles and help maintain a positive carbon balance in lower canopy positions (Brix 1971). Fertilization with phosphorus in addition to nitrogen provides quantities of foliage similar to fertilization with nitrogen alone high in the crown for a given branch size. But with increasing distance from the top of the tree, foliage biomass again declines for a given branch size, indicating a stronger effect of light limitation. On this site, it appears that nitrogen plus phosphorus fertilization must be undertaken to increase canopy density to create by light limitations in the lower canopy positions, due to both nitrogen and phosphorus limitations.

Nitrogen fertilization and thinning treatments in stand 4 have provided only moderate treatment effects on foliage weight for a given branch size and position (Fig. 2). Nontreated trees show the greatest differentiation in foliage weight by canopy depth, again with decreasing foliage quantities lower in the crown. The nitrogen fertilization treatment in stand 4 also reduces the effect of canopy depth as in stand 2. However, the thinning and thinning plus fertilization treatments have the least impact on foliage biomass of a given branch with increasing canopy depth. This is most likely due to the removal of any light limitation low in the canopy after thinning and the reallocation of nutrient resources to the remaining trees. Relative reductions in foliage biomass near the top of the tree for thinned and fertilized trees indicates a reallocation of resources to the lower crown positions. Though the mechanism is unknown, observations in these trials have shown reduced height growth following thinning (H.L. Allen, unpublished data).

When examining foliage display for nontreated trees of different size classes (stand 1), the developed regression equations show little differentiation in foliage weight on a given branch by canopy depth for dominant or large trees. One would expect little shading effect on the larger trees from neighboring crowns, and thus little differentiation, but also, branch size and foliage weights are smaller in this stand when compared with the other stands. Because total tree foliage biomass is less in stand 1 than in the other stands (Table 3), and because stand 1 is a poorer site with less basal area (Table 1), a nutrient limitation might be suspected. Foliage display for medium and small trees (codominant and intermediate) seems to substantiate this hypothesis. For these smaller trees, there is a relatively strong negative effect for increasing canopy depth. This effect implies at least partial shading. At the top of a tree, foliage weight is predicted to be greater for a given diameter as compared with dominant or large trees. However, the strong negative canopy depth effect quickly reduces foliage biomass to a level comparable with foliage biomass found at all canopy depths for a large tree.

Whole tree

Whole tree foliage biomass was dramatically affected by silvicultural treatment (Tables 3 and 4). Thinning in conjunction with nitrogen fertilization provided the largest crowns (predicted values) even though these trees were younger and smaller than those in stands 2 and 3. These treatment differences are due in part to the stand- or treatment-specific individual branch foliage equations (especially stand 2) (see Table 2). However, treatment-induced differences in the size and number of branches on a tree are also important contributors. The largest differences are seen in

