Mapping QTL for yield components, vigor, and resistance to *Phytophthora palmivora* in *Theobroma cacao* L.

D. Clement, A.M. Risterucci, J.C. Motamayor, J. N'Goran, and C. Lanaud

Abstract: Quantitative trait loci (QTL) mapping for agronomic traits was carried out in cocoa (*Theobroma cacao* L.). Regions of the genome involved in yield, vigor, and resistance to *Phytophthora palmivora* were identified. Three heterozygous clones, one upper Amazon Forastero (IMC78) and two Trinitario (DR1 and S52), were crossed with the same male parent, a lower Amazon Forastero (Catongo), known to be highly homozygous. Observations were made on progeny over nine consecutive years. One to three QTL related to yield were detected in each of the three populations, located on chromosomes 1, 2, 4, 5, 9, and 10. They explained between 8.1 and 19.3% of the phenotypic variation and showed various levels of repeatability. In IMC78, the QTL detected on chromosome 5 was the most repeatable over years. The QTL for the average individual pod weight on chromosome 4 was the most significant with an LOD of 17.3 and an R^2 of 43.7. QTL related to these traits were identified in the same region of the genome in clones of different genetic groups. This suggests that molecular markers can be used to improve cocoa varieties.

Key words: Theobroma cacao, agronomic traits, quantitative trait loci (QTL).

Résumé : La cartographie de locus à caractère quantitatif (QTL) a été réalisée chez le cacaoyer (*Theobroma cacao* L.) pour des caractères agronomiques. Des régions du génome impliquées dans le rendement, la vigueur et la résistance à *Phytophthora palmivora*, ont été identifiées. Trois clones hétérozygotes, un Forastero haut Amazonien (IMC78) et deux Trinitario (DR1 et S52) ont été croisés par le même parent mâle (Catongo), Forastero bas Amazonien qui est connu pour être hautement homozygote. Les observations ont été réalisées sur neuf années consécutives. Un à trois QTL impliqués dans le rendement ont été détectés chez chacune des trois populations, localisés sur les chromosomes 1, 2, 4, 5, 9 et 10. Ils ont expliqué entre 8,1 et 19,3% de la variation phénotypique et ont montré différents niveaux de répétabilité. Chez IMC78, le QTL détecté sur le chromosome 5 était le plus stable. Le QTL pour le poids moyen de la cabosse, sur le chromosome 4, était le plus significatif avec un LOD de 17,3 et un R^2 de 43,7. Des QTL impliqués dans ces caractères ont été identifiés dans les mêmes régions du génome chez des clones appartenant à différents groupes génétiques. Ceci laisse prévoir que les marqueurs moléculaires pourraient être utilisés pour améliorer les variétés de cacaoyers.

Mots clés : Theobroma cacao, caractères agronomiques, locus de caractères quantitatifs.

Introduction

Theobroma cacao was domesticated in pre-Columbian times by the Mayans and Aztecs (Paradis 1979). Today, *T. cacao* is cultivated in humid tropical regions. It is mainly cultivated by small holders along with their subsistence crops, providing them with a cash crop of cocoa. Africa produces 70% of the world cocoa supply, with Côte d'Ivoire being the leading producer. The improvement of *T. cacao*'s adaptation to various environments, particularly to areas with strong disease pressure, requires the accumulation of favorable alleles in new varieties.

The Criollo group, which can be found from Mexico to Colombia and Venezuela, has a narrow genetic base (Motamayor et al. 2002), whereas the Forastero group is composed of numerous heterogeneous wild populations and cultivated varieties that can be found from Guyana, lower Amazonia (Brazil), and the Orinoco valley (Venezuela) to upper Amazonia (Brazil, Peru, Ecuador, and Colombia) (Lanaud et al. 1999*a*). The Trinitario group is composed of hybrids between Criollo and lower Amazon Forastero and a better understanding on the origin of the Trinitario was proposed recently by Motamayor et al. (2002).

Criollo has been used in breeding programs less often than other types of cocoa generally because of its low productivity, as well as its frequent susceptibility to diseases. On the other hand, Trinitario and Forastero have been widely

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Table 1. Statistical analyses on yield and vigor traits in the progenies.

