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On the Number of Genes Controlling the Grass Stage in Longleaf Pine

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Abstract

The grass stage is an inherent and distinctive developmental trait of longleaf pine (*Pinus palustris*), in which height growth in the first few years after germination is suppressed. In operational forestry practice the grass stage extends for two to several years and often plays a role in planting failures and decisions to plant alternative species. Interspecies hybrids involving loblolly (*P. taeda*) and slash (*P. elliottii* var. *elliottii*) pines have been investigated as a means to produce planting stock with improved early height growth and to develop backcross populations for advanced generation breeding. We have reevaluated data from several interspecies populations, with the objective of estimating the number of genes contributing to the difference in first-year height growth between longleaf and loblolly pines. Estimates based on means and variances of parental and interspecies hybrid and backcross families suggest a minimum of 4 to 10 genes with standard errors less than half the estimates. These results suggest that the grass stage has evolved through the accumulation of alleles at several loci, each with small effects on various components of first-year height growth. Given the complexity of the grass-stage trait, tree breeders may need to combine genetic marker analysis with recurrent backcross breeding to efficiently develop longleaf pine planting stock for improved reforestation.

The juvenile development of longleaf pine (*Pinus palustris* Mill.) is characterized by the grass stage (Wahlenberg 1946). The grass stage is initiated, immediately following germination, with the nearly complete suppression of primary shoot elongation (Brown 1964). The length of time and the degree of suppression depend on genetic and environmental factors, including among- and within-family variation, degree of brown spot needle blight infection, level of competing vegetation, and nutrient and moisture availability (Layton and Goddard 1982). Selected families grown under optimal conditions begin to break the grass stage in the second year after field planting (Bey 1979; Schmidtling and White 1989). Under less favorable conditions the same families may remain in the grass stage for several years.

Longleaf pine is unique in being the only pine species native to the southeastern United States that exhibits the grass stage. The south Florida variety of slash pine (*P. elliottii* Engelm. var. *densa*) exhibits a slow-growing juvenile period relative to the typical variety (*P. elliottii* var. *elliottii*), but not a true grass stage (Little and Dorman 1954). Also, in the southwestern United States, Mexico, Cuba, and Asia at least six other species—*P. engelmannii* Carr., *P. pringlei* Shaw, *P. montezumae* Lamb., *P. devoniana* Lindley, *P. tropicalis* Morelet, and *P. merkusii* Jungh. and de Vriese—are known to exhibit a similar slow-growing or grass-stage juvenile phase (Brown 1964; Keeley and Zedler 1998; Little and Dorman 1954; Schmidtling RC, personal communication). The grass-stage trait is thought to be an adaptation to a predictable pattern of ground fires on low to moderate productivity sites (Keeley and Zedler 1998) and as such may have originated independently in different lineages. It is not known whether the slow juvenile growth characteristic of *P. elliottii* var. *densa* is a similar adaptation or possibly the result of gene flow from a grass-stage species—for example, longleaf pine or *P. tropicalis*—and natural selection in the south Florida environment.

Studies on the inheritance of the grass stage of longleaf pine have been limited to a genetic and physiologic study by Brown (1964) and several tree improvement screening studies (e.g., Derr 1969; Layton and Goddard 1982; Snyder 1969, 1973; Snyder and Derr 1972; Wells and Snyder 1976), including a full diallel cross (Snyder and Namkoong 1978). The screening studies revealed heritable variation in the duration of the grass stage and growth rate after emergence from the grass stage. Brown (1964), utilizing physiologic ex-

perimental techniques, showed that the grass stage was due to a disruption in the basipetal transport of auxin. As a result, cell division in the anticlinal plane was inhibited in favor of periclinal cell division. Both mature hypocotyl length and subsequent primary shoot growth were affected. Furthermore, using data from longleaf, loblolly (*P. taeda* L.) and their interspecies hybrids and backcrosses and Castle's (1921) corrected formula, Brown estimated that at least 10 genes were involved in the expression of primary shoot growth.

