

Bole Straightness Measurement for Advanced-Generation Loblolly Pine Genetic Tests¹⁾

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Summary

A relative straightness scoring system (REL) was compared with sweep, a product grading standard, in two genetic tests of loblolly pine (*Pinus taeda* L.). A third test was used to quantify repeatability and length of time required for each method of measurement. REL compared favorably with sweep at each location; it was least as heritable as sweep and its genetic correlation with sweep was 0.90 to 0.95. Repeatability values for two graders, one experienced and one inexperienced, were 0.78 and 0.73, respectively. The major limitation of the relative score was that genetic differences were inflated in one test which had exceptionally straight trees and undervalued at a second test which had extreme variation in bole straightness. An absolute score (ABS), based on sweep measurements, is suggested as an alternative for loblolly pine genetic tests.

Key words: Bole straightness, sweep, ocular score, *Pinus taeda* L., second generation genetic tests.

Introduction

Choice of traits in genetic improvement programs is determined by the influence each trait has on the value of the commercial product as well as its patterns of genetic and phenotypic variation. In the case of bole straightness traits, genetic gain in product value has been demonstrated repeatedly (BLAIR *et al.*, 1979). The appropriate trait measurement method for second generation loblolly pine (*Pinus taeda* L.) genetic tests is at issue since the tests are approaching selection age.

The primary function of genetic tests in an operational breeding program is to correctly order the genetic entries for selection. Selections will then be used in a production orchard or in recurrent breeding to increase the value of commercial plantations. Genetic tests may also be used to obtain estimates of realized gain or genetic parameters although these are ancillary to selection purposes. The merit of a straightness measurement method for second-generation tests lies in its correlation to sweep, a mill grading standard, (e.g. SCHROEDER *et al.*, 1968).

Quantitative measurement methods for bole straightness have traditionally been rejected in United States loblolly pine breeding programs because they are time-consuming and costly (e.g. SHELBORNE and NAMKOONG, 1966). Consequently a six-point relative score (REL) has been used for first generation tests in the North Carolina State-Industry breeding program because grader accuracy for absolute scoring was variable (PASCHKE, 1979). REL differs from an absolute score in that the score is relative to the trees in a single test location rather than relative to all trees in genetic tests.

Continued use of either a relative or absolute scoring system depends on its selection efficacy relative to sweep, a mill grading standard. We hypothesize that an absolute scoring system could substitute for sweep in young genetic tests without undue grader inaccuracy. Visual assessment of stem straightness in radiata pine (*Pinus radiata* D. DON.) approximated sweep in a milling study of a 21-year-old plantation (MILLER, 1975). Other bole defects such as spirality and lean are considered to be of negligible importance. Lean has no heritable basis (SHELBORNE and STONECYPHER, 1971) and spirality, a rare defect thought to be controlled by a few major genes (PERRY, 1960), was most likely eliminated in the initial natural stand selections.

The purpose of this study was to choose a cost-effective straightness measurement method for second generation genetic tests. Sweep was compared to single and repeated scoring. The repeated scoring was done because breeders of radiata pine have found that a second ocular measure improved accuracy without the need for the added labor of a quantitative measurement method (BANNISTER, 1979).

Materials and Methods

Sweep, the maximum deflection in the lower, most valuable portion of the bole, was measured in three loblolly pine genetic tests where the trees were old enough to have at least 2.4 to 8.4 meters of bole. Relative differences in sweep measured prior to half-rotation were assumed to be carried through harvest age although this assumption has not been validated to our knowledge. We also assumed that the results from these first generation genetic tests could be directly extrapolated to second generation tests which will be measured at four to six years of age (e.g. McKEAND, 1988).

a) Genetic and phenotypic parameter estimation

Two genetic tests were measured to compare sweep with the relative straightness score. A third test was used to compare the repeatability and time requirements for each of the methods. Bole sweep was measured as the maximum deflection from a 2.4 m pole set against the vertical axis of the tree. The pole was moved along the first log (4.8 m) to assess maximum deflection. Straightness scores were subjectively assessed on a scale of 1 (best) to 6 (worst) before sweep measurement.

Test 1 — Green County, Mississippi

This first-generation test had 53 full-sib families and a woods-run checklot, each represented by 5-tree row plots in twelve blocks. Fourteen parents were used in 3 or more specific crosses. The mean height of the test was 7.6 m at eight years after test establishment. Sweep was measured 8.5 years after planting.

