Genetic mapping of QTLs affecting productivity and plant architecture in a full-sib cross from non-inbred parents in cassava (*Manihot esculenta* Crantz)

[1,2]Okogbenin E. and [1]Fregene M.

[1]*International Center for Tropical Agriculture, AA6713, Cali, Colombia;* [2]*University of Ibadan, Ibadan, Nigeria*

Introduction

Rapid improvement of cassava to meet its expanding role in developing economies depend on a better understanding of the genetics underlying important economic traits for which this crop is highly valued both as food and as industrial use. Ideal and efficient plant architecture has long been identified as a key factor underlying the physiological basis of yield, thus providing the opportunity for yield improvement *(Cock and El-Sharkawy, 1988)*.

DNA markers and statistical methods for mapping quantitative trait loci (QTLs) represent powerful tools for understanding the inheritance of quantitative traits *(Rami et al 1998)*. The genetic map of cassava *(Fregene et al., 1997; Mba et al 2001)* provides DNA markers on genome wide basis to study the genetics of productivity and the plant architecture of cassava. Molecular information on the inheritance of traits will permit the design of appropriate breeding schemes to more efficiently produce improved genotypes and good parents. In the study presented here, we used a previously constructed linkage map of cassava to identify QTLs involved in cassava productivity and architecture (morphological) traits.

Materials and methods

The full-sib population of 144 individuals used in this study is from a cross between two elite clones TMS 30572 and CM 2177-2. This cross is highly heterozygous due to the fairly large number of diverse cassava accessions in their pedigrees. The genetic map constructed from a full-sib segregating mapping population using molecular markers has been described elsewhere *(Fregene et al., 1997; Mba et al 2001)*. The 144 individuals were evaluated in 1998 and 1999 for architecture and productivity traits in a field experiment using a partially balanced triple-lattice design at Palmira and Quilichao. The full-sib population was planted on ridges in plot sizes of 20 m² resulting in 20 plants per plot. Quantitative traits measured for QTL mapping are those, which reflect the most-important components of architecture and productivity. They include plant height (PH), first branching height (BH), stem portion with leaves (SPL), branching levels (BL) branching index (BI), fresh root yield (FRY), fresh shoot weight (FSW), number of storage roots (NR), leaf area index (LAI) and harvest index (HI). Combined analysis of variance (SAS ANOVA procedure) based on the type III sums of squares for unbalanced data, was used to estimate genetic and environmental effects, as well as to detect differences between locations and genotypes for each trait in the F_1. Phenotypic data were subjected to the QTL analysis using untransformed data and marker genotypic data from the male- and female- derived maps of the F_1 mapping population. Cassava genome was scanned for the presence of the QTL effect at 2.0 cM intervals using the computer package MAPMAKER/QTL 1.1 program and a free-model QTL effect *(Paterson et al. 1988)*. A LOD score of 2.0 was used to estimate the most likely position of the QTL on the linkage map.

Results

All traits analyzed exhibited continuous distribution in the full-sib population, typical of quantitative traits. All traits exhibited strong genotype-by-environment interactions thus QTL analysis was done for each year in each environment. Correlations among traits were similar at both sites (Palmira and Quilichao). Architecture traits were highly correlated with one another and similarly among productivity traits.

Interval mapping procedure detected a total of 33 primary QTLs using the single-QTL model *(Table 1)*. When the primary QTLs were fixed, and the genome re-scanned under a two QTL model, a total of 84 secondary QTLs were identified through interaction. Only significant interactions under the two-QTL model, resulting in PVE of 20% and above are shown in Table 2. The 16 significant interactions (with PVE above 20%) shown in Table 2 were all from the male-derived map. In general, the %PVE obtained for most of the traits were generally higher in effects for male alleles than for female alleles.

