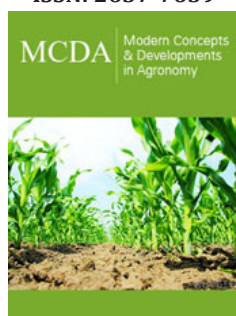


Effect of Time of Harvesting and Disease Resistance in Reducing Cassava (*Manihot esculenta* Crantz) Yield Losses by Two Viral Diseases

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Abstract

Cassava mosaic disease (CMD) and cassava brown streak disease (CBSD) are two important biotic constraints for cassava (*Manihot esculenta* Crantz) production in Eastern and Southern Africa. CMD causes a general decline in yield in affected plants of susceptible cassava varieties but CBSD causes rotting of edible roots. Delayed harvesting can increase rotting of roots and making them unfit for consumption or marketing, and thus affecting the livelihoods of poor farmers. This study investigated the effect of interaction between time of harvesting and levels of disease resistance to identify ideal harvesting times for reducing yield losses. The resistant cassava variety Namikonga remained in the field for the duration of the study, up to 24 months after planting without incurring significant yield losses, while the tolerant varieties Kiroba and Kizimbani could only be maintained up to 21 months. Susceptible varieties Mreteta and Albert suffered significant yield losses beyond 15 months. Among the varieties, Kizimbani had the least CBSD and CMD foliar symptoms as well as farmer desirable traits including high root weight, quantity of marketable roots and dry matter content. Harvesting of cassava can depend on the resistance or susceptibility of the varieties grown. Therefore, the above harvesting times for different varieties were recommended for minimizing yield losses due to the diseases and thus maximizing yields to the farmers.

Abbreviations: CBSD: Cassava Brown Streak Disease; CBSIs: Cassava Brown Streak Ipomoviruses; CBSV: Cassava Brown Streak Virus; CMBs: Cassava Mosaic Begomoviruses; CMD: Cassava Mosaic Disease; CMV: Cassava Mosaic Virus; UCBSV: Uganda Cassava Brown Streak Virus

Introduction

Cassava (*Manihot esculenta* Crantz) roots are an important staple food in sub-Saharan Africa (SSA) providing daily source of carbohydrates for over 450 million [1,2]. Apart from utilization as fresh roots, it can also be processed into flour, which may be consumed by the farmers, sold in market, or can be used in bakery, starch or ethanol production and paper making [3]. Cassava tolerates unpredictable drought periods and can grow on marginal soils with minimum inputs. Subsistence farmers rely on cassava as a vital source of energy since it can be harvested throughout the year. In addition, the average cassava yield in East and Southern Africa has, however, remained low since the 1990s, rarely exceeding 10.0t/ha, which is far below the estimated yield potential of 50-60t/ha [4,5]. Among the numerous factors, the biotic stresses: cassava mosaic disease (CMD) and cassava brown streak disease (CBSD) have greatly contributed to low cassava productivity in SSA [6-8].

CBSD is caused by two RNA viruses belonging to the genus *Ipomovirus* in the family *Potyviridae*: cassava brown streak virus (CBSV) and Ugandan cassava brown streak virus (UCBSV) [7,9-11], which are together called cassava brown streak ipomoviruses (CBSIs) [12]. CBSD symptoms are characterized by leaf chlorosis along the secondary and tertiary veins, and elongated necrotic lesions on stems [8,13,14]. The major economic damage arises from the dry, necrotic rotting of cassava roots which reduces nutritional and industrial quality and

renders the roots unpalatable and marketable [9,14]. In southern coastal Tanzania, for example, yield losses of up to 70% were caused by CBSD in susceptible cultivars [15]. The CMD is caused by 11 cassava mosaic begomoviruses (CMBs), (Family *Geminiviridae*: Genus *Begomovirus*) [7,16].

CMD symptoms typically include irregular yellow or yellow-green chlorotic mosaic pattern on leaves, leaf distortion, stunted plant growth and reduced root yields, but not rotting of roots [17-19]. Losses up to 100% have been reported in highly susceptible varieties [19,20] or in mixed infections of CMD and CBSD [21,22]. CMD-resistant varieties have been developed which express less severe symptoms than susceptible ones especially during the late stages of plant growth, when the resistant varieties become virtually symptomless [23]. Apart from plant genotype, environmental factors also influence symptom expression and leaves produced during periods of cool weather tend to have more severe symptoms than those produced under hotter conditions [24]. Moreover, some strains of viruses cause more severe symptoms than others and have greater effects on growth and yield [25].

Dual infections of CMD and CBSD are common and they are a serious threat to cassava production and food security in SSA. Deployment of cassava varieties with dual resistance to both diseases is the only sustainable way to control [26]. More recently, breeding has been focussing on varieties with dual resistance to both CMD and CBSD. Crossing the resistant cassava variety (var.) Namikonga (CBSD resistant but CMD susceptible) with var. AR42-4 (CBSD susceptible but CMD resistant) developed a new cassava hybrid Pwani which is resistant to CMD but tolerant to CBSD with no or delayed root necrosis [27]. However, the large-scale adaption of such varieties is yet to be achieved in the worst affected countries of eastern and southern Africa [7,16]. A property unique to cassava is its ability to store the roots in the ground beyond the optimum harvesting time without major reduction in yields. Cassava roots can stay underground for up to three years after planting, which is making it an important food security crop available at the time of needs when all other crops are not available [28]. Many farmers value long 'in-ground storage' of cassava roots especially in drought prone areas as they can harvest a few plants at a time (piecemeal harvesting) leaving others "stored" in the field for later harvest [29]. Preferences for long in-ground storage of cassava roots have been reported in Tanzania, Uganda, and Malawi [30,31]. Additionally, to ensure food security during adverse conditions, cassava farmers

in Tanzania plant both early maturing (6-9 months) and late maturing (12-18 months) varieties [31]. However, all the food security benefits of cassava are lost due to the infections of CBSD as root necrosis becomes increasingly severe with plant age and late harvesting which can result in significant yield losses.

