

Integrating within-crown variation in net photosynthesis in loblolly and slash pine families

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Summary We examined photosynthetic characteristics of two fast- and two slow-growing half-sib families of both loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* var. *elliottii* Engelm.) on two sites in northern Florida to: (1) quantify variation in light-saturated net photosynthesis (A_{\max}) associated with vertical crown position and foliage age; (2) quantify the amount and distribution of leaf area by foliage age class; and (3) determine whether photosynthetic indices, ranging from leaf-level through whole-crown A_{\max} , were related to growth differences among species and families. In both species, leaf-level A_{\max} was higher in more recently formed foliage both within the same year (where A_{\max} in the third flush averaged 10 to 30% higher than A_{\max} in the first flush) and between years (where A_{\max} in current-year foliage averaged 20 to 40% higher than A_{\max} in 1-year-old foliage). When expressed on a leaf area basis, A_{\max} of current-year foliage was higher in slash pine than in loblolly pine, but A_{\max} expressed on a mass basis did not differ between species. Loblolly pine had higher whole-tree leaf area than slash pine, whereas whole-tree A_{\max} did not differ between species. When the mean values for fast-growing families were compared with the mean values for slow-growing families, there were no differences in leaf-level characteristics, whereas at the whole-tree level, fast-growing families had higher leaf area and whole-tree A_{\max} than slow-growing families in both species. When comparisons were made among the individual fast- and slow-growing families, however, results were more variable. In both species, stem volume growth was strongly correlated with whole-tree A_{\max} , with most of the strength of the correlation deriving from the relationship between volume growth and tree leaf area.

Keywords: foliar nitrogen concentration, photosynthetic capacity, *Pinus elliottii*, *Pinus taeda*, specific leaf area.

Introduction

Growth in most forest tree species is moderately heritable; this fact has been successfully exploited in genetic tree improvement programs, resulting in enhanced growth rates and disease resistance of several commercial species. For example, genetically improved southern pines (primarily loblolly pine (*Pinus*

taeda L.) and slash pine (*Pinus elliottii* var. *elliottii* Engelm.)) currently being planted yield 20 to 40% more wood volume at rotation age than their unimproved predecessors (White et al. 1993, McKeand and Bridgwater 1998, McKeand et al. 2003). Although growth variation associated with genetic differences is well quantified for many forest tree species, the biological bases of these genetic differences among taxa (species, families and clones) are poorly understood (Martin et al. 2001).

Tree growth is a complex phenomenon that integrates many physiological processes. Of these processes, photosynthetic capacity and related indices of a tree's potential to fix carbon have received considerable attention as determinants of growth rate (e.g., Ledig and Perry 1967, Isebrands et al. 1988, Johnsen and Major 1995, Samuelson 1998, Will et al. 2001). Accordingly, some indicator of a tree's carbon fixation capacity, such as leaf net photosynthetic rate, tree crown size or stand leaf area index, is included in most process-based growth models (e.g., Host et al. 1990, Battaglia and Sands 1997, Landsberg and Waring 1997, Cropper 2000). Despite the expected linkage between carbon fixation and growth, however, studies examining this relationship have yielded conflicting results, showing weak or negative (Ledig and Perry 1967, Ottosen 1990, Samuelson et al. 1992, Marshall et al. 2001) as well as positive (Ceulemans and Impens 1983, Boltz et al. 1986, Major and Johnsen 1996) correlations between leaf net photosynthetic rate and plant growth. In some cases, measurements or indices that integrate photosynthetic capacity over space, time or both have been better correlated with growth than isolated measurements of leaf-level net photosynthesis that span short periods of time (Ledig and Perry 1969, Zelitch 1982, Boltz et al. 1986, Isebrands et al. 1988, Nicotra et al. 2003).

We examined photosynthetic characteristics of fast- and slow-growing half-sib families of loblolly pine and slash pine. These species occupy about 12×10^6 and 5.3×10^6 ha, respectively, in the southeastern USA (Sheffield and Knight 1982, Sheffield et al. 1983). Although the natural ranges of these species overlap (slash pine's range is contained within the range of loblolly pine) and both have considerable commercial value, there have been few studies comparing their photosynthetic characteristics (Samuelson 2000, Will et al. 2001)

and even fewer studies have examined net photosynthesis of slash pine in the field (Teskey et al. 1994, Will et al. 2001)

Our first objective was to quantify within-crown variation of light-saturated net photosynthetic rate (A_{\max}) in loblolly pine and slash pine to determine how vertical crown position and foliage age affect A_{\max} . Although many studies have described vertical variation in net photosynthesis in tree canopies, this information is better documented in loblolly pine (e.g., Gravatt et al. 1997, Maier et al. 2002) than in slash pine. In southern pines, formation of multiple growth flushes in a single season results in a complex foliage age structure. In some cases, juveniles may produce as many as seven or more flushes in one season (Lanner 1976) and retain these flushes for 18 months or longer (Hendry and Gholz 1986). Several reports have documented how A_{\max} varies between current-year and 1-year-old foliage in southern pines (Murthy et al. 1996, Ellsworth 2000, Will et al. 2001, Maier et al. 2002), but few papers have documented within-year (i.e., among flushes) variation in detail (Sasek et al. 1991).

Our second objective was to compare indices of carbon fixation among loblolly pine and slash pine half-sib families with contrasting growth rates. By calculating increasingly integrated indices of carbon fixation for each family, ranging from A_{\max} of a single flush of needles through estimated whole-crown A_{\max} , we hoped to determine whether incorporating additional information on within-crown variation in photosynthetic rates would be helpful in linking genetic differences in growth with underlying physiological and morphological drivers.

Our final objective was to make broad physiological genetic comparisons between loblolly pine and slash pine, to identify suites of traits (i.e., ideotypes; Donald 1968, Dickmann et al. 1994, Martin et al. 2001) that distinguish unique physiological phenotypes in these co-occurring species.

