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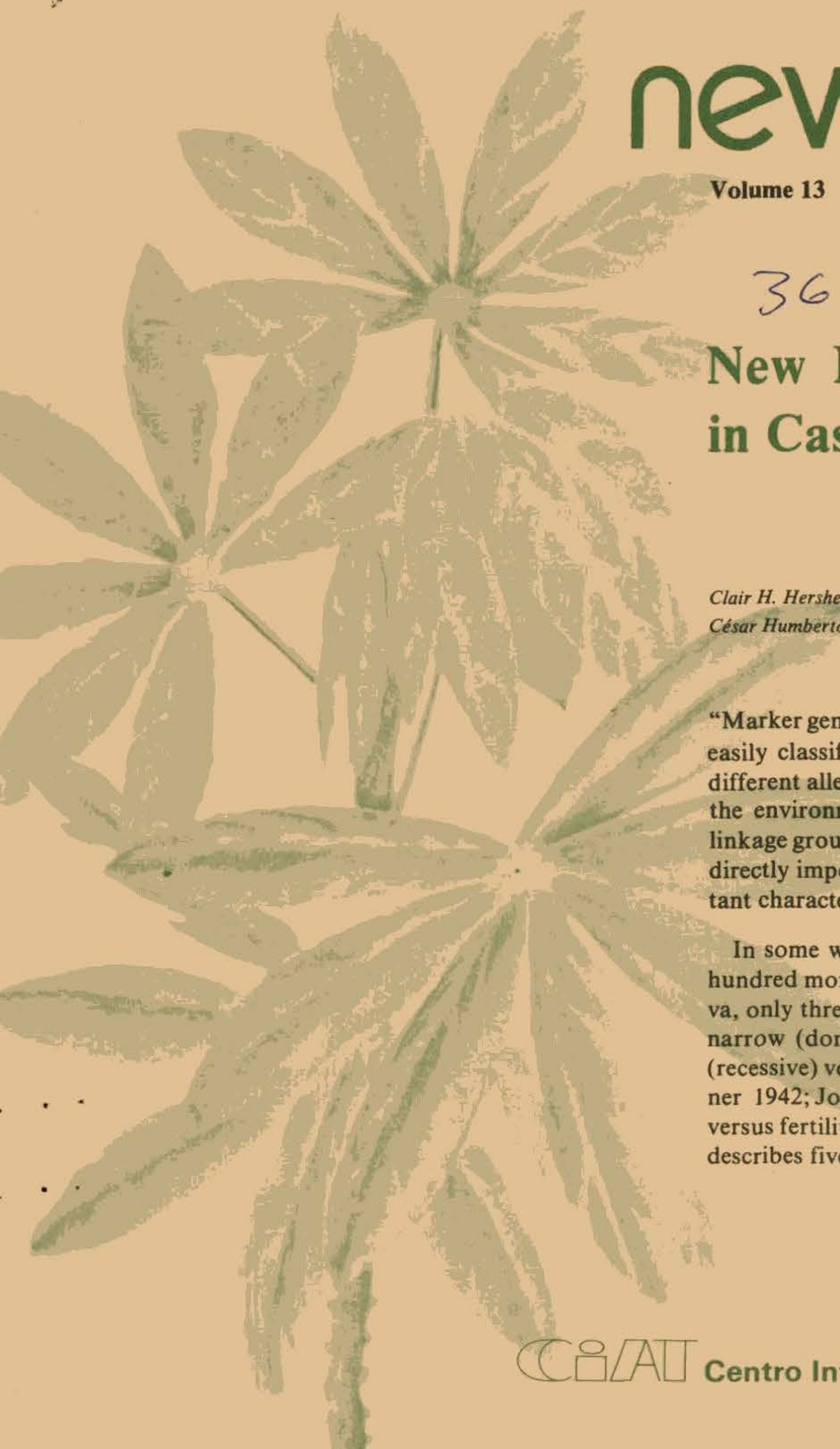

New Marker Genes Found in Cassava

Clair H. Hershey and
César Humberto Ocampo N.

"Marker genes" control the expression of traits which can be easily classified into distinct states, each controlled by a different allele, and whose expression is little influenced by the environment. Such genes can be a tool for studying linkage groups and mating systems; and sometimes they are directly important as determinants of economically important characters.

