Linear Mixed Model for Oil Palm Parents Selection

Abdullah Sonhaji[1*], **Udjianna S. Pasaribu**[2], **Sapto W. Indratno**[2], **Adi Pancoro**[3]

[1]Doctoral Program in Mathematics, Institut Teknologi Bandung, Bandung 40132, Indonesia
[2]Statistics Research Division, Institut Teknologi Bandung, Bandung 40132, Indonesia
[3]School of Life Sciences and Technology, Institut Teknologi Bandung, Bandung 40132, Indonesia

*Email: a.sonhaji@gmail.com

Abstract

The objective of plant breeding is to obtain superior seeds. These seeds originated from parents that can pass their superior traits to their progeny. The observed characteristics of the progeny (phenotype) determined the traits of these seeds. Therefore, we performed a progeny analysis. In this analysis, the data samples were collected from Riau in Sumatera and Kumai in Kalimantan (two locations). The main objective is to find superior parents from these two locations. The superiority of the selected parents lies not only in passing high production traits but also in adaptability (fit) to the diversity or variability of the environment or locations. This analysis calculates the General Combining Ability (GCA) values for both male and female parents using the Linear Mixed Model (LMM). The experimental design, as the source of data, was an alpha lattice design, so the LMM contains locations, replicas, blocks, male and female parents, and the progeny factors. The analyzed phenotype is Fresh Fruit Bunches of third-year production. Since the data sets of the two locations were non-intersect, the model uses the coefficient of parentage (additive relationship matrix) to link both. The results of the GCA analysis showed that selected female parents were 137, 155, 126, 147, and 159 (Dura), and 101, 113, 109, and 117 for male parents. They are among the parents with highly productive progenies. There are also new potential crossings not currently available on the plantation — for example, the crossing 137 x 101 with the additive genetic value of 35.37.

Keywords: breeding, oil palm, phenotype, general combining ability, linear mixed model

2020 MSC classification number: 60-08, 92-08

1. INTRODUCTION

The oil palm (Elaeis guineensis) is an industrial plant [24]. The cultivation and breeding of oil palm are ruled by specific laws and regulations [29]. Nowadays, oil palm become a strategic commodity. Crude Palm Oil (CPO) is a product of this plant that can be utilized as a renewable energy source [25], [15]. Soh stated that the high demand for palm oil as biofuel and in various products requires efficient production [35]. It triggers a need to increase the production. Increasing oil palm production was driven by many reasons. To improve the characteristics such as heavy bunches, oil yield, oil quality, stress tolerance or adaptability to new environments, and the need for new market niches. Despite those, there is a growing need to explore and develop new varieties with high potential yield and the genetic diversity required to maintain oil palm yield stability [17].

The oil palm has three varieties with different shell thickness characteristics: 1) Dura, 2) Pisifera, and 3) Tenera. Dura has a thick shell. Pisifera is known for having a very slim shell. The Tenera variety is a hybrid breeding between the Dura and Pisifera varieties [2], [36]. Figure 1 illustrates the three varieties of oil palm. Due to the wide range of male and female parental varieties, it would be ideal to breed all these parents to gather comprehensive information on the characteristics of the progeny [2], [36]. However, this task presents significant challenges. Therefore, the researchers employ an experimental method and design to minimize variations in breeding and planting. The Alpha Lattice Design application is widely used for oil palm planting designs [37], [7], [22], [33]. The breeding step applies the Connected Design principle. During its implementation, various obstacles may arise that cause the process and results to deviate from the ideal conditions. Given such circumstances, the challenge lies in determining or selecting the parent palm that can

---

*Corresponding author

Received May 7^{th}, 2024, Revised July 17^{th}, 2024 (first), Revised October 19^{th}, 2024 (second), Accepted for publication November 28^{th}, 2024. Copyright ©2025 Published by Indonesian Biomathematical Society, e-ISSN: 2549-2896, DOI:10.5614/cbms.2025.8.1.3

Figure 1: Cross section of the shell of the palm fruit a) Dura, b) Pisifera and c) Tenera.

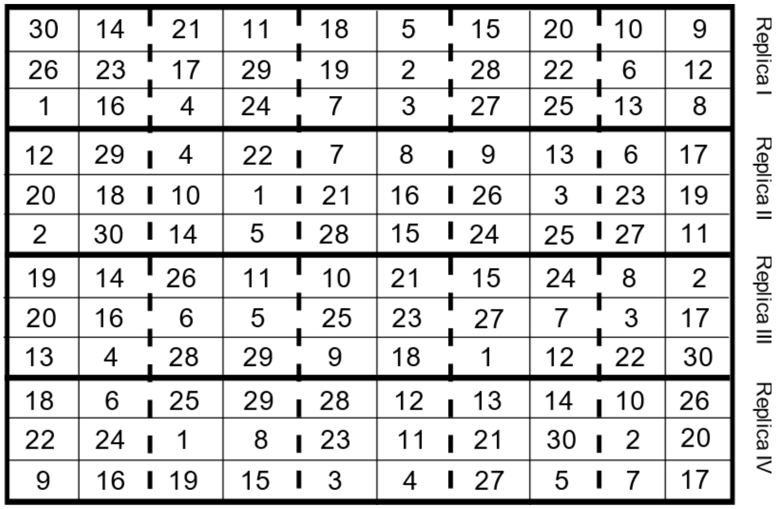
yield desirable progeny. Breeding between selected female and male parents aimed to determine parents that possess superior characteristics. The female parents are selected from various types of Dura oil palms, while the male parents are from various Pisifera and Tenera oil palms. Concisely, the aim was to determine the value of the phenotype of the progeny [2], [36] and to calculate the ability to transmit parental characteristics to their progeny in subsequent generations. This ability is referred to as General Combining Ability (GCA) and Specific Combining Ability (SCA) in breeding [19].

