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Comparison of quantitative trait loci (QTLs) associated with yield components in two commercial *Dura* × *Pisifera* breeding crosses

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Abstract The high yielding *tenera* is the commercial oil palm planting material of choice in Southeast Asia. Notwithstanding this, there is continuous effort to further improve the yield and one way to do this is by addressing the yield components (YCs). Using 4451 SNP and over 600 SSR markers, this study revealed quantitative trait loci (QTL) associated with YCs in two breeding populations, a Deli *dura* × Yangambi *pisifera* (P2) and a Deli *dura* × AVROS *pisifera* (KULIM DxP). Thirteen and 29 QTLs were identified in P2 and KULIM DxP, respectively. They were compared to other YC-linked QTLs reported previously for different genetic backgrounds by mapping the QTL-linked markers to the oil palm genome. The comparison revealed four common chromosomes containing QTLs influencing various YCs. The results reveal the possible presence of closely linked loci or pleiotropic genes influencing YCs in oil palm. Exploiting the genome data has also facilitated the discovery of candidate genes within or near the QTL regions including those related to glycosylation, fatty acid and oil biosynthesis, and development of flower, seed and fruit.

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Keywords Oil palm · DxP · Quantitative trait loci · Yield components · Comparative QTL mapping

Abbreviations

ABW	Average bunch weight
Acyl-ACP TE	Acyl-acyl carrier protein thioesterase
AFLP	Amplified fragment length polymorphism
AGL8	Agamous-like MADS-box protein
AP	Aspartic proteinase
Aux/IAA	Auxin/indole-3-acetic acid
BN, BNO	Bunch number
Bwt, BW	Bunch weight
CHR	Chromosome
CINV	Alkaline/neutral invertase
cM	Centimorgan
CTAB	Cetyl trimethylammonium bromide
DMWM	Dry mesocarp/wet mesocarp
EG5	*E. guineensis* genome build
FELDA	Federal Land Development Authority Malaysia
FFB	Fresh fruit bunch(es) weight
FTB, FB	Fruit/bunch
Fwt	Fruit weight
GATA	GATA-binding transcription factor
GA2OX	Gibberellin 2-beta-dioxygenase
GGPP	Geranylgeranyl diphosphate chloroplastic
GM	G model
GPAT	Glycerol-3-phosphate acyltransferase
GRF	Growth-regulating factor
GRP	Glycine-rich protein
GS	Genomic selection
HXK1	Hexokinase-1
IM	Interval mapping
KASII, III	Beta-ketoacyl-ACP synthases II, III
KTB	Kernel/bunch
KTF, KF	Kernel/fruit
KW	Kruskal–Wallis test
KY	Kernel yield
LG	Linkage group
LOD	Logarithm of odds
MAS	Marker-assisted selection
MBN	Mean bunch number
MBOAT	Membrane-bound O-acyltransferase
MFFB	Mean fresh fruit bunch(es) weight
MFW	Mean fruit weight
MKW	Mean kernel weight
ML	Maximum likelihood
MPW	Mean mesocarp weight
MSW	Mean shell weight
MTF	Mesocarp/fruit
MQM	Multiple-QTL model
NAC2	NAC domain-containing protein 2
NDL1	N-MYC downregulated 1
N.N. Stress	Nearest neighbor stress
OTB, OB	Oil/bunch
OTDP, O/DM	Oil/dry mesocarp
OTF, OF	Oil/fruit
OTWP	Oil/wet mesocarp
OY	Oil yield
PF	Pulp/fruit
PME	Pectinesterase
PG	Polygalacturonase
PO	Palm oil
QTL	Quantitative trait loci
RFLP	Restriction fragment length polymorphism
SAUR	Small auxin-up RNA-like auxin-responsive protein
SNP	Single nucleotide polymorphism
SRM1	Salt-related MYB1
STF	Shell/fruit
SSR	Simple sequence repeat
TF	Transcription factor
TOT	Total oil
UGT	UDP-glycosyltransferase
VQ	Valine-glutamine motif-containing protein
WMF	Wet mesocarp/fruit
WRI1	WRINKLED1
YC	Yield component

Introduction

Oil palm (*Elaeis guineensis* Jacq.) is the most productive oil crop in the world, and is currently grown on some 19 million hectares (ha) of land. This is only about 0.4% of the total world agricultural land but accounts for almost 40.0% of the global oils and fats (Kushairi et al. 2018). Comparatively, soybean (*Glycine max*) utilizes 40.1% of the total agricultural

land, followed by cottonseed (13.8%), rapeseed (13.0%) and sunflower (10.0%) (Pirker et al. 2016).

In traditional oil palm breeding, the parental lines are continuously crossed to generate superior progenies, similar to producing hybrids in other crops. The progeny from crosses however, are not automatically acceptable just because they come from good parents. Thus, each cross is progeny tested, and only the confirmed combinations with superior yield are used to produce commercial seeds (Soh et al. 2003). It takes on average 10–12 years to develop a new variety, sometimes even up to 20 years for commercial application (Rajanaidu et al. 2000). The question begged is obviously whether the time can be shortened. The main challenge is collection of phenotypic data which is time consuming and labour-intensive, requring years for reliable data compilation. Yield is recorded for at least five years, from six to 10 years after planting in the field and vegetative measurements have to be done several times (Corley and Tinker 2003; Swaray et al. 2020).

In introgressing good trait(s) from Palm A into Palm B, the whole gamut of genes from A, both good and bad, are first incorporated with those from B, and then the undesirable genes weeded out by repeated subsequent self-pollination and selection. It would be faster if only the good gene alleles could be introgressed, but the question has always been how to do so. In recent years, enabling technologies have emerged, such as marker-assisted selection (MAS) and genomic selection (GS). In MAS, markers are used to predict the phenotype, saving time and money in gathering the phenotypic data, as selection can be made even on seedlings when the adult features are yet to show (Collard et al. 2005; Nadeem et al. 2018). More recently, GS, which uses genome-wide markers to estimate the effects of all loci, makes it possible to compute a genomic estimated breeding value for specific traits (Wang et al. 2018) and this approach, is gaining prominence for crop improvement. Both, MAS and GS increase the rate of genetic gain by reducing the necessary selection time for the desired traits. MAS- and GS-based programmes have been applied to improve yield in soybean (Concibido et al. 1997; Sebastian et al. 2010; Jarquín et al. 2014; Fallen et al. 2015; Stewart-Brown et al. 2019) and maize (Yousef and Juvik 2001; Liu et al. 2015; Pace et al. 2015; Beyene et al. 2015; Wang et al. 2020) and have enhanced disease resistance, yield, plant height and flowering time in wheat and rice (Gupta et al. 2010; Poland et al. 2012; Ragimekula et al. 2013; Spindel et al. 2015; Thavamanikumar et al. 2015; Borrenpohl et al. 2020). These molecular strategies are also applicable to oil palm.

In oil palm, the required tools and techniques for MAS and GS have been developed over the last two decades. For example, DNA-based markers and identification of genomic loci associated with monogenic as well as polygenic traits have been reported (Jack and Mayes 1993; Singh and Cheah 2005). The causal genes regulating the two most important monogenic traits—shell and fruit colour—have been identified and the discoveries translated into commercial diagnostic assays (Singh et al. 2013a, 2014; Ooi et al. 2016). For yield, the QTLs associated with oil yield (OY) and various other yield components (YCs) have been reported by Rance et al. (2001), Billotte et al. (2010), Jeennor and Volkaert (2014), Pootakham et al. (2015), Seng et al. (2016), Teh et al. (2016, 2020) and Bhagya et al. (2020). Many QTLs and markers have been associated with OY and various YCs across different genetic backgrounds, suggesting a complex genetic mechanism determining oil palm yield. The QTLs were uncovered using different marker systems, starting with restriction fragment length polymorphism (RFLP), which were largely replaced by amplified fragment length polymorphism (AFLP), simple sequence repeat (SSR) and more recently, single nucleotide polymorphism (SNP) based markers. RFLP-based markers are codominant, but not popular at present as the technique for generating and identifying informative RFLP markers is expensive and laborious. To overcome these shortfalls, AFLP markers can be used instead (Singh and Cheah 1999; Kularatne et al. 2001; Seng et al. 2007) although their dominant nature also posed some limitations in application. Subsequently, SSR markers (also codominant but requiring less DNA and with high reproducibility across laboratories) have become popular in oil palm research (Ting et al. 2010; Zaki et al. 2012; Ting et al. 2013). More recently, SNP markers have gained importance and are preferred due to their wide distribution in the genome, codominant nature and amenability to high throughput analysis (Mishra et al. 2014; Nadeem et al. 2018).

This study constructed a genetic linkage map for a Deli *dura* × AVROS *pisifera* family, a commercial planting material, and updated the Deli

dura × Yangambi *pisifera* genetic map constructed previously by Ting et al. (2014). Both maps were constructed using the same oil palm customised array containing 4451 SNP markers and over 600 SSR markers, making the comparison possible. The genetic maps were then used to identify QTLs associated with OY and YCs, and the results were compared to the QTLs published previously for oil palm. Linking and cataloguing the QTLs identified in different studies and by different marker systems is challenging, but has fortunately been made easier with the publication of the oil palm genome build (EG5) (Singh et al. 2013b). It is now possible to compare QTLs from different crosses and publications to determine if they fall within the same chromosomal regions. The ability to identify overlapping QTLs linked to a trait in a similar chromosomal region, adds confidence to the postulation that the genomic region strongly influences the trait concerned. Inclusion of QTL-linked markers consistently associated with a trait in a panel has increased the prediction accuracy of GS models in cattle improvement (Brøndum et al. 2015). More importantly, candidate genes within or near the QTL regions can now be identified for subsequent analysis to determine the actual causative genes for the yield trait(s).

Materials and methods

Mapping families

The first mapping family—P2 (05 Trial 1)—is an advanced breeding cross between an Ulu Remis Deli *dura* (ENL48) and a Yangambi *pisifera* (ML161). The P2 population consisted of 87 F_1 *tenera* palms currently grown at FGV R&D Sdn. Bhd., Kota Gelanggi, Pahang, Malaysia. The second family namely, KULIM DxP consisted of 135 F_1 *tenera* palms, planted at the Tereh Utara plantation of Kulim Plantation Bhd., Johor, Malaysia. The KULIM DxP palms were generated from a cross between an ex-Ulu Remis Deli *dura* (KT 910512/0804) and an AVROS *pisifera* (KT 911101/1203). The maternal *dura* and the paternal *pisifera* palms are known to have contrasting yield parameters, as *pisifera* is female sterile and rarely produces fruit bunches to maturity (Wonkyi-Appiah 1987; Kushairi et al. 1999; Kushairi and Rajanaidu 2000; Swaray et al. 2020). The maternal Deli *dura* palms are known to have higher bunch weight and lower bunch number compared to the paternal *pisifera* and the resulting intraspecific progenies of these two parental palms show hybrid vigour for yield (Gascon and de Berchoux 1964; Durand-Gasselin et al. 2000; Jin et al. 2017; Singh et al. 2020). Leaf materials from all the palms, including the parental ones, were sampled for DNA extraction and marker analysis.

