

REVIEW

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Breeding for postharvest physiological deterioration in cassava: problems and strategies

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Abstract

Cassava is a major food crop for millions of people in Africa, Asia and South America, forming an essential food-security and income generation commodity for small-scale or subsistence farming communities. The storage root is the most important component of the crop that provides more calories than cereals. Immediately after harvest, cassava storage roots undergo complex biochemical and physiological changes known as postharvest physiological deterioration (PPD), which is influenced by genotype, environmental and agronomic factors, resulting to spoilage, rendering the storage roots unpalatable and unmarketable. This problem has remained unresolved over the years. This review describes the innovative breeding technologies which could be used to prolong cassava storage root shelf-life. In this review, we discuss the available knowledge on (i) physiology and biochemistry of cassava storage root with regard to PPD (ii) strategies for minimizing PPD in cassava storage roots (iii) traits associated with PPD tolerance as essential targets for prolonging cassava storage root shelf life, and (iv) suggestions for novel genomic tools and modern genetic and breeding approaches for prolonging shelf-life in cassava storage roots. With its extensive genomic resources including the public release of cassava reference genome sequence assembly and other and resources, and innovative plant breeding technologies, the crop offers an excellent opportunity to serve as a model to address postharvest spoilage and improve food security. Continuous improvements based on the new plant breeding technologies (genome editing, speeding breeding and RNA-dependent DNA methylation) in cassava and innovations in postharvest handling and storage of the storage roots are expected to provide sustainable solutions for PPD constraints and make cassava an important food security and nutrition and industrial crop.

Keywords: Cassava storage roots, Food security, New plant breeding technologies, Postharvest physiological deterioration

Introduction

Cassava (*Manihot esculenta* Crantz.) is the most widely cultivated storage root crop in tropical and subtropical regions of the world, serving as the main carbohydrate source after maize and rice. Cassava can grow and produce with reasonable yields in areas characterized by

low soil fertility and irregular rainfall patterns especially smallholder farmers (Ramcharan et al. 2017). Modeling studies have indicated that the crop can be highly resilient to future climate change scenarios (Jarvis et al., 2012). This offers adaptation opportunities for development and promotion of food and livelihood systems, which cannot be provided by other staple food crops Furthermore, cassava storage roots contain more than 800 g/kg starch (dry weight) (Li et al. 2017), which makes it an important raw material for production of starch, biofuel and other bio-based products including animal feed, beverages, paper,

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textiles, medicine, cosmetics, and biopolymers. Globally, over 303.6 million tons of cassava storage roots are harvested from approximately 28.2 million ha (FAOSTAT 2020). The African continent cultivates more than half of the global fresh cassava (79.8%) on 22.5 million ha; however, the continent's average yield (8.6 ton/ha) falls short of the global yield (10.7 ton/ha) (FAOSTAT 2020) and the maximum potential experimental yield (20–50 ton/ha) (Lebot, 2017). Africa's cassava output is entirely consumed domestically, which makes it prone to postharvest losses. Some reasons for lower yields include limited access to labor, poor soil quality, suboptimal agronomic practices, premature harvesting, diseases, pests. Other challenges which face cassava production include low protein and micronutrient contents, toxic levels of cyanogenic glycoside in leaves and storage roots, and short postharvest shelf-life of the storage roots, making it not a crop of choice (Bull et al. 2011). In sub-Saharan Africa, cassava productivity is severely limited by the cassava brown streak disease (CBSD) and the cassava mosaic disease (CMD), which are caused by the cassava brown streak virus and cassava mosaic virus, respectively (Mulenga et al. 2018). These two viral diseases collectively result in an annual loss of approximately US\$1 billion (IITA 2014), severely affecting the food security and nutrition of the entire region. African cassava cultivation is predominantly concentrated in West Africa (Nigeria, Ghana and Cameroon) and East Africa (Uganda, Kenya, Tanzania, Rwanda and Burundi). Upon harvesting, the cassava storage roots rapidly experience a complex biological phenomenon known as post-harvest physiological deterioration (PPD) within 12–72 h. PPD spoils the storage root quality by discolouring the vascular parenchyma to either blue/black or brown, rendering the storage root unpalatable and unmarketable, which significantly affects the crop's nutritional and economic value (Zeng et al. 2020). Progression of PPD degrades starch granules into monosaccharides, thereby destroying the structural characteristics of cassava starch of low gelatinization temperature, and high water-binding capacity and viscosity, which makes cassava starch suitable in food, feed, chemicals and pharmaceuticals applications (Li et al. 2017). Globally, postharvest losses have accounted for 19% of the total production mainly because of PPD, with losses in Asia, South America, and Africa estimated at 8, 10, and 29%, respectively (Salcedo and Siritunga 2011). Therefore, PPD is a major constraint for the subsistence as well as commercial production, and utilization of cassava, particularly in developing countries with poor road connectivity and supply chain networks.

This review discusses breeding strategies to improve cassava shelf-life, which is a target of the Sustainable Development Goal (SDG) 12.3 to reduce losses along

supply chains (United Nations 2015). We have also discussed current knowledge of phenological, physiological, biochemical, and metabolic mechanisms of PPD that can contribute to the realization of these goals. Further, we have suggested novel technologies that integrate high-throughput molecular phenotypic data obtained using genomics technologies with biological networks to increase the storage root crop's shelf-life.

Cassava storage root physiology and biochemistry during PPD

Cassava storage roots are inadvertently wounded during harvesting while the roots are detached from the stem. This mechanical wounding triggers a number of local and systemic reactions through an array of physiological, biochemical, and molecular responses to palliate the injury. In addition to inducing wound-healing processes, the responses form a barricade that protects the storage roots from potentially harmful micro-organisms. These responses include immediate reactions, such as electric signals that are immediately activated upon injury, oxidative bursts, associated cell wall reinforcements, cell wall repair (deposition of polysaccharides; callose, suberin, or aggregation of proteinase inhibitors and hydrolases), expression of injury stress-responsive genes and hormonal level adjustments. Late response due to PPD responses involve programmed cell death, and synthesis and accumulation of defence proteins and secondary metabolites (Rocha et al. 2021; Wang et al. 2019). Primarily, PPD in cassava storage roots is a physiologically active process that begins within 15 min of root wounding (Houmani et al. 2018). It is completely different from secondary deterioration caused by microbial infection, which results in rotting and softening of the root tissue (Luna et al. 2021).

