

Effects of inbreeding on growth and yield of oil palm

Inbreeding of oil palm

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Summary

The effects of inbreeding were studied in three oil palm (*Elaeis guineensis* Jacq.) trials in the Democratic Republic of Congo (Congo). In selfings, marked inbreeding depression was observed for yield of fruit bunches, mean bunch weight and bunch number, but there was little effect on bunch composition. Most vegetative measurements were significantly affected by selfing, but leaf production rate and leaf area ratio were unaffected. Sib-crossing had less depressive effect than selfing, and in some families sib-crosses were superior to outcrosses. Where selection needs to be done within inbred families, our study suggests that leaf area ratio and bunch composition would be useful criteria.

Abbreviations: Fx: inbreeding coefficient; FFB: fresh fruit bunches; F/B: fruit to bunch ratio; M/F: mesocarp to fruit ratio; O/M: oil/mesocarp ratio; K/B: kernel/bunch ratio; LAR: leaf area ratio; VDM: vegetative dry matter

Introduction

Oil palm seed for commercial planting is produced by crossing palms of the thick-shelled *dura* fruit form with the shell-less *pisifera* form to give thin-shelled *tenera* offspring. Several major oil palm breeding programmes are based on reciprocal recurrent selection (RRS), with *dura* and *pisifera* populations kept distinct; selfing and sib-crossing are usually included in these programmes to obtain parents for seed production, or for the next generation of crosses (Corley & Tinker, 2003). However, it is unusual for more than two consecutive generations of inbreeding to be done, partly for fear of inbreeding depression. Thus, while palms used as seed parents are homozygous for the gene controlling shell thickness, they remain highly heterozygous at other loci. In common with other

cross-pollinated and heterozygous species, inbreeding of oil palm has been shown to cause depression of yield (Gascon et al., 1969). Hardon (1970) found a highly significant negative correlation between inbreeding coefficient and yield of bunches in the widely used Deli *dura* population. The effects of inbreeding depression may complicate phenotypic selection, and the aim of our work is to try to identify parameters which are relatively unaffected by inbreeding, and which could thus be used as selection criteria. Various authors have suggested the use of vegetative measurements as selection criteria (Corley et al., 1971; Breure & Corley, 1983; Breure, 1986), so it is important to ascertain the effects of inbreeding on these parameters. In this paper we evaluate the effects of inbreeding on growth and yield in material from breeding programmes in Congo and Cameroun.

Material and methods

Trials

Trial 1 was planted at Binga Research Station (2° 22' N, 20° 31' E, 400 m asl). Trials 2 and 3 were at Yaligimba Research Station (2° 13' N, 22° 56' E, 460 m asl); both stations are in northern Congo. The annual rainfall at both stations is about 1700 mm, with a two to three-month dry season at Yaligimba, and three to four months at Binga. The soils in northern Congo have been described as hygro-kaolinitic ferral-sols (FAO-UNESCO, 1990). All trials were planted at 143 palms/ha, in randomised complete block designs, with nine palms per plot.

Trial 1

This trial included 22 *tenera* × *tenera* and 8 *dura* × *tenera* crosses among palms derived from four origins in the Yangambi programme (Figure 1; see Rosenquist, 1986, for more details). The crosses had inbreeding coefficients (F_x), calculated from pedigrees as described by Falconer (1981), ranging from $F_x = 0.03$ to $F_x = 0.75$. The trial was planted in 1973, with eight replicates. Yields of fresh fruit bunches (FFB) were recorded for 10 years from 1976 to 1985. Vegetative measurements were made in 1982, following the non-

destructive methods described by Corley et al. (1971). *Fusarium* wilt incidence records were based on external symptoms of the disease.

Seven families were excluded from the analyses, as the segregation of fruit forms differed significantly from expectation, indicating contamination or illegitimacy. One family, Bg143, a presumed self of parent palm 312/3, has been shown using RFLP markers to be at least partly an illegitimate outcross rather than a selfing (Mayes, 1995), although fruit form segregation was as expected. We also excluded that family from the analyses, but the legitimacy of the remaining crosses has not been checked.