In many countries, farmers have adopted early harvesting to cope with such CBSD losses and thus reducing the food security value of cassava [15,30,32,33]. Early harvesting, especially for varieties that accumulate starch late (late bulking) contributes to significant yield losses [33]. Cassava is harvested normally between 9 and 12 months after planting but little information is available on the optimum time of harvesting to reduce the impact of CBSD. To identify optimum harvesting times for cassava varieties with different levels of resistance to the two diseases, this study was carried out with the following objectives;

- (i) Determine the effect of harvesting time on cassava yields (root weight, marketable roots and dry matter content) in a 24 months growth cycle, and
- (ii) Testing the resilience of CBSD -resistant, -tolerant and -susceptible varieties to root necrosis damage and yield losses.

These results will help develop recommendations for farmers on the ideal harvesting times for different cassava varieties in disease affected areas.

Material and Methods

Cassava germplasm and screening location

Five popular cassava varieties; Namikonga, Kiroba, Kizimbani, Albert and Mreteta, grown in different regions of Tanzania were selected for evaluation based on their reaction to CMD and CBSD (Table 1). The field trial was established in February 2014 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 and is located at 10° 22' 20"S, 40° 10' 34"E and 111m above mean sea level. The area receives the main rainfall from December-May with second rains of scattered showers in August-October (TMA, 2009). The sandy soils of Mtwara region are considered poor for most crops. They are characterised by deep, well drained, weak structured, dark reddish-brown loamy sand topsoil over reddish brown moderately structured sandy loam to sandy clay loam subsoil [34].

Table 1: Pedigree of Tanzanian cassava varieties used to estimate the effect of CMD and CBSD, and the time of harvesting on cassava yield losses.

| Variety | Pedigree | Response to CBSD | Response to CMD | Notes | References |
|---------|--|------------------|-----------------|---|--|
| Albert | Putative full-sib of TME117 | Susceptible | Resistant | Popular landrace grown in Tanzania | Maruthi et al. [45]; Bredeson et al. [46]; Masumba et al. [47]. |
| Kiroba | Hypothesised to be a derivative from a <i>M. glaziovii</i> × <i>M. esculenta</i> interspecific cross | Tolerant | Susceptible | Popular landrace officially released for Tanzanian coastal lowlands | Muhana and Mtunda [48]; Ferguson et al. [49]; Nzuki et al. [50]. |

| | | | | | |
|-----------|--|-------------|-------------|--|---|
| Kizimbani | Kiroba half-sib (male parent unknown) | Tolerant | Resistant | High yielding improved variety grown in Zanzibar | Kanju et al. [59]. |
| Mreteta | Unknown | Susceptible | Susceptible | Local landrace | Kulembeka [44]. |
| Namikonga | Third back cross from inter-specific hybrid (46106/27) from <i>M. glaziovii</i> onto <i>M. esculenta</i> | Resistant | Susceptible | Late root bulking properties | Jennings [58]; Hillocks and Jennings [14]; Masumba et al. [47]. |

Experimental design

A split plot design with three replicates was used for the study. The varieties in the main plots were randomly assigned in replications while the different harvesting times were sub-plots randomized within the main plots. The main plots each measured 80m long and 16m wide while the sub-plots each measured 10m long and 2m wide. Mature cassava cuttings of about 25cm 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 var. Limbanga and CBSD susceptible var. Albert were planted around the experimental plots as spreader rows [35]. The trial was rain fed, kept weed free by monthly weeding and no fertilizer or chemical pesticides were applied.

Estimating the impact of CMD and CBSD on cassava yields

Data on several parameters required to assess the impact of CMD and CBSD on cassava yields were collected at 6, 9, 12, 15, 18, 21, and 24 months after planting. These included CMD and CBSD foliar incidences, foliar severities, root necrosis, yield loss, root weight (t/ha), marketable roots (t/ha) and dry matter content of cassava roots. Foliar incidences were calculated as a percentage of the plants showing symptoms while foliar severities were recorded based on a scale of 1-5 for both CMD and CBSD according to Hahn et al. [36] and Hillocks et al. [29], respectively (Table 2). Roots from each plant were harvested and chopped longitudinally and transversely to check for root necrosis on the starch bearing tissues. Scoring for root necrosis was done based on a 1- 5 scale by Gondwe et al. [30]. Root weight in tonnes per hectare (t/ha) was estimated according to Kamau et al. [37].

Table 2: CMD and CBSD foliar severity scoring scale.

| Scoring Scale | CMD Foliar Symptoms | CBSD Foliar Symptoms | CBSD Root Symptoms | General Description of Symptoms | Description of Varieties |
|---------------|---|---|---|---------------------------------|--------------------------|
| 1 | No visible symptoms | No visible symptoms | No visible symptoms | No symptoms | Highly resistant |
| 2 | A mild distortion only at the base of leaflets with the remainder of leaflets appearing green and healthy/mild chlorotic pattern over entire leaflets | Mild foliar mosaic on some leaves and no stem lesions | <5% of root necrotic | Mild | Resistant |
| 3 | Conspicuous mosaic pattern throughout leaf, narrowing and distortion of lower 1/3 of leaflets | Foliar mosaic with mild stem lesions and no die back | 5-25% of root necrotic | Moderate | Tolerant |
| 4 | Severe mosaic, distortion of two-thirds of leaflets and general reduction of leaf size | Foliar mosaic and pronounced stem lesions and no die back | 25-50% root necrotic & mild root constriction | Severe | Susceptible |
| 5 | Severe mosaic, distortion of ¾ of leaflets, twisted and misshapen leaves | Defoliation with pronounced stem lesions and die-back | >50% of root necrotic | Highly severe | Highly susceptible |

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

All roots with necrosis score of ≤2 was considered marketable as only tiny spots of root necrosis were observable at this score [38]. Severe root necrosis affects root quality, therefore reducing the quantity of marketable roots (t/ha). Marketable roots were determined by deducting the unmarketable roots which had root necrosis score >2. Each category was weighed separately, and yield loss was calculated by expressing the weight of the unmarketable

roots (t/ha) as a percentage of the total root weight (t/ha). Further, data were collected on root dry matter content using the specific gravity method [39].

