Reprinted from *Crop Science*
Vol. 27, No. 1

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ABSTRACT

Genetic and environmental variabilities of root dry matter content (RDMC) of cassava (*Manihot esculenta* Crantz) clones (accessions and breeding lines) were estimated at different harvest months (8 or 12 months), seasons (wet and dry), and locations (three altitudes). To assess the possibility of obtaining higher dry matter yield through selection for RDMC, genetic studies based on F_1 variability and parents-offspring regressions also were conducted. Age of plant, season, and location significantly affected root dry matter content. Temperature appeared to be an important factor related to the effect of location. The highest RDMC was obtained with 8 month-old plants harvested at the beginning of the dry season in the high altitude location, while the lowest occurred with 12-month-old plants harvested at the beginning of the wet season at the low altitude location. The clone effect was highly significant and a broad-sense heritability of 0.87 was obtained. Clone × location interaction was also significant, but the magnitude of this effect was much smaller than that of the clone effect. Genetic analyses suggested that inheritance of RDMC was controlled mainly by polygenic additive factors. Narrow-sense heritabilities ranging from 0.51 to 0.67 were obtained. There was no indication of negative response in root dry matter content after intensive mass selection for root fresh yield. The data indicate that RDMC can be increased by simple breeding techniques such as phenotypic mass selection. Selection of clones at one location was largely valid for other locations; however, final selection should be made at each specific location for maximum potential gain.

***Additional index words:* *Manihot esculenta* Crantz, Selection, Heritability, Genotype × environment interaction, Starch.**

CASSAVA (*Manihot esculenta* Crantz) is one of the most important calorie-producing crops in the tropics. It is efficient in carbohydrate production, adapted to a wide range of environments, and tolerant to drought and acid soils (Jones, 1959; Rogers and Appan, 1970; Cock and Rosas, 1975; Kawano et al., 1978; Cock, 1985). The major portion of the economic product, cassava roots, is consumed as human food, both processed and unprocessed.

The potential for genetic improvement of the crop has been demonstrated, and considerable progress has been made in increasing yield potential and stability (CIAT, 1977, 1978, 1981; Kawano et al., 1978). Cassava root yield traditionally is expressed as fresh weight; however significant varietal differences exist in root dry matter content (RDMC) (CIAT, 1975, 1976). Consequently, relatively little attention has been paid to genetic improvement of RDMC for an increased total calorie yield.

Fresh root yields of up to 80 t/ha per year with experiment station conditions and up to 60 t/ha per year under farm conditions have been reported, while RDMC varied from 20 to 40% (CIAT, 1978, 1979, 1980). On the average, about 90% of root dry matter is carbohydrates with 4% crude fiber, 3% ash, 2% crude protein, and 1% fat (Holleman and Aten, 1956; Barrios and Bressani, 1967; Lim, 1968). Root dry matter content is believed to be positively correlated with eating quality when the root is consumed after boiling. Moreover, most processing is oriented to reducing the moisture content of the root and recovering the starch in one form or another. Increasing dry matter content would thus improve the extraction efficiency of industrial processing and, because price differentials for roots are usually paid on the basis of dry matter content, it would increase farm incomes.

We measured RDMC of cassava clones in different environmental conditions and observed its genetic behavior. The objective of this work was to examine the genetic and environmental variability of root dry matter content, and to assess the possibility of obtaining higher dry matter yield through selection for RDMC.

MATERIALS AND METHODS

Experimental Sites. The CIAT Experiment Station is located in the medium altitude plateau in the Department of Valle, Colombia. The climate in Valle is usually characterized by two short dry seasons with relatively well-distributed rainfall, however, a departure from this general pattern occasionally occurs. The soils are generally fertile.

Carimagua Experiment Station, operated by the Instituto Colombiano Agropecuario (ICA) and CIAT, is located in the middle of the LLanos Orientales in the Department of Meta, Colombia. The soils are extremely poor, and the climate is characterized by pronounced dry and wet seasons.

Caribia Experiment Station, also operated by ICA, is located on the northern coast in the Department of Magdalena, Colombia. The soils are medium to high in fertility, and the climate is characterized by a moderate wet season, followed by a long dry season.

