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Environmental and genetic effects on crown shape in young loblolly pine plantations

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Abstract: Tree crown shape is an important trait affecting the light environment in forest canopies. We examined genetic and environmental effects on outer crown shape of young single-family stands of loblolly pine (*Pinus taeda* L.). Crown diameter profiles were measured after canopy closure at four experimental sites in the southeastern US. The two examined families of contrasting aboveground productivity differed in crown length but not in their outer crown shapes or crown shape ratios, defined as the ratio of crown diameter to crown length. Within each site, intensive silvicultural treatment, consisting of fertilization and control of competing vegetation, had little effect upon crown shape. A strongly significant effect of site on crown shape parameters was found in the family grown at all four experimental sites; however, density differences among the experimental series likely accounted for a part of the across-sites variation in crown shape. In contrast to other studies on crown shape in trees, and to findings at age 2 years in the same stands, we conclude that family effects on the outer crown shape were small compared with the environmental effects in these 5-year-old pine plantations, following canopy closure.

Résumé : La forme de la cime des arbres est un trait important qui influence l'environnement lumineux dans la canopée des forêts. Nous avons étudié les effets d'ordre génétique et environnemental sur la forme de la partie externe de la cime dans de jeunes peuplements composés de pin à encens appartenant à une même famille. Des profils du diamètre de la cime ont été mesurés après la fermeture du couvert dans quatre stations expérimentales situées dans le sud-est des États-Unis. Deux familles dont la productivité aérienne était différente ont été étudiées. Elles se distinguaient par la longueur de la cime mais non par la forme de la partie externe de la cime, c'est-à-dire le rapport du diamètre de la cime sur sa longueur. Dans chaque station, des traitements sylvicoles intensifs, incluant la fertilisation et la maîtrise de la végétation, ont eu peu d'effet sur la forme de la cime. Un effet très significatif de la station sur les paramètres de la forme de la cime a été noté dans le cas de la famille établie dans les quatre stations expérimentales. Cependant, des différences de densité entre les séries expérimentales expliquaient probablement une partie de la variation dans la forme de la cime d'une station à l'autre. Contrairement aux résultats d'autres études sur la forme de la cime des arbres et à ceux qui ont été obtenus dans les mêmes peuplements lorsqu'ils étaient âgés de deux ans, une fois le couvert fermé dans ces plantations maintenant âgées de cinq ans, nous concluons que la forme de la partie externe de la cime est influencée par des facteurs d'ordre environnemental beaucoup plus que génétique.

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Introduction

Crown shape, together with total leaf area and its distribution within the crown, affects light interception and photosynthesis in a forest canopy. Since stand growth is related to canopy carbon gain, differences in crown shape and associated leaf area distributions might render differences in growth among stands of trees varying in crown shape. Many

current process-based models of forest canopy photosynthesis require description of crown shape as an important component for simulation of light absorption (Brunner 1998). Modeling studies in Norway spruce (*Picea abies* Karst.) showed that different crown shape ratios, defined as the ratio of crown diameter to crown length, are favorable for light interception at different latitudes, in accordance with varying solar elevation angles (Oker-Blom and Kellomaki 1982;

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Table 1. Characteristics of experimental site locations and long-term (1971–2000) mean values of climatic data.

Site*	Series [†]	Latitude (N)	Longitude (W)	Elevation (m)	Soil order	Annual temperature (°C)			Precipitation sum (mm)
						Average	Max.	Min.	
Kirbyville Texas	WG	30°35'	93°59'	40	Ultisol	19.2	25.1	13.2	1339
DeRidder, Louisiana	WG	30°51'	93°21'	61	Alfisol	19.3	25.3	14.4	1560
Sanderson, Florida	AC	29°10'	82°19'	45	Spodosol	20.4	26.3	14.6	1361
Waverly, Georgia	AC	31°07'	81°45'	10	Ultisol	18.9	25.4	12.4	1316

*Long-term mean values are from the nearest National Oceanic and Atmospheric Administration (NOAA) recording station: for Kirbyville, nearest NOAA station is located at Town Bluff Dam, Texas; for Sanderson, nearest is in Lake City, Florida; and for Waverly, nearest is in Nahunta, Georgia.

[†]WG and AC refer to Western Gulf and Atlantic coastal plains series, respectively.

