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PERFORMANCE AND HERITABILITY ESTIMATIONS ON OIL PALM PROGENIES TESTED IN DIFFERENT ENVIRONMENTS

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ABSTRACT

*Forty oil palm (*Elaeis guineensis *Jacq.)* dura *x* pisifera *(DxP) crosses derived from the North Carolina Mating Design 1 (NCM 1) were evaluated in six locations (Kudat, Sabah; Beaufort, Sabah; Teluk Intan, Perak; Carey Island, Selangor; Kepong, Selangor and Kluang, Johor). Fifteen* pisifera *palms were chosen as male parents and each was crossed to two to four* dura *female parents.*

Environmental factors contributed to the phenotypic variability in all the agronomic characters. Hence, the variation in performance of the genotypes in the different locations was partly a reflection of the differences in soil type, soil fertility and rainfall. Generally, Carey Island and Teluk Intan were the more favourable environments for yield than the marginal environments, such as Kudat and Kluang.

The results showed that the environment had a great influence on the genetic variance components. In general, the heritability estimates for yield and its components and bunch quality characters fluctuated from location to location. However, the estimates for vegetative characters were fairly consistent and higher than those for yield and its components, and bunch quality characters.

Keywords: *dura* x *pisifera* progenies, genetic variance, different environments, heritability.

INTRODUCTION

Yield and other quantitative traits are not solely under genetic control. The phenotypic values observed are the sum of their genetic and environmental effects and, in most cases, their interactions as well. In fact, most of the economically important characters are controlled by polygenes and influenced by environmental factors, thus giving a normal distribution to their expressions. Quantitative estimations of genetic variances and heritabilities have been attempted by oil palm breeders to provide information to improve breeding efficiency (Hardon and Thomas, 1968; Soh and Tan, 1983; Hardon *et al.*, 1985).

Several researchers (Thomas *et al.*, 1969; Ooi *et al.*, 1973; Rajanaidu and Rao, 1988) have noted that the genetic variability for yield and its components is low. The early systematic studies on the variance were carried out by Thomas *et al.* (1969) and Ooi *et al.* (1973), both of who partitioned the genetic variance into additive and dominance components. The additive variances for bunch yield and its components, average bunch weight (ABW) and bunch number (BNO), were found to be small with higher values for dominance variances in Deli *dura* populations. The low additive variances are undoubtedly due to the limited genetic base of the oil palm breeding population in Malaysia (Hardon, 1970; 1976).

Estimates of the broad and narrow sense heritabilities for yield and its components have been computed by many researchers using classical methods of quantitative genetics. Hardon *et al.* (1985) concluded that the heritability for fresh fruit bunch (FFB) is generally low, moderately high for ABW and high for BNO. They also summarized that generally high narrow sense heritability values are obtained for the bunch quality parameters, *i.e.* mesocarp to fruit (MTF), shell to fruit (STF) and kernel to fruit (KTF) ratios.

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In this study, 40 DxP progenies derived from the NCM 1 design were evaluated in six locations to estimate the genetic control and heritabilities for yield and its components, bunch quality and vegetative characters in the oil palm population.

MATERIALS AND METHODS

Experimental Materials and Procedures

Forty DxP progenies were tested concurrently in each of six locations, namely, Kluang, Kudat, Beaufort, Teluk Intan, Carey Island and Kepong. Fifteen *pisifera* palms of AVROS, Serdang S27B, Serdang 29/36, Lever Nigeria and Lever Cameroons were chosen as the male parents and each mated to four Deli *dura* palms as female parents in the NCM 1 (Comstock and Robinson, 1948; 1952). The parental palms were selected based on their *dura* x *tenera* progeny test performances in the Sabah Breeding Programme (Rajanaidu *et al.*,1985). Only forty progenies were developed from the crosses between each *pisifera* male and its two to four *dura* females. The pedigrees of the progenies and locations have been given in a previous paper (Rafii *et al.*, 2001).

The progenies were planted in a completely randomized design (CRD) at 136 to 148 palms ha^{-1} with two replicates per location and five palms per progeny per replicate. Yield data were collected in all the six locations, but vegetative and bunch quality data in only four (Kluang, Carey Island, Kepong and Teluk Intan). Yield was recorded over four years - 1985 to 1988 in Kudat, Beaufort, Teluk Intan, Carey Island and Kepong, and 1986 to 1989 in Kluang. Each palm was inspected every 10 days and any ripe fruit bunch present was harvested and weighed using a simple spring balance. The weight of bunch(es) and the number of bunches were recorded for each palm. The method of bunch analysis developed by Blaak *et al.* (1963) and improved by Rao *et al.* (1983) was used to estimate the bunch quality characters. The vegetative data were scored using the method proposed by Corley and Breure (1981). The vegetative parameters were measured on frond 17 and palm height (HT), taken at seven years old, was the distance from the ground to the base of frond 41.

