

Literature Cited

- ASKEW, G. R.: Implications of non-synchronous flowering in clonal conifer seed orchards. In: IUFRO conference: a joint meeting of working parties on breeding theory, progeny testing and seed orchards. Williamsburg, Va. pp. 182—191 (1986). — BRAMLETT, D. L. and O'GWYNN, C. H.: Recognizing developmental stages in southern pine flowers: the key to controlled pollination. U.S.D.A. For. Ser. Gen. Tech. Rep. SE-18 14 pp. (1980). — EL-KASSABY, Y. A. and RITLAND, K.: Low levels of pollen contamination in a Douglas-fir seed orchard as detected by allozyme markers. *Silvae Genetica* 35 (5—6): 224—229 (1986). — EL-KASSABY, Y. A., FASLER, A. M. and SZIKLAI, O.: Reproductive phenology and its impact on genetically improved seed production in a Douglas-fir seed orchard. *Silvae Genetica* 33 (4—5): 120—125 (1984). — FRIEDMAN, S. T. and ADAMS, W. T.: Genetic efficiency in loblolly pine seed orchards. In: Proc. South. For. Tree Imp. Conf., Blacksburg, Va. pp. 213—224 (1981). — GRIFFIN, A. R.: Clonal variation in radiata pine seed orchards. I. Mating probabilities in a seed orchard of *Pinus sylvestris* L.. *Silvae Genetica* 31 (5—f): 188—197 (1982). — SHEN, H. H., RUDIN, D. and LINDGREN, D.: Study of the pollination pattern in a Scots pine seed orchard by means of isozyme analysis. *Silvae Genetica* 30 (1): 7—15 (1981). — SMITH, D. B. and ADAMS, W. T.: Measuring pollen contamination in clonal seed orchards with the aid of genetic markers. In: Proc. 17th South. For. Tree Imp. Conf. Univ. of Ga. pp. 69—77: (1983). — ZOBEL, B. J. and TALBERT, J. T.: Applied Forest Tree Improvement. J. Wiley and Sons, N.Y., 505 p. (1984).

Genetic Variation in Growth and Form Characteristics of *Pinus caribaea*

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Abstract

Significant difference in total height and highly significant difference in stem form were found among 16 provenances of a 10 year old provenance trial of *Pinus caribaea* in one location within the savanna region of Nigeria. No significant differences were found for dbh, branch thickness and branch angle. The average height of the 15 provenances of *P. caribaea* var. *hondurensis* was significantly better than the one provenance of *P. caribaea* var. *caribaea* represented in the study. However, the variety *caribaea* provenance had straighter stems than the variety *hondurensis* provenances.

Except in total height in which the Los Briones provenance had the lowest performance, no significant differences existed in the five characteristics examined among the provenances of *Pinus caribaea* var. *hondurensis*. As a result of this and because very low genetic parameters were recorded for all the characteristics, the conclusion is that limited genetic improvement can be obtained by selecting any one of these provenances for use in the savanna region of Nigeria. However, genetic improvement through the selection of individual trees with outstanding phenotypes across the provenances is feasible because of consistently large tree-to-tree variation. Moreover, moderately high heritability estimates were recorded for total height (0.46) and stem form (0.56).

Stem form had the highest heritability estimate (0.56) and the greatest potential for genetic advance (expressed as a percentage of the mean, 7.5%), among the characteristics examined. It is a possible characteristic to be selected for among the *Pinus caribaea* provenances tested.

Key words: *Pinus caribaea*, height diameter, stem form, branch thickness, branch angle, phenotypic coefficient of variation, genotypic coefficient of variation, heritability, genetic advance.

Introduction

Pinus caribaea MORELET, grown as an exotic tree species in Nigeria, has adapted itself well to many ecological zones of the country. For this reason and its well known economic values, considerable interest has developed for use of

this species in afforestation and reforestation programmes in different parts of the country.

