



Research article

Implications of genotypic and phenotypic variation in Dura × Dura oil palm for maternal selection

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Article Info

Article history:

Received 25 October 2023

Revised 14 February 2024

Accepted 14 February 2024

Available online 29 February 2024

Keywords:

Clustering,

Dura,

Genetic variation,

SSR markers

Abstract

Importance of the work: Selecting suitable maternal palms is essential for breeding high-yielding Tenera oil palms for commercial seed production.

Objective: To assess the genetic and physical characteristics of progenies from Deli Dura breeding population of oil palm for maternal selection.

Materials & Methods: The experiment applied using one-way analysis of variance to investigate 12 different traits in three Dura × Dura families: A (46 palms); B (40 palms); and C (41 palms). Genetic variation parameters, a phylogenetic tree and principal coordinate analysis were determined using 30 microsatellite markers, using the POPGENE program to cluster them among Dura and their offspring.

Results: The three investigated families of Dura × Dura showed clear separation into three genotype clusters. The observed heterozygosity value was higher than expected, indicating no inbreeding in this oil palm. Each family showed distinctive traits—family A exhibited sex ratio, fresh fruit bunch and oil yield, family B oil-to-bunch ratio and family C plant height and height increment. This information should help in the selection of Dura as the maternal palm for next-generation improvement or for producing new commercial Tenera.

Main finding: The variation observed in oil palms provided information on the immature phase of the new Dura as an elite line, with clustering of their SSR genotypes. The essential traits identified for genetic improvement were fresh fruit bunch, sex ratio, plant height and oil-to-bunch ratio.

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<https://doi.org/10.34044/j.anres.2024.58.1.14>

Introduction

The oil palm (*Elaeis guineensis* Jacq.) is highly valuable and widely used for producing cooking oil, consumer goods, and biodiesel feedstock (Kaniapan et al., 2021). However, the commercial breeding of oil palms has been limited due to the narrow genetic pool of breeding materials; thus, it is essential to introduce more significant genetic variation to enhance the breeding process (Rosenquist, 1986). The most common way of introducing desirable genes into new germplasms is through parental selection (Allard, 1960). The genetic variation in the breeding population can aid oil palm breeders in enhancing trait means in every breeding cycle, with progenies from the Deli Dura breeding population of oil palm showing improvements in bunch yield, number of bunches and weight of single bunches (Okwuagwu, 1996). Various morphological traits and yield components have also improved. For example, Digner et al. (2008) selected oil palm families derived from Dura × Dura to improve the genetic gain of their germplasm, resulting in the best phenotypic performance and value. Tupaz-Vera et al. (2021) studied families obtained from crosses between Deli Dura and African Dura to create dwarf progenies using genetic parameters. Their study identified two progenies as slow-growing cultivars, with high numbers of fresh fruit bunches and a high oil-to-bunch ratio. Developing and selecting elite Dura parents with slow growth characteristics and high bunch and oil production can prolong the crop's productive life, resulting in differentiated cultivars of oil palm with added value. Noh et al. (2014) introduced and cross bred Nigerian Dura and Deli Dura oil palm progenies. Their purpose was to evaluate their performance regarding bunch yield, yield attributes, bunch quality components and vegetative characters. Their study found that the progenies exhibited high genetic variability, indicating potential for further breeding and selection. Pedapati et al. (2021) assessed bunch quality components in Dura × Dura progenies developed from Zambia and Cameroon germplasm to select high oil-yielding female parent palms. Their results indicated that fresh mesocarp per fruit and number of fruit per bunch were improved, while the oil yield increased, with less shell and kernel content. Oil palm selection based on a high oil-to-bunch ratio is necessary before hybridization in a breeding program (Rajanaidu et al., 1989). Corley and Lee (1992) reported that after four generations of selection, the yield of the population selected from Deli Dura had increased by 60% compared to that of the original clones. A cross between Dura and Pisifera palm trees yielded