In some well-studied crops like maize and peas, several hundred morphological marker genes are known. In cassava, only three have been reported: broad (recessive) versus narrow (dominant) leaf lobe shape (Graner 1942); light (recessive) versus dark (dominant) root surface color (Graner 1942; Jos and Hrishi 1976); and male sterility (recessive) versus fertility (dominant) (Jos and Nair 1984). This report describes five new marker genes for cassava. ➪

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Contents

Keeping in touch

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Materials and Methods

During 1987 and 1988 the breeding section of CIAT's Cassava Program studied several other traits to determine whether segregation patterns were consistent with single-gene inheritance. Those showing two distinct states, and with little environmental influence, were preselected for more detailed genetic studies. The traits studied and the two contrasting states of each were: chlorophyll production (normal versus albino), growth habit of the stem (straight versus zigzag), stem collenchyma color (light versus dark green), root parenchyma color (white versus yellow), and leaf lobe shape (pandurate versus smooth) (Figure 1). In all cases, the plants studied were the first generation progeny (F$_1$) from highly heterozygous clones.

Hypotheses for the inheritance of the individual traits were developed on the basis of empirical evidence and then crosses chosen which would test the hypotheses. Statistical analysis of the results was by chi^2 to determine whether segregation ratios differed significantly from those hypothesized from a single-gene inheritance pattern.

Results and Discussion

Chlorophyll production

The clone CG 165-7, when selfed, produced progeny in the ratio of 3:1 (normal:albino). All other crosses resulted in all normal seedlings. It is concluded that albinism is the result of a single recessive gene. The authors propose that the name of the locus be "A". Thus, albino plants (homozygous recessive) are denoted "aa", and normal plants are either "Aa" or "AA". The clone CG 165-7 is a heterozygous carrier of the allele for albinism (Table 1).

Stem growth habit

In CIAT's germplasm collection, only three clones are recorded as having zigzag stem growth habit. Of these, only MVen 217 has produced sufficient seed for genetic studies. The selfed progeny of this clone were all zigzag, while all other crosses produced straight stems (Table 2). There is strong evidence to suggest that zigzag stem is controlled by a single recessive gene. The name proposed for this locus is "Z". Thus, the genotype of MVen 217 is "zz", and the other clones crossed onto MVen 217 were all "ZZ".

This character is especially interesting as a marker gene in cassava since it is the only nonlethal, single-gene-seedling trait so far identified. One practical use of this gene would be to study outcrossing versus selfing rates in a given open pollination situation.

Stem collenchyma color

The stem collenchyma can be observed easily by scraping off the outer epidermis of a mature stem. The most common external stem colors in cassava are the result of the four possible combinations of light or dark brown epidermis, and light or dark green collenchyma.

From preliminary observations of the data from several crosses, the authors developed the hypothesis that stem collenchyma color is controlled by a single gene, with light green dominant to dark green. The (chi)^2 analyses in Table 3 confirm the hypothesis. The authors propose to name this locus "G". Plants with light green collenchyma may be "Gg", or "GG", and those with dark green are "gg".

Root parenchyma color

In the initial phase of this study on genetic markers, the observations on root parenchyma color were divided into just two classes: white and yellow. Data from several crosses were used to hypothesize single gene control for the trait, with yellow dominant to white (Table 4).

