

Article

Combining Ability and Genetic Components of Yield Characteristics, Dry Matter Content, and Total Carotenoids in Provitamin A Cassava F1 Cross-Progeny

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Abstract: Cassava is an important root crop in sub-Saharan Africa, largely cultivated for its starchy edible roots. Biofortified cassava varieties with enhanced provitamin A carotenoid content (PVAC) developed through conventional breeding provide a solution for vitamin A deficiency among vulnerable communities. The aim of this study was to use diallel analysis of six provitamin A cassava genotypes to determine the combining ability, genetic components, heritability, and heterosis of the most important yield characteristics and total carotenoids. Genetic variability for measured characteristics were evident. Fresh root yield was mainly determined by non-additive genetic effects, while dry matter content and total carotenoids were determined by additive effects. Total carotenoids were negatively correlated with fresh root yield, indicating that selection for higher provitamin A content could reduce yield. Mid and higher parent heterosis was seen in some of the crosses for fresh root yield, dry matter content, and total carotenoids. Narrow sense heritability was moderate for fresh root yield and dry matter content, and was high for total carotenoids. This study indicated that yield and dry matter content can be improved in provitamin A cassava but that increased provitamin A content may carry a yield penalty.

Keywords: cassava; heterosis; vitamin A; dry matter content; root yield

1. Introduction

Cassava (*Manihot esculenta* Crantz) is a shrubby perennial crop with edible storage roots, widely cultivated in the tropics, and ranked as the third largest source of calories after wheat and rice in the world [1]. Cassava grows best on well-drained light to medium soils, with a pH of 4.5–7.5. It is well adapted to various environments with low input amendment requirements and can generally withstand biotic and abiotic stress [2,3]. Storage root yield is the key objective of cassava breeding programs and farmers attach the highest importance to good storage root yield with higher dry matter content (DMC) [4–6]. Increasing emphasis is being placed on the nutritional value of cassava. This has led to the breeding of provitamin A cassava, which has more total carotenoids (TCs) than white cassava. Carotenoids are essential due to their conversion to vitamin A. Vitamin A deficiency (VAD) is a major

global public health challenge, particularly in tropical sub-Saharan Africa [7]. Hence, provitamin A cassava is vital given the status of cassava as a major staple crop in the tropics.

The DMC trait in cassava is a component of storage root yield, a complex quantitatively inherited trait [8]. Knowledge of the mode of inheritance of quantitative characteristics helps breeders to employ suitable breeding strategies for their improvement. The diallel mating design is a popular design employed by cassava breeders to obtain information on the value of the hybrids and parents. It is used to assess the gene action involved in various characteristics [9–14] and in applying appropriate selection procedures. It also helps to understand heterotic patterns of progeny at an early stage of hybridization programs [14]. Genetic variation exists among cassava genotypes for all important characteristics, thus providing an opportunity for exploiting this variation through selection [15]. The predominance of additive gene effects in controlling the expression of DMC has been previously reported [12]. This was confirmed by another study [14] that reported additive gene effects to be double that of non-additive gene action for DMC, while non-additive genetic effects were relatively higher for root yield. The yellow pulp color, indicating beta-carotene in cassava, was found to be controlled by non-additive gene effects [3]. Hybrid vigor for root yield over better-parent values and root yield performance associated with heterosis for yield components has been reported [15], indicating that hybrids can be exploited in heterosis breeding in order to develop superior genotypes. Heritability plays a predictive role in breeding, expressing the reliability of phenotype as a guide to breeding value [16,17]. Genetic advance is an important selection parameter that explains the degree of gain obtained in a characteristic under particular selection pressure. High genetic advance coupled with high heritability estimates offers the opportunity to predict the effect of selecting superior genotypes [18,19]. This aids breeders in a selection program to identify the best responses based on a given selection intensity, for genetic improvement of characteristics [20].

The objective of this study was to do a diallel analysis of six yellow-fleshed parents to determine the combining ability and gene action controlling the expression for TC, storage root yield, and percentage DMC of storage roots, and to estimate the heterosis relative to the mid parent (MPH) and better parent (BPH) for TC, storage root yield, and percentage DMC of storage roots.

