Journal of Soil Science and Plant Nutrition (2023) 23:71–91
https://doi.org/10.1007/s42729-023-01127-4

REVIEW

Morphophysiological Responses and Tolerance Mechanisms in Cassava (*Manihot esculenta* Crantz) Under Drought Stress

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Received: 29 May 2022 / Accepted: 3 January 2023 / Published online: 26 January 2023

Abstract

Cassava (*Manihot esculenta* Crantz), a ”miracle of the tropics,” is a critical component of the approaches to alleviate poverty, hunger, and malnutrition and increase livelihood security. Its high inherent photosynthetic efficiency and ability to sustain growth in challenging environments make it a potential food and nutrition security crop. However, water remains the most limiting factor for future cassava production, particularly under anticipated climatic variability. Though cassava is popularized as a drought-tolerant crop, seasonal or intermittent water stress episodes affect cassava productivity by influencing plant growth, storage root yield, and quality. Successful cassava production in drought-prone areas relies on the development of drought-tolerant cultivars along with tailored agronomic practices. We reviewed multi-faceted responses from morphological level to tissue/cell level biochemical changes, root development responses, and storage root quality alterations occurring under drought and potential targets for the future breeding program. This knowledge will pave the way for developing breeding strategies and implementable agronomic methods.

Keywords Drought tolerance · Drought adaptive responses · Food security · *Manihot esculenta* Crantz · Storage root quality

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Abbreviations

A	Carbon assimilation
ABA	Abscisic acid
Cal	Calorie
CAT	Catalase
CG	Cyanogenic glycosides
C_i/C_a	Ratio of internal (C_i) to atmospheric CO_2 concentration
C_a	Leaf internal carbon dioxide concentration
DAP	Days after planting
DEGs	Differentially expressed genes
DIRT	Digital imaging of root traits
E	Transpiration
ETR	Electron transfer rate
FC	Field capacity
FW	Fresh weight
g	Gram
GR	Glutathione reductase
g_s	Stomatal conductance
h	Hour
ha	Hectare
HCN	Hydrogen cyanide
HI	Harvest index

K^+	Potassium ion
kg	Kilogram
LAI	Leaf area index
m	Meter
MAP	Months after planting
NSC	Nonstructural carbohydrates
OA	Osmotic adjustment
PAR	Photosynthetically active radiation
PCD	Program cell death
PEPC	Phosphoenolpyruvate carboxylase
PSII	Photosystem II
qP	Photochemical quenching coefficient
ROS	Reactive oxygen species
RSA	Root system architecture
RuBisCO	Ribulose-1,5-bisphosphate carboxylase-oxygenase
s	Second
SOD	Superoxide dismutase
t	Ton
UN	United Nations
US$	United States dollars
WDS	Water-deficit stress
WP	Water potential
WUE	Water use efficiency
ΦPSII	Effective quantum yield
ICAR	Indian Council of Agricultural Research

1 Introduction

Environmental changes associated with global warming are potential threats to global food demand (FAO 2017) as the world population is projected to increase by 9–12.3 billion from 2050 to 2100 (Gerland et al. 2014; Frona et al. 2019). Furthermore, the increased drought and heatwave frequency (Naumann et al. 2018) will likely aggravate the anticipated limited land and water resource availability (Arora 2019). Moreover, the projected decline in productivity of major food crops will have severe implications for rural and semi-urban global populations in developing countries (Leng and Hall 2019; FAO 2020, 2021). Cassava, a staple for one billion people worldwide (Lebot 2020), thrives in challenging environments where other major food crops struggled, making it an ideal climate-resilient crop (Pushpalatha and Byju 2020). Cassava is generally grown by marginal and smallholder farmers, but its perception as a “poor man’s food” (FAO 2014) and “food-feed-fuel” crop (Howeler et al. 2013) has recently changed to a “future smart/climate-resilient crop” (Rosenthal and Ort 2012; Mukherjee et al. 2019; Pushpalatha and Byju 2020), “crop of industrial significance,” and “twenty-first century crop” (Howeler et al. 2013). It has immediate benefits against hunger, poverty, and malnutrition (Anikwe and Ikenganyia 2018; FAO 2018; Amelework et al. 2021) due to its higher energy production efficiency than maize and wheat (Howeler et al. 2013; Nayar 2014). The recent production statistics by FAOSTAT (2022) indicates that its production has increased significantly since 1961, and the global cassava market will reach up to US$66.84 billion by 2026, exhibiting a compound annual growth rate (CAGR) of 6.50% (GlobeNewswire 2021), showcasing its economic robustness, and importance. Apart from the cassava’s storage root, leaves are also consumed as a valuable protein source (Latif and Muller 2015), and extractable starch from storage roots forms the basis for numerous essential industrial products (Ravi et al. 2021; More et al. 2021).

The average productivity of cassava is still far lower than its potential yield suggesting broad scope for genetic improvement and the development of agronomic practices to narrow yield gaps. Drought alone can lead to a notable reduction in storage root yield, though the quantum of reduction depends on genotype and the severity and timing of drought during the growing season (Fig. 1). Water deficit during early growth (1–3 MAP, months after planting) causes more yield losses as this period coincides with the critical yield attributes *viz.* root system development, canopy establishment, storage root initiation, multiplication, bulking, and starch accumulation (El-Sharkawy 2007; Duque and Setter 2019). The crop simulation model predicted the region-specific drought-induced yield reduction of cassava storage root ranging from − 3.7 to 17.5% across Africa (Jarvis et al. 2012), − 17.24 to − 21.26% in Thailand (Pipitpukdee et al. 2020) and − 10 to 12% in India (Pushpalatha et al. 2021) under various future climatic scenarios.

Additionally, drought alters storage roots’ physical and chemical properties hampering the remuneration potential for marginal cassava growers, end-product utilization, and consumption pattern (Santisopasri et al. 2001; Nhassico et al. 2008; Gleadow et al. 2016; Jyothi and Sajeev 2021). Understanding stage-specific crop responses and the underlying physiological process is a prerequisite to reducing the negative impacts of drought on cassava productivity (Zhu et al. 2020). There is a plethora of studies on drought stress in cereal (rice, wheat and maize), vegetables, fruits and other crops (Havrlentova et al. 2021; Giordano et al. 2021; Dietz et al. 2021). However, cassava remained neglected, and information on drought responses is limited. In the present review, we have revisited the detrimental effect of drought stress on the quality aspect of cassava and its impact on growth and yield. Moreover, this will help develop knowledge and understanding of cassava drought tolerance, which would help in the development of suitable traits tailored to region-specific cultivars and appropriate management practices to ameliorate the adverse effects of drought.

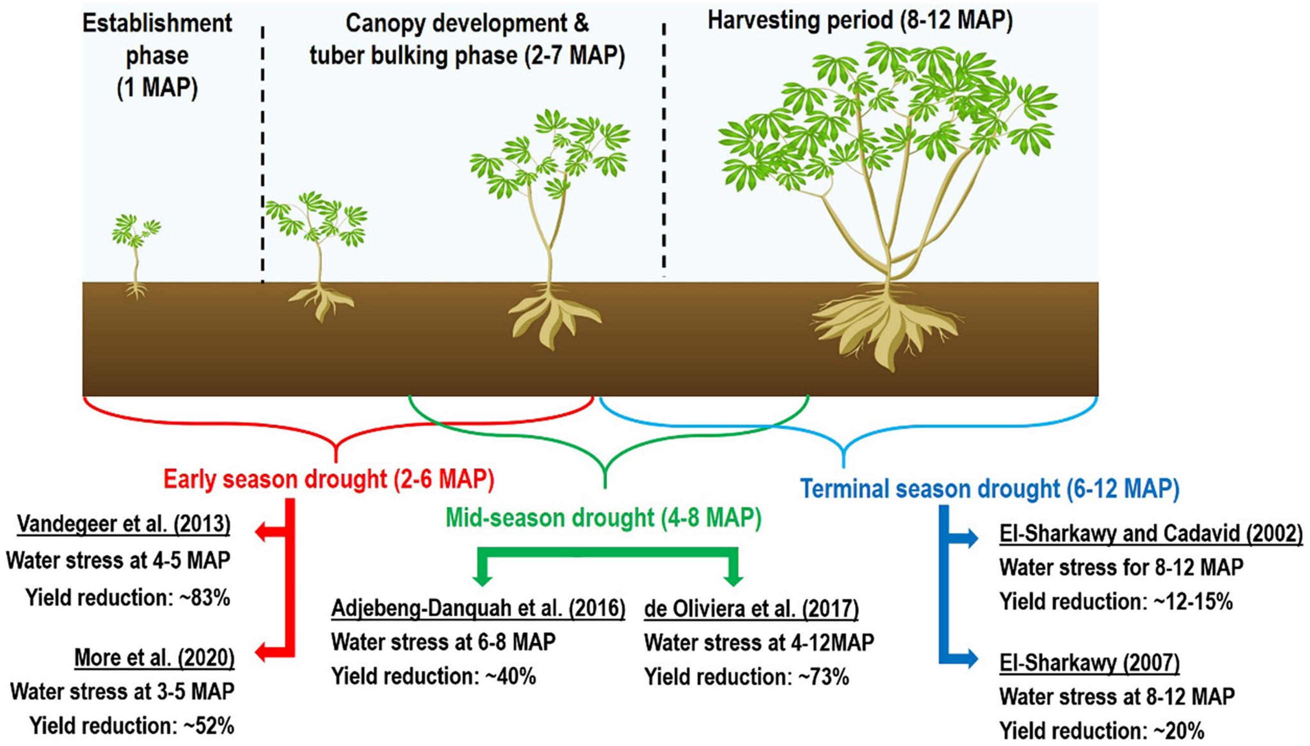

Fig. 1 Quantum of yield loss in cassava subjected to early, mid, or terminal season drought stress

