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Varietal response of cassava root yield components and root necrosis from cassava Brown streak disease to time of harvesting in Uganda

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ABSTRACT

Cassava brown streak disease (CBSD) is the most important biotic constraint threatening cassava (*Manihot esculenta* Crantz) production in eastern and southern Africa, and the food and income security of millions of rural farmers. With no tangible solution in view, farmers cope with the disease by harvesting the crop early, a practice that also leads to yield losses owing to small root size. This study evaluated CBSD root necrosis (RN), the total fresh root yield (TFRY), percentage marketable fresh root yield (PMFRY) and dry matter content (DMC) of six cassava varieties (MM, 2006/90, MM, 2006/123, MM, 2006/128, MM, 2006/130, MM 96/4271, and TME14) at different times of harvesting after the recommended 12 months after planting (MAP). Trials were planted during April 2012 at Sendusu and Serere located in the Wakiso and Serere districts of Uganda, respectively. The two sites are distinct in climatic, soil and CBSD disease pressure conditions. A split-plot design was used with cassava varieties as the main plots and times of harvesting (12, 16, 20 and 24 MAP) as sub-plots. Highly significant differences ($P \leq 0.001$) were detected between sites (S), varieties (V) and time of harvesting (T) for TFRY, PMFRY and RN, whereas only V effects were highly significant ($P \leq 0.001$) for DMC. The $V \times S$ interactions were highly significant for TFRY, PMFRY and RN, while the $V \times T$ interactions were highly significant for PMFRY and significant ($P \leq 0.01$) for TFRY and DMC. The PMFRY decreased by about 14–27% as the plants remained in the field after 12 MAP. There was a great difference among clones, depending on location. Variety MM 2006/128 performed the best, with virtually no root damage even at 24 MAP at both sites. The mean CBSD root necrosis severity score among the varieties at each site increased from 2.6 (at 12 MAP) to 3.1 (at 24 MAP) at Sendusu, and from 1.9 (at 12 MAP) to 2.4 (at 24 MAP) at Serere. However, for MM2006/128 which was the best performing variety, the root necrosis score remained about 1.0 at Sendusu and about 1.3 at Serere. Time of harvesting had no significant effect on DMC. This study showed it is possible to breed new cassava varieties that combine tolerance to CBSD with long periods of in-ground storability. Genotype and environment had a profound effect on all the traits analysed, suggesting that genotypes should be selected for specific environments and harvest times. The results indicate that some of the clones (MM, 2006/128, MM, 2006/123 and MM, 2006/130) investigated in this study will be useful in the fight against CBSD in the region especially for the mid-altitude areas, which have recently been seriously affected by the virus disease.

1. Introduction

Cassava (*Manihot esculenta* Crantz), originally from South America, is the fourth most important source of dietary energy in the developing world after the cereals wheat, maize, and rice, feeding an estimated 800 million people worldwide (FAO, 2013). Its ability to stay in the ground for up to three years makes it an excellent food security crop (Nweke et al., 2002). Other desirable attributes include drought tolerance, provision of reasonable yields in poor soils and weed suppression when the canopy is fully developed. Cassava is the second most important

Non-standard abbreviations: CBSD, Cassava brown streak disease; DMC, dry matter content; PMFRY, percentage marketable fresh root yield; MAP, months after planting; RN, root necrosis; RNI, root necrosis incidence; RNS, root necrosis severity; SG, specific gravity; TFRY, total fresh root yield; TSS, total sum of squares.

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source of starch in the world (FAO, 2013). The high starch content (20–40%) makes cassava a desirable energy source for both human and industrial usage. Moreover, cassava has been projected to be highly resilient to future climatic changes compared with other major staples such as maize, sorghum and millet, which could provide Africa with options for adaptation (Jarvis et al., 2012). For these reasons, cassava has been recognized as a powerful tool in fighting/alleviating poverty both through food security and commercialization (FAO, 2013).

Total cassava production in Africa exceeded 146 million tons in 2014 (61.9% of total global production), more than any other crop in Africa (FAO, 2013). However, Africa had the lowest productivity in the world with an average yield of 10.8 t/ha compared with that of Latin America and Asia where average yields were 12.9 and 19.6 t/ha, respectively (FAO, 2013). The low average yields in Africa are caused by many factors including the susceptibility of commonly grown varieties to major diseases and pests, including cassava mosaic disease (CMD) and cassava brown streak disease (CBSD) (Uzokwe et al., 2016).

In Uganda, CBSD was first observed in the 1940s on cassava genotypes introduced from Tanzania. The disease was, however, eradicated through the implementation of phytosanitary measures (Jameson, 1964). However, it re-emerged in 2005 and has since reached epidemic proportions (Alicai et al., 2007). A nationwide survey in 2013 recorded CBSD in 50 out of 55 districts of Uganda (Ogwok et al., 2014). An upsurge in the population of *Bemisia tabaci* (the whitefly vector) appears to be the key driver of the outbreak, though farmers play a significant role in the dissemination of CBSD through infected cuttings. CBSD is severely affecting cassava production as the CMD-resistant varieties that were widely grown in and around Uganda have become susceptible to the disease because they were not initially bred for CBSD resistance. CBSD causes losses in production through reduced growth, but the major economic damage is from the spoilage of the roots due to necrotic rot (Hillocks et al., 2001). In southern coastal Tanzania yield losses of up to 70% were reported in susceptible cultivars (Hillocks et al., 2001). It has been noted that root symptoms become increasingly severe as plants mature, and a secondary effect of CBSD is early harvesting by farmers to prevent severe root spoilage, which also contributes to yield losses (Hillocks et al., 2001; Gondwe et al., 2002; Adjebeug-Danquah et al., 2016). It is appropriate to regard CBSD as one of the most serious threats to food security in the world (Pennisi, 2010; Legg et al., 2014). Developing and deploying dual-resistant cassava varieties is the only sustainable way of controlling both diseases (Mohammed et al., 2015).

