Journal of Agricultural, Food Science & Biotechnology

JAFSB, 3(1), 48-59, 2025
https://doi.org/10.58985/jafsb.2025.v03i01.65
ISSN (Print): 2959-3417

*Research Article*

# Evaluation of cassava genotypes (*Manihot esculenta* Crantz) for drought tolerance and susceptibility under water deficit conditions

**Charles Orek***

Department of Agriculture, Murang'a University of Technology, P.O Box 75-10200, Murang'a, Kenya.

*Article Information*
*Received:* *11 November 2024*
*Revised:* *10 December 2024*
*Accepted:* *11 December 2024*
*Published:* *24 December 2024*

*Academic Editor*
Prof. Dr. Gian Carlo Tenore

*Corresponding Author*
Charles Orek
E-mail:
corek.publish@gmail.com
Tel: +254 795 193 570

*Keywords*
Cassava, drought stress, drought-tolerance, morphology, breeding.

## Abstract

Drought stress detriments crop yields and exacerbates food insecurity. Cassava, an inherently drought tolerant crop, is a sustainable solution. This study evaluated cassava genotypes' varied responses to drought enabling selection of superior candidates with improved performance. Field-assessed drought tolerant (DT) and drought susceptible (DS) genotypes varied in leaf wilting, abscission, staygreen, root development and bulking. Under greenhouse experiments, well-watered (WW) plants showed significantly ($P \leq 0.001$) higher vegetative growth and physiological response than plants exposed to water deficit (WD). Relative to WW treatment, WD reduced total leaves formed by ~20%, leaf retention by ~67%, plant height by ~26%, shoot fresh weight by ~62%, shoot dry weight by ~41% and shoot water content by ~49%. These generally implied negative effects of water deficit on cassava growth and development. Amongst genotypes, DT candidates (98/0002, 95/0306, M98/0068, I92/0067 & 94/0039) exhibited the least decline for most of these traits compared to DS counterparts (92/0427, TME-419 & I96/1439) under WD treatments. Physiologically, significantly ($P \leq 0.001$) higher leaf stomatal conductance (Gs) was measured from WW plants than WD-plants. Genotypically, a decrease in higher, moderate and lower Gs was recorded between the DT and DS genotypes. Cessation of leaf Gs after 10 days of WD and increased Gs rates after a day of re-watering respectively, mimicked drought-induced stomatal closure and stomatal re-opening. These results imply the potential use of either parameter(s) for rapid screening for drought stress tolerance in cassava genotypes and thus benefit breeding programs for drought-tolerant cassava. Selected morpho-physiologically superior genotypes such as 98/0002, 95/0306, M98/0068, I92/0067 and 94/0039 could be cultivated for better cassava productivity under drought stress.

## 1. Introduction

Drought stress has become an important factor in crop productivity and ultimately food security and nutrition due to climate change [1]. Drought stress causes low crop yields worldwide [2, 3] by severely affecting plant morphological, physiological, biochemical and molecular attributes that adversely impact their photosynthetic capacity [4]. Since crop growth and yields are negatively affected by sub-optimal water supply [1], development of drought tolerant crop varieties has become an important strategy to meet global food demands with less water [5], thus improving food security, nutrition and income levels, especially for people living in adverse or marginal environments [6]. Indeed, breeding stress tolerant staple crop varieties with higher yield under drought is a sustainable mitigation measure [7] that can extend agriculture to low rainfall areas [8]. Among such crops include cassava, an important food security crop for millions of people in sub-Saharan Africa [9]. Cassava is a 'miracle of the tropics' forming a critical component of the approaches to alleviate poverty, hunger, and malnutrition and increase livelihood security [10]. Despite this significance, cassava production is affected by both biotic and abiotic stresses [11] such as weeds, arthropod pests and diseases [12, 13], extreme temperatures, salinity and drought stress [14, 7, 10]. However, the crop has a broad agroecological adaptability, is considered inherently drought tolerant and can produce adequately well under drought stress conditions [15, 16].

Cassava plants respond to drought stress through multiple mechanisms at morphological, physiological and molecular levels [17, 7]. The crop's primary response to water stress is stomatal closure [18]. It rapidly and partially closes its stomata without changes in leaf water potential thus buffering the leaf against severe dehydration [19, 20]. Further, expansion of existing leaves, formation of new leaves and leaf area development are restricted or halted under drought [21, 22]. Although a substantial fraction of the leaves abscises reducing its canopy [23, 24], some staygreen genotypes maintains longer leaf longevity or leaf retention with a given leaf area index, permitting extended photosynthesis for better yield performance under drought [23, 21, 7]. The plant also halts formation of biomass, plant heights and stem diameter or girth under drought [25-28]. Below ground, production and growth of cassava's fibrous root systems of adventitious and lateral roots are suppressed by deficient soil moisture [29, 30]. However, the sparse fine roots are capable of penetrating into deeper and wetter soil enhancing the crop's access to deep soil water [20, 21]. Cassava plants that bulk early, of medium or short-stems, with extensive fine roots or deep rooting capacities, should be generated for semi-arid conditions [31]. Okogbenin et al. [32] recommended breeding for growth vigor under early drought stress.

Cassava's morphological responses to drought stress as reviewed above, depend on the duration and severity of water deficit, stage of development and the genotype or cultivar [33-35]. Some genotypes exhibit better adaptability through morphology that allows them to grow and yield more under drought stress compared to drought-susceptible counterparts. For instance, drought tolerant cassava genotypes that expressed higher morphology under drought stress [28] could be considered for improved productivity. Therefore, the present study compared variations in morpho-physiological descriptors for several droughts tolerant and drought susceptible cassava genotypes subjected to water deficit treatment under controlled or greenhouse conditions. Such rapid or short-term experiments that generate morpho-physiological differences between cassava genotypes and associated descriptors could aid quicker selection of drought tolerant candidates for improved productivity especially with the current global climatic changes.

## 2. Materials and methods

### 2.1 Germplasm establishment

Cassava germplasms used in this study were among several candidates that were previously evaluated for drought stress tolerance under field conditions in Kenya by Orek [6] and Orek et al. [7]. Morphological descriptors used to analyze differences between the genotypes under field conditions were measured as described by Fukuda et al. [36]. Out of 37 cassava genotypes [7], five tolerant (M98/0068, 94/0039, 95/0306, 98/0002 & I92/0067) and three susceptible (92/0427, TME-419 & I96/1439) candidates were selected for further morpho-physiological assessment under controlled and greenhouse conditions. To minimize growth variations often associated with direct propagation of different parts of the parental stem [37, 38], *in vitro* plantlets were generated from stakes or cuttings of these genotypes using cassava basic media as described by Bull et al. [39]. The plantlets were then transferred to 4-litre potted soil for hardening and establishment under controlled conditions, i.e. 26°C/17°C (day/night) temperatures; 60/50% (day/night) relative humidity, 14 hours of light at 35 K-lux intensity and average air ventilation rate of 84.7% [7]. The soil texture was 40% sand, 35% clay and 25% silt (RICOTER Erdaufbereitung AG, Aarberg, Switzerland). These conditions had been tested and optimized for uniform cassava plant growth and development under greenhouse

https://doi.org/10.58985/jafsb.2025.v03i01.65

conditions [7].