a Tenera fruit type with a thinner shell and 30% more oil. Corley et al. (1971) determined that the growth rate and leaf area index were critical factors in enhancing the growth and yield of Dura palms. Tanya et al. (2013) conducted a research study to explore the correlations among yield components in oil palm. Specifically, they examined fresh fruit bunch (FFB), bunch weight (BW) and number of bunches (BN) to determine their impact on oil palm yield. Their study found that FFB and BW had the greatest and significant influence on oil palm yield. In addition, Okoye and Okwuangwu (2008) reported a negative correlation between BN and BW and suggested that enhancing these traits should be prioritized in a cycle of an oil palm breeding program. The breeding cycle required for oil palm evaluation involves extensive data collection, leading to a bottleneck in oil palm breeding. The efficiency of molecular markers is used in breeding to save time and field space for data collection, with standard genetic features, such as Random Amplified Polymorphic DNA (RAPD), Inter Simple Sequence Repeat (ISSR), Random Fragment Length Polymorphism (RFLP), Amplified Fragment Length Polymorphism (AFLP) and Single Nucleotide Polymorphism (SNP), being proposed and applied. Simple sequence repeat (SSR) is the most popular marker because of its high accuracy, efficiency, heterozygosity and repeatability (Mohan et al., 1997). Thongthawee et al. (2010) applied 64 SSR markers on 245 palms from 6 families in a breeding population to analyze relationships among their parents'.

Abdullah et al. (2011) used microsatellite markers to evaluate the genetic relationship between the parents (Dura × Pisifera) and their progenies. They used this information to select the parental palms based on genetic distance. The current study estimated the phenotypic and genotypic variation of three Dura oil palm families to determine Dura parents for subsequent generations.

Materials and Methods

Plant materials

Three superior Dura oil palm plants (R10/1, R8/9 and A43/9) were selected from the improved oil palm germplasm of Golden Tenera Company Limited in Krabi province, Thailand. To create three distinct families, 127 oil palm seeds were obtained from the Golden Tenera Co. Ltd. field, which covers an area of approximately 1 ha, with a plant grid spacing of 9 m. Family A was produced by crossbreeding R10/1 and A43/9,

resulting in 46 palms. Family B was derived by crossbreeding R10/1 with R8/9, resulting in 40 palms. Finally, family C was created by crossbreeding A43/9 with R8/9, resulting in 41 palms.

Phenotyping and analysis

Phenotypic data were recorded on individual plants for three consecutive years (palm age 3–6 yr) after planting in the field. The vegetative characteristics were collected twice per year and consisted of: leaf area (LA, measured in square meters), frond dry matter weight (FDMW, measured in kilograms), frond length (FL, measured in meters), number of fronds (NF) per palm per year, plant height (PH, measured in centimeters), height increment per year (HI, measured in centimeters) and sex ratio (the proportion of females to total inflorescences). The number of bunches per palm per year (BN), the bunch weight (BW, measured in kilograms) and the total weight of fresh fruit bunches per palm per year (FFB, measured in kilograms) were measured every 2 wk. Additionally, the percentage of oil per bunch (O/B) was measured and used to calculate the oil yield per palm per year (OY, measured in kilograms). Phenotypic variation was calculated using a one-way analysis of variance (ANOVA), with Duncan's new multiple range test determined using the R program (R Core Team, 2014). A Gaussian frequency distribution was drawn using the GraphPad Prism software (version 6.00 for Windows, Free Trial, 2015 available at <https://www.graphpad.com/demos/>) and a normality test was conducted using the Excel software (version 2010; Microsoft Corp.; Redmond, WA, USA).

Genotyping and analysis

Oil palm DNA was extracted from the leaves using the method described by Tanya et al. (2011). Genotypic data were analyzed using 64 SSR primers, as reported by Billotte et al. (2005) based on polymerase chain reaction. Each reaction required a total volume of 10 μ L containing 10 ng/ μ L of genomic DNA, 1 $\times$ Taq buffer with $(\text{NH}_4)_2\text{SO}_4$ (Fermentas; Vilnius, Lithuania), 2 mM MgCl_2 , 10 mM dNTP, 5 μ M each of forward and reverse primers, and 1 U Taq DNA polymerase. The amplification process was carried out using a PCT-100TM thermal controller (MJ Research; Watertown, MA, USA) at 94°C for 5 min, followed by 35 cycles of 30 s each at 94°C, 55°C, and 72°C, respectively. DNA fingerprints were identified using silver staining. The polymorphic alleles obtained from each primer were analyzed to determine the polymorphic information content (PIC), expected heterozygosity (H_e) and observed heterozygosity (H_o) using the POPGENE Version 1.31 software (Yeh et al., 1999). Phylogenetic trees were constructed using the DARwin5 software (Perrier et al., 2003; Perrier and Jacquemoud, 2006) based on Jaccard's similarity coefficient and principal coordinate analysis (PCoA).