Statistical and Heritability Analyses

The analysis was done using individual palm data. Analysis of variance (ANOVA) for the individual locations and over all the locations was based on a random model with the variance components estimated from the mean squares. However, only the pooled analysis is presented in this paper. The outlines for ANOVA and expected mean squares across locations are given in *Table 1*. The tests for significance are:

D/P x R/L : MS8/MS9
P x R/L : MS7/MS8
D/P x L : MS5/MS8
P x L : $\frac{MS4 + MS8}{MS5 + MS7}$

Replicates within L (R/L) : MS6 / MS7

Location (L) : $\frac{(MS3 + MS7)}{(MS4 + MS5)}$

Duras within *pisifera* (D/P) : MS2/MS5

Pisifera (P) : $\frac{(MS1 + MS5)}{(MS2 + MS4)}$

The degrees of freedom (df) for the F-ratio on the composite item *pisifera* was derived from the approximation suggested by Satterthwaite (1946) (as quoted by Cochran and Cox, 1959):

$$n'_1 = \frac{(MS1 + MS5)^2}{\frac{MS1^2}{n_1} + \frac{MS5^2}{n_5}}$$

where n_1 = df for *pisifera* (P)
n_5 = df for D/P x L

$$n'_2 = \frac{(MS2 + MS4)^2}{\frac{MS2^2}{n_2} + \frac{MS4^2}{n_4}}$$

where n_2 = df for D/P
n_4 = P x L

The df for the F-ratio in P x location and location items were obtained as for the *pisifera* item. The variance components were estimated from the expected mean squares in *Table 1* by:

$$\sigma^2_w = MS9$$

$$\sigma^2_{(d/p)(r/l)} = \frac{MS8 - MS9}{n'}$$

$$\sigma^2_{p(r/l)} = \frac{MS7 - MS8}{n'd'}$$

$$\sigma^2_{(d/p)l} = \frac{MS5 - MS8}{n'r}$$

$$\sigma^2_{pl} = \frac{(MS4 + MS8) - (MS5 + MS7)}{n'rd'}$$

$$\sigma^2_{d/p} = \frac{MS2 - MS5}{n'rl}$$

$$\sigma^2_{p} = \frac{(MS1 + MS5) - (MS2 + MS4)}{n'rd'l}$$

where *r* is the number of replicates, *n'* the harmonic mean for palms within *dura*/replicate, *d'* the harmonic mean for *duras* within *pisifera*, and *l* the number of locations.

Under the assumptions (inbreeding coefficient F = 0, and no epistasis) listed by Comstock and Robinson (1952):

$$\sigma^2_p = \mathrm{Cov(HS)} = 1/4\,\sigma^2_A$$

$$\sigma^2_{d/p} = \mathrm{Cov(FS)} - \mathrm{Cov(HS)} = 1/4\sigma^2_A + 1/4\sigma^2_D$$

where:

Cov(HS) = covariance half-sibs

Cov(FS) = covariance full-sibs

σ^2_A = additive variance

σ^2_D = dominance variance

The heritabilities for the 21 characters were estimated from the variance components by:

Pisifera component heritability:

$$h^2_p = \frac{4\,\sigma^2 p}{\sigma^2 ph}$$

Dura component heritability:

$$h^2_d = \frac{4\,\sigma^2_{d/p}}{\sigma^2_{ph}}$$

where:

σ^2_{ph} (phenotypic variance - derived from ANOVA pooled data across locations)

$$= \sigma^2_w + \sigma^2_{(d/p)(r/l)} + \sigma^2_{p(r/l)} + \sigma^2_{(d/p)l} + \sigma^2_{pl} + \sigma^2_{d/p} + \sigma^2_p$$

σ^2_{ph} (phenotypic variance - derived from ANOVA at each location)

$$= \sigma^2_w + \sigma^2_{(d/p)r} + \sigma^2_{pr} + \sigma^2_{d/p} + \sigma^2_p$$

The heritability based on the $\sigma^2_{d/p}$ component is always an overestimate of the narrow sense heritability (h^2_d) if $\sigma^2_{d/p} > \sigma^2_p$. According to Falconer (1989), the two estimates of heritability from the male *(pisifera)* and female *(dura)* components are therefore equally reliable and their combination, based on the resemblance between full-sibs, may be taken as the best estimate.

