The Inheritance of Bole Straightness in Young Loblolly-Pine

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Introduction

Bole straightness is a morphological feature of the tree of considerable importance to wood utilization and consequently to silviculture and tree breeding. It is desirable for the tree breeder to know the degree to which various aspects of bole straightness are inherited and the degree of genetic correlation among them and with other characteristics. Such information is needed in planning selection programs to help in allocating priorities to different characteristics, and to predict gains.

The objectives of the studies reported in this paper are:

1. To obtain estimates of heritability of different parameters of bole straightness for loblolly pine (P. taeda L.).
2. To determine the genetic and phenotypic correlations of various parameters of bole straightness with each other.
3. To develop and use different techniques of quantifying bole straightenss''.

Bole straightness has always been regarded as important by foresters, and the earlier workers in tree improvement believed that the variation they observed in this character was heritable. Early clonal work demonstrated that straightness was genetically controlled, but evidence for appreciable additive genetic variation was not available prior to the studies of McWilliam and Florence (1955). Their studies on slash pine revealed considerable increases in the frequency of "acceptable" straight stems in plantations where open pollinated seed from selected parents had been used.

Perry (1960) made crcsses between two very crooked and two quite straight loblolly pines and reported differences between the progenies based on an index of crook determined by the number of crooks per meter and deviations of the crook nearest breast height. There were highly significant differences in crook index between progenies and a continuous gradation in crookedness between the most crooked (from crosses of crooked parents) and the most straight (from crosses of straight parents). Transgressive variation in straight X crooked crosses and continuous variation within families indicated that considerable numbers of genes were involved in the control of straightness. It might be predicted from these results that heritability of straightness would be appreciable. In 1964, Goddard and Strickland remeasured the same progenies and found differences among progenies similar to those reported by Perry. Their results indicated the correlation between two-year and seven-year measurements was quite good ($r = 0.83$), so that early assessments of straightness were thus quite adequate predictors of bole characters up to age seven.

In the published heritability estimates of traits of forest trees, neither Hattemer (1963) nor Namkoong et al. (1966) found any references to bole straightness in their extensive surveys of the literature. However, visual examination of open- and controlled-pollinated progenies of various pine species by many tree breeders has always suggested that this trait was under genetic control.

The series of studies reported here deals with the inheritance of various parameters of bole straightness and their genetic and phenotypic correlation with each other for loblolly pine aged from two to five years. These trees had average heights from about 4 to 15 feet. The older trees are of a sufficient size for the results to be some value to the tree breeder.

Materials

Two different field experiments (the open-pollinated and control-pollinated studies of the International Paper Company-North Carolina State Cooperative Loblolly Pine Heritability Study[4]) planted on adjacent sites, formed the material used in these studies. The parent tree population, experimental designs and forms of analysis for the heritability studies are fully described by Stonecypher (1967), and will merely be outlined here.

The open-pollinated study consists of progenies of 280 randomly chosen loblolly pine parent trees. These were randomly divided into 10 sets of 28 families each. The material was planted at two locations with contrasting environments with two replicates of 25-tree, square plots at each. A proportion of the total material was examined in this assessment.

The mating design used in the control pollinated study was N.C. State Design I (Comstock and Robinson 1948, 1952), a nested design in which each member of a group of parents used paternally is mated to a different group used maternally. Sixty-five male groups, each consisting of five females pollinated by a single male tree were randomly chosen from the parent population. The male groups were divided into eleven sets, and were planted in 1962, '63 and '64, but only the male groups planted in 1962 are involved in this study. Sets contained an average of 20 full-sib families with each family planted in a 12-tree row plot.

Measurements and Assessments

1. *Control-pollinated* families — Age two years:

The control-pollinated N.C. State Design I experiment was assessed at age 2 years. A single numerical, subjective rating was assigned to seedlings on a scale from one to five (from straight to very crooked). Four sets planted in January 1962, were assessed February 1964. All six replications of these sets in both locaticns were assessed by two observers, one observer for each location. Nineteen male groups, 74 families, 444 plots and slightly fewer than 5,000 seedlings were examined.

The subjective rating was based on an overall appraisal of the straightness of the seedling with equal weight being given to sweep, crook and lean. Seedlings that were severely damaged or distorted by such causes as tip moth attack and Cronartium fusiforme were not assessed.

