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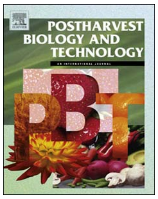

Review

# Cassava post-harvest physiological deterioration: From triggers to symptoms

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## ABSTRACT

The production of cassava, the most important staple root crop in the world, is constrained by the short shelf life of the cassava storage roots that are undergoing post-harvest physiological deterioration (PPD) shortly after harvest. PPD reduces starch quality and renders the roots unpalatable and unmarketable. PPD is a complex process involving enzymatic stress responses to wounding, changes in gene expression and protein synthesis as well as accumulation of secondary metabolites. PPD can be strongly influenced by environmental factors making the identification of genotypes with delayed PPD trait difficult. In the present review, we propose an integrative presentation of PPD phenomenon based on a comprehensive analysis of several key PPD studies. We discuss recent progress in the standardization of methods to assess and score PPD tolerance in cassava roots. Traditional and improved storage techniques to extend cassava shelf-life are presented and prospects of transgenic approaches to delay PPD are discussed.

## 1. Introduction

Cassava (*Manihot esculenta* Crantz) originates from South America and was first distributed to Africa by the Portuguese in the eighteenth century, and now it is commonly cultivated in many countries across Africa, Asia and Latin America (Nhassico et al., 2008; Olsen and Schaal, 2001; El-Sharkawy, 2012). Cassava, also called manioc or tapioca, is the most important staple root crop in the world and its production ranks sixth after maize, rice, wheat, potatoes, and soybeans (FAOSTAT, 2013). It provides the food energy intake for nearly a billion people in 105 countries worldwide and is considered as the cheapest source of starch used in more than 300 industrial products ("Cassava for Food," 2008). While initially considered as a "food for the poor", cassava has grown significantly in importance in world agriculture and is now a multipurpose crop that responds to the priorities of developing countries, to the trends in the global economy, and to the challenge of climate change (Lobell et al., 2008; Howeler et al., 2013). Cassava plays an important role in food security due to its beneficial traits such as drought tolerance and its ability to grow in marginal environments where many other crops perform poorly (Morante et al., 2010; Iyer et al., 2010). Despite good agronomic performance, cassava production remains constrained by several factors including biotic and abiotic stresses (Waddington et al., 2010; Campo et al., 2011). One of the major constraints is that cassava roots have a short postharvest shelf life, which severely limits their potential in the market and their benefits to cassava farmers. The roots exhibit visible symptoms of postharvest physiological deterioration (PPD) within only 24 to 72 h of harvest (Morante et al., 2010; Salcedo and Siritunga, 2011; Vanderschuren et al., 2014).

## 2. Post-harvest physiological deterioration (PPD)

PPD has become one of the major constraints to commercial cassava production and utilization because it is triggered by the inevitable physical damage of the roots during harvesting (Wenham, 1995; Buschmann et al., 2000a; Beeching, 2001; Iyer et al., 2010; Salcedo and Siritunga, 2011; Saravanan et al., 2016). PPD is a complex process that is linked to enzymatic stress responses to wounding, involving changes in gene expression, protein synthesis as well as accumulation of secondary metabolites and can be influenced by environmental factors. Visually, PPD is characterized by a blue/black or brown discoloration of the vascular parenchyma, which starts to appear within 24–72 h of harvest (Reilly et al., 2004; Beeching et al., 1998a, 1998b) (Fig. 1). This response initiates from the wound sites, caused during the harvesting and handling processes, and spreads from these to the storage parenchyma. This wounding of the root triggers an oxidative burst of the

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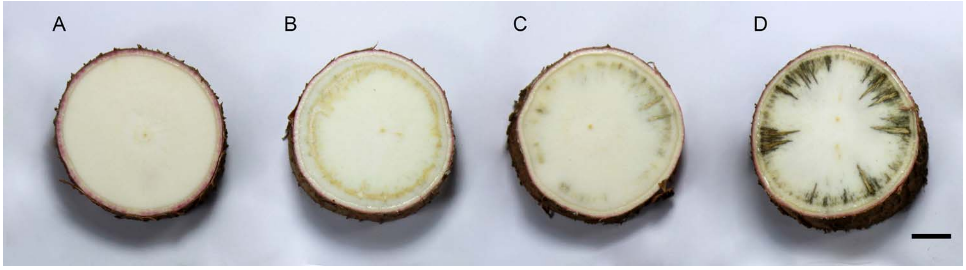

**Fig. 1.** PPD in field-grown cassava storage roots: A. root slice at harvest, B. root slice at 2 dph (days post-harvest), C. root slice at 4 dph, D. root slice at 7 dph. Black coloured bar = 11.6 mm.

superoxide radical ($O_2^-$) within 15 min, which is followed by the further production of reactive oxygen species (ROS), such as superoxide radical ($O_2^-$), hydroxyl radical (OH), and hydrogen peroxide ($H_2O_2$), altered gene expression, and the accumulation of secondary metabolites (Beeching, 2001; Huang et al., 2001; Reilly et al., 2004, 2007; Bayoumi et al., 2008a; Iyer et al., 2010; Zidenga et al., 2012). These findings are supported by the fact that oxygen exclusion can prevent PPD (Noon and Booth, 1977; Beeching et al., 1998a) and cassava roots with higher antioxidant content, such as β-carotene, tend to be more tolerant to PPD (Sánchez et al., 2006). Compared to other tuber and root crops, such as sweet potato and taro, cassava shows some differences in response to wounding. For instance, in sweet potato and taro, wounds rapidly seal through the production of a lignin layer, while in the detached roots of cassava, a lignin layer is not produced and no wound sealing occurs (Uritani, 1999). This is probably due to cassava roots not being propagules and, as a result not serving any biological function once detached from the plant. Wounded storage roots remaining attached to the plant are capable of wound repair (Beeching et al., 1994).