2 Cassava Water Relations Under Drought

Leaf water potential and relative water content are water stress indicators reflecting plant water availability (Alves and Setter 2004) as CO_2 enters the leaf via stomata, the same channel as transpiration. Water availability controls the trade-off between CO_2 absorption and water loss (Bhattacharya 2019).

The total water, free water, and the ratio of free water and bound water levels reduced in cassava leaves, while the bound water content increased with the intensification of drought (Shan et al. 2018). Reduced osmotic potential by osmotic adjustment under water stress facilitates turgor maintenance, stomatal regulation, CO_2assimilation, and increased tolerance to dehydration (Alves and Setter 2004; Helal et al. 2013). Osmotic adjustment regulates turgidity so that plants can sustain low soil water potentials and create sufficiently low tissue water potential for continued soil water extraction. Under water stress, mature and expanding cassava leaves decreased osmotic potential to a relatively limited extent or had relatively modest osmotic potential, whereas immature leaves osmotically adjust to a greater extent than mature leaves (Ike and Thurtell 1981; Alves and Setter 2004). The majority (nearly 60%) of osmotic adjustment (OA) occurs as a result of the accumulation of K^+salts in mature and expanding leaves, which is positively correlated with the extent of OA, while organic solutes such as sugars accounted for 25% of OA and their concentrations decreased as water stress progressed (Alves and Setter 2004; Okogbenin et al. 2013). Osmotic adjustment helps to increase water use efficiency and the water resupply system from stem to leaves during drought (Itani et al. 1999). However, OA alone is insufficient to provide drought tolerance and higher yields (Helal et al. 2013).

Water use efficiency [WUE; agronomic (yield produced per unit of water applied) or physiological, i.e., instantaneous WUE (A/E) and intrinsic WUE (A/g_s)] is important for analyzing plant growth under water-deficit conditions (Hatfield and Dold 2019). In cassava, the WUE is highly dependent on water supply, stomatal conductance, photosynthetic efficiency, transpirational losses, growth stage, and atmospheric condition (El-Sharkawy 2006). Interestingly, cassava crop growth rate and short-term WUE are similar to C_4 crops, which are considerably higher than other C_3crops (El-Sharkawy 2004, 2006). However, optimizing WUE under water-limited environments would also enhance cassava's productivity in challenging environments (Wongnoi et al. 2020).

3 Growth and Morphological Responses

3.1 Leaf and Shoot Growth Dynamics

Cassava leaves can take 10–12 days for emergence to full expansion (Cock 1984), with a leaf life of up to 30–180 days, depending on the cultivar, water availability, shade level, temperature, and growing conditions (Phosaengsri et al. 2019). Maximum leaf formation is completed within the first 90 DAP, followed by steady canopy development throughout the growing period (Alves and Setter 2004). Cassava canopy area increases significantly from 3 to 5 MAP, followed by a progressive decline in total canopy area during 8–9 MAP due to leaf loss (El-Sharkawy and De Tafur 2007). The canopy development phase (3–5 MAP) is critical as storage root initiation, and bulking co-occurs, significantly affecting the storage root yield (Ceballos et al. 2012). Accumulation of optimum canopy with desirable leaf growth during the storage root bulking phase is critical to achieving higher productivity irrespective of the water status of the location (Phosaengsri et al. 2019). Prolonged water deprivation harmed leaf development, leaf cell division, leaf angle, leaf expansion, leaf retention capacity, and leaf area index (LAI), and leaf abscission was accelerated (de Oliviera et al. 2017; More et al. 2020) (Fig.2). According to Connor and Cock (1981), leaf expansion/leaf size was more sensitive to water deficit than the leaf production rate. Thus, leaf area is the key determinant factor for canopy development and productivity under water stress, not the leaf loss. Water stress within 2–3 MAP produced half the leaf area of non-stressed plants (Turyagyenda et al. 2013a, b) and caused 84.27% mortality (Turyagyenda et al. 2013a). Furthermore, diminished leaf area was associated with ethylene accumulation (Ogaddee and Girdthai 2019), which might be related to accelerated leaf senescence and ROS generation (Liao et al. 2016). Reduced leaf area is the first line of defense, which reduces the transpirational loss but substantially affects the photosynthetic efficiency (Pacheco et al. 2019), with improved water use efficiency (Vandegeer et al. 2013).

Plant height, stem diameter, and shoot biomass were decreased significantly, varying with the different genotypes, in response to water stress (Aina et al. 2007; Okogbenin et al. 2013; Shan et al. 2018), owing to the downregulation of proteins and photosynthetic activity resulting into impaired cell development and division (Shan et al. 2018) and overall plant vigor. Tissue turgidity is maintained to a minimum to prevent cell death by limiting cell growth (Calatayud et al. 2000). Inhibited apical meristem cell development and elongation, loss of turgor, significant leaf fall and senescence, and altered biomass partitioning contributed to decreased shoot growth (Helal et al. 2013; Shan et al. 2018; More et al. 2020). This information on leaf and stem is essential to understand response mechanism that cassava showcases under drought.

3.2 Root Growth and Development

The formation of roots is critical for the growth and productivity of cassava shoots (Duque and Villordon 2019). Investigating root development kinetics in resource-constrained production environments may provide additional insight into cassava crops' drought-tolerance mechanisms (Adu et al. 2018). However, relatively few studies have identified the role of root growth and development in root and tuber crops, including

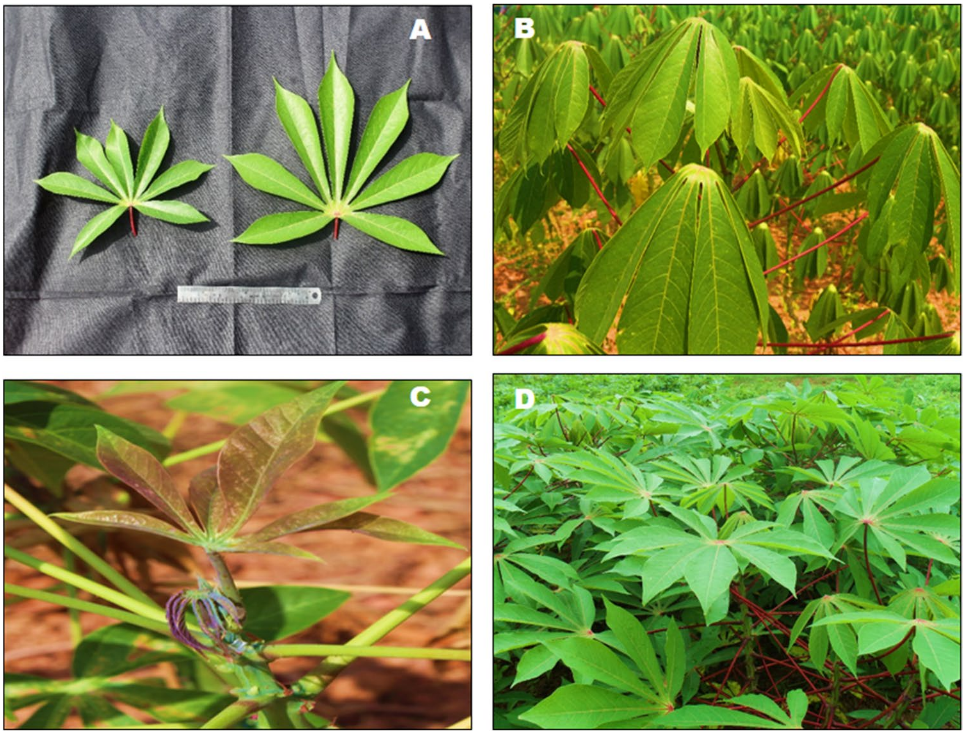

Fig. 2 Cassava plants under drought show reduced canopy development. The most notable change in the leaf trait is the reduction in leaf area in stressed plants as compared to the leaf area of well-irrigated plants (**A**). In order to regulate the use of limited available water, cassava leaves are known to employ heliotropic effect to reduce the harmful effect of radiation caused by drought-induced high-temperature stress (**B**). While leaves continue to develop, they are smaller and grow more slowly, and the older leaves are lost (**C**). Cassava demonstrated remarkable post drought recovery. The newly developed leaves from the previously stressed plants had similar leaf area and photosynthetic efficiency as that of well-irrigated plants (**D**)

