Family x Environment Interaction for Sweep in Local and Nonlocal Seed Sources of Loblolly Pine.

S. D. Douglass,[1] C.G. Williams,[2] C.C. Lambeth,[1] D.A. Huber[1], L.C. Burris[1]

Abstract -- Eight tests were planted in Mississippi, Arkansas and Oklahoma across diverse physiographical areas with each test containing five loblolly pine *(Pinus taeda* L) seed sources: coastal North Carolina, piedmont North Carolina, northern Mississippi/Alabama, central Mississippi/Alabama and Arkansas/Oklahoma. Each seed source consists of the best eight open-pollinated families for volume available from first generation seed orchards. The fastest growing seed source across sites at age eight was coastal North Carolina (28.24 dm^3/tree) and the slowest was Arkansas/Oklahoma (22.60 dm^3/tree). Piedmont North Carolina had less sweep (2.80 cm) than all other seed sources while the central Mississippi/Alabama seed source was the most crooked (3.13 cm). There was considerably more G x E for sweep among seed sources than families within seed sources. Conversely, for volume there was slightly less G x E at the seed source level than for families within seed sources for volume per tree. The more unstable seed sources for sweep were the coastal North Carolina source which dropped significantly in rank at two Mississippi sites and the central Mississippi/Alabama source which slightly dropped rank when planted northwest of its origin. There was no correlation among families for sweep and volume.

Keywords: Bole straightness, genetic stability, *Pinus taeda* L.

INTRODUCTION

Stem straightness has been an important trait in conifer breeding programs worldwide, especially in breeding programs which focus on improved sawlog grade. An ocular score based on an absolute rather than relative scale has proven the most beneficial (Miller 1975; Bannister 1979; Mullin et al. 1969). With the absolute score, grades assigned to each tree are based on the actual amount of defect observed; the score value is not relative to other trees at the location. There are three primary benefits of using an absolute value for stem straightness rather than a relative score: 1) maladaptability and other types of genotype x environment interaction (GxE) can be readily detected across locations, 2) score values can be translated into financial values at a

---

[1] Weyerhaeuser Southern Tree Improvement Program, P.O. Box 1060 Hot Springs AR 71901
[2] Dept. of Genetics, North Carolina State University, Raleigh NC 27675-7614

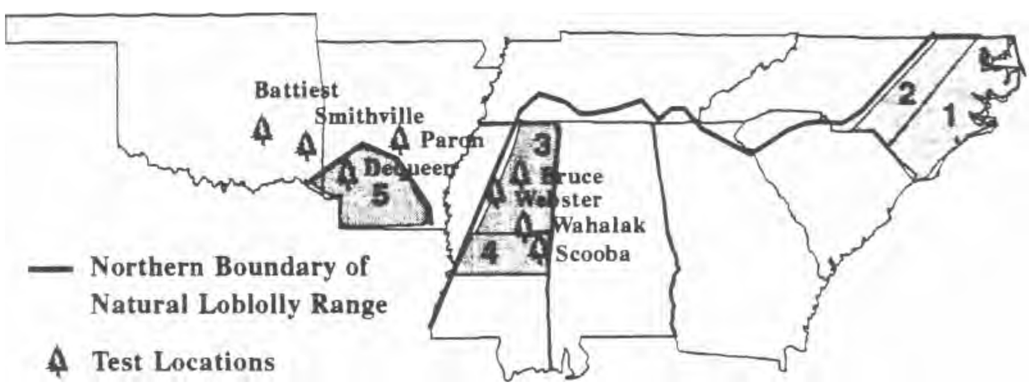
mill conversion facility and 3) selection for straight trees is more efficient across locations. In Weyerhaeuser's loblolly pine breeding program, a six-point absolute ocular score is used to measure sweep in the first log (Williams and Lambeth 1989).

Maladaptability has been observed in sweep measured in southerly seed sources of loblolly pine *(Pinus taeda L)* planted at a single Arkansas location. However, without multiple planting locations of the same seed sources, the study could not be used to ascertain whether significant G x E existed for sweep (Williams and Lambeth 1989). In other studies, stem straightness showed less GxE than diameter in radiata pine *(Pinus radiata* D. Don.) in Australia (Pederick 1986). Stem straightness in loblolly pine *(Pinus taeda* L.) from the "Lost Pines" area in Texas showed no significant GxE although GxE was strong for height and volume per tree (van Buijtenen 1978). However, neither study used a fixed ocular score based on sweep. Due to observed sweep problems with some non-local seed sources in Arkansas and Oklahoma (Lambeth, et. al. 1984), further study is needed to see whether local and non-local seed sources and families are stable (low G x E) for sweep ranking across a large number of sites.

