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Post-harvest physiological deterioration of cassava (*Manihot esculenta*) – A review

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ABSTRACT

Cassava (*Manihot esculenta* Crantz) is a valued root crop grown throughout the tropics for food, feed and biofuel and industrial uses. Fresh cassava roots have short shelf-life due to an endogenous phenomenon called Post-harvest Physiological Deterioration (PPD). The estimated losses fresh cassava roots due to PPD is nearly 1/3rd of total harvest world-wide. PPD symptom starts within 24 hr after harvest, initially as blue black discolouration in the storage parenchyma which quickly spread to entire root. The roots become unfit for consumption within 2-3 days after the harvest in most cases. Several lines of evidence suggest that the PPD of cassava roots is an enzymatic, endogenous oxidative process. Reactive Oxygen Species (ROS) have been shown to increase very early during PPD and strongly correlated with the symptoms and also evidenced by the active involvement of key ROS enzymes during PPD. Increase of phenolic compounds in freshly harvested roots (e.g. scopoletin), accumulation of H_2O_2 and other wound induced changes and inherently low protein content of roots tissue are also implicated for the rapid deterioration. Conventional PPD managements like waxing of fresh cassava roots and polybag storage with suitable fungicides are normally recommended and offer relief to certain extent. Efforts to breed delayed PPD in cassava had met with little success. Several attempts to manipulate the ROS metabolism through recombinant technologies proved little success at field level. Understanding the wound response of cassava roots and its signalling network is essential to evolve strategies to delay the PPD and prolong the shelf-life of fresh cassava roots.

Key words: Cassava, Post-harvest physiological deterioration

Cassava (*Manihot esculenta* Crantz) is ranked as the sixth most important food crop and consumed by 800 million people worldwide (Lebot 2009). The storage roots are edible as they are the main carbohydrate storage organs and stores up to 85% starch on dry weight basis. The starchy roots of cassava are the staple food consumed by large populations and it is the fourth most important crop in developing countries. It is an attractive commercial crop for small-scale farmers with limited resources and can grow well even in marginal soil (Ceballos *et al*. 2004). It is a subsistence crop in many parts of the world, as well as industrial crop for the production of starch, biofuel and animal feed (Beeching *et al*. 2002). The crop is well adapted to traditional mixed cropping agricultural systems and subsistence farming system. Cassava crop can withstand multiple stresses and thereby helps the farmers to minimize the risk of total crop failure (FAO 2013). The estimated increase in global harvested area of cassava was 44% between 1980 and 2011, from 13.6 to 19.6 million ha, respectively, which is the maximum increase among the world's five major food crops (FAO 2013). The global harvest in 2013 was more than 278 million tonnes, representing a 60% increase since 2000 and an annual growth rate double that of the previous two decades. It is the cheapest source of calories for both human nutrition and animal feeding (Tonukari 2004). Cassava production in India assumes significance due to its highest productivity in the world (35.65 tonnes/ha) with a cultivated area of 220 000 ha and producing 8.14 million tonnes during the year 2014 (FAOSTAT 2016). It is one of the most efficient producers of edible carbohydrates among the world's major food crops. It is estimated that cassava yields more energy per hectare (1045 KJ/ha) than other major crops (Montagnac *et al*. 2009). Global cassava production is expected to increase further due to increasing demand as food, feed and its value as raw material for industrial proposes, particularly in Africa (Tonukari 2004). Cassava roots are processed in a variety of ways like boiling, mashing, frying and drying and are widely used to produce granules, flour and chips that have a seemingly endless list of food and feed applications. In Asia and South East Asia, cassava is grown mainly for animal feed, biofuel and raw material for industry. The industrial demand is increasing for the production of sweeteners, organic acids, alcohol,

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biodegradable plastics and biofuel mainly ethanol (Balat and Balat 2009, Janssen *et al*. 2009). Hence, it is a versatile, food, feed and industrial crop of 21st century for food security and climate change (FAO 2013).