Yield-related phenotypic data

Ripe bunches from both families were analysed for their YCs over a 5-year period according to the standard protocol used by oil palm breeders (Blaak et al. 1963; Rao et al. 1983; Isa et al. 2011). The standard protocol for determining YCs is also cited in the National standards (SIRIM standard MS157), as the recommended methodology to determine the suitable parental palms for commercial seed production. A minimum of three bunches per palm were analysed for 16 YC parameters: mean bunch number (MBN, no/palm/year), mean fresh fruit bunch weight (MFFB, kg/palm/year), mean fruit weight (MFW, g/fruit), total mesocarp and kernel oils (TOT, ton/ha/year), mesocarp oil yield (OY, ton/ha/year), oil/bunch (OTB, %), oil/wet mesocarp (OTWP, %), oil/dry mesocarp (OTDP, %), mean mesocarp weight (MPW, g/fruit), mesocarp/fruit (MTF, %), kernel yield (KY, ton/ha/year), mean kernel weight (MKW, g/fruit), kernel/fruit (KTF, %), kernel/bunch (KTB, %), mean shell weight (MSW, g/fruit) and shell/fruit (STF, %). The distribution and correlations between the parameters were evaluated using the Kolmogorov–Smirnov normality and Pearson correlation tests in SPSS 16.0.

Genomic DNA extraction

Extraction of genomic DNA from frozen leaves stored at − 80 °C was done using the modified CTAB method (Doyle and Doyle 1990). DNA quality was checked by digestion with *Eco*RI and *Hae*III and electrophoresed on 0.8% agarose gel (Rahimah et al. 2006). The acceptable purity values were 1.8–2.0, as measured by the NanoDrop spectrophotometer (NanoDrop Technologies Inc., Wilmington, DE).

SNP and SSR analyses

SNP genotyping was performed by a service provider using the oil palm customized OPSNP3 Illumina Infinium II Bead-Chip array (Illumina Inc., San Diego, CA) containing 4451 SNPs. For SSR genotyping, fragment analysis was carried out using the ABI PRISM® 3100 Genetic Analyzer (Applied Biosystems, Foster City, CA). The SNP and SSR genotyping analyses were as described by Ting et al. (2013, 2014).

Construction of genetic linkage maps

An integrated genetic map of P2 was constructed previously (Ting et al. 2014). Additional SSR markers (sMo, sMh, sMg, _oSSR, sTE, sEg, sOleiSc, p5sc322 and sPSc) from the MPOB SSR database (http://opsri.mpob.gov.my/opsri/welcome.php) and Billotte et al. (2010) (mEgCIR) were genotyped and added to the P2 map. The KULIM DxP genetic map was constructed using JoinMap® 4.1 (van Ooijen 2006) as described by Ting et al. (2014). In brief, the independent parental and integrated KULIM DxP genetic maps were constructed simultaneously using the maximum likelihood (ML) mapping algorithm, where each linkage group (LG) was formed from marker pairs with recombination frequency ≤ 0.2. The Haldane mapping function was used to determine the map distance in centimorgan (cM) and markers with nearest neighbor stress (N.N. Stress) value > 4 cM were excluded from the individual parental and integrated maps. Finally, a consistent marker-order was determined by four iterations of map calculation. The integrated genetic linkage maps for P2 and KULIM DxP were labeled as DP and DPK, respectively.

QTLs analysis

QTL analysis was carried out separately for DP and DPK as described by Ting et al. (2016). The default parameters in Interval Mapping (IM), the Multiple-QTL Model (MQM) and Kruskal–Wallis non-parametric ranking tests (KW) were used in MapQTL®6 (van Ooijen 2009). The 95.0% genome-wide (GW) and chromosome-wide (CW) LOD significance thresholds for each YC was determined by 1000 permutations. In addition, G model (GM) (Bernardo 2013) was used to estimate the individual marker effect for the QTLs linked to each YC.

Mapping of QTLs to the oil palm genome build

Markers from the QTL regions were aligned to the oil palm reference genome (EG5) (Singh et al. 2013b) to identify their positions on the corresponding pseudo-chromosome using the Exonerate (Slater and Birney 2005) program with its default parameters. Markers with low scores ($< 90.0\%$ matched) and not uniquely mapped were removed. The genomic region corresponding to the QTLs were searched against the predicted oil palm gene model database (Chan et al. 2017) in PalmXplore (http://palmxplore.mpob.gov.my, Sanusi et al. 2018) to identify putative genes and their functions.

Results and discussion

Comparison of DP and DPK genetic maps

A DP (P2) genetic linkage map was constructed previously using AFLP, RFLP, SSR and SNP markers by Ting et al. (2014). A further 240 SSR markers, 151 from MPOB and 89 from Billotte et al. (2010) were added to the current DP map. The updated DP map now contains 1595 markers across 16 LGs, spanning 1714.3 cM. Interestingly, a small number of SNP markers (23 SNPM) that failed to map previously, are now in DP although the same mapping parameters were used. They helped bridge some gaps in the original map and further saturate some regions linked to QTLs e.g. OTB on LGDP2 and MSW and MKW on LGDP3. The DPK genetic map (KULIM DxP) had slightly fewer markers, only 57 SSRs and 1449 SNPs in 16 LGs, covering a total map length of 1902.3 cM. The average map distance per marker in DPK was 1.3 cM, which as expected was close to the 1.1 cM observed in DP. In DP, the LGs were 66.2–193.2 cM, and in DPK, the range observed was 60.7–192.4 cM. In both populations, LGDP/DPK5 was the shortest, and the longest was—LGDP/DPK4. There were in total 746 common markers across the 16 LGs, a comparison of which revealed relatively high collinearity of the markers in both maps (Supplementary Figure 1). This is likely due to both populations having female parents of the Deli *dura* pedigree. This suggests that major chromosomal rearrangements have not yet occurred in domestication of the closely

related parental lines, as also observed for watermelon (Ren et al. 2014).

Yield components (YCs) and correlations between them

Of the 16 YCs evaluated, 11 were common in both P2 and KULIM DxP families—MBN, MFFB, TOT, OY, KY, OTB, KTF, KTB, MKW, MSW and OTWP. The data for MFW, MPW, STF, OTDP and MTF were only available for KULIM DxP. Almost all the YCs (except MSW) had a continuous and significant normal distribution ($p > 0.05$) in both populations. Normality of YC data was also observed in other oil palm mapping families analysed by Billotte et al. (2010), Seng et al. (2016) and Teh et al. (2020). For P2, YC data were available for 75 of its 87 palms, of which three outliers were removed for MBN based on a Boxplot analysis comparing the observed and expected mean values (5.0% trimmed mean, SPSS 16.0). For KULIM DxP, the data was available for all of its 135 palms. However, for MSW, MPW and MKW, one, two and four outliers were removed, respectively, following Boxplot analysis.

MBN was determined for an average of 13 bunches/palm for both families, where the range of observations made for individual palms of P2 and KULIM DxP was 6–16 and 6–19, respectively. As MFFB is influenced by MBN, variation was also observed for it, 72.04–210.53 kg/palm/year in the two populations, while OY was 2.53–7.92 ton/ha/year. The variations for the different YCs are summarized in Supplementary Table S1. Wide distribution was also observed for fruit components, such as mesocarp measurements and their derivatives (MPW, OTWP, OTDP and MTF) as well as the kernel (KY, MKW, KTF and KTB) and shell-related traits (MSW and STF), suggesting that both populations are suitable for QTL analysis for all their YCs measured in this study.

The correlations between the various YCs were consistent in both P2 and KULIM DxP families, with three levels of positive relationships (Fig. 1). Strong correlations were observed among MBN, MFFB, TOT and OY with r = 0.63–0.99. The second level of positive correlations was among the mesocarp and endocarp components. The mesocarp components (OTB, OTDP and MTF) and MPW had moderate correlation with r = 0.20–0.28 for KULIM DxP. Moderate to strong correlations (r = 0.30–0.77) were recorded among the endocarp components where KTF, STF, KY and KTB were correlated with MKW and MSW. Finally, the mesocarp and endocarp components contributing to MFW showed strong correlations with MPW (r = 0.87) and moderate correlations with MKW (r = 0.49). A graphical view of the correlations between the YCs is shown in Fig. 1, while Supplementary Table S2 demonstrates the relationships of both the direct (those categorized in the same group) and contributory effects (those at different levels) of the YCs to the overall yield in oil palm.

Pearson correlation was negative between some YCs, mainly between the mesocarp (OTB, OTPM, OTDP, MPW and MTF) and endocarp (KTF, STF, KY, KTB, MKW and MSW) components. Among them, negative correlations with r = − 0.29 to − 0.95 occurred between MTF and the endocarp components in KULIM DxP. This clearly indicates that increasing mesocarp reduces kernel and shell, and vice versa, suggesting competition among the sinks for assimilates. Strong correlations among the YCs were also reported by Kushairi et al. (1999), Okwuagwu et al. (2008), Okoye et al. (2009), Seng et al. (2016), Osorio-Guarín et al. (2019) and Teh et al. (2020).

