adaptation with a desired level of mean performance. The wide unpredictable variations in agro-climatic conditions found in *Hevea* growing areas of Sri Lanka make it important that clones with general adaptition or stability to agro-climatic variability should be selected for commercial planting.

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Karyotype Analysis in Pinus caribaea var. hondurensis Barr. and Golf¹)

By R. SALAZAR

Tropical Agricultural Research and Training Center (CATIE),
Department of Renewable Natural Resources,
Turrialba, Costa Rica.

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Summary

The karyotypes of six provenances of *Pinus caribaea* var. *hondurensis* BARR. and GOLF. were analysed using the Feulgen technique on meristematic cells of the root tips.

Significant differences were detected in some of the chromosomes, mainly due to the provenances Limones and Guanaja.

The haploid number of chromosomes is n=12 in this variety; chromosomes are simple, long, and very similar between pairs, as has been found in most of the pine species.

The first 11 chromosomes are metacentric. Three secondary constrictions were observed but two were more persistent within the first six chromosomes. It was not possible to stain the heterochromatin regions using the Giemsa technique.

Key words: Pinus caribaea var. hondurensis BARR. and Golf., Provenances, Karyotype, Chromosomes, Analysis of variance.

Zusammenfassung

Es wurden die Karyotypen von 6 Provenienzen von Pinus caribea var. hondurensis Barr. and Golf. analysiert, indem die Feulgen-Technik an Meristemzellen der Wurzelspitzen angewandt wurde. In einigen Chromosomen wurden signifikante Unterschiede gefunden, hauptsächlich in solchen der Provenienzen Limones und Guanaja.

Die haploide Chromosomenzahl ist bei dieser Varietät n=12; die Chromosomen sind einfach, lang und innerhalb der Paare sehr ähnlich, wie von den meisten Kiefernarten bekannt ist.

Die ersten 11 Chromosomen sind metazentrisch. Drei sekundäre Einengungen wurden beobachtet, wobei zwei innerhalb der ersten 6 Chromosomen beständiger waren.

Es war nicht möglich, die Heterochromatin-Regionen mit der Giemsa-Technik anzufärben.

Introduction

The haploid number of chromosomes in all the species of the genus *Pinus* already studied has been reported as n=12. The chromosomes are very similar and only a small amount of inter specific differences has been found (Sax and Sax, 1933; Saylor 1964; Pederick 1970; Borzan and Papes 1978).

According to Sax and Sax (1933), Santamour (1960) and Saylor (1961) the stability in the morphology of the chromosomes in the conifers may indicate that evolution in this group of plants has passed the climax and the existing forms are survivors of a long natural selection.

They also suggested that it is possible that the intraand interspecific variation that is visible could be the result of alterations at gene level. Pederick (1970) suggested that small but significant differences in arm length in the corresponding chromosomes of certain pine species may be attributed to the gradual accumulation of duplications.

Saylor (1961) in a comparative study between the karyotypes of *P. strobus* L., *P. taeda* L., *P. palustris* Mill., *P. virginiana* Mill. and *P. resinosa* Ait., did not find intraspecific variation in terms of the relative arm length. However, it was possible to detect interspecific variation with respect to arm length. The secondary constrictions proved to be an unreliable diagnostic trait.

The present is the first attempt to determine morphological variations in the karyotype of six different collections of *P. caribaea* var. *hondurensis* at the chromosomal level; the populations represent extreme points in the distribution of the variety. Any difference detected could

The paper is adapted from part of the author's D. Phil. thesis, Forestry Department, Oxford University, England, 1981.

be of great value in present and future breeding programmes of the variety.

Materials and Methods

The study was carried out at the Botany School, Oxford University, using seeds supplied by the Commonwealth Forestry Institute (CFI), Oxford, England.

Seeds from six locations, representing the extreme points of the variety's natural distribution, were used in the study. The assessment was carried out on root tips of seedlings growing in a mixture of sand and peat (1:1) under greenhouse conditions, with temperatures of 18—22° C during the day, and 10—12° C at night.