Materials and methods

Site description

Two installations of an experiment designed by the University of Florida's Cooperative Forest Genetics Research Program (CFGRP) were in their fourth and fifth growing seasons at the time of this study. Site 1 was located southeast of Palatka, FL, in Putnam County (29°42.1' N, 81°42.1' W) and Site 2 was located northwest of Dunnellon, FL, in Levy County (29°4.6' N, 82°33.0' W). In Year 1, both sites received fertilizer treatments of 280 kg ha⁻¹ of diammonium phosphate (50 kg ha⁻¹ N, 56 kg ha⁻¹ P) and 224 kg ha⁻¹ of potassium chloride (117 kg ha⁻¹ K). A subsequent application of fertilizer was made to Site 1 of 600 kg ha⁻¹ of N,P,K (10,10,10) + micronutrients in Year 3 (60 kg ha⁻¹ N, 26 kg ha⁻¹ P, 50 kg ha⁻¹ K). Glyphosate was applied to control competing vegetation, both before planting and during the first growing season at Site 1. Site 2 received only pre-planting herbicide treatments. In Year 1, insecticide treatments of esfenvalerate (AsanaXL, DuPont, Wilmington, DE), diomethorate or pyridine were applied to prevent infestation by tip moth (*Rhyacionia* spp.). Soils at Site 1 are in the

Adamsville series, classified as hyperthermic, uncoated Aquic Quartzipsamments, and composed of very deep, somewhat poorly drained, rapidly permeable fine sands without a spodic horizon. Site 2 soils are in the Smyrna series, classified as sandy, siliceous, hyperthermic Aeric Alaquods, and consist of very deep, poorly to very poorly drained sands with a spodic horizon located 33–71 cm below the surface. Mean monthly temperatures at both sites ranged from 14 to 27 °C (mean annual temperature 21 °C), with a mean annual rainfall of 1320 mm. Lopez-Upton et al. (2000) provide a detailed description of the experimental installations.

Genetic material and experimental design

The study was arranged in a randomized complete block, nested split-plot design, with three blocks per site. Families were planted in five-tree row plots that were grouped into species plots within blocks. Trees were planted 1.5 m apart in beds that were spaced 3 m apart, producing a planting density of 2222 trees ha⁻¹. At the time of the study, trees at Site 1 (where growth rates were higher) were nearing canopy closure, whereas trees at Site 2 were not. Two fast- (F) and two slow- (S) growing families of *P. taeda* and *P. elliotii* were selected for net photosynthetic measurements based on CFGRP and North Carolina State University Industry Cooperative Tree Improvement Program breeding values and 2-year-old tree height data from these study installations reported by Lopez-Upton (1999). One sample tree was randomly chosen from each selected family row plot in each block at each site. Trees with disease symptoms, stem deformities, or located in anomalous microenvironments (i.e., openings in adjacent planting positions or overshadowing by trees in adjacent planting positions) were excluded from sampling. During the study, the families designated as fast-growing had higher stem volume growth rates than the slow-growing families, confirming the validity of the fast- versus slow-growing family selection criteria. At the end of the study, mean heights of the loblolly and slash pine trees were 6.6 and 7.3 m, respectively.

Data were taken over three sampling periods to account for seasonal variation in both photosynthetic rates and phenology. Winter measurements were made from December 1998 to February 1999, summer sampling occurred from June to August 1999, and a fall sampling was taken from October to December 1999. To account for seasonal adjustments in physiology between sampling periods, Site 1 was measured first on each sampling occasion. Sites were sampled sequentially, with all data being collected at one site before measurements were begun at the next.

Leaf-level measurements

Light-saturated net photosynthesis was measured on all age classes of foliage on a single branch in both the upper and lower halves of the crown of each tree. Branches were assigned to upper and lower crown layers based on their attachment point to the stem. Sampling order of blocks within site, species within blocks, family within species and crown layer within families was selected at random. Within a crown layer, foliage was sampled in order from oldest growth flush to the

most recently formed for each of the 48 sample trees.

Light-saturated net photosynthesis was measured with a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, NE). In the winter and summer sampling periods, all gas exchange measurements were made with one system. In the fall sampling period, measurements were made with two identically configured instruments. Each instrument was assigned randomly to one of the species in each block, with operators assigned randomly to each instrument within each block, so that both operator and instrument error were confounded with the error term for species. About 10 cm² of all-sided leaf area (generally four fascicles from loblolly pine and six from slash pine) was detached and placed in the sample chamber within 20 s. Pilot studies indicated that carbon assimilation remained stable for at least 7 min after needles were detached from the tree. Other researchers have shown that detached *Pinus* fascicles yield results similar to those for attached needles (Samuelson et al. 1992, Porte and Loustau 1998, Samuelson 2000). Conditions within the sample chamber were: [CO₂] = 370 μmol mol⁻¹; block temperature = 20 °C (winter and fall sampling dates) or 25 °C (summer sampling dates); photosynthetic photon flux (PPF) = 2000 μmol m⁻² s⁻¹; and mean vapor pressure deficit (VPD), which was set to approximate the prevailing seasonal VPD, was 1.69, 2.05 and 1.49 kPa for the winter, summer and fall measurement periods, respectively. Fascicles were allowed to acclimate in the chamber for about 3 min, and measurements were recorded when the sum of the coefficients of variation (calculated on a 22.5 s moving window) for chamber [CO₂], chamber VPD and flow rate dropped below 0.3%. Data were expressed on an all-sided leaf area basis, which was calculated from measurements of fascicle radius, assuming that each needle formed a section of a cylinder.

After the gas exchange measurements in the fall sampling period, the needles were dried, ground and analyzed for total N concentration in an elemental analyzer (NCS 2500, CE Elantech, Lakewood, NJ). During the same sampling period, additional fascicles were collected for measurement of specific leaf area. Groups of about 20 fascicles for each cohort and flush on each sample branch were measured (excluding the fascicle sheath) as described previously for leaf area, and then dried and weighed.

