

## Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine

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**Abstract:** We investigated above- and below-ground biomass allocation and allometric relationships of canopy dominant and suppressed loblolly pine (*Pinus taeda* L.) trees from a range of diameters at breast height (DBH = 3.5–35.6 cm) to determine if shifts in allocation may influence the growth and persistence of suppressed trees in the understory. Using mass and volume conversions from harvested trees (15 dominant and 15 suppressed), we developed regressions to predict total and component biomass from DBH. Bole, branch, needle, and total mass differed between dominance categories (ANCOVA,  $P < 0.10$ ). For a representative size (15 cm DBH), dominant trees allocated 63.4, 13.2, 11.3, and 12.0% of biomass to bole, branch, needle, and root tissue compared with 75.9, 6.7, 5.6, and 11.7% for suppressed trees. At any given DBH, suppressed trees were also taller than dominant trees and had a greater proportion of heterotrophic (bole plus branch plus root mass) to autotrophic (needle mass) tissue. Percent carbon and nitrogen of tissues did not differ between dominance categories. Unlike the increased investment in leaf area observed for seedlings and saplings of shade-tolerant species, suppressed loblolly pine increased allocation to bole mass and height growth. An increase in height for this shade-intolerant species may enable some suppressed individuals to escape competition for light. However, increased allocation to heterotrophic versus autotrophic tissue in suppressed trees may confer a cumulative disadvantage over time because of increased respiratory load.

**Résumé :** Nous avons examiné l'allocation de biomasse vers les parties aérienne et souterraine ainsi que les relations allométriques chez des pins à encens (*Pinus taeda* L.) dominants et supprimés dont le diamètre à hauteur de poitrine (DHP) variait de 3,5 à 35,6 cm. L'objectif consistait à déterminer si des changements dans l'allocation pouvaient influencer la croissance et la persistance des arbres supprimés en sous-étage. Grâce à des conversions de masse et de volume établies à l'aide d'arbres abattus (15 dominants et 15 supprimés), nous avons développé des équations de régression capables de prédire les diverses composantes de la biomasse et la biomasse totale à partir du DHP. La masse du fût, des branches, des aiguilles et la masse totale différaient selon l'étage (ANCOVA,  $P < 0,10$ ). Pour une dimension représentative (DHP de 15 cm), les arbres dominants allouaient respectivement 63,4, 13,2, 11,3 et 12,0% de la biomasse au fût, aux branches, aux aiguilles et aux racines comparativement à 75,9, 6,7, 5,6 et 11,7% chez les arbres supprimés. Pour un DHP donné, quel qu'il soit, les arbres supprimés étaient plus hauts que les arbres dominants et avaient une plus forte proportion de tissu hétérotrophe (masse du fût + branches + système racinaire) qu'autotrophe (masse des aiguilles). Le pourcentage de carbone et d'azote dans les tissus ne changeait pas en fonction de l'étage. Contrairement à un investissement accru dans la surface foliaire observé chez les semis et les jeunes tiges des espèces tolérantes à l'ombre, les pins à encens supprimés augmentaient leur allocation vers la masse du fût et la croissance en hauteur. Une augmentation en hauteur dans le cas de cette espèce de lumière peut faire en sorte que certains individus supprimés évitent de compétitionner pour la lumière. Cependant, une plus forte allocation vers les tissus hétérotrophes que vers les tissus autotrophes chez les arbres supprimés peut entraîner un désavantage cumulatif dans le temps à cause d'une charge respiratoire accrue.

[Traduit par la Rédaction]

### Introduction

Even-aged populations of trees may arise in the initial stages of forest succession or with the establishment of a plantation. In such populations, differences in seedling per-

formance quickly sort individual plants into canopy dominance categories (e.g., Nilsson and Albrektson 1994). Canopy category descriptions such as "dominant" and "suppressed" describe relative size or canopy position (e.g., Spurr and Barnes 1980). Suppressed trees experience greater competition for light, water, and nutrients (Kozłowski et al. 1991) than dominant trees. However, the functional consequences of these differences are not entirely clear.

Since tree stands self-thin over time, early establishment of dominance categories may determine which individuals survive to maturity (Weiner and Thomas 1986; Peet and Christensen 1987). Initiation of self-thinning depends on initial planting density and stand age (Fig. 1); therefore, suppressed trees may persist in the canopy for many years before mortality occurs. Understanding mechanisms by

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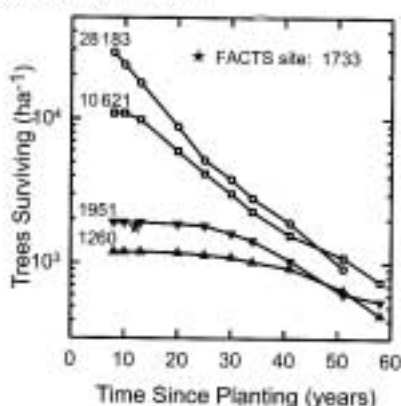
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**Table 1.** Site characteristics for harvested loblolly pine trees and the number of dominant (D) and suppressed (S) trees harvested from each site.