Results and Discussions

The ANOVA results showed that the three oil palm families were significantly ($p \leq 0.01$) different in all traits observed, except for NF and BW (Table 1). The mean comparison revealed the difference between families: B versus (A and

Table 1 Coefficient of variation and mean of vegetative growth and bunch yield components in three oil palm families

Traits	CV (%)	Families		
		A (R10/1 $\times$ A43/9)	B (R10/1 $\times$ R8/9)	C (A43/9 $\times$ R8/9)
Leaf area (m^2)**	13.21	6.17 $\pm$ 0.95 ^b	7.65 $\pm$ 0.94 ^a	6.42 $\pm$ 0.76 ^b
Frond dry matter weight (kg)**	17.69	3.07 $\pm$ 0.60 ^a	3.23 $\pm$ 0.61 ^a	2.64 $\pm$ 0.30 ^b
Frond length (m)**	6.86	4.80 $\pm$ 0.39 ^b	5.12 $\pm$ 0.35 ^a	4.73 $\pm$ 0.24 ^b
Number of fronds (fronds/palm/year) ^{ns}	7.44	27.22 $\pm$ 2.18	26.85 $\pm$ 1.82	27.49 $\pm$ 2.03
Plant height (cm)**	14.54	184.15 $\pm$ 23.66 ^a	158.48 $\pm$ 24.19 ^b	130.80 $\pm$ 21.28 ^c
Height increment (cm/year)**	28.71	55.24 $\pm$ 16.20 ^a	51.03 $\pm$ 15.26 ^a	38.73 $\pm$ 8.98 ^b
Sex ratio**	12.90	0.97 $\pm$ 0.06 ^a	0.93 $\pm$ 0.12 ^a	0.87 $\pm$ 0.16 ^b
Number of bunches (bunches/palm/year)**	20.50	26.24 $\pm$ 2.60 ^a	22.58 $\pm$ 4.36 ^b	22.88 $\pm$ 3.63 ^b
Bunch weight (kg/bunch) ^{ns}	17.97	8.29 $\pm$ 1.04	8.36 $\pm$ 1.52	8.34 $\pm$ 1.12
Fresh fruit bunch (kg/palm/year)**	21.66	219.21 $\pm$ 24.67 ^a	188.67 $\pm$ 38.08 ^b	191.62 $\pm$ 33.48 ^b
Oil/bunch (%)**	11.24	24.77 $\pm$ 2.30 ^b	28.20 $\pm$ 2.77 ^a	25.48 $\pm$ 3.64 ^b
Oil yield (kg/palm/year)**	24.75	54.28 $\pm$ 7.68 ^a	52.99 $\pm$ 10.84 ^a	48.96 $\pm$ 11.59 ^b

** = highly significant ($p < 0.01$); ns = non-significant ($p \geq 0.05$);

Values (mean $\pm$ SD) within rows superscripted with different lowercase letters are significantly ($p < 0.05$) different.

C) for LA, FL and O/B; (A and B) versus C for FDMW, HI, sex ratio and oil yield; A versus (B and C) for BN and FFB; and A versus B versus C for PH, as shown in Table 1. The highest values in each trait found in family A were PH (184.15 cm), HI (55.24 cm), sex ratio (0.97), BN (26.24 bunches/palm/year), FFB (219.21 kg/palm/year) and oil yield (54.28 kg/palm/year), in family B were LA (7.65 m²), FDMW (3.23 kg), FL (5.12 m) and O/B (28.20%), and in family C were NF (27.49 fronds/palm/year) and BW (8.34 kg/bunch).

The traits significantly ($p \leq 0.01$) differed in the frequency distribution of the progenies, as shown in Fig. 1. Based on Table 2, some characteristics—LA, FL, PH, FFB, O/B and oil yield—had a normal frequency distribution ($p \geq 0.05$). However, FDMW, HI, sex ratio and BN were highly skewed toward 1.23, 0.70, -2.42 and -0.46, respectively, and were not

normally distributed ($p \leq 0.05$), suggesting that a small number of loci in the gene may influence these traits.