Kuuluvainen and Pukkala 1989). These studies, however, considered only crown shape ratios, which may not be a good description of particular crown shapes. MacFarlane et al. (2003) used a detailed model of crown shape in their study of canopy dynamics and light interception in loblolly pine (*Pinus taeda* L.) stands. They concluded that light capture was sensitive to the shape parameter of the crown portion above the height of maximum crown width but that sensitivity varied by both stand spacing and age. Wang and Jarvis (1990) argued that crown shape was of minor importance for light interception compared with the total leaf area and its distribution within crowns of Sitka spruce (*Picea sitchensis* (Bong.) Carr.). In contrast, Duursma and Makela (2007) concluded that at a given crown volume, conical crowns of Scots pine (*Pinus sylvestris* L.) might intercept more light than ellipsoid ones.

Crown shape is often identified as one of the important morphological attributes of a tree ideotype (Dickmann 1985; Martin et al. 2001). The concept of an ideotype, defined as a biological model of a tree in terms of its productivity, and the development of associated selection criteria in tree improvement programs require information concerning the genetic and environmental influences on crown shape. Genetic variation in tree crown shape has not been studied extensively (St. Clair 1994; Isik and Isik 1999). However, if genetic differences in crown shapes exist, they may need to be incorporated into models simulating canopy light interception and photosynthesis in forest plantations and may be useful in tree improvement programs (Martin et al. 2001). We found differences in outer crown shape among families differing in aboveground productivity in single-family plots of loblolly pine and slash pine (*Pinus elliottii* Engelm.) at age 2 years, prior to canopy closure (Chmura et al. 2007). The most productive family in that study had relatively wider crowns in the middle canopy than the two other families. In the current study, we explored the following questions: (i) Do family differences in crown shape persist following canopy closure? (ii) Do contrasting environments, including sites and stand densities, affect crown shape of a highly productive family, planted at multiple experimental sites across the southeastern United States?

Materials and methods

Experimental sites and planting material

The Pine Productivity Interaction on Experimental Sites study consists of two series: the AC series, located in the Atlantic Coastal Plain of Florida and Georgia, and the WG series

in the West Gulf Coastal Plain of Texas and Louisiana (Table 1). The AC series was established in January 2000 at four locations as described in Roth et al. (2007), and plots in the WG series were planted between November 2001 and January 2002 at three locations (Chmura et al. 2007). In both series, full-sibling families of loblolly and slash pine were deployed in replicated single-family plots in two contrasting silvicultural treatments: control (C, fertilization and control of competing vegetation at planting only) and high intensity (HI, repeated fertilization and vegetation control, see Chmura et al. 2007 and Roth et al. 2007 for details on treatments). Each site was planted in a randomized complete-block, split-plot design with treatments as a whole-plot level and families as a subplot level. Only one planting density of 1223 trees·ha⁻¹ (2.4 × 3.3 m; 72 trees·plot⁻¹) was used in the WG series; whereas two planting densities were used in the AC series, 1334 trees·ha⁻¹ (2.75 × 2.75 m; 80 trees·plot⁻¹) and 2990 trees·ha⁻¹ (1.22 × 2.75 m; 128 trees·plot⁻¹) at each site. Only trees from the center of the plots were measured to limit the effect of competitive interactions to within-full-sib competition.

In the WG series, we measured two loblolly pine families: Lob 1 and Lob 5. The latter family was represented in both experimental series (WG and AC), which enabled investigation of the same family across multiple sites in the southeastern United States and the environmental effects on its traits. This family ranked first or second among multiple families in terms of aboveground production at all locations of the experiment at the early stand ages (Chmura et al. 2007; Roth et al. 2007; Chmura and Tjoelker 2008).

Measurements

To test for family differences in crown shape after canopy closure, which occurred in the fifth growing season (2006), we measured trees from the faster-growing Lob 5 family and the other, average-growing loblolly pine family (Lob 1, Chmura et al. 2007) at two experimental sites of the WG series, Kirbyville, Texas, and DeRidder, Louisiana. Twenty-four trees per family (four trees × two treatments × three blocks) were chosen as a subsample to represent variation in tree sizes at each family plot.

Crown diameters were measured in two directions, parallel and perpendicular to planting beds, at four points along the crown, which represented 0.25 increments of relative crown length from the base of the live crown. Two height poles with attached post levels were extended to each measurement position along the crown, and the horizontal distance between poles was measured with a tape measure to

Table 2. Analysis of variance $P > F$ values for tree and crown traits measured for the Western Gulf series.