This study examines the magnitude of genotype x environment interaction for sweep in the first log as compared to volume per tree at age eight years. Sweep and growth were measured in tests planted in Mississippi, Arkansas and Oklahoma which had open-pollinated families within five loblolly pine *(Pinus taeda* L) seed sources of both local and non-local origin.

METHODS AND MATERIALS

Test description



Seed Source Origin

1 Coastal North Carolina	**4 Central Mississippi/Alabama**
2 Piedmont North Carolina	**5 Arkansas/Oklahoma**
3 Northern Mississippi/Alabama	

Figure 1. Eight test locations of the Long-Term Seed Source Study are shown in relation to the northern boundary of the natural range of Loblolly pine (dashed line) and the seed source origin (shaded). A set of four tests were established in each of two years starting in 1982.

Eight test sites were planted with eight wind-pollinated families within each of five loblolly

Mississippi/Alabama (N-M/A), central Mississippi/Alabama (C-M/A) and Arkansas/Oklahoma A/O). The families in each source were the best available for volume production from first generation seed orchards. The trees were protected from insect attack for the first three years. Also, competition from hardwoods was kept to a minimum.

Measurements

Sweep, survival, fusiform rust infection, height, and diameter at 4.5 feet (1.37 meters) were measured at age eight years. Sweep was measured using a six-point ocular scoring method with each point being a one centimeter deflection from a eight-foot straight edge. The maximum deviation in the first twelve feet (3.66 meters) of the main stem, excluding the butt swell and lean, was scored. Each tree was thoroughly examined to locate the maximum deviation and quantitative measurements were periodically scored to maintain accuracy. Individual tree volume was calculated for inside bark of the entire stem (Smalley and Bower 1968).

Statistical analyses

An analysis of variance was used to test significant differences among seed sources, families and G x E interactions. Each test was planted in a split-block design with the five seed sources as main plots and eight wind-pollinated families within each seed source as five-tree row plots.

$$Y_{ijklm} = \mu + L_i + B(L)_{ij} + S_k + F(S)_{l(k)} + S \times L_{ki} + S \times B(L)_{ijk} + F(S)_{l(k)} \times L_i + \varepsilon_{ijklm}$$

where:

Y_{ijklm}	value of tree *m* in family *l*, seed source *k* within block *j* block at location *i*
μ	experimental mean
L_i	effect of the *i*th location
$B(L)_{ij}$	effect of the *j*th block within *i*th location
S_k	effect of the *k*th seed source
$F(S)_{l(k)}$	effect of the *l*th family within the *k*th seed source
$S \times L_{ki}$	effect of the seed source by location interaction
$S \times B(L)_{ijk}$	effect of the seed source by block within location interaction
$F(S)_{l(k)} \times L_i$	effect of the family within seed source by location interaction
ε_{ijklm}	pooled error term

Variances associated with each effect were derived from the expected mean squares and the average genetic correlation among environments associated with families within seed sources was calculated as follows:

$$r_{f(s)} = \frac{\sigma^2_{f(s)}}{\sigma^2_{f(s)} + \sigma^2_{f(s) \times l}}$$

where $\sigma^2_{f(s)}+\sigma^2_{f(s)xl}$ = family within seed source and family x location interaction variance components respectively.

The genetic correlation among sites was adjusted for interactions associated with heterogeneity (not due to true rank changes) of family variance components among sites:

$$r'_{f(s)} = \frac{\sigma^2_{f(s)}}{\sigma^2_{f(s)} + [\sigma^2_{f(s)\mathrm{x}l} - \mathrm{var}(\sigma_{f(s)i})]}$$

where $\mathrm{Var}(\sigma_{f(s)i})$ is the variance of the $\sigma^2_{f(s)}$ for locations i = 1 to 8

The average genetic correlation (and adjusted correlation) among environments associated with seed sources was calculated similarly:

$$r_s = \frac{\sigma^2_s}{\sigma^2_s + \sigma^2_{s\,\mathrm{x}\,l}} \qquad r'_s = \frac{\sigma^2_s}{\sigma^2_s + \sigma^2_{s\,\mathrm{x}\,l} - \mathrm{Var}\,(\sigma s_i)}$$

