GENETIC IMPROVEMENT OF CASSAVA (*Manihot esculenta* Crantz) FOR PRODUCTIVITY

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Cassava (*Manihot esculenta* Crantz) is one of the most important calorie producing crops in the tropics. It accounts for 54% of tropical root and tuber acreage and covers 57% of root and tuber production (FAO, 1971). Nestel (1974) calculated that approximately 300 million people in the tropics depend on cassava as a major source of their calorie intake. According to a World Bank analysis (Anon, 1976), nearly a third of the world population or 75% of the population of underdeveloped countries in the tropics suffers from simple calorie deficiency. Cassava's high calorie yield per hectare therefore makes it a primary means of relieving this food deficit (Nestel, 1973). Furthermore, cassava has important uses as an animal feed and in starch and alcohol production. The demand for cassava as an animal feed is expected to rise rapidly in an attempt to expand the production of animal protein in the tropics (Phillips, 1974). Cassava is widely believed to be highly efficient in carbohydrate production, adapted to a wide range of environmental diversity and tolerant to drought and acid soils. The potential of cassava in tropical agriculture has attracted attention within and outside the tropics (de Vries, Ferwerda and Flach, 1967; Martin, 1970; Nojima and Hirose, 1977).

Limited research has been conducted on cassava despite its importance. Cassava yields of up to 50 ton/ha (fresh weight) are occasionally reported under experimental conditions (Arraudeu, 1969) but farmer's yields are usually from 10 to 15 ton/ha. A world center for cassava research has been established at CIAT with the objective of providing a technical package based on improved germplasm to increase the efficiency of cassava production.

CIAT's cassava breeding program aims to obtain new genotypes that give the maximum calorie yield per unit area per unit time over a wide range of environmental conditions. I define a genetic improvement program for major food crops as a research effort designed to reach the maximum level of productivity by genetically modifying the plant structure and protecting this high level of productivity from yield-reducing factors. We are on the way to upgrading cassava germplasm to its maximum productivity level. The importance of breeding work against yield reducing factors such as disease and insect resistances and tolerances to special soil problems should not be neglected. However, in recent years, our primary interest has been to realize the highest yield potential of cassava. For these reasons, the present paper deals with the methodology of cassava breeding for higher productivity.

Botanical characteristics related to breeding work

The chromosome number of *Manihot esculenta* is 36 and the species is generally regarded as an allotetraploid (Umanah and Hartman, 1972). Cassava is a highly heterozygous species (CIAT, 1975; Kawano *et al*, in press) and this heterozygosity is easily maintained through vegetative propagation.

Both cross-pollination and self-pollination occur naturally. The proportion of cross-pollination depends on the flowering habit of the genotypes and the physical arrangement of the population (CIAT, 1975; Kawano *et al*, in press). Cassava is a monoecius species with the stigma and anther usually separated in different flowers on the same plant. The male and

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Table 1. Comparison between self-pollinated offspring (S_1) and parents. *

	No. of S_1 genotypes	Yield (k/plant)		Total plant (k/plant)		Harvest index		Plant height (m)	
		S_1	Parent	S_1	Parent	S_1	Parent	S_1	Parent
Llanera	9	1.9	4.5	4.1	8.7	.32	.52	1.67	1.82
M Col 9	6	0.9	4.0	4.7	12.6	.20	.32	1.64	2.43
M Col 51	23	1.3	3.0	2.8	5.1	.52	.60	1.40	1.67
M Col 173	20	1.3	2.6	5.6	8.2	.21	.31	2.72	2.77
M Col 340	26	1.8	4.8	6.5	12.0	.28	.40	1.78	2.30
MCol 562	14	1.6	3.2	3.7	7.5	.41	.50	1.82	2.30
M Col 647	36	2.0	4.0	4.4	9.8	.45	.40	1.58	2.30
M Col 667	5	0.6	4.8	1.6	11.0	.38	.44	1.52	2.80
M Col 688	10	2.5	4.2	5.3	7.8	.45	.53	2.14	2.43
M Col 971	15	3.8	3.1	9.5	5.4	.40	.57	1.97	1.50
Extranjera	12	1.4	2.9	3.2	7.7	.41	.38	1.43	2.43
M Ven 179	16	1.4	3.5	5.4	13.4	.44	.25	2.00	2.00
Average		1.71	3.72	4.73	9.10	.373	.466	1.81	2.23

* Data from single-row trials (2m between genotypes, 1m between plants of the same genotype, average of 3 plants per genotype).

female flowers almost never open simultaneously on the same branch; however, it is common that the female flowers and the male flowers on different branches of the same plant open at the same time. There is no physiological or genetic mechanism to prevent self-pollination and cross-incompatibility has not been found up to now.

