

More Than Skin Deep: Native Periderm Development and Lignin-mediated Durability in Sweetpotato Storage Roots

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Abstract. The sweetpotato native periderm is a critical protective tissue that replaces the epidermis during secondary growth in storage roots and plays a central role in determining postharvest quality and marketability. Damage to this tissue during harvest increases water loss and susceptibility to pathogen infection, necessitating post-harvest curing to induce wound periderm formation. Although wound periderm development has been extensively characterized, particularly in model systems, the formation and regulation of native periderm remain comparatively underexplored. This imbalance limits the translation of mechanistic insights from wound healing to strategies to improve the durability of native periderm under diverse production conditions. A key but underexamined factor contributing to this gap is lignification. Lignin deposition has been largely interpreted in the context of wound responses, where it is viewed as a terminal structural outcome, thus potentially obscuring its broader role in the development of native periderm. As a result, the contribution of lignification to variations in native periderm structure and function remains unresolved. This review synthesizes the current understanding of native periderm formation in sweetpotato by drawing on model and well-characterized species and repositions lignin and lignification as important contributors to native periderm development. By integrating developmental and applied perspectives, this work identifies key knowledge gaps and provides a framework to improve the durability of native periderm, storage root quality, and crop resilience. These insights position lignification as a tractable target for improving sweetpotato skin quality across diverse production systems.

Introduction

Sweetpotato (*Ipomoea batatas*) is widely recognized as the third most important root or tuber crop in the world after potato (*Solanum tuberosum*) and cassava (*Manihot esculenta*) (Food and Agriculture Organization 2023). It is a versatile root crop that is grown in diverse production ecologies. Globally, sweetpotato production is centered in Asia, with China being the largest producer, and Sub-Saharan Africa ranks second (Food and Agriculture Organization 2023). Although leaves are consumed as vegetables in some regions, the fleshy storage roots are the main economically important organ of the crop. The crop is a source of starch, ethanol, and animal fodder in most of Asia, but

it is considered a subsistence or security crop in Sub-Saharan Africa (Firon et al. 2013). In many production environments, the storage root is also the basis of propagation. The United States, Israel, Japan, Australia, New Zealand, and South Africa are among the few countries with developed economies that grow and market sweetpotatoes as a vegetable. Sweetpotato is a perennial, but it is grown as an annual crop in the United States and other subtropical growing regions. In the mainland United States, year-round availability of sweetpotatoes became common approximately 40 years ago, when growers and shippers built environmentally controlled storage facilities, adopted improved curing (Table 1) and storage technologies, and minimized major pest and disease problems in

stored sweetpotatoes (Estes 2009). Postharvest curing is a crucial step that enables the US sweetpotato industry to provide a year-round supply of consistent quality (Edmunds et al. 2008). In tropical growing regions where post-harvest curing and similar environmentally controlled storage technologies are not typically used, sweetpotatoes are grown and available year-round. For example, in Australia, planting is staggered throughout the year, and storage roots are not cured or stored on-site; the crop is harvested, packed, and shipped by refrigerated transport to retail channels and consumed within 1 month of harvest (Bourke 2009). Studies conducted in Sub-Saharan Africa show that root rot, shriveling, and weight loss during transport are directly associated with skinning injury and other periderm wounds (Tomlins et al. 2000). In the United States, consumers perceive gradients in skinning injury, which can influence retail purchase decisions (Collart et al. 2019). In all growing environments, periderm loss or “skinning” (Table 1) has been identified as a critical postharvest and marketing constraint because it leads to reduced shelf life, increases the susceptibility of storage roots to pathogen infection in storage, and reduces marketability (Firon et al. 2013; Klipcan et al. 2020; LaBonte and Wright 1993; Wang et al. 2013).