Mechanisms underlying cassava root formation have not been extensively studied, unlike tuberization in potato. These mechanisms can provide insights into cassava root formation, even though the mechanisms governing root formation in the two plants might be significantly different. Cassava storage roots are parts of the root system that originate from the basal and nodal root structures (Chaweewan and Taylor 2015), whereas, potato tubers originate from stolons emanating from the basal node on the main shoot of the underground stem (Yousaf et al. 2021). Cassava root formation and growth has been postulated to occur when fibrous roots develop from the stem through formation of the vascular cambium and subsequent secondary root growth, wherein a large amount of starch is synthesized and deposited in non-lignified xylem parenchyma cells (Rüscher et al. 2021). Mechanical wounding of cassava storage roots alters their quality along with physiological, biochemical,

and transcriptional changes corresponding to the defence response systems, including those involved in signalling pathways and production of secondary metabolites. Moreover, wounding stress elicits multiple changes in primary metabolism, such as cellular respiration, photosynthesis, source-sink relations, and programmed cell death (Torres-Contreras et al. 2018; Sooklal et al. 2020). Therefore, wounding results in complex cross-talk between the primary and secondary metabolism. PPD initially occurs in parenchymal tissue, which is the edible part of the cassava storage root. PPD is characterised by discoloration of the storage root cross section to black-blue or brown (Fig. 1), followed by formation of dark streaking on the xylem vascular vessels (Fig. 1) that are associated with formation of wound-induced vascular occlusions (tyloses) in the dead xylem cells, which can be oxidized (Djabou et al. 2017). Subsequently, PPD starts affecting neighboring storage parenchymal cells causing the stored starch to undergo structural and chemical degradation to form free sugars and organic acids. Once primary PPD sets in, the storage roots become infested with microorganisms that further degrade the sugars through microbiological PPD, which is characterised by the presence of organic acids (Uarrota et al. 2015). In addition to cell death, downstream phases of PPD include callus formation to heal the gap at the wound site (Lee et al. 2018).

Several factors including cassava genotype, moisture content of the storage root, temperature, and type of invading microbes affect the type and rate of PPD. This

genetic variability is essential for plant breeding, demonstrating that considerable genetic gain is attainable by phenotypic selection for PPD tolerance. Luna et al. (2021) and Tumuhimbise et al. (2015) have revealed significant genotypic differences among cassava varieties in response to PPD stress. Another crucial factor that affects PPD is the interaction between the genotype and the environment ($G \times E$). $G \times E$ influences not only the moisture content of the storage roots, but also other important traits associated with PPD (Nduwumuremyi et al. 2017). Consequently, assessing cassava genotypes in multiple environments is critical for breeders to account for the effects of $G \times E$ interactions, before recommending appropriate genotypes for specific agro-ecological regions.

Injury to cassava storage roots through cuts and abrasions also triggers a complex metabolic machinery that responds rapidly by producing proteins and secondary metabolites to ensure physiological modifications for survival and protection of the injured tissue. Previous studies have shown that water loss and increased respiration rate are some pivotal wound-response mechanisms in lettuce (Ripoll et al. 2019), carrot (Becerra-Moreno et al. 2015), and cassava (Hu et al. 2016a, b; Marriott et al. 1978). In these experiments, water loss and increased respiration rate were found to synergistically activate the primary and secondary metabolisms of the respective plants, leading to higher biosynthesis of shikimic acid, phenolic compounds, and lignin. Not much is known about the molecular mechanisms controlling wound-induced

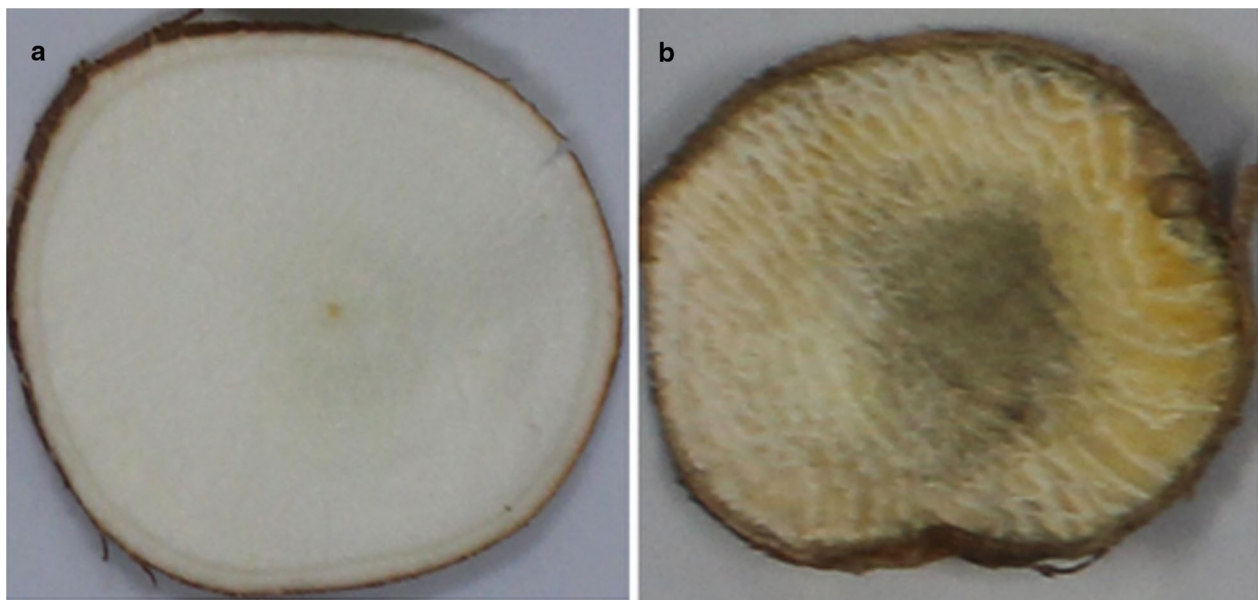


Fig. 1 Cassava roots showing progression of PPD. **a.** Freshly harvested cassava roots before undergoing PPD, **b.** Cassava roots with PPD syndrome 12 days after harvest.

biosynthesis and accretion of secondary metabolites in cassava storage roots. However, several plant hormones including jasmonic acid, salicylic acid, ethylene, and abscisic acid, as well as biomolecules including acetone, lipids, carbohydrates, catechins, phenols, leucoanthocyanidins, and reactive oxygen species (ROS) are upregulated upon tissue injury to regulate various signalling pathways, thereby alleviating the negative effects of injury stress (Guan et al. 2021). Phenolic compounds are produced in wounded plant tissues to enhance lignin biosynthesis to prevent more water loss (Ripoll et al. 2019), whereas elevated respiration activates the conversion of starch into soluble sugars. Furthermore, loss of water increases the dry-matter content in cassava storage roots, which is directly associated with PPD (Luna et al. 2021). Ethylene production increases steadily from six hours after storage root harvesting (Hirose et al. 1984), whereas emission of other volatile metabolites including ketones, cyanohydrin, aldehydes, and alcohols have been associated with PPD (Iyer et al. 2010).