Quantitative genetic theory explains the process of character inheritance [20]. Quantitative character analysis began with Brownian motion [4]. This analysis was applied to wheat races and commercial cultivars [12] and soybeans [21]. It evaluated the genetic value passed on from the parents to an individual (offspring). Estimation of this genetic value can use phenotype or genomic data. Two components, GCA and SCA, are commonly assessed. GCA is the deviation of an individual's mean value from the population's mean value [18]. The higher the value of this ability, the higher the genetic traits inherited by the parent. SCA results from dominant effect and allele interaction in loci [18]. In other words, the interaction between parents (male and female) has significant value. Estimation can be done in many ways, for example, with a regression model like that done by Fernandez and Miller [10], but the model commonly used today is the Linear Mixed Model (LMM).

In a study by Oliveira et al. [27], mixed models, multivariate analysis, and traditional phenotype selection methods were compared to determine superior maize genotypes in the breeding field. The result was a selection based on the LMM, complemented by multivariate analysis with means, which increased the accuracy of determining the best genotype. In that same year, the same model was used to evaluate and predict the yield of the new wheat genotype [1], demonstrating its stability compared to traditional approaches, where percentage yield determined the genotype performance. Next, Baeza-Rodriguez et al. used a generalized LMM to compare three multiracial population models: the linear animal, the linear sire, and the logistic sire. Their study aimed to evaluate the fertility of heifers on Simmental-Simbrah cattle farms [1]. Specifically in oil palm breeding, Soh used the Best Linear Unbiased Predictor (BLUP) of the LLM in ranking oil palm parents [34]. Likewise, Purba et al. stated that this model helped determine and select the oil palm parents for nurseries [30]. In the past few years, Peixoto et al. have also used this formula for selecting oil palms [28]. Based on the description above, we examine the problems still open for research, including in the multi-site experimental design with repeated measurements. This study is devoted to oil palms where the progenies were planted in two locations. The problem is that the two sets of progenies were inherited from different parents. Hence, the subject under study is the determination of the method of selecting the parent (male and female) of oil palm with the conditions previously mentioned. This study aims to determine the method of oil palm parent selection with certain constraints, as stated in the research problem above. In this case, to link two different sets of progenies, the element of kinship can be used; that is, the closer the kinship, the more genetically similar they are. Therefore, this method will use pedigree information. The next goal is to develop a mathematical model to determine GCA and SCA. We propose the LMM that accommodates the alpha lattice design factors. By accommodating the factors, the model error will be reduced and the likelihood of LMM maximized. In addition to the two general objectives above, we also design specific objectives, namely 1) exploring the heritability of the oil palm trait, and 2) deepening the model by utilizing pedigree information. After conducting several comparative studies over the years, we observed the potential novelty that this research would bring. It is a method of determining and selecting oil palm parents, calculating combining power values, and predicting progeny and parent values in breeding techniques. The method is LMM with alpha lattice design components as linear terms, including the additive relationship matrix that forms the parent and progeny covariance matrices. This model will benefit the breeder facing the indicated conditions. The paper is organized as follows: 1. Introduction, 2. Data Preparation, 3. Research and Methodology, 4. Result and Discussion, 5. Conclusion, 6. References, and 7. Appendices.

2. DATA PREPARATION (EXPERIMENTAL DATA)

The experiment carried out by the research team followed the Reciprocal Recurrent Selection (RRS) design [8]. This method has been used for genetic improvement [32] and increased Orange-Flashed Sweet potato production [14]. A private incorporation gave access to the experimental data with Non-Disclosure Agreement (NDA) permission. It was collected from Riau in Sumatra and Kumai in Kalimantan, Indonesia (two locations). The data contained three main characteristics. The first was phenotypes. They were the fresh fruit bunch (FFB) of the first three-year productions (FFB1, FFB2, FFB3). FFB is the weight of the oil palm fruit in kg/tree/year. The second was the structure of the experimental design. It consisted of location, replica, block, and plot factors. It constructed an alpha lattice design. The last one was the progenies and their parents. The complete data structure consisted of location, replica, block, progeny, female parent, male parent, FFB1, FFB2, and FFB3 factors. The progeny sets of the two locations are different. No progeny of the same parents was planted in the two locations. The progeny's female parents are Dura. The males are Pisifera and Tenera. Sumatra has 24 Dura, 4 Pisifera, and 9 Tenera varieties. Kalimantan has 19, 2, and 7, respectively. Sumatra has 24 blocks in 4 replicas, 48 plots with 16 same progenies planted on each. Kalimantan has 20 blocks in 4 replicas, 30 plots with 16 same progenies planted on each. The parent selection used third-year production, FFB3. Figure 2 displays the alpha lattice design applied in Kumai.



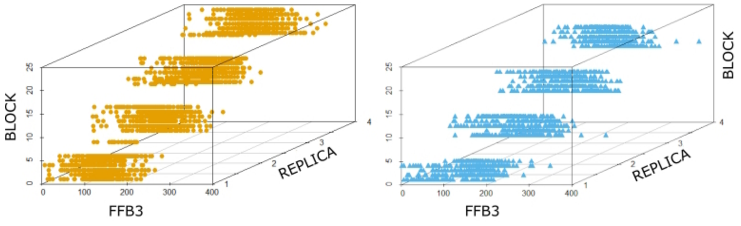
30	14	21	11	18	5	15	20	10	9	Replica I
26	23	17	29	19	2	28	22	6	12	
1	16	4	24	7	3	27	25	13	8	
12	29	4	22	7	8	9	13	6	17	Replica II
20	18	10	1	21	16	26	3	23	19	
2	30	14	5	28	15	24	25	27	11	
19	14	26	11	10	21	15	24	8	2	Replica III
20	16	6	5	25	23	27	7	3	17	
13	4	28	29	9	18	1	12	22	30	
18	6	25	29	28	12	13	14	10	26	Replica IV
22	24	1	8	23	11	21	30	2	20	
9	16	19	15	3	4	27	5	7	17	

Figure 2: Alpha lattice design of plantation in Kumai Kalimantan.