A total of 26 primary QTLs were detected for architecture traits by interval mapping. Phenotypic variance explained (PVE) by individual QTLs for all architecture traits ranged from 6.8 to 23.4%. The results of QTL analyses for productivity traits are presented in Table 2. For productivity traits a total of seven primary QTLs were detected. The PVE by individual primary QTL for productivity traits ranged from 9.1 to 15.5%. A total of 10 secondary QTLs were identified through interactions for productivity traits.

Several QTLs (both primary and secondary QTLs) for productivity and morphological traits were detected in the same genomic regions. A total of 28 intervals (in both male and female derived maps) were found to be involved in the control of two or more architecture traits. In many genomic regions where QTLs were identified for productivity traits, QTLs were also detected for architecture traits. We identified 8 intervals in both maps controlling both architecture and productivity traits. The number of QTLs detected in more than one trial for each trait, vary from 1 (fresh root yield) to 13 (branching index). We identified 29 QTL s in two trials, 11 QTLs in three trials and 1 QTL in four trials *(Table 3)*.

Discussion

As expected our results shows that these traits are controlled by several genes with small effects. Several QTLs were identified for each of the traits. We observed that 35% of the QTLs were detected in more than one trial while others were found only in only one trial hence QTLs for the different traits showed different stability. Many genomic regions were identified with significant effects on more than one trait. QTLs for a number of architecture and productivity traits were found to coincide with each other. Our results also identified common genomic regions among productivity traits. Thus it should be feasible to manipulate total biomass in plant breeding for increased yield through component traits of productivity *(Okogbenin and Fregene 2002)*. All identified primary and secondary QTLs detected for yield were found associated with one or more other traits (productivity and architecture traits) indicating yield as complex trait. This suggests that either some individual QTLs have pleiotropic effects *(Gruneberg 1998)* or that different QTLs tend to cluster together into groups *(Paterson et al 1991)*. The identification of QTLs of positive and negative effects underlying the relationship between productivity and architecture traits promises the utility of ideotype concept in cassava breeding. Thus, through ideotype breeding, architecture traits could be manipulated, using QTLs with effects of opposite direction, to maintain storage root and top growth balance toward achieving high root yield which is the most important productivity trait of cassava. Ideotype breeding has been explored in trees. Such an approach could be adapted for yield improvement in cassava.

Conclusion

The detection of QTLs controlling related traits holds promise for the easier manipulation of yield in cassava through molecular marker-assisted breeding (MAB). It is therefore expected that markers associated with such QTLs will help improve the efficiency of the development of the ideal plant morphology essential to improved yield potential and general crop performance by selecting early in the crop cycle for these loci through marker assisted selection.

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Table 1. Summary of significant primary effect QTLs detected using interval mapping analysis.

