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# Diallel analysis of cassava brown streak disease, yield and yield related characteristics in Mozambique

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**Abstract** Cassava brown streak disease (CBSD) reported from 1999 in Mozambique, now constitutes the main production constraint in the country. CBSD may be found in all plant parts, affecting food security and availability and quality of planting material. The aim of this study was to evaluate the relative importance of general (GCA) and specific combining ability (SCA), and inheritance of relevant traits and to identify superior parents for use in further improvement of genotypes for yield and CBSD resistance. The parents were selected from a region where CBSD is the main economic constraint. Chigoma mafia was the best general combiner for average root number and CBSD resistance, Mulaleia also combined well for CBSD resistance. Clone IMM 30025 was the best general combiner for root pulp hardness, but combined poorly for CBSD resistance. Chigoma mafia × Mulaleia had the best mean performance for fresh root yield and CBSD resistance. Macia 1 × Chigoma mafia had the best SCA for fresh root yield, CBSD resistance and root pulp hardness. MZ 89186 × IMM 30025 and the reciprocals IMM 30025 × MZ 89186, Chigoma mafia × Macia 1 and MZ 89186 × Mulaleia had the best resistance to CBSD. This indicates that there is good parental material for CBSD resistance breeding. Chigoma × Mulaleia, MZ 89185 × IMM 30025 and MZ 89186 × Macia 1 had good mid-parent heterosis for the most important traits. Broad sense heritability estimates varied from 38.9 for fresh root yield to as high as 95.5 for harvest index, indicating the potential for effective response to selection.

**Keywords** Cassava brown streak disease · Combining ability · Heritability · Resistance · Yield

## Introduction

Cassava is a staple food for more than 50% of the population in the main production areas of Mozambique. The roots and leaves are used daily as a main source of carbohydrates and vitamins. The outbreak of cassava brown streak disease (CBSD) reported from 1999, now constitutes the main production constraint in the country. CBSD may be found in all plant parts, affecting food security and availability and quality of planting material. The root symptoms are a yellow–brown, corky necrosis in the starch-bearing tissue, making the most severely affected roots unfit for consumption. Losses in root yield may

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reach 60–70% due to CBSD in susceptible cultivars (Hillocks and Thresh 2001; Cuambe et al. 2007), resulting in food security problems. Survey reports conducted in northern Mozambique, have shown that farmers have identified local varieties that are tolerant or resistant to CBSD (Hillocks et al. 2002; Zacarias and Cuambe 2004). Some of these varieties are Chigoma mafia, Nikwaha, Mucudo muevia, Mulaleia, Likonde and Mocuba, which were included in this study.

CBSD is caused by Cassava Brown Streak Virus of the genus *Ipomovirus*, family *Potyviridae* (Monger et al. 2001). CBSD was first reported by Storey (1936) in the then called Tanganyika. The disease is endemic in East African coastal cassava-growing areas from southern Kenya, through Tanzania to the Zambezi River in Mozambique, and also occurs in some inland areas of Malawi, Uganda and the Democratic Republic Congo (DRC) (Hillocks et al. 2002; Legg and Raya 1998; Benesi 2005).

The first attempt to select for resistance to CBSD dated from 1937 at Amani Research Station (Hillocks and Jennings 2003), the area where the disease was confined at the time. Crosses were made between wild *Manihot* species, collected in Surinam and Brazil. However, only the hybrids from *M. glaziovii* and *M. melanobasis* were promising and contained a combination of other required traits in cassava (Hillocks and Jennings 2003). Seventy years have passed and little is still known about the disease, which has since spread to more areas in different countries. More breeding for resistance to CBSD is necessary. It is known that development of resistant varieties could potentially form the basis of a sustainable management strategy for this disease (Asiedu et al. 1998; Mahungu et al. 1994; DeVries and Toenniessen 2001). Selection of resistant varieties and continuous breeding appears to be the most efficient way to control CBSD.

Studies on improvement for resistance to CBSD are scarce. All breeding programmes in the affected areas should pool information that will help to formulate an efficient strategy for incorporating the resistance genes into high yielding and adapted lines. It is known that the development of new varieties depends greatly on the screening of parental lines to be used for hybridisation programmes. The overall objective of this study was to evaluate the relative importance of general and specific combining ability, inheritance of relevant traits and to identify superior parents for use in further improvement of cassava genotypes for yield and CBSD resistance.

## Materials and methods

### Parental material

Eighteen entries maintained at the national cassava gene bank were screened for their performance based on agronomic traits, CBSD tolerance, adaptation to the environment and farmer preference (Zacarias et al. 2003). From this material, two CBSD-resistant parents (Chigoma mafia and Mulaleia), one CBSD-moderately resistant parent (Macia 1) and two CBSD-susceptible parents (MZ 89186 and IMM 30025) were selected. The varieties Chigoma mafia, Mulaleia and Macia 1 are landraces collected in Cabo Delgado and Zambezia, while IMM 30025 and MZ 89186 are improved clones selected from true seed received from the International Institute of Tropical Agriculture (IITA), batches of 1986 and 1989 respectively (Table 1).

### Development of progeny

The five parents were planted in the breeding nurseries at Posto Agronomico de Nampula (PAN) on 15 October in the 2002 season. Controlled pollinations were performed following the standard procedures described by Kawano (1980). The parents were crossed in a full diallel mating design (Griffing 1956) to produce 20 $F_1$ crosses, including reciprocals. Twenty seeds from each cross were harvested. The seeds were germinated and grown in a greenhouse in plastic bags at PAN. Forty five days after planting (DAP) the plants were transported and transplanted (10 December 2003) to the experimental field in Mogincual Substation, in the rainy season as a seedling nursery. Established seedlings were planted in a single row, 50 cm and 1 m spacing within and between rows, respectively, to produce enough woody cuttings for the study. Mature stems (25 cm long) of the five parents were also planted in the field. No irrigation and fertiliser was applied at this stage. At harvest time, 12 months after planting (MAP), five vegetative cuttings for each of the 20 genotypes of each $F_1$ family and parents were obtained. They were selected based on the capacity of the plant to produce five good quality vegetative cuttings to proceed with evaluation.

