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

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1 **Key words:** General combining ability; specific combining ability; additive effects,
2 dominance, super elongation disease.

3

4 **Abstract**

5 There is a limited knowledge on the inheritance of traits with agronomic relev-
6 ance in cassava. A diallel study among ten parental clones was conducted in the
7 acid-soils environment in the eastern savannas of Colombia. Thirty clones were
8 obtained for each F1 cross. Each clone was represented by six plants, which
9 were distributed in three replications at two locations. Therefore the same 30 ge-
10 notypes of each F1 cross were planted in the three replications at the two loca-
11 tions. Analysis of variance suggested significant effects for five of the six va-
12 riables analyzed (harvest index, dry matter content, height of first branching,
13 reaction to super elongation disease and plant type scores). Fresh root yield
14 showed strong genotype x environment interaction and differences between
15 crosses reached statistical significance in only one of the two environments ana-
16 lyzed. General and specific combining ability effects and their interaction with the
17 environment were significant for most of the variables as well. Results suggested
18 that dominance plays an important role particularly in the cases of fresh root yield
19 and harvest index.

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21 **Abbreviations:** CBB (cassava bacterial blight); SED (super elongation disease);
22 WA (weight in the air); WW (weight in water); GCA (general combining ability);
23 SCA (specific combining ability).

1 **Introduction**

2 Cassava (*Manihot esculenta* Crantz), along with maize, sugarcane and rice con-
3 stitute the most important sources of energy in the diet of most tropical countries
4 of the world. Cassava is the fourth most important basic food after rice, wheat
5 and maize and is a fundamental component in the diet of million of people
6 (FAO/FIDA, 2000). The species originated in South America, and was domesti-
7 cated about 5000 years ago (Allem, 2001; Olsen & Schaal, 2001). The first Euro-
8 pean sailors soon recognized the advantages of the crop and spread it through
9 Asia and Africa. Until recently, cassava and its products were little known outside
10 the tropical and subtropical regions where it grows. Compared with other staple
11 foods, little scientific efforts had been made to improve the crop (Cock, 1989).
12 However, with the creation of the International Institute of Tropical Agriculture (II-
13 TA) in Nigeria and the International Center of Tropical Agriculture (CIAT) in Co-
14 lombia in the early 1970's a new era began for cassava with the implementation
15 of successful breeding projects, modernization of cultural practices and develop-
16 ment of new processing methods (Cock, 1989; Jennings & Iglesias, 2002). Na-
17 tional research centers in India, Thailand, Colombia, Cuba and Brazil, among few
18 other countries, have conducted successful research on cassava as well.

19

20 Cassava is a very rustic crop that grows well in conditions where few other
21 crops could survive: it is drought tolerant, can produce in degraded soils, and of-
22 fers resistance to its most important diseases and pests. It is naturally tolerant to
23 acidic soils and offers the convenient flexibility to be harvested when the farmers

1 need it. Cassava has benefited from technological inputs in the area of breeding
2 (Kawano et al. 1998; 2003) to successfully satisfy the needs of farmers and pro-
3 cessors. The general scheme for cassava breeding is indeed a phenotypic mas-
4 sal selection. Large number of segregating genotypes is evaluated in a lengthy
5 process that requires as many as six year for completion (Ceballos et al.,
6 2004;Jennings & Iglesias, 2002). Individual genotypes (clones) are selected and
7 then multiplied to take advantage of the vegetative propagation of the crop.

8

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

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20

21 **Materials and methods**

22 Controlled pollinations among several parents were performed following the
23 standard procedures described by Kawano (1980). Several thousand pollinations

1 are routinely made among 25-30 elite cassava clones adapted to the acid soil
2 environment (Ceballos et al., 2004). The specific parents used in this study
3 where those that had produced enough botanical seeds for each of the required
4 F1 crosses in a complete, balanced diallel set. That was the main selection crite-
5 ria used for determining which parental materials would be included in the study.

