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ORIGINAL ARTICLE

Impact of viral diseases and whiteflies on the yield and quality of cassava

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Abstract

Here we investigated the effect of the insect pest whitefly (*Bemisia tabaci)*, cassava mosaic disease (CMD) and cassava brown streak disease (CBSD) on cassava root yield and quality in two cropping seasons 2014–2015 and 2015–2016 on ten cassava varieties in Tanzania. ANOVA (sum of squares or SS) revealed that the time of planting (42.7%) and cassava variety (29.5%) had the largest effect on whitefly population. Not surprisingly, cassava varieties also had the highest effect (SS 39.8 to 70.4%) on both diseases and yield. An increase in whitefly population led to higher disease incidences and severity in 2015–2016 compared to 2014–2015. Some CBSD-resistant and tolerant cassava varieties like Namikonga and Kiroba, respectively, harboured high whitefly populations. The CMD, CBSD and whitefly-susceptible variety, Mreteta, showed highest yield losses of up to 60%, while the resistant variety NDL 2005/1471 had approximately 1% loss. Deployment of varieties resistant to both diseases and whitefly is thus necessary to safeguard cassava production and food security of vulnerable communities in the affected African countries.

Keywords Epidemiology · Whitefly · Cassava brown streak disease · Cassava mosaic disease · Insect and disease resistance

Introduction

Cassava (*Manihot esculenta* Crantz) is an important staple food in sub-Saharan Africa (SSA), ranked second after maize in Eastern and Southern African countries (FAOSTAT 2020). With approximately 200 million metric tonnes of annual root production, cassava is a major source of carbohydrates in the diet of about 450 million people in SSA. It is also grown as a famine reserve crop owing to its tolerance to harsh environmental conditions (Jarvis et al. 2012). The crop has enormous potential as an essential economic driver within the agriculture sector in SSA countries for exploitation in industries to produce high-quality cassava flour, starch, beverages and animal feed (Luar et al. 2018). Despite its importance, the average cassava yield in Africa is, however, about 9.0 t/ha (FAOSTAT 2020), which is well below the yield potential of 50–90 t/ha achieved under optimal conditions (Ntawuruhunga et al. 2006; El-Sharkawy 2004; Obiero 2004). However, average yields in the Eastern African countries of Uganda, Tanzania and Kenya are very low at 3.3, 7.3, and 14.5 t/ha, respectively (FAOSTAT 2020).

One of the factors for the low yield is severe damage caused by insect pests and diseases that hinder cassava production (Ekeleme et al. 2017; Ezui et al. 2016). Two of the most critical current biotic constraints in Eastern and Southern Africa are viral diseases: cassava mosaic disease (CMD) caused by cassava mosaic begomoviruses (CMBs) (family *Geminiviridae*) and cassava brown streak disease (CBSD) caused by cassava brown streak ipomoviruses (CBSIs) (family *Potyviridae*) (Legg et al. 2011, 2015; Mohammed et al. 2012). CMD symptoms typically include irregular yellow or yellow-green chlorotic mosaic pattern on leaves, leaf distortion, stunted plant growth and reduced or complete root yields, but not rotting of roots (Storey and Nichols 1938; Thresh and Cooter 2005; Tembo et al. 2017). The most

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damaging effect of CBSD is root necrosis, causing yield losses of up to 75% as the root is unmarketable or inedible in the most susceptible varieties (Maruthi et al. 2020). These diseases together can severely reduce cassava productivity in sub-Saharan Africa, causing annual losses of up to US$3 billion to resource poor farmers (Thresh et al. 1997; Hillocks and Maruthi 2015).

The whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), is a serious plant pest and is the sole vector of CMBs and CBSIs in cassava (Legg 2010; Maruthi et al. 2005, 2017). Whitefly feeding on cassava can also damage plants causing chlorotic mottling, twisting or curling, particularly on upper leaves (Bellotti and Arias 2001). Large populations that develop early in the crop's life reduce plant vigour and tuber sizes and cause stunted growth leading to more than 50% loss in yield (Legg et al. 2004). A large whitefly population can also produce honeydew, which leads to the production of black sooty mould on lower leaves, reducing the photosynthetic ability of the plant, further contributing to yield losses (Legg et al. 2004; Omongo et al. 2004). However, the most significant economic threat is spread of CMD and CBSD.

Disease and whitefly prevalence surveys have been conducted in the past to assess the epidemiology of both CMD and CBSD (Muhindo et al. 2020; Tairo et al. 2019; Harimalala et al. 2015; Legg et al. 2011). These findings had shown high whitefly abundance with high CMD and CBSD severity and incidences. However, few studies have investigated the cumulative effects of damage by whiteflies and viral diseases on cassava. To investigate this, we evaluated the spread of whiteflies, CMD, CBSD and their impact on cassava yield and quality in two cropping seasons in Tanzania.

Materials and methods

Cassava germplasm and screening location

Ten popularly grown cassava varieties and advanced breeding lines were selected for this study (Table 1). The field trials were established in 2014–2015 and 2015–2016 cropping seasons in the CMD and CBSD hot spot research fields of the Tanzania Agricultural Research Institute (TARI)—Naliendele in the Mtwara region of southern Tanzania. TARI-Naliendele lies on the coastal belt of the Indian Ocean at 10° 22′ 20"S, 40° 10′ 34"E and 111 m above mean sea level. The area receives the main rainfall from December to May, with second rains of scattered showers in August–October (Dondeyne et al. 2003). The sandy soils of

the Mtwara region are considered poor for most crops. They comprise deep, well-drained, weak-structured dark reddish-brown loamy sand topsoil over reddish brown moderately structured sandy loam to sandy clay loam subsoil (Dondeyne et al. 2003).

Experimental design

The field trials were laid out using the Randomised Complete Block Design (RCBD) with three replications and a plot size of 4 m × 10 m. The first trial was planted on 12 January 2014 and harvested on 20 January 2015, while the second was planted on 16 March 2015 and harvested on 19 March 2016 at the Naliendele site. Both trials consisted of 10 cassava varieties and advanced breeding lines, namely NDL2003/031, NDL2003/111, NDL2005/1471, KBH96/1056, KBH 2002/494, KBH2002/482, Kiroba and Mreteta. The control checks included Namikonga (susceptible and resistant to CMD and CBSD, respectively) and Albert (resistant to CMD and susceptible to CBSD) (Table 1). Mature cassava cuttings of about 25 cm long and having 4–5 nodes with viable buds were collected for each variety from TARI—Makutupora in Tanzania (a disease-free site used for seed multiplication). To increase disease inoculum, CMD-susceptible variety Limbanga and CBSD-susceptible variety Albert were planted around the experimental plots as spreader rows (Kundy et al. 2014). The trial was rain-fed and kept weed-free by monthly weeding, and no fertiliser was applied.

