Journal of Oil Palm Research
DOI: https://doi.org/10.21894/jopr.2025.0018

TRUE-TO-TYPE VERSION 2 - HIGH RESOLUTION GENOTYPING PLATFORM FOR PARENTAL IDENTIFICATION IN OIL PALM

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ABSTRACT

This study reports on developing the TRUE-TO-TYPE VERSION 2 DNA genotyping platform. Relative to SureSawit™ TRUE-TO-TYPE (Version 1), the new platform has improved genotyping resolution for high-precision parental identification in Elaeis guineensis*, allowing accurate assignment of a palm to their actual parents even if the parentage information is not available. The feature was developed by increasing the marker-set from 24 (in Version 1) to 108 stably inherited SNPs. The optimal performance of TRUE-TO-TYPE VERSION 2 was confirmed by analysing the genotypes of 2,301 offspring from three genetic backgrounds. A total of 17 panels with different numbers of SNP markers were evaluated for this purpose. The finalised panel was validated in 460 offspring and 41 candidate parents from 20 families of diverse genetic backgrounds. Our data demonstrated >99.4% accuracy in predicting the true parents for the palm materials analysed using TRUE-TO-TYPE VERSION 2. The platform retains the ability to detect illegitimates and track genetic lineage accurately. It is a quality control tool for managing palm materials in seed-gardens, breeding programs, commercial nurseries and tissue-culture laboratories. The genetic information obtained will also facilitate the establishment of a comprehensive DNA fingerprint database for the palm materials.*

Keywords: advanced breeding lines, germplasm, parentage analysis, purity testing, SNP panel.

Received: 13 August 2024**; Accepted:** 3 December 2024**; Published online:** 25 March 2025.

INTRODUCTION

Oil palm is an important commodity crop, especially in Malaysia and Indonesia, contributing to approximately 2.5% and 4.5% of the Gross Domestic Product (GDP) in 2022. Its economic importance has resulted in the wide-scale cultivation of oil palm in these two countries. In Malaysia alone, the planting areas across the Peninsular, Sabah and Sarawak were estimated at about 5.7 million hectares (Parveez *et al.*, 2023). The hectarage consists of >770 million standing palms at a modest planting density of 136 palms/ha, not including seedlings in the nurseries and ramets produced in the tissue culture laboratories.

Therefore, a reliable and efficient management system is required for the large-scale production of good quality planting materials. Most oil palm plantation companies have established their best-practice system in managing the germplasm (Germ), advanced breeding lines (ABL) and materials produced for commercial planting in the production fields. The system is also in place to manage seedlings in nurseries and ramets produced via tissue culture. However, the management systems practised currently mostly rely on paper-trail which involves physically tracking the movement of materials, starting from the crossing of selected

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palms to the seed production facility, followed by tracking seedlings in nurseries and planting in the breeding or commercial fields. A similar exercise is carried out throughout the tissue culture process where plantlets (ramets) are moved from laboratories to nurseries and transferred to the field (Rohani *et al.,* 2000; Soh *et al.,* 2011). Undeniably, as thousands of breeding crosses are made yearly and dozens of ortets are cloned (each giving several lines), mislabelling and other mistakes in tracking are likely common.

A significant concern is the presence of illegitimates in the controlled crosses and mix-up of clones which, cannot be identified based on their physical appearance, especially at the early stages. The occurrence of such incidents has been well documented (Corley, 2005; Hama-Ali *et al*., 2014; Teh *et al.,* 2019). There are also potential yield losses if illegitimates or unintended clones are embedded in the commercial fields, as demonstrated in the large-scale screening of 1,150,827 palm materials by Malaysian Palm Oil Board (MPOB) (Ooi *et al.,* 2016; 2023; Singh *et al.,* 2021), using the first available oil palm Deoxyribonucleic acid (DNA) diagnostic test. The survey revealed unexpectedly high levels of contamination (ranging from 10.7%-2.8%) in the *dura* x *pisifera* controlled crosses, causing losses in billions of Malaysian ringgit to the industry. The single nucleotide polymorphism (SNP) markers used by Ooi *et al.* (2019) and Singh *et al.* (2018) targeted a particular gene – *SHELL* – that differentiates the commercially acceptable fruit form (*tenera*) from the undesired planting materials (non-*tenera*). Other studies using SSR markers have detected illegitimates ranging from 8.3%-98.0% (Zolkafli *et al.,* 2021) and recommended different numbers of SSR markers that could be utilised for each of the genetic backgrounds screened. The limitation in the SSR studies mentioned above is that, the known parental pair is required, and if an illegitimate is detected, it cannot be accurately assigned to the correct parental pair with high confidence, even when a set of possible parents are genotyped.