6

7 Based on the seeds obtained a complete diallel set from 10 parents was
8 prepared. Botanical seed produced from the crosses were planted in screen
9 houses and transplanted to the field after 2 months at CIAT station in Palmira
10 (Valle del Cauca Department, Colombia). A total of 12,022 genotypes were pro-
11 duced with maximum and minimum number of seeds for each F1-cross of 791
12 and 73, respectively. A total of 4697 were planted and 4251 could be trans-
13 planted to the field. From the transplanted seedlings, a total of 3871 (or 91.0%)
14 developed into vigorous plants from which vegetative cuttings could be obtained.
15 Unavoidably there is a selection at this stage, which is based on the capacity of
16 the plants to produce a minimum of six good quality vegetative cuttings. This was
17 also the main criterion for selecting the sample of 30 clones that would represent
18 each F1 cross. At harvest time six vegetative cuttings from 30 plants were ob-
19 tained for all crosses except CM 4574-7 x SM 2058-2, which was represented by
20 only 18 clones. For this particular cross, 12 plants (from a regional check) were
21 added to complete the 30 plants required to maintain experimental units with uni-
22 form size and plant density. These 12 plants, however, were not considered in
23 the analysis.

1

2 Two locations with different soil conditions were used for this diallel evalua-
3 tion. Both locations were at the Experimental Station in CORPOICA La Libertad
4 near Villavicencio in Meta Department, Colombia (4° 06' N, 73° 29' W and at 400
5 meters above sea level). In spite of their proximity, the two environments were
6 very different. *Loma* plot had severe edaphic constraints related to soil acidity
7 (4.33 pH, 15.7 ppm P and 66.9% aluminum saturation). The environmental condi-
8 tions in this plot generally allow for high disease pressure from super elongation
9 disease (SED) induced by the fungus *Sphaceloma manihoticola* and cassava
10 bacterial blight (CBB) induced by *Xanthomonas axonopodis* pv. *Manihotis*. Both
11 diseases are endemic in this region and evaluation of the reaction of cassava to
12 them is based on their natural incidence. *Porcinos* field had much better soil con-
13 ditions (4.73 pH, 24.7 ppm P and only 28.5% aluminum saturation). Before plant-
14 ing 0.5 t ha⁻¹ of dolomitic lime was applied to the soil. One month after planting
15 the stakes 0.5 t ha⁻¹ of 10-20-02 NPK fertilizer was applied following the standard
16 recommendations for cassava grown in this kind of environments.

17

18 A randomized complete block design with three replications per location
19 was used. The evaluation was similar to a split-plot design. Each replication con-
20 tained 45 main plots, one for each of the 45 F₁ crosses of the diallel. Each F₁
21 cross was, therefore, randomly allocated within each replication. Main plots con-
22 tained eight rows with seven plants per row. The first and last rows and the first
23 and last plant within each row were filled with border plants. The rest of the plot

1 (6x5= 30 subplots) was used to plant the experimental material. The 30 clones
2 constituting each F₁ cross were planted together in the respective main plots of
3 each replication. Row-to-row distances and separation of plants within row were
4 1 m for a final plant density of 10000 plants ha⁻¹.

5
6 Trials were harvested in April 2002, ten months after planting (the usual age
7 for harvesting cassava in this environment). Harvest is planned to take place just
8 before the beginning of the rains. Root dry matter content drops drastically with
9 the advent of the rains because the plant uses some of the energy accumulated
10 in the roots to restart growth after the dry period. However, plants cannot be har-
11 vested too early because the vegetative cuttings obtained from them loose
12 sprouting capacity and, therefore, additional evaluation and selection could be
13 hampered. To take advantage of the large number of segregating progenies the
14 results of this study were also used to continue the standard selection process in
15 search of elite clones. Therefore the best performing clones in this diallel analysis
16 were selected and planted in a preliminary yield trial (Ceballos et al., 2004)

17
18 Plants were hand harvested individually and results averaged across the 30
19 clones of each F₁ cross. All the roots produced by each plant were weighted as
20 well as the above ground biomass (stem and foliage). Harvest index was meas-
21 ured as the ratio between root weight and total biomass. Dry matter content in
22 the roots was estimated using the specific gravity methodology (Kawano et al.,
23 1987). Approximately five kilograms of roots were weighed in a hanging scale