Effect	df	Tree height	DBH	Crown length	Height to live crown	Crown shape ratio across beds	Crown shape ratio along beds
DeRidder							
Block	2	0.2667	0.4986	0.0187	0.1133	0.2172	0.2204
Treatment	1	0.0754	0.0579	0.0199	0.3655	0.6633	0.1211
Block × treatment*	2	0.6021	0.5927	0.9250	0.4373	0.4919	0.3432
Family	1	0.0630	0.2639	0.0259	0.9690	0.5291	0.4288
Family × treatment	1	0.6555	0.7331	0.5435	0.3655	0.8016	0.0228
Error	4						
Kirbyville							
Block	2	0.3582	0.0510	0.1423	0.7995	0.8248	0.0080
Treatment	1	0.1392	0.0006	0.0665	0.9104	0.1078	0.0096
Block × treatment*	2	0.3284	0.9839	0.4398	0.1429	0.7950	0.9636
Family	1	0.1238	0.8844	0.0114	0.3086	0.3416	0.0273
Family × treatment	1	0.6479	0.8979	0.6151	0.9296	0.8937	0.6022
Error	4						
Both WG series sites (DeRidder and Kirbyville)							
Site	1	0.4008	0.0361	0.0927	0.0681	0.1566	0.0265
Block (site) [†]	4	0.2516	0.3577	0.0252	0.3052	0.2338	0.0146
Treatment	1	0.0186	0.0004	0.0054	0.5652	0.0934	0.0059
Treatment × site	1	0.8165	0.0494	0.1823	0.7110	0.2281	0.7525
Treatment × block (site) [‡]	4	0.4431	0.8661	0.7140	0.1469	0.7932	0.8283
Family	1	0.0130	0.3347	0.0005	0.3935	0.2367	0.0094
Family × site	1	0.6955	0.4430	0.5516	0.4215	0.6001	0.0347
Family × treatment	1	0.5104	0.7317	0.9269	0.4778	0.7988	0.2441
Family × treatment × site	1	0.9892	0.8758	0.4175	0.5629	0.9825	0.0550
Error	8						

Note: Individual tree values were averaged at the family-plot level before the analysis. Bold-faced values show statistically significant effects.

*Used as an error term for block and treatment effects.

[†]Error term for site effect.

[‡]Error term for treatment, treatment × site, and block (site) effects.

the nearest 5 cm. Crown diameter was set to zero at the top of the crown. Subsequently, a relative crown radius (relative to the maximum in the crown) was calculated at each crown position. To describe the vertical distribution of crown radii, we estimated parameters of a modified equation of Baldwin and Peterson (1997):

$$[1] \quad RCR = a \left(\frac{RHIC - 1}{RHIC + 1} \right) + b(1 - RHIC)^c$$

where RCR is the relative crown radius; RHIC is the relative height in the crown (from 0 at the bottom to 1 at the top); and a , b , and c are the estimated parameters.

Similar measurements were taken for the Lob 5 family after the fifth growing season (2004) at two experimental sites of the AC series, Sanderson, Florida, and Waverly, Georgia. In the AC series, only trees from the high planting density (2990 trees·ha⁻¹) in three blocks were selected as part of a larger, independent allometry study. We sampled 18 trees, nine from each of the HI and C treatments at the Sanderson site (three trees × two treatments × three blocks), and nine trees at the Waverly site from the HI treatment only (three trees × three blocks). This sampling scheme provided a test of family, silvicultural treatment and the interactive effects of family × treatment at two of four

experimental sites (WG series), and treatment effects in the Lob 5 family at the Sanderson site of the AC series. Planting density effects were not directly tested; however, a comparison of a single family performance between the two experimental series (WG vs. AC) at a common stand age (5 years) provided an indirect test of the effects of planting density.

Statistical analysis

Analysis of variance (ANOVA), testing family, treatment, and their interactive effects according to the split-plot design (Table 2), was performed on the family-plot means for tree and crown traits — tree height, diameter at 1.3 m above the ground (DBH), crown length, height to live crown, and crown shape ratio (the ratio of maximum measured crown diameter to crown length) — separately by site in the WG series according to the model

$$[2] \quad Y_{ijkl} = \mu + B_i + T_j + BT_{ij} + F_k + FT_{jk} + e_{ijkl}$$

where Y_{ijkl} is the response variable of the l th plot of k th family in j th treatment of i th block, μ is the overall mean, B_i is the random effect of i th block ($i = 1, 2, 3$), T_j is the fixed effect of j th treatment ($j = 1, 2$), BT_{ij} is the random interaction of i th block and j th treatment, F_k is the fixed effect of

Table 3. Means (SE) of tree and crown traits for loblolly pine families after the fifth growing season.