Post-harvest physiological deterioration of cassava roots

PPD is a complex phenomenon which involves an elaborate network of cellular functions occurring simultaneously in the harvested cassava roots. Harvested cassava roots are highly perishable and undergo rapid deterioration within 48-72 h after harvest. The roots can't be stored satisfactorily for more than two to three days under ambient conditions as they become unfit for human and animal consumption and also for industrial uses. PPD depends on the genotypic as well as the environmental conditions and is followed by microbial infection (Ravi and Aked 1996, Reilly *et al*. 2004). The deterioration of cassava roots generally starts with a black-blue to black vascular discoloration (vascular streaking) which quickly spreads to the parenchyma tissue. PPD results in sizeable quantitative and striking qualitative post-harvest losses of the fresh cassava roots.

PPD of cassava is recognized as one of the major constraints for expansion of its cultivation in many parts of the world (Sayre *et al*. 2011). PPD is a major constraint when cassava is processed on industrial scale or when transported long distances to reach the industry and consumers (Westby 2002). Earlier estimates peg the losses due to PPD in cassava to be in the range of 5–25% of the total expected value of the crop. Recently, an estimate by Rudi *et al*. (2010) envisages the economic benefits of extending the shelf life of cassava to several weeks would reduce financial losses by $2.9 billion in Nigeria alone over a 20-year period. The traditional practice of partial harvesting of roots in subsistence farming communities can delay the complete use of the roots per cassava plant, but the practice is unsuitable for commercial cultivation. Furthermore, the remaining roots after partial harvest, are subjected to a loss of starch content, decline of palatability due to the increase of fibre content and an associated increase in cooking time. High temperatures >30°C prevailing in India hastens PPD of cassava root, which is again a major concern in the context of climate change. Increasing the shelf-life of cassava storage roots is desirable not only to solve problems of utilization and marketing but also to facilitate the conversion of cassava from a traditionally rural food staple to a commercial crop. Therefore, research directed towards introducing resistance to PPD, or delaying its progress, is considered a priority by international bodies such as the Food and Agriculture Organisation of the United Nations (FAO) and the Cassava Biotechnology Network and ICAR-Central Tuber Crops Research Institute had initiated multipronged strategy to overcome the problem of cassava PPD.

At present, evaluation of PPD of roots is subjective and mainly based on visual symptoms. With a increasing demand for cassava genotypes for low PPD and longer shelf-life, there is an urgent need for an objective technique to screen the genotypes. To develop an appropriate method to evaluate PPD that is both practical and quantitative and links phenotypic tolerance/susceptibility to PPD level, understanding the biochemical and molecular pathways associated with PPD and its components will be helpful. This article reviews the recent advances on understanding PPD of cassava roots and focuses on the future road map for achieving PPD tolerance/resistance in cassava.

Role of phytohormones in wound signal transduction and PPD response

PPD of cassava root is considered as a complex abiotic wound response (Westby 2002, Beeching *et al*. 2002). Being a root and storage organ for photosynthates with no regenerative function, cassava roots lack the biological requirement to repair wounds when detached from the plant (Reilly *et al*. 2004). The development of PPD throughout the storage tissue of cassava root after wounding while detaching from the plant suggests the transmission of intercellular signals from the site of damage to distal region. Mechanical wounding and subsequent pathogen infection in plants may involve the induction, perception and transmission of wound signals which are capable of inducing defence related gene expression. Wound activated responses directly to the plant for the healing of damaged tissues and the activation of defence mechanisms that prevent further damage by inhibiting the defence signals. The defence signalling pathways are mediated by many structurally different molecules including the oligopeptide *systemin*, molecules with hormonal activity such as jasmonic acid (JA), salicylic acid (SA), ethylene (Reymond and Farmer 1998) and hydrogen peroxide H_2O_2 (Orozco-Cardenas and Ryan 1999) which further orchestrate the induction of defence responses. Cassava, like all other plants rely on various defence mechanisms for protection against injury from insects, microorganisms or mechanical wounding. Cassava storage roots are essentially predisposed to wounding that usually accompanies harvesting and handling. Physiological deterioration of cassava storage roots shares many features of plant wound responses; however, the wound repair and subsequent down modulation of the signals necessary for restoration of integrity of damaged tissues are inadequate in cassava roots. This deficiency leads to continuous cascades of wound responses that spread through the entire root. Interestingly, wounded cassava roots that remain attached to the plant are capable of normal wound repair, suggesting that an efficient wound repair mechanism of the detached root was lost during evolution because the root has no biological function once detached from the plant.