2. Materials and Methods

2.1. Experimental Site

The experiment was conducted at the International Institute of Tropical Agriculture (IITA), at Ibadan and Ikenne research stations in 2012–2015. Ibadan, Oyo State is located at latitude 7°24' N, longitude 3°55' E, and altitude 273 m above sea level while Ikenne, Ogun State is located on latitude 6°53' N, longitude 3°42' E, and altitude 60 m above sea level. Both locations are in the southern rainforest vegetation belt of Nigeria and are characterized by nitosol soils with an annual rainfall range of about 1200–1515 mm and temperature range of about 22–32 °C.

2.2. Experimental Material

The experimental material comprised of six elite yellow cassava parental genotypes (Table 1) (details provided at <https://cassavabase.org/>). The genotypes were all IITA material, selected for provitamin A content, early bulking, yield, and yield-related characteristics. The pedigree shows the two parents that were crossed (female to male) to obtain each of these genotypes. All the genotypes were full-sibs except for genotype IITA-TMS-IBA070337, which is a half-sib with high DMC. The first three genotypes are part of the first group of biofortified cassava varieties released in Nigeria.

Table 1. Pedigree information of the six parents used in this study.

S/N	Parent	Female	Male	Pedigree
1	IITA-TMS-IBA011368	IITA-TMS-IBA940561	IITA-TMS-IBA940263	IITA-TMS-IBA940561/IITA-TMS-IBA940263
2	IITA-TMS-IBA011371	IITA-TMS-IBA940561	IITA-TMS-IBA940263	IITA-TMS-IBA940561/IITA-TMS-IBA940263
3	IITA-TMS-IBA011412	IITA-TMS-IBA950971	IITA-TMS-IBA940561	IITA-TMS-IBA950971/IITA-TMS-IBA940561
4	IITA-TMS-IBA070337	IITA-TMS-IBA920429		IITA-TMS-IBA920429/
5	IITA-TMS-IBA070553	IITA-TMS-IBA011663	IITA-TMS-IBA011335	IITA-TMS-IBA011663/IITA-TMS-IBA011335
6	IITA-TMS-IBA070593	IITA-TMS-IBA011277	IITA-TMS-IBA990067	IITA-TMS-IBA011277/IITA-TMS-IBA990067

2.3. Generation of F_1 Progenies

The six parental genotypes were planted in a 6×6 half diallel design to generate 15 F_1 full-sib families (Table 2) through controlled pollination of immature flowers following standard procedures [4]. F_1 botanical seeds were harvested three months after pollination. The seeds were placed in a labeled paper bag and stored for three months to break seed dormancy. Seeds were sown directly into a nursery field at $0.25 \text{ m} \times 1 \text{ m}$ intra- and inter-row spacing in a family row plot that was partitioned into a block ridge 20 m long and arranged in a serpentine pattern with no replicates. An alley of 1 m was maintained between families. The resulting F_1 seedlings were harvested at 12 months after planting (MAP). Selection of plants from the nursery field trial for inclusion in the clonal evaluation trial was based on the ability of each plant to produce five to six good plant stakes. A total of 1581 healthy F_1 plants were selected from the nursery trial and advanced to the clonal trial in the second year. For the clonal trial, the F_1 genotypes were cut into stakes of about 20 cm with approximately four to five nodes and planted at a spacing of $0.5 \text{ m} \times 1 \text{ m}$ arranged in an augmented design with no replicates. Parents and checks were included in the trials. Morphological evaluation was carried out at different growth stages (1, 3, 6, 9, and 12 MAP). Selection of plants from the clonal trial for inclusion in the preliminary yield trial stage was based on performance of each clone based on a selection index rating that considers four key characteristics (TC, DMC, cassava mosaic disease resistance, and plant architecture). Forty clones per family (for most families) were obtained, but there were cases where some clones failed to develop or died and thus could not be evaluated.

Table 2. Frequency table of the size of each family.

S/N	Genotype	N
1	I011368/I011368	4
2	I011368/I011371	28
3	I011368/I011412	80
4	I011368/I070337	42
5	I011368/I070553	32
6	I011371/I011371	4
7	I011371/I011412	64
8	I011371/I070337	42
9	I011371/I070553	56
10	I011412/I011412	4
11	I011412/I070337	28
12	I070337/I070337	4
13	I070553/I011412	40
14	I070553/I070337	42
15	I070553/I070553	4
16	I070593/I011368	66
17	I070593/I011371	62
18	I070593/I011412	83
19	I070593/I070337	52
20	I070593/I070553	42
21	I070593/I070593	6

2.4. Experimental Design

The preliminary yield trial was arranged in a randomized complete block design with two replicates. Planting was done in September 2014. A total of 379 clones consisting of the 15 cross progenies with the six parents were included in the respective plots of each replicate. Each plot consisted of a single row of 10 plants for each of the clones. The spacing between plants was 0.8 m × 1 m. The field was kept free of weeds for the duration of the growing cycle and neither fertilizer nor irrigation was applied.