*2.2 Experimental design*

The greenhouse experiment was conducted at the ETH-Zurich research station located in Lindau-Eschikon, 20 km North-East of Zurich, Switzerland on latitude 47°26'N, longitude, 8°40'E and altitude of 540 m above sea level [40]. Four biological replicates of the 60-day old plants per genotype and treatments were arranged in a complete randomized design (CRD), with the induction of the three treatments modified from a procedure described by Vandegeer et al. [38] and Alves and Setter [41]. The treatments were water deficit (WD) followed by re-watering (WDR) and well-watered (WW) or positive control. Withholding total irrigation was used to attain WD, while WW plants were maintained at ~ 100% pot soil moisture content or pot capacity (PC) as described by Alves and Setter [41]. At 70 days after planting (DAP), WDR plants were first subjected to 10 days of WD then re-irrigated and maintained at ~ 100% PC for five days, after which the WDR treatment was terminated. For WD plants, the WD treatments were stopped once contrasting leaf retention or abscission and wilting response amongst genotypes was observed under the WD treatment. This was approximately after 3 weeks of WD or 80 - 85 DAP. Control plants were continuously maintained under WW treatment.

*2.3 Data collection and analysis*

Genotypic variations for WD tolerance under controlled conditions were assessed through measurement and analysis of morpho-physiological parameters such as total number of leaves (TL), leaf retention (LR), plant heights (PH), shoot fresh weight (SFW), shoot dry weight (SDW), shoot water contents (SWC) and stomatal conductance (G*s*). Using SC-1 Leaf Porometer (Decagon Devices Inc., Pullman, WA), G*s* was quantified from three young fully expanded leaves previously tagged from four randomly selected plants per treatment. At the terminal stage of experiments, total leaf scars were tallied to determine LR, PH was measured from soil level to the peak of the plant canopy using a meter rule [15, 36], whole plant shoots were weighed as SFW and SDW were determined after oven drying the shoots at 85°C for 48 hours [42, 43]. The weight differences between SFW and SDW were used to compute SWC, which was then expressed in grams of water per gram dry weight of plant (g/gDW plant$^{-1}$) [44]. Variations amongst genotypes and between treatments for all these traits were tested by subjecting all collected data to analysis of variances (ANOVA) using SigmaPlot analysis software version 12.2, San Jose, CA. Differences between groups of means were separated by Fischer's LSD (α=0.05) procedure.

## 3. Results and discussion

*3.1 Field-based drought stress response*

Both drought tolerant and drought susceptible cassava genotypes used in this study, were selected from multi-locational and multi-seasonal drought stress experiments under field conditions in Kenya. The key field data that was used to classify these genotypes into either drought tolerant or drought susceptible candidates included field-based leaf retention or staygreen trait, number of storage roots and yield/weight of fresh storage roots. These were analyzed by Orek [6] and Orek et al. [7]. The figures (Figs. 1 and 2) show the characteristic response of these cassava genotypes to non-irrigation or drought stress treatment and irrigated treatment (positive control) under field conditions.

Like any other plant, cassava respond to moisture scarcity through leaf wilting and abscission or shedding off leaves. In this study, leaf drying, wilting and abscission were observed during field-based drought stress trials (Fig. 1a and Fig. 1b).

**Figure 1a.** Rapid leaf fall

**Figure 1b.** Gradual wilting

Similarly, Yan et al. [45] reported that drought stress triggers drying and wilting of cassava leaves with a consequent decrease in relative water content of the leaf. Although, cassava escapes drought stress through leaf abscission [46], excessive leaf fall reduces the photosynthetic capacity of the crop leading to reduced yield. Due to this, cassava varieties with short leaf life spans that result in low root yield under drought stress are classified as drought susceptible, while genotypes with longer leaf longevity that sustain higher storage root yield are considered drought tolerant. This characteristic has been respectively categorized as non-staygreen (Fig. 2a and Fig. 2b) conferring drought susceptibility and staygreen (Fig. 1c and Fig. 2c) that confers tolerance to drought stress.


**Figure 2a.** Non-staygreen

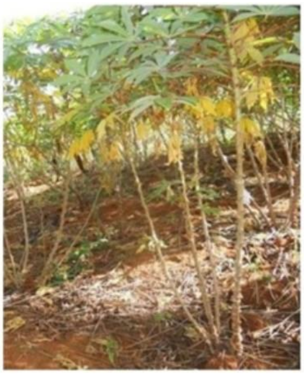
**Figure 2b**. Leaf senescence

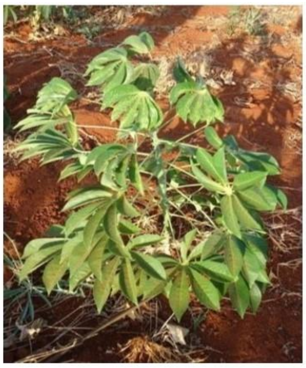
**Figure 1c.** Delayed wilting


**Figure 2c**. Staygreen

Staygreen cassava retain their leaves longer during drought conditions, maintaining photosynthesis and reducing yield loss [47]. Such genotypes can produce more biomass and have higher root dry matter compared to their non-staygreen counterparts [7, 23, 47]. Indeed, increased leaf longevity has been associated with increased cassava production [48].

Belowground carbon fixation by cassava is allocated for the growth and development of its fibrous roots for nutrient and water uptake, which later thickens than a given diameter and develops into storage roots with high starch content [49]. Despite cassava's inherent tolerance to drought stress, it's storage root yield is easily threatened by water stress [50]. This was clearly shown in this study by the morphological differences between fibrous and storage roots under the two different treatments. For instance, relatively longer fibrous roots with early bulking response and more storage root numbers were recorded under irrigation (Fig. 3a and Fig. 4a), compared to non-irrigated treatments or drought stress, which produced few and shorter fibrous roots and lesser storage root numbers of smaller sizes (Fig. 3b and Fig. 4b).


**Figure 3a.** Root development under irrigated/control treatment.


**Figure 4a.** Storage root yield under irrigated/control treatment.


**Figure 3b.** Root development under non-irrigated/drought stress treatment.


**Figure 4b.** Storage root yield under non-irrigated/drought stress treatment (drought susceptible).

Similarly, Duque and Setter [19] observed reduced growth of fibrous roots in cassava plants under water stress. Cassava's fibrous roots can grow as long as 2 meters below ground, allowing access to deep water layers, enabling the crop to escape or evade water stress [13, 51]. A large genotypic difference for fibrous root weight and root length observed between 2 – 5 weeks after planting under water deficit, enabled the adoption of early root growth as a selection criterion for adaptation to drought stress [15]. Underwater scarcity, storage root growth, development and bulking suffer amongst susceptible genotypes (Fig. 4b) while superior or tolerant genotypes (Fig. 4c) sustain storage root growth and bulking.