In particular, the skewness of HI skewed right, revealing slow height increment, sex ratio skewed left, with tail extreme indicating that there were more female inflorescences than male inflorescences, according to which all crosses had a high yield performance, while the number of bunches skewed right, indicating that most of the progenies produced a higher number of bunches per year than the average (24 bunches/palm/year). The distribution of individual progenies was observed for each trait and grouped into three groups, as shown in Table 3 and Fig. 1. The palms from family A were high on sex ratio, BN, FFB and oil yield. Family B had more plants with high LA, FL, and O/B, while family C had low PH (<120 cm). Individuals in family C were classified as having low PH and HI compared to the other families and might have been affected by maternal A43/9 being shorter than R10/1. All progenies in these families had low HI. In addition, families A and B had more plants with a high FDMW, while family C had a low FDMW. Most of the progenies from families A, B and C had a high sex ratio.

This information effectively supports the parental selection of oil palm breeding programs by focusing on desirable traits, such as height value in sex ratio, O/B, FFB and OY, contrasting to low height increments for short palms. Progenies with vegetative characteristics were selected to produce new parental germplasm, as shown in Table 3. Family C chose PH and HI palms with height ≤ 120 cm and growth rate < 35 cm/year. The sex ratio can be selected based on progenies from all families with a value higher than 0.9. FFB, O/B and short palm were chosen as the progenies in the maximum family A, B and C groups, respectively—however, the selection process aimed to fix phenotypes and genotypes in each breeding program.

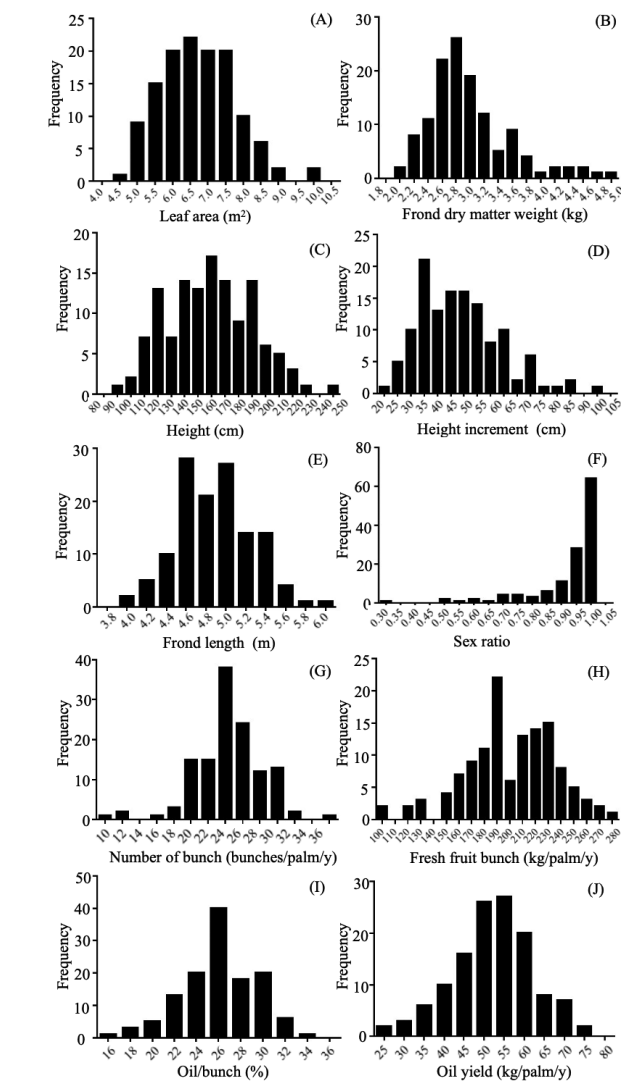


Fig. 1 Frequency histograms of vegetative growth and bunch yield for progenies obtained from three families of Dura × Dura oil palm

Table 2 Normality and skewness tests of vegetative growth and bunch yield components

Traits	Skewness	Probability of normal distribution
Leaf area (m ²)	0.45	0.0907*
Frond dry matter weight (kg)	1.23	< 0.0001 ^{ns}
Frond length (m)	0.17	0.8200*
Plant Height (cm)	0.21	0.5906*
Height increment (cm/year)	0.70	0.0026 ^{ns}
Sex ratio	-2.42	< 0.0001 ^{ns}
Number of bunches (bunches/palm/year)	-0.46	0.0023 ^{ns}
Fresh fruit bunch (kg/palm/year)	-0.37	0.2728*
Oil/bunch (%)	-0.23	0.7453*
Oil yield (kg/palm/year)	-0.21	0.5703*

* = significant ($p < 0.05$); ns = non-significant ($p \geq 0.05$)