P2: QTLs linked to YCs

In the DP genetic map, 10 QTLs, significant at GW, were associated with various YCs. The traits for the QTLs and their LGs were MBN (LGDP13A), OTB (LGs DP2 and DP12), OTWP (LGDP12), KY (LGDP15), MKW (LGs DP3 and DP10), MSW (LGs DP2, DP3 and DP16) (Table 1). A QTL associated with MBN was identified at map interval 0.0–5.0 cM on LGDP13A. An AFLP marker, EAAG/MCTC-125, was closest to the QTL peak detected at LOD 3.9 for MBN. Both the IM and MQM methods revealed that the QTL explained ~ 20.5% of the phenotypic variation for MBN, and a negative (paternal) effect (− 0.59) was estimated using GM. When associating the MBN phenotype with the observed genotype profiles, without the AFLP locus from the paternal palm (denoted *aa* genotype) (Fig. 2A) MBN increased to 13.30 ± 1.53 bunches from 12.11 ± 1.53 bunches. The limitation of an AFLP marker here was its dominant nature, and it was not clear if the marker concerned, EAAG/MCTC-125, amplified a homozygous or heterozygous DNA

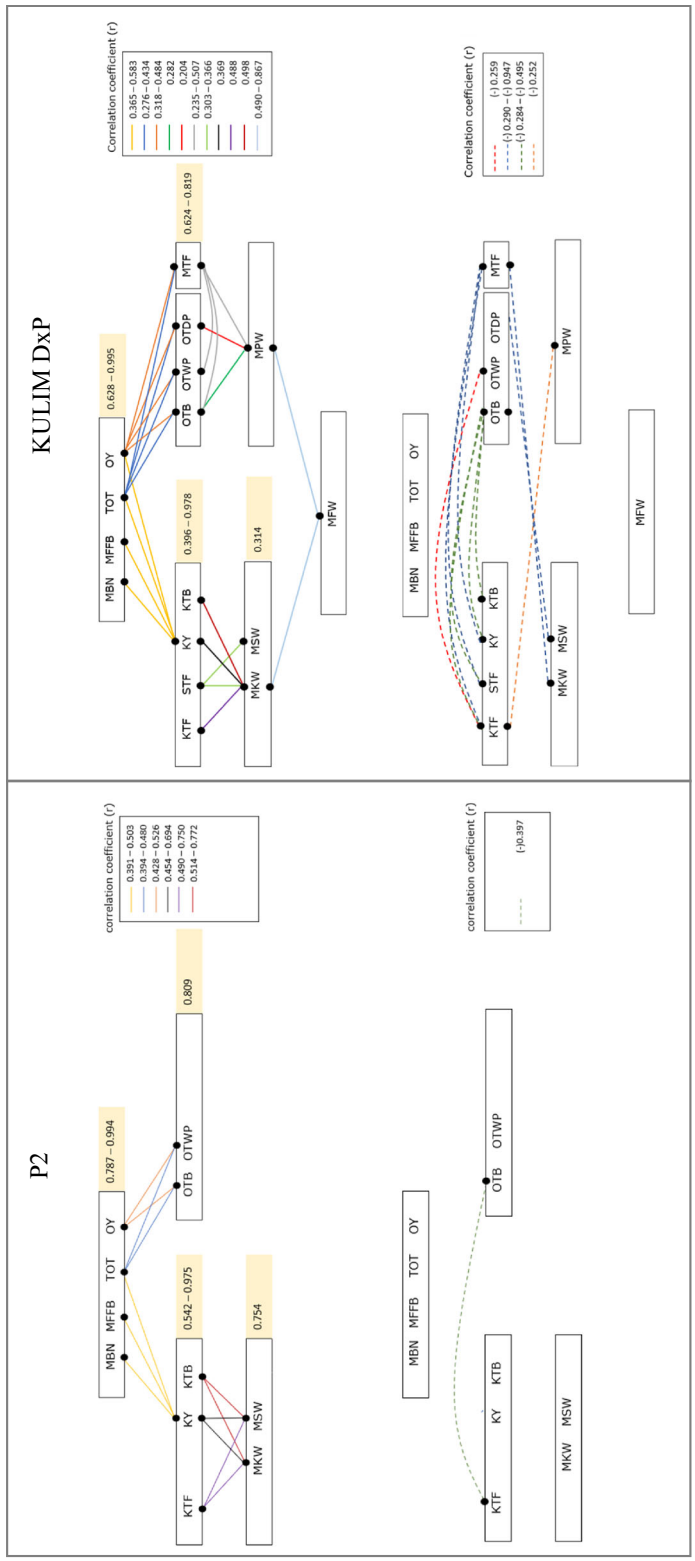

Fig. 1 Significant ($p \leq 0.01$, 2-tailed) positive (solid lines) and negative (dotted lines) correlations between YCs in P2 and KULIM DxP families

Table 1 Genome-wide (GW) significant QTLs detected for YCs in P2

Trait	IM					MQM		KW		GM	
LG	QTL interval (cM)	QTL peak (cM)	QTL peak (LOD)	Closest marker	Variation (%)	LOD	Variation (%)	K value	*p* value	Marker effect	*p* value
Mean bunch number (MBN) (GW:3.4)											
DP13A	0–5.0	0	3.9	EAAG/MCTC-125	20.5	3.9	20.6	11.4	0.0010	0.59(−)	0.000969
Oil/bunch (OTB) (GW:3.2)											
DP2	48.0–52.0	48.7	3.8	SNPM02314	22.4	3.6	20.5	8.3	0.0050	0.92(−)	0.007228
				SNPM03157						0.92(−)	0.007228
				SNPM01965						0.92(−)	0.007228
				SNPM03715						0.92(−)	0.007228
DP12	34.3–42.8	39.8	3.6	SNPM04433	20.4	3.6	20.4	14.7	0.0005	1.20(−)	0.000160
Oil/wet mesocarp (OTWP) (GW:3.2)											
DP12	38.0–40.0	39.8	3.3	SNPM04433	18.8	3.3	18.8	15.3	0.0001	2.14(−)	0.000263
Kernel yield (KY) (GW:3.3)											
DP15	75.0–82.1	77.0	3.6	SNPM01951	34.1	3.6	34.1	5.4	0.0500	0.07(+)	0.013897
Mean kernel weight (MKW) (GW:3.4)											
DP3	54.2–58.5	54.2	3.8	mEgCIR3301	21.1	3.8	21.1	15.5	0.0050	0.18(−)	0.037698
				SNPM01588						0.11(+)	0.000661
				sPSc00682						0.09(−)	0.000187
DP10	11.7–22.9	20.7	3.7	EAGC/MCAA-302	22.7	3.4	22.5	4.3	0.0500	0.05(+)	0.043500
Mean shell weight (MSW) (GW:3.3)											
DP2	8.6	8.6	3.4	SNPM02999	19.1	3.4	19.1	9.0	0.0050	0.10(+)	0.002726
				mEgCIR2149						0.08(+)	0.002726
				SNPM03213						0.06(+)	0.029294
				sMg00194						0.07(+)	0.016289
DP3	53.0–57.5	54.2	4.6	mEgCIR3301	25.3	4.6	25.3	19.3	0.0005	0.25(−)	0.042563
				SNPM01588						0.16(+)	0.000064
				sPSc00682						0.12(−)	0.000046
DP16	0.5–2.5	1.2	3.8	SNPM02704	21.3	3.8	21.5	13.4	0.0050	NA	NA
				SNPM04360						NA	NA

QTLs identified using Interval Mapping (IM), Multiple-QTL Model (MQM), Kruskal–Wallis non-parametric tests (KW) and G Model (GM)

NA: Not analysed using GM as both parents have same '*ab*' genotype <*ab*x*ab*>

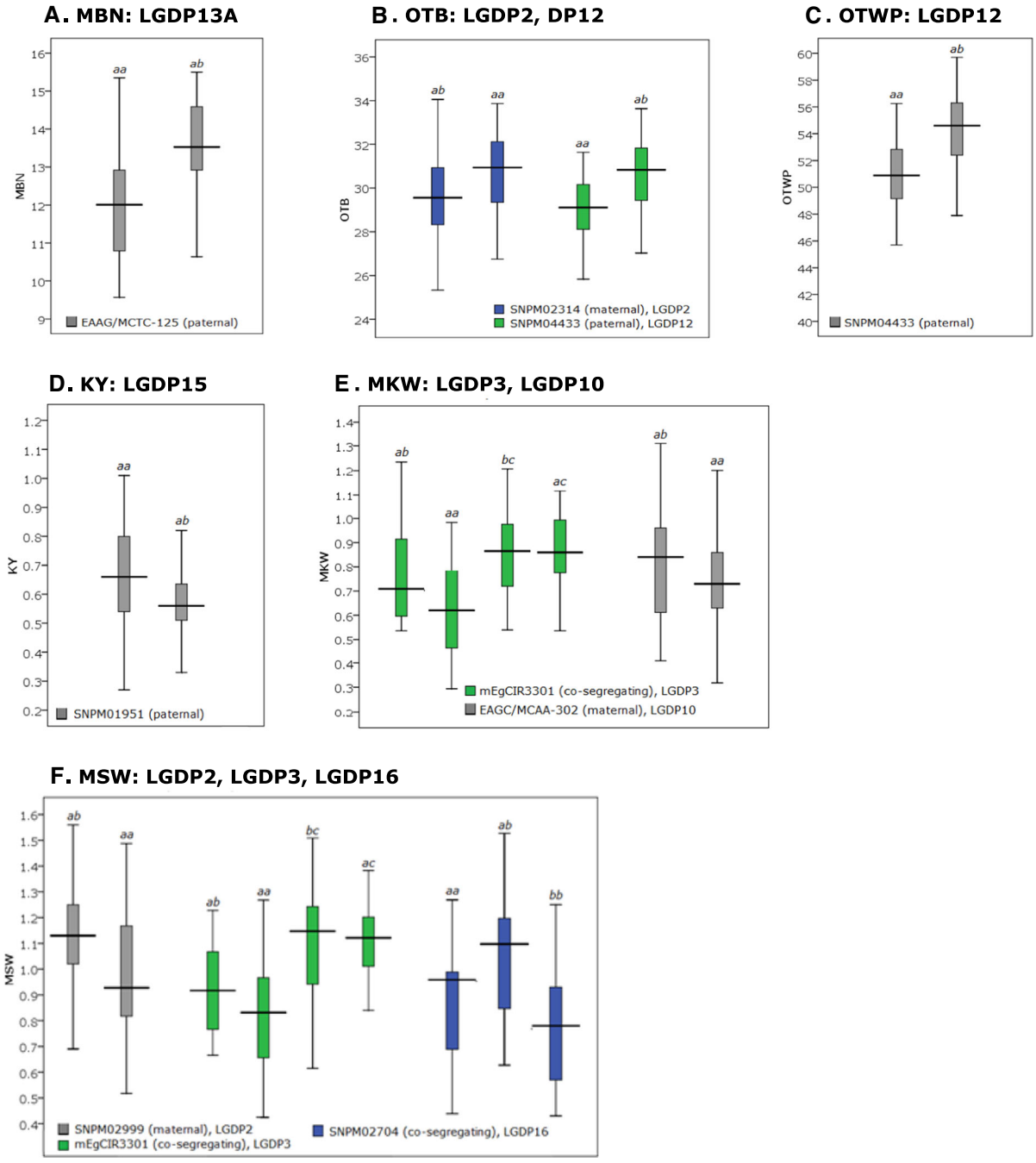

Fig. 2 Boxplot distribution of YCs by genotype of closest markers to QTL peaks in P2

segment. Therefore, other flanking markers (LOD 3.6)—namely, sMo00166, sMo00196, SNPM04999 and SNPM03169—located ~ 2.6 cM (Figure S1) away were used as proxies, although the phenotypic variation explained was slightly reduced to 18.6.

