

Skinning Injury Responses in Sweetpotato

Respons Cedera Kulit pada Ubi Jalar

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ABSTRACT

*In sweetpotatoes (*Ipomoea batatas* L. Lamb), the loss of skin from the surface of the storage roots is known as skinning injury. It is responsible for significant postharvest loss resulting from moisture increase and weight reduction, wrinkling, and susceptibility to pathogen attack. Reduced root weight by water loss is associated with a higher rate of rot predominantly occurred in the developing and underdeveloped countries which can count of 8-20% of postharvest loss. Plants have different adaptation to protect themselves against skinning injury. Lignification, suberization, and increased sugar at the wound site have been shown to be correlated with wound healing. Changing in gene expressions have been associated with skinning injury. Genes associated in the biosynthesis of lignin and suberin, protein fate, cell-wall modification, transcription and protein synthesis, and stress responses and defense have been associated with skinning injury responses in plants. Understanding the skinning injury responses and how to regulate them can be used to produce a more desirable plant resistant to skinning injury. This paper especially reviews and discusses skinning injury responses in sweetpotato, a root crop which product may severely be affected by skinning injury.*

Keywords: gene expression, *Ipomoea batatas*, lignification, postharvest loss, wounding

ABSTRAK

Pada ubi jalar (*Ipomoea batatas* L. Lamb), cedera kulit adalah hilangnya kulit dari permukaan umbi. Cedera kulit ini bertanggung jawab atas kerugian pascapanen yang signifikan akibat peningkatan laju kelembaban dan penurunan berat umbi, pengerutan, dan kerentanan terhadap serangan patogen. Berat umbi yang berkurang karena kehilangan air dikaitkan dengan tingkat pembusukan yang lebih tinggi, terutama terjadi di negara-negara berkembang dan yang kurang berkembang dengan kehilangan hasil panen umbi 8-20%. Tanaman memiliki adaptasi yang berbeda untuk melindungi diri dari cedera kulit. Lignifikasi, suberisasi, dan peningkatan gula di lokasi pelukaan telah terbukti berkorelasi dengan penyembuhan luka. Perubahan ekspresi gen telah dikaitkan dengan cedera kulit. Gen-gen yang terlibat dalam jalur biosintesis lignin dan suberin, protein tujuan akhir, modifikasi dinding sel, transkripsi dan sintesis protein, serta respons stres dan pertahanan telah dikaitkan dengan respons cedera kulit pada tanaman. Memahami respons cedera kulit dan bagaimana cara mengaturnya dapat digunakan untuk menghasilkan tanaman yang diinginkan yang tahan terhadap cedera kulit umbi. Paper ini secara khusus mengulas dan membahas respon cedera kulit pada ubi jalar, suatu tanaman umbian yang hasilnya sangat terpengaruh oleh cedera kulit.

Kata kunci: ekspresi gen, *Ipomoea batatas*, lignifikasi, kehilangan pascapanen, pelukaan

INTRODUCTION

Sweetpotato, with an annual yield of about 91.8 million metric tons and a planted area of 7.77 million hectares, is the seventh important food crop, slightly behind cassava (FAO, 2019). It is a staple food in many nations and produces steady crop yields under a variety of environmental cues. More than 95% of the world's sweetpotato crop is cultivated in developing nations, where it ranks fifth in terms of fresh weight after rice, wheat, maize, and cassava (Plucknett, 1991).

The internal flesh of sweetpotato storage roots is mostly constituted of parenchyma cells with starch granules (storage parenchyma) and is covered by the epidermis. The skin, also known as the periderm, is made up of three layers: phellem, phelloderm, and phellogen (Järvinen *et al.*, 2011). The phellogen produces the phelloderm on the inside of the root and the phellem on the outside of the root. The phellem is made up of numerous layers of cells that are free of starch granules and arranged radially toward the phellogen. The phelloderm is more difficult to distinguish from cortical cells since it resembles them, and it is usually differentiated by the radial position of the cells in relation to the phellogen (Kono and Mizoguchi 1982; Villavicencio *et al.*, 2007; Firon *et al.*, 2009).

During sweetpotato growth, the outer peridermal cells get partially lignified and are gradually shed off. The phellogen layer, on the other hand, remains active until harvest, causing the periderm layer thickness to stay unchanged (Artschwager and Starrett, 1931; Villavicencio *et al.*, 2007; Firon *et al.*, 2009). All parenchyma tissues in the tuber maintain the ability to produce new periderm in response to wounding, but it is most prevalent close to the original, native periderm (Artschwager 1927). The phellem cells are characterized in both wound and native periderm by their rectangular form and columnar row structure, and their walls autofluoresce under UV light (Ginzberg, 2008). The autofluorescence is due to presence of aromatic suberin polymers in their cell walls (Bernards and Lewis, 1998). This columnar pattern is a result of their emergence from periclinal division in the phellogen cell layer (Artschwager, 1924).

