GSC Advanced Research and Reviews
eISSN: 2582-4597 CODEN (USA): GARRC2
Cross Ref DOI: 10.30574/gscarr
Journal homepage: https://gsconlinepress.com/journals/gscarr/

(RESEARCH ARTICLE)

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Microsatellite-based QTL mapping for yield and horticultural traits in cacao (*Theobroma cacao* L.)

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GSC Advanced Research and Reviews, 2025, 25(02), 390-406

Publication history: Received on 02 October 2025; revised on 22 November 2025; accepted on 25 November 2025

Article DOI: https://doi.org/10.30574/gscarr.2025.25.2.0351

Abstract

In cacao, a perennial crop, SSR could ease/facilitate and speed up/accelerate selection for yield, vigour and their components. This investigation was conducted to identify Quantitative Trait Loci (QTL) underlying these traits in three hybrid progenies created, at CNRA in Côte d'Ivoire, from crosses (SCA6 x H) x C1, (P7 x ICS100) x C1 and (P7 x ICS95 x) x C1 and, encompassing, respectively, 179, 173 and 183 plants. Yield related-traits were recorded during three full campains years. In each progeny, Kruskal-Wallis test and interval mapping were applied on a SSR based-linkage map. QTLs detected are: 18 for yield components (healthy ripe pods number, pods weight, dried beans weight, one-hundred dried beans weight) on chromosomes 1, 2, 4, 6, 10, with a major for PW (R^2 = 34.3 %) borded by markers mTcCIR168 and mTcCIR18 on chromosome 4 of the parent derived from "P7 x ICS95", two for trunk girth on chromosome 4, three for yield efficiency. Some clusters of QTLs of yield components were observed on chromosomes 1, 4 and 6, 6 suggesting pleiotropic and/or polysgenic effects. The chromosome 4 carried most of QTLs. Some QTLs of the healthy ripe pods number, pods weight, dried beans weight, stable across progenies, genetic backgrounds and years, and moreover linked to markers mTcCIR168 and smTcCIR18, are useful in breeding programs.

Keywords: *Theobroma cacao* L.; Simple Sequence Repeats (SSR); Quantitative trait loci (QTL); Yield components; Horticultural vigour

1. Introduction

Cacao (*Theobroma cacao* L.) is an important export commodity crop in many countries in Latin America, sub-saharan Africa and Asia. In 2014, [1] reported that cocoa provided a livelihood for over 120 million people worldwide. However, cocoa production has been constrained by a number of factors, including climate changes, low productivity. The annual average production of cocoa beans is very low on farms, particularly in Africa, varying between 218,64 and 600 kilograms per hectare [2, 3]. This low productivity is, to a certain extent, due to genetic facors.

Yield and vigour are complex traits controlled by many genes. Their oligogenic inheritance system has been demonstrated and is still being well unknown.

Since many decades, steps towards high yield in cocoa breeding programs by means of traditional methods, crosses and generations of phenotypic backcrossing or selfing, have been limited. This phenotypic-based selection is laborious and

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time consuming for a slow-growing plant, cacao; in addition to be expensive. Thus, despite these efforts, up to now, no genotype with high yield level has been found or created. Thus, the introduction of molecular markers in the selection process, via markers-assisted selection, should improve the efficiency and should be a convenient alternative to phenotypic selection. Indeed, DNA markers are very efficient and powerful tools in plant breeding for the genetic dissection of quantitative traits and the early screening of desired genotypes in perennial crops, such as cacao, thereby offering new opportunities for genetic improvement in cacao.

In cacao, few studies have been conducted to analyze markers-trait associations and to detect QTL for yield and vigor [4, 5, 6, 7, 8, 9, 10, 11]. In these studies, markers were combined: either, markers other than microsatellite or a few SSR with markers of other types. In these cases where different types of markers were mixed, problems occurred in interpreting the results with complex profiles [12] and accordingly should be so in implementing MAS.

Microsatellite, (SSR), is an ideal PCR-based DNA marker for genetic mapping and MAS because of their multiple advantageous features [13, 14, 15, 16] that make them more suited for molecular genetic studies in developing countries like Côte d'Ivoire.

The present study aimed at identifying SSR markers-based QTLs for yield and its components (pods number, pods weight, beans weight) and adult tree vigor in three related hybrid populations monitored over a 3-year period. QTL stability across time was also analyzed.

2. Materials and methods

2.1. Plant materials

The study was conducted on three mapping hybrid progenies, comprising, respectively, 179, 173 and 183 plants, derived from crosses (SCA6 x H) x C1, (P7 x ICS100) x C1 and (P7 x ICS95) x C1. These were set up at the Centre National de Recherche Agronomique (CNRA) research station in Bingerville, South-Eastern Côte d'Ivoire. Their male parent, C1 (or IFC1), is a highly homozygous [17] Lower Amazon Forastero clone local type Amelonado. It is a relatively high or good yielding clone [18, 19] with a relatively good adult vigor [18]. ICS100, ICS95 and H are Trinitario clones, from Trinidad, known for the big size of their beans. ICS95 is one of the best and precious clones owing to its high yielding level and excellent or good pod filling [20, 19, 21]. While ICS100 presents a relatively good yield level and a good adult vigor (trunk girth) [22, 23]. P7 (or Pound 7), an Upper Amazon Forastero clone, from wild origin, was one of the progenitors of commercial varieties in Côte d'Ivoire, especially in crosses with Lower Amazon Forastero clones (Amelonado). It exhibits a good production [23, 21] and a very good adult vigor (trunk girth) [23]. SCA6, an Upper Forastero amazon clone from wild origin [22], is known for, on one hand, and, one the other hand, a high cocoa yielding [22], high yield efficiency and yield/vigour relationship [22, 19].

Thus, C1, P7 and SCA6 are used as parents for high-yielding hybrid families with good pod filling and good grain formation [24, 25, 26, 27, 28].

2.2. Methods

2.2.1. Experimental design and trial monitoring

The three studued hybrid progenies were planted according to a completely randomized mating design of rows with border (guards). Each plant (tree) represented a unique genotype. The plants spacing was 3 m both between rows and in row. Pollination was not controlled. Weedings in t**he fields** were performed manually and, if needed, supplemented with chemical treatments by spraying Kalach 360 SL (360 g/L) at the rate of 10 mL/L water. Pests were controlled with direct applications of Thiodan 50 CE at the rate of 12.5 mL/L water. Regular pruning was performed on the exceeding plagiotropic and orthotropic branches, along with the removal of parasitic epiphytes (*Loranthus spp*). No fertilizer was applied.

2.2.2. Traits measurements

Traits measurements were done on an individual tree basis.

Yield related-traits scoring

The following traits were recorded for each of the 179, 173 and 183 trees of the three studied progenies. During four cocoa campaigns (from september to august), cacao healthy ripe pods monthly harvested were weighted. The cocoa yield was expressed as cumulated pods number (PN), pods weight (PW) and dried beans weight (DBW) by transforming the wet beans weight (WBW) as follows: WBW = PW x α, with α a transformation coefficient **[20]**. DBW = WBW x *d* x α', where *d* is the planting density (in our case *d* = 1,337 trees/ha) and α' is a coefficient of transformation of WBW to DBW, generally fixed at 0.35. In addition, for only trees of progenies derived from (P7 x ICS100) x C1 and (P7 x ICS95) x C1, a sample of about 400 g of fresh beans was micro-fermented and sun dried at every harvest. Then, one-hundred dried beans weight (W_{100}) was recorded and its average values were calculated per year and over the three-year period. The yield efficiency (YE) was, also, estimated as the ratio of the cumulated healthy ripe pods weight data over the three years to the trunk cross-section (cm^2).