Strong inbreeding depression has been observed in characters such as root yield and total plant weight (Table 1). This strong inbreeding depression, in addition to the vegetatively propagated nature of the species, is the biological mechanism through which the high heterozygosity of the species is maintained. Male-sterility is frequent and this is effective in preventing any self-pollination from taking place.

Vegetative propagation is of great advantage to breeders. Once a favorable type is obtained, the genotype can be multiplied indefinitely.

Existing germplasm

Cassava originated and completed the major part of its diversification in Latin America (Leon, 1976). The CIAT germplasm collection comprises approximately 2,400 cultivars which have been collected from Colombia, Venezuela, Ecuador, Peru, Mexico, Brazil, Panama, Puerto Rico, Costa Rica, The Dominican Republic, Bolivia and Paraguay. The collection represents the major genetic diversity of the species. Tens of thousands of seeds obtained in this collection have been sent to other cassava breeding programs in Latin America, Asia and Africa.

In this germplasm, enormous genetic variability in such characters as harvest index and root yield is found (Fig. 1). As well, resistances to the major cassava diseases such as cassava bacterial blight *Phoma* leaf spot, superelongation disease and *Cercospora* leaf spot have been identified (CIAT, 1973, 1974, 1975). However, no cultivar in the collection has been found to meet the standard which we consider the newly recommended cultivars should satisfy. Thus, producing a quantity of recombination types through hybridizations is necessary.

Plant type

The identification of an optimum leaf area index for root yield (CIAT, 1975; Cock *et al* in press) may be the most significant contribution of cassava production physiology to the

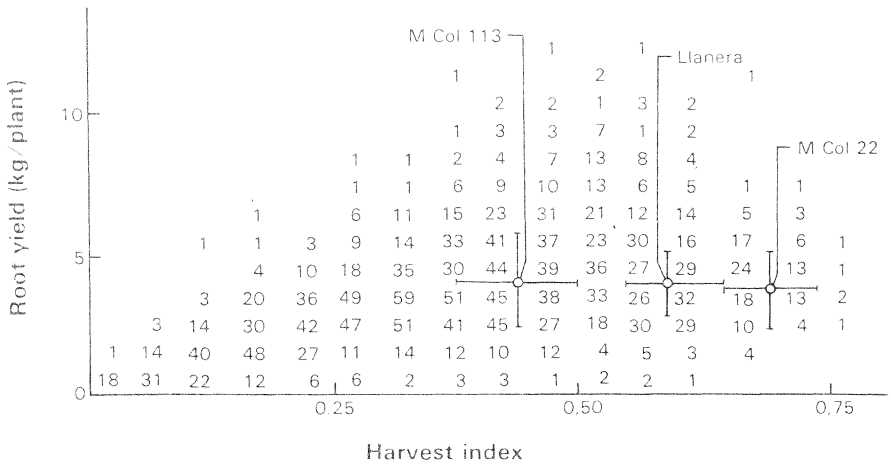

Fig. 1. Relationship between harvest index and root yield of 1,900 cultivars evaluated in single-row trial at CIAT. (The number represents the number of cultivars and the values of control cultivars are shown with standard deviation).

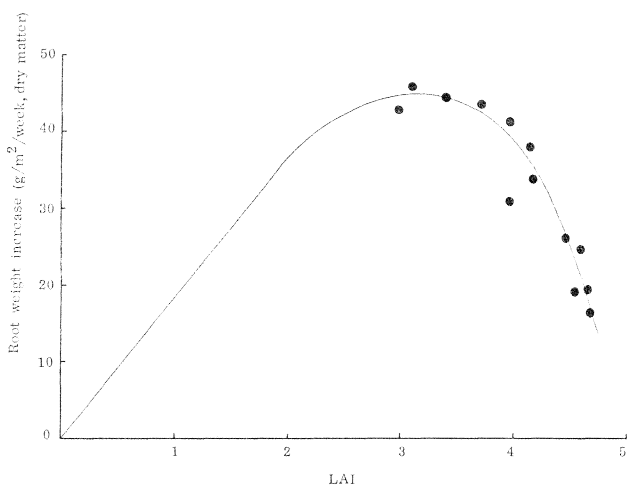

Fig. 2. Root weight increase as a function of LAI in a cultivar M Col 113 at CIAT (Cock-CIAT, 1975).

breeders' work up to the present. The optimum LAI exists between 3 and 3.5 (Fig. 2). It stays phenotypically constant over a wide range of temperature variation, although the genotype which attains the optimum LAI may be different under different temperatures (CIAT, 1976; Irijura, Cock and Kawano, in press).

