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Prediction of oil palm (*Elaeis guineensis*, Jacq.) agronomic performances using the best linear unbiased predictor (BLUP)

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Abstract Reciprocal recurrent selection (RRS) has been adopted for oil palm breeding in Indonesia. Due to a long selection cycle and the large area required, a satisfactory oil palm progeny trial is difficult to conduct. Knowledge of the parental genetic parameters is very important in achieving the expected genetic progress, but the evaluation of these parameters is constrained by highly unbalanced data sets. In this study, the unbalanced agronomic data sets and the pedigree information of an oil palm breeding programme in Indonesia were analysed by using the restricted maximum likelihood (REML) and the best linear unbiased predictor (BLUP) methods. The characters analysed were bunch and oil yields of the adult period (from 7 to 9 years after planting). The coefficients of parentage varied from 0.125 to 0.891 and from zero to 0.750 between parents in the Deli and African groups, respectively. The average coefficients of inbreeding were 0.269 and 0.166 for the parents within the Deli and African groups, respectively. The additive variances of the bunch number, industrial oil-extraction rate and oil yield characters were higher in the parents of the Deli group than those in the African ones. The coefficients of correlation between the predicted and observed hybrids performances varied from 0.55 to 0.64 for oil yield, 0.49 to 0.71 for bunch number, 0.47 to 0.58 for bunch production, 0.48 to 0.64 for industrial oil-extraction rate and 0.42 to 0.56 for plant-height increment. For selection on the basis of oil yield character, BLUPs ability to predict single-cross performance should be sufficient, and will result in a significant contribution to the oil palm seed and clone productions.

Keywords *Elaeis guineensis* · RRS · BLUP · Prediction · Unbalanced data

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Introduction

Reciprocal recurrent selection (RRS) has been adopted for oil palm breeding in Indonesia. In RRS, the parental values are evaluated through their progenies, generally tested during at least 9 years of field observation. The parents whose progenies perform better are considered to have good genetic values. Therefore, these parents can be used in the next selection cycle and/or for seed production through their descendants (Comstock et al. 1949). In oil palm breeding, the source materials were grouped using two parameters: (1) the complementarity of production components, and (2) the degree of relationship between the origins in each group. Palms with a low number of big bunches (Deli, Angola) are in one group, palms with a high number of small bunches (La Me, Yangambi, Yocoboue, Nigeria and Cameroon) in another (Meunier and Gascon 1972).

Due to a long selection cycle (10–12 years), undertaking oil palm progeny trials is difficult, and these trials require a large area. As an example, even though Indonesian oil palm breeding started in the early 20th century, a properly organized programme was established only in the early 1970s (Lubis 1985). Corresponding results have been used to estimate the general combining abilities (GCA) of the populations (Lubis et al. 1989; Purba et al. 1993). The parental evaluations were constrained by highly unbalanced data sets due to improperly designed trials. Among the causes were: (1) the large variations in the number of partners (from 1 to 13) crossed with each parent, (2) the number of tested parents was not the same from one population to another (from 3 to 79), and (3) check crosses were not made. Meanwhile, the performances of the parents *per se* and their relative rank in the progeny tests are very important in achieving the expected genetic progress (White and Hodge 1988). Thus, to perform selection it will be interesting to use genetic values and combinations of the parent candidates, as well as the values of parental relationships.

Recently, unbalanced data sets from an apple tree breeding programme have been satisfactorily analysed. The restricted maximum-likelihood method for (co)variance component estimations (REML VCE) was found to be better than other methods in estimating genetic parameters by using pedigree information (Durel et al. 1998). Another method, the best linear unbiased predictor (BLUP), has been widely used in livestock breeding (Henderson 1975). Both BLUP and the best linear predictor (BLP) were suited to forest tree breeding (White and Hodge 1988). In maize, the BLUP method was also effective in predicting single-cross performance by using agronomic data and information on relationships obtained from the pedigree, as well as the molecular, data (Bernardo 1994, 1995, 1996). Furthermore, this approach is as efficient as factorial regression models (Charcosset et al. 1998). Even if the BLUP has not been widely used in tree or crop breeding, its ability to handle the messy unbalanced data will be a great advantage. Thus, this method is believed to be widely used in predicting genetic values (White and Hodge 1989).