1 (WA) and then, the same sample, was weighed with the roots submerged in wa-
2 ter (WW). Dry matter content was estimated utilizing the following formula:

3

$$4 \quad \text{Dry matter content (\%)} = \{ [WA / (WA - WW)] * 158.3 \} - 142$$

5

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

7

8 Reaction to SED and plant type architecture were scored using a 1 to 5
9 scale where 1=resistant or excellent plant type and 5=susceptible or very poor
10 plant type. Plant type score took into consideration several important characteris-
11 tics such as plant vigor, erect architecture with few branches and reduced
12 branching angle, adequate capacity to produce vegetative cuttings, amount of fo-
13 liage present and absence of foliar diseases.

14

15 The analysis of variance follows the method 4 proposed by Griffing (1956).
16 Genotypes and environments were considered fixed and random effects, respec-
17 tively.

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1 **Results**

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

11

12 *Analysis of variance*

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

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2 The sum of squares due to crosses was further partitioned in two orthogon-
3 al components represented by the general (GCA) and specific (SCA) combining
4 ability effects. The proportion of the sum of squares for crosses explained by
5 GCA and SCA effects is an estimation of the relative importance of additive and
6 non-additive effects in the expression of each variable. SCA effects accounted for
7 53 % of the variation due to crosses for fresh root yield, 38% for harvest index
8 and 33% for height of first branching. For the remaining variables non-additive ef-
9 fects accounted for less than 20% of the cross sum of squares. These results are
10 consistent with those observed in two additional diallel studies for the sub-humid
11 and mid-altitude valleys (CIAT, 2003). Across the three studies, SCA accounted
12 for 51% (fresh root yield), 40% (harvest index), 28% (dry matter content), 25%
13 (height of first branching) and 29% (plant type score) of the sum of squares due
14 to crosses (CIAT, 2003).

15

16 *General combining ability effects*

17 General combining ability effects were highly significant ($P \geq 0.01$) for height
18 of first branching and SED score, significant ($P \geq 0.05$) for dry matter content and
19 non-significant for fresh root yield, harvest index and plant type score. Specific
20 combining ability effects were highly significant ($P < 0.01$) for height of first
21 branching and plant type score, significant ($P \geq 0.05$) for dry matter content and
22 SED score, and non-significant for fresh root yield and harvest index. However,
23 the combined analysis for genetic effects should, for most variables, be done in-

1 individually for each location, due to the significance of their respective interactions
2 with the environment, particularly for the GCA effects.

3

4 The best two parents for fresh root yield, across the two locations, were SM
5 2219-11 and CM 4574-7 (Table 2). On the other hand, parent MPER 183 pro-
6 duced clearly mediocre progenies regarding fresh root productivity. SM 1219-9
7 and CM 6740-7 also produced better than average progenies for this trait. The
8 former was also found to be a good parent for the sub-humid environment and
9 the mid-altitude valleys. CM 6740-7 was officially released as a cultivar with the
10 name CORPOICA-REINA in 2001. SM 2219-11 not only had the highest positive
11 GCA effects for fresh root yield, but also for harvest index (0.042) and positive
12 GCA effects (but not the highest) for dry matter content in the roots (0.485).
13 Moreover, the progeny from this clone had a good performance with low scores
14 for SED (-0.205) and plant type (-0.147). Its progeny tended to have a high first
15 branching (0.158), which is generally a desirable trait.

16

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

23

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

5
6 In the analysis of individual locations the GCA effects for fresh root yield
7 from the *Loma* field were highly significant. SM 2219-11 showed the highest posi-
8 tive value, which was also found for the *Porcinos* field (Table 2). CM 4574-7 and
9 SM 1565-15 also showed significant positive GCA effects for fresh root yield. SM
10 1565-15, however, showed the lowest value at the *Porcinos* field. It is clear that
11 progenies from this particular clone have good adaptation to the more limiting
12 conditions to the typical acid-soil savannas, which agrees with previous findings
13 (CIAT, 2003) but cannot compete successfully in the better conditions at *Porci-*
14 *nos* field. MPER 183 had negative GCA effects, and in the case of the results
15 from the *Loma* field, it was the lowest among all parents.