2.5. Data Collection

Data were collected at harvest (12 MAP). Eight central plants, excluding the first and last plants in a plot, were assessed for their number of storage roots per plant, root weight (kg plant⁻¹), and total shoot weight (kg plant⁻¹). Storage root yield (t ha⁻¹), DMC (%), and harvestable index were estimated [21]. Total carotenoids (µg g⁻¹) in fresh weight were estimated following the IITA standard laboratory procedure, using the iCheck Device [22].

2.6. Data Analysis

The data were analyzed using SAS version 9.3 [23]. Diallel analysis was done following method 2, model 1 of Griffing [24] to determine the combining ability and separate components of genetic variance. The mixed model procedure based on the restricted maximum likelihood (REML) estimation method was fitted to the data, where the replication effect is considered fixed, while parent and cross effects were considered random, to estimate the GCA and SCA variance components, respectively [25].

The distribution of crosses in relation to GCA and SCA effects was determined by denoting significant positive combining ability effects as high, non-significant as average, and significantly negative as low, for fresh root weight, DMC, and TC [15]. The GCA/SCA ratio of mean squares for the studied characteristics was determined to predict the gene effects for a trait [14,26]. Baker's prediction ratio [27] was used to determine progeny performance. The closer this ratio is to one, the better the chances of predicting progeny performance based on GCA. A value of less than 1 was taken as predominance of non-additive gene action, and higher than 1 as predominance of additive gene action. Heterosis relative to mid-parent and better parent values were estimated as deviation of the F₁ value from the mid-parent (MP) and the better-parent (BP) values, respectively [28].

Phenotypic correlations (r_p) were estimated for each pair of characteristics as the Pearson product moment correlation coefficient using the CORR procedure of SAS version 9.3 [23]. Genetic correlations (r_G) were estimated as previously described [29].

Estimates of variance components for genotypic and phenotypic variances were determined from the estimated values of the mean squares obtained from the ANOVA [19]. Phenotypic coefficient of variation (PCV) and genotypic coefficient of variation (GCV) were also estimated [30]. PCV and GCV values of more than 20% were regarded as high, whereas values less than 10% were considered as low and values between 10% and 20% as average [31]. Broad and narrow sense heritability (h^2_b and h^2_n) were calculated as the ratio of genotypic variance to the phenotypic variance. The broad sense heritability estimates were classified as low (0–30%), moderate (30–60%), and high (60% and above) [1]. Expected genetic advance with one cycle of selection and expected genetic advance as a percentage of the mean was calculated to compare the extent of predicted genetic advance of different characteristics under selection [32]. Genetic advance as a percent of the population mean was categorized as follows: less than 10% as low, 10–20% as moderate, and above 20% as high.

3. Results

3.1. Analysis of Variance

Highly significant ($p < 0.001$) genotype effects were observed for all the characteristics (Table 3). Significant SCA mean squares were observed for FYLD and TC. The GCA/SCA ratio was higher

than unity for DMC (12.46) and TC (1.17) but less than one for FYLD (0.16). In addition, the Baker's prediction ratio was low for FYLD (0.24) but closer to 1 for DMC (0.96) and TC (0.70), respectively.

Table 3. Analysis of variance for the genotypes and for the combining ability of the studied characteristics.

Source	Df	Mean Squares		
		FYLD (t ha ⁻¹)	DMC (%)	TC (µg g ⁻¹ Fresh Weight)
Genotype	20	647.99 ***	319.24 ***	30.93 ***
GCA	5	1.65	4.61	0.34
SCA	14	10.32 *	0.37	0.29 *
Residual	723	113.96	39.6	3.19
GCA/SCA	-	0.16	12.46	1.17
Baker's ratio	-	0.24	0.96	0.70

* $p < 0.05$; *** $p < 0.001$, FYLD = Fresh yield, DMC = Dry matter content, TC = Total carotenoids, GCA = general combining ability, SCA = specific combining ability.

