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Interrelations among vegetative, yield and bunch quality traits in short-stem oil palm progenies

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Summary

Breeders usually obtain information on a large number of traits in their breeding and selection programmes. However, since some or many of these traits could be related, it is desirable to reduce the number being handled to the barest minimum without sacrificing efficiency. Breeders often use correlations, stepwise multiple regressions and path coefficient analyses to determine the nature of relationships among such characteristics. The objective of this study was to use these statistical methods to determine traits that could be useful in predicting number of bunches (NB), fresh fruit bunch yield (FFB) and mean bunch weight (MBW) for 13 backcross progenies of oil palm (*Elaeis* sp.) grown in four replications with 12 palms per replication. Data were collected over a period of 3 or 11 years, depending on the trait. Progeny means and individual palm data, averaged across replications and years, were used for each of these analyses.

Results showed that correlations involving individual palm data were similar to the progeny mean correlations. Five to seven traits accounted for about 70–90% of the variations in the dependent variables. Traits that showed the highest correlations with the dependent variables always accounted for the largest proportion of the variation (r^2) in multiple regression models, but did not always have the highest direct effect (i.e. path coefficients) in path analysis of the dependent trait. Number of leaves per palm had the highest correlation ($r = 0.729$) with, and accounted for 53.2% of the variation in NB. Path analysis however showed that percentage fruit per bunch (% F/B) was the most important determinant of NB. It exerted the highest direct effect of 0.537. The highest correlation with FFB involved number of leaves ($r = 0.660$), which, in multiple regression models also accounted for the largest proportion (44.0%) of the variation in FFB. Path analysis showed that percentage mesocarp per fruit gave the highest direct effect ($p = -0.974$) for this trait. It was concluded that various combinations of number of leaves per palm, sex-ratio, percentage fruit per bunch and percentage mesocarp per fruit would be effective as indirect selection criteria for NB, FFB and MBW in this set of material.

Introduction

Earlier studies on the relationships among traits in oil palm (*Elaeis guineensis*) involved mostly yield and its components (Corley et al., 1971; Ooi et al., 1973; Van der Vossen, 1974; Hartley, 1977; Obisesan, 1981) and less commonly vegetative traits (Akpan et al., 1982). Relationships among traits are useful in making decisions in breeding and selection programmes, because they indicate changes that may occur in unselected traits when single-trait or index selection is practised. Such changes are called correlated responses. In the oil palm, significant negative phenotypic and genotypic correlations have been found to occur between number of bunches (NB) and mean bunch weight (MBW); while NB and MBW were positively correlated with fresh fruit bunch (FFB) (Corley et al., 1971; Ooi et al., 1973; Van der Vossen, 1974; Hartley, 1977; Obisesan, 1981). Earlier studies indicated that percentage mesocarp per fruit (%M/F) had significant negative correlations with percentage kernel per fruit (%K/F) and percentage shell per fruit (%S/F) (Van der Vossen, 1974; Obisesan, 1981). The latter was also observed to be negatively correlated with %M/F and percentage oil per mesocarp (%O/M).

In contemporary plant breeding some or many of the traits measured by the breeder could be related. It is desirable, therefore, to reduce the number of traits to the barest minimum without sacrificing efficiency. Correlations, stepwise multiple regression and path coefficient analyses could be used to determine the nature of relationships among traits. The objectives of the investigation reported here were to (i) determine the nature of trait relationships in some oil palm backcross progenies and (ii) use the above methodologies to determine traits that would be useful in predicting NB, FFB, and MBW.

Materials and methods

Thirteen backcross progenies from Field 46-12 of the Nigerian Institute for Oil Palm Research (NIFOR) were used in this study. This field was planted to seedlings from 15 crosses in four replications and 12 palms per plot, using randomized complete block design. However, only 14 of the crosses were backcross progenies and one of the 14 was a duplication entry (i.e. the cross was repeated in error at planting). Thus information on the two similar progenies were pooled to represent one cross in the analysis. The fifteenth entry was on F_1 interspecific hybrid (*Elaeis guineensis* x *Elaeis oleifera*) which was used as check for comparing the backcross progenies. This was eliminated from the analysis reported here, since the primary interest was on the backcross progenies. The progenies were the first backcross generation of F_1 interspecific hybrid (*E. guineensis* x *E. oleifera*) to *E. guineensis*. The field was planted in 1969 and covered an area of 6.3 ha with the usual spacing of 8.84 m triangular. Vegetative data collected include trunk height and crown diameter from 1969 to 1979 inclusive; the period 1969 to 1972 represented the juvenile period as palms had not come into bearing when the measurements were determined. Leaf and flowering measurements (number of leaves, number of male and female inflorescence, and sex-ratio determined as