Ethylene levels in damaged cassava roots increased after an initial lag period of 6 h and the levels remained high over a 22 h period**.** Ethylene levels in cassava peaked after 16 h lag period. Pre-harvest pruning of cassava shoot suppressed root PPD development (van Oirschot *et al*. 2000). However, pre-harvest shoot pruning had no significant influence on ethylene production following wounding and the exogenous application of ethylene on wounded roots does not affect the wound responses (Bleecker and Kende 2000, Wang *et al*. 2002). These observations led to the speculation that ethylene may be involved albeit indirectly in signal transduction during PPD. The ACC oxidase gene associated with ethylene biosynthesis was up-regulated during cassava root PPD**.**

The rapid appearance of vascular streaking in harvested cassava roots is a result of membrane destabilization resulting in a loss of cellular compartmentation. Lipid changes in harvested cassava roots have shown a progressive decline in phospholipid content indicating membrane degradation. These changes indicate structural alterations to membranes which may allow the interaction of substrates and enzymes producing dark streaking. The role of SA and JA in wound response in cassava is not fully understood and warrants investigation.

Enzymatic activity during PPD

Several key enzymes of the phenylpropanoid pathway including activities of phenylalanine ammonia lyase (PAL), cinnamate 4-hydroxylase were induced after harvest of cassava root. Levels of peroxidase involved in biosynthesis of lignin as well as detoxification of hydrogen peroxide were lower in cassava. Several enzymes were shown to be differentially regulated during PPD. The increase in PAL activity closely followed the progress of cassava root PPD, and peaked after approximately 2 days after wounding. Peroxidases at the wounded site of cassava root act upon the phenolic compounds generated by PAL. Apparently, accumulation of the PAL occurs by *de novo* synthesis and is induced after a 24 h lag period. Using sequentially sectioned cassava roots, it was found that superoxide dismutase (SOD), catalase, and peroxidase were predominantly expressed in regions adjacent to the wound site. Emissions of aldehydes, derived from fatty acid oxidation, have been detected from harvested cassava root (Iyer *et al*. 2010). Given the detection of aldehydes and only trace quantities of alcohols at 3 h after root detachment, the ADH pathway appears to operate during cassava root PPD. Recently, Uarrota *et al*. (2016) found increased activities of ascorbate peroxidase (APX), guaiacol peroxidase (GPX) in the stored roots during PPD and correlated with antioxidant mechanism against ROS. They also indicated a potential role of proteins in PPD delay by the negative correlation between PPD and total proteins.

Gene expression and molecular response to PPD

Several transcripts involved in important biochemical and physiological processes are associated with PPD in cassava root (Huang *et al*. 2001). In an attempt to identify the entire subset of genes that are differentially regulated in cassava during PPD, Reilly *et al*. (2007) carried out a large-scale cDNA microarray analysis of the cassava root transcriptome. They found 72 differentially regulated ESTs, of which 63 were upregulated and 9 were downregulated. Many of the upregulated PPD-specific ESTs were predicted to play roles in cell wall repair, reactive oxygen species (ROS) generation and turnover, programmed cell death, ion/water/metabolite transport, signal transduction, stress response and metabolism, and protein synthesis. Vanderschuren *et al*. (2016) identified significant abundance of 300 proteins involved in oxidative stress, phenylpropanoid biosynthesis (including scopoletin), the glutathione cycle, fatty acid oxidation, folate transformation, and the sulphate reduction II pathway during cassava PPD. Transgenic cassava overexpressing a cytosolic glutathione peroxidase in storage roots had delayed PPD and reduced lipid peroxidation as well as decreased H_2O_2 accumulation (Vanderschuren *et al*. 2016). Cinnamyl-alcohol dehydrogenase involved in coumarin synthesis, was downregulated during PPD. Cassava variety having high susceptibility to post-harvest deterioration showed higher formate dehydrogenase (involved in the oxidation–reduction process and the wounding response) protein abundance (Schmitz *et at*. 2016). However, the early events in the PPD development and molecular mechanism behind the events linked to wound response is still poorly understood.