Site	No. of trees harvested		Age (years)	No. of stems ( $\text{ha}^{-1}$ )	Basal area ( $\text{m}^2\text{ha}^{-1}$ )	Average height (m)	Average DBH (cm)
	D	S					
Durham C-53	3	3	10	9386	39	5.8	5.7
Blackwood C-4	4	3	18	1371	42	14.6	17.5
Blackwood C-6	6	7	17	1445	44	13.1	18.7
Blackwood C-8	1	1	32	790	39	21.9	27.2
Blackwood C-12	1	1	48	420	35	22.4	35.4

Note: Site data were collected 2.5 years after harvesting.

**Fig. 1.** Survivorship versus age in even-aged loblolly pine stands of different initial planting densities. Initial density, to the left of each line, is reported as trees per hectare. Data are replotted from Peet and Christensen (1987). Density ( $1733 \text{ trees}\cdot\text{ha}^{-1}$ ) of loblolly pine at the Forest Air Carbon Transfer and Storage-1 (FACTS-1) research site in 1995 (prior to initiation of treatment) is indicated by a star. Only trees over 2.5 cm DBH were recorded at the FACTS-1 site whereas the original graph included trees down to 1.25 cm.



which suppressed trees survive in the understory or escape suppression may facilitate predictions of forest productivity under current and future environmental conditions.

Although it is well known that growth of trees can increase in response to disturbance events that increase resource availability, such as canopy gaps (e.g., Canham and Marks 1985) and thinning (e.g., Pothier and Margois 1991; Willey and Zeide 1992), mechanisms by which trees survive under long-term competition are less clear. Changes in allocation patterns may facilitate the persistence of suppressed trees under conditions of resource limitation. For example, competition for light can result in C deficiencies that may be offset by adjusting the balance of light-acquiring to nutrient-acquiring tissues (decreasing root to shoot ratio) or by decreasing the ratio of heterotrophic (boles, branches, and roots) to autotrophic (needles) tissue. Acquisition of water and nutrients may increase with root to shoot ratio, and a decrease in the leaf area to sapwood cross-sectional area ratio may indicate an increase in the ability to provision the canopy with water. Actual changes in the storage of limited resources such as C and N will be reflected by changes in percent C (%C) and N (%N) content of plant tissues. Also,

an increase in sapwood volume may indicate greater capacity for water storage. Such changes in the ability to acquire, store, or distribute limited resources may offset resource deficiencies (Cannell and Dewar 1994), thus facilitating persistence of suppressed trees in the understory.

The objective of this study was to determine if patterns of biomass allocation differ between canopy dominant and suppressed loblolly pine (*Pinus taeda* L.) trees. Since patterns of biomass allocation change as trees grow larger, we compared size-dependent allometries of dominant and suppressed trees from stands of different ages. Loblolly pine is shade intolerant (Baker and Langdon 1990); therefore, we expected allocation patterns in suppressed trees to be mostly driven by light limitation. Since overtopping by dominant neighbors is the primary cause of limited light interception, suppressed trees may preferentially allocate resources to height growth despite other potential resource deficiencies (King and Loucks 1978). To provide regression equations for nondestructively predicting growth of loblolly pine in response to elevated  $\text{CO}_2$ , we selected trees for this study of sizes that encompass those growing at the FACTS-1 (Forest Air Carbon Transfer and Storage-1) site, a Free-Air  $\text{CO}_2$  enrichment (FACE) experiment (Hendrey and Kimball 1994; Lewin et al. 1994) recently (August 1996) established in the Blackwood division of Duke Forest (Chapel Hill, N.C.). The FACTS-1 site is not yet in the self-thinning stage, and suppressed trees in this stand have 20–30 years before significant mortality will begin (Fig. 1).

## Materials and methods

### Tree selection

In September 1995, 15 canopy dominant and 15 suppressed loblolly pine trees were harvested from five sites (7–45 years old at the time of harvest) located within the Blackwood and Durham divisions of Duke Forest in the Piedmont region of North Carolina ( $35^{\circ}97'N$ ,  $79^{\circ}09'W$ ). These stands were established as plantations on soils of the Enon series but have not been managed since planting. Site characteristics were determined at the harvest locations in April 1998 (2.5 years postharvest); therefore, density was somewhat higher and basal area, height, and diameter at breast height (DBH, 140 cm) lower at the time of harvest than the reported values (Table 1). Trees were selected based on height and location of the live crown in relation to the canopy of surrounding trees. We defined dominant individuals as trees with a majority of the live crown within or above the canopy of surrounding trees. Suppressed trees had a majority of the live crown located in the lower portion or below the canopy of surrounding trees. The range of stand ages

provided trees with a range of DBH (3.5–35.6 cm). Harvests were conducted and regressions generated as in Callaway et al. (1994).