The loss of the epidermis/skin from the surface of the root, referred to as "skinning," is the major constrain in postharvest handling of sweetpotato roots. Skinning arises when the periderm's superficial layers detach from the underlying tissue, resulting in increased moisture loss, weight loss, shriveling of the root surface, greater vulnerability to pathogen infestations, and an unappealing appearance. 'Beauregard', is the most favored cultivars due to its smooth skin, color and high harvest cultivars in the United States. Unfortunately, following harvest and handling, this cultivar is very susceptible to skin damage (Firon *et al.*, 2009).

Desiccation of the surface cell layers, lignification of the underlying cell layers, and eventually the development of a wound periderm by cell division are all steps in the wound-healing process in sweetpotato storage roots (Artschwager and Starrett, 1931). Improper wound healing is related with a thick dried layer and delayed incomplete lignifications when the humidity is low (van Oirschot *et al.*, 2006). Continuity of the lignified layer is critical for wound healing, apparently to function as a barrier to manage water, mineral nutrients, and vital gas fluxes, as well as to protect against toxic chemical incorporation, water loss, insect infestation, and pathogen attack (van Oirschot *et al.*, 2006; Ranathunge *et al.*, 2011). Van Oirschot *et al.*, (2002) developed a method for measuring wound-healing efficiency using phloroglucinol staining (lignifications score: LS), which has been used to screen sweetpotato cultivars (van Oirschot *et al.*, 2002; 2006).

Because skin loss is caused by the breakdown of peridermal cell walls, Villavicencio *et al.*, (2007) hypothesized that lignin content and polygalacturonase (PG) and pectin methylesterase (PME) activities could be part of the processes or factors that cause raised or lowered skin adhesion in sweetpotato roots. If this is the case, skin adhesion may be related to these factors, allowing them to be used as markers of skinning susceptibility.

SKINNING INJURY AND POSTHARVEST LOSS

Physical Factors

Mechanical breakage is the most significant harvest component, with much of it occurring during harvest, transportation, and marketing. In the tropics, harvesting is often done by hand with a range of instruments such as digging sticks, spades, hoes, and knives. Harvesting tools frequently cut, skinned, and bruise sweetpotato storage roots.

Physiological Factors

Excessive respiration and transpiration in sweetpotato lead to weight loss and changes in internal and external appearance. The evaporative loss of cellular water induced by the vapor pressure differential between the root interior and the outside environment causes transpiration losses. Furthermore, injuring sweetpotato roots led in an increase in both respiration rate and weight loss. Moreover, a condition known as pithiness is defined by the formation of cavities within the tissues as a result of moisture loss. Long-term moisture losses, such as those found in tropical climates, can induce tissue collapse near the root's distal end. This is commonly found in small sized root which could lead to total desiccation (Picha, 1986).

Biological Factors

Pre-harvest and postharvest infestations by pathogenic microorganisms (mainly fungus, but also bacteria) are major factors of sweetpotato root postharvest loss (Snowdon, 1990). The relative significance of the main diseases varies a lot depending location and environmental situation (Ray and Byju, 2003).

STRATEGIES ADOPTED BY PLANTS TO AVOID SKINNING INJURY

Plants have evolved diverse ways to defend themselves against insect and microorganism due to skinning injury. Structurally, plants have a polyester coating composed of cutin and suberin (Kolattukudy, 1980). This coating normally isolates the plant tissues from competing organisms and plants are therefore relatively immune from the presence of these competitors even on their surface. However, if a break or wound occurs in this surface coating, then competing organisms gain entrance into the plant's tissues where they can cause injurious damage to those tissues. Consequently, plants have developed a complex response to wounding that dramatically alters the cellular physiology of plant tissues and results in the production of defenses. These defenses are particularly protection against microorganisms and are effective against small herbivores (Constabel *et al.*, 2000).

A major phase of the wound-response is a generalized activation of plant defenses. Because the majority of microbial infections occur in plants following a wound, plants have developed a range of biochemical defenses to inhibit invading pathogens and small herbivores (Zhou and Thornburg, 1999). The accumulation of phytoalexins after wounding has been a worldwide area for study. Phytoalexin, a small molecular weight defensive compounds, has been shown to have a biological activity against microorganisms or herbivores. For example, phenolic, terpenoid, and alkaloid compounds are a major component of plant secondary metabolism (Zhou and Thornburg, 1999).

