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ORIGINAL PAPER

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

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**Abstract** An attempt was made to identify quantitative trait loci (QTLs) for several productivity and plant architecture traits in a full-sib progeny of 144 individuals from two non-inbred parents in cassava. A molecular linkage map of this cross constructed previously with over 250 markers was the source of molecular markers. The progeny were grown under field conditions at two locations (Palmira and Quilichao) in Colombia and evaluated in 2 years (1998 and 1999) for architecture and productivity traits. Architecture traits evaluated were plant height (PH), branching height (BH), branching levels (BL), branching index (BI), stem portion with leaves (SPL) and leaf area index (LAI). Productivity traits were those related to total dry matter production and distribution, namely fresh root yield (FRY), fresh shoot yield (FSY), harvest index (HI) and the number of storage roots (NR). Phenotypic evaluation of the traits in this population revealed continuous variation for all traits. Broad-sense heritability estimates, ranged from 36% (for NR) to 94% (for BH). Several significant phenotypic correlations were observed between architecture and productivity traits. Primary QTLs, using the single-QTL model, and secondary QTLs, by a primary QTL interaction model, were detected by interval mapping. A total of 30 primary QTLs and 84 secondary QTLs were detected. We identified 35% of detected QTLs in two or more trials, the other QTLs were environment-specific. These results underscore the significant genotype × environment interactions found for most of the traits. Several genomic segments affecting multiple traits were identified and were in agreement with correlation among traits. All QTLs identified for FRY were found associated with either component traits of productivity or architecture traits. This study suggests that QTLs for plant architecture can be used to improve productivity. However an exhaustive search and analysis of QTLs controlling architecture is required before marker-assisted selection (MAS) for increasing productivity can be initiated.

**Key words** Cassava · Genetic mapping · Architecture and productivity traits · QTL

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## Introduction

Cassava (*Manihot esculenta* Crantz) is the fourth major food crop in the tropics, grown principally by poor farmers (Cock 1985). It is one of the least researched among the major crops of the world and the potential for genetic improvement is considerable. Cassava is monoecious, and predominantly out-crossing, mediated by protogyny, which leads to a high degree of heterozygosity that considerably complicates breeding (Hershey and Jennings 1992). Rapid improvement of cassava to meet its expanding role in developing economies will therefore 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.

Breeders seek to develop high yielding crop varieties by understanding how various parts of a plant interact with each other to produce the best performance in a specific environment (Wu 1998). Several studies have been conducted by physiologists to relate yield in cassava with plant architecture, photosynthesis, biomass partitioning and leaf area (Cock et al. 1979; Lian and Cock 1979a, b; Cock and El-Sharkawy 1988; Lenis et al. 2003). These studies have been carried out at the level of individual leaf, the branch, canopy and stem. 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. In a recent study,

Lenis et al (2003) demonstrated the effect of leaf retention or stem portion with leaves on productivity; clones that retained leaves at 5-months of age yielded 33% more root dry matter at harvest time around 10 months of age. Plant architecture also has implications for yield through canopy information, incident light absorption by leaves and branching habit (CIAT 1975; Hunt et al. 1977; Cock 1985; Iglesias et al. 1994; Nweke et al. 1994).

Leaves are traditionally considered the most important components of canopy. Canopy with a larger leaf area can produce more growth than a smaller canopy. However, a larger leaf area requires support tissues of branches that competes with the allocation of biomass to the storage roots of cassava (Lian and Cock 1979a). Thus a way to balance maximum photosynthetic surface (leaf area) and minimum energy investment (branches) can potentially increase productivity (Farnsworth and Niklas 1995). This functional relationship can be incorporated into genetic-improvement programs if its underlying genetic mechanisms are understood.

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). A linkage map of cassava has been developed from a full-sib-segregating mapping population using molecular markers (Fregene et al. 1997). The genetic map of cassava provides DNA markers on a genome-wide basis to study the genetics of productivity and the plant architecture of cassava. Genetic factors controlling these traits can be studied in terms of the size of their effects on the phenotype, gene action, the source of the favorable QTL alleles and the relationship between QTLs underlying the different physiological processes. Molecular information on the inheritance of traits will permit the design of appropriate breeding schemes to more-efficiently produce improved genotypes and good parents. (Wu 1998).

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. The implications of these results for the development of improved cassava varieties are discussed briefly.

## Materials and methods

### Plant materials and field experiment

The full-sib population of 144 individuals used in this study is from a cross between two elite clones TMS 30572 (the female parent) developed at the International Institute of Tropical Agriculture (IITA), Nigeria, and CM 2177-2 (the male parent) produced at Centro Internacional de Agricultura de Tropical, Colombia. This cross is highly heterozygous due to the fairly large number of diverse cassava accessions in their pedigrees. The genetic map constructed from this cross 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 CIAT headquarters, Palmira, and at the sub-station in Santander de Quilichao; both classified as the mid-altitude tropics of Colombia. The full-sib population was planted on ridges, in plot sizes of 20 $m^2$ (of 5 rows×4 columns), with a spacing of 1×1 m, resulting in 20 plants per plot at a population density of 10,000 plants $ha^{-1}$. By this arrangement, each plot had 14 border plants and six central plants.

