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Diallel analysis of early storage root yield and disease resistance traits in cassava (*Manihot esculenta* Crantz)

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ABSTRACT

Little progress has been made in determining the combining ability and gene action controlling early storage root yield (SRY) and disease resistance traits in the Ugandan cassava germplasm. Such information is important in the selection of parents and breeding strategies for an effective breeding programme. The objective of this study was to estimate the general combining ability (GCA) of nine cassava parents and their specific combining ability (SCA) for early SRY and disease resistance traits, as well as to determine the gene action controlling these traits. Thirty-six full-sib cassava families were generated from a 9 × 9 half-diallel mating design and were evaluated in two distinct environments in Uganda using a 3 × 12 row by column design. Family, GCA and SCA effects and their interactions with environments were significantly different for most traits, indicating, respectively significant differences in the mean performances of the families, additive and non-additive gene action in the expression of the traits, and the non-additive influence of the environments. The relative importance of additive and non-additive gene action varied between traits, indicating the need for specific breeding strategies for each trait. Parents with desirable GCA effects for most traits were developed from cassava introductions from South America, highlighting their importance and possibility of widening genetic variability of African cassava germplasm. The GCA effects for the parents did not always correlate with their *per se* performance, implying that selection of parents based on their *per se* performance may not necessarily lead to development of superior hybrids.
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1. Introduction

Cassava (*Manihot esculenta* Crantz) is an important storage root crop worldwide. In Uganda, it is the second most important food crop providing food and income for the majority of smallholder farmers (Ministry of Agriculture, Animal Industry and Fisheries (MAAIF), 2007). Among the key traits farmers look for when selecting cassava cultivars are: high storage root yield, earliness, resistance to pests and diseases, and dry mass content (Tumuhimbise et al., 2012). Early storage root yield (SRY), in particular, is currently a key farmer preferred trait due to its perceived importance of providing quick food and income to farmers, as well as in escaping late season droughts, pests and diseases (Suja et al., 2009; Tumuhimbise et al., 2012). The Root Crops Programme in Uganda (RCP) has responded to farmers' preferences by developing and/or introducing improved cultivars from the International Institute of Tropical Agriculture (IITA) and International Centre for Tropical Agriculture (CIAT) (Kawuki et al., 2011). Nonetheless, some farmers have continued to grow landraces that are important as potential genetic resources for cassava breeding programmes. However, little progress has been done in determining the combining ability and inheritance of agronomic and disease resistance traits of the genotypes grown in Uganda and/or used by the RCP. As a result, there is insufficient information on the combining ability and inheritance of yield and other important traits in cassava in Uganda, a situation that frustrates efforts to improve cassava through breeding.

Traits such as yield are quantitatively inherited and the knowledge about their mode of inheritance helps breeders to employ suitable breeding strategies for their improvement (Calle et al., 2005; Zacarias and Labuschagne, 2010). A number of mating designs including: polycross (Amini et al., 2011); North Carolina (Comstock and Robinson, 1948); line × tester (Basbag et al., 2007) and diallel (Griffing, 1956) have been developed to serve this purpose. Of these designs, the diallel mating design has been widely used by cassava breeders to generate full-sib progeny for genetic studies (Calle et al., 2005; Perez et al., 2005; Cach et al., 2006; Zacarias and Labuschagne, 2010; Kulembeka et al., 2012).

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Diallel analysis provides information on gene action controlling plant traits, general combing ability (GCA) and the specific combining ability (SCA) of parents in crosses (Griffing, 1956). Several analysis methods have been devised for the diallel mating design (Hayman, 1954; Griffing, 1956; Gardner and Eberhart, 1966). Among these methonds, Griffing's (1956) diallel analysis method has been widely used to estimate the GCA of parents and SCA of families in a breeding programme. Estimating GCA of parents helps in developing superior genotypes, while estimating SCA effects, helps in determining the performance of hybrids (Griffing, 1956; Dudley and Moll, 1969; Parkes et al., 2013). Estimation of combining ability also provides knowledge of the gene action controlling traits, which is critical in deciding on the type of breeding methods that would successfully improve the performance of the traits of interest (Dudley and Moll, 1969). The objectives of this study therefore, were: (1) to estimate the combining ability of nine cassava parents for early SRY, resistance to cassava mosaic disease (CMD) and cassava brown streak disease (CBSD), and related traits; and (2) to determine gene action controlling the expression of early SRY, resistance to CMD and CBSD, and related traits. Previous research by Okechukwu and Dixon (2009) and Kamau et al. (2011) has shown that early yielding cassava genotypes are harvested ≤12 months after planting (MAP). Therefore, in that context the performance of the genotypes were evaluated for SRY, defined as early SRY and related traits at 8 MAP.

2. Materials and methods

2.1. Experimental sites

Experiments were conducted at Namulonge and Bulindi Agricultural Research Institutes in Uganda during 2012/13. Namulonge is located in central Uganda at 32°36′E and 0°31′N, at 1134 m above sea level (masl) while Bulindi is located in north-western Uganda at 31°28′E and 01°28′N, at 1230 masl. The two sites experience a bimodal rainfall pattern, with two distinct rainy seasons and dry seasons of nearly equal length. Peak rainfall occurs between March to May and September to November. The minimum and maximum temperature, and mean rainfall for the two sites during the experimental period as well as the soil properties at the commencement of the experiment were recorded (Table 1).