			Statistical analysis			Correlation coefficients (Pearson)					
Traits	Female parent	*N*	Mean	Range	CV (%)	PN	PW	RP	SD	CW	TC
WBW	DR1	96	1.9	0.4–7.7	56.1	0.95**		–0.22*		0.47**	0.71**
	S52	94	2.1	0.1–6.1	47.5	0.95**			0.38**	0.42**	0.79**
	IMC78	125	4.1	0.6–8.1	39.9	0.89**		0.38**		0.48**	0.66**
PN	DR1	96	19.6	3.8–73.2	51.4					0.46**	0.64**
	S52	94	21.4	2.3–69.2	50.9				0.35**	0.41**	0.78**
	IMC78	125	32.6	9.0–75.5	38.3		–0.25*			0.36**	0.45**
PW	DR1	96	513	342–731	15.6			–0.20*			0.34**
	S52	94	491	330–684	13.5						
	IMC78	125	676	443–926	15.6			–0.34**			0.42**
RP	DR1	90	9.6	0.0–38.6	69.6						
	S52	91	11.8	1.2–45.0	64.7						
	IMC78	117	10.1	1.8–29.7	65.1					–0.23*	0.44**
CW	DR1	96	9.3	2.7–24	36.2						0.54**
	S52	94	7.3	1.9–17.3	44.7						0.44**
	IMC78	125	11.9	1.5–25.8	37.8						0.54**
TC	DR1	96	44.6	30–66	18.5						
	S52	94	44.2	28–68	16.7						
	IMC78	125	57.1	34–88	16.2						

Note: Correlation coefficient corresponds to the values of the Pearson correlation only indicated at significance of $p < 0.05$ (*) and $p < 0.001$ (**). WBW, average wet bean weight per tree and per year in kilograms, from accumulated harvest data over nine years (1990 to 1998); PN, average pod number per year from accumulated harvest data over nine years (1990 to 1998); PW, average weight of single pods in grams, from accumulated harvest data over nine years (1990 to 1998); RP, average percentage of rotten pods from accumulated data over six years (1990–1995); TC, trunk circumference (cm) (measured the 12th year after planting); CW, estimation of the canopy width (m^2) (measured nine years after planting).

used (Eskes and Lanaud 1997). In Côte d'Ivoire, where part of this study was carried out, the first plantations were established with cocoa pods of a lower Amazon Forastero type, Amelonado. In this country, breeding programs have generally used hybrids between Amelonado or Trinitario genotypes and the Amazon Forastero (Besse. 1977; Clément et al. 1999). Selected hybrids of clones revealed a higher yielding capacity, but resistance to the main diseases like black pod (caused by *Phytophthora palmivora*) still needs to be improved. In cocoa, a selection cycle usually requires 6–8 years of observations. Development of effective early screening methods is therefore of great interest.

Molecular markers have provided a clearer understanding of the genetic basis of important agronomic traits and their use has considerably developed over recent years. The first cocoa linkage map was constructed by Lanaud et al. (1995) and a high-density linkage map with 424 markers was recently built (Risterucci et al. 2000). Genetic mapping of agronomic traits has been carried out from data coming from population studies and several regions of the genome involved in yield and *Phytophthora* sp. resistance have been identified (Lanaud et al. 1999*b*; Crouzillat et al. 2000*a*, 2000*b*; Flament et al. 2001).

The objective of this study was to identify QTL for yield, yield components, adult tree vigor, and *Phytophthora* resistance from three populations assessed over a 9-year period. Prospects for the use of molecular markers in cocoa breeding are discussed.

Materials and methods

Plant material

Three segregating populations planted in 1981 at Abengourou, an experimental station of Centre National de Recherche Agronomique (CNRA) in Côte d'Ivoire, were assessed. The three female parents, two Trinitario clones, DR1 and S52, and IMC78, an upper Amazon Forastero clone, were known to be heterozygous with rates of 37, 27, and 27%, respectively (C. Lanaud, unpublished data). The common male parent, Catongo, is a lower Amazon Forastero clone, known to be highly homozygous (Crouzillat et al. 1996). The main criteria for selecting these clones for crossing were that they showed promise for yield and bean traits. At the start of the program, no clones with reliable data on black pod resistance were available. However, because the two Trinitario clones are derived from a hybridization between Criollo and Forastero, with Criollo reputedly less resistant than Forestero, segregation for this trait was expected among the progeny. The number of individuals in the popu-

Fig. 1. Yield trends. Yield is expressed in tons of dry beans per hectare and YM is the mean yield over the 9-year period (1990–1998).