The parents of the cross, TMS 30572 and CM 2177-2, were also evaluated in both locations. The parents were planted adjacent to the field experiment for the progeny in a randomized complete block design, based on 20 plants per plot in three replications. Quantitative traits measured for QTL mapping were 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) and the derived trait; branching index (BI) being expressed as the ratio of BH to PH. The six central plants in each plot were used for all measurements. Branching levels or the total number of branches was also determined for each genotype. Morphometric measurements were done 2 weeks before harvest. Leaf area index (LAI), because of its influence on leaf development and hence canopy formation, was also measured. LAI was measured at 4-weekly intervals between three months after planting (3 MAP) and six months after planting (6 MAP) and averaged. At 11 months after planting (11 MAP), the trials were harvested in both locations and evaluated for productivity traits, namely (FRY), fresh shoot weight (FSW), number of storage roots (NR) and harvest index (HI). The central six plants of each plot was used in all measurements as with the architecture traits. The number of thickened storage roots per plant was also recorded. Aerial parts (stems and leaves) of the plants were weighed to measure fresh shoot weight and to derive harvest index, the ratio of root yield to the total plant biomass. All trait values were determined per plot and averaged over the three replications.

### Data analyses

Data analyses include calculation of mean values, determination of the statistical significance of the sources of variation and calculation of estimates of variance components. Distribution analyses were performed for each trait using the SAS UNIVARIATE procedure (SAS institute 1996). Normality of distribution was tested ($P<0.05$) with the W-statistic test described by Shapiro and Wilk (1965). Separate analyses of variance for progeny data were conducted for each trait evaluated. All phenotypic analyses were performed on untransformed data. Normalizing data through transformation may misrepresent differences among individuals by pulling skewed tails toward the center of the distribution (Doerge and Churchill 1994; Mutschler et al. 1996; Bryne et al. 1998). Nine genotypes in the $F_1$ progeny had establishment problems, arising from the poor vigor of the mother plants from which cuttings were made, and some few plots corresponding to these genotypes resulted in some missing data points. The final data were therefore analyzed as a RCB experiment (Cochran and Cox 1957) with all effects considered as random. 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 years, locations and genotypes for each trait in the $F_1$. The sources of variation were partitioned into main effects and their interactions. The mean squares for the sources of variation were determined and appropriate *F*-tests were used to assess the probability that a source of variation was significant. Components of variance were calculated for the main effect of genotype and its interactions with years and locations. We applied the following linear model (Johnson et al. 1955) for our statistical analysis of the progeny:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + r(\alpha\beta)_{ijk} + \lambda_l + \alpha\lambda_{il} + \beta\lambda_{jl} + \alpha\beta\lambda_{ijl} + \varepsilon_{ijkl},$$

where $Y_{ijkl}$ is the observed phenotypic value of the *i*th genotype in the *k*th replication in the *j*th location and the *i*th year, $\mu$ is the

overall population mean of the trait, $\alpha_i$ is the year effect ($i$=1, 2), $\beta_j$ is the location effect ($j$=1, 2), $\alpha\beta_{ij}$ is the year × location effect, $r(\alpha\beta)_{ijk}$ is the replication within year x location interaction effect ($k$=1,2, 3), $\lambda_l$ is the genotype effect ($l$=1, 2, 3, ..., 144), $\alpha\lambda_{il}$ is the year × genotype interaction effect, $\beta\lambda_{jl}$ is the effect associated with location by genotype interaction, $\alpha\beta\lambda_{ijl}$ is the year × location × genotype interaction effect, and $\varepsilon_{ijkl}$ is the random error associated with each observation.

Broad-sense heritability ($H^2$) is defined as the ratio of genotypic variance to phenotypic variance. $H^2$, on an entry mean basis, was estimated for each trait using the variance components of the expected mean squares (Fehr 1987) from our analysis of variance of the $F_1$ population. Spearman's rank correlation coefficients were calculated and tested for significance ($P$<0.05) among traits for each location.

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; Lincoln et al. 1992). A LOD score of 3.0 was used to estimate the most-likely position of the QTL on the linkage map. For each LOD peak we determined the LOD 1.0 support interval, that is the region in which the LOD score remains within 1.0 unit of the peak. The percent phenotypic variation explained by an individual QTL and effects were estimated at the most-likely QTL position. Primary QTLs identified from the above step were fixed and the genome scanned again to search for other QTLs (secondary QTLs). Likewise, when linked QTLs with no overlapping 1.0 LOD support intervals were detected, the locus with the highest LOD score was fixed and the linkage group scanned again for the linked effect.