During the initial stages of PPD, the produced signalling compounds trigger the biosynthesis of various metabolites associated with plant defence responses, including carbohydrates, lipids, phenolic compounds, flavonoids, carotenoids, as well as anthocyanidins and catechins in the root xylem tissue, which accelerates the rate of PPD progression (Uarrotta et al. 2014, Reilly et al. 2003). The precise roles of these bio-compounds such as flavonoids have not been investigated in PPD development because they begin accumulating after four to six days of the storage root harvest, when PPD is completely established (Uarrotta and Maraschin 2015). Another important defence response to cassava storage root tissue injury is the accumulation of the following coumarins: 6-(β -D-glucopyranosyloxy)-7-hydroxy-2H-1-benzopyran-2-one (esculin), 6,7-dihydroxy-2H-1-benzopyran-2-one (esculetin), 7-(β -D-glucopyranosyloxy)-6-methoxy-2H-1-benzopyran-2-one (scopolin), and 7-hydroxy-6-methoxy-2H-1-benzopyran-2-one (scopoletin). Of these four coumarins, scopoletin is the most abundant and its oxidation by ROS and peroxidase yields a blue-black color, confirming its predominant involvement in PPD development (Liu et al. 2017). Feruloyl CoA 6'-hydroxylase is a pivotal enzyme in the biosynthesis of scopoletin (Luna et al. 2021). It catalyses a rate limiting step of where 6'-hydroxyferuloyl-CoA is converted into coumarin scopoletin (Sun et al. 2015). Several studies have shown scopoletin as the most abundant secondary metabolite during progression of PPD. Feruloyl CoA 6'-hydroxylase has been in focus for development of cassava lines with delayed PPD. Decreases in phospholipids and glyceroglycolipids levels and accumulation of sterol-containing lipids have also been linked to PPD of cassava storage

roots (Beeching et al. 1998). Increased sterol-to-lipid ratio has been widely reported as an indicator of aging and senescence of plant tissue (Rogowska and Szakiel 2020).

Biosynthesis of ROS and reactive nitrogen species (RNS) through oxidative burst is an important response to tissue injury in plants. After mechanical injury, plant tissues discharge oligosaccharide cell wall detritus, which are crucially involved in the signalling cascades, which immediately induce local and systemic participation of ROS and RNS metabolism (Kapoor et al. 2019). Synthesis of ROS and RNS commences within minutes in response to different developmental signals and other abiotic and biotic stresses (Fichman and Mittler 2021). Some ROS produced after plant tissue injury include superoxide anion radicals ($O_2^{\bullet-}$), hydroperoxyl radicals (HO_2^{\bullet}), hydrogen peroxide (H_2O_2), hydroperoxide ($ROOH$), hydroxyl radicals ($\bullet OH$), peroxy radicals (ROO^{\bullet}), alkoxyl radicals (RO^{\bullet}), and singlet oxygen (1O_2) (Fichman and Mittler 2021). RNS involved in these responses include nitric oxide ($\bullet NO$), S-nitrosoglutathione (GSNO), S-nitrosothiols (RSNOs), peroxynitrite ($ONOO^-$), and S-nitrosogluthathione reductase (Corpas et al. 2008; Ross et al. 2006). The participation of enzymatic metabolic processes that regulate the synthesis of these essential antioxidant molecules illustrates that their redox states are crucial in the regulation mechanisms of plant cells including tissue injury responses. Although their exact connection to PPD has not been entirely elucidated, the shelf-life of cassava storage root has been extended by reducing ROS production (Zidenga et al. 2012; Noon and Booth 1977) and using scavenging molecules such as methyl jasmonate (Liu et al. 2019a, b), ethanol (Liu et al. 2019a, b), melatonin (Ma et al. 2016), and β -carotene (Sánchez et al., 2006). These few studies have demonstrated the crucial involvements of ROS and RNS in attenuating PPD. However, further investigation is required to elucidate their involvement in cassava storage root deterioration.

Plants and other eukaryotes undergo apoptosis (regulated programmed cell death), a highly regulated system wherein a cell decides when and how it dies, forming a part of the natural mechanism that functions as a survival system under stressful circumstances (Iakimova and Woltering 2018). In plants, programmed cell death is utilized for developmental functions including vascular tissue differentiation, selective stage-specific floral organ abortion in unisex plants, and suspensor decadence during seed development and organ senescence (An et al. 2019). Complex interplays between tissue injury, cellular water loss, and dark-induced apoptosis are considered to result in PPD symptoms. Wound-induced local cell death at the tissue damage site implies that apoptosis effectively

sequesters the wound using a barricade of dead cells. However, cell death occurring at sites far from the wound indicates that long-distance wound messengers get dispersed, eventually triggering tissue senescence. Apoptosis as well as related gene expression and enzyme activity have been found to be integral for wounding in lettuce (Iakimova and Woltering 2018), peach fruits (An et al. 2019), and potato (Partington et al. 1999). Therefore, it is important to determine the factors that affect PPD development in cassava roots and senescence from the perspective of apoptosis. This can be useful to elucidate the molecular mechanisms underlying PPD and senescence, in addition to improving cassava packing and storage methods.

Strategies to minimise PPD in cassava storage roots

Efforts to delay PPD in cassava storage roots that can ensure greater flexibility in marketing the crop have had limited success. In small farming communities, cassava storage roots are usually left in the ground after an optimal period of root development, and are only harvested when required for immediate consumption, processing, or sale. However, cassava is typically cultivated through mixed cropping, which makes the land utilised by the standing crop inaccessible, thereby hampering the subsequent agricultural output. Additionally, storage roots can remain in the soil for up to 36 months. Although the storage roots may grow in size, they become woody and fibrous, which reduces their palatability and lengthens cooking time (Luna et al. 2021). Roots stored in the ground are also susceptible to pathogens and uncertain weather conditions, which substantially reduces the extractable quantity and quality of starch.

Partial or total pre-harvest pruning of the cassava plant above the ground has been reported by several researchers to be effective in reducing PPD of the storage roots (Luna et al. 2021; Morante et al. 2010). Lengthening cassava storage root shelf-life through pruning method is advantageous compared to postharvest storage approaches that usually involve chemical application. However, pre-harvest pruning influences the storage root quality including considerable reductions in the dry matter and starch contents, which are essential to their texture, flavour, and general acceptability (Luna et al. 2021). This strategy can only be applied to small farms. The mechanism underlying pruning effects on cassava storage roots is still unknown and requires investigation.

Applying various compounds to plant harvests is a common practice to prolong their shelf-life, while preserving nutritional quality, flavour, and controlling chilling injury, browning, and decay (Ali et al. 2021; Nyamende et al. 2021). Pre-treatment and postharvest treatment

products that can delay PPD progression in cassava storage roots during storage can provide a solution to the entire value chain. These chemicals can modulate various plant hormones, ROS metabolism, and plant tissue respiration. Chemical compounds (Shen & Yang, 2017), plant extracts (Blasi and Cossignani 2020), nanoparticles (Niu et al. 2021), have been used to control postharvest losses.