QTLs associated with OTB were found in the 48.0–52.0 cM (4.0 cM confidence interval) and 34.3–42.8 cM (8.5 cM confidence interval) regions of LGs DP2 and DP12, respectively. Markers from the two intervals showed negative effects from 0.9 to

1.2% ($p = 0.007$). The closest markers flanking the QTLs were SNPM02314 (LGDP2) and SNPM04433 (LGDP12). Palms categorized in the genotypes *ab* and *aa* had significant differences in OTB ($p \leq 0.05$ T test, SPSS 16.0). For the marker from the maternal palm—SNPM02314—the homozygous genotype *aa* showed increased OTB (31.4 ± 2.6%), ~ 1.9% higher than the *ab* genotype (29.6 ± 2.9%). The genotype of the paternal marker SNPM04433, meanwhile, had an opposite effect on OTB. The *aa* genotype (28.7 ± 2.8%) had 2.6% lower OTB than *ab* (31.3 ± 2.6%) (Fig. 2B).

In addition to OTB, LGDP12 also hosted another GW significant QTL, OTWP, which interval overlapped that for OTB, with the same marker, SNPM04433, located closest to the QTL peaks for both traits. This explained why the two YCs were strongly correlated (r = 0.81). However, SNPM04433 had a stronger effect of − 2.14 ($p = 0.000263$) for OTWP than for OTB (only − 1.20, $p = 0.000160$). This was likely due to the larger variation for OTWP (3.2%) in the two genotypes *ab* (54.0 ± 3.5%) and *aa* (50.9 ± 3.2%) (Fig. 2C). QTLs associated with kernel and shell components, such as KY, MSW and MKW, were also identified on DP. The markers linked to them explained less of the phenotypic variation than those linked to the QTLs for fruit bunch, whole fruit and mesocarp components (Table 1). This is demonstrated for KY where marker SNPM01951 from the QTL interval 75.0–82.1 cM in LGDP15 showed an effect of only 0.07 ($p = 0.013897$). The average KY for the two genotypes *ab* and *aa* were 0.57 and 0.66 ton/ha/year, respectively, a difference of only 0.09 ton/ha/year (Fig. 2D). Similar observations were made for MSW and MKW where the genotypes *ab* and *aa* of SNPM02999 (LGDP2) and EAGC/MCAA-302 (LGDP10) showed only a small difference of not more than 0.18 g (Fig. 2E, F). Additional QTLs for MSW and MKW were observed in LGs DP3 and DP16 where markers showing clear codominant segregating profiles were detected close to their QTL peaks. The SSR marker mEgCIR3301 had three alleles <*ab*x*ac*> , which segregated into four genotype classes—*ab*, *aa*, *bc* and *ac*. Interestingly, *ab* and *aa* showed lower phenotypic values than *bc* and *ac* (Fig. 2E, F). Another interesting marker was SNPM02704 at the QTL interval associated with MSW on LGDP16. The two parental palms showed the same genotype <*ab*x*ab*> and therefore, their parental effects and contribution to the trait could not be determined via GM. However, among the three observed genotypes, *bb* had the lowest MSW (0.79 ± 0.3 g) compared to *aa* (0.96 ± 0.2 g) and *ab* (1.10 ± 0.2 g) (Fig. 2F).

In this study, QTL analysis also revealed a number of putative QTLs for YCs (Table 2). By permutating the entire 16 LGs, these QTLs had LOD scores lower than their GW significance thresholds but higher than their 95.0% significant thresholds at the chromosome level. In this respect, three CW significant QTLs, termed putative, were identified for MBN, TOT and OY in LGDP2. Interestingly, these three production components are strongly related to each other (r = 0.79–0.99). In oil palm, a common QTL interval on the genetic map for related YCs, such as OTB, OTF, STF, KTF and DMWM, was also reported by Jeennor and Volkaert (2014). Similarly, in other crops, clustering of QTLs was reported for fiber quality and various yield traits in cotton (Keerio et al. 2018), weight, length, diameter and peduncle length in tomato (Portis et al. 2014), grain yield, harvesting index and grain weight in rice (Zhu et al. 2017) as well as maturity date, fruit development, fruit structure and the solid soluble content in sweet cherry (Calle and Wünsch 2020). The co-localization of multiple QTLs suggests the presence of closely linked loci or pleiotropic genes (Billotte et al. 2010; Lemmon and Doebley 2014).

KULIM DxP: QTLs linked to YCs

In this population, GW-significant QTLs were identified for nine YCs (Table 3). The YCs with their associated QTLs and LGs were MBN and MFFB (LGDPK1), OTB (LGDPK8), OY and TOT (LGDPK1 and DPK8), KTB, KTF and MTF (LGDPK14) and STF (LGDPK4). A QTL was associated with MBN at interval 0–7.2 cM on LGDPK1, explaining ~ 15.9% of the phenotypic variation for the trait. The QTL peak had LOD 5.1 and the closest marker was a SSR, mEgCIR3803, with four genotype classes among the progenies, namely *ac*, *ad*, *bc* and *bd*. Palms with the *ac* and *bc* genotypes had lower MBN of 12.61 ± 0.39 and 12.76 ± 0.38, respectively, than those with the *bd* (13.90 ± 0.33) and *ad* (14.85 ± 0.36) genotypes (Fig. 3A). Within the same QTL interval, a smaller region (0.75–7.58 cM) was associated with MFFB, where the SNP marker, SNPM01086 was located

Table 2 Chromosome-wide (CW) QTLs detected for YCs in P2

Trait	CW	IM					MQM		KW		GM	
LG		QTL interval (cM)	QTL peak (cM)	QTL peak (LOD)	Closest marker	Variation (%)	LOD	Variation (%)	K value	*p* value	Marker effect	*p* value
Mean bunch number (MBN)												
DP2	2.7	12.9	12.9	2.8	SNPM01194	14.6	2.8	14.6	12.0	0.0050	NA	NA
Total oil (TOT)												
DP2	3.1	12.7–12.9	12.9	3.2	SNPM01194	18.2	3.2	18.2	8.9	0.0500	NA	NA
Oil yield (OY)												
DP2	3.0	12.7–12.9	12.9	3.1	SNPM01194	17.6	3.1	17.6	7.8	0.0500	NA	NA

QTLs identified using Interval Mapping (IM), Multiple-QTL Model (MQM), Kruskal–Wallis non-parametric tests (KW) and G Model (GM)

NA: Not analysed using GM as both parents have same '*ab*' genotype <*ab*x*ab*>

closest to the QTL peak. In fact, MFFB is one of the most important traits that indicates the productivity of oil palm. This co-segregating <*ab*x*ab*> marker demonstrated that both the *aa* (157.92 ± 3.30 kg) and *ab* (156.56 ± 2.52 kg) genotypes contributed to significantly higher MFFB production than palms with the *bb* genotype (143.02 ± 4.28 kg) (Fig. 3B). On LGDPK1, the slightly extended interval from 0.00 to 7.60 cM also hosted QTLs for OY and TOT, where the co-segregating marker SNPM01086 was closest to the QTL peak. Higher OY (6.1 ± 0.2 ton/ha/year) and TOT (6.60 ± 0.1 ton/ha/year) were observed for the *aa* than in the *ab* (5.8 ± 0.1 ton/ha/year OY and TOT) and *bb* (5.24 ± 0.18 ton/ha/year OY and 5.76 ± 0.19 ton/ha/year TOT) genotypes.

The QTLs associated with OY and TOT were also identified on LGDPK8 (92.3–105.2 cM), with two SNP markers, SNPM02425 and SNPM02400, located closest to the QTL peaks, respectively. The OY-linked SNPM02425 showed a co-segregating profile <*ab*x*ab*>, i.e., palms with the *bb* genotype had higher OY (6.18 ± 0.13 ton/ha/year) than those with *aa* (5.26 ± 0.2 ton/ha/year) and *ab* (5.76 ± 0.1 ton/ha/year). For the QTL associated with TOT, the maternally inherited marker SNPM02400 revealed significantly higher TOT (6.6 ± 0.1 ton/ha/year) for the homozygous genotype (*aa*) than *ab* (5.83 ± 0.1 ton/ha/year). Interestingly, SNPM02400 also pointed to another QTL associated with OTB located at the 101.1–103.4 cM interval. The *aa* genotype of this marker was also responsible for higher OTB (28.2 ± 0.2%) than *ab* (26.8 ± 0.2%) (Fig. 3C). The three YCs discussed above—OTB, OY and TOT—were significantly related with each another. Therefore, selection for higher OTB will also increase OY and TOT, although these three YC traits are highly influenced by the environment (Soh et al. 2017). The heritability for the three YCs are low, so their breeding improvement will be highly dependent on the environment and general operational management of the trials. If the environment is unfavourable and operational management is poor, the gains from MAS will be tentative.

On LGDPK4, the QTL interval associated with STF was 3.5–16.2 cM. It explained 18.6% of the phenotypic variation in STF and the closest marker to the QTL peak was SNPM00151, which revealed a marker effect of − 0.73% (heterozygous in the paternal palm). The heterozygous (*ab*) group showed a

Table 3 Genome-wide (GW) significant QTLs detected for YCs in KULIM DxP

Trait	IM					MQM		KW		GM	
LG	QTL interval (cM)	QTL peak (cM)	QTL peak (LOD)	Closest marker	Variation (%)	LOD	Variation (%)	K value	*p* value	Marker effect	*p* value
Mean bunch number (MBN) (GW = 4.5)											
DPK1	0.7–7.2	4.2	5.1	mEgCIR3803	15.9	5.1	15.9	22.7	0.0001	NA	NA
Mean fresh fruit bunch (MFFB) (GW = 4.5)											
DPK1	0.7– 7.6	2.3	5.4	SNPM01086	16.8	5.4	16.8	11.4	0.0050	NA	NA
Oil/bunch (OTB) (GW = 4.5)											
DPK8	101.1–103.4	102.8	4.6	SNPM02400	14.5	4.6	14.5	17.4	0.0001	0.72(+)	0.000011
Oil yield (OY) (GW = 4.3)											
DPK1	0.0–7.6	2.27	5.4	SNPM01086	16.5	5.3	16.5	23.6	0.0001	NA	NA
DPK8	92.3–105.2	98.8	5.1	SNPM02425	16.0	5.1	16.0	19.6	0.0001	NA	NA
Kernel/bunch (KTB) (GW = 4.6)											
DPK14	46.9–64.8	54.0	6.9	SNPM04522	21.1	6.9	21.1	28.5	0.0001	0.37(−)	0.000000
				SNPM04938	21.1	6.9	21.1	28.5	0.0001	0.37(−)	0.000000
Kernel/fruit (KTF) (GW = 4.5)											
DPK14	48.9–62.8	54.0	6.1	SNPM04938	18.8	6.1	18.8	24.6	0.0001	0.50(−)	0.000000
				SNPM04522	18.8	6.1	18.8	24.6	0.0001	0.50(−)	0.000000
Mesocarp/fruit (MTF) (GW = 4.4)											
DPK14	53.5–60.4	57.4	4.9	SNPM01100	15.6	5.0	15.8	20.2	0.0001	0.85(+)	0.000002
		54.0	4.7	SNPM04522	14.9	4.7	14.9	20.2	0.0001	0.94(+)	0.000005
				SNPM04938	14.9	4.7	14.9	20.2	0.0001	0.94(+)	0.000005
Shell/fruit (STF) (GW = 4.5)											
DPK4	3.5–16.2	6.7	6.0	SNPM00151	18.6	6.0	18.6	24.6	0.0001	0.73(−)	0.000000
Total oil (TOT) (GW = 4.5)											
DPK8	93.1–102.8	102.8	4.7	SNPM02400	14.8	4.7	14.9	19.3	0.0001	0.38(+)	0.000006
DPK1	0.0–7.6	2.3	5.2	SNPM01086	16.2	5.2	16.2	14.2	0.0010	NA	NA

