

QUANTITATIVE TRAIT LOCI (QTL) LINKED TO COMPACTNESS IN AN INTERSPECIFIC BACKCROSS TWO (BC₂) POPULATION OF OIL PALM

ZULKIFLI, Y*; RAJINDER, S*; TING, N C*; MARHALIL, M*; XAVIAR, A**; RAJANAIDU, N*; JANSEN, J†; MOHD DIN, A*; ONG-ABDULLAH, M*; CHIE, T Y‡ and KUSHAIRI, A*

ABSTRACT

Conventional quantitative trait loci (QTL) analysis of a mapping family is carried out to generate molecular tools for development of compact interspecific hybrid palms that can be planted more closely for higher yields per unit land area. Genetic maps were constructed for an interspecific backcross two (BC₂) oil palm population using single nucleotide polymorphism (SNP) and simple sequence repeat (SSR) markers. A total of 1744 markers were mapped onto 16 linkage groups, spanning 1499.5 cM with an average marker interval of 0.86 cM. Using empirical genome and chromosome-wide thresholds, QTL analysis yielded a number of significant associations with vegetative characters for palm compactness. Subsequent QTL analysis revealed two major and two putative QTL linked to rachis length and petiole cross-section, two important characters for palm compactness. The QTL identified are an important step towards the implementation of marker assisted selection (MAS), enabling breeders to make early informed decisions on improving interspecific hybrids.

Keywords: oil palm, interspecific hybrids, quantitative trait loci, compactness.

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INTRODUCTION

The African oil palm (*Elaeis guineensis*) is already the highest yielding oil crop per unit area (Kushairi *et al.*, 2018). Nevertheless, it is being improved for yet higher yield, possibly up to its theoretical potential of 18.2 t ha⁻¹ yr⁻¹ palm oil (Corley *et al.*, 1998). Apart

from improving the African species, breeders are also interested in the interspecific hybrid between *E. guineensis* and the South American oil palm, *Elaeis oleifera* (Zulkifli *et al.*, 2017). Although it produces much less oil, *E. oleifera* has certain interesting characteristics, *e.g.*, dwarfness, as it grows only 5-10 cm yr⁻¹ *vs.* 45-75 cm yr⁻¹ by *E. guineensis*. Its oil is also more liquid (less saturated), similar to olive oil, and it is resistant to certain diseases, such as fatal yellowing (Corley and Tinker, 2003). This has led to interspecific hybrids to introgress the desired characteristics of *E. oleifera* into *E. guineensis*. Further steps, *e.g.*, selfing, intercrossing of the F₁ or backcrossing to *E. guineensis*, have been proposed to improve the yield and vegetative traits of the F₁.

Improvement by conventional breeding will be long, tedious and expensive. However, marker assisted selection (MAS) can be used to incorporate the desirable traits from *E. oleifera* into

* Malaysian Palm Oil Board,
6 Persiaran Institusi, Bandar Baru Bangi,
43000 Kajang, Selangor, Malaysia.
E-mail: zulkifly@mpob.gov.my

** United Plantations Bhd, Jendarata Estate,
36009 Teluk Intan, Perak, Malaysia.

† Biometris, Wageningen University and Research Centre,
P.O. Box 100, 6700 AC Wageningen,
The Netherlands.

‡ Codon Genomics Sdn Bhd,
26, Jalan Dutamas 7,
Taman Dutamas, Balakong,
43200 Seri Kembangan, Selangor, Malaysia.

E. guineensis faster and more efficiently. For starters, the quantitative trait loci (QTL) linked to fatty acid composition in the interspecific hybrids (Singh *et al.*, 2009) and backcrosses (Montoya *et al.*, 2013) have been identified. Identifying the markers linked to compactness will also help realise the full potential of the interspecific hybrids. Generally, compact palms demonstrate lower height increment and have shorter fronds. Some studies have also shown that small petioles contribute to compactness (Noh *et al.*, 2014; Barcelos *et al.*, 2015). The trait, however, is not a direct measure for compactness, but is one of the parameters to determine vegetative dry matter to compute bunch index to select physiologically efficient palms. For compact palms, if their individual palm yield can be maintained, they can be planted at higher density to give higher yield per unit area (Escobar and Alvarado, 2004). Interspecific hybrid breeding is an excellent way to develop compact palms.