To identify the most suitable seed source of *Pinus caribaea* for use in afforestation programmes in the savanna region of Nigeria, provenance trials were started in 1968. They were established at three locations, and contained nine provenances covering the three described varieties — *hondurensis*, *caribaea* and *bahamensis*. Subsequent reports on this trial by OJO and SHADO (1973), OTEGBEYE (1980), and OTEGBEYE and SHADO (1984) showed that variety *hondurensis* was superior to the other two varieties in growth rate. It was closely followed by variety *caribaea* while variety *bahamensis* had the least growth rate.

Since *Pinus caribaea* var. *hondurensis* has the best growth rate among the tree varieties tested in Nigeria, subsequent provenance trials were composed almost solely of that variety. One such trial, established at Afaka in 1973, contains 16 provenances of the species, 15 of which were of variety *hondurensis* and one of variety *caribaea*.

The objectives of the study were to: determine the variation pattern in some growth and morphological characteristics among 16 provenances of *Pinus caribaea* and estimate some genetic parameters for each of the characteristics under consideration.

Materials and Methods

Fifteen provenances of *Pinus caribaea* var. *hondurensis* and one of var. *caribaea* were assessed for total height, diameter at breast height (dbh), stem form, branch thickness and branch angle in 1983 at 10 years of age. A description of the seed sources is given in Table 1. The trees were planted at Afaka in June, 1973 using potted seedlings raised in Savanna Forestry Research Nursery at Samaru. Afaka is about 30 km south of Kaduna at altitude 10°37'N, longitude 7°17'E, altitude of about 600 m; it has a mean annual rainfall of about 1290 mm.

The experimental design was a randomized block with five replications. The trees were planted at an espacement

Table 1. — Description of the sixteen provenances of *Pinus caribaea* tested at Afaka.

PROVENANCES	LATITUDE	LONGITUDE	ALTITUDE (m)	MEAN ANNUAL RAINFALL (mm)
Karawala, Nicaragua	12°58'N	83°34'W	< 10	4,200
Alamicamba, Nicaragua	13°34'N	84°17'W	20-30	2,900
Rio Cogo, Nicaragua	14°45'N	83°55'W	50-100	2,800
Brus Lagoon, Honduras Republic	15°45'N	84°40'W	< 10	2,654
Guanaja, Honduras Republic	16°27'N	85°54'W	50-100	2,300
Poptum, Guatemala	16°21'N	89°25'W	500	1,690
Manuel, Cuba	22°37'N	83°40'W		
Los Briones, Honduras Republic	15°34'N	86°44'W	600	912
Limonas, Honduras Republic	14°03'N	86°42'W	700	663
Culmi, Honduras Republic	15°06'N	85°37'W	500-600	1,325
Potosi, Honduras Republic	15°20'N	88°25'W	600-700	1,205
Mt. Pine Ridge, Belize	17°00'N	88°55'W	400	1,600
Santa Clara, Nicaragua	13°48'N	86°12'W	700	1,800
Byfield, Queensland (1)				
Melinda, Belize	17°01'N	88°20'W		
Byfield, Queensland (2)				

of 2.7 m × 2.7 m with 36 trees per plot. Because of a large number of missing trees in one replication, only four replications were used for analysis. The data were subjected to analysis of variance, using plot means.

Silvicultural treatments applied included application of 113 gm of superphosphate fertilizer about six weeks after planting, treatment with Aldrin dust to check termite attack, and clean weeding until the trees closed canopy.

Tree height was measured with a Haga altimeter, dbh was measured with a diameter tape and stem form, branch thickness and branch angle were assessed subjectively. The scoring system for stem form ranges from 0 for straight trees to 5 for crooked ones. For branch thickness and branch angle, trees with very fine or flat-angled branches were scored 0 while those with coarse or acute-angled branches received a score of 3.

Phenotypic coefficients of variation (PCV) and genotypic coefficients of variation (GCV) were estimated for each of the five characteristics using the relationships suggested by BURTON (1952), JOHNSON *et al.* (1955) and HANSON *et al.* (1956):

$$PCV (\%) = \sqrt{\frac{\sigma_{ph}^2}{\bar{X}}} \times 100$$

$$GCV (\%) = \sqrt{\frac{\sigma_g^2}{\bar{X}}} \times 100$$

where σ_{ph}^2 = phenotypic variance of the characteristic
 σ_g^2 = genetic variance of the characteristic
 \bar{X} = mean of the characteristic.