**Table 1** List of parents and F1 progeny used in the diallel trial

| Entry codes | Pedigree | Remarks |
|---|---|---|
| Parents | | |
| 1 | Chigoma mafia | Landrace |
| 2 | Mulaleia | Landrace |
| 3 | MZ 89186[a] | Improved clone |
| 4 | MZ IMM 30025[a] | Improved clone |
| 5 | Macia 1 | Landrace |
| F1 | | |
| 1 × 2 | Chigoma mafia × Mulaleia | F1 |
| 1 × 3 | Chigoma mafia × MZ 89186 | F1 |
| 1 × 4 | Chigoma mafia × IMM 30025 | F1 |
| 1 × 5 | Chigoma mafia × Macia 1 | F1 |
| 2 × 1 | Mulaleia × Chigoma mafia | Reciprocal |
| 2 × 3 | Mulaleia × MZ 89186 | F1 |
| 2 × 4 | Mulaleia × IMM 30025 | F1 |
| 2 × 5 | Mulaleia × Macia 1 | F1 |
| 3 × 1 | MZ 89186 × Chigoma mafia | Reciprocal |
| 3 × 2 | MZ 89186 × Mulaleia | Reciprocal |
| 3 × 4 | MZ 89186 × IMM 30025 | F1 |
| 3 × 5 | MZ 89186 × Macia 1 | F1 |
| 4 × 1 | IMM 30025 × Chigoma mafia | Reciprocal |
| 4 × 2 | IMM 30025 × Mulaleia | Reciprocal |
| 4 × 3 | IMM 30025 × MZ 89186 | Reciprocal |
| 4 × 5 | IMM 30025 × Macia 1 | F1 |
| 5 × 1 | Macia 1 × Chigoma mafia | Reciprocal |
| 5 × 2 | Macia 1 × Mulaleia | Reciprocal |
| 5 × 3 | Macia 1 × MZ 89186 | Reciprocal |
| 5 × 4 | Macia 1 × IMM 30025 | Reciprocal |

[a] Selection from IITA seeds received in batch 1986–1989

## Field experiments

A randomised complete block design with five replicates was used to plant a total of 25 entries consisting of 10 $F_1$, 10 reciprocals and five parents (Table 1). The experiment was planted in two consecutive years, 2004 and 2005 at Mogincual Experimental Station. The planting dates were 15/12/2004 and 18/12/2005. The planting period started at the beginning of the raining season. Each replication contained the 25 entries (parents and crosses), planted together in the respective plots of each replication. The plant spacing was 1 m between and within rows, giving a plant population of 10,000 plants per hectare. The field was kept weed free manually and no supplement of irrigation or fertiliser was applied during the growth period. Data from three plants (inner plants), of each entry was averaged before analysis.

Trials were planted at Mogincual, a district of the Nampula province (Fig. 1). The soils are predominantly sandy, brown-grey, deep with good drainage, however they were moderately acidic with low organic matter (INIA 1995). Mogincual is located at 15°34′ latitude south and 40°45′ longitude east, 35 m above sea level (INIA 1995). It is situated along the coast with an average incidence of CBSD of 90% annually (Zacarias and Cuambe 2004).

## Agronomic characters measured

During the growth period, data was collected on morphological traits. Plants were hand-harvested individually and results averaged across plants from each $F_1$ cross. The roots were counted and weighed separately. Every root was sliced to score for necrosis caused by CBSD where 1 = no symptoms, 5 = totally damaged (Hillocks et al. 1996). Harvest index was measured as a ratio of root weight to total biomass. Root taste was scored using the scale 1 = bitter and 2 = sweet, using adapted sensorial methodology described by Padonou et al. (2005). Root pulp hardness was measured using a subjective scale of 1–5, where 1 = very hard, 2 = hard, 3 = moderate, 4 = soft and watery, 5 = soft and very watery. Farmers frequently use the chewing technique to get an indication of the pulp texture. Roots with a lower score (1–3), are the best, while the ones with a high score (4–5), will be rejected because such roots will be too soft. Cassava mealybug infestation was scored on a scale from 1 to 5 with 1 having no infestation and 5 severe infestation.

Fresh root and harvest index are important traits related to yield (Byrne 1984). Root pulp hardness is of the same importance as dry matter content in cassava. CBSD is the most important economical constraint in the region (Hillocks and Jennings 2003; Zacarias and Cuambe 2004).

## Data analysis

Analysis of variance and diallel analysis (Griffing, Method 1, fixed model) were done using Agrobase (2000). Analysis of general (GCA) and specific (SCA) combining ability for individual experiments was

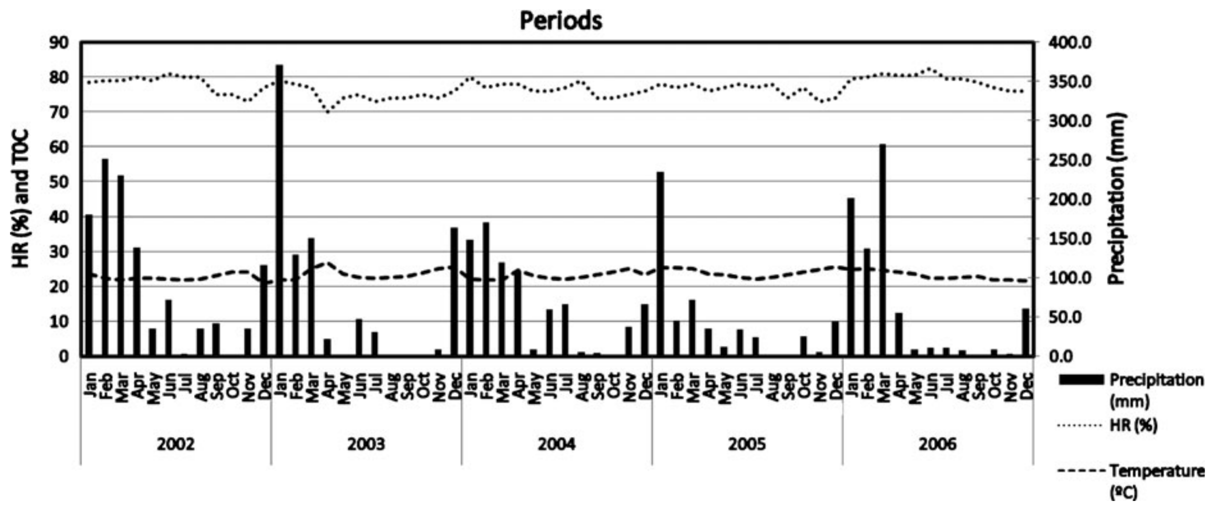


**Fig. 1** Average monthly temperature, rainfall and relative humidity of Mogincual data collected from January 2002 to December 2006 (*Source*: IIAM 2006)

performed, and mean squares of GCA and SCA were used to determine GCA:SCA ratios (Beil and Atkins 1967; Haussmann et al. 1999).