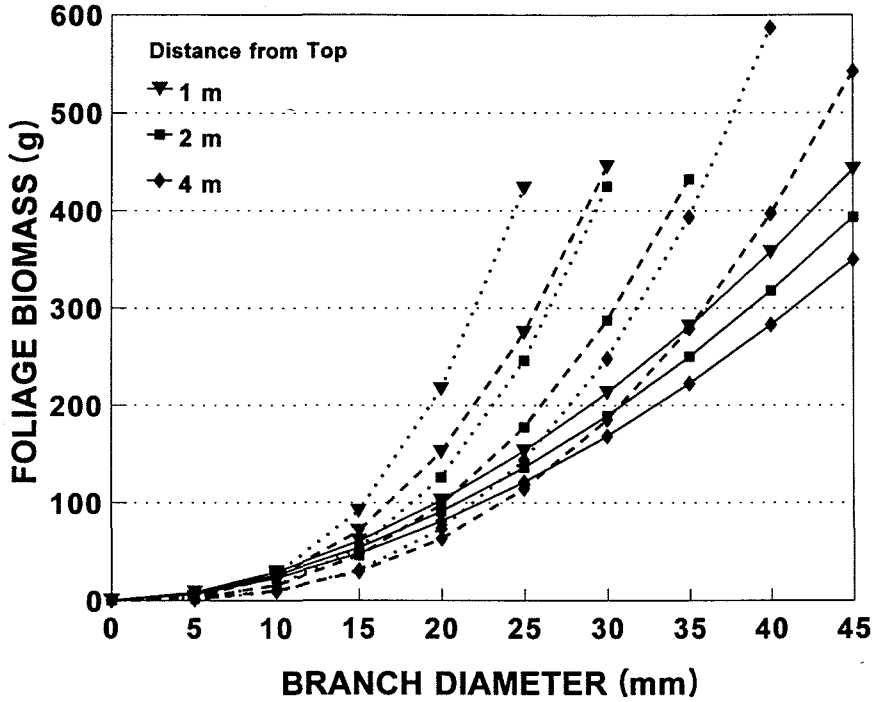

FIG. 3. Individual loblolly pine branch foliage biomass as a function of branch diameter and distance from the top (DFT) of the tree for trees of different size in stand 1. Solid lines represent the larger size class of trees, dotted lines represent the middle size class of trees, and broken lines represent the smallest size class of trees.

TABLE 3. Treatment means and standard errors for individual loblolly pine tree foliage, stem, and branch parameters

	Tree height (m)	Diameter (cm)	Crown length (cm)	Crown ratio (%)	Average branch size (mm)	No. of branches	Foliage biomass (g)
Stand 1							
Large*	7.9	11.0	497	63.3	13.6	47.3	2366
Medium	6.0	9.2	417	69.5	11.4	51.0	1946
Small	4.9	6.5	353	71.8	9.7	39.0	902
SE†	0.755	1.199	0.501	0.045	0.903	7.32	416.676
Stand 2							
C	10.0	18.4	590	58.9	17.9	48.5	2522
N	9.7	26.5	575	60.1	19.2	45.8	5550
P	9.6	24.0	585	61.4	19.0	45.5	4982
N+P	10.1	18.2	542	53.2	19.6	40.2	4668
SE	0.685	2.182	0.532	0.045	1.918	5.813	680.575
Stand 3							
C	14.2	16.4	587	41.2	16.4	40.5	2267
N	15.7	17.1	711	45.6	17.7	52.8	4606
P	13.9	15.8	636	45.4	14.8	52.0	2435
N+P	15.0	17.0	694	46.4	16.9	47.0	3802
SE	0.987	0.336	0.841	0.032	1.695	6.891	378.303
Stand 4							
C	9.0	13.0	507	56.0	16.5	43.3	3283
N	9.4	14.2	567	60.2	15.3	51.0	4152
Thin	9.0	14.2	618	68.9	15.3	61.7	5310
N + Thin	8.9	15.9	608	68.3	17.1	58.3	5765
SE	0.283	0.326	0.632	0.063	1.792	6.910	501.495

*Stand characteristics separate tree size (stand 1) and silvicultural treatments (stands 2, 3, and 4) including control (C), nitrogen (N) and phosphorus (P) fertilization, and thinning (Thin). Treatments are defined in Table 1.
†ANOVA root mean square error.

stand 1 where tree size affected both branch number and size, with large trees clearly having a greater support structure (larger branches). Treatment effects in stands 3 and 4 (only codominant trees sampled) were less pronounced. In these two stands, branch numbers were more highly impacted by fertilization and (or) thinning.

TABLE 4. Summary of probability values for ANOVA treatment effects for individual loblolly pine tree foliage, stem, and branch parameters

	Tree height	Diameter	Crown length	Crown ratio	Average branch size	No. of branches	Foliage biomass
Stand 1							
Tree size*	0.0030	0.0035	0.0184	0.1155	0.0017	0.1199	0.0040
Stand 2							
N	0.7500	0.3094	0.5267	0.3879	0.3522	0.1939	0.0032
P	0.9717	0.2554	0.1665	0.1136	0.4281	0.1694	0.0458
N × P	0.2098	0.0001	0.5862	0.5885	0.7247	0.6748	0.0008
Stand 3							
N	0.0261	0.0003	0.1136	0.5095	0.0652	0.3134	0.0001
P	0.3045	0.0469	0.6665	0.1606	0.1997	0.4203	0.1278
N × P	0.7128	0.1534	0.1368	0.0688	0.6724	0.0277	0.0303
Stand 4							
N	0.3938	0.0003	0.4671	0.5651	0.7635	0.6091	0.0625
Thin	0.1767	0.0003	0.0755	0.0227	0.7794	0.0136	0.0008
N × thin	0.1767	0.3273	0.3747	0.5606	0.1955	0.2138	0.4959