Treatment*	Family†	<i>n</i>	Tree height (m)	DBH (cm)	Crown length (m)	Height to live crown (m)	Crown shape ratio across planting beds	Crown shape ratio along planting beds
DeRidder, Louisiana								
C	Lob 1	12	7.35 (0.286)	12.11 (0.388)	5.70a (0.189)	1.65 (0.214)	0.54 (0.012)	0.46 (0.021)
	Lob 5	12	7.87 (0.162)	12.53 (0.495)	6.48b (0.160)	1.39 (0.119)	0.52 (0.026)	0.41 (0.014)
	Mean		7.61 (0.170)	12.32 (0.310)	6.09a (0.146)	1.52 (0.123)	0.53 (0.014)	0.43 (0.013)
HI	Lob 1	12	7.88 (0.240)	13.34 (0.631)	6.20a (0.320)	1.69 (0.253)	0.55 (0.025)	0.45 (0.023)
	Lob 5	12	8.65 (0.187)	14.10 (0.541)	6.73b (0.275)	1.92 (0.251)	0.54 (0.018)	0.48 (0.016)
	Mean		8.27 (0.169)	13.72 (0.414)	6.46b (0.214)	1.80 (0.176)	0.54 (0.015)	0.46 (0.014)
Site mean			7.94 (0.128)	13.02 (0.276)	6.28 (0.131)	1.66 (0.108)	0.54 (0.010)	0.45 (0.010)
Kirbyville, Texas								
C	Lob 1	12	7.63 (0.233)	12.49 (0.531)	4.92a (0.287)	2.71 (0.181)	0.57 (0.032)	0.53a (0.026)
	Lob 5	12	8.00 (0.327)	12.50 (0.718)	5.64b (0.358)	2.36 (0.186)	0.53 (0.025)	0.48b (0.025)
	Mean		7.81 (0.200)	12.50a (0.437)	5.28 (0.236)	2.53 (0.132)	0.55 (0.020)	0.50a (0.018)
HI	Lob 1	12	8.25 (0.202)	14.83 (0.427)	5.50a (0.233)	2.74 (0.193)	0.61 (0.022)	0.58a (0.026)
	Lob 5	12	8.87 (0.195)	14.96 (0.384)	6.42b (0.284)	2.45 (0.291)	0.58 (0.037)	0.51b (0.026)
	Mean		8.56 (0.152)	14.89b (0.281)	5.96 (0.204)	2.60 (0.173)	0.59 (0.021)	0.54b (0.020)
Site mean			8.18 (0.136)	13.69 (0.311)	5.62 (0.162)	2.57 (0.108)	0.57 (0.015)	0.52 (0.014)
Sanderson, Florida								
C	Lob 5	9	7.31 (0.408)	8.89a (0.519)	4.40a (0.114)	2.91 (0.130)	0.45 (0.010)	0.34 (0.007)
HI	Lob 5	9	9.20 (0.219)	11.58b (0.611)	5.29b (0.098)	3.91 (0.099)	0.51 (0.009)	0.33 (0.005)
Site mean			8.26 (0.321)	10.23 (0.507)	4.84 (0.088)	3.41 (0.097)	0.48 (0.007)	0.34 (0.005)
Waverly, Georgia								
HI	Lob 5	9	8.37 (0.247)	12.53 (0.397)	5.02 (0.074)	3.34 (0.043)	0.48 (0.006)	0.36 (0.016)

Note: Values followed by different letters within a column denote significantly different pairs for family and treatment comparisons within site. Indicated are only statistically significant comparisons, $P \leq 0.05$.

*C and HI refer to the control and high intensity treatments, respectively.

†Lob 1 and Lob 5 refer to the two loblolly pine families.

k th family ($k = 1, 2$), FT_{jk} is the interaction effect of j th treatment and k th family, and e_{ijkl} is the random error.

The analysis of both sites in the WG series (Table 2) was performed according to the model

$$[3] \quad Y_{ijklm} = \mu + S_i + B(S)_{ij} + T_k + TS_{ik} + B(S)T_{ijk} + F_l + FS_{il} + FT_{kl} + FTS_{ikl} + e_{ijklm}$$

where Y_{ijklm} is the response variable of the m th plot of l th family in k th treatment of j th block within the i th site; μ is the overall mean; S_i is the fixed effect of site ($i = 1, 2$); $B(S)_{ij}$ is the random effect of j th block within i th site ($j = 1, 2, 3$); T_k is the fixed effect of k th treatment ($k = 1, 2$); $B(S)T_{ij}$ is the random interaction of j th block within i th site and k th treatment; F_l is the fixed effect of l th family ($l = 1, 2$); FS_{il} , FT_{kl} , and FTS_{ikl} are the interaction terms; and e_{ijklm} is the random error.