In the present paper, the unbalanced agronomic data sets and the pedigree information of an oil palm trial in Indonesia were analysed by using the REML and the predictor of BLUP. Our objectives were to: (1) estimate the parental genetic parameters through progeny tests, and (2) predict the performances of oil palm crosses.

Materials and methods

Data sets

Between 1974 and 1980, 401 hybrids were planted in 26 progeny trials in the Bah Jambi and Tinjowan plantations (North Sumatra, Indonesia). These hybrids were obtained by crossing 154 Deli parents with 135 parents from various African sources (79, 39, 14 and 3 parents were from the populations of Zaire, Cameroon, Côte d'Ivoire and Nigeria, respectively). As a whole, they constituted the first-cycle breeding programme of the Marihat Research Station (now the Indonesian Oil Palm Research Institute/IOPRI). All but two trials, were conducted on a flat area with homogeneous soil conditions. In most cases, the randomized complete block design was applied with 5 or 6 replications, each elementary plot containing 12 to 16 palms.

The pedigree information of all parents was obtained from Lubis (1985), Rosenquist (1986) and archives (file of International Experiments) documented at the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD). The PROC INBREED of SAS software (SAS Institute Inc. 1996a) was used to calculate the coefficient of parentage between the parents. In this calculation procedure, the initial covariance among the parents from the first generation of the Deli selection was set at 0.25.

Table 1 Oil palm characters analysed from observations at the adult period (7–9 years after planting)

Character	Abbreviation	Unit
Oil yield	OYD	Ton/ha/year
Bunch number	BNO	–
Average bunch weight	ABW	Kg
Fresh fruit bunches	FFB	Kg/palm/year
Industrial extraction rate	IER	%
Height increment	HIT	Cm/year

The characters analysed were bunch and oil yields for the period of 7–9 years after planting, the oil extraction rate, and the height increment measured 6 and 8 years after planting (Table 1). They are considered as the best predictors for the whole economic cycle of the oil palm (Lubis et al 1991). The fresh fruit bunches (FFB) were calculated by multiplying the bunch number (BNO) by the average bunch weight (ABW), measured per tree, on all the palms in the trials. The industrial oil extraction rate (IER) was calculated by multiplying the factory correction factor (0.855) by the percentage of fruits to bunch (F/B), the percentage of mesocarp to fruit (M/F) and the percentage of oil to mesocarp (O/M). The oil yield (OYD) was the fresh fruit bunches (FFB) corrected for 95% standing palms and multiplied by the oil extraction rate (IER) according to Nouy et al. (1989). All the data used in this study were the average performances of a hybrid in each trial.

Genetic model

Let us assume that A and A′are two parents belonging to group A (the Deli group in the RRS scheme), and B and B′ are parents from group B (the African group in the RRS scheme). Suppose that there is no epistasis and that all populations in both groups are in Hardy-Weinberg equilibrium, then the genetic model of Stuber and Cockerham (1966) can be expressed as:

$$Cov(AB,A'B') = f_{AA'}V_{A(A)} + f_{BB'}V_{A(B)} + f_{AA'}f_{BB'}V_{D(AB)} \quad (1)$$

where,

AB and A′B′ are the mean values of the A × B and A′ × B′ crosses, respectively,

$f_{AA'}$ and $f_{BB'}$ are the coefficients of parentage between A and A′ and B and B′, respectively,

$V_{A(A)}$ and $V_{A(B)}$ are the additive variances of alleles of A and B, and $V_{D(AB)}$ is the dominance variance between parents of A and B.