Although preliminary findings on the use of chemical compounds such as ethanol (Liu et al. 2019a, b), calcium (Hu et al. 2018), and melatonin (Hu et al. 2018; Ma et al. 2016) to reduce or delay PPD in cassava storage roots were encouraging, they were inconclusive. Further research is required to optimise the dosage and application timings. However, the presence of chemical residues in plant products and in the environment is a global public health concern, which negatively impacts the markets. This challenge has prompted researchers to devise alternative strategies to prolong shelf-life. These strategies include thermal or non-thermal treatments with high levels of radiation, which have emerged as effective and safe alternative methods (Nyamende et al. 2021). Waxing the roots and drying the storage root chops are other approaches that are used, even though their efficacy and economic value is low (Luna et al. 2021). Minimising PPD in cassava roots through these anti-PPD procedures is challenging because they are expensive for small-scale farmers, and they are unsuitable for industrial use because of their low customer acceptance, high cost, inability to be mechanised, and their adverse effects to human health and the environment. Sustainable approaches that overcome these challenges are expected to guarantee their application. Furthermore, extensive studies are required to determine the effects of these treatments on the nutritional, sensory, and functional properties of the treated cassava roots as well as the socio-economic impacts of the treatments.

Biotechnological techniques that regulate gene expression in the storage root is a promising strategy to increase cassava root shelf-life. There are various genes that have been found to be up- or down-regulated during storage (Hu et al. 2016a, b), and their modulation at either genomic, transcriptomic, or proteomic level can effectively delay PPD. Overexpression of alternative oxidase (Zidenga et al. 2012) and co-overexpression of proteins for superoxide dismutase and catalase (Xu et al. 2013), have effectively slowed down PPD responses. Using RNAi technology, Liu et al. (2017) have completely inhibited expression the feruloyl CoA 6'-hydroxylase gene in cassava, concomitantly blocking scopoletin biosynthesis, a critical metabolite in PPD development. Recently, Beyene et al. (2020) have employed virus induced gene silencing to modulate PPD development in Cassava roots. Taken together, these findings demonstrate the great potential

of biotechnological tools in mitigating the effects of PPD in cassava roots. Application of new plant breeding technologies in efforts to prevent PPD in cassava remains to be examined.

Breeding strategies

Conventional breeding has been successful in addressing the constraints of cassava farmers and users, making it the main strategy for crop trait improvement (Malik et al. 2020). Similar to other clonally propagated crops, traditional cassava breeding is performed through phenotypic recurrent selection. Although clonal propagation facilitates the exchange of stem-cuttings, it also increases the spread of diseases; bacteria, fungi, phytoplasmas, and the most devastating viral diseases, CMD and CBSD (Mulenga et al. 2018). Cassava breeding is complicated because of the crop's high heterozygosity that produces genetically diverse progeny. Moreover, recalcitrant cross-pollination caused by poor flower setting, asynchronous and long flowering cycles, with certain genotypes not producing any flowers, making it difficult to synchronise planned crosses. Furthermore, cassava takes more than a year to establish viable seeds after crossing (Ceballos et al. 2020).

Impressive advancements in marker-assisted breeding, genomics-assisted breeding, and computational science have substantially enhanced cassava improvement programmes, including development of CMD- (Fondong 2017) and CBSD- resistant lines (Beyene et al. 2017), reducing toxic levels of cyanogenic glucosides (Jørgensen et al. 2005; Siritunga, and Sayre 2004), biofortification (Narayanan et al. 2019; Beyene et al. 2018), improving starch yield and quality (do Carmo et al. 2020; Karlström et al. 2016), and reducing PPD (Liu et al. 2017). To date, there is no cassava cultivar with a long shelf-life available for cultivation.

Although some cassava genotypes with relatively longer shelf-lives have been identified, they could not be successfully bred to delay PPD because of the polygenic nature of the PPD trait and its correlation with low water content and preferably high dry-matter content in the storage roots (Luna et al. 2021). For decades, cassava researchers have applied molecular breeding methods to discover QTL. Even with the large amounts of QTL mapping data collected so far, there is no successful application of marker-assisted breeding (MAB) strategy for postharvest attributes that have been documented. Fregene et al. (1997) have developed the first molecular map for cassava, which has been applied in QTL to map various traits. Since then, several QTL have been identified that confer different root traits such as productivity during high dry matter, drought stress, morphological and quality traits, as well as resistance to pests and diseases

(Ewa et al. 2021; Ezenwaka et al. 2020; Garcia-Oliveira et al. 2020; Masumba et al. 2017; Nzuki et al. 2017). Therefore, it is quite clear that the molecular map has assisted in speeding up the development of improved cassava cultivars. However, to our best knowledge, no QTL associated with PPD have been mapped thus far. The first tentative QTL for PPD in cassava roots were mapped by Corte's group (2002); they identified the major genomic regions that were associated with PPD.

Although MAB and genomic selection have advantages over classic breeding strategies by permitting efficient and early germplasm selection at the seedling stage, large amounts of phenotyping material and lengthy selections periods impose challenges because it can take over ten years to produce an improved cultivar (Scheben et al., 2017). For example, it took over 20 years for Beneforté to release a broccoli hybrid developed through wild allele introgression with three times higher concentrations of glucoraphanin, a metabolite with health-promoting activities (Traka et al. 2013). A longer period of breeding is expected because of the complicated genetic structure of PPD trait, which comprises several low-effect QTL that are difficult to precisely detect using genome-wide linkage and association mapping methods. The low power and accuracy of QTL discovery in mapping populations owing to the low recombination rates of chromosomes, and interactions of the environment with the QTL can be difficult to understand in QTL mapping experiments, which are often duplicated over definite growing seasons and/or environments (Cockram et al. 2018). Therefore, identifying powerful and dynamic QTL commensurate to the period taken and the heavy financial investment is a drawback of MAS. As the biotechnological methods to provide valuable insights into the biochemical and genetic mechanisms governing PPD in cassava storage roots, which can guide approaches for shelf-life extension of the harvested cassava storage roots. The publication of a high-resolution linkage map and chromosome-scale genome assembly of cassava (ICGMC 2015) provides a framework to assist in identification of markers for PPD traits.

Genetic manipulation to increase PPD tolerance in cassava storage roots

Over the years, cassava root responses to PPD have been studied at the ecological, phenotypic, cellular, physiological, biochemical, and molecular levels. Findings from these studies establish a firm foundation to mitigate the perishability of cassava roots through genetic alterations. At the expression level, microarray assays (Reilly et al. 2007) and total RNA sequencing (Yan et al. 2021) have been utilized to explicate the differential expressions of RNA transcripts and protein profiles involved in PPD

response. Moreover, PPD-related proteins (Owiti et al. 2011), microRNAs (Khatabi, et al. 2016), hormones (Liu et al. 2019a, b), ROS (Xu et al. 2013), secondary metabolites (Uarrotta et al. 2015), and QTL (Fernando et al. 2002) are crucial in PPD signalling.