In the present study, we reanalyzed Brown's data, using more recent developments in the theory of estimating the number of genetic factors controlling trait expression, with the objective of estimating the minimum number of genes controlling hypocotyl length, primary shoot length, and total seedling height during the first year of development. Additionally, we analyzed data collected in a similar experiment conducted with seedlings from an unrelated longleaf × loblolly cross and its backcross and F_2 generations. Finally, we compared these results to those obtained by Weng et al. (2002) in a QTL analysis of early height growth in an interspecies backcross family of slash pine × (longleaf pine × slash pine), and we discuss the implications of these results for understanding the evolution of longleaf pine and their application to tree improvement programs.

Materials and Methods

Brown's Experiment

Controlled pollinations using two loblolly (S2Pt7 and S2Pt9), two longleaf (Ppa1 and Ppa2), and three natural longleaf × loblolly hybrids (X *P. sondereggeri* Chapm.; Hyb1, Hyb2, and Hyb3) were made to produce seed for six populations: Loblolly (S2Pt7 × S2Pt9); Longleaf (Ppa2 × Ppa1); F_1 (Ppa2 × S2Pt7, S2Pt7 × Ppa2); BC1-loblolly (S2Pt7 × Hyb2); BC1-longleaf (Hyb2 × Ppa2); and F_2 (Hyb1 × Hyb1, Hyb2 × Hyb3, Hyb3 × Hyb3, Hyb2 × Hyb1). Parent trees were selected in natural stands in the vicinity of Groveton, Texas (Trinity County), with morphological and species range data to ensure true-to-species selections (Brown 1964). Seedlings were germinated and grown under uniform conditions in a greenhouse. Detailed height measurements were taken during germination and early development through the end of one year's growth. Because the raw data were lost from Brown (1964), the primary shoot length by hypocotyl length scatter plots (Brown 1964, figures 61–70) were scanned and analyzed with Un-Scan-It software (version 2, Silk Scientific, Inc., Orem, UT). Five replicate runs of Un-Scan-It were made on the scanned images and then averaged to determine the X (hypocotyl length) and Y (primary shoot length) coordinates of each data point (tree). The sum of the hypocotyl and primary shoot lengths was used as a measure of total seedling height.

Snow's Experiment

Open- and control-pollinated seeds from 10 families were stratified, germinated, and transplanted essentially as described by Snow et al. (1990). The 10 families could be grouped into six populations representing parental and interspecies crosses of loblolly and longleaf pine and a loblolly × slash pine F_1 hybrid. The six populations and their constituent families were as follows: Loblolly (B-144-L and B-145-L open-pollinated); Longleaf (3–356 and 27–168 open-pollinated); F_1 (27–168 × B-144-L); BC1-loblolly (B-145-L × 2–7); BC1-longleaf (27–168 × 2–7); and F_2 (open-pollinated F_1s: 3–356 × B-144-L and 2–7). The loblolly × slash pine F_1 was not used in this analysis. Tree 2–7 had been identified as a natural longleaf × loblolly hybrid (X *P. sondereggeri*) through morphological analysis. Subsequent chloroplast DNA testing supported this conclusion (Nelson CD, unpublished data), but neither test is definitive for species classification. Longleaf trees 3–356 and 27–168 were selected from a seedling seed orchard located on the Harrison Experimental Forest in southeast Mississippi (Snyder EB, study information on file at SIFG). Loblolly trees B-144-L and B-145-L were selected for bark beetle resistance in natural stands in southeast Texas (Coyne JL, study information on file at SIFG). Six to 8 weeks after transplanting, the seedlings were inoculated with one of two multigall composite cultures of *Cronartium quercuum* f.sp. *fusiforme*, the causative organism of fusiform rust disease. Nine months after transplanting, the seedlings were scored for fusiform rust galls and measured for total height.