This leads to the conclusion that to obtain the highest yield, a cassava population must reach the optimum LAI as soon as possible and maintain it as near by as possible until the harvest. Analysis of the components of leaf area suggests that long leaf life and late branching are the most important among others (CIAT, 1976; Cock *et al* in press).

Hybridization

Pollination is easy. Genotypes differ greatly in their efficiency when used as a female parent for hybridization while they all seem to function well as a male parent (Table 2). Approximately 30,000 hybrid seeds are being produced yearly from the controlled-pollination of approximately 22,000 female flowers at CIAT.

Open-pollinations offer a fair chance of obtaining high-yielding hybrid selections (CIAT, 1976). However, a high proportion of seeds obtained by open-pollinations can be a result of self-pollination and the evidence suggests that self-pollination is self-destructive in many cases (Table 1).

Table 2. Genotypic difference in seed setting after pollination

Cross	No. of female flowers pollinated	No. of seeds obtained		No. of seeds set per female flower
M Col 1684 x M Col 22	91	72		0.79
M Col 1684 x M Col 638	350	63		0.18
M Col 1684 x M Mex 55	78	40		0.51
M Col 1684 x CM 309-56	225	53		0.24
M Col 1684 x CM 309-239	115	65		0.57
M Col 1684 x CM 309-260	130	20		0.15
			Average	0.41
M Col 638 x M Col 1684	274	268		0.98
M Col 638 x M Mex 55	220	284		1.29
M Col 638 x M Ven 218	357	402		1.13
M Col 638 x M Pan 70	324	257		0.79
M Col 638 x M Pan 114	217	313		1.44
M Col 638 x Popayan	285	484		1.70
M Col 638 x CM 309-11	105	191		1.82
M Col 638 x CM 309-26	144	212		1.47
M Col 638 x CM 309-29	99	154		1.56
M Col 638 x CM 309-56	143	206		1.44
M Col 638 x CM 309-143	64	136		2.13
			Average	1.43
M Col 755 x Llanera	161	279		1.73
M Col 755 x M Col 22	278	500		1.80
M Col 755 x M Col 647	233	424		1.82
M Col 755 x M Col 667	144	234		1.63
M Col 755 x M Mex 55	284	517		1.82
M Col 755 x M Mex 59	154	284		1,84
M Col 755 x M Ven 185	90	157		1.74
M Col 755 x M Ven 209	162	204		1.88
M Col 755 x M Ven 270	163	308		1.89
M Col 755 x M Ven 307	203	379		1.87
			Average	1.80
SM 76-66 x M Col 638	488	946		1.94
SM 76-66 x M Mex 59	59	132		2.24
SM 76-66 x Popayan	221	427		1.93
SM 76-66 x CM 157-9	111	186		1.68
SM 76-66 x CM 170-2	106	239		2.25
SM 76-66 x CM 204-5	75	156		2.08
SM 76-66 x CM 309-37	112	218		1.95
SM 76-66 x CM 309-56	143	221		1.55
SM 76-66 x CM 334-19	119	241		2.03
			Average	1.96

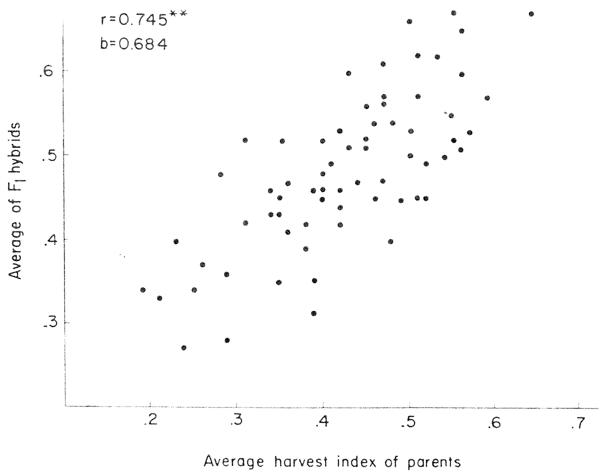

Fig. 3. Regression of F_1 average on the mid-parent value in harvest index (Data taken from single-row trials at CIAT).