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

All data were subjected to ANOVA to obtain the contribution of all sources of variation to the total sum of squares. The analysis was carried out using the PROC GLM procedure of SAS 13.1 [40] (SAS Institute Inc, 2013) and means for varieties and harvest times

were separated using Tukey’s HSD test at 95% confidence level. Graphs were also plotted to show the trend of disease incidences, severities, and yield losses for different varieties.

Result

CMD foliar incidences and severity

CMD foliar incidence varied significantly ($P \leq 0.05$) among the varieties (Figure 1). Mreteta maintained the highest incidence ranging from 47.5 to 90.0%, while Kizimbani and Albert had the least, rarely exceeding 10.0% throughout the growing season.

Kiroba and Namikonga had moderate incidence ranging from 19.7 to 52.9%. Similarly, CMD foliar severity varied significantly ($P \leq 0.05$) among the varieties (Figure 1). Mreteta and Kiroba had the highest severity ranging from 2.0 to 3.5 while Kizimbani and Albert had the least ranging from 1.0 to 1.1 throughout the growing season. Moderate severity was recorded on Namikonga. Combined means for all time points showed a similar trend where both CMD foliar incidence and severity increased from 6 MAP, peaked at 15 MAP then dropped gradually till the end of the growing season at 24 MAP (Table 3).

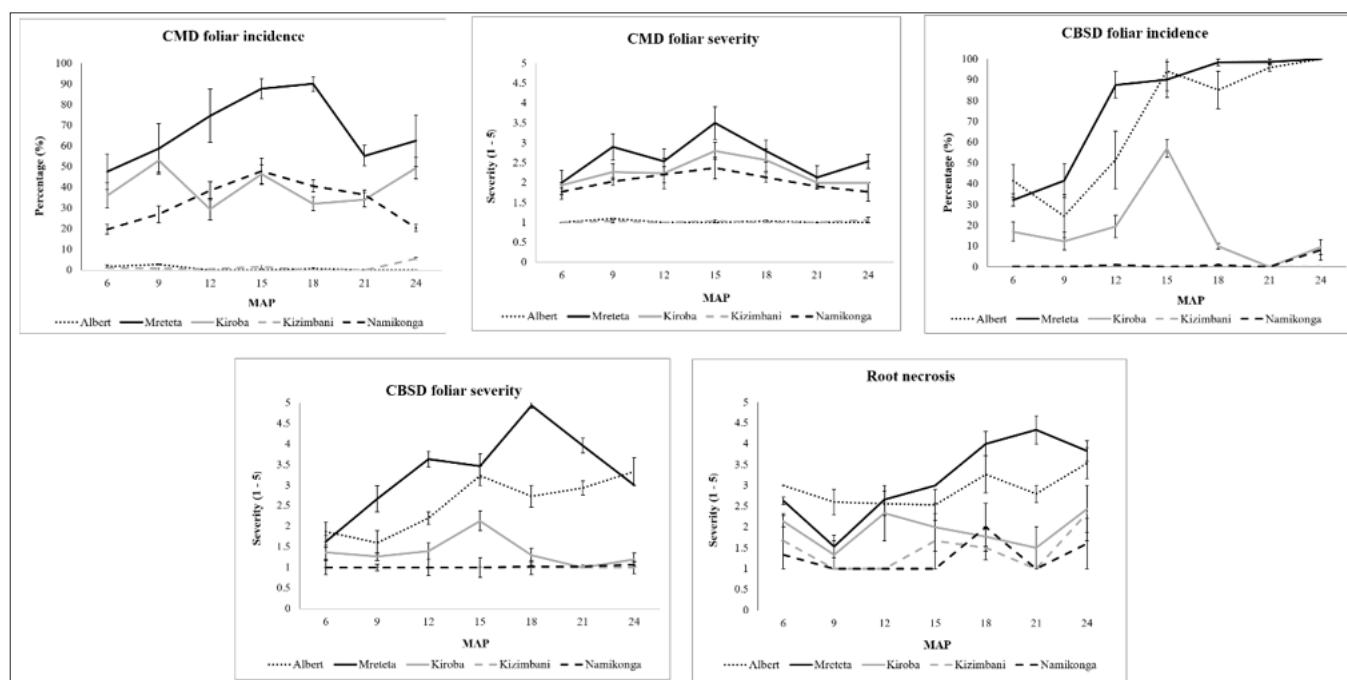


Figure 1: CMD/CBSD incidence and severity of cassava varieties at different harvesting times from 6-24 months after planting (MAP). Vertical bars denote the standard errors of the means with 95% confidence interval.

Table 3: Combined means of disease and yield traits for different times of harvesting (6 to 24 months after planting).