Trial 2

This trial included 15 *tenera* × *tenera* crosses between palms selected in code Bg143 in Trial 1, and palms of the Ekona population (Rosenquist, 1986) from Lobe, Cameroun. There were nine outcrosses, all between palms in Bg143 and either Ekona palm 2/2311 or its selfed offspring. There were also three Ekona selfs, and three selfs in Bg143. Although Bg143 is known to be at least partly illegitimate (see above), the parents of the three selfings could all have been legitimate (ie. they did not have marker bands not shown by the parent palm 312/3). Thus we have assumed the selfings to have $F_x = 0.75$.

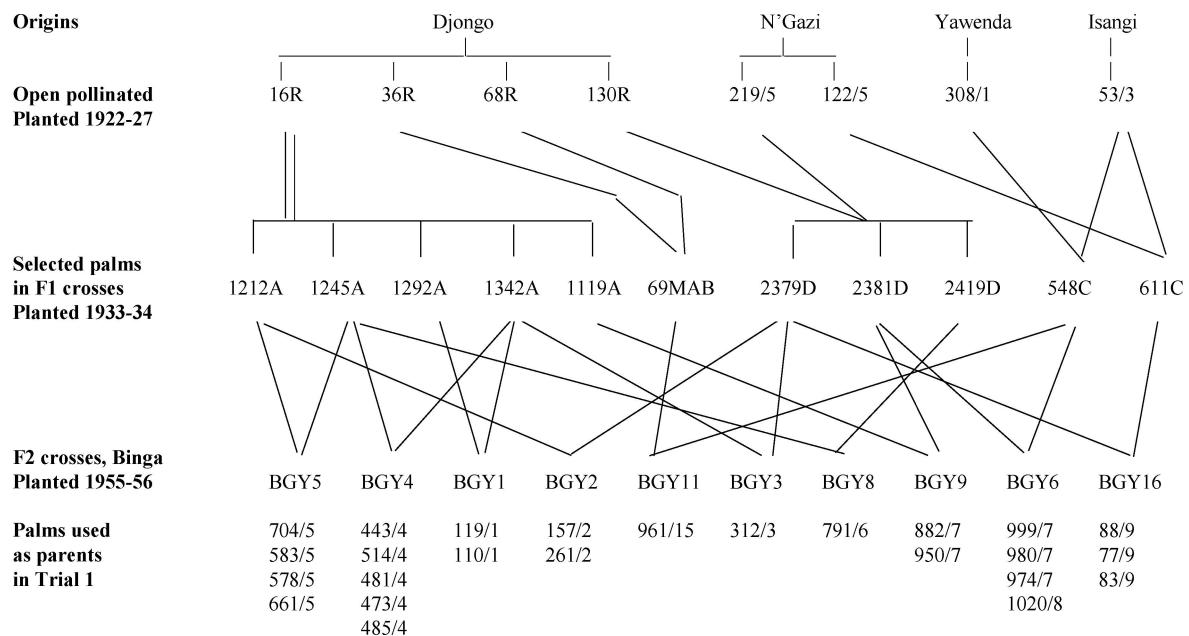


Figure 1. Ancestry of parental palms used in Trial 1 (based on Hardon et al., 1976; Rosenquist, 1986).

The trial was divided into two parts, adjacent to each other. Trial 2A included 11 families, with eight replicates, while Trial 2B included four families, with four replicates; data from the two parts of the trial have been combined. The trial was planted in 1985, and yields were recorded for 5 years from 1988 to 1992. Vegetative measurements are the means of three sets of data, collected in 1990, 1991 and 1993.

Trial 3

Results for some of the crosses in each of seven field experiments have been combined here. The trials were all contiguous, and linked by a common standard cross. The parents were taken from four families at Binga (details of the families were given by Rosenquist et al., 1990). We have used data from six palms which had been selfed; these palms were also involved in 18 sib-crosses and 11 outcrosses (with palms in the other three families). The one palm from Bg143 which was included was known to be illegitimate, so its selfing had $F_x = 0.5$; crosses between it and other palms in Bg143 were assumed to be half-sib crosses.