Because family x location interaction was statistically significant at the 1% level or higher for volume and sweep, the Finlay and Wilkinson (1963) method of regressing family mean against an environmental index was used to determine whether some families were more or less stable than others. To test for linearity, we used the R^2 from the slope values from the regression analysis. Any R^2 greater than 0.80 was considered high (McKeand, et al. 1988). With large numbers of families there was little value in recalculating the site mean after subtracting each family mean value in question as is recommended when only a few families are used.

$$X_{ij} = X_i + \mathrm{B}_j\,(X._j - X..) + \varepsilon_{ij}$$

where:

X_{ij}	mean of family *i* at environment *j* (*i*=1 to 40, *j*=1 to 8)
X_i	mean of family *i* over all environments
B_j	coefficient for family mean regressed against environment mean
X_j	mean of all families over all environments
ε_{ij}	deviation or residual from a linear response

RESULTS AND DISCUSSION

Sweep exhibited more G x E interaction at the seed source level than at the family within seed sources level (Table 1). In contrast, volume appears to have slightly less G x E interaction with seed sources than families within seed sources (Table 1). A closer look at interactive seed sources and families are more relevant to decision-making in a seed source movement program than the analyses of variance alone.

Table 1. Genetic correlations among sites at the seed source *(rs)* and family within seed source (rf(s)) levels. The prime (') indicates that the correlations were adjusted for scale effects.

Trait		*r'f(s)*		r'_c
Sweep	0.86	0.89	0.10	0.15
Volume per Tree	0.68	0.74	0.80	0.85

Seed Sources

Seed sources for both sweep and volume at age eight years were generally stable across diverse physiographic areas with a few notable exceptions. For sweep, the coastal North Carolina source performed well for sweep across sites except at the two most crooked at Wahalak and Webster County, Mississippi. The decrease in rank was not related to longitude, latitude or proximity to the edge of the species range. Also, the central Mississippi/Alabama families showed a slight drop in rank with some sinuous stem growth observed when planted northwest of their origin. The piedmont North Carolina source was generally the straightest across all sites with central Mississippi/Alabama as the most crooked (Table 2). No genetic entries were severely maladapted with respect to volume production.

Table 2. Seed source means for sweep (cm) at age eight years across eight locations. Ranks in parenthesis range from the straightest (1) to the most crooked (5). Locations are ordered from least to most sweep.

Seed Source	Battiest, OK.	**Smithville,** OK..	Dequeen, AR.	Bruce, **MS.**	Scooba, **MS.**	Paron, AR.	Webster Co. , MS.	Wahalak, MS.
NC-P	1.96 (1)	2.37 (2)	2.56 (3)	3.04 (4)	2.77 (1)	3.06 (1)	3.15 (1)	3.71 (1)
NC-C	2.26 (2)	2.06 (1)	2.15 (1)	2.55 (1)	2.83 (2)	3.29 (3)	3.59 (5)	4.16 (5)
MA-N	2.27 (3)	2.57 (4)	2.53 (2)	2.97 (2)	2.97 (3)	3.12 (2)	3.22 (2)	4.00 (2)
A/0	2.32 (4)	2.49 (3)	2.85 (4)	3.23 (5)	3.23 (5)	3.60 (5)	3.38 (3)	4.04 (3)
M/A-C	2.36 (5)	2.72 (5)	2.86 (5)	3.04 (3)	3.19 (4)	3.35 (4)	3.51 (4)	4.12 (4)

There were relatively small seed source differences in sweep means at this age but they were statistically important and unrelated to volume or survival (Table 3) at age eight years. Seed sources which exhibited high volume such as central Mississippi/Alabama had as much sweep as a seed source with considerably less volume such as Arkansas-Oklahoma. Coastal North Carolina was first for volume production and second for sweep. Although the Arkansas/Oklahoma and central Mississippi/Alabama both displayed more sweep than other seed sources, Arkansas/Oklahoma had the best survival across all sites with central Mississippi/Alabama having the worst.

Table 3. Seed source means across eight locations for individual-tree volume (dm ^{3}), sweep (cm), and cumulative percent mortality at age eight years. Standard errors of the means. are in parentheses.