Role of low molecular weight secondary metabolites during PPD

The blue/black product synthesized during PPD is due to the oxidation of hydroxycoumarins (secondary metabolites that are involved in plant defence and include esculetin and scopoletin) with hydrogen peroxide (H_2O_2) by peroxidases. Hydroxycoumarins are fluorescent and can be visualised under ultraviolet (UV) light. Application of phenolic compounds to freshly harvested root sections revealed that only scopoletin caused a rapid and intense discolouration indicative of PPD. The synthesis of scopoletin, via. the phenylpropanoid pathway increased during PPD, peaking 24 h after harvest, before gradually returning to basal levels in subsequent days (Buschmann *et al*. 2000). However, no correlation between fluorescence intensity and PPD severity was observed after five days storage. This discrepancy was attributed to hydroxy coumarins accumulation and gradual degradation of their content prior to symptom development (Salcedo *et al*. 2010). The involvement of scopoletin in defence and PPD was implicated further because, PAL a key enzyme in its production was up-regulated following treatment of cassava cell suspension cultures with pathogens including *Fusarium oxysporum* (Gómez-Vásquez *et al*. 2004). Increase in activity of PAL was detected within 24 h after harvest of cassava root (Owiti *et al*. 2011). Similarly, a 17% increase in PAL activity has been also reported in sweet potato following wounding and storage for two days at 15°C (Reyes *et al*. 2007).

Melatonin (N-acetyl-5-methoxy tryptamine) significantly delayed PPD and reduced the accumulation of hydrogen peroxide (H_2O_2) while increasing the activity of superoxide dismutase (SOD), catalase (CAT), and glutathione reductase (GR), but not ascorbate peroxidase (APX) (Ma *et al*. 2016). Further expression of copper/zinc *SOD* (*MeCu/ZnSOD*), *MeCAT1,* glutathione peroxidase (*MeGPX*), peroxidase 3 (*MePX3*), and glutathione S-transferases (*MeGST*) was higher in cassava roots treated with 500 mg/l melatonin than in those not exposed to exogenous melatonin. Tocopherol which can scavenge reactive oxygen and interacts with other antioxidants (e.g. ascorbate) and phytohormones did not have relation with cassava PPD, whereas acidic polysaccharides may act as barrier components of plant cell walls play an important role in PPD delay (Uarrota *et al*. 2016).

Role of reactive oxygen species (ROS) in PPD

ROS have been shown to increase very early during PPD and several studies indicated the role of ROS (singlet oxygen (O_2), superoxide anion radical (O_2), H_2O_2 and hydroxyl radical ($HO^{\bullet}$) associated with PPD in cassava root (Ravi *et al*. 1996b). Reilly *et al*. (2004) reported a rapid oxidative burst within 15 min of harvest, signalling the start of PPD, predominantly due to a rapid production of superoxide and hydrogen peroxide. An increase in phenolic compounds (e.g. scopoletin) and H_2O_2 had a definite relation with PPD in cassava (Buschmann *et al*. 2000). Cyanogenic glycosides, upon wounding and mechanical damage, break down to release cyanide following cellular disruption and release of the cyanogens from the vacuole (Siritunga and Sayre 2003, Siritunga *et al*. 2004). Toxic levels of cyanogenic glycosides has also been implicated for the oxidative burst initiated by cyanide release that occurs after wounding of cassava in cassava root (Zidenga *et al.* 2012). The cyanide inhibition of mitochondrial cytochrome oxidase is the major source of ROS production in damaged cassava roots (Zidenga *et al.* 2012). Increases in both peroxidase and catalase activity involved in turnover of H_2O_2, have been shown to occur during PPD in cassava root. The genes encoding for ascorbate peroxidase, catalase, secretory peroxidase, thioredoxin peroxidase, glutathione S-tranferase involved in ROS turnover are upregulated and changes in expression patterns of suggest probable involvement of ROS in PPD (Reilly *et al*. 2007). The over-expression of individual ROS regulating genes may typically increase oxidative stress resistance in plants and could enhance the ROS scavenging capacity in cassava storage roots thereby delaying PPD. Carotenoids with their antioxidant activity protect cells and tissues from ROS induced oxidative damage. Cassava varieties with elevated β-carotene content had extended shelf-life (Chávez *et al.* 2005). Indeed, the shelf-life of green house grown transgenic plants with elevated β-carotene (40 ppm) content was extended to four weeks (Zidenga *et al*. 2012). Desirable level of PPD tolerance in cassava from transgenic approach is still remains to be achieved.