### Genetic parameters

The relative contribution of genetic components was determined to obtain estimates of GCA variance ($\delta^2_{gca}$) and SCA variance ($\delta^2_{sca}$) for each characteristic. Additive ($V_a$) and dominance ($V_d$) variance were estimated as $V_a = 2(\delta^2_{gca})$ and $V_d = (\delta^2_{sca})$. Phenotypic ($V_p$) and genotypic variance ($V_g$) were also estimated as

$$V_g = V_a + V_d,\ \text{where } V_p = V_g + V_e(\text{environmental variance}).$$

Broad ($h^2b$) and narrow ($h^2n$) sense heritability was calculated from the estimated components of variance as:

$$h^2_b = V_g/V_p \text{ and } h^2_n = V_a/V_p,\ \text{respectively.}$$

The relative size of variances due to GCA and SCA on progeny performance was estimated following Baker's prediction ratio (PR) (Baker 1978) as:

$$PR = 2\delta^2_{gca}/(2\delta^2_{gca} + \delta^2_{gca}),$$

The average degree of dominance was estimated as $\sqrt{H/D} = \sqrt{(\delta^2_{gca}/\delta^2_{sca})}$ (Singh and Chaudhary 1979).

### Estimates of heterosis

Heterosis was calculated as:

$$\text{Mid-parent heterosis (MPH)(\%)} = (F_1 - MP)/MP \times 100$$

where, $F_1 = F_1$ hybrid performance, $MP = (P1+P2)/2$ where $P1$ and $P2$ are the performance of inbred parents, respectively.

## Results and discussion

Analysis of variance of the characters evaluated during 2004 and 2005 in Mogincual, showed that the mean squares of genotypes were significant for all measured characteristics (Table 2).

### Weather and climate at trial site

Mogincual has 4 months of effective rain per season. Annual rainfall showed a reducing tendency from 2001 to 2005. The total rainfall was 1137 mm for 2001, 921.6 mm for 2002, 790.9 mm for 2003, 524 mm for 2004 and 769.7 mm for 2005. The effective rain period is only for 4 months with varied rainfall distribution (Fig. 1). The season 2004/05 was the most irregular with January receiving 234 mm and other months less than 100 mm. For all seasons the

**Table 2** Mean squares for GCA and SCA and GCA:SCA ratios for different cassava characters studied in a diallel trial during 2004 and 2005

| Source | Df | ARN (kg/pl) | | FRW (kg/pl) | | CBSD score (1–5) | | RTST (1–2) | |
|---|---|---|---|---|---|---|---|---|---|
| | | 2004 | 2005 | 2004 | 2005 | 2004 | 2005 | 2004 | 2005 |
| Genotypes | 24 | 214* | 1694* | 0.14** | 34.5** | 1.03** | 2.1* | 0.26* | 0.24** |
| GCA | 4 | 8.15 | 402 | 0.03 | 2.88 | 0.2** | 0.48** | 0.14* | 0.13* |
| SCA | 10 | 3.73* | 168* | 0.02 | 14.9 | 0.32** | 0.57** | 0.06** | 0.05** |
| Reciprocal | 10 | 3.7 | 485 | 0.04 | 0.48 | 0.09 | 0.23 | 0.01 | 0.01 |
| Error | 96 | 3 | 227 | 0.03 | 2.5 | 0.07 | 0.26 | 0.02 | 0.2 |
| GCA:SCA | | 2.19 | 2.39 | 1.87 | 0.19 | 0.63 | 0.84 | 2.33 | 2.6 |

| Source | Df | RPH (1–5) | | CM (1–5) | | HI (%) | |
|---|---|---|---|---|---|---|---|
| | | 2004 | 2005 | 2004 | 2005 | 2004 | 2005 |
| Genotypes | 24 | 2.04** | 3.2* | 0.41* | 0.41* | 0.01* | 0.02** |
| GCA | 4 | 0.87** | 1.1* | 0.17 | 0.03 | 0.04 | 0.01 |
| SCA | 10 | 0.45** | 0.88** | 0.13 | 0.08 | 0.03* | 0.01* |
| Reciprocal | 10 | 0.18 | 0.22 | 0.04 | 0.11 | 0.01** | 0.02** |
| Error | 96 | 0.1 | 0.17 | 0.01 | 0.01 | 0.03 | 0.02 |
| GCA:SCA | | 1.93 | 1.25 | 1.31 | 0.38 | 1.33 | 1.2 |

*ARN* average root number, *FRW* average fresh root yield per plant, *CBSD* cassava brown streak necrosis, *RTST* root taste, *RPH* root pulp hardness, *CM* cassava mealybug infestation, *HI* harvest index, *Df* degrees of freedom, *GCA* general combining ability, *SCA* specific combining ability

* $P \leq 0.05$

** $P \leq 0.01$

peak of rainfall was observed between February to March. The average monthly and maximum temperatures ranged between 21.9 and 23.5°C for 2001, 20 and 29.8°C for 2002, 21.4 and 25.4°C for 2003, 22.05 and 24.4°C for 2004 and 21.6 and 25.1°C for 2005.

### Estimation of combining ability variances

Evaluation of combining ability of additive and non-additive gene performance within breeding populations is important to determine the type of breeding methods that will successfully improve the performance of the studied characters (Dudley and Moll 1969).

General combining ability (GCA) mean squares were highly significant for CBSD resistance (both years), and root pulp hardness (2004). Specific combining ability (SCA) was significant in both years for average root number, CBSD resistance, root taste, root pulp hardness and harvest index (Table 2). Reciprocal effects were significant only for harvest index.

The GCA:SCA ratios indicated that GCA was higher than SCA for average root number, root taste, root pulp hardness and harvest index, for 2 years of evaluation, where a ratio closer or higher than a unit indicates the predominance of additive gene action (Table 2). However, the GCA was lower than SCA for fresh root yield and cassava mealybug infestation for the second year of evaluation, showing the influence of the environment on these traits. The SCA was higher than GCA for CBSD resistance, demonstrating that these characters are largely under the influence of non-additive gene action.