Scope of the problem

Despite its central role in determining periderm integrity, postharvest performance, and resistance to abiotic and biotic stresses, native periderm development in sweetpotato remains comparatively understudied, particularly relative to the extensive body of work regarding wound periderm formation. Early foundational work in the 1950s and 1960s almost exclusively focused on postharvest curing and the physiological processes underlying wound periderm formation (Fig. 1). These studies established the importance of temperature and humidity in promoting wound healing and reducing storage losses (Kushman and Wright 1969; Morris and Mann 1955). Subsequently, the anatomical and chemical bases of wound periderm formation were characterized (Walter and Schadel 1983). In contrast, studies of native periderm and preharvest treatments to reduce skinning were not reported until the 1970s (Austin and Graves 1970). A key finding by Walter and Schadel (1983) demonstrated that the wound periderm was histochemically similar to the native periderm, consisting of suberized and lignified phellem cells arranged in protective layers. They also highlighted the critical role of lignification in the early response to wounding and in the completion of the curing process (Walter and Schadel 1982, 1983). Except for a report linking ethylene to wound healing (St. Amand and Randle 1991), research of wound periderm experienced a lull in momentum during the 1990s and 2000s, followed by renewed interest using molecular approaches. During the same timeframe, research of native periderm focused on biochemical and functional properties, including allelopathic and insecticidal activities (Harrison et al. 2001, 2003;

Table 1. Glossary.

Lignin	Structural phenolic polymer in cell walls
Lignification	Process of lignin deposition and polymerization
Native periderm	Periderm is formed during normal development
Periderm	Secondary protective tissue replacing the epidermis (phellem, phellogen, phelloderm)
Phellem (cork)	Outermost layer of dead, suberized cells
Phellogen	Meristematic layer generating periderm tissues
Phelloderm	Tissue resembling cortical parenchyma produced centripetally by the phellogen
Phenylpropanoid pathway	Metabolic pathway producing lignin precursors
Storage root	Root swelling because of secondary growth, usually comprising the formation of secondary vascular tissues from a vascular cambium and periderm from phellogen
Skinning injury	Detachment of periderm during harvest/handling
Wound periderm	Periderm formed after injury

Peterson and Harrison 1991; Truong et al. 2007). From the early 2000s onward, research of wound periderm shifted toward gene expression and enzymatic regulation associated with wound healing. In a synthesis of the available literature, Firon et al. (2013) highlighted that lignin content and activities of polygalacturonase and pectin methylesterase may be involved in processes or factors associated with increased or decreased periderm loss in sweetpotato. The study by Efendy et al. (2013) is one of the earliest attempts to characterize the molecular basis of wound periderm formation in sweetpotato. This study demonstrated that wound periderm formation is an active, transcriptionally regulated process rather than a passive structural response. More importantly, it confirmed the activity of enzymes associated with lignin biosynthesis, thus supporting the conclusion of Walter and Schadel (1983). Recent transcriptomic analyses have further confirmed the essential role of lignification in wound periderm formation. Transcriptomic studies by Ji et al. (2022) and Xuan et al.

(2024) documented that wound healing was associated with upregulation of genes involved in phenylpropanoid metabolism, lignin biosynthesis, and cell wall remodeling. In contrast, research of native periderm around this time was firmly in the physiological and agronomic era. Among the limited studies that directly addressed native periderm, Villavicencio et al. (2007) demonstrated that substrate temperature influenced skin adhesion, lignin content, and periderm histochemistry, thus providing evidence that lignification is associated with increased periderm durability. Klipcan et al. (2020) reported that potassium nutrition increased periderm thickness, thus demonstrating that native periderm quality can be agronomically manipulated; however, the underlying mechanisms, including potential effects on lignification, remain unexplored.

Collectively, these studies indicate that although the body of research regarding native periderm remains limited compared with that regarding wound periderm, published works to date support an important role for lignification in determining periderm durability. Despite this, lignification has often been treated as a secondary component relative to suberin and has been overlooked in discussions of periderm strength and skinning resistance. Emerging evidence of sweetpotato complemented by findings of studies of other storage organs and model systems support the hypothesis that native periderm lignification is associated with structural integrity. Wound periderm studies provide a mechanistic framework for evaluating lignification as a tractable trait that can be influenced through genetic and agronomic approaches. Durable native periderm reduces wounding during harvest, extends storage life, and improves the overall marketability of sweetpotatoes. In this literature review, we synthesize current knowledge of native periderm development in sweetpotato within a broader comparative context and integrate insights from other species when relevant. We highlight lignification as an emerging structural and functional trait associated with reduced skinning injury, improved postharvest performance, and enhanced resilience to abiotic and biotic stresses.