### Bole allocation

Prior to harvesting, diameter at 10 and 140 cm (DBH) above ground was recorded for root and whole-plant regressions, respectively. Breast height was marked as a reference point for measuring total tree and branch heights, and the tree was felled below this mark. Attachment height and basal diameter were recorded for each branch on the tree, as were height and diameter of the bole at the base of the live crown and total height of the tree. Thin discs (2–3 cm) were cut at 1-m intervals along the bole of the tree, and the outline of the bark (perimeter outline of the section), sapwood, the most recent 5-year growth interval, heartwood, and pith were traced onto clear acetate. Wood was stained with ferric chloride to differentiate sapwood from heartwood (Shelburne et al. 1993). The area of each component was determined by cutting out and weighing the traced section and multiplying by the specific area (square centimetres per gram) for each acetate sheet. Total and component volumes of the bole were determined using the formula for the volume of a frustum of a cone:  $V = \pi h / 3(r_1^2 + r_1r_2 + r_2^2)$ , where  $h$  is the height (1 m) of each bole segment and  $r_1$  and  $r_2$  are the radii of the bottom and top of the frustum. The mean radius at each metre section was calculated from the area of the disc. Total bole volume was derived by summing all sections for each tree.

Volume was converted to mass using the specific gravity (grams per square centimetre) of wood and bark. To determine the specific gravity of wood samples, a strip 2–3 cm wide was cut from the middle (passing through the center) of three discs per tree (one each from the bottom, middle, and top) and wood and bark were separated. Wood segments included sapwood, pith, and heartwood; bark segments included cortex. The volume of each wood and bark segment was determined by the displacement of water. Although specific gravity (density) of wood increased with height (ANCOVA;  $n = 76$ ,  $P < 0.05$ ) and that of bark decreased with height ( $n = 78$ ,  $P < 0.01$ ), there was no difference in these relationships between dominant and suppressed trees ( $P > 0.10$ ) (see Statistical analysis section), and the regressions had very low coefficients of determination (wood,  $r^2 = 0.07$ ; bark,  $r^2 = 0.12$ ). Therefore, mean wood density (0.427 g·cm<sup>-3</sup>) and bark density (0.279 g·cm<sup>-3</sup>) for dominant and suppressed trees combined were used to determine total and component biomass of the boles of each tree.

### Foliage and branch allocation

Needles on four arbitrarily selected branches per tree were removed and separated into cohorts (needles that emerged at different times). Stripped branches were then divided into primary (main axis attached to the bole), secondary (attached directly to primary), tertiary (attached directly to secondary), and quaternary (attached directly to tertiary) branches, and the total length of all branches in each branch order was measured. Primary branches were cut into 25- or 50-cm segments and total and sapwood diameter were measured in two perpendicular directions on the distal end of each segment. Cross-sectional areas of bark and sapwood were calculated from diameter measurements and were multiplied by the length of each segment to determine the total and component volumes of primary branches. Higher order branches were cut into small segments and total and sapwood diameter were measured on three to five segments. Average cross-sectional areas were multiplied by total length of branch in each branch order to determine total and component volumes, and branch mass was either directly measured or calculated from volume and specific gravity. Pith was included in sapwood estimates and cortex was included in bark estimates. None of the branches contained heartwood. Total mass, needle mass, wood mass (including bark), and sapwood volume of

branches were regressed against basal branch diameter and the resulting equations used to estimate total and component biomass of all branches on the tree (Table 2).

Fresh needle (3–10 fascicles) subsamples were collected from one to four of the harvested branches on a subset of trees (nine dominant and four suppressed) for determination of leaf area to dry mass regressions. For each fascicle, total length and diameter near the middle of each fascicle were measured by holding the needles together to form a cylinder. Assuming that the cross section of each needle was one third of the cylinder, total surface area (SA) of each needle was calculated as  $SA = [1/3(2\pi r) + 2r]L$ , where  $r$  and  $L$  are the radius and length of the entire fascicle. Projected leaf area of a needle is determined by the length and radius of the fascicle, the angle of the needle from horizontal, and the degree of rotation of the needle around its central axis. Assuming that all needles were horizontal, the average projected area was determined as a function of  $r$  and  $L$  by averaging the projected areas of the needle at each degree of needle rotation around the central axis from 1 to 360°. Mean projected needle area (PA) was thus calculated as  $PA = 1.30rL$ . Only projected needle areas are reported here, but a combination of the above equations reveals that  $SA = 3.15PA$ .

Needles present on the foliated portion of the bole (near the top of the tree) were collected, dried, weighed, and added to the values determined by the branch regressions to determine the total needle biomass on each tree.

### Root allocation

The roots of nine trees (four dominant and five suppressed) were excavated with a backhoe to estimate below-ground biomass. This sample size is insufficient to draw conclusions about potential differences in root allocation between dominant and suppressed trees, but enabled us to make preliminary estimates for coarse root allocation at this site. For each root system, the basal diameter of each primary lateral root (attached to the taproot) was recorded and the taproot was dried and weighed. The mass of the lateral roots was determined using a logarithmic regression of basal root diameter on dry mass ( $r^2 = 0.97$ ) generated from a subset ( $n = 20$ ) of lateral roots (lumping dominant and suppressed trees). The total mass of the root system was regressed against the diameter at 10 and 140 cm (DBH) above the soil. Both regressions were significant, so the regression on DBH ( $\log(\text{root}) = 1.368 + 2.064 \log(\text{DBH})$ ;  $n = 9$ ,  $r^2 = 0.82$ ) was used to simplify calculations, as most other parameters are regressed against this variable. This regression was then used to estimate the root biomass of each of the 30 original trees from their DBH.