2. *Open-pollinated* families — Aged *three-and-a-half* years:

One set of 28 open pollinated families which has grown uniformly in both replications was selected in location A, and a plot of 25 trees of each family in each replication was assessed for (i) the maximum amplitude of stem deviations and (ii) the number of helical rotations, both of the current year's growth.

The former were measured using a plexiglass viewer. This was constructed by fixing a 12-inch-long by three-inch-wide piece of plexiglass in a 12-inch-long holder.

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[3]) A photogrammetric technique (Shelbourne and Namkoong, 1966) was used for a group of families not reported here but was found to be too time-consuming in field and laboratory for making assessments of the thousands of trees necessary to estimate genetic variances.

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Parallel vertical lines were drawn on the plexiglass at .125 inch intervals. When the plexiglass was held 12 inches from the eye, a single interval between two lines measured one inch at a range of eight feet. The main objective of this relatively small study was to gain experience in the application of two techniques of measuring bole straightness, as well as to obtain a preliminary estimate of heritability of the two characteristics measured.

3. Open-pollinated families — Aged five years (wood study families):

Further open-pollinated families which had been studied previously in a nursery experiment and which were scattered at random through the sets of the field experiment were also assessed when aged five years and with heights up to 20 feet at Location B. It was desired to compare the straightness of these families growing in the field with the amount of compression wood that individuals of the same families had developed in the nursery (SHELBOURNE *et al.* 1969). The data however were also suitable for obtaining estimates of additive genetic variance and narrow sense heritability of straightness traits. In all, 37 open-pollinated families common to both the wood study and field planting were assessed for straightness in both replications at Location B.

Trees were given subjective ratings of one to five (ranging from straight to very crooked) for each of three characteristics, crook, sweep and straightness. Crook was defined as the random or helical deviations about the axis of the stem, whether this axis was straight or curved. Sweep was defined as the degree of curvature of the tree's axis or the extent of large curvilinear deviations of the stem. There is, of course, some intergradation between crook and sweep when they are assessed subjectively, and it is difficult to clearly differentiate between the two. The straightness rating was based on an ocular combination of crook and sweep characteristics and was estimated on a scale from one to five. It was necessary to view the stem from at least two directions at right angles to each other when rating crook, sweep or straightness. An attempt was made to subjectively assign an index for angle of lean, but this was found to be impracticable.

4. Open pollinated families — Aged five years:

Three sets, each of 28 families, were assessed using the same methods as described in the above paragraph. Assessment was restricted to two replications in Location B, so that a total of 84 half-sib families, 168 plots and slightly fewer than 4,000 trees were measured. In addition to crook, sweep and straightness assessed by a single observer, another rating of straightness was made by several different observers working at random within the experiment. The objectives of this study were to obtain estimates of heritability and genetic correlations among different subjective measures of straightness. A secondary objective was to see how satisfactorily estimates of straightness could be made by several observers.

Statistical Analysis

1. Control pollinated families — Aged two years:

The N.C. State Design I data on a single measure of straightness were subjected to analysis of variance. Components of variance were then computed to obtain estimates of additive and dominance (genetic) variance and heritability.

The genetic interpretation of components of variance for this analysis and the necessary assumptions about the nature of the population being sampled, as well as methods

Table 1. — Analysis of variance combined over sets and locations[1]) for the control pollinated families.

Source of Variation	Degrees of Freedom	Expected Mean Squares[2])
Sets	3	
Locations	1	
Reps. in locations	4	
Sets × locations	3	
Sets × reps. in locations	12	
Males in sets	18	$\sigma^2_w/k + \sigma^2_p + k1\sigma^2_{fs} + k2\sigma^2_{ms} + k3\sigma^2_f + k4\sigma^2_m$
Females in males in sets	52	$\sigma^2_w/k + \sigma^2_p + k1\sigma^2_{fs} + k3\,\sigma^2_f$
Males in sets × locations	18	$\sigma^2_w/k + \sigma^2_p + k1\sigma^2_{fs} + \; + k2\sigma^2_{ms}$
Females in males in sets × locations	52	$\sigma^2_w/k + \sigma^2_p + k1\sigma^2_{fs}$
Pooled error	280	$\sigma^2_w/k + \sigma^2_p$
Within plot		σ^2_w

[1]) As derived by STONECYPHER (1967).