Treatment effects were tested at the Sanderson site of the AC series in a manner similar to the model in eq. 2, but without the terms involving family and interaction effects (there was only one family measured). Site effects across multiple locations for the Lob 5 family, planted at all experimental sites, were analyzed in the HI treatment only. Least squares means were compared using the Tukey's Honestly Significant Difference test or the Student's t test. The effects reported as significant refer to $P \leq 0.05$. Analysis of variance was performed using JMP statistical software (JMP 5.0.1., SAS Institute Inc., Cary, North Carolina, USA).

Parameters of eq. 1 describing the outer crown shape were estimated at the family-plot level with a nonlinear procedure in JMP statistical software (JMP 5.0.1.). Because it is possible to obtain similar crown shapes with different sets of parameter values in eq. 1, the analysis of differences among families, treatments, and sites should compare all three parameters simultaneously. All analyses of differences in the sets of three crown shape parameters were performed using PROC MIXED in SAS (SAS 9.1). Parameters were treated as repeated measurements, which took into account the correlations among parameters. Analyses were done similarly to the analyses of variance described above, testing family and treatment effects at single sites, and site and interaction effects using multiple sites. The least squares means were compared with a DIFF procedure, performing all possible comparisons among combinations of factors. Differences reported as significant refer to $P \leq 0.05$.

Results and discussion

Family differences

The two families examined in the WG series differed in crown length, with the Lob 5 family having longer crowns than Lob 1 at both locations, and the height to live crown did not differ between families (Tables 2 and 3). Crown shape ratios were also similar in the two families except when measured along planting beds at the Kirbyville site (Tables 2 and 3). Family and treatment effects were not in-

Table 4. Least squares means estimates (SE) of parameters (a, b, and c) fitted to eq. 1, describing the vertical distribution of relative crown radii for two loblolly pine families in two silvicultural treatments of the Western Gulf series.

Treatment*	Family [†]	Across planting beds			Along planting beds		
		a	b	c	a	b	c
DeRidder, Louisiana							
C	Lob 1	1.97 (0.79)	2.65 (0.71)	0.77 (0.06)	1.89 (0.49)	2.52 (0.44)	0.72 (0.04)
	Lob 5	2.77 (0.79)	3.35 (0.71)	0.88 (0.06)	1.96 (0.49)	2.56 (0.44)	0.71 (0.04)
	Mean	2.37a (0.53)	3.00a (0.48)	0.83a (0.04)	1.92a (0.45)	2.54a (0.41)	0.71a (0.05)
HI	Lob 1	4.07 (0.79)	4.61 (0.71)	1.04 (0.06)	4.97 (0.49)	5.30 (0.44)	1.03 (0.04)
	Lob 5	4.53 (0.79)	4.99 (0.71)	1.01 (0.06)	3.93 (0.49)	4.33 (0.44)	0.99 (0.04)
	Mean	4.30b (0.53)	4.80b (0.48)	1.03b (0.04)	4.45b (0.45)	4.81b (0.41)	1.01b (0.05)
Site mean		3.33 (0.38)	3.90 (0.34)	0.93 (0.03)	3.19 (0.32)	3.68 (0.29)	0.86 (0.04)
Kirbyville, Texas							
C	Lob 1	3.92 (0.70)	4.37 (0.62)	0.94 (0.06)	3.44 (0.76)	3.86 (0.68)	0.87 (0.10)
	Lob 5	3.23 (0.70)	3.63 (0.62)	0.83 (0.06)	4.33 (0.76)	4.63 (0.68)	0.94 (0.10)
	Mean	3.58 (0.53)	4.00 (0.48)	0.88 (0.04)	3.89 (0.45)	4.24 (0.41)	0.90 (0.05)
HI	Lob 1	3.00 (0.70)	3.47 (0.62)	0.82 (0.06)	3.28 (0.76)	3.64 (0.68)	0.76 (0.10)
	Lob 5	5.39 (0.70)	5.53 (0.62)	0.99 (0.06)	4.63 (0.76)	4.74 (0.68)	0.92 (0.10)
	Mean	4.20 (0.53)	4.50 (0.48)	0.91 (0.04)	3.95 (0.45)	4.19 (0.41)	0.84 (0.05)
Site mean		3.89 (0.38)	4.25 (0.34)	0.89 (0.03)	3.92 (0.32)	4.22 (0.29)	0.87 (0.04)

Note: All R^2 values are ≥ 0.80 , P values are < 0.0001 . Values followed by different letters within a column denote significantly different pairs for treatment comparisons within site. Indicated are only statistically significant comparisons, $P \leq 0.05$.