The other mapping procedure used was based on the single-marker model, using simple regression. A significant association between the traits and the marker ($P$<0.005) was considered an evidence of a QTL in the region of the marker. Simple regression of the phenotypic data on marker genotype classes as the independent variable was done using the computer software QGENE (Nelson 1997). The amount of phenotypic variance explained by allelic differences at a marker locus ($R^2$) was estimated. This test statistic is based on only one segregating marker and has the tendency to bias estimates of QTL effects, due to the non-independence among the hypothesis tests for linked markers. We also analyzed our phenotypic data using the single-marker model $t$-test with conditioning analysis of the PGRI QTL analysis package (Liu and Lu 1995), to detect other loci with significant association to traits ($P$<0.005). When three or more linked markers were associated with a trait from the single-marker analysis, these markers were subjected to multiple regression for further analysis to determine the marker most strongly linked to the trait and to eliminate the possibility of collinearity among markers. Multiple regression was done according to the linear regression model (Sills et al. 1995):

$$Y_{ij} = \mu + A_i + B_i + C_i + ..... + Z_i + \in_{ij},$$

where $Y_{ij}$ is the trait value of phenotype $j$ with marker score $I$, $\mu$ is the overall mean for the trait, $A_i$+$B_i$+$C_i$+.....,and $Z_i$ represent the linked markers associated with the trait loci and $\in_{ij}$ is the random error. In this paper, we report only QTLs that explained 6% or more of the phenotypic variance observed for analyzed traits.

## Results

### Trait means, variation and heritability

Mean phenotypic values, standard errors, ranges, the W-statistic for traits measured in the parental lines and the full-sib family, are shown in Table 1. All traits analyzed exhibited continuous distribution in the full-sib population, typical of quantitative traits. Analysis of variance detected significant differences between the genotypes for each trait measured (data not shown). Broad-sense heritability estimates based on plot entry means for architecture traits were 91% for plant height, 83% for branching levels, 94% for branching height, 80% for leaf length, 90% for leaf width and 27% for length of stems

**Table 1** Statistical parameters for the distributions of morphological traits of the $F_1$ population

| Trait[a] | Location-year[b] | Female (m±SE) | Male (m±SE) | $F_1$ Range | $F_1$ (m±SE) | Kurtosis | Skewness | $F_1$ W statistic |
|---|---|---|---|---|---|---|---|---|
| PH (cm) | Q-98 | – | – | 44.08–227.01 | 141.91±29.47 | 0.52 | –0.13 | 0.99 ns |
| | Q-99 | 152.50±6.91 | 173.06±13.44 | 63.33–216.39 | 148.23±31.10 | –0.20 | –0.09 | 0.98 ns |
| | P-98 | – | – | 109.76–260.21 | 205.87±30.80 | 0.48 | –0.71 | 0.95* |
| | P-99 | 108.33±10.02 | 108.00±6.92 | 55.42–184.44 | 119.94±25.51 | –0.05 | –0.01 | 0.98 ns |
| BH (cm) | Q-98 | – | – | 24.44–134.44 | 68.07±22.58 | –0.04 | 0.60 | 0.96* |
| | Q-99 | 56.39±6.71 | 50.00±2.04 | 22.50–131.67 | 57.53±22.07 | 1.03 | 1.04 | 0.92* |
| | P-98 | – | – | 24.17–179.17 | 82.64±31.01 | 0.02 | 0.50 | 0.96* |
| | P-99 | 45.83±1.18 | 36.56±2.60 | 28.33–60.28 | 43.22±13.60 | 1.13 | 1.10 | 0.91* |
| BL | Q-98 | – | – | 1.72–4.87 | 3.39±0.70 | –0.48 | –0.21 | 0.97 ns |
| | Q-99 | 4.06±0.21 | 5.10±0.50 | 1.94–5.77 | 4.06±0.71 | 0.33 | –0.33 | 0.98 ns |
| | P-98 | | | 1.67–5.83 | 3.83±0.77 | 0.17 | –0.51 | 0.97* |
| | P-99 | 3.28±0.34 | 4.68±0.39 | 2.42–4.61 | 3.79±0.81 | –0.37 | –0.26 | 0.97 ns |
| BI | Q-98 | – | – | 0.15–0.84 | 0.48± | –0.31 | 0.01 | 0.98 ns |
| | Q-99 | 0.37±0.06 | 0.29±0.03 | 0.16–0.67 | 0.39± | –0.32 | 0.46 | 0.96* |
| | P-98 | – | – | 0.10–0.73 | 0.40± | –0.15 | 0.21 | 0.97* |
| | P-99 | 0.42±0.03 | 0.34±0.02 | 0.17–0.66 | 0.37± | –0.20 | 0.63 | 0.94* |
| SPL (cm) | Q-98 | – | – | 5.1–38.49 | 16.43±4.80 | 3.78 | 1.20 | 0.94* |
| | Q-99 | 10.00±0.00 | 14.61±3.38 | 6.67–29.78 | 16.39±4.62 | –0.14 | 0.28 | 0.98 ns |
| | P-98 | – | – | 8.20–71.68 | 48.99±11.81 | 0.76 | –0.67 | 0.96* |
| | P-99 | 15.28±3.75 | 21.72± 3.10 | 9.86–77.50 | 34.43±11.96 | 0.74 | 0.59 | 0.97 ns |

* Distribution is significantly different from normal; ns—distribution is not significantly different from normal

[a] PH, plant height; BH, branching height; BL, branching level, BI, branching index; SPL, stem portion with leaves