3.2. Mean Performance of Parents and Their Hybrid Progenies

Parent IITA-TMS-IBA070337 had the highest mean values for root number, root weight, FYLD, DMC, and harvest index while parent IITA-TMS-IBA070593 had the highest mean value for TC (Table 4). Crosses IITA-TMS-IBA011368/IITA-TMS-IBA070337 had the highest values for root number, root weight, and FYLD while IITA-TMS-IBA011412/IITA-TMS-IBA070337 had the highest value for DMC and harvest index. The highest mean value for TC was recorded in IBA070593/IBA011368. The lowest value for FYLD and DMC was recorded in parent IBA070553, while parent IITA-TMS-IBA070337 recorded the lowest value for TC. For the crosses, IBA011368/IITA-TMS-IBA011371 gave the lowest values for FYLD, while IITA-TMS-IBA070553/IITA-TMS-IBA011412 and IITA-TMS-IBA011368/IITA-TMS-IBA070337 had the lowest values for DMC and TC, respectively.

Table 4. Mean performance of parents and F1 hybrids for studied characteristics.

Genotype	Trait	RTWT	DMC	FYLD	TC	HI
	RTNO	(kg)	(%)	(t ha ⁻¹)	(µg g ⁻¹)	
IITA-TMS-IBA011368	40.500	15.85	21.10	19.81	5.86	0.42
IITA-TMS-IBA011371	27.25	13.70	21.04	17.13	6.66	0.48
IITA-TMS-IBA011412	36.25	24.60	15.53	30.75	6.52	0.52
IITA-TMS-IBA070337	43.75	27.50	35.73	34.38	3.90	0.53
IITA-TMS-IBA070553	22.00	8.75	20.89	10.94	7.96	0.41
IITA-TMS-IBA070593	34.33	19.33	24.23	24.17	9.67	0.45
IITA-TMS-IBA011368/IITA-TMS-IBA011371	20.19	4.91	22.84	6.14	7.59	0.25
IITA-TMS-IBA011368/IITA-TMS-IBA011412	34.39	13.44	21.45	16.79	6.21	0.38
IITA-TMS-IBA011368/IITA-TMS-IBA070337	39.26	16.82	24.82	21.03	4.73	0.4
IITA-TMS-IBA011368/IITA-TMS-IBA070553	23.94	7.67	21.8	9.59	6.98	0.26
IITA-TMS-IBA011371/IITA-TMS-IBA011412	24.16	9.50	23.37	11.88	6.46	0.33
IITA-TMS-IBA011371/IITA-TMS-IBA070337	34.69	15.48	28.29	19.35	5.40	0.42
IITA-TMS-IBA011371/IITA-TMS-IBA070553	25.80	10.26	23.24	12.82	6.08	0.32
IITA-TMS-IBA011412/IITA-TMS-IBA070337	16.30	10.43	29.40	13.04	5.14	0.51
IITA-TMS-IBA070553/IITA-TMS-IBA011412	28.40	9.99	18.71	12.48	7.07	0.33
IITA-TMS-IBA070553/IITA-TMS-IBA070337	30.12	11.09	24.76	13.86	6.10	0.33
IITA-TMS-IBA070593/IITA-TMS-IBA011368	23.29	8.15	26.15	10.19	8.13	0.29
IITA-TMS-IBA070593/IITA-TMS-IBA011371	22.97	8.85	23.86	11.06	7.11	0.32
IITA-TMS-IBA070593/IITA-TMS-IBA011412	28.27	13.6	24.89	17.00	6.69	0.38
IITA-TMS-IBA070593/IITA-TMS-IBA070337	32.18	14.08	29.35	17.61	5.93	0.33
IITA-TMS-IBA070593/IITA-TMS-IBA070553	26.74	10.10	24.98	12.63	6.96	0.33
Grand mean	29.28	13.05	24.12	16.32	6.53	0.38
SE±	1.57	1.21	0.92	1.51	0.27	0.02

RTNO = Root number, RTWT = Root weight, FYLD = Fresh yield, DMC = Dry matter content, TC = Total carotenoids, HI = Harvest Index, SE± = Standard error.