cassava, compared to aboveground morphophysiological traits (Adu et al. 2018; Duque and Villordon 2019), particularly under conditions of water stress (Adu et al. 2020). Root emergence occurs 1 to 2 weeks after planting, followed by significant fibrous and lateral root development (Izumi et al. 1999). Early water stress coincides with the period of highest relative growth rate of root system during the first 30 DAP, which subsequently decreases to a nearly constant rate after 30–60 DAP (Adu et al. 2018) and becomes more detrimental to crop yield. The fibrous root system grows up to 1.4–2 m in depth to increase access to deeper water (de Tafur et al. 1997), or even up to 2.4–2.6 m Ekanayake et al. 1994, 1996) depending upon the timing of the water stress, and soil texture also significantly affected due to water stress (Adu et al. 2018). Aina et al. (2007) reported that drought reduced root growth more than shoot growth in cassava, depending on the timing and severity of the drought. Strikingly, reduced lateral and total root numbers; root length and diameter; adventitious root number and length; basal root branching density; lower and upper nodal root numbers; first, second, and third lateral root numbers; and root dry weight as a result of water stress cause sizeable reduction in storage root yield (Pardales and Yamauchi 2003; Helal et al. 2013; de Oliveira et al. 2015; Kengkanna et al. 2019; Adu 2020). Developing a cassava root phenotyping protocol and platform and identifying phenotypic variation in root systems is essential for developing highly drought-tolerant cassava genotypes. Recently developed root shovelomics-based phenotyping techniques combining manual and semi-automatic DIRT measurements (Kengkanna et al. 2019) or easy and low-cost three-dimensional cassava root crowns phenotyping platform (Sunvittayakul et al. 2022) could be proven extremely useful for root architectural trait phenotyping in cassava under various growing conditions. Moreover, a substantial amount of germplasm maintained at the International Center for Tropical Agriculture (CIAT), Colombia, Central Tuber Crops Research Institute (CTCRI), India, and other premier research institutes could be assessed in collaborative breeding program for identification of root-related traits for drought-tolerance.

4 Physiological-Biochemical Responses

4.1 Photosynthesis

Cassava is a biologically efficient crop with a higher leaf photosynthetic rate, as high as 40–50 µmol CO_2 m^{-2} s^{-1}under favorable environments (El-Sharkawy 2007). In a series of experiments, aboveground dry weight and storage root yield were positively correlated with the single-leaf photosynthesis or mean seasonal upper canopy photosynthesis (El-Sharkawy et al. 1990; El-Sharkawy 2006). However, this correlation depends on optimum PAR, plant age, leaf position, LAI, leaf duration, leaf anatomy, and the environment under which the leaves were formed (El-Sharkawy 2014; De Souza and Long 2018).

Inhibited CO_2assimilation rate under water stress was primarily attributed to reduced leaf area, reduced stomatal conductance (Adjebeng-Danquah et al. 2016; Morgante et al. 2020), and reduced photosynthesis-related proteins (Chang et al. 2019; Wang et al. 2021a, b). The sensitivity of cassava's stomata to varying water regimes and atmospheric humidity has been reviewed in detail (El-Sharkawy 2007). The presence of higher stomatal density on the abaxial side than on the adaxial side of the leaf also reduced gaseous exchange under water stress conditions due to leaf bending/rolling (El-Sharkawy and Cock 1987). Asymmetric stomatal density reduced gas exchange which optimized water use but impaired carbon gain. This is further affected due to restricted flow of water from leaf veins to guard cells (Ooba and Takahashi 2003). Hydro active stomatal closure (referred to as stomatal closure due to localized dehydration of guard cells and accessory cells as per the relative change in air humidity) was induced by the upregulation of ABA-dependent (ABA-D) and ABA-independent genes associated with decreased stomatal activity (El-Sharkawy 2006; Orek et al. 2020; Fu et al. 2016; Li et al. 2017a, b). Carbon isotope ratios ($\Delta^{13}C$), a key parameter to assess water use efficiency in relation to stomatal activity and gaseous exchange capacity remained more negative under water stress (Adjebeng-Danquah et al. 2016; More et al. 2019a, b2019, 2022). Drought-sensitive cultivars had lower photosynthetic quantum efficiency (Fv/Fm) than drought-tolerant cultivars (Zhao et al. 2015). The quantum yield of the light-adapted leaf (F′v/F′m), effective quantum yield (ΦPSII), photochemical quenching coefficient (qP), and ETR were decreased significantly under water stress. Efficiency of photosystem II and electron transport rate was reduced significantly as a result of water stress (Pereira et al. 2018), however, contrary to these findings, Shan et al. (2018) reported increased PS II and PS I subunits to modulate the photosystem repair and electron transfer to maintain photosynthetic efficiency to reduce the negative effect of water deficiency (Shan et al. 2018). These changes are ascribed to damage to the chlorophyll membrane, chlorophyll degradation, and associated photoinhibition (Morgante et al. 2020); downregulation of PSII synthesis; decreased oxygen-evolving complex protein production; and structural changes in oxygen-evolving complex proteins (Dalal and Tripathy 2018). Additionally, photosynthetic activity was harmed by ROS generation, decreased RuBisCO activity, and damage to multiple cellular components (Zhu et al. 2020), as well as downregulation of sedoheptulose-1,7-bisphosphatase (SBPase) and fructose-bisphosphate aldolase (both of which are required for the supply of RuBP to Rubisco) (Shan et al. 2018).

Reduced stomatal activity and carbon assimilation and the reduction in leaf area were the strategic responses to optimize the water use efficiency (Duque and Setter 2013; Zhao et al. 2015; Adjebeng-Danquah et al. 2016). Consequently, high water use efficiency will not always result in high yield, as it may be the result of reduced water consumption due to leaf abscission and consequently less CO_2fixation (Blum 2009). A delicate balance between transpiration and CO_2diffusion is crucial for optimizing water use efficiency and productivity under drought conditions in cassava. Evapotranspiration increases with a simultaneously higher stomatal conductance (Oguntunde 2005; El-Sharkawy 2012; Shan et al. 2018; Morgante et al. 2020). Transpiration also declined abruptly in conjunction with leaf ABA accumulation and severe leaf abscission (Duque and Setter 2013). Genotypic variation for gaseous exchange under varied ecosystems exists (Shan et al. 2018; More et al. 2020), which could be useful in fine-tuning the dual function of the stomatal aperture. More research is warranted to decipher biochemical and molecular characteristics of cassava photosynthesis in relation to storage root yield.

4.2 Assimilate Partitioning

Storage root yield of cassava is a function of source-sink interactions and the photosynthetic efficiency (Orek et al. 2020). It is severely impeded by water stress episodes (El-Sharkawy 2014) (Fig.3). Partitioning index (PI), a ratio of storage root yield to total biomass (aboveground biomass + storage root weight + fibrous root weight) determined at 4-6 MAP (Duque and Setter 2019), is an indicator of biomass accumulation efficiency of storage roots. Duque (2012) had established profuse relationship especially under water stress among PI and HI, for 45 diverse cassava genotypes. PI at 7 MAP and HI at 12 MAP (at harvesting) were significantly and positively correlated for drought-tolerant genotypes (Olasanmi 2010). Duque and Setter (2019) also suggested that root yield is the function of PI, based on observed correlation patterns. Water stress occurred during the 3–4 MAP period, significantly decreased PI, biomass, and yield. Assessment of PI at an early stage could have additional benefits as an indicator of higher storage root yield. Significantly less attention has been given to this particular trait in cassava, and further studies are sought to determine the pattern and quantum to which cassava alters carbohydrate accumulation and pattern of its diversion among different organs to sustain its partitioning capacity to sustain yield.