2.2. Plant germplasm

Nine genetically diverse parents (Table 2) were selected from farmers' fields and the RCP at the National Crops Resources Research Institute, Uganda. Parents from farmers' fields were landraces, while parents from the RCP were composed of introductions from IITA and genotypes generated by crossing lines from CIAT with those of Uganda. The selection of parents was based on their *per se* performance for early SRY, dry mass content (DMC), flowering ability and relative degrees of field resistance to CMD and CBSD. Parents were planted in a crossing block under irrigation in paired rows to facilitate generation of 36 full-sib families of F_1 progeny of a 9 × 9 half-diallel design. Controlled pollinations were performed following the standard procedures described by Kawano (1980). Three months after pollination, botanical seeds were harvested and stored in labelled paper bags for three months to break seed dormancy. Afterwards, 100 seeds from each family were germinated in a greenhouse in plastic bags filled with sterile forest topsoil. The resulting seedlings were planted in a seedling evaluation trial (SET) that was laid out as a 6 × 6 triple lattice design with three replications. After harvesting the SET, 30 genotypes per family that produced at least 12 cuttings were planted in clonal evaluation trials (CET) at Namulonge and Bulindi.

2.3. Experimental design

The CET at each site, comprising of 1080 F_1 genotypes, was planted in a 3 × 12 row by column design with three replications. Two 25 cm long cuttings of each selected genotype per family were planted contiguously within the rows of the respective family plots per replication. The trials were planted in the first week of September 2012 at a spacing of 1.0 × 1.0 m between and within rows, providing a population density of 10 000 plants ha^{-1}. The trials were conducted without supplemental irrigation and weeded regularly.

2.4. Data collection

At harvest 8 MAP, plants were individually measured for height (PHT) (cm) and then uprooted. The storage roots of two plants per genotype in a plot were counted and weighed to obtain storage root number (SRN) and mass (SRM) (kg), respectively. Shoot mass (STM) (kg plant^{-1}) of each genotype was obtained by weighing the total shoot (kg). Storage root yield (t ha^{-1}) was estimated from SRM (kg plant^{-1}) as:

$$\text{SRY} = \frac{\text{SRM} \times 10\ \ 000}{1000}$$

Storage root girth (SRG) was measured as the circumference (cm) at the widest point of the mid-section of a storage root. Harvest index (HI) was calculated as the ratio SRM to total plant biomass (TBM) on a fresh mass basis (kg) as:

$$\text{HI} = \frac{\text{SRM}}{\text{TBM}}$$

Percentage storage root DMC was determined by selecting at least two storage roots from a bulk of storage roots per genotype, which were washed, peeled and sliced using a knife. The sliced samples were weighed to obtain 0.1 kg before being dried for 48 h in a forced-drought oven at 80 °C. The dried samples were weighed to obtain the dry mass and DMC% was calculated as:

$$\text{DMC} = \left(\frac{\text{DRM}}{\text{FRM}}\right) \times 100$$

where: DRM = dry storage root mass (kg); FRM = fresh sample storage root mass (kg).

Because the main damage (necrosis) caused by CBSD is to the storage roots, the cassava brown streak disease root necrosis (CBSD–RN) rating was done on storage roots. Six randomly selected storage roots of each genotype per family were sliced and scored for CBSD-RN on a scale of 1 to 5 where: 1 = no visible root necrosis, and 5 = severe root necrosis (Hillocks et al., 1996). Data on cassava mosaic disease severity (CMD-S) were collected per plot at 6 MAP as most cassava genotypes within families expressed severe CMD symptoms beyond 5MAP. The CMD-S assessment was done on a score scale of 1 to 5 where: 1 = no mosaic symptoms, and 5 = very severe mosaic symptoms.

2.5. Data analysis

The data collected for each site were first analysed individually and then the error variances between sites tested for homogeneity using Hartley's Fmax test (Hartley, 1950). As the differences were not significant, an unweighted combined analysis of variance of the data for the two locations was conducted. Data for the respective 36 families were independently averaged for statistical analysis. As it is always the case with most field experiments, a few plants died or failed to develop normally to be evaluated. Hence, in a few F_1 families fewer than 30 clones were actually evaluated in the field in each of the three replications. To deal with this problem,

Table 1
Description of the weather and soil conditions at Namulonge and Bulindi.

Location	Weather data		pH	Soil chemical elements						
	Rainfall (mm)	Temp (°C)		OC	OM	N	P	Ca	Mg	K
	Sept 2012–May 2013	Min–max		%			(ppm)			
Namulonge	1206	15.1–28.5	6.1	4.2	7.3	0.33	0.7	1276.0	762.1	435.7
Bulindi	760	16.9–29.8	6.0	2.6	4.5	0.23	3.2	971.0	334.4	476.4

Table 2
Nine cassava parental lines crossed in a 9 × 9 half-diallel design and their special attributes.