[a]Trait	[b]QTL	Linkage group	Interval	Position	LOD	[c]%PVE	Phenotypic effects	[d]Loc. (year)
Male map								
FRY	fryH-m	H	GY77-rGY31-1	0.8	3.05	15.5	-583.99	Q ('98)
		J	AE10A-CDY76	0.0	2.07	10.4	369.45	Q ('98)
SW	swH-m	H	GY77-rGY31-1	0.0	2.32	13.4	-312.22	Q ('98)
PH	phG-m	G	GY6-rCDY16-1	4.0	2.59	13.4	18.64	P ('99)
BH	bhJ-m	J	GY34-1-K10	14	2.61	21.3	28.76	P ('98), Q('99)
BL	blD-m	D	GY57-GY25	0.0	2.46	13.9	0.53	P ('98)
	blN-m	N	rGBSSII-rCDY44	0.0	2.11	13.1	0.56	P ('98)
	blR1-m	R	rGY48-AE2	6.0	2.30	13.5	0.52	P ('98)
	blR2-m	R	AE2-U1	6.0	2.61	16.9	0.63	P ('98)
BI	biD1-m	D	J1A-GY57	12.0	2.05	14.0	-0.10	P ('98)
	biD2-m	D	GY57-GY25	0.0	2.02	10.5	-0.07	P ('99)
	biJ-m	J	GY34-1-K10	16.0	2.84	23.4	0.13	P ('98)
	biR-m	R	rGY48-AE2	8.0	2.05	13.6	-0.10	P ('98
RN	rnH-m	H	AE10A-CDY76	0.0	2.65	12.7	2.30	P ('99)
Female map								
FRY	fryM-f	M	GY154-rGY215	32.0	2.04	10.6	-372.41	Q ('99)
SW	swF-f	F	GY203-GY218	0.0	2.94	9.1	-256.15	Q ('98)
HI	hiF-f	F	GY204-GY194	6.0	4.18	12.3	0.07	P ('99)
PH	phD-f	D	rGY180-GY222	0.0	2.18	6.8	-16.05	P ('98)
	phF1-f	F	GY203-GY218	0.0	2.84	8.7	-17.49	P ('98)
	phF2-f	F	GY196-GY203	2.0	2.5	8.4	-14.81	P ('99)
BH	bh1A-f	A	GY12-GY28	8.0	2.34	8.6	18.26	P ('98, '99)
	bhA2-f	A	GY28-GY203	0.0	2.17	7.0	11.67	Q ('99)
BL	blD1-f	D	rGY167-rGY180	0.0	2.37	7.5	-0.42	P ('98)
	blD2-f	D	GY222-GY181	0.0	2.05	6.8	-0.37	P ('98)
BI	biD1-f	D	rGY167-rGY180	0.0	2.3	7.3	0.07	P ('98)
	biD2-f	D	GY42-GY219	0.0	3.0	9.8	0.07	P ('99)
	biM-f	M	GY154-rGY215	0.0	2.01	7.1	-0.05	P ('99)
SPL	splA-f	A	GY12-GY28	12.0	3.51	11.8	8.1	P ('98)
	splF1-f	F	GY203-GY218	0.0	2.83	9.1	-7.24	P ('99)
	sSplF2-f	F	GY196-GY203	4.0	2.54	8.3	-2.78	Q ('98)
	splI-f	I	rD5a-rB3a	0.0	2.18	7.5	-2.63	P ('98)
	splM-f	M	rGY215-L7	0.0	2.58	11.4	-3.14	Q ('99)
LAI	LaiC-f	C	r011a-rGY74	4.0	2.76	13.9	0.07	P ('99)

[a]See Materials and Method section for abbreviation
[b]Individual QTL loci are named by trait abbreviation (in small letters), linkage groups (in alphabets in capital letters), map (separated by hyphen: -m =male, -f =female). In cases where multiple QTLs affecting a trait were found along the same linkage group, the QTLs are distinguished by numbers indicating the temporal order in which QTLs were discovered (e.g. splR1-f, splR2-f) [c]%PVE-Percent phenotypic variation explained [d]Location- Palmira (P), Quilichao (Q); year- '98 (1998), '99 (1999)

Table 2. Significant interactions between primary and secondary QTL with PVE above 20%

Map	[a]Trait	[b]LG	Interval	[c]Pri. QTL Pos	LG	Interval	[d]Sec. QTL Pos	LOD	[e]% PVE	[f]Loc.
Male										
	FRY	J	AE10A-CDY76	0.0	N	rGY47-nGY143	4.0	3.81	20.9	Q ('98)
	SW	H	GY77-rGY31-1	0.0	A	rGY7-1-rBEST2	10.0	4.84	26.3	Q ('98)
		H	GY77-rGY31-1	0.0	G	GY6-rCDY16-1	4.0	3.81	20.4	Q ('98)
	PH	J	GY6-rCDY16-1	4.0	C	GY54-GY81-1	0.0	4.47	23.5	P ('99)
	BH	J	GY34-1-K10	14.0	D	JIA-GY57	23.3	4.29	29.3	P ('98)
		J	GY34-1-K10	0.0	J	GY7-GY34-1	0.0	3.91	40.2	P ('98)
		J	GY34-1-K10	0.0	Q	GY74-AM12	14.0	2.87	22.8	P ('98)
	BL	N	rGBSSII-rCDY44	0.0	D	JIA-GY57	22.0	5.50	33.6	P ('98)
		N	rGBSSII-rCDY44	0.0	H	GY77-rGY31-1	2.0	3.90	22.1	P ('98)
		R	AE2-U1	6.0	D	GY65-PASK1	4.0	3.36	20.4	P ('98)
		R	AE2-U1	6.0	Q	GY74-AM12	14.0	4.04	24.1	P ('98)
	BI	D	JIA-GY57	12.0	E	r14A-G13	20.0	3.71	24.5	P ('98)
		D	JIA-GY57	12.0	N	rCDY99-rGBSSII	6.0	4.60	32.2	P ('98)
		J	GY34-1-K10	16.0	G	GY62-rGY97	2.0	3.32	25.1	P ('98)
		J	GY34-1-K10	16.0	H	rGY99-rGY8-1	6.0	4.20	33.1	P ('98)
		J	GY34-1-K10	16.0	J	GY7-GY34-1	0.0	4.59	44.8	P ('98)