Test 2 — Perry County, Arkansas

Fifty-nine open-pollinated families were planted north of the loblolly pine range in the Ouachita Mountains. Each family was planted in 5-tree row plots in eight blocks. Of the total, 55 families came from seed collected from selec-

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tions made in natural stands in southeast Texas, northern Louisiana-southern Arkansas and central Arkansas-southeast Oklahoma. The remaining 4 families originated in first-generation seed orchards. Sweep and straightness score were measured eight years after test establishment. Only the 37 families from central Arkansas and southeast Oklahoma were used to estimate genetic and phenotypic parameters since they represent the most local seed source for the Perry County test.

b) Repeatability and timing estimates

Test 3 — Wake County, North Carolina

The test was a pairwise comparison of plantlets and seedlings from six open-pollinated families, measured seven years after establishment. Three plots established in four of the eight blocks of the test were used to compare repeatability among graders for the two straightness methods. Three plots were marked off in each of four blocks (60 trees measured for each trait). No attempt was made to discern differences between seedlings and plantlets.

Each plot was measured twice, each time with one of the two methods assigned randomly to the graders. Two graders participated: Grader A had over ten years' experience and Grader B had negligible experience. The first two blocks were measured a second time for each method to get a measure of repeatability for each grader (30 trees per trait per grader).

The other four blocks of the study were used to simulate actual genetic test measurement (height, diameter, straightness) in order to obtain the time required to measure sweep or straightness score. A sampling design similar to the one used in the first four blocks of Test 3 was employed: two plots in each of the four blocks were measured and the time of measurement was recorded.

Statistical analyses

The analyses of variance was based on the following random model:

$$Y_{ijk} = m + b_i + f_j + bf_{ij} + e_{ijk}$$

where Y_{ijk} = value of the k th tree in the j th family, i th block

m = experimental mean
 b_i = effect of the i th block
 f_j = effect of the j th cross or half-sib family
 bf_{ij} = block by family interaction effect
 e_{ijk} = within-plot error

The estimates for the Mississippi test were based on 53 full-sib families; the estimates of narrow-sense heritability include some in estimable portion of the dominance variance. Heritability was estimated on an individual and family mean basis according to NAMKOONG (1979, pp. 70 to 78). Genetic gain (G) from selection of family means for the score and for sweep is as follows:

$$G = i \text{Cov}_{A, P} / \sigma_P \quad (\text{Equation 1})$$

where i = selection intensity
 $\text{Cov}_{A, P}$ = covariance between the breeding value of sweep and the phenotypic value of the selection criterion
 σ_P = the phenotypic standard deviation of family means

For sweep as a selection criterion and the selection goal, the covariance term is a quarter (or half in the case of full-sibs) of the additive genetic covariance:

$$G_1 = i h^2 \sigma_{P_{swp}} \quad (\text{Eq. 2})$$

where h^2_{swp} = heritability on a family mean basis

For the score, the selection goal is sweep and the selection criterion is the score so the covariance term is a quarter (or half) of the additive genetic covariance between score and sweep.

$$G_2 = i h_{str} h_{swp} r_G \sigma_{P_{swp}} \quad (\text{Eq. 3})$$

where $r_{G_{str, swp}}$ = genetic correlation between two traits measured on the same individual at a single point in time

The efficiency (E) of selection of score on sweep relative to direct selection on sweep is estimated as a percentage:

$$E = \frac{(h_{str} h_{swp} r_{G_{swp, str}}) \times 100}{h^2_{swp}} \quad (\text{Eq. 4})$$

The Pearson product moment correlation was used to estimate family mean correlation (r_{pf}). Tests for statistical significance are described in SNEDECOR and COCHRAN (1967).