Source	Mean Volume - dm (STDERR)	Mean Sweep - cm (STDERR)	Cumulative Mortality
Coastal North Carolina	28.24 ± (.30)	2.83 ± (.03)	6.0%
Central Mississippi/Alabama	26.93 ± (.29)	3.13 ± (.03)	8.1%
North Mississippi/Alabama	25.75 ± (.29)	2.93 ± (.03)	5.7 %
Piedmont North Carolina	24.43 ± (.27)	2.80 ± (.03)	5.1%
Arkansas/Oklahoma	22.60 ± (.25)	3.12 ± .03)	3.7%

Seed source stability across sites was tested using the Finlay and Wilkinson (1963) method of regressing the environmental source mean against the location source means (all R^2 values were greater than 0.90). A regression slope of b=1.0 indicates an average stability across sites and a response in direct proportion to site change. A slope of b > 1.0 indicates a source is unstable and that it is more responsive to site changes. A slope of b < 1.0 indicates the source is stable and that it is less sensitive to site changes.

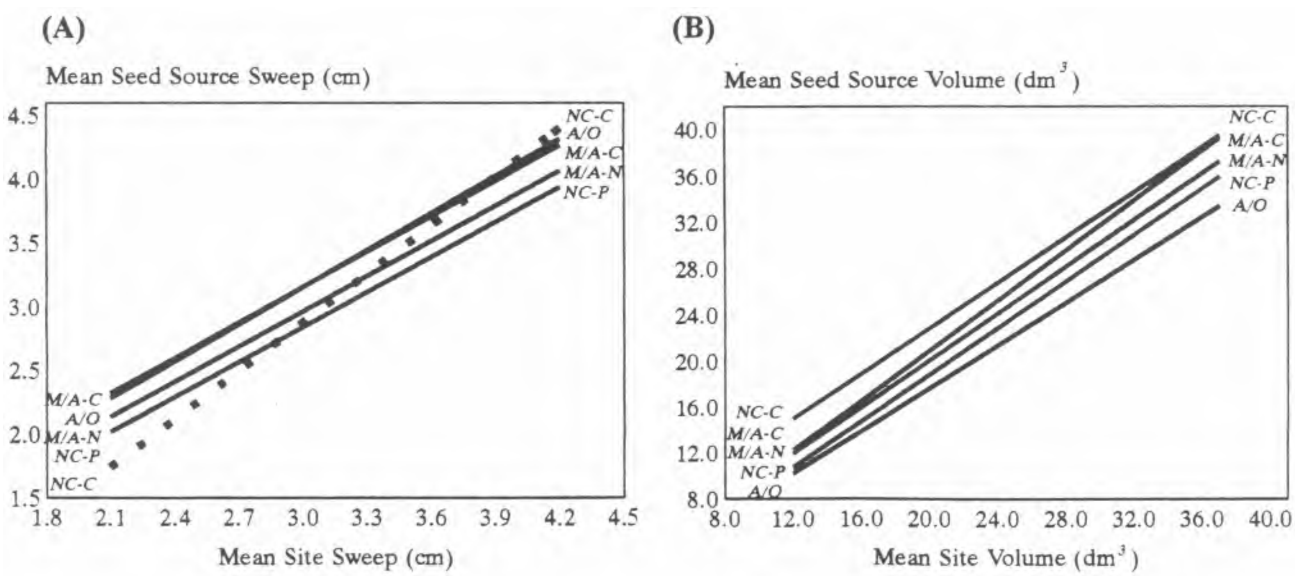


Figure 2. A) Seed source regression slope (b) for sweep at age eight years across eight locations, B) Seed source regression slope (b) for volume at age eight years across eight locations.

For sweep, coastal North Carolina proved to be the least stable across physiographic areas (Figure 2A). In contrast, the Arkansas/Oklahoma seed source was stable but exhibited poor sweep. The central Mississippi/Alabama seed source was generally stable at all locations except the northeastern Arkansas and Oklahoma sites where it dropped slightly in rank. Piedmont North Carolina and northern Mississippi/Alabama sources showed average stability for sweep and were generally the straightest across test locations (Figure 2A). All seed sources were stable across locations for volume (Figure 2B)

Families within seed sources

Stability of families within seed source was also tested using the Finlay and Wilkinson (1963) method of regressing the environmental family means against the location family means. Of the 40 families, 32 had $\mathbf{R}^2$ values higher than 0.80. Of the remaining eight families with R^2 values which fell between 0.54 and 0.80, four of these were the extremely straight piedmont North Carolina families which exhibited negligible variation for sweep. In addition, 17 out of 40 families had slope (b) values for sweep which were significantly different than b=1 at the 10% level. Of these 17 families, 10 came from the more unstable stable seed sources: coastal North Carolina and central Mississippi/Alabama.