Branch and tree leaf area

To account for the distribution of foliage among crown layers and age classes, total leaf area was measured on two branches of each sample tree in each sampling period. One representative branch in each of the upper and lower crown layers was selected, with care taken to include branches with a wide range of basal diameters. The foliated length of each foliage age class (flush) for all primary, secondary and tertiary branches on the sample branch was measured with a ruler. Fascicle density was calculated by counting the number of fascicles in a 5-cm length of foliated branch. Total number of fascicles per flush was counted if flush length was less than 5 cm, or if fascicles were sparsely or unevenly distributed along the foliated length. Total leaf area per flush was calculated by multiplying

mean fascicle area by the total number of fascicles per flush. Branch leaf area was determined by summing the foliage areas of each individual flush. These data were used to develop a regression model that predicted branch leaf area from inputs of sampling period, site, species, family, crown layer and branch basal area (R^2 of full model = 0.73, $n = 288$). Leaf area of all branches on each sample tree was then predicted from branch diameter measurements taken with digital calipers on each sample tree in each sampling period. Trees had an average of 35 living branches (range 20 to 62 branches). Leaf area of each crown layer was partitioned into foliage age classes based on the mean fractional distribution of foliage age classes from the foliage sample branches for each family for each sampling period. This approach invokes the simplifying assumption that the age class distribution on the sample branch was representative of all branches for that crown layer.

Expression of photosynthetic capacity

Comparison of A_{\max} among half-sib families was based on several indices of carbon fixation potential that were measured or calculated at the leaf level. The simplest index was A_{\max} of the first flush of foliage formed in the current growing season, designated $A_{\max(\text{cf})}$. The next level of integration accounted for variation in photosynthetic capacity when A_{\max} was averaged across all age classes of foliage present on any given tree and was designated the mean light-saturated photosynthetic rate, or $A_{\max(\text{m})}$. The most complex leaf-level index of carbon fixation potential was a weighted mean ($A_{\max(\text{wm})}$) that incorporated both functional variation in A_{\max} , as well as structural variation in terms of the relative amounts of foliage in each age class. This index was calculated by weighting A_{\max} of each age class of foliage by the fraction of leaf area occupied by that same age class.

To scale carbon fixation potential from the leaf-level to the tree-level, leaf area of individual foliage age classes from each crown position were combined with leaf-level A_{\max} values of those age classes. Crown-layer light-saturated photosynthetic capacity was calculated as:

$$A_{\max(k)} = \sum ((LA_{ij})_k (A_{\max(ij)})_k) \quad (1)$$

where $(LA_{ij})_k$ is the amount of leaf area represented by cohort i and flush j in crown layer k , and $(A_{\max(ij)})_k$ is equal to the corresponding light-saturated photosynthetic rate for the cohort/flush component ij in crown layer k . For each sample tree, $A_{\max(k)}$ for each crown layer was added to determine whole-tree light-saturated photosynthetic capacity ($A_{\max(\text{wt})}$), an estimate of the amount of carbon an entire tree could fix per second if all foliage were illuminated with saturating PPF. The equivalent calculation of $A_{\max(\text{wt})}$ was obtained by multiplying whole-tree leaf area (LA_{wt}) by $A_{\max(\text{wm})}$. Although the complete light-saturation conditions inherent in $A_{\max(\text{wt})}$ represent a biologically unrealistic situation, it sets a theoretical maximum carbon fixation capacity for each tree that incorporates both structural and functional information.

Data analysis

Statistical differences in measured parameters were subjected to analysis of variance (ANOVA) using the Mixed procedure of the SAS Version 8.0 statistical software package (SAS Institute, Cary, NC). Differences were declared significant at $\alpha < 0.05$. Single degree of freedom contrasts were used to test for differences between the means of the fast- and slow-growing families. Correlations of stem growth during the study with $A_{\max(\text{cf})}$, $A_{\max(\text{m})}$, $A_{\max(\text{wm})}$, LA_{wt} and $A_{\max(\text{wt})}$ were calculated to determine which expression of carbon fixation capacity was the best predictor of growth. For these correlations, stem growth was considered the stem volume gain from winter 1998–1999 to winter 1999–2000, as estimated by measurements of diameter along each meter of stem at the beginning and end of the study.

Statistical comparisons of within-crown variation in A_{\max} were difficult because of inherent imbalance in the data set caused by phenology and season. Consequently, we chose biologically relevant and nearly balanced data sets for some analyses to ensure that the hypotheses being tested by ANOVA were valid. To test A_{\max} for foliage cohort (year of formation) effects, a balanced data set was developed by averaging all upper-crown A_{\max} measurements of each cohort in the summer and fall sampling periods only (measurements from the winter sampling period were excluded because most foliage present was from only one growing season). To test A_{\max} for crown layer effects, a balanced data set was developed by taking the mean of leaf-level photosynthetic measurements of upper- and lower-crown foliage formed during the 1998 growing season.

Results

Phenological variation in A_{\max}

The total number of flushes (foliage age classes) present increased through the year for both species, from about three flushes in the winter sampling period to about five in the fall (Table 1). In the fall sampling, loblolly pine had a larger number of current-year flushes than slash pine (2.6 versus 2.1); for

all other sampling periods and foliage age categories, the species did not differ. Some trees of both species accumulated as many as nine age classes of foliage by the fall sampling period (Table 1). Upper-crown A_{\max} varied consistently with foliage age for both species, with the earliest formed foliage having lower A_{\max} than foliage formed later in the growing season (Figure 1, trend only for slash pine, statistically significant for loblolly pine, statistics not shown), and with current-year foliage having greater A_{\max} than previous-year foliage (Table 1). The differences in A_{\max} of current- and previous-year foliage were greatest during the fall sampling period. In loblolly pine, A_{\max} was 44% lower in 1-year-old foliage than in current-year foliage; slash pine showed a 31% reduction in A_{\max} from current-year to 1-year-old foliage (Table 1).