| Time (MAP) | CMD Incidence | CMD Severity | CBSD Incidence | CBSD Severity | Root Necrosis | Yield Loss | Root Weight (t/ha) | Marketable Roots (t/ha) | Dry Matter Content |
|------------|--------------------|--------------------|--------------------|-------------------|-------------------|--------------------|--------------------|-------------------------|--------------------|
| 6 | 22.0 ^d | 1.6 ^d | 18.2 ^d | 1.4 ^e | 2.2 ^b | 8.3 ^d | 7.4 ^e | 6.6 ^e | 22.3 ^c |
| 9 | 30.7 ^{bc} | 1.9 ^b | 15.8 ^d | 1.5 ^c | 1.5 ^d | 4.4 ^e | 10.9 ^d | 10.3 ^d | 24.9 ^b |
| 12 | 29.5 ^{bc} | 1.8 ^{bc} | 31.9 ^c | 1.9 ^b | 1.9 ^c | 10.8 ^{cd} | 12.6 ^d | 11.4 ^d | 20.0 ^d |
| 15 | 38.2 ^a | 2.2 ^a | 48.3 ^a | 2.2 ^a | 2.0 ^{bc} | 12.1 ^c | 18.8 ^c | 16.2 ^c | 28.7 ^a |
| 18 | 33.4 ^{ab} | 2.0 ^{ab} | 38.9 ^{bc} | 2.2 ^a | 2.5 ^a | 20.5 ^b | 23.9 ^b | 18.9 ^b | 25.1 ^b |
| 21 | 25.8 ^{cd} | 1.6 ^d | 38.9 ^{bc} | 2.0 ^{ab} | 2.2 ^b | 20.9 ^b | 24.1 ^b | 17.8 ^{bc} | 21.2 ^c |
| 24 | 30.2 ^{bc} | 1.7 ^{bcd} | 43.4 ^{ab} | 1.9 ^{ab} | 2.7 ^a | 27.8 ^a | 28.7 ^a | 20.8 ^a | 25.8 ^b |
| MSE | 35.7 | 0.1 | 58.6 | 0.1 | 0 | 6.5 | 3.6 | 2.5 | 1.1 |
| HSD | 6.7 | 0.3 | 8.5 | 0.3 | 0.2 | 2.8 | 2.1 | 1.7 | 1.2 |

MSE=mean square error, HSD: tukey’s honest significant difference; different letters indicate that means within a column are significantly different ($P \leq 0.05$).

CBSD foliar incidences and severity

CBSD foliar incidence also varied significantly ($P \leq 0.05$) among the cassava varieties. The highest incidences were recorded on Albert and Mreteta, which gradually increased throughout the 24 months growing period and ranged from 25.0 to 100% (Figure 1). Namikonga and Kizimbani maintained low foliar CBSD incidences not exceeding 10.0% while Kiroba had intermediate incidence ranging from 9.5 to 57.1%. Similarly, CBSD foliar severity increased throughout the growing period on Albert and Mreteta with the highest severity ranging from 1.6 to 4.9 while Namikonga and Kizimbani maintained the least < 1.5 (Figure 1). Kiroba had an intermediate foliar severity ranging from 1.3 to 2.1. Comparable to CMD foliar incidence and severity, combined means for all time points showed a similar trend for CBSD foliar incidence and severity, which increased from 6 MAP, peaked at 15 MAP then decreased gradually till 24 MAP (Table 3).

Root damage by CBSD infection

CBSD root necrosis and rotting varied significantly ($P \leq 0.05$) among the varieties (Figure 1). Mreteta and Albert had the most

damaged roots with severities ranging from 1.5 to 4.3 throughout the growing season. Namikonga had the least damage with severity not exceeding 1.7 while Kizimbani and Kiroba had intermediate severities ranging from 1.0 to 2.3. Combined means for all the harvesting time points showed that root necrosis was high at 6 MAP with a severity of 2.2. The severity decreased to 1.5 at 9 MAP before beginning to rise again from 1.9 at 12 MAP to 2.7 at 24 MAP (Table 3).

Yield losses due to CBSD infection

Yield losses occur due to necrosis and rotting of infected roots and in this study, losses varied among the varieties (Figure 2). Mreteta had the highest losses with a maximum of 76.9% at 21 MAP. Although Albert had moderate root losses of $< 30.0\%$ between 6-21 MAP, it nevertheless had a high loss of 50.4% at 24 MAP. Kizimbani and Kiroba maintained low losses of $< 12.0\%$ between 6-21 MAP, but the losses increased to 23.0% at 24 MAP. Finally, Namikonga had the least losses of $< 10.0\%$ throughout the growing season. Combined means for all the harvesting time points showed that losses reduced at 9 MAP before rising again at 12 MAP till the end of the growing season at 24 MAP (Table 3).

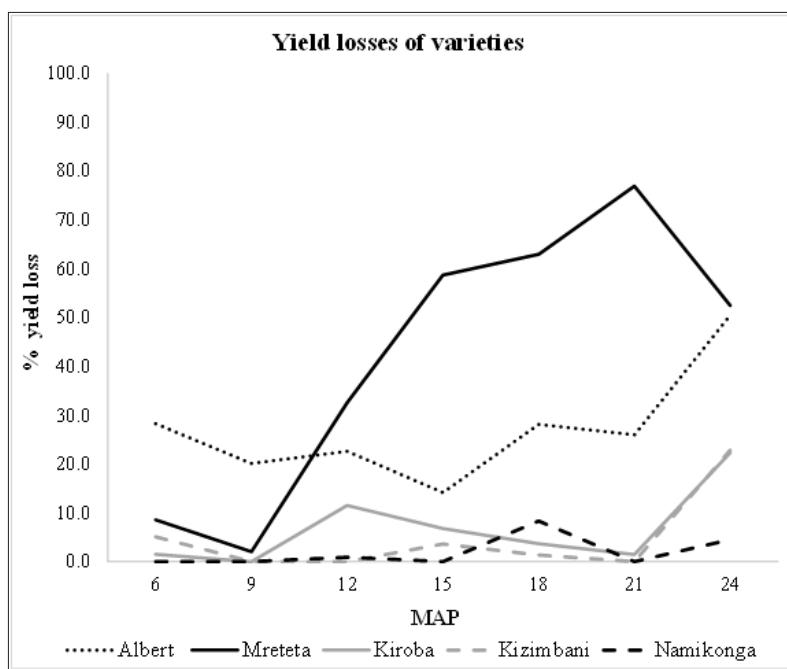


Figure 2: Means for yield losses of varieties at different harvesting times from 6 to 24 months after planting (MAP).