Epidemiology and effect of cassava viral diseases and insect pests on yield

Twenty plants per plot were selected from the two inner rows for data collection from 1 to 12 months after planting. The data collected included whitefly adult count on top five leaves, CMD and CBSD foliar severities, CBSD root symptoms (root necrosis), root weight (t/ha), marketable roots (t/ha) and dry matter content from 20 plants/plot/variety. The foliar severity for CMD was scored on a 1–5 scale where: 1 = no visible symptoms; 2 = mild distortion only at the base of leaflets with the rest of leaflets appearing green and healthy/mild chlorotic pattern over the entire leaflets; 3 = conspicuous mosaic pattern throughout the leaf, narrowing and distortion of lower 1/3 of leaflets; 4 = severe mosaic, distortion of two-thirds of leaflets and general reduction in leaf size; and 5 = severe mosaic, distortion of ¾ of leaflets, twisted and malformed leaves (Hahn et al. 1980). Foliar severity for CBSD was scored on a 1–5 scale where: 1 = no visible symptoms; 2 = mild foliar mosaic on some leaves and

no stem lesions; 3 = foliar mosaic with mild stem lesions and no dieback; 4 = foliar mosaic and pronounced stem lesions and no die back; and 5 = defoliation with pronounced stem lesions and dieback (Hillocks et al. 1996).

At about 12 MAP, plants were harvested, and roots were examined for root necrosis. Roots from each plant were chopped longitudinally and transversely to identify the presence of necrotic patches on the starch-bearing tissues. Scoring for root necrosis severity was also done based on a 1–5 scale where: 1 = no clear symptoms; 2 = < 5% of root necrotic; 3 = 5 –25% of root necrotic; 4 = 25–50% root necrotic and mild root constriction; and 5 = > 50% of root necrotic (Masinde et al. 2016; Hillocks and Maruthi 2015; Gondwe et al. 2002). All roots with a necrosis score of ≤ 2 were considered marketable as only tiny spots of root necrosis were observable at this score (Masinde et al. 2016). Severe root necrosis affects root quality, reducing the quantity of marketable roots. Marketable roots per variety were determined by deducting the unmarketable roots with root necrosis score > 2 from the total roots.

Root weight in tonnes per hectare (t/ha/) was estimated according to Masinde et al. (2017).

$$\text{Root weight}\left(\frac{t}{\text{ha}}\right) = \frac{\text{root weight}\left(\frac{\text{kg}}{\text{m}^2}\right) \times 1000}{1000}$$

Further, the specific gravity method collected data on root dry matter content (Kawano 1987).

$$\text{Dry matter content} = 158.3 \times \left[\frac{\text{weights of roots in air}}{\text{weights of roots in air} - \text{weights of roots in water}}\right] - 142$$

Data analysis

Data analysis was performed using R packages multcomp, agricolae and emmeans. A 3-way ANOVA was performed on the effect of time of planting (months after planting, MAP), variety and season for whitefly infestation, CMD and CBSD foliar severities. A 2-way ANOVA was performed on the effects of variety and season for root necrosis and yield parameters including root weight, marketable roots and dry matter content. Treatment means were separated using the LSD test at a 95% confidence level. Graphs were plotted for whitefly abundance and yield traits, while means were calculated for the ratings on colour, smell and taste of cassava products used in the organoleptic test.

Results

Evaluation of different traits

The time of planting (MAP) had the largest effect on whitefly abundance (Table 2) (42.7% of the total SS), followed by variety (29.5%) and interaction effect between MAP and season (13.7%). Additionally, the mean squares were highly significant ($P \le 0.001$) for the factors and their interactions. The cassava varieties contributed to the maximum differences (39.8 to 70.4% of SS) observed for CMD, CBSD, root necrosis, root weight and marketable roots (Table 2 and 3). Seasonal effect accounted for 12.4 to 43.1% SS, while variety by season interaction accounted for 5.1 to 16.9% differences. The mean squares for the factors and most of their interactions were significant ($P \le 0.05$) (Table 2 and 3). Finally, the season (time of harvesting) had the largest effect (83.7% SS) on dry matter content (Table 3) with minor effect by the varieties (9.7%).

Table 1 Pedigree of cassava varieties and advanced breeding lines used in the study

Variety	Pedigree	Status
Albert	Putative full-sib of TME117	Popular landrace grown in Tanzania. CBSD susceptible/CMD resistant
KBH 2002/482	Kiroba half-sib (male parent unknown)	Released
KBH 2002/494	Kiroba half-sib (male parent unknown)	Not released
KBH 96/1056	Kiroba half-sib (male parent unknown)	Candidate for official release
Kiroba	Hypothesised to be a derivative from *M. glaziovii* × *M. esculenta* interspecific cross	Popular landrace officially released for Tanzanian coastal lowlands. CBSD tolerant/CMD susceptible
Mreteta	Unknown	Local landrace. CBSD susceptible/CMD susceptible
Namikonga	Third back cross from inter-specific hybrid (46,106/27) from *M. glaziovii* onto *M. esculenta*	Popular landrace with late root bulking properties. CBSD resistant/CMD susceptible
NDL 2003/031	Nachinyaya × Kiroba full-sib	Candidate for official release
NDL 2003/111	Namikonga × Kalulu full-sib	Candidate for official release
NDL 2005/1471	Nachinyaya half-sib (male parent unknown)	Candidate for official release

Fullsib genotypes with known male and female parents, *Halfsib* genotypes with a known mother that was open pollinated; hence, male parent is unknown

Table 2 Mean and sum of squares of whitefly count on 10 cassava varieties in 2014–2015 and 2015–2016 seasons

3- way ANOVA (F stat.)