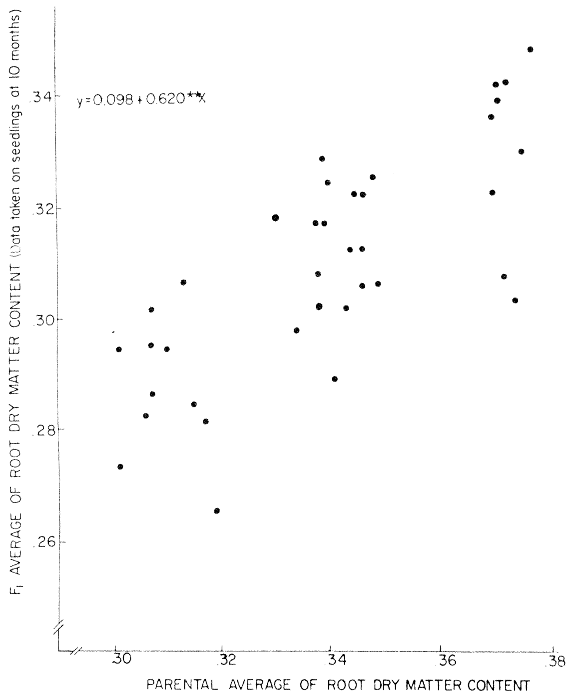

Fig. 4. Regression of F_1 average on the mid-parent value in root dry matter content (Data taken from single-row trials at CIAT).

The inheritance of such important characters as harvest index (Fig. 3), root dry matter content (Fig. 4) and post-harvest root perishability (Fig. 5) follows a simple additive gene manner. Resistances to important diseases such as cassava bacterial blight and *Cercospora* leaf spot can be transmitted relatively easily to offspring when the resistant genotypes are included in the hybridizations (CIAT, 1975, 1976). A great number of high-yielding genotypes

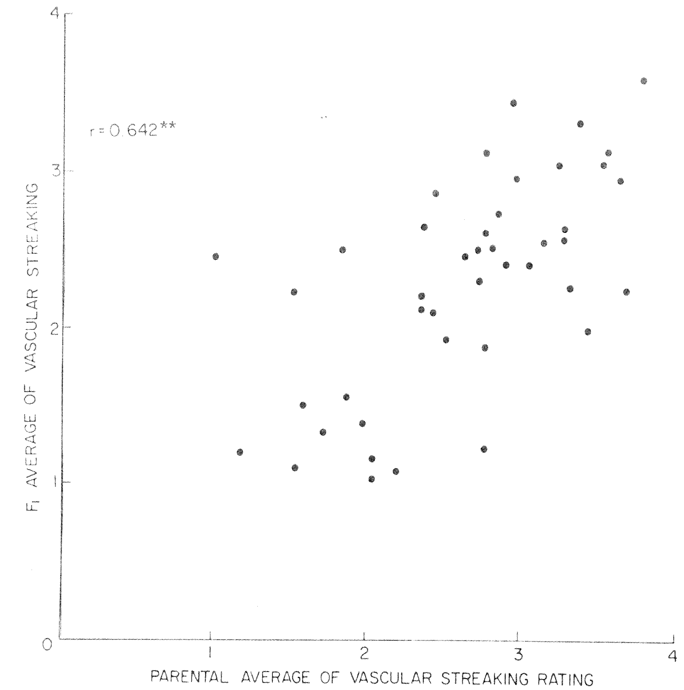

Fig. 5. Regression of F_1 average on the mid-parent value in post-harvest root deterioration (Vascular streaking rating; O-no damage, 4-full damage).

resulted from the crosses which had included genotypes with a high harvest index (CIAT, 1977; Kawano *et al* in press). Controlled hand pollination with selected parents is recommended as a general tool of breeding cassava. When a breeder has to choose open-pollination, the use of male-sterility is recommended.

The simple inheritance mode for many important characters and vegetative propagation makes the method of cassava breeding simple. The details of methodology are not important at this moment. The basic germplasm on which the breeder works and the efficiency of selection both of cross parents and hybrid lines are most important.

Selection

1. Seedling trial

Sixty to 95% germination is obtained depending on genotypes. The germination percentage seems to be highest about five months after seed harvest (or eight months after pollination) and it drops dramatically when the seeds are stored more than two years at room temperature (Fig. 6).