### Growth analysis

Using the allometric relationships to calculate total biomass at the time of harvest and 5 years prior to harvest (using diameter estimated from tree rings), relative growth rate (RGR), leaf area ratio (LAR), and net assimilation rate (NAR) were calculated according to Hunt (1990). The three smallest trees in each dominance category were excluded from this analysis, as they were less than 5 years old. Growth analysis variables were then regressed against DBH and values computed for a theoretical tree of 15 cm DBH (see Table 4).

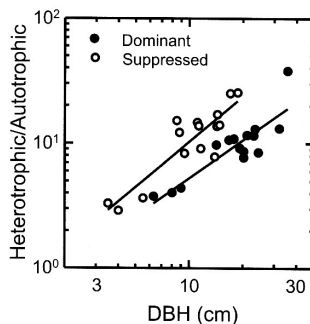
### Nutrient analysis

Tissue samples were oven-dried at 60°C to a constant mass and weighed to the nearest 0.01 g. Samples were ground in a Tecator Cyclotec 1093 sample mill, and subsamples were weighed (3–6 mg for needles and 8–12 mg for stems, bark, bole, and roots) into tin cups. Total C and N were determined following Dumas combustion with a Carlo Erba NA 1500 N, C, S elemental analyzer (Fisons Instruments, Valencia, Calif.).

**Table 2.** Allometric equations for branches of dominant (D) and suppressed (S) loblolly pine trees.

<i>Y</i>		$b_1$	$b_0$	$r^2$
Total branch mass (g)	D and S	2.505 ns	1.671 ns	0.97
Branch wood plus bark mass (g)	D	3.035 ns	1.152***	0.98
	S	3.049	1.123	0.96
Branch needle mass (g)	D and S	2.044 ns	1.484 ns	0.88
Branch sapwood volume (cm <sup>3</sup> )	D	3.289 ns	1.249***	0.99
	S	3.288	1.355	0.96

**Note:** Replicate sizes were four branches from each of 15 D and 15 S trees ( $n = 120$ ). Equations are in the form  $\log(Y) = b_1 \log(\text{basidia}) + b_0$ , where basidia is basal branch diameter (cm). Differences between D and S trees were tested with an ANCOVA. If the slopes (the interaction term) were not different ( $P > 0.10$ ), this term was dropped from the ANCOVA model to test for differences (\*\*\*,  $P < 0.01$ ) in the intercepts.

**Fig. 2.** Ratio of heterotrophic (bole plus branch plus root mass) to autotrophic (needle mass) tissue for dominant (solid circles) and suppressed (open circles) loblolly pine trees across a range of DBH. Regression equation coefficients and statistics are given in Table 3.

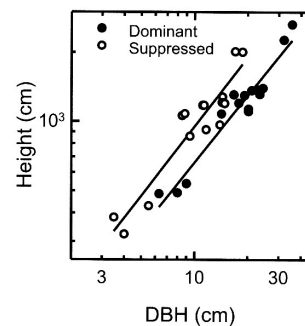
### Statistical analysis

Data were log-transformed before analysis because of the large range in tree size. Two outliers (with Student's residuals greater than three) were removed for the variable LAR and one was removed for RGR. Analysis of covariance (ANCOVA) was used to compare dominant and suppressed trees across a range of tree sizes. If the interaction term (slopes) was not significant ( $P > 0.10$ ), this term was dropped from the model to test for differences in intercept. If either intercepts or slopes were different ( $P < 0.10$ ), linear regression was performed for dominant and suppressed trees separately to obtain regression coefficients. Otherwise, dominant and suppressed trees were combined for regression analysis.

Nutrient data were analyzed with a nested analysis of variance (ANOVA) for each tissue component (needles, branches, bole wood, bole bark, and roots) separately. Sample size (see Table 5) varied according to the number of needle cohorts, branching orders, bole discs, and roots sampled from each tree. Samples were nested within branch, tree, and dominance category. Nutrient data were transformed where appropriate to meet the assumptions of the model. All procedures were performed using SAS statistical software (version 6.11, SAS Institute Inc., Cary, N.C.).

### Results

By harvesting trees from even-aged stands of different ages, we were able to generate a range of DBH for both dominant and suppressed trees. By using DBH as a covariate, we were able to examine potential allocation differ-

**Fig. 3.** Height versus DBH for dominant (solid circles) and suppressed (open circles) loblolly pine trees across a range of DBH. Regression equation coefficients and statistics are given in Table 3.

ences between dominant and suppressed trees independently of differences resulting from size alone.

For individual branches, the regressions of total branch mass (wood plus bark plus needles) and branch needle mass did not differ between dominant and suppressed trees ( $P > 0.10$ ); however, branches on dominant trees had greater wood plus bark mass and greater sapwood volume than those on suppressed trees across the range of branch sizes (equal slopes, different intercepts) (Table 2).