4.3 Biochemical Changes

Drought episodes triggered the biosynthesis of protective biochemicals and secondary metabolites in cassava to counteract the water-deficit stress (Nuwamanya et al. 2014). Most changes were associated with the increases in the synthesis of defensive proteins (e.g., lectins and protease inhibitors) and other biomolecules like phenolics, proline, and tannins (Isah 2019). Cassava leaves accumulated significantly higher quantities of trehalose and proline during early drought stress (Ren et al. 2017). Sugar content in stems and immature/mature leaves decreased as water stress progressed (Duque and Setter 2013; Koundinya et al. 2018). Duque and Setter (2013) reported that while evaluating the composition of nonstructural carbohydrates in cassava organs under water stress, sugar was the primary form of nonstructural

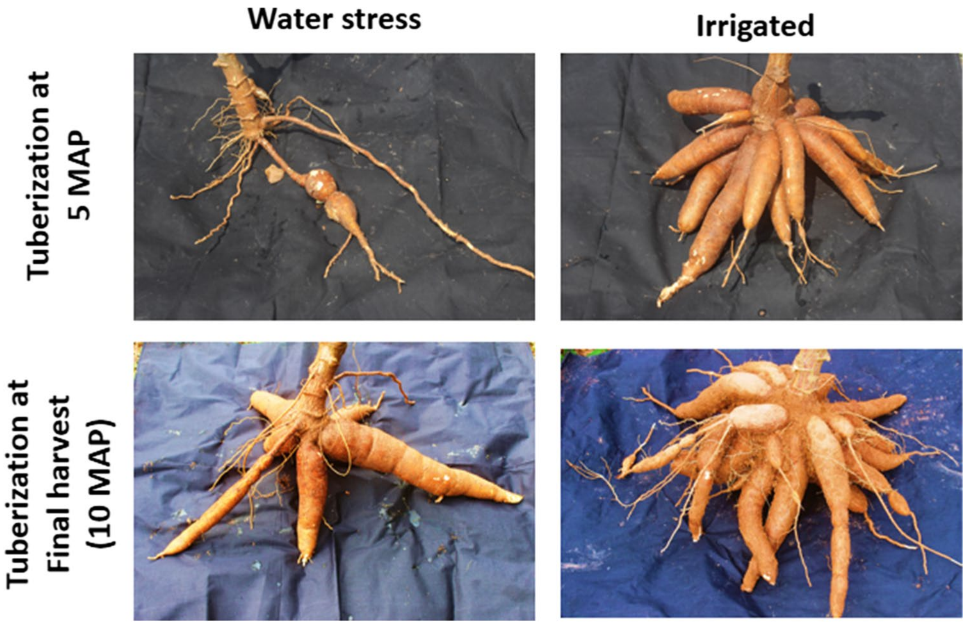

Fig. 3 Tuberization at 5 and 10 months (harvesting) after planting in a variety H 165 subjected to drought from 61 to150 days after planting

carbohydrate in the leaf blade and leaf petiole, while starch comprised approximately one-third. Contrastingly, stem and storage roots contained relatively high starch content. The stem's starch reserves were remobilized in numerous organs to maintain development via storable carbohydrates depleted during periods of water stress due to reduced canopy photosynthesis and the generation of secondary metabolites and defense proteins (Duque and Setter 2013). However, they remained unaffected in tolerant and susceptible genotypes under water stress (Duque and Setter 2019). The accumulation of total reducing sugars (glucose) was negatively correlated with starch yield and positively correlated with protein and phenolic contents (Nuwamanya et al. 2014). Reverse translocation of sugars from storage roots occurred to cater for leaf and stem growth. Bound reducing sugars increased more than free reducing sugars with increasing water stress, suggesting possible losses in storage starch. Understanding biochemical responses is essential for a holistic perception of drought resistance mechanism that cassava adopts under drought

Reactive oxygen species (ROS) are generated during water-deficit stress, causing oxidative damage. ROSs are responsible for the negative impact on physiological processes leading to programmed cell death (PCD). Under oxidative stress, relative leaf electrical conductivity and malondialdehyde and hydrogen peroxide contents significantly increased with increasing drought stress (Petrov et al. 2015). Enzymatic (superoxide dismutase, ascorbate peroxidase, peroxidase, glutathione reductase, catalase) and non-enzymatic (ascorbic acid, glutathione, total phenolics, and total flavonoids) antioxidant mechanisms form to counteract the oxidative damage occurring under water stress (Zhu et al. 2020). Almost all antioxidants enhanced manifold under water stress, depending on the genotype. Some cultivars accumulated more ascorbic acid, glutathione, and superoxide dismutase triggered by the upregulation of Mn-SOD and CAT genes, while others synthesized more glutathione reductase and total phenols due to the upregulation of the GR gene (Zhu et al. 2020). Furthermore, drought abruptly affected the thylakoid membrane and grana stacking, and grana lamellae structure significantly affecting biochemical and physiological processes, whereas no change was observed in the thylakoid granum structure (Chang et al. 2019). Hence, it is needed to explore the role of chloroplast in drought resistance and adaptation in cassava.

Cassava's complex multi-level drought responses involve employment of the antioxidant system (Yan et al. 2021). Proteomic analysis is a useful technique to reveal the role of genes associated with a specific protein involved with drought responses and adaptation mechanisms (Aslam et al. 2017). However, information regarding this aspect in cassava is very limited (Yan et al. 2021). In a Kyoto Encyclopedia of Genes and Genomes (KEGG)-based proteomics analysis in cassava, Wang et al. (2021a, b) reported distinct drought response and adaptation mechanisms in leaf vasculature and leaf mesophyll, respectively. Genes associated with amino acid biosynthesis (e.g., alanine, aspartic acid, and glutamic acid), pyruvate metabolism, and starch and sucrose metabolism were upregulated in leaf mesophyll, while genes associated with carbon metabolism, plant hormone signal transduction, pyrophosphatase activity, and oxidative phosphorylation were upregulated in leaf vasculature. In addition, the increased arginine biosynthesis in leaf mesophyll tissue was associated with enhanced adaptation to water deficiency. Shan et al. (2018), under long-term drought conditions, reported upregulation of 262 proteins potentially involved in carbohydrate energy metabolism, heat shock proteins, protein homeostasis, transcription, cell structure, cell membrane transport, signal transduction, and stress responses. Numerous reports depict the role of 90 kDa heat shock protein (HSP90, highly conserved molecular chaperone) as an aid in coping with multiple biotic and abiotic stresses in plants and animals. However, its role in cassava regarding drought resistance is not yet studied in detail (Wei et al. 2020). *MeHSP90* proteins were identified as a critical factor for enhanced stress resistance. Out of 10 identified *MeHSP90s*, the *MeHSP90.9* was abundantly induced as a result of drought stress. Apart from these, two potential HSP90 client proteins, viz., *MeWRKY20*, and *MeCatalase1* interacted significantly with *MeHSP90.9* to foster stress resistance. *MeHSP90.9* proteins regulated the accumulation of ABA hormone through targeting the ABA biosynthesis gene *MeNCED5* whereas along with *MeCatalase1*, it regulated the catalase activity and H_2O_2accumulation to facilitate cassava plants to cope up with drought. Li et al. (2021) characterized the functions of drought-responsive genes such as*SQUAMOSA promoter binding protein-like 9 (SPL9)* and *MeSPL9*. *MeSPL9* and *rMeSPL9-SRDX*conferred drought tolerance with enhanced accumulation of proline, anthocyanin, jasmonic acid (JA), and soluble sugars. Chang et al. (2019) elucidated photosynthesis-related proteins' downregulation, significantly affecting photosynthesis efficiency. However, the cassava plant could cope with the drought situation with the upregulation of carbon and nitrogen metabolism–associated proteins. In the very first report of integration of transcriptomic and proteomic analysis in cassava, Ding et al. (2019) reported 237 and 307 differentially expressed proteins (DEPs), in cassava leaf and root, enabling heat shock protein, secondary metabolism biosynthesis, and hormone biosynthesis to sustain under water-deficient environments.*MeMYB1*, *MeMYB2*, *MeMYB4*, and *MeMYB9*transcription factors belonging to the myeloblastosis (MYB) superfamily were involved in stress response mechanisms in cassava (Ruan et al. 2017). RNAi-driven repression of*MeMYB2*resulted in drought and cold tolerance in transgenic cassava (Ruan et al. 2017).

Wang et al. (2021a, b) reported that the MYB family protein*MeMYB26*, a typical transcription factor with two MYB DNA-binding and transcriptional activation domains, was exclusively involved in water stress signal transduction in the root portion of cassava and crucial for plant stress resistance, growth, and biomass development. MeMYB transcription factors were differentially expressed in leaves upon exposure to cold and drought stress and thus could be important for signal transduction of abiotic stress responses (Ruan et al. 2017; Wang et al. 2021a, b). However, more experiments are needed to re-confirm these findings.

