

Diallel inheritance of relevant traits in cassava (*Manihot esculenta* Crantz) adapted to acid-soil savannas

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Summary

There is a limited knowledge on the inheritance of traits with agronomic relevance in cassava. A diallel study among 10 parental clones was conducted in the acid-soils environment in the eastern savannas of Colombia. Thirty clones were obtained for each F1 cross. Each clone was represented by six plants, which were distributed in three replications at two locations. Therefore, the same 30 genotypes of each F1 cross were planted in the three replications at the two locations. Analysis of variance suggested significant effects for five of the six variables analyzed (harvest index, dry matter content, height of first branching, reaction to super elongation disease, and plant type scores). Fresh root yield showed strong genotype \times environment interaction and differences between crosses reached statistical significance in only one of the two environments analyzed. General and specific combining ability effects and their interaction with the environment were significant for most of the variables as well. Results suggested that dominance plays an important role particularly in the cases of fresh root yield and harvest index.

Abbreviations: CBB, cassava bacterial blight; SED, super elongation disease; WA, weight in the air; WW, weight in water; GCA, general combining ability; SCA, specific combining ability

Introduction

Cassava (*Manihot esculenta* Crantz), along with maize, sugarcane, and rice constitute the most important sources of energy in the diet of most tropical countries of the world. Cassava is the fourth most important basic food after rice, wheat, and maize and is a fundamental component in the diet of millions of people (FAO/FIDA, 2000). The species originated in South America, and was domesticated about 5000 years ago (Allem, 2002; Olsen & Schaal, 2001). The first European sailors soon recognized the advantages of the crop and spread it through Asia and Africa. Until recently, cassava and its products were little known outside the tropical and subtropical regions where it grows. Compared with other staple foods, little scientific ef-

forts had been made to improve the crop (Cock, 1985). However, with the creation of the International Institute of Tropical Agriculture (IITA) in Nigeria and the International Center of Tropical Agriculture (CIAT) in Colombia in the early 1970s a new era began for cassava with the implementation of successful breeding projects, modernization of cultural practices, and development of new processing methods (Cock, 1985; Jennings & Iglesias, 2002). National research centers in India, Thailand, Colombia, Cuba, and Brazil, among few other countries, have conducted successful research on cassava as well.

Cassava is a very rustic crop that grows well in conditions where few other crops could survive: it is drought tolerant, can produce in degraded soils, and offers resistance to its most important diseases and pests.

It is naturally tolerant to acidic soils and offers the convenient flexibility to be harvested when the farmers need it. Cassava has benefited from technological inputs in the area of breeding (Kawano, 2003; Kawano et al., 1998) to successfully satisfy the needs of farmers and processors. The general scheme for cassava breeding is indeed a phenotypic massal selection. Large number of segregating genotypes is evaluated in a lengthy process that requires as many as 6 years for completion (Ceballos et al., 2004; Jennings & Iglesias, 2002). Individual genotypes (clones) are selected and then multiplied to take advantage of the vegetative propagation of the crop.

However, in spite of the importance of this crop, very little progress has been done to understand the inheritance of traits with agronomic relevance. Very few articles regarding the inheritance of quantitative traits have been published (Easwari Amma et al., 1995; Easwari Amma & Sheela, 1993, 1995, 1998). Cassava shows in this regard a unique situation because a molecular map has been already developed (Fregene et al., 1997; Mba et al., 2001) and yet very little knowledge based on traditional genetics has so far been produced. The objective of this study was to obtain information on the inheritance of traits with agronomic relevance in cassava so that a more scientifically based approach for improving them could be implemented.

Materials and methods

Controlled pollinations among several parents were performed following the standard procedures described by Kawano (1980). Several thousand pollinations are routinely made among 25–30 elite cassava clones adapted to the acid soil environment (Ceballos et al., 2004). The specific parents used in this study were those that had produced enough botanical seeds for each of the required F₁ crosses in a complete, balanced diallel set. That was the main selection criteria used for determining which parental materials would be included in the study.