All the trials, planted in 1987, had eight replications. Yields were recorded for 5 years from 1991 to 1995; vegetative measurements were made in 1992. Yields of the standard crosses did not differ much between trials, with coefficients of variation between trials of 5% for yield, 6% for bunch number and 4% for bunch weight. Thus we considered that all trial sites had similar yield potential, and we did not make any adjustments to the data before combining results from different trials.

Recording

Yields of fruit bunches (FFB) were recorded by weighing all bunches immediately after each harvest round; the tables give means for the *dura* and *tenera* fruit forms. Bunch composition was determined on a sample of *tenera* bunches, following the methods described by Blaak et al. (1963) and Rao et al. (1983). An average of 55 bunches were sampled per family in Trial 1, and 51 per family in Trial 2; in Trial 3, an average 12 bunches per family were analysed. Oil yield was estimated from the product of FFB yield and oil/bunch; in Trial 1, this was done for individual plots, so that oil yield data could be analysed statistically, but the data did not permit this in the other trials. Vegetative measurements and non-destructive estimates of dry matter production were made for all palms, following the methods described by Corley et al. (1971). *Fusarium* wilt incidence was recorded in Trial 1, based on exter-

nal symptoms of the disease; in Trials 2 and 3 incidence was very low, and the data are not considered here.

Results

Trial 1

Results for this trial are given in Table 1. In Table 2, the data for yield and its components are summarised for four levels of inbreeding. There was a highly significant trend towards lower yield with larger F_x . In terms of yield components, mean bunch weight was most strongly affected; the correlations of F_x with bunch number and oil/bunch, though negative, were not significant. However, Table 2 shows that mean bunch numbers for the inbred groups were significantly below the mean for outcrosses. None of the bunch components was significantly correlated with F_x , although there was some indication of depression of mesocarp/fruit. Results for code Bg143 are included in Table 1, but because it has been shown to be partly illegitimate, it was excluded when calculating the correlations.

Vegetative growth was also affected by inbreeding, with height increment, leaf weight, leaf area and annual vegetative dry matter production all being negatively correlated with F_x (Tables 1 and 3). Annual leaf production and leaf area ratio (the ratio of area to weight) were not affected. Incidence of *Fusarium* wilt was positively (but not significantly) correlated with inbreeding coefficient.

Trial 2

Results of this trial are summarised in Tables 2 and 3. Yield and its components were significantly depressed by selfing; first and second generation selfs were very similar, but there was only one first generation self in the trial. Mean bunch weight and bunch number per palm were both significantly reduced in the selfs, with the effect on bunch weight being greater. Oil/bunch was slightly lower, because of lower oil/mesocarp. All vegetative parameters were reduced in the second generation selfs (Table 3).

Trial 3

Results of this trial are summarised in Tables 2 and 3. As in the other trials, yields were lower in the inbred crosses than in outcrosses, with the effect on bunch weight being slightly greater than that on bunch number. Oil/bunch was slightly affected, through lower

Table 1. Correlations between inbreeding coefficient (Fx) and yield and growth of inbred oil palm families in Trial 1