Phenotypic and genotypic coefficients of variation show the degree of phenotypic and genotypic variance respectively existing for a characteristic. The higher the value of

genotypic coefficient of variation, for instance, the higher is the genetic variance (AL-JIBOURI *et al.*, 1958).

Heritability (h^2) of provenance means was estimated using the relationship given by BURLEY and WOOD (1976):

$$h^2 = \frac{\sigma_p^2}{\sigma_p^2 + \sigma_e^2} \frac{r}{r}$$

where σ_p^2 = genetic variance among provenances
 σ_e^2 = error variance
 r = number of replications.

Genetic advance (GA) was computed as the product of heritability ratio and selection differential as suggested by JOHNSON *et al.* (1955):

$$GA = \frac{\sigma_p^2}{\sigma_{ph}^2} \times k\sigma_{ph}$$

where σ_p^2 and σ_{ph}^2 are as previously defined
 $k\sigma_{ph}$ = selection differential expressed in phenotypic standard deviation.

The assumption was made that K was 2.06 which is the expectation when 5% selection is made from the population.

The genetic advance obtained for each characteristic was also expressed as percentage of the mean of the characteristic. Genetic advance increases the usefulness of heritability estimates (JOHNSON *et al.*, 1955).

Results and Discussion

The results of the analyses of variance for the five characteristics examined are presented in Table 2. Differences in total height among the 16 *Pinus caribaea* provenances

Table 2. — Analyses of variance for five growth and morphological characteristics of 10-year-old provenances of *Pinus caribaea* tested at Afaka.

SOURCE	df	MEAN SQUARE ^a				
		HEIGHT	DIAMETER AT BREAST HEIGHT	STEM FORM	BRANCH THICKNESS	BRANCH ANGLE
Block	3	4.36	2.39	0.49**	0.14	0.03
Provenance	15	2.75*	3.34	0.18**	0.04	0.01
Error	45	1.46	2.78	0.08	0.08	0.02

^a * Significant at 5% level
 ** Significant at 1% level

were significant at 5% level while the differences in stem form were significant at 1% level. There was no significant difference in dbh, branch thickness and branch angle among these provenances. The mean values of the five characteristics of the provenances were 14.8 m, 18.0 cm, 2.7 (score), 1.6 (score) and 1.5 (score) for height, dbh, stem form, branch angle and branch thickness, respectively (Table 3).

Duncan's Multiple Range test showed that except for the Los Briones provenance which had the lowest total height, no significant difference existed in the height of the provenances of *Pinus caribaea* var. *hondurensis*. This tends to support an earlier finding that significant differences do not exist among limited provenances of the variety at a

location separate from Afaka (OTEGBEYE, 1980). Similarly no significant difference was found at Afaka in the stem form of the 15 provenances of the variety. It thus appears that members of this variety have similar inherent ability to grow fast and exhibit similar stemform and branching characteristics in the savanna region of Nigeria.

The t-test revealed that *Pinus caribaea* var. *hondurensis* was significantly taller at 10 years than *P. caribaea* var. *caribaea*. This in part supports reports by OJO and SHADO (1973), OTEGBEYE (1980), and OTEGBEYE and SHADO (1984) who showed that variety *hondurensis* has superior growth to that of variety *caribaea* in all of the savanna regions of Nigeria where they have been tested. However, the Manuel

Table 3. — Mean values of five growth and morphological characteristics of 10-year-old provenances of *Pinus caribaea* tested at Afaka.