QTLs identified using Interval Mapping (IM), Multiple-QTL Model (MQM), Kruskal–Wallis non-parametric tests (KW) and G Model (GM)

NA: Not analysed using GM as both parents have same '*ab*' genotype <*ab*x*ab*>

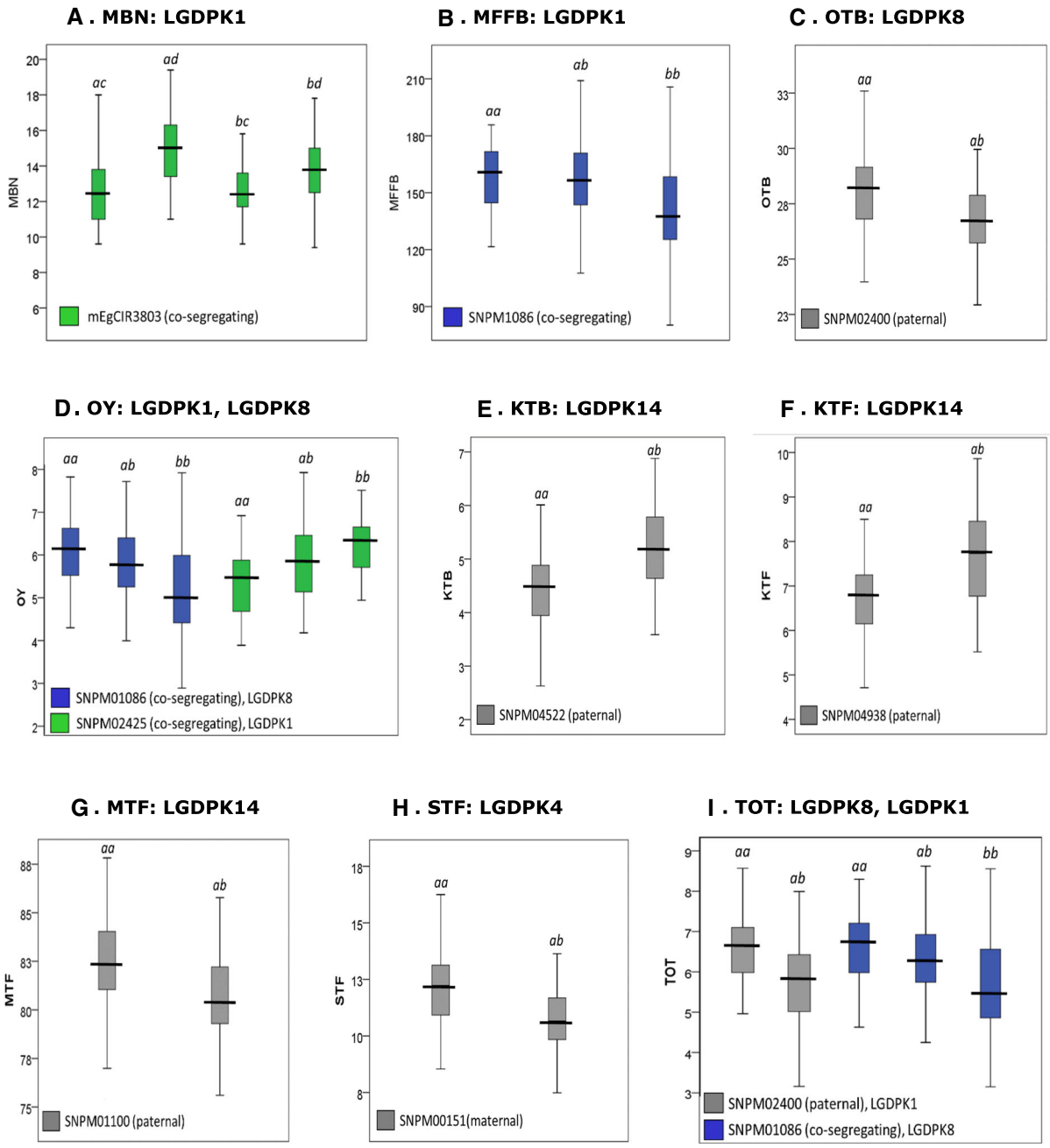

Fig. 3 Boxplot distribution of YCs by genotype of closest markers to QTL peaks in KULIM DxP

significantly lower STF (10.60 ± 0.19%) than *aa* (12.06 ± 0.19%) (Fig. 3H). On DPK14, the QTLs for three highly correlated traits—KTF, KTB and MTF were found within the same map interval (46.9–64.8 cM). For KTF and KTB, the markers closest to the QTL peak (54.0 cM) were SNPM04522 and SNPM04938 which mapped on the same locus, indicating they had similar segregation profiles in the mapping family. The phenotypic variation explained by the QTL for KTF (18.8%) was higher than that for KTB (21.1%). Based on the genotypes of both markers, higher KTF and KTB were observed for the *ab* (7.69 ± 0.13% KTF and 5.20 ± 0.09% KTB) than the homozygous *aa* genotype (6.70 ± 0.13% KTF and

4.46 ± 0.09% KTB) (Fig. 3E, F). Within the same map interval, SNPM01100, located closest to the QTL peak (57.4 cM), accounted for 15.6% of the MTF phenotypic variation. In contrast with KTF and KTB, the *aa* genotype of SNPM01100 showed significantly higher MTF (82.45 ± 0.31%) than *ab* (80.4 ± 0.28%) (Fig. 3G). Interestingly, marker SNPM01100 was also significantly associated with KTF and KTB, although it was not closest to their QTL peaks. This indicates that within the QTL interval, this marker influences multiple traits differently depending on its genotype, which is supported by the significant correlations of KTF and KTB with MTF. This suggests that the genes that contribute to increased kernel size (larger KTF and KTB) will reduce mesocarp (MTF). So, selection for MTF will reduce KTF, boosting the mesocarp oil yield (Kushairi et al. 1999).

This study also identified a number of putative QTLs for various YCs on LGs DPK2 (OTDP), DPK4 (MFW, MPW, MSW and KY), DPK5 (MPW, MFW, OTB, OTWP and OTDP), DPK7 (OTWP), DPK8 (MBN), DPK13 (KTF) and DPK14 (MKW, STF and KY). Information on the putative QTLs is summarized in Table 4.

Comparison of common QTLs between P2 and KULIM DxP

This study identified 42 QTLs (21 putative) in P2 and KULIM DxP, distributed across 12 LGs (except 06, 09 and 11). Within each family, a number of the QTLs were co-localized on the same regions, such as on LGs DP1 (MFFB, TOT and OY), DP2 (MBN, OY and TOT) and DP12 (OTB and OTWP) in P2. In KULIM DxP, common QTLs were found on LGs DPK5 (MFW, MPW, OTB, OTDP and OTWP), DPK8 (OTB and TOT) and DPK14 (MTF and STF and; KTB and KTF). However, comparing P2 and KULIM DxP, only a few QTLs were detected in the same LGs for both. The QTLs on the same LGs were those associated with OTB, MBN, OY, TOT and MSW with OTDP in LG2, and MBN with KTF in LG13. However, the QTLs in the same LGs in P2 and KULIM DxP did not overlap, either in the genetic or physical map.

The lack of common QTLs in both families is likely due to differences in their genetic backgrounds, especially as their *pisifera* parents were different. The *pisifera* of P2 was Yangambi and that of KULIM DxP was AVROS, of quite separate origins. The *pisifera* of KULIM DxP contributed most of the alleles that revealed the GW QTLs for OTB (LGDPK8), KTB, KTF, MTF (LGDPK14) and TOT (LGDPK1). The maternal *dura*, as expected, contributed the alleles for the STF-related QTLs, as the shell trait is maternally inherited. However, in P2, the GW QTLs detected were contributed in equal numbers by both the paternal and maternal parents. Its paternally inherited QTLs were those associated with MBN (LGDP13A), OTB, OTWP (LGDP12) and KY (LGDP15).

QTLs from different studies

The QTLs identified in this study were compared with 144 previously reported for several oil palm crosses (Billotte et al. 2010; Jeennor and Volkaert 2014; Pootakham et al. 2015; Seng et al. 2016; Teh et al. 2016; Bai et al. 2017; Ithnin et al. 2017). Comparison was also made to the QTLs already detected for MFW, MPW, STF, MTF and OTDP in P2 (Ting et al. 2018). The sequences of all the published QTL-linked markers were first mapped to the EG5 genome build to locate them in their pseudo-chromosomes. The results showed that most of the QTLs identified in our study were unique to P2 or KULIM DxP, and have not been reported in other oil palm crosses. Nevertheless, genomic regions on CHR09 and 14 that hosted QTLs in LGs DP7 and DP3 was common to those reported in different genetic backgrounds (discussed below). And, another five QTLs detected in our study are located as close as 2792 bp to the QTLs reported previously in CHR02, 06 and 15 (Fig. 4).

In CHR02, marker SNPM00151, linked to the QTLs for STF and MSW, was located only ~ 236.4 kb away from the SSR marker sMg00022 that was reported to be associated with KB and KF by Seng et al. (2016). Interestingly, STF is positively related with both KB and KF, which explains why the same genomic region may influence both traits. In the window (2,092,554–2,328,938 bp) which encompasses both the QTL intervals, we identified two genes—*acyl-acyl carrier protein thioesterase* (*Acyl-ACP TE*) and *UDP-glycosyltransferase* (*UGT*) involved in the fatty acid (FA) biosynthesis and glycosylation modification, respectively, during fruit development and ripening (Pulsifer et al. 2014; Jing et al. 2011; Sun et al. 2017; Wu et al. 2017; Peng et al.