Code	Parents		Yield per palm				Yield components			Bunch components (<i>tenera</i>)					Growth parameters				Fusarium wilt %		
	Female	Male	FFB kg/year	Oil kg/year	Bunch		Oil/bunch %	F/B %	M/F %	O/M %	K/B %	Fruit wt g	Leaf area m ²	Leaf wt kg	Leaf prodn /p.yr	VDM kg/year	LAR m ² /kg cm/yr	Height incr. cm/yr			
					No. p.yr	Bunch wt/kg															
217	88/9	×	1020/8	0.09	90.4	18.1	10.7	8.7	21.3	54.1	83.8	47.8	4.5	10.2	7.9	2.6	19.1	60	2.56	50	31
219	974/7	×	77/9	0.09	83.4	16.9	9.8	9.1	18.4	56.7	78.5	49.9	6.3	11.8	7.5	2.6	19.9	63	2.38	46	52
111	77/9	×	312/3	0.14	80.0	17.5	7.5	11.4	21.9	53.6	79.1	50.4	5.5	11.4	7.6	2.6	20.6	66	2.38	46	25
114	83/9	×	980/7	0.09	78.7	17.0	10.6	7.6	20.2	51.7	82.3	50.2	4.7	11.3	7.8	2.5	16.6	53	2.13	51	14
112	312/3	×	443/4	0.28	73.7	15.8	8.1	9.6	21.7	56.6	76.8	50.9	5.3	12.2	7.5	2.5	21.1	62	2.53	41	25
140	950/7	×	661/5	0.16	79.3	15.4	9.3	8.8	21.2	53.1	75.9	49.8	5.9	9.8	8.1	3.0	19.6	72	2.12	44	18
211	961/15	×	999/7	0.14	74.4	15.3	7.6	10.5	17.3	50.6	81.1	51.2	5.3	11.5	8.0	2.8	19.1	64	2.36	47	11
108	157/2	×	77/9	0.15	72.4	15.2	6.8	11.6	21.6	56.5	75.5	52.7	5.8	10.2	6.8	2.3	20.9	58	2.28	45	57
192	83/9	×	261/2	0.15	70.8	15.3	7.4	10.4	21.3	43.4	78.3	45.5	4.1	9.9	7.7	2.2	20.9	54	2.93	44	85
183	578/5	×	481/4	0.37	57.6	12.4	7.2	8.5	19.8	50.3	72.6	45.3	5.0	8.7	6.7	2.3	19.8	57	2.33	43	50
157	1020/8	×	119/1	0.03	77.4	16.9	10.9	7.8	19.1	48.3	80.5	49.8	4.8	10.0	7.7	2.5	19.8	59	2.58	46	45
124	999/7	×	119/1	0.03	74.8	13.4	8.2	9.8	21.7	47.7	77.2	48.2	6.1	11.6	8.2	2.6	20.2	61	2.54	44	29
144	999/7	×	514/4	0.03	71.2	12.9	7.0	10.8	22.2	50.4	78.0	50.6	6.0	11.5	8.3	2.9	19.9	67	2.30	45	25
176	882/7	×	704/5	0.16	48.6	12.6	6.2	7.6	21.9	59.0	77.6	51.8	5.7	9.6	6.4	2.4	16.6	51	1.99	32	53
79	119/1	selfed		0.75	68.9	11.0	11.7	6.1	21.6	48.5	72.8	48.8	6.0	10.2	6.7	2.2	20.7	55	2.60	41	46
110	443/4	selfed		0.75	39.9	10.0	5.3	7.7	19.4	56.0	78.2	50.1	4.4	11.0	5.3	1.6	20.9	41	2.32	37	76
113	583/5	×	514/4	0.37	57.1	11.0	7.6	7.6	21.9	50.0	75.5	51.5	5.2	9.5	7.1	2.5	21.4	65	2.36	39	43
122	473/4	×	110/1	0.37	66.1	11.1	8.8	7.7	19.6	47.9	75.6	44.9	5.9	9.7	6.8	2.5	20.6	62	2.24	38	6
116	485/4	×	119/1	0.37	69.9	10.7	8.9	8.3	23.7	45.4	71.8	43.3	5.7	9.6	7.4	2.5	19.8	59	2.33	44	40
174	791/6	selfed		0.53	50.6	10.1	8.1	6.4	20.1	52.3	79.8	50.3	4.1	11.3	5.9	2.0	19.7	48	2.30	35	35
218	704/5	selfed		0.75	37.8	7.6	6.2	6.5	21.5	59.8	72.2	51.6	6.6	9.2	7.3	2.7	18.3	58	2.20	35	68
249	514/4	selfed		0.75	44.2	7.2	6.3	7.2	18.5	42.8	81.0	47.6	3.9	9.7	6.1	2.1	19.4	50	2.29	34	16
143	312/3	×	unknown		83.2	17.0	9.0	9.8	20.0	55.5	81.6	49.9	5.3	12.0	8.4	3.0	19.8	68	2.33	44	7
Standard Error				3.3	0.93	0.44	0.42	1.31	—	—	—	—	—	—	0.33	0.12	0.68	3.6	0.13	1.8	—
Correlation with Fx (df = 20)				-0.77*	-0.83*	-0.28	-0.67*	-0.09	-0.03	-0.39	-0.10	-0.15	-0.34	-0.68*	-0.53*	0.13	-0.45*	-0.00	-0.64*	0.24	—

Abbreviations: Fx: inbreeding coefficient; F/B: fruit/bunch; M/F: mesocarp/fruit; O/M: oil/mesocarp; K/B: kernel/bunch; Leaf prodn: number of new leaves produced per year; VDM: vegetative dry matter production; LAR: leaf area ratio.