Methods developed by Lande (1981) and Cockerham (1986) were used to estimate the minimum (or effective) number of freely segregating genetic factors (n_e) contributing to various stages of first-year height growth in longleaf pine and its hybrids with loblolly pine. Lande's methods extend Castle's (1921) and Wright's (1968) procedure to genetically heterogeneous parental populations, assuming an appropriate (i.e., all genetic variance is additive) scale of measurement can be determined. Four estimates can be computed based on different formulas for calculating the segregation variance (i.e., variance due to genes causing the difference in trait means between parental populations). The estimated minimum number equals the squared difference in means of the parental populations divided by 8 times the segregation variance. Before computing the estimates and standard errors, measurement scales for each trait were evaluated as suggested by Wright (1968). Based on this evaluation, a transformation was selected for each trait according to criteria reviewed by Lande (1981); namely, additivity of the mean phenotypes in parental, F_1, F_2, and backcross populations and constancy or linearity of parental and F_1 variances. In some cases transformations could not be found to meet these criteria for all six populations, resulting in invalid estimates of the minimum number of genes. Estimates are reported here for valid cases only, and when the values exceed their standard errors.

QTL Mapping Experiment

An interspecies BC1 family was produced by controlled pollination, 18–27 × 488. Slash pine, 18–27, was selected from a natural stand in Harrison County, Mississippi, and is

Table 1. Population sizes, means, and variances for first-year height growth traits in two studies

	Brown's Data							Snow's Data		
	Hypocotyl (mm)			Primary shoot (mm)		Total height (mm)		7-month height (cm)		
Population	*N*	Mean	Var.	Mean	Var.	Mean	Var.	*N*	Mean	Var.
Longleaf	70	6.1	2.46	7.5	5.70	13.5	10.31	90	2.94	0.724
BC1-longleaf	50	20.4	106.70	64.7	2146.30	85.0	3047.90	48	4.22	1.510
F_1	93	21.2	13.96	39.2	271.23	60.4	318.69	20	13.38	14.313
F_2	155	21.2	40.66	45.1	543.47	66.4	719.66	20	6.60	19.674
BC1-loblolly	38	37.1	37.84	126.0	791.86	163.0	812.57	106	19.21	33.716
Loblolly	75	50.9	62.52	145.7	1497.60	196.7	1692.80	138	35.66	43.425

currently an established clone in the research clone bank at the Harrison Experimental Forest. Hybrid tree 488 was selected on the Palustris Experimental Forest near Pineville, Louisiana, from a full-sib hybrid family, longleaf 8R × slash 51 (Derr 1966). Like 18–27, tree 488 is currently an established clone at the Harrison Experimental Forest, as are the longleaf and loblolly parents described under Snow's Experiment. Seeds from 18–27 × 488 were stratified and germinated in containers in a greenhouse and grown under uniform conditions for 7 months. At that time, total seedling heights (n = 258) were measured, and the seedlings were organized for field planting. Because our present interest is in the grass-stage trait as expressed in the first year of growth, we limited our analysis to this one measure.

Single-marker ANOVA and interval mapping were used to identify QTLs specific to each parent, hybrid 488 (150 markers) and slash 18–27 (116 markers). Significance levels of .005 were used for the ANOVA analyses, and LOD scores of >2.0 were used for interval mapping. The number of unlinked QTLs at these significance levels were counted and compared to the effective number estimates developed from Brown's and Snow's data.

Results

Brown's Experiment

Data were successfully obtained from figures 61–70, providing pairs of hypocotyl and primary shoot lengths for each tree in all six required populations. Total heights were obtained by adding the hypocotyl and primary shoot lengths for each tree. The selfed F_2 families (Brown 1964, figures 67 and 69) were significantly shorter (hypocotyl and primary shoot lengths) than the two outcrossed F_2 families (figures 68 and 70) and were thus omitted from further analysis. Means and standard errors for the three first-year height measurements are given in Table 1. Loblolly parental means were 8.5 to 19.5 times larger than longleaf means, and the F_1 and F_2 means were similar and slightly larger than intermediate to the parental populations.