Hence, it is important to develop a marker panel that has sufficient discriminating power and is amenable to high-throughput genotyping. Exploring the genomic resources available at MPOB namely, the resequencing of selected Germ (unpublished data) anchored to the oil palm genome (Singh *et al.,* 2013), SureSawit™ TRUE-TO-TYPE genotyping platform (Version 1) consisting of 24 genome-wide SNP markers was developed in 2018 (Ooi *et al*., 2019; Singh *et al*., 2018). The Version 1 genotyping platform proved useful in detecting illegitimates, discriminating individual palms according to their genetic lineage, and allowing parentage assignment when the true parents are known. In such a guided-analysis, Version 1 was used to effectively validate the legitimacy of controlled crosses across a broad range of genetic backgrounds. However, in cases where the parentage information was unavailable, reduced accuracy was observed in assigning the individuals to their biological parents.

As Version 1 had limitations, an advanced platform for parental identification was thus needed. This study describes the steps taken in selecting, optimising, and subsequently, validating the SNP panel for that purpose. For fish and mammals, parentage analysis has been well established where many studies reported a range of 50-150 (Abadía-Cardoso *et al.,* 2013; Beacham *et al.,* 2018; Dussault & Boulding 2018; Liu *et al.,* 2016; Tong *et al.,* 2023) and 84-700 (Bell *et al.,* 2013; Calvo *et al.,* 2020; Clarke *et al.,* 2014; Gebrehiwot *et al.,* 2021; Heaton *et al.,* 2014; Holl *et al.,* 2017; Strucken *et al.,* 2015; Tortereau *et al.,* 2017) SNP markers can reliably resolve parentage assignment. For oil palm, accurately assigning every individual to their biological parents, especially in the breeding programs, is very important to ensure that the parental combining ability is accurately accessed. As making controlled crosses is an expensive and laborious exercise, the ability to assign the individual palms accurately to their respective parental pair will improve efficiency in breeding programs. Since the palms in such trials are the selected high-yielding breeding stocks, establishing a DNA database for these materials will be especially beneficial, as it will be valuable for the overall management system of important breeding lines as well as for protecting possible intellectual property (IP) related to the palm materials.

MATERIALS AND METHODS

Plant Materials

In this study, a total of 2,301 confirmed offspring resulting from 22 crosses involving 25 parental palms (18 maternal and seven paternal palms) was used for developing a suitable SNP marker panel. They were categorised under seven progeny groups based on the common paternal palm (*Table 1*). For the validation experiment, the sample panel consisted of 460 offspring palms derived from 21 crosses, where the 41 candidate parental palms were of diverse genetic backgrounds, including ABL and Germ (*Table 2*). The number of offspring for the individual crosses was relatively small, ranging from 10-30 palms.

Development of SNP Panel

Information on a total of 2,280 SNP markers, previously genotyped in the 78K and 92K high-density SNP arrays (Ting *et al.,* 2023a; 2023b) on

the families listed in *Table 1*, was extracted from MPOB's in-house database. Selection of these markers was based on three parameters: 1) Evenly distributed across the 16 pseudo-chromosomes in the *E. guineensis* genome; 2) showed the Mendelian segregation profiles across the three genetic backgrounds and; 3) had high minor allele frequencies ranging from 10.0%-5.00% (average 40.0%) across the three genetic backgrounds.

For determining the optimum number of SNP markers, 17 panels with increasing number of SNP markers ranging from 24 (of Version 1) to 50, 70, 80, 90, 100, 110, 120, 130, 140, 150, 160, 180, 200, 500, 1,000 and 2,280 SNPs were evaluated. For each panel, the selection of SNP markers was carried out in six independent repetitions where, the first round only picked markers that were evenly spaced and the following five rounds involved random sampling.

TABLE 1. SAMPLES USED FOR DEVELOPING AN OPTIMAL SIZE OF SNP MARKER PANEL

Family type	Genetic background	Progeny group	Number of offspring	Number of parent(s) involved
Full-sib	Deli *dura* x AVROS *pisifera*	1	995	2
Full-sib	Nigeria *tenera* selfed	2	223	1
Linked half-sib	Deli *dura* x Nigeria *pisifera*	3	275	6
		4	112	3
		5	452	9
		6	112	3
		7	157	4
Total			**2,326***	**25**

Note: * - Including 25 suspicious palms.