Climatic and edaphic data for the three locations are presented in Table 1. In general, CIAT, Carimagua, and Caribia represent high, low, and medium yielding environments, respectively, for cassava production. The genotype × environment experiment was conducted in these three stations. All the other field experiments were conducted at the CIAT station.

Genotype × Environment Experiment. Eight germplasm accessions and breeding lines (Llanera, M Col 22, M Col

Table 1. Climatic and edaphic data for three experimental sites.

	CIAT	Carimagua	Caribia
Altitude (m)	1000	200	50
Annual avg temperature (°C)	24	26.5	28
Annual precipitation (mm)	900–1200	1800–2600	1150–1450
Length of dry season (months with less than 50 mm rainfall)	2–4 (twice)	4	5
Soil pH	7.4–7.8	4.1–4.7	6.2–6.8
Soil organic matter (%)	6.8	4.3	2.1
P (Bray II) (mg/kg)	45–55	1–2	69–114
K [cmol(K^+)/kg]	0.44	0.08	0.16
Al (% sat)	0	85	0
Al [cmol(⅓Al^{3+})/kg]	0	3.5	0
Soil texture	Clay	Clay loam	Sandy loam

[1] Contribution from the Centro Internacional de Agricultura Tropical (CIAT), A.A. 67-13, Cali, Colombia. Received 6 Mar. 1986.

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Published in *Crop Sci.* 27:69–74 (1987).

1468, M Col 1684, CM 342-170, CM 507-37, CM 523-7, and CM 728-2) were planted in yield trials at the three experimental sites, following the method established by the CIAT cassava breeding program (Kawano et al., 1978). The planting and harvesting times were adjusted such that harvests at 8 and 12 months after planting corresponded to the beginning of the wet season or the beginning of dry season, at each site (Fig. 1). Neither irrigation nor application of fungicide or pesticide was made at any experimental site. A total of 500 kg/ha of dolomitic lime, 75 kg/ha N, 150 kg/ha P_2O_5 and K_2O, and 10 kg/ha Zn were applied only to the experiments at Carimagua. Each clonal plot was 5 × 6 m in size in which cassava stem cuttings were planted at 1- × 1-m distance. Each yield trial had two replications. Root samples for determining dry matter content were taken from the inside plants in each clonal plot for each replication, age (8 and 12 months), season (wet and dry), and location.

Genetic Study. Fifty-six unselected F_1 hybrid clones from a cross between M Col 22 and M Ven 270 (moderately high × high RDMC) and 133 F_1 clones from a cross between M Col 22 and M Mex 59 (moderately high × low) were planted in an unreplicated single-row trial at CIAT in May 1975. Five 20-cm stem cuttings of each clone were planted in each of 189 rows. The planting distance was 1 m between plants and 2 m between rows. Twelve rows of each of the three parental clones, for a total of 36 control rows, were also planted in four replications. A year later, the three inside plants in each row were harvested.

A total of 435 unselected F_1 clones from 37 crosses were planted in the same manner. These clones included a wide variation of root dry matter content in their parentage, and each cross was represented by at least six unselected F_1 clones. Three rows of each parental clone were also planted in three replications. Similar trials with different set of crosses were continued in succeeding years, consisting of 32 crosses in 1976, 45 in 1977, 25 in 1978, 23 in 1979, and 30 in 1980.

Selection. One-thousand eight-hundred and fifty cassava accessions collected throughout Latin America were planted in a single-row trial in May 1973 (Yield Trial 1). Five 20-cm stem cuttings per accession were planted in each row. The planting distance was 1 m between plants and 1.4 m between rows. Twelve months after planting, the three inside plants were harvested, and fresh root yield, harvest index (root fresh weight/total plant fresh weight), and RDMC were determined.

Based on harvest index and root fresh yield, 230 accessions were selected and further evaluated in a yield trial planted in November 1974 (Yield Trial 2), following the same procedure as for the genotype × environment experiment (Kawano et al., 1978).

Based on root fresh yield and harvest index, superior clones were selected from every yield trial as parents for the hybridization program. The resulting F_1 hybrid progenies were selected through F_1 seedling trials and single-row trials. Selected clones were planted in yield trials and superior clones were recycled in hybridization, selection, and yield trials. This cycle was continued until the May 1980 planting of Yield Trial 12 in which a total of 286 selected hybrid clones were evaluated in the same manner as described above.