Transformations of the form $\log_{10}(x + a)$, where x = value on original scale, and a = a correction factor, were necessary to appropriately scale the data for each trait (Wright 1968). On the transformed scale, the loblolly parental means were 10.1 to 11.7 phenotypic standard deviations larger than those of the longleaf (Table 2). However, even with the best transformation, the backcross populations failed to conform to the additive model with no interaction (Figure 1, upper panels and lower left panel). The BC1-longleaf population had the highest variances of all, and its means were as large as the F_1 and F_2 means. The means of the BC1-loblolly population were about as expected; however, the variances were much lower than expected.

Given the unexpected means and variances of the backcross populations, methods 3 and 4 of Lande (n_{e3} and n_{e4}) could not be used to provide valid estimates of effective gene number. However, using the other four populations and methods 1 and 2 (n_{e1} and n_{e2}), valid estimates could be computed. Methods 1 and 2 suggest a minimum of 6 segregating genes for hypocotyl length, 7 for primary shoot length, and 8 for total height (Table 2). In addition, using all populations and Cockerham's (1986) unweighted least squares method, the estimated minimum gene numbers ($n_{e(uwls)}$) are 4.1, 3.9, and 4.4 for hypocotyl length, primary shoot length, and total height, respectively. In all cases the standard errors are well less than one-half the estimated effective number values (Table 2).

Snow's Experiment

Open-pollinated F_2 family 2–7 developed similarly to BC1-loblolly family B-145-L × 2–7 in terms of both height growth and fusiform rust disease, so it was classified as a BC1-loblolly before analysis. All other families responded in growth and disease development as expected. In addition, the data were evaluated for the effect of fusiform rust disease on seedling height. The presence of a fusiform rust gall had a significant and nearly constant effect on height in the loblolly (5 cm average effect), BC1-loblolly (6 cm), and F_1 (7 cm) populations. To adjust for this effect, the average difference between galled and nongalled trees was added to each galled tree in the affected populations. Rust-adjusted heights were then utilized in subsequent analyses. The loblolly mean was 12.1 times larger than the longleaf mean, and the F_1 and F_2 means were larger and smaller, respectively, than intermediate to the parental means (Table 1).

A transformation of the same form, $\log_{10}(x + a)$, as used for Brown's data was used for rust-adjusted height. On the transformed scale the loblolly parental mean was 9.7 phenotypic standard deviations larger than the longleaf

Table 2. Statistics for the minimum or effective number of genes segregating for first-year height growth traits in two studies

	Brown's data									Snow's data		
	Hypocotyl length $\log_{10}$(mm + 5.03)			Primary shoot length $\log_{10}$(mm + 1.60)			Total height $\log_{10}$(mm + 1.97)			Total height Log_{10}(cm + 1.91)		
Population	*N*	Mean	Var.	*N*	Mean	Var.	*N*	Mean	Var.	*N*	Mean	Var.
Longleaf	70	1.040	0.00425	70	0.943	0.01463	70	1.180	0.00914	90	0.679	0.00605
BC1-longleaf	50	1.364	0.03800	50	1.680	0.14880	50	1.827	0.11401	48	0.778	0.00821
F_1	93	1.414	0.00420	93	1.574	0.03440	93	1.777	0.01660	20	1.169	0.01498
F_2	155	1.403	0.01434	155	1.615	0.05027	155	1.801	0.03137	20	0.887	0.03500
BC1-loblolly	38	1.610	0.00388	38	2.096	0.00913	38	2.211	0.00548	106	1.310	0.01321
Loblolly	75	1.743	0.00403	75	2.153	0.01437	75	2.289	0.00857	138	1.568	0.00677
	$n_{e1} = 6.1 \pm 1.1$			$n_{e1} = 11.5 \pm 5.5$			$n_{e1} = 10.4 \pm 3.1$			$n_{e1} = 4.9 \pm 3.0$		
	$n_{e2} = 6.1 \pm 1.0$			$n_{e2} = 7.1 \pm 1.7$			$n_{e2} = 8.2 \pm 1.7$			$n_{e2} = 4.1 \pm 1.9$		
	$n_{e(uwls)} = 4.1 \pm 0.6$			$n_{e(uwls)} = 3.9 \pm 0.7$			$n_{e(uwls)} = 4.4 \pm 0.7$			$n_{e(uwls)} = 4.7 \pm 2.0$		