ABA, a stress hormone, plays a vital role in controlling the leaf development rate to reduce water losses. ABA accumulation is a part of the regulatory system to cope with water deficit (Alves and Setter 2000). ABA restricted stomatal activity, cell growth cycle and division, shoot and root growth, and leaf area growth to manage limited water availability under water stress (Alves and Setter 2004; Duque and Setter 2013; Felemban et al. 2019). Under water stress, young and mature leaves accumulate ABA. Strikingly, young leaves doubled the ABA content on a leaf area basis and always had higher ABA concentrations than mature leaves (Alves and Setter 2004; Duque and Setter 2013) because of their lesser metabolic breakdown capacity and translocation of ABA from mature leaves (Alves and Setter 2004). In addition to ABA, ethylene accumulation also increased due to drought stress, leading to the senescence of older leaves (Liao et al. 2016; Ogaddee and Girdthai 2019). Over a period of time, ABA has been referred to as principal drought-responsive hormone, but there are several drought-responsive hormones, namely, ethylene, jasmonic acid, and salicylic acid whose role under drought in cassava remained neglected.

5 Molecular Responses

Deciphering the molecular drought responses is the essential component for designing a breeding program to develop drought-tolerant crop species. Drought response in cassava involves the complex multi-faceted mechanisms with upregulation or downregulation of multiple genes and proteins (Muiruri et al. 2021). Upregulation of ABA-D genes and the downregulation of a large number of genes were observed during post-stress withdrawal. ABA-D genes regulate stress-related responses by mediating stomatal activity and ABA accumulation in cassava leaves (Orek et al. 2020). In addition to this, water stress induced ABA biosynthesis genes (*NCED* and *ABA1*) and ABA signaling elements (*PP2C*, *SnRK2*, and *ABF*) in vascular cells of cassava leaves. Gene expression pattern analysis revealed that the leaf vascular bundle responded more actively than mesophyll cells (Wang et al. 2021a, b). Ruan et al. (2018) identified 18 cassava-specific CC-type GRXs across the cassava genome, of which*MeGRXC3*, *C4*, *C7*, *C14*, *C15*, and *C18*were involved in ABA signaling. Recently, Ruan et al. (2022) revealed that overexpression of*MeGRXC3*, a cassava-specific CC-type glutaredoxin essential for redox homeostasis and ROS signaling, induced stress-related transcription factor genes in *Arabidopsis*. Ren et al. (2017) employed bioinformatics approaches to identify and characterize candidate*Manihot esculenta* ethylene receptor genes and transcription factor genes. The highest and the lowest expression of these genes was in the leaf and tuberous roots, respectively, subjected to drought stress through the ethylene signaling pathway.

Shang et al. (2021) elucidated the tissue-specific *SOD*, *CAT*, and *APX* gene expression consequent to osmotic stress, postharvest physiological deterioration (PPD) of storage roots, ABA, and *Xanthomonas axonopodis* infection. Seven SODs, 6 CATs, and 6 APX genes were identified in this research, of which *SODs*showed high expression levels. Long non-coding RNAs (lncRNAs), important drought response regulators, were reported in autotetraploid cassava which conferred drought tolerance by increasing the stomatal density (Li et al. 2017b; Xiao et al. 2019). Li et al. (2017b) identified 318 long non-coding RNAs associated with biosynthesis of secondary metabolite, transduction of hormone signals, and sucrose metabolism in cassava. Yu et al. (2016) isolated stress-inducible homologous cassava plasma membrane gene,*MePMP3-2*, for the first time from cassava. The expression of this gene was upregulated under NaCl and PEG-mediated water stress suggesting its role in triggering stress responses. According to Yan et al. (2021), transcription factor*MeRAV5* interacts physically with *MePOD* (peroxidase) and *MeCAD15*(lignin-related cinnamyl alcohol dehydrogenase 15), to govern hydrogen peroxide and lignin accumulation, respectively, to enhance drought resistance. Astonishingly, this pathway was ABA independent as it had no significant effect on ABA content of the leaves. Recently, genetic mechanism and genomics research focusing on drought tolerance is reviewed in detail by Muiruri et al. (2021).

5.1 GWAS Approaches for Identifying Breeding Targets

Cassava hybridization is challenging due to its long-life cycle (Bull et al. 2017), asynchronized flowering and sterility or non-flowering (Pineda et al. 2020), and polygenic nature of abiotic stress tolerance (Koundinya and More 2021). Marker-assisted selection (MAS) and quantitative trait loci (QTL) have been used to analyze genetic linkage maps of cassava for drought tolerance (Setter and Fregene 2007; Turyagyenda et al. 2013a, b). For example, the KASPar SNP genetic map was used to explore productivity-associated traits in cassava exposed to moderate drought stress in Africa using 505 polymorphic SNP markers distributed across 21 linkage groups, with 27 QTL identified for 11 productivity traits from 267 F_1progeny (Ewa et al. 2021). The QTLs*c3loc84.0*, *c6loc0.0*, and *c7loc13.0* were associated with stable productivity under moderate stress. However, according to Jannink et al. (2010), MAS may not improve polygenic traits as it ignores genes with minor effects when selecting quantitative traits such as drought tolerance. Genome-wide association studies (GWAS) can better analyze genomic regions associated with water deficit using genome-wide marker data. In a GWAS, Feng et al. (2019) observed that the abscisic acid (ABA)-responsive element (ABRE)-binding factors (ABFs) gene regulated the expression of target genes under drought stress by binding to *ABRE* (abscisic-acid-response element). *Manihot esculenta ABFs* (*MeABFs*) regulated the expression of *Manihot esculenta betaine aldehyde dehydrogenase* (*MeBADHs*) genes by binding the *MeBADH1* promoter to modulate the accumulation of glycine betaine (GB) in cassava leaves to cope against drought stress. dos Santos Silva et al. (2021) identified 62 single nucleotide polymorphisms (SNPs) across 18 cassava chromosomes associated with drought-responsive-tolerance protein synthesis, including APETALA 2 domain (AP2), photosystem II oxygen-evolving enhancer protein, PR5-like receptor kinase-related, beta-fructofuranosidase/saccharase, leucine zipper, and bZIP transcription factors. Furthermore, numerous transcription factors associated with abiotic stresses identified in cassava, such as filamentous temperature-sensitive protein Z (Tubulin/FtsZ) and *Manihot esculenta* Crantz, 23 *tubulin* genes (*MeTubulins*) having important roles in IAA and GA_3stress-induced responses (Li et al. 2021). GWAS is one of the feasible approaches for rapid identification of new/target genes and demands development of high-throughput phenotyping tool for GWAS in cassava to identify novel genes conferring drought tolerance.

5.2 Key genes for Transgenic Approaches

Molecular characterization of drought-responsive and tolerant genes is needed to improve drought tolerance in cassava. Researchers are keen to develop transgenic cassava plants with greater drought tolerance. Possible targets include the genes underlying the major QTL discussed previously, but other genes can also be considered. Cassava clone TMS 60444 was transformed with isopentenyl transferase (*ipt*) gene conferring drought tolerance via enhanced cytokinin production under drought (Zhang et al. 2010). Turyagenda et al. (2013) identified potential drought-tolerant candidate genes to develop transgenic cassava regulating oxidative stress by moderating reactive oxygen species (*MeMSD* and *MeALDH*) and osmotic adjustment (*MeZFP* and *MeRD28*). Application of PEG and ABA treatments significantly induced the expression of *MeDREB1A*, responsible for enhanced abiotic stress tolerance in transgenic *Arabidopsis*and cassava plants (An et al. 2017). Expression of the*aquaporin* (*AQP*) gene conferring drought tolerance has been characterized in cassava (Putpeerawit et al. 2017; Wahyuni et al. 2020). Wahyuni et al. (2020) observed differential expression of the*AQP* gene in three cassava varieties subjected to drought stress. Genome-wide analysis of the aquaporin gene family in cassava revealed the availability of many aquaporin isoforms. Expression analysis of the *MeAQPs* gene family under water stress confirmed the upregulation of *MePIP2-1* and *MePIP2-10*. *AQP*gene enhanced drought tolerance through AQ PIP2-mediated greater water permeabilities in cellular membranes, influencing water efflux in guard cells to regulate stomatal activities (Putpeerawit et al. 2017). A recent study identified a novel gene,*lncRNA*, *DROUGHT-INDUCED INTERGENIC lncRNA* (*DIR*), enhancing proline accumulation and drought tolerance in transgenic cassava (Dong et al. 2022). In another study,*MeHSP90.9* promoted the transcriptional activation of *MeWRKY20* associated with ABA biosynthesis and the activation of *MeCatalase1*, conferring drought tolerance in cassava (Wei et al. 2020). According to Xu et al. (2013), transgenic cassava cultivars with increased expression of cytosolic*MeCu/ZnSoD* and peroxisomal *MeCat1*had greater drought tolerance than non-transgenic plants due to increased water content, proline content, superoxide dismutase, and catalase. Ethylene response factor family genes are involved in abiotic stress tolerance, inducing ethylene-mediated responses, and have been identified and characterized in cassava (Fan et al. 2016). Drought-stressed cassava had upregulated expression of TCP transcription factors (Lei et al. 2017), mitogen-activated protein kinase kinase kinases (MAPKKKs) genes (Ye et al. 2017), and the late embryogenesis abundant protein family (Wu et al. 2018), instrumental in stress responses through the ABA signaling pathway. In addition, calcium (Ca^{2+}) sensors such as calmodulins (CaMs), calmodulin-like proteins (CMLs), and calcineurin B-like proteins (CBLs) are crucial for calcium-based abiotic stress sensing (Wei et al. 2018), and KT/HAK/KUP family genes crucial for potassium ion (K^+) transport during stress (Ou et al. 2018) have been identified in cassava and could be used in breeding programs. Furthermore, Li et al. (2022) recently reviewed drought- and cold-responsive and tolerance genes in cassava. A summary of selected genomic studies on drought tolerance in cassava is presented in Table1.