Horticultural traits measurement

Three horticultural vigor traits, namely the trunk girth (TG), the jorquette height (JH) and the canopy size (CS), were scored in both half-sib families (progenies) derived from crosses (P7 x ICS100) x C1 and (P7 x ICS95) x C1. The trunk girth (TG) was measured at about 10 cm above the soil, in the 6th and 10th years after planting. When the tree presented two trunks, TG has been adjusted as follows: TG = $\sqrt{(TG1 \times TG1 + TG2 \times TG2)}$ **[22]**, TG1 and TG2 being girths of trunks 1 and 2, respectively. The jorquette height (JH) was measured as the height (cm), from the soil surface, to the first jorquette (first point at which trunk breaks into lateral branches), in the 6th and 10th years after planting. When the tree presented two trunks, the highest height value has been taken into account in analyses. The canopy surface (CS) was estimated, in the 10th year after planting, as an approximation of the surface of the crown calculated from its projection on the soil, as follows: CS (m^2) = π x CD1/2 x CD2/2, with CD1 the maximal canopy diameter measured in the direction of the row in which the tree is and CD2 the maximal one measured in the perpendicular direction.

2.2.3. Molecular evaluations

DNA evaluation and SSR analyses are fully described in **[29]**.

2.2.4. Data analyses

Phenotypic data

Normal distribution of the data of each trait was verified applying the chi square test (χ^2) and/or the Agostino test at the threshold α = 5 %. Variances homogeneity was also checked by the test of Bartlett and/or the test of Brown-Forsythe. Descriptive statistical analyses (means and coefficients of variation), correlation coefficients (r) according to Pearson among traits and analyses of variance were calculated or performed with STATISTICA 7.1 software (StatSoft Group Inc., Tulsa, Okla.). Trees that did not produce any pod were discarded from descriptive statistical analyses. Natural logarithm transformation, square root transformation or arc sine transformation were applied, according to the type of trait analyzed, in case of evident anormality. Non parametric tests were performed when transformations did not achieve a sufficiently normal distribution.

2.3. Molecular data

The linkage maps used for the QTL mapping were constructed and published by **[29]**. Also, QTL mapping strategy is the one described in this previous paper.

2.3.1. QTL stability across time

For analyzing QTL stability across harvesting years, five times were defined: the three full years of the study (monitoring and scoring traits), the main and accessory harvest periods. The main harvest period (from september to january) was defined as the sum of the main harvest periods of the three years and the accessory harvest period (from april to july) as the sum of the accessory harvest periods of these three years. The QTL stability analysis was performed with phenotypic data collected during each of these five times. Thus, a stable QTL (QTL_{ST}) is defined as a QTL detected in the three years. While a specific QTL (QTL_{SP}) was a QTL detected only in any one given of the five times (year or period) and in the three progenies simultaneously.

2.3.2. Pleiotropic and polygenic QTLs determination

QTLs positions on linkage groups of the different parents were compared and discussed for determining pleiotropic and polygenic QTLs in relation to traits controlled. Pleiotropic QTLs, associated with different traits are, normally, detected in the same genomic region, and polygenic QTLs in different genomic regions.

3. Results

3.1. Phenotypic data distribution

Distributions of phenotypic data were normal ($p > 0.05$) for jorquette height (JH), canopy size (CS), one-hundred dried weight (W_{100}) in both half-sib families, besides for trunk girth (TG) in the family derived from (P7 x ICS95) x C1. But almost normal for TG in the family derived from (P7 x ICS100) x C1 and for TG and JH in the family derived from (P7 x ICS95) x C1. Whereas, a group presented high deviation to normal distribution. This group is composed of healthy ripe pods number (PN), pods weight (PW), dried beans weight (DBW) in the three families, besides yield efficiency (YE) in the family derived from (P7 x ICS100) x C1 and YE in the family derived from (P7 x ICS95) x C1. For these traits, distributions remained non normal despite transformations performed. Non-parametric tests were, thus, applied. Homogeneity of variances was observed for the quasi-totality of traits analyzed.

3.2. Correlations between traits

Of the 28 correlations tested among the height traits studied (five for yield: PN, PW, DBW, W_{100}, YE; three for vigor: TG, JH, CS) in each one of the two half-sib progenies, respectively, 17 and 18 were significant ($p < 0.05$, $p < 0.01$ and $p < 0.001$) (Tables 1 and 2). All these correlations are positive. No correlation was found between W_{100} and the other seven traits. TG and CS have the highest number (six) of significant correlations with the other six traits. The strongest correlations coefficients, ranging from 0.96 to 1.00, were observed, unsurprisingly, among PN, PW and DBW. These yield components (PN, PW, DBW) are strongly correlated ($0.77^{***} \leq r \leq 0.81^{***}$) with TG and relatively strongly correlated ($0.57^{***} \leq r \leq 0.68^{***}$) with CS. The JH was correlated only with the other two vigor traits (TG and CS) in the progeny derived from (P7 x ICS100) x C1, while it was correlated with YE, besides these other two vigor traits in the progeny derived from (P7 x ICS95) x C1. In the population derived from (SCA6 x H) x C1, each of the yield traits PN, PW and DBW were highly strongly ($0.92 \leq r \leq 1.00$) correlated with the two others (Table 3).

Table 1 Pearson's phenotypic correlation coefficients among traits analyzed in the population derived from (P7 x ICS100) x C1

	PN	**PW**	**DBW**	**W_{100}**	**TG**	**JH**	**CS**
PW	0.96***						
DBW	0.96***	0.99***					
W_{100}	Ns	Ns	Ns				
TG	0.78***	0.80***	0.81***	ns			
JH	Ns	Ns	Ns	ns	0.36***		
CS	0.63***	0.67***	0.68***	ns	0.81***	0.23**	
YE	0.87***	0.89***	0.88***	ns	0.64***	Ns	0.55***

ns : non significant ; significant * at $p < 5$ % ; ** at $p < 1$ % ; *** at $p < 0,1$ %..

PN: healthy ripe pods number; PW: pods weight; DBW: dried beans weight; W_{100}: one hundred dried beans weight; TG: trunk girth; JH: jorquette height; CS: canopy size; YE: yield efficiency.

Table 2 Pearson's phenotypic correlation coefficients among traits analyzed in the population derived from (P7 x ICS95) x C1

	PN	**PW**	**DBW**	**W_{100}**	**TG**	**JH**	**CS**
PW	0.97***						
DBW	0.97***	1.00***					

W_{100}	Ns	Ns	Ns				
TG	0.77***	0.81***	0.81**	ns			
JH	Ns	Ns	Ns	ns	0.31***		
CS	0.59***	0.58***	0.57***	ns	0.84***	0.18*	
YE	0.94***	0.93***	0.93***	ns	0.76***	0.16*	0.60***

ns : non significant ; significant * at $p < 5$ % ; ** at $p < 1$ % ; *** at $p < 0{,}1$ %..

