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Full Length Research Paper

Combining the yield ability and secondary traits of selected cassava genotypes in the semi-arid areas of Eastern Kenya

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Despite the importance of cassava for food security in semi-arid areas of Kenya, there is a lack of information regarding gene action determining yield of local varieties. Therefore the objective of this study was to estimate the combining ability for yield and associated secondary traits by crossing popular local varieties with some varieties from IITA using a NC II mating design. The F1 progenies were evaluated in a seedling trial laid out as a 7 × 7 simple lattice with two replicates. Results indicated significant variation among progenies for shoot weight, root number, root weight, root yield, biomass, harvest index, percentage dry matter, dry matter yield, cyanide content, and resistance to cassava mosaic disease and green mites. Average fresh root weight at 6 mo ranged from 1.1 kg to 1.4 kg plant^{-1}. To a great extent SCA effects (57 to 75%) explained variation for shoot weight, root weight, harvest index, dry matter content, root cyanide content and resistance to cassava mosaic, while GCA effects (55%) were more important for root number. Thus, our results suggested that non-additive gene action was more important than additive gene action in influencing yield and most of its associated traits in this cassava population. Overall, the results suggested that the success of cassava breeding in the semi-arid areas would depend on the ability of breeders to assemble heterotic groups of germplasm that combine well in order to achieve early vigour, disease and pest resistance, root quality and high yield potential.

Key words: Cassava, yield, secondary traits.

INTRODUCTION

Cassava is one of the leading staples in the world with a global total production of 233 million metric tones from 18.6 million ha (FAOSTAT, 2008). It was long ago established as the fourth most important staple food in the tropics (De Vries et al., 1967). For, example in topical Africa, total cassava production was about 118 million metric tones in 2008 (FAOSTAT, 2008). It is commonly cultivated in areas considered marginal for most other crops and is adaptable to low soil fertility and erratic rainfall ranging from less than 600 mm in semi-arid tropics to more than 1000 mm in the humid tropics. It survives prolonged drought of 4 to 7 mo during the growing cycle in north eastern Brazil (El-Sharkawy, 2003). It requires minimum inputs, which makes it ideal for drought prone areas in tropical and sub-tropical Africa, Asia and America (El-Sharkawy, 2003).

In Kenya, cassava is grown in both semi-arid and high rainfall areas for food security and as a cash crop. Surplus cassava is sold to earn income for the family. However, the varieties grown by farmers in this region are landraces that are late bulking and have low root yield potential. In order to improve the yield potential of these landraces, an understanding of the gene effects controlling root yield and secondary traits affecting yield is important. Such knowledge would assist in devising the best breeding strategy to improve early bulking and yield potential (Kariuki et al., 2002).

Improving the local landraces requires a hybridisation programme to generate hybrid progenies for selection and recombination (Fehr, 1984). Population improvement and recurrent selection in cross-pollinated crops progressively increases the frequencies of genes for specific

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specific desirable traits (Hahn et al., 1980). However, the success of population breeding depends largely on the choice of parents. Parental genotypes are usually selected on the basis of their performance or the performance of their F_1 progenies (Banziger and Paterson, 1992). In maize, selection of parental genotypes to produce F_1 hybrids is usually based on the performance of their progenies (Fehr, 1984; Lee, 1995). However, experienced breeders with fully characterised core germplasm, also use direct evaluation of parents, when breeding, for simply knowing the inherited traits in maize (Lee, 1995). Cassava breeders have traditionally used performance *per se* of parental genotypes (CIAT, 2004). In the current study, parental genotypes were selected based on their performance *per se* in semi-arid Eastern Kenya. The local varieties, though late bulking, have good root qualities and are popular with the farmers in the area (Kiarie et al., 1991). The IITA varieties, used to cross with the local produced popular varieties that were early bulking, but lacked certain attributes acceptable to farmers (Kamau et al., 1998). It was assumed that crossing the two groups (local and IITA), would result in new genotypes, which combine early bulking with acceptable root qualities.

Plant breeders and geneticists frequently use diallel-mating design to obtain genetic information (Sprague and Tatum, 1942; Griffing, 1956; Eberhart and Gardner, 1966). Analyses of broad based populations were generally conducted according to Eberhart and Gardner (1966) analyses I, II and III. Apart from diallel design, breeders also use factorial mating designs such as the North Carolina (NC) mating designs I, II, and III (Comstock and Robinson 1948; 1952) to generate genetic information on parents based on progeny performance. Genetic information generated by these mating designs is used to estimate general combing ability of the parental genotypes and specific combining ability of the progenies (Sprague and Tatum, 1942; Haulauer and Miranda, 1995).