[b] Q = Quilichao, P = Palmira, 98=1998, 99=1999

**Table 2** Pearson phenotypic correlations in the cassava F1 population at Palmira and Quilichao in 1998 (top number) and 1999 (bottom number)

| Location | | FRY[a] | FSW | HI | NR | PH | BH | BL | BI | SPL |
|---|---|---|---|---|---|---|---|---|---|---|
| Palmira | FSW | 0.51 | | | | | | | | |
| | | 0.65 | | | | | | | | |
| | HI | 0.50 | –0.42 | | | | | | | |
| | | ns | –0.58 | | | | | | | |
| | NR | – | – | – | | | | | | |
| | | 0.76 | 0.41 | 0.22 | | | | | | |
| | PH | 0.44 | 0.73 | –0.31 | – | | | | | |
| | | 0.68 | 0.78 | –0.35 | 0.44 | | | | | |
| | BH | 0.29 | ns | ns | – | 0.41 | | | | |
| | | 0.52 | 0.39 | ns | 0.44 | 0.46 | | | | |
| | BL | ns | 0.32 | ns | – | 0.27 | –0.62 | | | |
| | | ns | 0.31 | –0.31 | ns | 0.43 | –0.49 | | | |
| | BI | ns | ns | 0.24 | – | ns | 0.90 | –0.80 | | |
| | | ns | –0.18 | 0.29 | ns | –0.30 | 0.69 | –0.87 | | |
| | SPL | 0.44 | 0.64 | –0.20 | – | 0.74 | 0.39 | 0.21 | ns | |
| | | 0.49 | 0.80 | –0.57 | 0.21 | 0.76 | 0.29 | 0.39 | –0.30 | |
| | LAI | – | – | – | – | – | – | – | – | – |
| | | 0.41 | 0.33 | ns | 0.40 | 0.35 | ns | ns | ns | 0.17 |
| Quilichao | FSW | 0.62 | | | | | | | | |
| | | 0.64 | | | | | | | | |
| | HI | 0.24 | –0.55 | | | | | | | |
| | | 0.50 | –0.20 | | | | | | | |
| | NR | – | – | – | | | | | | |
| | | 0.84 | 0.49 | 0.45 | | | | | | |
| | PH | 0.57 | 0.82 | –0.38 | – | | | | | |
| | | 0.59 | 0.83 | ns | 0.43 | | | | | |
| | BH | 0.51 | 0.35 | ns | – | 0.51 | | | | |
| | | 0.40 | 0.33 | ns | 0.38 | 0.57 | | | | |
| | BL | ns | 0.48 | –0.37 | – | 0.54 | ns | | | |
| | | 0.22 | 0.53 | –0.22 | ns | 0.50 | –0.20 | | | |
| | BI | ns | –0.22 | 0.34 | – | –0.18 | 0.73 | –0.60 | | |
| | | ns | ns | 0.26 | 0.19 | ns | 0.80 | –0.58 | | |
| | SPL | 0.51 | 0.63 | –0.22 | – | 0.76 | 0.54 | 0.37 | ns | |
| | | 0.51 | 0.76 | –0.21 | 0.33 | 0.77 | 0.32 | 0.45 | ns | |

[a] Trait abbreviations: FRY—fresh root yields, FSW—fresh shoot weight, HI—harvest index, NR—number of roots, PH—plant height, BH—branch height, BL—branching levels, BI—branching index, SPL—stem portion with leaves

with leaves. For productivity traits, heritability estimates were 87% for HI, 71% for FSW, 50% for FRY and 36% for NR. Low to intermediate heritability estimates for SPL, NR and FRY indicated a marked influence of environment on these traits. All traits exhibited strong genotype-by-environment interactions (data not shown), thus QTL analysis was done for each year in each environment. A total of 58 and 55 phenotypic correlations, respectively, were significant at Palmira and Quilichao for architecture and productivity traits (Table 2). Correlations among traits were similar at both sites. Architecture traits were highly correlated with one another and similarly among productivity traits. For architecture traits, the most significant correlations were observed for PH and SPL (0.74–0.77), BH and BI (0.69–0.90), as well as for BL and BI (–0.58––0.80). The most significant correlation among productivity traits were observed between FRY and SW (0.51–0.65), as well as between FRY and NR (0.76–0.84). Significant correlations were also observed between architecture and productivity traits with the most significant being between PH and FSW, and between SPL and FSW. With the exception of BI, root yield was significantly correlated with all other traits in at least one location.

## QTL detection and localization

Interval mapping procedure detected a total of 33 primary QTLs using the single-QTL model (Table 3). Significant peak values of LOD scores, the position of these peaks, the percentage of phenotypic variance explained and estimated phenotypic effects are shown in Table 3. When the primary QTLs were fixed, and the genome re-scanned under the two-QTL model, a total of 84 secondary QTLs were identified for seven of the nine traits studied (excluding LAI and NR). Only significant interactions under the two-QTL model, resulting in the percentage of phenotypic variance explained (PVE) by 20% and above are shown in Table 4. The 16 significant interactions (with PVE above 20%) shown in Table 4 were all from the male-derived map. In general, the %PVE obtained for most of the traits were generally higher in effects for alleles from the male parent than for the female. The results obtained with single-marker analysis were similar to those obtained with interval mapping for primary QTLs (data not shown). Only a small proportion of the secondary QTLs detected by interval mapping were found with single-marker analysis. This may have been due to the stringent threshold value of $P<0.005$ chosen to