Based on the seeds obtained a complete diallel set from 10 parents was prepared. Botanical seed produced from the crosses were planted in screen houses and transplanted to the field after 2 months at CIAT station in Palmira (Valle del Cauca Department, Colombia). A total of 12,022 genotypes were produced with maximum and minimum number of seeds for each F₁-cross of 791 and 73, respectively. A total of 4697 were planted and 4251 could be transplanted to the field.

From the transplanted seedlings, a total of 3871 (or 91.0%) developed into vigorous plants from which vegetative cuttings could be obtained. Unavoidably, there is a selection at this stage, which is based on the capacity of the plants to produce a minimum of six good quality vegetative cuttings. This was also the main criterion for selecting the sample of 30 clones that would represent each F₁ cross. At harvest time six vegetative cuttings from 30 plants were obtained for all crosses except CM 4574-7 × SM 2058-2, which was represented by only 18 clones. For this particular cross, 12 plants (from a regional check) were added to complete the 30 plants required to maintain experimental units with uniform size and plant density. These 12 plants, however, were not considered in the analysis.

Two locations with different soil conditions were used for this diallel evaluation. Both locations were at the Experimental Station in CORPOICA La Libertad near Villavicencio in Meta Department, Colombia (4°06'N, 73°29'W, and at 400 m above sea level). In spite of their proximity, the two environments were very different. *Loma* plot had severe edaphic constraints related to soil acidity (4.33 pH, 15.7 ppm P, and 66.9% aluminum saturation). The environmental conditions in this plot generally allow for high disease pressure from super elongation disease (SED) induced by the fungus *Sphaceloma manihoticola* and cassava bacterial blight (CBB) induced by *Xanthomonas axonopodis* pv. *manihotis*. Both diseases are endemic in this region and evaluation of the reaction of cassava to them is based on their natural incidence. *Porcinos* field had much better soil conditions (4.73 pH, 24.7 ppm P, and only 28.5% aluminum saturation). Before planting 0.5 t ha⁻¹ of dolomitic lime was applied to the soil. One month after planting the stakes 0.5 t ha⁻¹ of 10-20-20 NPK fertilizer was applied following the standard recommendations for cassava grown in this kind of environments.

A randomized complete block design with three replications per location was used. The evaluation was similar to a split-plot design. Each replication contained 45 main plots, one for each of the 45 F₁ crosses of the diallel. Each F₁ cross was, therefore, randomly allocated within each replication. Main plots contained eight rows with seven plants per row. The first and last rows and the first and last plant within each row were filled with border plants. The rest of the plot (6 × 5 = 30 subplots) was used to plant the experimental material. The 30 clones constituting each F₁ cross were planted together in the respective main plots of each replication. Row-to-row distances and separation of plants within

row were 1 m for a final plant density of 10,000 plants ha^{-1} .

Trials were harvested in April 2002, 10 months after planting (the usual age for harvesting cassava in this environment). Harvest is planned to take place just before the beginning of the rains. Root dry matter content drops drastically with the advent of the rains because the plant uses some of the energy accumulated in the roots to restart growth after the dry period. However, plants cannot be harvested too early because the vegetative cuttings obtained from them lose sprouting capacity and, therefore, additional evaluation and selection could be hampered. To take advantage of the large number of segregating progenies the results of this study were also used to continue the standard selection process in search of elite clones. Therefore, the best performing clones in this diallel analysis were selected and planted in a preliminary yield trial (Ceballos et al., 2004).

Plants were hand harvested individually and results averaged across the 30 clones of each F1 cross. All the roots produced by each plant were weighted as well as the above ground biomass (stem and foliage). Harvest index was measured as the ratio between root weight and total biomass. Dry matter content in the roots was estimated using the specific gravity methodology (Kawano et al., 1987). Approximately 5 kg of roots were weighed in a hanging scale (WA) and then, the same sample, was weighed with the roots submerged in water (WW). Dry matter content was estimated utilizing the following formula:

$$\begin{aligned} \text{Dry matter content (\%)} \\ = \{[\text{WA}/(\text{WA} - \text{WW})] \times 158.3\} - 142 \end{aligned}$$

where WA = weight in the air and WW = weight in water.