In this study, the NC II mating design was used to generate the progenies from crosses between two groups of parents (local versus IITA varieties). Several researchers have used this design in, for example, sugar cane (Hogarth et al., 1981), variety crosses in maize (Eberhart and Gardner, 1966), maize (Pixley and Bjamason, 1993; Derera et al., 2000) and even feed conversion in broiler rabbits (Dedkova et al., 2002). In cassava, the design has been used to study resistance to cassava mosaic disease (Lokko et al., 2004). Combining abilities in cassava were creatively estimated, because of the difficulties of obtaining reliable family (cross combination) mean values for traits. In most cases, data collected on plants were selected from the seedling and later selection stages. Thus, the combining ability information on cassava lines is estimated from a small group of superior progenies, which germinated or a few advanced into the clonal trials (Ceballos et al., 2004). In addition, the problem with this approach is that the combining ability estimates will not be based on a random, unselected progeny population and will therefore be biased. With selection, non-additive effects tend to increase.

MATERIALS AND METHODS

Selection of parents

The selection of parents, to build the population of the future cassava breeding work for the mid-altitude eastern semi-arid areas of Kenya, began when open pollinated derived seeds were introduced from IITA, Ibadan, Nigeria from 1994 to 2000. The seeds were mainly bulk collections from the trials. Selected genotypes were evaluated on station trials at KARI-Katumani main centre, Kampi Ya Mawe, and Ithookwe sub-centres over several seasons. The superior genotypes were advanced by subjecting them to on-farm testing by farmers. Farmers used their experience to observe the growing habit of the various genotypes and performed a palatability test at the end of each trial. Palatability tests of raw and boiled roots were based on appearance of fresh and boiled roots, taste (bitter or sweet) and fibre (presence or absence) (Kamau et al., 1998; Githunguri and Migwa, 2003). The four local entries were popular local varieties with high root yield, good root quality and were tolerant to cassava mosaic disease. Their selection for this research was based on their performance *per se* and not on the performance of their progenies.

Crossing block

A crossing block was established at KARI-Kiboko farm in 2004 with four popular, but late, bulking varieties and six early bulking varieties from the IITA germplasm. The varieties were crossed following the NC II mating design. The local varieties were used as the females and the IITA as the males. The method of pollination was a modification of that employed by IITA (IITA, 1982).

Seedling nursery

Preliminary experiments were done at KARI-Katumani to establish optimum conditions for uniform germination of the cassava seeds. The hybrid seeds were germinated at 36℃ in the laboratory. The germinated seeds were planted in 5 cm × 8 cm black polythene bags and grouped according to family. The bags were filled with forest soil that had been cooked for 4 d to kill most of the microorganisms. Soil analysis was conducted to determine the mineral composition of the forest soil (Table 1).

The seedbeds were covered with a clear polythene sheet that created a humidity chamber. The temperature inside a seedbed without the seedlings rose up to 50℃ when the outside air temperature was 30℃. Therefore, to keep the seedbeds temperature at 2℃ above the air temperature, the sides of the seedbeds were lifted between 9.00 am and 4.00 pm every day.

After 21 d the seedlings were transported to KARI-Kiboko farm where they were, once again, arranged into family groups. They were left in the open for 4 d to harden up and were watered twice daily.

Seedling field trial

KARI-Kiboko farm is located along the Mombasa-Nairobi road located at 2° 10’S; 37° 40’ E and 975 m altitude. The KARI-Kiboko farm, at which the F_1 seedling trial was conducted, receives bimodal rainfall although there are yearly variations with peaks usually between March - May and from October – December. The monthly

Table 1. Mineral composition of the forest soil.

Sample	pH	P	K	Ca	Mg	Na	Zn	Fe	Mn	Cu	N
Description	**Unit**					**(ppm)**					**(%)**
Forest soil	4.1	10	248	585	140	27	1.54	168	26	0.98	0.31

Analysed at the Del Monte Kenya limited, Thika.

Table 2. KARI-Kiboko farm monthly rainfall data (mm) between November 2003 and June 2006

Months	Period of experimentation			
	2003	2004	2005	2006
January		143.0	6.5	12.4
February		49.0	0.0	6.0
March		22.5	40.5	85.7
April		70.8	186.5	205.8
May		0.0	13.8	43.5
June		0.0	0.0	0.0
July		0.0	0.0	0.0
Aug		0.0	2.5	0.0
September		5.0	0.5	
October		15.0	20.5	
November		49.5	57.5	
December	31.5	113.6	9.2	
Total	31.5	468.4	337.5	353.4

rainfall for the period of experimentation, December 2003 to August 2006, is provided in Table 2. The soil at Kiboko farm is ferric luvisols (Hornetz et al., 2000).