In all the yield trials, six relatively high-yielding accessions (Llanera, M Col 22, M Col 113, M Col 1468, M Col 1684, and M Ven 218) were included as controls.

All the experiments described here were part of a comprehensive breeding program, and a complete randomization of entries in yield trials was not made. However, the six control entries were randomized in each experiment with

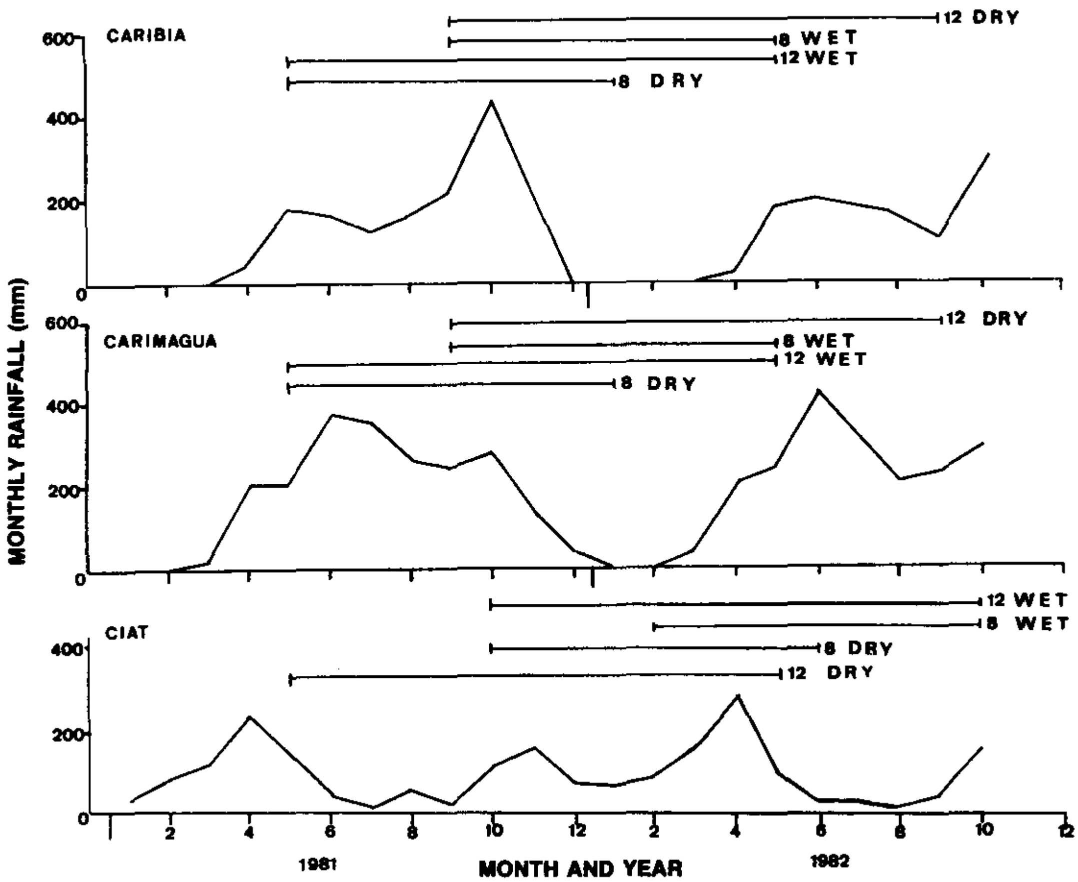

Fig. 1. Monthly rainfall and dates of plantings and harvests of genotype × environment experiments at three locations. (Harvest month, 8 or 12; and season, dry or wet, are indicated at each harvest).

Table 2. Starch, carbohydrate, and dry matter content in cassava root parts of 20 germplasm accessions.

Part of root	Mean ± SD†
	%
Parenchyma	
Starch	31.0 ± 3.1
Soluble carbohydate	34.1 ± 3.0
Dry matter	37.7 ± 2.4
Peel	
Starch	17.1 ± 2.1
Soluble carbohydrate	19.4 ± 2.1
Dry matter	24.2 ± 1.9
Whole root	
Starch	28.5 ± 2.7
Soluble carbohydrate	31.5 ± 2.6
Dry matter	35.3 ± 2.4
Peel/Whole root fresh weight	18.1 ± 2.3

† Based on variation among clone means.

two to four replications. All the breeding lines in yield trials were planted with two replications.