Repeatability was estimated as an intraclass correlation, r , from the following analysis of variance model (FALCONER, 1981, p. 127).

$$Y_{ijk} = m + g_i + t_j + e_{ijk}$$

where Y_{ijk} = value of the k th measurement for the i th tree for the j th grader

m = experimental mean
 g_i = effect of i th grader
 t_j = effect of j th tree
 e_{ijk} = residual error

$$r = \frac{MS_t - MS_e}{MS_t + MS_e} \quad (\text{Eq. 5})$$

Phenotypic variance decreased and heritability increased as variance due to measurement error is removed. Relative efficiency of the two measurement techniques relative to one, K , was multiplied by the heritability to adjust for the reduction in measurement error:

$$K = n / (1 + (n-1) r) \quad (\text{Eq. 6})$$

where n = number of measurements
 r = correlation of repeated measurements of the same individual

Results

The genetic relationship between sweep and the relative score (REL) were the same at both test locations. The genetic correlations were nearly unity and heritability was slightly higher for REL than for sweep (Table 1). REL allowed families to be ranked similarly to sweep for both tests (family mean correlations, Table 1). This occurred in Test 1 despite the low variance among families for sweep (Test 1 family variance is 0.0017 compared to 0.0479 in Test 2). The trees in Test 1 were extremely straight compared to the trees in Test 2 (Table 2). Families were statistically different ($P \geq 0.05$) for both traits at both locations.

Gain efficiency for indirect selection from a single REL scoring was over 100% (Table 3). Use of two measurements of score increased efficiency further although selection on values obtained from a single scoring alone surpassed use of sweep as a direct measure of bole straightness. The efficiency of indirect selection was high because the genetic correlation was nearly 1; REL's heritability score was higher than that for sweep and its repeatability was moderately high (Table 3).

REL was measured in less time although it was less repeatable than sweep. Measurement of sweep, height and diameter required a mean of 3.44 minutes per 5-tree plot compared to 2.55 minutes required for measurement of the score, height and diameter. At this rate, a single second-

Table 1. -- Heritabilities for sweep and ocular score and genetic and family mean correlations between traits by test location. Test 1 is located in Green County, Mississippi and Test 2 is located in Perry County, Arkansas.

TEST LOCATION	SWEEP (cm)		STRAIGHTNESS SCORE (1-6) (REL)		CORRELATIONS AMONG TRAITS	
	family heritability	individual heritability	family heritability	individual heritability	genetic	family mean
1	.59	.06	.80	.13	.90	.65
2	.64	.13	.71	.24	.95	.82

Table 2. -- Genetic test means (and standard deviations) for sweep and straightness scores (REL). Bole straightness is given for seed sources planted in Test 2.

TEST/SEED SOURCE	METHOD	
	SWEEP (cm)	REL SCORE (code 1-6)
1 Greene County, MS	0.27 + .24	4.16 + .86
2 Perry County, AR	4.20 + 3.88	3.00 + 1.08
Arkansas/ Oklahoma	3.60 + 1.98	2.67 + 0.96
Northern Louisiana	3.87 + 3.97	2.85 + 0.99
Southeast Texas	5.82 + 4.11	3.80 + 1.06

generation genetic test of at least 1224 trees (TALBERT *et al.*, 1981) would require 14 hours for measurement of sweep and growth traits. Conversely, measuring REL and growth traits score would require 10.4 hours, a savings of 3.6 hours.

The score's repeatability (r) is 0.78 compared to 0.89 for sweep in Test 3. By grader, the correlation between the first and second score of the same trees was 0.78 for the experienced versus 0.73 for the inexperienced grader (Table 4).

Discussion

a) Merits of the relative scoring system

REL was a good approximation of sweep and it can be

measured quickly. Little benefit was derived from a second scoring and genetic gains from a single measure of the score were higher than gains from direct selection on sweep. The difference in the outcome of the loblolly pine and radiata pine studies (BANNISTER, 1979) may lie in the portion of the bole which is scored. REL includes the entire stem for loblolly pine but in New Zealand, the bole is scored 2 meters above ground level (BANNISTER, 1979). Sinuosity of new growth increment may be poorly correlated with sweep in the lower 2 meters. A second reason for the difference is that trait and species differences may be too great to permit extrapolation from radiata to loblolly pine bole straightness.

Table 3. — Genetic gain efficiency of straightness score as a selection criterion for sweep, a mill standard. Test 1 is located in Green County, Mississippi, Test 2 is located in Perry County, Arkansas. Test 3 is located in Wake County, North Carolina. K is a repeatability coefficient.