Under the skin: Clarifying periderm terminology

Periderm terminology is among the most difficult in plant anatomy (Crang et al. 2018; Serra et al. 2022). The term “skin” has been used to refer to the periderm (Blankenship and Boyette 2002; Villavicencio et al. 2007). However, Klipcan et al. (2020) defined the sweetpotato “skin” as the phellem layer. Variable definitions of skin can lead to differences in interpretation and compromise direct comparisons of results across studies with different definitions of “skin.” Considering prior work, we defined “skin” in this review as the periderm tissue composed of the following three layers: phellem, phellogen, and phelloderm (Table 1). Unless otherwise indicated as wound periderm, the terms “periderm” and “native periderm” are used interchangeably throughout this review. The onset of periderm formation has been associated with secondary growth (Campilho et al. 2020; Esau 1977; Wunderling et al. 2018). In sweetpotato, the appearance of secondary vascular tissue, cambium, and anomalous cambium marks the onset of secondary growth or storage root formation (Table 1).

Building the barrier: Ontogeny and chemical composition

Despite substantial advances in our understanding of storage root formation, the origin and development of the sweetpotato native periderm are incompletely understood. Current knowledge has been derived largely from isolated anatomical studies and extrapolations from model systems, with limited integration across developmental and biochemical scales. This section addresses this gap by synthesizing current published work regarding the development of the native periderm and chemical composition, thus highlighting insights regarding lignin as a key structural component.

Origins of the periderm: Pericyclic or cortical? Current anatomical evidence suggests that native periderm development is closely associated with the onset of storage root formation (Esau 1977), yet the precise cellular origin of the tissue remains unresolved. Early anatomical observations by Artschwager (1918) described the gradual replacement of the epidermis by a periderm derived from superficial cell layers, including the epidermis and peripheral cortex. As periderm formation progressed, the original cortex and endodermis became thinner, indicating a developmental transition toward a protective outer tissue. Subsequent studies provided more explicit evidence of a nonpericyclic origin. Kono and Mizoguchi (1982) reported that the sweetpotato periderm arises from periclinal divisions in the sub-exodermal cell layer rather than from the pericycle. This interpretation is further supported by anatomical observations by Villordon et al. (2009), who demonstrated that native periderm formation occurs early during the transition from primary growth to storage root initiation (Fig. 2). At 5 d after planting, adventitious roots undergoing primary growth exhibit typical root anatomy, including epidermis, cortex,

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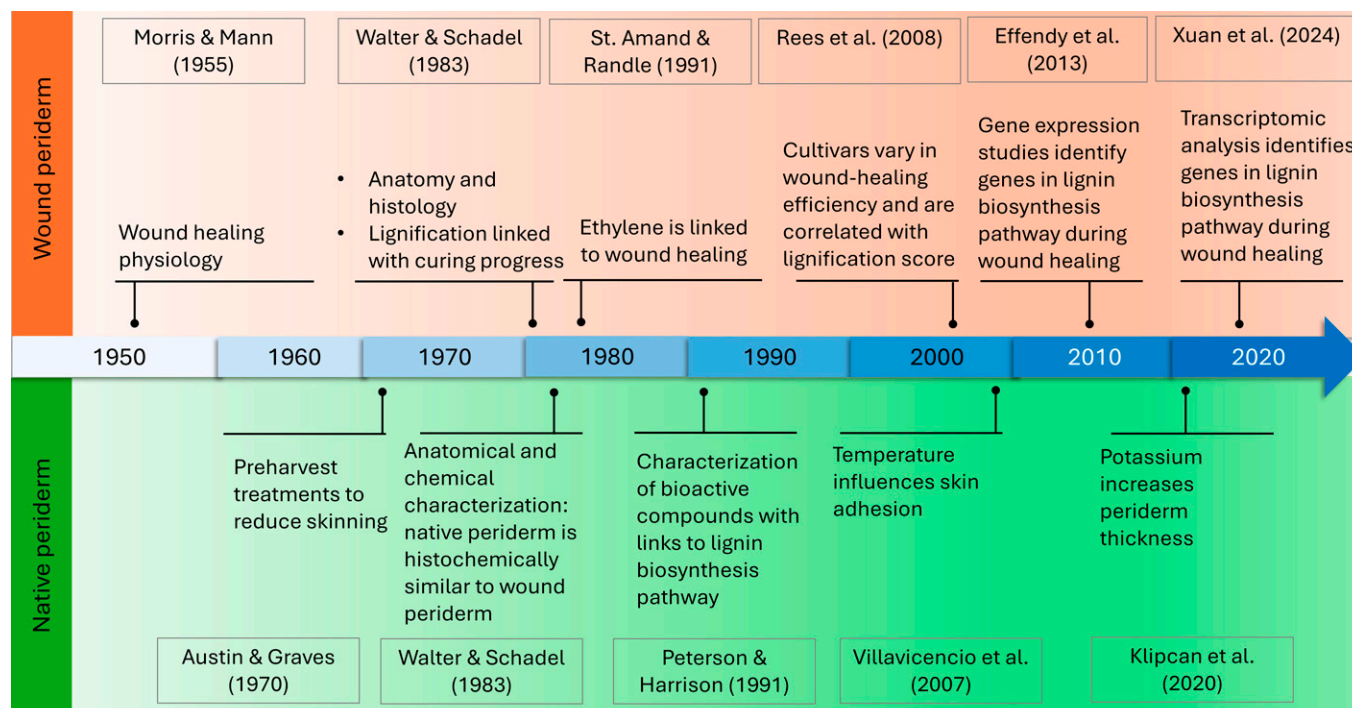