	df	Whiteflies			CBSD			CMD		
		SS	SS (%)	MS	SS	SS (%)	MS	SS	SS (%)	MS
MAP	11	26,229.2	42.7	3475.3***	27.5	5.7	2.5***	14.1	9.0	1.3***
Variety	6	18,143.3	29.5	3023.9***	276.0	57.2	30.7***	62.4	39.8	6.9***
Season	1	1508.1	2.5	1507.7***	59.7	12.4	59.7***	29.3	18.7	29.3***
MAP*Variety	99	4280.1	7.0	43.2***	33.9	7.0	0.3***	13.9	8.9	0.2***
MAP*Season	11	8395.9	13.7	763.3***	2.4	0.5	0.2	2.2	1.4	0.2**
Variety*Season	9	432.4	0.7	47.9***	70.1	14.5	7.8***	26.5	16.9	2.9***
MAP*Variety*Season	99	2433.5	4.0	24.6***	12.5	2.6	0.1	8.9	5.7	0.1
Total	480	61,422.5			482.2			157.1		

df degrees of freedom, *MS* mean squares, *SS* sum of squares, *MAP* month after planting, statistical significance *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$

Table 3 Mean and sum of squares of root necrosis, root weight, marketable roots and dry matter content of 10 cassava varieties

2-way ANOVA (F stat.)

	df	Root necrosis			Root weight			Marketable roots			Dry matter content		
		SS	SS (%)	MS	SS	SS (%)	MS	SS	SS (%)	MS	SS	SS (%)	MS
Season	1	5.7	20.8	5.7***	265.7	23.5	265.7***	510.4	43.1	510.4***	557.5	83.7	557.5***
Variety	9	15.6	67.8	1.7***	797.2	70.4	88.6***	587.4	49.5	65.3***	64.4	9.7	7.2***
Variety*Season	9	3.7	11.4	0.4**	57.9	5.1	6.4**	64.8	5.5	7.2*	44.1	6.6	4.9**
Total	36	25.0			1129.8			1185.7			666.0		

df degrees of freedom, *MS* mean squares, *SS* sum of squares, statistical significance *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$
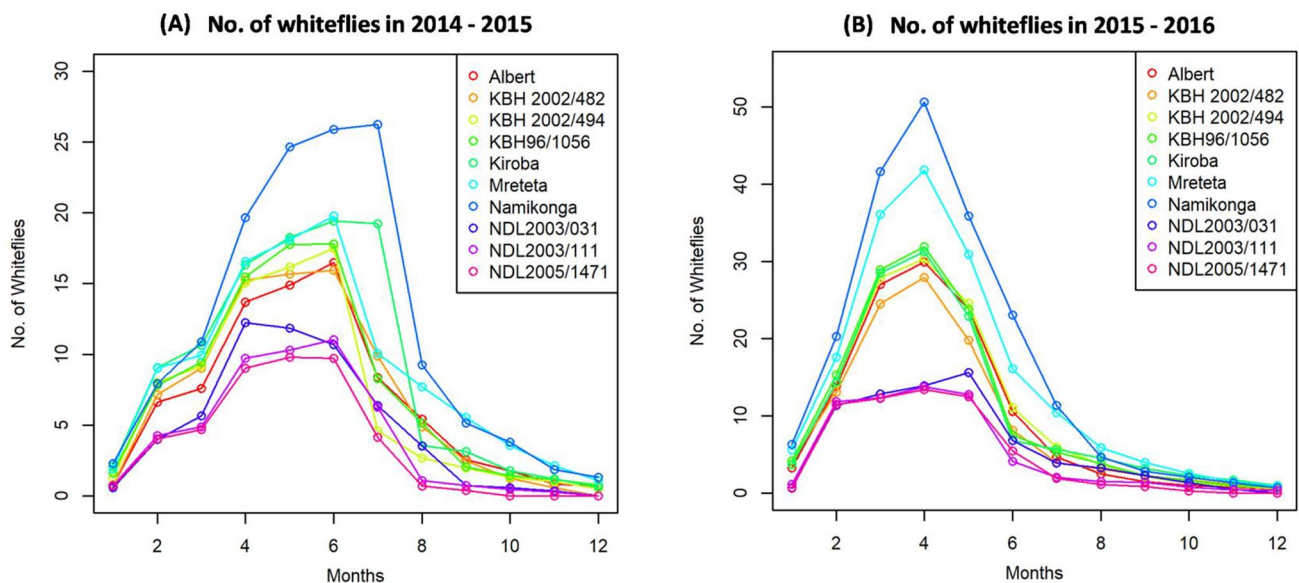

Fig. 1 Number of whiteflies on different cassava varieties in **A** season 2014–2015 and **B** season 2015–2016 from 1 to 12 months after planting

Fig. 2 Leaf morphological features of cassava varieties. **A** Albert, **B** KBH 2002/482, **C** KBH 2002/494, **D** KBH 96/1056, **E** Kiroba, **F** Mreteta, **G** Namikonga, **H** NDL 2003/031, **I** NDL 2003/111, and **J** NDL 2005/1471

Generally, a large SS for a factor indicates that it contributes to most variations observed.

Whitefly abundance and morphological characterisation of varieties

Cropping season 2015—2016 had a slightly higher mean number of whiteflies ranging from 0.5 to 28.5 compared to 2014–2015 (0.5–16.4) (Figs. 1 and 2). The mean whitefly population increased from 1 MAP and peaked at approximately 6 MAP (16.4) and 4 MAP (28.5) in 2014–2015 and 2015–2016, respectively. The population declined sharply after with the lowest count of 0.5 by 12 MAP in both seasons. Whitefly count varied significantly ($P \leq 0.05$) among the varieties. Vars. Namikonga and Mreteta had the highest count ranging from 1.1 to 50.7, while Albert, KBH 2002/482, KBH 2002/494, KBH 96/1056 and Kiroba had

moderate counts (0.0–31.3) across the seasons. Vars. NDL 2003/031, NDL 2003/111 and NDL 2005/1471 had the least count ranging from 0.0 to 13.9 across the seasons.