Measurement of Root Dry Matter Content. Eight bulked 12-month-old roots were sampled at harvest from each of 38 accessions randomly selected from a yield trial in May 1975, 16 hybrid clones in November 1975, and 25 hybrid clones in May 1976. Specific gravity of each sample (of the whole root, including the peel) was determined from the weights in air and in water. The same samples were chopped, sliced, dried in a forced-air drying oven at 70°C for 3 days, and weighed. Root dry matter content obtained from fresh and dry root weight was regressed on the root specific gravity. The resulting regression equation was used to estimate RDMC of several thousand samples evaluated in this study.

Determination of Components of Root Dry Matter. Eight bulked roots, from each of 20 moderate to high-yielding germplasm accessions with different RDMC, were sampled in two replications after the November 1975 harvest (Yield Trial 2). The sampled roots were separated into parenchymas and peels, then analyzed for dry matter content, soluble carbohydrates, and starch, using the methods described by Moretzki et al. (1966) and Yoshida et al. (1972).

RESULTS AND DISCUSSION

Components of Root Dry Matter. The peel comprised about 18% of the fresh weight of the root (Table 2). Starch, soluble carbohydrate, and dry matter contents were much higher in the parenchyma than in the peel. Dry matter content of the whole root seems to

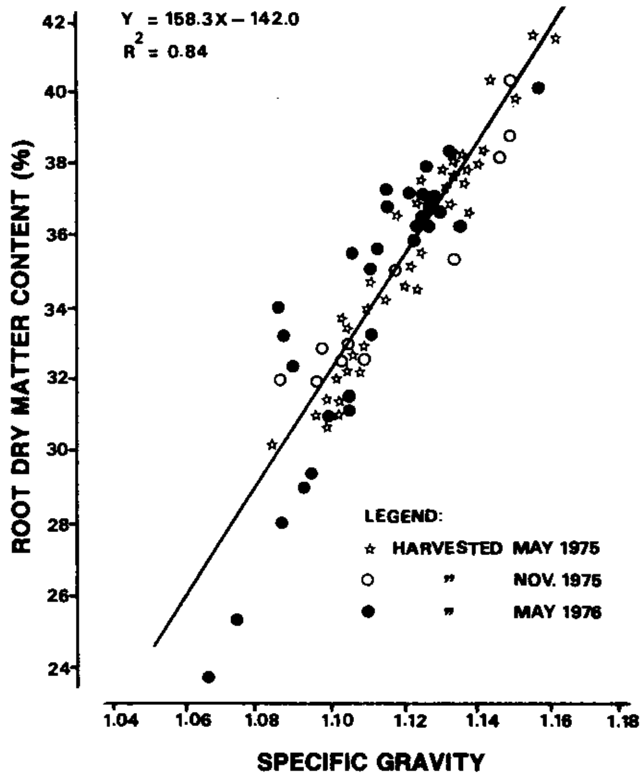

Fig. 2. Regression of RDMC on root specific gravity.

be the most recommendable unit for field studies because it is the simplest to define and measure.

Regression on Root Specific Gravity. Regression of RDMC on specific gravity was highly significant in each harvest, and the regressions of different harvests did not differ (Fig. 2). Thus, the common regression equation $Y = 158.3X - 142.0$ ($r^2 = 0.84$), where Y represents the percentage of RDMC and X is the root specific gravity, was used to estimate RDMC from the root specific gravity measurements taken in other samples.

Our regression equation was nearly indentical to those obtained by Grossman and Freitas (1950), Keating et al. (1981), and Umemura et al. (1983) in their studies of the relationship between cassava RDMC and specific gravity in Brazil, Austrialia, and Thailand,

Table 3. Root dry matter content (%) of eight clones harvested at different locations, harvest months, and seasons.