[2]) σ^2_w = within plot variance for both locations combined over sets.

σ^2_p = plot to plot variance (pooled interactions, females in males x reps. and males x reps for both locations, combined over sets).

σ^2_f = variance due to differences among females mated to the same male for both locations combined over sets.

σ^2_m = variance due to differences among progenies from the same male, for both locations combined over sets.

k = harmonic mean of number of plants per plot.

k1, k2, k3, k4, = appropriate coefficients for variance components.

σ^2_{fs} = variance due to interaction of females in males in sets and locations, combined over sets.

σ^2_{ms} = variance due to interaction of males in sets and locations, combined over sets.

of computing heritability and standard errors of variance components are discussed by STONECYPHER (1967). Assumptions are the same for open- and control-pollinated studies except that with open-pollinated progenies, the additional assumption of a half-sib relationship must be made.

Narrow sense heritability was estimated thus:

$$h^2 = \frac{4\,\sigma^2_m}{\sigma^2_m + \sigma^2_f + \sigma^2_p + \sigma^2_w + \sigma^2_{fs} + \sigma^2_{ms}}$$

For meanings of these symbols see *Table 1*.

Three replications of four sets, in two locations, were analysed by separate sets using plot means. Estimates of within-plot variance were made separately using individual seedling data from a random sample of plots. The separate set analyses were then pooled over sets and locations. The form of this analysis is shown in *Table 1*.

2. Open pollinated families — Aged 3½ and 5 years:

Analyses of variance and covariance were made on one or more sets of 28 open-pollinated families and in one case a sample of 37 families from several sets, in two replications at single locations using the form of analysis shown in *Table 2*. Heritabilities of different parameters of straightness and their genetic and phenotypic correlations with each other were computed. Standard errors were computed for the family components of variance, using the methods of ANDERSON and BANCROFT (1952).

The genetic interpretation of components of variance and covariance for open pollinated family analyses as well as methods of computing genetics and phenotypic correlations are detailed in STONECYPHER (1967) and also in STONECYPHER *et al.* (1964). Narrow sense heritability was computed for all open pollinated family analyses thus:

$$h^2 = \frac{4\,\sigma^2_f}{\sigma^2_w + \sigma^2_{rf} + \sigma^2_f}$$

For meaning of these symbols, see *Table 2*.

Some further statistics were calculated for the group of 37 families (wood study) scattered through most of the sets in two replications at Location A; simple correlation coefficients between family means were computed for different parameters of straightness with percentage by volume of compression wood assessed in other trees of the same families growing in a nursery experiment. Correlations were also computed between straightness parameters of progeny and straightness and spiral ratings of the female parent tree.

Table 2. — Form of analysis of variance for open-pollinated families at one location.

Source of Variation	Degrees of Freedom	Expected Mean Squares[1])
Replications	r — 1	$\sigma^2_w/k + \sigma^2_{rf} + f\sigma^2_r$
Families	f — 1	$\sigma^2_w/k + \sigma^2_{rf} + r\sigma^2_f$
Replications × Families	(r — 1) (f — 1)	$\sigma^2_w/k + \sigma^2_{rf}$
Within plot		σ^2_w

[1]) σ^2_{rf} = variance due to replication × family interaction, or „plot error".
σ^2_f = variance between half sib families.
σ^2_r = variance due to replications.
σ^2_w = variance within plots
k = harmonic mean number of trees per plot.
r = number of replications.
f = number of families.

Results and Discussion

1. Control pollinated families — Aged two years:

An assessment of the control pollinated study at age two years, showed a heritability of .20 for the single subjective rating of bole straightness used and gave adequately precise estimates of genetic variance components. The heritability for straightness was the highest of several morphological and growth rate traits measured on this material, although it was still quite low.