$$\frac{\text{female inflorescence } (♀)}{\text{total inflorescence } (♀ + ♂ + ⚥)} \times 100$$

were obtained from 1974 to 1976. Stem circumference was measured in two years, 1969 and 1970. Bunch quality traits, which include %F/B, %M/F, %K/F, %S/F and %O/M, were determined between the first two years of production as recommended by Van der Vossen (1974). Yield components, including NB, FFB and MBW, were determined from 1973 to 1980. Annual trunk increase was determined on progeny basis using regression analysis, i.e.

$$y = b_0 + b_1 x_1 + e,$$

where y = predicted trunk height
b_0 = intercept
b_1 = regression coefficient due to x_i (= annual trunk increment)
x_i = year of measurement
e = error term.

Phenotypic correlations among the traits were computed using progeny means and individual palm data across replications and years. Observations for bunch quality traits was not determined on all palms in a plot; therefore for the individual palm analysis a total of only 6 palms per plot was used. Stepwise multiple regression analysis was carried out on the data, with NB, FFB or MBW as the dependent variable and the other traits the independent variables. In addition, path coefficient analysis, developed by Wright (1923) was used to determine the interrelationships among all variables in a set of data. This method aids the partitioning and interpretation of cause-and-effect relationships among a set of variables. A direct casual effect (p) of a trait on the dependent trait (y) is indicated by a single one-directional arrow in Fig. 1. Indirect casual effects are indicated by alternate paths from a trait, i, through another trait, j, to the dependent trait. Thus a single indirect effect is equal to the product of path coefficient along a given path; i.e., Indirect effect = $(r_{ij})(p_{jy})$

where r_{ij} = correlation coefficient of trait i with j; $i \neq j$

p_{jy} = direct effect (or path coefficient) of trait j on the end product, y.

Total indirect effects (I) is the sum of individual indirect effects. The effect coefficient (C) is the sum of direct and total indirect effects, while residual or non-casual correlation (E) is the coefficient of total correlation (r_{iy}) minus the effect coefficient.

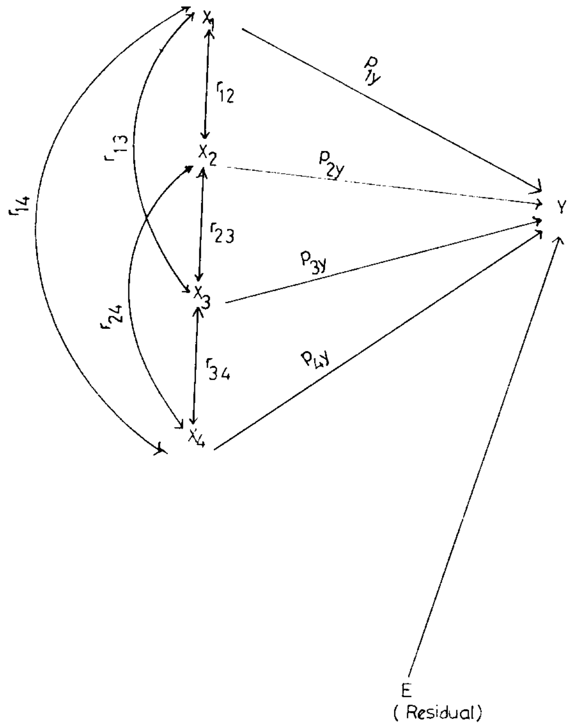

Fig. 1. Path diagram of four variables on yield (Y). One directional arrow indicates direct effects or path coefficients while double arrows indicate correlation coefficients.