The seedlings were planted at Kiboko farm in a 7 × 7 simple lattice design with two replications on 2nd December 2004, where only the families were replicated. Sixteen full-sibs from a family were planted in each plot per replication at the commercial spacing of 1 m × 1 m. The plots and blocks were separated by 1.5 and 2.0 m wide alleys, respectively, to avoid competition from neighbouring families. Stakes were used to plant the parental genotypes in the trial. No mineral fertilizer was applied at planting and during growing period. Sprinkler irrigation was used to supplement the rains when necessary. The experiment was weeded once every month and no fertiliser was added.

The trial was harvested by hand when the plants were 6 mo old. The individual plants were assessed for their number of storage roots per plant and root yield per plant. Shoot weight was determined by weighing the stems and leaves of each plant. Plot data on number of tuberous roots and yield was averaged over the plants harvested in each plot.

Specific gravity of root samples was measured on an individual plant basis. Dry matter content was determined indirectly based on the correlation between root specific gravity and dry matter (Kawano et al, 1987). Measurement of specific gravity was obtained by weighing roots in air and then in water. The weight in water was measured by submerging the roots in a net into a 200 L container with water. Dry matter content (DM %) percentage was determined using the formula:

$$DM\ \% = 158.3 \times \text{weight in air} / (\text{weight in air} - \text{weight in water}) - 142.$$

Dry matter yield (DMY) per hectare was estimated by multiplying the fresh root yield per hectare by the dry matter content (Kawano et al., 1987):

$$DMY = (DM\ \% /100) \times \text{fresh root yield}$$

Harvest index (HI %) was computed as the ratio of root weight to the total harvested biomass per genotype on fresh weight basis:

$$HI\ \% = (\text{root weight}/ \text{biomass}) \times 100$$

Cyanide content in the roots of each genotype was estimated using the semi-quantitative determination (O'Brien et al., 1994). Cyanide content was determined by colour change from pale green to dark brown of the picrate on the paper strip (125 mm Whatman® filter paper).

Reaction to cassava mosaic disease and green mites were assessed on individual F_1 genotypes at 3, 4 and 5 mo after planting. A scale of 1 – no apparent symptoms, 2 – mild symptoms and 3 – severe symptoms was used to rate the genotypes for resistance to cassava mosaic disease (CMD) and green mites.

Data analysis

The parental varieties were considered as a fixed reference population; consequently results only pertain to this set of heterozygous genotypes. Even though the selected parents represent the superior groups for the breeding programme at KARI-Katumani, the inferences drawn from this study are not to be generalised. The REML (residual maximum likelihood) procedure in the Genstat Version 9 statistical software package was used to analyse the data. General combining ability (GCA), effects and

Table 3. Mean square values for yield, secondary traits, disease and pests

Source	df	Mean square value										
		TSW	**RTN**	**RTW**	**RTY**	**Biomass**	**HI**	**DM**	**DMY**	**RCNP**	**CMD**	**CGM**
Crosses	23	1.80*	2.30**	2.53**	2.53**	1.82**	2.36**	1.50*	2.32**	1.84**	2.73**	1.46
GCA (IITA)	5	2.24	5.92**	2.98*	2.98*	2.24*	1.80	2.28*	3.35**	0.19	1.04	2.43*
GCA (LOCAL)	3	1.89*	0.29	0.77	0.77	2.16	0.58	1.17	0.36	0.07	5.17**	0.38
SCA (Local × IITA)	15	0.04*	1.66*	1.74*	1.74	1.61	2.19**	1.34	1.83*	0.02*	2.83**	1.25
ERROR	23	0.30	0.66	0.02	2.21	0.36	6.31	6.25	0.44	0.05	0.01	0.01

*, ** Significant at P≤ 0.05 and P ≤ 0.01 probability, respectively. Shoot weight (TSW kg plant^{-1}), root number (RTN count), root weight (RTW kg plant^{-1}), root yield (RTY t ha^{-1}), total biomass (kg plant^{-1}), harvest index (HI %), dry matter (DM %), dry matter yield (DMY t ha^{-1}), root cyanide content (RCNP score), cassava mosaic disease (CMD score) and cassava green mite attack (CGM score)

Table 4. Proportion (%) of GCA and SCA effects relative to the sum of squares for the crosses.

Trait	GCA (%)		SCA (%)
	IITA	**Local**	**Local × IITA**
Shoot weight (kg plant^{-1})	26.38	13.33	60.30
Root number (count)	53.49	1.55	44.95
Root weight (kg plant^{-1})	34.43	5.32	60.25
Total biomass (kg plant^{-1})	26.76	15.47	57.77
Harvest index (%)	20.69	3.97	75.34
Dry matter content (%)	32.49	9.99	57.52
Dry matter yield (t ha^{-1})	37.03	2.41	60.57
Root cyanide content (score)	17.78	16.61	65.61
Cassava mosaic disease (score)	8.22	24.57	67.21
Cassava green mites (score)	37.94	3.53	58.52
GCA – general combing ability, SCA – specific combing ability			

specific combining ability (SCA) effects were estimated using the following model:

$$Y_{ijk} = \mu + Fg_i + Mg_j + FMs_{ij} + R_k + E_{ijk},$$

Where,

Y_{ijk} is the observed value for a cross between the ith and jth parents in the kth replication;
μ is the general population mean;
Fg_i is the GCA value of the ith maternal parent;
Mg_j is the GCA value of the jth paternal parent;
FMs_{ij} is the SCA value for the cross between the ith and jth parent;
R_k is the replication effect;
E_{ijk} is the experimental error.