Reaction to SED and plant type architecture were scored using a 1–5 scale where 1 = resistant or excellent plant type and 5 = susceptible or very poor plant type. Plant type score took into consideration several important characteristics such as plant vigor, erect architecture with few branches and reduced branching angle, adequate capacity to produce vegetative cuttings, amount of foliage present, and absence of foliar diseases.

The analysis of variance follows the method 4 proposed by Griffing (1956). Genotypes and environments were considered fixed and random effects, respectively.

Results

There was little development of CBB in both fields and, therefore, reaction to this disease was not analyzed. Pressure from SED was low or negligible at the *Porcinos* field, which is characterized by considerably better soil conditions. This is why SED scores could only be taken at the *Loma* plot. Table 1 presents the analysis of variance combined across locations. Environments were significantly different for fresh root yield, height of first branching, and plant type score but did not show significant differences for harvest index and dry matter content. In general, the coefficients of variability (Steel & Torrie, 1960) were acceptable for the relatively large trials involving cassava evaluations in the field.

Analysis of variance

Differences among the averages of the 45 crosses evaluated were highly significant ($P \geq 0.01$) for dry matter content, height of first branching, SED, and plant type score, significant ($P \geq 0.05$) for harvest index and non-significant for fresh root yield (Table 1). All variables (except SED which was measured only in one environment) showed highly significant ($P \geq 0.01$) interactions between crosses and the environments ($C \times L$). The error term for crosses in this analysis was the respective interaction with the environment. The large $C \times L$ interaction for fresh root yield explains the lack of statistical significance for differences among crosses for this variable. Individual locations analyses revealed highly significant differences ($P \geq 0.01$) among crosses for the *Loma* field and non-significant at the *Porcinos* one (data not presented).

The sum of squares due to crosses was further partitioned in two orthogonal components represented by the general (GCA) and specific (SCA) combining ability effects. The proportion of the sum of squares for crosses explained by GCA and SCA effects is an estimation of the relative importance of additive and non-additive effects in the expression of each variable. SCA effects accounted for 53% of the variation due to crosses for fresh root yield, 38% for harvest index, and 33% for height of first branching. For the remaining variables non-additive effects accounted for less than 20% of the cross sum of squares. These results are consistent with those observed in two additional diallel studies for the sub-humid and mid-altitude valleys (CIAT, 2002). Across the three studies, SCA accounted for 51% (fresh root yield), 40% (harvest index), 28% (dry matter content), 25% (height of first branching),

Table 1. Mean squares from the analysis of variance, combined across locations, for the diallel study from 10 parental cassava clones evaluated in two soil conditions in Meta Department, Colombia

Source of variation	Degrees of freedom	Fresh root yield (kg pl ⁻¹)	Harvest Index (0–1)	Dry matter content (%)	Height 1st branching (m)	SED ^a score (1–5)	Plant type (1–5)
Locations (L)	1	172.8**	0.232	144.25	680.48**	n.a.	22.634**
Rep/L	4	3.8	0.060	55.49	23.51	1.804	0.624
Crosses (C)	44	0.6	0.014*	17.27**	23.59**	0.813**	0.927**
GCA	9	1.4	0.043	68.96*	76.87**	3.421**	3.783
SCA	35	0.4	0.007	3.98*	9.89**	0.142*	0.192**
C × L	44	0.5**	0.008**	5.82**	2.35**	–	0.374**
GCA × L	9	1.2**	0.022**	21.27**	4.27**	–	1.578**
SCA × L	35	0.3*	0.005*	1.84	1.85*	–	0.064
Error	176	0.2	0.003	1.34	1.22	0.086	0.067
Total	357	0.8	0.006	4.53	5.97	0.264	0.264
CV (%) ^b		21.40	14.09	3.70	10.40	10.01	7.44
%SS crosses due to GCA ^c		47	62	82	67	86	83
%SS crosses due to SCA ^c		53	38	18	33	14	17

^aSED: Super elongation disease evaluated only at *Loma* plot.

^bCV = Coefficient of variability.

^cSS = Sum of squares.

*Significant at the $P < 0.05$ probability level.

**Significant at the $P < 0.01$ probability level.

and 29% (plant type score) of the sum of squares due to crosses (CIAT, 2002).