**Figure 4c.** Storage root yield under non-irrigated treatment (drought tolerant).

*3.2 Morphological response to water deficit under greenhouse*

All morphological traits: total leaves (TL), leaf retention (LR), plant height (PH), shoot fresh weight (SFW), shoot dry weight (SDW) and shoot water contents (SWC) significantly differed (P≤0.001) amongst genotypes and between treatments *(Supplementary Table S1).* The genotype*treatment (G*T) interactions for all the parameters were insignificant (P>0.05) except LR which exhibited significant (P≤0.011) differences *(Supplementary. Table S1).* Higher performance for all traits was observed in WW than in WD treatment (Table 1). Relative to WW, WD treatment reduced TL formed by 20.43% and LR by 67.31%, shortened PH by 25.93%, lessened SFW and SDW by 62.15 and 41.26% respectively and lowered SWC by 48.72% (Table 1). These results indicated the negative effects of moisture deficiency on cassava morphology under greenhouse conditions.

Under WD, TME-419 maintained the least TL, 98/0002 & 94/0039 expressed higher LR and 92/0427 showed the least LR compared to other genotypes and higher and shorter PH were respectively measured from M98/0068 and I92/0067 (Table 2). Additionally, relatively higher SFW was weighed from all tolerant genotypes compared to susceptible ones, three tolerant (95/0306, M98/0068 & 94/0039) genotypes and one susceptible 92/0427 expressed relatively higher SDW compared to lower SDW weighed from tolerant I92/0067 and 98/0002 and susceptible I96/1439 and TME-419 and the SWC of tolerant 98/0002 was significantly higher than all other genotypes (Table 2).

Under control or WW treatment, significantly higher TL was counted from M98/0068 and I96/1439 and lower TL was noted in 98/0002 and TME-419 (Table 3). Percent LR did not significantly differ between most genotypes and M98/0068 and I92/0067 were respectively taller and shorter than other genotypes under this treatment (Table 3). Genotypes 95/0306, M98/0068 and 92/0427 accumulated significantly higher SFW than other genotypes and lower SFW was weighed from I92/0067, 96/1439 and TME-419. Relatively higher SDW was recorded in 92/0427 95/0306 and M98/0068 and the least SDW from I92/0067. Genotypes 98/0002, I92/0067, M98/0068 and I96/1439 exhibited significantly higher SWC than 92/0427 and TME-419 (Table 3).

Based on percent reduction relative to WW treatment (Table 4), TL was reduced by more than 20% in two tolerant (M98/0068 & 95/0306) and three susceptible (I96/1439, 92/0427 & TME-419) genotypes, while the least TL decrease (7.58%) was registered in tolerant 98/0002. Apart from 98/0002 and 94/0039, more than 60% LR decline was observed in all genotypes, with the highest LR decline observed in susceptible 92/0427 (88%) and tolerant M98/0068 (82%) (Table 4). The least (9.63%) PH decline was exhibited by TME-419; the maximum PH decline (>30%) was recorded in 98/0002 & I92/0067. The SFW of tolerant genotypes 94/0039, 95/0306 & 98/0002 declined by approximately 55%, while 64 – 67% SFW reduction was computed in all susceptible candidates and two tolerant (M98/0068 & I92/0067) genotypes. The least (34 - 38%) SDW decline was observed among tolerant 95/0306, 94/0039 & I92/0067 and a higher SDW decline (41 – 49%) was recorded in all susceptible candidates and 2 tolerant (98/0002 & M98/0068) genotypes (Table 4). Two susceptible genotypes 92/0427 and I96/1439 and one tolerant candidate (I92/0067) exhibited more than 55% SWC decrease compared to the least SWC reduction (33%) observed in tolerant 98/ 0002 (Table 4). The other genotypes showed 41 – 47% SWC loss (Table 4). Water stress results in a substantial decrease in the growth of all plant parts [19]. Indeed, variations amongst genotypes and between treatments for morphological traits, as well as reductions in shoot

**Table 1.** Overall means of traits (plant$^{-1}$) under WW and WD treatments

| Trait | WW | WD | Diff. of Means | LSD (0.05) | Diff. (%) |
|---|---|---|---|---|---|
| TL | 18.813 | 14.969 | 3.844* | 0.725 | 20.43 |
| LR | 75.585 | 24.706 | 50.879* | 4.342 | 67.31 |
| PH | 44.156 | 32.703 | 11.453* | 1.618 | 25.93 |
| SFW | 28.228 | 10.685 | 17.543* | 1.728 | 62.15 |
| SDW | 7.302 | 4.288 | 3.013* | 0.490 | 41.26 |
| SWC | 2.939 | 1.516 | 1.432* | 0.188 | 48.72 |

*= Variations btw treatments significant at P≤0.001; % Diff. = differences between WD treatment means relative to WW

**Table 2.** Genotypic variations for traits under WD treatment

| Traits<br>Genotypes | TL (# plant$^{-1}$) | LR (% plant$^{-1}$) | PH (cm plant$^{-1}$) | SFW (g plant$^{-1}$) | SDW (g plant$^{-1}$) | SWC (g/gDW plant$^{-1}$) |
|---|---|---|---|---|---|---|
| DT_98/0002 | $15.25^{ac}$ | $45.74^{a}$ | $26.325^{g}$ | $12.185^{ad}$ | $3.728^{bcd}$ | $2.269^{a}$ |
| DT_I92/0067 | $15.5^{ac}$ | $16.65^{bd}$ | $20.8^{c}$ | $7.117^{bef}$ | $3.025^{b}$ | $1.36^{b}$ |
| DT_M98/0068 | $16.25^{ac}$ | $12.19^{bd}$ | $46.375^{a}$ | $11.92^{ae}$ | $4.582^{ad}$ | $1.598^{b}$ |
| DT_94/0039 | $16.75^{a}$ | $23.99^{bc}$ | $35.125^{bd}$ | $8.303^{bcdef}$ | $3.523^{bd}$ | $1.368^{b}$ |
| DT_95/0306 | $15.5^{ac}$ | $35.49^{ac}$ | $36.125^{b}$ | $12.525^{ac}$ | $4.925^{ac}$ | $1.553^{b}$ |
| DS_I96/1439 | $14.25^{bc}$ | $22.914^{b}$ | $30.875^{cdef}$ | $14.025^{a}$ | $5.775^{a}$ | $1.427^{b}$ |
| DS_92/0427 | $14.25^{bc}$ | $8.71^{d}$ | $34.25^{be}$ | $10.9^{af}$ | $5.25^{a}$ | $1.08^{b}$ |
| DS_TME - 419 | $12^{d}$ | $31.97^{bc}$ | $31.75^{bf}$ | $8.5^{bcdef}$ | $3.5^{bd}$ | $1.472^{b}$ |
| LSD (0.05) | 2.05 | 12.282 | 4.576 | 4.888 | 1.385 | 0.532 |

Means denoted by the same letter (s) within column are not significantly different (P>0.05); Means denoted by different letter (s) within column are significantly different (P≤0.05). DT = drought tolerant genotype; DS = drought susceptible genotype.