In this model, the terms Fg_i and Mg_j estimated GCA effects due to the local varieties and IITA varieties, respectively, while the interaction term, *FMsij*, estimated SCA effects. The GCA and SCA variances provide an indication of the levels of additive and non-additive variance in a population respectively (Falconer and Mackay, 1996). Pearson's phenotypic correlation coefficients were also calculated between root yield and the following: shoot weight, root number, root weight per plant, root yield, biomass yield, harvest index, dry matter content and dry matter yield.

RESULTS

REML analysis of variance for agronomic traits

Among the crosses, significant differences (p<0.05) were identified for shoot weight (TSW) and percentage dry matter content (Table 3). Other traits that were significantly different (p<0.01) were root weight (RTW kg plant^{-1}), root yield (RTY t ha^{-1}), total biomass, harvest index, root dry matter yield and resistance to cassava mosaic disease. However, resistance to cassava green mites was not significantly different. The IITA varieties did not differ significantly for shoot weight, harvest index, root cyanogenic potential and reaction to cassava mosaic disease. Also, the local varieties differed significantly in shoot weight (p<0.05) and reaction to cassava mosaic disease (p<0.01). General combining ability (GCA) effects were estimated for those traits that were significant (Table 4). The SCA effects were significant (p<0.05) for shoot weight, root number, dry matter yield and root cyanide content, while harvest index and reaction to cassava mosaic disease were highly significant

Table 5. GCA effects of genotypes for shoot weight and root number.

Genotypes	Source	Shoot weight			Root number		
		Mean (kg plant^{-1})	GCA (kg plant^{-1})	GCA (SE)	Mean	GCA	GCA (SE)
820001	Local	3.35	-0.37*	0.16	8.63	-0.05	0.23
820058	Local	3.58	-0.14	0.16	8.35	-0.16	0.23
990010	Local	4.18	0.46*	0.16	8.73	0.06	0.23
990014	Local	3.78	0.06	0.16	8.67	0.15	0.23
960249	IITA	3.32	-0.41*	0.19	8.03	-0.48	0.29
990056	IITA	4.26	0.53*	0.19	9.82	1.03*	0.29
990067	IITA	4.11	0.39*	0.19	9.25	0.54*	0.29
990072	IITA	3.51	-0.21	0.19	7.51	-0.99**	0.29
990127	IITA	3.82	0.10	0.19	8.75	0.19	0.29
990183	IITA	3.31	-0.41*	0.19	8.21	-0.30	0.29

*, **, *** Significant at 0.05, 0.01 and 0.001; GCA – general combining ability, SE - standard error.

Table 6. The genotypes GCA effect for root weight.

Genotypes	Source	Root weight		
		Mean (kg plant^{-1})	GCA (kg plant^{-1})	GCA (SE)
820001	Local	1.06	-0.04	0.04
820058	Local	1.04	-0.05	0.04
990010	Local	1.17	0.08	0.04
990014	Local	1.11	0.01	0.04
960249	IITA	1.20	0.10	0.05
990056	IITA	1.03	-0.07	0.05
990067	IITA	1.24	0.14*	0.05
990072	IITA	1.10	0.00	0.05
990127	IITA	1.05	-0.05	0.05
990183	IITA	0.97	-0.13*	0.05

*, **, *** Significant at 0.05, 0.01 and 0.001; GCA – specific combining ability, SE – standard error.

the sum of squares for crosses between the local and IITA varieties were very variable. The local varieties contributed less GCA effects for most of the traits, except for the reaction to cassava mosaic disease, for which they contributed 24.57%. The SCA effects were more important for most of the traits except for root number, which had 53.49% GCA from the IITA lines (Table 4).

General combining ability

Among the parental genotypes, 990056 from IITA had the highest GCA effects for shoot weight and root number. Although the GCA values were low, some progenies from the crosses of the 990010 (Local) and 990056 and 990067 (both IITA) had positive and significant ($P<0.005$) GCAs for shoot weight, while 990056 and 990067 had significant GCAs for root number (Table 5). The GCA effects for the mean root number were significant for the IITA varieties 990056 and 990067 (Table 5).