*Correlation significant at $P = 0.05$ or less.

Table 2. Mean yield and yield components for groups of families with different levels of inbreeding

Trial	Cross type	No. of crosses	Mean Fx	Yield of fruit		Yield of oil		Bunch No.		Mean bunch wt		Bunch components (%)					
				kg/year	S.E.	kg/year	S.E.	kg/year	S.E.	kg	S.E.	Oil/B	S.E.	F/B	M/F	O/M	K/B
1	Fx = 0.03–0.09	6	0.06	79.2	1.9	15.7	0.48	9.5	0.28	9.0	0.23	20.5	0.59	51.5	80.1	49.4	5.4
	Fx = 0.14–0.28	7	0.17	72.6*	1.9	15.7	0.47	7.7*	0.27	10.0	0.22	21.0	0.51	53.3	77.8	50.3	5.4
	Fx = 0.37–0.53	5	0.40	60.5*	2.1	11.1*	0.52	8.2*	0.30	7.7*	0.24	21.0	0.61	49.2	75.1	47.1	5.2
	Fx = 0.75	4	0.75	48.7*	2.4	9.3*	0.63	7.6*	0.35	6.8*	0.28	20.3	0.68	51.8	76.1	49.5	5.2
2	Outcrosses	9	0	57.5	1.7	15.2	–	12.1	0.28	4.8	0.09	26.4	–	62.6	78.0	54.1	4.5
	Selfs	1	0.50	33.7*	4.7	8.7	–	9.1*	0.75	3.7*	0.23	25.9	–	65.4	78.3	50.6	4.1
	Selfs (S2)	5	0.75	34.1*	2.2	8.8	–	9.2*	0.35	3.7*	0.11	25.8	–	63.0	79.6	51.4	3.9
3	Outcrosses	11	0	46.2	–	13.0	–	10.4	–	4.7	–	28.2	–	63.3	81.6	54.4	3.5
	Sibs, ½-sibs	18	0.22	42.9	–	12.1	–	9.7	–	4.6	–	28.4	–	63.8	81.7	54.5	3.6
	Selfs	6	0.50	39.4	–	10.8	–	9.7	–	4.1	–	27.6	–	62.5	82.0	53.5	3.4

Abbreviations: Fx: inbreeding coefficient; Oil/B: oil/bunch; F/B: fruit/bunch; M/F: mesocarp/fruit; O/M: oil/mesocarp; K/B: kernel/bunch.
*Significantly below outcrosses or smallest Fx class.

Table 3. Mean growth parameters for groups of families with different levels of inbreeding

Trial	Cross type	No. of crosses	Mean Fx	Leaf area		Leaf weight		Leaf production		VDM		LAR		Height increment	
				m ²	S.E.	kg	S.E.	/p.yr	S.E.	kg/year	S.E.	m ² /kg	S.E.	cm/yr	S.E.
1	Fx = 0.03–0.09	6	0.06	7.90	0.16	2.61	0.06	19.2	0.33	60.4	1.76	2.40	0.06	47	0.91
	Fx = 0.14–0.28	7	0.17	7.51	0.16	2.59	0.06	19.8	0.32	62.7	1.70	2.34	0.06	43*	0.89
	Fx = 0.37–0.53	5	0.40	6.78*	0.18	2.38*	0.07	20.3	0.35	58.4	1.89	2.31	0.06	40*	0.98
	Fx = 0.75	4	0.75	6.45*	0.20	2.22*	0.08	19.8	0.41	52.2*	2.19	2.36	0.07	37*	1.13
2	Outcrosses	9	0	5.23	–	1.86	–	30.6	–	64.8	–	2.47	–	50	–
	Selfs	1	0.50	4.64	–	1.60	–	29.0	–	53.5	–	2.52	–	44	–
	Selfs (S2)	5	0.75	4.45	–	1.76	–	29.2	–	57.9	–	2.24	–	39	–
3	Outcrosses	11	0	3.89	–	1.31	–	30.0	–	39.9	–	3.03	–	24	–
	Sibs, ½-sibs	18	0.22	3.92	–	1.28	–	29.4	–	38.4	–	3.08	–	23	–
	Selfs	6	0.50	3.74	–	1.25	–	28.5	–	35.4	–	3.02	–	20	–