For volume, families with stabilities that are responsive to site conditions are desired to maximize productivity through intensive silvicultural practices. In contrast, when it is uncertain what factors directly influence sweep, selecting a family exhibiting straight stems and average stability (b=1) may be more advisable.

There were several interesting exceptions for sweep at the family level. One top-ranking coastal North Carolina family for volume proved to be highly unstable for sweep and quite crooked (Figure 3A). However, four coastal North Carolina families were well-adapted to non-local sites with high volume production and exceptionally straight stems.

(A) **(B)**

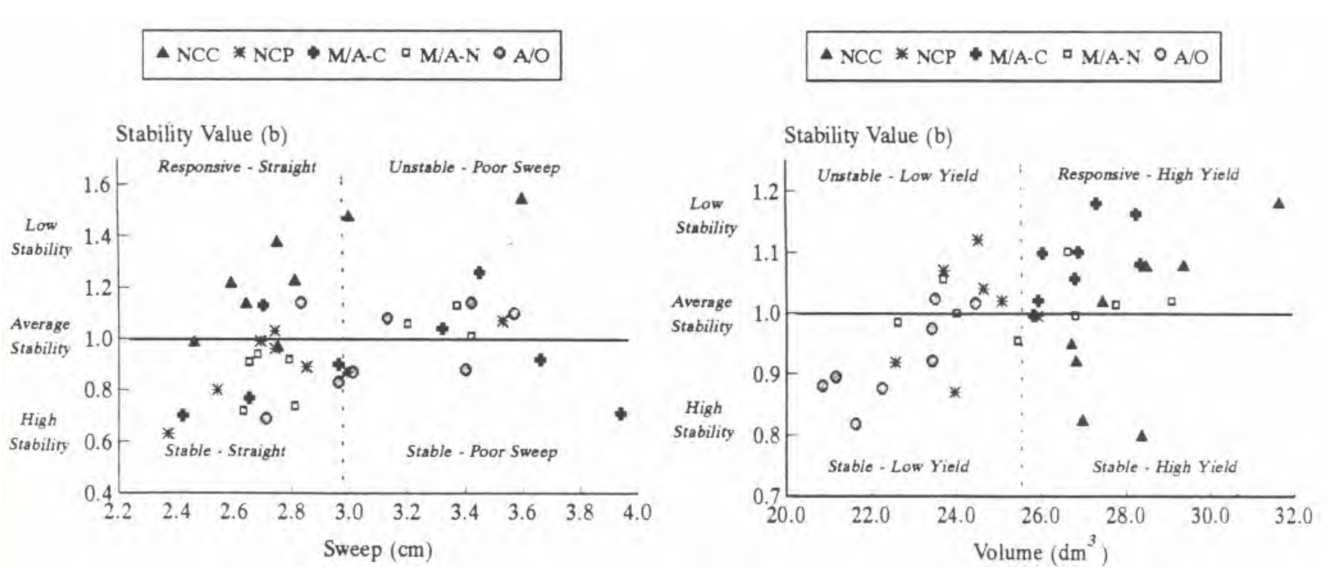


Figure **3.** A) Family stability for sweep at age eight years across eight locations, **B)** Family stability for volume at age eight year across eight locations. Each point on the graph represents an open-pollinated family within the indicated seed sources.

Central Mississippi/Alabama demonstrated the widest spread in sweep among families (range=1.5 cm) (Figure 3A). Some families within this seed source were among the straightest and most stable in the tests while others were very unstable and crooked (Figure 3A). Three other sets of families, northern Mississippi/Alabama, piedmont North Carolina and Arkansas/Oklahoma were generally stable with family performance in sweep overlapping among seed sources (Figure 3A).

Results differed greatly at the family level between volume and sweep. For volume, central Mississippi/Alabama families responded well to site conditions favoring high volume production (Figure 3B). In contrast, sweep had more variability among families. The coastal North Carolina families generally were stable to responsive and were among the best for both growth and straightness. Piedmont North Carolina, northern Mississippi/Alabama, and Arkansas/Oklahoma families also exhibited high to average stability with less respect to volume production.