Biomass allocation differed between dominant and suppressed loblolly pine trees. The significant interaction between needle mass and DBH ( $P < 0.10$ ) coupled with no significant difference in intercept demonstrates that large dominant trees allocated more biomass to needles than large suppressed trees (Table 3). However, dominant trees of all sizes allocated less biomass to boles and branches than suppressed trees (no interaction, lower intercepts,  $P < 0.01$ ) (Table 3). Allocation to root biomass did not differ between dominant and suppressed trees (see Materials and methods). Total biomass (including bole, needle, branch, and root mass) for trees of the same diameter was greater in small suppressed trees than in small dominant trees ( $P < 0.05$ ), but a significant ( $P < 0.10$ ) interaction (slope) term indicated that for larger trees, this relationship converged (Table 3). Bole mass was, by far, the greatest component of total mass, with the majority of this being allocated to sapwood.

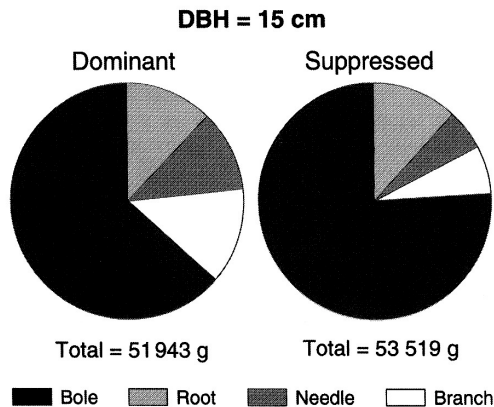
Suppressed trees also had a greater proportion of heterotrophic (bole plus branch plus root mass) to autotrophic (needle mass) tissue ( $P < 0.01$ ) (Table 3; Fig. 2)

**Table 3.** Equations of allometric relationships for dominant (D,  $n = 15$ ) and suppressed (S,  $n = 15$ ) loblolly pine trees.

Y	X		$b_1$	$b_0$	$r^2$
Bole mass (g)	DBH (cm)	D	2.708 ns	1.333***	0.98
		S	2.549	1.611	0.98
Needle mass (g)	DBH (cm)	D	1.567*	1.927 ns	0.92
		S	1.198	2.072	0.85
Branch mass (g)	DBH (cm)	D	2.308 ns	1.122***	0.92
		S	1.882	1.345	0.86
Total mass (g)	DBH (cm)	D	2.464*	1.830**	0.99
		S	2.250	2.082	0.98
Heterotrophic/autotrophic (g)	DBH (cm)	D	1.009 ns	-0.287***	0.90
		S	1.202	-0.190	0.82
Height (cm)	DBH (cm)	D	0.967 ns	1.854***	0.93
		S	1.002	1.976	0.88
Root mass (g)	Shoot mass (g)	D	0.811*	0.007*	0.99
		S	0.890	-0.369	0.98
Projected leaf area (cm <sup>2</sup> )	Sapwood area at the base of the live crown (cm <sup>2</sup> )	D and S	1.003 ns	2.923 ns	0.94
Sapwood volume/projected leaf area (cm <sup>3</sup> /cm <sup>2</sup> )	DBH (cm)	D	1.221 ns	-1.432***	0.80
		S	1.360	-1.313	0.80
Sapwood volume (cm <sup>3</sup> )	DBH (cm)	D	2.788*	1.597**	0.99
		S	2.558	1.929	0.98
Sapwood mass (g)	DBH (cm)	D	2.788*	1.228**	0.99
		S	2.558	1.560	0.98

**Note:** Equations are in the form  $\log(Y) = b_1 \log(X) + b_0$ . Differences between D and S trees were tested with an ANCOVA. If the slopes (the interaction term) were not different ( $P > 0.10$ ), this term was dropped from the ANCOVA model to test for differences (\*,  $P < 0.10$ ; \*\*,  $P < 0.05$ ; \*\*\*,  $P < 0.01$ ) in the intercepts.

**Fig. 4.** Proportional allocation of bole, root, needle, and branch biomass for a dominant and suppressed tree of equal DBH. Total and component masses (except for root mass) for the dominant and suppressed trees were calculated separately from regression equations reported in Table 3 prior to calculating percentages. Root mass for both trees was calculated from the same regression equation (see Materials and methods).



and were taller than dominant trees ( $P < 0.01$ ) (Table 3; Fig. 3) across the range of DBH. The ratio of root to total shoot (bole plus branch plus needle) biomass was less in small suppressed trees than in small dominant trees ( $P < 0.10$ ), although the greater slope in suppressed trees ( $P < 0.10$ ) indicates that this relationship was similar in larger trees (Table 3).