Measurement of cassava yield traits

The root weight increased throughout the growing season and the cumulative root weight varied significantly for each variety ($P \leq 0.05$) (Tables 4&5). Kizimbani and Kiroba had significantly highest cumulative root weight of 21.0t/ha and 20.8t/ha, respectively, while Namikonga had the least at 14.7t/ha (Table 4). The mean marketable roots increased throughout the growing season and cumulative marketable roots for each variety varied

significantly ($P \leq 0.05$) (Tables 4&6). Kizimbani had the highest cumulative marketable roots of 19.7t/ha and was significantly different from Kiroba (15.9t/ha), Namikonga (14.3t/ha), Albert (12.0t/ha) and Mreteta (10.9t/ha). The mean dry matter content fluctuated throughout the growing season depending on the weather patterns (Table 7) (Figure 3). Low dry matter content was recorded in months with high rainfall for example at 12 and 21 MAP and it increased in the rest of the drier months including at 9, 15 and 24 MAP. The highest cumulative dry matter content was recorded

in Namikonga at 24.7% and was not significantly different from Kiroba (24.4%) and Kizimbani (24.3%) (Table 3). Albert (23.7%) and Mreteta (22.7%) had the lowest dry matter content and were not significantly different from each other.

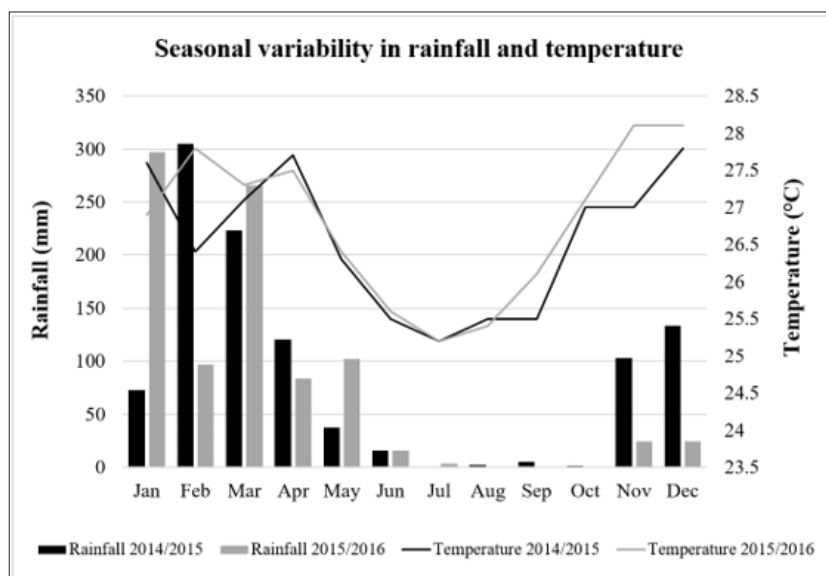


Figure 3: Variability in rainfall and temperature for 2014/2015 and 2015/2016 growing season.

Table 4: Combined means of disease and yield traits for cassava varieties.

| Variety | CMD Incidence | CMD Severity | CBSD Incidence | CBSD Severity | Root Necrosis | Yield Loss | Root Weight (t/ha) | Marketable Roots (t/ha) | Dry Matter Content (%) |
|-----------|-------------------|-------------------|-------------------|------------------|------------------|-------------------|--------------------|-------------------------|------------------------|
| Albert | 0.7 ^c | 1.0 ^c | 70.4 ^b | 2.6 ^b | 2.9 ^a | 27.1 ^b | 16.7 ^b | 12.0 ^d | 23.7 ^{ab} |
| Kiroba | 44.2 ^b | 2.4 ^{ab} | 17.9 ^c | 1.4 ^c | 1.9 ^b | 5.3 ^c | 17.0 ^b | 15.9 ^b | 24.4 ^a |
| Kizimbani | 1.2 ^c | 1.0 ^c | 0.1 ^d | 1.0 ^c | 1.4 ^c | 3.7 ^{cd} | 21.0 ^a | 19.7 ^a | 24.3 ^a |
| Mreteta | 68.0 ^a | 2.6 ^a | 78.4 ^a | 3.3 ^a | 3.1 ^a | 37.2 ^a | 20.8 ^a | 10.9 ^d | 22.7 ^b |
| Namikonga | 33.9 ^b | 2.1 ^b | 1.1 ^d | 1.0 ^c | 1.3 ^c | 1.7 ^d | 14.7 ^c | 14.3 ^c | 24.7 ^a |
| MSE | 258.4 | 0.2 | 35.8 | 0.2 | 0.1 | 8.9 | 3.4 | 1.3 | 1.1 |
| HSD | 17.1 | 0.5 | 6.4 | 0.5 | 0.4 | 3.2 | 2 | 1.2 | 1.1 |

MSE=mean square error, HSD: tukey’s honest significant difference; different letters indicate that means within a column are significantly different (P≤0.05).

Table 5: Mean root weight (t/ha) and standard errors of means (SEM) for varieties at different harvesting times from 6 to 24 months after planting (MAP).

| Variety | Root Weight (t/ha) ± SEM MAP | | | | | | |
|-----------|------------------------------|------------------------|-----------------------|------------------------|-----------------------|------------------------|-----------------------|
| | 6 | 9 | 12 | 15 | 18 | 21 | 24 |
| Albert | 9.0±0.5 ^a | 12.9±0.4 ^a | 12.5±0.7 ^b | 18.1±0.6 ^{bc} | 19.6±0.8 ^b | 21.2±1.1 ^{bc} | 23.7±0.8 ^c |
| Kiroba | 6.9±0.3 ^b | 9.5±0.3 ^{bc} | 9.9±0.2 ^b | 16.4±0.5 ^{bc} | 21.0±0.7 ^b | 27.3±1.7 ^{ab} | 28.0±0.5 ^b |
| Kizimbani | 6.8±0.2 ^b | 11.4±0.5 ^{ab} | 16.5±0.8 ^a | 15.9±0.5 ^c | 30.4±0.2 ^a | 23.8±1.3 ^b | 42.3±2.2 ^a |
| Mreteta | 9.4±0.3 ^a | 11.7±0.6 ^a | 11.6±0.9 ^b | 24.5±0.8 ^a | 29.3±0.5 ^a | 31.1±1.6 ^a | 27.7±0.3 ^b |
| Namikonga | 4.7±0.3 ^c | 8.9±0.1 ^c | 12.7±1.0 ^b | 19.0±0.5 ^b | 19.3±0.4 ^b | 16.9±1.5 ^c | 21.5±1.0 ^c |
| Mean | 7.4±0.5 | 10.9±0.4 | 12.6±0.7 | 18.8±0.9 | 23.9±1.3 | 24.1±1.4 | 28.6±2.0 |

±=95% confidence interval for means; different letters indicate that means within a column are significantly different (P≤0.05).