Fig. 1. A historical timeline of differential progress in research conducted to enhance the understanding of wound periderm and native periderm in sweetpotato. The top half of the timeline (green) tracks progress in wound periderm research over the past 75 years, and the bottom half (orange) tracks progress in native periderm research.

pericycle, phloem, and protoxylem, with no evident well-developed periderm (Fig. 2A). By the onset of secondary growth, meristematic activity becomes visible around the vascular cylinder, including the initial appearance of

vascular cambium (Fig. 2B). As development proceeds, a well-defined periderm composed of phellem, phellogen, and phelloderm is evident concurrently with a fully established vascular cambium and the early onset of anomalous

cambium activity (Fig. 2C). The close connection between lateral roots and the main vascular system further illustrates the integration of vascular development with storage root formation (Fig. 2D). By the initial bulking phase, the

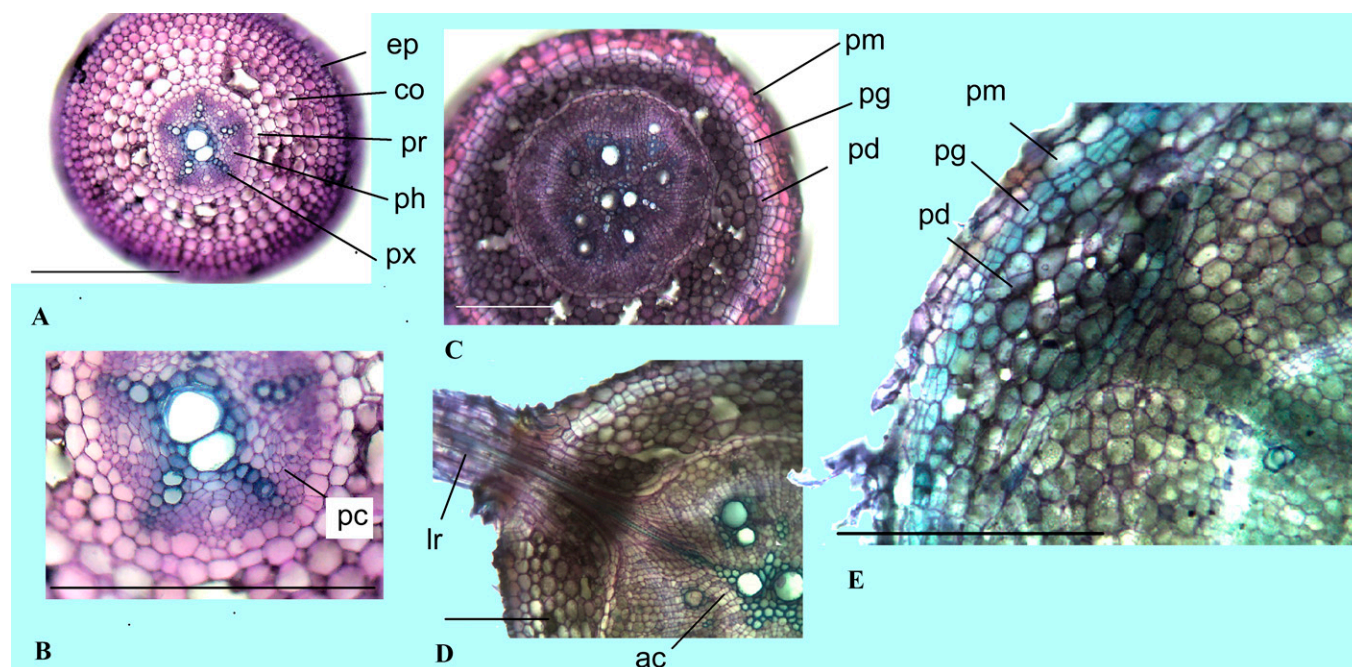


Fig. 2. Anatomical progression of storage root development and periderm formation in sweetpotato. Primary growth stage [5 d after planting (DAP)] showing typical adventitious root anatomy before secondary growth (A). Onset of secondary growth (15 DAP) with the initial appearance of the vascular cambium (B). Development of a well-defined periderm concurrent with a fully established vascular cambium and onset of anomalous cambial activity (C). A cross-section illustrates a lateral root connected to the main vascular tissue and associated anomalous cambium (D). Storage root at the initial bulking phase (15–25 DAP) with the outer phellem partially removed, thus revealing underlying periderm layers (E). ac = anomalous cambium; co = cortex; ep = epidermis; lr = lateral root; pc = procambium; pd = phelloderm; pg = phellogen; ph = phloem; pm = phellem; pr = pericycle; px = protoxylem. Scale bars = 0.5 mm. Adapted from Villordon et al. (2009).

storage root shows a distinct outer periderm, with the phellem layer visible at the root surface (Fig. 2E). Together, these observations suggest that native periderm formation is initiated early during storage root development and closely associated with secondary growth, but it may precede or occur concurrently with anomalous cambium development.