To determine the capacity for water transport and storage, we calculated the ratio of leaf area to sapwood area at the base of the live crown and the total amount of sapwood located in boles and branches of the tree. Dominant and suppressed trees had the same amount of projected leaf area per unit sapwood area at the base of the live crown ( $P > 0.10$ ) (Table 3). However, total sapwood volume (including bole and branch sapwood) per unit projected leaf area (calculated from leaf mass) was greater in suppressed trees than in dominant trees across all sizes ( $P < 0.01$ ) (Table 3). Total sapwood volume was also greater for small suppressed trees than for small dominant trees (intercept  $P < 0.05$ ), but the significantly greater slope in dominant trees ( $P < 0.10$ ) indicates that larger trees were similar (Table 3). Sapwood mass was calculated from sapwood volume and wood density (see Materials and methods); therefore, relationships between dominant and suppressed trees for sapwood mass and volume are the same (Table 3).

Bole, branch, and needle biomass were calculated separately from regression equations reported in Table 3 for a theoretical dominant and suppressed tree of equal size (15 cm DBH). Root mass for both categories of trees was calculated from the same regression equation (see Materials and methods). The resulting mass values were then used to calculate proportional allocation of component tissues for the theoretical trees. Total biomass was calculated by adding the biomasses derived from the component equations. Total biomass for a 15 cm DBH tree was similar, but dominant trees allocated 63.4, 13.2, 11.3, and 12.0% of biomass to bole, branch, needle, and root tissue compared with 75.9, 6.7, 5.6, and 11.7% for suppressed trees (Fig. 4).

**Table 4.** Reconstructed growth analysis for dominant (D,  $n = 12$ ) and suppressed (S,  $n = 12$ ) loblolly pine trees.

$Y$		$b_1$	$b_0$	$r^2$	Diameter = 15 cm
RGR ( $\text{g}\cdot\text{g}^{-1}\cdot\text{year}^{-1}$ )	D	-0.893 ns	0.417***	0.88	0.233
	S	-0.854	0.139	0.88	0.136
LAR ( $\text{m}^2/\text{g}$ )	D	-0.742***	-3.071 ns	0.99	$1.138 \times 10^{-4}$
	S	-0.859	-3.120	0.99	$7.409 \times 10^{-5}$
NAR ( $\text{g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ )	D	-0.281 ns	3.674**	0.27	2205
	S	-0.267	3.547	0.19	1710

**Note:** Relative growth rate (RGR), leaf area ratio (LAR), and net assimilation rate (NAR) were regressed against the estimated diameter 5 years prior to harvest (dia-5; see Materials and methods). Equations are in the form  $\log(Y) = b_1 \log(\text{dia-5}) + b_0$ . Differences between D and S trees were tested with an ANCOVA. If the slopes (the interaction term) were not different ( $P > 0.10$ ), this term was dropped from the ANCOVA model to test for differences (\*\*,  $P < 0.05$ ; \*\*\*,  $P < 0.01$ ) in the intercepts. Calculations are reported for a theoretical D and S tree of equal diameter 5 years ago.

**Table 5.** Mean, standard error (in parentheses), and total number of samples ( $n$ ) for %N, %C, and C/N of tissue from dominant (D) and suppressed (S) loblolly pine trees combined.

Tissue	$n$	%C	%N	C/N
<b>Needle cohort</b>				
All	454	51.5 (0.0)	1.25 (0.01)	43.1 (0.4)
1	118	51.0 (0.1)	1.43 (0.02)	36.4 (0.0)
2	118	51.5 (0.1)	1.30 (0.02)	40.6 (0.7)
3	97	51.7 (0.1)	1.12 (0.02)	47.5 (1.0)
4	69	51.8 (0.2)	1.09 (0.02)	49.2 (1.1)
5	18	51.9 (0.3)	0.97 (0.05)	55.7 (2.9)
6	4	51.6 (0.5)	0.97 (0.10)	55.2 (5.8)
On bole	30	51.5 (0.2)	1.28 (0.05)	42.0 (1.7)
<b>Branch order</b>				
All	312	51.0 (0.1)	0.49 (0.01)*	112.3 (1.8)*
1st	120	50.8 (0.1)	0.46 (0.01) <i>a</i>	115.2 (2.3) <i>a</i>
2nd	106	51.0 (0.1)	0.45 (0.01) <i>a</i>	121.4 (3.0) <i>a</i>
3rd	68	51.3 (0.2)	0.56 (0.02) <i>b</i>	102.3 (4.2) <i>b</i>
4th	18	51.4 (0.4)	0.73 (0.05) <i>c</i>	76.0 (5.0) <i>c</i>
<b>Bole</b>				
Wood	76	45.4 (0.2)	0.26 (0.00)	177.0 (3.8)
Bark	30	52.6 (0.3)	0.70 (0.01)	75.6 (1.3)
<b>Roots</b>				
All	29	50.0 (0.4)	0.37 (0.03)*	173.0 (20.0)*
Taproot	9	48.6 (0.8)	0.18 (0.02) <i>a</i>	288.6 (38.8) <i>a</i>
Lateral	20	50.7 (0.4)	0.46 (0.03) <i>b</i>	121.1 (10.8) <i>b</i>

**Note:** Nested ANOVA was performed on needles, branches, bole wood, bole bark, and roots separately. There were no significant differences ( $P > 0.05$ ) between D and S trees for any variable. %N and C/N differed between different branching orders and between lateral and taproots (\*,  $P < 0.05$ ); therefore, individual group means are also shown and significant differences are indicated by means followed by different letters.