Abbreviations: Fx: inbreeding coefficient; Leaf production: number of new leaves produced per year; VDM: vegetative dry matter production; LAR: leaf area ratio.

*Significantly below outcrosses or smallest Fx class.

oil/mesocarp in the selfs. Vegetative measurements (with the exception of leaf area ratio) were depressed in the selfs, but less affected in the sib-crosses.

In Table 4, the results for each of the four parental families in Trial 3 are considered separately. In most cases, yield and vegetative growth of selfs were reduced relative to sib-crosses, but the performance of outcrosses varied between parental families, depending on the relative merit of the family. Thus for crosses derived from Bg143, which is inherently high yielding, and also vegetatively vigorous (Table 1; also Rosenquist et al., 1990), mean yield and vegetative parameters were higher in the sib-crosses than in outcrosses. Yield

was reduced more by outcrossing to palms from other, inferior families than by sib-crossing. Conversely, for Bg30 and Bg271, which did not give particularly high yields, outcrosses were superior to sib-crosses. For Bg142, which had exceptionally high oil/bunch, outcrossing caused a noticeable reduction in that parameter. In the other families, there may be a slight depression of oil/bunch in selfings.

Discussion

Results of all three trials, summarised in Table 5, show that yield of fruit is severely depressed by inbreeding.

Table 4. Effect of inbreeding on yield and growth in families with four different ancestries, in Trial 3

Origin	Parent palms in Trial 3	No. of crosses	Fx	Yield, kg/palm.yr		Yield components		Bunch components			Growth parameters			Height incr.				
				Fruit	Oil	Bunch number	Bunch wt, kg	Oil/ bunch	F/B	M/F	O/M	K/B	Leaf area		Leaf wt, kg	Leaf prodn	VDM	LAR
Bg143	A86/21	3	0	44.0	11.8	10.3	4.2	26.9	62.3	79.6	54.3	4.1	3.69	1.24	29.7	36.9	3.00	18
		4	0.125	51.4	13.9	10.2	5.4	26.9	63.1	76.8	55.5	4.8	4.28	1.36	32.0	44.8	3.18	20
		1	0.50	46.1	11.9	9.2	5.3	25.8	62.5	77.7	53.1	4.5	4.22	1.48	27.0	39.4	2.89	15
Bg30	D47/33, D05/17	6	0	44.0	12.5	9.5	4.8	28.3	63.5	82.6	54.0	3.1	3.85	1.27	30.3	38.7	3.08	24
		8	0.25	38.3	10.8	8.9	4.4	28.4	63.8	83.4	53.3	2.9	3.82	1.24	28.4	35.1	3.13	23
		2	0.50	41.8	11.2	9.4	4.6	26.6	63.0	82.0	51.6	3.2	3.80	1.22	28.0	33.8	3.16	20
Bg142	B78/19, B61/02	3	0	41.7	11.5	9.6	4.5	27.7	63.3	80.9	55.0	3.7	3.60	1.18	31.3	33.5	3.08	19
		3	0.25	44.7	13.4	10.5	4.4	30.2	64.8	82.4	56.6	4.2	3.96	1.32	29.7	41.3	2.95	26
		2	0.50	36.7	11.4	9.4	3.9	31.3	64.5	85.3	56.8	3.4	3.65	1.19	29.5	35.6	3.07	22
Bg271	E37/08	3	0	52.9	15.0	12.5	4.4	28.5	64.1	82.7	53.7	3.2	4.15	1.37	29.3	40.5	3.12	27
		3	0.25	41.8	11.9	10.5	4.1	28.6	63.8	83.0	54.0	3.2	3.61	1.24	28.7	35.9	2.93	23
		1	0.50	33.4	8.0	11.3	2.9	24.0	57.4	81.4	51.4	3.1	3.34	1.19	29.0	34.3	2.80	18
Mean, all outcrosses		11	0	46.2	13.0	10.4	4.7	28.2	63.3	81.6	54.4	3.5	3.89	1.31	30.0	39.9	3.03	24