The short shelf-life of harvested cassava roots limits market potential and discourages all stakeholders in the value chain (Howeler et al., 2013). PPD causes reduced incomes for cassava farmers and lowers the reliable supply of cassava as raw material for industry (Salcedo and Siritunga, 2011). Globally, cassava post-harvest losses in production were estimated to account for 19% of total cassava production (FAO and IFAD, 2000) but higher rates of losses are reported in countries where the PPD problem is more dominant in the cassava value chain (Naziri et al., 2014).

Several *ex ante* studies have calculated the potential economic impact of reducing PPD. In Thailand, extending the storability of cassava to 45 days could lead to an increase in annual benefits of approximately US $ 35 million (Vlaar et al., 2007; García et al., 2013). In Nigeria, Ghana, and Uganda, benefits of cassava genotypes with delayed PPD have been estimated to US $ 2.9 billion, $ 855 million, and $ 280 million, respectively, over a 20 year time period (Rudi et al., 2010). In recognition of the economic impacts caused by PPD, the necessity to improve cassava storage life to a minimum of two weeks has long been considered a priority by the Food and Agriculture Organization of the United Nations (FAO) (Wenham, 1995). Breeding programs have successfully generated cassava genotypes with improved performance in drought and disease-prone areas (Okogbenin et al., 2013; Lenis et al., 2006). However, root traits such as delayed PPD onset and/or limited symptoms remain difficult to breed for due to a) the necessity to complete a lengthy crop cycle to produce storage roots b) the correlation between high dry-matter content, a desirable character, and PPD (Wenham, 1995; Chávez et al., 2005), and c) the large experimental errors typically associated with the available PPD scoring protocols (García et al., 2013). Evaluation of genotype susceptibility to PPD is another issue, as this trait is not only determined by genetic but also by environmental factors (Kawano and Rojanaridpiched, 1983; Wheatley and Schawabe, 1985; Wheatley and Gomez, 1985), making performance assessment of genotypes and breeding lines a challenge.

## 3. Assessment of PPD

A robust method for PPD initiation and PPD scoring is particularly essential to identify stable traits for susceptibility and tolerance to PPD. The International Center for Tropical Agriculture (CIAT) scientists introduced a standard method to induce PPD by removing the proximal and distal ends of storage roots, covering the distal end with a PVC film to prevent water loss and securely storing the wounded storage roots for three days in the shade outside (Booth, 1976; Wheatley and Gomez, 1985; Wheatley et al., 1985). Despite the establishment of other methods (Table 1), the assessment of PPD remains challenging due to discrepancies between different scoring methods. For instance, the PPD results generated with the so-called slice method, which uses 5–10 mm thick storage root slices and is reasonably efficient to generate variation in PPD symptom appearance and to rank selected genotypes accordingly, differ from those produced with other methods, including the CIAT standard method (Wheatley and Schawabe 1985; Wheatley and Gomez, 1985; Buschmann et al., 2000a).

The method of leaving the roots untouched and incubating them for prolonged periods (up to 40 days) showed no PPD symptoms over the long evaluation periods in some genotypes and a large variation in others (Morante et al., 2010). The slice method induces early and homogenous PPD symptoms in greenhouse-grown cv. 60444 cassava storage roots and was used for greenhouse-grown storage roots in transcriptomics and proteomics studies to investigate changes in gene expression and protein levels associated with PPD (Huang et al., 2001; Owiti et al., 2011; Vanderschuren et al., 2014; Hu et al., 2016). However, the slice method is a harsh treatment of root tissues that is not necessarily representative of the post-harvest stresses encountered by cassava storage roots in the value chain. For this reason, the slice method might not be the most appropriate method to discriminate PPD tolerant varieties from those that are susceptible.

Several studies have reported important experimental errors for the onset of PPD symptoms using various PPD assessment methods (Kawano and Rojanaridpiched, 1983; Buschmann et al., 2000a; García et al., 2013; Tumuhimbise et al., 2015a,b). Moreover, factors such as dry matter content, which are correlated with PPD susceptibility, are under strong environmental influence. Harvest period (i.e. rainy season or dry season), soil preparation and physiological state of the plant are factors reported to alter the level of deterioration within the same genotype (Kawano and Rojanaridpiched, 1983). Hence it is of high importance to account for environmental interferences when assessing PPD tolerance in the cassava germplasm. Multi-location trials over several years and assessment at different harvesting times are required to estimate the level of PPD tolerance (Kawano and Rojanaridpiched, 1983; Tumuhimbise et al., 2015a, 2015b). Sufficient numbers of evaluated roots are also required to reduce experimental errors. Some studies reported using five, ten, and fifteen storage roots in their PPD assessment (Salcedo et al., 2010; Morante et al., 2010; García et al., 2013). Root size homogeneity and age can also be considered in order to limit PPD variation, such as by using cassava roots with a minimum girth of 10 cm (Tumuhimbise et al., 2015a, 2015b). Depending on the aim of the study, the preferred methods for triggering PPD might have to be adjusted to the specific applications.