Understandably, most work in identifying markers linked to height, rachis length (RL) and petiole cross-section (PCS) has been on the African species. Previous studies Rance *et al.* (2001) and Billotte *et al.* (2010) reported QTL regions associated with RL and PCS in *E. guineensis*. More recently, two reports revealed the QTL and candidate genes influencing height in *E. guineensis* (Lee *et al.*, 2015; Pootakham *et al.*, 2015).

The rachis of *E. oleifera* is shorter than that of *E. guineensis*, while the interspecific hybrid has longer fronds than both parents (Sterling *et al.*, 1999), most likely due to over dominance in expression of the trait. Nevertheless, palms with shorter fronds have been successfully developed by repeated backcrossing to selected *E. guineensis* (Sterling *et al.*, 1988), indicating the usefulness of interspecific hybrids in producing compact palms. This present study focused on examining the QTL of RL and PCS in interspecific hybrid palms, as both characters contribute to compactness.

MATERIALS AND METHODS

Palm Materials, Marker Genotyping and Data Analysis

The mapping family used in this study was an interspecific hybrid backcross two (BC₂) population consisting of 74 palms. The BC₂ population was derived from a cross involving a *E. guineensis tenera* (female), with an interspecific backcross one (BC₁) palm (male) generated from *E. guineensis* (female) crossed with Colombian *E. oleifera* (male). The single nucleotide polymorphism (SNP) and simple sequence repeat (SSR) data on the mapping population was generated and analysed as described previously by Zulkifli *et al.* (2014).

Vegetative Measurement

Measurement of vegetative traits was carried out using the non-destructive method described by Breure and Powell (1988). Frond measurements involving RL and PCS were carried out using frond number 17. RL was measured from the first rudimentary leaf at the petiole to the tip of the rachis. With respect to PCS, the measurement was recorded at the first rudimentary leaflet at the petiole. Petiole width and depth were measured to obtain PCS area (width x depth).

Linkage Map Construction and QTL Analysis

Genetic linkage map was constructed using the JoinMap 4.1 software (Van Ooijen, 2006). Regression mapping algorithm with the default parameters (minimum logarithm of the odds (LOD) score threshold of 1.0, recombination fraction threshold of 0.4, ripple value of 1.0 and jump threshold of 5.0) were used to assign markers to individual linkage groups. Haldane's mapping function was then used to determine map order. Only markers with < 5% of missing data and following Mendelian inheritance ratio were used in map construction. Markers showing nearest-neighbour stress of more than 3 cm were also omitted.

The QTL were analysed using the interval mapping (IM) and the multiple-QTL model (MQM) implemented via the MapQTL 6 software (Van Ooijen, 2009). A mapping step size of 1 cM was used for both the IM and MQM analyses. Permutation of 1000 iterations were performed for each trait to establish experimental-wise LOD cut-off values for declaring QTL significant at $P < 0.05$, at the genome-wide (GW) and chromosome-wide (CW) levels. QTL were considered present only at positions where a LOD score exceeded the corresponding significance threshold. The confidence interval of each significant QTL by IM was determined by the LOD -1 method (Van Ooijen, 1992). A non-parametric Kruskal-Wallis (K-W) test was also employed to detect association between markers and traits individually at $P < 0.05$ using the MapQTL 6 software.

Identification of QTL Markers on EG5 Genome

A total of 15 markers (Table 1) associated or in close proximity with the linkage groups (LG) and QTL were identified from this study and a previous study by Billotte *et al.* (2010). These markers were mapped to the oil palm genome EG5 build, retrieved from GenomSawit web (<http://genomsawit.mpob.gov.my/genomsawit/>). Sequences of SNP markers were retrieved from GenomSawit web. All sequences were BLASTn (v2.2.26+) search against the EG5 build. Coordinates of BLAST search were used to identify position of these markers on the EG5 build.