The best stage for measuring mitotic chromosomes is at the metaphase stage, where they appear more contracted, well spread and less tangled (Mergen and Novotny, 1957; Burley, 1965; Thomas and Ching, 1968).

It was found that a higher number of cells at the metaphase stage were present between 11 and 12 in the morning. The slide preparation followed the Feulgen technique described by Darlington and La Cour (1962). As the chromosomes appeared too long and twisted, the pretreatment in colchicine was modified by soaking the root tips in a colchicine solution of 0.15% for 36 hours at room temperature.

Measurement of the chromosomes was by the photographic method which is more objective and forms a permanent record as explained by Burley (1965). The photographs were taken with a microscope ULTRAPHOT 11 (Carl Zeiss) with RECORDAK microfilm, using 500X magnification. They were printed on photographic paper at 7.5X magnification; resulting in a final magnification of 3750X, from which the measurements were taken to the nearest 0.1 mm., using a map measurer.

The short arm (a) and the long arm (b) of each of the 24 chromosomes were recorded and arranged in descending order, on the basis of their relative value as described by Thomas and Ching (1968). In this case, the system was modified because the relative values were calculated on the haploid number, selecting the member of each chromosome pair that gave the most confident measurement.

The analysis of variance was performed to detect the degree of variation between provenances, and between chromosomes within provenances, in terms of short and long arm length and total length, as a preliminary assess-

Table 1. — Provenance Location.

ORIGIN				Lati-	Longi-	Alti-	Rain-	Dray	Mean
No.	Country	Location		(°N)	tude (°W)	tude (masl)	fall (mm)	months	Temperature ° C
1	Nicaragua	Alamicamba	(ALA)	13° 34'	84* 14'	25	2610	3	27
2	Honduras	Los Limones	(LIM)	14" 03'	86° 42'	700	663	7	22
3	Belize	Mountain Pine Ridge	(MPR)	16° 58'	89° 00'	487	1558	3	23
4	Honduras	Guanaja	(GUA)	16* 27'	85° 54'	75	2308	3	27
5	Belize	Melinda	(MEL)	17* 01'	88* 201	12	2137	2	26
6	Honduras	Bruslagoon	(BRU)	15° 45'	84* 40*	10	2840	2	26

Table 2. — Shows the analysis of variance and the expectation mean squares for chromosome size assessment between popultions.

Entry No.	Sources of Variation	d.f.	Test against entry	Expectation mean square
1	Provenances (P)	(P-1)	4	σ ² + +tcσ ² P
2	Chromosomes (C)	(C-1)	3	σ_2 + t σ_2 PC + tp σ_C σ + t σ PC
3	PxC	(P-1)(C-1)	4	σ + t σ PC
4	Trees (T) in C in P	PC(T-1)		σ^{2}

Table 3. — Analysis of variance and expectation mean squares for individual chromosome assessment between populations.

Entry	Sources of variation	d.f.	Test against entry	Expectation mean square
1	Provenances (P)	(P-1)	2	$\sigma^2 + t \sigma_p^2$
2	Trees (T) in P	P(T-1)		σ2

Table 4. — Analysis of variance and expectation mean squares for individual chromosome analysis from Limones and Guanaja.

Entry No.	Sources of variation	d.f.	Test against entry	Expectation mean square
1	Provenance (P)	(P-1)	2	σ ² + s σ ² _{T/P} + st σ ² p
2	Trees (T) in P	P(T-1)	3	σ ² + s σ ² _{T/P}
3	Slides (S) in T in P	PT (S-1)		o ²

ment of six populations and six trees per provenance. The following mixed model was adopted, where chromosomes were considered to have fixed effects (*Table 2*):

$$Y_{ijk} = \mu + P_i + C_j + (PC)_{ij} + T_{ijk}$$

 Y_{ijk} = mean value of k^{th} tree in j^{th} chromosome in i^{th} provenance;