	Location												
	CIAT-Palmira				Carimagua				Caribia				
	Harvest month												
	8		12		8		12		8		12		
	Season												
Clone	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Mean
	%												
Llanera	30.8	31.8	26.4	30.6	30.3	35.8	33.0	32.3	29.1	28.9	24.3	30.7	30.3
M Col 22	34.5	35.6	27.1	32.0	28.2	30.6	30.5	30.6	32.6	33.8	28.9	31.4	31.3
M Col 1468	28.8	33.8	30.1	27.5	28.4	27.7	19.5	28.9	27.8	26.0	20.2	29.1	27.3
M Co. 1684	32.1	32.5	28.1	29.2	27.8	29.1	27.6	29.3	30.2	34.1	29.2	32.0	30.1
CM 342-170	35.0	35.4	28.6	33.4	29.2	31.8	26.6	28.1	29.3	32.3	27.7	29.1	30.5
CM 507-37	30.1	30.5	27.8	30.0	28.1	33.7	31.4	32.0	29.1	31.0	26.1	30.7	30.0
CM 523-7	37.1	37.8	34.6	37.4	33.2	32.7	33.8	35.5	34.2	35.4	31.4	30.2	34.4
CM 728-2	29.7	32.7	29.2	31.2	29.0	32.6	28.3	31.0	29.5	32.4	26.6	30.9	30.3
Avg	32.3	33.8	29.0	31.4	29.3	31.8	28.8	31.0	30.2	31.7	26.8	30.5	30.5
LSD (0.05) = 2.62													

† Wet = beginning of wet season; dry = beginning of dry season.

Table 4. Root dry matter content at different harvest month, seasons, and locations.

	Harvest month						
	8			12			
	Season			Season			
	Wet	Dry	Mean	Wet	Dry	Mean	Grand mean
	%						
Location							
CIAT	32.3	33.8	33.1	29.0	31.4	30.2	31.6
Carimagua	29.3	31.8	30.6	28.8	31.0	29.9	30.2
Caribia	30.2	31.7	31.0	26.8	30.5	28.7	29.8
Avg	30.6	32.4	31.6	28.2	31.0	29.6	30.5
Season							
Wet							29.4
Dry							31.7

† Wet = beginning of wet season; dry = beginning of dry season.

respectively. The estimation of root dry matter from specific gravity measurement may have a universal application in cassava.

Genotype × Environment Interaction. Root dry matter content varied from 20 to 38% depending on clone and environment (Table 3). In all locations RDMC tended to be higher at 8 rather than at 12 months after planting, and higher at the beginning of the dry season rather than the beginning of the wet season. The CIAT location gave the highest RDMC, followed by Carimagua and Caribia (Table 4). An analysis of variance indicated that the effects of clone, location, month of harvest, and season were highly significant. The interactions between clone and location, and between location and month of harvest were also statistically significant but the magnitude of these effects was much smaller compared with that of clone,

Table 5. Heritability of RDMC based on parent-offspring regression.

Year of planting	No. of crosses included	Heritability (*b*)
1975	37	0.62**
1976	32	0.63**
1977	45	0.51**
1978	25	0.59**
1979	23	0.63**
1980	30	0.67**

** Significant at the 0.01 probability level.

Table 6. Comparison of fresh root yield and RDMC between two trials.

	Yield trial no.	
	1	12
Planting date	May 1973	April 1980
Kind of clones	Unselected germplasm accessions	Selected hybrid clones
No. of clones	1850	286
	Mean ± SD	
Fresh root yield of controls (t/ha)	36.8 ± 4.2†	31.8 ± 4.1†
Fresh root yield of all entries (t/ha)	25.2 ± 14.4‡	45.2 ± 10.2‡
Root dry matter content of controls (%)	35.5 ± 1.8†	32.2 ± 1.5†
Root dry matter content of all entries (%)	35.4 ± 4.4‡	33.0 ± 2.9‡
	r	
Correlation coefficient between root fresh yield and RDMC§	0.295	0.234

† Standard deviation based on variation within clone (nongenetic variation).
‡ Standard deviation based on variation among clonal means (genetic and nongenetic variation).
§ Phenotypic correlation.