*C and HI refer to the control and high intensity treatments, respectively.

[†]Lob 1 and Lob 5 refer to the two loblolly pine families.

dependent (significant family \times treatment interaction effect) for the crown shape ratio measured along rows at the DeRidder site (Tables 2 and 3). The two examined families did not differ significantly in either tree height or diameter when the two WG sites were analyzed separately (Tables 2 and 3). However, measured trees in our study were only a subsample of trees for the family \times treatment combination. Therefore, the absolute values of growth traits should be judged cautiously because they may differ from means based on the inventory when all trees are measured. For the same reason, because the absolute values of crown dimensions are correlated with tree size, comparison of relative crown dimensions, such as the crown shape described by eq. 1 or crown shape ratios, provides a useful means to compare trees of differing size.

The overall fit of crown shape by eq. 1 for two loblolly pine families examined in the WG series was very good, (R^2 values ranged from 0.80 to 0.91 among the treatment combinations, $P < 0.0001$ (Table 4)). Crown shapes described by these equations did not differ between the two families in the WG series ($P > 0.05$) after the fifth growing season in the field, following canopy closure (Table 4).

The maximum outer crown radius in the WG series occurred between 0.3 and 0.45 of crown length and was independent of family and silvicultural treatment effects. These estimates compare well with the relative heights to maximum crown width reported from loblolly pine trees older than those in our stands (30 years) (Baldwin and Peterson 1997), where outer crown shapes were generally similar to those of the present study. Thus, crown shapes described by the parameters of eq. 1 were not specific to the two contrasting families in our study. This contrasts with the results of our previous study in the same stands at age 2 years before the onset of intertree competition. At that time, the two ex-

amined loblolly pine families had different crown shapes, particularly with respect to the width in the middle of the live crowns (Chmura et al. 2007), with the faster-growing family (Lob 5) exhibiting wider crowns. These findings indicate that inherent variation in crown shape discernible before the onset of canopy closure was likely muted when within-canopy competition began.

Treatment effects

The silvicultural treatment effect on crown length was significant at DeRidder but not at Kirbyville (Tables 2 and 3). At the Kirbyville site, trees had significantly greater DBH and crown shape ratio along rows in the HI treatment than in the control; however, crown shape ratio was affected differently by treatment in two families at the DeRidder site when measured along planting rows (significant family \times treatment interaction; Tables 2 and 3). In addition, when analyzed across sites in the WG series, the treatment effect was statistically significant for tree height, diameter, crown length, and crown shape ratio along planting beds (Table 2), with higher values in the HI treatment than the C treatment. HI treatment perhaps accelerated canopy closure and self-pruning (Albaugh et al. 2006), as the height to the live crown tended to be greater in the HI treatment than in the control treatment at both sites of the WG series, although not significantly (Table 3).

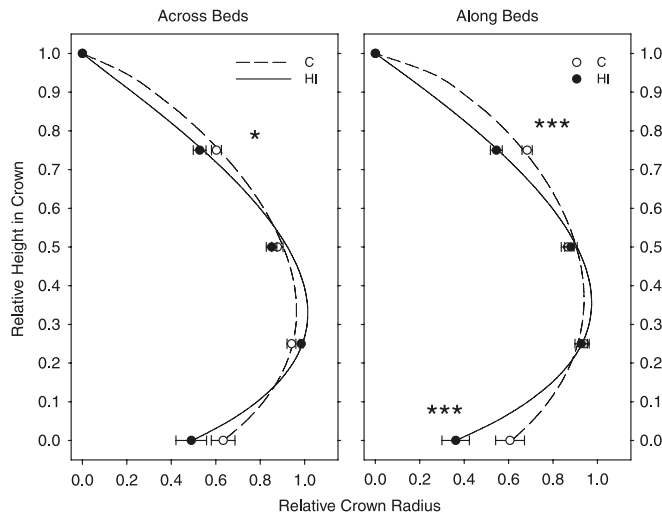
Silvicultural treatment effects on crown shape parameters (eq. 1) were statistically significant only at one of the two WG sites, the DeRidder site (Fig. 1; Table 4). Compared with the control, crowns in the HI treatment were relatively narrower at 0.75 of the relative height in the crown and at the base of live crown in both directions of measurement (Fig. 1). However, the overall crown shape was similar in both treatments (Fig. 1).

Table 5. Least squares means estimates (SE) of parameters (a, b, and c) fitted to eq. 1 describing the vertical distribution of relative crown radii for the Lob 5 family at four experimental sites in the high intensity treatment.