Table 3 Distribution of traits observed from progenies of 3 Dura × Dura oil palm families

Traits	Mean±SD	Family	Number of progeny in ranges of observed values		
Leaf area (m ²)	6.72±1.09		< 6	6–7.5	> 7.5
		A	24	16	6
		B	0	17	23
		C	12	27	2
Frond dry matter weight (kg)	2.98±0.58		< 2.6	2.6–3	> 3
		A	10	15	21
		B	4	16	20
		C	21	18	2
Frond length (m)	4.88±0.37		< 4.6	4.6–5	> 5
		A	14	18	14
		B	3	11	26
		C	12	24	5
Plant height (cm)	158.84±31.85		< 120	120–190	> 190
		A	0	31	15
		B	2	35	3
		C	13	27	1
Height increment (cm/year)	48.58±15.53		< 35	35–65	> 65
		A	6	29	11
		B	5	30	5
		C	14	22	5
Sex ratio	0.92±0.13		< 0.5	0.5–0.9	> 0.9
		A	0	4	42
		B	1	9	30
		C	1	18	22
Number of bunches (bunches/palm/year)	24.00±3.92		< 24	24–26	> 26
		A	7	20	19
		B	22	13	5
		C	26	11	4
Fresh fruit bunch (kg/palm/year)	200.68±34.93		< 180	180–210	> 210
		A	1	17	28
		B	17	11	12
		C	16	12	13
Oil/bunch (%)	26.08±3.26		< 24	24–27	> 27
		A	17	23	6
		B	3	14	23
		C	12	14	15
Oil yield (kg/palm/year)	52.15±10.26		< 50	50–60	> 60
		A	14	18	14
		B	15	17	8
		C	24	10	7

Low genetic variability has been maintained over long periods of oil palm improvement while preserving its perennial nature. For the established superior hybrid, it is necessary to cross elite parents selected for good performance. Dura × Dura is one of the valuable crossing populations implicated in parental selection and progeny testing for new germplasm. Of the 12 traits observed from the progenies of the three tested Dura × Dura families, 10 significantly differed among families. NF and BW were not entirely different among families because the general oil palm produced approximately 24 fronds per palm per year, and the juvenile stage of oil palm bunches was still small, with an average of 7–10 kg per bunch.

Family A had a lower O/B than family C but had a similar oil yield because family A had a higher yield of FFB and BN. The frequency distribution of the progenies approximated continuous variation, showing that several genes control these traits, except for FDMW, HI, sex ratio and BN. The number of bunches is the primary product of progenies, whereas the bunch weight is responsible for the secondary trend in the relationship between FFB and BN. The principal role of BN in FFB is that moderately high BN should be given substantial weight in any selection purposed to increase FFB in oil palms. Therefore, choice based on BN and BW is reliable for FFB improvement (Okoye et al., 2007; Tanya et al., 2013).

Digner et al. (2008) improved five Dura × Dura families in Ecuador by evaluating two traits (BN and FFB), without using genotype data. They found that the progenies from the Equador Deli Dura parent had the highest bunch yield due to the combination of the number of harvested bunches and average bunch weight. Pedapati et al. (2021) conducted a study to support the selection of mother oil palms for an oil palm breeding program. They evaluated 77 Dura × Dura progenies for bunch quality components. They found that the oil-to-wet mesocarp ratio had the highest positive direct effect on the oil-to-bunch ratio, followed by the mesocarp-to-fruit ratio. Their study suggested that additional hybridization programs to produce hybrid seeds achieved desirable outcomes; breeders should consider the ratio of mesocarp-to-fruit and the ratios of oil-to-dry mesocarp and oil-to-bunch since these characteristics significantly impact the oil content.

Okwuagwu et al. (2008) conducted a study on Deli Dura x Tenera in which they found that BN and FFB were crucial criteria for oil palm selection. The study involved checking the genotype data and background of all offspring of Deli × Tenera before continuing the breeding program. In the current study, family A produced the most significant offspring with high BN and FFB among the families. It makes an ideal choice for plant breeders to select Dura parental plants based on the performance of family members. This approach would help produce Tenera plants using the genotypes and phenotypes of each family as female parents. For example, when choosing Dura parents, priority is usually given to those with short PH and low HI. In this case, progenies from family C would be preferred as their offspring had a PH of less than 120 cm and HI of less than 35 cm per year. A comparison between families showed that the parents significantly affected the phenotypic

expression. Families A and B had the same maternal plant, R10/1, but crossed with different paternal plants (A43/9 and R8/9, respectively). Both families had similar offspring and no significant differences in their values for FDMW, HI, sex ratio and oil yield. Families B and C had R8/9 as their common paternal plant, with their offspring showing similar traits for BN and FFB.