Statistical Model

In order to estimate the variances in equation (1), the following mixed linear model has been applied to the *n* experimental observations resulting from *p* crosses derived from p_A parents of A and p_B parents of B which have been tested in *t* progeny tests:

$$y_{AB} = X\beta + Z_1a_{(A)} + Z_2a_{(B)} + Zd + e \quad (2)$$

where,

$y_{AB} = n \times 1$ vector of the observed characters,

$\beta = t$ x 1 vector of the trial effects (fixed effect),

$a_{(A)} = p_A \times 1$ vector of the additive genetic effects of the parents from A (random effect), with Var $[a_{(A)}] = V_{A(A)} \times A_1$ (see below),

$a_{(B)} = p_B$ x 1 vector of the additive genetic effects of the parents from B (random effect), with Var $[a_{(B)}] = V_{A(B)} \times A_2$ (see below),

$d = p \times 1$ vector of the dominance genetic effects (random effect), with Var $(d) = V_D \times D$ (see below),

$e = n \times 1$ vector of the residual effects with Var $(e) = V_R \times I_n$,

$X(n \times t)$, $Z_1(n \times p_A)$, $Z_2(n \times p_B)$ and $Z\ (n \times p)$ are the incidence matrices that connect the above effects with *y*,

$A_1\ (p_A \times p_A)$ and $A_2\ (p_B \times p_B)$ are the matrices of the coefficient of parentage between the parents in both groups, and

D is the $p \times p$ matrix whose term at the crossing between the row corresponding to the A × B cross and the column corresponding to the A′ × B′ cross is equal to $f_{AA'} \times f_{BB'}$.

It can be shown that with this model the covariance between two observed values y_{ABi} (A × B cross in the trial i) and $y_{A'B'j}$ (A′ × B′ cross in the trial j) respects the equation [1] and is equal to $f_{AA'}V_{A(A)} + f_{BB'}V_{A(B)} + f_{AA'}\,f_{BB'}V_D$. The fixed effect β was estimated and all of the random effects were predicted by the mixed-model equation of Henderson (1985). The genetic and non-genetic variances were estimated by using the REML method explained by Bernardo (1994, 1995, 1996). The calculation was done using the PROC MIXED procedure of SAS software (SAS Institute Inc. 1996b).

Hybrid-performance prediction

The phenotypic value of a hybrid was computed as the average of its observed value corrected for the trial effect. If Z is the (n × p) design-incidence matrix that relates each observed value to its cross, then the vector y_P of the phenotypic value is $(Z'Z)^{-1}\,Z'\,(y_{AB} - X_\beta)$. Any random vector y_M of untested (missing) hybrid performances correlated with y_P can then be estimated by:

$$y_M = Cov\,(y_M, y_P)\;V\,(y_P)^{-1}\,(y_P),$$

which is its best linear unbiased predictor. The elements of $Cov\,(y_M, y_P)$ and $V\,(y_P)$ were estimated with equation (1) where $V_{A(A)}$ and $V_{A(B)}$ were replaced by their estimations. The variance due to the environmental effect e, i.e. the quantity V_R/number of observations of the ith hybrid, was added to the ith diagonal element of $V\,(y_P)$.

Test precision

To assess the precision of BLUP estimations, the observed performances of some tested hybrids were compared with their estimations when using the other hybrids as predictors. A total of p = 60, 90, 120, 150, 180 and 240 hybrids were used as predictors. For a given number of predictor hybrids, 100 samples of p hybrids were chosen at random and, for each sample, the performances of the (401 – p) missing hybrids were predicted and the correlation between the predicted and observed values was computed.

Results and discussion

Coefficient of parentage, coefficient of inbreeding

The coefficients of parentage between parents in the Deli group (A) varied from 0.125 to 0.891 and were higher than those in the African group (B), which varied from zero to 0.750 (Table 2). The average coefficients of parentage were 0.178 and 0.055 for the parents within the Deli and African groups, respectively.