Table 1 shows the snippet of the data. The 3D view of the data of the two locations in Figure 3 illustrates the spread of the data over the replicas and blocks. The statistical description of Sumatra, Kalimantan, and the joined data are displayed in Tables 2, 3, and 4, respectively. Based on those tables, the FFB has an increasing trend. For the joined data, the mean value of the first year is 86.9, 143.6 in the second year (56.7 increase), and 158.3 in the third (14.7 increase). The size of the observation data is 4832. Since there are 36 FFB3 missing values of Sumatra and 26 of Kalimantan, the size reduces to 4770.

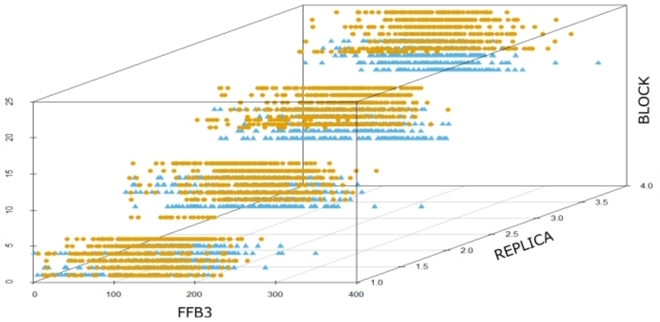
Table 1: The snippet of oil palm trial data, that is the fresh fruit bunch of third year yield.

Trials	Rep	Block	Plot	Progeny	Female	Male	FFB
Sumatera	1	4	203	160	121	110	109.4
							137.5
							143.4
							142.9
			202	168	147	107	130.3
							234.3
							78.2



a. Sumatera

b. Kalimantan



c. Sumatera and Kalimantan

Figure 3: 3D view of the data of the two locations (a) Sumatra (b) Kalimantan and (c) both joined.

Table 2: Descriptive statistics of FFB1, FFB2, FFB3 - Sumatra.

Phenotype	Min	Q1	Med	Mean	Q3	Max	NA's
FFB1	1.2	72	97.4	96.55	122	226.8	48
FFB2	1.5	111.2	141.8	140.9	172.7	292.9	30
FFB3	3.3	127.6	157.7	157.1	187.5	331.1	36

Table 3: Descriptive statistics of FFB1, FFB2, FFB3 - Kalimantan.

Phenotype	Min	Q1	Med	Mean	Q3	Max	NA's
FFB1	0.9	47.3	72.2	72.23	96.9	183.9	29
FFB2	1.2	113.1	149.5	147.8	183.6	307.6	23
FFB3	1.6	125.6	163.7	160.1	197.3	368.8	26

Table 4: Descriptive statistics of FFB1, FFB2, FFB3 - Sumatra and Kalimantan.

Phenotype	Min	Q1	Med	Mean	Q3	Max	NA's
FFB1	0.9	61.1	87.1	86.9	113.4	226.8	77
FFB2	1.2	112.0	144.5	143.6	176.6	307.6	53
FFB3	1.6	126.9	160.1	158.3	191.9	368.8	62

Figure 4 displays the histograms of FFB data and their correlations. The FFB data are from two locations and the three years of observation. Visually, in the first year, the histograms tend to skew left, and for the next two years, they are almost symmetric and normally distributed. The correlation between FFB3 and FFB2 is 0.52, and between FFB3 and FFB1 is 0.43. These correlation values are not high. These show that the production is not mature yet. The production is also still increasing. The LMM analysis will use the phenotype of FFB3.

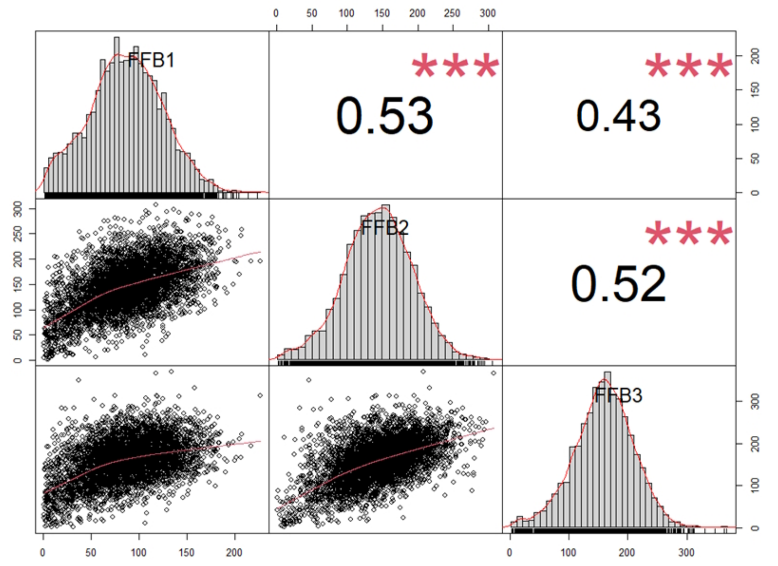


Figure 4: Histogram plots of FFB for the three years of total observation from Sumatera (top), Kalimantan (middle) and both locations (bottom).

3. RESEARCH METHODOLOGY

The Linear Mixed Model was developed by Henderson in 1975 [16] and applied in animal breeding. This model is commonly represented by the following equation.

$$\mathbf{y} = X\beta + Z\nu + \epsilon. \tag{1}$$

In Equation (1), X represents the design matrix of size $n \times p$, β is a vector of parameters for the fixed effects of size p, Z is an observed random effect design matrix with dimensions $n \times q$, ν is the random effect parameter vector with a size of q and is assumed to be normally distributed with mean 0 and covariance G, and ϵ is an unobserved error term that follows a normal distribution with $E[\epsilon] = 0$ and $Var[\epsilon] = \sigma_\epsilon^2 I$, denoted as $\epsilon \sim \mathcal{N}0, \sigma_\epsilon^2 I)$ with I is an $n \times n$ identity matrix. The elements of the matrix Z typically take values of 0 and 1.