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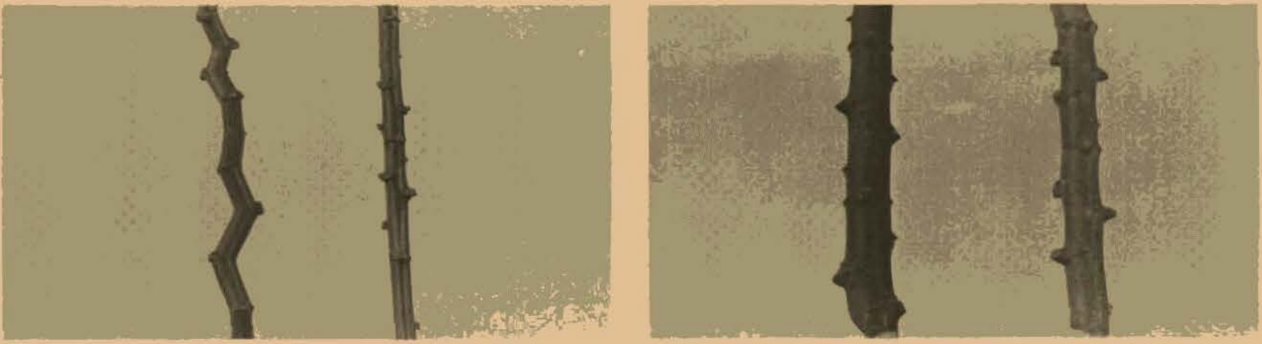
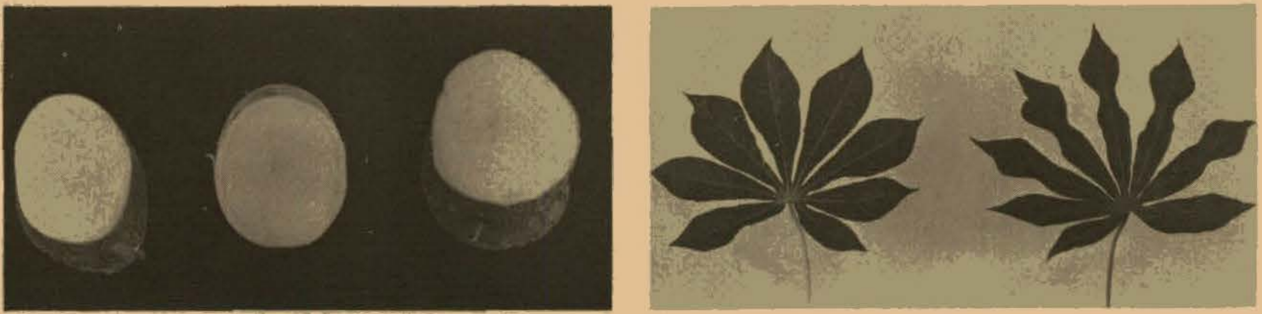
Chlorophyll production: Albino plant (left) versus normal plant.



Stem growth habit: Zigzag stem growth habit (left) versus straight stem.

Stem collenchyma color: Dark green (left) versus light green.



Root parenchyma color (left to right) white, light yellow, intense yellow.

Leaf lobe shape: Normal lobe (left) versus pandurate lobe.

Figure 1. *Constrasting phenotypes of the genetic markers studied.*

Table 1. Crosses used to study inheritance of seedling albinism in cassava.

	Parent phenotype		Parent genotype		Progeny (no.)		Expected	
Cross	♀	♂	♀	♂	Normal	Albino	ratio	(chi)^2
CG 165-7 ⊗	Normal	Normal	Aa	Aa	55	21	3:1	0.28
CM 523-7 ⊗	Normal	Normal	AA	AA	22	0	1:0	0.00
CG 165-7 x CM 523-7	Normal	Normal	Aa	AA	60	0	1:0	0.00
CM 523-7 x CG 165-7	Normal	Normal	AA	Aa	31	0	1:0	0.00

Table 2. Crosses used to study inheritance of stem growth habit.

Cross	Parent phenotype		Parent genotype		Progeny (no.)		Expected	
	♀	♂	♀	♂	Straight	Zigzag	ratio	(chi)²
Mbra 12⊗	Straight	Straight	ZZ	ZZ	4	0	1:0	0.00
MVen 217⊗	Zigzag	Zigzag	zz	zz	0	17	0:1	0.00
Mbra 12 x MVen 217	Straight	Zigzag	ZZ	zz	18	0	1:0	0.00
MVen 217 (O.P.)	Zigzag	?	zz	?	71	6	?	—

Table 3. Sample of crosses (from total of 67) used to study inheritance of stem collenchyma color.