Table 6: Mean marketable roots and standard errors of means (SEM) for varieties at different harvesting times from 6 to 24 months after planting (MAP).

| Variety | Marketable Roots (t/ha) ± SEM MAP | | | | | | |
|-----------|-----------------------------------|------------------------|-----------------------|-----------------------|-----------------------|------------------------|------------------------|
| | 6 | 9 | 12 | 15 | 18 | 21 | 24 |
| Albert | 6.0±0.3 ^{bc} | 10.4±0.1 ^{ab} | 9.3±1.0 ^b | 15.6±0.3 ^b | 14.8±0.7 ^c | 15.8±2.1 ^{ab} | 12.3±6.1 ^b |
| Kiroba | 6.8±0.4 ^b | 9.5±0.5 ^{ab} | 9.2±0.6 ^b | 15.3±0.3 ^b | 20.2±0.5 ^b | 27.0±3.1 ^a | 23.4±2.8 ^{ab} |
| Kizimbani | 6.5±0.1 ^b | 11.4±0.7 ^a | 16.5±0.8 ^a | 15.2±0.8 ^b | 30.1±0.4 ^a | 23.8±3.9 ^a | 34.1±1.8 ^a |
| Mreteta | 8.7±0.6 ^a | 11.5±0.6 ^a | 9.4±0.6 ^b | 15.7±0.4 ^b | 11.5±0.7 ^d | 5.6±2.2 ^b | 13.7±4.2 ^b |
| Namikonga | 4.7±0.3 ^c | 8.9±0.1 ^b | 12.5±0.9 ^b | 19.0±0.5 ⁺ | 17.8±0.6 ^b | 16.9±3.3 ^{ab} | 20.4±2.8 ^{ab} |
| Mean | 6.6±0.4 | 10.3±0.3 | 11.4±0.8 | 16.2±0.4 | 18.9±1.7 | 17.8±2.3 | 20.8±2.6 |

±=95% confidence interval for means; different letters indicate that means within a column are significantly different ($P \leq 0.05$).

Table 7: Mean % dry matter content and standard errors of means (SEM) for cassava varieties at different harvesting times from 6 to 24 months after planting (MAP).

| Variety | Dry Matter Content (%) ± SEM MAP | | | | | | |
|-----------|----------------------------------|------------------------|-----------------------|------------------------|-----------------------|-----------------------|------------------------|
| | 6 | 9 | 12 | 15 | 18 | 21 | 24 |
| Albert | 21.8±0.1 ^a | 25.1±0.1 ^{ab} | 19.2±1.1 ^a | 28.2±0.6 ^{ab} | 23.9±0.5 ^b | 20.9±1.9 ^a | 24.1±0.4 ^b |
| Kiroba | 22.3±0.3 ^a | 25.8±0.8 ^a | 19.5±1.0 ^a | 30.2±0.4 ^a | 26.0±0.2 ^a | 22.3±1.3 ^a | 25.0±0.1 ^{ab} |
| Kizimbani | 23.4±1.0 ^a | 25.1±0.1 ^{ab} | 20.4±1.0 ^a | 28.2±0.3 ^{ab} | 26.2±0.4 ^a | 20.9±0.4 ^a | 25.6±0.7 ^{ab} |
| Mreteta | 21.4±0.6 ^a | 22.6±0.8 ^b | 21.0±1.5 ^a | 26.7±0.6 ^b | 23.5±0.3 ^b | 20.2±0.7 ^a | 23.7±0.1 ^b |
| Namikonga | 22.4±0.4 ^a | 25.9±0.5 ^a | 19.7±0.8 ^a | 30.3±0.5 ^a | 25.8±0.2 ^a | 21.6±0.9 ^a | 27.3±1.1 ^a |
| Mean | 22.3±0.3 | 24.9±0.4 | 20.0±0.5 | 28.7±0.4 | 25.1±0.3 | 21.2±0.5 | 25.8±0.4 |

±=95% confidence interval for means; different letters indicate that means within a column are significantly different ($P \leq 0.05$).

Sum of squares (SS) for traits evaluated

The ANOVA revealed that a larger percentage of total sum of squares (SS) ranging from 53.8 to 81.9% was attributed to variety for foliar incidence and severity for both diseases, root necrosis and yield loss (Tables 8&9). The larger SS indicated that the genetic makeup of the varieties highly influenced the expression

of disease symptoms. On the contrary, a larger percentage of SS ranging from 47.5 to 80.9% was attributed to time for yield traits evaluated including: root weight, marketable roots, and dry matter content. This indicated that time contributed to the most variations observed in the yield traits analysed. Lastly, variety and time interaction had the least SS (6.5-29.7%) for all traits analysed since it had minimal effect on trait expression.