16
17 The GCA effects for harvest index of SM 2219-11 were the highest at both
18 locations. The better adaptation of SM 1565-15 to the conditions represented by
19 the *Loma* field is also reflected in the case of harvest index with the third highest
20 value, a sharp contrast with that from *Porcinos* field, which was the lowest among
21 the ten parents. MPER 183 had negative GCA effects for harvest index at both
22 locations, with the one from the *Loma* field being the lowest among all parents.

23

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

13

14 GCA effects for plant type score identified CM 4574-7 as one of the best
15 parents with negative values for both environments, particularly for the *Loma*
16 field. CM 6740-7 and SM 2219-11 also showed good GCA effects for plant type
17 at both locations. Clone SM 1565-15 showed again a particular adaptation to the
18 savannas conditions represented by the *Loma* field, with a significantly negative
19 GCA effect which contrasted with that from the *Porcinos* field, which was positive
20 (although not statistically different from zero). In general, good (negative) GCA
21 effects for plant type was associated with positive ones for height of first branch-
22 ing. Farmers generally prefer an erect, non-branching architecture because it fa-
23 cilitates cultural practices after the third-fourth month of grow and the production

1 and handling of the planting materials is facilitated. A first branching high above
2 the ground also results in a more erect type.

3

4 *Specific combining ability effects*

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

18

19 In the case of resistance to super elongation disease, on the other hand,
20 the lowest ratings were not necessarily associated with negative SCA effects with
21 the exception of the first cross (CM 4574-7 x CM 6740-7) which showed the low-
22 est SCA effect. It is reasonable, therefore to assume that for this trait additive ra-
23 ther than non-additive effects would control most of the reaction to the disease.

1 These results reinforce those obtained from the analysis of variance in Table 1,
2 where SCA accounted for less than 20% of the sum of squares due to crosses.
3 The correlation coefficient between average SED score performance for the F1
4 crosses and their respective SCA effects was 0.37, much lower than that found
5 for fresh root yield.

6

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

14

15 *Phenotypic correlations between evaluated traits*

16 Table 4 presents the phenotypic correlation coefficients among the aver-
17 ages of the 45 crosses analyzed in this study. As expected, negative correlations
18 ($\rho < -0.70$) were observed between SED score and root and foliage yields as well
19 as for dry matter content. It should be pointed out that lower scores for SED
20 meant better (resistant) reaction to the disease. SED was also negatively asso-
21 ciated with harvest index ($\rho = -0.61$). Positive correlation coefficients were also
22 found for SED score and plant and root scores. This was also expected because

1 in these variables a lower value represented better phenotypes as in the case of
2 the SED score.

3

4 The height of the first branch showed a high correlation coefficient ($\rho = -$
5 0.79) only with plant type score. In general, however, a high first branching
6 tended to have higher root and foliage yields (correlation coefficients of 0.38 and
7 0.40, respectively). In addition to the correlations already mentioned, fresh root
8 yield showed a highly positive coefficient with harvest index ($\rho = 0.73$) and nega-
9 tive ones with plant ($\rho = -0.52$) and root type ($\rho = -0.84$) scores.

10

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

17

18 **Discussion**

19 Mean fresh root yield across the experiment was 20.4 t ha^{-1} , but was considera-
20 bly higher in the *Porcinos* (36.1 t ha^{-1}) than in the *Loma* field (12.4 t ha^{-1}). Several
21 families, however, showed mean productivities across the two environments
22 above 25 t ha^{-1} , illustrating the excellent productivity of this crop, even in the limit-
23 ing conditions of the *Loma* field. It should be emphasized that these are averages

1 across the 30 clones representing each F1 family. The performance of the best
2 clones within each family offers even wider ranges of variations. It is the perfor-
3 mance of the individual clone that cassava breeders are most interested in.