Selection criterion	Selection goal	Gain efficiency (%)		Test 3
		Test 1	Test 2	K
Sweep	Sweep	100	100	
Straightness score (REL) One measurement	Sweep	105	104	
Straightness score (REL) Two measurements	Sweep	110	112	1.126

b) Disadvantages associated with the relative scoring system

The major limitation of REL in this study was that genetic differences at young ages cannot be used to predict product value. Genetic differences in sweep are potentially over- or under-valued. For example, REL in Test 1 inflated differences in sweep which are too small to influence the product value (Table 5). Use of the relative score suggested large genetic differences yet sweep differences were so

Table 4. — Correlation between measurements by grader for sweep and relative straightness score (REL).

-----Experienced grader-----

SWEEP (cm)	REL SCORE (code 1-6)
.87	.78

-----Inexperienced grader-----

SWEEP (cm)	REL SCORE (code 1-6)
.82	.73

Table 5. — Sweep values by relative score (REL) category for two genetic tests.

RELATIVE SCORE	SWEEP (cm)	
	TEST 1	TEST 2
1	-	2.16
2	0.15	2.90
3	0.18	3.68
4	0.24	5.25
5	0.33	7.94
6	0.57	19.71

poorly expressed in Test 1 that it was difficult to sort genetic entries.

At the second test, REL undervalued genetic differences which influence product value as well as seed source deployment decisions. The score did not yield information which could be used to detect maladapted genotypes. This is a disadvantage in recurrent breeding programs where an

Table 6. — A proposed absolute score (ABS) for loblolly pine.

ABS	Sweep (cm)
1	0 - 2.4
2	2.5 - 4.9
3	5.0 - 7.4
4	7.5 - 12.4
5	12.5 - 17.4
6	17.5 +

improved seed source is deployed outside its breeding region (LAMBETH *et al.*, 1984).

If these results are indicative of family performance across multiple sites, then genetic potential for bole sweep may not be optimally expressed on all test sites. A survey of second generation tests planted in Arkansas and North Carolina suggests that expression of sweep varies greatly across tests of the same families⁴⁾. This implies difference in the degree to which bole straightness is expressed for all genetic entries. Optimal trait expression of sweep might be compared to adaptability traits such as cold hardiness: site conditions must be conducive to good trait expression. If the trait is poorly expressed then the magnitude of genetic differences will be too limited for effective selection.

The utility of REL is limited by the extent to which the trees in each test approximate straightness found in all loblolly pine genetic tests. Continued use of REL could stymie genetic progress as well as deployment decisions. If sites influence the degree of trait expression, then use of a relative score will give suboptimal response to multiple trait index selection. For example, REL overestimates the amount of sweep at one test (Test 1) and underestimates sweep in a second test (such as Test 2) such that relative scores are not consistent with the absolute scores used to develop the economic weights for selection indexes (e.g. TALBERT, 1984). Economic weights for the index are determined with absolute scores of trees which represent the range of bole straightness in loblolly pine (BRIDGWATER and STONECYPHER, 1979; TALBERT, 1984; BRIDGWATER and SQUILLACE, 1986).

Measurements of growth and straightness are weighted according to the index which is derived in part from the economic weights. If the relative scores exaggerate the amount of sweep (as in Test 1), then a tree with an unfavorable relative score may be incorrectly downgraded even though it exhibits desirable characteristics. Ultimately, the deviation of REL from absolute values will cause breeders to make selections which do not maximize product value.

c) A proposed absolute score

Our results suggest relative score should be avoided if genetic expression varies widely across test sites and if selection is based on a multiple trait index. An absolute score is a promising alternative which would permit a low-cost straightness assessment which would relate to econom-

⁴⁾ WILLIAMS, unpub. data.

ic value and to maladaptability when non-local seed sources are used.

The absolute score (ABS) would also serve the ancillary purpose of genetic tests: realized gain estimation. It would slightly undervalue extremes greater than 17.5 cm of sweep but the result should be a conservative gain estimate. Since ABS would be based on sweep, genetic gain projections could be assigned a monetary value. ABS should be scored on a basis consistent with the sweep measurement.

An absolute score based on sweep must represent the entire range of sweep values likely for loblolly pine. The scoring system should have an even number of categories to avoid grader ambivalence (i.e. avoid scoring most trees with an "average" score). At least six categories will ensure that ABS discriminates within any test in the southeastern United States, despite a wide range in sweep across sites (Table 6). This approximates the number of categories for absolute scoring systems successfully used for pine genetic improvement programs worldwide (MULLIN *et al.*, 1978; BANNISTER, 1979; ARBEZ *et al.*, 1974). The six categories for ABS is based on the range of sweep values represented in both Test 1 and Test 2 (Tables 2 and 6).