PN: healthy ripe pods number; PW: pods weight; DBW: dried beans weight; W_{100}: one hundred dried beans weight; TG: trunk girth; JH: jorquette height; CS: canopy size; YE: yield efficiency.

Table 3 Pearson's phenotypic correlation coefficients among traits analyzed in the population derived from (SCA3 x H) x C1

	PN	**PW**
PW	0.93***	
DBW	0.92***	1.00***

ns : non significant ; significant; *** at $p < 0.1$ %; PN: healthy ripe pods number; PW: pods weight; DBW: dried beans weight.

3.3. Plant influence on traits variability

The analysis of variance revealed different influences of the factor genotype (a tree = a single genotype) on the variation of traits: significant ($p < 5$ %) for TG, YE, highly significant ($p < 1$ %) for PN and DBW, very highly significant ($p < 0.1$ %) for PW.

3.4. QTL identified

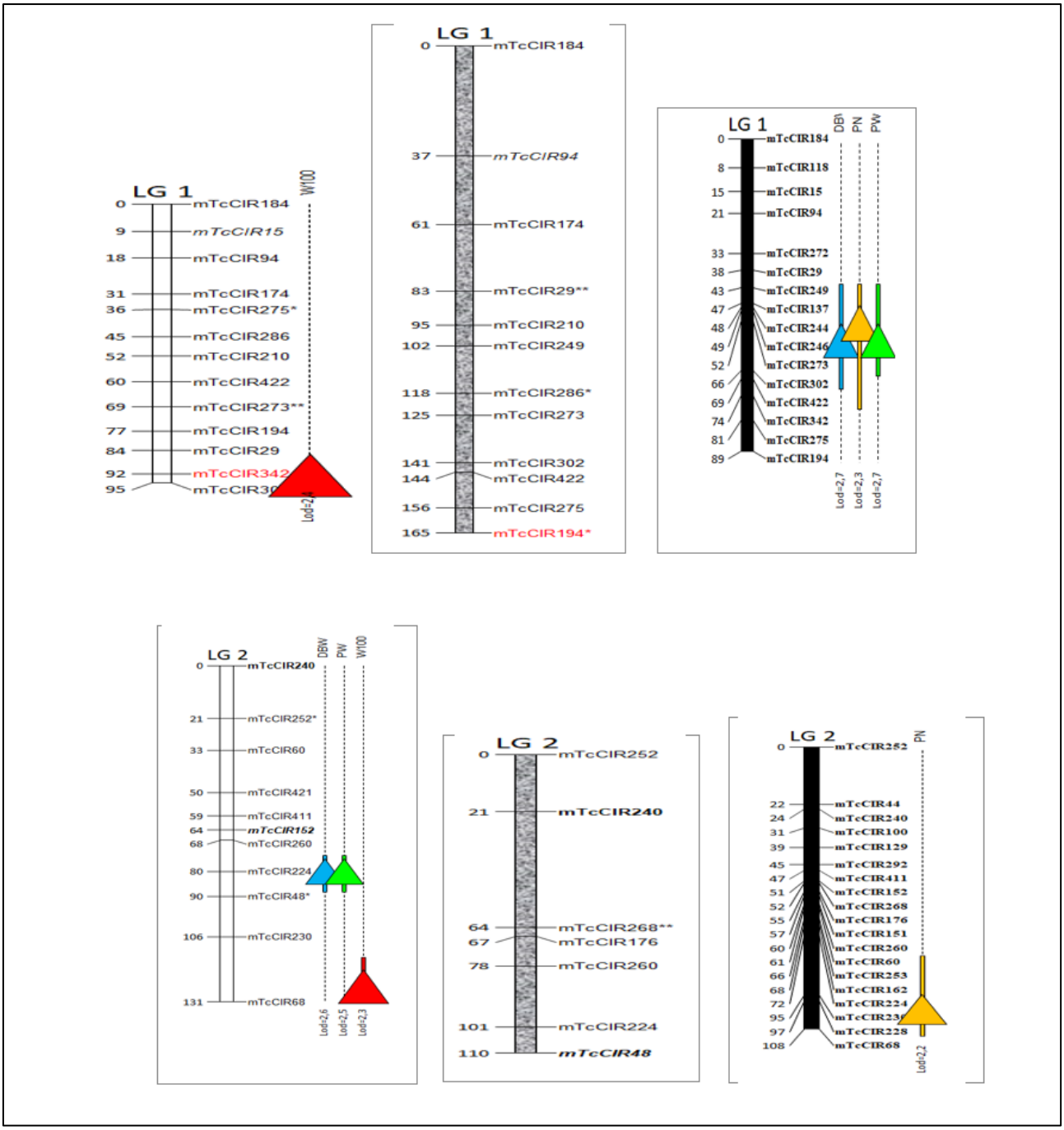
QTLs detected in the three progenies for the eight traits anslyzed are summarized in table 4. For each yield related-trait, three to five QTLs were identified on three to five linkage groups. While two QTLs of one horticultural trait was detected on one linkage group.

3.4.1. QTL of yield components

sNo QTL of healthy ripe pods number (PN) was found in the parent derived from "P7 x ICS100". Three QTLs for PN were identified on linkage groups (LGs) 1, 2 in parent derived from "SCA6 x H" and 4 of parent derived from "P7 x ICS100" (Figure 1; Table 4). The most significant were those on LGs 2 and 4 (Table 4). Five QTL of healthy ripe pods weight (PW) were identified (Figure 1; Table 4): two in each parent derived from "SCA6 x H" and "P7 x ICS100" and one in parent derived from "P7 x ICS95". The LG 4 carried one in two parents. That of the parent derived from (P7 x ICS95) had a major effect '(R^2 = 34,3 %). No QTL of dried beans weight (DBW) was found in the parent derived from "P7 x ICS95". Five QTLs for DBW were detected, with two in the parent derived from "SCA6 x H" and three in the parent derived from "P7 x ICS100". Five QTLs for one-hundred dried beans weight (W_{100}) were identified, with four in the parent derived from ''P7 x ICS100" and one in the parent derived from "P7 x ICS95". The phenotypic variation for the trait explained by these QTLs varied from 15.6 to 20.9 %. Three QTLs of yield efficiency (YE) were mapped: one and two, respectively, in the parent derived from "P7 x ICS100" and "P7 x ICS95". The LG 6 carried one in both parents. The R^2 varied from 8.5 to 13.6 %.