The National Research Organization (NARO) in Uganda officially released two varieties in 2015 with dual resistance and/or tolerance to CMD and CBSD. One of them, NARO-CASS 2, was developed by the breeding program of the International Institute of Tropical Agriculture (IITA) as breeding line MM 2006/130. The IITA program has also developed two other breeding lines MM 2006/123 and MM 2006/128 that have resistance to CMD and tolerance to CBSD and these are potential candidates for future official release in Uganda and elsewhere. The recommended time of harvesting for officially released varieties is 12 months, but there is no information on how the new CBSD-tolerant varieties would perform with respect to CBSD root necrosis damage if they were left in-ground beyond the recommended time. However, long in-ground storage of cassava roots is one of the traits subsistence farmers value for food security. This has been documented in Tanzania where farmers plant both short (6–9 months) and long (12–18 months) duration landraces to ensure food security during adverse conditions (Mtunguja et al., 2014). Protracted in-ground storage is particularly important in areas with a prolonged dry season during which farmers only harvest a few plants at a time leaving others 'stored' in the field well beyond the optimum harvest date (Hillocks et al., 1996). Other farmers may harvest only some roots from a plant at any one time (piecemeal harvesting) when cassava is grown as a famine-reserve crop (Fresco, 1986). A survey conducted in Malawi documented that the mean crop age in Salima Division, was 16 months (Gondwe et al., 2002). In Uganda, farmers grow long-in-ground-storage cultivars for food security (Tumuhimbise et al., 2012).

The present study aimed to determine whether time of harvesting had any effect on fresh root yield and resilience to CBSD root necrosis damage by the new disease-resistant cassava varieties. Our hypotheses were that: 1) tolerance to CBSD in the new varieties, compared with the control TME14, would lead to a higher yield at harvest because of reduced loss through necrosis; 2) even with disease tolerant varieties, harvesting after 12 months will reduce the marketable fresh root yield; and 3) varieties will perform differently across locations due to environmental conditions and the disease prevalence. These results will help to develop recommendations for farmers on the optimum harvesting time in Uganda.

2. Material and methods

Six varieties were selected for evaluation based on their reaction to CBSD (Table 1). Two varieties MM96/4271 and MM2006/130 are CBSD tolerant and have been officially released as NASE14 and NARO-CASS1, respectively. Three varieties MM 2006/90, MM 2006/123 and MM 2006/128 are also classified as CBSD tolerant, but have not been officially released, while TME14 is CBSD-susceptible and so was included as a control. MM 2006/90, MM 2006/123, MM 2006/128 and MM2006/130 were selected from half-sib families of CBSD-tolerant parents introduced from Tanzania to Uganda in 2005 (Kanju et al., 2012). These varieties have been under evaluation under very high CBSD and CMD pressure at Sendusu (a disease hot spot) for six seasons (2006–2012).

The trial was planted in April 2012 at Sendusu, near Namulonge, Wakiso District in Central Uganda and Serere, Serere District in Eastern Uganda. The site characteristics are presented in Table 2.

A split-plot design with three replications was used. The varieties were the main plots randomly assigned in a replication, while different times of harvesting were sub-plots randomized within the main plot. The sub-plots each measured 10 m long and 3 m wide, i.e., three rows each measuring 10 m long. Stem cuttings of each variety were obtained from plants with no visible CBSD foliar and root necrosis in the germplasm maintenance field at Serere (with low CBSD pressure) and were used in planting the trial, by placing one cutting per hole 1 m apart within the row. The rows were kept 1 m apart. The plots were kept weed free and no fertilizers or chemical pesticides were applied during the crop growth cycle.

Harvesting was done at 12, 16, 20 and 24 months after planting (MAP) by uprooting all the plants in the net plot area (eight plants in the middle row). Cassava roots were detached from the plants and separated into marketable (CBSD root necrosis severity score of class ≤ 2) and unmarketable (CBSD root necrosis severity score of class ≥ 3), counted and weighed to estimate marketable (MFRY), non-marketable and total fresh root yield (TFRY) components. The roots were cut transversally about 5 cm from both ends and the maximum root necrosis severity score was used to separate the root into the marketable or non-marketable category. Root necrosis was scored visually by the same technician based on a score of 1–5 where 1 indicated no visible symptoms and 5 indicated very severe symptoms. The maximum necrosis score was used to estimate the average root necrosis score for the plot. The number of roots with a score of 3–5 were counted and this number was used to get the root necrosis incidence, namely by dividing the total number of roots from the harvest area by the number of roots with a score of 3–5 (Gondwe et al., 2002; Okul Valentor et al., 2018). Each category was weighed separately for each plot. The percentage marketable fresh root yield (PMFRY) was calculated as the ratio of MFRY (t/ha) to TFRY (t/ha) expressed as a percentage. Root samples were taken on a sub-plot basis to determine root dry matter content using the specific gravity (SG) method as described by Kawano et al. (1987). The SG was determined by weighing approximately 3 kg of fresh roots in air and re-weighing the same roots when completely submerged in water. SG was then calculated using the following formula:

Table 1
Characteristics of cassava varieties used in the study.

Clone name	Accession Number	Resistance to CBSD	Resistance to CMD	Fresh Root Yield (t/ha)	Dry Matter Content (%)	Release status
MM 2006/90	Kibaha HS[a]	Moderate tolerance	Resistant	11.8	30.5	Not released
MM 2006/123	Kibaha HS	Tolerant	Resistant	20.0	32.3	Not released
MM 2006/128	Kigoma Red HS	Tolerant	Resistant	6.7	39.2	Not released
MM 2006/130	Kitumbua HS	Tolerant	Resistant	10.7	36.4	Released (NARO-CASS 2)
MM 96/4271	I92/0248 HS	Moderate tolerance	Resistant	7.4	33.4	Released (NASE 14)
TME14	Abbey Ife HS	Susceptible	Resistant	14.0	35.2	Not released

[a] HS = Half-sib (male parent not known).
Source: Kanju et al. (2012).