PROVENANCE	CHARACTERISTICS				
	HEIGHT (cm)	DBH (cm)	STEM FORM (SCORE)	BRANCH ANGLE (SCORE)	BRANCH THICKNESS (SCORE)
Karawala, Nicaragua	15.4	17.6	2.6	1.5	1.5
Alamicamba, Nicaragua	16.0	19.4	2.9	1.7	1.5
Rio Coco, Nicaragua	15.2	16.7	2.8	1.6	1.5
Brus Lagoon, Honduras Republic	15.1	17.7	2.8	1.6	1.4
Guanaja, Honduras Republic	15.1	17.4	2.8	1.7	1.4
Poptum, Guatemala	14.0	17.5	2.9	1.7	1.6
Manuel, Cuba ¹	13.3	16.1	2.3	1.4	1.5
Los Briones, Honduras Republic	12.8	17.9	2.5	1.6	1.5
Limonas, Honduras Republic	14.9	17.7	2.6	1.7	1.5
Culmi, Honduras Republic	14.9	19.5	2.8	1.7	1.6
Potosi, Honduras Republic	15.6	18.6	3.1	1.7	1.5
Mt. Pine Ridge, Belize	15.1	18.7	2.7	1.7	1.5
Santa Clara, Nicaragua	15.2	18.3	2.5	1.6	1.5
Byfield, Queensland (1)	14.9	18.4	2.5	1.6	1.5
Melinda, Belize	14.9	18.6	2.8	1.6	1.4
Byfield, Queensland (2)	15.1	17.5	2.6	1.5	1.5
Mean	14.8	18.0	2.7	1.6	1.5
LSD _{0.5}	1.7		0.4		
RANGE	12.8-16.0	16.1-19.5	2.3-3.1	1.4-1.7	1.4-1.6

¹ *Pinus caribaea* var. *caribaea*; all others are *P. caribaea* var. *hondurensis*.

Table 4. — Some genetic parameters of five growth and morphological characteristics of sixteen provenances of *Pinus caribaea* ^{a)}.

CHARACTERISTICS	MEAN	PCV %	GCV %	HERITABILITY	GA	GA AS % OF MEAN
Height	14.8	8.2	14.7	0.46	0.8	5.4
Diameter at breast height	18.0	9.3	8.8	0.17	0.3	1.7
Stem form	2.7	10.5	8.9	0.56	0.2	7.5
Branch thickness	1.6	17.7	-	-	-	-
Branch angle	1.5	9.4	-	-	-	-

^{a)} PCV = Phenotypic coefficient of variation
 GCV = Genotypic coefficient of variation
 GA = Genetic advance

(Cuba) provenance, which was the only variety *caribaea* provenance tested, had significantly straighter stems than did the 15 provenances of variety *hondurensis*. This trend was also reported by GREAVES (1980).

The results from this study suggest that almost all sources of variety *hondurensis* adapt equally well to the environmental conditions existing at Afaka. This trend probably applies to other parts of the savanna region where pines can be grown, based upon results reported by OREGBEYE (1980). It therefore appears that limited genetic improvement of the population can be achieved by carrying out selection among these provenances in the savanna region of Nigeria.

Negative genetic variances among the tested provenances of *Pinus caribaea* were obtained for branch angle (−1.25) and branch thickness (−0.01). The genetic variance for each of the two characteristics was therefore assumed to be zero.

The phenotypic coefficient of variation for the five characteristics examined and genotypic coefficient of variation for total height, dbh and stem form are shown in Table 4. The low coefficients of variation further indicate limited provenance variation for the five characteristics. Only total height had a genotypic coefficient of variation greater than its phenotypic coefficient of variation. The highest (14.7%) genotypic coefficient of variation was also recorded for this characteristic while dbh had the lowest value (8.8%). The limited difference between the phenotypic and genotypic coefficients of variation of dbh and stem form suggests that environmental influences had little more impact on these characteristics than did genetic influences.

The heritability, estimated on a plot mean basis, was 0.46, 0.17 and 0.56 for total height, dbh and stem form respectively. Although the highest genotypic coefficient of variation was recorded for total height, stem form had the highest heritability. Thus the genotypic coefficient of variation is not a good measure of a trait's heritability.