In total, 30 SSR markers from the 64 primers tested could amplify 67 polymorphic alleles, with a mean of 2.23. The amplified fragments had a range of 90–480 base pairs. The samples had alleles in the range 2–3 and the PIC values were in the range 0.23–0.57, with an average of 0.38.

Table 4 shows the genetic variation parameters, in which He was in the range 0.26–0.64 with an average of 0.47, and Ho was in the range 0.21–0.98 with an average of 0.61. Primer mEgCIR0173 had the highest values for PIC, He and Ho. The phylogenetic tree constructed based on Jaccard’s similarity coefficient of the 127 progenies had three distinct groups based on their families, as shown in Fig. 2. The study aimed to examine the genetic relationships among various palm families. According to the results, parent R8/9 was genetically different from the other parents, whereas R10/1 and A43/9 were genetically similar to the offspring in family A, as shown in Fig. 2. Additionally, the study found that palms B7/1 and B7/9 in family B were genetically identical to the offspring of family C. The PCoA analysis was classified into three family populations (A, B and C) based on the discriminant axes 1 and 2. Fig. 3 shows that the families B and C had the same paternal genetic background; in addition, the families A and B had the same maternal genetic background. The genetic distances between parents R10/1 and A43/9, R10/1 and R8/9, and A43/9 and R8/9 were 0.48, 0.67 and 0.72, respectively.

Table 4 Genetic variation parameters of 127 progenies derived from three combinations (R10/1×A43/9, R10/1×R8/9 and A43/9×R8/9) and three superior Dura, based on 30 single sequence repeat primers, as reported by Billotte et al. (2005)

Locus name	Allele size (base pair)	Number of amplified alleles	PIC	He	Ho
mEgCIR0173	110–130	3	0.57	0.64	0.98
mEgCIR0192	200–240	2	0.36	0.47	0.62
mEgCIR0580	230–270	2	0.28	0.33	0.21
mEgCIR0782	180–220	3	0.51	0.59	0.76
mEgCIR0788	140–170	3	0.55	0.62	0.78
mEgCIR0790	350–370	2	0.35	0.46	0.40
mEgCIR0800	250–270	2	0.37	0.50	0.66
mEgCIR0801	285–360	2	0.37	0.49	0.55
mEgCIR0844	260–270	2	0.37	0.49	0.40
mEgCIR0878	190–220	3	0.53	0.61	0.96
mEgCIR0882	165–170	2	0.38	0.50	0.58
mEgCIR0912	140–145	2	0.25	0.29	0.34
mEgCIR2144	195–200	2	0.34	0.44	0.63
mEgCIR2212	140–160	2	0.37	0.49	0.62

Table 4 Continued

Locus name	Allele size (base pair)	Number of amplified alleles	PIC	He	Ho
mEgCIR2291	250–260	2	0.27	0.32	0.40
mEgCIR2332	340–360	2	0.37	0.49	0.73
mEgCIR2409	270–290	3	0.56	0.64	0.48
mEgCIR2422	280–290	2	0.37	0.48	0.80
mEgCIR2427	150–170	2	0.34	0.44	0.63
mEgCIR2440	410–440	2	0.36	0.46	0.69
mEgCIR2450	120–150	2	0.26	0.31	0.37
mEgCIR2492	340–370	2	0.23	0.26	0.31
mEgCIR2538	285–290	2	0.34	0.43	0.63
mEgCIR2577	100–110	2	0.34	0.44	0.63
mEgCIR3400	170–190	2	0.37	0.49	0.71
mEgCIR3534	440–480	3	0.48	0.53	0.37
mEgCIR3535	190–195	2	0.34	0.43	0.63
mEgCIR3557	260–270	2	0.37	0.49	0.82
mEgCIR3684	220–230	2	0.37	0.50	0.73
mEgCIR3705	90–130	3	0.55	0.62	0.85
Mean		2.23	0.38	0.47	0.61
SD		0.43	0.09	0.10	0.20

PIC = polymorphic information content; He = expected heterozygosity; Ho = observed heterozygosity