Modern tools for estimation of PPD

Application of metabolomics and chemometrics : Low molecular weight phytochemicals (secondary metabolites) synthesized during PPD have significant role and hence monitoring them is gaining importance to understand the mechanism and identify biochemical markers associated with PPD. The changes in the chemical and enzymatic composition during PPD can be monitored using Mid-infrared Vibrational Fourier Transform Spectroscopy (ATR-FTIR) (Uarrota *et al*. (2014). High Performance Thin Layer Chromatography (HPTLC) was employed to screen several cassava genotypes and to classify the genotypes based on chemical finger printing (Saravanan *et al.* 2015). The scope of NIR in analyzing the PPD of cassava root is emerging as a tool that it can be used as a replacement of time-consuming manual methods.

Approaches for delaying PPD

Conventional methods of PPD management : Shelf-life of cassava tubers can be extended through traditional as well as modern methods (Ravi *et al*. 1996). Several simple, low-cost traditional methods such as under-ground storage, wood and cardboard box, polybag and modern techniques such as refrigerated cold storage, freezing, chemical treatments, wax coating are being followed to prolong the shelf-life of cassava roots (Ravi *et al*. 1999b).

Breeding and improvement of cassava for delayed PPD

Conventional breeding and selection for tolerance to PPD : Breeding cassava for longer shelf-life has met with little success due to lack of an objective scoring methodology, quantitative nature and complexity of the trait controlled by many genes, lack of sufficiently accurate linkage map for PPD for locating PPD related markers, high heterozygosity, poor flowering and the cross-pollinating nature of cassava. Cassava's highly differentiated gene pools and the large percentage of dominant/recessive gene action loci makes it highly heterotic (Fregene and Puonti-Kaerlas, 2002). Furthermore, although substantial genetic variability exists among cassava genotypes for PPD trait (Tumuhimbise *et al.* 2015) the prevailing agroclimatic conditions and associated pre-harvest stress masks genetic variability pertaining to PPD.

Cassava improvement programmes aim for high dry matter content. However, there is negative correlation reported to exist between PPD and high dry matter. It is hard to separate these two important traits through conventional breeding. Increase in ploidy level up to 3 increased yield starch content and dry matter (Sreekumari *et al.* 1999). However, an inverse relationship exists between PPD and ploidy level (Morante *et al*. 2010). This and the persistent but moderate negative correlation between low deterioration rate and high dry matter content (Sanchez *et al*. 2006) limits the scope of conventional breeding for delayed PPD (Ceballos *et al*. 2004). Nevertheless, conventional breeding tool like selection can be utilized effectively and there is a high probability that PPD trait can be improved through selection (Morante *et al*. 2010). Insights into the genetics of PPD trait have yielded some positive indications in this line. Cassava genotypes with delayed-PPD trait was identified (Morante *et al*. 2010, Moyib *et al.* 2015). Ten and three putative QTLs, respectively, which explain between 5 and 13% of the phenotypic variance of PPD linked quantitative trait loci (QTLs) influencing PPD of cassava have been identified and hence useful variability among the genotypes for PPD can be exploited for breeding PPD tolerant varieties. Cassava breeding at CIAT (*Centro Internacional de Agricultura Tropical*) for PPD tolerance revealed that genetic variability for this trait accounted for 52% of the total observed phenotypic variability and hence, there is a scope to improve low PPD clones by breeding or through selection (Morante *et al.* 2010). The broad-sense heritability (0.38 ± 0.04) and average heritability (0.52) for PPD trait imply high genetic control of PPD tolerance (Venturini *et al.* 2016). These studies offer considerable scope for enhancing shelf-life through selection.