The parent Chigoma mafia had positive GCA effects for average root number per plant (both years), and root taste (both years), but negative GCA for root pulp hardness (2005) and CBSD resistance for both years, but positive in 1 year and negative in the other year for harvest index (Table 3). However, Chigoma mafia had the best combining ability for CBSD resistance followed by Mulaleia (for 2004). Mulaleia had poor GCA effects for average root number, fresh root yield (2004 only), root taste (2004

**Table 3** Estimates of general combining ability (GCA) effects for various characters evaluated during 2004 and 2005

| Parent | ARN (kg/pl) | | | FRW (kg/pl) | | | CBSD (1–5) | | | RTST (1–2) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2004 | 2005 | Mean | 2004 | 2005 | Mean | 2004 | 2005 | Mean | 2004 | 2005 | Mean |
| Chigoma mafia | 1.18** | 9.73** | 6.98 | 0.03 | 0.07 | 3.22 | −0.03* | −0.35** | 1.55 | 0.2** | 0.19** | 1.56 |
| Mulaleia | −0.5 | −0.26 | 5.46 | −0.05 | 0.55* | 2.07 | −0.18* | −0.03 | 1.34 | −0.12 | 0.11** | 1.13 |
| MZ 89186 | −1.1 | 0.74 | 5.32 | −0.05 | −0.49 | 3.32 | 0.01 | 0.08 | 2.59 | −0.03 | 0.01 | 1.12 |
| IMM 30025 | 0.65 | 0.67 | 7.55 | 0.07 | 0.53 | 2.96 | 0.22** | 0.24** | 2.32 | −0.01 | 0.02 | 1.3 |
| Macia 1 | −0.3 | −0.81 | 7.84 | −0.13 | 0.57* | 2.82 | −0.01* | 0.06 | 2.92 | −0.04 | 0.04 | 1.04 |
| SD ($G_i$) | 0.49 | 4.25 | 6.63 | 0.05 | 0.44 | 2.88 | 0.07 | 0.14 | 2.14 | 0.03 | 0.04 | 1.23 |
| SD ($G_i - G_j$) | 0.77 | 6.7 | 2.63 | 0.11 | 0.71 | 0.99 | 0.19 | 0.23 | 0.67 | 0.06 | 0.06 | 0.23 |

| Parent | RPH (%) | | | CM (1–5) | | | HI (%) | | |
|---|---|---|---|---|---|---|---|---|---|
| | 2004 | 2005 | Mean | 2004 | 2005 | Mean | 2004 | 2005 | Mean |
| Chigoma mafia | −0.3 | −0.4** | 2.27 | 0.11** | −0.01 | 1.1 | 0.05** | −0.02 | 0.5 |
| Mulaleia | −0.3 | −0.27** | 3.04 | −0.1** | 0.03 | 1.02 | 0.05** | 0.01 | 0.55 |
| MZ 89186 | 0.13 | 0.31** | 3.32 | −0.09** | −0.09** | 1.1 | 0.03** | 0.02** | 0.63 |
| IMM 30025 | 0.39** | 0.31** | 4.06 | −0.1** | 0.02 | 1.11 | −0.01 | 0.03** | 0.47 |
| Macia 1 | 0.07 | 0.05 | 2.62 | 0.18** | 0.05* | 1.32 | 0 | −0.03 | 0.39 |
| SD ($G_i$) | 0.08 | 0.11 | 3.1 | 0.02 | 0.02 | 1.07 | 0.01 | 0.01 | 0.51 |
| SD ($G_i - G_j$) | 0.14 | 0.18 | 0.6 | 0.04 | 0.04 | 0.22 | 0.01 | 0.01 | 0.1 |

*ARN* average root number, *FRW* average fresh root yield, *CBSD* cassava brown streak necrosis, *RTST* root taste, *RPH* root pulp hardness, *CM* cassava mealybug infestation, *HI* harvest index, *SD* ($G_i$) standard error for any GCA effect, $SE(G_i - G_j)$ standard error of the difference between any two effects

* $P \leq 0.05$

** $P \leq 0.01$

only) and root pulp hardness (2004 only). The parent MZ 89186, had negative GCA effects for average root number (2004), fresh root yield (both years), root taste and mealy bug infestation (both years). MZ 89186 had the second best GCA score for root pulp hardness (2004). The clone IMM 30025 had a positive significant GCA effect for plant CBSD resistance (both years) and root pulp hardness (both years). The parent Macia 1 had negative GCA effect for average root number (not significant).

The GCA effects contributed 21.4 and 25.1%, during year 1 and 2 respectively while SCA contributed 78.6 and 74.9%, to the sum of squares for CBSD resistance, indicating the importance of non-additive gene action in the expression of CBSD (data not shown). Negative GCA effects for CBSD resistance indicated better performance based on the scales used.

The differences observed between years of evaluation might be due to differences in environmental conditions, especially rainfall, which differed in amount and pattern during the 2 years of the trial (Fig. 1). During 2004, the rainfall was better distributed compared to 2005, where half of the total amount (524.4 mm) fell in only 1 month (January). Significant GCA × environment interaction effects for fresh root yield and dry matter content were reported by Jaramillo et al. (2005).

Overall, Chigoma mafia was the best general combiner for CBSD resistance and average root number and IMM 30025 for root pulp hardness (Table 3). The best average performance for root number was observed in crosses MZ 89186 × IMM 30025 (8.5) and MZ 89186 × Macia 1, while the highest SCA effect was in the cross Chigoma mafia × IMM30325 (0.9) (Table 4). The fresh root yield Chigoma mafia × MZ 89186 had the best performance and the best SCA effect was observed in crosses Macia 1 × Chigoma mafia followed by IMM 30325 × MZ 89186. For root necrosis, the best performance was observed in the combination Chigoma mafia × Mulaleia followed by Macia 1 × Chigoma mafia, but the

**Table 4** Specific combing ability effects and mean performance of different characteristics evaluated during 2004 and 2005