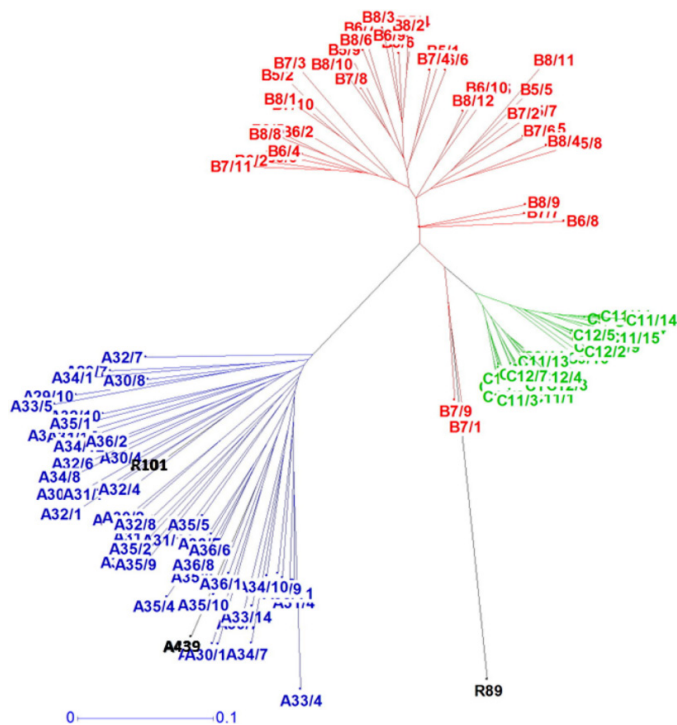


Fig. 2 Unrooted neighbor-joining tree, where colors of tree branches indicate three groups as families A (blue), B (red) and C (green)

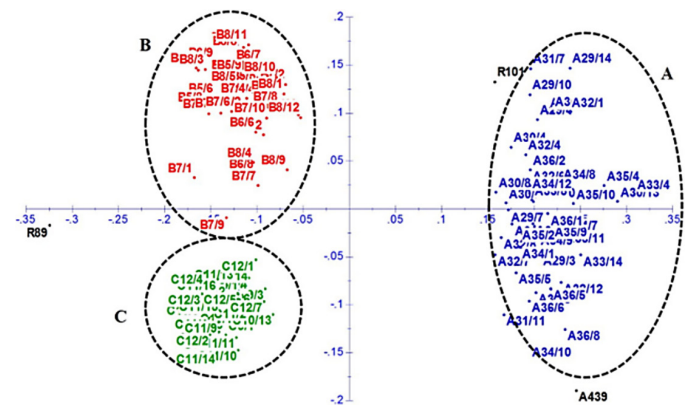


Fig. 3 Principal coordinate analysis from dissimilarity matrix calculated using Jaccard's similarity based on 30 single sequence repeat primers, where A, B and C represent families studied

A study was conducted to assess the genetic variability among the parents and offspring of Dura oil palm. Corley and Lee (1992) stated that oil palm parents with greater genetic distances generate more-variable offspring. The low average PIC (0.38) indicated a low number of detectable alleles and distribution of their frequency. The average Ho (0.61) was higher than for He (0.47), indicating that the high genetic variation among the 127 progenies was similar to the results of the tree and PcoA, while within families there was low variation. Crossing between palms within families should be avoided to increase the variation in heterozygosity in the next cycle of breeding programs.

The current study, which combined phenotypic and genotypic information for parental selection, has provided essential data for oil palm pre-breeding programs. The parents in this study and the progenies selected were suitable as new parents for the next cycle. On this basis, the frequency distribution results may predict a superior progeny in each trait. In this study, essential agronomic characteristics such as height, sex ratio and FFB, were analyzed in oil palm trees using 30 SSR primers. The results revealed significant genetic variation, providing essential genetic parameters. These data are a valuable resource for future research on oil palm germplasm.

Conflict of Interest

The authors declare that there are no conflicts of interest.

Acknowledgments

This research was partially supported by: 1) the Center of Excellence on Biotechnology of Oil Palm for Renewable Energy, Ministry of Higher Education, Science, Research, and Innovation; (2) the Center of Advanced Study on Agriculture and Food of Kasetsart University, Bangkok, Thailand (project no. CASAF 147); and (3) Golden Tenera Co. Ltd., who provided the oil palm materials for this study.

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