4

5 The results of this study indicate a large influence of genotype by environ-
6 ment interactions, which are particularly problematic in the case of cassava.
7 These effects were highly significant for all the variables analyzed in the two loca-
8 tions. Because the low multiplicative rate of cassava's planting material, it takes
9 several years until the first multi-location trial can be conducted (Ceballos et al.,
10 2004; Jennings & Iglesias, 2002). This implies that a large proportion of the se-
11 lection process is affected by the lack of replication in different environments.
12 One alternative would be to split the first clonal evaluation (Ceballos et al., 2004),
13 which is typically based on 6-8 plants, in two locations (where each clone would
14 be represented by 3-4 plants). Harvest index has been successfully used to
15 overcome some of the problems related to interfamily competition in the first
16 clonal evaluation stages (Kawano et al., 1998; Kawano 2003) when not enough
17 planting material is available for replicated trials. Harvest index, however, also
18 showed highly significant genotype by environment effects suggesting that even
19 this variable is also very much influenced by this interaction. The use of border
20 rows is not feasible in the large clonal evaluation trials because it would double
21 the size of an already large trial. The approach currently used by CIAT to reduce
22 interfamily competition in these trials is to widen row-to-row distance (from 1.0 to
23 1.2 m) and reduce plant-to-plant spacing within the row (from 1.0 to 0.8 m). This

1 layout increases within-row competition and reduces the between-row one, while
2 maintaining the overall plant density almost unchanged.

3

4 Another important conclusion from this study is the unexpectedly high role
5 that SCA effects had for fresh root yield. SCA effects accounted for more than
6 half of the crosses sum of squares for this variable. Non-additive effects also ex-
7 plained a considerable proportion of the cross sum of squares for harvest index
8 and height of first branch and had little influence in dry matter content, SED and
9 plant type score.

10

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

19

20

21 **Acknowledgments:**

22 This research was conducted with the partial support of the Ministerio de Agricul-
23 tura y Desarrollo Rural of Colombia.

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1 Table 1. Mean squares from the analysis of variance, combined across locations,
 2 for the diallel study from ten parental cassava clones evaluated in two soil
 3 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 1 st branching (m)	SED ^a score (1-5)	Plant type (1-5)
Locations (L)	1	172.8**	0.232	144.25	680.48**	n.a. ^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 x L	44	0.5**	0.008**	5.82**	2.35**	-	0.374**
GCA x L	9	1.2**	0.022**	21.27**	4.27**	-	1.578**
SCA x 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

4 ^a SED: Super elongation disease evaluated only at *Loma* plot. * Significant at the P < 0.05 proba-
 5 bility level ** significant at P < 0.01 probability level. ^b CV = Coefficient of variability; ^c SS = sum
 6 of squares.

1 Table 2. General combining ability effects, combined across locations, for the di-
 2 allele study from ten parental cassava clones evaluated in two soil condi-
 3 tions in Meta Department, Colombia.

Parental clone or parameter	Fresh root yield kg pl ⁻¹	Harvest Index (0-1)	Dry matter content (%)	Height 1 st branching (m)	SED score (1-5) ^a	Plant type (1-5) ^a
<i>Combined across locations</i>						
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
<i>Loma field</i>						
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
<i>Porcinos field</i>						
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