The genetic advance estimated for total height, dbh and stem form was 0.8, 0.3 and 0.2 respectively. When expressed as a percentage of the mean, the respective low values of 5.4, 1.7 and 7.5 percent were obtained. According to JOHNSON *et al.* (1955), high heritability coupled with high genetic

advance is the true index for effective selection. It is therefore clear that selection based on the mean performance of the *Pinus caribaea* provenances of this study will not result in genetic improvement of the species. However, because of the high heritability and genetic advance values, genetic improvement in stem form can likely be made from selecting in this population. Although limited differences existed among the *Pinus caribaea* var. *hondurensis* provenances, good prospect exist for genetic improvement of the population. This is especially so for total height, dbh and stem form. Individual tree values of the entire population ranged from 7.1 m to 21.5 m for total height, 8.6 cm to 26.3 cm for dbh and 1 to 5 for stem form. This range of values indicates that individual tree selection across the provenances can be used to a large extent in the improvement of the population.

Conclusion

Genetic improvement of forest trees has generally been achieved to a greater extent through provenance selection than by any other method. However, selection among provenances of *Pinus caribaea* var. *hondurensis* of the present study will result in limited genetic improvement. The cause of the limited improvement is the low degree of phenotypic and genotypic variation and the low genetic parameters estimated for the characteristics studied. For any meaningful improvement to be made, more seed sources will have to be tested along with all or some of the present ones to adequately exploit the genetic diversity that is associated with the species.

Although *Pinus caribaea* var. *hondurensis* excelled *P. caribaea* var. *caribaea* in total height, the latter had straighter stems than the former; the dbh and branching characteristics of the two varieties were essentially the same.

Since limited differences were exhibited in the performance of the *Pinus caribaea* var. *hondurensis* provenances examined, they will be maintained for the *P. caribaea* afforestation programme in the savanna region of Nigeria, pending the establishment of seed orchard. The situation offers a good opportunity for the collection of seeds from a

large number of trees when they eventually start producing viable seeds.

References

- AL-JIBOURI, H. A., MILLER, P. A. and ROBINSON, H. F.: Genotypic and environmental variances and covariances in an upland cross of interspecific origin. *Agron. J.* 50, 633 (1958). — BURLEY, J. and WOOD, P. J.: A manual on species and provenance research with particular reference to the tropics. *Tropical Forestry Papers* No. 10. Dept. Forestry, Commonwealth Forestry Institute, Univ. of Oxford, 226 pp. (1976). — BURTON, G. W.: Quantitative inheritance in grasses. *Proceedings Vth International Grassland Cong.* 1: 277–283 (1952). — GREAVES, A.: Review of the *Pinus caribaea* MOR. and *Pinus oocarpa* SCHIEDE international provenance trials. 1978. C.F.I. Occasional Paper No. 12, Dept. of Forestry Institute, Univ. of Oxford. 89 pp. (1980). — HANSON, C. H., ROBINSON, H. F. and COMSTOCK, R. E.: Biometrical studies of yield in segregating population of Korean *Lespedeza*: *Agron. J.* 48, 268–272 (1956). — JOHNSON, H. W., ROBINSON, H. F. and COMSTOCK, R. E.: Estimate of genetic and environmental variability in soybeans. *Agron. J.* 47, 314–318 (1955). — OJO, G. O. A. and SHADO, M. B.: Preliminary results of pine provenance trials in the savanna area of Nigeria. Research Paper No. 19, Savanna Forestry Research Station, Samaru-Zaria, Nigeria (1973). — OTEGBEYE, G. O.: Provenance trials of *Pinus caribaea* in some parts of the Savanna region of Nigeria. Paper presented at the 10th Annual Conference of the Forestry Association of Nigeria, Sokoto, Nigeria (1980). — OTEGBEYE, G. O. and SHADO, M. B.: Geographic variation in *Pinus caribaea* MORELET. In "Provenance and genetic improvement strategies in tropical forest trees". Mutare, Zimbabwe (Eds. BARNES, R. D., and GIBSON, G. L.). Commonwealth Forestry Institute, Oxford, and Forest Research Centre, Harare: 428–431 (1984).