The local parental genotypes had non-significant GCA effects for root yield (Table 6). However, among the IITA varieties, 990067 had the highest, significant ($P<0.005$) GCA effects for root weight per plant (Table 6).

Total biomass GCA effects for 990056 and 990067 (IITA) were significant ($p=0.05$). Genotype 960249 had the highest and significant ($P<0.01$) GCA effects for harvest index (Table 7).

The GCA effects for dry matter content were quite low except for 990127, which was significant ($P<0.05$) and positive. In dry matter yield, only the highest yielding genotype, 990067, had positive and significant ($P<0.01$) GCA effects (Table 8).

The local varieties, 820058 and 990010, had significant GCA effects of ($P<0.05$) and ($P<0.01$), respectively, for low and high root cyanide content respectively (Table 9). The two local cultivars, 990014 and 620001, had significant (negative and positive, respectively) GCA effects for reaction to cassava mosaic diseases.

Table 7. Parental varieties GCA effects and standard errors for biomass and harvest index.

Genotypes	Source	Biomass (kg plant^{-1})			Harvest index (%)		
		Mean	GCA	GCA (SE)	Mean	GCA	GCA (SE)
820001	Local	4.41	-0.41*	0.17	25.17	1.24	0.73
820058	Local	4.62	-0.20	0.17	23.24	-0.7	0.73
990010	Local	5.36	0.54**	0.17	24.00	0.07	0.73
990014	Local	4.89	0.06	0.17	23.33	-0.60	0.73
960249	IITA	4.52	-0.30	0.21	26.66	2.72**	0.89
990056	IITA	5.28	0.46*	0.21	22.95	-0.98	0.89
990067	IITA	5.35	0.53*	0.21	23.85	-0.09	0.89
990072	IITA	4.61	-0.21	0.21	24.30	0.36	0.89
990127	IITA	4.87	0.05	0.21	22.62	-1.32	0.89
990183	IITA	4.29	-0.53*	0.21	23.23	-0.71	0.89

*, **, *** Significant at 0.05, 0.01 and 0.001; GCA – general combining ability, SE – standard error.

Table 8. The genotype GCA effects for dry matter content and dry matter yield.

Genotypes	Source	Dry matter content (%)			Dry matter yield (t ha^{-1})		
		Mean	GCA	GCA (SE)	Mean	GCA	GCA(SE)
820001	Local	38.23	0.07	0.72	4.30	-0.13	0.20
820058	Local	38.95	0.79	0.72	4.30	-0.11	0.20
990010	Local	38.04	-0.12	0.72	4.70	0.28	0.20
990014	Local	37.43	-0.73	0.72	4.40	-0.10	0.20
960249	IITA	37.77	-0.39	0.88	5.00	0.06	0.20
990056	IITA	38.26	0.10	0.88	4.20	-0.20	0.20
990067	IITA	38.75	0.59	0.88	5.10	0.60**	0.20
990072	IITA	35.08	-3.08**	0.88	4.20	-0.30	0.20
990127	IITA	40.01	1.85*	0.88	4.20	-0.20	0.20
990183	IITA	39.09	0.93	0.88	4.00	-0.50*	0.20

*, **, *** Significant at 0.05, 0.01 and 0.001; GCA – general combining ability, SE – standard error.

Table 9. Genotype GCA for root cyanide ratio and reaction to cassava mosaic disease.

Genotypes	Source	Root cyanide ratio			Cassava mosaic disease		
		Mean	GCA	GCA (SE)	Mean	GCA	GC (SE)
820001	Local	4.26	-0.07	0.07	1.22	0.11**	0.03
820058	Local	4.16	-0.17*	0.07	1.09	-0.02	0.03
990010	Local	4.55	0.22**	0.07	1.08	-0.03	0.03
990014	Local	4.36	0.03	0.07	1.05	-0.06*	0.03
960249	IITA	4.21	-0.12	0.08	1.07	-0.04	0.03
990056	IITA	4.49	0.15	0.08	1.13	0.03	0.03
990067	IITA	4.37	0.04	0.08	1.09	-0.02	0.03
990072	IITA	4.31	-0.02	0.08	1.13	0.02	0.03
990127	IITA	4.20	-0.13	0.08	1.16	0.05	0.03
990183	IITA	4.41	0.08	0.08	1.06	-0.04	0.03

*, **, *** Significant at 0.05, 0.01 and 0.001; GCA – general combining ability, SE – standard error.

Table 10. Mean and SCA effects of crosses for shoot weight (kg plant^{-1}), root number and root weight (kg plant^{-1}).