TABLE 2. DETECTION OF ILLEGITIMATE PALMS IN VARIOUS CROSSES INVOLVING ABL AND GERM MATERIALS USING TRUE-TO-TYPE VERSION 2

No.	Material	Genetic background	Parental fruit form	Number of offspring	Number of illegitimate
1	ABL x ABL	Banting x Ulu Remis	D X D	23	0
2	ABL x ABL	Pamol x Ulu Remis	D X D	23	0
3	ABL x ABL	Johor Labis x AVROS	D X P	23	0
4	ABL x ABL	Ulu Remis x Yangambi	D X P	20	0
5	ABL x ABL	Deli x AVROS	D X P	10	1
6	ABL x ABL	Deli x AVROS	D X P	10	0
7	ABL x ABL	Serdang x Banting	D X D	23	1
8	ABL x ABL	Deli x Serdang	D X D	23	2
9	ABL x ABL	Marihat/Klanang/Ulu Remis x Yangambi	D X P	20	1
10	ABL x Germ	Ulu Remis x Nigeria	D X P	30	0
11	ABL x Germ	Ulu Remis x Nigeria	D X P	29	0
12	ABL x Germ	Klanang/Marihat x Yocoboue/IRHO	D X P	20	3
13	Germ x ABL	Zaire x AVROS	D X P	23	1
14	Germ x ABL	Angola x AVROS	D X P	22	2
15	Germ x ABL	Tanzania x AVROS	D X P	23	5
16	Germ x Germ	Sierra Leone x Sierra Leone	D X D	23	0
17	Germ x Germ	Nigeria	T selfed	29	0
18	Germ x Germ	Nigeria	D X D	17	8
19	Germ x Germ	Guinea	D X D	23	1
20	Germ x ABL	Cameroon x AVROS	D X T	23	4*
21	Germ x Germ	Nigeria x Nigeria	D X D	23	3*
Total				**460**	**32**

Note: * - Including both parents.

Parental prediction via Cervus 3.0 (Marshall *et al.*, 1998) was first performed for the five progeny groups in Deli *dura* × Nigeria *pisifera* to evaluate the efficiency of the markers in identifying the true parents when no information was provided on the identity of the parental pair (maternal-unfixed mode) in comparison to when only paternal was made unknown (maternal-fixed mode). The subsequent parental blinded analyses aimed to predict maternal and paternal parents.

Validation of TRUE-TO-TYPE VERSION 2

Primer-pairs were designed for the optimised SNP panel using a proprietary primer selection pipeline, similar to Primer3 (Koressaar *et al.*, 2018) and subsequently, used to genotype the 501 samples derived from diverse genetic backgrounds (*Table 2*), using an in-house amplicon sequencing platform similar to Multiplex PCR targeted amplicon sequencing (Onda *et al.*, 2018). Reproducibility of genotyping was determined by genotyping a subset of samples in two to four replicates and parentage assignment was carried out as described above.

RESULTS AND DISCUSSION

Optimal SNP Panel Size for TRUE-TO-TYPE VERSION 2

The main objective in designing the present assay was to identify the true parents for palms analysed, especially when both parents are unknown. The maternal-unfixed mode (available in Cervus 3.0) is an ideal option for such analysis; hence, the 13 marker panels' efficiency in assigning the true parental pair of the five Deli *dura* × Nigeria *pisifera* progeny groups was evaluated. The test revealed consistently high levels of prediction accuracy in the marker panels containing ≥110 SNPs, similar to the analyses performed with informed maternal palm (maternal-fixed mode). However, for smaller panels especially those containing ≤70 SNP markers, the prediction accuracy was reduced drastically (*Figure 1*), suggesting why Version 1 which had only 24 SNP markers was ineffective in identifying the true parents from a panel of possible parental pairs.

Using the maternal-unfixed mode, the blinded parentage analysis was extended to 17 marker panels involving all seven progeny groups (*Table 1*). The result showed that the panel with 110 markers was optimal for high accuracy (99.4%) parental prediction (*Figure 2*). Increasing the number of markers beyond 110 provided minimal additional parental identification benefits.

TRUE-TO-TYPE VERSION 2 Validation

Genotyping assay design was attempted for the 110 selected SNPs and primer-pairs could be designed for 109 SNPs. The 109 primer-pairs were used for genotyping 501 palms (and their replicates) derived from various genetic backgrounds of which, 99.6% of samples generated amplicons. Of the 109 markers genotyped, one completely failed to yield genotype data whereas, 99.0% (108 markers) were successfully called (99.0% call rate) and were 100.0% reproduced across replicates, indicating that they were high-performing SNPs. These 108 SNP markers were evenly distributed across the 16 pseudo-chromosomes of the latest oil palm (EG11) reference genome build (Low *et al.*, 2024) (*Figure 3*). The genotype data obtained was subsequently examined for legitimacy and identification of true parents in the individual families.