Physical barriers (such as wax coats and hardened tissues) and chemical metabolites protect plants from outside harm (Chen *et al.*, 2005). Plants are stimulated to create local and systemic signals in response to mechanical injury and pathogen infestation, which activate signal cascade inside cells (Bergey *et al.*, 1999). Several chemicals were found to be involved in the signaling cascades of defense systems, including hydrogen peroxide, nitric oxide, calcium, protein kinase, jasmonate, salicylic acid, and ethylene (Delaney *et al.*, 1994; Song *et al.*, 1995; O'Donnell *et al.*, 1996; McConn *et al.*, 1997; Zimmermann *et al.*, 1997; Foissner *et al.*, 2000; Orozco-Cárdenas *et al.*, 2001; Gould *et al.*, 2002; Jih *et al.*, 2003; Deng *et al.*, 2013).

SKINNING INJURY INDUCED CHANGES IN GENE EXPRESSION

Sweetpotato storage roots are underground storage organs with a suberized covering that preserves the interior flesh from dryness and infections. Understanding the molecular mechanisms that lead to the development of periderm is critical for gaining a better understanding of this protective tissue and extending the storage life of storage roots. Moreover, understanding the molecular mechanisms underlying skinning injury, attempts have turned toward the isolation of genes regulated by skinning injury. This also permits insight into their functions and the pathways that lead to their expression. Although several responses of plants to skinning injury, including short-term metabolic and physiological changes are anticipated to be independent of changes in gene expression, the large number are predicted to rely on modification in gene expression.

A common technique that has been used to identify and isolate skinning/wound injury responsive has been the screening of cDNA library constructed from poly(A)⁺ RNA from skinning injury plants. The encoded products of the genes isolated by this technique are believed to play a role in a number of processes including lignin and suberin biosynthesis pathways, protein fate, cell wall modification, transcription and protein synthesis, and stress response and defense.

Genes Involved in Lignin and Suberin Biosynthesis Pathways

Suberin is a polymer that has both aliphatic and aromatic domains (Bernards, 2002). The aliphatic suberin is a glycerol-based polyester containing a long and very long chain of ω -hydroxyacids and fatty α , ω -diacids, as well as minute quantities of esterified hydroxycinnamic acids, primarily ferulic acid. Aromatic suberin is a lignin-like polymer that is primarily composed of hydroxycinnamic acids. Longchain acyl-CoA synthetase (LACS), which appears to be involved in the activation of fatty acids prior to elongation (Pollard *et al.*, 2008), and a cytochrome P450 of the CYP94A subfamily, whose putative orthologue in *Nicotiana tabacum* catalyzes the oxidation of fatty acids to, α , ω -diacids, are two up-regulated genes for the aliphatic suberin pathway (Le Bouquin *et al.*, 2001). The presence of phenylalanine ammonia lyase (PAL) and caffeic acid 3-*O*-methyl transferase (COMT) in the aromatic suberin pathway should be emphasized. The enzyme PAL catalyzes the initial step in the phenylpropanoid pathway (Kolattukudy 1981), and its enzymatic activity in the periderm associates with the accumulation of suberin (Bernards *et al.*, 2000; Lulai, 2008). COMT catalyzes the methylation of hydroxylated monomeric lignin precursors in several steps. It is thought to play a key part in the lignin biosynthesis pathway. Wheat cDNA (TaCM) was isolated and shown to be expressed constitutively in the stem, leaf, and root tissues (Ma and Xu, 2008). TaCM's deduced amino acid sequence has a high similarity with COMT from other plants, especially in the SAM binding motif and the catalytic and substrate specificity regions (Ma and Xu, 2008).

Genes Involved in Protein Fate

PPIase (parvulin-type peptidyl-prolyl cis-trans isomerase) is thought to be involved in protein folding by catalyzing the cis-trans isomerization of X-Pro peptide bonds. Plant responses to various environmental cues were observed to accumulate PPIase mRNA (Godoy *et al.*, 2000; Reilly *et al.*, 2007; Effendy *et al.*, 2013; 2017). SmTCTP (*Soy max* translationally controlled tumor protein) gene has a role in protein fate (Gnanasekar *et al.*, 2009). SmTCTP was found to attach to native proteins and conserve them against denaturation due to heat. In bacterial cells, overexpression of TCTP can protect them against heat shock-induced cell death. This result implies that TCTP is a new small molecular weight heat shock protein that functions as a molecular chaperone to guard cellular proteins from heat shock damage (Gnanasekar *et al.*, 2009).

Genes Involved in Cell Wall Modification

As a result of cell expansion and suberin deposition, changes in cell wall alterations are critical during tuber periderm development. Suberin is accumulated into the main cell wall at the subcellular level. Suberin consists of three components within subdomains of cell walls, depending on the developmental stage of the suberized tissue (Ranathunge *et al.*, 2011). In the potato skin SSH library (Soler *et al.*, 2011), genes involved in cell wall growth and remodeling have been characterized, including pectin-glucuronyltransferase (Iwai *et al.*, 2002; Soler *et al.*, 2011), extensin (Cannon *et al.*, 2008; Soler *et al.*, 2011; Effendy *et al.*, 2013; Neubauer *et al.*, 2013), xyloglucan endotransglucosylase/hydrolase (Fry, 2004; Soler, 2011) and β -D-glucan exohydrolase (Hrmova and Fincher, 2001).