Cross	Shoot weight		Root number		Root weight	
	Mean	SCA	Mean	SCA	Mean	SCA
820001 × 960249	3.43	0.49	8.47	0.50	1.14	-0.02
820001 × 990056	3.33	-0.55	9.69	0.13	0.94	-0.05
820001 × 990067	3.46	-0.28	7.96	-1.83**	0.97	-0.23*
820001 × 990072	3.62	0.49	7.82	0.36	1.12	0.05
820001 × 990127	2.95	-0.50	10.38	1.53*	1.11	0.10
820001 × 990183	3.30	0.37	7.47	- 0.69	1.09	0.16
820058 × 960249	3.88	0.71	7.00	-0.87	1.11	-0.03
820058 × 900056	3.58	-0.53	10.47	1.09	1.24	0.26**
820058 × 900067	3.96	0.00	9.41	0.52	1.17	-0.02
820058 × 990072	3.24	-0.12	6.87	-0.49	1.02	-0.03
820058 × 990127	3.75	0.07	7.74	- 0.81	0.80	-0.19
820058 × 990183	3.04	-0.12	8.60	0.55	0.92	0.01
990010 × 960249	2.58	-1.19*	8.82	0.73	1.35	0.07
990010 × 990056	5.70	0.99*	8.73	-1.87**	0.99	-0.12
990010 × 990067	5.38	0.81*	9.92	0.81	1.46	0.15
990010 × 990072	4.11	0.14	8.47	0.90	1.27	0.10
990010 × 990127	3.68	-0.60	8.11	-0.65	0.96	-0.16
990010 × 990183	3.63	-0.14	8.33	0.07	1.01	-0.04
990014 × 960249	3.37	-0.01	7.82	-0.36	1.20	-0.02
990014 × 990056	4.41	0.10	10.39	0.65	0.95	-0.09
990014 × 990067	3.65	-0.52	9.69	0.49	1.36	0.11
990014 × 990072	3.05	-0.51	6.89	-0.78	0.99	-0.12
990014 × 990127	4.92	1.04*	8.78	- 0.08	1.32	0.26*
990014 × 990183	3.26	-0.10	8.43	0.07	0.86	-0.13
Statistics						
Mean	3.72		8.59		1.10	
SED	0.68		1.01		0.18	
SCA SE		0.39		0.57		0.11
Correlation		0.75		0.66		0.77

*, ** Significant at 5 and 1%, respectively; SCA - specific combining ability.

Specific combining ability effects

The crosses had an average TSW of 3.72 kg plant^{-1}, with a range between 2.58 and 5.70 kg plant^{-1} (Table 10). The SCA effects of crosses were significant (P<0.05) and positive for crosses 990014 × 990127, 990010 × 990056 and 990010 × 990067. Other significantly different SCA effects were negative, for example, cross 990010 × 960249 (Table 10). There was significant interaction (p<0.05) between the local and IITA varieties in RTN (Table 3). The specific combining abilities (SCA) effects of RTN were significant (P<0.01) but negative for 990010 × 990056 and 820001 × 990067, while cross, 820001 × 990127 had a positive and significant SCA (P<0.05) (Table 10). Root weight per plant ranged from 0.80 to 1.46 kg/plant (Table 10). A few of the crosses, 990014 × 990127 and 820058 × 900056, had positive and significant (P<0.05 and 0.01, respectively) SCA effects, while for cross 820001 × 990067, this was negative (Table 10).

Biomass of the crosses ranged from 3.93 to 6.85 kg plant^{-1} (Table 11). The SCA effects for biomass were significant and positive (P<0.01) for the crosses 990014 × 990127; 990010 × 990056; and 990010 × 990067. The SCA effects of 990010 × 960249 were negative and significant (Table 11). The harvest index of all the crosses was low, ranging from 18.08 to 32.85% with an overall average of 23.93% (Table 11). The SCA effects for harvest index were significant and positive for 820001 × 990127, 820058 × 990056 and 990010 × 960249 but negative for 820058 × 990127 and 820058 × 960249.

Dry matter content of all the crosses ranged from 32 to 42% with an overall average of 38% (Table 12). The SCA effects for dry matter among the crosses were all significant

Table 11. Mean and SCA effects of the crosses for the agronomic traits, total biomass (kg plant^{-1}) and percentage harvest index.