TABLE 1. MARKERS ASSOCIATED WITH THE LINKAGE GROUP OR QUANTITATIVE TRAIT LOCI (QTL)

No.	Markers	Traits	Sequence	Coordinate (start)	Coordinate (end)	Position source	Query coverage (%)	Sequence accession	Forward primer	Reverse primer
1	mEgCIR0059	RL	EG5_Chr2	58 197 428	58 197 651	ePCR	61.3	AJ578499	TGCAGGGGATGCTTTTATT	CCCTTAATTCCTGCCTTATT
2	mEgCIR0912	P_T	EG5_Chr14	10 191 655	10 191 830	Blast	98.3	AJ578566	CCATACATAATGTTTGGTGTG	TCTGTGCAITGGATTACTG
3	mEgCIR2144	P_T	EG5_Chr10	19 807 179	19 807 469	Blast	99.7	AJ578581	ACAAGGCTCTTCAAAGAGAT	CCACTGCCCCAACACTAGTAC
4	mEgCIR3321	RL	EG5_Chr6	4 194 678	4 194 906	Blast	99.1	AJ578647	CAAGGAGGAGCAGGTGAG	TACGGCCTCGGTTCTACAC
5	mEgCIR3574	P_W, RL	EG5_Chr16	3 581 226	3 581 667	Blast	99.6	AJ578686	AGAGACCCCTATTGTCTTGAT	GACAAAAGAGCTTGTCCACAC
6	mEgCIR3293	RL	EG5_Chr4	33 597 087	33 597 442	ePCR ^a	84.7	AJ578635	ACAACCACAAAGAGTCCTAAC	CTGCGAAATCAATAAAAAGTA
7	mEgCIR3400	RL	EG5_Chr4	31 138 393	31 138 632	ePCR	79.1	AJ578662	CAATTCACAGCGTCACTATAG	AGTGGCAGTGGAAAAAACACAGT
8	mEgCIR3755	RL	EG5_Chr4	36 105 406	36 105 694	ePCR	63.7	AJ578721	GCTCACCAAAAAGTGTAAAGTC	AGTTTCAACGGCAGGTATAT
9	mCnCIR0038	P_T	EG5_Chr12	18 048 052	18 048 101	Blast ^b	46.2	AJ865151	-	-
10	SEg00117 ^c	PCS	EG5_Chr6	34 867 089	34 867 716	Blast	100.0	-	GAGTGTAGTGGCTATGGTCT	CCGTTGTAICTGTTCTCGTACTG
11	SNPM00151	PCS	EG5_Chr2	2 328 817	2 329 058	Blast	100.0	-	-	-
12	SNPM00323	FL	EG5_Chr4	45 556 649	45 556 889	Blast	100.0	-	-	-
13	SNPM00339	PCS	EG5_Chr1	58 404 464	58 404 704	Blast	100.0	-	-	-
14	SNPM01114	FL	EG5_Chr2	1 151 052	1 151 292	Blast	100.0	-	-	-
15	SNPM03620	FL	EG5_Chr1	34 618 763	34 618 996	Blast	97.1	-	-	-

Note: ^a One mismatch on forward primer.

^b Low query coverage in blast result.

^c Primer and sequence of SEg00117 obtained from in-house study.

Source: identified from this study and Billette *et al.* (2010).

Circos was used to visualise the position of the markers on the genome (Krzywinski *et al.*, 2009).

RESULTS

Vegetative Measurement

All palms in the mapping population were measured for RL and PCS. The values obtained for the traits in the BC₂ mapping progeny and their parent are presented in Table 2, and both traits are segregating in this population. Although the mean of the RL is similar to the current commercial DxP *E. guineensis* (Noh *et al.*, 2012), the range observed in the BC₂ population highlights the fact that palms with RL as short as 2.5 m can be obtained via interspecific hybrid breeding. The mean for RL was in between both parental values, although it was closer to the BC₁ male parent. The mean value for PCS, on the other hand, was slightly higher than that of the both parental values, although the coefficient of variation (CV) observed was large (~20%). Adherence to normal distribution was assessed by using the Shapiro-Wilk test implemented via the SAS version 9.3 software.