**Table 3.** Genotypic variations for traits under WW treatment

| Traits<br>Genotypes | TL (# plant$^{-1}$) | LR (% plant$^{-1}$) | PH (cm plant$^{-1}$) | SFW (g plant$^{-1}$) | SDW (g plant$^{-1}$) | SWC (g/gDW plant$^{-1}$) |
|---|---|---|---|---|---|---|
| DT_98/0002 | $16.50^{z}$ | $78.79^{yz}$ | $42.325^{yzp}$ | $27.715^{xz}$ | $6.35^{xt}$ | $3.400^{w}$ |
| DT_I92/0067 | $19.25^{xy}$ | $74.12^{yz}$ | $32.75^{t}$ | $21.038^{y}$ | $4.93^{p}$ | $3.288^{w}$ |
| DT_M98/0068 | $21.75^{w}$ | $69.05^{xy}$ | $57.175^{w}$ | $33.148^{w}$ | $8.238^{wz}$ | $3.034^{wy}$ |
| DT_94/0039 | $19.00^{xy}$ | $76.22^{yz}$ | $46.625^{xz}$ | $28.075^{xz}$ | $7.70^{xyz}$ | $2.633^{xy}$ |
| DT_95/0306 | $18.75^{x}$ | $70.54^{xy}$ | $37.875^{y}$ | $32.35^{wx}$ | $8.85^{wy}$ | $2.639^{xy}$ |
| DS_I96/1439 | $21.00^{wy}$ | $84.50^{wz}$ | $49.00^{x}$ | $25.498^{yz}$ | $6.02^{pt}$ | $3.379^{w}$ |
| DS_92/0427 | $19.00^{xy}$ | $72.53^{yz}$ | $46.125^{xp}$ | $33.15^{w}$ | $9.35^{w}$ | $2.548^{xy}$ |
| DS_TME - 419 | $15.25^{z}$ | $78.92^{yz}$ | $41.375^{y}$ | $24.85^{yz}$ | $6.975^{xzt}$ | $2.592^{xy}$ |
| LSD (0.05) | 2.05 | 12.282 | 4.576 | 4.888 | 1.385 | 0.532 |

Means denoted by the same letter (s) within column are not significantly different (P>0.05); Means denoted by different letter (s) within column are significantly different (P≤0.05). DT = drought tolerant genotype; DS = drought susceptible genotype.

growth, plant height, number of leaves, leaf retention, fresh and dry weight of the shoots, reported in this study, have been reported under greenhouse water scarcity tests [24, 52-54]. Shan et al. [25] reported that under drought stress conditions, cassava plants showed a substantial decline in plant height, stem diameter, leaf number and leaf water content. Previously, screenhouse-based moisture stress treatment reduced cassava plant heights by 21.2%, stem girth by 21.7%, number of roots and root weight by more than 90% [53], total leaves by 45% and lowered tuber yield by 83% compared to well-watered plants [38].

Vigorous cassava clones are likely to shed more leaves or exhibit severe leaf abscission under stress than less vigorous types [15, 19]. This concept can explain the

**Table 4.** Percent reduction of traits amongst genotypes

| Traits Genotypes | TL | LR | PH | SFW | SDW | SWC |
|---|---|---|---|---|---|---|
| DT_98/0002 | $7.58^{h}$ | $41.95^{h}$ | $37.80^{a}$ | $56.03^{g}$ | $41.29^{e}$ | $33.26^{h}$ |
| DT_I92/0067 | $19.48^{f}$ | $77.54^{c}$ | $36.49^{b}$ | $66.17^{c}$ | $38.64^{f}$ | $58.64^{b}$ |
| DT_M98/0068 | $25.29^{a}$ | $82.35^{b}$ | $18.90^{c}$ | $64.03^{e}$ | $44.38^{b}$ | $47.33^{d}$ |
| DT_94/0039 | $18.42^{g}$ | $53.44^{g}$ | $10.50^{g}$ | $55.39^{h}$ | $36.04^{g}$ | $41.02^{g}$ |
| DT_95/0306 | $24.00^{c}$ | $67.52^{e}$ | $18.48^{d}$ | $56.65^{f}$ | $34.75^{h}$ | $45.93^{e}$ |
| DS_I96/1439 | $20.23^{e}$ | $71.61^{d}$ | $13.88^{e}$ | $67.44^{a}$ | $41.48^{d}$ | $59.51^{a}$ |
| DS_92/0427 | $25.00^{b}$ | $87.99^{a}$ | $11.88^{f}$ | $67.12^{b}$ | $43.85^{c}$ | $57.61^{c}$ |
| DS_TME - 419 | $21.31^{d}$ | $59.49^{f}$ | $9.630^{h}$ | $65.79^{d}$ | $49.82^{a}$ | $43.21^{f}$ |

Percent reduction of traits was calculated relative to WW treatment; Letters (a –> h) used to rank genotypes in a descending order i.e. from highest (a) to least (h) reduced per trait. DT = drought tolerant genotype; DS = drought susceptible genotype.

higher LR decline in two drought tolerant (I92/0067 & M98/0068) compared to one susceptible genotype TME-419. The number of leaf scars has been strongly associated with the number of leaves formed [15] and the reduction in total leaves is primarily due to leaf abscission or senescence [52], either due to aging or water stress. No report has described correlations between plant height and drought tolerance (high yield) in cassava [52]. The significant effect of soil moisture regime, such as the reduction of cassava shoot development determined through plant height, shoot fresh weight and shoot dry weight have also been observed by Agili and Pardales [55].

In the present study, most of the drought tolerant genotypes expressed relatively lower percent reduction of SFW, SDW and SWC compared to susceptible candidates. This probably is an indication of the tolerant genotype's capacity to reduce transpirational water loss or leaf conductance, an adaptation that conserves water and shields the plant from severe dehydration. This is a drought avoidance mechanism. Susceptible genotypes are most likely unable to effectively control their transpiration rates under WD thereby rapidly collapsing under severe water shortage. In conclusion, moisture stress cause considerable reduction in both cassava's morphology or vegetative growth that can inadvertently reduce yield. A sustainable solution could involve setting up irrigation systems in drought-prone cassava growing regions or development of drought tolerant cassava varieties.

### *3.3 Effect of water deficit on stomatal conductance*

Measurement of stomatal control of water loss can be valuable in identifying desirable cassava genotypes or in pre-selecting sources of germplasm conferring adaptation to prolonged dry periods [7, 15, 20]. In this study, ANOVA revealed significant (P≤0.001) differences for Gs between treatments, amongst genotypes and genotype*treatment interactions across the 15 days of the experiment *(Supplementary Table S2 and S2.1).* WD caused an overall reduction in Gs as reflected by higher Gs measured from WW compared to WD and WDR treatments (Fig. 5a).