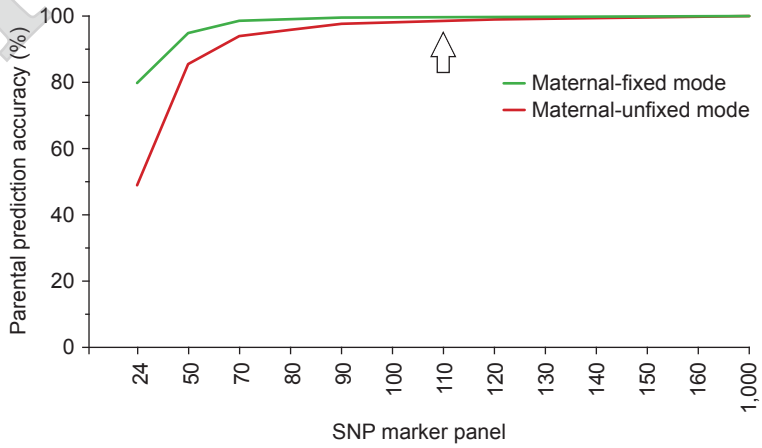

Figure 1. Comparing the prediction accuracy between the maternal-fixed and -unfixed modes in parentage analysis. The respective one- and both-parent blinded-analyses for five progeny groups under the Deli dura *x Nigeria* pisifera *background were performed across 13 panels containing different numbers of SNP markers.*

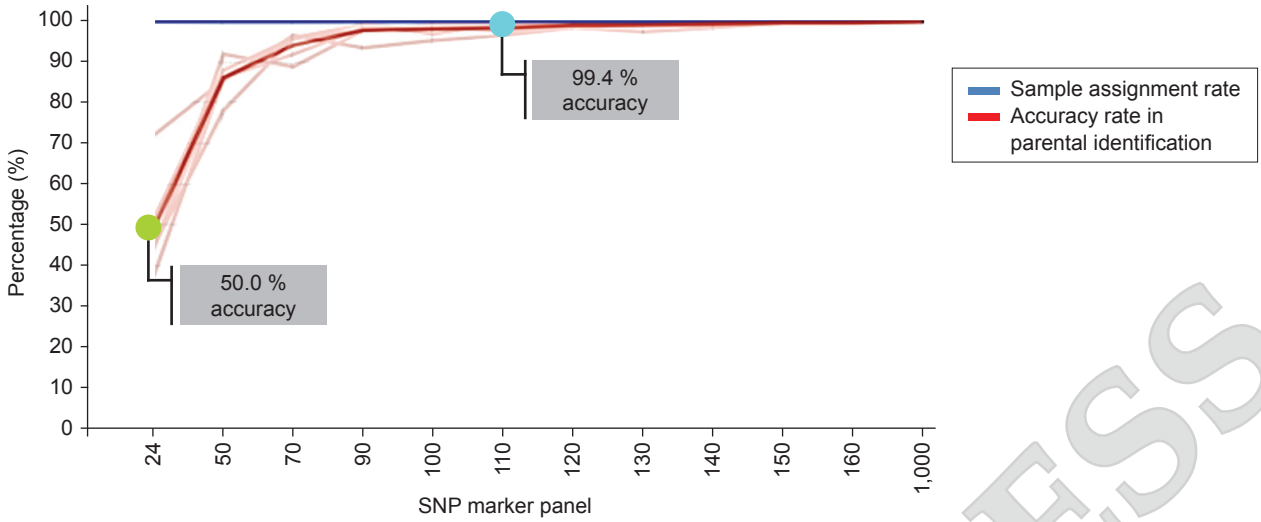

Figure 2. Determining the optimal SNP panel size for TRUE-TO-TYPE VERSION 2 by repeating blinded-analyses. The marker panel with 110 SNPs (indicated by the fluorescent blue dot) was selected as the optimal size for high confident (>95.0%) parental prediction while the 24-SNP panel of Version 1 (indicated by the fluorescent green dot) only encountered ~50.0% accuracy.