[a]See Materials and Method section for abbreviation
[b]LG-Linkage group [c]Pri. QTL pos. – Primary QTL position [d]Sec QTL pos – Secondary QTL position
[e]%PVE- Percent phenotypic variation [f]Location- Palmira (P), Quilichao (Q); year - '98 (1998), '99 (1999)

Table 3. Summary of QTLs (primary and secondary) detected in more than one trial in the F_1 population at Quilichao and Palmira (1998 and 1999)

[a]Trait	Map	Linkage group	Interval	Palmira (1998)	Palmira (1999)	Quilichao (1998)	Quilichao (1998)
FRY	Male	J	AE10a-CDY76	nd	nd	*	*
BH	Male	J	GY34-1-K10	*	nd	nd	*
		J	GY7-GY34-1	*	nd	nd	*
		Q	GY74-AM12	*	nd	nd	*
	Female	A	GY28-GY213	*	*	nd	nd
		A	rGY75-GY12	*	*	nd	nd
		C	GY174-rGY119	*	*	nd	*
		E	rGY118-rGY176	*	*	nd	*
		G	rGY94-AM1890	*	*	nd	*
		K	rGA127-CDY106	*	*	nd	nd
BL	Male	A	GY28-GY32	*	nd	nd	*
		C	rGY26-rGY89-1	*	nd	nd	*
		G	GY6-rCDY16-1	*	nd	nd	*
		H	GY77-rGY31-1	*	nd	nd	*
		L	CDY131-1-U2c	*	nd	*	*
		N	GY10-GY52	*	nd	nd	*
		Q	GY74-AM12	*	nd	nd	*
BI	Male	A	GY28-GY32	*	nd	nd	*
		E	r14a-G13	*	nd	nd	*
		G	rGY62-GY97	*	nd	nd	*
		H	GY77-rGY31-1	*	nd	nd	*
		L	CDY131-1-U2c	*	nd	*	*
		Q	GY74-AM12	*	nd	nd	*
	Female	A	GY12-GY28	*	*	nd	*
		C	rGY89-rGY177	*	*	nd	*
		C	rGY176-rGY190	*	*	nd	*
		E	rGY94-AM18	*	nd	nd	*
		G	H14b-GY128	*	*	nd	nd
		I	rGY164-GY223	*	*	nd	nd
		Q	rGY172-rP3	*	*	nd	*
SPL	Female	A	GY12-GY28	*	nd	nd	*
		C	GY174-rGY119	ns	*	*	nd
		G	rGY94-AM18	*	*	*	nd
		H	OJ1-rGY199	*	*	*	nd
		L	CBB1-rAF149	ns	*	nd	*
		O	rGY164-GY223	*	*	*	*
		Q	rGY172-rP3	*	*	*	*
PH	Female	A	GY213-GY209	nd	*	nd	nd
		C	rGY177-O11a	*	*	nd	nd
		E	rGY118-rGY176	*	*	nd	nd

[a]See Materials and Method section for abbreviation