A high relationship within the A group reflected the assumption that all the parents of this group derived from four ancestral Deli palms, introduced to Indonesia in 1848. Those palms are supposed to have originated from the same mother palm even though some reports showed different histories (cited by Hartley 1988). In contrast, within the Zaire population of the B group, only the progenies of SP 540 T and the Yangambi parents are related through their ‘‘Djongo’’ common parent, planted at the Eala Botanical Garden, Zaire. The other sub-populations from Zaire (Bangun and Bah Jambi/Dolok Sinumbah) are supposed to have no relationship with the first, even though they also originated from Zaire. Within the Côte d’Ivoire population, the La Mé parents are supposed to be half-sibs, although no data could ascertain that they originated from the same parents. Other populations, Nifor and Cameroon, are unrelated to each other as well as to the rest. An AFLP marker study has also shown that the Bah Jambi/Dolok Sinumbah sub-population and the Cameroon population could be distinguished from the others of Zaire or from those of the Côte d’Ivoire populations (Purba et al. 2000).

Table 2 Coefficient of parentage of the Deli and African parents used in the oil palm breeding programme at IOPRI

Item	Parents	
	Deli (n = 154)	African (n = 135)
Minimum	0.125	0.000
Average	0.178	0.055
Maximum	0.891	0.750

Table 3 Coefficient of inbreeding of the Deli and African parents used in the oil palm breeding programme at IOPRI

Item	Parents	
	Deli (n = 154)	African (n = 135)
Minimum	0.125	0.000
Average	0.269	0.166
Maximum	0.781	0.500

The coefficient of inbreeding of a parent X was calculated as $(2 \text{ x } f_{XX}) - 1$, where f_{XX} is the coefficient of parentage of the parent X with itself. The average coefficients of inbreeding were respectively 0.269 and 0.166 for the parents within the Deli and African groups (Table 3).

Previous estimation showed a slightly higher coefficient for the Deli materials. Rosenquist (1986) estimated the average coefficients of inbreeding as 0.29 from a pathway analysis of one progeny of Deli. This difference depends upon the coefficient of parentage assumed for the ancestral Deli palms. The coefficient obtained by Rosenquist (1986) was based on the coefficient of parentage of ancestral palms, ranging from 0.219 to 0.381, as proposed by Hardon (1970).

Means and variances

The mean and variance components of each trait are presented in Table 4. The mean oil yield was 5.75 ton/ha peryear, whereas the means bunch number, average bunch weight, fresh fruit bunches, industrial extraction rate and height increment were 10.28, 18.79 kg, 187.93 kg/palm per year, 22.66% and 73.19 cm/year, respectively. For characters such as bunch number, industrial oil extraction and oil yield, the additive variances contributed by the parents of the Deli population were higher than those of the African ones (Table 4). Meanwhile the dominance variance for all the characters observed is not significantly different from zero. Their proportions, V_D/V_G, where V_G is equal to $[V_{A(A)}+V_{A(B)}+V_D]$, were less than

Table 4 Means and variances for all oil palm hybrids tested

Characters[a]	Means	Variances[b]			
		$V_{A(A)}$	$V_{A(B)}$	V_D	V_R
OYD	5.75	0.30	0.25	0.00^{ns}	0.21
BNO	10.28	3.49	2.50	0.24^{ns}	0.52
ABW	18.79	6.34	8.28	0.79^{ns}	0.80
FFB	187.93	170.96	212.78	8.54^{ns}	149.99
IER	22.66	1.44	1.40	0.21^{ns}	0.68
HIT	73.19	49.58	53.55	Zero*	35.22

[a] BNO = bunch number; FFB = fresh fruit bunches; IER = oil industrial extraction rate ; OYD = oil yield; HIT = height increment;
[b] $V_{A(A)}$ = additive variance of parents of the A group; $V_{A(B)}$ = additive variance of parents of the B group; V_D = dominance variance; V_R = residual variance
ns = not significant at $\alpha = 0.05$; * = negative value is taken as zero

Table 5 Correlation coefficients between predicted and observed performances in oil palm

Character	Number of predictor hybrids (p)[a]						
	60	90	120	150	180	210	240
OYD	0.55	0.58	0.60	0.61	0.62	0.63	0.64
BNO	0.49	0.55	0.60	0.64	0.66	0.69	0.71
ABW	0.37	0.45	0.53	0.58	0.63	0.67	0.70
FFB	0.47	0.51	0.53	0.55	0.56	0.57	0.58
IER	0.48	0.53	0.57	0.58	0.60	0.62	0.64
HIT	0.42	0.45	0.48	0.51	0.52	0.54	0.56

[a] Degrees of freedom for each value of $p = 401 - p - 1$

10%, indicating that dominance is unimportant in the tested materials.