Collectively, these observations suggest that sweetpotato may deviate from the classical pericyclic model of periderm origin. In many model systems, including *Arabidopsis*, it is well-documented that periderm formation originates from the pericycle following the initiation of secondary growth (Campilho et al. 2020; Wunderling et al. 2018). However, in storage organs such as potato tubers, the periderm originates from subepidermal cells that dedifferentiate into phellogen initials (Serra et al. 2022). This suggests that periderm origin may be strongly influenced by organ type and developmental context, with storage organs favoring cortical or subepidermal origins rather than pericyclic derivation.

Taken together, the available anatomical evidence supports a model in which sweetpotato native periderm originates from subepidermal or cortical tissues early in storage root development. However, this conclusion is largely inferential because of the lack of lineage-tracing or molecular marker studies. Resolving the cellular origin of the native periderm remains a critical gap, particularly because of its implications for understanding how structural and chemical traits, such as lignification, are established during development.

Chemical composition and the emerging role of lignification. Compared with anatomical studies, the chemical composition of sweetpotato native periderm remains poorly characterized. Most studies have focused on biological activity rather than structural function. Foundational work by Walter and Schadel (1983) compared native and wound periderms and reported broadly similar lignin aromatic components, although wound periderm contained substantially lower suberin content. These findings, together with comparable observations of other species (Pearce 1996), suggest that lignification is an early and conserved response associated with periderm formation, particularly under stress conditions.

More broadly, insights regarding periderm chemistry have been largely derived from model systems. In these systems, periderm cell walls are primarily composed of suberin, lignin, waxes, and polysaccharides (Barros et al. 2024). Traditionally, suberin has been emphasized for its role in water impermeability; however, lignin significantly contributes to mechanical strength and structural integrity (Barros et al. 2015; Boerjan et al. 2003) and plays an important role in both passive and active defense (Bhuiyan et al. 2009; Moura et al. 2010). Lignin is the most abundant aromatic polymer produced in plants (Dixon and Barros 2019). It is a complex cell wall-binding phenolic polymer derived from the phenylpropanoid pathway (Choi et al. 2023; Liu et al. 2018) that is deposited in the apoplast, thus forming a critical component of secondary

cell walls along with cellulose and hemicellulose (Boerjan et al. 2003). Its evolutionary significance is well-established because lignification is a key adaptation that enabled terrestrial plants to withstand mechanical and environmental stresses (Tobimatsu and Schuetz 2019).