3.3. Combining Ability

Parent IBA070337 had a highly significant ($p < 0.01$) positive GCA effect for DMC and a significant ($p < 0.05$) negative GCA effect for TC (Table 5). IITA-TMS-IBA011368/IITA-TMS-IBA070337 and IITA-TMS-IBA011371/IITA-TMS-IBA070337 had significant positive SCA effects for FYLD, while IITA-TMS-IBA011368/IITA-TMS-IBA011371 had significant negative SCA effects for FYLD (Table 6). For TC, significant positive SCA effects were exhibited for IITA-TMS-IBA070593/IITA-TMS-IBA011368 while significant but negative SCA effects were also recorded for IITA-TMS-IBA011368/IITA-TMS-IBA070337 for FYLD.

Table 5. Estimates of parental general combining ability effects for fresh yield, dry matter content, and total carotenoids.

Parent	FYLD				DMC				TC			
	Estimate	SE±	df = 714 t Value	Pr > t	Estimate	SE±	df = 507 t Value	Pr > t	Estimate	SE±	df = 721 t Value	Pr > t
IITA-TMS-IBA011368	-0.35	1.09	-0.33	0.745	-1.16	1.04	-1.11	0.267	0.28	0.34	0.82	0.415
IITA-TMS-IBA011371	-0.61	1.09	-0.56	0.575	-0.17	1.04	-0.17	0.868	0.07	0.34	0.19	0.847
IITA-TMS-IBA011412	0.26	1.09	0.24	0.814	-1.62	1.03	-1.57	0.116	-0.13	0.34	-0.37	0.708
IITA-TMS-IBA070337	1.36	1.09	1.25	0.212	3.23**	1.04	3.09	0.002	-0.95**	0.34	-2.79	0.005
IITA-TMS-IBA070553	-0.62	1.09	-0.56	0.573	-1.98	1.05	-1.90	0.059	0.20	0.34	0.59	0.554
IITA-TMS-IBA070593	-0.04	1.09	-0.04	0.972	1.70	1.03	1.65	0.099	0.53	0.34	1.58	0.116

** $p < 0.01$. FYLD = Fresh yield, DMC = Dry matter content, TC = Total carotenoids.

3.4. Estimates of Heterosis

Estimated values for MPH ranged from -49.81% to 30.51% for FYLD, -15.1% to 10.93% for DMC, and -19.12% to 12.79% for TC while values for BPH ranged from -58.92% to 21.67% for FYLD, -16.82% to 7.94% for DMC, and -23.74% to 7.47% for TC (Table 7). The cross with the best and positive MPH and BPH values for FYLD was IITA-TMS-IBA011368/IITA-TMS-IBA070337, while for DMC it was for IITA-TMS-IBA070593/IITA-TMS-IBA070337. For TC, IITA-TMS-IBA011368/IITA-TMS-IBA011371 and IITA-TMS-IBA011368/IITA-TMS-IBA070553 had the best MPH and BPH, respectively.

3.5. Estimates of the Phenotypic and Genetic Correlations

Genetic correlations (r_G) were higher than phenotypic correlations for all measured characteristics (Table 8). HI showed a positive and high correlation with the number of roots per plant and FYLD. A negative correlation was observed for DMC and TC with FYLD.

Table 6. Estimates of specific combining ability effects for fresh yield, dry matter content, and total carotenoids.