General combining ability effects

General combining ability effects were highly significant ($P \geq 0.01$) for height of first branching and SED score, significant ($P \geq 0.05$) for dry matter content and non-significant for fresh root yield, harvest index, and plant type score. Specific combining ability effects were highly significant ($P \geq 0.01$) for height of first branching and plant type score, significant ($P \geq 0.05$) for dry matter content and SED score, and non-significant for fresh root yield and harvest index. However, the combined analysis for genetic effects should, for most variables, be done individually for each location, due to the significance of their respective interactions with the environment, particularly for the GCA effects.

The best two parents for fresh root yield, across the two locations, were SM 2219-11 and CM 4574-7 (Table 2). On the other hand, parent MPER 183 produced clearly mediocre progenies regarding fresh root productivity. SM 1219-9 and CM 6740-7 also produced better than average progenies for this trait. The former was also found to be a good parent for the sub-humid environment and the mid-altitude valleys (CIAT, 2002).

CM 6740-7 was officially released as a cultivar with the name CORPOICA-REINA in 2001. SM 2219-11 not only had the highest positive GCA effects for fresh root yield, but also for harvest index (0.042) and positive GCA effects (but not the highest) for dry matter content in the roots (0.485). Moreover, the progeny from this clone had a good performance with low scores for SED (–0.205) and plant type (–0.147). Its progeny tended to have a high first branching (0.158), which is generally a desirable trait.

A second outstanding clone, based on the average performance of its progeny across the two locations was CM 4574-7. It had the second highest GCA effects for fresh root yield as well as for dry matter content in the roots. The progeny from this clone also had the lowest GCA estimates for SED and plant type. In addition, the height of first branching was high indicating a rather late branching in the life of the plant, a trait generally preferred by most farmers.

As it is frequently the case for other crops, it was difficult to find a clone whose progeny was outstanding for most variables. In this experiment the progeny of MPER 183 was the worst for every variable and was among the poorer for height of first branching.

In the analysis of individual locations the GCA effects for fresh root yield from the *Loma* field were highly significant. SM 2219-11 showed the highest

Table 2. General combining ability effects, combined across locations, for the diallel study from 10 parental cassava clones evaluated in two soil conditions in Meta Department, Colombia

Parental clone or parameter	Fresh root yield (kg pl ⁻¹)	Harvest Index (0–1)	Dry matter content (%)	Height 1st branching (m)	SED score (1–5) ^a	Plant type (1–5) ^a
Combined across locations						
1 = CM 4574-7	0.178	–0.003	0.996	0.133	–	–0.428
2 = CM 6740-7	0.071	–0.008	0.075	0.122	–	–0.160
3 = CM 7033-3	–0.108	–0.007	–0.457	0.081	–	–0.146
4 = SM 1219-9	0.095	0.026	0.566	0.023	–	–0.020
5 = SM 1565-15	–0.069	–0.002	1.324	–0.073	–	–0.135
6 = SM 2058-2	0.071	0.006	–0.411	0.015	–	–0.070
7 = SM 2219-11	0.275	0.042	0.485	0.158	–	–0.147
8 = HMC 1	–0.128	0.013	–0.140	–0.178	–	0.435
9 = MPER 183	–0.323	–0.073	–2.987	–0.100	–	0.437
10 = MTAI 8	–0.063	0.006	0.547	–0.180	–	0.234
Std. Dev. G_i	0.151	0.020	0.632	0.028	–	0.172
Std. Dev. ($G_i - G_j$)	0.225	0.030	0.941	0.042	–	0.256
Loma field						
CM 4574-7	0.186	–0.003	1.871	13.619	–0.445	–0.741
CM 6740-7	0.029	–0.002	0.324	8.712	0.180	–0.234
CM 7033-3	–0.073	–0.016	–0.106	3.742	–0.308	–0.186
SM 1219-9	0.056	0.033	0.818	0.433	–0.016	–0.010
SM 1565-15	0.206	0.030	1.319	–5.237	–0.359	–0.284
SM 2058-2	–0.025	–0.008	–0.472	–0.391	–0.139	0.074
SM 2219-11	0.319	0.060	0.934	18.379	–0.205	–0.215
HMC 1	0.073	0.028	–0.408	–12.773	0.143	0.441
MPER 183	–0.621	–0.118	–4.616	–10.828	0.784	0.792
MTAI 8	–0.150	–0.006	0.336	–15.656	0.364	0.364
Std. Dev. G_i	0.058	0.013	0.229	1.953	0.057	0.052
Std. Dev. ($G_i - G_j$)	0.086	0.019	0.341	2.911	0.085	0.078
Porcinos field						
CM 4574-7	0.171	–0.004	0.122	12.970	–	–0.115
CM 6740-7	0.113	–0.014	–0.174	15.653	–	–0.086
CM 7033-3	–0.143	0.002	–0.808	12.361	–	–0.106
SM 1219-9	0.135	0.020	0.315	4.069	–	–0.031
SM 1565-15	–0.343	–0.035	1.330	–9.277	–	0.015
SM 2058-2	0.168	0.019	–0.350	3.421	–	–0.213
SM 2219-11	0.232	0.024	0.036	13.204	–	–0.078
HMC 1	–0.330	–0.002	0.128	–22.864	–	0.428
MPER 183	–0.025	–0.027	–1.358	–9.162	–	0.082
MTAI 8	0.024	0.019	0.759	–20.375	–	0.104
Std. Dev. G_i	0.105	0.009	0.220	2.309	–	0.048
Std. Dev. ($G_i - G_j$)	0.156	0.013	0.328	3.442	–	0.071