 $\mu = \text{true mean effect};$

 $P_i \,=\, effect\ of\ i^{th}\ provenance;\ i\,=\,1.2,$ ---6

 C_i = effect of jth chromosome; j = 1,2, ---12

 $(PC)_{ij}$ = interaction effect ith provenance with jth chromosome:

 $T_{ijk}=$ residual associated with k^{th} tree in j^{th} chromosome in i^{th} provenance; k=1,2 ---6

The degree of variation of the arms a, b, and a + b of each individual chromosome among the six provenances was analysed using the following random model of the analysis of variance (*Table 3*):

$$Y_{ij} = \mu + P_i + E_{ij}$$
 where:

 Y_{ij} = mean value of jth tree in ith provenance;

 $\mu = \text{true mean effect};$

 $\dot{P}_{i} = effekt of i^{th} provenance; i = 1,2, ---6$

 $E_{ij}=$ residual associated with j^{th} tree in i^{th} provenance; j=1,2, ---6

Nonlinear regression analyses were performed in order to detect any relationships between morphology of the chromosomes and latitude, longitude and temperature at the site of origin. As a result of the previous analyses a more intensive study was carried out in the karyotype of the populations Los Limones (high elevation) and Guanaja (low elevation) to confirm the differences found in the preliminary analyses. Two provenances, five trees per provenance, and five slides per tree, were assessed using the following mathematical model (Table 4):

$$Y_{ijk} = \mu + P_i + T_{j/i} + E_{ijk}$$

where:

 Y_{ijk} = mean value of k^{th} slide in j^{th} tree in i^{th} provenance;

 $\mu = \text{true mean effect};$

 $P_i = effect of i$ th provenance; i = 1,2

 $T_{j/i} = \text{effect of } j^{\text{th}} \text{ tree in } i^{\text{th}} \text{ provenance; } j = 1,2,$ ---5

 E_{ijk} = residual associated with kth slide in jth tree in ith provenance; k = 1,2,---5

Results and Discussion

The classification of the 12 chromosomes in terms of centromere location as explained by Simak (1962) shows

Table 5. — Mean arm ratios of each chromosome.

Chromosome	Ratio (a/b)	Chromosome	Ratio (a/b
1	0.92	7	0.89
2	0.91	8	0.90
3	0.92	9	0.89
4	0.90	10	0.88
5	0.91	11	0.84
6	0.92	12	0.60

Table 6. - General chromosome means, arm ratios and Studentized range test (P < 0.05).

Chromosome	Short arm (a)	Long arm (b)	Total length (a+b)	a/b
No.	mean	mean	mean	
1	58.05	63.23	121.28	0.92
2	53.67	59.13	112.86	0.91
3	52.52	57.31	109.93	0.92
4	50.87	56.55	107.77	0.90
5	50.17	54.91	105.09	0.91
6	49.56	53.64	102.94	0.92
7	47.42	53.58	101.19	0.89
8	46.36	51.52	97.89	0.89
9	44.60	50.52	94.85	0.89
10	42.95	48.80	91.75	0.88
11	38.52	46.03	85.17	0.84
12	26.20	43.78	69.69	0.60

that only chromosome 12 is acrocentric and the rest are metacentric (Table 5). In the median position group, the a/b arm ratio ranked from 0.84 to 0.92. In the accrocentric one the arm ratio was 0,60.

The largest differences in relative total length occurred between chromosomes 1 and 2 (8,4 units), chromosomes 10 and 11 (6.6 units), and chromosomes 11 and 12 (15.5 units) (Table 6). Between chromosomes 1 and 12 there is a difference in relative length of 51.6 units, which means that the chromosome 1 is 42.5% bigger than chromosome 12. The bigger difference in these two chromosomes is in the short arm that has 31.8 units less than the long arm.