**Table 3** Summary of significant primary effect QTLs detected using interval mapping analysis

| Trait[a] | QTL[b] | Linkage group | Interval | Position | LOD | %PVE[c] | Phenotypic effects | Loc. (year)[d] |
|---|---|---|---|---|---|---|---|---|
| Male-derived 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 | Q ('99) |
| | *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 | Q ('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 | Q ('99) |
| Female-derived 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 | Q ('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 | Q ('99) |
| 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 | Q ('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 | Q ('98) |
| | *splM-f* | M | rGY215-L7 | 0.0 | 2.58 | 11.4 | –3.14 | Q ('99) |
| LAI | *LaiC-f* | C | rO11a-rGY74 | 4.0 | 2.76 | 13.9 | –0.3 | P ('99) |

[a] See Table 2 for abbreviations
[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)

declare QTLs in single-marker analysis, which while reducing the chance of Type-I errors (false positives), would have also excluded a high frequency of Type-II errors (not detecting valid QTLs).

## Architecture traits

A total of 26 primary QTLs were detected for architecture traits by interval mapping. Phenotypic variance explained by individual QTLs for all architecture traits ranged from 6.8 to 23.4%. Four primary QTLs were detected for PH. The QTL *phG-m* in the interval GY6–rCDY16-1 on linkage group G of the male-derived map had the largest effect and increased plant height by 19-cm (LOD 2.59, PVE 13.4). The interaction of this QTL with a secondary QTL on linkage group C in the interval GY54–GY81-1 accounts for 23.5% of PVE and a LOD score of 4.47. The other three primary QTLs located in the female-derived map reduced plant height between 14 and 16 cm (Table 3). A total of 12 secondary effect QTLs were detected for PH. Results obtained at Palmira in 1999 suggest evidence of partial-dominance allele action for plant height, with the $F_1$ mean primarily in the direction of the female parent. The $F_1$ mean in 1999 was 148.23 cm, which was lower than the plant height of the male parent but similar to the female parent (152.50 cm). Thus, female alleles tended to reduce plant height in this cross.

BH, measured as height of the first branch, was affected by one major primary QTL (*bhJ-m*) in the interval GY341–K10 on linkage group J of the male-derived map with PVE of 21.3% (LOD 2.61). Two other primary QTLs affecting BH were located in adjacent intervals (GY12–GY28, GY28–203) in the female-derived map on linkage group A (Table 3). All three primary QTLs increased branching height between 12 and 29 cm.

**Table 4** Significant interactions between primary and secondary QTL with PVE above 20%

| Map | Trait[a] | LG[b] | Interval | Pri. QTL Pos[c] | LG | Interval | Sec. QTL Pos.[d] | LOD | %PVE[e] | Loc.[f] |
|---|---|---|---|---|---|---|---|---|---|---|
| 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 | G | 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 | B | 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 abbreviations in Table 2
[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)

A total of 13 secondary QTLs were detected for this trait. Three highly significant QTL interactions for BH (each with PVE above 20%) were detected (Table 4). The most significant interaction was observed between *bhJ1m* on linkage group J and another QTL in the interval GY7–GY34-1 of the same linkage group accounted for phenotypic variation of 40%. At Quilichao in 1999, BH in the $F_1$ ranged from 22.50 to 131.67 cm. The $F_1$ mean (57.53 cm) for branching height was closer to the value for the female parent (56.39 cm) as compared to the male parent, which was 50.00 cm (Table 1). This suggests that the maternal alleles were dominant to the paternal alleles for this trait.

BL, an indicator trait for flowering pattern, revealed six primary QTLs with individual QTLs accounting for between 7 and 17% of the phenotypic variation. Primary QTLs detected segregating from the male parent increased BL, while those from the female reduced BL. Seventeen secondary QTLs were also detected, and five of these QTLs resulted in PVE ranging from 20.4 to 33.6%. The highest significant interaction was observed between the QTL *blN-m* in the interval rGBSII–rCDY44 on linkage group I of the male map and a secondary QTL in the interval JIA–GY57 on linkage group D (LOD 5.50 and PVE 33.6%). This trait was generally in the direction of reduced branching in the $F_1$ population, suggesting that most of the contributing alleles for lower BL came from the female parent. This parent had lower BL compared to the male parent. At Quilichao in 1999, the $F_1$ mean for BL was 4.06, the same as observed for the female parent (Table 1).

BI, a derived trait expressing branching height as a proportion of plant height, is a standardized relative term for characterizing BI. A cassava plant is considered "low branching" if the first branch occurs at a point below a third of the total height; and "high branching" if the point of first branching is above a third of the total height. Six primary QTLs were detected for branching index on linkage groups D, J and R of the male-derived map and on linkage groups D on the female-derived map. The individual effects of the QTLs ranged between 7% and 23% (Table 3). Except for the QTL *blJ-m* on linkage group J of the male parent, all others decreased BI. QTL *blJ-m* had the strongest effect with a PVE of 23.4% and LOD 2.84. A total of 16 secondary QTLs were detected for BI. PVE resulting from QTL interaction between primary and secondary QTLs ranged between 24.5 and 45% (Table 4). The highest PVE (45%) was detected in the interaction between a primary QTL (*biJ-m*) in the interval GY34-1–K10 and a secondary QTL in the interval GY7–GY34-1 on linkage group J of the male map.