Results

All possible correlation coefficients are presented in Table 1. Generally, correlations of progeny means gave similar coefficients in sign, magnitude and level of significance as those involving individual palm data. Significant associations occurred in many cases, but only those involving NB, FFB and MBW in relation to other traits will be discussed. NB was positively correlated with FFB and MBW on individual palm basis but only with FFB using progeny means. However, in both cases FFB and MBW were positively correlated. On individual palm basis, each of NB, FFB and MBW were positively correlated with stem circumference, juvenile crown diameter, trunk height and crown diameter. In addition, NB and FFB were positively associated with number of leaves and female inflorescence; both of FFB and MBW were also positively correlated with %K/F and male inflorescence. Observations based on progeny means showed NB and FFB to be positively correlated with number of leaves and number of female inflorescence; while MBW showed positive associations with %F/B, %K/F, juvenile crown diameter, adult crown diameter and sex-ratio.

Stepwise multiple regression models involving progeny means (Table 2) showed that only five to seven traits accounted for about 70–90% of the variation in the dependent traits. Number of leaves was the most important trait influencing NB and FFB; it accounted for 53.2 and 43.6% of the variation in the two traits, respectively. For NB, %F/B, trunk height, number of female inflorescence and %S/F were identified in that order, by the regression model, and these traits accounted for an additional 20% of the variation in NB. For FFB, the regression model identified %K/F as the second most important variable and this accounted for 18.3% of the variation in FFB. An additional 31.2% was explained by sex-ratio, %M/F, number of male and female inflorescence and annual trunk increase. A total of six traits accounted for 96.7% of the variation in MBW, with the most important trait being crown diameter which alone accounted for 52.5% of the variation in MBW.

Results on individual palm basis (Table 3) showed that eight of the 14 traits accounted for 44 and 42% of the variation in NB and FFB, respectively. The inclusion of the other six traits in the model increased the R^2 only by an additional 2–4%. Thus the 14 traits considered were effective in explaining only 46% of the variation in NB and FFB, respectively. The most important trait influencing MBW was crown diameter which accounted for 36.2% of its variation. The addition of other traits in the regression models for MBW increased the R^2 to 57%.

A comparison of the stepwise multiple regression models (Tables 2 and 3) revealed that for NB, three of the five traits (number of leaves, %F/B, number of female inflorescence) in the regression model for progeny means were also identified in the model involving individual palm data. For FFB, four traits were common to both models, and only two for MBW.

Path coefficient analysis was used to further investigate the cause-and-effect relationships among the progeny means for these traits. For NB, number of leaves had the highest correlation ($r = 0.729$) and accounted for the largest proportion of the variation (53.2%) but %F/B had the largest direct ($p_{2y} = 0.537$) effect (Table 4). Direct effect of number of leaves ($p_{1y} = 0.445$) and number of female inflorescence ($p_{4y} = 0.497$) were also relatively large and positive. Trunk height had negative direct effect ($p_{3y} = -0.406$) although, it had positive correlations ($r = 0.197$) with NB. Similarly, %S/F had negative correlation ($r = -0.103$) but its direct effect on NB, though fairly low, was positive. Indirect effects of %F/B via trunk height ($r_{23}\, p_{3y} = -0.259$) and %S/F ($r_{25}\, p_{5y} = -0.151$) were negative. Generally, single indirect effects were low, but the effects of number of leaves via number of female inflorescence ($r_{14}\, p_{4y} = 0.352$), trunk height via %F/B ($r_{32}\, p_{2y} = -0.343$), number of female inflorescence via number of leaves ($r_{41}\, p_{1y} = 0.316$), and %S/F via %F/B ($r_{52}\, p_{2y} = -0.348$) were moderate. Trunk height had the largest total indirect effect ($I = 0.603$) on NB while number of leaves ($C = 0.728$) and number of female inflo-

Table 1. Phenotypic Correlations of backcross progenies using individual palms and progeny mean in oil palm.