Table 2
Site description of locations used for the time of harvesting analysis.

Parameter	Site	
	Sendusu	Serere
Latitude	0° 31′ N	1° 32′ N
Longitude	32° 36′ E	32° 25′E
Altitude	1,134 m	1,085 m
Agroecology	Tropical rain forest	Tall savannah
Soil type	Sandy clay	Sandy loam
Soil pH	4.9–5.0	5.8–6.2
Temperature	22.2 °C	18.0–31.3 °C
Rainfall	1,500 mm	1,000–1,300 mm

$$SG = \text{Weight in air} / (\text{Weight in air} - \text{Weight in water}) \quad (1)$$

The SG was then used to calculate dry matter content (DMC) using the following formula as used by Kawano et al. (1987).

$$DMC = (158.3 \times SG) - 142.0 \quad (2)$$

Data were subjected to analyses of variance (ANOVA) using the GenStat Discovery software (VSN International, http://www.vsni.co.uk) separately for each site and combined for the two sites. The least significant difference (LSD) was used to separate the means. Contributions of all the sources of variation to sum of squares were calculated from the combined ANOVA. The broad-sense heritability (H2) was calculated for each variable using the variances generated from the Residual or Restricted Maximum Likelihood (REML) analysis. Finally, the Best Linear Unbiased Predictions (BLUPs) were estimated.

3. Results

3.1. Total fresh root yield (t/ha)

There were significant differences ($P \leq 0.01$) between sites (S), whereas for varieties (V), and time of harvesting (T) the differences were highly significant ($P < 0.001$) for TFRY (Table 3). The sites contributed the highest percentage (37.2%) of the total sum of squares (TSS) for TFRY. Conversely, harvesting time contributed only a small percentage of the TSS for TFRY (7.8%). The S × V interactions were highly significant ($P < 0.001$) and accounted for 12.2% of the TSS. Although the S × T interactions were significant ($P < 0.01$), they contributed only slightly (1.7%) to the TSS. Similarly, V × T interactions were significant ($P < 0.01$) but made a small contribution to TFRY (4.4%). The interactions S × V × T were significant ($P \leq 0.05$) but with a very low percentage proportion of the TSS (4.0%).

At both sites, TFRY doubled when harvesting was done at 16 MAP (Table 4). Thereafter, TFRY decreased slightly. Varieties MM 2006/90 and MM 2006/123 were the highest yielding varieties at both sites and across all harvesting dates. The average TFRY at Serere was almost three times greater than that at Sendusu (9.8 vs. 28.3 t/ha) across varieties and harvesting dates (Table 4). At Sendusu the best performing varieties were MM 2006/90 and MM 2006/123 (23.2 and 15.1 t/ha, respectively) whereas at Serere the best performers were MM 96/4271and MM 2006/123 (39.8 and 32.9 t/ha, respectively (Table 4). The highest yielding variety at 12 MAP at Sendusu and Serere was MM 2006/123 (12.0 and 27.9 t/ha, respectively), which was significantly better ($P < 0.001$) than other varieties except MM 2006/90 at Sendusu (Table 4). At 16 MAP MM 2006/128 was significantly outperformed by other varieties at both sites, except for MM 2006/130. This trend was also observed at 20 and 24 MAP.

3.2. Marketable fresh root yield (t/ha)

There were significant differences ($P \leq 0.01$) for S whereas for V and T the differences were highly significant ($P < 0.001$) for MFRY (Table 3). The sites contributed the highest percentage (30.7%) of the total sum of squares (TSS) for MFRY. Conversely, harvesting time contributed only a small percentage of the TSS for MFRY (3.7%). The S × V interactions were highly significant ($P < 0.001$) and accounted for 15% of the TSS. Although the S × T interactions were significant ($P < 0.01$), they contributed only slightly (2%) to the TSS. Similarly, V × T interactions were significant ($P < 0.01$) but made a small contribution to TSS (4.7%).

Table 3
ANOVA for total fresh root yield (TFRY), marketable fresh root yield (MFRY), percentage marketable root yield (PMFRY), cassava brown streak disease (CBSD) root necrosis incidence (RNI), CBSD root necrosis severity (RNS) and dry matter content (DMC).

Source of Variation	DF	TFRY (t/ha)	MFRY (t/ha)	PMFRY (%)	RNI (%)	RNS	DMC (%)
Site (S)	1	12,404.4** (37.2)	99,964.6** (30.7)	21,986.8*** (11.5)	9865.2*** (5.8)	13.4444*** (7.3)	16.54 (0.7)
Residual	4	226.85 (2.7)	297.2 (4.1)	334.8 (0.7)	102.1 (0.2)	0.0903 (0.2)	40.79 (3.7)
Variety (V)	5	702.1*** (10.5)	871.7*** (16.0)	14,773.2*** (38.7)	14,735.5*** (43.0)	17.5444*** (47.7)	261.66*** (59.4)
S × V	5	813.2*** (12.2)	819.2*** (15.0)	8580.1*** (22.5)	6739.1*** (19.7)	5.8778*** (16.0)	27.62 (6.3)
Residual	20	64.3 (3.8)	60.4 (4.4)	316.9 (3.3)	177.6 (2.1)	0.6236 (6.8)	22.22 (10.08)
Time (T)	3	866.9*** (7.8)	333.1*** (3.7)	4567.1*** (7.2)	6849.1*** (12.0)	2.537*** (4.1)	50.02 (6.8)
S × T	3	193.4** (1.7)	186.0** (2.0)	568.2* (0.9)	361.3 (0.6)	0.2407 (0.4)	152.00** (6.9)
V × T	15	98.0** (4.4)	84.9** (4.7)	629.8*** (5.0)	639.3*** (5.6)	0.3259 (2.7)	55.79** (38.0)
S × V × T	15	89.2* (4.0)	73.030* (4.0)	314.4 (2.5)	309.6 (2.7)	0.5407* (4.4)	32.61 (7.4)
Residual	72	41.7 (9.6)	34.4 (9.1)	205.9 (7.8)	208.9 (8.7)	0.2662 (10.4)	18.04 (19.6)
ssTotal	143	31,167.4	27,145.7	19,0822.7	17,1228.6	183.9	2019.9
Heritability (H^2)		0.08	0.19	0.48	0.52	0.51	0.25

*** Significant at $P \leq 0.001$, ** significant at $P \leq 0.01$, *significant at $P \leq 0.05$, H^2 = Broad-sense heritability.