Cross	Biomass		Harvest index	
	Mean	SCA	Mean	SCA
820001 × 960249	4.58	0.47	25.38	-2.51
820001 × 990056	4.27	-0.60	23.17	-1.02
820001 × 990067	4.43	-0.52	23.54	-1.54
820001 × 990072	4.74	0.54	24.68	-0.85
820001 × 990127	4.06	-0.41	29.54	5.69**
820001 × 990183	4.39	0.51	24.70	0.24
820058 × 960249	5.03	0.70	22.43	-3.53*
820058 × 900056	4.81	-0.28	27.65	5.40**
820058 × 900067	5.13	-0.02	23.90	0.75
820058 × 990072	4.26	-0.15	24.76	1.16
820058 × 990127	4.55	-0.13	18.08	-3.84*
820058 × 990183	3.96	-0.13	22.58	0.05
990010 × 960249	3.93	-1.13*	32.85	6.13**
990010 × 990056	6.69	0.87*	21.08	-1.94
990010 × 990067	6.85	0.95*	21.98	-1.94
990010 × 990072	5.38	0.23	23.76	-0.60
990010 × 990127	4.64	-0.77	20.27	-2.42
990010 × 990183	4.67	-0.15	24.06	0.77
990014 × 960249	4.54	-0.04	25.96	-0.09
990014 × 990056	5.36	0.01	19.91	-2.44
990014 × 990067	5.01	-0.41	25.97	2.73*
990014 × 990072	4.04	-0.63	23.98	0.29
990014 × 990127	6.24	1.30**	22.58	0.57
990014 × 990183	4.12	-0.23	21.57	-1.05
Statistics				
Mean	4.82		23.93	
SED	0.74		3.11	
SCA SE		0.42		1.78
Correlation		0.74		0.86

*, ** Significant at 5 and 1% respectively; SCA – specific combining ability.

significant (P<0.01) except for 820001 × 990072 and 820058 × 9900127 (Table 12). At 6 mo, the crosses produced from 3.20 to 6.20 t ha^{-1} had root dry matter yield (Table 12). The SCA effects for dry matter yield of most crosses were not significant except for crosses 990014 × 990067 and 990014 × 990127 (P<0.05). The root cyanide content of 6 mo old cassava plants had a range of 4 to 5. The SCA effects for root cyanide content were significant (P<0.05) and positive for 820001 × 990127, and 820058 × 900056; and negative for 820058 × 990127 (Table 12).

Phenotypic correlations

The phenotypic correlations among the family averages for shoot weight, root yield, root weight and number, dry matter and biomass evaluated in this study are presented in Table 13. Most of the traits were positively and significantly correlated, except for dry matter content with harvest index, cyanide content, harvest index with biomass and shoot weight, which were negatively correlated. Biomass was highly correlated with shoot weight (0.969). However, root weight was highly correlated with dry matter yield and harvest index.

DISCUSSION AND CONCLUSION

The aim of the study was to generate a segregated population from crosses between the late bulking local and the early IITA varieties to study gene action for root yield and related traits. Crosses were segregated for shoot weight, root number, root weight, root yield, early

Table 12. Mean and SCA effects of the crosses for the agronomic traits, dry matter content (%), dry matter yield (t ha^{-1}) and root cyanide content SCA - specific combining ability.

Cross	Dry matter content		Dry matter yield		Root cyanide content	
	Mean	SCA	Mean	SCA	Mean	SCA
820001 × 960249	39.44	1.61**	4.80	-0.10	4.19	0.05
820001 × 990056	40.74	2.41**	4.00	-0.10	4.33	-0.08
820001 × 990067	39.79	0.97**	4.00	-0.90	4.10	-0.19
820001 × 990072	35.25	0.10	4.50	0.40	3.94	-0.30
820001 × 990127	37.12	-2.96**	4.30	0.20	4.53	0.40*
820001 × 990183	37.02	-2.13**	4.50	0.60	4.48	0.13
820058 × 960249	36.80	-1.76**	4.90	0.00	4.15	0.11
820058 × 900056	37.74	-1.31**	4.60	0.50	4.71	0.40*
820058 × 900067	40.99	1.45**	5.10	0.10	3.98	-0.22
820058 × 990072	35.09	-0.78**	3.90	-0.20	4.38	0.24
820058 × 990127	40.85	0.05	3.50	-0.70	3.51	-0.51*
820058 × 990183	42.22	2.35**	4.10	0.20	4.22	-0.02
990010 × 960249	39.53	1.88**	5.90	0.60	4.47	0.05
990010 × 990056	35.35	-2.79**	4.50	0.00	4.55	-0.15
990010 × 990067	33.99	-4.64**	5.00	-0.30	4.83	0.25
990010 × 990072	38.28	3.32**	5.10	0.60	4.37	-0.16
990010 × 990127	40.53	0.64*	3.80	-0.70	4.64	0.23
990010 × 990183	40.56	1.60**	4.10	-0.20	4.43	-0.21
990014 × 960249	35.30	-1.73**	4.60	-0.40	4.03	-0.20
990014 × 990056	39.22	1.69**	3.80	-0.30	4.35	-0.16
990014 × 990067	40.23	2.22**	6.20	1.10*	4.56	0.16
990014 × 990072	31.72	-2.63**	3.30	-0.80	4.55	0.21
990014 × 990127	41.54	2.27**	5.30	1.20*	4.12	-0.11
990014 × 990183	36.54	-1.81**	3.20	-0.70	4.54	0.10
Statistics						
Mean	38.16		4.50		4.33	
SED	1.61		0.85		0.29	
SCA SE		0.11		0.50		0.17
Correlation		0.79		0.78		0.79

*, ** Significant at 5 and 1%, respectively.

early shoot vigour, the breeder should select and identify lines that combine well. Families 990010 and 990014 had the highest shoot weight and their crosses, 990010 × 990056; 990014 × 990072; 990014 × 990056; and 990014 × 990127 had the highest positive SCA effects, suggesting that these two parents could belong to two separate heterotic groups that can be used for future breeding for early shoot vigour.