Site	Across planting beds			Along planting beds		
	a	b	c	a	b	c
DeRidder, Louisiana	4.53ab (0.80)	4.99ab (0.73)	1.01a (0.09)	3.93a (0.48)	4.33a (0.44)	0.99a (0.08)
Kirbyville, Texas	5.39a (0.80)	5.53a (0.73)	0.99a (0.09)	4.63a (0.48)	4.74a (0.44)	0.92ab (0.08)
Sanderson, Florida	2.19bc (0.80)	3.05bc (0.73)	0.94a (0.09)	1.45b (0.48)	2.29b (0.44)	0.81ab (0.08)
Waverly, Georgia	1.70c (0.80)	2.49b (0.73)	0.79a (0.09)	1.63b (0.48)	2.36b (0.44)	0.69b (0.08)

Note: Values followed by the same letters within a column are not significantly different for a given parameter ($P > 0.05$; site comparisons). All R^2 values are ≥ 0.82 ; P values are < 0.0001 .

Fig. 1. Outer crown shapes of loblolly pine trees at the DeRidder experimental site in two contrasting silvicultural treatments (C, control; HI, high intensity). Points and error bars show means and standard errors, respectively, at each measurement position along the live crown ($n = 24$ at each crown position and treatment). Lines show crown shapes fitted with eq. 1 separately for each silvicultural treatment. Asterisks indicate significance level for comparisons between treatments at each crown position: *, $P \leq 0.05$; ***, $P \leq 0.001$.



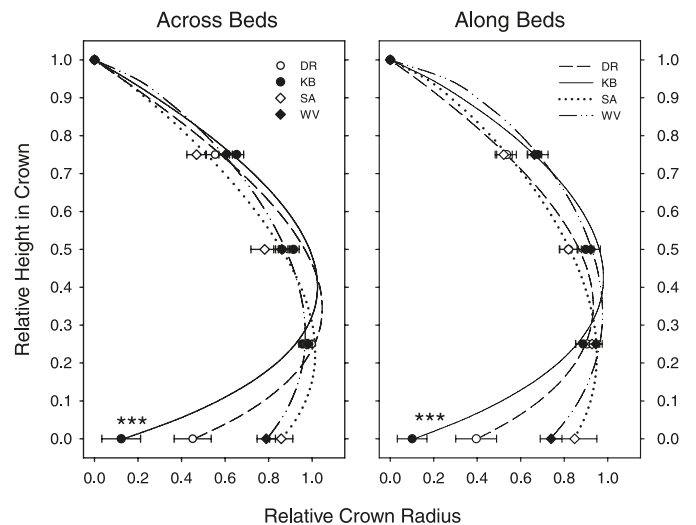
The treatment effect was not significant for crown shape parameters in the Lob 5 family at the Sanderson site in the AC series (data not shown). However, in the HI treatment at that site, trees had significantly greater DBH with longer crowns than trees in the C treatment (Table 3).

Environmental effects

Analysis of tree and crown traits across two sites of the WG series revealed a significant site effect for DBH and family \times site interaction for crown shape ratio along planting beds (Table 2). However, the significant interaction resulted from the effect of scale rather than from a change in family rankings (Table 3). When tree and crown traits of the Lob 5 family were analyzed across all planting sites (HI treatment only), the site effect was highly significant ($P \leq 0.036$), except for tree height ($P = 0.308$) and for crown shape ratio across planting beds ($P = 0.121$). These findings indicate that crown traits in our experiment were affected more by environment than by family.

The effect of site on crown shape parameters (eq.1) in the WG series was obscured by significant interactions. A three-way site \times treatment \times family interaction was significant when measured across planting beds ($P = 0.0137$). The val-

Fig. 2. Outer crown shapes (lines) of the Lob 5 family fitted with eq. 1 at four experimental sites (DR, DeRidder; KB, Kirbyville; SA, Sanderson; WV, Waverly) after the fifth growing season. Points and error bars show means and standard errors, respectively, at each measurement position along the live crown in the high intensity treatment ($n = 12$ at DR and KB; $n = 9$ at SA and WV). Asterisks indicate significance level for comparisons among sites at each crown position: ***, $P \leq 0.001$.



ues of all three parameters across beds were lower in the HI treatment than in the C treatment for the Lob 1 family at the Kirbyville site, whereas the opposite trend was found in all other combinations of factors (Table 4). A significant two-way site \times treatment interaction was found along planting beds ($P = 0.0171$), with greater differences between silvicultural treatments at DeRidder than at the Kirbyville site (Table 4).