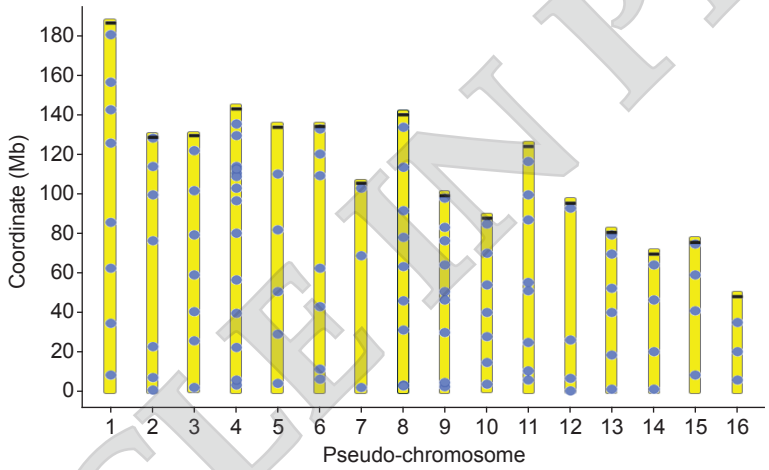

Figure 3. Distributions of TRUE-TO-TYPE VERSION 2 SNPs on the oil palm genome assembly. Yellow vertical bars represent the pseudo-chromosomes of EG11. Blue circles represent the positions of 108 SNP markers, except three SNPs that mapped to the unplaced scaffolds. Black horizontal bars represent the uppermost coordinate of each pseudo-chromosome.

Detection of illegitimates. Marker data for the 21 full-sib crosses involving a total of 460 offspring (*Table* 2) was used to construct a weighted Neighbor-Joining dendrogram using DARwin version 6 (Perrier & Jacquemoud-Collet, 2006), to visualise the genetic relatedness among the samples (*Figure 4*). The samples were clustered into 20 genetic groups, instead of the 21 families that were expected. Crosses No. 5 and 6 (*Table* 2) were obtained from the same parental pair. The dendrogram also showed the presence of several outliers that are possibly illegitimate. The subsequent legitimacy check using a pool of 41 candidate parents confirmed the observation. A total of 32 illegitimate palms (with a triad score ≥0.05) were identified where one to eight offspring were contaminants in the first 19 crosses. None of the assumed parental palms were the true parents for Crosses No. 20 and 21 (*Table 2*), suggesting a possible mix-up when samples were moved from the seed production facility to the nursery and subsequently, to the field. This demonstrates that the TRUE-TO-TYPE VERSION 2 can screen illegitimate palms efficiently at both offspring and parent levels, across a wide range of genetic backgrounds.

Parental identification efficiency. The 389 confirmed offspring palms from Crosses No. 1-19 (*Table 2*) were subjected to the predictions of both parents (maternal-unfixed mode). The result showed 100.0% accuracy in all the predictions made across the offspring of different genetic backgrounds, demonstrating that the TRUE-TO-TYPE VERSION 2 is highly reliable for parental identification even when the number of palms analysed was as few