Parent	Entry code	Type	Special positive attributes	Special negative attributes
Bukalasa11	Bukalasa11	Landrace	High DMC, early bulking, sweet	Very *S* to CMD
Nyaraboke	Nyaraboke	Landrace	High DMC, sweet	Very *S* to CMD
TME14	TME14	Improved variety[a]	*R* to CMD, *T* to CBSD, high DMC	Medium bulking
TMS30572	NASE3	Improved variety[a]	*R* to CMD, *T* to CBSD, sweet	Late bulking
FS37-4	CT1	New genotype[b]	*R* to CMD, *T* to CBSD, high yielding	Medium bulking
FS25-5	CT2	New genotype[b]	*R* to CMD, high yielding, early bulking	Very *S* to CBSD
FS7-18	CT3	New genotype[b]	*R* to CMD, early bulking, high DMC	*S* to CBSD
FS27-15	CT4	New genotype[b]	*R* to CMD, *T* to CBSD	Low yield
FS1-4	CT5	New genotype[b]	*R* to CMD, early bulking, sweet	*S* to CBSD

DMC = dry mass content; CMD = cassava mosaic disease; CBSD = cassava brown streak disease.
[a] IITA introductions.
[b] Genotypes developed between CIAT and Uganda lines, *R* = resistant; *T* = tolerant; *S* = susceptible.

harmonic mean instead of arithmetic mean for the families was used (Cach et al., 2005). The analysis of variance (ANOVA) for the traits were done using Genstat 14th edition (Payne et al., 2011). Pearson's phenotypic correlations between traits based on family means were also performed using Genstat 14 version (Payne et al., 2011). The diallel analysis was conducted using the DIALLEL-SAS05 programme (Zhang et al., 2005). Griffing's (1956) diallel method 4, model 1 for a fixed model was fitted to estimate the GCA and SCA:

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + b_k + e_{ijkl}$$

where: Y_{ij} = observed value of the cross between parent i and j; μ = overall mean; g_i = GCA of the parent i; g_j = GCA of the parent j; s_{ij} = SCA of the cross between parents i and j; b_k = effect of the kth block; and e_{ijkl} = experimental error.

The relative importance of GCA and SCA effects for each trait was determined from their percentages of the family sum of squares (SS) due to GCA and SCA (Kulembeka et al., 2012; Were et al., 2012).

3. Results

3.1. Diallel analysis of variance for traits

Environment effects were significantly different for: early SRY, DMC, SRG and CMD-S ($P < 0.001$); PHT and SRN ($P < 0.01$); and CBSD-RN ($P < 0.05$) (Table 3). Family effects weresignificantly different for: HI, DMC, SRG, CBSD-RN and CMD-S ($P < 0.001$); and PHT, early SRY and SRN ($P < 0.01$).

Families SS were partitioned into that due to parents (GCA effects) and the interaction between parents (SCA effects). General combining ability effects weresignificantly different for: HI, early SRY, DMC, SRN, SRG, CBSD-RN and CMD-S ($P < 0.001$); and PHT ($P < 0.01$). Specific combining ability effects were significantly different for: DMC, CBSD-RN and CMD-S ($P < 0.001$); HI and SRG ($P < 0.01$); and early SRY ($P < 0.05$). Environment × family interaction effects were significantly different for: DMC ($P < 0.001$) and PHT ($P < 0.01$). Environment × GCA interaction effects were significantly different for: early SRY ($P < 0.001$) and DMC ($P < 0.01$), while the environment × SCA interaction effects were significantly different for: DMC ($P < 0.01$) and CMD-S ($P < 0.05$).

The proportion of the families SS due to GCA and SCA effects expressed as a percentage provides an indication of the relative importance of additive and non-additive gene effects in the expression of the trait evaluated. The GCA effects accounted for over 50.0% of the variability expressed by the families in DMC, SRG, CBSD-RN and CMD-S, while SCA effects accounted for over 50% of the variability expressed by the families in early SRY, SRN, HI and PHT (Table 3).

3.2. Estimates of general combining ability effects

All five parents of CIAT ancestry had positive GCA effects for early SRY, which were significantly different for CT1 and CT5 ($P < 0.05$) (Table 4). In addition, CT5 had positive and significant GCA effects for: HI and SRN ($P < 0.001$); and PHT ($P < 0.01$), and a negative, significant GCA effect for CMD-S ($P < 0.01$). It, however, recorded an undesirable significant, negative GCA effect for DMC ($P < 0.001$) as well as a positive, but non-significant GCA effect for CBSD-RN. CT1 also had a desirable negative, significant GCA effect for CBSD-RN ($P < 0.05$). With the exception of Nyaraboke, Bukalasa11 and NASE3, the other parents had desirable negative GCA effects for CMD-S, which was expected given the low scores for CMD-S of these parents. TME14 recorded the lowest negative and significant ($P < 0.001$) GCA effect of −0.17 for CMD-S followed by CT2 with a significant ($P < 0.01$) GCA effect of −0.15. Similarly, negative and significant GCA effects for CBSD-RN were recorded in CT4 and NASE3 ($P < 0.001$); and CT1 ($P < 0.05$), and non-significant for Nyaraboke, with CT4 recording the lowest negative GCA effect of −0.58 for the trait. Bukalasa11 had the best positive, significant GCA effect for DMC ($P < 0.001$) and CT5 the best positive, significant GCA effect for PHT ($P < 0.01$). CT2 had the highest significant GCA effect for SRG ($P < 0.01$). Overall, CT5 was the best general combiner for most of the traits assessed.