^aSED and plant type scores based on a 1 (resistant to SED or good plant type) to 5 (susceptible to SED or poor plant type).

positive value, which was also found for the *Porcinos* field (Table 2). CM 4574-7 and SM 1565-15 also showed significant positive GCA effects for fresh root yield. SM 1565-15, however, showed the lowest value at the *Porcinos* field. It is clear that progenies from this particular clone have good adaptation to the more limiting conditions to the typical acid-soil savannas, which agrees with previous findings (CIAT, 2002) but cannot compete successfully in the better conditions at *Porcinos* field. MPER 183 had negative GCA effects, and in the case of the results from the *Loma* field, it was the lowest among all parents.

The GCA effects for harvest index of SM 2219-11 were the highest at both locations. The better adaptation of SM 1565-15 to the conditions represented by the *Loma* field is also reflected in the case of harvest index with the third highest value, a sharp contrast with that from *Porcinos* field, which was the lowest among the 10 parents. MPER 183 had negative GCA effects for harvest index at both locations, with the one from the *Loma* field being the lowest among all parents.

Clone SM 1565-15 showed the best GCA effects for dry matter content at the *Porcinos* field, and the second best at the *Loma* field. GCA effects for this trait from CM 4574-7 were also outstanding in both environments. The progeny from this clone showed the best reaction to SED (GCA effect = -0.445), followed by SM 1565-15, CM 7033-3, and SM 2219-11, all with significantly negative values. MPER 183 produced the most susceptible progenies (GCA effect = 0.784) followed by MTAI 8 (GCA effect = 0.364). The joint Thailand-CIAT breeding program developed the latter, which was released in 1987 as Rayong 60. Since SED is not present in Thailand, it is not surprising to observe that the progenies from MTAI 8 were found to be susceptible to this disease. MTAI 8 was included as parent because of its outstanding root yield potential and high dry matter content in the roots.

GCA effects for plant type score identified CM 4574-7 as one of the best parents with negative values for both environments, particularly for the *Loma* field. CM 6740-7 and SM 2219-11 also showed good GCA effects for plant type at both locations. Clone SM 1565-15 showed again a particular adaptation to the savannas conditions represented by the *Loma* field, with a significantly negative GCA effect which contrasted with that from the *Porcinos* field, which was positive (although not statistically different from zero). In general, good (negative) GCA effects for plant type was associated with positive ones for height of first branching. Farmers generally prefer an erect, non-branching

architecture because it facilitates cultural practices after the third-fourth month of growth and the production and handling of the planting materials is facilitated. A first branching high above the ground also results in a more erect type.