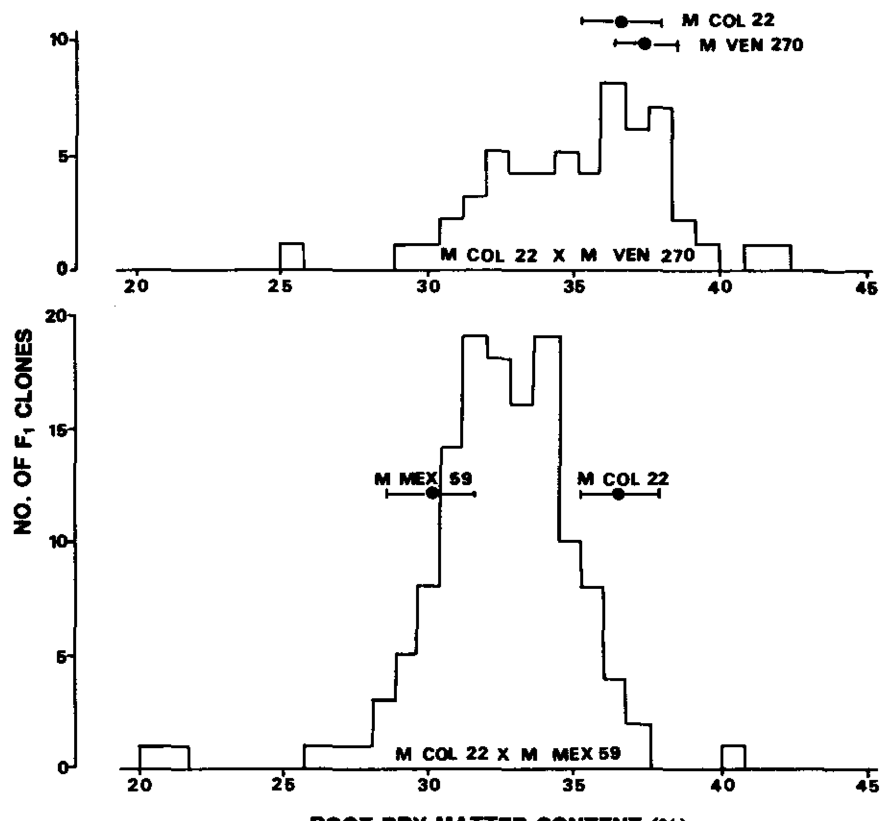

Fig. 3. Segregation of two crosses (F_1 populations) for RDMC. (Parental values are indicated with standard deviation).

location, or month of harvest alone. Other interactions were not statistically significant.

Temperature is reported to be inversely related to RDMC, within a certain temperature range (CIAT, 1978; Irikura et al., 1979). Thus, the lower average temperature at CIAT may be the primary factor for higher RDMC there than at the other locations (Table 1). Resumption of growth, using stored carbohydrate that occurs after a long dry season, may be the main reason for low RDMC in the beginning of the wet season.

The highly significant clone effect indicates that RDMC is a relatively stable character and that selection at one environment would be largely effective for other environments. From the variance analysis, a broad-sense heritability estimate of 0.87 was obtained for the clonal mean. However, the existence of clone × location interaction, though small in magnitude, suggests that final selection has to be made at each location.

Genetic Study at CIAT. The F_1 clones from crosses between M Col 22 and M Ven 270, and between M Col 22 and M Mex 59 showed a wide variation in RDMC (Fig. 3).

Regressions of F_1 means on midparent value, in RDMC, were highly significant in all the trials (Table 5, Fig. 4). A parent offspring regression coefficient gives an estimate for heritability based on the relative effect of additive genetic factors or narrow-sense heritability. Heritability estimates thus calculated were from 0.51 to 0.67. Because the parents and offspring were evaluated in the same environment, these heritabilities are probably biased upward due to correlations of errors.

Selection. The average yield of all germplasm accessions was 25 t/ha of fresh weight with 35% dry matter content (Table 6, Trial 1). With selection for harvest index and root fresh yield, average yield increased gradually from 1973 to 1980 (Fig. 5). Neither 1973–1974 nor 1980–1981 were exceptional years in climatic terms, nevertheless, average fresh yields of the later