The physiological changes that occur during cassava storage root development are caused by stage-dependent control of metabolic pathways, which is also reported in other plants (López-Ruiz et al. 2020; Sun et al. 2019). Several researchers have highlighted numerous genes that are crucial in dry matter accumulation, cytosolic processes, oxidative mechanisms, stress responses, programmed cell death, cellular metabolism, as well as biosynthesis and activation of protein syntheses and secondary metabolites involved in PPD specific-stage mechanisms (Uarrotta et al. 2015; Morante et al. 2010; Reilly et al. 2004). All these studies have confirmed that PPD in cassava roots is a multitrait phenomenon and the feasibility of developing cassava cultivars with delayed PPD is challenging through conventional breeding because of the complex cross-talk involved in PPD. Other alternatives include genetic engineering and synthetic biology.

Genes conferring PPD tolerance

Extensive studies conducted in tuber crops such as potato (Krunić et al. 2018), sweetpotato (Fan et al. 2021), and eggplant (Liu et al. 2021) have disclosed the regulatory mechanisms underlying carbohydrate metabolism and starch deposition in tubers, tuber wounding, and postharvest internal browning. However, the mechanisms underlying these processes in cassava can be drastically different from that of other plant species. Findings from potato and sweetpotato provide some insights on the possible regulatory mechanisms involved in PPD in cassava. Therefore, various studies have been conducted over the last two decades to unveil various important and essential genes for PPD and its components in cassava (Table 1). PPD responses in cassava storage roots are executed by various genes, transcription factors, miRNAs, long noncoding RNAs (lncRNAs), proteins, hormones, secondary metabolites, cofactors, and ions (Hu et al. 2018). More recently, the mechanisms that govern PPD development and progression in cassava roots were examined using cDNA microarray, proteomics, metabolomics, and large transcriptomic analyses (Fu et al. 2021; Zeng et al. 2020). Previously genome assembly at chromosome level, *Manihot esculenta* v6, provided genomic resource (Bredeson et al. 2016). Fortunately, a whole genome reference sequence for cassava with improved resolution and completeness *M.esculenta_v8* (GenBank Assembly Accession GCA_001659605.2) was released in 2021. The current reference sequence will provide a unifying platform for cassava research on with genome

editing using the CRISPR/Cas system, gene content and genetic variation. Nevertheless, comprehensive genome-wide expression profiling data for cassava at various PPD development stages are missing, which restricts the ability to understand the molecular responses connected to various physiological, biological, and molecular mechanisms. In order to stabilize cassava yield under various agro-ecological conditions and to reduce its storage root perishability, it is essential to investigate the changes of pan-genome genes and pathways for determining principal candidates that improve PPD tolerance in cassava.

Using the identified genes and their components, transgenic cassava plants have been developed to regulate specific metabolic or physiological processes related to PPD tolerance. For example, down regulation of MeF6'H (feruloyl CoA 6'-hydroxylase) genes using RNAi technology reduced scopoletin biosynthesis and PPD occurrence in cassava storage roots (Liu et al. 2017). Transgenic cassava plants overexpressing alternative oxidase (AOX), a cyanide insensitive gene, have exhibited extended storage root shelf-life of up to 21 days under greenhouse and field conditions by reducing ROS accumulation. The transgenic cassava lines had lower yield of the root biomass compared to wildtypes (Zidenga et al. 2012). Similarly, known-out of cytochrome P450 gene, CYP79D1 and CYP79D2 in cassava resulted in cassava storage roots with low cyanogenic glycosides but longer shelf-life than the wildtypes (Schmidt et al. 2018). CYP79D1 and CYP79D2 encode for enzymes that hydroxylates valine (95%) and isoleucine (5%) to form the N-hydroxyl derivative, linamarin, a toxic cyanogenic glucoside (Schmidt et al. 2018). Cyanogenic glycosides shorten the shelf-life of harvested cassava storage roots via cyanide inhibition of mitochondrial respiration, and associated cellular production of ROS that accelerates PPD (McMahon et al. 2022). More recently, transgenic cassava lines with silenced MeAPL3 gene displayed a substantial decrease in storage root starch and dry matter contents. Cassava storage roots with substantially low starch and dry matter contents also exhibited either considerably reduced or no PPD compared to wildtype plants (Beyene et al. 2020). MeAPL3 is key isoform that is responsible for accumulation of starch and dry matter in cassava storage roots.

Transcription factors and the components of signal transduction pathways that regulate expression of downstream regulons have been identified as crucial molecular targets to engineer complex traits such as drought tolerance (Manna et al. 2021). Although there are no examples of PPD tolerance using transcription factor components of signal transduction pathways, a transgenic tomato engineered with basic leucine zipper transcription factor SlbZIP1 (Zhu et al. 2018) serves as a relevant example. The SlbZIP1-RNAi transgenic tomato plants displayed

Table 1 Genes conferring PPD tolerance in cassava

Gene(s)	Encoded Enzyme	Function	References
MePAL1, MePAL2, MePAL3, MePAL4, MePAL5 and MePAL6	Phenylalanine ammonia-lyase (PAL)	Deamination of L-phenylalanine to (E)-cinnamate	Lim, 2019
MeC4H1	Cinnamate 4-hydroxylase (C4H)	C4H is a member of the cytochrome P450-dependent monooxygenase family (P450s) that catalyzes the hydroxylation of (E)-cinnamate into (E)-p-coumarate (also known as 4-coumarate)	Lim, 2019
Me4CL1, Me4CL2, Me4CL3 and Me4CL4	4-Coumarate CoA-Ligase (4CL)	Catalyze p-coumarate to form p-coumaroyl CoA in an ATP dependent formation of the thioester bond between coenzyme A (CoA) and its carboxyl group	Lim, 2019
MeHCT1, MeHCT2	Hydroxycinnamoyl-CoA Shikimate: Quinate Hydroxycinnamoyl-transferase (HCT)	Catalyses the transfer of the p-coumaroyl group in p-coumaroyl CoA to shikimate to produce p-coumaroyl shikimate (Hoffmann et al., 2003)	Lim, 2019
MeCCoAOMT1, MeCCoAOMT2	Caffeoyl CoA 3-O-methyltransferase (CCoAOMT)	Catalyzes the transfer of the methyl group of Caffeoyl CoA to yield feruloyl CoA	Lim, 2019
MeF6'H1, MeF6'H2, MeF6'H3, MeF6'H4, MeF6'H5, MeF6'H6 and MeF6'H7	F6'H (Feruloyl CoA 6'-Hydroxylase)	During scopoletin biosynthesis, F6'H incorporates a hydroxyl group to feruloyl-CoA, turning it to 6'-hydroxyferuloyl CoA (Liu et al. 2017)	Lim, 2019, Liu et al. 2017
MeCOMT1, MeCOMT2	Caffeic acid O-Methyltransferase (COMT)	Catalyze methoxylation of esculetin to produce scopoletin	Lim, 2019
MecCAT1 (DT883577, AF170272)	Catalase	Involved in turnover of ROS where they detoxify harmful ROS or indirectly utilise ROS in cellular functions	Reilly et al. 2007, Reilly et al. 2001
MecPX3 (DN740367, AY973612)	Secretory peroxidases	Play a role in vascular streaking reaction of PPD	Reilly et al. 2007
DT883578	Thioredoxin peroxidase	Catalyse the reduction of either H ₂ O ₂ or various alkyl hydroperoxides to water and the corresponding alcohol in the presence of thioredoxin proteins	Reilly et al. 2007
DT883579	Thioredoxin-like protein		
DT883580	Glutathione-S-transferase	Catalyse the conjugation of glutathione to a range of electrophilic, hydrophobic and cytotoxic substrates, thereby reducing their toxicity. During oxidative stress they detoxify metabolites resulting from oxidative damage such as lipid peroxidation and oxidative DNA degradation products	Rentel and Knight, 2004
DT883581	Metallothionein	ROS scavenging and metal homeostasis	Wong et al. 2004
DT883582	Quinine oxidoreductase	Break down quinones and semiquinone intermediates resulting from the reduction of quinones. Semiquinones in particular can donate electrons to oxygen, causing the production of superoxide anions	Matvienko et al. 2001
DN740363	Similar to plant auxin-induced aldo/keto reductase (AKR)	Detoxification of ROS produced during plant stress	Zhang et al. 2005
DT883583	Similar to early light inducible protein (ELIP),	Detoxification of ROS produced during plant stress	Zhang et al. 2005