Cross	FYLD		df = 714		DMC		df = 507		TC		df = 721	
	Estimate	SE±	t Value	Pr > t	Estimate	SE±	t Value	Pr > t	Estimate	SE±	t Value	Pr > t
IITA-TMS-IBA011368/IITA-TMS-IBA011371	-4.75 *	2.04	-2.32	0.020	-0.12	0.58	-0.22	0.83	0.57	0.38	1.49	0.136
IITA-TMS-IBA011368/IITA-TMS-IBA011412	2.72	1.74	1.57	0.118	-0.15	0.55	-0.27	0.79	-0.33	0.35	-0.93	0.354
IITA-TMS-IBA011368/IITA-TMS-IBA070337	4.93 **	1.90	2.59	0.010	-0.30	0.56	-0.53	0.60	-0.82	0.37	-2.22	0.027
IITA-TMS-IBA011368/IITA-TMS-IBA070553	-2.38	2.00	-1.19	0.233	0.17	0.58	0.29	0.78	0.07	0.38	0.18	0.854
IITA-TMS-IBA011371/IITA-TMS-IBA011412	-1.33	1.79	-0.74	0.459	0.04	0.56	0.06	0.95	0.07	0.36	0.20	0.839
IITA-TMS-IBA011371/IITA-TMS-IBA070337	3.80	1.90	2.00	0.046	0.25	0.56	0.44	0.66	-0.11	0.37	-0.31	0.755
IITA-TMS-IBA011371/IITA-TMS-IBA070553	0.21	1.83	0.12	0.908	0.17	0.56	0.3	0.77	-0.52	0.36	-1.44	0.151
IITA-TMS-IBA011412/IITA-TMS-IBA070337	-1.69	2.04	-0.83	0.409	0.38	0.58	0.65	0.52	-0.16	0.38	-0.42	0.674
IITA-TMS-IBA070553/IITA-TMS-IBA011412	-0.74	1.91	-0.39	0.697	-0.44	0.57	-0.77	0.44	0.44	0.37	1.19	0.234
IITA-TMS-IBA070553/IITA-TMS-IBA070337	-0.54	1.90	-0.28	0.776	-0.13	0.57	-0.22	0.83	0.33	0.37	0.90	0.368
IITA-TMS-IBA070593/IITA-TMS-IBA011368	-2.73	1.79	-1.53	0.127	0.31	0.56	0.56	0.58	0.74 **	0.36	2.09	0.037
IITA-TMS-IBA070593/IITA-TMS-IBA011371	-1.75	1.80	-0.97	0.331	-0.34	0.56	-0.61	0.54	0.05	0.36	0.14	0.892
IITA-TMS-IBA070593/IITA-TMS-IBA011412	2.63	1.73	1.52	0.128	0.04	0.55	0.08	0.94	-0.13	0.35	-0.38	0.706
IITA-TMS-IBA070593/IITA-TMS-IBA070337	2.00	1.88	1.06	0.288	0.06	0.56	0.1	0.92	-0.06	0.36	-0.150	0.880
IITA-TMS-IBA070593/IITA-TMS-IBA070553	-0.39	1.96	-0.20	0.843	0.07	0.57	0.12	0.91	-0.15	0.37	-0.400	0.688

* $p < 0.05$, ** $p < 0.01$, FYLD = Fresh yield, DMC = Dry matter content, TC = Total carotenoids.

Table 7. Heterosis (%) relative to mid parents (MPH) and better parents (BPH) for studied characteristics.

Cross	FYLD		DMC		TC	
	(t ha ⁻¹)		(%)		(µg g ⁻¹) Fresh Weight	
	MPH	BPH	MPH	BPH	MPH	BPH
IITA-TMS I011368/IITA-TMS I011371	-49.81	-58.92	-0.91	-2.95	12.79	4.58
IITA-TMS I011368/IITA-TMS I011412	12.05	11.72	-4.79	-4.94	-2.55	-5.12
IITA-TMS I011368/IITA-TMS I070337	30.51	21.67	-0.25	-8.74	-19.12	-23.74
IITA-TMS I011368/IITA-TMS I070553	-28.62	-35.83	-5.28	-7.06	9.35	6.25
IITA-TMS I011371/IITA-TMS I011412	-18.64	-20.97	-1.26	-5.92	2.48	-1.37
IITA-TMS I011371/IITA-TMS I070337	23.03	11.96	8.72	4.02	-6.40	-10.75
IITA-TMS I011371/IITA-TMS I070553	-1.73	-9.53	-3.75	-6.45	-3.65	-7.45
IITA-TMS I011412/IITA-TMS I070337	-14.01	-24.57	3.90	0.00	-3.27	-6.34
IITA-TMS I070553/IITA-TMS I011412	-11.52	-16.95	-15.10	-16.82	7.72	7.47
IITA-TMS I070553/IITA-TMS I070337	-9.05	-19.83	1.50	-8.96	1.06	-7.28
IITA-TMS I070593/IITA-TMS I011368	-15.07	-26.19	0.81	0.00	7.40	0.00
IITA-TMS I070593/IITA-TMS I011371	-5.13	-19.87	-3.16	-7.28	-0.37	-2.09
IITA-TMS I070593/IITA-TMS I011412	17.92	13.11	3.21	-3.27	-1.30	-4.55
IITA-TMS I070593/IITA-TMS I070337	13.25	1.86	10.93	7.94	-5.07	-15.34
IITA-TMS I070593/IITA-TMS I070553	-1.87	-8.56	1.59	-2.91	2.45	-0.72

FYLD = Fresh root yield, DMC = Dry matter content, TC = Total carotenoids.