Only the PCS trait followed a normal distribution (P>0.05). The correlation study using Pearson's correlation showed that both traits are positively correlated with each other (r = 0.45).

Linkage Map Construction

The consensus genetic map is shown in Figure 1 while Table 3 summarises marker composition and lengths of individual linkage group (LG). The individual female and male parental maps had 1268 and 963 markers, covering 1706.9 and 1250.3 cM, respectively (Table 4). The parental maps were successfully integrated into a single consensus map (Figure 1) of 16 groups. LG5 had two sub-groups (LG 5a and b) and integration of the two groups formed a marker free region of 15 cM which could be due to a large homozygous block possibly due to the small marker set employed. Therefore, we decided to keep it as two separate sub-groups.

Identification of QTL Associated with RL and PCS

Results of the QTL analysis are summarised in Figure 1, Tables 5 and 6. The significant threshold

TABLE 2. PHENOTYPIC DATA OF VEGETATIVE MEASUREMENTS FOR INTERSPECIFIC BACKCROSS TWO (BC₂) PROGENIES AND THE PARENT

Trait	Parent		Mean of BC ₂ progenies (n=74)	Range	Variance	Coefficient of variation (CV)
	<i>E. guineensis tenera</i> (female)	BC ₁ (male)				
Rachis length (m)	4.86	5.68	5.3	2.45-6.8	0.46	12.78
Petiole cross-section (cm ²)	24	24	26	10-41	31.09	20.95

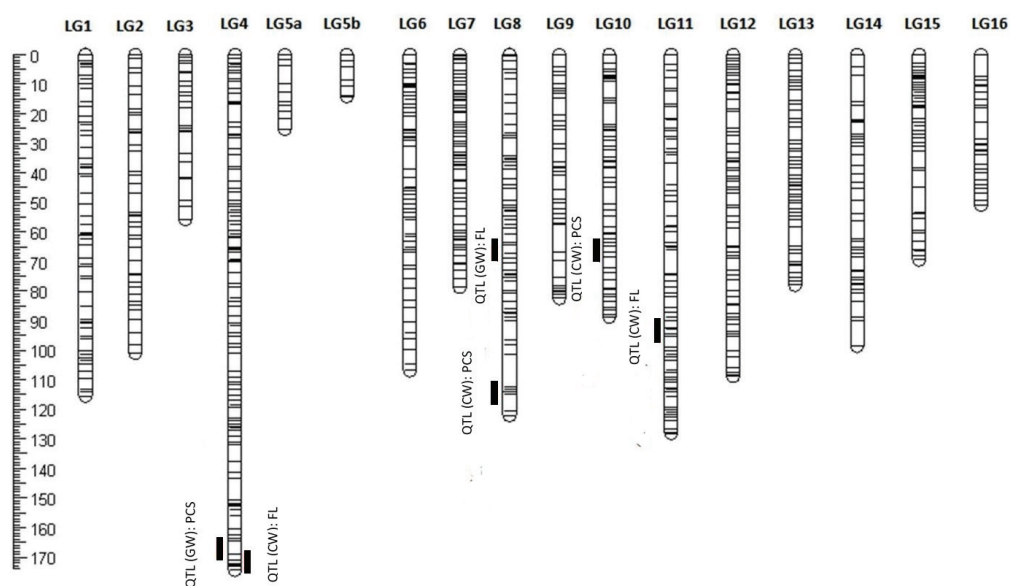


Figure 1. Linkage group (LG) 1-16 of interspecific backcross two (BC₂) population and distribution of quantitative trait loci (QTL) associated with rachis length (RL) and petiole cross-section (PCS) for both genome-wide (GW) and chromosome-wide (CW).