There was no correlation among families for sweep and volume (Figure 4). Therefore, it is possible to select for both high volume production and straight stems among families within seed sources.

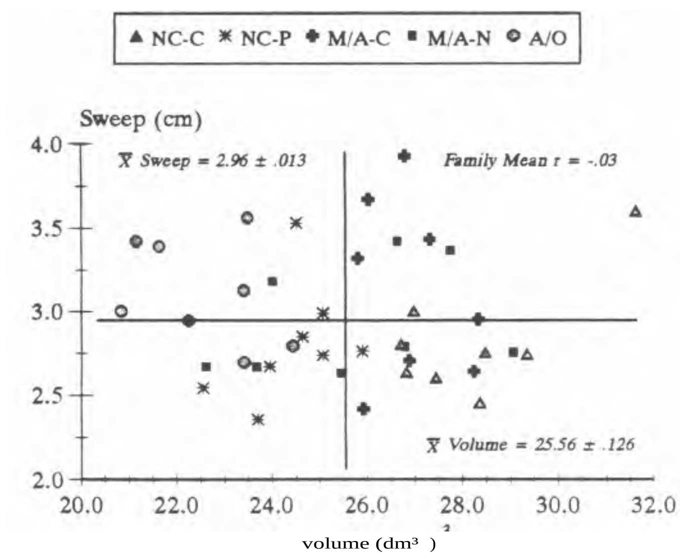


Figure 4. Scatter diagram of family mean for sweep and individual tree volume at age eight years across eight locations.

CONCLUSIONS

- For sweep, there was more G x E at the seed source level than for families within seed sources.
- For volume, it was reversed with slightly less G x E for volume at the seed source level than for families within seed sources.
- None of the seed sources or families exhibited serious maladaptation on any of the eight sites for sweep at age eight years..

. There was no correlation between sweep and volume at the seed source or family level.

ACKNOWLEDGMENTS

We thank the following individuals for their helpful manuscript reviews: Dr. Bailian Li, University of Minnesota, Dr. Colin Matheson, currently visiting University of Florida from Canberra, Australia, and Barbara Jones, Weyerhaeuser Company,

LITERATURE CITED

Bannister, M.H. 1979. An early progeny test in Pinus radiata. 2. Subjective assessment of crookedness. N. Z. J. For. Sci. 9(3): 241-261.

Finlay, K. W. and G. N. Wilkinson. 1963. The analysis of adaptation in a plant breeding programme. Austr. J. Agric. Res. 14: 742-754.

Lambeth, C. C., P. M. Dougherty, W. T. Gladstone, R. B. McCullough and O. O. Wells. 1984. Large-scale planting of North Carolina loblolly pine in Arkansas and Oklahoma: a case of gain versus risk. J. of For. 82(12): 736-741.

McKeand, S. E., B. Li, A. Hatcher, R. Weir 1988. Stability Parameter Estimates for Stem Volume for Loblolly Pine Families Growing in Different Regions in the Southeastern United States. For. Sci. 38(1): 10-17.

Miller, R.G. 1975. Visual assessment of stem straightness in radiata pine. Austr. For. Res. 7: 45-46.

Mullin, L. J., R. D. Barnes and M. J. Prevost. 1969. Review of the Southern Pines in Rhodesia. Rhod. Bull. For. Res. 7. 328 p.

Pederick, L.A. 1986. Family x site interactions in Pinus *radiatain* Victoria. p. 66. In Proc. IUFRO Conference, a joint meeting of working parties on Breeding Theory, Progeny Testing and Seed Orchards, Oct. 13-17, Williamsburg VA (Abstract).

Smalley, G. W. and D. R. Bower 1968. Volume Tables and Points - Sampling Factors for Loblolly Pines in Plantations on Abnormal Fields in Tennessee, Alabama, and Georgia Highlands. Forest Service Research Paper SO-32.

van Buijtenen, J. P. 1978. Response of the "Lost Pines" seeds sources to site quality. pp. 228-234. In Proc. 5th North American Forestry Biology Wkshp, Gainesville FL.

Williams C.G. and C. C. Lambeth. 1989. Bole straightness measurement for advanced-generation loblolly pine genetic test. Silv. Gen. 38(5/6): 212-217.