A pooled analysis was made over the four sets and two locations of the control pollinated experiment that were assessed, and the pooled estimates of variance components are shown in *Table 3*, part 1. The effect due to locations was not significant, neither were the interactions between males in sets × locations or females in males in sets × locations. Estimates of σ^2_m, the component due to males and σ^2_f, the component due to females in males, were quite similar (.0190 and .0217) and had standard errors amounting to 52% and 29% of each components respectively. This provided some indication that the extra dominance variance included in σ^2_f was small, ($\sigma^2_m = \sigma^2_A/4$* and $\sigma^2_f = \sigma^2_A/4 + \sigma^2_D/4$). However, this indication is only very tentative in view of the relatively high standard errors of these components.

2. Open pollinated families — Aged 3½ years:

An assessment of two traits in this 3½ year, 10 feet high material, namely deviations of the current annual shoot and the number of spiral rotations in this section of the stem, revealed moderate heritabilities of these traits (.42 and .35, respectively).

The assessment was restricted to 28 half-sib families in two replications at a single location, but yielded adequately precise estimates of the family components of variance and thus of heritability. Variance components, standard errors and heritabilities are shown in *Table 3*, part 2. Standard errors of components were 18% and 68% respectively, of the family component of variance for deviations and numbers of spiral rotations.

The increase in heritability of straightness from the measurements made on two-year-old seedlings in the control pollinated study (h^2 = .20) to the value of .42 (stem deviations) for 3½ year old trees can be partly explained by the restriction of measurement to the current year's growth. This is likely to decrease environmental variation and raise heritability. However, it is also probable that once trees grow beyond the seedling stage, they become less affected by environmental changes and the heritability of straightness is likely to increase. For instance, tip moth attack and bird damage decrease after the first five years.

Use of the plexiglass viewer proved quite satisfactory for this young material. Its use for measuring stem deviations over the whole stem would however be limited by the poor visibility of the stem due to needles and branches at this age. It should be satisfactory in considerably older stands providing only the lower portion of the bole is required to be assessed.

3. Open pollinated families — Aged five years (Wood Study Families):

The same open pollinated families assessed for compression wood and other traits in a wood property study planted in a nursery (SHELBOURNE *et al.*, 1969), were assessed in the

* σ^2_A = additive genetic variance and σ^2_D = dominance (genetic) variance.

Table 3. — Components of variance and heritability estimates for different parameters of straightness, from four studies.

Experimental Material	Trait	Components of Variance	Estimated Value of Component	Standard Error of Component	F Ratio	Herit-ability
1. Two-year-old Controlled Pollinated	Straightness	σ^2_m	.0190	.0098	2.5**[1])	.20
		σ^2_f	.0217	.0064	3.2**	
		σ^2_{ms}	.0009		1.1	
		σ^2_{fs}	.0015		1.1	
		σ^2_p	.0225		1.7**	
		σ^2_w	.3129			
2. 3½-year-old Open Pollinated	Helical Rotations	σ^2_f	.0297	.0201	1.8*	.35
		σ^2_{rf}	.0580		5.6**	
		σ^2_w	.2511			
	Stem Deviations	σ^2_f	.0218	.0040	3.1**	.42
		σ^2_{rf}	.0122		2.4*	
		σ^2_w	.1727			
3. 5-year-old Open Pollinated (wood study)	Crook	σ^2_f	.0303	.0138	2.3*	.32
		σ^2_{rf}	0.295		2.7**	
		σ^2_w	.3243			
	Sweep	σ^2_f	.0231	.0126	2.0*	.23
		σ^2_{rf}	.0306		2.7**	
		σ^2_w	.3497			
	Straightness	σ^2_f	.0284	.0121	2.5**	.36
		σ^2_{rf}	.0244		2.8**	
		σ^2_w	.2637			
4. 5-year-old Open Pollinated	Crook	σ^2_f Set 1.	.0264	.0137		.28
		Set 2.	.0383	.0172		.38
		Set 3.	.0405	.0182		.40
		σ^2_{rf}	.0272			
			.0304			
			.0312			
		σ^2_w	.3292			
			.3392			
			.3351			
	Sweep	σ^2_f	.0090	.0109		.11
			.0226	.0103		.25
			.0156	.0115		.14
		σ^2_{rf}	.0329			
			.0128			
			.0235			
		σ^2_w	.3297			
			3272			
			.3952			
	Straightness	σ^2_f	.0198	.0111		.26
			.0404	.0154		.52
			.0287	.0141		.36
		σ^2_{rf}	.0248			
			.0014			
			.0280			
		σ^2_w	.2612			
			.0171			
			.2631			

[1]) ** significant at 1% probability level.
* significant at 5% probability level

field for crook, sweep, and overall straightness by means of subjectively assigned indices. Heritabilities of these traits were found to be moderate; .32 for crook, .23 for sweep, and .36 for straightness. Genetic and phenotypic correlations between these traits were all high except between sweep and crook indicating that these traits could be considered separately.