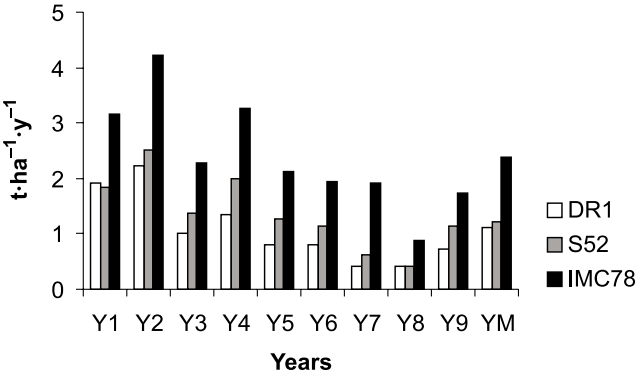

Table 2. QTL related to yield and yield component, average weight of single pods, vigor, and percentage of rotten pods.

				CIM		
Traits	Progenies	L.G	Marker interval	LOD peak	R^2	QTL effect[a]
WBW	DR1	4	AF12/6–gTcCIR136	3.9	16.6	1.0
		9	cTcCIR228–gTcCIR102	3.0	10.4	–0.8
	S52	1	CCG1285–cTcCIR46	2.8	12.9	–1.4
	IMC78	2	mTcCIR19–gTcCIR161	2.7	10.0	–9.0
		4	AF15/20–AF14/4	2.7	8.1	–1.1
		5	gTcCIR106–AF15/11	3.1	11.2	–1.1
PN	DR1	4	AF12/6–gTcCIR136	4.1	19.3	10
		9	cTcCIR228–gTcCIR102	5.5	18.8	–12
	IMC78	5	gTcCIR106–AF15/11	3.7	11.8	–9
PW	DR1	1	CCG1285–mTcCIR15	7.9	23.6	83
		4	AF55/3–mTcCIR18	5.0	21.9	–84
	S52	2	AF12/27–AF50/5	3.4	13.0	–47
		3	AF27/2–AF52/6	3.7	10.9	–45
		5	gTcCIR148–AF39/1	4.8	13.8	–54
		7	AF6/12–AF54/4	3.7	14.7	54
	IMC78	4	AF15/20–AF11/17	17.3	43.5	–141
RP	DR1	4	AF55/3–mTcCIR18	2.5	10.1	4.2
	IMC78	4	AF15/20–AF11/17	7.4	22.6	6.2
CW	DR1	10	gTcCIR126–cTcCIR239	3.1	9.7	–2.1
	IMC78	4	AF32/10–AF15/20	5.0	16.7	–3.7
TC	DR1	4	CCG1419–gTcCIR129	4.4	15.4	6.7
	S52	2	gTcCIR151–cTcCIR76	4.1	13.6	–5.6
	IMC78	4	AF15/20–AF11/17	9.4	24.9	–9.4

Note: WBW, average wet bean weight per tree and per year; PN, average pod number per year; PW, average weight of single pods; RP, average percentage of rotten pods; CW, estimation of the canopy width; TC, trunk circumference (cm) (measured the 12th year after planting).

[a]The QTL effect was estimated by the difference ($A - H$) between the mean of the two genotypes of individuals obtained in the test-cross progeny (A and H).

lations involving DR1, S52, and IMC78, were 96, 94, and 125, respectively.

Traits measured

Yield components

Yield performance was analyzed from data obtained over nine consecutive years, between the 8th and 16th year after planting (1990–1998). For this 9-year period, yield analyses were carried out on annual and accumulated harvest data. For each harvest, healthy and rotten attached pods were counted for each tree, and the healthy pods were weighed. Yield was estimated from the average total number of harvested pods (PN) and the total wet bean weight (WBW). WBW was calculated from the transformation of healthy pod weight to wet bean weight using a transformation coefficient called "α" (Lachenaud 1991). This coefficient is applied in cocoa selection trials and is estimated at each harvest from a random sample of about 200 pods. Yield is given in tonnes of dry cocoa per year and per hectare by the relation WBW × d × α′, where d is the planting density, (i.e., 1666 trees/hectare) and α′ is a coefficient of transformation of wet bean weight to dry bean weight, generally fixed at 0.35.