| Crosses and reciprocals | ARN (kg/pl) | | | FRW(kg/pl) | | | CBSD score (1–5) | | | RTST (1–2) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | 2004 | 2005 | Mean | 2004 | 2005 | Mean | 2004 | 2005 | Mean | 2004 | 2005 |
| 1×2 | 6.35 | 0.45* | 0.55 | 2.06 | 0.01 | −0.53* | 1.63 | 0.20* | −0.09 | 1.20 | −0.20** | −0.19** |
| 1×3 | 6.11 | 0.33* | 0.59 | 3.54 | 0.20** | −0.42* | 2.13 | 0.35** | 0.10* | 1.58 | 0.05* | 0.04* |
| 1×4 | 6.94 | 0.90* | −0.03 | 2.69 | 0.13** | −1.59** | 2.32 | 0.01 | 0.24** | 1.44 | 0.03* | 0.02 |
| 1×5 | 5.59 | −0.33 | −1.71** | 1.59 | −0.04 | −2.15** | 1.57 | −0.11* | 0.12* | 1.29 | −0.20** | −0.20** |
| 2×3 | 6.97 | 0.13 | 0.89* | 2.07 | −0.02 | −0.66* | 2.02 | 0.16* | 0.60** | 1.29 | 0.19** | 0.18** |
| 2×4 | 5.21 | 0.79* | −0.75* | 2.09 | −0.04 | −1.23* | 1.93 | −0.03 | 0.31** | 1.29 | −0.04* | −0.04* |
| 2×5 | 6.43 | 1.10* | 0.14 | 2.99 | 0.07 | −2.16** | 2.08 | −0.10* | 0.19* | 1.42 | 0.10 | 0.10* |
| 3×4 | 8.50 | 0.21 | 1.33** | 2.26 | −0.08 | −1.55** | 1.75 | −0.27* | −0.59** | 1.34 | −0.11** | −0.11** |
| 3×5 | 7.73 | 0.43* | −0.62** | 2.63 | −0.09 | −0.03 | 1.76 | −0.47** | −0.90** | 1.21 | 0.10* | 0.07* |
| 4×5 | 5.22 | −0.21 | −2.23** | 2.09 | −0.04 | −1.99** | 1.87 | −0.36** | −0.02 | 1.32 | 0.18** | 0.17** |
| 2×1 | 1.07 | 0.04 | −1.13 | 2.70 | −0.15** | −0.27* | 2.01 | −0.11 | −0.20* | 1.26 | 0.04* | 0.04 |
| 3×1 | 7.57 | 0.23** | −1.61** | 2.58 | −0.10 | −0.55 | 1.74 | −0.05 | 0.10 | 1.28 | 0.07* | 0.07 |
| 3×2 | 7.26 | 0.01 | −0.27 | 2.31 | 0.09 | −0.22 | 2.41 | 0.27* | −0.52** | 1.34 | 0.07* | 0.07 |
| 4×1 | 6.94 | 0.34** | −0.92 | 2.53 | 0.09 | −0.44 | 1.83 | −0.03 | 0.20 | 1.47 | −0.06 | −0.03 |
| 4×2 | 6.60 | −0.13 | −1.40 | 3.26 | 0.03 | −0.58 | 2.68 | −0.14 | −0.40** | 1.11 | 0.06 | 0.06 |
| 4×3 | 7.36 | −0.11 | 1.80 | 2.70 | 0.14** | 0.41 | 2.06 | −0.02 | −0.60** | 1.11 | −0.20** | −0.02 |
| 5×1 | 5.47 | −0.26 | −0.18 | 2.72 | 0.26** | −0.78 | 1.70 | −0.51** | −0.10 | 1.59 | 0.06* | 0.06* |
| 5×2 | 4.89 | −1.12 | 0.52 | 2.14 | 0.09 | 0.41* | 2.10 | 0.03 | −0.50** | 1.03 | 0.17** | 0.17** |
| 5×3 | 4.12 | 1.10** | 2.02 | 1.09 | 0.21** | 0.69* | 1.70 | 0.07 | 0.10 | 1.12 | 0.08* | 0.07 |
| 5×4 | 4.43 | −0.23 | 0.72 | 3.13 | 0.02 | −0.22 | 2.70 | −0.19* | −0.05 | 1.30 | 0.02 | 0.01 |
| SE ($S_{ij}$) | 6.04[a] | 0.18 | 0.61 | 2.46[a] | 0.21 | 0.22 | 1.99[a] | 0.10 | 0.14 | 1.30[a] | 0.03 | 0.04 |
| SE ($S_{ij} - S_{kl}$) | 2.63[b] | 1.34 | 1.17 | 0.99[b] | 0.13 | 1.33 | 0.67[b] | 0.31 | 0.39 | 0.23[b] | 0.11 | 0.11 |
| SE ($R_{ij}$) | | 1.22 | 10.64 | | 0.12 | 1.12 | | 0.19 | 0.36 | | 0.06 | 0.10 |

| Crosses and reciprocals | RPH (%) | | | CM (1-5) | | | HI (%) | | |
|---|---|---|---|---|---|---|---|---|---|
| | Mean | 2004 | 2005 | Mean | 2004 | 2005 | Mean | 2004 | 2005 |
| 1×2 | 2.77 | −0.08* | 0.03 | 1.00 | −0.10** | −0.16** | 0.4 | 0.02* | −0.02** |
| 1×3 | 3.26 | 0.33** | 0.05 | 1.00 | −0.12** | 0.01 | 0.39 | 0.03** | 0.03** |
| 1×4 | 3.90 | 0.27** | −0.01 | 1.00 | −0.11** | −0.10** | 0.47 | 0.01* | 0.01* |
| 1×5 | 3.34 | 0.32** | 0.10* | 1.88 | 0.64** | 0.29** | 0.34 | 0.02* | 0.02** |
| 2×3 | 3.77 | 0.54** | −0.13* | 1.00 | 0.09** | 0.43** | 0.41 | −0.07** | −0.07** |
| 2×4 | 3.79 | 0.12* | −0.20** | 1.00 | 0.09** | −0.18** | 0.53 | 0.02* | 0.02** |
| 2×5 | 3.68 | 0.42** | −0.10 | 1.00 | −0.18** | −0.03 | 0.46 | −0.01* | −0.01 |
| 3×4 | 3.73 | −0.33** | −0.19** | 1.00 | 0.09** | −0.03 | 0.43 | −0.03** | −0.03** |
| 3×5 | 3.99 | 0.02 | −0.01 | 1.00 | −0.16** | −0.06 | 0.42 | −0.02* | −0.02* |
| 4×5 | 2.97 | 0.03 | −0.14** | 1.00 | −0.18** | −0.17** | 0.47 | 0.04** | 0.04** |
| 2×1 | 2.79 | −0.09* | 0.25** | 1.00 | 0.01 | 0.01 | 0.45 | −0.02* | −0.02* |
| 3×1 | 3.78 | −0.32** | 0.19* | 1.00 | 0.01 | 0.01 | 0.45 | −0.03* | −0.03** |
| 3×2 | 4.21 | −0.35** | 0.01 | 1.06 | 0.00 | − 0.03 | 0.41 | 0.01 | 0.01 |
| 4×1 | 3.64 | 0.37** | 0.16 | 1.00 | 0.01 | 0.01 | 0.45 | 0.01 | 0.01 |
| 4×2 | 3.94 | 0.18 | −0.04 | 2.16 | 0.01 | −0.58** | 0.47 | 0.03 | 0.03** |
| 4×3 | 3.97 | −0.15 | 0.05 | 1.00 | 0.01 | 0.01 | 0.51 | −0.04** | −0.04** |
| 5×1 | 4.06 | −0.49** | 0.36* | 1.00 | −0.14** | 0.44** | 0.42 | −0.04** | −0.04** |