Traits	NB		FFB		MBW	
	Indiv. palm	Progeny mean	Indiv. palm	Progeny mean	Indiv. palm	Progeny mean
NB			0.834**	0.923**	0.329**	0.519
FFB					0.704**	0.770**
MBW						
%O/M						
%F/B	0.037	0.341	0.080	0.461	0.144	0.623*
%M/F	− 0.029	− 0.067	− 0.075	− 0.095	− 0.030	0.111
%K/F	− 0.062	− 0.103	− 0.075	− 0.177	− 0.145	− 0.433
%K/F	0.175	0.310	0.367**	0.515	0.489**	0.654*
Stem circumference	0.233*	0.071	0.414**	0.288	0.523**	0.519
Crown diameter⁺	0.350**	0.359	0.450**	0.463	0.518**	0.615*
Trunk height⁺	0.022	− 0.063	0.142	− 0.225	0.197	− 0.346
Trunk height	0.291**	0.197	0.434**	0.304	0.384**	0.413
Crown diameter	0.279*	0.349	0.505**	0.507	0.602**	0.725**
Number of leaves	0.393**	0.729**	0.309**	0.660*	0.056	0.265
No. of female inflorescence	0.415**	0.657*	0.287*	0.589*	− 0.069	0.230
No. of male inflorescence	0.095	0.045	0.241*	0.194	0.398**	0.543
Sex-ratio	0.157	0.471	− 0.170	0.538	− 0.065	0.576*

*, ** Significant at 0.05 and 0.01 levels of probability, respectively.

⁺ measurements taken before palms came into bearing (juvenile measurements).

rescence (C = 0.656) had the largest effect coefficients.

For FFB, %M/F exerted the largest direct effect ($p_{4y} = -0.974$) although it was negative (Table 5). Large positive direct effects were also observed for sex-ratio, number of male inflorescence and number of female inflorescence. Direct effect of annual trunk increase was moderate and negative while those for the other two traits were low. Indirect effects of sex-ratio via %M/F ($r_{34}\, p_{4y} = -0.499$), number of male inflorescence via %M/F ($r_{54}\, p_{4y} = -0.468$), number of female inflorescence via %M/F ($r_{64}\, p_{4y} = -0.416$), and trunk height via number of male inflorescence ($r_{75}\, p_{5y} = 0.557$) and via number of female inflorescence ($r_{76}\, p_{6y} = 0.408$) were moderate.

Table 2. Coefficients of determinatic (R^2) and R^2 change (DR^2) from stepwise multiple regression for each of NB, FFB and MBW on vegetative and yield traits using progeny means

Traits	R^2	DR^2
	NB	
Number of leaves	0.53*	0.53
%F/B	0.59*	0.06
Trunk height	0.65*	0.06
Number of female inflorescence	0.71*	0.06
%S/F	0.73*	0.02
	FFB	
Number of leaves	0.44*	0.44
%K/F	0.62**	0.18
Sex-ratio	0.70**	0.08
%M/F	0.75*	0.05
Number of male inflorescence	0.82*	0.07
Number of female inflorescence	0.89*	0.07
Annual trunk increase	0.93*	0.04
	MBW	
Crown diameter	0.53**	0.53
%K/F	0.64**	0.11
Sex-ratio	0.79**	0.15
%S/F	0.87**	0.08
Number of male inflorescence	0.93**	0.06
%F/B	0.97**	0.04

*, ** Significant F-test at 0.05 and 0.01 levels of probability, respectively.

Table 3. Coefficients of determination (R^2) and R^2 change from stepwise multiple regression for each of NB, FFB and MBW on vegetative and yield traits using individual palm means

Traits	R^2	DR^2
	NB	
Number of female inflorescence	0.17**	0.17
Crown diameter (juvenile)	0.25**	0.08
%O/M	0.29**	0.04
Trunk height (juvenile)	0.33**	0.04
%M/F	0.37**	0.04
Number of leaves	0.39**	0.02
%F/B	0.41**	0.02
Crown diameter	0.44**	0.33
	FFB	
Crown diameter	0.26**	0.26
%K/F	0.30**	0.04
Number of leaves	0.35**	0.05
Sex-ratio	0.37**	0.02
%O/M	0.38**	0.01
Number of female inflorescence	0.40**	0.02
Stem circumference	0.41**	0.01
Trunk height (juvenile)	0.42**	0.01
	MBW	
Crown diameter	0.36**	0.36
%K/F	0.45**	0.09
Number of female inflorescence	0.49**	0.04
Stem circumference	0.52**	0.03
Trunk height (juvenile)	0.55**	0.03