The additional objective of measuring straightness in these 37 families was to determine whether there was any relationship between their average compression wood percent, determined when grown under crowded but controlled conditions in a nursery, and the straightness of their half sib relatives when grown under normal plantation conditions in the field. The correlation between these traits was negative and weak ($r = -.17$) contrary to what was originally expected, but in agreement with results from other studies (SHELBOURNE, 1966) where a weak inverse relationship was demonstrated between amounts of slight and moderate forms of compression wood and various parameters of straightness.

The components of variance, standard errors of components and heritabilities for crook, sweep and straightness are shown in *Table 3*, part 3. Standard errors of σ^2_f, the family component, were in all cases about 50% of the component.

Phenotypic and genetic correlation coefficients between crook, sweep, and straightness are shown in *Table 4*. As expected, the phenotypic correlations were all somewhat lower than genetic. The phenotypic correlation coefficient for sweep with straightness was .77 and was .93 for crook with straightness, indicating that the latter was being given more weight in the straightness assessment.

Correlation coefficients were also computed between family mean values of the different straightness measures with the straightness and the number of turns of the stem spiral of the female parent which had been previously subjectively evaluated by STONECYPHER (1967). Parent-offspring correlation coefficients for parent straightness were .22 with crook, .22 with straightness, and .16 with sweep. These correlations are of the same order as those found between 18-month-old control-pollinated progeny and parent straightness ratings in another study (SHELBOURNE, 1966). Correlations of different straightness parameters of the offspring with parent spiral were all negligible. Although these parent-offspring correlations fail to reach significance at the 5% level it is believed they are meaningful and indicate that, in spite of a tremendous difference in size and age between 40-year-old parent and 5-year-old open pollinated offspring, heritability is appreciable.

4. Open pollinated families — Aged five years:

Estimates of heritability of crook, sweep and straightness, as made above, were made on an additional 84 open pollinated families grouped in three sets of 28 at Location B. Heritability values for these traits computed for each set were similar to those found above, with heritability estimates ranging from .28 to .40 for crook, .11 to .25 for sweep, and .26 to .51 for straightness.

In addition, separate measurements of straightness were made by a number of different observers working in different parts of the experiment, and their pooled estimates of heritability of straightness varied from zero to .47 in the three sets and showed poor correlation with the estimate of overall straightness made by a single observer ($r = .52$ to $.57$). Because of their evident unreliability they will not be considered further.

Analyses of variance were carried out on each set of 28 families individually. Components of variance, their standard errors and heritabilities are shown in *Table 3*, part 4. Standard errors of family components are mostly about 50% of the component indicating that the precision of these estimates was barely adequate. There were considerable differences in heritability estimates between different sets, and these were generally lower for set two. Mean heritabilities for crook, sweep and straightness averaged over sets, including estimates obtained from 37 wood study families, were .35, .18, and .38 respectively.

Genetic and phenotypic correlations between the straightness traits measured are shown in *Table 4*, where the genetic correlations are, in all instances, higher than their respective phenotypic correlations. Being based on the family components of variance and covariance, they are somewhat less reliable than these components themselves (whose standard errors indicate their reliability is usually barely adequate). Phenotypic correlations, which are more reliable, range from .50 to .76 between crook and sweep, but for these traits with straightness are from .83 to .94 indicating that in this study their relationship with straightness is equally strong.