Table 1 (continued)

Gene(s)	Encoded Enzyme	Function	References
DN740375	ACC oxidase sequence	Encodes a novel cassava phospholipase. Plants phospholipases are activated in response to cellular and environmental cues and play a role in signal transduction during stress responses via the formation of lipid-derived messengers, as well as in membrane remodeling and degradation	Yuan et al. 2010
DN740369	Immunophilin	Their function in plants is not yet clear; however, they are proposed to be involved in trafficking of signal proteins in plants. Several plant FKBP are induced by heat and other stress	Krishna and Kanelakis 2003
DN740364	Cysteine protease	The cysteine proteases are proteolytic enzymes involved in the hydrolysis of proteins. Specific proteases may also act as mediators of signal transduction and/or effectors of programmed cell death. They have been implicated in senescence and in response to stresses, such as drought, cold, wounding, ethylene treatment and glucose starvation	Reilly et al. 2007
DN740377	Class IV chitinase	Catalyse hydrolysis of chitin, a major component of fungal cell walls. Class IV chitinase are proposed to be involved in programmed cell death	
DT883584	Dehydrin	They are expressed during periods of water stress, or in response to other environmental stresses where osmotic stress is a component of the stress mechanism. May function as structure stabilizers with detergent and chaperone-like properties	Reilly et al. 2007 , Heyen et al. 2002
DT883585	Hsp70 sequence	Induced by a variety of stress conditions including heat shock, wounding, water deficit, ABA and cold, and could play a general role in stress adaptation	Reilly et al. 2007 , Li et al. 1994
DN740371	PIP1 type aquaporins	Regulate water permeability by increasing water permeation across biological membranes	Reilly et al. 2007
DN740353	PIP2 type aquaporins		
DN740350	Gamma adaptin	Subunits of adaptor protein complexes, which are involved in intracellular vesicle transport	Reilly et al. 2007 , Krishna and Kanelakis 2003
DN740360	Pyrophosphatase (H ⁺ PPase)	Hydrolyses pyrophosphate, a by-product of metabolic processes such as protein, starch and cellulose synthesis, coupled to active proton transport across the vacuolar membrane and leading to acidification of the vacuole	Reilly et al. 2007
DT883571	ATP/ADP translocase	An anti-porter of the inner plastid and mitochondrial membrane. ATP is usually exported to the cytoplasm and ADP imported for further ATP synthesis	Reilly et al. 2007

Table 1 (continued)

Gene(s)	Encoded Enzyme	Function	References
DT883569	Xyloglucan endotransglycosylase (XET)	Breaks and join xyloglucan polymers, the major hemicellulose of the primary cell wall, thereby reinforcing the wall during growth and in response to mechanical strain	Reilly et al. 2007, Antosiewicz et al. 1997
DT883565	Uridine diphosphate (UDP)-glucose dehydrogenase	Up-regulated in response to wounding and involved in biosynthesis of sugar nucleotides required for biosynthesis of hemicellulose components	Reilly et al. 2007, Tenhaken and Thulke 1996
DN740379	Germin-like protein (GLP)	Cell wall remodeling during both development and stress responses though exact nature of their role in these processes is unclear	Reilly et al. 2007, Mathieu et al. 2003
AOX1A	Alternative oxidase cyanide-resistant terminal oxidase	Lowers mitochondrial reactive oxygen production in plant cells	Zidenga et al. 2012
CYP79D1, CYP79D2	Cytochrome P450 enzymes	Involved in the synthesis of the cyanogenic glycosides linamarin and lotaustralin in the root	Reilly et al. 2007, Andersen et al. 2000
DT883570	Cytochrome b5 reductase	Proposed to act as a direct or indirect electron donor in the biosynthesis of products such as sterols, terpenoids and gibberellic acids	Reilly et al. 2007, Martsinkovskaya et al. 1999
DN740366, DT883564	UDP glycosyltransferases	Biosynthesis of disaccharides, oligosaccharides and polysaccharides and catalyze the formation of glycosidic bonds	Reilly et al. 2007
DT883572	Enzyme L-asparaginase	Involved in asparaginase hydrolysis in plants. Ammonia is released in the reaction and is utilized for the synthesis of nitrogen containing compounds, including amino acids required for protein synthesis	Reilly et al. 2007, Casado et al. 1995
DT883574	Ketol-acid reductoisomerase	An enzyme involved in synthesis of branched chain amino acids including isoleucine and valine	Reilly et al. 2007, Dumas et al. 1993
DT883573	Transaldolase	An enzyme of the non-oxidative branch of the plant pentose phosphate pathway that is involved in transfer of carbohydrates from primary to secondary metabolism allowing synthesis of aromatic amino acids, flavonoids and lignin	Caillau and Quick 2005
DT883575	Arginine decarboxylase	Involved in the synthesis of putrescine in response to plant stress and wounding	Perez-Amador et al. 2002
DN740380	Auxin-repressed protein-like protein ARP1	Potential roles in signal transduction or perception	Reilly et al. 2007
EC591276	GTP-binding protein	Potential roles in signal transduction or perception	Reilly et al. 2007
EC591277	Nuclear transport factor, putative	Potential roles in signal transduction or perception	Reilly et al. 2007
EC591278	Cell wall-plasma membrane linker protein	Potential roles in cell wall metabolism and remodeling	Reilly et al. 2007
EC591279	Translation initiation factor	Roles in transcription or translation	Reilly et al. 2007
EC591280	Putative ribosomal protein L10a	Roles in transcription or translation	Reilly et al. 2007