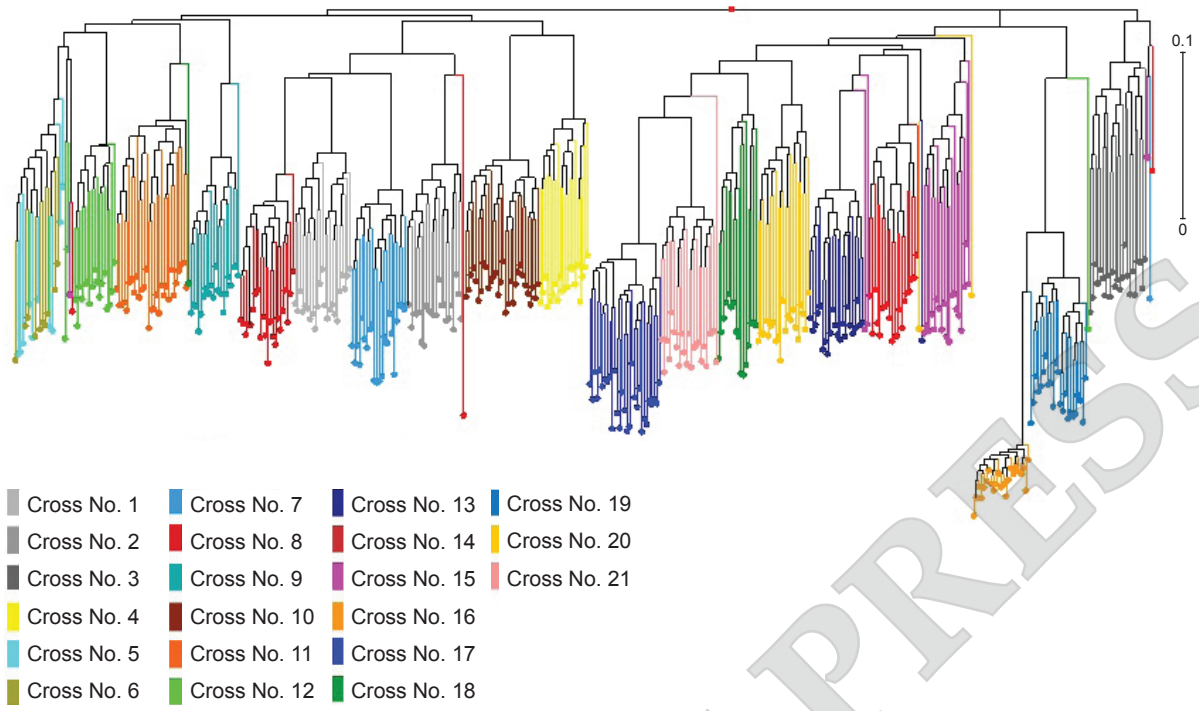

Figure 4. Genetic tree for 460 offspring collected from 21 crosses. Each dot represents an offspring and each family is given in different colour.

as nine. The accuracy rate for the similar parental prediction using the 24 SNP markers of Version 1 was only 79.0%.

For a more detailed examination, the estimated LOD scores for the individual offspring in a representative cross – Ulu Remis *dura* x Yangambi *pisifera* (Cross No. 4 in *Table 2*) were compared between Version 1 and 2 (*Figure 5*). Using the present 108 SNP markers, both parents of all 20 offspring were accurately predicted and a large gap in LOD scores was observed between the true and false parental pairs in the blinded analysis. A similar pattern was not observed when Version 1 was used. In contrast, the LOD scores observed for the samples analysed with the 24-SNP panel were at much lower levels (LOD ≤12) and failed to separate the true from the predicted false parental pairs. This explains the lower rate of identifying the significant parental pair and subtly, lower accuracy of the parental prediction in Version 1 if the actual parental pair was unknown.

Feasibility of Establishing a DNA Fingerprint Database Using TRUE-TO-TYPE VERSION 2

The TRUE-TO-TYPE VERSION 2 platform, which uniquely identifies individual palms and assigns them to specific parents across a wide range of genetic backgrounds, represents a core set of 108 universal SNP markers that can help establish an oil palm DNA fingerprint database. The database captures unambiguous genotype data for the individual palms and if generated for their parental palms, could help establish the DNA fingerprint of an invaluable asset. This will be useful for integrating into a company's management system to protect the IP related to key breeding lines used for commercial seed production. Although morphological traits are widely used to determine distinctness, uniformity, and stability (DUS) for plant variety protection (Plant Varieties Board Malaysia, http://pvpbkkt.doa.gov.my), the narrow genetic pool of commercially produced oil palm materials in Malaysia and other oil palm producing countries (Hartley, 1967; Kushairi & Nookiah, 2000), severely limits the ability to use phenotypes for this purpose. Therefore, a DNA database can protect the existing key breeding lines and new varieties being developed by a particular company. Such DNA fingerprint databases have been established for specific plant species such as maize, where an SSR-based DNA fingerprint database was established to better manage the maize varieties in China (Wang *et al.*, 2017). More recently, SNP markers have been the popular choice which, a core set ranging from 18-200 markers has been developed for setting-up DNA fingerprint databases for variety protection and to overcome potential intellectual disputes in maize (Jiang *et al.*, 2020; Tian *et al.*, 2021; Zhao *et al.*, 2021), tobacco (Wang *et al.*, 2021), cauliflower (Yang *et al.*, 2022) and tomato (Zhang *et al.*, 2023).

The DNA fingerprint database generated using the TRUE-TO-TYPE VERSION 2 platform will also be very useful in deciphering genetic information for important breeding lines which can help characterise the level of diversity within an organisation's seed garden. The various genetic parameters that can be obtained include the genetic diversity or relatedness of the materials, which can be easily visualised as demonstrated for the samples analysed in this study (*Figure 6*). In addition, the allelic information including the number of alleles per locus (k), observed heterozygosity (H_{Obs}), expected heterozygosity (H_{Exp}), polymorphic information content (PIC) and frequency of null alleles (F_{null}) (*Figure 7*), are important parameters to help evaluate the diversity of the materials in the seed garden. Interestingly for all crosses analysed in this study, the H_{Obs} on average were higher than H_{Exp}, suggesting high genetic variability and low levels of inbreeding, contributed by the fact that the crosses involved two parents, with one exception, Cross 17 (selfed cross).