3.4.2. QTL related to plant vigor

No QTL was detected for the jorquette height (JH) and the canopy size (CS). Two QTLs of the trunk girth (TG) were found on LG 4 of the parent derived from "P7 x ICS100", with R^2 varying from 10.7 to 11.9 %.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9 mTcCIR15
18 mTcCIR94
31 mTcCIR174
36 mTcCIR275*
45 mTcCIR286
52 mTcCIR210
60 mTcCIR422
69 mTcCIR273**
77 mTcCIR194
84 mTcCIR29
92 mTcCIR342
95 mTcCIR30
W100
Lod=2,4
LG 1
0 mTcCIR184
37 mTcCIR94
61 mTcCIR174
83 mTcCIR29**
95 mTcCIR210
102 mTcCIR249
118 mTcCIR286*
125 mTcCIR273
141 mTcCIR302
144 mTcCIR422
156 mTcCIR275
165 mTcCIR194*
LG 1
0 mTcCIR184
8 mTcCIR118
15 mTcCIR15
21 mTcCIR94
33 mTcCIR272
38 mTcCIR29
43 mTcCIR249
47 mTcCIR137
48 mTcCIR244
49 mTcCIR246
52 mTcCIR273
66 mTcCIR302
69 mTcCIR422
74 mTcCIR342
81 mTcCIR275
89 mTcCIR194
DBI
PN
PW
Lod=2,7
Lod=2,3
Lod=2,7
LG 2
0 mTcCIR240
21 mTcCIR252*
33 mTcCIR60
50 mTcCIR421
59 mTcCIR411
64 mTcCIR152
68 mTcCIR260
80 mTcCIR224
90 mTcCIR48*
106 mTcCIR230
131 mTcCIR68
DBW
PW
W100
Lod=2,6
Lod=2,5
Lod=2,3
LG 2
0 mTcCIR252
21 mTcCIR240
64 mTcCIR268**
67 mTcCIR176
78 mTcCIR260
101 mTcCIR224
110 mTcCIR48
LG 2
0 mTcCIR252
22 mTcCIR44
24 mTcCIR240
31 mTcCIR100
39 mTcCIR129
45 mTcCIR292
47 mTcCIR411
51 mTcCIR152
52 mTcCIR268
55 mTcCIR176
57 mTcCIR151
60 mTcCIR260
61 mTcCIR60
66 mTcCIR253
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72 mTcCIR224