Table 4
Total fresh root yield (t ha^{-1}) of six cassava landraces evaluated in two sites in Uganda at four different harvesting rounds (MAP).

	Sendusu					Serere				
	12 MAP	16 MAP	20 MAP	24 MAP	Mean[a]	12 MAP	16 MAP	20 MAP	24 MAP	Mean[a]
MM 2006/90	10.7	26.1	34.5	21.6	23.2	12.8	28.1	30.4	34.2	26.4
MM 2006/123	12.0	19.4	14.0	15.0	15.1	27.9	35.0	39.2	29.6	32.9
MM 2006/128	2.2	3.1	4.5	6.6	4.1	11.2	23.1	22.1	20.5	19.2
MM 2006/130	3.4	9.7	2.8	7.3	5.8	18.1	25.4	15.1	25.6	21.1
MM 96/4271	0.6	1.8	0.4	1.0	0.9	14.3	53.3	44.4	47.1	39.8
TME14	6.7	11.3	12.4	7.5	9.5	21.2	30.0	40.2	31.2	30.7
Mean[b]	5.9	11.9	11.5	9.8	9.8	17.6	32.5	31.9	31.4	28.3
CV (%)	39.2	43.7	68.8	31.0	48.4	31.2	30.5	24.6	25.3	27.6
LSD_V	4.2***	9.4***	14.3***	5.5***	6.1***	10.0*	18.0*	14.2**	14.5**	8.3**
LSD_T					3.2**					5.3***
$LSD_{V\times T}$					8.8*					13.4*

CV, Coefficient of variation; LSD, Least significant difference; V, Varieties; MAP, Months after planting; T, Time of harvesting (MAP).
***P ≤ 0.001, **P ≤ 0.01, *P ≤ 0.05.
[a] Mean over three harvest rounds.
[b] Overall landrace site mean.

The interactions S × V × T were significant (P ≤ 0.05) but with a very low percentage proportion of the TSS (4.0%).

At Serere, MFRY almost doubled when harvesting was done at 16 MAP (Table 5). Thereafter, MFRY decreased slightly at both sites. At Sendusu, varieties MM 2006/123 and MM 2006/90 had the highest MFRY from 12 MAP to 20 MAP whereas at Serere it was varieties MM 2006/123 and MM 2006/130, but only at 12 MAP. Thereafter, it was varieties MM 96/4271 and MM 2006/123 (Table 5). The average MFRY at Serere was almost three times greater than that at Sendusu (5.1 vs. 15.3 t/ha) at 12 MAP across varieties. Thereafter, it was almost four times greater (Table 5).

3.3. Percentage marketable fresh root yield (%)

Highly significant (P < 0.001) S, V, T, S × V, and V × T effects were observed for PMFRY. The S × T effects were significant at P < 0.05 (Table 3). The V effects contributed the highest percentage (38.7%) to the TSS followed by the S × V interaction effects (22.5%).

The quantity of marketable fresh roots was significantly lower at Sendusu (76.5%) than that at Serere (89.7%) at 12 MAP (Table 6). There was a sharper decline in PMFRY at Sendusu (22%) than at Serere (6%) from 12 MAP to 16 MAP. At 12 MAP, only two varieties (MM, 2006/123 and MM, 2006/128) had 100% PMFRY at both sites meaning that all roots were marketable. However, at Sendusu only MM 2006/128 maintained this status throughout the successive harvesting dates whereas at Serere both varieties maintained the same performance. It was interesting to note that the worst variety at Sendusu was MM 96/4271 whereas at Serere it was TME14 across all harvesting dates. By 20 MAP MM 96/4271 had completely no marketable yield at Sendusu (Table 6).

3.4. CBSD root necrosis incidence (%)

Highly significant (P < 0.001) S, V, T, S × V and V × T effects were observed for RNI (Table 3). The V effects contributed the highest percentage (43%) to the TSS followed by the S × V interaction effects (19.7%) and T (12%).

The number of roots affected by CBSD was significantly higher at Sendusu than at Serere across the harvesting dates. At both sites the RNI increased as harvesting was delayed. However, the increase was highest at Sendusu (24%) when harvesting was done at 16 MAP. At Serere the highest RI increase (13.5%) was from 16 MAP to 20 MAP (Table 7).

At 12 MAP, only two varieties (MM, 2006/123 and MM, 2006/128) had no roots affected by CBSD at both sites. However, at Sendusu only MM 2006/128 maintained this status throughout the successive harvesting dates. At Serere MM 2006/128 had no roots affected up to 16 MAP. Thereafter, it had the lowest RNI of 2.4% and 3% at 20 MAP and 24 MAP, respectively. It was noted that the worst variety at Sendusu was MM 96/4271 whereas at Serere it was TME14 across all harvesting dates. By 20 MAP, MM 96/4271 had all its roots completely damaged by CBSD at Sendusu (Table 7).

Table 5
Marketable fresh root yield (t ha^{-1}) of six cassava landraces evaluated in two sites in Uganda at four different harvesting rounds (MAP).