3.3. Mean performance and estimates of specific combining ability

The best mean performance for early SRY (17.0 $t\,ha^{-1}$) was recorded by family CT3 × Nyaraboke, whereas the best significant ($P < 0.05$), positive SCA effects of 3.50 early SRY was recorded by family CT1 × Nyaraboke (Table 5). Family TME14 × Nyaraboke had the best mean performance for DMC (38.2%) and significant ($P < 0.01$), positive SCA effect of 2.40. For the SRN, the highest mean

Table 3
Diallel analysis of variance for eight traits of 36 cassava F_1 families evaluated at eight months after planting across two sites in Uganda.

Sources of variation	DF	Mean squares			
		SRY	HI	DMC	SRN
Environment (E)	1	1361.7***	0.008 ns	239.78***	22.43**
Families	35	27.8**	0.007***	13.62***	3.54**
GCA	8	51.0***	0.015***	32.25***	7.51***
SCA	27	21.0*	0.005**	8.10***	2.37
E × Families	35	20.5	0.003	8.74***	2.38
E × GCA	8	3.5***	0.003	10.93**	2.67
E × SCA	27	0.8	0.003	8.10**	2.30
% Families SS due to GCA		41.9	49.5	54.1	48.4
% Families SS due to SCA		58.1	50.5	45.9	51.6
Error	140	14.2	0.002	3.16	1.83
CV (%)		31.0	14.200	5.10	22.8
Sources of variation	DF	Mean squares			
		SRG	CBSD-RN	CMD-S	PHT
Environment (E)	1	316.00***	1.14*	2.96***	8581.9**
Families	35	4.58***	1.92***	0.71***	2371.0**
GCA	8	10.30***	5.06***	1.62***	4455.4**
SCA	27	2.88**	0.98***	0.43***	1753.4
E × Families	35	2.15	0.16	0.15	2371.0**
E × GCA	8	2.84	0.13	0.11	1357.4
E × SCA	27	1.94	0.16	0.17*	785.9
% Families SS due to GCA		51.5	60.3	52.3	42.3
% Families SS due to SCA		48.5	39.7	47.7	57.7
Error	140	1.43	0.27	0.10	1220.9
CV (%)		9.50	19.10	19.20	23.0

DF—degrees of freedom; PHT—plant height (cm); HI—harvest index; SRY—storage root yield ($t\,ha^{-1}$); DMC—dry mass content (%); SRN—storage root number $plant^{-1}$; SRG—storage root girth (cm); CBSD-RN—cassava brown streak disease root necrosis scored on a scale of 1–5; CMD-S—cassava mosaic disease severity scored on a scale of 1–5; GCA—general combining ability; SCA—specific combining ability; SS—sum of squares; CV—coefficient of variation.
* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.

performance of 7.6 was recorded in family CT5 × CT4, while the best positive but non-significant SCA effect of 0.96 was recorded in family NASE3 × Bukalasa11 followed by family CT4 × Nyaraboke with SCA effect of 9.0.

Family CT2 × Bukalasa11 recorded the highest mean performance for SRG of 15.4 cm and positive significant ($P<0.05$) SCA effect of 1.92. The lowest mean score for CBSD-RN of 1.8 was recorded by CT4 × Nyaraboke while the lowest and significant ($P<0.001$), negative SCA effect of 0.82 was recorded by TME14 × CT3. Families, CT5 × Bukalasa11 and TME14 × Nyaraboke recorded the lowest mean score of 1.2 for CMD-S, with TME14 × Nyaraboke also recording the lowest and significant ($P<0.001$), negative SCA effect for the trait.

The highest mean of 199.6 cm and significant ($P<0.05$), positive SCA effect of 29.44 for PHT were observed in CT4 × CT3 (Table 5). For HI, CT5 × TME14 had the highest mean performance of 0.42 and a significant ($P<0.01$), positive SCA effect of 0.05, followed by CT5 × Nyaraboke with a mean performance of 0.41 and a significant ($P<0.05$), positive SCA effect of 0.04.

3.4. Phenotypic correlations—among traits

Most of the traits were positively and significantly correlated with one another, except CMD-S and CBSD-RN (Table 6). With the exception of CBSD-RN and CMD-S, there were significant ($P<0.001$), and positive correlations between early SRY and all

Table 4
Estimates of general combining ability effects for eight traits of nine cassava parental line used in 9 × 9 half-diallel analysis of 36 F_1 clonal stage families evaluated eight months after planting and averaged across two sites in Uganda.

	Estimates of general combining ability effects							
Parents	SRY	HI	DMC	PHT	SRN	SRG	CBSD-RN	CMD-S
Bukalasa11	−0.58	0.011	1.25***	14.37***	−0.32	0.31	0.06	0.07
CT1	1.60*	0.001	0.27	−0.25	−0.01	0.20	−0.18*	−0.03
CT2	0.06	0.015*	−0.78*	−8.61	−0.33	0.70**	0.65***	−0.15**
CT3	0.13	−0.010	0.27	−9.84	−0.17	0.04	0.21**	−0.04
CT4	0.05	−0.036***	−0.51	3.34	0.59**	−0.25	−0.58***	−0.14**
CT5	1.67*	0.030***	−1.53***	16.40**	0.79***	0.48	0.11	−0.13**
NASE3	−0.95	−0.011	0.03	−9.99	0.08	−0.90**	−0.28***	0.43***
Nyaraboke	−0.24	0.005	−0.09	3.48	−0.35	−0.10	−0.12	0.16**
TME14	−1.74**	−0.007	1.09**	−8.89	−0.29	−0.46	0.13	−0.17***
$LSD_{0.05}$	2.36	0.017	1.11	12.36	0.22	0.27	0.07	0.05
SE	0.73	0.008	0.34	5.06	0.55	0.57	0.12	0.11