Comparative studies across storage organs further reinforce the importance of lignification in periderm function. In cassava, phenylpropanoid pathways are strongly induced in response to wounding, resulting in increased lignin accumulation during postharvest storage (Wang et al. 2023). In radish (*Raphanus sativus*) and carrot (*Daucus carota*), lignified and suberized periderm layers contribute to barrier function and mechanical stability, with variation in lignin composition (e.g., glucose-to-starch ratio) influencing tissue properties (Kováč et al. 2018; Schäfer et al. 2018). Similar patterns are observed in turnip (*Brassica rapa*), where lignin contributes to both structural reinforcement and chemical defense (Wen et al. 2022). These cross-species observations suggest that lignification is a conserved feature of periderm development, with functional roles extending beyond simple barrier formation.

Despite this broader context, direct evidence linking lignification to the function of the native periderm in sweetpotato remains limited. Existing studies provided indirect but compelling support. For example, environmental and physiological studies have shown that increased lignin content is associated with improved skin adhesion and reduced susceptibility to skinning injury (Villavicencio et al. 2007). Similarly, agronomic studies indicate that nutrient management, particularly potassium supply, can influence periderm characteristics, potentially through effects on cell wall composition and structural reinforcement (Klipcan et al. 2020). However, these studies stop short of mechanistically linking lignin biosynthesis to periderm development.

This disconnect highlights a critical gap in current understanding. While lignification is well-established as a key component of wound periderm formation and strongly implicated in the durability of the native periderm, it has not been systematically investigated as a developmental trait in sweetpotato. As a result, lignin remains underrepresented in discussions of periderm structure relative to suberin despite mounting evidence of its importance. In this context, lignification should not be viewed merely as a secondary component of periderm chemistry because it may function as a key structural component with direct implications for periderm strength, adhesion, and resistance to mechanical and biological stress. Advancing our understanding of lignin deposition, composition, and regulation in native periderm will be essential for developing strategies to improve sweetpotato skin quality and postharvest performance.

Building the barrier: Genes and pathways shaping periderm formation and lignification

Direct molecular evidence of sweetpotato remains limited, and much of our understanding

of lignin biosynthesis and its regulation in periderm tissues is derived from model systems such as *Arabidopsis* and potato (*Solanum tuberosum*). Nevertheless, lignin biosynthesis is highly conserved across plant species and originates from the phenylpropanoid pathway, which also produces a wide range of secondary metabolites, including hydroxycinnamic acids, flavonoids, and lignans (Weng and Chapple 2010; Xu et al. 2009; Yao et al. 2021). This conserved framework provides a foundation for interpreting lignification processes in sweetpotato periderm, particularly in the context of structural reinforcement and stress response.

From phenylpropanoid to monolignols: blueprint for periderm lignification. Lignin biosynthesis proceeds through three coordinated stages: monolignol biosynthesis through the phenylpropanoid pathway in the cytoplasm; transport of lignin precursors in the apoplast; and polymerization in the cell wall (Choi et al. 2023; Jalal et al. 2025; Liu et al. 2018). The pathway begins with the conversion of phenylalanine to cinnamic acid by phenylalanine ammonia-lyase (PAL), followed by hydroxylation by cinnamate 4-hydroxylase (C4H) to *p*-coumaric acid (Fig. 3). Then, this compound is activated by 4-coumarate:CoA ligase (4CL) to *p*-coumaroyl-CoA, a key branch point linking lignin biosynthesis to other phenylpropanoid-derived pathways (Jalal et al. 2025). Downstream reactions modify these intermediates through hydroxylation, acyl transfer, methylation, and reduction, thereby determining the composition of lignin. Key enzymes include hydroxycinnamoyl-CoA shikimate/quinate hydroxycinnamoyl transferase, *p*-coumarate 3-hydroxylase, caffeoyl shikimate esterase, caffeoyl-CoA O-methyltransferase (CCoAOMT), caffeic acid O-methyltransferase (COMT), cinnamoyl-CoA reductase (CCR), and cinnamyl alcohol dehydrogenase (CAD). Together, these reactions generate three major monolignols, *p*-coumaryl alcohol, coniferyl alcohol, and sinapyl alcohol, which give rise to H, G, and S lignin units, respectively. Formation of S units also requires ferulate 5-hydroxylase and COMT activity. The relative abundance of H, G, and S units influences lignin structure, cross-linking, rigidity, and resistance to degradation (Choi et al. 2023; Jalal et al. 2025; Liu et al. 2018; Yao et al. 2021; Yoon et al. 2015; Xie et al. 2018).