Despite the fact that the Deli parents originated from a restricted genetic base, their genetic variability is similar to that in the African group. Such a difference in additive variance may be related to the breeding stage of the parents from both groups. The Deli parents have been selected from several selection programmes conducted separately by different research centres or private companies (Lubis 1985). This makes for gene dispersion among different individuals. The high divergence of the selected individuals, chosen as the parents of tested hybrids, could enhance the genetic variability which is expressed in the higher additive variances contributed by the parents of the Deli group.

Almost all of the parents of the Côte d'Ivoire, Nigeria and Zaire populations were elite materials from the Institut de Recherche pour les Huiles et Oléagineux (IRHO, now CIRAD) or from AVROS (now IOPRI). These materials, in fact, derived from a very limited number of ancestral palms. As an example, the La Mé sub-population originated from only two parents: Brt 10 and Teis 3. Likewise, Yangambi and SP 540 T and its descendant sub-populations originated from an out-cross harvested from a single palm, ‘‘Djongo’’. This limited number of ancestral parents could explain the low genetic variation in the African group.

Correlation between predicted and observed performances

The coefficients of correlation between the predicted and observed hybrid performances are reported in Table 5. These correlations varied from 0.55 to 0.64 for oil yield, 0.49 to 0.71 for bunch number, 0.37 to 0.70 for average bunch weight, 0.47 to 0.58 for bunch production, 0.48 to 0.64 for industrial oil-extraction rate, and 0.42 to 0.56 for height increment. The t test showed that all these coefficients were significantly different from zero. The coefficients increased with the number of hybrids used as a predictor (Table 5). This indicates that the precision increased with the number of hybrids tested. Nevertheless, the present study showed that for oil yield, bunch number, average bunch weight and industrial oil-extraction rate, 120 to 180 hybrids are needed to achieve a high (0.60) correlation coefficient. For fresh fruit bunches and height increment, having a large number of predictor hybrids may be necessary to achieve a sufficiently high correlation.

Use of BLUP in oil palm breeding

The sufficiently high correlation between predicted and observed hybrid performances, for most of the important traits, was obtained with highly unbalanced data sets. The BLUP coefficient should be sufficient for selection on the basis of the oil yield character, which is the main objective in most oil palm breeding programmes. Bernardo (1992) showed theoretically that with a coefficient of 0.60, the probability for the best single-cross to be included in the 20% selected hybrids is higher than 80%. Thus, breeders could expect to have a best hybrid after the re-test of their 20% selected hybrids.

One follow up the RRS scheme of oil palm improvement is to test the best hybrids that have been predicted to give a good performance. The BLUP analysis, in fact, yielded a prediction of the performances of all possible parent combinations (a total of 20665 combinations from 153 and 135 Deli and African parents, respectively). Reducing the model by supposing neglected dominant and epistasis effects, the predicted performance of a hybrid is simply the sum of the additive values of its parents. Thus, the parents for the next cycle could be chosen based on the basis of their additive genetic values. The standard errors of prediction of these additive values, $\hat{\gamma}_i$, which are the square root of $V(\hat{\gamma}_i - \gamma_i)$, can be estimated by considering that $\hat{\gamma}_i$ is a solution of the mixed-model equations (SAS Institute Inc. 1996b). These errors in the Deli part were higher than those of the African and decreased as the number of parent partners increased in the progeny tests, as shown for the oil yield character (Fig. 1A and B).