It was observed that there is great similarity in the relative length of neighboring chromosomes. The difference in the pairs from 2 to 9 ranged from 1.7 to 3.3 units; making identification rather inaccurate and difficult. Only chromosomes 1, 11 and 12 can be properly identified by length. As the chromosomes are too long it is necessary to have a strong contraction to avoid overlapping, but if the contraction is not uniform the measurements can not be accurate. Figure 1 shows the somatic chromosomes.

Due to the contraction effect, it was not possible to find consistent secondary contrictions in all the slides. Three of them were observed frequently but two were more prominent, located in any one of the first six chromosomes. It is possible that the technique described by Darlington and LA Cour (1962) is not adequate to detect these regions in P. caribaea var. hondurensis. Pederick (1967, 1970) and Bor-ZAN, and PAPES, (1978) demonstrated that in several pine species these constrictions have a great value in chromosomes identification. The sticky phenomenon described by Borzan (1977) was observed in some slides.

The preliminary statistical assessment (Table 7) of the karyotype as a whole showed that only arm a was significantly different (P < 0.05) between the six populations, but the variation was only 0.19% of the total variation, which is an irrelevant amount.



Figure 1. - Somatic chromosomes of P. caribaea var. hondurensis (2n = 24) at metaphase stage (1300x).

Table 8 shows that in the individual chromosome analysis, only long arm and total length in chromosome 2 and total length in number 6 were significantly different (P \leq 0.05); respectively they represent 23.4, 27.3, and 25.0% of the total variation observed. This percentage of variation is relevant, and it could be the result of accumulations of DNA duplications in the case of the total length, and translocations of chromosome sections in the case of the long arm. Because only six slides were scanned per population, these observations can not be conclusive, mainly because inversion and misclassification could have taken place in the adjacent chromosomes 2-3-4-5-6-7 and 8 which have similar dimensions (idiograms Figure 2).

The Studentized range test (Table 8) supports the previous analysis showing that there are no significant differences in the morphology of the chromosomes of the six

Table 7. - Summary of analysis of variance and variance components for short arm, long arm and total length in six prove-

Entry No.					SHORT AF	.		LONG ARM		T	OTAL LENGT	H
	Sources of variation	d.f.	Test against entry	Mean square	Variance ratio(F)	Variance components	Hean square	Variance ratio(P)	Variance component		Variance ratio(F)	Variance component
,	Provenan- ces (P)	5	4	19,04		0.19	5,60	NS	0.00	10.83	NS	0.00
2	Chromoso- nes (C)	11	3	2472.00		89,01	1079,00	•••	73.84	6706.00	•••	94.36
3	PXC	55	4	8.07	NS	0.00	13.27	NS	1.36	9.60	NS	0.00
4	Residual	360		8.30		10.79	9.97		24.79	11.12		5.64

Table 8. — Summary of analysis of variance and variance components for individual chromosome assessment between populations.