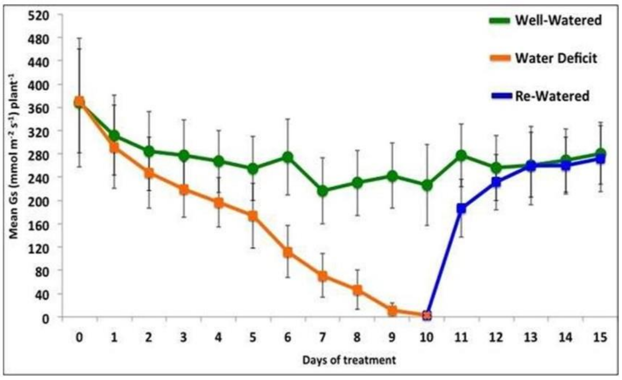

**Figure 5a.** Mean Gs under treatments (WW, WD and WDR). Mean ± SD; N = 12 i.e. 4 plants @ 3 leaves per plant; SD = standard deviation.

Previous studies equally showed higher and lower Gs respectively, measured in cassava plants under WW and WD treatments [24, 52]. The rapid leaf Gs decline between 0 to 10 days of WD treatment (Fig. 5a) was halted once water was re-supplied (~100% PC) from day 11 (Fig. 5b). This produced non-significant leaf Gs differences between WDR and WW plants between 13 – 15 days (Fig. 5a). *Supplementary Tables S3 and S3.1* show the actual mean treatment Gs differences based on LSD (α=0.05). A drastic decrease in Gs of cassava

https://doi.org/10.58985/jafsb.2025.v03i01.65

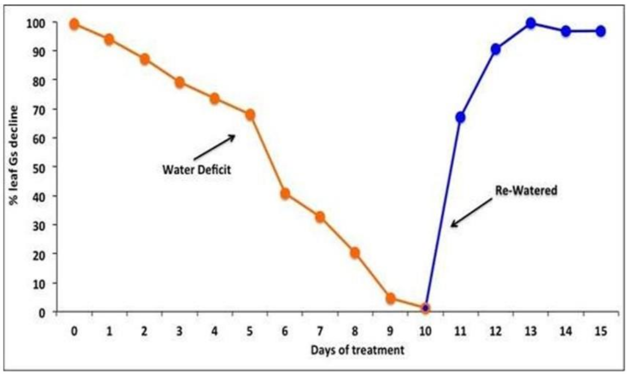

**Figure 5b.** Overall percent Gs decrease and regained relative to WW treatment. Gs decrease = WD relative to WW; Gs regain = WDR relative to WW treatments.

during stress [21] is often punctuated by rapid recovery once water or rain re-occurs [56, 57]. Once freed from water stress, cassava rapidly recovers by forming new leaves with higher leaf conductance and photosynthetic rates compared to non-stressed plants, thereby ameliorating loss in root yield [6, 31, 58].

Genotypic variations for Gs were also observed in this study. Relatively higher Gs were measured in three tolerant (95/0306, 94/0039 & M98/0068) and two susceptible (92/0427 & TME-419) genotypes, compared to lower Gs observed in two other tolerant (98/0002 & I92/0067) and one susceptible I96/1439 candidate *(Supplementary Table S4).* Upon WDR, genotypes M98/0068, 95/0306 and I96/1439 sustained faster recovery and maintained relatively higher Gs compared to other genotypes for the five days *(Supplementary Table S4.1).* Genotypes 98/0002, I92/0067 and 94/0039 showed the least Gs recovery (least stomatal re-opening) compared to genotypes 95/0305, I96/1439 and M98/0068 with higher Gs recovery *(Supplementary Table S4.1).*

However, the percent (%) Gs decline relative to WW treatment also showed genotypic differences for Gs. For example, susceptible I96/1439 exhibited rapid Gs decline under WD compared to the two tolerant genotypes 94/0039 with gradual Gs decline (Fig. 6). Upon rewatering, tolerant M98/0068 and susceptible 92/0427 respectively, regained higher and lower Gs (Fig. 6). Generally, under WW, tolerant 95/0306 showed higher Gs for most of the days compared to other genotypes.

The findings from this study on Gs differences corroborate earlier data which showed that drought-induced decreases in stomatal aperture or pore size that can limit leaf Gs [59], and that high humidity or well-watered treatment favorably sustains stomatal opening for high Gs in cassava [20]. Under drought stress, cassava plants showed substantial decline in Gs compared to well-watered plants [25]. Decreasing the irrigation dose to 30% lowered stomatal conductance by 41% [27].

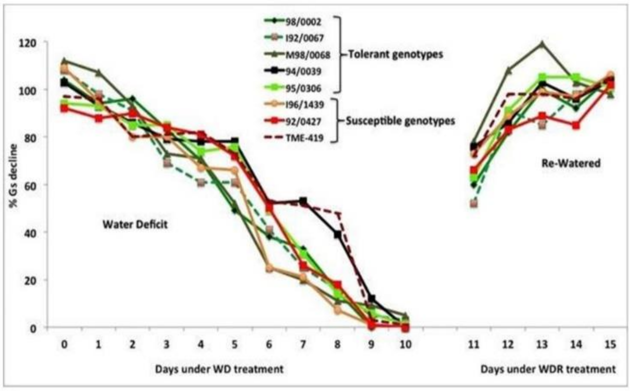

**Figure 6.** Genotypic percent Gs decline relative to WW treatment.

The genotypic differences for Gs either under water deficit or re-watered treatments, enabled the selection of physiologically superior genotypes. For instance, susceptible (I96/1439 & 92/0427) candidates showed rapid Gs decline or lower Gs recovery compared to tolerant genotypes (94/0039 & M98/0068) with gradual Gs decline or higher Gs recovery. Similar genotypic variations for Gs under water deficit have been reported. For example, Turyagyenda et al. [54] reported more than two times lower Gs in an improved cassava variety, MH96/0686 compared to a local landrace, Nyalanda, under drought stress. de Souza et al. [60] also observed higher Gs in a cassava landrace compared to an improved cultivar under drought.

Orek [61] and Ngugi et al. [62] reported variations for Gs between two transgenic cassava lines (529-28 & 529-48), their wild type TMS 60444 and non-transgenic genotypes 98-0002, 98-2226, TME-3, 95-0306 and 91-02322 subjected to different water deficit levels. Recently, Santanoo et al. [63] observed high Gs variations in cassava genotypes RY9, RY72, KU50, CMR38-125-77, CMR35-91-63 and CM523-7 under early drought stress treatment. Reduction in Gs under drought is linked to the closing of stomata by cassava

*https://doi.org/10.58985/jafsb.2025.v03i01.65*

as a drought avoidance strategy. The rapid closure of cassava stomata and the decline in water loss lead to stable leaf water contents, thus protecting leaf tissues from desiccation [6, 56]. Leaf G*s* to water vapor has been evaluated as an indicator of the capacity of different cassava genotypes to prevent water loss under prolonged drought [60, 64]. Further, drought-driven stomatal closure with consequent decreases in $CO_2$ intake and net photosynthesis, reduces cassava growth [25], a typical response to drought stress conditions. In this study, it can be hypothesized that the gradual Gs reduction in drought tolerant genotypes compared to their susceptible counterparts with rapid Gs decline, indicated increased crop water use efficiency amongst tolerant candidates [60]. In summary, cassava's ability to rapidly decrease leaf stomatal conductance is a physiological adaptation to drought stress that enables the crop to avoid significant decline in leaf water potential, thus protecting its photosynthetic apparatus [60].