6 Storage Root Quality

6.1 Physicochemical Properties

Cassava storage roots are a huge reservoir of starchy carbohydrates. In its original or modified form, starch is used in various industries due to its functional and chemical properties (Jyothi and Sajeev 2021). Starch accumulation in storage root initiates 4–6 weeks after planting (Cock 1984; El-Sharkawy 2004) and continues even when the root growth rate has declined until the harvest (Sriroth et al. 2001). Though the accumulation capacity of roots depends on the inherent varietal behavior, the reduced starch yield and quality are the likely consequence of water stress (Connor et al. 1981; Santisopasri et al. 2001). After prolonged water stress, water availability restores plant growth and starch synthesis (regardless of the stage of water stress, i.e., early/mid or terminal stress), but the effect on starch quality is compromised and cannot compare to the starch quality of plants supplemented with sufficient irrigation (Santisopasri et al. 2001; Sriroth et al. 2001). Starch physiochemical properties viz., hydration, gelatinization, and peak viscosity, were altered significantly under different water regimes (Teerawanichpan et al. 2008). Starch granules extracted from roots during early growth under normal moisture conditions had greater swelling capacity than those extracted from plants under moisture stress, which might be due to the moisture deficit significantly decreasing the granule size (Teerawanichpan et al. 2008) and influenced the paste viscosity with increased water absorption. Water stress had minimal influence on amylose: amylopectin contents (Defloor et al. 1998; Janket et al. 2020), though starch content (%) remained significantly lower in the plants exposed to water stress (Santisopasri et al. 2001). This reduction may help support aboveground growth by remobilization of starch under limited photosynthesis during water stress (Setter and Fregene 2007). Cassava starch grown under initial moisture stress has a considerably higher pasting temperature than cassava starch cultivated under no first moisture stress. In comparison, the peak viscosity of cassava starch extracted under early water stress was substantially lower than that extracted under normal conditions (Santisopasri et al. 2001). Water availability significantly changes the chloroplast structures. Chloroplasts from droughted plants were round in shape and further swollen with the progressive stress accumulating higher quantities of starch granules. On the other hand, chloroplast determined from the control plants was typically fusiform. Formation of higher number of starch granules might help plant to generate extra energy to combat drought (Chang et al. 2019).

The effect of drought on the physiochemical properties of cassava starch is inevitable (Santisopasri et al. 2001). Industrial application of cassava starch is predominantly reliant upon quality (Odeku 2013). As the economy of many countries (West and Central Africa, China, Thailand, Brazil, and India) revolves around cassava starch, undesired changes in yield and quality will lead to reduction in farm income. Therefore, additional research is needed to determine the effect of water availability on the functional, physiochemical, and structural features of starch.

6.2 Anti-nutritional Factors

Cassava is one of over 2000 plant species, including fruits and vegetables, which contain cyanogenic glycosides (CG) that release cyanide upon hydrolysis as a defense mechanism against herbivores (Møller 2010). It interacts with stress hormones and initiates actions, allowing plants to become used to biotic and abiotic challenges (Siegien and Bogatek 2006). Moreover, CG served as a storage house for nitrogen, which could be used in nitrogen assimilation under moisture stress to support the nitrogen-demanding sites to sustain growth (Mtunguja et al. 2016). Growing conditions, location, varietal differences, edaphic stresses, nutrient supply, and water availability are the crucial determinants of hydrogen cyanide (HCN) production in cassava leaves and storage roots (Burns et al. 2012; Imakumbili et al. 2019). Under water stress, HCN accumulation in leaves increased by 1.8–2.7 times as compared to leaves under no stress (Imakumbili 2019; Hular-Bograd et al. 2011) and increased with drought intensity (Santisopasri et al. 2001). The HCN content in dried storage roots of droughted plants was twofold higher than in control plants (Vandegeer et al. 2013). Higher HCN contents in roots could be due to the mobilization of resources, including HCN, from growing young leaves and tuberous roots (Vandegeer et al. 2013). According to the hypothesis of Vedengeer et al. (2013), if HCN is constitutive in nature, then accumulation of HCN as a result of water-stress will persist even after availability of sufficient water. Contrary to this hypothesis, if accumulating HCN is labile in nature, then glucosides synthesized under drought will be of same quantity as that of non-droughted plants (Møller 2010; Vandegeer et al. 2013). Quantification of HCN accumulation in leaves and storage roots under drought is extremely important and cannot be neglected while developing drought-tolerant cassava variety. The morphological, physiological, and molecular responses of cassava subjected to drought stress and their effects are summarized in Figs. 4 and 5.

7 Water Stress Adaptation Strategies

Cassava exhibited several strategies ranging from morphophysiological-biochemical responses to changes at the molecular level to mitigate drought-related consequences (Table 2). These strategies enable the plant to escape the drought by modifying life cycle/phenology or by regulating physiological functions. Strategies like stomata closure, shedding leaves, and regulating root system architecture (Muiruri et al. 2021) facilitate the reduction in photosynthetic leaf area, transpiration losses, and optimize water use (Okogbenin et al. 2013; Wongnoi et al. 2020). These changes correspond with impaired mesophyll conductance significantly hampering photosynthetic efficiency to manage

Table 1 Summary of genomic studies on drought tolerance in cassava

Sl. no.	Genomic approach	Genes identified	Description	Reference
1.	Expressed sequence tags (ESTs)	A total of 18,166 ESTs lead to the identification of 8577 unique gene clusters	Osmoprotective genes, transcription factors, and heat-shock proteins modulate signal transduction	Lokko et al. (2007)
2.	60-mer high-density oligomicroarray	1300 drought stress upregulated genes	Putative genes conferring stress recovery and high starch content	Utsumi et al. (2012)
3.	Micro(mi) RNAs	821 potential cassava-specific miRNAs and 60 miRNAs conserved in other crops species	Critical role in role in stress-induced post-transcriptional regulation	Ballen-Taborda et al. (2013)
4.	iTRAQ-based proteomic analysis	Aquaporin, myo-inositol 1-phosphate synthases, protein kinases, two 14-3-3 proteins, several RNA-binding proteins, transcription factors and two histone deacetylases	Critical role in role in drought signaling or gene regulation	Zhao et al. (2015)
5.	Transcriptome analysis/RNA sequencing analysis	Identification of ABA-dependent and ABA-independent regulatory networks underlying water stress	Genes related to glycolysis, abscisic acid and ethylene biosynthesis, lipid metabolism, protein degradation, and second metabolism of flavonoids were significantly induced	Fu et al. (2016)
6.	Sequence tags-simple sequence repeat (EST-SSR) markers	53 markers were significantly associated with drought-related traits.	Associated with peroxidase, superoxide dismutase, catalase, proline, aboveground fresh weight, and storage root-related traits	Wang et al. (2017)
7.	RNA sequencing analysis	A catalogue of 682 high-confidence lncRNAs	lncRNAs were associated with hormone signal transduction, secondary metabolite biosynthesis, and sucrose metabolism pathway	Li et al. (2017b)
8.	RNA sequencing analysis	1666 differentially expressed genes	Involved in the cell wall, protein synthesis, light reaction of photosynthesis, and ethylene metabolism	Zeng et al. (2017)
9.	RNA sequencing analysis	18 CC-type GRXs of which six (*MeGRXC3*, *C4*, *C7*, *C14*, *C15*, and *C18*) were induced by drought stress	ABA-mediated drought signaling	Ruan et al. (2018)
10.	Transcriptome analysis	Identified 2372 lncRNAs, and 86 autotetraploid-specific lncRNAs	Associated with galactose metabolism, pentose phosphate pathway and brassinosteroid biosynthesis	Xiao et al. (2019)
11.	RNA sequencing analysis	91 cassava POD genes (*MePODs*)	Associated with drought response and postharvest physiological deterioration	Wu et al. (2019)
12.	RNA sequencing analysis and Kyoto Encyclopedia of Genes and Genomes (KEGG)	116 DEGs involved in leaf mesophyll; 108 DEGs involved in the mid-vein vasculature	Stimulation of the biosynthesis/metabolism of amino acids, glutamic acid, starch and sucrose	Wang et al. (2021a, b)