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

1 Table 3. Averages and specific combining ability effects (SCA), combined across
 2 locations, for the most relevant traits in the diallel study evaluated in the
 3 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 x 2	25.90	2.98	0.44	0.046	32.7	0.327	2.3	-0.418
1 x 3	19.99	-1.14	0.38	-0.015	31.3	-0.597	2.2	0.007
1 x 4	23.53	0.36	0.43	-0.001	32.6	-0.316	2.4	-0.113
1 x 5	17.82	-3.70	0.37	-0.032	34.4	0.731	2.2	0.068
1 x 6	25.39	2.46	0.43	0.024	31.5	-0.422	2.6	0.205
1 x 7	26.50	1.53	0.45	0.007	31.8	-1.014	2.6	0.286
1 x 8	16.24	-4.69	0.37	-0.048	32.3	0.152	2.5	-0.139
1 x 9	21.49	2.51	0.38	0.047	31.0	1.647	3.2	-0.030
1 x 10	21.27	-0.31	0.38	-0.029	32.4	-0.508	3.0	0.135
2 x 3	19.12	-0.94	0.37	-0.024	31.7	0.766	3.0	0.160
2 x 4	18.59	-3.50	0.37	-0.060	31.5	-0.498	3.3	0.223
2 x 5	21.38	0.93	0.40	-0.001	33.9	1.189	2.5	-0.295
2 x 6	22.63	0.78	0.43	0.022	30.6	-0.340	2.9	-0.038
2 x 7	24.96	1.07	0.45	0.010	32.3	0.427	3.1	0.190
2 x 8	17.39	-2.46	0.38	-0.030	30.0	-1.229	3.5	0.281
2 x 9	16.83	-1.08	0.32	-0.006	27.3	-1.097	3.9	-0.010
2 x 10	22.73	2.22	0.45	0.043	32.4	0.454	3.4	-0.093
3 x 4	21.52	1.22	0.46	0.036	32.3	0.832	2.4	-0.167
3 x 5	19.80	1.14	0.38	-0.019	32.5	0.290	2.2	-0.021
3 x 6	21.77	1.71	0.39	-0.021	30.0	-0.415	2.7	0.225
3 x 7	18.94	-3.17	0.42	-0.022	30.5	-0.825	2.4	-0.031
3 x 8	17.11	-0.95	0.40	-0.018	30.2	-0.521	2.7	-0.095
3 x 9	18.72	2.60	0.36	0.029	28.8	0.905	3.5	0.081
3 x 10	18.25	-0.47	0.46	0.053	31.0	-0.434	2.8	-0.160
4 x 5	21.89	1.19	0.42	-0.010	32.1	-1.133	3.0	0.445
4 x 6	21.50	-0.59	0.40	-0.037	31.2	-0.307	3.1	0.307
4 x 7	25.13	0.99	0.50	0.029	32.5	0.131	2.6	-0.156
4 x 8	18.68	-1.42	0.46	0.011	32.6	0.904	2.8	-0.236
4 x 9	17.13	-1.02	0.37	0.007	28.9	0.051	3.5	-0.248
4 x 10	23.52	2.77	0.46	0.023	32.8	0.337	3.2	-0.055
5 x 6	19.59	-0.87	0.42	0.005	33.1	0.896	2.3	-0.160
5 x 7	20.61	-1.88	0.46	0.012	33.0	-0.086	2.2	-0.185
5 x 8	22.76	4.31	0.46	0.047	32.4	-0.103	2.9	0.184
5 x 9	18.68	2.16	0.36	0.031	28.7	-0.931	3.3	-0.023
5 x 10	15.83	-3.28	0.38	-0.035	32.3	-0.853	2.9	-0.013
6 x 7	18.62	-5.27	0.44	-0.014	30.7	-0.671	2.6	0.052
6 x 8	21.08	1.23	0.43	0.008	31.9	1.110	2.5	-0.413
6 x 9	18.25	0.34	0.35	0.014	27.7	-0.190	3.5	-0.125
6 x 10	20.74	0.23	0.42	-0.002	31.8	0.337	3.1	-0.054
7 x 8	26.53	4.63	0.48	0.014	31.7	-0.006	2.7	-0.132
7 x 9	19.06	-0.89	0.34	-0.034	29.7	0.869	3.5	0.006
7 x 10	25.54	2.99	0.45	-0.002	33.5	1.175	3.1	-0.030
8 x 9	15.35	-0.56	0.34	-0.010	27.7	-0.528	4.2	0.315
8 x 10	18.43	-0.09	0.45	0.026	31.9	0.220	3.7	0.236
9 x 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

4 ^a Codes for identifying the parents at top of Table 2; ^b SED evaluated only at *Loma* plot; ^c Standard
 5 deviation for S_{ij}; ^d Standard deviation for (S_{ij}-S_{ik}).
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1 Table 4. Phenotypic correlations from the averages, combined across locations,
 2 for the most relevant traits in the diallel study evaluated in the acid-soil
 3 conditions of eastern savannas of Colombia.

	SED score (1-5)	Height 1 st 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 1 st 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

4 * Significant at the P < 0.05 probability level ** significant at P < 0.01 probability level.