The structure of the experimental data consists of alpha lattice design components (location, replica, block, and plot) and the genetic factors (male and female parent). Since the two locations are separated (each located on a different island), each replica and associated blocks are assumed to be samples of all possible locations. So, the replicas and blocks are considered random effects. The male, the female, the interaction between the male and female parents, and the interaction between blocks and the progeny are random effects [11]. The only fixed effect is the location.

LMM which accommodates alpha lattice design (the environment), the genetics, and their interaction factors can be represented by Equation (2).

$$\mathbf{y} = X\beta + Z_1\nu_{Loc:Rep} + Z_2\nu_{Loc:Rep:Block} + Z_3\nu_{Loc:Rep:Block:P} + Z_M\nu_M + Z_F\nu_F + Z_{F:M}\nu_{F:M} + \epsilon, \quad (2)$$

where X is the fixed effect design matrix, Z_1, Z_2, Z_3, Z_M, Z_F, and $Z_{F:M}$ are the design matrices of replicas in location, blocks in replicas in location, the interaction between blocks in replicas in location and progeny, the male, the female, and the progeny factors, respectively. The parameters β is the location fixed effect factor, $\nu_{Loc:Rep}$, $\nu_{Loc:Rep:Blok}$, $\nu_{Loc:Rep:Blok:P}$, ν_M, ν_F, and ν_P are the random effects of replicas in location, blocks in replicas in location, the interaction between blocks in replicas in location and progeny, the male, the female, and the progeny factors, respectively, and ϵ is the error random effect. Based on the data, the size of each component in Equation (2) is $y : 4770 \times 1$, $X : 4770 \times 2$, $\beta : 2 \times 1$, $Z_1 : 4770 \times 8$, $\nu_{Loc:Rep} : 8 \times 1$, $Z_2 : 4770 \times 192$, $\nu_{Loc:Rep:Block} : 192 \times 1$, $Z_3 : 4770 \times 14976$, $\nu_{Loc:Rep:Block:P} : 14976 \times 1$, $Z_M : 4470 \times 22$,$\nu_M : 22 \times 1$, $Z_F : 4770 \times 41$, $\nu_F : 41 \times 1$, $Z_{F:M} : 4770 \times 78$, $\nu_{F:M} : 78 \times 1$, $\epsilon : 4770 \times 1$. The factor of parent interaction effect will be approximated by the progeny effect because the progeny is a result of crossing the parents:

$$\nu_{F:M} \approx \nu_P.$$

Each of the random effect factors in Equation (2) is assumed to be normally distributed with mean **0**. The distribution of each of them is shown in Equation (3).

$$\nu_{Loc:Rep} \sim \mathcal{N}(\mathbf{0}, G_1), \nu_{Loc:Rep:Block} \sim \mathcal{N}(\mathbf{0}, G_2), \nu_{Loc:Rep:Block:P} \sim \mathcal{N}(\mathbf{0}, G_3),$$

$$\nu_M \sim \mathcal{N}\mathbf{0}, G_M), \nu_F \sim \mathcal{N}\mathbf{0}, G_F), \nu_P \sim \mathcal{N}\mathbf{0}, G_P).$$

The solution of the LMM equation (2) is

$$\begin{aligned} \hat{\beta} &= (X^tV^{-1}X)^{-1}X^tV^{-1}\mathbf{y}, \\ \hat{\nu} &= (Z^t\Sigma^{-1}Z + G^{-1})^{-1}Z^t\Sigma^{-1}(\mathbf{y} - X\hat{\beta}), \end{aligned} \quad (3)$$

where

$$G = \begin{bmatrix} G_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_M & 0 & 0 \\ 0 & 0 & 0 & 0 & G_F & 0 \\ 0 & 0 & 0 & 0 & 0 & G_P \end{bmatrix}, \quad Var(\mathbf{y}) = V = ZGZ^t + \Sigma,$$

and $G_1, G_2, G_3, G_M, G_F, G_P$ are the covariance matrices of the replicas in location, the blocks in replicas in location, the interaction between blocks in replicas in location and progeny, the male, the female, and the progeny factors, respectively, and Σ is the covariance of error. The solution depends on the variance of random variable $\mathbf{y}, V$.

GCA analysis was performed on data obtained from the two locations. But the progeny sets of two locations did not intersect, no progeny of the same parent was planted in either location. It violated the alpha lattice design principle where all the progenies must be planted on all replicas. This problem can be overcome by linking the two sets with pedigree information. This information is transformed into a coefficient of parentage or additive relationship matrix. The additive relationship is used as a measure of the covariance of breeding values between relatives. Nilforooshan et al. [26] showed how to calculate this type of matrix. In this analysis, the following assumption is held.

$$G_1 = \sigma_1^2 I, G_2 = \sigma_2^2 I, G_3 = \sigma_3^2 I, G_M = \sigma_M^2 A_M, G_F = \sigma_F^2 A_F, G_P = \sigma_P^2 A_P, \Sigma = \sigma_\epsilon^2 I,$$
$$\nu_{Loc:Rep} \sim \mathcal{N}(\mathbf{0}, \sigma_1^2 I), \nu_{Loc:Rep:Block} \sim \mathcal{N}(\mathbf{0}, \sigma_2^2 I), \nu_{Loc:Rep:Block:P} \sim \mathcal{N}(\mathbf{0}, \sigma_3^2 I),$$
$$\nu_M \sim \mathcal{N}(\mathbf{0}, \sigma_M^2 A_M), \nu_F \sim \mathcal{N}(\mathbf{0}, \sigma_M^2 A_F), \nu_P \sim \mathcal{N}(\mathbf{0}, \sigma_M^2 A_P),$$

where A_M, A_F, and A_P are the additive relationship matrices of the male parent, the female parent, and the progeny, respectively.