Table 4 Chromosome-wide (CW) QTLs detected for YCs in KULIM DxP

Trait	CW	IM					MQM		KW		GM	
LG		QTL interval (cM)	QTL peak (cM)	QTL peak (LOD)	Closest marker	Variation (%)	LOD	Variation (%)	K value	*p* value	Marker effect	*p* value
Mean bunch number (MBN)												
DPK8	3.1	157.4–162.0	7.9	3.61	SNPM00157	11.6	3.6	11.6	12.9	0.0005	0.79(+)	0.000097
Mean fruit weight (MFW)												
DPK5	2.6	24.3–54.7	43.8	3.56	SNPM01913	11.6	3.6	11.5	14.0	0.0005	0.52(+)	0.000155
DPK4	3.5	147.1–171.9	159.5	4.11	SNPM01593	12.9	4.3	13.7	17.0	0.0001	0.57(+)	0.000017
Mean mesocarp weight (MPW)												
DPK4	3.2	150.5–174.8	159.5	4.2	SNPM01593	13.5	3.6	11.6	14.6	0.0005	0.46(+)	0.000077
DPK5	2.7	38.8–52.7	43.8	3.25	SNPM01913	10.6	3.3	10.6	16.6	0.0005	0.45(+)	0.009190
Mean shell weight (MSW)												
DPK4	3.3	3.8–9.7	6.7	3.56	SNPM00151	11.5	3.51	11.3	16.5	0.0001	0.10(−)	0.008394
Mean kernel weight (MKW)												
DPK14	3.0	61.4–65.8	62.8	3.3	SNPM00455	10.9	3.21	12.1	10.3	0.005	0.02(−)	0.000105
Kernel yield (KY)												
DPK14	3	101.6–106.0	101.6	4.0	SNPM03523	12.9	3.0	10.8	12.1	0.0010	NA	NA
DPK4	3.4	54.0–62.8	55.7	3.1	SNPM00230	10.4	3.4	11.0	13.1	0.0050	0.06(−)	0.000529
Oil/wet mesocarp (OTWP)												
DPK7	3.1	29.2–31.9	31.9	3.4	SNPM04582	13.1	2.7	10.9	4.0	0.0500	0.64(−)	0.000709
DPK5	2.8	4.5–32.0	20.5	3.8	SNPM03432	12.8	3.7	12.0	12.7	0.0005	0.64(−)	0.000709
Oil/dry mesocarp (OTDP)												
DPK5	2.6	17.4–22.5	20.5	2.9	SNPM03432	10.3	2.8	9.2	4.0	0.0500	0.78(−)	0.000482
DPK2	2.9	101.0	101.0	2.9	SNPM03435	9.4	3.0	9.7	12.5	0.0050	NA	NA
Oil/bunch												
DPK5	2.8	15.4–20.5	20.5	2.9	SNPM03432	9.8	2.8	9.2	8.1	0.0050	0.45(−)	0.007484
Kernel/fruit (KTF)												
DPK13	2.9	52.3	52.3	2.9	SNPM00839	9.4	2.7	8.7	10.5	0.0100	NA	NA
Mesocarp/fruit (MTF)												
DPK16	2.9	43.7–52.8	48.4	3.8	SNPM01404	12.3	3.8	12.2	8.0	0.005	0.72(−)	0.001453
Shell/fruit (STF)												
DPK14	2.9	54.0–57.4	57.4	3.4	SNPM01100	10.9	3.5	11.4	15.0	0.0005	0.56(−)	0.000111

Table 4 continued

Trait	CW	IM				MQM		KW		GM	
LG		QTL interval (cM)	QTL peak (cM)	QTL peak (LOD)	Closest marker	Variation (%)	LOD	Variation (%)	K value	*p* value	Marker effect	*p* value
DPK16	3.0	44.1–52.7	48.4	4.0	SNPM01404	13.0	4.0	13.0	8.8	0.0050	0.49(+)	0.000790

QTLs identified using Interval Mapping (IM), Multiple-QTL Model (MQM), Kruskal–Wallis non-parametric tests (KW) and G Model (GM)

2020). In the oil palm fruit, the *Acyl-ACP TE* genes such as *FATA* and *FATB* encode protein that hydrolyse the FA acyl chains from ACPs. *FATA* is quite specific for unsaturated acyl ACPs e.g. C18:1-ACP for release of C18:1, and *FATB* for saturated acyl-ACPs, e.g. C16:0-ACP and C14:0-ACP for release of C16:0 and C14:0, respectively thus, playing essential roles in determining the FA composition of palm oil (Sambanthamurthi et al. 2000; Othman et al 2001). *UGT* is involved in anthocyanin glycosylation, the process of accumulating phenolic compounds which are responsible for the customary deep orange-to-red colour of oil palm exocarp. Based on their biological activities, the two genes have a direct impact on the composition of palm oil produced. However, their impact on the shell (and kernel) components, if any, require further investigation.

In CHR06, the marker EAGC/MCAA-302 closest to the QTL peak for MKW—was in the same QTL interval (37,012–38,280 kb) associated with PF and aBWT in a multi-parental DxP cross (Billotte et al. 2010). In the interval, a *valine-glutamine motif-containing protein* (*VQ*) was identified at chromosomal position 37,411,925 bp. In many plants, *VQ* has been reported to be responsive to biotic and abiotic stress, including pathogen infection, when interacting with the *WRKY* transcription factor (TF) (Chen et al 2012; Pecher et al. 2014; Liu et al. 2020). The specific interaction between the *VQ* motif FXhVQChTG (pfam05678) containing the gene *IKU1* and a *WRKY*, *MINI3,* reportedly controls endosperm growth and seed size in *Arabidopsis* (Wang et al. 2010). Therefore, *VQ* is a good candidate gene to investigate for its regulatory effect on kernel and seed in oil palm. Additional analysis of the MKW-QTL region revealed that *VQ* was flanked by *gibberellin 2-beta-dioxygenase* (*GA2OX*) and a *GATA* TF (*GATA*), the putative functions of which are summarized in Table 5. Interestingly, these genes are significantly differentially expressed in low- and high-yielding oil palm (Wong et al. 2017). Furthermore, *GATA* is known to regulate biological functions in various plant organs, including the flower and seed.

In CHR09, the genomic region corresponding to 74.8–84.5 cM on LGDP7 of P2 was previously reported to be associated with MTF and STF (Ting et al. 2018). The same genomic region was also associated with QTLs for Bwt and Fwt which were identified in populations derived from Deli, La Me and

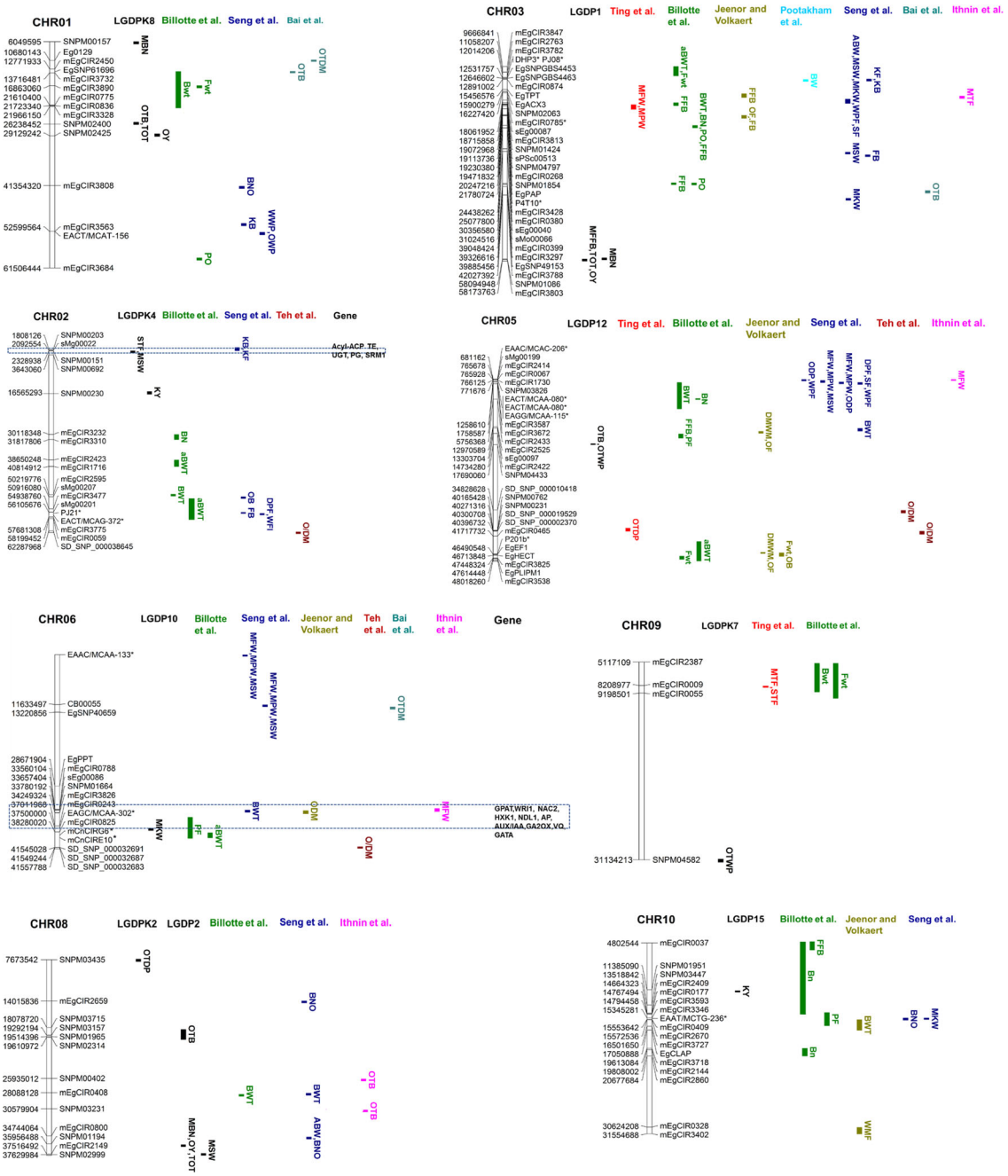

Fig. 4 Comparison of QTLs from different studies by mapping relevant information to oil palm EG5 genome build. Only closely linked markers defined the QTL regions for each trait on the chromosomes are shown

Yangambi genetic backgrounds (Billotte et al. 2010). Although the correlations between MTF, Bwt and Fwt are not known, it is postulated that increased MTF (or decreased STF) will increase Fwt. A search for genes of interest was performed in the genomic region 8,208,977–9,198,501 bp, and two, *C3HC4-type zinc finger* TF (*RING finger*) and a *membrane-bound O-acyltransferase* (*MBOAT*), were shortlisted. In