Conclusions

Results from four studies involving both control and open pollinated families of loblolly pine from age two to five years indicate that bole straightness is a heritable trait which becomes more strongly genetically controlled as the tree increases in age and height. This is possibly because the environment has less deformatory effect on the leading shoot growth of the tree as it becomes more firmly established on the site. In addition the juvenile morphology of young pines including loblolly is different from that of the mature tree and probably the morphogenesis of the leading shoots from mature trees is more stable. The heritability of straightness estimated from these experiments increased from .20 at age two years to an average of .38 at age five years. Sweep or bole curvilinearity was generally much less heritable with values from .10 to .25 at age five years. This was expected from an understanding of the environmental causes of sweep (i. e. competition from other trees or weeds, poor planting, partial wind-blow etc.). Estimates of heritability of straightness at this age varied from .26 to .52 for different groups of families within the experiment. Poor height growth and subsequent deformation by tip-moth attack affected different parts of the field

Table 4. — Genetic and phenotypic correlations between straightness traits for 5-year-old open pollinated families.

Traits	Crook		Sweep	
	Genetic	Phenotypic	Genetic	Phenotypic
Straightness	.87[1]	.83	.97	.83
	1.00[2]	.92	.93	.89
	1.05[3]	.94	1.04	.85
	.93[4]	.86	.77	.77
Crook	—	—	.71	.50
			.94	.76
			1.20	.76
			.52	.42

[1]) Set 1.
[2]) Set 2.
[3]) Set 3.
[4]) Wood study families.

experiment. The plot size was rather large (25 trees) and resulted in a block size of over one acre which increased within block variability, reduced the precision of the experiment, and was probably the main reason for this variability in heritability estimates.

The relationships of crook, sweep and straightness to each other are best portrayed by phenotypic correlation coefficients; genetic correlations were much less precise and usually higher. Crook was more closely correlated with overall straightness than sweep ($r = .93$ compared with $r = .77$). Sweep thus showed some independence of the other straightness parameters.

The correlation between 40-year-old female parent and five-year-old offspring gives an additional measure of the inheritance of straightness, though, owing to the tremendous age and size difference, it might be effectively considered as two different traits. Correlations were not significant for the 37 parents studied ($r = .22$ for parent straightness and offspring crook).

A weak negative relationship ($r = -.17$) was demonstrated between amounts of compression wood in a group of 37 open pollinated families grown at close spacing in a nursery for destructive examination of wood properties, and the straightness of other members of the same families grown in the field. The absence of a strong relationship between percentage volume of compression wood and straightness is in agreement with other studies (SHELBOURNE, 1966).

The value of the studies reported here in elucidating the inheritance pattern and relationships of bole straightness was limited mainly by the low age and relatively small size of the material. Greater precision of variance component estimation would have been possible if it had been practicable to assess all 280 open pollinated families from the whole experiment. The effects of tip moth attack and site were highly variable and often prevented the proper expression of the potential bole morphology so that any numerical estimate of straightness was unrealistic. Such variation when confounded with family differences markedly reduced the precision of the experiment and also lowered heritability.

Use of subjective rating techniques for evaluating straightness proved quite satisfactory. Use of several different observers working at random within the experiment gave very unreliable results however. Ideally it is best to use repeated observations of each tree by several observers. Other less desirable, though more economical alternatives. are to use a single observer throughout the experiment or to restrict each observer to a single replication so that bias due to individual observers can be removed statistically along with the replication effects. Subjective ratings appeared to be the only practicable method for making extensive field measurements of straightness though the plexiglass viewer shows promise for certain situations. To obtain reliable estimates of genetic variances and heritability, a very large number of trees must be examined and any technique must be very fast in use.

Summary

Four studies on two- to five-year-old control and open pollinated families of loblolly pine (heights from three to 20 feet) indicated that straightness is heritable and becomes more strongly genetically controlled with increasing size and age of tree — h^2 (heritability in narrow sense) = .20 at age two, .38 at age five.

Two experiments with control and open pollinated families planted in incomplete block field designs with families confounded with blocks, were assessed for various aspects of bole straightness. Genetic and phenotypic correlations between traits indicated that sweep (stem curvilinearity) showed some independence from crook (random stem deviations) but was appreciably less heritable (h^2 = .10 to .23) than either crook (h^2 = .28 to .40) or overall straightness (h^2 = .26 to .52), all traits being assessed by subjective ratings. Such methods of assessment proved to be satisfactory and to be the most practicable means of assessing large numbers of trees.

A weak negative relationship was found between amounts of compression wood in a group of 37 open pollinated families grown in a nursery, and the straightness of the other members of these families grown in the field.

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