Specific combining ability effects

Table 3 presents a summary of averages for each cross (combined across both locations) as well as the respective SCA effects. Fresh root production is presented in t ha^{-1} units to illustrate the outstanding yield potential of this crop. The highest yielding crosses were concentrated in combinations of certain progenitors. SM 2219-11 was a parent in five of the best 10 yielding crosses followed by CM 4574-7, which participated in four such crosses. As expected this agrees with the results from the GCA effects from Table 2, which showed these clones to be the best two for fresh root yield. The highest fresh root yields were always associated with positive SCA effects, which were frequently statistically significant. This would suggest that these good performances were closely associated with non-additive, rather than additive genetic effects. An observation coherent with those obtained from Table 1. The correlation coefficient between F1 average yield performances and their respective SCA effects was 0.73.

In the case of resistance to super elongation disease, on the other hand, the lowest ratings were not necessarily associated with negative SCA effects with the exception of the first cross (CM 4574-7 \times CM 6740-7) which showed the lowest SCA effect. It is reasonable, therefore, to assume that for this trait additive rather than non-additive effects would control most of the reaction to the disease. These results reinforce those obtained from the analysis of variance in Table 1, where SCA accounted for less than 20% of the sum of squares due to crosses. The correlation coefficient between average SED score performance for the F1 crosses and their respective SCA effects was 0.37, much lower than that found for fresh root yield.

The correlation coefficients between average harvest index and dry matter content with their respective SCA values were, respectively, 0.62 and 0.43. These values would also support the finding that non-additive effects play an important role for harvest index, which accounted for 38% of the sum of squares due to crosses (Table 1) but are not so important for dry matter content (for which only 18% of the sum of squares of crosses was accounted for by SCA effects, Table 1).

Table 3. Averages and specific combining ability effects (SCA), combined across locations, for the most relevant traits in the diallel study evaluated in the acid-soil conditions of eastern savannas of Colombia

Cross ^a or parameter	Fresh root yield		Harvest Index		Dry matter content		SED score ^b	
	t ha ⁻¹	SCA	0–1	SCA	%	SCA	1–5	SCA
1 × 2	25.90	2.98	0.44	0.046	32.7	0.327	2.3	−0.418
1 × 3	19.99	−1.14	0.38	−0.015	31.3	−0.597	2.2	0.007
1 × 4	23.53	0.36	0.43	−0.001	32.6	−0.316	2.4	−0.113
1 × 5	17.82	−3.70	0.37	−0.032	34.4	0.731	2.2	0.068
1 × 6	25.39	2.46	0.43	0.024	31.5	−0.422	2.6	0.205
1 × 7	26.50	1.53	0.45	0.007	31.8	−1.014	2.6	0.286
1 × 8	16.24	−4.69	0.37	−0.048	32.3	0.152	2.5	−0.139
1 × 9	21.49	2.51	0.38	0.047	31.0	1.647	3.2	−0.030
1 × 10	21.27	−0.31	0.38	−0.029	32.4	−0.508	3.0	0.135
2 × 3	19.12	−0.94	0.37	−0.024	31.7	0.766	3.0	0.160
2 × 4	18.59	−3.50	0.37	−0.060	31.5	−0.498	3.3	0.223
2 × 5	21.38	0.93	0.40	−0.001	33.9	1.189	2.5	−0.295
2 × 6	22.63	0.78	0.43	0.022	30.6	−0.340	2.9	−0.038
2 × 7	24.96	1.07	0.45	0.010	32.3	0.427	3.1	0.190
2 × 8	17.39	−2.46	0.38	−0.030	30.0	−1.229	3.5	0.281
2 × 9	16.83	−1.08	0.32	−0.006	27.3	−1.097	3.9	−0.010
2 × 10	22.73	2.22	0.45	0.043	32.4	0.454	3.4	−0.093
3 × 4	21.52	1.22	0.46	0.036	32.3	0.832	2.4	−0.167
3 × 5	19.80	1.14	0.38	−0.019	32.5	0.290	2.2	−0.021
3 × 6	21.77	1.71	0.39	−0.021	30.0	−0.415	2.7	0.225
3 × 7	18.94	−3.17	0.42	−0.022	30.5	−0.825	2.4	−0.031
3 × 8	17.11	−0.95	0.40	−0.018	30.2	−0.521	2.7	−0.095
3 × 9	18.72	2.60	0.36	0.029	28.8	0.905	3.5	0.081
3 × 10	18.25	−0.47	0.46	0.053	31.0	−0.434	2.8	−0.160
4 × 5	21.89	1.19	0.42	−0.010	32.1	−1.133	3.0	0.445
4 × 6	21.50	−0.59	0.40	−0.037	31.2	−0.307	3.1	0.307
4 × 7	25.13	0.99	0.50	0.029	32.5	0.131	2.6	−0.156
4 × 8	18.68	−1.42	0.46	0.011	32.6	0.904	2.8	−0.236
4 × 9	17.13	−1.02	0.37	0.007	28.9	0.051	3.5	−0.248
4 × 10	23.52	2.77	0.46	0.023	32.8	0.337	3.2	−0.055
5 × 6	19.59	−0.87	0.42	0.005	33.1	0.896	2.3	−0.160
5 × 7	20.61	−1.88	0.46	0.012	33.0	−0.086	2.2	−0.185
5 × 8	22.76	4.31	0.46	0.047	32.4	−0.103	2.9	0.184
5 × 9	18.68	2.16	0.36	0.031	28.7	−0.931	3.3	−0.023
5 × 10	15.83	−3.28	0.38	−0.035	32.3	−0.853	2.9	−0.013
6 × 7	18.62	−5.27	0.44	−0.014	30.7	−0.671	2.6	0.052
6 × 8	21.08	1.23	0.43	0.008	31.9	1.110	2.5	−0.413
6 × 9	18.25	0.34	0.35	0.014	27.7	−0.190	3.5	−0.125
6 × 10	20.74	0.23	0.42	−0.002	31.8	0.337	3.1	−0.054
7 × 8	26.53	4.63	0.48	0.014	31.7	−0.006	2.7	−0.132