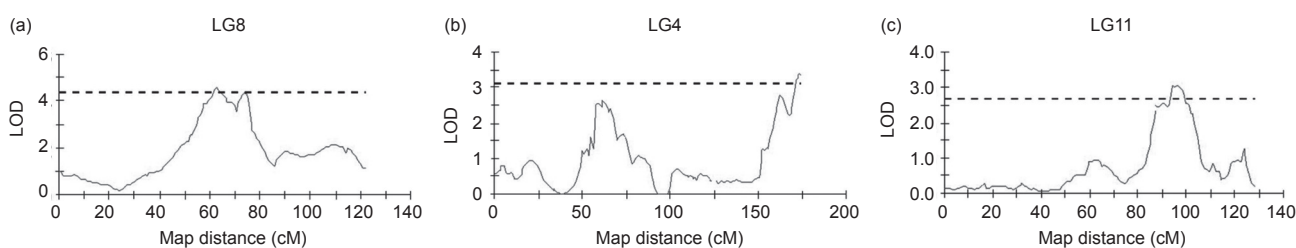
levels were calculated independently for each of the traits. At GW thresholds, two QTL were found to be associated with the traits of interest via IM analysis. QTL detected at empirical CW thresholds ($P < 0.05$) were also considered in this study. Additional two QTL for each trait were detected at CW level as presented in Table 6. The LOD score profiles obtained are shown in Figures 2 and 3. Interestingly, a CW QTL for RL was detected in the same region as the QTL for PCS at GW on LG4. Meanwhile, a CW QTL for PCS was detected in the same group with GW QTL for RL in LG8. In addition, putative QTL at CW were also detected for PCS and RL on LG10 and LG11, respectively.

In the subsequent MQM analysis, markers with highest LOD score for a trait were used as cofactors. The genomic region associated with PCS was maintained in MQM mapping. However, for RL, the LOD peak for the genome region falls slightly below the threshold level. All the significant QTL detected at CW in the initial round of IM were maintained in MQM. The non-parametric Kruskal-Wallis test was subsequently employed to confirm whether the individual markers associated to the QTL were actually significant. The test is a method for testing whether genotypic and phenotypic data originate from the same distribution. Thus, the results of the QTL analysis were not affected

by marker segregation distortion or non-normal distribution of phenotypic traits. As a result, all the linked markers (both at GW and CW) were significant at $P < 0.05$, providing further confidence to the QTL regions detected in this study.

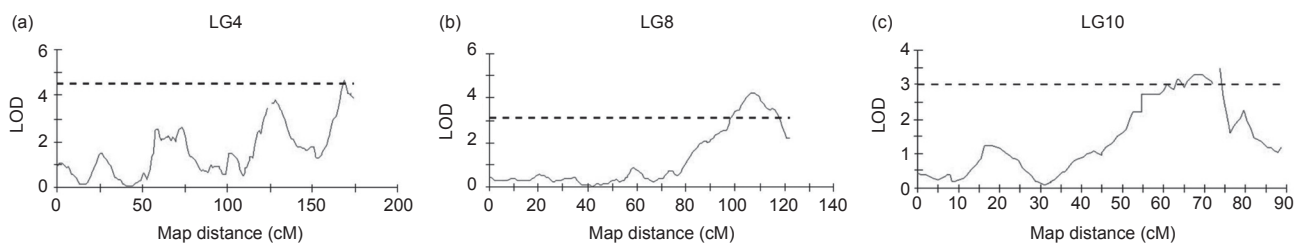
Comparison to Previous Published Results

Comparison was made to the previous study by Billotte *et al.* (2010), who found five QTL each associated with RL and PCS in *E. guineensis*. The markers associated with the QTL identified in this study were located in the oil palm genome build (Singh *et al.*, 2013) as shown in Figure 4. Markers identified previously to be influencing trait linked to RL and PCS (described as P_W and P_T) in an *E. guineensis* population were also located on the genome build for comparison purposes. The CW QTL for RL in this study was close to the QTL for similar trait described by Billotte *et al.* (2010) on LG11. Another QTL for RL (also at CW) was detected on LG10, similar to one of the QTL for RL by Billotte *et al.* (2010) but at opposite end of the LG. However, the two major QTL detected for the two traits in the BC₂ were in different LG, indicating that separate genomic regions are likely influencing compactness in both *E. guineensis* and interspecific hybrids.