95 mTcCIR23
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PN
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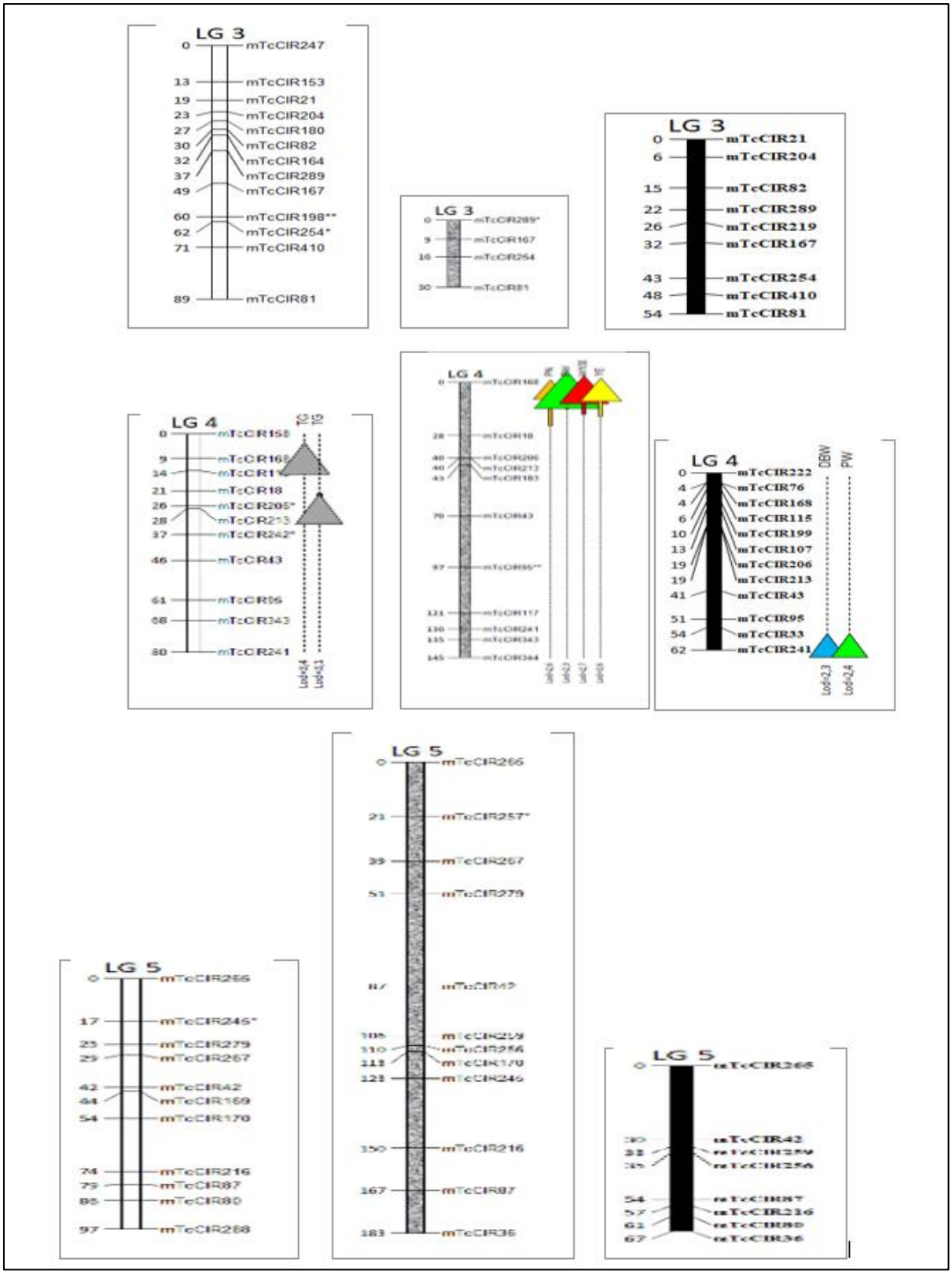
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32 mTcCIR164
37 mTcCIR289
49 mTcCIR167
60 mTcCIR198**
62 mTcCIR254*
71 mTcCIR410
89 mTcCIR81
LG 3
0 mTcCIR289*
9 mTcCIR167
16 mTcCIR254
30 mTcCIR81
LG 3
0 mTcCIR21
6 mTcCIR204
15 mTcCIR82
22 mTcCIR289
26 mTcCIR219
32 mTcCIR167
43 mTcCIR254
48 mTcCIR410
54 mTcCIR81
LG 4
0 mTcCIR155
9 mTcCIR168
14 mTcCIR1
21 mTcCIR18
26 mTcCIR205*
28 mTcCIR213
37 mTcCIR242*
46 mTcCIR43
61 mTcCIR86
68 mTcCIR343
80 mTcCIR241
LG 4
0 mTcCIR168
28 mTcCIR18
40 mTcCIR205
40 mTcCIR213
43 mTcCIR183
70 mTcCIR43
97 mTcCIR95**
121 mTcCIR117
130 mTcCIR241
135 mTcCIR343
145 mTcCIR344
LG 4
0 mTcCIR222
4 mTcCIR76
4 mTcCIR168
6 mTcCIR115
10 mTcCIR199
13 mTcCIR107
19 mTcCIR206
19 mTcCIR213
41 mTcCIR43
51 mTcCIR95
54 mTcCIR33
62 mTcCIR241
DBW
PW
LG 5
0 mTcCIR266
21 mTcCIR257*
39 mTcCIR267
51 mTcCIR279
87 mTcCIR42
105 mTcCIR219
110 mTcCIR256
113 mTcCIR170
123 mTcCIR246
150 mTcCIR216
167 mTcCIR87
183 mTcCIR36
LG 5
0 mTcCIR266
17 mTcCIR245*
25 mTcCIR279
29 mTcCIR267
42 mTcCIR42
44 mTcCIR169
54 mTcCIR170
74 mTcCIR216
79 mTcCIR87
85 mTcCIR80
97 mTcCIR268
LG 5
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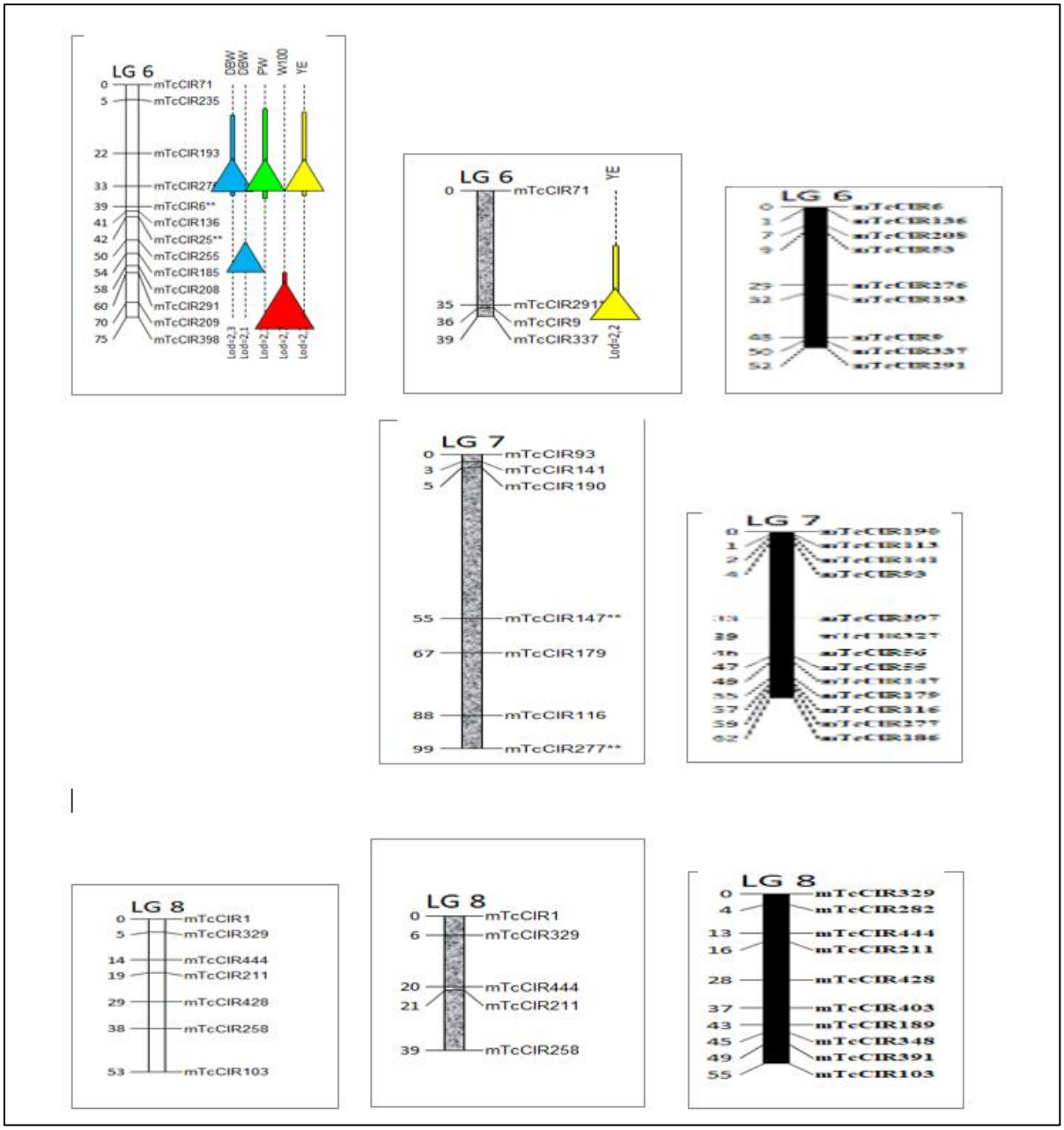
57 mTcCIR216
61 mTcCIR80
67 mTcCIR36