Genetics of *Cunninghamia lanceolata* Hook.

1. Genetic Analysis

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Summary

As a first step in the study of genetics of *Cunninghamia lanceolata*, the genetic control and the inheritance of the polymorphism revealed by gel electrophoresis for six enzyme systems is elucidated. By analysing endosperm and embryo of individual seeds from single maternal clones, genetic analyses are based on the segregation of enzyme phenotypes among the haploid female gametes and the association of phenotypes in diploid zygotes. The latter method turned out to be an efficient tool for inferring on the inheritance of the observed enzyme phenotypes where offspring from controlled crossings are not available. It is concluded that the six enzyme systems are coded by ten enzyme gene loci, which show a considerable number of codominant alleles in addition to the phenomenon of lacking enzyme activity ("null alleles"). Interactions between 26 pairs of gene loci were studied on the basis of gametic segregation among single tree progenies. Considerable variation with respect to the estimated recombination frequencies can be observed for the same pair of loci among some progenies. In such cases inferences on linkage should be drawn with care. Analogously to other coniferous species, linkage between GOT- and PGI-loci is evident.

Key words: Enzyme, gene marker, genetic control, inheritance, linkage, seed, *Cunninghamia lanceolata*.

Zusammenfassung

Als erster Schritt in den genetischen Untersuchungen an *Cunninghamia lanceolata* Hook. wurde die genetische Kontrolle und der Vererbungsmodus für den von 6 Enzymsystemen in der Gel-Elektrophorese gezeigten Polymorphismus nachgewiesen. Ausgehend von Untersuchungen an Endosperm und Embryo der Samen aus Nachkommenschaften einzelner Bäume, stützte sich die genetische Analyse auf die Aufspaltung der Enzym-Phänotypen zwischen den haploiden weiblichen Gameten und die Assoziation der Phänotypen in den diploiden Zygoten. Die zuletzt genannte Methode erwies sich als geeignetes Instrument zum Nach-

weis des Vererbungsmodus gegebener Enzym-Phänotypen für Fälle, in denen Nachkommenschaften aus kontrollierten Kreuzungen nicht zur Verfügung stehen. Es wird gefolgert, daß die 6 Enzymssysteme von 10 Genorten kodiert werden, welche eine beträchtliche Anzahl von kodominanten Allelen aber auch das Phänomen der fehlenden Enzymaktivität ("Nullallele") zeigen. Auf der Basis der gametischen Segregation innerhalb von Einzelbaum-Nachkommenschaften wurden Interaktionen für 26 Paare von Genorten untersucht. Zwischen einigen Nachkommenschaften besteht eine beträchtliche Variation der Schätzwerte für Rekombinationshäufigkeiten bezüglich derselben paarweisen Kombination von Genorten. In solchen Fällen sollten Rückschlüsse auf Kopplung mit Vorsicht gezogen werden. Analog zu anderen Nadelbaumarten zeigt sich Kopplung zwischen GOT- und PGI-Genorten.

Introduction

Cunninghamia lanceolata is a coniferous tree species which is widespread in the subtropical regions of the southern part of China. The economic importance of this species is substantial, due to its fast growth, the high quality of its timber and its multiple use potential. It constitutes approximately one-quarter of the total marketed timber production of China.

Cunninghamia lanceolata is known as a species which shows considerable variation in morphological characters and in growth (e.g. YE PEIZHANG, SHEN XIHUAN, CHEN YUEWU, pers. comm.). A genetic characterization of provenances of this species has not as yet been attempted, nor has, to our knowledge, any study dealing with environmentally independent markers been published. Studies in this field are in progress at the Beijing Forestry University (SHEN, pers. comm.). The lack of studies concerns the whole family of *Taxodiaceae* — the only population genetic investigations by means of genetic markers in this family deal with *Cryptomeria japonica* (e.g. SAKAI and PARK, 1971) and *Sequoiadendron giganteum* (FINS and LIBBY, 1982).

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