**Table 4** continued

| Crosses and reciprocals | RPH (%) | | | CM (1-5) | | | HI (%) | | |
|---|---|---|---|---|---|---|---|---|---|
| | Mean | 2004 | 2005 | Mean | 2004 | 2005 | Mean | 2004 | 2005 |
| 5×2 | 3.00 | −0.19 | −0.11* | 1.00 | 0.00 | 0.00 | 0.37 | 0.05** | 0.05** |
| 5×3 | 3.60 | 0.34** | 0.01 | 1.00 | 0.03 | 0.00 | 0.42 | 0.01 | 0.01 |
| 5×4 | 4.10 | −0.31** | −0.15 | 1.00 | 0.00 | 0.00 | 0.5 | 0.01 | 0.01 |
| SE ($S_{ij}$) | 3.61[a] | 0.08 | 0.11 | 1.11[a] | 0.02 | 0.07 | 0.44[a] | 0.01 | 0.01 |
| SE ($S_{ij} - S_{kl}$) | 0.60[b] | 0.24 | 0.31 | 0.23[b] | 0.08 | 0.08 | 0.11[b] | 0.03 | 0.02 |
| SE ($R_{ij}$) | | 0.22 | 0.29 | | 0.07 | 0.07 | | 0.03 | 0.02 |

*Parent*: 1 = Chigoma mafia, 2 = Mulaleia, 3 = MZ 89186, 4 = IMM 30025, 5 = Macia 1, *ARN* average root number, *FRW* average fresh root yield, *CBSD* cassava brown streak necrosis, *RTST* root taste, *RPH* root pulp hardness, *CM* cassava mealybug infestation, *Y* year, *HI* harvest index, *SE* Standard error

[a] average

[b] LSD (5%)

* $P \leq 0.05$

** $P \leq 0.01$

highest SCA effects were observed in the reciprocal Chigoma mafia × Macia 1.

The best average performance and SCA effect for root taste was observed in the cross Chigoma mafia × Mulaleia. Root pulp hardness has been used to classify the root quality. In this study, it was classified using a scale of 1 to 5, where the lower classes (1–3) were the best, and the higher (4–5) the poorest and rejected by farmers. The best performance was found in the cross Chigoma mafia × Mulaleia, and the best SCA effect between Macia 1 × Chigoma mafia in 2004. For root pulp hardness, these results were similar to findings reported by Jaramillo et al. (2005) and this was a confirmation of the importance of non-additive effects for root pulp hardness in cassava.

The GCA effect was lower than SCA for CBSD resistance. Thus the GCA:SCA ratio was lower than unit, suggesting the presence of non-additive gene action (Baker 1978). A negative GCA effect in the parent line for disease, in this case CBSD resistance, is an indication of the contribution towards resistance to the disease (Owolade et al. 2006), while a positive value represents the susceptibility due to the scale used. Chigoma mafia ranked as the best general combiner for CBSD resistance, followed by Mulaleia. During the field trips and surveys conducted from 1999 to 2004 in the affected region (Hillocks 2003; Zacarias and Cuambe 2004), farmers ranked these cultivars as resistant to CBSD. However, in this study, the best average performance was observed in the cross Chigoma mafia × Mulaleia, but the best SCA effects with the combinations with the lowest values were those between MZ 89186 × IMM 30325, susceptible × resistant parents, and the cross Macia 1 × Chigoma mafia, moderate × resistant parents, according to the available information so far collected in the affected areas. The magnitude of GCA and SCA for a given trait depends on the environment and genotypes involved (Ntawuruhunga 2000; Ojulong 2006).

## Estimates of heterosis

The largest heterosis value was observed for root pulp hardness followed by average root number and fresh root yield (Table 5). Heterosis for harvest index was rarely observed. Average root number was observed with significant heterosis values that varied from 2.09 to 34.69. MZ 89186 × Mulaleia, MZ 89186 × IMM 30325, and MZ 89186 × Chigoma mafia had the highest values.

Four combinations were observed with positive and significant heterosis for fresh root yield: Chigoma mafia × Mulaleia, MZ 89186 × IMM 30025, MZ 89186 × Macia 1 and the reciprocals IMM 30025 × Mulaleia.

Negative but therefore desirable, significant heterosis values were observed for CBSD resistance and the combinations were variable, compared to the others already reported in this study. The best four mid-parent

**Table 5** Mean performance and percentage of mid-parent heterosis (MPH) for various characters evaluated during the 2004 and 2005 seasons