** Significant F-test at 0.01 level of probability.

Results for MBW (Table 6), showed that the highest direct effect were those for sex-ratio ($p_{3y} = 0.948$) and number of male inflorescence ($p_{5y} = 0.949$). Although crown diameter had the highest correlation (r = 0.725) with MBW, its direct effect was negligible ($p_{1y} = 0.126$). However, its indirect effect via number of male inflorescence was the highest ($r_{15}\, p_{5y} = 0.822$). %F/B had negative direct effect on MBW ($p_{6y} = -0.449$), although the two traits were positively correlated (r = 0.623). Direct effects of %K/F ($p_{2y} = 0.631$) and %S/F ($p_{4y} = 0.735$) were also high. Total indirect effects for %S/F and %F/B were greater than unity, suggesting that the error variance attacked to these traits were high.

Table 4. Direct (on diagonal) and indirect (off diagonal) effects of vegetative and yield traits on number of bunches in the oil palm

Trait i	Trait j 1	2	3	4	5	Total indirect effect (I)	Effective coefficient (C)	Total correlation (r)	Non-casual correlation (E)
1. Number of leaves	0.445	0.074	−0.126	0.352	−0.017	0.283	0.728	0.729	0.001
2. %F/B	0.061	0.537	−0.259	0.153	−0.151	−0.196	0.341	0.341	0.000
3. Trunk height	0.138	0.343	−0.406	0.270	−0.148	0.603	0.197	0.197	0.000
4. No. of female Inflor.	0.316	0.165	−0.221	0.497	−0.101	0.159	0.656	0.657	0.001
5. %S/F	−0.031	−0.348	0.259	−0.215	0.233	−0.336	−0.103	−0.103	0.000

Discussion

The possibility of elucidating the underlying relationships among yield and other traits aids the breeder in ascertaining how improvement in one trait would cause simultaneous changes in others. Traits more directly associated with the dependent trait could be easily determined. In our study, NB was positively correlated with FFB and MBW. Earlier studies have reported negative correlations between NB and MBW (Corley et al., 1971; Ooi et al., 1973; Van der Vossen, 1974; Hartley, 1977; Obisesan, 1981). According to Van der Vossen (1974), this negative correlation is due to a yield ceiling which is imposed by genetic factors plus the effects of environmental factors, particularly climatic and edaphic factors. Obisesan (1981) suggested that if the two traits respond differently to the same environmental conditions a negative correlation would occur between them. The positive correlation observed between the two traits (NB and MBW) in this study is probably a consequence of crossing genetically diverse palms. The F_1 interspecific hybrid used in this study was obtained by crossing *E. oleifera*, commonly called the South American oil palm, with *E. guineensis*, the African oil palm. *E. oleifera* is characterised by a procumbent trunk and slow stem growth, with a mature height of 1.5 to 2.7 m, while *E. guineensis* is characterised by rapid height increment and the trunk reaches a height of 15 to 18 m. *E. oleifera* is generally lower yielding than *E. guineensis* and results summarized by Mennier & Hardon (1976) showed NB to be comparable in both species but MBW is

Table 5. Direct (or diagonal) and indirect (off diagonal) effects of vegetative traits and yield traits on fresh fruit bunch yield in the oil palm

Trait i	Trait j 1	2	3	4	5	6	7	Total indir. effect I	Effective Coeff. C	Total Correlation r	Non-casual Corr. E
1. Number of leaves	0.111	−0.012	0.332	0.015	−0.122	0.477	−0.140	0.549	0.660	0.660	0
2. %K/F	0.015	−0.087	0.016	0.183	0.455	0.013	−0.081	0.601	0.514	0.515	0.001
3. Sex-ratio	0.051	−0.002	0.726	−0.499	0.044	0.388	−0.169	−0.187	0.539	0.538	−0.001
4. %M/F	−0.002	0.016	0.372	−0.974	0.421	0.287	−0.215	0.880	−0.094	−0.095	−0.001
5. No. of male inflorescence	−0.015	−0.045	0.036	−0.468	0.877	0.060	−0.252	−0.684	0.193	0.194	0.001
6. No. of female inflorescence	0.079	−0.002	0.418	−0.416	0.078	0.673	−0.241	−0.083	0.590	0.589	−0.001
7. Annual trunk increase	0.039	−0.018	0.309	−0.527	0.557	0.408	−0.397	0.769	0.372	0.371	−0.001