Dominant trees had higher RGR and NAR over the 5 years prior to harvest than suppressed trees of all sizes (same slopes,  $P > 0.10$ ; greater intercepts,  $P < 0.01$  and  $P < 0.05$ , respectively). LAR was similar in small suppressed and dominant trees (same intercept,  $P > 0.10$ ), but a less negative slope for dominants ( $P < 0.01$ ) indicated that for larger trees, LAR was greater for dominants than for suppressed trees (Table 4). These differences are demonstrated by the values calculated for a dominant and suppressed tree of equal diameter (Table 4).

Nested ANOVA on each tissue individually showed no significant differences in %N, %C, or C/N between domi-

nance categories; therefore, dominant and suppressed trees were combined to calculate means for these variables. For bole bark, there were no significant differences for any variable. For needles and bole wood, the only significant differences were between trees nested within dominance category for each variable; for simplicity, all trees were combined to calculate means (Table 5). For branches (samples included both wood and bark) and roots (lateral and taproots), there were no significant differences in %C, but %N and C/N differed between branches nested within a tree, between different branching orders nested within branch, and between lateral and taproots within a tree (Table 5). All differences reported in this analysis are at the  $P < 0.05$  level.

## Discussion

Within a closed-canopy forest, suppressed trees compete for limited light, water, and nutrients, and this competition drives substantial changes in the pattern of biomass allocation (Cannell and Dewar 1994). Suppressed loblolly pine trees allocated proportionally more biomass to boles and less to foliage and branches than dominant trees of the same diameter (Fig. 4). Previous studies also reported greater allocation of biomass to boles and less to branches (Van Lear et al. 1984) or to needles and branches (Scots pine (*Pinus sylvestris* L.), Nilsson and Albrektson 1993) in trees under competitive stress.

Our regression equations for loblolly pine branches agree with Baldwin et al. (1997) and Gillespie et al. (1994). A branch of 1.9 cm basal diameter, representing the mean of all branches in this study, had a total branch biomass of 234 g compared with 252–289 g reported by Baldwin et al. (1997). Foliage biomass per branch ranged from 62 to 177 g (Baldwin et al. 1997) or from 38 to 133 g (Gillespie et al. 1994), depending on distance from the top of the tree, compared with 113 g in our study. In contrast with branch regressions reported in the literature, we did not use height of the branch as a covariant in our equations.

In general, our allometric equations predict lower total above-ground biomass for loblolly pine than Van Lear et al. (1984) and Baldwin (1987) for stands with similar ranges of age and DBH. For a theoretical 15 cm DBH tree, our regression equations yield 47 030 and 47 225 g of above-ground biomass for a dominant and suppressed tree, respectively, compared with 64 303 g (Van Lear et al. 1984)

and 52 163 – 142 763 g (depending on tree height and age as well as DBH; Baldwin 1987). Our estimates of total foliage biomass for a 15 cm DBH tree (dominant, 5888 g; suppressed, 3027 g) were greater than those of Van Lear et al. 1984 (1814 g) but within the range reported by Baldwin (1987) (1610 – 18 416 g) and Baldwin (1989) (3728 g). The variation in these data suggest that regression equations for loblolly pine are site specific. Differences in soil moisture and nutrient availability between sites may influence these allometric relationships.

Total biomass was different between dominant and suppressed trees, although differences were greater for smaller trees than for larger ones (Table 3). Furthermore, suppressed trees contain a greater proportion of heterotrophic to autotrophic tissue ( $P < 0.01$ ) across the range of DBH (Table 3; Fig. 2). Rather than facilitating persistence in the understory, this allocation pattern suggests that respiratory costs may be relatively higher for suppressed trees, which, when combined with greatly reduced access to light and soil resources over time, is likely to contribute to their death.

Although seedlings and saplings of shade-tolerant hardwood species growing in low light generally allocate proportionally more biomass to leaf tissue (Givnish 1988), this may not hold true for larger trees, or for shade-intolerant conifer species. Loblolly pine allocates less to leaves and branches and more to boles in light-limited suppressed trees than in dominant trees of the same diameter (Fig. 4). The lower allocation to leaf and branch tissue in suppressed trees was likely a result of self-pruning in this shade-intolerant species. Greater allocation to bole biomass in suppressed trees was also associated with greater height. Suppressed trees were taller than dominant trees of the same DBH (Fig. 3). Taller trees generally allocate less total biomass to foliage than shorter trees (Givnish 1988; Roberts and Long 1992). Greater allocation to bole biomass suggests that for shade-intolerant loblolly pine trees growing under light-limited conditions, the drive to reach the top of the canopy may make investment in height growth a priority over increasing needle biomass. Also, since suppressed trees are buried within the canopy, their greater height for a given DBH may be facilitated by protection from wind stress (Jacobs 1954; Larson 1965). Other studies have also demonstrated greater height to diameter ratios in suppressed trees (Holbrook and Putz 1989; Gavrikov and Sekretenko 1996).