SRY—storage root yield ($t\,ha^{-1}$); HI—harvest index; DMC—dry mass content (%); PHT—plant height (cm); SRN—storage root number $plant^{-1}$; SRG—storage root girth (cm); CBSD-RN—cassava brown streak disease root necrosis scored on a scale of 1–5; CMD-S—cassava mosaic disease severity scored on a scale of 1–5; GCA—general combining ability; $LSD_{0.05}$—least significant difference at 5%; SE—standard error.
* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.

Table 5
Mean performance and estimates of specific combining ability effects for early storage root yield, dry mass content and storage root number of nine cassava parents used in a 9 × 9 half-diallel analysis of cassava F_1 clonal stage families evaluated eight months after planting and averaged across two sites in Uganda.

	SRY		DMC		SRN		SRG	
Families	Mean	SCA	Mean	SCA	Mean	SCA	Mean	SCA
Nyaraboke x Bukalasa11	10.6	- 2.28	36.6	0.57	4.5	- 0.78	12.0	- 0.71
CT1 x Bukalasa11	9.5	3.07	35.2	- 1.14	6.1	0.51	13.5	0.55
CT2 x Bukalasa11	13.4	1.75	35.5	0.12	6.4	0.33	15.4	1.92*
CT3 x Bukalasa11	9.3	0.51	37.1	0.79	5.3	- 0.13	12.8	0.01
TME14 x Bukalasa11	15.0	0.14	36.6	- 0.62	5.3	- 0.01	12.2	- 0.17
CT4 x Bukalasa11	10.3	- 2.36	34.0	- 1.67	5.6	- 0.61	11.7	- 0.85
CT5 x Bukalasa11	14.0	- 2.69	35.4	0.75	6.1	- 0.27	12.3	- 0.97
NASE3 x Bukalasa11	10.4	1.87	37.4	1.20	6.6	0.96	12.1	0.24
CT1 x Nyaraboke	16.2	3.50*	36.1	1.11	6.3	0.79	12.9	0.35
CT2 x Nyaraboke	10.0	- 1.68	32.4	- 1.62	4.9	- 0.30	13.1	- 0.02
CT3 x Nyaraboke	17.0	0.40	33.9	- 0.99	5.9	0.47	12.8	0.40
TME14 x Nyaraboke	12.1	0.74	38.2	2.40**	5.1	- 0.15	12.2	0.25
CT4 x Nyaraboke	14.3	1.18	34.2	- 0.07	7.1	0.90	12.4	0.32
CT5 x Nyaraboke	12.3	0.76	31.8	- 1.47	5.6	- 0.81	13.1	0.22
NASE3 x Nyaraboke	12.2	- 2.61	34.9	0.08	5.5	- 0.11	10.7	- 0.80
CT2 x CT1	12.2	0.15	34.9	0.61	5.8	0.18	12.8	- 0.56
CT3 x CT1	10.6	- 1.90	34.9	- 0.35	6.2	- 0.09	12.5	- 0.20
TME14 x CT1	9.5	- 2.96	36.7	0.63	4.6	- 1.02	11.7	- 0.48
CT4 x CT1	12.4	- 1.32	34.0	- 0.55	5.9	- 0.65	12.7	0.31
CT5 x CT1	12.0	- 0.10	32.4	- 1.18	7.1	0.40	12.9	- 0.27
NASE3 x CT1	11.5	- 0.46	35.9	0.84	5.9	- 0.12	12.1	0.30
CT3 x CT2	12.5	0.65	34.6	0.29	5.6	0.15	13.6	0.39
TME14 x CT2	14.9	- 0.06	36.0	0.83	5.5	0.18	12.5	- 0.24
CT4 x CT2	10.9	- 0.74	34.2	0.54	5.6	- 0.55	11.5	- 1.45*
CT5 x CT2	9.1	0.56	32.9	0.28	7.2	0.84	13.2	- 0.42
NASE3 x CT2	14.4	- 0.63	33.1	- 1.05	4.8	- 0.84	12.7	0.39
TME14 x CT3	14.4	- 0.97	35.2	- 0.84	5.7	0.28	11.9	- 0.15
CT4 x CT3	13.1	1.29	34.4	- 0.16	6.8	0.46	12.6	0.35
CT5 x CT3	12.5	- 1.77	34.7	1.23	7.2	- 0.38	12.8	- 0.23
NASE3 x CT3	10.6	1.79	35.0	0.00	5.1	- 0.76	11.0	- 0.58
CT4 x TME14	8.3	0.17	35.1	- 0.32	5.8	- 0.90	11.8	0.03
CT5 x TME14	13.0	2.91	34.6	0.27	6.8	- 0.38	13.2	0.75
NASE3 x TME14	13.1	0.02	33.5	- 2.35**	6.4	0.37	11.1	0.02
CT5 x CT4	15.3	1.02	33.4	0.53	7.6	0.26	13.6	0.88
NASE3 x CT4	9.6	0.74	36.1	1.70*	7.2	0.56	11.7	0.41
NASE3 x CT5	13.6	- 0.72	32.9	- 0.41	6.4	- 0.42	12.1	0.05
MEAN	12.2	-	34.8	-	6.0	-	12.5	-
SE	2.3	1.78	1.8	0.84	1.4	0.54	1.2	0.65
$LSD_{0.05}$	4.5	2.51	2.0	2.06	1.6	1.09	1.4	1.01