(Continued on next page)

Table 3. (Continued)

Cross ^a or parameter	Fresh root yield		Harvest index		Dry matter content		SED score ^b	
	t ha ⁻¹	SCA	0–1	SCA	%	SCA	1–5	SCA
7 × 9	19.06	−0.89	0.34	−0.034	29.7	0.869	3.5	0.006
7 × 10	25.54	2.99	0.45	−0.002	33.5	1.175	3.1	−0.030
8 × 9	15.35	−0.56	0.34	−0.010	27.7	−0.528	4.2	0.315
8 × 10	18.43	−0.09	0.45	0.026	31.9	0.220	3.7	0.236
9 × 10	12.51	−4.06	0.26	−0.078	28.2	−0.727	4.1	0.034
Mean	20.43	1.92 ^c	0.41	0.025 ^c	31.32	0.489 ^c	2.9	0.150 ^c
LSD (5%)	8.03	2.88 ^d	0.11	0.038 ^d	2.804	0.733 ^d	0.477	0.224 ^d

^aCodes for identifying the parents at top of Table 2.

^bSED evaluated only at *Loma* plot.

^cStandard deviation for S_{ij} .

^dStandard deviation for $(S_{ij} - S_{ik})$.

Phenotypic correlations between evaluated traits

Table 4 presents the phenotypic correlation coefficients among the averages of the 45 crosses analyzed in this study. As expected, negative correlations ($\rho < -0.70$) were observed between SED score and root and foliage yields as well as for dry matter content. It should be pointed out that lower scores for SED meant better (resistant) reaction to the disease. SED was also negatively associated with harvest index ($\rho = -0.61$). Positive correlation coefficients were also found for SED score and plant and root scores. This was also expected because in these variables a lower value represented better phenotypes as in the case of the SED score.

The height of the first branch showed a high correlation coefficient ($\rho = -0.79$) only with plant

type score. In general, however, a high first branching tended to have higher root and foliage yields (correlation coefficients of 0.38 and 0.40, respectively). In addition to the correlations already mentioned, fresh root yield showed a highly positive coefficient with harvest index ($\rho = 0.73$) and negative ones with plant ($\rho = -0.52$) and root type ($\rho = -0.84$) scores.