From a practical point of view, BLUP's ability to predict single-cross performance will result in a significant

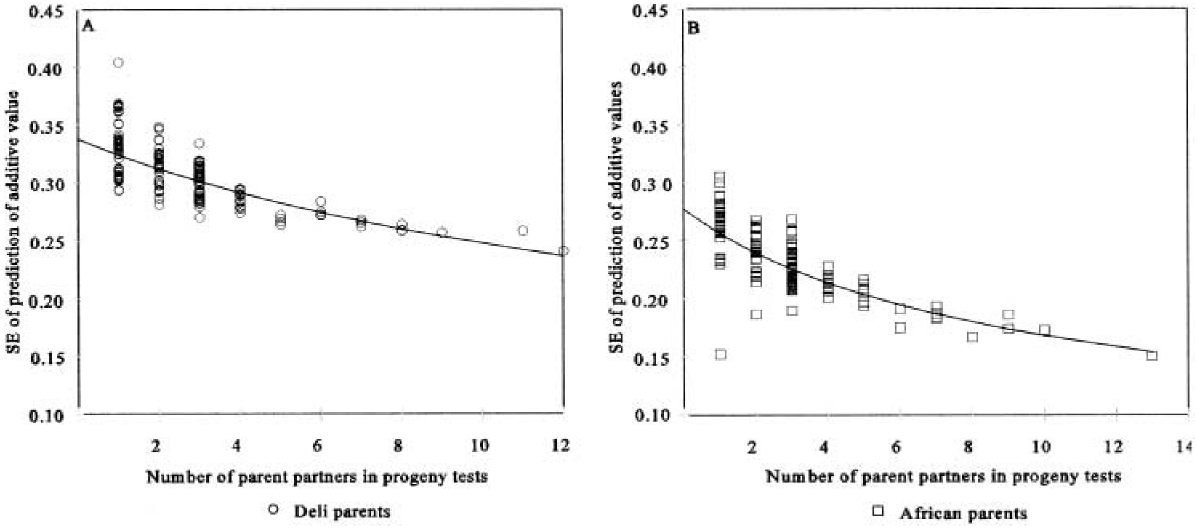

Fig. 1 Relationship between the standard error of prediction of parental additive values and the number of parent partners in the progeny tests of a parent from the Deli group (**A**) and the African group (**B**) for the oil yield of oil palm

contribution to oil palm seed production. In the RRS scheme, the commercial seeds are made by reproducing the hybrids, which have the highest performances in the progeny tests, by selfing of their parents (Jacquemard et al. 1981). The ‘‘best’’ male parent has a high sex ratio, and consequently produces few male inflorescences (Baudouin 1995). Thus, the best hybrids can not always be reproduced due to the lack of appropriate pollen. The BLUP strategy could solve this problem by proposing some male parents that are known to have a good prediction value when crossed with the female parents of those hybrids.

The BLUP strategy also contributes to the creation of oil palm clonal-planting materials. Work carried out to produce the oil palm clonal materials through an in vitro vegetative propagation process was started in the early 70 s (Duval et al. 1988). Soh (1986) proposed that cloning young seedlings of superior hybrids could lead to a 13% increase in yield if there is no somaclonal variation. Those seedlings could also be re-created from the untested single-crosses that have a high predicted yield from an analysis with BLUP.

It is clear that the BLUP method is based on several assumptions such as the equilibration of the populations and the parent representativeness within the populations studied. The parents used in the present study were formerly selected, or elite, materials and the populations were not in Hardy-Weinberg equilibrium, as shown by an isoenzymatic analysis (Purba et al. 2000). However, the coefficient of correlation between the predicted and observed performances could justify the use of a simplified model if we assume that the gamete is in equilibrium and that epistasis can be neglected (Bernardo 1994).

In conclusion, the present study has shown the effectiveness of the BLUP method in predicting hybrid performance, even when the data are unbalanced. The additive model [i.e. by removing the dominance effect from equation (2)] may be appropriate in predicting the performances of untested hybrids. The high correlation obtained between predicted and observed hybrid performances, not only for highly heritable characters such as bunch number but also for a complex character such as oil yield, confirms the usefulness of BLUP in helping to choose the hybrids to be tested in next cycle. In practice, the use of the BLUP method will eliminate the poorest potential hybrids and simplify the selection scheme.

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