Marker assisted breeding : The marker assisted selection (MAS) and the mapping of quantitative trait loci (QTLs) linked to PPD are yet to be done to identify strong markers for this trait in cassava. The evaluation of all biochemical constituents involved in PPD and further comparison of cassava cultivars with contrasting PPD tolerance may reveal basic insights into the PPD problem. A negative correlation between PPD and carotenoid content suggests that carotenoids may help in delaying PPD (Sanchez *et al*. 2006). This makes possible the identification of molecular markers linked to PPD. Cortes *et al*. (2002) identified a set of 10 molecular markers with a significant association with putative QTLs for PPD. As the delayed

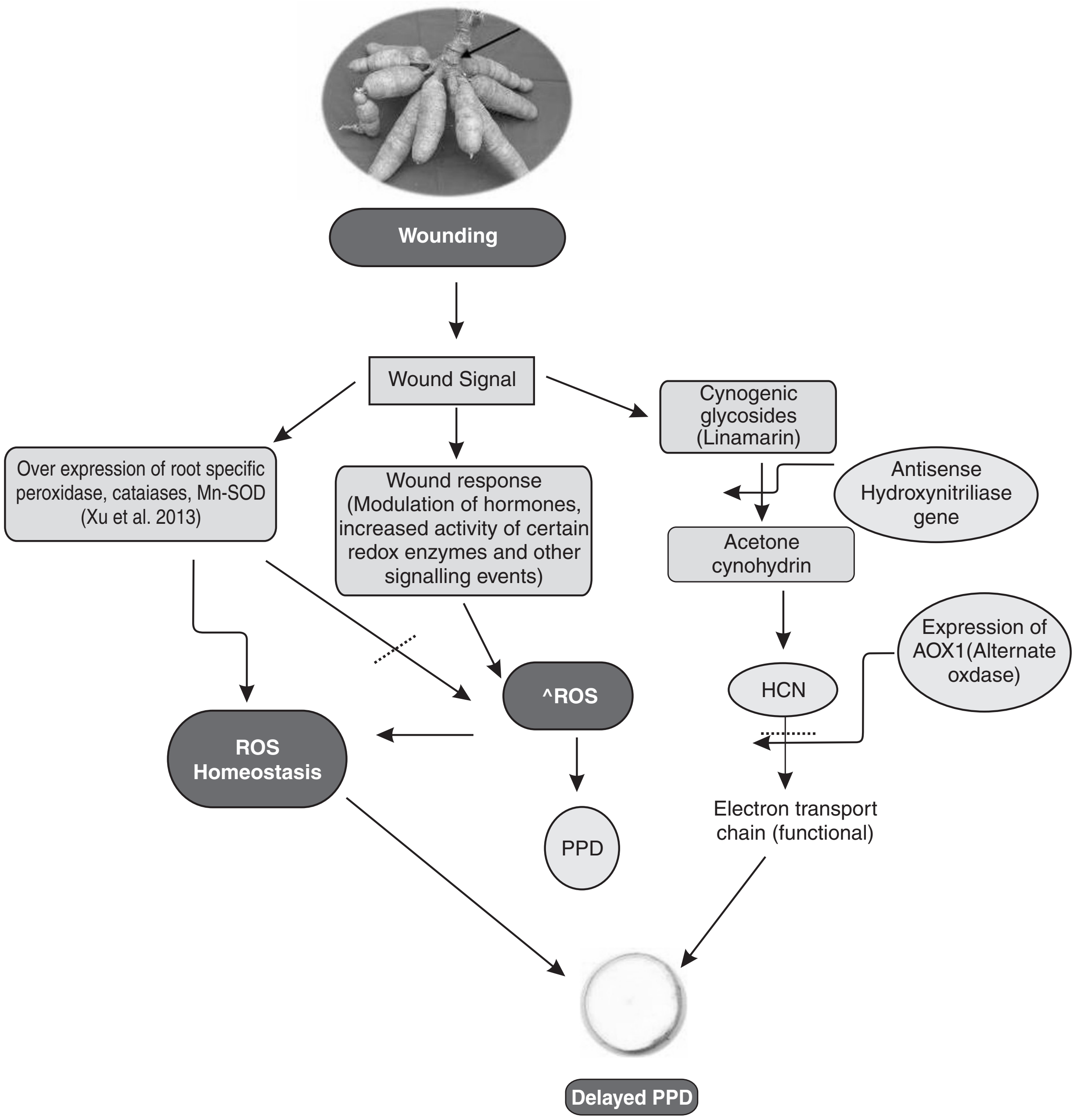

Fig 1 Delaying PPD through genetic manipulation of wound response pathway in cassava.

PPD has been identified in the storage root of *Manihot walkerae*, a wild relative of cassava, the development of inter-specific hybrids between cassava and *M. walkerae*, offers possibilities for mapping PPD related genes (Cortes *et al*. 2002). Identification of major cassava genome regions related to post-harvest deterioration may provides tools for the identification of gene(s) controlling this trait.

Genetic engineering to delay PPD : Cassava roots are subjected to mechanical damages such as abrasion, bruising, cut etc., during harvest which trigger the generation of reactive oxygen species (ROS). In a wound healing response in plant tissues, the ROS's act as a signalling molecule that induces programmed cell death or antioxidant defences against ROS. These biochemical changes are too late or inadequate to complete wound repair in cassava (Reilly *et al*. 2004). Analyses of genes expressed during cassava PPD revealed an altered regulation of genes and enzymes involved in signal transduction, regulation of reactive oxygen species (ROS), phytohormone synthesis, senescence, programmed cell death (PCD) responses, and the formation of compounds involved in the synthesis of cell wall components (Gunawardena *et al*. 2001, Pieterse *et al*. 2012). Endogenous melatonin acts as a signal modulator of cassava PPD and that manipulation of melatonin biosynthesis genes through genetic engineering may prevent cassava root deterioration (Ma *et al*. 2016).