Dry matter content was positively correlated with harvest index ($\rho = 0.63$) and fresh root yield ($\rho = 0.51$). The latter is a fortunate association because breeders are generally interested in developing cassava germplasm that has high fresh root yield as well as high dry matter content (Jennings & Iglesias, 2002; Kawano, 2003). Finally, high dry matter content was also associated, negatively as expected, with plant type score ($\rho = -0.53$).

Table 4. Phenotypic correlations from the averages, combined across locations, for the most relevant traits in the diallel study evaluated in the acid-soil conditions of eastern savannas of Colombia

	SED score (1–5)	Height 1st branch (m)	Plant type (1–5)	Root score (1–5)	Fresh root yield (kg pl ⁻¹)	Fresh foliage yield (kg pl ⁻¹)	Harvest Index (0–1)	Dry matter content (%)
Height 1st branch	−0.41**	1.00						
Plant type	0.78**	−0.79**	1.00					
Root score	0.78**	−0.38*	0.64**	1.00				
Fresh root yield	−0.74**	0.38*	−0.52**	−0.84**	1.00			
Foliage yield	−0.77**	0.40**	−0.52**	−0.41**	0.42**	1.00		
Harvest Index	−0.61**	0.13	−0.30*	−0.77**	0.73**	−0.14	1.00	
Dry matter content	−0.73**	0.11	−0.53**	−0.71**	0.51**	0.25	0.63**	1.00

*Significant at the $P < 0.05$ probability level.

**Significant at the $P < 0.01$ probability level.

Discussion

Mean fresh root yield across the experiment was 20.4 t ha^{-1} , but was considerably higher in the *Porcinos* (36.1 t ha^{-1}) than in the *Loma* field (12.4 t ha^{-1}). Several families, however, showed mean productivities across the two environments above 25 t ha^{-1} , illustrating the excellent productivity of this crop, even in the limiting conditions of the *Loma* field. It should be emphasized that these are averages across the 30 clones representing each F1 family. The performance of the best clones within each family offers even wider ranges of variations. It is the performance of the individual clone that cassava breeders are most interested in.

The results of this study indicate a large influence of genotype \times environment interactions, which are particularly problematic in the case of cassava. These effects were highly significant for all the variables analyzed in the two locations. Because of the low multiplicative rate of cassava's planting material, it takes several years until the first multi-location trial can be conducted (Ceballos et al., 2004; Jennings & Iglesias, 2002). This implies that a large proportion of the selection process is affected by the lack of replication in different environments. One alternative would be to split the first clonal evaluation (Ceballos et al., 2004), which is typically based on 6–8 plants, in two locations (where each clone would be represented by 3–4 plants). Harvest index has been successfully used to overcome some of the problems related to interfamilial competition in the first clonal evaluation stages (Kawano, 2003; Kawano et al., 1998) when not enough planting material is available for replicated trials. Harvest index, however, also showed highly significant genotype \times environment effects suggesting that even this variable is also very much influenced by this interaction. The use of border rows is not feasible in the large clonal evaluation trials because it would double the size of an already large trial. The approach currently used by CIAT to reduce interfamilial competition in these trials is to widen row-to-row distance (from 1.0 to 1.2 m) and reduce plant-to-plant spacing within the row (from 1.0 to 0.8 m). This layout increases within-row competition and reduces the between-row one, while maintaining the overall plant density almost unchanged.

Another important conclusion from this study is the unexpectedly high role that SCA effects had for fresh root yield. SCA effects accounted for more than half of the crosses sum of squares for this variable. Non-

additive effects also explained a considerable proportion of the cross sum of squares for harvest index and height of first branch and had little influence in dry matter content, SED, and plant type score.

Progenies from clones CM 4574-7, CM 6740-7, and SM 2219-11 showed an above average performance suggesting a higher breeding value for these three parental lines. Clone SM 1565-15 can be used as source of increased dry matter content in the roots and resistance to SED. In general, the progenies from this clone were outstanding in the more limiting conditions of the *Loma* field, but could not compete well in the more favorable conditions of the *Porcinos* field. On the other hand, clones MPER 183, HMC 1, and CM 7033-3 should not be used as progenitor of cassava clones targeting this environment.

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