TABLE 1. OUTLINE OF ANALYSIS OF VARIANCE AND EXPECTED MEAN SQUARES FOR NORTH CAROLINA MATING DESIGN 1 ANALYSIS OVER LOCATIONS

Source	df	MS	EMS
Pisifera (P)	(p - 1)	MS1	$\sigma^2_w + n'\sigma^2_{(d/p)(r/l)} + n'd'\sigma^2_{p(r/l)} + n'r\sigma^2_{(d/p)l} + n'rd'\sigma^2_{pl} + n'rl\sigma^2_{(d/p)} + n'rd'l\sigma^2_p$
Duras within *pisifera* (D/P)	p (d - 1)	MS2	$\sigma^2_w + n'\sigma^2_{(d/p)(r/l)} + n'r\,\sigma^2_{(d/p)l} + n'rl\,\sigma^2_{(d/p)}$
Location (L)	(*l* - 1)	MS3	$\sigma^2_w + n'\sigma^2_{(d/p)(r/l)} + n'd'\sigma^2_{p(r/l)} + n'd'p\sigma^2_{r/l} + n'r\,\sigma^2_{(d/p)} + n'rd'\sigma^2_{pl} + n'rd'p\sigma^2_l$
P x L	(p-1)(*l*-1)	MS4	$\sigma^2_w + n'\sigma^2_{(d/p)(r/l)} + n'd'\sigma^2_{p(r/l)} + n'r\sigma^2_{(d/p)l} + n'rd'\sigma^2_{pl}$
D/P x L	p (d-1)(*l*-1)	MS5	$\sigma^2_w + n'\sigma^2_{(d/p)(r/l)} + n'r\sigma^2_{(d/p)l}$
Replication within L (R/L)	*l* (r - 1)	MS6	$\sigma^2_w + n'\sigma^2_{(d/p)(r/l)} + n'd'\sigma^2_{p(r/l)} + n'd'\sigma^2_{r/l}$
P x R/L	(p - 1) *l* (r - 1)	MS7	$\sigma^2_w + n'\sigma^2_{(d/p)(r/l)} + n'd'\sigma^2_{p(r/l)}$
D/P x R/L	p*l* (d - 1) (r - 1)	MS8	$\sigma^2_w + n'\sigma^2_{(d/p)(r/l)}$
Within palms	pd*l*r (n' - 1)	MS9	σ^2_w

Notes: n' = harmonic mean for palms in *dura*/replicate.
d' = harmonic mean for *duras* in *pisifera*.
r = number of replications.
P = number of *pisiferas*.
l = number of locations.

RESULTS AND DISCUSSION

Population Performance

The performances of the DxP progenies in each location are shown in *Tables 2* and *3*. Carey Island was the best environment for FFB (184.63 kg palm^{-1} yr^{-1}). However, Duncan's new multiple range test (DNMRT) determined that the FFB yields at Teluk Intan and Carey Island were not significantly different, although both were significantly higher than in the other environments. BNO for the individual progenies ranged from 8.82 (Kudat) to 20.23 (Carey Island). The mean BNOs for the locations were significantly different. ABW was the highest at Teluk Intan, followed by Beaufort, Kudat, Kluang, Carey Island and Kepong, ranging from 7.82 kg to 12.53 kg.

The bunch quality and vegetative characters at each location are given in *Table 3*. In general, MTF was higher on the inland (Kluang) than coastal (Teluk Intan and Carey Island) soils. Carey Island was the most favourable environment for KTF (10.04%) and kernel to bunch (KTB) (5.51%). Fruit to bunch (FTB) was the highest at Kluang (63.18%) and lowest at Kepong (55.76%). Kluang was significantly higher than the other locations. Oil to bunch (OTB) in the four locations ranged from 22.25% (Carey Island and Kluang) to 23.77% (Teluk Intan). Teluk Intan was the best environment for oil/palm/year (OPY) among the four locations although it was not significantly higher than Carey Island. A similar trend was observed for kernel/palm/year (KPY) where the coastal soils (Teluk Intan and Carey Island) produced about similar amounts but more than the inland soil (Kluang).

Clear and consistent differences were detected between the environments for all the vegetative characters except leaflet length (LL), leaflet width (LW) and leaflet number (LN). The highest progeny means over locations were observed in Carey Island, followed by Teluk Intan, Kepong and Kluang for HT, leaf area (LA) and leaf area index (LAI).

Analysis of Variance (ANOVA)

Tables 4 to *7* present the ANOVA and variance components for the NCM 1 analyses over locations

TABLE 2. LOCATION MEANS FOR YIELD AND ITS COMPONENTS

	Character		
Location	**FFB (kg palm^{-1} yr^{-1})**	**BNO (No. palm^{-1} yr^{-1})**	**ABW (kg)**
Kudat	86.06^{d}	8.82^{f}	9.97^{b}
Beaufort	142.65^{b}	11.67^{d}	12.17^{a}
Teluk Intan	177.86^{a}	14.51^{c}	12.53^{a}
Carey Island	184.63^{a}	20.23^{a}	9.31^{c}
Kepong	135.58^{b}	17.49^{b}	7.82^{d}
Kluang	96.22^{c}	9.75^{e}	9.89^{b}
Mean	137.17	13.74	10.28

Note: Means within the same column with the same letter are not significantly different at P - 0.05 from Duncan's new multiple range test.