The yield data of seedling plants are highly correlated with those of the same genotype planted with stakes (Fig. 7). This clearly indicates that the seedling selection is highly effective. In cassava, inter-genotypic competition is highly significant especially when different genotypes are planted close together (CIAT, 1975; Kawano *et al* in press). Thus it is important to plant segregating materials with enough spacing among them. At CIAT, the seedlings are planted at 2 x 1 m distance.

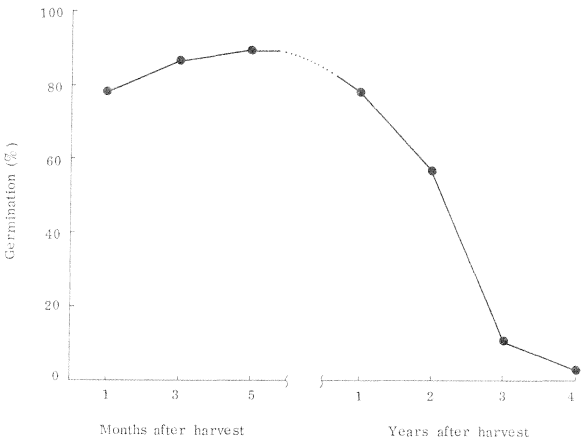

Fig.6 Germination of cassava seeds at different periods of storage at room temperature (24° C) (each point represents the average of several genetic populations).

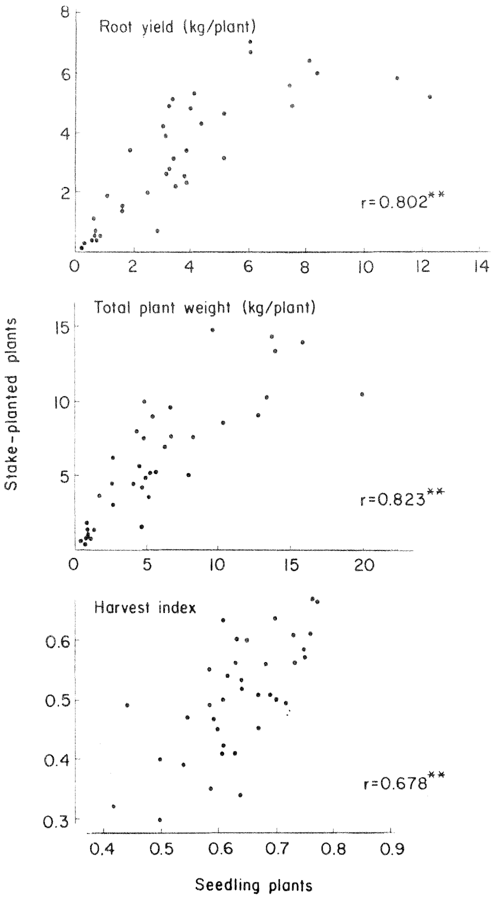

Fig. 7. Correlation of seedling plant data harvested 7 months after transplanting with that of stake-planted plants of the same genotype at CIAT.

2 Single-row and population trials

The selected seedling plants are passed immediately to a single-row trial. Those selected lines from the single-row trial are then evaluated in a replicated population trial in which only the central plants free from border effect are harvested.

There is no correlation between root yield data obtained in single-row trials and those obtained in population trials (Fig. 8). Since the valid yield data should come from replicated population trials, the root yield data obtained in single-row trials have virtually no meaning.

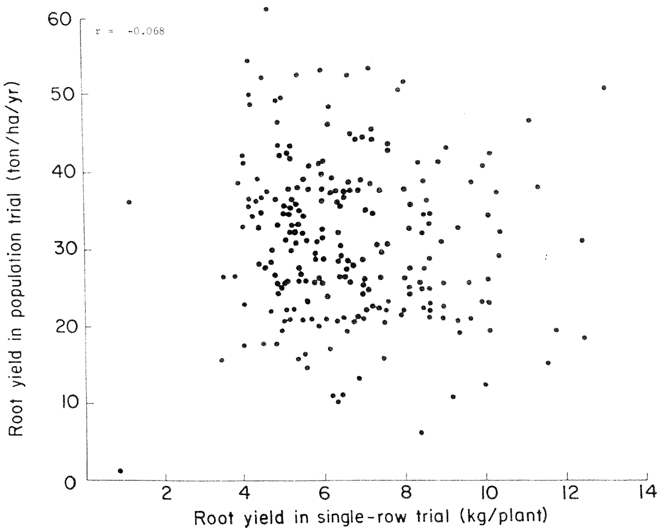

Fig. 8. Relationship between root yield data weight in fresh weight in single-row trial and that in population trial at CIAT.