drought episodes (El-Sharkawy 2004). The leaves became smaller with the progression of drought coupled with leaf rolling and change in leaf angle to prevent light interception and photooxidative damage (Calatayud et al. 2000). Along with leaves, stem length and thickness are greatly reduced to balance canopy growth and storage root development under drought. Balanced above-belowground growth under drought is achieved by modulating utilization of starch reserves. Non-structural carbohydrate reserves from leaves and stem are likely to be diverted to support the storage root growth under drought. It can be a potential strategy against drought stress (Duque and Setter 2013).

The employment of antioxidant system induces drought tolerance in cassava by scavenging harmful ROS generated under drought condition (Xu et al. 2013; Xu et al. 2013; Liao et al. 2016). Drought-tolerant cultivars tend to have a lower

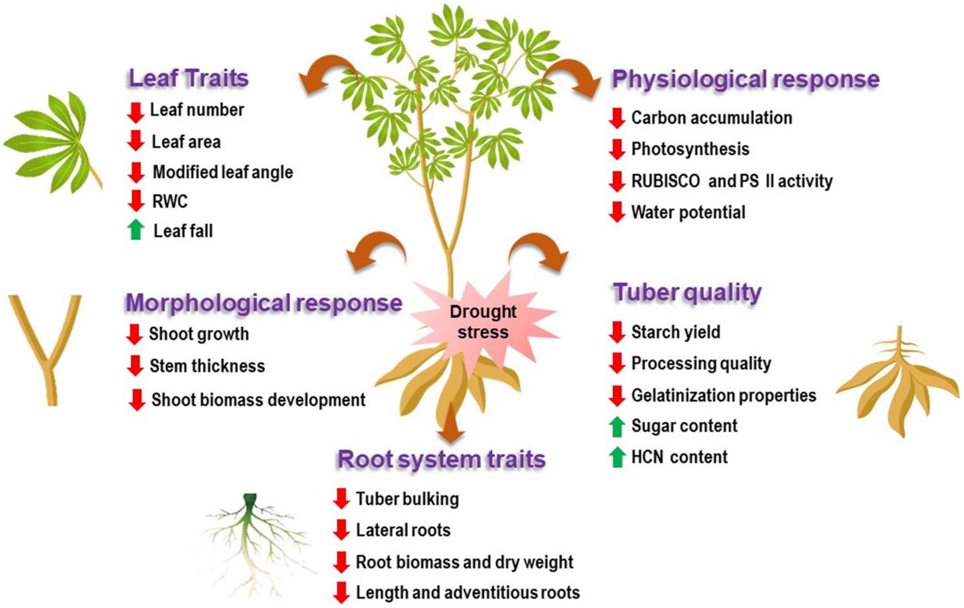

Fig. 4 Morphological and physiological responses of cassava subjected to drought stress and their effect on storage root and processing quality

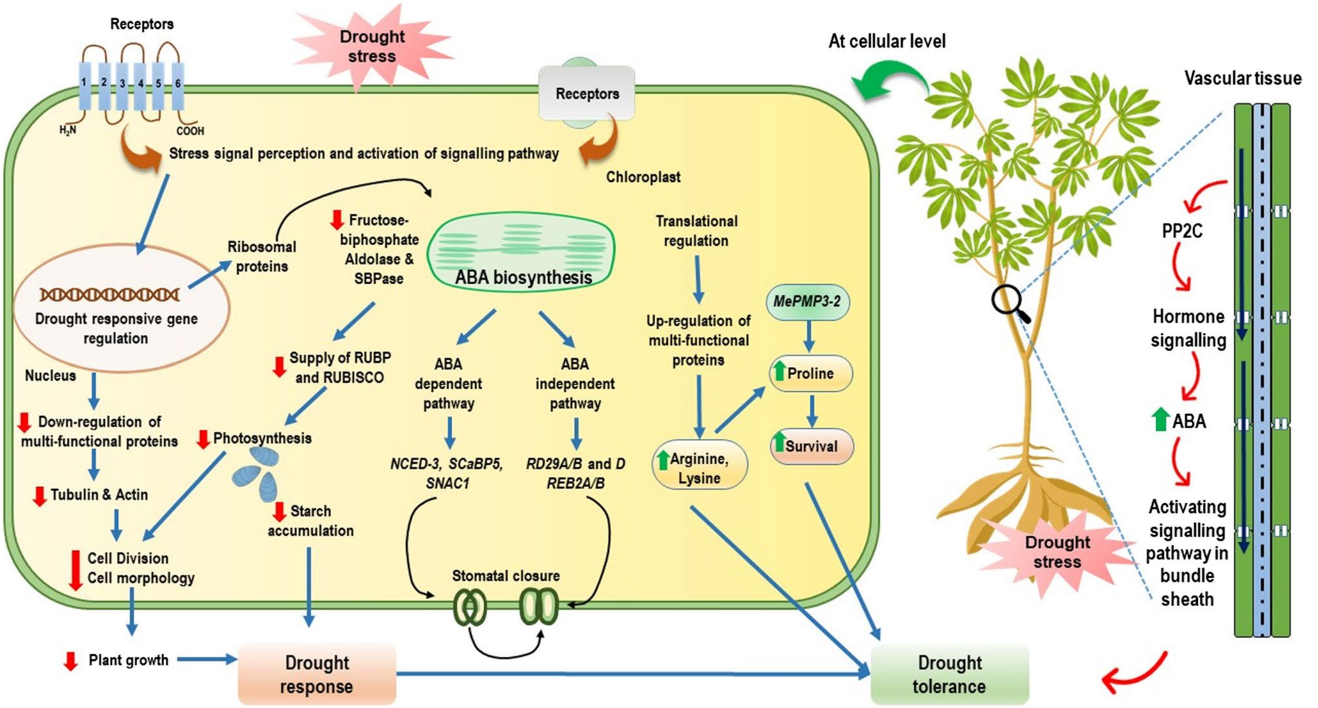

Fig. 5 Physiological and biochemical responses of cassava subjected to drought

Table 2 An overview of multi-level drought adaptation strategies of cassava

Sl. no.	Traits	Adaptation strategy	Reference
1.	Leaf	• Change in leaf angle • Leaf wilting/drooping • Leaf shedding • Higher leaf retention • Higher leaf life • Carbohydrate reserve in leaves during drought	Calatayud et al. (2000), Lenis et al. (2006), El-Sharkawy (2004), De Souza et al. (2017), Shan et al. (2018), More et al. (2020)
2.	Stem	• Higher pith density • Higher pith biomass • Higher carbohydrate reserve during drought	- - Duque and Setter (2013)
3.	Canopy	• High vigor index • Branching type canopy • Higher leaf area index	El-Sharkawy (2012), El-Sharkawy (2016), More et al. (2020)
4.	Photosynthetic efficiency	• Higher net photosynthetic rate • Stomatal closure • Increased PEPC activity • Higher carotenoid synthesis	El-Sharkawy (2004), El-Sharkawy (2007), El-Sharkawy (2012), El-Sharkawy (2016), Pereira et al. (2018), Shan et al. (2018)
5.	Biochemical	• Osmotic adjustment • Up-regulation of chlorophyll a/b binding proteins • Regulation of nitrogen metabolism • Employment of antioxidant system • Increment in PS-I and PS-II subunits (CP43 and R subunits) • Increased peptidyl-prolyl cis-trans isomerase activity • Enhanced arginine biosynthesis and 20S-19S proteasome • Up-regulation of drought-related proteins	Helal et al. (2013), Nuwamanya et al. (2014), Shan et al. (2018), Zhu et al. (2020), Wang et al. (2021a, b), Li et al. (2021)
6.	Molecular	• Regulation of *OPEN STOMATA 1 (OST1)*, protein phosphatase 2C and outer membrane tryptophan-rich sensory protein (TSPO) • Heat shock proteins • Enhanced Arginine biosynthesis • Enhanced *FtsZ2-1* and *MeSPL9* genes expression	Utsumi et al. (2019), Wang et al. (2021a, b), Li et al. (2021)
7.	Hormonal regulation	• Accumulation of ABA and ethylene	Duque and Setter (2013), Liao et al. (2016), Ogaddee and Girdthai (2019)
8.	Belowground Portion	• Higher root numbers • Higher axle length • Higher lateral root growth • Narrow root angle • Early bulking • Higher HI and sink strength • Resource remobilization particularly starch • Extensive root system	Izumi et al. (1999), Jarvis et al. (2012), Rogers and Benfey (2015), Turyagyenda et al. (2013a), Adu et al. (2020)