*Stand characteristics separate tree size (stand 1) and silvicultural treatments (stands 2, 3, and 4) including control (C), nitrogen (N) and phosphorous (P) fertilization, and thinning (Thin). Treatments are defined in Table 1.

TABLE 5. Weibull parameter estimates for loblolly pine branch size and foliage biomass distributions for each treatment

	Branch diameter		Foliage biomass	
	α	β	α	β
Stand 1				
Large*	2.281 (2.074–2.488)	0.650 (0.500–0.800)	2.488 (0.970–4.006)	0.666 (0.512–0.820)
Medium	2.169 (1.962–2.376)	0.630 (0.480–0.780)	2.243 (0.725–3.761)	0.615 (0.461–0.769)
Small	2.228 (2.021–2.435)	0.612 (0.462–0.762)	2.329 (0.811–3.847)	0.576 (0.422–0.730)
Stand 2				
C	2.097 (1.714–2.340)	0.632 (0.585–0.679)	2.530 (1.726–3.334)	0.646 (0.557–0.735)
N	2.142 (1.829–2.455)	0.622 (0.575–0.669)	2.532 (1.728–3.336)	0.676 (0.587–0.765)
P	2.167 (1.854–2.480)	0.606 (0.559–0.653)	2.731 (1.927–3.535)	0.626 (0.537–0.715)
N+P	2.225 (1.912–2.538)	0.636 (0.589–0.683)	2.599 (1.795–3.403)	0.653 (0.564–0.742)
Stand 3				
C	2.251 (1.845–2.657)	0.627 (0.517–0.737)	2.306 (1.749–2.863)	0.587 (0.466–0.708)
N	2.064 (1.658–2.470)	0.598 (0.488–0.708)	2.295 (1.738–2.852)	0.594 (0.473–0.715)
P	2.137 (1.731–2.543)	0.598 (0.488–0.708)	2.305 (1.748–2.862)	0.596 (0.475–0.717)
N+P	2.056 (1.650–2.462)	0.590 (0.480–0.700)	2.177 (1.620–2.734)	0.583 (0.462–0.704)
Stand 4				
C	2.329 (1.928–2.730)	0.647 (0.598–0.696)	2.473 (1.859–3.087)	0.626 (0.584–0.668)
N	2.136 (1.735–2.537)	0.606 (0.557–0.655)	2.495 (1.881–3.109)	0.630 (0.588–0.672)
Thin	1.974 (1.573–2.375)	0.588 (0.539–0.637)	2.514 (1.900–3.128)	0.608 (0.566–0.650)
N + Thin	2.130 (1.729–2.531)	0.615 (0.566–0.664)	2.597 (1.983–3.211)	0.618 (0.576–0.660)
Overall average	2.153 (2.090–2.216)	0.617 (0.606–0.628)	2.434 (2.331–2.537)	0.619 (0.605–0.633)

NOTE: Values are parameter estimates with 95% confidence intervals given in parentheses.
*Stand characteristics separate tree size (stand 1) and silvicultural treatments (stands 2, 3, and 4) including control (C), nitrogen (N) and phosphorus (P) fertilization, and thinning (Thin). Treatments are defined in Table 1.