Table 1 (continued)

Gene(s)	Encoded Enzyme	Function	References
EC591281	Structural constituent of ribosome	Roles in transcription or translation	Reilly et al. 2007
EC591282	Nucleic acid binding	Roles in transcription or translation	Reilly et al. 2007
EC591275	Electron transporter/thiol-disulphide exchange	Roles in protein modification	Reilly et al. 2007
EC591283	Polyubiquitin	Roles in protein modification	Reilly et al. 2007
DN740383	Arabidopsis expressed	Role unknown or uncharacterized	Reilly et al. 2007
EC591291	Unknown protein	Role unknown or uncharacterized	Reilly et al. 2007
EC591292	Conserved hypothetical protein	Role unknown or uncharacterized	Reilly et al. 2007
EC591284	Unknown protein	Role unknown or uncharacterized	Reilly et al. 2007
EC591285	Unknown protein	Role unknown or uncharacterized	Reilly et al. 2007
EC591286	Unknown protein	Role unknown or uncharacterized	Reilly et al. 2007
EC591289	No protein match	Role unknown or uncharacterised	Reilly et al. 2007
EC591290	No protein match	Role unknown or uncharacterized	Reilly et al. 2007
EC591287	M. esculenta allergenic-related protein Pt2L4I	Role unknown or uncharacterized	Reilly et al. 2007
DT883602	Translationally controlled tumour protein	Role unknown or uncharacterized	Reilly et al. 2007
DT883603	Cystatin-like protein	Role unknown or uncharacterized	Reilly et al. 2007

reduced tolerance to drought and salinity stresses compared to the wildtype plants by evaluating various physiological parameters associated with stress mechanisms, such as decreased abscisic acid, chlorophyll content, and catalase activity, as well as increased malondialdehyde content. Metabolic engineering to regulate contents of intracellular organic osmolytes was successful in several plants subjected to abiotic and biotic stresses, albeit the actual benefits of such an approach are debated (Baillio et al. 2019). Lei et al. (2017) have reported differential phytogetic and expression patterns of TCP transcription factors in cassava seedlings exposed to cold and drought stress conditions. These analogies serve as an applicable approach to mitigate the adverse effects of PPD in cassava storage roots.

Harnessing wild relatives for cassava improvement

The genus *Manihot* from the Euphorbiaceae family is considered to comprise about 98 species spread throughout the Central and South America. *Manihot flabellifolia* and *Manihot peruviana* are believed to be the primary gene pool for domesticated cassava (Allem 1999). Cultivated cassava, *Manihot esculenta* ssp. *esculenta*, was domesticated from *M. esculenta* ssp. *flabellifolia*. Its hybridizing relative, *M. pruinosa* has no contribution to the germplasm of cassava. However, *M. pruinosa*, is considered the nearest species to the primary cassava gene pool and can barely be separated from its wildtype strain *M. flabellifolia* based on morphological characteristics (Allem et al. 2001). Comparative genome-wide analyses between wild relatives and cultivated cassava varieties have revealed that wild cassava relatives have more genetic variation than the cultivated cassava (Zou and Yang 2019; Wang et al. 2014). Unfortunately, some wild relatives of cassava are on the verge of extinction, and may be extinct in the near future (Nassar et al. 2007). This will deprive the gene reservoir for cassava breeding programs. Natural hybridization occurs among wild *Manihot* species as well as between them and domesticated cassava varieties. For example, controlled crossings of cassava with *M. glaziovii*, *M. pseudoglaziovii*, *M. aesculifolia*, *M. pilosa*, *M. dichotoma*, *M. pohlii*, *M. neusana*, and *M. anomala* yielded interspecific hybrids. However, the frequency was low (Nassar et al. 2007).

Successful interspecific hybridization of cassava genotypes and *Manihot walkerae* for delayed PPD (Morante et al. 2010) signify that genetic improvement for PPD tolerance can be accomplished by using wild relatives. However, cassava domestication has resulted in a number of fundamental features that distinguish modern cultivated cassava from its inedible wild ancestor (Piperno et al. 2006). Consequently, using wild cassava progenitors may be a disadvantage to broaden the genetic pool for cassava

pre-breeding, as opposed to using them directly in MAB approaches, because of the adverse effects of linkage drag of interspecific hybrid progenies (Ewa et al. 2021).

Genomics-informed breeding of cassava root for long shelf-life

Genomic selection

As an alternative to MAB, genomic selection that uses all molecular markers for genomic-enabled prediction of the performance of the candidates for selection, facilitates an accelerated selection of superior genotypes, thereby expediting the breeding cycle. This presents a unique opportunity to develop cassava varieties with longer shelf-lives and higher storage root yields in a short period of time. Genomic selection integrates genotypic (first) and phenotypic (trait of interest) data in a population referred as 'training population', to predict genomic estimated breeding values of individuals within a testing population, usually genotyped, but not phenotyped (Gaynor et al. 2017). As global climate change continues to cause more intense and frequent environmental variations than before, the stability for complex traits is crucial. Several studies have proposed various concepts and statistical methodologies to assess trait stability. The genomic estimated breeding values can be evaluated using only genotypic data from a collection of breeding material, allowing for speedy selection of appropriate breeding material. The relative cost effectiveness of high-throughput genotyping-by-sequencing over the last decade has supported large-scale genotyping, making genomic selection attainable. Although genomic selection has the capability of speeding up marker-assisted-breeding, this strategy is still constrained by the following three main factors: (i) genotyping costs are still high and unavailable to developing countries where cassava is predominantly grown, (ii) crop generation time and existing genetic variation of cassava cultivars, and their sexual incompatibility with wild relatives, (iii) lack of definite guidelines for implementation of genomic selection in a breeding programme. Although wild relatives of cassava present a large pool of new allelic variations, it also presents an additional burden of ensuring that only favourable loci are introgressed, because of disadvantages of genetic linkage drag (Cobb et al. 2019), as witnessed during the development of Beneforté.

Speed breeding

New breeding technologies aim to shorten plant generation periods, thereby increasing genetic acquisition by reducing breeding cycles. One such technology, termed as "Speed breeding", or rapid generation advancement, shortens the breeding cycle by adjusting environmental conditions such as temperature, prolonged photoperiod,

humidity control, plant growth regulators such as gibberellic acid, and use of haploids to maximize the rate of development and flowering of plants thereby, quickening the genetic gain (Ghosh et al. 2018). Speed breeding has been applied effectively in long-day crops such as barley, wheat, canola, chickpea (Ghosh et al. 2018), and some few short-day crops plants such as soybean (Nagatoshi and Fujita 2019) and peanut (O'Connor et al. 2013). To date, no speed breeding technique has been applied for cassava. Therefore, there is an urgent need to formulate a cassava genotype-independent high-density planting to trigger early flowering for speed breeding. Accelerated breeding of cassava will be instrumental for crop research and breeding, particularly in introducing traits in response to emerging threats and needs.