GCA effects (53%) were mainly responsible for determining the root numbers; but a breeder should also consider SCA effects, which accounted for 45% of the variation. The small difference between GCA and SCA effects suggested that it is possible to breed for increased root yield by selecting parents with high GCA for root number. Alternatively, the breeder can use germplasm that combines well for increased root numbers. Our results were in agreement with previous studies. Whyte (1985) reported that both additive and non-additive gene action influenced root number. Root number was found to be positively correlated (r = 0.33) with root yield, indicating that selection for large number of roots would increase root yield. Kawano et al. (1987) obtained similar results.

Predominantly, SCA (at 60% of crosses variance) controlled root yield, indicating the importance of non-additive gene action in influencing yield. The GCA, due to IITA varieties, accounted for 34% of crosses variance, indicating that these genotypes made a significant ($p<0.05$) contribution to early root bulking in the crosses. The proportionally higher SCA effects indicated that the individual genotypes of the two groups of parents, IITA and local, combined specifically well for root yield. Perez

Table 13. Phenotypic correlations between yield and secondary traits.

	DMY	%DM	%HI	Biomass	RTW	RTN	TSW
RCNP (score)	0.102**	-0.015**	0.034ns	0.069*	0.104**	-0.044ns	0.043ns
DMY (t ha^{-1})		0.44***	0.501***	0.378***	0.873***	0.361ns	0.186***
DM (%)			-0.026***	0.042ns	0.04ns	0.102**	0.039ns
HI (%)				-0.186***	0.602***	0.089*	-0.353***
Biomass					0.429***	0.29***	0.969***
RTY (t ha^{-1})					1.00***	0.382***	0.206***
RTW (kg)						0.382***	0.206***
RTN (count)							0.22***

RCNP – root cyanide content, DMY - dry matter yield, DM -dry matter content, HI- harvest index, RWT – root weight (kg $plant^{-1}$), RTN –root number per plant, TSW – shoot weight (kg $plant^{-1}$). *, ** - Significantly different from zero at the 0.05 and 0.01 probability levels, respectively (two-tailed test).

et al. (2005) also reported predominance of SCA, while GCA was not significant for yield in a diallel analysis. Jaramillo et al. (2005) reported 59% and 41% for SCA and GCA, respectively, for root yield, which is highly consistent with these findings.

For dry matter yield, 37% of the crosses sum of squares were accounted for by GCA effects mainly due to the IITA varieties, and were significant ($P<0.05$) (Table 19), while SCA was responsible for 61% of the crosses sum of squares, again suggesting the predominance of non-additive gene action. A similar trend was observed with cyanide content with SCA effects accounting for 66% of crosses' sums of squares. Jaramillo et al. (2005) did not measure cyanide content, but reported that SCA accounted for 37%, while GCA explained 63% of the crosses variation in a diallel analysis. However, Perez et al. (2005) reported that GCA was not significant for dry matter content, which supports the predominance of SCA, and thus has no additive effects in determining dry matter content in cassava.

The local varieties had more GCA effects for reaction to cassava mosaic compared to the IITA varieties. In particular, the local genotype 990014 had negative GCA effects which reflect the involvement of additive genes in the resistance it expresses. Resistance was, however, mostly explained by SCA, 67% of crosses sum of squares, suggested predominance of non-additive gene action for disease resistance. There is a need for continuous improvement of genotypes for disease resistance, because the disease is prevalent in all cassava-growing areas in Africa.

Significantly, high correlations between SCA and mean values for all traits of the F_1 progeny indicated that performance of crosses *per se* could be used to predict their SCA values (Tables 10, 11, 12 and 13). Jaramillo et al. (2005) reported similar results.

Harvest index was positively associated with root yield, indicating that selecting high harvest index will not compromise yield. There will be declining returns on selected harvest index in order to increase root yield until a fall off occurs. Redesigning the crop morphology and physiology then becomes necessary. Harvest index is an important trait as it measures the efficiency of a genotype in partitioning dry matter to the storage roots. Positive correlation between root yield and harvest index confirmed previous results (Kawano et al, 1978). There were positive associations among shoot weight, root yield, root weight, root number, dry matter content and biomass, suggesting that breeding for any of these traits will not reduce the desired level of the other.

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