SRY = storage root yield (t ha^{-1}); DMC = dry mas content (%); SRN = storage root number $plant^{-1}$; SRG = storage root girth (cm); SCA = specific combining ability; $LSD_{0.05}$ = least significant difference at 5%; SE = standard error; * = P<0.05; ** = P<0.01; *** = P<0.001.

the other traits assessed. Of the traits significantly correlated with early SRY, SRG had the highest correlation ($r = 0.70$). The CBSD-RN had a significant ($P < 0.001$), negative correlation with CMD-S and a significant ($P < 0.01$), positive correlation with SRG. The CMD-S on the other hand had negative but non-significant correlations with: early SRY, HI and SRN. For HI, significant positive correlations were recorded with early SRY ($P < 0.001$) SRG ($P < 0.001$) and DMC ($P < 0.01$).

4. Discussion

An understanding of the gene action controlling traits of interest forms the basis for selection of appropriate parental lines and breeding strategies for a successful breeding programme. Consequently, precise selection of parental lines and subsequent development of a few manageable specific crosses are important steps for an effective and efficient plant breeding programme (Dudley and Moll, 1969).

The findings of this study revealed that the main effects for environment (site) were significantly different for most of the traits evaluated, indicative of significant differences in the mean performances of the sites. Namulonge and Bulindi have distinctly different climatic conditions (National Agricultural Research Organisation (NARO), 2001) and experience different pressures for CMD and CBSD. Namulonge, situated in central Uganda, experiences higher levels of CMD and CBSD due to its high whitefly (*Bemisia tabaci*) populations compared to Bulindi, situated in north-western Uganda. In addition, the soil sample analyses conducted for the two sites before establishment of trials revealed significant differences, with Namulonge recording more fertile soils. Also, the rainfall and temperatures recorded at these two sites during the experimental period confirmed the differences between them. Bulindi recorded higher temperatures, while Namulonge recorded higher rainfall. Aina et al. (2009) indicated that rainfall is the critical climatic factor that discriminates different agro-ecological zones for cassava.

Significant differences between family effects for all traits indicated significant genotypic differences between the families. Although significant genotype × environment interaction effects have been recorded for most agronomic and morphological traits in cassava (Calle et al., 2005; Cach et al., 2006; Were et al., 2012), in this study significant interaction between environment and family effects were only recorded for DMC and PHT possibly because the genotype × environment interaction effects for other traits could

Table 5 *(Continued)*
Mean performance and estimates of specific combining ability effects for cassava brown streak disease root necrosis, cassava mosaic disease severity, plant height and harvest index in a 9 × 9 half-diallel analysis of cassava F_1 clonal stage families evaluated eight months after planting and averaged across two sites in Uganda.