mean (Table 2). The transformation was generally effective in meeting Lande's criteria, except that the variances of both backcross populations were less than the F_1 variance (Figure 1, lower right). This resulted in invalid estimates based on the backcross populations (i.e., methods 3 and 4). Methods 1 and 2 and the unweighted least squares method all produced similar estimates for the effective number of genes, ranging from 4.1 to 4.9 with standard errors less than 3 (Table 2).

QTL Mapping Experiment

Total tree heights at 7 months from germination were normally distributed as determined by a Wilk-Shapiro test, obviating the need for transformation before analysis. Three unlinked QTL were detected for 7-month seedling height (Weng et al. 2002). All three were detected with both analysis methods—single-marker ANOVA and interval mapping. Each QTL accounted for about 4–6% of the phenotypic variation, while the three together accounted for 14.5% of the variation. All 7-month height QTL were contributed by the hybrid parent; however, the recurrent slash pine parent contributed several QTLs for stem diameter (data not reported).

Discussion

The number of genes controlling first-year height growth in longleaf pine remains an elusive parameter to estimate. Our current estimates range from a count of 3, based on QTL detection in one backcross family, to 11.5, based on one method as described by Lande (1981), using data on F_1, F_2, and parental generations reported by Brown (1964). Brown's own estimate of 10 genes for first-year height was based on Lande's method 1 (also Castle 1921) and our reanalysis confirms this value with a standard error of 3. The unweighted least squares method (Cockerham 1986) provided consistent estimates of about 4 to 5 genetic factors, with standard errors less than 2. However, given the generally poor fit of some of the populations to the additive model, we suspect that these estimates are biased downward, although, estimates of 4 to 5 factors were obtained using methods 1 and 2 (Lande 1981) and Snow's data. The F_1, F_2, and parental populations fit the additive model well, so these estimates appear to be sound, although it is important to emphasize that these estimates represent the minimum number of genes, because linkage and variable allelic affects will cause the actual number to be higher (Lande 1981; Zeng 1992).

The lower number of genetic factors as detected by QTL analysis was not unexpected, given the less than full marker coverage of the genome and less than 100% heritability of early height growth. Weng et al. (2002) estimated that the linkage maps for both parents covered less than 75% of the genome each, so at least 25% of the genome was not evaluated for QTL. In addition, estimates of the heritability of early height growth in longleaf pine vary widely from 15–65% (Layton and Goddard 1982; Snyder and Namkoong 1978; Snyder et al. 1977), with the higher estimates being based on cross or family means. However, none of these estimates considers specifically first-year growth under closely controlled environmental conditions. Using an assumed individual tree heritability of 50% and extrapolating from 14.5% phenotypic variation explained by 3 QTL suggests that about 10 QTL of the magnitude detected would be required to account for the additive genetic variation.

The current evidence suggests that 10 is a good estimate for the effective number of genes contributing to the difference in first-year height growth between longleaf and loblolly pines. In some crosses fewer genes may be segregating, as suggested by data from Snow's experiment; however, in all cases these should be viewed as estimates of the minimum number. According to Brown's data and reasonably supported by QTL analysis, it seems that about 6 of these factors are directly involved in determining hypocotyl length and that some of these, and at least 4 others, are involved in primary shoot growth after the full extension of the hypocotyl. QTL analysis of height data collected in the field suggests that same sort of phenomena. That is, growth QTLs detected at an early age are not necessarily detected at later ages (Weng et al. 2002). This result is consistent with the general finding in pine