| Entries | ARN (kg/pl) | | FRW (kg/pl) | | CBSD (1–5) | | RTST (1–2) | | RPH (%) | | HI (%) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | MPH | Mean | MPH | Mean | MPH | Mean | MPH | Mean | MPH | Mean | MPH |
| P1 | 6.98 | | 3.22 | | 1.55 | | 1.56 | | 2.27 | | 0.50 | |
| P2 | 5.46 | | 2.07 | | 1.34 | | 1.13 | | 3.04 | | 0.55 | |
| P3 | 5.32 | | 3.32 | | 2.59 | | 1.12 | | 3.32 | | 0.63 | |
| P4 | 7.55 | | 2.96 | | 2.32 | | 1.30 | | 4.06 | | 0.47 | |
| P5 | 7.87 | | 2.82 | | 2.92 | | 1.04 | | 2.62 | | 0.39 | |
| 1 × 2 | 6.35 | 2.09** | 3.50 | 32.33** | 1.63 | 12.80* | 1.20 | −10.78** | 2.77 | 4.33 | 0.40 | −23.81* |
| 1 × 3 | 6.11 | −0.65* | 2.26 | −30.89 | 2.13 | 2.90 | 1.58 | 17.91* | 3.26 | 16.64 | 0.39 | −30.97* |
| 1 × 4 | 6.94 | −4.47* | 2.69 | −12.94* | 2.32 | 19.90 | 1.44 | 0.70* | 3.90 | 23.22 | 0.47 | −3.09* |
| 1 × 5 | 5.59 | −24.71* | 1.59 | −47.35 | 1.57 | −29.75** | 1.29 | −0.77** | 3.34 | 36.61 | 0.34 | −23.60* |
| 2 × 3 | 6.97 | 1.58** | 2.07 | −0.63** | 2.02 | 0.06 | 1.29 | 0.17* | 3.77 | 18.55 | 0.41 | −0.18 |
| 2 × 4 | 5.21 | −0.65* | 3.10 | 0.29* | 1.93 | 0.05 | 1.29 | 0.04* | 3.79 | 6.76 | 0.53 | 0.01** |
| 2 × 5 | 6.43 | −13.40* | 2.99 | −0.99 | 2.08 | −6.94 | 1.42 | 9.23* | 3.68 | 50.51* | 0.46 | 3.37** |
| 3 × 4 | 8.50 | 32.09** | 3.54 | 12.74** | 1.75 | −28.72* | 1.34 | 10.74** | 3.73 | 1.08 | 0.43 | −21.82 |
| 3 × 5 | 7.73 | 17.21** | 3.50 | 14.01* | 1.76 | -36.12* | 1.21 | 12.04* | 3.99 | 34.34 | 0.42 | −17.65 |
| 4 × 5 | 5.22 | −32.30* | 2.09 | −27.68* | 1.87 | −28.63* | 1.32 | 12.82 | 2.97 | −11.08** | 0.47 | 9.30** |
| 2 × 1 | 1.07 | −82.80* | 2.70 | 2.08 | 2.01 | 39.10* | 1.26 | −6.32* | 2.79 | 5.08* | 0.45 | −14.29 |
| 3 × 1 | 7.57 | 23.09** | 2.58 | −21.10 | 1.74 | −15.94** | 1.28 | −4.48** | 3.78 | 35.24 | 0.45 | −20.35* |
| 3 × 2 | 7.26 | 34.69** | 2.31 | −14.29 | 2.41 | 22.65* | 1.34 | 19.11* | 4.21 | 32.39* | 0.41 | −30.51* |
| 4 × 1 | 6.94 | −4.47* | 2.53 | −18.12 | 1.83 | −5.43 | 1.47 | 2.80 | 3.64 | 15.01 | 0.45 | −7.22* |
| 4 × 2 | 6.60 | −14.40* | 3.26 | 12.80** | 2.68 | 2.29 | 1.11 | −5.13 | 3.94 | 17.96** | 0.47 | 9.30** |
| 4 × 3 | 7.36 | 14.37** | 2.70 | −14.01 | 2.06 | −16.09** | 1.11 | −8.26* | 3.97 | 7.59* | 0.51 | −7.27* |
| 5 × 1 | 5.47 | −26.33* | 2.72 | −9.93 | 1.70 | −23.94** | 1.59 | 22.31** | 4.06 | 66.05** | 0.42 | −5.62* |
| 5 × 2 | 4.89 | −34.14* | 2.14 | −29.14 | 2.10 | −6.04* | 1.03 | −20.77** | 3.00 | 22.70* | 0.37 | −16.85* |
| 5 × 3 | 4.12 | −37.53* | 1.09 | −64.50* | 1.70 | −38.29** | 1.12 | 3.70* | 3.60 | 21.21** | 0.42 | −17.65* |
| 5 × 4 | 4.43 | −42.54* | 3.13 | 8.30** | 2.70 | 3.05 | 1.30 | 11.11* | 4.10 | 22.75* | 0.50 | 16.28** |

*Parent*: 1 = Chigoma mafia, 2 = Mulaleia, 3 = MZ 89186, 4 = IMM 30025, 5 = Macia 1, *ARN* average root number, *FRW* fresh root weight, *CBSD* cassava brown streak necrosis, *RTST* root taste, *RPH* root pulp hardness; HI=harvest index

* $P \leq 0.05$

** $P \leq 0.01$

values observed were Macia 1 × MZ 89185, MZ 89186 × Macia 1, Chigoma mafia × Macia 1, MZ 89286 × IMM 30025 and Macia 1 × Chigoma mafia.

Lower root taste values identifies the sweet tasting roots and were observed for Macia 1 × Mulaleia, while the most bitter was Macia 1 × Chigoma mafia. In the small-scale farms it is common to find mixtures of varieties grown by farmers in Africa (Jones 1959; Chiwona-Karltun et al. 2004). Sweet types are commonly used fresh and as snack, while the bitter ones are processed into flour prior to consumption and they are usually correlated to high levels of cyanogenic glucosides (Chiwona-Karltun et al. 2004).

Root pulp hardness is also one of the traits of commercial importance in cassava. The only combination observed with highly significant and negative values for root pulp hardness was IMM 30025 × Macia 1. The classes used in this study, varied from 1 to 5, where the lowest was better, which means that for among all hybrid combinations for MPH, IMM 30025 × Macia 1 was the best.

Harvest index had only four combinations that had positive and significant mid-parent heterosis. They were Mulaleia × Macia 1, IMM 30025 × Mulaleia, IMM 30025 × Macia 1 and its reciprocal Macia 1 × IMM 30025.

From this analysis it can be observed that it is difficult to produce hybrids with a combination of the most important economic traits, such as fresh root yield, CBSD resistance and root pulp hardness.

Estimates of genetic parameters

The general combing ability variances ($\delta^2_{gca}$) were low, in general, compared to SCA variances ($\delta^2_{sca}$). When $\delta^2_{gca}$, is higher than $\delta^2_{sca}$, it indicates the contribution of both additive and non-additive variability to inheritance of traits in this study. For the characters with $\delta^2_{gca}$ higher than $\delta^2_{sca}$, it is an indication that they should respond favourably to direct selection. This is more reliable in cases when parents are selected randomly. In this case, cassava is a highly heterozygous crop and in particular for this study the parents were selected for their performance in a high pressure CBSD environment in Mozambique, capacity of seed production and the capacity of their $F_1$ progeny to produce five stem cuttings. The relative amount of GCA variance measured in this case, might have been under-estimated. However, significant SCA effects were also observed, which Stuber (1970) suggested were probably the result of additive × additive epistatic effects. Negative variances are not subject to analysis in this study, but their calculations were represented in the table.

Of all the characters, root taste, root pulp hardness, CM and harvest index, had the highest heritability values (Table 6). Score scales are subject to change depending on the objective, for example using different scales, the results may differ to that obtained in this study. The heritability of CBSD resistance was lower due to its poor GCA:SCA ratios, which consequently produced negative $\delta^2_{gca}$ and $\delta^2_A$, a clear indication that it is a polygenic trait. The SCA variance was higher than the GCA variance, thus, the SCA is more important in predicting progeny performance for expression of resistance to CBSD.

High broad sense heritability indicated that the characteristics had high genetic variance, both additive and non-additive. In this study, most of the characteristics measured had high broad sense heritability. Narrow sense heritability is important for breeding programmes as it estimates the relative importance of the additive portion of the genetic variance that can be transmitted to the next generation. In this case, the narrow sense heritability of all characteristics was relatively low except for harvest index. Falconer and Mackay (1996) reported that the lower narrow sense heritability was caused by low additive effects and high dominant gene action.