The leaf colour, the shape of the central leaflet, the orientation of petioles and the hairiness/smoothness of leaves formed the basis for the morphological characterisation of cassava varieties for whiteflies' preference and colonisation. Accordingly, varieties with the highest whiteflies count, including Namikonga and Mreteta, had light green foliage, unlike the rest, which had dark green foliage (Fig. 3). Varieties with least whiteflies count, including NDL 2003/031, NDL 2003/111 and NDL 2005/1471, had lanceolate-shaped central leaflets, unlike the others whose leaves were elliptical–lanceolate. Petioles for Albert and KBH 2002/494 were inclined downwards, Kiroba and KBH 96/1056 inclined horizontally, while KBH 2002/482, Namikonga, Mreteta, NDL 2003/031, NDL 2003/111, and NDL 2005/1471 had
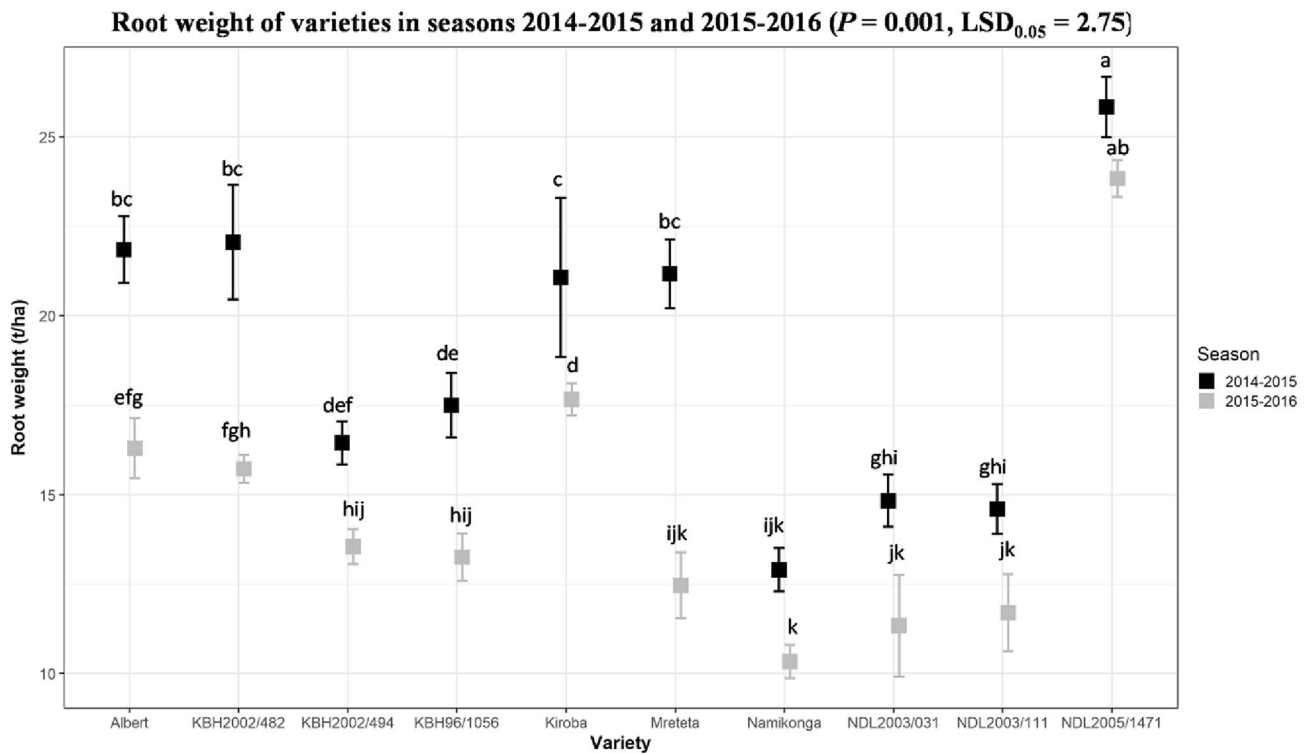
Fig. 3 Root weight of varieties in 2014–2015 and 2015–2016 cropping seasons

petioles facing upwards. NDL 2003/031, NDL 2003/111 and NDL 2005/147, the least infested varieties, possessed slightly hairy leaves while the rest had smooth leaves.

CMD foliar incidence and severity

2015–2016 had the highest mean CMD foliar severities and whitefly count (Table 4). In 2014–2015, CMD foliar symptoms were first observed at 2 MAP, while in 2015–2016 were observed very early at 1 MAP. In most varieties, CMD foliar severity increased throughout the two growing seasons and peaked between 6 and 8 MAP before dropping up to 12 MAP. Var. Mreteta had the highest CMD foliar severity ranging from 1.0 to 3.0, while KBH 96/1056 had the least ranging from 1.0 to 1.2 across the seasons.

CBSD foliar incidence, severity and root necrosis

CBSD foliar symptoms were first observed at 3 and 2 MAP in 2014–2015 and 2015–2016, respectively. 2015–2016 also had the highest mean CBSD foliar severities and whitefly count (Table 5). In 2014–2015, the mean CBSD foliar severity increased throughout the growing season until 9 MAP, then dropped from 10 to 12 MAP. In contrast, the mean CBSD foliar severity

increased to 7 MAP in 2015–2016, then dropped from 8 to 12 MAP. Varieties with significantly ($P \geq 0.05$) high CBSD foliar severity also had high root necrosis and vice-versa. Accordingly, var. Albert had the highest CBSD foliar severity ranging from 1.0 to 3.1 and root necrosis severity ranging from 2.4 to 2.7 across the seasons while Namikonga had the least CBSD foliar severity (1.0–1.3) and root necrosis (1.0–1.1).

Cassava yield traits

2014–2015 had significantly ($P \geq 0.05$) higher root weight, marketable roots and dry matter content, and it also received higher rainfall and had the least disease and whitefly incidences (Figs. 4 and 5). Varieties with significant differences between the two seasons in disease and whitefly incidences also had significant differences in root weight. For example, var. Mreteta had a low CMD incidence of (0.0–14.7%) with a root weight of 21.5 t/ha in 2014–2015, while it had a higher incidence of (44.1–75.6%) with a low root weight of 12.8 t/ha in 2015–2016 (Table 4, Fig. 4). On the other hand, NDL 2005/1471 had low CMD severities in both seasons and hence the minimal difference in root weight of 25.4 t/ha and 23.4 t/ha in 2014–2015 and 2015–2016, respectively (Table 4, Fig. 4).