Effects of crown position on A_{\max} and foliar nitrogen concentration

Expressed on a leaf area basis, $A_{\max(\text{cf})}$ was significantly higher in slash pine than in loblolly pine ($P = 0.0083$), with rates of 5.0 and 5.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the upper- and lower-crown layers, respectively, compared with 4.2 and 3.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the upper- and lower-crown layers of loblolly pine, respectively (Table 2). Light-saturated net photosynthesis on a leaf area basis did not differ between the upper and lower crown in either species. When $A_{\max(\text{cf})}$ was expressed per unit leaf biomass, there were no differences in rates between species. Specific leaf area (SLA) was significantly higher in loblolly pine than in slash pine ($P = 0.0104$). In both species, SLA was higher in the lower crown than in the upper crown.

The effect of crown position on foliar nitrogen concentration ([N]) depended on whether [N] was expressed on a mass or leaf area basis. Leaf-area-based [N] ($[N]_{\text{LA}}$) did not differ between species, but differed between crown layers, with upper-crown foliage having 0.98 g N m⁻² versus 0.84 g N m⁻² in lower-crown foliage (Table 2). In contrast, dry-mass-based [N] ($[N]_{\text{LM}}$) did not vary by crown layer, but differed by species (12.2 g N kg⁻¹ DW for slash pine and 13.6 g N kg⁻¹ DW for loblolly pine).

Table 1. Seasonal variation in number of flushes in two cohorts of needles, and light-saturated net photosynthesis (A_{\max}) by cohort in loblolly and slash pine trees at two sites in north-central Florida. Data are from the upper-crown layer.

Sampling period	Number of foliage flushes present ¹			A_{\max} by cohort ² ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	
	1998 Cohort	1999 Cohort	Total (range)	1998	1999
<i>Loblolly pine</i>					
Winter	2.8	–	3.1 (2–5)	3.49	–
Summer	2.8	1.2	3.9 (3–5)	3.18 *	4.45 *
Fall	2.6	2.6 *	5.2 (3–9)	2.57 *	4.63 *
<i>Slash pine</i>					
Winter	2.6	–	2.8 (2–7)	3.61	–
Summer	2.5	1.1	3.6 (3–6)	3.53 *	4.39 *
Fall	2.7	2.1 *	4.8 (3–9)	3.52 *	5.08 *

¹ Within a column and sampling period, asterisks indicate a significant difference between species ($P < 0.05$).

² Values within a row followed by asterisks are significantly different ($P < 0.05$).

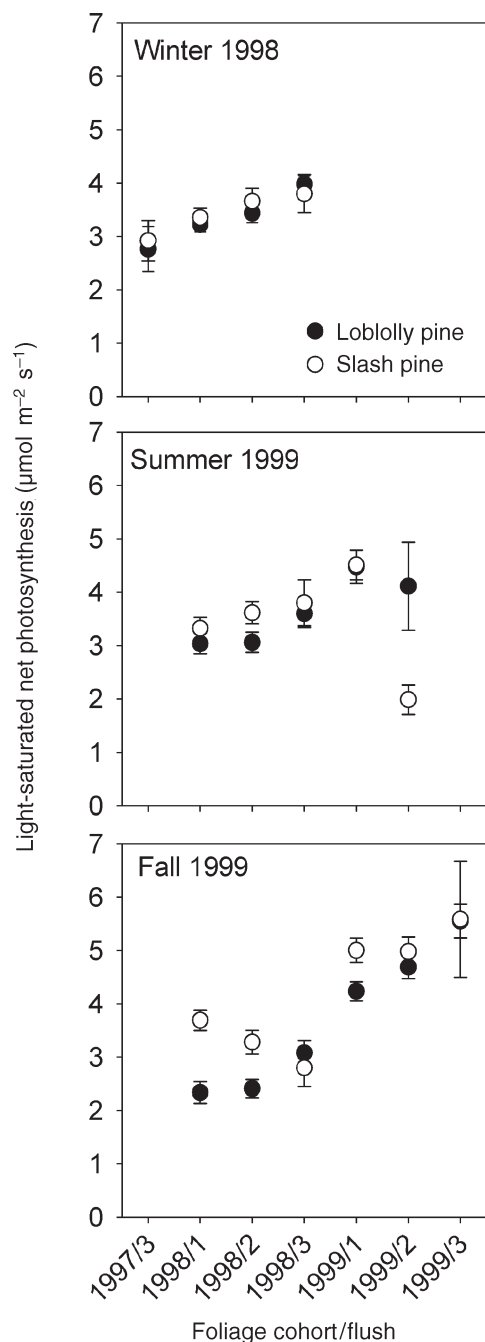


Figure 1. Variation in upper-crown light-saturated net photosynthesis with foliage age class for loblolly and slash pine trees during three sampling periods at two sites in north-central Florida. Error bars are SE, $n = 6$ for each symbol.

Photosynthesis–nitrogen relationships

The relationship between A_{\max} and foliar [N] varied depending on the units of expression of the two variables (Figure 2). The strongest relationship occurred when leaf-mass-based measures were regressed together: $[N]_{LM}$ explained 34% of the variation in mass-based A_{\max} (Figure 2A). Both measures of foliar [N] explained about 20% of the variation in area-based

A_{\max} (Figures 2C and 2D). The relationship between mass-based photosynthesis and $[N]_{LA}$ was not significant (Figure 2B). For all relationships, there was no effect of species or site on the regression parameters, so a single regression equation could be used to explain variation in photosynthetic rates of both species on both sites.

Species- and family-level variation

When expressed on a leaf area basis, leaf-level A_{\max} was consistently about 15% higher in slash pine than in loblolly pine, whether expressed as $A_{\max(cf)}$, $A_{\max(m)}$ or $A_{\max(wm)}$ (Tables 2 and 3). In contrast, mean whole-tree leaf area was 16% higher in loblolly pine than in slash pine ($P = 0.076$; Table 3). Whole-tree A_{\max} did not differ between species ($P = 0.725$; Table 3).

Among loblolly pine families, there were no differences in any of the leaf-level measures of photosynthetic capacity, whether the families were considered individually, or the mean of the fast-growing families was compared with the mean of the slow-growing families (Table 3). At the whole-tree level, however, the fast-growing loblolly pine families had higher mean LA_{wt} and $A_{\max(wt)}$ than the slow-growing families. This response appeared to be dominated by family F1, which generally had higher LA_{wt} and $A_{\max(wt)}$ than the other loblolly pine families.