## 4. Conclusions

This study was designed to evaluate differences in morphological and physiological mechanisms or responses of drought tolerant and drought susceptible cassava genotypes under drought stress or water deficit conditions. Variations between the genotypes were exhibited through leaf wilting, abscission, staygreen, fibrous root growth and development, storage root bulking and stomatal conductance. Data collected from these descriptors enabled the selection of drought tolerant genotypes which exhibited better or superior performance compared to their susceptible counterparts. The selected drought tolerant candidates or genotypes including 98/0002, 95/0306, M98/0068, I92/0067 and 94/0039 could be promoted for adoption as climate smart technologies for improved productivity and adaptation under changing climatic conditions. These genotypes could potentially be used as parents to benefit breeding programs for introgression of drought-tolerant traits in susceptible but highly yielding cassava varieties.

## Supplementary material

*Supplementary Table S1 – S4.*

Supplementary material to this article can be found online at https://www.currentsci.com/images/articlesFile/supplementary.1735051870.pdf

## Authors' contributions

Conceptualization, methodology, data analysis; resources, writing original draft preparation, writing review and editing and submission to the journal for publication, O.C.

## Acknowledgements

The authors acknowledge the contributions of IITA and KALRO – Kiboko and Kibwezi in Kenya for supplying the germplasm.

## Funding

This research received no external funding.

## Availability of data and materials

All data will be made available on request according to the journal policy.

## Conflicts of interest

The author declares no conflict of interest

## References

1. Fahad, S.; Bajwa, A.A.; Nazir, U.; Anjum, S.A.; Farooq, A.; Zohaib, A; Sadia, S; Nasim, W. Crop production under drought and heat stress: Plant responses and management options. Front. Plant Sci. 2017, 8, 1147. https://doi.org/10.3389/fpls.2017.01147
2. Bodner, G.; Nakhforoosh, A.; Kaul, H.P. Management of crop water under drought: a review. Agron. Sustain. Dev. 2015, 35, 401 – 442. https://doi.org/10.1007/s13593-015-0283-4
3. Pereira, L.F.M.; Santos, H.L.; Zanetti, S.; Brito, I.A.D.; Tozin, L.R.D.; Rodrigues, T.M.; Silva, M.D.A. Morphology, biochemistry and yield of cassava as functions of growth stage and water regime. South Afr. J. Bot. 2022, 149, 222 – 239. https://doi.org/10.1016/j.sajb.2022.06.003
4. Seleiman, M.F.; Al-Suhaibani, N.; Ali, N.; Akmal, M.; Alotaibi, M. Drought stress impacts on plants and different approaches to alleviate its adverse effects. Plants. 2021, 10(2), 259. https://doi.org/10.3390/plants10020259
5. ISAAA. Biotechnology for the development of drought tolerant crops. Pocket K No. 32, 2008.
6. Orek, C.O. Morphological, physiological and molecular characterization of drought tolerance in cassava

(*Manihot esculenta* Crantz). PhD thesis, 2014. https://doi.org/10.3929/ethz-a-010114812

7. Orek, C.; Gruissem, W.; Ferguson, M.; Vanderschuren, H. Morpho-physiological and molecular evaluation of drought tolerance in cassava (*Manihot esculenta* Crantz). Field Crop Res. 2020, 255, 107861. https://doi.org/10.1016/j.fcr.2020.107861
8. Muiruri, S.K.; Ntui, V.O.; Tripathi, L.; Tripathi, J.N. Mechanisms and approaches towards enhanced drought tolerance in cassava (*Manihot esculenta* Crantz). Curr. Plant Biol. 2021, 28, 100227. https://doi.org/10.1016/j.cpb.2021.100227
9. Mbanjo, E.G.N.; Rabbi, I.Y.; Ferguson, M.E.; Kayondo, S.I.; Eng, N.W.; Tripathi, L.; Kulakow, P.; Egesi, C. Technological innovations for improving cassava production in Sub-Saharan Africa. Front. Genet. 2021, 11, 623736. https://doi.org/10.3389/fgene.2020.623736
10. More, S.J.; Bardhan, K.; Ravi, V. Morphophysiological responses and tolerance mechanisms in Cassava (*Manihot esculenta* Crantz) under drought stress. J. Soil Sci. Plant Nutr. 2023, 23, 71–91. https://doi.org/10.1007/s42729-023-01127-4
11. Devi, B.; Kumar, M.N.; Chutia, M.; Bhattacharyya, N. Abiotic and biotic stress challenges of Cassava in changing climate and strategies to overcome: A review. Sci. Hort. 2022, 305, 111432**.** https://doi.org/10.1016/j.scienta.2022.111432
12. Orek, C. A review of management of major arthropod pests affecting cassava production in Sub-Saharan Africa. Crop Protect. 2024, 175, 106465. https://doi.org/10.1016/j.cropro.2023.106465
13. Orek, C.; Kyallo, M.; Yao, N. Analysis of local cassava landraces and improved genotypes in response to infections by cassava mosaic begomoviruses under field conditions in Kenya. Trop. Plant Pathol. 2023, 48, 182–198. https://doi.org/10.1007/s40858-023-00558-9
14. Ikeogu, U.N.; Okereke, N.R.; Uchendu, K.; Okwuonu, I.C.; Onyeka, J.T.; Egesi, C.N. Genomic designing for abiotic stress-resistant Cassava. In: Kole, C. (eds) genomic designing for abiotic stress resistant technical crops. Springer, Cham, 2022. https://doi.org/10.1007/978-3-031-05706-9_1
15. Okogbenin, E.; Setter, T.L.; Ferguson, M.; Mutegi, R.; Ceballos, H.; Olasanmi, B.; Fregene, M. Phenotypic approaches to drought in cassava: review. Front. Physiol., 2013, 4(93), 1 – 15. https://doi.org/10.3389/fphys.2013.00093
16. Zhao, P.; Liu, P.; Shao, J.; Li, C.; Wang, B.; Guo, X.; Yan, B.; Xia, Y.; Peng, M. Analysis of different strategies adapted by two cassava cultivars in response to drought stress: ensuring survival or continuing growth. J. Experimen. Bot. 2014. https://doi.or/10.1093/jxb/eru507
17. Avivi, S.; Sanjaya, B.R.L.; Ogita, S.; Hartatik, S.; Soeparjono, S. Morphological, physiological and molecular responses of Indonesian cassava to drought stress. AJCS, 2020, 14(11), 1723-1727. https://doi.org/10.21475/ajcs.20.14.11.p1961
18. Pipatsitee, P.; Eiumnoh, A.; Praseartkul, P.; Taota, K.; Kongpugdee, S.; Sakulleerungroj, K.; Cha-um, S. Application of infrared thermography to assess cassava physiology under water deficit condition, Plant Prod. Sci. 2018, 21(4), 398-406. https://doi.org/10.1080/1343943X.2018.1530943
19. Duque, L.O.; Setter, T.L. Cassava response to water deficit in deep pots: root and shoot growth, ABA, and carbohydrate reserves in stems, leaves and storage roots. Trop. Plant Biol. 2013, 6, 199–209. https://doi.org/10.1007/s12042-013-9131-3
20. El-Sharkawy, M.A. Physiological characteristics of cassava tolerance to prolonged drought in the tropics: Implications for breeding cultivars adapted to seasonally dry and semiarid environments. Braz. J. Plant Physiol. 2007, 19(4), 257 – 286.
21. Setter, T.L.; Fregene, M.A. Recent advances in molecular breeding of cassava for improved drought stress tolerance. In: MA Jenks, PM Hasegawa and SM Jain: Advances in molecular breeding toward drought and salt tolerant crops', Springer: Dordrecht, The Netherlands, 2007, 701 – 711.
22. Alves, A.A.C.; Setter, T.L. Abscisic acid accumulation and osmotic adjustment in cassava under water deficit. Environ. Experimen. Bot. 2004, 51, 259 – 271. https://doi.org/10.1016/j.envexpbot.2003.11.005
23. Lenis, J.I.; Calle, F.; Jaramillo, G.; Pérez, J.C.; Ceballos, H.; Cock, J. Leaf retention and cassava productivity. Field Crops Res. 2006, 95, 126 – 134. https://doi.org/10.1016/j.fcr.2005.02.007
24. Calatayud, P.A.; Llovera, E.; Bois, J.F.; Lamaze, T. Photosynthesis in drought-adapted cassava. Photosynth. 2000, 38, 97–104 https://doi.org/ 10.1186/1471-2164-13-64
25. Shan, Z.; Luo, X.; Wei, M.; Huang, T.; Khan, A.; Zhu, Y. Physiological and proteomic analysis on long-term drought resistance of cassava (*Manihot esculentta* Crantz). Sci. Report. 2018, 8, 17982. https://doi.org/10.1038/s41598-018-35711-x
26. Pacheco, R.I.L.; Macias, M.P.; Campos, F.C.F.; Izquierdo, A.J.R.; Izquierdo, G.A.R. Agronomic and physiological evaluation of eight cassava clones under water deficit conditions. Rev. Fac. Nac. Agron. Medellín. 2020, 73(1), 9109-9119. https://doi.org/10.15446/rfnam.v73n1.75402