Table 8. Estimates of phenotypic (upper diagonal) and genetic (lower diagonal) correlations for characteristics evaluated in 21 cassava genotypes.

	DMC	TC	FYLD	HI	RTNO	CMD
DMC	-	0.08	0.07	0.15 ***	0.04	-0.06
TC	-0.17 ***	-	-0.16 ***	-0.14 ***	-0.12 ***	-0.07
FYLD	0.16 ***	-0.29 ***	-	0.69 ***	0.74 ***	-0.45 ***
HI	0.17 ***	-0.30 ***	0.80 ***	-	0.47 ***	-0.34 ***
RTNO	0.01	-0.26 ***	0.94 ***	0.63 ***	-	-0.46 ***
CMD	-0.03	-0.08 *	-0.63 ***	-0.44 ***	-0.61 ***	-

* $p < 0.05$, *** $p < 0.001$, DMC = Dry matter content, TC = Total carotenoids, RTNO = Root number, FYLD = Fresh yield, HI = Harvest Index, RTNO = root number, CMD = cassava mosaic disease.

3.6. Estimates of Variance Components, Broad and Narrow Sense Heritability, and Genetic Advance

FYLD, DMC, TC, and cassava mosaic disease (CMD) exhibited high genotypic (σ^2_G) and phenotypic (σ^2_P) variances (Table 9). The genotypic variance was separated into the additive (σ^2_A) and non-additive/dominance (σ^2_D) variance components. Additive variance (σ^2_A) values were higher for DMC, TCC, and CMD than their corresponding non-additive variance (σ^2_D) except for FYLD, where the non-additive variance was higher than its corresponding additive variance. The difference between the σ^2_G and σ^2_P was high for all the characteristics evaluated except for CMD. High genotypic (GCV) and phenotypic (PCV) coefficient of variances were observed for all characteristics except for DMC, which recorded high PCV but average GCV (Table 9). Phenotypic coefficient of variability (PCV) values ranged from 31.24% for TC to 69.24% for FYLD, while the genotypic coefficient of variability (GCV) ranged from 18.50% for DMC to 42.39% for FYLD. PCV values were generally higher than their corresponding GCV values for all the characteristics considered. Broad sense heritability (h^2_b) was higher than the corresponding narrow sense heritability (h^2_n) for all the characteristics. Estimated values of h^2_b values ranged from 22.58% for CMD to 60.58% TC whereas the h^2_n ranged from 5.18% for FYLD to 37.49% for DMC. Genetic advance as a percentage of the mean was high (>20) for all the studied characteristics. This ranged from 24.58 for CMD severity to 53.59 for FYLD.

Table 9. Estimates of genetic variance components, heritability (%), and genetic advance (%) of the studied characteristics in yellow cassava genotypes.

Trait	Mean	Variance Components							Genetic Advance		
		σ^2_A	σ^2_D	σ^2_e	σ^2_P	PCV (%)	GCV (%)	h^2_b (%)	h^2_n (%)	GA	GAM (%)
FYLD	16.32	6.61	41.26	113.96	127.58	69.24	42.39	37.52	5.18	8.75	53.59
DMC	24.12	18.44	1.48	39.60	49.19	29.06	18.50	40.50	37.49	5.86	24.30
TC	6.53	1.36	1.16	3.19	4.16	31.24	24.31	60.58	32.69	2.55	39.05
CMD	2.11	0.20	0.08	1.12	1.24	57.76	25.08	22.58	16.13	0.52	24.58

σ^2_A = Additive genetic variance, σ^2_D = Dominance genetic variance, σ^2_e = Environmental variance, σ^2_P = Phenotypic variance, PCV = Phenotypic coefficient of variation, GCV = Genotypic coefficient of variation, h^2_b = Broad-sense heritability, h^2_n = Narrow-sense heritability, GA = Genetic advance and GAM = Genetic advance as percent of mean.