oxidative response than drought-susceptible cultivars (Zhu et al. 2020). According to Nuwamanya et al. (2014), cultivars with enhanced nitrogen metabolism enabled higher photosynthetic efficiency under water tress. Substantial quantities of osmolytes and biochemical factors are accumulated to maintain the physiology of plants. Proline and glycine-betaine accumulation has been found in plants after stress episodes (Ren et al. 2017; Wang et al. 2021a, b). Glutathione and ascorbic acid accumulation act as a protectant against water-stress–induced oxidative stress. Cultivars with higher mineral, osmoprotectant, osmolyte, and ascorbic acid contents had a higher degree of drought tolerance (Okogbenin et al. 2013; Zhu et al. 2020). Higher quantities of superoxide dismutase, peroxidase, catalase, ascorbate peroxidase, glutathione reductase, and ascorbic acid are part of the plant-defensive system (Zhu et al. 2020). At the molecular-genomic level, the genes, transcriptome, and enzymes expressed in cassava under drought conditions have been extensively studied and are covered in the preceding section. According to Zhao et al. (2015), boosting sucrose synthase substrate and aquaporin proteins is another technique for minimizing damage and enhancing protein stability, antioxidant activity, and secondary metabolism during times of water stress condition.

Plants under drought stress develop long deep roots as an escape mechanism to evade water stress (Okogbenin et al. 2013). A steeper root angle is associated with drought tolerance in various agronomic crops, including wheat (Comas et al. 2013), maize (Lynch 2013), and rice (Saengwilai et al. 2018). However, in cassava, wide root angle may not help in drought tolerance possibly due to the very shallow root system and complex storage root arrangements (Kengkanna et al. 2019). Accumulation of ABA and ethylene further increased the sustainability of plants under drought (Alves and Setter 2000; Duque and Setter 2013; Liao et al. 2016; Ogaddee and Girdthai 2019). Non-photochemical dissipation of energy mediated by enhanced carotenoid synthesis and enhanced PS-I and PS-II subunits (CP43 and R subunits) can be used as a protective mechanism against photooxidation in cassava (Pereira et al. 2018; Shan et al. 2018). Understanding the precise molecular, biochemical, and physiological level mechanism of drought tolerance is pivotal for enhancing storage root yield as the predicted climate change is likely to aggravate the drought intensity.

8 Key Traits for Enduring Drought Tolerance in Cassava

Selection based on highly heritable morphological, molecular, and physiological traits contributes directly to storage root yield under drought stress. Rapid storage root development followed by early bulking has been identified as one of the most important traits to enhance drought tolerance. This trait can be an effective drought avoidance strategy during early water stress period or intermittent water stress episode. Early bulking variety could have the upper hand over mid or late bulking varieties as late or mid bulking variety may not accumulate desired quantities of biomass under water limiting condition. Moreover, late bulking varieties might increase the cropping period beyond harvesting (12 months after planting in general) with serious implications in terms of storage root quality. Breeding cassava cultivars with highly regulated root system architecture with higher lateral branching density could result into drought tolerant cultivar. Additional traits like higher root length and number, dry biomass, higher axle length, and density of upper nodal roots can further intensify drought tolerance. Screening cassava genotypes for photosynthetic efficiency is easy and widely followed. Maintenance of reasonable photosynthetic rate under drought is essential to sustain higher productivity. It is suggested to breed varieties with a lower stomatal density on the abaxial surface of hypostomatous leaves in wet/humid zones or in ecosystems with short intermittent water drought episodes. On the other hand, selecting cultivars with a higher stomatal density on the abaxial surface of hypostomatous leaves would optimize water use efficiency and sustain productivity under prolonged drought period in subhumid/semi-arid ecosystems.

Selecting/development of medium or short canopy genotypes (one with developing extra branches late) with optimum LAI, HI, and PI is one of the strategies for developing drought-tolerant variety as storage root weight is positively correlated with leaf number, and cultivars that retained many leaves were high yielders. Increased leaf life under water stress is an important drought-tolerant trait. An evaluation of modern cassava cultivars based on leaf life, leaf turnover rate, leaf retention or recovery index interception efficiency of photosynthetically active radiation (PAR), and efficiency of conversion of that intercepted PAR have major opportunities for genetic improvement in water-deficient environments as it will help in sustaining optimum LAI throughout the growing season under stress. Furthermore, integrating anatomical plastic traits viz. increased epidermis thickness and blade adaxial face, increased palisade and spongy parenchyma thickness, and decreased xylem vulnerability would give additional benefit to drought-tolerant cultivars.

In the view of reduced photosynthesis under drought, the storage root bulking process becomes increasingly reliant of carbohydrate reserve in stem and leaves. Therefore, improving drought tolerance may involve selection of varieties based on regulation of carbohydrate reserves and its judicious use during drought episodes for canopy and storage root development. Additionally, increased pith density and pith biomass could serve as potential drought tolerance traits to develop drought-tolerant cultivars. The number of storage roots and storage root biomass are potential indicators of drought tolerance in cassava and should be incorporated into breeding programs. Cassava's capacity to cope against drought is associated with accumulation of osmolytes to regulate osmotic adjustment. These traits have not been explored in detail in cassava. Yu et al. (2016) developed transgenic rice plants with constitutively expressing cassava plasma membrane–specific*MePMP3-2* gene, conferring drought tolerance by upregulating stress-related genes *OsProT* and *OsP5CS*, enhanced proline content and lowered malondialdehyde (MDA) content. There is great scope for developing drought-tolerant transgenic cassava with increased *MePMP3-2* gene expression. Integrating multiple traits into a comprehensive breeding program using advanced genomic and phenotyping tools could accelerate the development of high-yielding drought-tolerant cassava varieties with increased genetic gain.

9 Conclusion

Drought limited cassava plant's productivity, by reducing leaf area, photosynthetic efficiency, biochemical parameters and quality. Phenotypic plastic responses instrumental in enhancing drought tolerance of cassava include abscission of old leaves, continued but limited photosynthetic area, highly regulated stomatal activity and starch reserve utilization, increased proline content, and modified sink-source relations. Screening and phenotyping drought adaptation traits during early stage would expedite the development of drought-tolerant varieties. While new omics-driven high-throughput techniques can be used to identify new genes linked with drought resistance, the immediate goal is to confirm the QTL and genes that have already been identified and include them in the breeding program. Starch exhibited vast portfolio of changes in its yield, quality, hydration, and functional properties. However, this aspect demands urgent intervention as very little information is available on changes in the physical, mechanical, and processing qualities of cassava starch under drought stress. In addition, these parameters should be integrated into breeding program to ensure nutritional benefits and its suitability for industrial application in the future. Furthermore, developing high-yielding drought-tolerant cassava cultivars with high starch content and low cyanogenic glucoside potential will be challenging for breeders as consumption of high HCN is associated with several diseases and disorders in humans. There remains a paucity of information on rhizospheric changes, viz., nutrient imbalance, microbial populations, and diversity associated with drought and their implications for the aboveground growth of cassava. Integrating multi-level adaptive traits and eco-physiological approaches will be essential to sustain the productivity and quality of cassava under drought stress.

Author Contribution SJM and KB: conceived the idea and design the outline of the first draft, designed the figures, and wrote the first draft. VR and RP: interpretation and critical revision. MKL: critical revision and designed the figures. AKC and KHMS: critical revision for important intellectual content and provided critical feedback. All the authors read and approved the final manuscript.

Data Availability Data sharing does not apply to this article as no datasets were generated or analyzed during the current study.

Declarations

Competing Interests The authors declare no competing interests.

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