TABLE 3. LOCATION MEANS FOR BUNCH QUALITY AND VEGETATIVE CHARACTERS

Location	**Character**									
	MTF (%)	**STF (%)**	**KTF (%)**	**KTB (%)**	**FTB (%)**	**OTB (%)**	**OTDM (%)**	**OTWM (%)**	**OPY (kg palm^{-1} yr^{-1})**	**KPY (kg palm^{-1} yr^{-1})**
Teluk Intan	78.44^{b}	13.24^{a}	8.37^{b}	5.15^{b}	61.47^{b}	23.77^{a}	76.71^{a}	49.26^{a}	42.55^{a}	9.20^{a}
Carey Island	75.68^{c}	12.84^{a}	10.04^{a}	5.51^{a}	59.14^{c}	22.25^{b}	74.83^{c}	48.98^{a}	41.37^{a}	9.74^{a}
Kepong	78.59^{b}	13.19^{a}	8.07^{b}	4.67^{c}	55.76^{d}	22.65^{b}	75.36^{bc}	47.43^{b}	31.47^{b}	6.08^{b}
Kluang	80.09^{a}	11.66^{b}	8.26^{b}	5.29^{ab}	63.18^{a}	22.25^{b}	75.55^{b}	44.03^{c}	22.10^{c}	5.27^{c}
Mean	78.22	12.73	8.77	5.15	59.89	22.73	75.41	47.42	34.37	7.69

	HT (m)	**PCS (cm^{2})**	**RL (m)**	**LL (cm)**	**LW (cm)**	**LN (No.)**	**LA (m^{2})**	**LAI**
Teluk Intan	1.95^{b}	27.13^{b}	5.15^{b}	89.83^{a}	5.58^{a}	145.46^{c}	8.34^{b}	4.94^{b}
Carey Island	2.43^{a}	32.34^{a}	5.50^{a}	89.98^{a}	5.40^{b}	170.22^{a}	9.24^{a}	5.59^{a}
Kepong	1.74^{c}	25.14^{c}	4.85^{c}	85.06^{b}	4.78^{c}	155.84^{b}	7.26^{c}	4.30^{c}
Kluang	1.14^{d}	19.84^{d}	4.64^{d}	80.30^{c}	4.62^{d}	154.85^{b}	6.63^{c}	3.93^{d}
Mean	1.81	26.11	5.04	86.29	5.09	156.59	7.87	4.69

Note: Means within a column with the same letter are not significantly different at P - 0.05 with Duncan's new multiple range test.

for yield and its components, bunch quality and vegetative characters. The appropriate expected mean squares were used to test the items (Cochran and Cox, 1959; Satterthwaite, 1946). The *duras* within *pisifera* effect was highly significant for BNO and ABW, and significant for FFB, indicating that the variation conferred by different *duras* mated to the same *pisifera* was high for these characters. In contrast, the *pisifera* item was non-significant for the three characters. These results indicated that the highly significant progeny differences for FFB, BNO and ABW were mainly due to the *duras* within *pisifera* effect rather than the contribution from *pisifera* (*Table 4*).

Highly significant effects of *pisifera* x location and *duras* within *pisifera* x location were recorded for yield and its component characters except for *pisifera* x location for FFB (*Table 4*). For the second order interactions, D/P x R/L was highly significant for ABW, and P x R/L significant for FFB. The estimates for $\sigma^2_{d/p}$ (1.28% to 6.52%) were larger than those for σ^2_p (0% to 1.26%) for all the characters (*Table 4*). It was also noted that $\sigma^2_{(d/p)l}$ was larger than σ^2_{pl} for all the characters except ABW.

Tables 5 and *6* show the ANOVA for the bunch quality characters. For the half-sib families, highly significant differences between *pisiferas* were detected for MTF and STF, and significant differences for KTB and OPY (*Tables 5* and *6*). The variation from *duras* within *pisifera* was very high for KTF, KTB, oil to wet mesocarp (OTWM) and KPY, but not significant for the other characters.

The interactions between *pisifera* and location were highly significant for FTB and significant for KTB and OTB. The D/P x L interaction was highly significant for most of the bunch quality characters except oil to dry mesocarp (OTDM) and OPY which were significant, and for FTB, which was non-significant (*Tables 5* and *6*). None of the second order interactions, *viz.* P x R/L and D/P x R/L, were significant for any character. The estimates for σ^2_p were larger than those for $\sigma^2_{d/p}$ for MTF, STF and OPY. In contrast, the estimates for $\sigma^2_{d/p}$ were larger than the σ^2_p component for the other bunch quality characters (*Tables 5* and *6*). The contributions of σ^2_p and $\sigma^2_{d/p}$ towards the phenotypic variance ranged from 0% to 10.98% and 0% to 9.32%, respectively.