The magnitude of heritability of a given trait is affected by the type of genetic material involved

**Table 6** Estimates of genetic parameters for various characters evaluated during two seasons in Mogincual

| Character | Years | Genetic parameter | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | $\delta^2_{gca}$ | $\delta^2_{sca}$ | $\delta^2_e$ | $\delta^2_A$ | $\delta^2_D$ | $H^2$ (b) (%) | $h^2$(n) (%) | PR | $\sqrt{H/D}$ |
| ARN | 2004 | −0.122 | 0.545 | 0.412 | −0.245 | 0.545 | 42.2 | −34.35 | −0.81 | |
| | 2005 | −0.241 | −3.116 | 4.574 | −0.481 | −3.116 | −36.8 | −49.28 | 0.13 | 0.31 |
| FRW | 2004 | 0.054 | 0.134 | 0.227 | 0.108 | 0.134 | 51.6 | 23.03 | 0.45 | 1.58 |
| | 2005 | 0.041 | 0.075 | 0.251 | 0.083 | 0.075 | 38.6 | 20.23 | 0.52 | 1.35 |
| CBSD | 2004 | −0.037 | 0.241 | 0.074 | −0.074 | 0.241 | 69.3 | −30.71 | −0.44 | – |
| | 2005 | −0.030 | 0.300 | 0.260 | −0.060 | 0.300 | 48.0 | −12.00 | −0.25 | – |
| RTST | 2004 | 0.023 | 0.041 | 0.019 | 0.047 | 0.041 | 82.2 | 43.75 | 0.53 | 1.33 |
| | 2005 | 0.030 | 0.030 | 0.020 | 0.060 | 0.030 | 81.8 | 54.55 | 0.67 | 1.00 |
| RPH | 2004 | 0.140 | 0.350 | 0.100 | 0.280 | 0.350 | 86.3 | 38.36 | 0.44 | 1.58 |
| | 2005 | 0.068 | 0.710 | 0.166 | 0.135 | 0.710 | 83.6 | 13.38 | 0.16 | 3.24 |
| CM | 2004 | 0.015 | 0.117 | 0.009 | 0.030 | 0.117 | 94.2 | 19.23 | 0.20 | 2.79 |
| | 2005 | −0.017 | 0.070 | 0.010 | −0.033 | 0.070 | 78.6 | – | – | – |
| HI | 2004 | 0.001 | 0.001 | 0.001 | 0.003 | 0.001 | 78.6 | 57.14 | 1.00 | 0.00 |
| | 2005 | 0.009 | 0.001 | 0.001 | 0.019 | 0.001 | 95.2 | 90.32 | 0.95 | 0.33 |

*ARN* average root number, *FRW* average fresh root yield, *CBSD* cassava brown streak necrosis, *RTST* root taste, *RPH* root pulp hardness; *CM* cassava mealybug infestation, *HI* harvest index, $h^2(b)$ broad sense heritability, $h^2(n)$ narrow sense heritability

(Ceccarelli 1994). Cassava is a vegetatively propagated crop with the advantage that in every new hybrid the genes are fixed, as the new commercial variety is produced by simply multiplying the stem cuttings. For this reason Kawano et al. (1998) suggested that heritability of cassava after hybridisation is mainly broad-sense in nature.

The average degree of dominance ($\sqrt{H/D}$) for the characters was less than unit for average root number and harvest index (Table 6), suggesting partial dominance. The opposite suggests the presence of dominance. The degree of dominance was greater than unit for fresh root yield, root taste, root pulp hardness and cassava mealybug infestation, indicating the presence of over-dominance for these characters.

The predictability ratio (PR) is important to estimate the relative importance of progeny performance. Baker (1978) indicated that when SCA means are not important, the hypothesis is that performance of single-cross progeny can be adequately predicted on the basis of GCA. Moreover, if the SCA mean squares are significant, the relative importance of GCA and SCA should be determined by estimating components of variance to predict the progeny performance. The closer the ratio is to a unit, the greater the predictability based on GCA alone. The predictability ratio in this study varied from 0.1 to 1.0. The character with the ratio closest to 1 was harvest index. Jaramillo et al. (2005), using a different approach for analysis, found similar results for harvest index and suggested that GCA effects were more important than SCA for harvest index.

The analysis of variance and the GCA: SCA ratio indicated that the GCA was larger than SCA for average root number, average fresh root yield, root taste, root pulp hardness yield and harvest index, indicating the presence of additive gene effects and a possibility for improvement for this characters.

The parental genotypes were selected from a particular region where CBSD is the main economic constraint. Chigoma mafia had the best GCA effect for average root number and CBSD resistance, while the clone IMM 30025, had the best GCA effect for fresh root yield and root pulp hardness. However, the combination Chigoma mafia × Mulaleia, had the best mean performance for fresh root yield and CBSD resistance. While the combination with parents Macia 1 × Chigoma mafia had the best SCA for fresh root yield, CBSD resistance and root pulp hardness. With considerations to the CBSD constraint, the combinations MZ 89186 × IMM 30025 and the reciprocal IMM 30025 × MZ 89186, Macia 1 × Chigoma mafia and MZ 89186 × Mulaleia were the best for resistance to CBSD. The two sets are important for different traits and should be considered as parents in the next hybridisation scheme.

In terms of mid-parent hybrid performance, three had combinations with traits of interest for the breeding programme. Chigoma × Mulaleia for average root number, fresh root yield and root pulp hardness; MZ 89185 × IMM 30025 for average root number, fresh root yield, root taste and CBSD resistance, and MZ 89186 × Macia 1 for average root number, fresh root yield, CBSD resistance and root taste.

The broad sense heritability estimates were moderate to high. It varied from 38.9 observed for fresh root yield to as high as 95.5 for harvest index, as clear indication that the phenotypic variance was additive. However, some characteristics showed non-additive gene action. Harvest index had a GCA variance higher than SCA variance. Its predictability ratio was close to unit, confirming that this character is highly heritable and under additive gene action.

## Conclusions

Chigoma mafia was the best general combiner for average root number and CBSD resistance, Mulaleia also had good GCA for CBSD resistance. Clone IMM 30025 was the best general combiner for root pulp hardness, but combined poorly for CBSD resistance and should not be used in crosses. Chigoma mafia × Mulaleia had the best mean performance for fresh root yield and CBSD resistance. Macia 1 × Chigoma mafia had the best SCA for fresh root yield, CBSD resistance and root pulp hardness. MZ 89186 × IMM 30025 and the reciprocals IMM 30025 × MZ 89186, Chigoma mafia × Macia 1 and MZ 89186 × Mulaleia had the best resistance to CBSD. This indicates that there are good potential parents that can be used in crosses to improve CBSD resistance, while maintaining good yield and root characteristics.

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