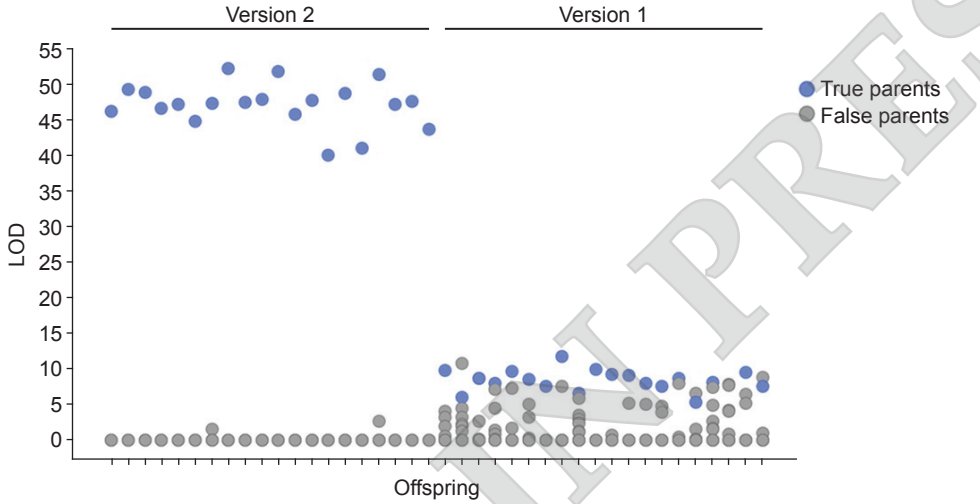

Figure 5. Blinded parental analysis for 20 confirmed offspring in a representative full-sib cross. Positive LOD scores for the true (blue dots) and false parent pairs (grey dots) are plotted for each offspring palm when tested with 24 (Version 1) and 108 (Version 2) SNP markers.

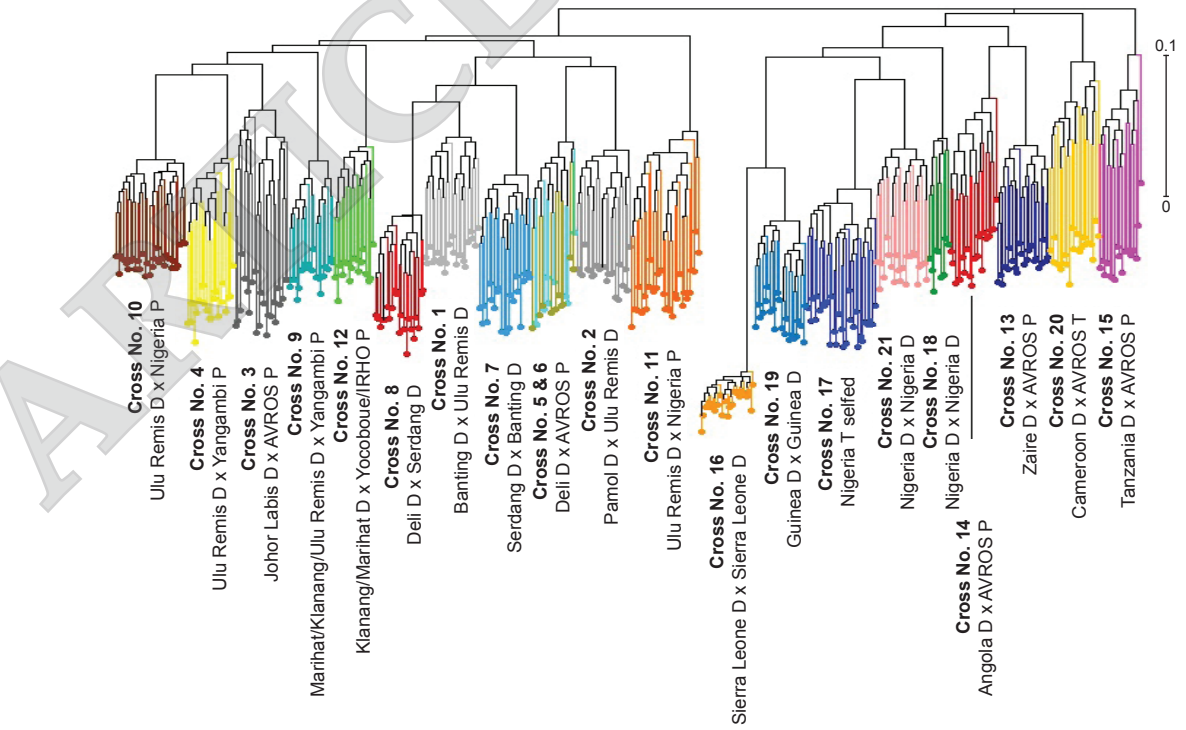

Figure 6. Genetic distances and diversity among legitimate palms of 20 different families validated by TRUE-TO-TYPE VERSION 2.