LG 6
DBW
DBW
PW
W100
YE
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5 mTcCIR235
22 mTcCIR193
33 mTcCIR27
39 mTcCIR6**
41 mTcCIR136
42 mTcCIR25**
50 mTcCIR255
54 mTcCIR185
58 mTcCIR208
60 mTcCIR291
70 mTcCIR209
75 mTcCIR398
Lod=2,3
Lod=2,1
LG 6
YE
0 mTcCIR71
35 mTcCIR291
36 mTcCIR9
39 mTcCIR337
Lod=2,2
LG 6
LG 7
0 mTcCIR93
3 mTcCIR141
5 mTcCIR190
55 mTcCIR147**
67 mTcCIR179
88 mTcCIR116
99 mTcCIR277**
LG 7
LG 8
0 mTcCIR1
5 mTcCIR329
14 mTcCIR444
19 mTcCIR211
29 mTcCIR428
38 mTcCIR258
53 mTcCIR103
LG 8
0 mTcCIR1
6 mTcCIR329
20 mTcCIR444
21 mTcCIR211
39 mTcCIR258
LG 8
0 mTcCIR329
4 mTcCIR282
13 mTcCIR444
16 mTcCIR211
28 mTcCIR428
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49 mTcCIR391
55 mTcCIR103

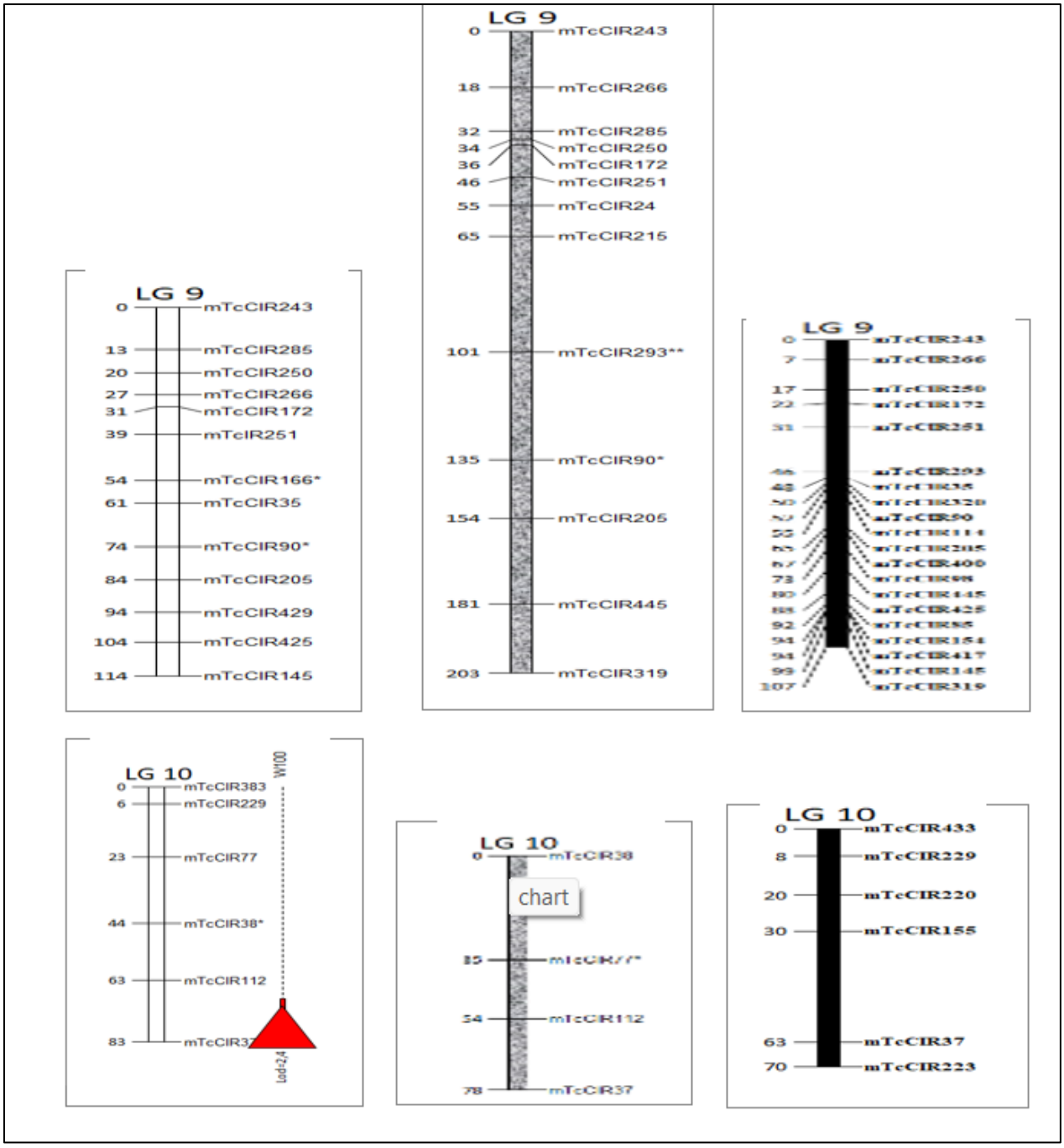

Figure 1 Graphical representation of the linkage groups (LGs) of the three female parents carrying their respective detected QTLs

Vertical lanes representing LGs of the female parent "P7 x ICS100" in white, those of the female parent "P7 x ICS95" in white-black and of the female parent "SCA6 x H" in black. On the right side of the LG, the triangle is proportional to the percentage of the phenotypic variance of the trait explained by the QTL. On the left, cumulative map distances in cM and the locus names are indicated. Markers loci with asterisks deviated significantly from a 1:1 ratio.

Table 4 Summary of QTL data for yield components, vigour and resistance traits to *Phytophthora palmivora*

Traits	Progeny derived from cross	chr	KW (SMA)		SIM			
			K*	SL	Position	Bording marlers	LOD peak	R^2

					LOD peak			
PN	(SCA6 x H) x C1	1	7,982	4*	50,400	mTcCIR246 – mTcCIR273	2,31	8.8
		2	16,416	7*	97,260	mTcCIR230 – mTcCIR228	2.16	11.4
	(P7 x ICS100) x C1	-	-	-	-	-	-	-
	(P7 x ICS95) x C1	4	17.927	7*	4.000	mTcCIR168 – mTcCIR18	2,55	9.6
PW	(SCA6 x H) x C1	1	10,840	4*	55,300	mTcCIR273 – mTcCIR302	2,72	7,9
		4	7,875	4*	57,500	mTcCIR33 – mTcCIR241	2,35	5,9
	(P7 x ICS100) x C1	2	8,785	4*	80,326	mTcCIR224 – mTcCIR48	2,54	8,8
		6	8,154	4*	28,964	mTcCIR193 – mTcCIR276	2,09	9,2
	(P7 x ICS95) x C1	4	14,454	6*	4,000	mTcCIR168 – mTcCIR18	2,29	34,3
DBW	(SCA6 x H) x C1	1	10,483	4*	55,300	mTcCIR273 – mTcCIR302	2,71	7,9
		4	7,949	4*	57,500	mTcCIR33 – mTcCIR241	2,34	5,9
	(P7 x ICS100) x C1	2	8,274	4*	80,326	mTcCIR260 – mTcCIR24	2,58	8,9
		6	8,884	4*	28,964	mTcCIR193 – mTcCIR276	2,33	10,3
		6	8,519	4*	55,241	mTcCIR185 – mTcCIR208	2,08	8,3
	(P7 x ICS95) x C1	-	-	-	-	-	-	-
W_{100}	(P7 x ICS100) x C1	1	9,375	4*	90,636	mTcCIR342 – mTcCIR302	2,41	18,5
		2	13,347	6*	125,151	mTcCIR230 – mTcCIR68	2,28	15,6
		6	10,747	4*	70,774	mTcCIR209 – mTcCIR398	2,73	20,9
		10	10,442	4*	77,903	mTcCIR112 – mTcCIR37	2,41	16,8
	(P7 x ICS95) x C1	4	10,413	4*	4,000	mTcCIR168 – mTcCIR18	2,72	19,4
TG	(P7 x ICS100) x C1	4	18,847	7*	9,210	mTcCIR168 – mTcCIR115	3,45	11,9
		4	14,530	6*	27,641	mTcCIR18 – mTcCIR213	3,08	10,7
	(P7 x ICS95) x C1	-	-	-	-	-	-	-

YE	(P7 x ICS100) x C1	6	9,213	4*	28,984	mTcCIR193 – mTcCIR276	2,07	9,2
	(P7 x ICS95) x C1	4	23,029	7*	4,000	mTcCIR168 – mTcCIR18	3,65	13,6
		6	8,196	4*	35,000	mTcCIR71 – mTcCIR291	2,19	8,5

chr : chromosome ; KW : Kruskal-Wallis test ; K*: Kruskal-Wallis statistic value; SL: significance level; 1*0.1; 2*0.05; 3*0.01; 4*0.005; 5*0.001; 6*0.0005; 7*0.0001; SIM : Simple Interval Mapping ; R^2 : Phenotypic variation for traits explained by individual QTL.

Legend : PN : healthy ripe pods number; PW: healthy ripe pods weight; DBW: dried beans weight; W_{100} one-hundred dried beans weight; TG: trunk girth; YE: yield efficiency.

3.4.3. QTL stability across time

Any QTL was considered stable (QTL_{ST}), when detected in each of the three years of the study. Such QTL_{ST} were found for dried beans weight (DBW): one on each of LGs 1 and 4 in the parent derived from "SCA6 x H" and one on LG 6 of the parent derived from "P7 x ICS100''.

3.4.4. Pleiotropic and polygenic QTLs

Pleiotropic and polygenic (polymeric) co-localizations were highlighted. Regarding pleiotropic co-localization, in the parent derived from "SCA6 x H", QTLs of PN, PW (or DBW) were found in the same position on LG 1. In the parent derived from "P7 x ICS95", on LG 4, a tight cluster of QTL of PW, W_{100}, YE and PN was observed and in the parent derived from "P7 x ICS100", on LG 6: a region grouping QTLs of PW, DBW, YE was identified. In regards polygenic co-localization, several regions of certain LGs were associated with a trait. That was observed, in the parent derived from "P7 x ICS100", for trunk girth (TG) on LG 4, DBW on LG 6.