SPL measures the ability of cassava plants to maintain a leaf area close to optimum at maturity, and it is a highly important attribute for productivity (Lenis et al. 2003). Six primary QTLs were detected for SPL in the female map with PVE ranging from 7.5% to 11.8%. A QTL (*splA-f*) in the interval GY12–GY28 increased SPL by 8.1 cm (peak LOD=3.51, PVE=12%). The observed mean of SPL in the $F_1$ was generally higher than obtained in the male parent (which had a higher SPL than the female parent) at both Palmira and Quilichao. Such high mean values of SPL in the $F_1$ population at both locations may be due to transgressive segregation and/or heterosis. Two-QTL model analysis identified 13 secondary QTLs for SPL.

Leaf area index, which is related to leaf development and canopy formation, is an important feature in the

**Table 5** Summary of QTLs (primary and secondary) detected in more than one trial in the $F_1$ population at Quilichao and Palmira (1998 and 1999)

| Trait[a] | Map | Linkage gp. | Interval | Trials | | | |
|---|---|---|---|---|---|---|---|
| | | | | Palmira (1998) | Palmira (1999) | Quilichao (1998) | Quilichao (1999) |
| 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 | nd | * |
| | | E | rGY118–rGY176 | * | nd | 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 | rGY10–GY52 | * | nd | nd | * |
| | | Q | GY74–AM12 | * | 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 | nd | * |
| | | Q | GY74–AM12 | * | nd | nd | * |
| | Female | A | GY12–GY28 | * | * | nd | * |
| | | C | rGY89–rGY177 | * | * | nd | * |
| | | E | rGY176–rGY190 | * | * | nd | * |
| | | G | rGY94–AM18 | * | nd | nd | * |
| | | I | H14b–GY128 | * | * | nd | nd |
| | | O | rGY164–GY223 | * | * | nd | * |
| | | Q | rGY172–rP3 | * | * | nd | * |
| SPL | Female | A | GY12–GY28 | * | nd | * | * |
| | | C | GY174–rGY119 | nd | * | * | * |
| | | G | rGY94–AM18 | * | nd | * | nd |
| | | H | OJ1–rGY199 | * | nd | * | nd |
| | | L | CBB1–rAF149 | nd | nd | * | * |
| | | O | rGY164–GY223 | * | * | * | * |
| | | Q | rGY172–rP3 | * | nd | nd | * |
| PH | Female | A | GY213–GY209 | * | * | nd | nd |
| | | C | rGY177–O11a | * | * | nd | nd |
| | | E | rGY118–rGY176 | * | * | nd | nd |

* QTL detected with LOD of >3.0; nd: not detected
[a] See abbreviation in Table 2

architectural development of cassava. This data was evaluated only in one season (1999) and one location (Palmira). Only one primary QTL was detected for LAI with a PVE value of 14%. No secondary QTL was detected for this trait.

## Productivity traits

The results of QTL analyses for productivity traits are presented in Table 3. For the four productivity traits evaluated (FRY, FSW, HI and NR), a total of seven primary QTLs were detected. The number of primary QTLs identified for each trait ranged between one (for HI and NR) and three (for FRY). PVE by individual primary QTLs ranged from 9.1 to 15.5%. A total of ten secondary QTLs were identified through interactions for productivity traits.

FRY, which is the economic part of the plant, yielded three QTLs with PVE ranging from 10 to 15.5%. Four secondary QTLs were discovered associated with this trait. The most significant QTL interaction for this was observed between the primary QTL, *fryJ-f*, within the interval AE10A–CDY76 on linkage group J and a secondary QTL in the interval rGY47–nGY143 on linkage group N of the male map (PVE=20%, peak LOD=3.81).

Two primary QTLs were identified for FSW, one each in the male-derived and female-derived map. QTL *fswH-m* within the interval GY77–rGY31-1 in the male-derived map accounted for phenotypic variation of 13.4% while QTL *fswF-m,* within the interval GY203–GY218 in the

female-derived map explained 9.1% of the phenotypic variation. Four secondary QTLs were also found associated with this trait. QTL interaction involving two of the secondary QTLs resulted in PVE values of 20% and above (Table 4).

One primary QTL each was discovered for NR and HI. The primary QTL for NR (*nrH-m*) was detected in the female-derived map with LOD 2.65 (PVE=12.7%) in the interval AE10A–CDY76. This QTL increased NR. No secondary QTL was detected for NR. The QTL detected for HI increased HI and was found in the interval GY204–GY218 on linkage F of the female-derived map (PVE=12.3%, LOD=4.18). Only one secondary QTL was identified for HI.

### Co-localization of QTLs

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. For example, interval GY34-1–K10 in the male-derived map was found associated with BH, BL and PH, which is in agreement with the significant correlations observed better than these architecture traits. Similarly, PH and SPL, which were found to be significantly correlated had QTLs that were found in the same genomic region. Two of the three intervals (GY203–GY218, GY196–GY-203) associated with primary QTLs for PH also had QTLs for SPL. Genomic regions associated with more than one productivity trait were also detected. Three intervals in the male-derived map were found to be involved in the control of two productivity traits. These are GY77–rGY31-1 (FRY, FSW), AE10A–CDY76 (FRY, RN) and GY–rCDY16-1 (FRY, NR) on linkage groups H, J and G respectively.