Table 4 Means of CMD severity in 2014–2015 and 2015–2016 cropping seasons

Variety	Months after planting (MAP)											
	1	2	3	4	5	6	7	8	9	10	11	12
2014–2015												
Albert	1.0[a]	1.0[b]	1.1[bc]	1.1[bc]	1.2[cde]	1.2[cd]	1.1[bc]	1.2[c]	1.2[ab]	1.2[ab]	1.2[bc]	1.0[ab]
KBH 2002/482	1.0[a]	1.2[a]	1.3[ab]	1.4[ab]	1.5[abc]	1.6[abc]	1.8[ab]	1.4[abc]	1.2[ab]	1.2[ab]	1.2[bc]	1.1[ab]
KBH 2002/494	1.0[a]	1.0[ab]	1.1[bc]	1.3[abc]	1.3[bcde]	1.3[bcd]	1.1[bc]	1.1[c]	1.1[b]	1.0[b]	1.0[c]	1.0[b]
KBH 96/1056	1.0[a]	1.0[b]	1.0[c]	1.0[c]	1.0[e]	1.0[d]	1.0[c]	1.0[c]	1.0[b]	1.0[b]	1.0[c]	1.0[b]
Kiroba	1.0[a]	1.2[a]	1.4[a]	1.6[a]	1.8[a]	1.8[ab]	1.9[a]	2.0[a]	1.8[a]	1.6[ab]	1.5[ab]	1.4[a]
Mreteta	1.0[a]	1.1[ab]	1.1[bc]	1.4[ab]	1.4[bcd]	1.4[abcd]	1.5[abc]	1.4[bc]	1.3[ab]	1.3[ab]	1.1[c]	1.2[ab]
Namikonga	1.0[a]	1.2[a]	1.4[a]	1.4[ab]	1.6[ab]	2.0[a]	2.0[a]	2.1[a]	1.9[a]	1.7[a]	1.6[a]	1.1[ab]
NDL 2003/031	1.0[a]	1.0[b]	1.0[c]	1.0[c]	1.0[e]	1.0[d]	1.0[c]	1.0[c]	1.0[b]	1.0[b]	1.0[c]	1.0[b]
NDL 2003/111	1.0[a]	1.1[ab]	1.1[bc]	1.1[bc]	1.0[e]	1.0[d]	1.0[c]	1.0[c]	1.0[b]	1.0[b]	1.0[c]	1.0[b]
NDL 2005/1471	1.0[a]	1.0[b]	1.1[bc]	1.2[bc]	1.1[de]	1.2[cd]	1.1[bc]	1.0[c]	1.0[b]	1.0[b]	1.0[c]	1.0[b]
Mean	1.0	1.1	1.2	1.2	1.3	1.3	1.4	1.3	1.3	1.2	1.2	1.1
HSD	–	0.2	0.3	0.4	0.6	0.6	0.7	0.7	0.7	0.6	0.4	0.4
CV	–	11.8	13.8	19.5	16.2	15.0	18.6	17.0	19.8	16.5	19.8	12.7
2015–2016												
Albert	1.1[c]	1.1[c]	1.2[c]	1.2[c]	1.5[cd]	1.5[bc]	1.4[c]	1.5[bc]	1.4[bc]	1.3[bcd]	1.3[bcde]	1.3[bc]
KBH 2002/482	1.2[bc]	1.3[bc]	1.4[c]	1.5[bc]	1.5[cd]	1.8[abc]	1.9[bc]	1.7[bc]	1.5[bc]	1.5[bc]	1.6[bc]	1.4[b]
KBH 2002/494	1.2[c]	1.2[c]	1.3[c]	1.2[c]	1.7[bcd]	2.0[abc]	1.7[bc]	1.5[bc]	1.3[bc]	1.3[bcd]	1.3[bcde]	1.2[bc]
KBH 96/1056	1.0[c]	1.1[c]	1.1[c]	1.1[c]	1.1[d]	1.1[c]	1.2[c]	1.2[c]	1.0[c]	1.0[d]	1.0[de]	1.0[c]
Kiroba	2.2[a]	2.2[a]	2.3[a]	2.3[ab]	2.3[b]	2.5[ab]	2.6[ab]	2.3[ab]	1.9[b]	1.6[b]	1.5[bcd]	1.5[b]
Mreteta	2.1[ab]	2.1[ab]	2.2[a]	2.7[a]	3.0[a]	3.0[a]	3.0[a]	3.0[a]	3.0[a]	2.9[a]	2.8[a]	2.7[a]
Namikonga	1.3[bc]	1.4[abc]	1.5[bc]	1.7[bc]	1.8[bcd]	1.8[abc]	2.5[ab]	1.8[bc]	1.7[bc]	1.7[b]	1.7[b]	1.3[bc]
NDL 2003/031	1.8[abc]	1.9[abc]	2.0[ab]	2.0[abc]	2.1[bc]	2.2[abc]	1.5[c]	1.4[c]	1.0[c]	1.1[d]	1.0[e]	1.0[c]
NDL 2003/111	1.3[bc]	1.4[abc]	1.6[bc]	1.6[bc]	1.7[bcd]	1.7[abc]	1.5[c]	1.1[c]	1.0[c]	1.0[d]	1.0[e]	1.0[c]
NDL 2005/1471	1.3[bc]	1.4[abc]	1.5[bc]	1.6[bc]	1.6[bcd]	1.6[bc]	1.5[c]	1.5[bc]	1.4[bc]	1.2[bcd]	1.1[cde]	1.1[c]
Mean	1.5	1.5	1.6	1.7	1.8	1.9	1.9	1.7	1.5	1.5	1.4	1.3
HSD	0.9	0.9	0.6	1.0	0.7	1.4	0.8	0.9	0.8	0.4	0.5	0.3
CV	19.9	20.1	20.0	20.6	21.9	24.2	25.9	18.2	17.9	16.3	19.3	13.1

HSD Tukey's honest significant difference, *CV* coefficient of variation; different letters indicate that means within a column are significantly different ($P \leq 0.05$)

Varieties with least root necrosis severity and high root weight also had higher quantities of marketable roots. Accordingly, NDL 2003/1471 had the highest quantity of marketable roots of 25.3 t/ha in 2014–2015 and 23.0 t/ha in 2015–2016, while Albert had the least: 11.0 t/ha in 2014–2015 and 3.9 t/ha in 2015–2016 (Fig. 5). Although Namikonga had low root necrosis severity in both seasons, it had a low quantity of marketable roots, 14.7 t/ha in 2014–2015 and 10.7 t/ha in 2015–2016 due to its low root yield.

Higher levels of dry matter content (22.9–28.4%) were recorded in 2014–2015 compared to 2015–2016 (18.8–20.1%). Season 2015–2016 had higher whitefly and disease incidences, which may have contributed to the low dry matter content recorded (Table 4, 5). Further, a higher quantity of rainfall between January and March in season 2015–2016 may have contributed to lower dry matter content.