Since the model contains the genetic effects (the male and female parents), we will use the coefficient of parentage (additive relationship matrix) to link the progeny of Sumatra and Kalimantan. We will focus on block matrix

$$\begin{bmatrix} G_M & 0 & 0 \\ 0 & G_F & 0 \\ 0 & 0 & G_P \end{bmatrix}.$$

Define the additive relationship matrices

$$A_M = \begin{bmatrix} A_{M_S} & A_{M_{S:K}} \\ A_{M_{K:S}} & A_{M_K} \end{bmatrix}, \quad A_F = \begin{bmatrix} A_{F_S} & A_{F_{S:K}} \\ A_{F_{K:S}} & A_{F_K} \end{bmatrix}, \quad A_P = \begin{bmatrix} A_{P_S} & A_{P_{S:K}} \\ A_{P_{K:S}} & A_{P_K} \end{bmatrix},$$

where A_{M_S}, A_{M_K}, A_{F_S}, A_{F_K}, A_{P_S}, A_{P_K} are additive relationship matrices of the male parent of Sumatra, the male parent of Kalimantan, the female parent of Sumatra, the female parent of Kalimantan, the progeny of Sumatra, and the progeny of Kalimantan, respectively, $A_{M_{S:K}}$, $A_{F_{S:K}}$, and $A_{P_{S:K}}$ are additive relationship matrices of the male parent of Sumatra and Kalimantan, the female parent of Sumatra and Kalimantan, and the progeny of Sumatra and Kalimantan, respectively. The distribution of ν_M, ν_F, and ν_P are:

$$\nu_M \sim \mathcal{N}(\mathbf{0}, \begin{bmatrix} A_{M_S} & A_{M_{S:K}} \\ A_{M_{K:S}} & A_{M_K} \end{bmatrix}), \quad \nu_F \sim \mathcal{N}(\mathbf{0}, \begin{bmatrix} A_{F_S} & A_{F_{S:K}} \\ A_{F_{K:S}} & A_{F_K} \end{bmatrix}), \quad \nu_P \sim \mathcal{N}(\mathbf{0}, \begin{bmatrix} A_{P_S} & A_{P_{S:K}} \\ A_{P_{K:S}} & A_{P_K} \end{bmatrix}).$$

Hence, the variance of $\mathbf{y}$ is

$$V = [Z_1 Z_2 Z_3 Z_M Z_F Z_P] \begin{bmatrix} \sigma_1^2 I & 0 & 0 & 0 & 0 & 0 \\ 0 & \sigma_2^2 I & 0 & 0 & 0 & 0 \\ 0 & 0 & \sigma_3^2 I & 0 & 0 & 0 \\ 0 & 0 & 0 & \sigma_M^2 A_M & 0 & 0 \\ 0 & 0 & 0 & 0 & \sigma_F^2 A_F & 0 \\ 0 & 0 & 0 & 0 & 0 & \sigma_P^2 A_P \end{bmatrix} \begin{bmatrix} Z_1^t \\ Z_2^t \\ Z_3^t \\ Z_M^t \\ Z_F^t \\ Z_P^t \end{bmatrix}.$$

Appendix 1 Table 10 lists the pedigree information of the oil palm used in this analysis and Table 11 lists its corresponding additive relationship matrix (snippet).

Several researchers have conducted the oil palm selection for breeding programs, including Purba et al. [30], Soh [35], and Peixoto et al. [28]. Table 5 shows the summary of the differences between this model and theirs. In summary, the model in this analysis focuses on male and female parent selection by treating the replicas, blocks, interaction between blocks and progeny, male and female parent, and progeny as random effects. The aim of accommodating the mentioned factors, is that the parents selected will pass down the character of adaptability to different locations to their offspring. We ran the LMM using the R library Sommer version 4.3.4 [5] [6], and calculated the Additive Relationship matrix using the R library Pedigreemm version 0.3-4 [3]. The R version is 4.3.2 for Windows [31].

Table 5: The differences between the model other previous researches.

Factor	**Soh (1994)**	**Purba (2001)**	**Peixoto (2015)**	**This model (2024)**
Fixed Effects	Genetic group	Trail	Trail	Location
Random Effects	Progeny, male parent, female parent	Parent of group A, parent of group B, interaction between parent of group A and B	Progeny, male parent, female parent	Replica in location (loc:rep), blocks in loc:rep (loc:rep:block), interaction between loc:rep:block and progeny, male parent, female parent, progeny
Experimental design	Randomized Block	Randomized Complete Block (mostly)	Randomized Complete Block	Alpha Lattice Design/Randomized Incomplete Block
Selection	Male parent	Parent	Family	Male and female parent

4. RESULTS AND DISCUSSION

The variance components of LMM equation (2) are shown in Table 6 and the fixed effect estimations in Table 7. The variance component of female parents is 834.77. It is higher than the male parents which is 51.56. The ratio is about 16.2 times. In inheriting the trait, the female has a higher impact than the male. Although small enough compared to the female, the male effect cannot be neglected [35]. For a female parent, the highest GCA value is 30.23 and the lowest is -59.04 while for the male parent are 5.14 and -4.88, respectively. The location effect estimation values of Sumatra and Kalimantan are 142.0 and 144.4, respectively. They are very close. The heritability value is 0.81 based on Gioia et al. [13]. The value is high. This shows that there is high genetic control for the trait. Parent selection will be advantageous, particularly for the female parent. The first 5 of the highest GCA females are the candidates of superior female parents.

Table 6: Variance components of LMM equation 2.

Factor	Variance-covariance component
Loc:Rep	35.24
Loc:Rep:Block	213.34
Loc:Rep:Block:P	371.93
Progeny	59.87
Female	834.77
Male	51.56
Error	1807.31

Table 7: The Fixed effect estimation values.

Factors	Estimation value
Location 1	142.0
Location 2	144.4

The GCA values of these females are above 25. They are ID 137, 155, 126, 147, and 159. ID 137, 126, and 159 are of Kalimantan and ID 155 and 147 are of Sumatra. The first 4 of the highest GCA are ID 101, 113, 109, and 117. ID 117 is of Kalimantan and the rest are of Sumatra. The GCA values of the parent is displayed in Table 8.

Table 9 shows the average weight of the oil palm bunch of the female and male parents. The selection is reasonable. The selected female parents are among the top 5. For the male parents, 3 of 4 are among the top 5, and only ID 113 is not. This shows that their corresponding progenies' performances are among the top productive yields.