Highly significant *pisifera* and *duras* within *pisifera* effects were detected for all the vegetative characters except for the *pisifera* effect on LL (*Table 7*). There was considerable variation between the *pisifera* and *duras* within *pisifera* effects evaluated. The P x L and D/P x L interactions were non-significant for all the characters except D/P x L on LA and LAI. For the

TABLE 4. MEAN SQUARES AND VARIANCE COMPONENTS FROM NORTH CAROLINA MATING DESIGN 1 ANALYSIS OVER LOCATIONS FOR FRESH FRUIT BUNCHES, BUNCH NUMBER AND AVERAGE BUNCH WEIGHT

Source	df	FFB	BNO	ABW
Pisifera (P)	14	7 715.65	110.81	12.26
Duras within *pisifera* (D/P)	25	3 691.49*	88.35**	20.03**
Location (L)	5	639 948.25**	7 882.22**	1 234.28**
P x L	70	2 789.95	26.24	5.94**
D/P x L	125	2 265.37**	20.98**	6.14**
Rep within location (R/L)	6	25 545.66**	81.75**	29.49
P x R/L	84	2 283.11*	15.93	3.53
D/P x R/L	150	1 732.18	12.91	6.06**
Within palms	1 866	1 762.78	15.34	4.73
σ^2_p		24.00	0.12	0.00
		(1.26)	(0.67)	(0.00)
$\sigma^2_{d/p}$		24.45	1.16	0.24
		(1.28)	(6.52)	(4.49)
σ^2_{pl}		0.00	0.09	0.10
		(0.00)	(0.51)	(1.87)
$\sigma^2_{(d/p)l}$		54.85	0.83	0.01
		(2.87)	(4.67)	(0.19)
$\sigma^2_{p(r/l)}$		45.34	0.25	0.00
		(2.37)	(1.41)	(0.00)
$\sigma^2_{(d/p)(r/l)}$		0.00	0.00	0.27
		(0.00)	(0.00)	(5.05)
σ^2_w		1 762.78	15.34	4.73
		(92.22)	(86.23)	(88.41)

Notes: * , ** Significant at P - 0.05 and P - 0.01, respectively. The value in brackets below each variance component expresses it as a percentage of the phenotypic variance. Harmonic means for palms in female (n') and D/P (d') = 4.86 and 2.50, respectively. Negative estimate for the variance component for which the most reasonable value is zero.

TABLE 5. MEAN SQUARES AND VARIANCE COMPONENTS FROM NORTH CAROLINA MATING DESIGN 1 ANALYSIS OVER LOCATIONS FOR BUNCH QUALITY CHARACTERS

Source	df	MTF	STF	KTF	KTB	FTB	OTB	OTDM	OTWM
Pisifera (P)	14	470.82**	330.81**	47.50	28.54	342.73	61.31	16.51	77.12
Duras within *pisifera* (D/P)	25	95.47	41.49	22.68**	10.72**	96.53	39.35	17.32	72.29**
Location (L)	3	512.60**	123.35	373.69**	49.90**	3 307.68**	158.56	184.27**	1 712.68
P x L	42	83.31	61.97	9.29	4.26*	169.69**	37.37*	10.78	44.68
D/P x L	69	58.68**	61.02**	7.09**	3.28**	68.20	24.52**	11.58*	34.21**
Rep within location (R/L)	4	10.38	2.54	6.26	2.45	118.43	61.31**	85.30**	74.54*
P x R/L	56	30.52	19.07	4.16	1.94	54.81	12.55	8.65	27.96
D/P x R/L	92	31.50	20.26	4.69	2.79	62.17	13.71	8.01	21.84
Within palms	1 011	36.81	25.86	3.79	2.23	72.34	14.96	8.87	21.84
σ^2_p		4.67	3.84	0.30	0.22	1.93	0.12	0.00	0.00
		(9.85)	(10.98)	(5.70)	(7.38)	(2.36)	(0.68)	(0.00)	(0.00)
$\sigma^2_{d/p}$		1.16	0.00	0.49	0.23	0.89	0.47	0.18	1.20
		(2.45)	(0.00)	(9.32)	(7.72)	(1.09)	(2.66)	(1.88)	(4.57)
σ^2_{pl}		1.36	0.11	0.15	0.10	5.80	0.75	0.00	0.23
		(2.87)	(0.31)	(2.85)	(3.36)	(7.08)	(4.25)	(0.00)	(0.88)
$\sigma^2_{(d/p)l}$		3.43	5.15	0.30	0.06	0.96	1.36	0.45	1.56
		(7.23)	(14.73)	(5.70)	(2.01)	(1.17)	(7.70)	(4.70)	(5.94)
$\sigma^2_{p(r/l)}$		0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.65
		(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.00)	(0.73)	(2.47)
$\sigma^2_{(d/p)(r/l)}$		0.00	0.00	0.23	0.14	0.00	0.00	0.00	0.00
		(0.00)	(0.00)	(4.37)	(4.70)	(0.00)	(0.00)	(0.00)	(0.00)
σ^2_w		36.81	25.86	3.79	2.23	72.34	14.96	8.87	22.64
		(77.61)	(73.97)	(72.05)	(74.83)	(88.31)	(84.71)	(92.69)	(86.15)

Notes: * , ** Significant at P - 0.05 and P - 0.01, respectively. The value in brackets below each variance component expresses it as a percentage of the phenotypic variance. Harmonic means for palms in female (n') and D/P (d') = 3.96 and 2.37, respectively. Negative estimate for the variance component for which the most reasonable value is zero.