	CBSD-RN		CMD-S		PHT		HI	
Families	Mean	SCA	Mean	SCA	Mean	SCA	Mean	SCA
Nyaraboke x Bukalasa11	2.2	- 0.50**	2.7	0.73***	165.3	- 4.41	0.33	- 0.021
CT1 x Bukalasa11	2.1	- 0.56**	1.8	0.03	171.1	5.15	0.37	0.005
CT2 x Bukalasa11	3.9	0.401*	1.8	0.14	182.3	24.70*	0.38	0.014
CT3 x Bukalasa11	3.5	0.49**	1.5	- 0.20	134.4	- 21.96	0.36	0.005
TME14 x Bukalasa11	3.0	0.07	1.5	- 0.08	163.3	6.00	0.34	- 0.006
CT4 x Bukalasa11	2.4	0.15	1.6	- 0.01	134.1	- 35.39**	0.30	- 0.011
CT5 x Bukalasa11	3.2	0.29	1.2	- 0.44***	199.6	17.00	0.36	- 0.023
NASE3 x Bukalasa11	2.2	- 0.34	2.0	- 0.15	165.1	8.90	0.37	0.035*
CT1 x Nyaraboke	2.6	0.19	1.9	0.12	175.6	20.57	0.36	0.010
CT2 x Nyaraboke	3.3	0.03	1.3	- 0.37	132.4	- 14.33	0.34	- 0.014
CT3 x Nyaraboke	2.9	0.08	1.9	0.09**	153.5	8.06	0.35	- 0.000
TME14 x Nyaraboke	3.1	0.38*	1.2	- 0.46***	154.5	8.06	0.35	0.016
CT4 x Nyaraboke	1.8	- 0.25	1.5	- 0.17	174.4	15.74	0.28	- 0.032
CT5 x Nyaraboke	2.7	0.01	1.5	- 0.23	145.5	- 26.20*	0.41	0.040*
NASE3 x Nyaraboke	2.4	0.06	2.6	0.29*	137.8	- 7.50	0.33	0.002
CT2 x CT1	3.5	0.28	1.3	- 0.25*	150.1	7.13	0.36	- 0.007
CT3 x CT1	3.7	0.95***	1.5	- 0.11	126.4	- 15.30	0.39	0.033
TME14 x CT1	2.5	- 0.20	1.7	0.21	124.9	- 17.75	0.33	- 0.011
CT4 x CT1	2.0	- 0.01	1.5	- 0.04	159.9	4.97	0.33	0.011
CT5 x CT1	2.2	- 0.53**	1.8	0.25*	175.1	7.17	0.33	- 0.053**
NASE3 x CT1	2.2	- 0.13	1.9	- 0.20	129.6	- 11.96	0.35	0.014
CT3 x CT2	3.2	- 0.38*	1.5	- 0.05	132.1	- 1.27	0.37	0.015
TME14 x CT2	3.7	0.17	1.5	0.17	114.4	- 19.89	0.35	- 0.001
CT4 x CT2	2.6	- 0.18	1.5	0.09	147.0	0.43	0.33	0.013
CT5 x CT2	3.6	0.06	1.3	- 0.10	156.4	- 3.20	0.37	- 0.0111
NASE3 x CT2	2.7	- 0.39*	2.3	0.37**	139.7	6.43	0.33	- 0.009
TME14 x CT3	2.3	- 0.82***	1.6	0.16	129.0	- 4.11	0.36	0.036*
CT4 x CT3	2.2	- 0.19	1.4	- 0.02	174.8	29.44*	0.29	- 0.014
CT5 x CT3	3.1	0.05	1.7	0.14	170.6	12.21	0.34	- 0.030
NASE3 x CT3	2.5	- 0.18	2.1	- 0.02	124.9	- 7.07	0.30	- 0.031
CT4 x TME14	2.2	- 0.13	1.4	0.07	138.1	- 8.21	0.27	- 0.029
CT5 x TME14	3.1	0.12	1.6	0.23	175.0	15.63	0.42	0.048**
NASE3 x TME14	3.0	0.42*	1.6	- 0.31*	153.2	20.27	0.28	- 0.043*
CT5 x CT4	2.3	0.02	1.5	0.10	161.3	- 10.27	0.36	0.030
NASE3 x CT4	2.5	0.59**	2.0	- 0.02	148.5	3.28	0.32	0.033
NASE3 x CT5	2.5	- 0.03	2.0	0.04	145.9	- 12.35	0.35	- 0.003
MEAN	2.7	-	1.7	-	151.8	-	0.34	-
SE	0.5	0.18	0.3	0.13	34.8	12.30	0.03	0.018
$LSD_{0.05}$	0.6	0.29	0.4	0.30	39.8	20.33	0.06	0.037

CBSD-RN = cassava brown streak disease root necrosis scored on a scale of 1-5; CMD-S = cassava mosaic disease severity scored on a scale of 1-5; PHT = Plant height (cm); HI= Harvest index; (0-1); SCA = specific combining ability; $LSD_{0.05}$ = least significant difference at 5%; SE = standard error; * = P<0.05; ** = P<0.01; *** = P<0.001.

not be detected very well due to limited sites. This also implies that families in this study recorded stable performance across the two test environments for all traits except DMC and PHT, and that selection for all the family traits assessed except DMC and PHT could be done at either site. Significant interaction between environment and GCA MS for early SRY and DMC as well as significant interaction between environment and SCA MS for DMC and CMD-S implied that evaluation and selection of suitable genotypes for

Table 6
Phenotypic correlation coefficients for agronomic and disease resistance traits of 36 cassava F_1 families harvested at eight months after planting and averaged across two sites in Uganda.

Traits	SRY	SRN	SRG	DMC	HI	PHT	CMD-S	CBSD-RN
SRY	1.00							
SRN	0.51***	1.00						
SRG	0.70***	0.13*	1.00					
DMC	0.20***	−0.13*	0.24***	1.00				
HI	0.33***	0.11ns	0.29***	0.19**	1.00			
PHT	0.28***	0.22***	0.22***	0.09ns	−0.04	1.00		
CMD-S	0.10ns	−0.03ns	0.05ns	−0.12*	−0.04ns	0.02ns	1.00	
CBSD-RN	−0.01ns	−0.15*	0.20**	0.01ns	0.14ns	−0.14ns	−0.23***	1.00

SRY—storage root yield ($t\,ha^{-1}$); SRN—storage root number $plant^{-1}$; SRG—storage root girth (cm); DMC—dry mass content (%); HI—harvest index; PHT—plant height (cm); CMD-S—cassava mosaic disease severity scored on a scale of 1–5; CBSD-RN—cassava brown streak disease root necrosis scored on a scale of 1–5; ns—correlation not significant at 0.05.

* Significant at $P<0.05$.
** $P<0.01$.
*** $P<0.001$ level.

commercial production or as parents for these traits should be based on multilocation testing. Those that show high GCA and SCA effects across environments are the best genotypes. However, due to low multiplication rate of cassava planting materials (Ceballos et al., 2004), it is a tradition by most cassava breeding programmes that the first clonal evaluation trials are established at one location and to some extent not replicated (Ceballos et al., 2004). For example, in this study the data presented are from two plant plots replicated three times at each location because there was lack of enough planting materials of each genotype to establish larger plots, considering the low seed multiplication rates of cassava at the early stages of breeding. There is therefore a need to develop technologies that can improve the multiplication rate of cassava such as tissue culture or the cut-back method reported by Were et al. (2012) to conduct larger replicated trials in several locations.