Table 8: Sum of squares for CMD and CBSD foliar incidence, severity and root necrosis.

| Source of Variation | Df | CMD Incidence | | CMD Severity | | CBSD Incidence | | CBSD Severity | | Root Necrosis | |
|---------------------|-----|---------------|--------|--------------|--------|----------------|--------|---------------|--------|---------------|--------|
| | | SS | SS (%) | SS | SS (%) | SS | SS (%) | SS | SS (%) | SS | SS (%) |
| Replicate | 2 | 280.3 | 0.3 | 0.2 | 0.3 | 182.6 | 0.1 | 0.5 | 0.4 | 0.11 | 0.12 |
| Variety | 4 | 68058.6 | 81.9 | 47.3 | 77.3 | 1E+05 | 74.4 | 90.9 | 71.5 | 58.7 | 65.2 |
| Replicate*Variety | 8 | 2067.4 | 2.5 | 1.9 | 3.1 | 286.2 | 0.2 | 0.8 | 0.6 | 0.91 | 1 |
| Time (MAP) | 6 | 2399 | 2.9 | 4.4 | 7.2 | 137,33.7 | 8.4 | 9.6 | 7.6 | 13.8 | 15.3 |
| Variety*Time (MAP) | 24 | 8137 | 9.8 | 4.2 | 6.8 | 24170 | 14.8 | 21.3 | 16.8 | 15.4 | 17.1 |
| Residual | 60 | 2142.1 | 2.6 | 3.4 | 5.6 | 3514 | 2.2 | 4.1 | 3.2 | 1.9 | 2.1 |
| Total | 104 | 83084.4 | - | 61.4 | - | 2E+05 | - | 127.2 | - | 90 | - |

Table 9: Sum of squares for yield loss, root weight, marketable roots, and dry matter content.

| Source of Variation | df | Yield Loss | | Root Weight (t/ha) | | Marketable Roots (t/ha) | | Dry Matter Content | |
|---------------------|-----|------------|--------|--------------------|--------|-------------------------|--------|--------------------|--------|
| | | SS | SS (%) | SS | SS (%) | SS | SS (%) | SS | SS (%) |
| Replicate | 2 | 50.9 | 0.1 | 8.7 | 0.1 | 1.2 | 0 | 0.6 | 0.1 |
| Variety | 4 | 21809 | 53.8 | 631.8 | 8.1 | 1003.1 | 19.6 | 51.8 | 5.2 |
| Replicate*Variety | 8 | 71.3 | 0.2 | 27.3 | 0.4 | 10.3 | 0.2 | 8.9 | 0.9 |
| Time (MAP) | 6 | 6154.4 | 15.2 | 5667.8 | 73.5 | 2435.1 | 47.5 | 812 | 80.9 |
| Variety*Time (MAP) | 24 | 11999 | 29.7 | 1161.8 | 15.1 | 1529.1 | 29 | 64.8 | 6.5 |
| Residual | 60 | 389.3 | 1 | 215.2 | 2.8 | 146.8 | 2.9 | 66.2 | 6.6 |
| Total | 104 | 40474 | - | 7712.6 | - | 5125.6 | - | 1004.3 | - |

Discussion

Cassava production in eastern and southern Africa is severely constrained by two major viral diseases: CMD and CBSD. Deployment of varieties resistant to both diseases is urgent and is the only sustainable way to control the diseases. Cassava is an important food security crop in Africa due to its ability to remain in the ground without deterioration for more than two years after reaching physiological maturity [28]. Farmers keep cassava in the ground typically for 12 to 18 months and practice piece meal harvesting for home consumption when all other crops not available [30,31]. However, the contribution of cassava to food security has been under severe threat by CBSD because it causes rotting of affected roots in susceptible varieties. To make matters worse, the damage by CBSD will not be apparent until the crop is harvested, and roots processed for cooking. This can be a sudden loss of the only source of food for millions of households relying solely on cassava during extreme times such as droughts. Delayed harvesting increases CBSD severity and the number of affected roots, thus farmers can no longer depend on cassava for food. To minimize CBSD damage, farmers have adopted early harvesting before the full physiological maturity of cassava plants. Although this may reduce CBSD damage, however, it can significantly reduce yields due to the low accumulation of starch in root tissues. Understanding the effect of time of harvesting and the levels of resistance of cassava varieties to both CMD and CBSD is therefore important for safeguarding the food security of millions of poor farmers. In this study, we investigated the interaction between times of harvest with resistance levels of the cassava varieties for identifying optimum cassava harvest times. The genetic make-up of the cassava varieties had the highest SS, therefore contributing significantly to the variations observed in disease traits including incidences and severity of foliar and root symptoms for both diseases. This is good news because the findings indicated that the traits are heritable and thus can be selected in breeding programmes. The foliar disease incidences and severities increased till 15 MAP, during active plant growth, and then declined till 24 MAP. This confirms that CMD symptoms decrease with increasing plant age as the older leaves are less susceptible than new growth [41]. Similarly, CBSD foliar symptoms mask in older plants and are

difficult to recognize as the lower leaves with prominent symptoms senesce and fall off [42].

On the contrary, root necrosis severity and yield losses increased with delayed harvesting as expected. Chipeta et al. [43] reported similar findings where yield loss due to CBSD was significantly associated with increased root severity at different harvest times and yield loss increased from 10.9% to 43.1% between 6 and 12 MAP. Var. Mreteta was the most affected with the maximum foliar incidences of >90.0% for both CMD and CBSD. It also had the highest foliar and root necrosis severities ranging from 3.5 to 4.9, confirming that Mreteta is susceptible to both diseases [44]. Albert showed low and high foliar incidences and severity for CMD and CBSD, respectively, which confirms its classification as CMD-resistant but CBSD-susceptible [45-47]. Although susceptible to CMD, Kiroba has been previously reported to be tolerant to CBSD since it expresses CBSD foliar symptoms with delayed or no root symptoms [48-50]. Kizimbani showed minimal CMD and CBSD foliar incidences (<6.0%) and severities (<1.1) but with moderate root necrosis severity (<2.3). Namikonga had the lowest CBSD foliar incidence (<8.2%), severity (<1.1) together with low root necrosis severity (<1.6).