TABLE 6. MEANS SQUARES AND VARIANCE COMPONENTS FROM NORTH CAROLINA MATING DESIGN 1 ANALYSIS OVER LOCATIONS FOR OIL/PALM/YEAR AND KERNEL/PALM/YEAR

Source	df	OPY	KPY
Pisifera (P)	14	584.19*	64.58
Duras within *pisifera* (D/P)	23	180.19	36.41**
Location (L)	3	27 405.86**	1 470.42**
P x L	42	191.93	11.20
D/P x L	69	165.61*	14.35**
Rep within location (R/L)	4	825.21**	14.86
P x R/L	56	124.21	8.62
D/P x R/L	92	118.27	11.61
Within palms	1 005	124.21	9.21
σ^2_p		5.07	0.42
		(3.98)	(3.72)
$\sigma^2_{d/p}$		0.46	0.70
		(0.36)	(6.20)
σ^2_{pl}		1.09	0.00
		(0.86)	(0.00)
$\sigma^2_{(d/p)l}$		6.02	0.35
		(4.73)	(3.10)
$\sigma^2_{p(r/l)}$		0.64	0.00
		(0.50)	(0.00)
$\sigma^2_{(d/p)(r/l)}$		1.46	0.61
		(1.15)	(5.40)
σ^2_w		112.53	09.21
		(88.42)	(81.58)

Notes: * , ** Significant at P - 0.05 and P - 0.01, respectively. The value in brackets below each variance component expresses it as a percentage of the phenotypic variance. Harmonic means for palms in female (n') and D/P (d') = 3.93 and 2.37, respectively. Negative estimate for the variance component for which the most reasonable value is zero.

TABLE 7 . MEAN SQUARES AND VARIANCE COMPONENTS FROM NORTH CAROLINA MATING DESIGN 1 ANALYSIS OVER LOCATIONS FOR VEGETATIVE CHARACTERS

Source	df	HT	PCS	RL	LL	LW	LN	LA	LAI
Pisifera (P)	14	2.13**	600.71**	1.77**	674.27	3.75**	2 188.54**	21.08**	7.39**
Duras within *pisifera* (D/P)	25	0.60**	170.14**	0.58**	533.50**	0.89**	615.38**	7.49**	2.63**
Location (L)	3	108.12**	10 293.16**	53.08**	8 115.84**	81.76**	39 585.02**	580.25**	203.35**
P x L	42	0.11	4.59	0.28	52.43	0.36	227.32	1.96**	0.69
D/P x L	75	0.16	44.40	0.27	59.74	0.30	163.62	1.74	0.60
Rep within location (R/L)	4	0.96**	294.80**	0.58	449.04**	16.20	1 592.92**	64.70**	22.65**
P x R/L	56	0.10	33.93	0.23	65.04	0.25	146.30	2.01	0.70
D/P x R/L	100	0.15*	44.33*	0.27	60.84	0.33	116.59	2.13	0.75
Within palms	1 211	0.11	34.28	0.25	60.17	0.31	158.50	2.13	0.75
σ^2_p		0.02	4.54	0.01	1.57	0.03	15.96	0.14	0.05
		(13.33)	(10.14)	(3.57)	(2.10)	(7.89)	(8.18)	(5.76)	(5.81)
$\sigma^2_{d/p}$		0.01	3.32	0.01	12.52	0.02	11.94	0.15	0.05
		(6.67)	(7.42)	(3.57)	(16.57)	(5.26)	(6.12)	(6.17)	(5.81)
σ^2_{pl}		0.00	0.49	0.00	0.00	0.01	1.44	0.01	0.01
		(0.00)	(1.09)	(0.00)	(0.00)	(2.63)	(0.74)	(0.41)	(1.16)
$\sigma^2_{(d/p)l}$		0.00	0.01	0.00	0.00	0.00	4.79	0.00	0.00
		(0.00)	(0.02)	(0.00)	(0.00)	(0.00)	(2.45)	(0.00)	(0.00)
$\sigma^2_{p(r/l)}$		0.00	0.00	0.00	0.36	0.00	2.51	0.00	0.00
		(0.00)	(0.00)	(0.00)	(0.48)	(0.00)	(1.29)	(0.00)	(0.00)
$\sigma^2_{(d/p)(r/l)}$		0.01	2.12	0.01	0.16	0.01	0.00	0.00	0.00
		(6.67)	(4.74)	(3.57)	(0.19)	(2.63)	(0.00)	(0.00)	(0.00)
σ^2_w		0.11	34.28	0.25	60.17	0.31	158.50	2.13	0.75
		(73.33)	(76.59)	(89.29)	(80.48)	(81.58)	(81.22)	(87.65)	(87.21)