Table 8: GCA values of female and male parents (ordered from largest to smallest).

ID Female	GCA	ID Female	GCA	ID Male	GCA
137	30.2378891	139	15.3943678	101	5.1399761
155	30.1729883	134	15.1107185	113	4.9548271
126	29.3908126	151	15.0924924	109	4.9353
147	27.0855274	158	14.3700068	117	4.5638783
159	25.9571829	149	13.6106632	100	4.2169756
125	23.965404	141	12.8018348	116	4.0216417
128	23.5795049	157	11.7099035	114	3.9338027
136	22.8887212	129	11.5627134	99	3.8246342
124	22.6749783	123	10.953722	115	3.5878338
150	22.0557911	156	10.2557247	102	2.9622833
154	21.3618275	144	7.5875052	104	1.3317078
148	21.158078	131	7.2298169	112	0.655304
127	20.1315429	133	5.8275816	108	-0.4901503
153	19.1152555	121	4.9835485	105	-0.9552536
119	18.8412355	145	4.9716269	96	-1.1201911
142	18.1976069	118	3.1870911	111	-1.403554
143	17.5823985	122	0.9664901	98	-1.4743577
152	17.0222825	132	0.5985304	107	-1.5822143
138	16.5874891	135	-5.4666733	106	-1.9428063
146	16.2486114	140	-59.035955	110	-3.7566837
130	15.9270587			97	-4.0268603
				103	-4.8786914

Table 9: The 5 highest average FFB values of female and male parent.

No	Female ID	Progeny Average FFB	Male ID	Progeny Average FFB
1	159	187.9062	117	177.0016
2	147	186.3766	116	172.3350
3	137	183.2984	101	171.8451
4	155	179.2489	100	170.5906
5	126	177.0012	109	168.1410

There are new crossings between the selected female and male parents that are not on the plantation yet. They are candidates for the new superior seeds. They have the high potential to pass down superior traits to offspring: 1) high oil yield, and 2) ability to adapt to the two locations. For example, the crossing between ID 137 of Kalimantan and ID 101 of Sumatra has the highest total additive genetic value (35.37) among the selected parents. Potentially, all possible crossings between selected female and male parents have these characteristics. This result is beneficial to the breeder and feasible for commercial seeds. Both industry and homeland farmers will have an alternative source of superior seeds. This will minimize the risk of loss because of getting low-production oil palm seeds.

Although the aim is to get the parents whose progeny is adaptable to any location or environment, we performed the analysis using the data from two locations. To make the analysis more robust, more samples from various locations are required. The model might be improved by accommodating the weather, season, soil, and other natural factors. The assumption of no dominant, epistatic, or other genetic effect might be violated, as well. Since the phenotype analyzed was FFB3 (6 years after planting), it might not represent the true productive progeny. The mature productivity of oil palm is in the 8-14 years after planting [23]. Purba et al. [30] use 7-9 years after planting as a mature oil palm tree. Danylo et al. [9] quoted that the oil palm reaches a high mature productivity at the age of 7-15 years after planting.

5. CONCLUSION

Oil palm parents (both female and male) having potential superior genetic characteristics are selected using an LMM. The LMM accommodates the following random effects factors: 1) location, 2) replica, 3) block, 4) interaction between blocks in replicas in location and progeny, 5) female parent, 6) male parent, and 7) progeny. The location is considered a fixed effect. There are two locations in which the sets of their progenies are non-intersect. The model uses pedigree information to link the progenies. This pedigree information contributes to the variance-covariance structure of the LLM. We use the phenotype FFB3 in this analysis. The selected female parents are ID 137, 155, 126, 147, and 159. All of them are Dura varieties. The selected male parents are ID 101, 113, 109, and 117. ID 101 and 117 are Pisifera. The rest are Tenera. The oil palm female parents have a higher impact than the male in inheriting the trait. The variance component of the female parent is greater than that of the male parent. The selection is advantageous for the superior characteristics because the heritability is high. This selection also results in new potential crossings. The crossings will inherit the following traits: 1) a high productive yield and 2) adaptability to different locations.

REFERENCES

[1] Baeza-Rodríguez, J.J., Montaño-Bermúdez, M., Vega-Murillo, V.E. and Arechavaleta-Velasco, M.E., Linear and logistic models for multiple-breed genetic analysis of heifer fertility in Mexican Simmental–Simbrah beef cattle, Journal of Applied Animal Research, 46(1), pp. 534-540, 2018.

[2] Bai, B., Wang, L., Zhang, Y.J., Lee, M., Rahmadsyah, R., Alfiko, Y., Ye, B.Q., Purwantomo, S., Suwanto, A., Chua, N.H. and Yue, G.H., Developing genome-wide SNPs and constructing an ultrahigh-density linkage map in oil palm, Scientific Reports, 8(1), p. 691, 2018.

[3] Bates, D., Rodriguez, P.P. and Vazquez, A.I., _pedigreemm: Pedigree-based mixed-effects models_, R package version 0.3-4. https://github.com/anainesvs/pedigreemm/, 2023.

[4] Blomberg, S.P., Rathnayake, S.I. and Moreau, C.M., Beyond Brownian motion and the Ornstein-Uhlenbeck process: stochastic diffusion models for the evolution of quantitative characters, The American Naturalist, 195(2), pp. 145-165, 2020.

[5] Covarrubias-Pazaran, G., Genome-assisted prediction of quantitative traits using the R package sommer, PloS One, 11(6), p. e0156744, 2016.

[6] Covarrubias-Pazaran, G., Software update: Moving the R package sommer to multivariate mixed models for genome-assisted prediction, BioRxiv, p. 354639, 2018.

[7] Crain, J., Mondal, S., Rutkoski, J., Singh, R.P. and Poland, J., Combining high-throughput phenotyping and genomic information to increase prediction and selection accuracy in wheat breeding, The Plant Genome, 11(1), p. 170043, 2018.