The crowns of codominant loblolly pine trees respond very well to fertilization or thinning treatments (see also Vose and Allen 1988; Allen and Gillespie 1991) just as for species like Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; Brix 1981), Scots pine (*Pinus sylvestris* L.; Linder and Axelsson 1982), slash pine (*Pinus elliotii* Engelm.; Colbert et al. 1990), and many others. It appears that for stands with low to moderate stocking (stand 2 and thinned plots in stand 4), the fertilizer-induced increase in crown size will be a function of the increase in the amount of foliage carried by a branch of a given size and an increase in average branch size. In well-stocked stands (stand 3 and unthinned plots in stand 4), foliage responses to fertilization will be due primarily to an increase in the amount of foliage for a given branch size and the number of live branches on the stems. These factors will lead to increased foliage density within the crown. The relative contributions of these mechanisms for increasing foliage biomass following fertilization in these young to midrotation stands will be a function of stocking decisions such as initial planting density and (or) precommercial thinning. Nutrient availability will also regulate the magnitude of response and the mechanisms

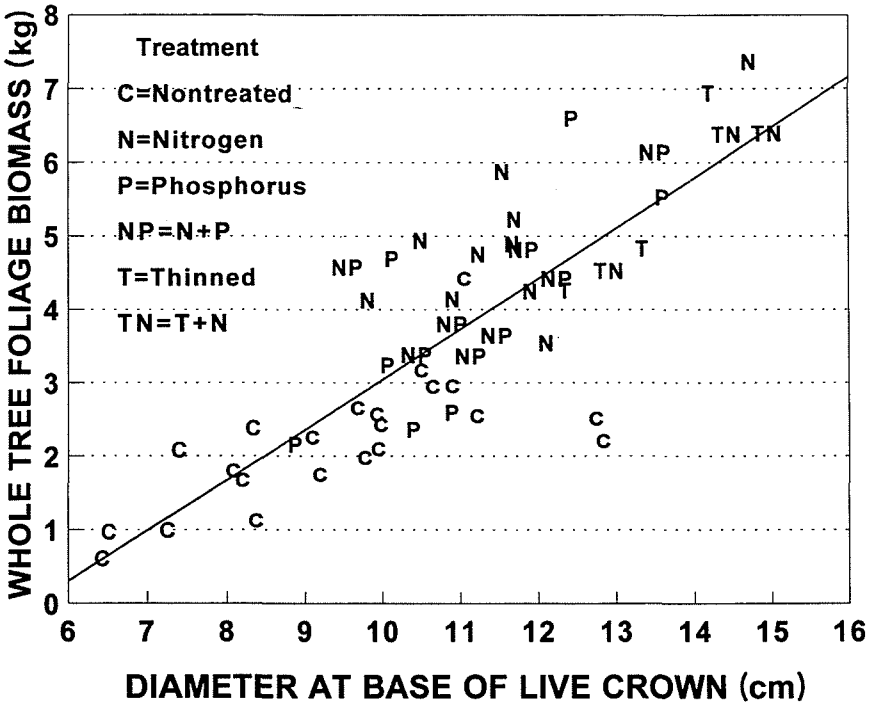

FIG. 4. The effect of silvicultural treatment on the relationship of individual tree foliage biomass and diameter at the base of the live crown for loblolly pine.

of response in these stands where light limitations may not be as important as previously thought for determining canopy architecture.

Vertical profiles

Comparison of the α- and β-parameters for branch diameter and foliage biomass reveals overlapping confidence intervals for all stand treatment combinations (Table 5). Branch diameter and foliage biomass distributions were, on average, skewed (bunched toward the bottom of the tree) for all treatments. Loblolly pine (Kinerson et al. 1974) and other species crowns or canopies (e.g., Scots pine, Whitehead 1978; deciduous forests, Rauner 1976) have been modelled as normally distributed. Our sample of 55 loblolly pine trees from different stands having different treatments indicates that young to midrotation loblolly pine trees have vertical branch or foliage distributions that are not normally distributed. Because treatment seems to have little effect on shifting the shape or density of branch and foliage distributions, an average value for both Weibull parameters could be used to adequately characterize the vertical canopy architecture of loblolly pine in similar stands. Some authors propose simpler models for characterizing canopies (e.g., Norman 1979 for radiation modelling), however, the Weibull provides a more accurate canopy description for microenvironmental and physiological modelling.