Notes: * , ** Significant at P - 0.05 and P - 0.01, respectively. The value in brackets below each variance component expresses it as a percentage of the phenotypic variance. Harmonic means for palms in female (n') and D/P (d') = 4.73 and 2.50, respectively. Negative estimate for the variance component for which the most reasonable value is zero.

second order interactions, only the D/P x R/L interaction for HT and petiole cross-section (PCS) was significant. The estimates for σ^2_p were higher than those for $\sigma^2_{d/p}$ for HT, PCS, LW and LN, but the latter variance was larger for LL and LA. The σ^2_p component ranged from 2.10% to 13.38%, while $\sigma^2_{d/p}$ ranged from 3.57% to 16.75 % of the phenotypic variance.

Heritability Estimates Based on the *Pisifera* (σ^2_p) and *Duras/Pisifera* ($\sigma^2_{d/p}$) Components

The heritability values estimated for the individual locations are tabulated in *Table 8*. In general, they differed from location to location. The values based on the *pisifera* and *dura* components were greatly influenced by the environment.

For yield and its components, and the bunch quality characters, the heritability estimates were low and not consistent between the locations. Higher estimates for the bunch quality traits were obtained from most of the locations (*Table 8*). In general, the estimates from all locations were more consistent for the vegetative than yield and bunch quality characters (*Table 8*).

The heritabilities over locations for half-sib analysis are presented in *Table 9*. The estimates based on the *dura* component (h^2_d) were higher than those based on the *pisifera* component (h^2_p) for FFB, BNO, ABW, KTF, KTB, OTB, OTDM, OTWM, KPY, LL and LA. In contrast, the latter estimates were higher for MTF, STF, FTB, OPY, HT, PCS, LW and LN. They were similar amounts for rachis length (RL) and LAI.

Quantitative characters controlled by polygenes are strongly influenced by the environment (Kang, 1994). In this study, the DxP population showed wide genetic variation and heritability values over the range of environments. Thus, the environment had a great influence on the magnitude of the σ^2_p and $\sigma^2_{d/p}$ components although there was no clear trend over the locations. The estimates of σ^2_p and $\sigma^2_{d/p}$ were either positive or negative depending upon the environment under which the trial was conducted. Besides the genotype x environment interaction, a few other explanations can be proffered for such a situation. One explanation for the negative variance components is the large within palms mean squares. Another is the limited germplasm used - only 15 males (unequally) mated with two to four females in developing the half-sib families. Sanchez and Hallauer (1970), in their study on sample size in the estimation of genetic variance in maize, found that negative variances frequently arose in trials with a small number of male groups or too few females mated to a male. They suggested that at least four females should be mated to a male.