	Sendusu					Serere				
	12 MAP	16 MAP	20 MAP	24 MAP	Mean[a]	12 MAP	16 MAP	20 MAP	24 MAP	Mean[a]
MM 2006/90	7.8	13.8	9.7	1.9	8.3	12.2	26.5	19.2	17.9	18.9
MM 2006/123	12.0	15.2	12.3	9.6	12.3	27.9	35.0	39.2	29.6	32.9
MM 2006/128	2.2	3.1	4.5	6.6	4.1	11.2	23.1	22.1	20.5	19.2
MM 2006/130	3.3	4.2	1.2	4.0	3.2	17.3	24.0	15.1	20.8	19.3
MM 96/4271	0.1	0.1	0.0	0.0	0.0	12.9	51.2	44.4	36.7	36.3
TME14	5.0	5.0	6.3	2.5	4.7	10.4	6.9	4.0	1.7	5.7
Mean[b]	5.1	6.9	5.7	4.1	5.4	15.3	27.8	24.0	21.2	22.1
CV	53.5	62.5	58.4	66.2	54.7	26.9	40.1	31.4	35.7	35.1
LSD_V	4.9***	7.8***	6.1***	4.9***	4.2***	7.5***	20.3*	13.7***	13.8**	9.0***
LSD_T					NS					5.2***
$LSD_{V\times T}$					5.8*					13.7*

CV, Coefficient of variation; LSD, Least significant difference; V, Variety; MAP, Months after planting; T, Time of harvesting.
NS, Not significant; ***: P ≤ 0.001, **: P ≤ 0.01, *: P ≤ 0.05.
[a] Mean over three harvest rounds.
[b] Overall landrace site mean.

Table 6
Percentage marketable fresh root yield (%) of six cassava landraces evaluated in two sites in Uganda at four different harvesting rounds (MAP).

	Sendusu					Serere				
	12 MAP	16 MAP	20 MAP	24 MAP	Mean[a]	12 MAP	16 MAP	20 MAP	24 MAP	Mean[a]
MM 2006/90	71.1	54.4	28.1	9.2	40.7	96.2	90.1	63.4	48.2	74.2
MM 2006/123	100.0	78.2	88.9	64.1	82.8	100.0	100.0	100.0	100.0	100.0
MM 2006/128	100.0	100.0	100.0	100.0	100	100.0	100.0	100.0	100.0	100.0
MM 2006/130	95.9	47.1	36.2	52.4	55.4	96.1	93.7	100.0	83.1	93.2
MM 96/4271	19.7	5.6	0.0	0.0	6.3	92.4	95.5	100.0	79.2	91.8
TME14	72.2	43.5	45.1	36.4	49.3	54.6	22.7	10.9	6.1	23.6
Mean[b]	76.5	54.8	48.1	43.7	55.8	89.7	83.7	79.1	69.4	80.5
CV	19.6	29.9	31.7	25.0	24.1	18.8	16.9	17.2	27.6	18.9
LSD_V	27.3***	29.8***	27.7***	19.9***	16.6***	30.7*	25.8***	24.8***	34.8***	15.7***
LSD_T					9.1***					10.3**
$LSD_{V\times T}$					24.4**					NS

CV, Coefficient of variation; LSD, Least significant difference; V, Variety; MAP, Months after planting; T, Time of harvesting (MAP).
NS, Not significant; ***P ≤ 0.001, **P ≤ 0.01, *P ≤ 0.05.
[a] Mean over three harvest rounds.
[b] Overall landrace site mean.

Table 7
Cassava brown streak disease (CBSD) root necrosis incidence (%) of six cassava landraces evaluated in two sites in Uganda at four different harvesting rounds (MAP).

	Sendusu					Serere				
	12 MAP	16 MAP	20 MAP	24 MAP	Mean[a]	12 MAP	16 MAP	20 MAP	24 MAP	Mean[a]
MM 2006/90	30.3	66.1	72.2	91.3	65.0	5.7	16.2	59.2	53.6	33.7
MM 2006/123	0.0	15.7	12.4	26.8	13.7	0.0	3.1	13.4	38.5	13.7
MM 2006/128	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	3.0	1.4
MM 2006/130	2.8	49.6	71.0	39.2	40.6	5.3	18.2	27.0	16.9	16.8
MM 96/4271	64.7	94.1	100.0	100.0	89.7	10.2	9.3	14.9	39.9	18.6
TME14	35.7	54.7	54.8	58.9	51.0	37.8	81.3	91.9	95.2	76.5
Mean[b]	22.3	46.7	51.7	52.7	43.3	9.8	21.3	34.8	41.2	26.8
CV	67.7	34.3	29.7	20.3	31.7	156.1	46.4	34.3	44.6	56.4
LSD_V	28.2**	29.1***	28.0***	19.4***	13.4***	NS	18.0***	21.7***	33.4**	10.7***
LSD_T					9.3***					10.2***
$LSD_{V\times T}$					23.0*					23.6*

CV, Coefficient of variation; LSD, Least significant difference; V, Variety; MAP, Months after planting; T, Time of harvesting (MAP).
NS, Not significant; ***P ≤ 0.001, **P ≤ 0.01, *P ≤ 0.05.
[a] Mean over three harvest rounds.
[b] Overall landrace site mean.

3.5. *CBSD root necrosis severity scores*

Highly significant ($P < 0.001$) S, V and T effects were detected. The S × V interaction effect was also highly significant (Table 3). The S × V × T interaction effects were significant ($P < 0.05$). The V effects contributed the highest percentage (47.7%) to the TSS, followed by S × V interaction effects (16%) and S effects (7.3%).

At Sendusu, the mean RN scores were higher than at Serere across all the harvesting dates (Table 8). At both sites, MM 2006/128 had the lowest RNS score across all the harvesting dates. As anticipated, the RN score increased with delayed harvesting at both sites. At Sendusu, variety MM 96/4271 had the highest RN score across all harvesting dates, while variety TME 14 had the highest score at Serere (Table 8).

Table 8
Cassava brown streak disease (CBSD) root necrosis severity of six cassava landraces evaluated in two sites in Uganda at four different harvesting rounds (MAP).