Abbreviations: Fx: inbreeding coefficient; F/B: fruit/bunch; M/F: mesocarp/fruit; O/M: oil/mesocarp; K/B: kernel/bunch; Leaf prodn: number of new leaves produced per year; VDM: vegetative dry matter production; LAR: leaf area ratio.

Table 5. Effects of different levels of inbreeding in the three trials, expressed as percentage change relative to outcrosses¹

Parameter	Yield of fruit			Bunch No.			Bunch Wt			Oil/bunch			Fruit/bunch			Mesoc./fruit			Oil/mesocarp		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Sib-crosses	-10	-	-7	-21	-	-7	+11	-	-2	+2	-	+1	+3	-	+1	-3	-	0	+2	-	0
S1 selfs	-24	-	-15	-	-7	-14	-	-13	+3	+3	-	-2	-4	-	-1	-6	-	0	-5	-	-2
S2 selfs	-40	-41	-	-23	-24	-	-23	-23	-	-1	-2	-	+1	+1	-	-5	+2	-	0	-5	-
Parameter	Leaf area			Leaf weight			Leaf prodn			VDM			LAR			Height incr.			Fruit No./bunch		
Trial	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Sib-crosses	-6	-	+1	-3	-	-2	+3	-	-2	+1	-	-4	-2	-	+2	-9	-	-4	+20		
S1 selfs	-14	-	-4	-10	-	-5	+5	-	-5	-4	-	-11	-4	-	0	-15	-	-17	-6		
S2 selfs	-15	-15	-	-12	-5	-	+3	-5	-	-10	-10	-	0	-9	-	-20	-22	-	-15		

Abbreviations: Leaf prodn: number of new leaves produced per year; VDM: vegetative dry matter production; LAR: leaf area ratio.

¹For trial 1, the average inbreeding coefficient for outcrosses was Fx = 0.06, for 'sib-crosses' Fx = 0.17, and for 'selfs' Fx = 0.40.

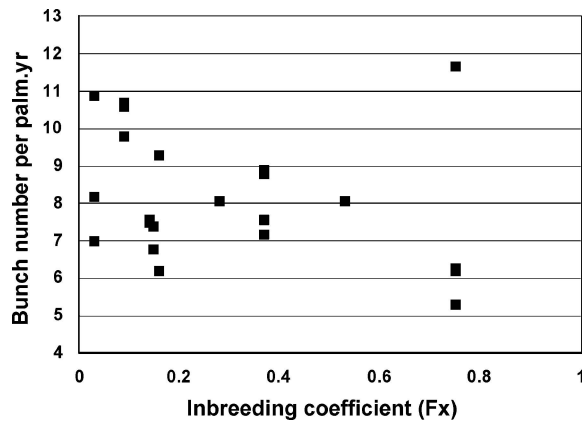


Figure 2. Relationship between bunch number per palm and inbreeding coefficient, Trial 1.

This is typical of normally cross-pollinated species (Falconer, 1981), and is in agreement with the results of Hardon (1970) for oil palm. With $F_x = 0.4-0.5$, Hardon found an average depression of yield of about 30% both in Deli *duras* and in Yangambi *teneras* (the F2 crosses in Figure 1). In our trials, the effect was rather less, at 15 - 24%, but was over 40% in S2 selfs. In Deli *duras*, Hardon found that mean bunch weight was affected, but not the number of bunches. In Table 5 bunch weight was depressed in selfs, and more so in S2 selfs. The effect of inbreeding on bunch number did not show the same progression, but Figure 2 shows that in Trial 1, in contrast to Hardon's result, there was a clear downward trend in bunch number with increasing F_x , with the exception of one anomalous S2 self.