Discussion

The cassava varieties, season and their interactions were significant ($P \geq 0.05$) in all the parameters evaluated in this study. The MAP had the largest SS, signifying that it contributed to the major variations observed for the whitefly population. Cassava leaves began emerging 7 and 10 days after planting, and adult whitefly were detected at 1 MAP. The whitefly population peaked at 6 and 4 MAP in 2014–2015 and 2015–2016, respectively, before dropping sharply by 12 MAP. It has been known that suitability of cassava for whitefly feeding decreases as it matures due to the hardiness of leaves.

Whitefly population usually starts building up early when leaves are young and just formed, and peaks between 5 and 7 MAP when the foliage is well formed and succulent, after which it drops drastically as the plant grows

Table 5 Means of CBSD foliar and root necrosis severity in 2014–2015 and 2015–2016 cropping seasons

| Variety | CBSD foliar severity | | | | | | | | | | | | Root Necrosis |
| | Months after Planting (MAP) | | | | | | | | | | | | |
	1	2	3	4	5	6	7	8	9	10	11	12	
2014–2015													
Albert	1.0[a]	1.0[a]	1.5[a]	1.8[a]	2.1[a]	2.1[a]	2.2[a]	2.3[a]	2.4[a]	2.0[b]	1.9[a]	1.8[a]	2.4[a]
KBH 2002/482	1.0[a]	1.0[a]	1.2[ab]	1.3[ab]	1.3[bc]	1.5[bcd]	1.6[bc]	1.8[ab]	1.9[ab]	1.2[cd]	1.1[bc]	1.1[c]	1.1[c]
KBH 2002/494	1.0[a]	1.0[a]	1.2[ab]	1.2[ab]	1.3[bc]	1.4[bcde]	1.6[bc]	1.7[abc]	1.7[ab]	1.3[cd]	1.1[bc]	1.0[c]	1.0[c]
KBH 96/1056	1.0[a]	1.0[a]	1.0[b]	1.0[b]	1.0[c]	1.0[e]	1.0[d]	1.0[c]	1.0[c]	1.0[d]	1.0[c]	1.0[c]	1.0[c]
Kiroba	1.0[a]	1.0[a]	1.3[ab]	1.4[ab]	1.5[bc]	1.6[abc]	1.6[abc]	1.7[ab]	1.7[ab]	1.4[c]	1.3[b]	1.3[b]	1.0[c]
Mreteta	1.0[a]	1.0[a]	1.4[ab]	1.6[ab]	1.6[ab]	1.8[ab]	2.1[ab]	2.1[a]	2.3[a]	2.3[a]	2.1[a]	1.8[a]	1.8[b]
Namikonga	1.0[a]	1.0[a]	1.0[b]	1.2[b]	1.2[bc]	1.2[cde]	1.2[cd]	1.3[bc]	1.3[bc]	1.0[d]	1.0[c]	1.0[c]	1.0[c]
NDL 2003/031	1.0[a]	1.0[a]	1.0[b]	1.0[b]	1.0[c]	1.0[e]	1.0[d]	1.0[c]	1.0[c]	1.0[d]	1.0[c]	1.0[c]	1.1[c]
NDL 2003/111	1.0[a]	1.0[a]	1.0[b]	1.0[b]	1.0[c]	1.1[de]	1.0[d]	1.0[c]	1.0[c]	1.0[d]	1.0[c]	1.0[c]	1.0[c]
NDL 2005/1471	1.0[a]	1.0[a]	1.0[b]	1.0[b]	1.0[c]	1.0[e]	1.0[d]	1.0[c]	1.0[c]	1.0[d]	1.0[c]	1.0[c]	1.0[c]
Mean	1.0	1.0	1.2	1.3	1.3	1.4	1.4	1.5	1.5	1.3	1.3	1.2	1.2
LSD	–	–	0.4	0.6	0.5	0.5	0.6	0.7	0.7	0.3	0.3	0.2	0.2
CV	–	–	11.7	16.5	13.6	12.3	14.3	15.5	15.4	12.1	8.1	5.4	18.5
2015–2016													
Albert	1.0[a]	1.7[a]	2.1[a]	2.5[a]	2.5[a]	2.6[ab]	2.5[ab]	2.7[a]	3.1[a]	2.6[a]	2.5[a]	2.4[a]	2.7[ab]
KBH 2002/482	1.0[a]	1.0[c]	1.1[c]	1.3[bc]	1.4[bc]	1.7[bcd]	1.9[abcd]	2.2[abc]	2.0[abc]	1.6[ab]	1.1[c]	1.1[bc]	1.1[d]
KBH 2002/494	1.0[a]	1.0[c]	1.3[bc]	1.7[bc]	1.7[bc]	1.7[bcd]	2.0[abcd]	1.6[bcd]	1.1[c]	1.0[c]	1.0[c]	1.0[c]	2.2[bc]
KBH 96/1056	1.0[a]	1.0[c]	1.0[c]	1.1[c]	1.1[c]	1.2[d]	1.4[cd]	1.3[cd]	1.1[c]	1.0[c]	1.0[c]	1.0[c]	1.8[cd]
Kiroba	1.0[a]	1.6[ab]	1.8[ab]	1.9[ab]	2.2[ab]	2.5[abc]	2.9[a]	2.6[ab]	2.3[ab]	2.2[ab]	2.0[ab]	1.9[ab]	1.7[cd]
Mreteta	1.0[a]	1.2[bc]	1.5[abc]	1.9[ab]	2.2[ab]	2.8[a]	2.8[a]	2.7[a]	2.9[ab]	2.7[a]	2.0[ab]	2.0[a]	3.3[a]
Namikonga	1.0[a]	1.0[c]	1.1[c]	1.3[bc]	1.3[c]	1.1[d]	1.0[d]	1.0[d]	1.0[c]	1.0[c]	1.0[c]	1.0[c]	1.1[d]
NDL 2003/031	1.0[a]	1.0[c]	1.1[c]	1.4[bc]	1.6[bc]	1.8[bcd]	2.2[abc]	2.5[ab]	1.9[bc]	1.6[bc]	1.3[bc]	1.0[c]	1.2[d]
NDL 2003/111	1.0[a]	1.0[c]	1.1[c]	1.3[bc]	1.4[c]	1.6[cd]	1.6[bcd]	1.3[cd]	1.0[c]	1.0[c]	1.0[c]	1.0[c]	1.8[cd]
NDL 2005/1471	1.0[a]	1.1[c]	1.1[c]	1.1[c]	1.1[c]	1.1[d]	1.2[cd]	1.0[d]	1.0[c]	1.0[c]	1.0[c]	1.0[c]	1.1[d]
Mean	1.0	1.2	1.3	1.6	1.6	1.8	2.0	1.9	1.7	1.6	1.4	1.3	1.8
HSD	–	0.5	0.6	0.8	0.8	0.9	1.1	1.0	1.2	0.8	0.8	0.9	0.9
CV	–	14.1	16.1	16.7	15.5	17.6	19.0	18.7	22.7	29.2	19.9	21.7	28.4