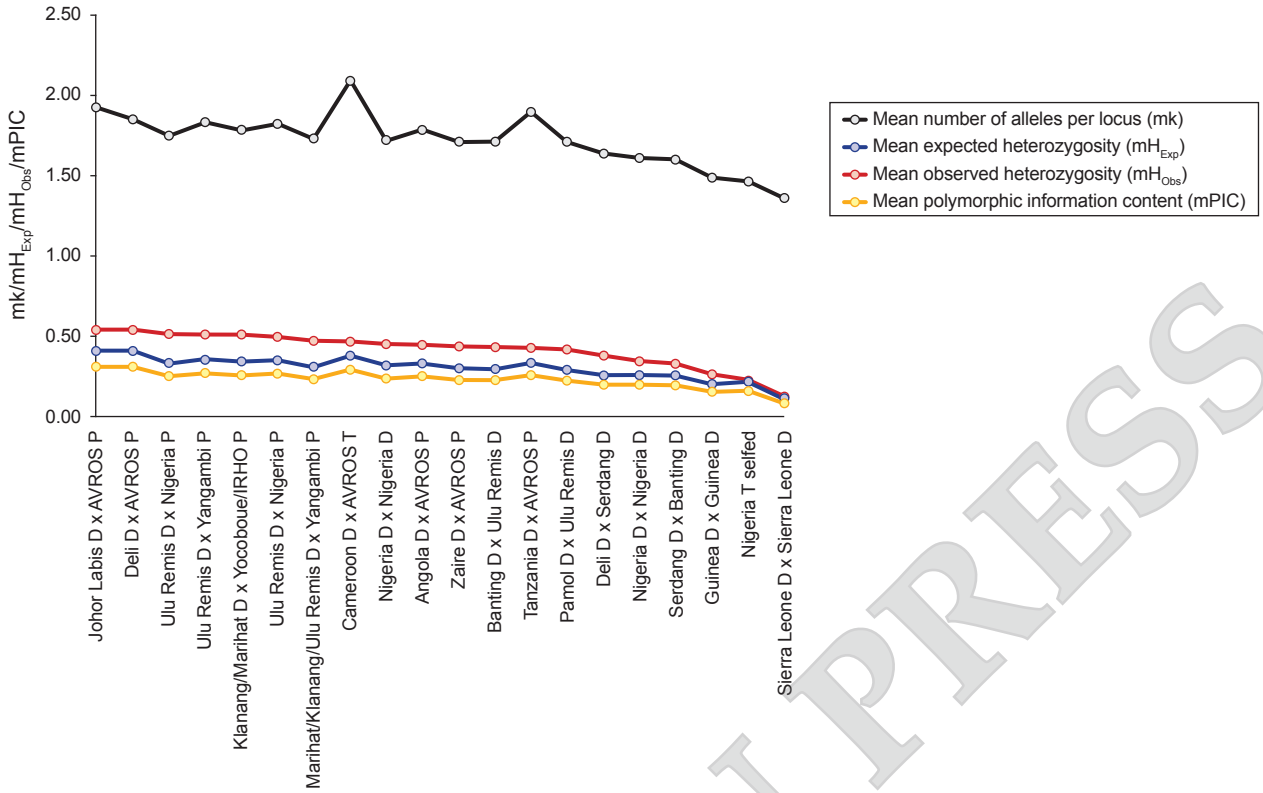

Figure 7. Summary of the allelic information for palm families genotyped by TRUE-TO-TYPE VERSION 2.

CONCLUSION

The genotyping resolution of TRUE-TO-TYPE VERSION 2 has been maximised with a powerful set of 108 SNP markers, four times more relative to Version 1 introduced six years ago. This study has demonstrated the efficiency of TRUE-TO-TYPE VERSION 2 in assigning legitimate palms to their true parental pair in crosses of various genetic backgrounds. This improvement is significant to ensure the parental lines for various palm materials are genetically traceable, particularly in breeding and improvement programs. As a result, other features originally designed for Version 1 such as detecting illegitimates and tracking genetic lineage are also further improved in this new genotyping platform. The new genotyping platform as such, can be utilised for better quality control and to significantly improve breeding and tissue culture procedures' efficiency, which will help accelerate the development of new varieties. More importantly, the new genotyping platform will facilitate the establishment of an unambiguous DNA fingerprint database for the palm materials owned by an organisation. This is useful to avoid infringement of their respective company brand name and fraud concerning the illegal use of a particular company name to sell inferior oil palm seeds and seedlings.

ACKNOWLEDGEMENT

The authors thank the Director-General of the MPOB for the permission to publish this paper. This work was funded by the Twelfth Malaysia Plan (RMKe-12: P2011101202002).

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