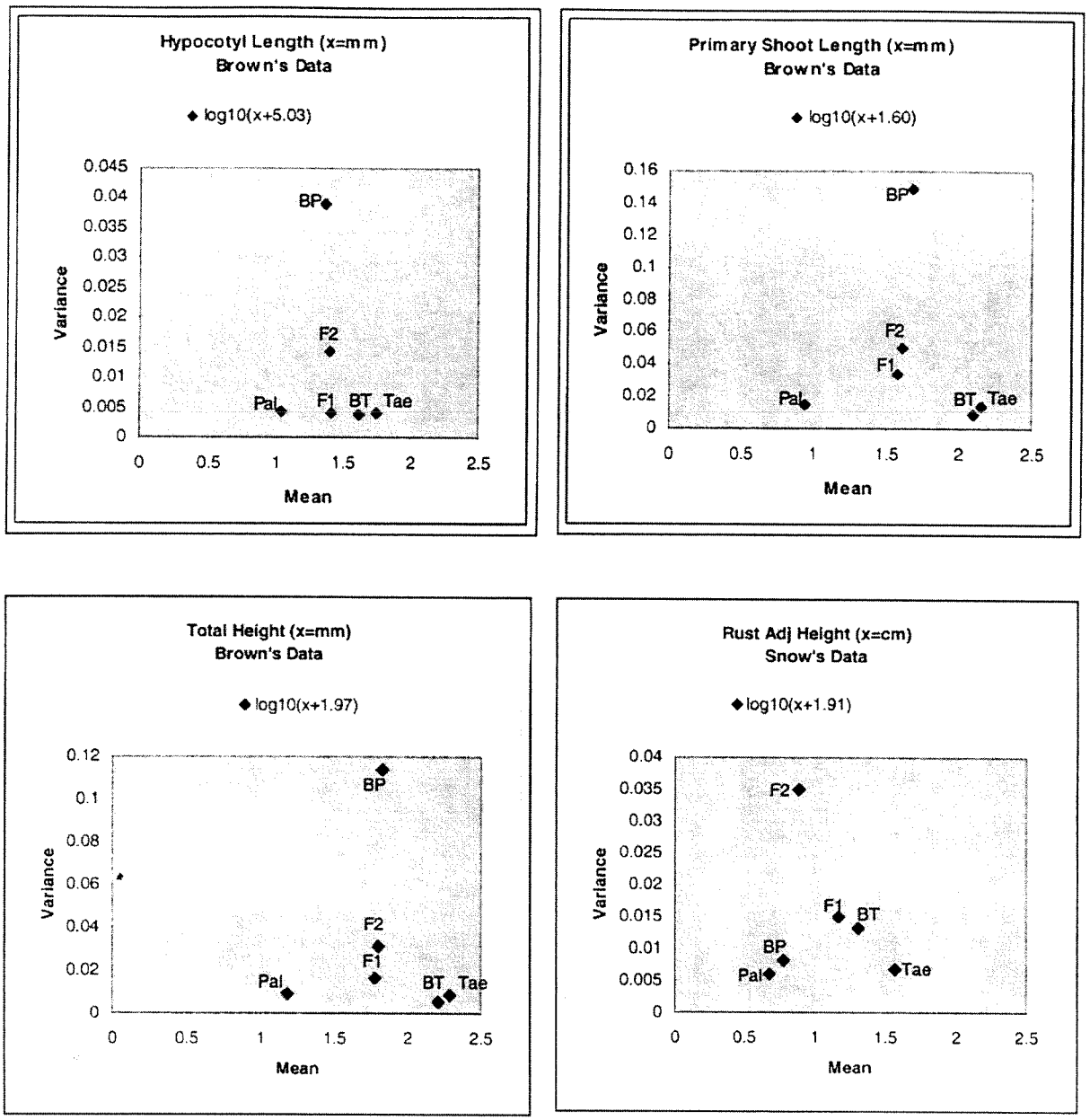

Figure 1. Variance by mean plots for Brown's and Snow's data, transformed as described in the text (Pal = Longleaf, Tae = Loblolly, BP = BC1-longleaf, BT = BC1-loblolly).

improvement studies that early heights (age < 3 years) are not highly correlated with medium (>7 years) and longer-term (>15 years) heights.