4. Discussion

The mean performance of the clones within each family showed significant variations. This confirmed the possibility of selection for these characteristics through hybridization of respective parents. A similar trend was reported previously [13,14]. The significant variation in values observed for the genotypes for the different characteristics (Table 4) indicate the presence of genetic variability among the genotypes. High genetic variability for different characteristics has also been reported in other studies [8,13]. The significant estimates of SCA mean squares for FYLD and TC presented in this study indicates that non-additive gene effects are more important than additive gene effects in the control of these characteristics. The significant SCA effects for FYLD observed in this study agreed with previous findings [9,13] while that of TC was in agreement with a previous study [3]. Higher values than unity for the GCA/SCA ratio for DMC and TC is an indication that the additive gene effects make a larger contribution in the control of DMC and TC than non-additive effects, while for FYLD, the non-additive gene effects predominated. Similarly, a Baker's ratio close to one for DMC and TC is an indication that progeny performance is based on GCA [16]. Nonetheless, the predicted GCA/SCA ratio and Baker's prediction ratio may not always project the true picture of the gene action for a trait due to the differential parental ability to combine well. The performance of the crosses with respect to the parental genotypes suggests that progeny performance cannot be predicted from the performance of the parents per se. Performance also depends upon the complex interaction between the genotype and environment [9,16].

GCA and SCA effects show both the magnitude and direction of genetic effects. The significant positive and negative GCA effects recorded for parent IBA070337 for DMC and TC, respectively, indicate that the genotype contributed highly to DMC but very little to TC. Thus, this genotype was the most superior and best general combiner for DMC but a poor combiner for TC. For the cross progenies, the significant positive SCA effects obtained for IITA-TMS-IBA011368/IITA-TMS-IBA070337 and IITA-TMS-IBA070593/IITA-TMS-IBA011368 for FYLD and TC, respectively, indicate that these cross progenies are the best specific combiners for these characteristics. More than one-third of the cross progenies showed desirable positive (though not significant) SCA effects for DMC. This suggests average SCA for DMC. SCA of contrasting parent genotypes used for genetic improvement of a trait can transmit the desirable specific trait to the next generation [10].

There was good mid and better parent heterosis for the studied characteristics in some of the cross progenies. This may indicate that additive and non-additive genetic effects in the crosses are acting in the same direction. It also suggests that these cross progenies can be exploited in heterosis breeding to develop superior genotypes to take full advantage of these specific characteristics. Heterosis over mid and better parents were previously reported for cassava characteristics, which varied according to the cross combinations and measured characteristics, and it played a very important role in cassava performance [9,12,14].

Phenotypic correlation is the correlation of the genotype means for characteristics and this is partitioned into genetic and environmental sources. However, genetic correlation is heritable and of more practical importance. Higher genetic than the phenotypic correlations observed for all evaluated

characteristics is an indication that genetic factors were major contributors to correlations among characteristics, and this is favorable for the selection process. Positive correlation between the harvest index and number of roots per plant ($r_G = 0.63$) and FYLD ($r_G = 0.80$) is an indication that the increase of one trait will simultaneously increase the other. These results agree with previous findings [6], where positive and high genetic correlations between tuberous root yield and shoot biomass yield were reported. The presence of a positive correlation may indicate a balance in the source sink relationship. Negative correlations of TC with DMC and FYLD were observed in this study as was previously reported [33,34], where an inverse relationship of β -carotene content with DMC as well as FYLD was seen.

The higher phenotypic coefficient of variance than the genotypic coefficient of variance observed for all characteristics agrees with a previous study [31]. Considering the benchmark for broad sense heritability (0–30% as low, 30–60% as moderate, and 60% and above as high), h^2_b for CMD severity was low (22.58%), moderate for FYLD (37.52%) and DMC (40.5%), and high for TC (60.58%). The relatively high estimates of broad sense heritability observed for FYLD, DMC, and TC gives an indication that these characteristics are primarily under genetic control. Selection for these characteristics should lead to genetic advance [18]. High heritability of a characteristic makes selection more effective. High heritability (>30) coupled with high genetic advance (>20) as a percent of the mean for FYLD, DMC, and TC gives an indication that selection for genetic improvement of cassava is reliable. High heritability with high genetic advance as a percentage of the mean for plant height and root fresh weight in cassava was previously reported [35].

5. Conclusions

The role of additive and non-additive gene action in the determination and control of FYLD, DMC and TC presented in this study suggests the possibility of effective selection for genetic improvement of cassava as applicable mainly to the genetic makeup of the parents presented. Families from crosses among elite cassava clones were very promising for genetic improvement for multiple important characteristics, taking full advantage of genetic variance inherent in cassava clones for high yield potential. High heritability (>30) with high genetic advance (>20) is important for selection and the genetic improvement of cassava. It is therefore necessary to conduct further studies with the test genotypes in bigger trials and in several locations and seasons to confirm the results presented in this study.

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