A putative wound response pathway with consequent PPD symptom development in harvested cassava roots and pathway interventions to delay the PPD expression is presented in Fig 1 (Saravanan 2015). Overexpression of *Arabidopsis* AOX in transgenic cassava roots resulted in substantially reduced ROS accumulation and delayed the onset of PPD by as much as three weeks (Zidenga *et al.* 2012) leaving enough time for the shipping or processing operations necessary after harvesting the crop. However, the growth abnormalities in the field grown transgenic cassava plants were an impediment in employing transgenic approach for developing tolerance to PPD. Storage roots of transgenic cassava lines with ectopic expression of Cu/ZnSOD and CAT showed an improved and synergistic ROS-scavenging capacity. Consequently, those lines showed a delay in their PPD response up to 10 days, accompanied by less mitochondrial oxidation and H_2O_2 accumulation compared with those of the wild type (Xu *et al*. 2013). Tailoring of genes to modify the expression of PPD traits through recombinant DNA technology may offer considerable hope for extending the shelf-life of fresh cassava roots.

Post-harvest physiological deterioration of cassava is a vexing problem for cassava farmers and processors and remains to be a major constraint for expansion of cassava cultivation. PPD starts in fresh tubers after harvest and renders them unfit for consumption due to the discoloration and associated foul smell with qualitative and quantitative losses. Alterations in various key enzymes of ROS metabolism such as peroxidise, SODs and catalase etc., during the storage and associated symptom development were reported. The role of wound induced ROS in modulating the PPD expression was demonstrated by several biochemical and molecular studies. Serious attempts were made to genetically engineer cassava for extended shelf-life but the field level success is still elusive. The wound signalling network of cassava storage roots and pathway of ROS metabolism and its constituents and their interplay is not yet fully understood. Understanding the genetics of PPD, development of robust and objective PPD screening methods will pave way to extend cassava root storage life. Marker aided selection and genetic engineering of cassava shall usher new avenues for long shelf-life of fresh cassava roots.

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