This depression of yield can cause problems in oil palm breeding programmes. Because of the long generation time and large scale of trials, phenotypic selection of parents is important, even in RRS programmes based mainly on progeny testing. However, if inbreeding depression results from the accumulation of homozygous recessive alleles (Falconer, 1981), then phenotypic selection will simply tend to bias towards the more heterozygous individuals, and may not result in selection progress when those individuals are subsequently outcrossed in a hybrid seed production programme. Selfing is a useful tool, but selection within selfings needs to be based on characters which are not depressed by inbreeding.

Oil to bunch ratio appears to be only moderately affected, and there are no large effects on any bunch components. This is consistent with the observation that inbreeding depression tends only to affect characters associated with fitness (Falconer, 1981). Fruit or seed

number, which is related to fitness, can be estimated from mean fruit weight, bunch weight and fruit/bunch ratio, and was negatively correlated with F_x in Trial 1 ($r = -0.49$, 20 d.f.). In contrast, the composition of the fruit has little consequence for fitness. The main function of the mesocarp in wild palms is probably to attract animals for fruit dispersal, and the mesocarp thickness and oil content are probably not critical; this may explain why these yield components were apparently little affected by inbreeding.

From our study, therefore, it appears that bunch composition could be used for selection within inbred families, at least in Congo and Cameroun material. Gascon et al. (1969) reported a decrease of 12% in oil/bunch of selfs in La Mé and Deli materials, but in practice bunch components have been used for selection in inbred Deli *dura* families (Jacquemard et al., 1981). Dumortier (2003) found good correlations between bunch characters in the selfed offspring of *duras* and the general combining abilities of the same *duras* in *dura* × *pisifera* progeny trials.

Vegetative measurements were made at different ages in the three trials: at 9 years after planting in Trial 1, and at 5 years in Trial 3. For Trial 2, the data are means of measurements made at 5, 6 and 8 years after planting. Oil palms produce successively larger leaves until about 10 years after planting, which explains why the mean values for vegetative parameters were largest for Trial 1, the oldest at time of measurement. However, the relative effects of inbreeding were quite similar in all three trials. Height was most strongly affected, and leaf area and weight are also depressed, but the rate of leaf production was not affected. Vegetative dry matter (above ground) consists of trunk and leaves, so VDM was also depressed. Leaf area ratio was not much affected, because leaf area and leaf weight were equally depressed. Breure (1986) showed that leaf area ratio was a useful selection criterion, and its relative insensitivity to inbreeding suggests that it could probably be used to select reliably within inbred families.

In Trial 1, *Fusarium* wilt incidence was positively (but not significantly) correlated with inbreeding. This may be because the most inbred families were all descended from palm 16R (see Figure 1), which is known to have given highly wilt susceptible offspring (de Franqueville & de Greef, 1988).

Rosenquist et al. (1990) suggested that palm 312/3, the parent of Bg143, appeared to be 'tolerant of inbreeding', because the supposed selfing of this palm was among the highest yielding families in Trial 1. However, the demonstration by Mayes (1995) that

Bg 143 was at least partly illegitimate probably explains why the family was higher yielding than expected for a selfing. The outlying S2 self in Figure 2 (code 79 in Table 1) may also be illegitimate, although segregation of fruit forms was in line with expectation. We have not been able to check its legitimacy with molecular markers.

Hardon & Ooi (1971) suggested that the oil palm as a species might be tolerant to low levels of inbreeding. They argued that, because the palm occurs naturally in small, sometimes isolated populations, some degree of inbreeding could be common, and deleterious recessive mutations might be rapidly eliminated rather than accumulating. Our results are somewhat equivocal on this point. In Trial 1, bunch number and yield from sib-crosses were significantly lower than from outcrosses (Table 2), and height was also significantly depressed (Table 3). However, bunch weight of sib-crosses was not depressed, and VDM and leaf weight were not affected. Results from Trial 3 were similar. An important point to note in this context is that the effect of inbreeding on sib-crosses appears to depend partly on the relative performance of the genotype. Superior genotypes might be more depressed by outcrossing to inferior genotypes than by sib-crossing (Table 4). The practical conclusion is that sib-crossing within superior families is an acceptable part of an oil palm breeding programme, and that phenotypic selection within such families may be quite reliable if based on appropriate parameters.

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