Average weight of single pods

The average weight of single pods (PW) was calculated from harvest data accumulated over the 9-year period.

Vigor traits

Adult tree vigor was estimated from the trunk circumference (TC) about 1 m from the ground, measured in the 12th year after planting. The canopy width (CW) was also estimated in the 9th year after planting. This measurement was an approximation of the surface of the crown, calculated from it projection on the soil.

Percentage of rotten pods

Pod losses owing to black pod disease incidence in the field (*Phytophthora palmivora*) were expressed as the percentage of rotten pods in relation to the total number of pods from data cumulated over six years between the 8th and 13th year after planting.

Data analysis

The mean, range, and coefficient of variation were estimated for all traits observed in the DR1, S52, and IMC78 progenies. Phenotypic correlations between traits were calculated using the Pearson method. Descriptive statistical

Table 3. QTL for yield (WBW) and pod number (PN) detected in DR1, S52, and IMC78 over 9 years of harvesting.

		DR1			S52			IMC78		
Year	Yield traits	Ch.	Marker interval	LOD	Ch.	Marker interval	LOD	Ch.	Marker interval	LOD
1990	WBW				1	CCG1285–cTcCIR46	2.8			
	PN									
1991	WBW							2	mTcCIR19–gTcCIR161	2.7
	PN	4	AF12/6–gTcCIR136	3.2						
1992	WBW	9	cTcCIR228–gTcCIR102	3.0						
	PN	9	cTcCIR228–gTcCIR102	5.5				5	gTcCIR106–AF15/11	2.5
1993	WBW	4	AF12/6-gTcCIR136	3.9				5	gTcCIR106–AF15/11	3.0
	PN	4	AF12/6-gTcCIR136	4.1				5	gTcCIR106–AF15/11	3.2
1994	WBW							5	gTcCIR106–AF15/11	3.1
	PN							5	gTcCIR106–AF15/11	3.7
1998	WBW							4	AF11/7–AF56/21	2.7
	PN							5	gTcCIR106–AF15/11	2.5
1990–1998	WBW	4	AF12/6-gTcCIR136	2.5				5	gTcCIR106–AF15/11	2.8
	PN	4	AF12/6-gTcCIR136	2.8				5	gTcCIR106–AF15/11	3.3

Note: Ch., chromosome.

analyses were carried out using STATISTICA software (StatSoft Group Inc., Tulsa, Okla.).

Map construction and QTL analysis

The female parents were partly heterozygous and Catongo, the common male parent, was homozygous. Therefore, the segregation of markers in the pseudo test cross only reflected the heterozygosity of the female parent. Restriction fragment length polymorphism (RFLP), microsatellite, and amplification fragment length polymorphism (AFLP) markers were used to construct linkage maps for each of the female parents. Recombination frequencies were converted into map distances with the Kosambi mapping function (Kosambi 1944). The genetic map was built using MAPMAKER/EXP version 3.0. (Lander et al. 1987). QTL analyses were carried out from maps with approximately 1 marker every 10 cM and the number of markers were 78, 64, and 84 in DR1, S52, and IMC78, respectively (Clément 2001). This average distance between markers is sufficient, considering the power of QTL detection in our study (Lincoln and Lander 1992).

QTL analyses were carried out using the composite interval mapping (CIM) module (Zeng 1994) in QTL-Cartographer software version 1.13 (Basten et al. 1997). Forward–backward stepwise regression was carried out to choose the most significant cofactors. A window size of 20 cM was chosen for the test interval. Significance thresholds were defined using the method proposed by Churchill and Doerge (1994), based on permutation testing (1000) by random sampling of phenotypic data. The LOD score thresholds were estimated from the mean of the value assessed for each trait. Significance levels of $\alpha = 0.10$, 0.05, and 0.01 across the genome corresponded to LOD score thresholds of 2.15, 2.40, and 3.20, respectively. A QTL was considered significant when the LOD score was greater than 2.4 The confidence interval for each QTL was determined from the value of one LOD on either side of the LOD peak. For each QTL, R^2 estimated the percentage of phenotypic variation explained by the QTL.