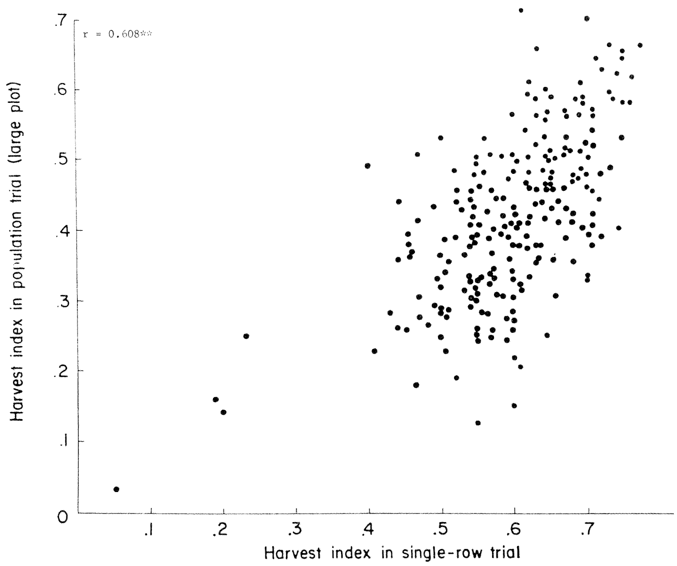

Fig. 9. Relationship between harvest indices in single-row trial and population trial at CIAT.

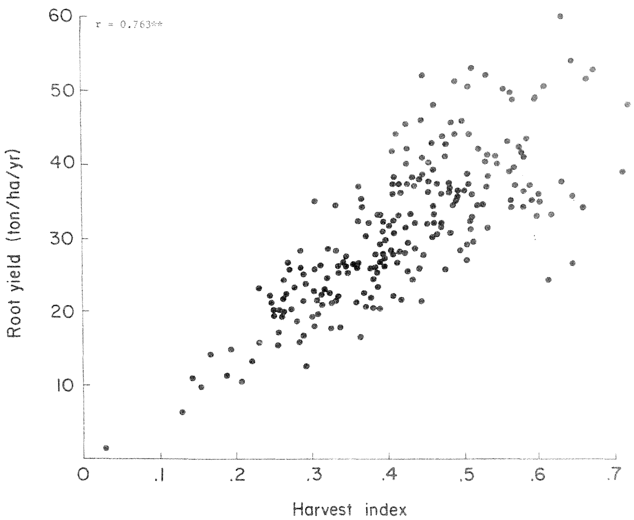

Fig. 10. Relationship between harvest index and root yield (fresh weight) in population trial at CIAT.

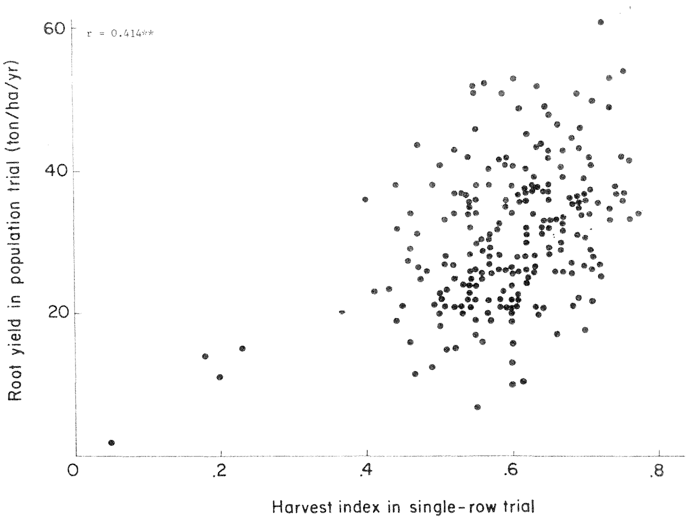

Fig. 11. Relationship between harvest index in single-row trial and root yield (fresh weight) in population trial at CIAT.