HSD Tukey's honest significant difference, *CV* coefficient of variation; different letters indicate that means within a column are significantly different ($P \leq 0.05$)

older, becomes woodier and sheds leaves (Macfadyen et al. 2018; Sseruwagi et al. 2005). The whitefly population was higher in season 2015–2016 than 2014–2015. This may be due to delayed planting in March 2015, which has allowed build of high number of whiteflies on neighbouring crops and weeds and moving on to the young succulent cassava plants in our trials (Mohamed 2012). The temperatures are generally high, above 30 °C, at the study site Naliendele from February to May (Kimata et al. 2021), which is highly favourable for whitefly development and will have also contributed to the early peaks in populations seen in this study (Shirima et al. 2019).

The varietal effect had the second largest SS, contributing to major variations observed for the whitefly population. Morphological characterisation of cassava varieties regarding whitefly preference and colonisation confirmed the characteristic traits of resistant and susceptible varieties. NDL 2003/031, NDL 2003/111 and NDL 2005/1471 were the least infested and were categorised as resistant, while Namikonga and Mreteta were susceptible. The resistant varieties had dark green foliage, slightly hairy leaves and lanceolate-shaped central leaflets, unlike the susceptible ones with light green foliage, smooth leaves and elliptical–lanceolate-shaped central leaflets. Similar results were observed when whiteflies preferentially fed and oviposited more on varieties with light green and smooth foliage (Gwandu et al. 2019). Leaf hairs interfere with whitefly landing and feeding on cassava; therefore, it is a likely trait of resistance (Gwandu et al. 2019; Byrne and Bellows 1991). Additionally, dark green leaf varieties are known to have higher phenolic

Marketable roots of varieties in seasons 2014-2015 and 2015-2016 ($P = 0.001$, LSD$_{0.05}$ = 3.36)
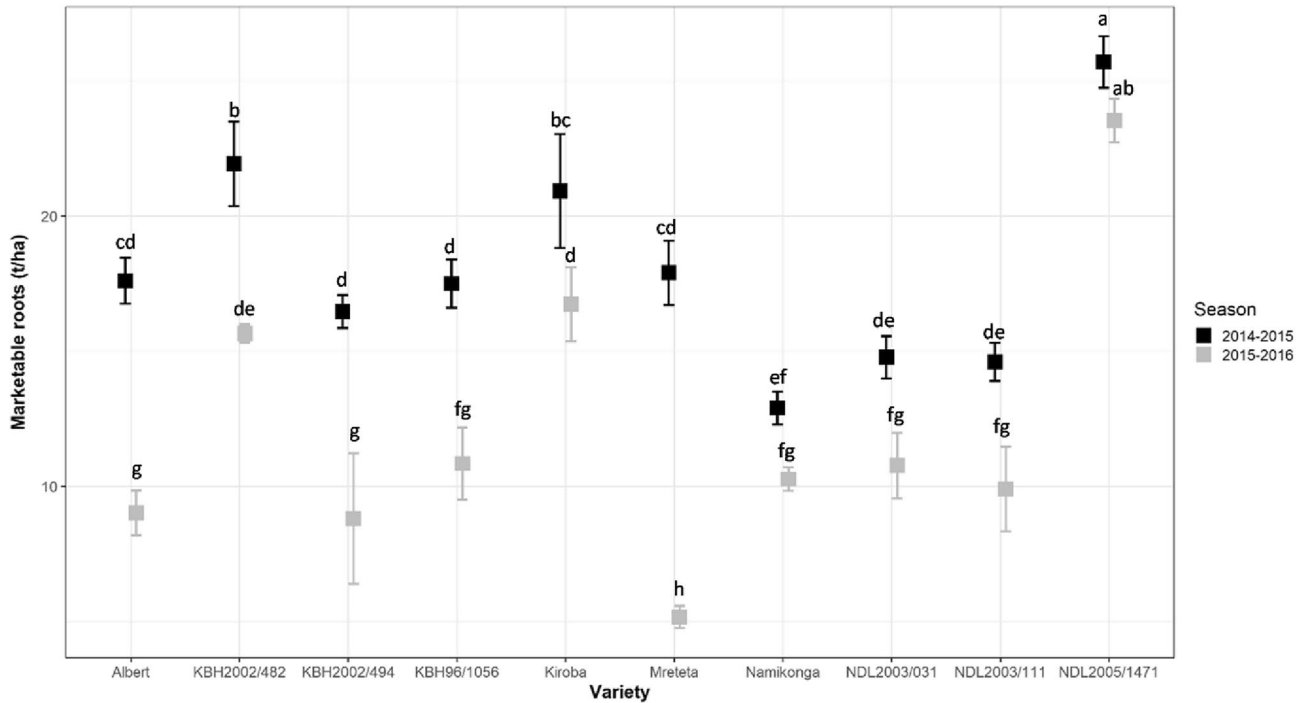