After monolignols are synthesized in the cytoplasm, they are transported to the apoplast, where oxidative polymerization occurs in the cell wall. This final step is primarily mediated by laccases and peroxidases (POD), which generate phenoxy radicals that couple nonenzymatically to form the lignin polymer (Alejandro et al. 2012; Lashbrooke et al. 2016; Miao and Liu 2010). At the regulatory level, lignin biosynthesis is controlled by transcriptional networks involving *NAC* and *MYB* transcription factors. The *NAC* proteins, such as SND1/NST1 homologs, function as master regulators of secondary wall formation, while downstream *MYB* transcription factors, such as *MYB46* and *MYB83*, activate lignin biosynthetic genes including *PAL*, *C4H*, *4CL*, *CCR*, and *CAD*. Additional *MYB*

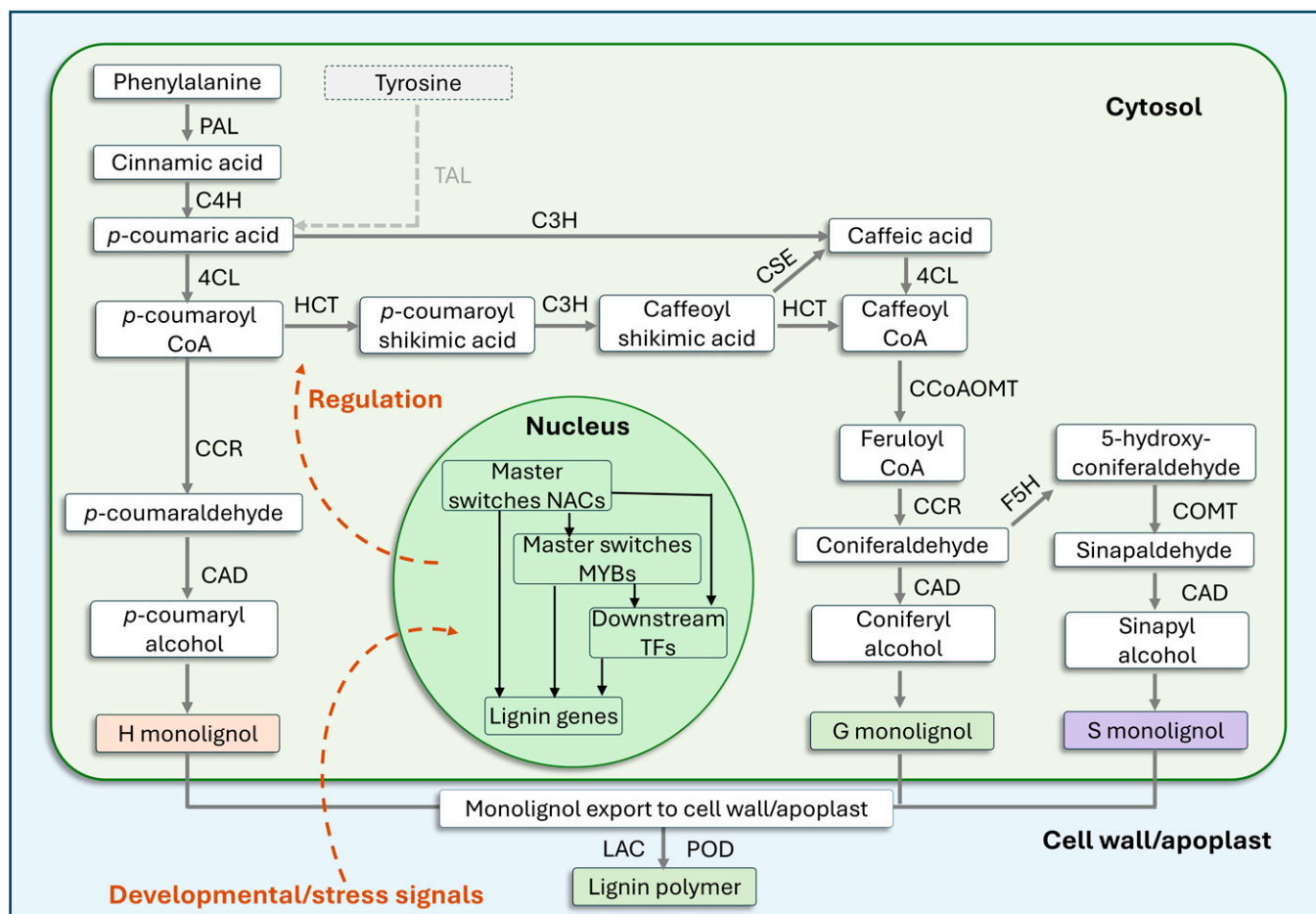


Fig. 3. Simplified conceptual model of lignin biosynthesis, transcriptional regulation, and polymerization during periderm lignification. The diagram summarizes the major cytosolic steps of the phenylpropanoid–monolignol pathway, starting from phenylalanine (with an alternative tyrosine route), culminating in the formation of the H, G, and S monolignols, and then undergoing oxidative polymerization in the cell wall to form lignin. A simplified nuclear regulatory module highlights the roles of NAC and MYB transcription factors as well as downstream transcription factors in controlling lignin biosynthetic genes. This figure was created by the authors as a conceptual synthesis based on multiple published sources, including Barros et al. (2015), Liu et al. (2018), Rao and Barros (2024), Yao et al. (2021), and Yoon et al. (2015); it was not reproduced from a single published figure. 4CL = 4-coumarate:CoA ligase; C3H = coumarate 3-hydroxylase; C4H = cinnamate 4-hydroxylase; CAD = cinnamyl alcohol dehydrogenase; CCoAOMT = caffeoyl-CoA O-methyltransferase; CCR = cinnamoyl-CoA reductase; CoA = coenzyme A; COMT = caffeic acid O-methyltransferase; CSE = caffeoyl shikimate esterase; F5H = ferulate 5-hydroxylase; G = guaiacyl; H = p-hydroxyphenyl; HCT = hydroxycinnamoyl-CoA shikimate/quinic acid hydroxycinnamoyl transferase; LAC = laccase; MYBs = MYB transcription factors; NACs = NAC transcription factors; PAL = phenylalanine ammonia-lyase; POD = peroxidase; S = syringyl; TAL = tyrosine ammonia-lyase; TFs = transcription factors.

factors (e.g., *MYB58* and *MYB63*) act as lignin-specific activators that fine-tune monolignol biosynthesis and composition (Choi et al. 2023; Zhong and Ye 2009). This regulatory framework provides a mechanistic basis for genotype-dependent variation in lignification observed across crops.