Silvicultural treatment impacts canopy foliage quantity through a modification of the branch size – foliage weight relationship and the number and (or) size of branches within a crown. As silvicultural treatment has no impact on foliage distribution, loblolly pine crowns could be quantified by predicting crown foliage – branch biomass. Distributions of the foliage–branch biomass could then be calculated using average Weibull distribution parameters derived from Table 5.

Foliage – tree dimensional relationships

Foliage biomass was significantly related to the tree dimensional characteristics measured except for total height ($R = 0.21$). Diameter at the base of the live crown had the strongest correlation with foliage biomass ($R = 0.82$). Unfortunately, this is not a characteristic normally measured in the field. Diameter at breast height had the next highest correlation with foliage biomass ($R = 0.71$), and live crown length the least ($R = 0.50$). Linear and nonlinear combinations of DBH, live crown length, and total height were attempted, but none proved to be as good as DLC alone. The importance of DLC as a predictor of foliage biomass suggests that a sapwood area approach to estimating foliage biomass might be successful. In loblolly pine, sapwood thickness has been linearly related to stem DBH and DLC so that sapwood and stem diameter provide similar information (Blanche et al. 1984). A similar study in loblolly pine found a constant leaf area – sapwood ratio with increasing tree size (Blanche et al. 1985). Thus, DBH (or DLC) should be a good estimator of foliage biomass or area. Certainly other studies provide the strong theoretical and experimental link between the measures (e.g., Whitehead 1978; Waring et al. 1982), but more recent work casts doubt on the constancy of the leaf area – sapwood ratio as sapwood area (tree size) increases (Long and Smith 1988). In our data, treatment appears to have introduced additional variation in the foliage biomass – DLC model (Fig. 4). From Fig. 4, foliage biomass is underestimated for positive treatments such as fertilization or thinning and overestimated for untreated, smaller (lower crown class), or phosphorus-fertilized trees (where stand densities, crown lengths, and crown ratios are essentially the same). This confounds our ability to predict foliage biomass from simple dimensional characteristics.

Because trees responding to treatment can be larger, it follows that their leaf area – sapwood ratio may also be increasing, explaining this apparent underestimation of foliage biomass in responding plots as shown in Fig. 4. But what is not consistent with the leaf area – sapwood approach is the variation in the leaf area – sapwood ratio for trees of the same DBH (or DLC) but having different treatments

(Fig. 4). There is quite a bit of overlap in diameter distributions for the different treatments within a stand. Trees of equal diameter (and presumably sapwood area) have varying levels of foliage biomass depending on whether they were fertilized with nitrogen or thinned (greater foliage biomass) or not (less foliage biomass). This is contrary to the results of Long and Smith (1988) where tree size and distance to the center of the live crown accounted for site quality and density variability in the curvilinear leaf area – sapwood relationship (in untreated stands). Using additional dimensional characteristics (cf. Long and Smith 1988) would not work here where tree height and crown length have not been significantly affected 2 years after treatment (Tables 3 and 4) and where we examined similar-sized trees in stands of similar density (fertilized stands). The leaf area – sapwood ratio must change with these site quality differences (natural or thinning and fertilizer induced) or there is a significant time lag in stem size and foliage adjustment to treatment. The time lag for the leaf area – sapwood ratios to return to untreated levels may be substantial. For example, Brix and Mitchell (1983) found treatment differences in leaf area – sapwood relationships in thinned and fertilized Douglas-fir 9 years after treatment. They found that nontreated trees had the smallest slope, or the least foliage for a given tree size, while thinning, fertilization, and thinning with fertilization (in this order) significantly increased the regression slope, i.e., the foliage carried by similar-sized trees. Thus, the sapwood area approach does not appear reliable in predicting individual tree foliage biomass when treatments are applied.

Unfortunately, from a modelling perspective, this treatment-induced variation in foliage biomass for a tree of a given size makes it most difficult to predict individual tree foliage biomass, the missing variable in parameterizing a crown foliage distribution model. The quantity of foliage on a given sized tree varies with past treatment and, apparently, the treatment's effect on nutrient status of the tree. Thus, for loblolly pine, any estimation of crown biomass must be site and treatment specific, requiring some investment in destructive harvesting for allometric analysis.

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