However, it had moderate CMD foliar severity and incidences of up to 51.7%, indicating its susceptibility to CMD. Namikonga has perpetually exhibited no or low CBSD symptoms severity for many years and has been used as one of the best CBSD progenitors in breeding programmes [45,47,51-53]. High root necrosis severity resulted in high yield losses at different time points [54]. The average yield loss was 8.3% at 6 MAP, which dropped to 4.4% at 9 MAP, then began rising again up to a maximum of 27.8% at the end of the experiment. Development of the fibrous roots of cassava into starchy tubers occurs between 2 and 9 MAP depending on the varieties [54]. Thereafter, tuberization stops and root bulking begins where the tubers increase in size and weight. At 6 MAP it is too early for harvesting most cassava varieties and thus the roots were fewer and smaller in size. CBSD infection at this stage can result in significant loss of the root in susceptible varieties and thus the losses can be proportionately higher. The yield losses decreased at 9 MAP mainly because this was the active bulking period for cassava

and thus the tubers can outgrow the damage caused by the disease. Farmers actively remove the minimally damaged portions of such roots and use the remaining healthy part for consumption which is contributing to the lower losses observed at 9 MAP. Moreover, during this period of active growth, several tubers escape disease infection and develop into completely healthy tubers, further contributing to observed lower losses. Time of harvest and disease resistance affected yield losses due to CBSD in different varieties [55]. The susceptible var. Mreteta developed the most severe root necrosis throughout the growing season and had the highest yield losses with a maximum of 80.0% at 21 MAP. On the contrary, the resistant var. Namikonga was least affected with correspondingly low losses not exceeding 9.0%. Tolerant var. Kiroba and Kizimbani developed moderate root necrosis therefore maintaining low losses below 12.0% between 6 and 21 MAP. The losses, however, increased to approximately 23.0% at 24 MAP in both varieties. Comparable to the tolerant varieties, the CBSD-susceptible var. Albert maintained yield losses below 30.0% from 6 to 21 MAP but 50.0% of its yield was lost during harvesting at 24 MAP. By 24 MAP, root bulking has stopped, and rapid virus accumulation may occur in the roots causing losses in tolerant and susceptible varieties. Root necrosis severity and yield loss were fluctuating in Kiroba, Kizimbani and Namikonga indicating the recovery of resistant and tolerant varieties to virus infection or localised infection in any given plant tissue [45].

Time of harvest highly influenced root weight as it increased throughout the growing season. The maximum root weights for most of the varieties were recorded at 24 MAP and they included Kizimbani (42.3t/ha), Mreteta (31.1 t/ha), Kiroba (28.0t/ha), Albert (23.7t/ha) and Namikonga (21.5t/ha). Similarly, the quantity of marketable roots increased with delayed harvesting apart from the times when the varieties had severe root necrosis and high yield losses. High root weights coupled with low yield losses resulted in high quantities of marketable roots [54]. The highest quantity of marketable roots was recorded in Kizimbani and Kiroba which are high yielding CBSD-tolerant varieties. Although Namikonga had the least losses, its marketable root quantity was significantly lower than that of Kizimbani and Kiroba since it is a late bulking and low yielding variety [56]. Albert was severely affected by CBSD; therefore, it had low quantities of marketable roots. Mreteta had the highest root weights but had the least marketable roots due to high susceptibility to CBSD. Although Mreteta was severely affected by both CBSD and CMD it still maintained a higher root weight not significantly different from Kizimbani. In the absence of diseases, Mreteta has the potential of producing higher yield. These findings emphasized on the importance of deploying varieties that are both disease resistant and high yielding to increase the quantity of marketable roots.

Dry matter content varied depending on the time of harvest. High mean dry matter content was recorded during low rainfall including at 9 MAP (24.9%), 15 MAP (28.7%), 18 MAP (25.1%) and 24 MAP (25.8%). On the contrary, low mean dry matter content was recorded at 12 MAP (20.0%) and 21 MAP (21.2%), which are periods

characterised by high rainfall. During the rainy season, cassava roots absorb more water which results in proportionally low dry matter content (Masinde et al., 2017). Additionally, varieties with the least CBSD root symptoms had the highest dry matter content (eg. Namikonga, Kiroba and Kizimbani) and vice versa (eg. Albert and Mreteta). This indicates that the presence of CBSD symptoms on either leaves or roots affects key agronomic traits such as dry matter content leading to loss in farmer desirable traits [54]. A combination of timely harvesting and deployment of resistant/tolerant varieties can reduce cassava losses due to CMD and CBSD. The recommended time of harvest for officially released varieties is 12 MAP although farmers prefer long 'in-ground storage' of cassava roots especially in drought prone areas. This study showed that beyond 12 MAP, CBSD resistant var. Namikonga could be harvested till 24 MAP because it had the least CBSD root losses throughout the growing season [57-60]. Tolerant vars. Kizimbani and Kiroba could stay in the field up to 21 MAP without significant losses while susceptible vars. Albert and Mreteta would be best harvested at or before 15 MAP. Although we do not recommend growing susceptible varieties, this study has also demonstrated that satisfactory yields can still be obtained from all varieties when using disease-free cassava as planting material and harvested no later than 15 MAP. The recommended harvesting time points maximize both root weight and marketable roots for different varieties categorised as resistant, tolerant, and susceptible. Therefore, each variety can be harvested at its own appropriate time depending on its resilience to CBSD.

Conclusion

The findings in this study have shown that CBSD -resistant, -tolerant, and -susceptible varieties can be harvested at different times to minimise CBSD root necrosis damage and yield losses. When disease-free planting materials are used for cultivation, the resistant, tolerant and susceptible cassava varieties can be left in the ground for up to 24, 21 and 15 months, respectively, without incurring significant losses to cassava yields. These results help seed specialists, agricultural extension officers to provide specific recommendations to farmers on each cassava variety grown, and thus maximising the food security value of cassava in the worst affected regions of eastern and southern Africa.

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