	Sendusu					Serere				
	12 MAP	16 MAP	20 MAP	24 MAP	Mean[a]	12 MAP	16 MAP	20 MAP	24 MAP	Mean[a]
MM 2006/90	3.3	3.7	3.7	4.3	3.7	1.7	2.0	2.7	3.0	2.3
MM 2006/123	1.7	2.3	2.0	2.7	2.2	1.0	1.7	2.0	1.7	1.6
MM 2006/128	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.7	1.7	1.3
MM 2006/130	2.3	3.0	3.3	3.0	2.9	2.3	2.0	2.0	2.3	2.2
MM 96/4271	4.0	3.7	4.7	4.3	4.2	2.3	2.3	2.0	2.3	2.2
TME14	3.0	3.0	3.0	3.0	3.0	3.0	3.0	5.0	3.8	3.7
Mean[b]	2.6	2.8	2.9	3.1	2.8	1.9	2.0	2.6	2.4	2.2
CV	22.2	15.6	21.2	14.2	15.0	46.0	35.4	11.7	28.6	26.7
LSD_V	1.0***	0.8***	1.1***	0.8***	0.6***	1.6*	1.3*	0.5***	1.3**	0.8***
LSD_T					0.3**					0.4**
$LSD_{V\times T}$					NS					NS

CV, Coefficient of variation; LSD, Least significant difference; V, Variety; MAP, Months after planting; T, Time of harvesting (MAP).
NS, Not significant; ***P ≤ 0.001, **P ≤ 0.01, *P ≤ 0.05.
[a] Mean over three harvest rounds.
[b] Overall landrace site mean.

3.6. Dry matter content

Highly significant (P < 0.001) V effects were detected for DMC (Table 3). The S × T and V × T interaction effects were significant (P < 0.01). The V effects contributed the highest percentage (59.4%) to the TSS, followed by V × T interaction effects (38%).

No significant differences were detected for DMC among the sites (Table 3). At Sendusu DMC increased from 16 to 20 MAP (33.1–35.9%, respectively), thereafter it slightly decreased (Table 9).

At Sendusu, no significant differences were detected among the varieties across all the harvesting dates. However, at Serere MM 2006/130 and MM 2006/128 had significantly (P < 0.01) higher DMC at 12 MAP than the rest of the varieties except TME14 (Table 9).

3.7. Broad-sense heritability (H) and Best Linear Unbiased Predictions (BLUPs)

Estimates of H for TFRY, MFRY, PMFRY, RNI, RNS and DMC are presented in Table 3. The estimates ranged from 0.08 (TFRY) to 0.52 (RNI). The estimates were low (as defined by Ewa et al., 2017) for TFRY (0.08), MFRY (0.19) and DMC (0.25); moderate for PMFRY (0.48) and high for RNS (0.51) and RNI (0.52).

Best Linear Unbiased Prediction (BLUP) estimates are presented in Table 10. For TFRY, the best varieties were MM 2006/90 (5.0) and MM 2006/123 (4.3). The worst varieties were MM 2006/128 (−6.4) and MM 2006/130 (−4.9). For MFRY, the best variety was MM 2006/123 (8.0) followed by MM 96/4241 (4.0), whereas the worst variety was TME14 (−7.7) followed by MM 2006/130 (−2.3). For PMFRY, the best variety was MM 2006/128 (30.6) followed by MM 2006/123 (22.3). The worst variety was TME14 (−30.4) followed by MM 96/4271 (−18.3). For RNI, the best variety was MM 2006/128 (−33.4) followed by MM 2006/123 (−20.9) whereas the worst variety was TME14 (27.4) followed by MM 96/4271 (19.7). For RNS, the best variety was MM 2006/128 (−1.3) followed by MM 2006/123 (−0.6), whereas the worst three varieties were TME14 (0.8), MM 96/4271 (0.7) and MM 2006/90 (0.5). Finally, for DMC, the best variety was MM 2006/128 (3.8) followed by MM 2006/130 (1.5). The worst varieties for DMC was MM 2006/90 (−3.2) followed by MM 2006/123 (−1.8).

3.8. Box-plot presentation of four of the variables

A box and whisker plot is a graphical method of displaying variation in a set of data. The display for RNI (CBSDRi), RNS (CBSDRs), DMC and TFRY is presented in Fig. 1. The data for RNS was more variable at 12 MAP and thereafter, the variability decreased with delayed time of harvesting. The data were negatively skewed for all harvesting dates except at 20 MAP. For RNI, the data were least variable at 12 MAP. The variability was highest at 20 MAP, although the data were almost normally distributed. For the rest of the harvesting dates, the data were positively skewed.

The data for DMC showed little variability across all the harvesting dates. However, the data at 20 MAP showed the highest variability. At 16 and 20 MAP the data were normally distributed but were positively skewed for 12 and 20 MAP. For TFRY, the data were least variable at 12 MAP. The highest variability occurred at 20 MAP. The data were normally distributed at 12, 20 and 24 MAP. At 16 MAP the data were negatively skewed.

Table 10
Best Linear Unbiased Predictions (BLUPs) for six traits evaluated at Sendusu and Serere.

Variety	TFRY	MFRY	PMFRY	DMC	RNI	RNS
MM 2006/90	4.99	−0.125	−10.20	−3.278	13.503	0.50
MM 2006/123	4.31	8.015	22.33	−1.8.15	−20.862	−0.63
MM 2006/128	−6.43	−1.879	30.58	3.804	−33.443	−1.32
MM 2006/130	−4.89	−2.280	5.94	1.539	−6.365	0.01
MM 96/4271	1.13	4.006	−18.29	−0.0855	19.715	0.66
TME14	0.89	−7.737	−30.37	0.605	27.452	0.78

TFRY, total fresh root yield; MFRY, marketable fresh root yield; PMFRY, percentage marketable root yield; DMC, dry matter content; RNI, CBSD root necrosis incidence; RNS, CBSD root necrosis severity.