Note: LOD - logarithm of odds.

Figure 2. Significant quantitative trait loci (QTL) detected for rachis length (RL) at genome-wide (GW) (a) and chromosome-wide (CW) (b and c). Horizontal line indicates the 95% significant threshold value for declaring a QTL.



Note: LOD - logarithm of odds.

Figure 3. Significant quantitative trait loci (QTL) detected for petiole cross-section (PCS) at genome-wide (GW) (a), and chromosome-wide (CW) (b and c). Horizontal line indicates the 95% significant threshold value for declaring a QTL.

TABLE 3. DISTRIBUTION OF MARKERS ON THE 16 LINKAGE GROUPS OF THE CONSENSUS INTERSPECIFIC BACKCROSS TWO (BC₂) GENETIC MAP

Linkage group (LG)	Number of markers			Map length (cM)	Average interval between markers (cM)
	SNP	SSR	Total		
1	119	2	121	115.5	0.95
2	87	0	87	101.0	1.16
3	46	2	48	55.8	1.16
4	174	4	178	174.4	0.98
5a	16	5	21	25.2	1.2
5b	17	0	17	14.8	0.87
6	120	9	129	106.9	0.83
7	168	5	173	78.7	0.45
8	132	0	132	122.1	0.93
9	51	5	56	82.5	1.47
10	125	4	129	88.8	0.69
11	161	5	166	128.1	0.77
12	125	5	130	108.8	0.84
13	121	6	127	78.0	0.61
14	74	3	77	98.6	1.28
15	115	4	119	69.4	0.58
16	32	2	34	50.9	1.50
Mean	99	3.6	102.6	88.2	0.86
Total	1 683	61	1 744	1 499.5	-

Note: SNP - Single nucleotide polymorphism.
 SSR - Simple sequence repeat.

TABLE 4. DISTRIBUTION OF MARKERS ON THE 16 LINKAGE GROUPS OF THE PARENTAL INTERSPECIFIC BACKCROSS TWO (BC₂) POPULATION

Linkage group (LG)	No. of markers		Length (cM)	
	Female parent	Male parent	Female parent	Male parent
1	90	78	144.2	85.6
2	51	56	113.5	80.2
3	36	34	53.1	58.6
4	115	131	209.1	137.0
5	11+13	16+11	23.1+13.3	27.2+14.9
6	94	74	122.3	88.8
7	139	57	96.6	60.8
8	85	81	143.3	99.5
9	40	42	94.1	65.2
10	96	59	100.0	77.7
11	132	70	162.8	93.3
12	96	84	117.1	100.5
13	102	38	85.0	69.6
14	60	46	117.4	72.8
15	79	56	62.0	71.1
16	29	30	50.0	47.5
Total	1 268	963	1 706.9	1 250.3

TABLE 5. THE QUANTITATIVE TRAIT LOCI (QTL) FOUND TO BE SIGNIFICANT AT THE EMPIRICAL GENOME-WIDE (GW) MAPPING THRESHOLD

Trait	Kruskal-Wallis	LG	Interval mapping analysis				Explained variance (%)	MQM analysis		
			GW threshold (p<0.05)	LOD	Closest marker	Position (cM)		Cofactor	LOD	Confidence interval (cM)
RL	0.005	8	4.4	4.42	SNPM03620	63.5	24.60	SNPM03620	4.21	55.88-75.34
PCS	0.0001	4	4.5	4.65	SNPM00151	168.9	25.70	SNPM00151	4.63	165.61-174.40

Note: RL - rachis length, PCS - petiole cross-section, LOD - logarithm of odds, LG - linkage group.