However, harvest index data obtained in single-row trials are highly correlated with those in population trials (Fig. 9). In population trials, harvest index is highly correlated with the root yield (Fig. 10). As a consequence, in the single-row trials harvest index is a better indicator of true yielding ability than the yield itself (Fig. 11).

This occurs as a result of competition between genotypes. Genotypes with high vegetative vigor and low harvest index can occupy a larger space resulting in higher root yield in seedling or single-row trials. However, when these types are planted in populations, they do not yield well.

Harvest index is an indicator of the balance between leaf and stem growth and root growth. There exists an enormous genetic variation in this character (Fig. 1) and it is highly heritable

(Fig. 3). Thus, harvest index is a highly effective character for use as an indicator for the selection of cross parents, seedling selections and single-row trials. We are eliminating the materials which have an harvest index lower than 0.60 and 0.55 in seedling and single-row trials, respectively.

Recent advances at CIAT

On the CIAT farm where the soil is fertile, several hybrid selections gave root dry-weight yields of 15 ton/ha/yr or more, outyielding a local cultivar by 100% with 65mm of rainfall and without any application of fertilizer, fungicide, insecticide or irrigation (Table 3). On the soil of the Llanos Orientales of Colombia which is so acid (pH 4. 3), so high in aluminium (exch. Al 3.5 me/100 g, 85% sat) and so low in phosphorus (1-2 ppm Bray II) that the majority of food crops can be grown only with a heavy application of lime and phosphorus, several hybrid selections gave root dry weight yields of 10 ton/ha/yr with a moderate application of

Table 3. Selected results of yield trials in three locations

Location	Genotype	Root yield (ton/ha/yr)	
		Dry wt.	Fresh wt.
CIAT	CM 309-211	17.9	50.8
	CM 308-197	17.6	50.3
	CM 323-30	16.6	48.3
	CM 308-1	16.3	43.3
	CM 321-15	15.9	46.1
	CM 321-170	15.8	47.8
	CM 317-16	15.4	48.1
	CM 307-135	15.4	44.0
	CM 309-84	15.4	41.1
	CM 152-12	14.7	45.0
	M Col 113 (local cultivar)	8.4	25.6
	Llanera (control)	7.9	24.7
	M Col 22 (control)	7.1	19.7
Carimagua	SM 92-73	10.6	33.0
	CM 323-52	10.0	33.0
	CM 308-197	9.9	30.6
	CM 314-2	8.4	25.7
	CM 323-99	7.8	24.3
	CM 323-142	7.5	26.0
	CM 309-2	7.5	23.3
	CM 321-88	7.1	21.5
	CM 305-11	6.9	24.0
	CM 323-41	6.6	24.0
	Llanera (local cultivar)	6.9	21.5
	M Col 22 (control)	6.0	19.4
	M Col 113 (control)	2.7	10.4
Caribia	CM 320-2	13.7	42.0
	CM 309-50	13.7	41.7
	CM 309-163	12.8	44.3
	CM 323-75	12.2	37.8
	CM 323-41	12.2	37.6
	CM 322-20	12.1	36.7
	CM 321-85	11.6	36.1
	CM 308-197	11.4	34.5
	CM 309-128	11.1	34.8
	CM 321-78	11.0	38.0
	M Col 22 (control)	11.4	33.6
	Llanera (control)	6.0	20.7
	Manteca (local cultivar)	5.0	18.1
	Montero (local cultivar)	4.3	12.6

lime and phosphorus, outyielding a local cultivar by 50% (Table 3). On the Northern Coast of Colombia, which is one of the cassava production centers of that country, several hybrid selections yielded more than 12 ton/ha/yr in root dry weight withstanding 5 months of dry season and outyielded local cultivars by more than 100% (Table 3). A hybrid selection such as CM 308-197 did well in all of these locations, always exceeding the yields of corresponding local cultivars by 50 to 150%.

To answer the question of whether we can go still further in selection for higher productivity, careful studies by physiologists and soil scientists will be required. However, the genotypes with this level of yielding capacity should be able to significantly increase the current yields at the farm level of 3 to 5 ton/ha/yr in root dry weight.

Conclusion

The productivity of the existing cassava germplasm is generally far below the potential of the species. Limited attention has been given to the genetic improvement of the species. Botanical characteristics of the species and genetic behavior of several important characters suggest that the genetic management of the species must be easy. Attaining the maximum level of productivity is easily within reach. One key factor for maintaining a high efficiency of genetic work is the use of harvest index in selection.