Cross	Parent phenotype		Parent genotype		Progeny (no.)		Expected	
	♀	♂	♀	♂	Light	Dark	ratio	(chi)²
MCol 948C⊗	Light	Light	Gg	Gg	43	15	3:1	0.02
MCol 948C x CM 847-11	Light	Light	Gg	GG	45	0	1:0	0.00
CG 165-7⊗	Dark	Dark	gg	gg	0	26	0:1	0.00
CG 165-7 x CM 523-7	Dark	Light	gg	Gg	30	25	1:1	0.45
CM 847-11 x CM 922-2	Light	Dark	GG	gg	36	0	1:0	0.00

Table 4. Sample of crosses (from total of 68) used to study inheritance of root parenchyma color.

Cross	Parent phenotype		Parent genotype		Progeny (no.)		Expected	
	♀	♂	♀	♂	Yellow	White	ratio	(chi)²
MCol 948C x CM 847-11	White	Yellow	yy	Yy	22	23	1:1	0.02
CM 1585-13⊗	Yellow	Yellow	Yy	Yy	12	7	3:1	1.42
CM 1999-5⊗	Yellow	Yellow	Yy	Yy	10	3	3:1	0.03
CM 1999-5 x CM 1585-13	Yellow	Yellow	Yy	Yy	33	8	3:1	0.66
MBra 12 x CG 165-7	White	White	yy	yy	0	33	0:1	0.00

However, in some of the segregating progeny, it was observed that there was an apparent segregation into three distinct classes: white, light yellow, and intense yellow. Therefore, some of the crosses which were still available in the field near the close of the study were reevaluated, and plants classified into three rather than two groups. The segregation patterns suggest that the gene may show a dosage effect, where the dominant homozygote shows an intense yellow, the heterozygote a light yellow, and the recessive homozygote is white (Table 5).

The authors propose "Y" as the name of this locus. Thus, "YY", "Yy", and "yy" are the intense yellow, light yellow, and white phenotypes, respectively.

Of the markers studied here, root parenchyma color is the one with the most obvious agronomic importance. In some markets, yellow fleshed roots are preferred. The yellow component of the roots is carotene, a precursor of Vitamin A, a nutrient that claims increasing attention among nutritionists because of deficiencies in large sectors of some populations. Knowing the genetics of the trait can greatly aid the plant breeder in selecting appropriate parents.

Leaf lobe shape

Of the clones used as parents, only CG 406-1 displayed the pandurate leaf character. All others had broad leaves, presumably homozygous recessive for leaf width (Table 6).

Segregation follows classical Mendelian patterns in some but not in all

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Table 5. Crosses used to test hypothesis of dosage effect of Y gene for root parenchyma color.

Cross	Parent phenotype		Parent genotype		Progeny (no.)			Expected ratio	(chi)^2
	♀	♂	♀	♂	Intense yellow	Light yellow	White		
CM 507-37 x CM 523-7	Yellow	White	Yy	yy	0	14	18	0:1:1	0.50
CM 430-37 x CM 996-6	Yellow	Yellow	Yy	Yy	14	24	14	1:2:1	0.46
CM 1585-13 x CM 1999-5	Yellow	Yellow	Yy	Yy	16	32	10	1:2:1	1.87

Table 6. Sample of crosses (from total of 22) used to study inheritance of pandurate leaf shape.

Cross	Parent phenotype		Parent genotype		Progeny (no.)		Expected ratio	(chi)^2
	♀	♂	♀	♂	Pandurate	Normal		
CG 401-6 x MCol 2016	Pandurate	Entire	Pp	pp	38	37	1:1	0.01
CG 403-18ⓧ	Entire	Entire	Pp	Pp	18	164	3:1	411.50
CG 403-18 x CG 354-12	Entire	Entire	Pp	pp	4	38	1:1	27.52
CG 401-6 x Cg 501-1	Pandurate	Entire	Pp	pp	64	60	1:1	0.13
MCol 1488 x MCol 2016	Entire	Entire	pp	pp	0	70	0:1	0.00

crosses. Excluding the crosses in which CG 403-18 is one of the parents, one can hypothesize a single dominant gene controlling pandurate leaf shape. If this is the case, then, the clone CG 403-18 could be suspected of having the dominant gene, but its expression masked by one or more nonallelic genes, which also serve to mask expression of the pandurate gene in some proportion of the progeny.