4. Discussion

Normal distribution of values of some investigated traits indicates their polygenic inheritance [30, 31, 32, 33]. That is the case of one-hundred dried beans weight (W_{100}) in the family derived from (P7 x ICS100) x C1, trunk girth (TG) and W_{100} in the family derived from (P7 x ICS95) x C1. Traits exhibiting non normal distribution of values can also be poly-genetically inherited. Besides, the polygenic inheritance is suggested by the transgressive segregation of phenotypic data in each family, as demonstrated in pea [34], french bean (*Phaseolus vulgaris* L.) for yield and its component traits [35], in modern plant breeding [36].

Significant and positive correlations were observed among yield components (healthy ripe pods number: PN; healthy pods weight: PW ; dried beans weight : DBW), in the three families. In both half-sib families studied, plant vigor related traits (trunk girth:TG, jorquette height: JH, canopy size: CS) were significantly positively correlated. Strong correlations found between yield components and TG and CS could mean that the more a cacao tree is vigorous, the higher its potential level of cocoa yield; these could also suggest that yield was largely due to TG and CS rather than JH, since there was no correlation between yield components and JH. Relationships between adult vigour and yield components are found mostly established separately. Thus, in their works [37] and [24] found, as in the current study, respecrively, strong and relatively strong positive correlation between trunk diameter or collar diameter (equivalent to TG) and JH or plant height. While, [26**]** reported such correlations between total number of pods and ~~p~~otential yield and, betwwen averahe fresh beans weight per pod and average single dried bean weight. Moreover, strong correlations were also highlighted between yield and, respectively, trunk circumference and plant height in *Cola nitida* [38], a fruity perennial species of Malvaceae family, to which cacao belongs.

The highly significant effects of the genotype (tree) on the variation of yield components and plant vigor predict high probabilities of detecting QTLs involved in the expression of these characters. [39] also found a high inter-clone yield variability and such a inter-tree yield variability in two populations of *Cola nitida*.

QTLs for healthy ripe pods number (PN) were detected on LGs 1 and 2 of the parent derived from "SCA6 x H" (2 QTLs) and on LG 4 in the parent derived from "P7 x ICS95" (1 QTL). QTLs of pods number were also localized by [6] on LGs 4, 5, 9 and [10] on LGs 1 and 4. Also, [7] detected associations SSR (mTcCIR) with such QTLs on LGs 4 and 9 in the Hawaiian cacao collection. Likese, [40] detected, in a population of Criollo/Trinitario from Venezuela, three significant associations markers-QTLs of pods number on LGs 1, 2 and 8. These results exhibit several common regions of LGs 1, 2 and 4 involved in pod number determinism.

Five QTLs for healthy ripe pods weight (PW) were detected, with one to two QTLs found in each female parent on LGs 1, 2, 4 and 6. In Hawaiian populations consisted of Trinitario, forastero upper amazon and forastero upper amazon/Trinitario'hybrids, [7] exhibited associations between PW and, on one hand, three markers on LG 2 and, one the other hand, markers mTcCIR115, mTcCIR18 and mTcCIR107 on LG 4. The marker mTcCIR18 is one of the bording markers of the major QTL (R^2 = 34.3 %) detected in the current work on LG 4. These findings demonstrate the necessity of increasing analyses of such kind across backgrounds and environments and comparing results so that to uniformize markers to be used in markers-aided selection programs.

QTLs of dried beans weight (DBW) were mapped on LGs 1 and 4 of the parent derived from ''SCA6 x H'' and on LGs 2 and 6 of the parent derived from ''P7 x ICS100''. [10] mapped such QTLs on LGs 1, 2, 3, 4, 5, 6, 8, 9 and in addition some of yield on LGs 3, 4, 9. Dried beans weight is related to fresh beans weight. QTLs of fresh beans weight were localized in Forastero/Trinitario and Forastero backgrounds on LG 2 by [41], on LGs 1, 2, 4, 5 and 9 by [6]. Likewise, [7] highlighted associations between QTL of fresh beans weight and, respectively, on the one hand two markers on each of LGs 2 and 9, and on the other hand markers mTcCIR115, mTcCIR18, mTcCIR107, mTcCIR12 on LG 4. Ten QTLs of DBW were mapped on LGs 2, 3, 4, 5, 7, 8, 9 and 10 in a Forastero background [4]. Our data and those of [4] show that QTL on LGs 2 and 4 are localized in the same genomic regions. Also, [40] detected 15 regions of LGs 1, 2, 3, 4, 5, 6, 7, 9 and 10 involved in the variation of fresh and dried beans weights, in Criollo/Trinitario hybrid varieties and in the international collection of CATIE in Costa Rica and in cultivated ones in Venezuela.

QTLs of one-hundred dried beans weight (W_{100}) were identified on LGs 1, 2, 6 and 10 in the parent derived from ''P7 x ICS100'' and, on LG 4 in the parent derived from ''P7 x ICS95''. Three QTLs of W_{100}, with total R^2 > 50 %, were found on LGs 6, 8 and 9 by [42]. [40] detected six associations between some markers and W_{100}. [43] localized, on LGs 2, 3, 4, 7 and 10, QTLs of number of fermented and dried beans for 100 g. That localized on LG 3 was regarded to be the most stable. In the current work, a QTl for W_{100}, with R^2 = 15,6 %, was mapped on LG 2, on which [4] localized one QTL of single fermented and dried bean weight, with R^2 = 21,2 %.

In the current study, LGs 5, 6 and 10 carried only QTL for yield and in progenies generated from a Trinitario background (clones ICS100 and ICS95). In **[6]**, LG 9 presented QTLs for yield in Tinitario background. All these findings show that some favorable alleles of yield seem to be inherited via particular chromosomes.

In this investigation, we highlighted the proximal extremety of chromosome 4 carrying QTLs of PN, PW, W100 and yield efficiency. Identical findings were made by **[10]** who mapped QTLs for the total pods number, the healthy pods number, dry bean weight, pod index and average yield. Moreover, these authors revealed that these QTL incease the most cocoa yield components.

The two QTLs of trunk girth (TG) (R^2 varying from 10.7 to 11.9 %) identified on LG 4 of the parent derived from "P7 x ICS100" represent more likely only one QTL, since their positions are adjacent between markers mTcCIR168 and mTcCIR18. TG is the only one character for which family (data non shown) and tree (genotype) effects were significant. That could be one reason of the failure in QTL detecting for JH and CS. However, [7] localized one significant association between marker mTcCIR223 on LG 10 and canopy width (CW). [37] identified on LG 4, one QTL of trunk diameter, with R^2 = 6.1. Two QTLs of trunk diameter or trunk circumference, R^2 = 15.4 and 24.9 % respectively, were also identified on LG 4 by [6]. In the same region of LG 4, [8] localized one QTL of the average trunk diameter growth rate, with R^2 = 13.1 %. In our study and in [8], marker mTcCIR168 is one of the bording markers of this QTL on LG 4, that appears to be one of the main and essential supports of TG. Trunk diameter or trunk circumference was identified to be the best parameter determining dried beans weight (DBW) [4]. In our work, the highest significant and positive phenotypic correlation between yield variables and vigor traits was found between TG and DBW. Marker mTcCIR18 on LG 4 is one of the bording markers of TG in our work and is associated with PW in [7].