Fig. 4 Marketable roots of varieties in 2014–2015 and 2015–2016 cropping seasons

Dry matter content of varieties in seasons 2014-2015 and 2015-2016 ($P = 0.001$, LSD$_{0.05}$ = 2.21)
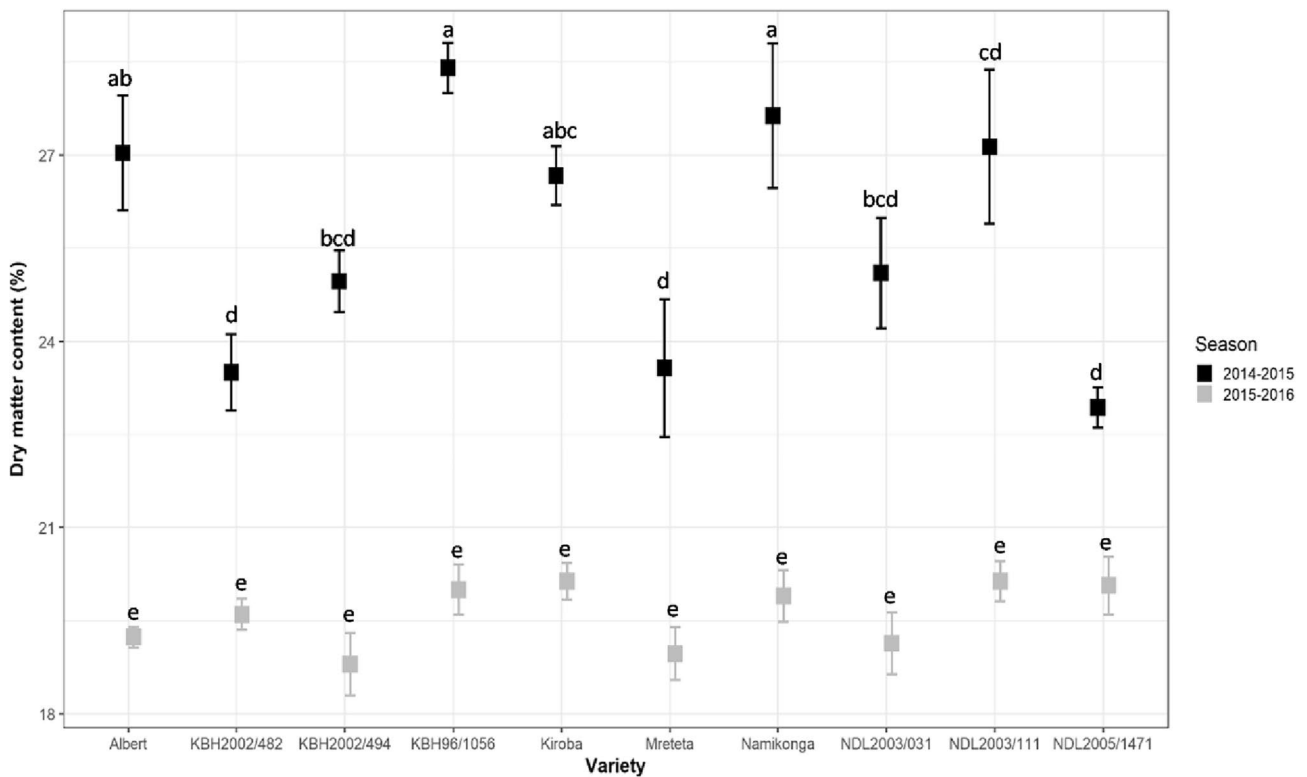

Fig. 5 Dry matter content of varieties in 2014–2015 and 2015–2016 cropping seasons

content, which act as feeding deterrents and ultimately providing resistance against insects such as whiteflies (Shibuya et al. 2010; Mwila et al. 2017; Chu et al. 2017). Selection of cassava for whitefly resistance can therefore include varieties with darker green foliage as a trait in cassava breeding.

The cassava variety contributed to the largest SS for CMD, CBSD and root necrosis. Vars. Namikonga, Mreteta and Kiroba had the highest CMD and/or CBSD severity and a high whitefly population. Vars. Namikonga and Kiroba expressed field resistance and tolerance, respectively, to CBSD, and breeders commonly use them as the best sources of CBSD resistance/tolerance in conventional breeding programs. This should be reconsidered to prevent the development of whitefly-susceptible varieties which was partially responsible for the development of high whitefly populations on cassava in eastern Africa (Macfadyen et al. 2018). The incidences of CBSD decreased after 9 MAP in both years, which is the result of severe dropping of older leaves with CBSD symptoms due to prolonged dry periods (less than 10 mm rainfall per month) experienced from May to October at the study site Naliendele (Kimata et al. 2021).

Season 2014–2015 had lower root weight, marketable roots and dry matter content, probably due to a higher disease incidence. Additionally, low dry matter content was recorded in all varieties due to harvesting during the rainy season in March 2016. Low root necrosis severity coupled with high root weight results in high quantity of marketable roots and vice versa (Maruthi et al. 2020; Masinde et al. 2017). Var. NDL 2005/1471 had the highest quantity of marketable roots, unlike Namikonga, which, although it expressed minimal root necrosis, still had low quantity of marketable roots due to an initial low root weight. Namikonga is a low-yielding variety besides developing CMD symptoms, reducing yield (Masumba et al. 2017; Kaweesi et al. 2014). The high whitefly population in Namikonga could also be contributing to its low yields since the pest feeds on the phloem.

In 2014–2015 season, which had a low disease and whitefly incidence, var. Mreteta had root weight (21.5 t/ha) and marketable roots (13.2 t/ha), translating to 37% yield loss. In 2015–2016, higher disease and whitefly incidence led to lower root weight of 12.5 t/ha and marketable root (5.0 t/ha), translating to 60% loss. In contrast, the resistant var. NDL 2005/1471 had root weight (25.8 t/ha) in 2014–2015 with marketable roots (25.8 t/ha), translating to 1.2% yield loss. Similarly, in 2015–2016, NDL 2005/1471 had approximately 0.4% yield loss. It is therefore important to grow cassava varieties that are resistant to both whiteflies and CMD and CBSD, to achieve the full yield potential of cassava and thus increase high cassava production by the farmers.

Conclusions

Whitefly can spread viruses causing both CMD and CBSD, and if they all occur concurrently in a cropping season, they can result in significant losses of cassava root yield and quality. Seasonable variations were observed as 2015–2016 had higher whitefly population than 2014–2015, resulting in higher CMD and CMD foliar severities and consequently lower root yield and quality. Varietal variations were also observed as whitefly had higher preference for Namikonga, Kiroba and Mreteta, which also developed severe symptoms of either CMD, CBSD or both diseases. Planting a variety like Mreteta, susceptible to whitefly, CMD and CBSD, can make a farmer incur significant losses up to 60%, while the resistant var. NDL 2005/1471 suffered an approximate loss of only 1%. This study demonstrated that some varieties popularly used as breeding sources for CMD and CBSD resistance are susceptible to whitefly (e.g. Namikonga). Considerations should therefore be given to deploying high-yielding varieties resistant to both whiteflies, and CMD and CBSD to increase cassava productivity and food security in African countries.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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