The mean responses of fast- and slow-growing slash pine families were similar to those of loblolly pine, with no difference in any of the leaf-level indices between fast- and slow-growing families, but with fast-growing families having, on average, higher LA_{wt} and $A_{\max(wt)}$ than the slow-growing families (Table 3). When families were considered individually, S1 had lower $A_{\max(cf)}$ and $A_{\max(wm)}$ than the other slash pine families.

Stem volume growth during the study was highly correlated with LA_{wt} and $A_{\max(wt)}$ for both species during all measurement periods (Pearson correlation coefficient from 0.73 to 0.83, Table 4). In almost every species \times season combination, LA_{wt} was more highly correlated with stem volume growth than was $A_{\max(wt)}$. During the summer, leaf-level indices of carbon fixation potential ($A_{\max(cf)}$, $A_{\max(m)}$ and $A_{\max(wm)}$) were moderately correlated with stem volume growth in both species (correlation from 0.35 to 0.58, Table 4); during the winter and fall, there was no correlation between the leaf-level measures and stem volume growth. Stem volume growth was not correlated with any measure of foliar [N] (data not shown).

Discussion

We examined carbon fixation capacity of loblolly pine and slash pine, as well as among families within each species. For the among-family comparisons, we examined indices of carbon fixation capacity at both the leaf level and the whole-tree level. This approach incorporated variation in leaf A_{\max} associated with leaf age and crown position with the quantity and distribution of leaf area in each foliage age class. Most physiological genetics comparisons of carbon fixation capacity have either focused on leaf-level A_{\max} of one or two standardized foliage age classes (e.g., Johnsen et al. 1999, Yang et al. 2002) or

Table 2. Upper- and lower-crown light-saturated net photosynthesis of current-year foliage ($A_{\max(cf)}$), foliar nitrogen concentration ([N]) and specific leaf area (SLA) of loblolly pine and slash pine at two sites in north-central Florida, and *P* values for the species and layer main effects and their interaction for each variable. Values in parentheses are SE. Data are from the fall measurement period.

Species	Crown layer	$A_{\max(cf)}$ ($\mu\text{mol m}^{-2}$ leaf area s^{-1})	$A_{\max(cf)}$ (nmol g^{-1} leaf biomass s^{-1})	Foliar [N] (g m^{-2} leaf area)	Foliar [N] ($\text{g kg}_{\text{DW}}^{-1}$)	SLA ($\text{cm}^2 \text{g}^{-1}$)
Loblolly pine	Upper	4.2 (0.9)	64.7 (14.1)	0.94 (0.22)	13.8 (1.7)	155.5 (49.1)
	Lower	3.9 (1.0)	74.2 (27.0)	0.77 (0.26)	13.4 (1.6)	187.3 (62.0)
Slash pine	Upper	5.0 (1.1)	65.6 (16.0)	1.01 (0.30)	11.9 (1.0)	128.1 (34.0)
	Lower	5.1 (1.2)	67.2 (14.7)	0.90 (0.15)	12.4 (1.3)	131.1 (19.8)
<i>Significance levels</i>						
Species		0.0083	0.25	0.11	0.0076	0.010
Layer		0.54	0.093	0.0023	0.13	0.048
Species \times layer		0.24	0.29	0.74	0.71	0.12

have investigated crown-level structural characteristics like leaf area index or leaf angle distribution without incorporating leaf-level physiology (e.g., McCrady and Jokela 1998, Xiao et al. 2003). Although these single-scale studies are informative,

genetics comparisons that integrate detailed leaf-level photosynthesis data to the crown scale afford more detailed information about the mechanisms underlying genetic differences in growth performance (Ledig and Perry 1969, Zelitch 1982,