Chromo-	Entry	Sources of variation	4.1.	Test				LONG ARM			TOTAL LENGTH		
		***************************************		entry	MS	7	VC (%)	MS		VC (%)	MS	r	VC (%)
,	,	Provenance (P)	5	2	6.81	NS	0.00	7.76	NS	0.00	11.43	NS	0.00
	2	Trees (T) in P	30		7.35		100.00	19.95		100.00	32,29		100.00
2	1	Provenance (P)	5	2	17.04	NS	7.25	28,34		23.39	24.39		27.16
	2	Trees (T) in P	30		11.60		92.75	10,01		76.71	7.33		72.8
3	1	Provenance (P)	5	2	8,11	NS	13,57	2,96	NS	0.00	9,20	NS	20.2
	2	Trees (T) in P	30		4,18		86.43	3.78		100,00	3.64		79.7
4	1	Provenance (P)	5	2	10.41	NS	6.43	14.18	NS	3,38	2.75	MS	0.00
	2	Trees(T) in P	30		7.37		93.57	11.60		96.42	4.50		100.00
5	1	Provenance (P)	5	2	4.95	NS	4.63	4.82	NS	8.89	3.10	NS	0.00
	2	Trees(T) in P	30		3.83		95.37	3.04		91,11	3.66		100.00
6	1	Provenance (P)	5	2	3.23	NS	0.00	5.90	NS	0.00	9.86		24.97
	3	Trees(T) in P	30		3,37		100.00	6,40		100.00	3.29		75.08
7	1	Provenance (P)	5	2	7.07	NS	11.69	13.45	NS	7.58	8.24	NS	20.04
	2	Trees(T) in P	30		3.94		88,31	9.01		92.48	3.49		79,96
8	1	Provenance (P)	5	2	5.50	NS	0.00	6.76	NS	0.00	8.45	NS	12.63
	2	Trees(T) in P	30		9.03		100.00	8.51		100.00	4.49		87.17
9	1	Provenance (P)	5	2	10.88	NS	0.00	8.34	NS	0.00	6.24	NS	0.00
	2	Trees(T) in P	30		12.41		100.00	9.67		100.00	6.32		100.00
10	1	Provenance (P)	5	2	8.08	NS	0.00	12,18	NS	19,11	7.62	NS	0.00
	2	Trees(T) in P	30		13.96		100.00	5.08		80.89	12,46		100.00
11	1	Provenance (P)	5	2	23.25	NS	3.87	26,96	NS	11.01	2.45	NS	0.00
	2	Trees (T) in P	30		18.73		96.13	13.09		84.99	27.71		100.00
12	1	Provenance (P)	5	2	2.46	NS	0.00	19,85	NS	0.24	22,17	NS	0.00
	2	Trees(T) in P	31)		3.42		100,00	19.56		99.76	23.91		100.00

Pr = Variance ratio = VC(8) = Variant component
Pr = Variance ratio = "Significant at P<0.05 of probability
Pr = Not significant at P<0.05 of probability

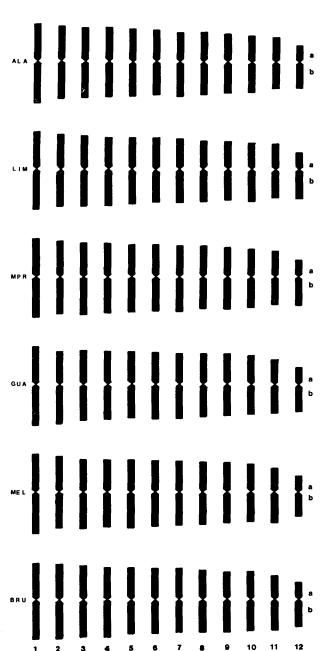


Figure 2. — Idiograms of six populations on the bases of relative length.

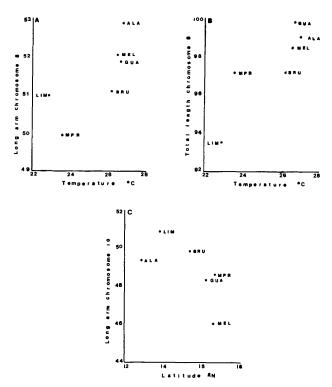


Figure 3. — Relationship of temperature with: a) long arm chromosome 8, b) total length chromosome 8, and of latitude with c) long arm chromosome 10.

provenances studied, with the exception of long arm in chromosome 10 where Limones has a longer long arm; and in total length where Brus Lagoon in chromosome 1, Alamicamba in chromosome 3, and Guanaja in chromosome 6 and 7 showed significant differences (P < 0.05). In the case of Limones the longer arm chromosome 10 could be related to the adaptation of this population to a dry condition (*Table 1*). In the case of Guanaja longer chromosomes 6 and 7 could be related with the evolutionary process of the species in its southern migration, and its adaptation to the isolated condition of an island.

Figure 3 is a scatter diagram which shows that long arm and total length in chromosome 8 distinguished the lowland populations analysed. Also the long arm in chromosome 10 shows a clear North-South clinal tendency to increase in size, which could be the result of accumulations of repeated DNA duplications during its southern migration.