4. Discussion

This study investigated the effect of time of harvesting on cassava root yield and quality using new disease-resistant varieties. For this purpose, six varieties were evaluated at two locations, with four harvesting times (12, 16, 20 and 24 MAP). The motivation for this study was to establish whether it was possible to maintain marketable root yield with delayed harvesting as practiced by most farmers. The most important finding from this study was that varieties differed significantly in all the traits evaluated. Furthermore, variety greatly contributed to the variation of the TSS for PMFRY, RNI, RNS and DMC suggesting that these traits are easy to breed for. For TFRY and MFRY, however, site was the main contributor to the variation of the TSS. This implies that for these two traits the breeding strategy should be to develop varieties for specific adaptation to the sites. The site-dependent differences might have been affected by environmental variables like rainfall, altitude, temperature, and soil characteristics of the test sites as suggested by Tumwegamire et al. (2016). These results agree with those of other researchers who have reported that cassava fresh root yield is significantly affected by genotype-environment interactions. For instance, in Malawi, Mkumbira et al. (2003) reported that the

Table 9
Dry matter content (%) of six cassava landraces evaluated in two sites in Uganda at four different harvesting rounds (MAP).

	Sendusu					Serere				
	12 MAP	16 MAP	20 MAP	24 MAP	Mean[a]	12 MAP	16 MAP	20 MAP	24 MAP	Mean[a]
MM 2006/90	30.6	29.8	29.5	28.6	29.6	33.1	33.1	33.1	31.0	32.1
MM 2006/123	32.7	32.0	32.6	32.6	32.5	34.4	34.4	43.4	29.2	31.6
MM 2006/128	30.0	36.4	42.1	45.9	38.6	41.6	41.6	41.6	38.9	40.9
MM 2006/130	38.9	36.1	36.7	31.2	35.7	42.2	42.2	42.2	33.2	38.4
MM 96/4271	29.8	27.4	38.7	37.4	33.3	32.5	32.5	32.5	34.8	33.4
TME14	36.3	37.0	35.7	35.7	36.2	35.9	35.9	35.9	30.9	33.6
Mean[b]	33.1	33.1	35.9	35.2	34.3	36.6	36.6	36.6	33.0	35.0
CV	7.4	8.2	16.4	18.6	13.8	6.8	6.8	6.8	7.7	NE
LSD_V	NS	NS	NS	NS	NS	6.4*	6.4*	6.4*	6.5*	NE
LSD_T					NS					NE
$LSD_{V\times T}$					NS					

CV, Coefficient of variation; LSD, Least significant difference; V, Variety; MAP, Months after planting; T, Time of harvesting (MAP), NE, Not evaluated.
NS, Not significant; ***P ≤ 0.001, **P ≤ 0.01, *P ≤ 0.05.
[a] Mean over three harvest rounds.
[b] Overall landrace site mean.

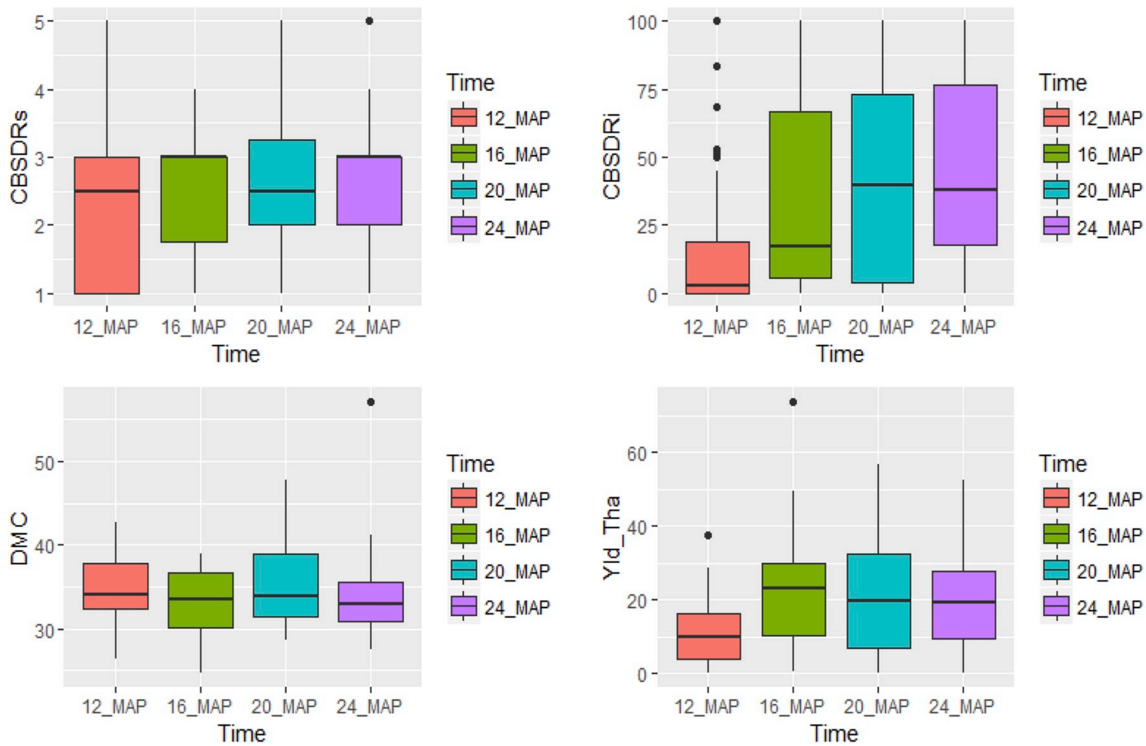

Fig. 1. Box and whisker depiction for CBSD root severity (CBSRs), CBSD root incidence (CBSDRi), dry matter content (DMC) and total fresh root yield (Yld_Tha).