Genome editing

Targeted mutagenesis, commonly known as genome editing, have revolutionized plant functional genomics research and their genetic improvement. These technologies that utilize various endonucleases to introduce site-specific DNA double-stranded breaks in the genome including meganucleases (Grabher and Wittbrod 2007), zinc finger nucleases (Kim et al. 1996), transcription activator-like effector nucleases (TALENs) (Christian et al. 2010), and CRISPR/Cas (Jinek et al. 2012), have made it possible for targeted genome modifications. The precision, simplicity, and affordability of using RNA-based CRISPR/Cas systems has emerged as more robust and convenient than protein-based techniques, facilitating the extensive use of the CRISPR/Cas systems to generate genome-edited plants. CRISPR/Cas technology's ability to perform multiplex genome editing, (simultaneous targeting of multiple related or unrelated targets) is greatly appealing, especially for complex and multigenic traits such as PPD. For example, four genes were simultaneously edited *Setaria viridis* in multiplexed CRISPR/Cas9 (Weiss et al. 2020). Achieving such a goal using MAB could take a long period of time rather than a single event. CRISPR/Cas technology could therefore be the most significant advancement in plant breeding since the Green Revolution; it will most certainly become the standard tool of crop breeding in future. CRISPR/Cas genome editing approaches also facilitate the modification of traits in plants that are difficult to acquire through conventional breeding approaches such as cassava, leaving no traces of foreign gene(s). The technology has already been applied to make profound discoveries in plant biology research, and it holds enormous promise for development of novel crops with preferred characteristics.

So far, CRISPR/Cas approaches have been used in precision plant breeding for yield improvement,

enhancement of crop resistance to biotic and abiotic stresses, and quality attributes through gene knock-outs (Shen et al. 2017), knock-ins (Asano et al. 2021), insertions (Svitashev et al. 2015), and replacements (Yu et al. 2017). Several reports of application of the CRISPR/Cas system in cassava currently exist (Gomez et al. 2019; Mehta et al. 2019; Rybick et al. 2019; Odipio et al. 2017). First, Odipio et al. (2017) successfully edited the phytoene desaturase gene using CRISPR/Cas9. Later, multiplex targeting of cassava eIF4E isoforms nCBP-1 and nCBP-2 reduced the severity and incidences of CBSD symptoms (Gomez et al. 2018). These practical cases exemplify the utility of CRISPR/Cas systems for stopping PPD progression. With the discovery of alternatives to Cas9 nuclease, such as Cpf1 (formally named Cas12a) and C2c1/2/3 which have higher precision, these variant proteins have expanded their applications (Nakade et al. 2017). CRISPR/Cas genome editing has been touted as the frontier for precision cassava breeding (Juma et al. 2021) and the great excitement towards CRISPR/Cas methods will also potentially assist in identifying unknown genes, that when edited, can generate cassava phenotypes with longer shelf-life. Combining CRISPR/Cas approaches and the traditional breeding methodologies will greatly expand the potential of genome-edited crops and their commercialization. One of the drawbacks of genome editing is the social politics and differential regulatory regimes that will probably restrict their application. The stringent and under-developed regulatory regimes in Africa pose a significant barrier to realize the potential of biotechnological technologies to enhance small-scale farmer livelihoods. A matter of great concern is how products of gene editing will be governed by African regulatory authorities as the development and application of such technologies will outmatch the statutory abilities and competences needed for prompt delivery to consumers. Although the European Union has a precedence on how to deal with genome edited products, African scientists, and all stakeholders should engage with regulators constructively on regulatory regimes of genome editing research and gene-edited plants to ensure that African farmers benefit from these revolutionary technologies in order to tackle the challenges facing cassava production. Other genomic based new plant breeding technologies such as RNA-dependent DNA methylation and cisgenesis should be explored to control PPD in cassava.

High-throughput phenotyping

Conventional phenotyping methods which rely on manual measurements and visual observation and scoring remains a technological challenge. As an alternative, deployment of high-throughput phenotyping pipelines that are faster, provide accurate assessment of plant

phenomes and they can be amenable to farm sizes, field conditions, and experimental designs in crop breeding programs is recommended. Application of high-throughput phenotyping tools has been shown to be effective for dissecting the genetic architecture in rice (Kim et al. 2020), canola (Knoch et al., 2020) and potato (de Jesus et al. 2021).

Some of the high-throughput phenotyping platforms include near-infrared and mid-infrared spectroscopy and hyperspectral imaging (Araus et al. 2014). A robust, simple and non-destructive high-throughput phenotyping platform known as CIAT Pheno-i, which is based on unmanned aerial vehicles and automated image processing was developed to monitor above and below-ground features in cassava (Selvaraj et al. 2020). Based on the proven records, efficient high-throughput phenotyping tools are therefore valuable in developing new improved cassava varieties for multiple traits including storage root quality traits, disease and pest resistance and tolerance to abiotic stresses, to mitigate the effects of climate change and address consumer and market preferences. Adoption of these high-throughput phenotyping techniques can require colossal investments. This therefore calls for development of affordable tools that can be used in mangy geographical locations, especially in remote regions to reduce transportation costs.

Conclusions and future prospects of mitigating PPD

Cassava storage roots will continue to remain an important calorie crop, widely consumed in countries along the tropics, especially in sub-Saharan Africa. As a result, supplying fresh and high-quality cassava roots with a longer shelf life is a major challenge, however, having such varieties will be highly beneficial for small holder farmers, industrialists and scientists. Despite the potential of cassava, postharvest quality traits have not been prominently factored in its breeding programs. To make an expeditious advancement in cassava PPD breeding, considerable germplasm and molecular tools are presently available. These include a reference genome, multiple cassava germplasm and wild relatives, an assortment of markers and sequence resources deposited in various genebanks, as well as cassava tissue culture, genetic engineering, and genome editing protocols. The future prospects of cassava PPD breeding should combine novel high-throughput phenotyping platforms with different innovative multi-omics-based genotyping technologies, and utilizing novel advanced and automated mathematical models to analyse the collected data to elucidate the biochemical and genetic mechanisms underlying complex plant traits, such as PPD tolerance. It will also be of

interest to focus on traits for CMD and CBSD resistance, nutrition, reduced cyanogenic compounds, and postharvest longevity, in delivering sustainable, high quality storage roots for the future.

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Author contributions

WM conceptualized and critically edited the manuscript for publication. WM and AM undertook the literature review and analysis and wrote the manuscript. Both authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on request.

Declarations

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Not applicable.

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Competing interests

All authors declare that they have no relevant financial or non-financial interests to disclose.

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