Genes Involved in Transcription and Protein Synthesis

Recent studies have revealed differentially expressed genes that involved in transcription and protein synthesis (Zhou and Wu, 2009; Gray *et al.*, 2012). In eukaryotes, transcriptional and posttranscriptional regulation are crucial for gene expression. Transcription factors complete the task of controlling plant stress responses through transregulation (Singh *et al.*, 2002). One of the largest families of plant-specific transcription factors is the NAC protein family (Olsen *et al.*, 2005; Zheng *et al.*, 2009). This family of genes is involved in a variety of biological processes, including biotic and abiotic stress responses, such as drought and salt stress (Zheng *et al.*, 2009). Zinc finger proteins are the most diverse group of transcription factors that regulate gene expression. They have a wide range of structures and functions, including RNA or DNA recognition, RNA packaging, transcriptional activation, protein folding and assembly, and lipid binding (Laity *et al.*, 2001; Zhou *et al.*, 2009a; Zhou and Wu, 2009).

Early in the formation of potato tubers, periderm replaces the epidermis (Reeve *et al.*, 1969). Periderm was shown to have a high level of external and endogenous oxidative stress (Pla *et al.*, 2000). Patatin-like phospholipase, catalase, and ascorbat peroxidase are among the genes implicated in abiotic and biotic stress tolerance found in both native and wound-healing periderm (Chávez *et al.*, 2005; Krits *et al.*, 2007; Barel and Ginzberg, 2008; Ginzberg *et al.*, 2009; Soler *et al.*, 2011). Bernards (2002) revealed that the presence of stress proteins in the periderm is linked to the detoxification of reactive oxygen species (ROS). Furthermore, genes that modulate protein redox status, such as thioredoxin, are induced in the periderm (Bernards, 2002) and storage roots. (Effendy *et al.*, 2013; 2017). The occurrence of genes involved in antioxidant activity and redox homeostasis indicates that redox signaling is important in periderm (Buchanan and Balmer, 2005; Foyer and Noctor, 2005).

Lectins have also been associated as proteins that are involved in defense. Viruses, bacteria, ants, and animals all have lectins, which are carbohydrate-binding proteins (Barondes 1988). Most lectins bind glycoproteins, glycolipids, and polysaccharides (Goldstein and Hayes 1977) and were presumed to assist plants defend themselves against pathogen or insect infestation (Zhu-Salzman *et al.*, 1998; Bandyopadhyay *et al.*, 2001). According to their structures and evolutionary origins, lectins are divided into seven families: legume lectins, type 2 ribosome inactivating proteins, chitin-binding lectins, monocot mannose-binding lectins, cucurbitaceae phloem lectins, jacalin-related lectins (Chang *et al.*, 2012) and others (Damme *et al.*, 1998).

Pathogenesis-related genes, general defense and stress-related genes, genes involved in fatty acid signaling and metabolism, genes for aromatic amino acid metabolism, and genes with unknown functions have all been identified in *Arabidopsis*. In addition, researchers have uncovered evidence that the octadecanoid signaling system promotes responses to mechanical injury, insect infestation, and UV irradiation. (Conconi *et al.*, 1996; Howe *et al.*, 1996). Wound-inducible genes encode proteins with a variety of functions. Some of them aid in the healing of injured tissue, while others may generate chemicals that suppress insect growth. Wound-inducible proteins were also involved in signaling pathway activation and plant metabolic regulation (León *et al.*, 2001). The sweetpotato ipomoelin (*IPO*) or sporamin (*spor*) gene, for example, was identified and its expression was up-regulated by methyl jasmonate and mechanical injury (Imanishi *et al.*, 1997; Chen *et al.*, 2003; Effendy *et al.*, 2013; 2017; 2019). Furthermore, results from feeding silkworms *spor* protein from *Escherichia coli* indicated that the *spor* protein was a protective protein that inhibited silkworm development and survival (Chen *et al.*, 2005).

CONCLUSIONS

From various previous studies it has been found that skinning injury clearly causes significant losses in sweetpotato storage root yield. However, plants have different mechanisms to prevent post-harvest losses. Upon harvesting, storage roots undergo post-harvest losses such as physical, physiological, and biological factors. In addition, plants have adopted different strategies to avoid further damage due to skinning injury by activating plant defenses, for example biochemical defenses, physiological barriers and chemical metabolites. Furthermore, changes in gene expression such as transcript accumulation associated with lignin and suberin biosynthesis pathways, cell wall modification, transcript and protein synthesis and stress responses and defense are up-regulated in response to skinning injury.

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