[8] Cros, D., Denis, M., Sánchez, L., Cochard, B., Flori, A., Durand-Gasselin, T., Nouy, B., Omoré, A., Pomiès, V., Riou, V. and Suryana, E., Genomic selection prediction accuracy in a perennial crop: case study of oil palm (Elaeis guineensis Jacq.), Theoretical and Applied Genetics, 128, pp. 397-410, 2015.

[9] Danylo, O., Pirker, J., Lemoine, G., Ceccherini, G., See, L., McCallum, I., Hadi, Kraxner, F., Achard, F. and Fritz, S., A map of the extent and year of detection of oil palm plantations in Indonesia, Malaysia and Thailand, Scientific Data, 8(1), p. 96, 2021.

[10] Fernandez, G.C.J. and Miller, J.C., Estimation of heritability by parent-offspring regression, Theoretical and Applied Genetics, 70, pp. 650-654, 1985.

[11] Gelman, A., Analysis of Variance: why it is more important than ever, The Annals of Statistics, 33(1), pp. 1-31, 2005.

[12] Gharib, M.A.A.H., Qabil, N., Salem, A.H., Ali, M.M.A., Awaad, H.A. and Mansour, E., Characterization of wheat landraces and commercial cultivars based on morpho-phenological and agronomic traits, Cereal Research Communications, 49, pp. 149-159, 2019.

[13] Gioia, T., Galinski, A., Lenz, H., Müller, C., Lentz, J., Heinz, K., Briese, C., Putz, A., Fiorani, F., Watt, M. and Schurr, U., GrowScreen-PaGe, a non-invasive, high-throughput phenotyping system based on germination paper to quantify crop phenotypic diversity and plasticity of root traits under varying nutrient supply, Functional Plant Biology, 44(1), pp. 76-93, 2016.

[14] Grüneberg, W.J., De Boeck, B., Diaz, F., Eyzaguirre, R., Low, J.W., Reif, J.C. and Campos, H., Heterosis and responses to selection in orange-fleshed sweetpotato (Ipomoea batatas L.) improved using reciprocal recurrent selection, Frontiers in Plant Science, 13, p. 793904, 2022.

[15] Gunny, A.A.N., Shahimin, M.F.M., Mohamed, A.R. and Jalil, M.F.A., Current status of renewable energy development, In Renewable energy from bio-resources in Malaysia, Springer Singapore, pp. 1-19, 2022.

[16] Henderson, C.R., Best linear unbiased estimation and prediction under a selection model, Biometrics, 31, pp. 423-447, 1975.

[17] John Martin, J.J., Yarra, R., Wei, L. and Cao, H., Oil palm breeding in the modern era: challenges and opportunities, Plants, 11(11), p. 1395, 2022.

[18] Isik, F., Holland, J. and Maltecca, C., Genetic data analysis for plant and animal breeding, Cham, Springer International Publishing, 2017.

[19] Bernardo Júnior, L.A.Y., Von Pinho, R.G., da Silva, C.P., Vieira Júnior, I.C., de Oliveira, L.A. and Silva, E.V.V., AMMI-Bayesian models and use of credible regions in the study of combining ability in maize, Euphytica, 217, pp. 1-19, 2021.

[20] Kearsey, M.J. and Pooni, H.S., The genetical analysis quantitative traits, 1st edition, Chapman & Hall, 1996.

[21] Krisnawati, A. and Adie M.M., Expression of heterosis, heterobeltiosis, and gene action in quantitative characters of soybean (Glycine max), Biodiversitas, 23(4), pp. 1745-1751, 2022.

[22] Kumar, A., Bharti, B., Kumar, J., Bhatia, D., Singh, G.P., Jaiswal, J.P. and Prasad, R., Improving the efficiency of wheat breeding experiments using alpha lattice design over randomised complete block design, Cereal Research Communications, 48, pp. 95-101, 2020.

[23] Woittiez, L.S., Van Wijk, M.T., Slingerland, M., Van Noordwijk, M. and Giller, K.E., Yield gaps in oil palm: A quantitative review of contributing factors, European Journal of Agronomy, 83, pp. 57-77, 2017.

[24] Murphy, D.J., Goggin, K. and Paterson, R.R.M., Oil palm in the 2020s and beyond: challenges and solutions, CABI Agriculture and Bioscience, 2, pp. 1-22, 2021.

[25] Ng, W.Z., Obon, A.A., Lee, C.L., Ong, Y.H., Gourich, W., Maran, K., Tang, D.B.Y., Song, C.P. and Chan, E.S., Techno-economic analysis of enzymatic biodiesel co-produced in palm oil mills from sludge palm oil for improving renewable energy access in rural areas, Energy, 243, p. 122745, 2022.

[26] Nilforooshan, M.A., Garrick, D. and Harris, B., Alternative ways of computing the numerator relationship matrix, Frontiers in Genetics, 12, p. 655638, 2021.

[27] Oliveira, G.H., Amaral, C.B., Silva, F.A., Dutra, S.M., Marconato, M.B. and Moro, G.V., Mixed models and multivariate analysis for selection of superior maize genotypes, Chilean Journal of Agricultural Research, 76(4), pp. 427-431, 2016.

[28] Peixoto, M.D.M., Friesen, P.C. and Sage, R.F., Winter cold-tolerance thresholds in field-grown Miscanthus hybrid rhizomes, Journal of Experimental Botany, 66(14), pp. 4415-4425, 2015.

[29] Presiden Republik Indonesia, Undang-Undang Republik Indonesia Nomor 29 tahun 2020 tentang perlindungan varietas tanaman, Jakarta, 2000.

[30] Purba, A.R., Flori, A., Baudouin, L. and Hamon, S., Prediction of oil palm (Elaeis guineensis, Jacq.) agronomic performances using the best linear unbiased predictor (BLUP), Theoretical and Applied Genetics, 102, pp. 787-792, 2001.

[31] Team, R.D.C., A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria, 2023. https://www.R-project.org/.