Results

Quantitative trait analyses

A summary of the statistical analysis is presented in Table 1. The IMC78 progeny showed the highest yield performance over the 9-year period, with an average of 4.1 kg of wet beans (WBW) per tree per year, corresponding to 2.4 $t \cdot ha^{-1} \cdot yr^{-1}$ of dry cocoa. Over the same period, the DR1 and S52 progenies were 50% less productive with around 1.1 $t \cdot ha^{-1} \cdot yr^{-1}$ of dry cocoa. Dry cocoa bean production trends over the 9-year period are illustrated in Fig. 1. Over the same analysis period, the average number of pods harvested per tree and per year (PN) strongly correlated with WBW (Table 1), as expected. The greatest adult tree vigor (TC and CW) was obtained in the IMC78 progeny. Yield traits were significantly correlated with adult tree vigor.

The percentage of rotten pods was calculated from cumulated data over a 6-year period between the 8th and 13th year after planting, and 9.6, 11.8, and 10.1% of rotten pods were obtained in the DR1, S52, and IMC78 progenies, respectively. This average level of black pod incidence in the

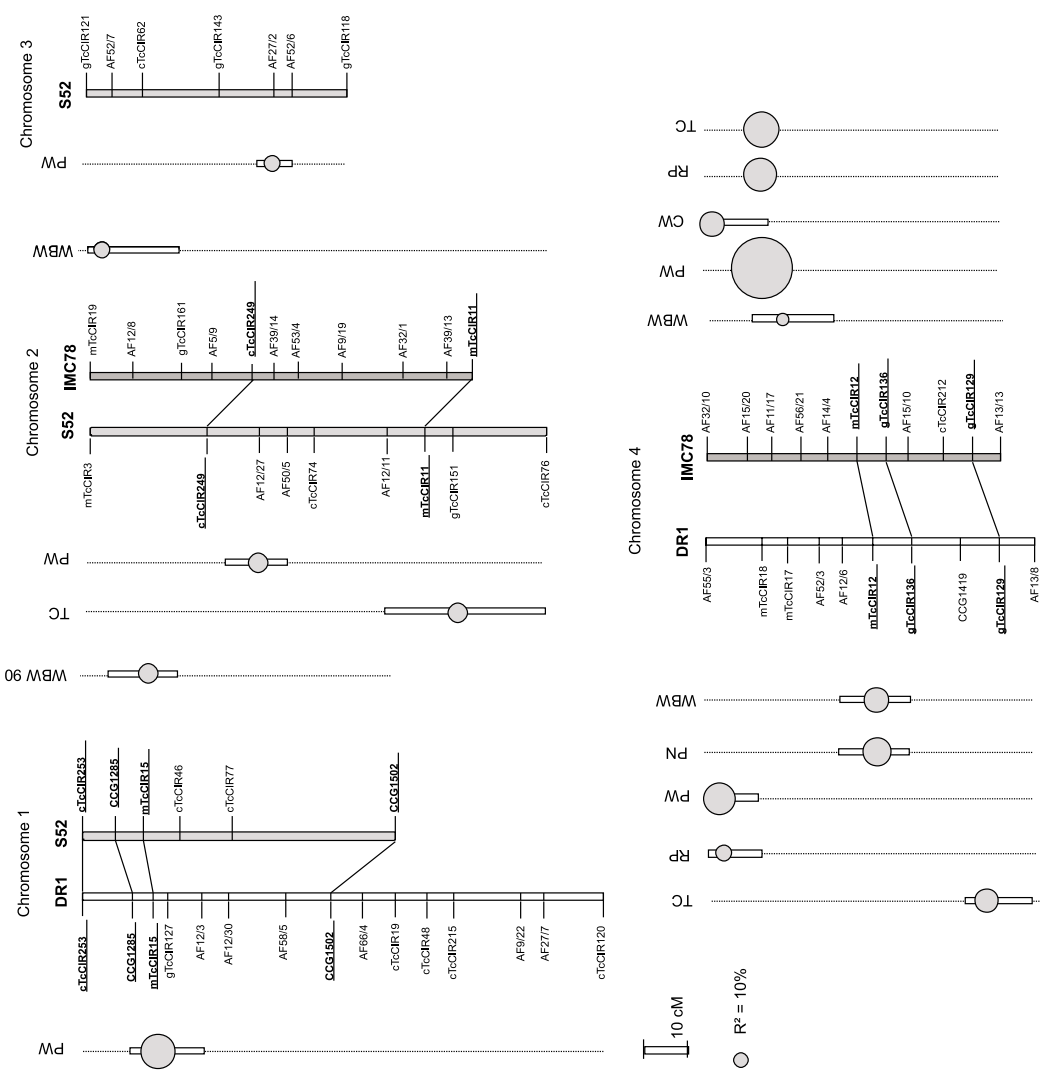

Fig. 2. QTL detected by CIM in DR1, S52, and IMC78. Each QTL is represented by a circle located on the LOD peak. The R^2 is proportional in size to the diameter of the circle. Common markers between the different maps are underlined and in bold. Linkage groups are assigned to chromosome numbers on the reference map using common specific markers.