TABLE 8. ESTIMATES OF HERITABILITY IN INDIVIDUAL LOCATIONS

Character	Location	h^2_p (%)	h^2_d (%)
FFB	Kudat	3.03	4.46
	Beaufort	0.00	25.94
	Teluk Intan	28.57	11.30
	Carey Island	24.11	31.45
	Kepong	0.00	9.98
	Kluang	20.27	0.00
BNO	Kudat	0.00	20.65
	Beaufort	0.00	44.04
	Teluk Intan	7.12	40.92
	Carey Island	41.26	70.51
	Kepong	7.49	0.00
	Kluang	0.00	100.00
ABW	Kudat	15.23	0.00
	Beaufort	0.00	32.86
	Teluk Intan	0.00	36.95
	Carey Island	0.00	40.34
	Kepong	0.00	0.00
	Kluang	17.32	31.39
MTF	Teluk Intan	98.31	35.09
	Carey Island	40.88	77.39
	Kepong	8.90	0.00
	Kluang	36.35	98.36
STF	Teluk Intan	100.00	41.33
	Carey Island	64.51	35.98
	Kepong	4.88	0.00
	Kluang	50.33	85.90
KTF	Teluk Intan	33.18	28.70
	Carey Island	32.89	100.00
	Kepong	24.39	0.00
	Kluang	36.21	96.35
KTB	Teluk Intan	43.70	5.04
	Carey Island	41.96	88.58
	Kepong	28.40	0.00
	Kluang	55.01	88.35
FTB	Teluk Intan	74.25	0.00
	Carey Island	18.40	45.56
	Kepong	24.49	0.00
	Kluang	32.42	48.86
OTB	Teluk Intan	86.53	6.49
	Carey Island	0.00	100.00
	Kepong	5.66	0.00
	Kluang	0.00	71.21
OTDM	Teluk Intan	2.91	0.00
	Carey Island	0.00	32.92
	Kepong	1.97	9.18
	Kluang	0.00	64.83
OTWM	Teluk Intan	0.00	16.35
	Carey Island	0.00	67.38
	Kepong	4.46	1.36
	Kluang	15.03	61.11
OPY	Teluk Intan	49.11	20.46
	Carey Island	15.09	42.44
	Kepong	0.00	4.27
	Kluang	8.69	5.87
KPY	Teluk Intan	22.67	11.86
	Carey Island	8.87	81.60
	Kepong	1.95	7.33
	Kluang	34.99	3.46
HT	Teluk Intan	80.00	53.33
	Carey Island	42.11	42.11
	Kepong	33.33	33.33
	Kluang	30.77	30.77
PCS	Teluk Intan	38.49	36.18
	Carey Island	46.70	67.38
	Kepong	47.01	30.65
	Kluang	42.13	0.00
RL	Teluk Intan	11.43	0.00
	Carey Island	40.00	20.00
	Kepong	32.00	16.00
	Kluang	13.33	13.33
LL	Teluk Intan	17.08	48.18
	Carey Island	19.71	52.08
	Kepong	0.00	75.87
	Kluang	9.47	81.17
LW	Teluk Intan	84.85	24.24
	Carey Island	33.33	33.33
	Kepong	25.53	8.51
	Kluang	17.78	8.89
LN	Teluk Intan	19.02	48.99
	Carey Island	60.38	45.16
	Kepong	20.96	31.35
	Kluang	41.86	12.00
LA	Teluk Intan	34.08	26.91
	Carey Island	29.09	34.55
	Kepong	10.07	20.14
	Kluang	31.23	0.00
LAI	Teluk Intan	35.90	25.64
	Carey Island	30.77	35.90
	Kepong	8.25	20.62
	Kluang	30.11	0.00

Notes: h^2_P = *pisifera* component heritability.
h^2_d = *dura* component heritability.
Negative estimate of heritability for which the most reasonable value is zero.
Estimates of heritability > 100% were recorded as 100%.

TABLE 9. ESTIMATES OF HERITABILTY OVER LOCATIONS

Character	h^2_p (%)	h^2_d (%)
FFB	5.02	5.12
BNO	2.70	26.08
ABW	0.00	17.94
MTF	39.38	9.78
STF	43.94	0.00
KTF	22.81	37.26
KTB	29.53	30.87
FTB	9.45	4.36
OTB	2.72	10.65
OTDM	0.00	7.52
OTWM	0.00	18.26
OPY	15.93	1.45
KPY	14.88	24.80
HT	53.33	26.67
PCS	40.57	29.67
RL	14.28	14.28
LL	8.40	66.99
LW	31.58	21.06
LN	32.68	24.45
LA	23.05	24.69
LAI	23.26	23.26

Notes: h^2_P= *pisifera* component heritability.
h^2_d= *dura* component heritability.
Negative estimate of heritability for which the most reasonable value is zero.

The heritability values were clearly also influenced by the environment. For example, h^2_p for FFB ranged from 0% (Beaufort) to 28.57% (Teluk Intan). However, pooling the data across locations, h^2_p was 5.02%. Gardner (1963) pointed out that heritability estimated in only one environment is biased upward because the genotype x environment interaction cannot be separated from the genetic effects. The degree of bias is obviously dependent on the magnitude of the genotype x environment interaction (Comstock and Moll, 1963).

According to Blum (1988), heritabilities are higher in better than poorer environments. However, in this study, there was no evidence to support this contention. The combined analysis across locations showed that h^2_d for FFB was low. Slightly higher values were obtained for ABW and BNO. The findings are in accordance with those of Hardon *et al.* (1985). However, all the values were low. It is interesting that these results are in contrast to several reports. Ahiekpor and Yap (1985) and Jacquemard *et al.* (1982) reported that yield (FFB) and its components (BNO and ABW) had high (>50%) broad sense heritabilities in different DxP populations, as did *dura* populations by other workers (Thomas *et al.*, 1969; Ooi *et al.*, 1973; Ooi, 1975). However, the low narrow sense heritabilities (h^2_p and h^2_d) found in this study are in agreement with those in other reports (Tan, 1978; Jacquemard *et al.*, 1982).

CONCLUSION

There was a marked influence by the environment on genetic variance in DxP progenies. Hence, the heritability estimates for yield and its components and bunch quality characters fluctuated greatly from location to location. Generally, the vegetative characters had higher heritabilities than yield and its components and most of the bunch quality characters, indicating a lower influence of the environment on them. Palm height showed the highest h^2_p, offering good potential in direct selection for dwarfness.

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