An absolute score based on sweep has an added advantage over REL: it can be converted to a relative score if needed. Deviations from the test mean based on ABS can be assigned a score value which will be relative to other trees in that test. Conversely, sweep can be sampled in each test to minimize grader inaccuracy with the use of ABS.

The sweep values assigned to each ABS category should ultimately reflect product value changes for multiple product use. Also, the merits of the proposed absolute score should be tested across different test sites composed of the same families. The effect of site differences in this study on the choice of a measurement method may be biased upwards for intrapopulation breeding programs because Test 2 had large seed source differences (Table 2).

Conclusions

Ocular scoring approximated of sweep in each of two genetic tests. Genetic gain from a single measure of the score was higher than gain obtained from direct selection on sweep so a second scoring was not necessary. The score could be measured with a 35% time savings over sweep and repeatability of the score was 0.78 compared to 0.89 for sweep in Test 3. However, the relative score distorted absolute genetic differences so that maladaptability was underestimated and the extreme bole straightness in a second test was overlooked. We propose a six point absolute score (ABS) based on sweep for use with multiple trait index selection.

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Genotypic Differentiation at PGM in Engelmann Spruce from Wet and Dry Sites

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Summary

Microgeographic variation of PGM allozymes was examined in 999 Engelmann spruce from 6 population samples. Field sites were categorized as wet or dry, and genotypic frequencies were compared between adjacent wet and dry sites. Dry sites had higher proportions of heterozygotes than wet sites, and the value of F at dry sites was generally lower than at wet sites. Comparisons of genotypic frequencies between age classes suggests that PGM heterozygotes have lower viability than homozygotes in wet sites.

Key words: Engelmann spruce, microgeographic differentiation, allozymes, natural selection.

Introduction

The high levels of outcrossing and the wind pollination common to all conifers produces the opportunity for high levels of gene flow among populations. Radioactively-labelled pollen has been observed to travel more than one kilometer, and pollen traps on ships 50 or more kilometers from shore capture conifer pollen (WOLFENBARGER, 1946). The great distances traveled by pollen lead us to expect relatively little geographic differentiation in conifers, and this expectation is usually consistent with empirical results. For example, HAMRICK (1983) examined modes of reproduction and patterns of population structure in different groups of plants, and found relatively little differentiation of populations in conifers. Despite the expectation of little differentiation among populations of conifers, biologists have found microgeographic differentiation among stands differing in elevation, aspect, or moisture

availability. For example, white fir, *Abies concolor*, in the mountains of Colorado and New Mexico is polymorphic for female cone color. Some trees produce exclusively green cones, while others produce exclusively purple cones. Populations at low elevations (2000 meters to 2500 meters) have predominantly trees bearing green cones, while the most common trees at the upper edge of the elevational distribution bear purple cones. Strong shifts in phenotypic frequencies have been documented over elevational distances of 1200 meters, and lateral distances of 10 km (STURGEON and MITTON, 1980; FARRIS and MITTON, 1985). There are also examples of differentiation of sites with respect to allelic frequencies for protein polymorphisms. For example, the peroxidase locus in ponderosa pine is differentiated both along elevational gradients and between adjacent north- and south-facing slopes (MITTON *et al.*, 1977; BECKMAN and MITTON, 1984), and peroxidases in both Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are differentiated among krummholz, flag and spire trees at tree line (GRANT and MITTON, 1977).

The high potential for gene flow in conifers helps us to identify the causes of microgeographic variation. Heterogeneity on a small scale that is not associated with environmental variation and is not replicable from site to site might well be attributed to familial structure in stands of forest trees (LINHART *et al.*, 1981). However, microgeographic patterns of differentiation that are repeatedly associated with environmental variation can be attributed to natural selection among heterogeneous environments.

This study of microgeographic variation follows comprehensive studies of inheritance, mating systems and microgeographic variation in both Engelmann spruce, (*Picea engelmannii*), and subalpine fir, (*Abies lasiocarpa*) SHEA, 1985, 1987, 1988). SHEA used six polymorphic allozyme loci in spruce to document variation in the mating system between sites and over years, and to reveal microgeogra-

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