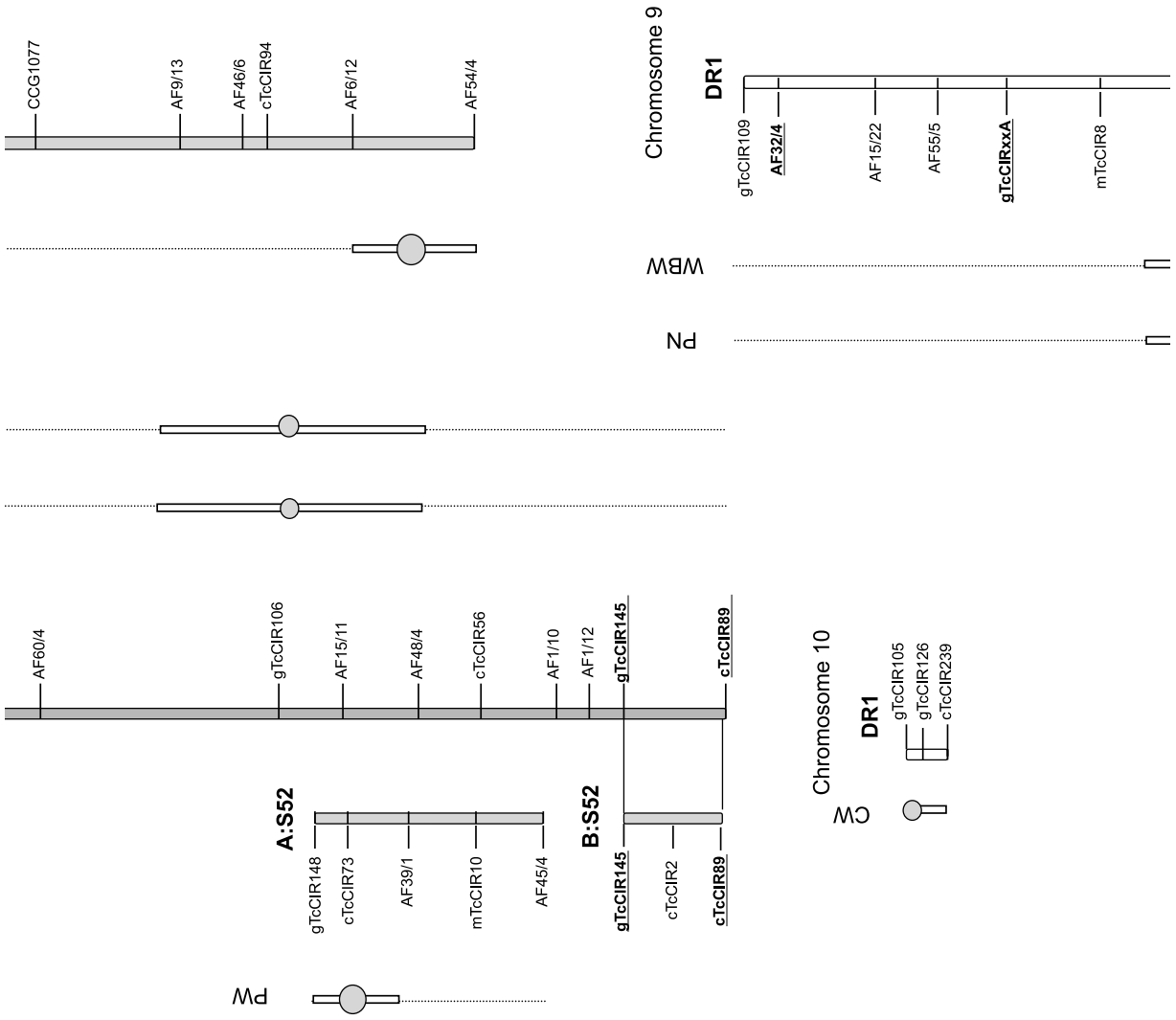

Fig. 2. (*concluded*).

field was moderate, but there was a substantial variability within each population (for example, a range of 1.2–45.0% for S52 progeny (Table 1). The correlation between the average weight of single pods and the percentage of rotten pods was negative and significant at $P = 0.05$ for DR1 and at $P = 0.001$ for IMC78.