27. Wasonga, D.O.; Kleemola, J.; Alakukku, L.; Mäkelä, P.S.A. Growth response of cassava to deficit irrigation and potassium fertigation during the early growth phase. Agronomy. 2020, 10(3), 321. https://doi.org/10.3390/agronomy10030321
28. Silim, N.H.; Kinoti, P.; Wainaina, C.M.; Ateka, E.M. Phenotypic evaluation of cassava genotypes (*Manihot esculenta*) under moisture stress. Afr. J. Agric. Res. 2021, 17(6) 836 – 843. https://doi.org/10.5897/ajar2020.14747
29. Pardales, J.R.; Yamauchi, A. Regulation of root development in sweet potato and cassava by soil moisture during their establishment period. Plant Soil. 2003, 255, 201 – 208. https://doi.org/10.1023/a:1026160309816
30. Subere, J.O.Q.; Bolatete, D.; Bergantin, R.; Pardales, A.; Belmonte, J.J. Genotypic variation in responses of cassava (*Manihot esculenta* Crantz) to drought and re-watering: Root system development. Plant Product. Sci. 2009, 12 (4), 462 – 474. https://doi.org/10.1626/pps.12.462
31. El-Sharkawy, M.A. International research on cassava photosynthesis, productivity, eco-physiology and responses to environmental stresses in the tropics. Photosynthetic. 2006, 44, 481 – 512. https://doi.org/10.1007/s11099-006-0063-0
32. Okogbenin, E.; Setter, T.L.; Ferguson, M.; Mutegi, R.; Alves, A.; Ceballos, H.; Fregene, M. Phenotyping cassava for adaptation to drought. In: Monneveux, P.; Ribaut, J.M. eds. Drought phenotyping in crops: from theory to practice. Texcoco, Mexico: CGIAR Generation Challenge Programme, pp.395-410, 2011.
33. Burns, A.; Gleadow, R.; Cliff, J.; Zacarias, A.; Cavagnaro, T. Cassava: The drought, war and famine crop in a changing world. Sustainability. 2010, 2, 3572 – 3607. https://doi.org/10.3390/su2113572
34. Lokko, Y.; Anderson, J.V.; Rudd, S.; Raji, A.; Horvath, D. Characterization of an 18,166 EST dataset for cassava (*Manihot esculenta* Crantz) enriched for drought-responsive genes. Plant Cell Report. 2007, 26, 1605 – 1618. https://doi.org/10.1007/s00299-007-0378-8
35. Okogbenin, E.; Fregene, M. Genetic mapping of QTLs affecting productivity and plant architecture in a full-sib cross from non-inbred parents in Cassava (*Manihot esculenta* Crantz). Theor. Appl. Genetic. 2003, 107(8), 1452-1462. https://doi.org/10.1007/s00122-003-1383-0
36. Fukuda, W.M.G.; Guevara, C.L.; Kawuki, R.; Ferguson, M.E. Selected morphological and agronomic descriptors for the characterization of cassava. International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria, p.19, 2010.
37. Jørgensen, K.; Bak, S.; Busk, P.K.; Sørensen, C.; Olsen, C.E.; Puonti-Kaerlas, J.; Møller, B.L. Cassava plants with a depleted cyanogenic glucoside content in leaves and tubers. Distribution of cyanogenic glucosides, their site of synthesis and transport, and blockage of the biosynthesis by RNA interference technology. Plant Physiol. 2005, 139(1), 363-374. https://doi.org/10.1104/pp.105.065904
38. Vandegeer, R.; Miller, R.E.; Bain, M.; Gleadow, R.M.; Cavagnaro, T.R. Drought adversely affects tuber development and nutritional quality of the staple crop cassava (*Manihot esculenta* Crantz). Function. Plant Biol. 2012, A – F. http://dx.doi.org/10.1071/FP12179
39. Bull, S.E.; Owiti, J.A.; Niklaus, M.; Beeching, J.R.; Gruissem, W.; Vanderschuren, H. Agrobacterium-mediated transformation of friable embryogenic calli and regeneration of transgenic cassava. Nature Protocol. 2009, 4(12), 1845 – 1854. https://doi.org/10.1038/nprot.2009.208
40. Schneider, D.N.; Freitag, N.M.; Liedgens, M.; Feil, B.; Stamp, P. Early growth of field-grown Swiss flint maize landraces. Maydica. 2011, 56, 1 – 9.
41. Alves, A.A.C.; Setter, T.L. The response of cassava leaf area expansion to water deficit: Cell proliferation, cell expansion and delayed development. Ann. Bot. 2004, 94, 605 – 613. https://doi.org/10.1093/aob/mch179
42. Percival, G.C.; Sheriffs, C.N. Identification of drought-tolerant woody perennials using chlorophyll fluorescence. J. Arboricul. 2002, 28 (5), 215 – 223. https://doi.org/10.48044/jauf.2002.032
43. Gajdos, E. Cadmium sensitivity of maize and sunflower hybrids, the possibility of reducing the harmful effects. PhD dissertation, 2013
44. Degenkolbe, T.; Thi, D.P.; Zuther, E.; Repsilber, D.; Walther, D.; Hincha, D.K.; Kohl, K.I. Expression profiling of rice cultivars differing in their tolerance to long-term drought stress. Plant Mol. Biol. 2009, 69, 133 – 153. https://doi.org/10.1007/s11103-008-9412-7
45. Yan, Y.; Wang, P.; Lu, Y.; Bai, Y.; Wei, Y.; Liu, G.; Shi, H. MeRAV5 promotes drought stress resistance in cassava by modulating hydrogen peroxide and lignin accumulation. The Plant Journal, 2021, 107(3), 847-860 https://doi.org/10.1111/tpj.15350
46. Liao, W.; Li, Y.; Yang, Y.; Wang, G.; Peng, M. Exposure to various abscission-promoting treatments suggests substantial ERF subfamily transcription factors involvement in the regulation of cassava leaf abscission. BMC Genomics, 2016, 17, 538. https://doi.org/10.1186/s12864-016-2845-5
47. Orek, C.; Zhang, P.; Gruissem,W.; Ferguson, M.; Vanderschuren, H. Gene expression associated with ‘staygreen’ trait for drought tolerance in cassava (*Manihot esculenta* Crantz). (researchgate.net), 2013
48. de Oliveira, C.R.S.; Borel, J.C.; Pereira, D.A.; de