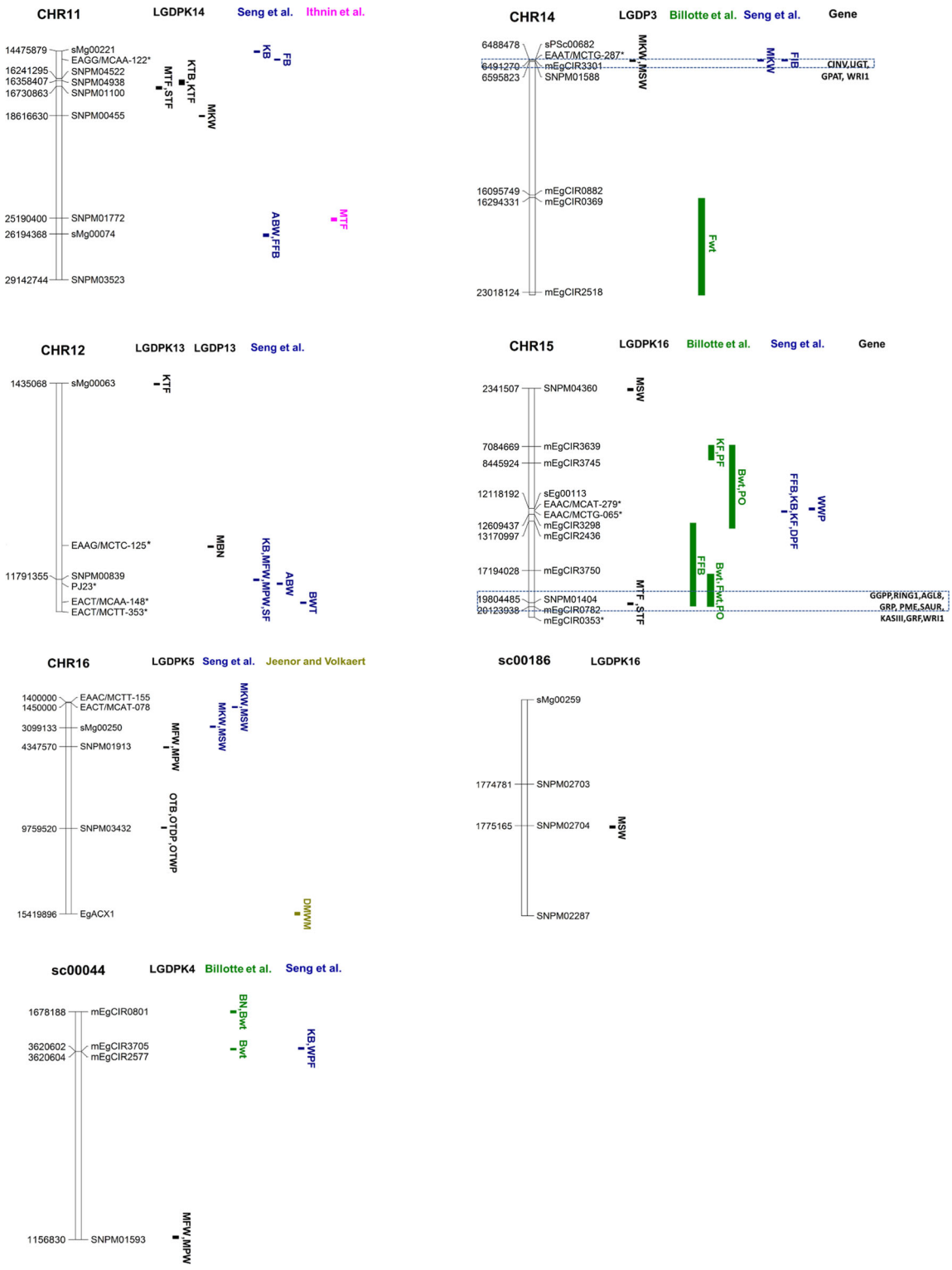

Fig. 4 continued

Table 5 Putative biological functions for the candidate genes, proteins and transcription factors identified within the QTL region associated with yield components in the P2 and KULIM DxP mapping populations

No	Chromosome	Position (bp)	Within/ flanking QTL region	Gene/transcription factor (TF)	NCBI accession number		Putative function for the encoded enzymes/protein/TF	References
					Gene	Protein		
1	CHR02	2,102,678–2,108,692	Within	*Acyl-acyl carrier protein thioesterase (Acyl-ACP TE)*	840418	Q9C7I5	*Acyl-ACP TE* plays an essential role in determining the fatty acid (FA) chain length by hydrolyzing the thioester bond which results in termination of acyl chain elongation during de novo biosynthesis of FAs in plants	Uniprot (https://www.uniprot.org/uniprot/Q9C7I5); Pulsifer et al. (2014), Jing et al. (2011)
2	CHR02	2,160,414–2,270,506	Within	*UDP-glycosyltransferase (UGT)*	N/A	K4CWS6	*UGT* mediates glycosylation modification such as anthocyanins, flavonols and flavor-related volatiles in development and ripening of fruits. It is also required for seed germination, abscisic acid (ABA)-mediated fruit ripening and negative responses to drought	Uniprot (https://www.uniprot.org/uniprot/K4CWS6); Sun et al. (2017), Wu et al. (2017)
3	CHR02	2,352,982–2,414,892	Flanking	*Polygalacturonase (PG)*	544051	P05117	*PG* is involved in pectin depolymerisation by hydrolyzing the O-glycosyl bonds in polygalacturonan, resulting in separation of cells in fruit abscission	Uniprot (https://www.uniprot.org/uniprot/P05117); Osteryoung et al. (1990), Watson et al. (1994), Cooley and Yoder (1998), Roongsattham et al. (2012)
4	CHR02	3,424,098–3,426,635	Flanking	*Salt-Related MYB1 (SRM1)*	830751	Q9FNN6	*SRM1* coordinates syntheses of ABA and signalling-related genes. In *Arabidopsis*, increasing ABA has negative effect on seed germination in saline conditions. It also promotes vegetative growth and leaf shape	Uniprot (https://www.uniprot.org/uniprot/Q9FNN6); Wang et al. (2015)
5	CHR06	33,837,283–33,840,111	Flanking	*Glycerol-3-phosphate acyltransferase (GPAT)*	836183	Q8GWG0	*GPAT* is involved in acylation of glycerol 3-phosphate in glycerolipid (e.g. triacylglycerol) biosynthesis in most plant seeds	Uniprot (https://www.uniprot.org/uniprot/Q8GWG0); Singer et al. (2016), Shockey et al. (2016)
6	CHR06	34,513,577–34,520,834	Flanking	*WRINKLED1 (WRI1)*	824599	Q6X5Y6	*WRI1* promotes sugar uptake and FA biosynthesis in developing seeds. The TF is also involved in embryo development, seed germination and seedling establishment	Uniprot (https://www.uniprot.org/uniprot/Q6X5Y6); Zhai et al. (2017)

Table 5 continued

No	Chromosome	Position (bp)	Within/ flanking QTL region	Gene/transcription factor (TF)	NCBI accession number		Putative function for the encoded enzymes/protein/TF	References
					Gene	Protein		
7	CHR06	34,771,741–34,779,694	Flanking	*NAC domain-containing protein 2 (NAC2)*	101248665	K4BNG7	*NAC2* is a plant-specific TF involved in regulation of leaf senescence, fruit yield and sugar content in fruit ripening by establishing ABA homeostasis	Uniprot (https://www.uniprot.org/uniprot/K4BNG7); Ma et al. (2018)
8	CHR06	35,270,178–35,283,392	Flanking	*Hexokinase-1 (HXK1)*	829034	Q42525	In plants, *HXK1* encodes hexokinase, a sugar sensor in the glucose-signalling network	Uniprot (https://www.uniprot.org/uniprot/Q42525); Dai et al. (1995), Granot et al. (2014)
9	CHR06	35,818,699–35,823,166	Flanking	*N-MYC downregulated1 (NDL1)*	835777	Q9FJT7	*NDL1* interacts with the *G protein beta subunit (GB1)* is involved in regulation of lateral root formation and basipetal inflorescence auxin transport. Its overexpression will affect root architecture and reproductive organ development	Uniprot (https://www.uniprot.org/uniprot/Q9FJT7); Mudgil et al. (2009, 2013)
10	CHR06	36,319,863–36,322,283	Flanking	*Aspartic proteinase (AP)*	820452	Q9LTW4	*AP* plays an essential role in regulation of endogenous sugar levels, photosynthetic carbon metabolism in chloroplasts and general morphology and development of plant	Uniprot (https://www.uniprot.org/uniprot/Q9LTW4); Paparelli et al. (2012), Al'bert et al. (2014)
11	CHR06	36,637,313–36,642,286	Flanking	*Aux/IAA gene family (Aux/IAA)*	N/A	Q38825	*Aux/IAA* plays an important role in development and growth of roots, shoots, flowers and fruits. It is also a repressor of early auxin-inducible gene expression by interacting with *auxin response factors (ARFs)*	Uniprot (https://www.uniprot.org/uniprot/Q38825); Liscum and Reed (2002), Luo et al. (2018)
12	CHR06	37,377,896–37,379,666	Within	*Gibberellin 2-beta-dioxygenase (GA2OX)*	4342182	Q8LGZ9	*GA2OX* regulates plant growth and architecture by inhibiting endogenous bioactive gibberellins	Uniprot (https://www.uniprot.org/uniprot/Q8LGZ9); Lo et al. (2008), Shan et al. (2014)
13	CHR06	37,411,925–37,413,912	Within	*Valine-glutamine motif-containing protein (VQ)*	6240987	Q1G3U8	*VQ* interacts with *WRKY* and is responsible for various developmental processes such as responses to biotic and abiotic stresses, seed development and size, and photomorphogenesis	Uniprot (https://www.uniprot.org/uniprot/Q1G3U8); Hu et al. (2013), Jing and Lin (2015), Wang et al. (2010), Cheng et al. (2012, Pecher et al. (2014)