QTL detection

Yield

QTL analyses for yield (WBW) and pod number (PN) were carried out each year over the 9-year analysis period. Significant QTL are shown in Tables 2 and 3. In each population, QTL for WBW and PN were identified in the same chromosome region (Table 3). Significant QTL for WBW and PN were detected in both Trinitario, between the 8th and 11th year after planting (1990–1993) in DR1 and only in 1990 in S52. In Forastero (IMC78), QTL were detected between the 9th and 16th year after planting (1991–1998) (Table 3). From harvest data summed over the analyzed period (1990–1998), QTL were detected for WBW and PN on chromosome 4 in DR1 and on chromosome 5 in IMC78. In IMC78, a QTL involved in both yield traits analyzed and located on chromosome 5 was the most repeatable (Table 3).

Average weight of individual pods

A total of 2, 4, and 1 QTL related to the average pod weight (PW) were detected in DR1, S52, and IMC78, respectively (Table 2). These QTL were more repeatable than QTL for yield. In fact QTL were detected most years over the 9-year period (data not presented) and the values noted in Table 2, which were assessed from the mean of PW over a 9-year period, were similar to that obtained in each of the analyzed years.

In DR1, two QTL detected on chromosomes 1 (LOD = 7.9) and 4 (LOD = 5.0) explained 23.6 and 21.9% of the phenotypic variation for pod weight, respectively. However, these two QTL had opposite effects on pod weight (Table 2).

In S52, four QTL were detected on chromosomes 2, 3, 5 and 7. LOD scores from 4.8 to 3.4 were obtained for the QTL identified on chromosome 5 and 2 respectively. The QTL identified on chromosome 7 had an opposite effect to that of the other QTL (chromosomes 2, 3, and 5).

In IMC78, the only major QTL (LOD = 17.3) related to pod weight was detected on chromosome 4 and explained 43.5% of the phenotypic variation.

Vigor traits

In DR1, significant QTL involved in TC and CW were detected on chromosomes 4 and 10, respectively. The QTL for TC and CW explained 15.4 and 9.7% of the phenotypic variation, respectively.

In S52, the QTL for TC detected on chromosome 2 explained 13.6% of the phenotypic variation.

In IMC78, the QTL for TC and CW were detected in the same region of chromosome 4 (Fig. 2). The QTL for TC was the most significant (LOD = 9.4) and explained 24.9% of the phenotypic variation.

Percentage of rotten pods in the field

An average of 10% rotten pods was found over the observation period. Resistance varied among progenies (Table 1), but significant QTL related to the percentage of rotten pods were detected only in DR1 and IMC78. The QTL of both parents were found in the same region of chromosome 4 (Fig. 2). These QTL explained 10.1% and 22.6% of the phenotypic variation in DR1 and IMC78, respectively (Table 2).

Discussion

QTL for yield components and vigor traits

QTL analyses for yield and growth traits have been carried out on fruit trees like apple (Conner et al. 1998) or forest trees like eucalyptus (Verhaegen et al. 1997), poplar (Bradshaw 1995 ; Wu 1998), and pine (Plomion et al. 1996; Kaya et al. 1999). These studies have mostly identified QTL that were repeatable throughout the harvest period, although some QTL were only detected in certain years and some were related to certain stages of plant development (e.g., early tree growth).

In our studies, QTL related to yield components were detected in the mature phase of tree development between the 8th and 16th years after planting. In IMC78, QTL for yield (Table 3) like the one identified on chromosome 5 was the most repeatable over time (the LOD score values for the years not presented in Table 3 and were mostly just below the threshold), unlike the QTL for yield detected in DR1 and S52. The higher levels of yield observed in IMC78 progeny, notably between Y6 and Y9 (Fig. 1), may have contributed to the QTL for yield being more repeatable in IMC78 than in DR1 and S52.