The pipe model theory of plant form suggests that the amount of leaves on a tree is proportional to the cross-sectional area of the stem at the base of the live crown (Shinozaki et al. 1964a, 1964b; Waring et al. 1982). Leaf area and leaf mass are also proportional to DBH, which is often a more convenient parameter to measure (Espinosa Bancalari et al. 1987; Baldwin 1989). This may be particularly true when the amount of heartwood is limited, as in this study (Espinosa Bancalari et al. 1987). We used DBH to calculate foliage biomass, but to determine the capacity for water transport to foliage, we examined the ratio of projected leaf area to sapwood area at the base of the live crown. This ratio did not differ between dominant and suppressed trees (Table 3), suggesting that lower amounts of leaf biomass in suppressed trees were more likely a consequence of reduced light availability than of limitations in

water supply to the crown. Dean and Long (1986) also saw no difference in the ratio of sapwood area to leaf area for trees of different canopy class. Other studies have reported lower ratios of leaf area to sapwood area at the base of the live crown in suppressed trees (Thompson 1989) or trees growing under competitive stress resulting from increased stand density (Keane and Weetman 1987; Shelburne et al. 1993), although this relationship appears to level off at stand densities above 3000 trees-ha<sup>-1</sup> (Hungerford 1986).

Lower sapwood permeability with lower dominance class has been reported in loblolly pine trees (Shelburne et al. 1993; Shelburne and Hedden 1996), suggesting that water supply may be limited by an increase in wood density (Edwards and Jarvis 1982). Although an increase in wood density has been reported for lodgepole pine (*Pinus contorta* Dougl. ex Loud.) trees growing in high stocking density versus low stocking density stands (Pearson et al. 1984; Keane and Weetman 1987), wood density did not differ between dominance classes in the current study (see Materials and methods). This supports our conclusion that dominant and suppressed trees did not differ in their ability to supply the canopy with water in this system.

The ratio of total sapwood volume (including both bole and branch sapwood) to projected leaf area was greater in suppressed trees across the range of DBH (Table 3). This was a result of both less leaf area and greater sapwood volume for suppressed trees ( $P < 0.05$ ) (Table 3). Suppressed trees had more sapwood volume for a given DBH because they were taller (Fig. 3; Table 3). These data suggest that suppressed trees may have a greater capacity for water storage than dominant trees of the same DBH. However, the greater amount of sapwood volume in suppressed trees contributes to the increase in the ratio of heterotrophic to autotrophic tissue (see above), which may move these trees closer to negative C balance.

Because of small sample sizes for harvested roots, we were unable to compare coarse root allocation between dominant and suppressed trees. Van Lear and Kapeluck (1995) found dominant trees to have a greater proportion of total biomass in lateral roots (including fine roots) than suppressed trees for a loblolly pine stand of similar age. They also found greater allocation to total below-ground biomass (20%) and less to foliage (2%) than in our study (roots, 12%; foliage, 6–11%) (Fig. 4). Our estimates of below-ground allocation do not include fine roots. However, although seasonal production of fine roots can be high (Nadelhoffer and Raich 1992), they contribute little (2%) to total standing biomass (Van Lear and Kapeluck 1995) and thus are unlikely to explain differences in total below-ground allocation between the two studies or between dominant and suppressed trees. Also, trees in the Van Lear and Kapeluck (1995) study tended to be larger (16–46 cm DBH) than trees in our study (3.5–35.6 cm DBH), which may explain the greater below-ground allocation. Differences in allocation patterns between dominant and suppressed trees may develop as trees grow larger.

Nitrogen concentration and C/N in various tissues did not differ between dominant and suppressed trees, suggesting that N may not be limiting in suppressed trees at this site. Our N values were similar to others reported for loblolly pine (Shelton et al. 1984; Blinn and Buckner 1989 and

references within; Zhang and Allen 1996) but were generally at the higher end of the range.

Shifts in biomass allocation in suppressed loblolly pine trees are primarily a result of increased allocation to bole mass and increased height. This suggests that competition for above-ground resources is more important for driving allocation changes in suppressed trees than competition for below-ground resources at this site. If these patterns continue over time, it is possible that some suppressed individuals may succeed in reaching the canopy, thus insuring their long-term survival. Rather than facilitating persistence in the understory, however, the increase in the ratio of heterotrophic to autotrophic tissue may eventually result in a respiratory load that cannot be offset. This increase in respiratory load in suppressed trees may explain why they had lower RGR over the 5 years prior to harvest than dominant trees. RGR is approximately equal to the product of NAR and LAR. In this study, lower RGR is explained by both allocation differences (lower LAR) and physiological differences (lower NAR) in suppressed trees (Table 4). Lower NAR is likely a result of light limitations that reduce C gain in suppressed trees.

Differences in allocation patterns in dominant and suppressed trees may cause them to respond differently to potential environmental changes such as elevated atmospheric CO<sub>2</sub>. Investigation of plasticity in biomass allocation of established trees under elevated CO<sub>2</sub> is currently underway at the FACTS-1 research site in Duke Forest and will provide insight into the response of forest stands to future elevated concentrations of atmospheric CO<sub>2</sub>.

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