TABLE 6. THE QUANTITATIVE TRAIT LOCI (QTL) FOUND TO BE SIGNIFICANT AT THE EMPIRICAL CHROMOSOME-WIDE (CW) MAPPING THRESHOLD

Trait	Kruskal-Wallis	LG	Interval mapping analysis				Explained variance (%)	MQM analysis		
			CW threshold (p<0.05)	LOD	Closest marker	Position (cM)		Cofactor	LOD	Confidence interval (cM)
RL	0.001	4	3.1	3.25	SNPM01114	172.4	18.80	SNPM01114	3.25	159.06 -174.03
	0.05	11	2.7	3.05	SNPM00323	94.6	17.70	SNPM00323	3.05	86.52-103.37
PCS	0.001	8	3.1	3.56	SNPM00339	115.0	20.40	SNPM00339	3.57	90.06-122.08
	0.0005	10	3.0	3.50	sEg00117	73.8	20.10	sEg00117	3.44	52.60-79.57

Note: RL - rachis length, PCS - petiole cross-section, LOD - logarithm of odds, LG - linkage group.

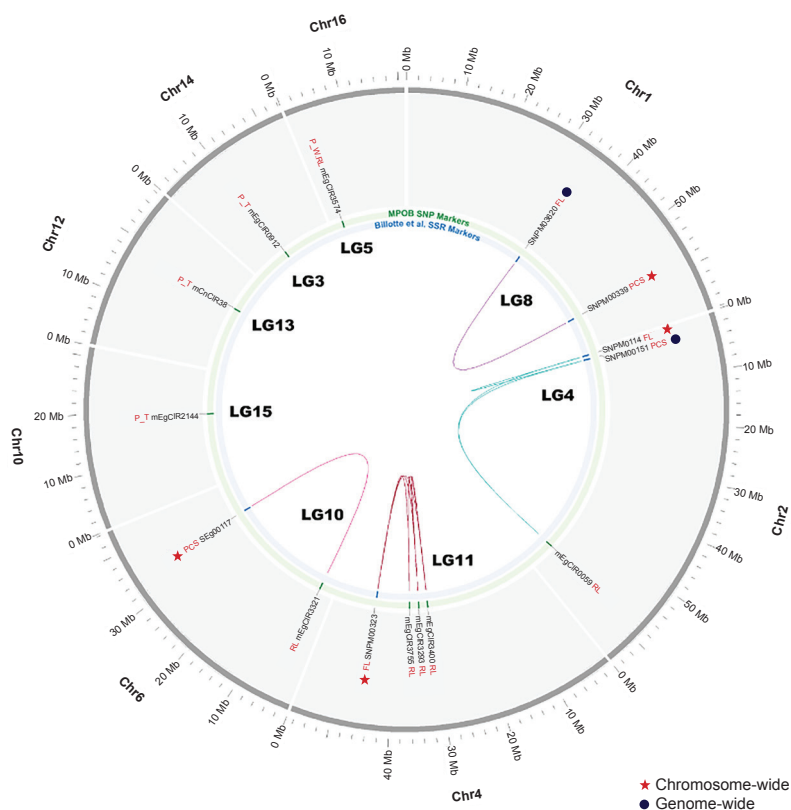


Figure 4. Location of 15 markers on oil palm genome EG5 build. From the outermost rings are 16 chromosomes of EG5, followed by the markers' ID and associated traits, locations of the markers on the chromosomes from two different sources, and linkage group of the markers. The chromosome-wide (CW) and genome-wide (GW) data are marked with red star and blue dot, respectively.

DISCUSSION

The two traits analysed in this study, RL and PCS are generally found to be highly heritable in oil palm populations (Hardon *et al.*, 1985). This indicates that these characters are amenable to selection and improvement either via conventional or molecular breeding. Among the two traits, only RL did not follow a pattern of continuous distribution around the mean. However, deviation from the normal distribution does not appear to significantly affect QTL detection (Septiningsih *et al.*, 2003).