A comparison of crown shape parameters for the Lob 5 family among the four sites revealed a significant site effect (Fig. 2). The overall fit with eq. 1 across sites was very strong (for individual sites, R^2 ranged from 0.82 to 0.95, $P < 0.0001$ (Table 5; Fig. 2)). Trees at the Sanderson site had relatively wider crowns than those in the WG series at the base of the live crown in both directions of measurement (Fig. 2). Maximum crown width occurred relatively higher within the live crown in the WG series than at the Sanderson site of the AC series (Fig. 2). Crown shape ratio measured along planting rows was affected by site and was significantly lower in the AC series than in the WG series ($P = 0.001$). Thus, even within the same family, crown shape was strongly affected by the environment, which

likely reflected differences in planting densities and other factors at the testing sites.

Stand density is one of the major factors affecting crown development through its effect on the amount of light and growing space available for individual crowns and branches (Oliver and Larson 1996). It is surprising, therefore, that within the same family, we observed more conical crown shapes at the closely spaced Sanderson site (2990 trees·ha⁻¹) than in the WG series with a much lower stand density (1334 trees·ha⁻¹; Table 5, Fig. 2). Contrary to our expectation, crowns were relatively wider at the base of the canopy in denser stands than in less dense stands (Fig. 2). However, as expected, crowns were shorter and occupied higher positions along the stem in the denser stands (Table 3). Crowns were not symmetrical in our trees, as reflected in higher values of crown shape ratios, when measured across than along planting beds (Table 3). Yet, although absolute crown dimensions were dependent upon direction within the crown, which was expected from a generally greater competition within the planting rows than between rows, the crown shapes described in relative terms were similar in both directions (Tables 4 and 5, Figs. 1 and 2). The significance of the site effect, the lack of significant between-family differences in crown shape parameters in the WG series, and the presence of interactions involving sites and families indicate that environmental effects on the outer crown shape in these young loblolly pine stands is strong relative to the family effects. Moreover, outer crown shapes described in our study seem to be general for loblolly pine trees, although they may also vary by tree size and age (Baldwin and Peterson 1997).

In contrast to our findings, crown form was under strong genetic control in Norway spruce and Scots pine families (Karki and Tigesrstedt 1985). However, this effect might perhaps not be detected without the presence of individual genotypes producing extreme phenotypes, such as columnar or pendulous crown forms (Karki and Tigesrstedt 1985). Crown shape ratios vary significantly among families in coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (St. Clair 1994) and among provenances in *Pinus brutia* Ten. (Isik and Isik 1999). These studies also reported moderate to high individual-tree heritabilities for that trait. Similarly, significant species differences and among-family variation in crown shape ratios were found in loblolly and slash pine plantations (McCrary and Jokela 1996; Xiao et al. 2003; Emhart et al. 2007), and low to moderate within-family broad-sense heritability for that trait in slash pine (Emhart et al. 2007). Moreover, the extent to which environmental vs. genetic effects influence crown shape ratio might depend on the genotypes examined (Emhart et al. 2007). In our experiment, however, both the fast-growing and average-growing family in the WG series had similar crown shapes and crown shape ratios. Consequently, if differences in aboveground growth and productivity among families in our experiment were associated with canopy carbon gain (Chmura and Tjoelker 2008), they were likely related more to the differences in overall crown size, accumulated leaf area, and perhaps branching pattern (Chmura et al. 2007; Emhart et al. 2007), than to variation in crown shape (Wang and Jarvis 1990).

To conclude, family differences in crown shape did not

persist after canopy closure at age 5 years in our experimental stands. Our results indicate that site-specific descriptions of crown shape might be required following crown closure rather than family-specific shapes, when used for modeling purposes in young loblolly pine plantations. Family-specific crown shapes may be important early in stand development prior to canopy closure or perhaps in the presence of highly contrasting crown forms, e.g., elongated columnar crowns vs. “egg-shaped” as in our study. Within a single family, differing site conditions, likely strongly affected outer crown shape. Caution is needed, however, as some of the cross-site comparisons confounded stand-spacing differences.

In our study of crown shape characteristics, we failed to distinguish a “crop ideotype,” characterized by efficient use of growing space and available resources for increased production per unit land area (Dickmann 1985; Martin et al. 2001; Chmura and Tjoelker 2008). In contrast, the most productive family in our study seems to demonstrate a “competition ideotype,” characterized by occupying available growing space with large crowns (Chmura and Tjoelker 2008). Crown shape following canopy closure in these experimental settings was of minor importance; however, it does not invalidate this trait as a selection criterion if strikingly different crown forms were present. Further study on the linkages between crown shape and growth in pine plantations is warranted.

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