In many regions where QTLs were identified for productivity traits, QTLs were also detected for architecture traits. We identified eight intervals in both maps controlling both architecture and productivity traits This co-segregation does not come as a surprise because of the high correlation coefficient between traits of both groups. Frequent co-localizations of QTLs involved in the control of related traits have been reported in many crop species (Lin et al. 1996; Bryne et al. 1997; Verhaegen et al. 1997; Chen et al. 1999).

## QTL by environment interaction

The phenotype of an individual is conditioned not only by its genotype, but also by the interaction of that genotype with the environment. By growing the $F_1$ population in two different environments and in 2 years (Quilichao and Palmira in 1998 and 1999), a total of four trials was possible to assess the influence of genotype × environment interaction, as reflected by the expression of individual QTLs. QTLs detected in more than one trial or location provided a test of the stability of QTLs in the four trials used for our study. Results indicate that QTLs for a different trait showed different stabilities. The number of QTLs detected in more than one trial for each trait vary from 1 (FRY) to 13 (BI). We identified 29 QTLs in two trials, 11 QTLs in three trials and 1 QTL in four trials (Table 5). Most of the QTLs associated with two or more related traits were easily detected. A summary of marker loci identified for each trait in more than one trial is presented in Table 5. Six of the traits evaluated (FRY, PH, BH, BL, BI and SPL) identified QTLs, which were detected in more than one trial. The detection of many QTLs in only one trial indicates that such individual QTLs are sensitive, and are likely to be environment-specific. Such QTLs are likely to change greatly across environments. This is in agreement with the results reported by Paterson et al. (1991).

### QTLs and transgressive segregation

Identification of transgressive segregants is likely in a full-sib segregating population from non-inbred parents because of the abundance of recombinant types (Foodlad et al. 1998). All architecture traits in the $F_1$ population showed extreme performance with values either much larger or much smaller than those of the parents (Table 2). Although few differences were found between the parental lines for architecture traits the progeny showed a wide range of variation for these traits, indicating that transgressive segregation has occurred. Transgressions were much higher in PH, BH and SPL than in any of the other traits. The QTL effect is the measurement of the change in a population-mean when an allele of a QTL is replaced or substituted. A negative value indicates a reduction in performance and vice versa. In a segregating population of the $F_1$ used in this study, the recombination of positive alleles would be the most-likely genetic basis for the transgression.

### Positive and negative effects of QTLs

This study identified QTLs in both male- and female-derived maps with effects of opposite direction for the traits studied. This observation is not uncommon and has been reported for many traits and various species (Weller et al. 1988; de Vincente and Tanksley 1993; Foodlad et al. 1998; Paterson et al. 1988). An almost equal proportion of primary QTLs with opposite effects were detected in this study. Presence of favorable QTL alleles in both parents suggests a strong likelihood of recovering transgressive segregants as was found for architecture traits in the $F_1$ population used in this study.

## Discussion

Ideal and efficient plant architecture has long-been identified as a key factor underlying the physiological basis of yield and an opportunity to increase yield. Studies on morphological traits of cassava, relating plant architecture to improvement in yield, have been published (CIAT 1975; Hunt et al. 1997; Lian and Cock 1979a, b; Cock 1985; Cock and El-Sharkawy 1988; Iglesias et al. 1994; Lenis et al 2003). Through such studies, morphological traits have been identified as traits of immense importance, critical to understanding the physiological basis of yield in cassava. The relationships between cassava-root yield and morphological traits are being exploited in cassava improvement strategies for enhanced and accelerated development of high yielding cultivars in several breeding programs, where these adaptive traits are used as selection criteria (Iglesias et al. 1994).

This paper is the first report on QTL analysis of architecture and their interactions with QTLs for productivity in cassava. The high heritability observed for most of the traits indicates that the phenotypic variation in these traits has a large genetic component, thus making this population suitable for QTL mapping. As expected our results show that these traits are controlled by several genes with small effects. With the exception of RN and LAI, one primary QTL was found each for RN and LAI, several QTLs were identified for all traits. QTLs explaining small portions of the phenotypic variance as identified in this study far outnumber those explaining large variance, with few explaining more than 15%. The smallest effect of PVE considered in this experiment was 6%. These results support a model for quantitative inheritance wherein effects of individual factors are small.