Although increased first-year height growth appears to be an advantage to survival of most southern pines, especially on highly productive sites, and set the stage for good growth in later years, for longleaf pine the opposite appears to be true, even if the effect is small. Lande (1981) provided the following formula for estimating the maximum proportion of the difference between parental populations attributable to the leading genetic factor: $p <= 1/n_e^{1/2}$. For Snow's data, this equates to as much as 0.50 (i.e., roughly one-half the difference in first-year height between longleaf and loblolly pine could be attributed to a single gene). On the transformed scale used here, this is 0.44 units or about 1.0 cm untransformed. As a percentage of the untransformed parental and F_1 population means, this effect is 33% of the longleaf mean, 3% of loblolly, and 7% of the F_1. The three detected QTL in the BC1-slash, 18–27 × 488 (Weng et al. 2002), population had from 0.75 to 1.0 cm effect or 7–9% of

the population mean. A 1 cm difference is a large effect relative to the longleaf mean height at 1 year, but in absolute terms it is clearly small enough that it can easily become diluted in environmental variation or by increasing growth rates in subsequent years, or both.

On drier and poorer sites, more typical of longleaf pine habitat, first-year height effects of 1 cm and less are apparently important for early survival and subsequent stand establishment. The reduction in height growth is concomitant with increased stem diameter and root development and herein a significant advantage on lowly productive sites and habitats, especially where periodic ground fires burn. The adaptation of longleaf pine to these sites appears to be the result of the accumulation of alleles at several loci, each with a small effect as measured on first-year height growth. Various combinations of these alleles control the grass-stage trait and thus provide longleaf pine with a selective advantage on these poorer sites.

Tree improvement programs aimed at increasing the early height growth of longleaf pine must recognize that reducing the grass stage may reduce long-term fitness in typical longleaf pine environments by making the seedlings susceptible to fire-induced mortality. Hybridization of longleaf pine with loblolly pine naturally occurs, producing Sonderegger pines (X *P. sondereggeri* Chapm.), providing a natural source of early height growth alleles for longleaf pine. However, because all longleaf pines exhibit the grass stage, there must be some barrier to introgression of loblolly genes into longleaf pine. One of the most likely mechanisms would be that, though the Sonderegger pines exhibit some early height growth (i.e., intermediate to longleaf and loblolly pines), they lose the fire-resistant characteristics of the grass stage, without becoming large enough, fast enough, to escape ground fires, and are strongly selected against in ecosystems with frequent fires.

Products of recurrent backcross breeding programs will need to be tested on an array of sites and management regimes in order ensure their proper place in reforestation plans. The use of these trees in reforestation programs may require exclusion of fire during early stand development and corresponding silvicultural treatments more similar to those used for loblolly or slash pines. During later stand development, the progeny of advanced backcross generations should appear morphologically similar to longleaf pine, and normal longleaf pine silvicultural treatments will most likely be appropriate.

This type of experiment needs to be carried out over a several-year period on various field sites and combined with high density QTL mapping to verify the existence and nature of genes affecting growth at different developmental stages and in different environments. Given the relatively small effects of these genes, larger populations (>200 for F_2 and BC1) will be required for both accurate estimation of the number of genes and their detection and mapping with genetic markers. Marker-assisted selection (MAS) applications in forest tree breeding require QTL that are effective in predicting longer-term growth rates. Combining early phenotypic data with QTL data predictive of later performance should effectively increase the heritability of growth rate and greatly increase the available genetic gain in both conventional and backcross breeding programs.

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References

Bey CF, 1979. Longleaf pine—a good candidate for genetic improvement. In: Proceedings of the Longleaf Pine Workshop. Mobile, AL, October 17–19, 1978. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station; 65–69.

Brown CL, 1964. The seedling habit of longleaf pine. Athens, GA: Georgia Forest Research Council and the University of Georgia, School of Forestry.