performance of genotypes in terms of fresh root yield varied across sites. Similar results were observed by Egesi et al. (2007) in Nigeria. Again, in Malawi, Benesi et al. (2008) reported that optimal harvest time was genotype- and environment-dependent. This underscores the fact that cassava, as a crop, is adaptable to a wide diversity of environmental conditions, but the usual ranges of most varieties are narrow and have large genotype-environment interaction effects (Dixon et al., 1994; Ngeve, 1994; Ntawuruhunga et al., 2001). It is interesting to note that, in general, fresh root yield increased (doubled) and reached a maximum at 16 MAP similar to the results reported in Tanzania (Mtunguja et al., 2016). This can be explained by the fact that the two sites in Uganda (Sendusu and Serere, respectively located in the central and eastern regions) normally do not experience a very long dry period. This means the plants do not deplete their reserves in trying to survive during the dry season as is the case in many other parts of sub-Saharan Africa (Mtunguja et al., 2016). It implies that the recommended time of harvest of 12 months after planting is not the optimum time for harvesting cassava in these environments. The present results showed that fresh root yield doubled at 16 MAP from 12 MAP. Further investigations are required to see if it will be economically beneficial to harvest at 16 MAP taking into account that the land is occupied by the crop for longer (Adjebeug-Danquah et al., 2016).

The fresh marketable root yield and the percentage of marketable fresh root yield were used to explain the adverse effects of CBSD infection on the root yield of cassava. This depicted the reality facing farmers because roots scoring class 3 and above cannot be marketed (Hillocks et al., 2015). As expected, both decreased with delayed time of harvesting. The significant genotype-environment interaction effects we observed implied that varieties responded differently within sites. Variety MM 96/4271 (NASE 14) proved to be very susceptible to CBSD root necrosis even at 12 MAP at Sendusu, the disease hotspot. However, these results contradict reports by other authors who have indicated that this variety is tolerant to CBSD and is currently recommended to farmers in Uganda (Ogwok et al., 2014). Our results agree with those recently reported by Okul Valentor et al. (2018), who used NASE 14 as a resistant check but reported that it showed severe root necrosis (class 3), high root incidence (65.7%) and stem die-back. They attributed this poor performance to the breakdown of its partial resistance under high disease pressure and to degeneration after more than 10 years of recycling. The present study showed that this variety should be recommended only for growing in areas where CBSD is not prevalent. On the basis of the present study it is recommended that varieties MM 2006/128, MM 2006/123 and MM 2006/130 should be grown and harvested at 12 MAP. The variety MM 2006/128 which showed good performance vis à vis CBSD in both locations and across different harvest times is recommended if harvesting has to be delayed. This variety has not been officially released in Uganda, but these findings might add to its merit for consideration for official release. The same applies to variety MM 2006/123. Both varieties were derived from half-sib seed derived from open pollination among mostly CBSD tolerant parents from Tanzania. The results indicated a clear trend of root necrosis becoming more severe with delayed harvesting. The effect of genotype-environment interaction was also evident for variety and site meaning that genotypes should be recommended based on specific adaptation. There was a marked difference in the response of varieties at the two sites. Sendusu was obviously a disease hotspot where varieties showed the highest severity symptoms, with MM 2006/4271 being the most susceptible from 12 MAP onwards. This supports the decision of farmers in badly CBSD-affected areas to harvest CBSD-susceptible cultivars earlier than 12 MAP. The strong influence of the environment on the expression of CBSD root necrosis can be attributed to variety susceptibility levels, predominant virus species, and climatic factors that influence the abundance of the whitefly vectors (Okul Valentor et al., 2018). There is a need for breeders to screen their germplasm for identification of clones with long in-ground storability like MM 2006/128 since our results indicates that there is genetic variability for this trait.

Dry matter content tended to increase to a maximum at 20 MAP and thereafter slightly declined. The influence of genotype-environment interactions was also evident, with varieties responding differently at the different harvesting times. These results agree with those reported from Tanzania by Mtunguja et al. (2016). Significant genotype × harvesting time effects were also reported by Adjebeng-Danquah et al. (2016) for Ghana. It is worth noting that variety MM 2006/128 had the highest mean DMC content at both sites and it also had the highest DMC at 24 MAP.

The main practical advantages of using BLUP is that it allows comparison of varieties over time and space, and allows the simultaneous correction for environmental effects, estimation of variance components, and prediction of genetic values. BLUP also deals with complex data structures and may be applied to unbalanced data and to non-orthogonal designs (de Resende, 2016). The BLUPs confirmed that MM 2006/0128 was the best variety to recommend where delayed harvesting is practiced. It was the only one that was not adversely affected by delayed harvesting with regards to root yield and quality traits.

5. Conclusions

Within limits, the datasets generated from this study highlighted three findings. Firstly, delayed harvesting almost doubled TFRY at 16 MAP. This needs further investigation to make a revised recommendation for time of harvesting, since it might be more economical to harvest at 16 MAP. Secondly, although harvesting time effects were highly significant for all variables, it was variety followed by variety × site effects that contributed the most to the TSS. This does not undermine the adverse effects of delayed harvesting on economic root yield. Thirdly, MM 2006/128 has proven to be the best variety to recommend where delayed harvesting under high CBSD pressure is practiced. This study has highlighted that it is possible to breed new cassava varieties that can combine tolerance to CBSD with long in-ground storability. This approach should be applied to all promising breeding lines that are in advanced stages of evaluation to identify suitable varieties before they are officially released. Genotype and environment had a profound effect on all the traits analysed. This implies that genotypes should be selected for specific adaptation to environments. Furthermore, the best harvesting time should also be based on the specific variety and location for all the traits we have investigated in this study. As far as we are aware, this is the first study on the relationship between time of harvesting and CBSD root necrosis that went on for 24 MAP. We propose that the promising varieties reported in this study be distributed to other countries in the region that are seriously affected by CBSD, where they can be evaluated for their response to CBSD and/or adaptation. The varieties can then be officially released if they are found to be superior to currently grown varieties. In addition, these varieties can serve as parents to be used as new sources of resistance to CBSD and CMD.

Declarations of interest

None.

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