QTL analyses were carried out by Crouzillat et al. (2000*a*) in a population (Catongo × Pound12) planted in Costa Rica. Pound12 and IMC78 are both genotypes originating from the upper Amazon and collected in the same region of Iquitos in Peru (Pound 1943). Indeed, according to Pound (1943), clones carrying his name were collected on the Nanay river, near the area where IMC trees were collected. Recent diversity studies on the upper Amazon Forastero showed that the genetic distance between Pound and IMC clones was small (Sounigo et al. 2001). QTL analysis for yield in Pound12 was carried out using 15 years of harvest observations. Two QTL for yield identified on chromosomes 4 and 5 were repeatable over time. These two QTL for yield, detected in Pound12, were located close to QTL related to yield and identified in IMC78 (Fig. 2). In Pound12, colocation between the QTL related to yield and vigor traits was also identified in the same region of chromosome 4 as in IMC78 (Fig. 2).

Common QTL have been found in another Trinitario clone studied: one QTL related to pod number and to the average weight of single pods was also detected on chromosome 1 of another Trinitario clone, UF676, close to mTcCIR15 (Lanaud et al. 1999*b*). The great majority of the Trinitario genotypes originate from a small number of genetic crosses (6–7) between one homozygous genotype of Criollo and a very few highly homozygous clones of Forastero (Motamayor et al. 2002). For this reason, it could be assumed that the linkage disequilibrium between molecular markers and agronomic traits in Trinitario was probably maintained. Identification of QTL for agronomic traits in genotypes belonging to this genetic group would enable the

use of molecular markers closely linked to these QTL to screen Trinitario germplasm.

QTL related to *Phytophthora* resistance in the field

The *Phytophthora* resistance of the parental clones was unknown at the start of the program. The disease pressure is generally not very strong in Côte d'Ivoire (10–25% pod loss owing to *P. palmivora*, (Kébé 1994), but the variation among the progeny was important (Cilas et al. 1999). A QTL was in turn mapped in two of the populations (DR1 and IMC78). This QTL was located on the same region of chromosome 4 in the maps of both clones, and colocated with a QTL for the weight of single pods (Fig. 2). This colocation is interesting, especially because the QTL for pod weight was having a negative effect. Berry and Cilas (1994) suggest that black pod resistance in the field could be the result of intrinsic resistance combined with the interaction of other biological traits like the time taken for pod ripening (smaller pods ripen more quickly than heavier ones, thus smaller pods may have a greater chance of escaping attack) or environmental conditions.

QTL for resistance to *P. palmivora* have already been studied on several populations at another CNRA research station and in other countries using various inoculation tests (leaf and pod tests) (Lanaud et al. 2000) and several colocations with QTL identified in our study could be seen. In UPA402, an upper Amazon Forastero clone, one putative QTL for resistance evaluated by a leaf inoculation test was detected in the same region of chromosome 4 as the QTL for resistance identified in IMC78 and DR1 (Fig. 2). UPA402 is a clone closely related to IMC78.

In Trinidad, leaf tests were carried out on a population involving another IMC clone (IMC58) (Motilal et al. 2000) and a QTL for resistance to *P. palmivora* was detected in the region close to the region already identified on chromosome 4. These results, obtained with IMC clones using various methods to evaluate resistance to *Phytophthora*, suggested that the QTL identified on chromosome 4 may be related to intrinsic resistance to *P. palmivora.*

In IMC78, a QTL for the percentage of the rotten pods (RP) was colocated on chromosome 4 with a QTL for the average individual pod weight (PW) and a QTL related to vigor (TC). In DR1, QTL for RP and PW were also identified in the same region of chromosome 4. These colocations could suggest a relationship between resistance to *Phytophthora* in the field and the morphological characteristics of the pods, included in the PW trait.

Molecular markers can be used in several ways to improve plant breeding efficiency (Dekkers and Hospital 2002; Stuber et al. 1999). QTL involved in important traits for breeding were identified in this study. The common location of some of them across different genetic groups confirms their existence and their potential use in marker-aided selection. Selection decision can be based on molecular markers alone or on a combination of molecular and phenotypic information. Schemes based on markers only capitalize on a large saving of time, particularly important in cocoa breeding where obtaining phenotypic information is a long and expensive process. However, for selection for yield and resistance to *Phytophthora* sp., both polygenic traits, an approach based on the marker–phenotype index as proposed by Lande and Thomson (1990) would allow the use of markers to improve the prediction of breeding value for each individual.

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