Conclusions

The studies reported here have resulted in the description of five new marker genes in cassava controlling the following traits: chlorophyll production in seedlings, stem growth habit, stem collenchyma color, root parenchyma color, and leaf lobe shape. Names are proposed for each loci, and dominant and recessive phenotypes described. In the case of parenchyma color, the dominant gene appears to have a dosage effect, resulting in more intense color in the homozygote as compared to the heterozygote. Pandurate leaf shape presents some unclear segregation patterns, suggesting epistatic effects of other genes.

Recriprocal crosses studied for segregation of seedling albinism, stem collenchyma color, and root parenchyma color show identical ratios regardless of which parent was male or female, indicating that inheritance is not influenced by cytoplasmic effects.

While CIAT has done some preliminary studies on linkages among the newly identified genes, more crosses need to be analyzed. It will also be important in the future to study possible linkages to multigenically controlled traits of economic importance.

CIAT has begun to establish a marker gene collection, consisting of known genotypes of all the described marker genes with the possible genotipic combinations for these markers. These will be available for study by any interested scientist.

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Performance of Cassava in Multitier Cropping Systems

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The southern state of Kerala, India, has led the country in area cultivated and production of cassava since its introduction in the 16th century. Nevertheless, there has been a steady decline in area cultivated as profitable rubber and other plantation crops have moved into the area to take advantage of desirable humid tropical conditions. This has necessitated a thorough analysis of existing cassava production systems in the state.

The use of multitier cropping with crops having differing canopies is seen as a realistic approach to sustaining cassava production in the region.

Layout

Field experiments were conducted on fairly large plots (700-800 m^2) on sloping land (8-9%) during 1983-86, at the Central Tuber Crops Research Institute (CTCRI) farm. Four perennial species—coconut, banana, *Eucalyptus*, and *Leucaena*—constituted the first-tier crops, while cassava occupied the second tier, and seasonals such as groundnut or vegetable cowpea for fresh consumption constituted the ground tier. Single stands of perennials and cassava and intercropped stands of cassava with groundnut and cassava with vegetable cowpea were also evaluated.

Performance of Perennials

Aerial growth

Intercropping with cassava and other seasonal crops promoted the growth of *Eucalyptus*, the effect being conspicuous at the six-month stage and gradually narrowing toward the 30-month stage. *Leucaena* growth was adversely affected by cassava during the first 12 months and flowering and fruiting in banana took place earlier in the pure stands. Total leaf production and girth at the collar region of the young coconut plants were greater in single stands at 30 months.

Root spread

Cassava intercropping restricted the spread of lateral roots of both *Eucalyptus* and *Leucaena* without affecting the number of first-order roots. In *Eucalyptus*, compared with the maximum lateral spread of 4.85 m in a pure stand at the 32nd month, the spread was only 2.68 m in plants raised in association with cassava. In banana plots, the interrow space (5 m) was not entirely covered by the banana roots even at the 32nd month. Apparently the central row of intercropped cassava did not encounter the roots of the banana plants. Cassava intercropping carried out for up to three years had no apparent effect on the maximum spread and mean length of the lateral roots of coconut, since basins were maintained at 60 cm below ground level.

Shade effect

The shade of *Eucalyptus* plants increased from 15.0% to 52.6% over a period of three years. The shade effect of other perennials could be observed only on the adjacent cassava rows, which did not change much in the case of banana and *Leucaena*. In the case of coconut, there was a gradual increase in shade from 5.5% to 18.2% in three years (Table 1).

Performance of Cassava

Growth

Cassava growth in association with banana was more vigorous when compared with other combinations in all three seasons. The result was more conspicuous, however, during the first-year crop cycle of cassava with banana. Cassava growth in association with *Eucalyptus* was very much reduced from the second year onward. Inclusion of the seasonal intercrop (groundnut) reduced the growth of cassava, though reductions were not marked in the case of vegetable cowpea.

Table 1. Shade effect (%) of perennials on cassava.

	Perennials			
Year	Banana	*Eucalyptus*	Coconut	*Leucaena*
1983-84	13.6	15.0	5.5	25.0
1984-85	11.2	22.5	9.7	20.5
1985-86	15.7	52.6	18.2	21.5