QTLs of yield efficiency (YE) were identified, respectively, in the progeny derived from (P7 x ICS100) x C1 on LG 6 and, in the progeny derived from (P7 x ICS95) x C1 on LGs 4 and 6. Neither on LG 4 nor LG 6 were detected QTLs for both PW and TG. However, YE was estimated with PW and TG. Thus, PW contributed more enough in detecting QTLs for YE in family derived from (P7 x ICS100) x C1 on LG 6 and in family derived from (P7 x ICS95) x C1 on LG4. For evidence, in the latter family on LG 4, the highest scores of LOD (3.63) and R^2 (13.6 %) were noted, since on this LG 4, a major QTL (R^2 = 34.3 %) of PW was identified. [44] mapped, in three different families, QTLs of yield-vigor ratio on LGs 2, 4 and 9 with R^2 values approximately identical to that (8.5 to 13.6 %) is obtained in this work.

In the three progenies studied, some QTLs for several traits, on different LGs, appeared stable during the strict minimum of the three-year period. It is established that major QTL may be identified at different times and in different environments [45, 46, 47, 48]. Our findings are in accordance with that, being beyond.

In the family derived from (SCA6 x H) x C1, one stable QTL (QTL_{ST}) of PW and DBW, each with R^2 = 7.9 %, were highlighted on LG 1 and one QTL of PN (R^2 = 11.4 %) on LG 2. [43] emphasized stable QTL of number of beans per 100 g (R^2 from 6.7 to 13.2 %) on LG 3. In the family derived from (P7 x ICS100) x C1, one stable QTL of DBW (R^2 = 10.3 %) was revealed on LG 6, while in the family derived from (P7 x ICS95) x C1, one stable QTL of PN (R^2 = 9,6 %) was declared on LG 4. [4] detected also stable QTL of yield (DBW) on LG 5 and 9. In [6], one stable QTL of fresh beans weight and pods number were localized on LG 5 of the clone IMC78

As distinguished by [4], QTLs of yield identified in the current study appear to be, in majority, QTLs for juvenile phase, since cacao trees aged 10 years at most. This could explain their non consistent detection across time, contrarily to [6] who found QTLs during the adult phase of plant development. In our study, we identified, however, on LGs 4 and 2, major QTLs upon which, according to [4], cocoa yield depends more.

In the current study, different markers-traits associations were observed, which are the same, either in the family derived from (SCA6 x H) x C1 and in one of the two half-sib families, or in both half-sib families.

QTLs of some yield components (PN, PW or DBW) were localized in the same position on LG 1. Likewise, QTLs of PW, W_{100}, YE, PN co-localized on LG 4. On LG 6, a region clustering QTLs of PW, DBW, YE was identified. A similar co-locating result has been obtained in cacao by [5, 6] on LG 4 and [10] for QTLs of yield components (pod and fresh beans weights, pods number), QTLs of vigour (trunk circumference, canopy width), [46] for QTLs of resistance to witches' broom disease on LG 9, [47] for yield components in wheat.

Several regions of different LGs have been involved in the expression of one or several agro-morphological traits. Similar results have been reported in many species. That is the case, in *Theobroma* spp. for yield components [37, 4, 6, 40, 9, 10, 11], resistance factors to *P. palmivora* [49, 6, 9], resistance factors to witches' broom disease [50, 9, 51, 46], resistance factors to Ceratocystis wilt of cacao due to *Ceratocystis cacaofunesta* [52], vigor traits [4, 6], butter content and hardness/quality product [53 11]. Several QTL localizations and co-localizations found in this work were similar to some in [44] and [5, 6] on chromosomes 1, 2, 4 and 9.

QTLs overlapping is in accordance with high values of highly significant correlations observed among yield components. Indeed, Pearson's phenotypic correlation coefficients vary from 0.89 to 1.00. Similar results have been reported in cacao [37, 4, 41, 5, 6)], in pepper [54], in wheat [47]. This suggests physiological mechanisms shared between characters contributing to yield, plant vigour and quality of products [54]. In rice, the major and stable QTL for narrow noot cone angle co-localized with the genes involved in abiotic stress stimulus response [55]. However, we observed that QTLs of some traits non correlated or negatively correlated co-localized. Indeed; the one-hundred dried beans weight (W_{100}) was not correlated with any other trait in this study.

QTLs co-locating, as on the chromosome 4, could suggest the presence of one gene with pleiotropic effect on traits controlled. Alternatively, it could be several closely linked genes (cluster of genes), each of which affecting a different trait and in this case the co-location of QTLs for different traits is simply a result of linkage. Albeit, the pleiotropism could be the most likely explanation of QTLs co-locating, in the current study, data and maps resolution were non sufficient to establish absolute distinction between pleiotropic effects of a single gene and independent effects of cluster of genes.

5. Conclusion

This investigation was performed to identify, on Microsatellite-based linkage maps, QTLs of yield components (healthy ripe pods number, pods weight, dried beans weight, one-hundred dried beans weight, yield efficiency) and vigor traits (trunk girth, jorquette height, canopy size) in three cacao progenies . In conjunction with that, positive significant phenotypic correlations have been found among traits, except one-hundred dried beans weight. Some of these correlations are strong as those among yield components (healthy ripe pods number, pods weight, dried beans weight, yield efficiency) and plant vigor-related traits (trunk girth, canopy size). While, no correlation was observed between yield components and jorquette height.

Also, data of healthy ripe pods number, pods weight, dried beans weight, yield efficiency, trunk girth varied significantly to very highly significantly among cacao trees.

Regarding the target subject, two to five QTLs were mapped, often on different chromosomes 1, 2, 4, 6, 10 for each one of the yield components studied. whereas, two QTLs for the trunk girth were identified on chromosome 4. Some QTLs of yield components co-locate on chromosomes 1, 4 and 6. These co-locations are in accordance of strong and positive

highly significant phenotypic correlations among traits. Of these QTLs, a pods weight major QTL (R^2 = 34.3 %) was borded by SSR markers mTcCIR168 and mTcCIR18 on chromosome 4 of the parent derived from "P7 x ICS95". Also, QTLs for one-hundred dried beans weight whose R^2 of 15.6 to 20.9 %, the most consistent, were found on five chromosomes in both half-sib populations.

Morever, a few QTLs for healthy ripe pods number, pods weight and dried beans weight were stable across time and progenies, in one to three genetic backgrouds (Trinitario and/or Forastero). Then, marker mTcCIR18 is linked to healthy ripe pods number, dried beans weight and, trunk girth besides marker mTcCIR168 one of the markers bording the major QTL of pods weight, on chromosome 4, were found across progenies, backgrousds. These markers linked to stable and/or major QTLs or poly linked-traits markers are valuable potential candidates for a future exploiting of these QTLs as selection tools.

Compliance with ethical standards

Acknowledgments

We highly and gratefully acknowledge the financial support of the Agropolis Fondation to the first author for molecular analyses implementation at CIRAD Biotrop in Montpellier France.

Disclosure of conflict of interest

The authors declare no conflict of interest.

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