[32] Yusop, M.R., Sukaimi, J., Amiruddin, M.D., Jalloh, M., Swaray, S., Yusuff, O. and Chukwu, S.C., Genetic improvement of oil palm through recurrent selection, The Oil Palm Genome, pp. 35-46, 2020.

[33] Sanadya, S. K., Sood, V. K., Kumar S. and Sharma G., Relative effectiveness of alpha lattice design and randomized complete block design in oats breeding experiment, Journal of Cereal Research, 14(Spl-2), pp. 27-32, 2022.

[34] Soh, A. C., Ranking Parents by Best Linear Unbiased Prediction (BLUP) breeding values in oil palm, Euphytica, 76, pp. 13-21, 1994.

[35] Soh, A.C., Wong, C.K., Ho, Y.W., Choong, C.W., Oil Palm, In J. Vollmann, J. and Rajcan, I (Eds.), Oil crops, Handbook of Plant Breeding, Springer, 4, pp. 333-367, 2009.

[36] Swaray, S., Din Amiruddin, M., Rafii, M.Y., Jamian, S., Ismail, M.F., Jalloh, M., Marjuni, M., Mustakim Mohamad, M. and Yusuff, O., Influence of parental dura and pisifera genetic origins on oil palm fruit set ratio and yield components in their D× P Progenies, Agronomy, 10(11), p. 1793, 2020.

[37] Verdooren, L.R., Use of alpha-designs in oil palm breeding trials, American Journal of Theoretical and Applied Statistics, 8(4), pp. 136-143, 2019.

APPENDIX

Table 10: Pedigree Information (F = Female Parent ID, M = Male Parent ID).

1	-	-	41	23	19	81	40	37	121	95	94	161	157	113	201	158	114
2	-	-	42	27	27	82	38	40	122	95	94	162	144	109	202	154	108
3	-	-	43	27	27	83	40	38	123	64	64	163	119	101	203	132	108
4	-	-	44	27	27	84	39	39	124	65	65	164	118	113	204	134	108
5	-	-	45	25	25	85	37	37	125	66	88	165	123	113	205	143	101
6	-	-	46	27	27	86	39	39	126	68	67	166	119	109	206	124	101
7	-	-	47	30	30	87	40	40	127	69	84	167	123	103	207	146	113
8	4	4	48	30	30	88	40	40	128	69	84	168	145	105	208	125	98
9	1	1	49	27	27	89	39	39	129	70	70	169	118	103	209	125	115
10	2	2	50	27	27	90	39	39	130	70	70	170	157	101	210	128	115
11	3	3	51	26	26	91	40	40	131	71	71	171	133	113	211	128	98
12	1	1	52	27	27	92	40	40	132	72	72	172	145	108	212	131	99
13	2	2	53	29	29	93	40	40	133	72	72	173	119	105	213	131	112
14	4	9	54	30	25	94	85	85	134	77	77	174	150	107	214	129	98
15	2	2	55	27	27	95	85	85	135	73	73	175	132	107	215	129	115
16	2	2	56	27	27	96	62	61	136	74	74	176	145	97	216	130	112
17	12	10	57	28	41	97	62	61	137	74	74	177	144	97	217	130	96
18	8	8	58	28	41	98	60	59	138	75	75	178	122	113	218	136	98
19	14	11	59	29	29	99	58	58	139	76	76	179	155	101	219	137	111
20	14	13	60	30	25	100	58	57	140	79	78	180	147	101	220	138	115
21	8	8	61	41	24	101	58	57	141	79	78	181	122	103	221	135	115
22	15	13	62	41	24	102	56	55	142	79	78	182	124	101	222	135	111
23	16	16	63	38	37	103	54	53	143	80	80	183	146	113	223	139	99
24	20	17	64	40	40	104	52	52	144	81	81	184	121	105	224	139	96
25	5	5	65	40	40	105	60	51	145	81	81	185	148	97	225	139	98
26	21	18	66	40	40	106	60	51	146	82	82	186	144	102	226	140	111
27	5	5	67	38	37	107	54	53	147	82	82	187	118	107	227	141	104
28	22	23	68	38	37	108	54	53	148	83	83	188	146	109	228	141	112
29	8	8	69	39	37	109	50	49	149	92	92	189	151	103	229	148	100
30	5	5	70	37	39	110	48	48	150	88	87	190	150	108	230	149	115
31	6	6	71	39	37	111	48	47	151	88	87	191	127	114	231	149	96
32	6	6	72	39	37	112	52	46	152	88	87	192	155	107	232	152	115
33	32	31	73	37	38	113	45	45	153	89	90	193	157	108	233	153	115
34	32	31	74	40	40	114	44	43	154	90	90	194	146	106	234	156	112
35	34	33	75	40	40	115	44	43	155	91	91	195	143	107	235	156	100
36	7	7	76	40	40	116	42	43	156	93	92	196	142	116	236	159	111
37	36	36	77	35	40	117	44	43	157	92	93	197	146	110	237	126	117
38	36	36	78	40	35	118	63	63	158	84	85	198	124	108			
39	36	36	79	35	40	119	83	83	159	86	85	199	120	114			
40	36	36	80	40	37	120	70	70	160	119	108	200	124	102			

Table 11: The snippet of Additive Relationship matrix.

		ID							
		98	99	100	101	102	103	104	...
ID	98	1.359375	0.9453125	0	0.640625	0.640625	0.640625	0	
	99	0.9453125	1.359375	0	0.640625	0.640625	0.640625	0	
	100	0	0	1	0	0	0	0.5	
	101	0.640625	0.640625	0	1.671875	1.15625	1.15625	0	
	102	0.640625	0.640625	0	1.15625	1.484375	1.15625	0	
	103	0.640625	0.640625	0	1.15625	1.15625	1.484375	0	
	104	0	0	0.5	0	0	0	1.75	
	105	0	0	0.6875	0	0	0	0.5	
	106	0	0	0.5	0	0	0	1.5	
	107	0	0	0.625	0	0	0	0.5	
	…								