Both traits measured showed intermediate mean values of the two parental palms. Thus, observation for the interspecific hybrids is in accordance with previous reported (Meunier and Boulin, 1975; Montoya *et al.*, 2013). The values are also intermediate to that observed by Mohd Din *et al.* (2000) in *E. oleifera* germplasm (4.2 m and 16.5 cm², respectively) and the study by Noh *et al.* (2012) in commercial *E. guineensis* (5.6 m and 29.0 cm², respectively). As expected, the range for the two vegetative traits measured is wide, indicating that variation exists in the BC₂ population and is ideal for further selection and improvement in breeding, as well as appropriate for use in mapping and QTL analysis.

Genetic Mapping

One of the major obstacles in genetic mapping of oil palm is the unavailability of inbred lines and true backcross. Nevertheless, being an outbreeding species, a high degree of heterozygosity is expected to occur in its genome. Subsequently, a second-generation interspecific pseudo-backcross (*E. guineensis* × *E. oleifera*) × *E. guineensis* was chosen as a mapping population. The number of LG observed in this study is 16, in agreement with cytogenetic analysis of oil palm chromosomes (Maria *et al.*, 1995). As such, the 16 LG obtained actually represent the 16 oil palm chromosomes in the genome. The genome length observed (1499.5 cM) was similar to that reported by Montoya *et al.* (2013) for an oil palm interspecific hybrid. Interestingly, the length is also similar to that reported by Billotte *et al.* (2010) for *E. guineensis*.

The average interval between two loci obtained in this study is much lower than previously reported which is in the range of 1.2 to 7.2 cM [(Singh *et al.*, 2009 (252 markers/7.2 interval); Montoya *et al.*, 2013 (362 markers/4.1 interval); Pootakham *et al.*, 2015 (1085 markers/1.26 interval)]. The average length of the LG is close to the expected size of 100-150 cM found in most agricultural crops (Malieepard *et al.*, 1998). Skewed segregation ratios are common phenomenon in hybrid species (Whitkus, 1998). Markers showing low levels of distorted segregation

ratios were also included in the mapping analysis. A total of 53 distorted markers were successfully mapped and distributed in linkage groups 1, 2, 4, 12 and 15. Those markers showed some tendency towards mapping in close proximity to one another. The number of SSR mapped in this study was lower compared to SNP and majority of the SSR were located at the ends of the linkage groups, which is in agreement with cytological location of SSR probes in oil palm (Castilho *et al.*, 2000).

QTL Associated with Frond Length and Petiole Cross-section

The high variance explained by the two QTL at the GW threshold (24.6% and 25.7%) indicates their potential use in a MAS programme designed to introgress the traits into elite breeding lines. The stringent GW empirical thresholds used to declare a QTL is important to avoid false positives. Nevertheless, adopting too high a significance level could ignore certain regions that deserve further investigation (Van Ooijen, 1999). A term 'suggestive linkage' was suggested by Lander and Kruglyak (1995) for regions that do not meet stringent thresholds but may be region of interest for the traits being evaluated. These regions were considered in the study as putative associations at CW threshold levels.

Considering markers that exceeded the LOD scores at CW threshold levels, a few additional QTL for the two traits concerned were revealed. As in GW thresholds, the experimental error rate of 5% was also accepted for CW significance level (Van Ooijen, 1999). The proposed suggestive-linkage threshold of LOD=2.7 for F₂ populations by van Ooijen (1999) is within the range of the empirical CW LOD threshold estimated in this study (LOD=2.7-3.1). Interestingly, the genomic region associated with PCS at CW was in close proximity to the QTL at GW for RL. Similarly, the associated genomic region for RL at CW was in the same location with QTL for PCS at GW.

CONCLUSION

As Malaysia is geographically small, land availability for further expansion to raise production is limited. The only way forward to increase yields is by increasing the number of palms per hectare. This can be achieved by developing compact palms for commercial planting. Future studies incorporating a larger population will also look at deciphering genomic loci influencing height increment in interspecific hybrids. These short and compact characteristics are also desirable as they will also prolong economic life, apart from allowing more palms to be planted per hectare of land.

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