Table 6. Direct (on diagonal) and indirect (off diagonal) effects of vegetative and yield traits on mean bunch weight in the oil palm

Trait i	Trait j 1	2	3	4	5	6	Total indir. effect I	Effective Coeff. C	Total Correlation r	Non-casual Correlation E
1. Crown diameter	0.126	0.320	0.382	− 0.541	0.822	− 0.384	0.598	0.724	0.725	0.001
2. %K/F	0.063	0.631	0.021	− 0.241	0.493	− 0.313	0.023	0.654	0.654	0.000
3. Sex-ratio	0.051	0.014	0.948	− 0.370	0.047	− 0.114	− 0.371	0.577	0.576	− 0.001
4. %S/F	− 0.093	− 0.207	− 0.477	0.735	− 0.683	0.291	− 1.169	− 0.434	− 0.433	0.001
5. No. of male inflorescence	0.109	0.327	0.047	− 0.529	0.949	− 0.360	− 0.405	0.544	0.543	− 0.001
6. %F/B	0.108	0.400	0.240	− 0.476	0.761	− 0.449	1.073	0.624	0.623	− 0.001

lower in *E. oleifera* and consequently FFB than in *E. guineensis*. The two species are sufficiently diverse for changes to occur in the association of traits among their progeny. This positive correlation further suggest that dry matter production is not limited thereby adequately fulfilling the need of the vegetative and reproductive traits in the plant.

Traits that had the highest correlation with the dependent traits were always identified as the most important in influencing the dependent trait in the stepwise multiple regression model. Correlation is a bi-variate relationship pairing two traits at a time without giving any consideration to other variables in the model. Thus, the true picture of relationship among a set of data is rarely accurately determined by means of correlation analysis alone. Multicollinearity and spurious correlations which are limitations in correlation analysis, are, to a large extent, still present in regression analysis (Fakorede, 1979; Fakorede & Opeke, 1985). Path coefficient analysis is useful in reducing the effect of both spurious correlations and multicollinearity.

Using this technique, it became clear that %F/B exerted the largest influence on NB, although number of leaves would have been identified as the most important, if only correlation and regression analyses were done. It seems therefore that palms having the potential to produce more fruits (i.e. high fruit set which is main contributor to %F/B) exhibited this by producing more bunches. Thus there is likely to be a ceiling in the number of fruits a bunch can subtend. Sex-ratio and number of male inflorescence were common factors that led to increases in both FFB and MBW. Thus increased sex-ratio, a measure of increase in the number of female inflorescence relative to total inflorescence, may increase FFB through a higher production of bunches. Higher production of male inflorescence suggests more pollen is produced and this increases fruit set as pollen is dispersed more effectively under the crop canopy. Hardon & Corley (1976) observed that assisted pollination by hand using a blower or duster) or increase in pollen production is beneficial to bunch yield as it increases fruit set and bunch weight. This shows the need for a substantial number of male inflorescence in order to improve fruit set and hence bunch weight. The use of correlations would have identified K/F, F/B and crown diameter as factors favouring increased MBW; however it became clear from path analysis that the number of male inflorescence is an important factor in the determination of MBW.

Furthermore, %K/F was also a major determinant of MBW. The negative direct effect of %F/B on MBW suggests that it is not the number of fruits per bunch *per se* that determines MBW but the weight of these fruits which is, in turn, influenced by kernel weight. Bunch weight depends, to a large extent, on weight of stalk, weight and number of spikelets, percentage fruit set and mean weight of fruits (Corley & Gray, 1976). Thus it is likely that %F/B is less important than the other traits in determination of MBW.

From this study, it seems that various combinations of number of leaves, number of male and female inflorescence, sex-ratio and %F/B would be effective as indirect selection criteria for NB, FFB and MBW.

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