Carvalho, B.P.; Medrado, E.; Ishikawa, F.H.; de Oliveira, E.J. Genetic parameters and path analysis for root yield of cassava under drought and early harvest. Crop Breed. Appl. Biotechnol. 2021, 21(3), e36162137. https://doi.org/10.1590/1984-70332021v21n3a46

49. Punyasu, N.; Thaiprasit, J.; Kalapanulak, S.; Saithong, T.; Postma, J.A. Modeling cassava root system architecture and the underlying dynamics in shoot–root carbon allocation during the early storage root bulking stage. Plant Soil. 2024. https://doi.org/10.1007/s11104-024-06771-y
50. Zhu, Y.; Luo, X.; Nawaz, G.; Yin, J.; Yang, J. Physiological and biochemical responses of four cassava cultivars to drought stress. Sci. Report. 2020, 10, 6968. https://doi.org/10.1038/s41598-020-63809-8
51. El-Sharkawy, M.A. Cassava biology and physiology. Plant Mol. Biol. 2004, 56, 481 – 501. https://doi.org/10.1023/b:plan.0000019109.01740.c6
52. Bergantin, V.R.; Yamauchi, A.; Pardales, J.R.; Bolatete, D.M. Screening cassava genotypes for resistance to water deficit during crop establishment. Philip. J. Crop Sci. 2004, 29 (1), 29 – 39.
53. Aina, O.O.; Dixon, A.G.O.; Akinrinde, E.A. Effect of soil moisture stress on growth and yield of cassava in Nigeria. Pak. J. Biol. Sci. 2007, 10 (18), 3085 – 3090. https://doi.org/10.3923/pjbs.2007.3085.3090
54. Turyagyenda, L.F.; Kizito, E.B.; Ferguson, M.; Baguma, Y.; Agaba, M.; Harvey, J.J.; Osiru, D.S. Physiological and molecular characterization of drought responses and identification of candidate tolerance genes in cassava. AoB Plants, 2013, 5, plt007. https://doi.org/10.1093/aobpla/plt007
55. Agili, S.M.; Pardales, J.R Jr. Influence of moisture and allelopathic regimes in the soil on the development of cassava and mycorrhizal infection of its roots during establishment period. Crop Sci. 1997, 22, 99 – 105.
56. El-Sharkawy, M.A. Drought tolerant cassava for Africa, Asia and Latin America. Biosciences, 1993, 43 (7), 441-451. https://doi.org/10.2307/1311903
57. El-Sharkawy M.A.; Cadavid, L.F. Response of cassava to prolonged drought stress imposed at different stages of growth. Exp. Agric. 2002, 38(3), 333 – 350. https://doi.org/10.1017/S001447970200306X
58. de Tafur, S.M.; El-Sharkawy, M.A.; Calle, F. Photosynthesis and yield performance of cassava in seasonally dry and semi-arid environments. Photosynthetic. 1997, 33 (2), 249 – 257. https://doi.org/10.1023/a:1022116414969
59. El-Sharkawy, M.A. Effect of humidity and wind on leaf conductance of field grown cassava. Braz. J. Plant Physiol. 1990, 2, 17 – 22.
60. de Souza, A.P.; Massenburg, L.N.; Jaiswal, D.; Cheng, S.; Shekar, R.; Long, S.P. Rooting for cassava: Insights into photosynthesis and associated physiology as a route to improve yield potential. New Phytologist. 2017, 213, 50–65. https://doi.org/10.1111/nph.14250
61. Orek, C. Analysis of ‘staygreen’ characteristics associated with drought tolerance in cassava (*Manihot esculenta* Crantz) under greenhouse conditions. MSc. Thesis, UoN, 2009, (uonbi.ac.ke)
62. Ngugi, K.; Orek, C.; Mwang’ombe, A. Morphological and physiological measurement of the stay-green trait in transgenic and non-transgenic cassava under greenhouse water stress conditions. J. Renew. Agric. 2013, 1(5), 77-83. https://doi.org/10.12966/jra.08.02.2013
63. Santanoo, S.; Ittipong, P.; Banterng, P.; Vorasoot, N.; Jogloy, S.; Vongcharoen, K.; Theerakulpisut, P. Photosynthetic performance, carbohydrate partitioning, growth, and yield among cassava genotypes under full irrigation and early drought treatment in a tropical Savanna climate. Plants. 2024, 13(15), 2049. https://doi.org/10.3390/plants13152049
64. Wang, S.; Lu, C.; Chen, X.; Wang, H.; Wang, W. Comparative transcriptome profiling indicated that leaf mesophyll and leaf vasculature have different drought response mechanisms in cassava. Trop. Plant Biol. 2021, 14, 396–407. https://doi.org/10.1007/s12042-021-09302-6