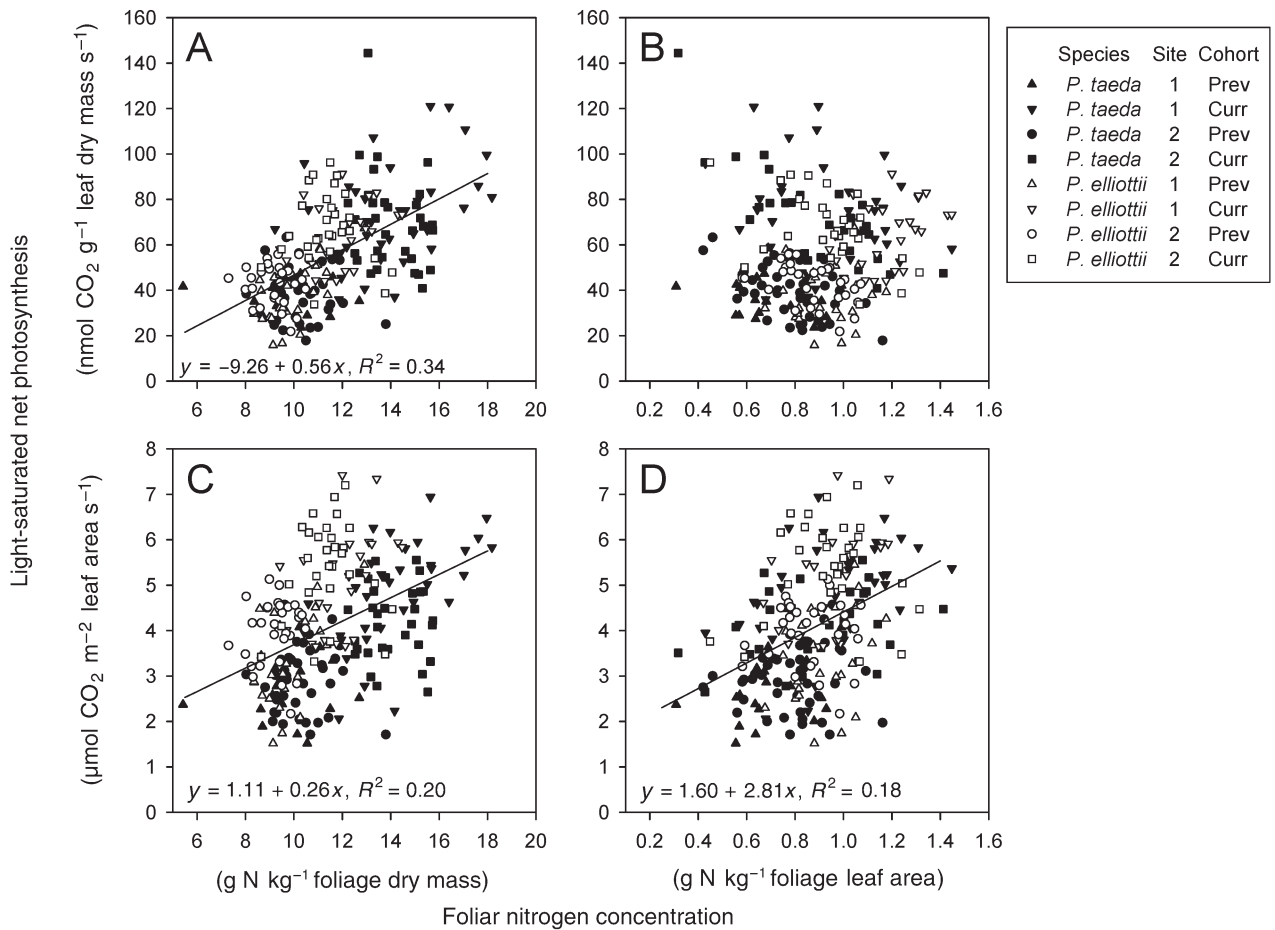


Figure 2. Relationships among leaf area (C and D) and leaf-mass-based light-saturated net photosynthesis (A and B), and leaf area (B and D) and leaf-mass-based foliar nitrogen concentration (A and C) for current-year (Curr) and previous-year (Prev) foliage of loblolly and slash pine trees at two sites in north-central Florida. Measurements are from the fall sampling period, $n = 288$.

Table 3. Variation of indices of carbon fixation for fast- (F) and slow-growing (S) half-sib families of loblolly and slash pine on two sites in north-central Florida. Data are averaged across winter, summer and fall measurement periods and across sites. Within a species and column, family means followed by the same lower case letter are not significantly different ($P > 0.05$). Abbreviations: A_{\max} = light-saturated net photosynthesis; $A_{\max(\text{cf})}$ = current-year foliage A_{\max} ; $A_{\max(\text{m})}$ = A_{\max} averaged across all flushes; $A_{\max(\text{wm})}$ = weighted mean A_{\max} ; LA_{wt} = whole-tree leaf area; and $A_{\max(\text{wt})}$ = whole-tree A_{\max} .

	Leaf level			Whole-tree level	
	$A_{\max(\text{cf})}$ ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	$A_{\max(\text{m})}$ ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	$A_{\max(\text{wm})}$ ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	LA_{wt} (m^2)	$A_{\max(\text{wt})}$ ($\mu\text{mol CO}_2 \text{ s}^{-1}$)
<i>Loblolly pine</i>					
Species mean	3.70	3.28	3.47	55.6	193.81
Family F1	3.69 a	3.26 a	3.40 a	69.5 a	241.05 a
Family F2	3.69 a	3.27 a	3.53 a	51.6 b	183.70 b
Family S1	3.41 a	3.15 a	3.35 a	47.4 b	153.46 b
Family S2	4.01 a	3.43 a	3.58 a	54.0 b	197.01 ab
<i>P</i> value (Fast versus slow family contrast)	0.96	0.88	0.97	0.011	0.039
<i>Slash pine</i>					
Species mean	4.28	3.77	3.93	47.9	188.24
Family F1	4.44 a	4.00 a	4.20 a	57.9 a	238.31 a
Family F2	4.57 a	3.84 a	4.02 a	50.4 ab	200.68 ab
Family S1	3.76 b	3.44 a	3.54 b	41.9 b	150.07 c
Family S2	4.33 a	3.80 a	3.94 ab	41.4 b	163.91 bc
<i>P</i> value (Fast versus slow family contrast)	0.099	0.53	0.48	0.0013	0.0007
<i>P</i> value (Species main effect)	0.0083	0.013	0.011	0.076	0.72

Boltz et al. 1986, Isebrands et al. 1988). Our leaf-level data provided insight into the sources of variation in A_{\max} in young southern pine crowns, and provided the basis for integrating A_{\max} data upward in scale, enabling comparisons among fast- and slow-growing families at the whole-tree level.

Foliage age effects on A_{\max}

Southern pines have a recurrent foliage production pattern, in which the initial, pre-formed foliage flush in the spring is followed by one or more additional flushes (Lanner 1976). Once produced, the life span of needles in these species is 18 to 24 months (Hendry and Gholz 1986, Sasek et al. 1991). These phenological characteristics lead to a complex and dynamic foliage age structure. In our study, trees held approximately three age classes of foliage in the winter, most of which were formed the previous spring (Table 1). As the subsequent growing season progressed and new flushes from the 1999 cohort were added to the aging flushes from the 1998 cohort, the total number of flushes present increased. By fall, the period of peak leaf area development in these species (Gholz et al. 1991, Martin and Jokela 2004), trees carried an average of five foliage flushes, with as many as nine age classes on some trees (Table 1). Several conifers bear many distinct foliage age classes at the same time (e.g., *Abies amabilis* (Brooks et al. 1996), *Picea abies* (Stenberg et al. 1995), *Pinus contorta* Dougl. ssp. *latifolia*, (Schoettle and Smith 1998), *Pseudotsuga menziesii* and *Abies grandis* (Balster and Marshall 2000), *Pinus sylvestris* (Molchonov 2000)), but in most cases, this variation results from the determinate production of one pre-

formed growth flush of foliage per year that lives for several years. In contrast, southern pines tend to produce many distinct age classes of foliage that have a relatively short (~18 months) life span.