Guanaja and Limones provenances, which are more than 250 kilometers (km) apart and under different climatic conditions, were assessed to prove the previous finding. Although significant differences were found (P < 0.05) in arm a and b in chromosomes 5 and 11 respectively (Table 9), these results do not support the previous results.

The Giemsa banding and fluorescense methods described by Vosa (1973, 1974), did not give positive results; which may be due to the small amount of heterechromatin present in the chromosomes of *P. caribaea* var. *hondurensis*.

Conclusions

Through the statistical analysis, it was possible to detect significant differences between provenances in some chromosomes. These differences are supposed to be due to the provenances Limones and Guanaja which also have showed differences in growth habits in other studies (Barnes et al., 1980; Salazar, 1981).

Table 9. — Summary of analysis of variance and variance components for individual chromosome for Limones and Guanaja.

Chromosome		Sources of	đ.f.	Test	Short	arm		Lo	ng arm	
No.	No.	variation		against entry	MS	r	CV (%)	MS	P	cv (v
	1	Provenances (P)	1	2	39,50		23.97			
5	2	Trees (T) in (P)	8	3	5.43	MS	4.78			
	3	Error	40		4.06		71.25			
	1	Provenances (P)	1	2				65.42	•	20.66
11	2	Trees (T) in (P)	8	3				7.47	NS	0.00
	3	Error	40					8,74		79.34

MS= Mean square F = Variance ratio * = Significant at P< 0.05 of probability NS = Not significant at P< 0.05 of probability

F = Variance ratio CV= Variance component

NOTA: This table is a summary of only those variables that present significant differences.

In *P. caribaea* var. *hondurensis* as in other pine species, it was found that the mitotic chromosomes are too long and of simple morphology. The similarity between chromosome pairs in terms or relative length, principally from chromosome 2 to 9, is such that misclassification can easily take place. The phenomenon of inversion with respect to arm a or b can occur, because 11 of the 12 chromosomes are metacentrics

The differences detected in this study may not be conclusive for the above mentioned difficulties. A more detailed analysis is necessary to confirm these findings.

The use of haploid tissue, such as female gametophyte tissue, is recomended because the chromosomes are not excessively compressed and their morphological details can be easily analysed in this material.

If differences at chromosome level are not detectable in this variety of Pinus, the phenotypic differences already observed between provenances in other studies (Barnes $et\ al.$, 1980; Salazar, 1981), could be the result of changes at the gene level.

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Limits of Artificial Selection under Balanced Mating Systems with Family Selection

By H. Kang

Forestry Sciences Laboratory, North Central Forest Experiment Station, Forest Service, U. S. Dept. of Agriculture, P. O. Box 898,

Rhinelander, Wisconsin 54501, USA

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Abstract

Two mating systems, pair mating and partial diallel mating, were evaluated with respect to three parameters single generation gene frequency advance (\bigtriangleup q), ultimate probability of allele fixation (u), and the time required to fix or lose an allele (t). These three parameters are useful in developing long-term breeding strategies. For a given population size the pair mating showed higher values of \bigtriangleup q, lower values of u, and shorter t than partial diallel mating. However, when the number of families was fixed, u of pair mating was greater than that of partial diallel mating. The impact of the results on tree breeding is discussed.

Key words: Selection limit, gene frequency, probability of allele fixation, pair mating, partial diallel mating.

Zusammenfassung

Zwei Paarungssysteme, die paarweise Kreuzung und das unvollständige diallele Kreuzungssystem, wurden bezüglich dreier Parameter: Änderung der Genhäufigkeit in einer Generation ($\triangle q$), Wahrscheinlichkeit der Fixierung eines Allels (u) und Zeit, die benötigt wird, um ein Allel zu fixieren oder zu verlieren (t), untersucht. Diese drei Parameter sind bei der Entwicklung von Langzeitzüchtungsstrategien von Nutzen. Für eine gegebene Populationsgröße zeigte die paarweise Kreuzung höhere $\triangle q$