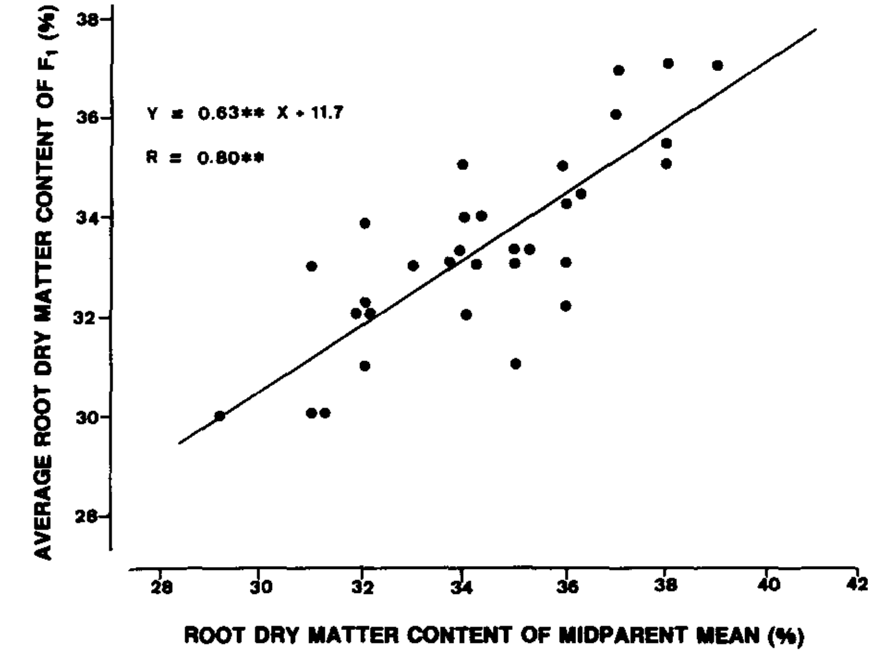

Fig. 4. Regression of F_1 mean on midparent value for RDMC. (May 1977 harvest).

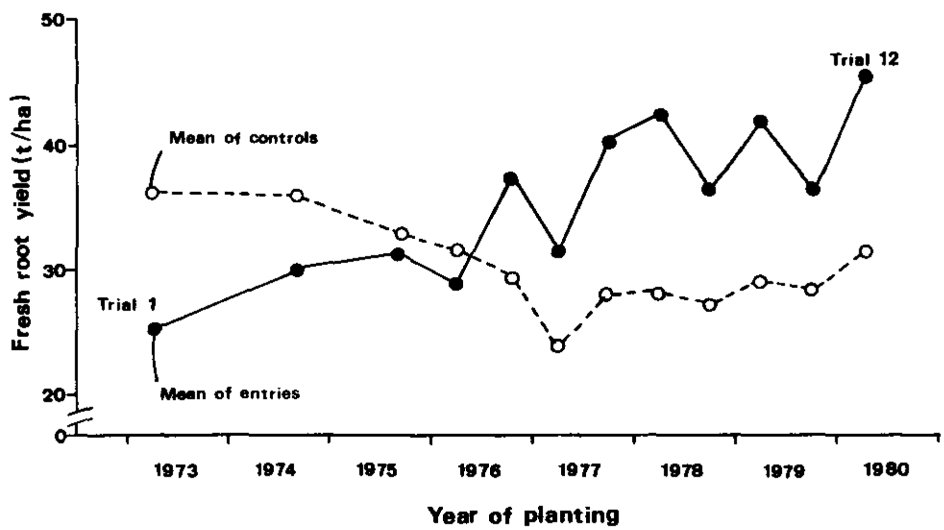

Fig. 5. Change in means of varietal entries and controls in selection trials from 1973–1974 to 1980–1981 cropping year at CIAT.

trials (for example, Trial 12, Table 6) were much higher than those of the earlier ones. This suggests that the yield level of the later population was 80% higher than that of the original germplasm accessions.

The average RDMC of the population and the controls tended to decrease slightly from 1973 to 1980; however, the change was not significant. This may indicate that the relative RDMC of breeding population did not decline during selection (Table 6).

One of the major selection effects during the early years was the elimination of low-yielding or low-dry-matter accessions. The genetic variability in these characters was somewhat reduced, although considerable genetic variability remained in the later cycles (Table 6).

In the original germplasm population, root fresh yield was not negatively correlated with RDMC (Table 6). This absence of negative correlation persisted in the later population.

Root dry matter yield is the product of root fresh yield and RDMC. Root fresh yield and dry matter content become competing components and a negative correlation should arise between them when the assimilation by the crop reaches physiological ceiling and the variability in dry matter yield becomes limited (Kawano and Takahashi, 1968). The fact that there is no indication of negative correlation between fresh yield and dry matter content suggests that a yield plateau has not been reached, and that selection for either RDMC or fresh root yield may not necessarily lead to a negative response in the other.

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