Southern pine A_{\max} varies with foliage age, with most studies demonstrating that needles formed in the year of measurement have higher A_{\max} than needles from the previous growing season (Murthy et al. 1996, Ellsworth 2000, Will et al. 2001, Maier et al. 2002). Similarly, we found that A_{\max} of current-year foliage was 40 and 24% higher than that of the previous-year foliage in loblolly and slash pine, respectively, in summer (Table 1). By fall, the difference in A_{\max} had increased to 80 and 44% for loblolly and slash pine, respectively (Table 1). Light-saturated net photosynthesis also varied by foliage age within a growing season, with the first flush in a year generally having lower A_{\max} than foliage formed later in the year (Figure 1), except in cases when foliage was near the beginning or end of its life span. For example, in summer 1999, A_{\max} of the second flush of the current-year cohort was considerably lower than the first formed flush of that year (Figure 1), probably because that foliage flush was still expanding and had not reached the A_{\max} typical of mature, fully developed leaves (Radoglou and Teskey 1997). The decline in A_{\max} with foliage age is partially developmental: A_{\max} typically increases as leaves develop, peaks near the time of foliage maturity, and then declines as leaves age and resources, especially mineral nutrients, are retranslocated to newer, expanding foliage (Chabot and Hicks 1982, Radoglou and Teskey 1997). However, changing light environments probably also induce down-

ward acclimation of A_{max} in aging foliage, which tends to become increasingly shaded as foliage develops higher in the crown (Brooks et al. 1994, Schoettle and Smith 1998). No studies have yet decoupled aging or senescence effects from shade acclimation effects on A_{max} in southern pine foliage.

Crown position effects on A_{max}

Foliage formed in low light often has lower A_{max} compared with foliage formed in bright microenvironments, and also generally has different morphological and biochemical characteristics, such as higher SLA and lower leaf [N] (Shelton and Switzer 1984, Cregg et al. 1993, Groninger et al. 1996, Stenberg et al. 1998, Jose et al. 2003, Nippert and Marshall 2003). Many studies have demonstrated significant declines in A_{max} from upper- to lower-crown foliage in southern pines (e.g., Tang et al. 1999, Maier et al. 2002) and in other conifers (Bond et al. 1999). In our study, SLA was higher in lower-crown needles than in upper-crown needles ($P = 0.048$; Table 2), and $[N]_{LA}$ declined from the upper to lower crown ($P = 0.0023$, Table 2). The change in $[N]_{LA}$ was caused solely by a shift in SLA, because $[N]_{LM}$ did not differ between the upper and lower crown. Although leaf morphology and chemistry changed in a predictable direction with crown position, there was no difference in $A_{max(cf)}$ between the upper and lower crown, whether expressed on a leaf area or a leaf mass basis (Table 2). It may be that, in this relatively young pine canopy, interception of light by the upper crown is sufficient to induce changes in lower-crown SLA and leaf [N], but is not yet large enough to cause detectable changes in A_{max} . Pine canopy structure is nonrandom, with considerable aggregation of foliage that results in less attenuation of radiation at a given leaf area index than would occur in species with a more random foliage distribution (Stenberg et al. 1994, Chen 1996).

Foliar nitrogen effects on A_{max}

In the fall measurement period, mass-based A_{max} of both loblolly pine and slash pine was moderately correlated with $[N]_{LM}$ ($R^2 = 0.34$; Figure 2A). Correlations of leaf area-based A_{max} with both $[N]_{LM}$ and $[N]_{LA}$ were also significant, although not as strong (Figures 2C and 2D). A positive response of A_{max} to foliar [N] has been observed in several species (Brix 1971, Evans 1989, Mitchell and Hinckley 1993, Bond et al. 1999), and many process models utilize foliar [N] as a scalar for integrating photosynthetic processes from leaves to canopies (e.g., Kull and Jarvis 1995, Leuning et al. 1995, Williams et al. 1996, Lai et al. 2002). However, a strong A_{max} -leaf [N] relationship may not exist for southern pines. Although several studies have reported a positive response of loblolly pine A_{max} to foliar [N] (Tjoelker and Luxmoore 1991, Green and Mitchell 1992, Tissue et al. 1993, Murthy et al. 1996, Samuelson 2000, Lai et al. 2002, Yang et al. 2002), other studies have shown little or no relationship between the two variables (Samuelson 1998, Tang et al. 1999, Samuelson et al. 2001, Munger et al. 2003). Maier et al. (2002) found that the strength and slope of the A_{max} -leaf [N] relationship varied seasonally. Studies with other conifers have also failed to show a strong A_{max} -leaf [N]

Table 4. Pearson correlation coefficients between stem volume growth (SVG; dm^3) over the course of the 2-year study and light-saturated net photosynthesis of current-year foliage ($A_{max(cf)}$), light-saturated net photosynthesis averaged over all foliage age classes ($A_{max(m)}$), light-saturated net photosynthesis expressed as a mean weighted by the proportion of leaf area in each foliage age class ($A_{max(wm)}$), whole-tree leaf area (LA_{wt}) and whole-tree light-saturated net photosynthesis ($A_{max(wt)}$) in each of the winter, summer and fall sampling periods for loblolly pine and slash pine on two sites in north-central Florida. Differences are considered statistically significant at $P < 0.05$.

	Winter					Summer					Fall				
	$A_{max(cf)}$	$A_{max(m)}$	$A_{max(wm)}$	LA_{wt}	$A_{max(wt)}$	$A_{max(cf)}$	$A_{max(m)}$	$A_{max(wm)}$	LA_{wt}	$A_{max(wt)}$	$A_{max(cf)}$	$A_{max(m)}$	$A_{max(wm)}$	LA_{wt}	$A_{max(wt)}$
Loblolly pine SVG	0.12	0.13	0.15	0.83	0.76	0.42	0.52	0.35	0.79	0.73	-0.19	-0.25	-0.17	0.80	0.52
P value	0.58	0.53	0.31	0.0001	0.0001	0.044	0.0097	0.015	0.0001	0.0001	0.38	0.24	0.27	0.0001	0.0095
Slash pine SVG	0.23	-0.09	0.12	0.79	0.79	0.58	0.56	0.58	0.73	0.75	-0.05	-0.10	0.02	0.81	0.77
P value	0.28	0.67	0.41	0.0001	0.0001	0.0029	0.0040	0.0001	0.0001	0.0001	0.81	0.65	0.90	0.0001	0.0001

relationship (Kloppell et al. 2000, Nippert and Marshall 2003). Although the scatter in Figure 2A is considerable, foliar [N] explains about a third of the variation in A_{\max} from widely varying genetic stock, crown positions, age classes and sites.