General combining ability and SCA effects were significantly different for most traits indicating the significance of additive and non-additive gene action in controlling the traits, respectively. The expression of all traits studied except PHT and SRN was significantly under the control of both additive and non-additive genes. The presence of family, GCA and SCA × environment interaction effects for early SRY, DMC and CMD-S implied that the gene action determining the expression of these traits, whether additive or non-additive or a combination of the two was site specific and was therefore not stably expressed across environments (Were et al., 2012).

General combining ability measures the average performance of a parent in its crosses while SCA refers to performance of a cross greater or less than what would be expected on the basis of the average performance of the parents involved (Griffing, 1956). The proportion of the SS for families due to GCA and SCA effects provides an indication of the relative importance of additive and non-additive gene effects in the expression of traits (Calle et al., 2005; Kulembeka et al., 2012). In this study, the GCA effects accounted for over 50.0% of the families SS for DMC, SRG, CBSD-RN and CMD-S, indicating the predominance of additive gene action in controlling these traits. In contrast, SCA effects for early SRY, SRN, HI and PHT accounted for over 50.0% of the families SS indicating that they were predominantly under non-additive gene control. Based on % families SS accounted for by SCA effects, Were et al. (2012) and Kulembeka et al. (2012) also reported that SRY was under the control of non-additive gene action. The relative importance of GCA effects for CBSD-RN observed in this study was in agreement with the observations of Kulembeka et al. (2012), but in disagreement with Zacarias and Labuschagne (2010). Cassava mosaic disease resistance was also found to be predominantly controlled by additive gene effects as previously reported by Parkes et al. (2013).

In terms of GCA and associated transmission of desirable additive gene action from parents to progeny, parents CT1 and CT5 had the highest significant positive GCA effects for early SRY and they were, therefore, the best parents to use when breeding for high SRY. In addition, CT5 had the highest significant positive GCA effects for PHT, HI and SRN. The parents with the highest significant positive GCA effects for DMC were Bukalasa11 and TME14. For CBSD-RN, CT1, CT4 and NASE3 had significant negative GCA effects, suggesting that they were best parents to use in breeding cultivars with resistance to CBSD. Parents CT2, CT4, CT5 and TME14 had very low mean scores, as well as significant negative GCA effect for CMD-S. Parents that had desirable GCA effects for early SRY and most other traits were derived from CIAT introductions, suggesting the importance and feasibility of CIAT progenitors in introducing and widening genetic variability of African cassava breeding populations.

The desirable SCA effect for early SRY was recorded in family CT1 × Nyaraboke, while the desirable SCA effect for DMC was recorded in TME14 × Nyaraboke. The best SCA effect for SRN was observed in NASE3 × Bukalasa11 followed by CT4 × Nyaraboke. Family CT2 × Bukalasa11 recorded the best SCA effect for SRG. The best SCA effect for CBSD-RN was recorded in TME14 × CT3 and the best SCA effects for CMD-S in TME14 × Nyaraboke. These results revealed that families developed from contrasting parents in terms of GCA effects for particular traits, generally had correspondingly high and significant SCA effects, suggesting that specific combinations of alleles may be important in controlling traits or that there could be some inter-locus gene interaction. Also, considering the mean performances of the families for different traits, for example, those developed from Bukalasa11 or Nyaraboke, it was apparent that the GCA effects for the parents did not generally correlate with their per se performance and that the best performing families were not always developed from parents with high GCA effects. This implied that selection of parents based on their *per se* performance may not necessarily lead to development of superior hybrids. Most of the yield and yield related traits were significantly positively correlated with one another demonstrating the interdependence of these traits. Early SRY was positively and significantly correlated with PHT, SRN, SRG, DMC and HI; with SRG recording the highest correlation. Harvest index and SRN recorded positive correlations with early SRY which confirms these traits as good indicators of early SRY (Okechukwu and Dixon, 2009). Cassava mosaic disease was negatively, but non-significantly correlated with early SRY, HI and SRN. This is in agreement with the findings that diseases and pests reduce SRY in cassava (Parkes et al., 2013).

5. Conclusion

Parents and families with desirable GCA and SCA effects, respectively for early SRY, resistance to CBSD and CMD, and other key cassava traits were identified and could be exploited in the cassava breeding programmes in Uganda. Both additive and non-additive gene actions were involved in the expression of cassava traits. For traits: DMC, SRG, CBSD-RN and CMD-S where additive genetic effects were predominant, a hybridisation scheme followed by phenotypic recurrent mass selection may be effective in identifying desirable recombinants. On the other hand, for traits: early SRY, SRN, HI and PHT; where there was predominance of non-additive genetic effects in their expression, a different approach might be used. For instance, cassava genotypes could be grouped into heterotic pools and specific hybrid combinations made in order to exploit non-additive gene action, which can be fixed through vegetative propagation of the subsequent generations. Earliness in cassava is an important strategy for avoiding disease loss from CBSD, but it could limit the ability to judge resistance or tolerance in the genotypes. There is therefore a need for further studies with the test genotypes in bigger trials and in several locations to confirm results presented in this research article.

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