There are a number of explanations for the small effects observed for most of the traits: firstly, important QTLs for these traits do not segregate in the cross chosen for the experiment as they have already been fixed in the population and will prevent their identification. Prior results with other crop species have shown that, as QTLs with large effects are fixed in a population, it becomes increasingly possible to detect those with smaller effects (Shrimpton and Robertson 1988; Paterson et al. 1990). For genetic improvement of crops, such genes of smaller effects could prove very valuable where QTLs of large effects have already been fixed. Secondly, the population structure of an $F_1$ from non-inbred parents is not adequate to identify these QTLs. Heterogeneity of different mating types in a $F_1$ population makes QTLs detection even more complex and less efficient compared to inbreds (Williams 1998). Thirdly, there are still gaps in the female and male genetic maps leading to some markers being unlinked. The availability of more markers will improve resolution of QTL mapping. Only 144 genotypes were evaluated in this cross, which could have some limitations for the detection of QTLs. As the variance explained by a QTL decreases, the number of progeny, which must be studied in order to detect QTLs, increases (Lander and Botstein 1989). Only QTLs with sufficient effects will be detected in a particular cross, while those with much smaller effects will go unnoticed (Paterson et al. 1991). Young (1999) reported that in the types of mapping population most often used with 100–200 progeny, only a fraction of true QTLs are discovered. The number of QTLs detected should therefore be considered as lower bounds. And fourthly, some of the QTLs might appear to have small effects because they are dependent upon interaction with other loci and in a relatively small population (less than 150 plants), as in this cross the optimal allele configurations might occur rarely (Paterson et al. 1991).

QTLs for different traits showed different stability. We observed that 35% of the QTLs were detected in more than one trial while others were found only in only one trial. Individual QTLs appear to show a range of sensitivities to the environment. Cassava plant-breeders routinely find that genotypes, which perform well in one environment, are not well suited to other environments. Differences in the adaptation ability of plant genotypes are due to environment-sensitive QTLs. QTLs, which function consistently over a range of environments, are preferred for breeding. However, the additional use of environment-specific QTLs may further improve cassava productivity in a specific environment. Furthermore, by combining several QTLs with different environment specificities into a single genotype, it is possible to attain a performance that is somewhat buffered against the vagaries of the environment (Paterson et al. 1991).

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. Some of the QTLs identified for branching traits (*biM-f, bhA1-f*) were found associated with genomic regions controlling SPL, FSW and FRY. The three branching traits (BH, BL and BI) studied tend to have a similar genetic basis as evidenced by common genomic segments shared by QTLs (*bhJ-m* and *biJ-m*, *blR1-m* and *biR-m*, *blD-m* and *biD-m*, *blD1-f* and *biD1-f*) of these traits. Branching pattern is the main determinant of the rates of increase in apices and leaves, and its manipulation through plant breeding and selection methods could possibly improve both LAI and harvest index. (Lian and Cock 1979a, b). Our results also identified common genomic regions among productivity traits (FRY, FSW, HI and NR). 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 a complex trait. Association between productivity and architecture traits have been reported in genomes of several crop species (Barua et al. 1993; Perreira and Lee 1995; Lin et al. 1998). The co-localization of QTLs involved in the control of related traits imply that QTLs affecting different traits are found near one another, more frequently than would be expected by chance. 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). Pleiotropy or close linkage has been suggested by various studies (Lin et al. 1996; Verhaegen et al. 1997; Zhuang et al. 1997) as a possible explanation for this phenomenon. Paterson et al. (1991) also explained the possibility that recombination suppression in some regions of the genome may make genes appear closer together recombinationally than they actually are physically. The distinction between linkage and pleiotropy is important for breeding purposes, but without high-resolution mapping such distinctions are difficult to resolve (Chen et al. 1999).

The principle of identifying a combination of form and function, optimal for plant growth and production, has been developed in crop physiology leading to the concept of ideotype breeding (Rosen 1967; Donald 1968). An ideotype is the gathering of many favorable characteristics, such as good growth, maximum plant biomass, reasonable morphological structure, yield and efficient physiological metabolism. The breeding of ideotypes attempts to combine favorable QTLs that determine various ideotype traits in specific traits of specific genotypes (Wu 1998).

The identification of QTLs with positive and negative effects underlying the relationship between productivity and architecture traits promises the utility of the ideotype concept in cassava breeding. QTLs of positive effects were detected for architecture traits, which were also implicated in increased productivity traits. QTLs of negative effects for architecture traits also hold some advantages for improved productivity, as evidenced from findings of past studies (Cock et al. 1979; Lian and Cock 1979a, b). For example, Cock et al. (1979) using a simulation model described late-branching (at 6 MAP) as one of the attributes of an "ideal plant type". Further study by Lian and Cock (1979a, b) associated late-branching (synonymous with increased BH and reduced BL, due to the significant negative correlation between both traits) to increased yield. They reported, however, that early branching (reduced BH) could be advantageous to high yield if top growth is not excessive (less branches). 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, the most-important trait in cassava. Ideotype breeding has been explored in trees, and theoretical models suggest that forest trees have optimal architecture for growth in a specific environment (Wu 1993; Chen et al. 1994; Farnsworth and Niklas 1995). Such an approach could be adapted for yield improvement in cassava. The efficiency of ideotype breeding using molecular marker-assisted breeding (MAB) holds promise if QTLs of sufficient sizes can be identified for the architecture traits. This will require better data from mapping multiple-families using denser genetic maps and more complex QTL mapping-algorithms suited to allogamous crops (Wu 1998).

Despite the limitations created by the ambiguities of mapping in a single full-sib cross, the information obtained about number and effect of loci controlling the different morphological traits is helpful in refining further studies. We have generated $F_2$ populations, which could further be used for marker fidelity studies, to examine and determine the genetic effects of the detected QTLs in a different genetic background. The detection of QTLs controlling related traits makes it easier for manipulation in a breeding program. It is expected that markers will be found to 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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