Genetic variation

Leaf structural and functional characteristics varied strongly between species. Leaf-area-based A_{\max} was higher in slash pine than in loblolly pine, regardless of how A_{\max} was averaged over crown layers or foliage age classes (Tables 2 and 3). In contrast, Samuelson (2000) and Will et al. (2001) reported no difference in A_{\max} between young loblolly and slash pine trees. Variation in leaf-area-based A_{\max} was linked to differences in SLA between species: mass-based A_{\max} was similar in both species, but loblolly pine had higher SLA than slash pine (Table 2). Mass-based foliar [N] was also higher in loblolly pine than in slash pine. Will et al. (2001) reported similar patterns of variation in SLA and foliar [N] in the same species. Species-level differences in SLA are generally linked to the development of higher leaf area in individual loblolly pine trees and higher leaf area indices in loblolly pine stands compared with slash pine trees and stands (Dalla-Tea and Jokela 1991, Jokela and Martin 2000, Will et al. 2001), and our results are consistent with this trend: LA_{wt} was, on average, 16% higher in loblolly pine than in slash pine ($P = 0.076$; Table 3). The species differences in leaf-level photosynthesis and tree-level leaf area were opposing and of similar magnitudes. As a result, $A_{\max(wt)}$, which is the product of $A_{\max(wm)}$ and LA_{wt} , did not differ between species ($P = 0.72$; Table 3). These results define contrasting physiological ideotypes for the two species: given equal amounts of crown foliage biomass, slash pine, with its lower SLA, will produce less leaf area with a greater rate of net photosynthesis per unit leaf area, whereas loblolly pine will produce more leaf area with a lower rate of photosynthesis per unit leaf area. Both combinations of traits will tend to produce a similar potential for crown-level carbon fixation.

Although comparison of species-level traits revealed easily interpretable patterns, there were few consistent trends in carbon fixation capacity at the leaf-level among fast- or slow-growing families within each species (Table 3). For loblolly pine, none of the families differed in any of the leaf-level carbon fixation indices. In slash pine, family S1 had lower $A_{\max(cf)}$ and $A_{\max(wm)}$ than either of the fast-growing families, but the second slow-growing family did not differ in leaf-level A_{\max} from the fast-growing families. At the whole-tree level in both loblolly and slash pine, fast-growing families on average had higher LA_{wt} and $A_{\max(wt)}$ than slow-growing families. The mean responses of fast- and slow-growing families suggest that there are whole-tree characteristics that are consistently associated with rapid growth, but analysis of individual families was more ambiguous. For example, loblolly pine family F1 had higher $A_{\max(wt)}$ than families F2 and S1, but similar whole-tree A_{\max} to family S2. Slash pine families showed similarly mixed results when considered individually. Of the eight half-sib slash pine families examined, only family S1 showed a consistent relationship between indices of C fixation (other than

LA_{wt}) and growth, and this family had the lowest leaf-level A_{\max} , low LA_{wt} and low $A_{\max(wt)}$ (Table 3). The S1 family might be characterized as one in which low photosynthetic rates, combined with low rates of leaf area accretion, result in slow growth rates. For the other families, variation in growth rates was attributable to factors other than leaf-level photosynthetic rates, such as whole-tree leaf area (Table 3), or variable allocation of C to roots (Bongarten and Teskey 1987, Johnsen et al. 1996).

In addition to analyzing mean family-level growth and photosynthetic characteristics, we examined the correlation of individual tree stem volume growth with carbon fixation indices (Table 4). In all sampling seasons, stem volume growth was highly correlated with both LA_{wt} and $A_{\max(wt)}$. Because the correlation of volume growth with LA_{wt} was almost always higher than the correlation with $A_{\max(wt)}$, and LA_{wt} is a component of $A_{\max(wt)}$, it appears that, in the winter and fall, greater growth is primarily associated with higher LA_{wt} , and not with photosynthetic characteristics at the leaf- or tree-level. Similarly, other studies have shown that leaf area development is more important than leaf-level photosynthetic rates in determining southern pine growth (Samuelson 1998, Maier et al. 2002, Yang et al. 2002, Munger et al. 2003). However, our summer data require a different interpretation, because the summer leaf-level photosynthetic measurements were also correlated with stem volume growth (Table 4), suggesting a role for leaf dark respiration in determining C fixation and growth. It is known that conifer foliage acclimates to changes in temperature by decreasing basal maintenance respiration rates as the prevailing temperature increases (Rook 1969, Teskey and Will 1999, Tjoelker et al. 1999, Will 2000). If some genotypes have increased plasticity in their acclimation of leaf maintenance respiration to elevated summer temperatures, they might be expected to maintain higher A_{\max} during the summer months, and as a result could have greater net C fixation and perhaps growth than trees that did not acclimate as readily and therefore have higher foliage maintenance respiration costs. Some evidence suggests that foliar respiratory costs can influence growth of different southern pine taxa (Samuelson 2000).

In conclusion, we identified several cases where southern pine taxa (species or families) demonstrated unique suites of traits that could be linked to some aspect of growth performance or C gain. In the case of loblolly pine and slash pine, contrasting species-specific combinations of leaf morphology, leaf physiology and whole-tree leaf area produced similar potential C fixation. In the case of slash pine family S1, low leaf-level net photosynthetic rates combined with reduced tree-level leaf area production likely contributed to the below-average growth of this taxon. In other cases, family-level growth appeared to be influenced primarily by leaf area. We also demonstrated that the suite of morphological, phenological and physiological traits controlling carbon fixation and growth may vary depending on the taxon.

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