After four years of work, the CIAT cassava breeding program has hybrid selections which outyield local cultivars by 50 to 150% under a wide range of environmental conditions. Some of the superior materials may be named as a recommended cultivar and distributed to national cassava programs in the tropics in the near future. The emphasis of breeders' work will gradually shift toward incorporating resistances to the yield-reducing factors such as resistance to diseases and insects.

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Discussion

K. Sakai, Japan: You mentioned that the yield in a single row was not correlated with that in the population trial.

1. What is meant by population?
2. How many replications did you make?
3. What is the reason for the low correlation? Is it due to inter-genotypic competition? If so, why are you interested in making replications which reduce the effect of inter-genotypic competition?

Answer:

1. Pure stand of a single genotype.
2. Two in the population trial and none in the single row trial.
3. Inter-genotypic competition and genotype-spacing interaction.

We are trying to minimize the inter-genotypic competition by planting the segregated materials at wide spacing.

J. T. Rao, India: You raise a large population and wait one year for determining the yield and carbohydrate content. Do you think that any correlated characters at the juvenile stage could help eliminate the very many undesirable effects?

Answer: Cassava seedling cannot provide a reasonable quality and quantity of stem cuttings for further propagation and evaluation within 8 months after planting. Thus, even if there were some screening method available at the very early stage of seedling growth, we would have to wait a minimum of 6 months for obtaining stem cuttings. Besides, at CIAT, land and labour are not a limiting factor. To develop a technique for early screening might not be too helpful.

S. Tsunoda, Japan: May I ask the reason why a leaf area index beyond 3.5 would not be more advantageous for getting high root yield. My assumption is that a high leaf area index and a low harvest index would bring about lower root yield. It seems that the most important point would be to get a good balance between the leaf expansion and the root development.

Answer: You are right, fundamentally. You could refer to the extensive study on cassava production physiology conducted at CIAT by J. H. Cock.

M. Iizuka, Japan: Could we expect seed propagating F1 breeding in cassava in the future?

Answer: It would be very difficult practically. Cassava has never been selected for higher seed production for the past 5000 years thus seed production rate is very low. Besides, the seeds crack off when they mature and fruit fly eats up about 80% of maturing seeds if not covered.

G. S. Khush, The Philippines: Cassava is a long duration crop. Do you have any variations for growth duration? Is early maturity one of the breeding objectives in cassava?

Answer: It is fairly difficult to define growth duration in the case of cassava. There are some genotypes which can give a fair amount of root yield six months after planting while the majority of cultivars hardly give any commercial size root at 6 months. However, even with so called early maturing cultivars, the yield is higher at 10 to 12 months even when the yield is based on ton/ha/month.

J. Soria, Costa Rica:

1. You showed that you could develop high-yielding hybrids adapted to acid soils, such as Carimagua in the Llanos Orientales. Did you make any selection for acid soils?

2. Yields seem to exceed those obtained by local farmers. Did you apply larger amounts of fertilisers and did you adjust the acidity?

Answer:

1. Yes. Besides, some genotypes are showing good results both at Carimagua (soil pH:4.2) and CIAT, Valle (pH:7.6)

2. Fertilisers were not applied at CIAT and Caribia (Northern Coast). A moderate level of N,P,K, and lime was applied at Carimagua, for Llanos conditions. No irrigation was supplied in either of the three locations.

J. T. Rao, India: The two important characters are yield and carbohydrate content. Are they inversely related? If so, what is the breeding system you adopt?

Answer: We pay more attention to root dry matter yield rather than to root fresh weight yield. Presently, there is no correlation between these two parameters. However, as the level of selection advances, it is likely that we will encounter a negative correlation between the two characters, especially if we concentrate our selection effort only on root fresh weight yield.

Y. Hojo, Japan:

1. In sweet potato there is not necessarily a correlation between dry matter content of tuber and dry weight of tuber per plant. Is there any relationship between dry matter content of root and dry weight of root per plant in cassava?

2. You showed the close relationship between harvest index and root yield. Is the harvest index related to top weight, root weight and total plant weight?

3. What are the main factors responsible for the high harvest index of cassava?

Answer:

1. For the time being we do not find any correlation between root dry matter content and root fresh weight yield. It may become different when the level for root fresh yield will advance.

2. Harvest index is negatively correlated with top weight.

3 The main factor is represented by high proportion of growth period which is directly related to root yield, filling in total growth duration (8 months out of 12 months).