Castle W, 1921. An improved method of estimating the number of genetic factors concerned in cases of blending inheritance. Science 54:223.

Cockerham CC, 1986. Modifications in estimating the number of genes for a quantitative character. Genetics 114:659–664.

Derr HJ, 1966. Longleaf × slash pine hybrids at age 7: survival, growth, and disease resistance. J Forestry 64:236–239.

Derr HJ, 1969. Intraspecific and interspecific crosses for testing brown-spot resistance of longleaf pine. Final Report on Study FS-SO-1152-5.2. New Orleans, LA: USDA Forest Service, Southern Forest Experiment Station (now Asheville, NC: USDA Forest Service, Southern Research Station).

Keeley JE and Zedler PH, 1998. Evolution of life histories in *Pinus*. In: Ecology and biogeography of *Pinus* (Richardson DM, ed). Cambridge, MA: Cambridge University Press; 219–249.

Lande R, 1981. The minimum number of genes contributing to quantitative variation between and within populations. Genetics 99:541–553.

Layton PA and Goddard RE, 1982. Environmental and genetics effects on the duration of the grass stage in longleaf pine. In: Proceedings of the Seventh North American Forest Biology Workshop, Lexington, KY, July 26–28, 1982. Lexington, KY: University of Kentucky; 131–136.

Little EL Jr and Dorman KW, 1954. Slash pine (*Pinus elliottii*) including south Florida slash pine, nomenclature, and description. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station.

Schmidtling RC and White TL, 1989. Genetics and tree improvement of longleaf pine. In: Proceedings of the Symposium on the Management of Longleaf Pine, Long Beach, MS, April 4–6, 1989. New Orleans, LA: USDA Forest Service, Southern Forest Experiment Station (now Asheville, NC: USDA Forest Service, Southern Research Station); 114–127.

Snow GA, Matthews FR, Nance WL, and Foster GS, 1990. Effects of pollen source on loblolly pine resistance to *Cronartium quercuum* f.sp. *fusiforme*. For Sci 36:304–312.

Snyder EB, 1969. Parental selection versus half-sib family selection of longleaf pine. In: Proceedings of the Tenth Southern Forest Tree Improvement Conference, Houston, TX, June 17–19, 1969. Macon, GA: USDA Forest Service, Eastern Tree Seed Laboratory; 84–88.

Snyder EB, 1973. Fifteen-year gains from parental and early family selection in longleaf pine. In: Proceedings of the Twelfth Southern Forest Tree Improvement Conference, Baton Rouge, LA, June 12–13, 1973. Baton Rouge, LA: Louisiana State University, Division of Continuing Education; 46–49.

Snyder EB and Derr HJ, 1972. Breeding longleaf pines for resistance to brown spot needle blight. Phytopathology 62:325–329.

Snyder EB, Dinus RJ, and Derr HJ, 1977. Genetics of longleaf pine. Washington, DC: USDA Forest Service.

Snyder EB and Namkoong G, 1978. Inheritance in a diallel crossing experiment with longleaf pine. New Orleans, LA: USDA Forest Service, Southern Forest Experiment Station (now Asheville, NC: USDA Forest Service, Southern Research Station).

Walhenberg WG, 1946. Longleaf pine: its use, ecology, regeneration, protection, growth, and management. Washington, DC: Charles Lathrop Pack Forestry Foundation.

Wells OO and Snyder EB, 1976. Longleaf pine half-sib progeny test. Forest Sci (Note) 22:404–406.

Weng C, Kubisiak TL, Nelson CD, and Stine M, 2002. Mapping quantitative trait loci controlling early growth in a slash pine × (longleaf pine × slash pine) BC1 family. Theor Appl Genet 104:852–859.

Wright S, 1968. Evolution and the genetics of populations, vol. 1: genetic and biometric foundations. Chicago, IL: The University of Chicago Press.

Zeng Z-B, 1992. Correcting the bias of Wright's estimates of the number of genes affecting a quantitative character: a further improved method. Genetics 131:987–1001.

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