Table 5 continued

No	Chromosome	Position (bp)	Within/ flanking QTL region	Gene/transcription factor (TF)	NCBI accession number		Putative function for the encoded enzymes/protein/TF	References
					Gene	Protein		
14	CHR06	37,839,335–37,841,673	Within	*GATA* TF *(GATA)*	835788	Q5HZ36	*GATA* is involved in regulation of chlorophyll biosynthesis, chloroplast development, germination, senescence, elongation growth, flowering time and leaf starch content	Uniprot (https://www.uniprot.org/uniprot/Q5HZ36); Mara and Irish (2008), Richter et al. (2010, 2013), Hudson et al. (2011), Chiang et al. (2012), Behringer et al. (2014)
15	CHR09	8,605,559–8,606,879	Within	*Zinc finger, C3HC4 type (RING finger)*	N/A	N/A	*RING finger* is involved in growth and fruit development	Wu et al. (2014)
16	CHR09	8,884,309–8,895,044	Within	*Membrane-bound O-acyltransferase (MBOAT)*	N/A	Q5GKZ7; Q9CAN8	Plant MBOATs, including *diacylglycerol acyltransferase* (*DGAT*) and *lysophospholipid acyltransferase* (*LPLAT*), play important role in lipid metabolism in developing seeds	Uniprot (https://www.uniprot.org/uniprot/Q5GKZ7); Li et al. (2013); (https://www.uniprot.org/uniprot/Q9CAN8); Wang et al. (2012), Rosli et al. (2018)
17	CHR14	6,284,291–6,291,463	Flanking	*Alkaline/neutral invertase (CINV)*	840454	Q9LQF2	*CINV* breaks sucrose down to fructose and glucose. It regulates root growth, leaf and silique development and floral transition	Uniprot (https://www.uniprot.org/uniprot/Q9LQF2); Xiang et al. (2011)
18	CHR14	6,369,304–6,371,721	Flanking	*UDP-glycosyltransferase (UGT)*	N/A	K4CWS6	In plants, *UGT* mediates glycosylation modification, such as in anthocyanins, flavanols and flavour-related volatiles, in development and ripening of fruits. It is also required for seed germination, ABA mediated fruit ripening and for negative response to drought	Uniprot (https://www.uniprot.org/uniprot/K4CWS6); Sun et al. (2017), Wu et al. (2017)
19	CHR14	6,480,850–6,486,840	Within	*Glycerol-3-phosphate acyltransferase (GPAT)*	836183	Q8GWG0	*GPAT* is involved in acylation of glycerol 3-phosphate in glycerolipid (e.g. triacylglycerol) biosynthesis in most plant seeds	Uniprot (https://www.uniprot.org/uniprot/Q8GWG0); Singer et al. (2016), Shockey et al. (2016)
20	CHR14	6,510,932–6,516,831	Within	*WRINKLED1 (WRI1)*	824599	Q6X5Y6	*WRI1* promotes sugar uptake and FA/oil biosynthesis in developing seeds which affects embryo development, seed germination and seedling establishment	Uniprot (https://www.uniprot.org/uniprot/Q6X5Y6); Zhai et al. (2017)

Table 5 continued

No	Chromosome	Position (bp)	Within/flanking QTL region	Gene/transcription factor (TF)	NCBI accession number		Putative function for the encoded enzymes/protein/TF	References
					Gene	Protein		
21	CHR15	19,353,857–19,357,974	Flanking	*Geranylgeranyl diphosphate chloroplastic (GGPP)*	N/A	N/A	*GGPP* is a precursor for various aspects of growth and development in plants, including biosynthesis of gibberellins, carotenoids, chlorophylls, isoprenoid quinones and geranylgeranylated proteins	Okada et al. (2000)
22	CHR15	19,399,974–19,400,633; 19,688,746–19,692,587	Flanking	*E3 ubiquitin-protein ligase RING1 (RING1)*	830902	Q9LX93	*RING1* is involved in development of plants, including dormancy and germination of seeds, root growth, flowering time and chloroplast development	Uniprot (https://www.uniprot.org/uniprot/Q9LX93); Lin et al. (2008), Shu and Yang (2017)
23	CHR15	19,500,133–19,510,818	Flanking	*Agamous-like MADS-box protein (AGL8)*	836212	Q38876	*AGL8* regulates development of flowers and fruits by interacting with other MADS-box genes. For example, it promotes early floral meristem identity by interacting with *APETALA1*, *CAULIFLOWER* and *LEAFY* genes and together with *FRUITFULL* gene promotes carpel and fruit development. Therefore, mutations in these MADS-box genes could cause non-flowering phenotypes	Uniprot (https://www.uniprot.org/uniprot/Q38876); Gu et al. (1998), Ferrándiz et al. (2000)
24	CHR15	19,688,746–19,692,587	Flanking	*Glycine-rich protein (GRP)*	N/A	N/A	*GRP* is involved in cellular stress responses and signalling, floral development and auxin signalling	Czolpinska and Rurek (2018)
25	CHR15	19,788,553–19,805,976	Flanking	*Pectinesterase (PME)*	544090	P14280	*PME* is involved in modification of cell wall during fruit development in preparation for ripening and softening (induced by *PG*)	Uniprot https://www.uniprot.org/uniprot/P14280
26	CHR15	20,058,133–20,059,096	Flanking	*Small auxin-up RNA-like auxin-responsive protein (SAUR)*	832205	Q29PU2	*SAUR* induced by auxin, is involved in various biological processes, including cell division, expansion and differentiation	Uniprot (https://www.uniprot.org/uniprot/Q29PU2); Markakis et al. (2013), Li et al. (2015)
27	CHR15	20,227,498–20,233,306	Flanking	*3-oxoacyl-[acyl-carrier-protein (ACP)] synthase III (KASIII)*	4348632	Q7XEM4	*KASIII* enzyme catalyses condensation of malonyl-ACP to initialize carbon chain elongation during FA biosynthesis	Uniprot (https://www.uniprot.org/uniprot/Q7XEM4); Alamin et al. (2017)

Table 5 continued

No	Chromosome	Position (bp)	Within/ flanking QTL region	Gene/transcription factor (TF)	NCBI accession number		Putative function for the encoded enzymes/protein/TF	References
					Gene	Protein		
28	CHR15	20,846,505–20,847,955	Flanking	*Growth-regulating factor (GRF)*	4330436	Q6ZIK5	*GRF* is involved in development and formation of root, leaf, stem, floral organ, seed and grain	Uniprot (https://www.uniprot.org/uniprot/Q6ZIK5); Hu et al. (2015), Che et al. (2015), Duan et al. (2015), Li et al. (2016)
29	CHR15	20,907,799–20,913,152	Flanking	*WRINKLED1 (WRI1)*	824599	Q6X5Y6	*WRI1* promotes sugar uptake and FA biosynthesis in developing seeds. The TF is also involved in embryo development, seed germination and seedling establishment	Uniprot (https://www.uniprot.org/uniprot/Q6X5Y6); Zhai et al. (2017)

Nicotiana benthamiana, *RING finger* is in the chloroplasts and silencing it stops the growth of fruits (Wu et al. 2014). *MBOATs,* such as *diacylglycerol acyltransferase* (*DGAT*) and *lysophospholipid acyltransferase* (*LPLAT*), are involved in catalysing the synthesis and accumulation of lipids in developing seeds, including in the mesocarp of oil palm (Tranbarger et al. 2011; Li et al, 2013; Wang et al. 2012; Jin et al. 2017; Rosli et al. 2018).

The SSR marker mEgCIR3301 mapped to 6,491,270 bp in CHR14 was found associated to MKW in P2 and an DxP mapping family by Seng et al. (2016) as both families shared the same paternal parent (coded ML161). Interestingly, mEgCIR3301 was flanked by a lipid acylation-related gene, *glycerol-3-phosphate acyltransferase* (*GPAT*), at 6,480,850 bp and *WRI1*, at 6,510,932 bp. In many plants, including oil palm, *WRI1* has been reported to regulate genes encoding a number of key enzymes along the FA and triacylglycerol synthesis pathways (Maeo et al. 2009; Bourgis et al. 2011; Tranbarger et al. 2011; Chapman and Ohlrogge 2012; Qu et al. 2012; To et al. 2012; Vanhercke et al. 2013; Tajima et al. 2013; Grimberg et al. 2020; Kong et al. 2020). In fact, a wider group of genes, such as the sugar- and carbohydrate-responsive genes, are also reported to be regulated by *WRI1* (Masaki et al. 2005; Cernac et al. 2006). The storage compounds regulated by these genes eventually will affect development of the seed, embryo and even seedling, suggesting a possible role for *WRI1* in regulating MKW of oil palm.

Another common genomic region is the 19,804–20,124 kb interval on CHR15, which was associated with MTF and STF in KULIM DxP. The region was also reportedly linked to other important YCs, such as FFB, Fwt, Bwt and PO (Billotte et al. 2010). We identified a *pectinesterase* (*PME*) and a *small auxin-up RNA-like auxin-responsive protein* (*SAUR*) at 19,788,553 bp (to 19,805,976 bp) and 20,058,133 bp (to 20,059,096 bp), respectively. Both are related to cell metabolism, *PME* degrading pectin and modifying the cell wall in preparation for fruit ripening and softening, and *SAUR* involved in cell division, expansion and differentiation (Markakis et al. 2013; Abu-Sarra and Abu-Goukh 1992; Li et al. 2015; Wen et al. 2020). The presence of these genes in QTL regions influencing various bunch components suggests the importance of genes regulating cell wall development, cell division, expansion

and differentiation for the appropriate development of all components in the fruit bunch. Extending the search beyond the common QTL regions (in CHR02, 06, 14 and 15), we also identified a number of genes and TFs involved in the regulation of sugar levels, FA/oil biosynthesis, growth and development of flower, seed and fruit (Table 5), all of which potentially impact development of the bunch components.

Conclusion

This study describes the QTLs associated with yield components in two advanced *dura* × *pisifera* populations. Several common QTLs were identified in both populations. The QTLs linked to MTF and OTWP in P2 and KULIM DxP that influence mesocarp formation, respectively, were located ~ 22,000 kb apart in CHR09 (LGDP/DPK7). In addition, another similar genomic region (~ 11,000 kb apart) in CHR08 (LGDP/DPK2) regulates OTB and OTDP in P2 and KULIM DxP, respectively, both directly contributing to oil yield. The QTLs associated with similar yield traits have been published previously in mapping populations of different genetic backgrounds. We collated all the information to identify the QTL regions influencing the related traits reported by the different studies in CHR02, 06, 09, 14 and 15. Search within and near the QTL regions in the different chromosomes revealed 29 candidate genes and transcription factors related to glycosylation, plant growth, development and architecture, glucose and hormone signalling, lipid metabolism, photosynthesis, flowering and fruit ripening. *UGT*, *PG*, *MYB*, *NAC2*, *AUX/IAA*, *RING finger* and *PME* are example of genes potentially regulating oil palm fruit formation, thus directly impacting yield. The current genome-based candidate gene approach is useful in identifying interesting genes that can assist in further understanding the genetic control of oil palm yield. In fact, *GATA* gene located within the QTL interval was shown previously to be differentially expressed in high- and low-yielding palms. Further validation of the association of the other candidate genes with the traits concerned can help develop useful tools for marker assisted selection in oil palm breeding. The markers linked to the QTLs could also be candidates for developing an appropriate marker panel for genomic selection in oil palm.

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Availability of data and materials Summary data and genetic linkage maps used for this study are included in supplementary material.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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