Although detailed biochemical characterization of sweetpotato remains limited, available data indicate that both native and wound periderms contain similar lignin aromatic components, with notable compositional differences. Walter and Schadel (1983) reported that wound periderm contains fewer S units than native periderm, suggesting that lignin formed during injury responses is structurally distinct and potentially less complex. More recent transcriptomic studies confirmed active phenylpropanoid metabolism during wound periderm formation, including the expression of key lignin biosynthetic genes and accumulation of monolignol precursors (Xuan et al. 2024). Together, these findings support a conserved

model in which lignification contributes to periderm structure through the regulated biosynthesis and polymerization of monolignols. However, although the biochemical pathway is well-defined, its developmental regulation and spatial dynamics in the sweetpotato native periderm remain largely unresolved.

Lignification as a trait: genetic variation for enhanced periderm durability. Emerging evidence supports the view that lignification is not merely a biochemical endpoint; it is a selectable trait that is likely to influence periderm strength, adhesion, and resistance to stress. Lignin content and composition can be genetically altered, and the effects of single or multiple lignin biosynthesis gene expression on phenotypic traits of transgenic plants have been characterized (Liu et al. 2018). In potato, which is the best-characterized system for periderm development, genetic and transgenic manipulations of lignin-related pathways have demonstrated clear functional outcomes. For example, silencing of the NAC transcription

factor *StNAC103* alters suberin-associated pathways and increases lignin deposition, resulting in firmer periderm and reduced susceptibility to mechanical damage and pathogen ingress (Verdaguer et al. 2016). Complementary studies showed that CCoAOMT was linked to lignification and associated with skin set in potato (Vulavala et al. 2019). In carrot, increased expression of *COMT* and *CAD* during maturation shifted lignin composition and improved periderm firmness (Schäfer et al. 2018). Cassava rapidly induced expression of phenylpropanoid genes in response to stress, with specific PAL alleles linked to tolerance to postharvest deterioration (Wang et al. 2023). Similar lignin-mediated responses have been observed in radish, turnip (*Brassica rapa*), and sugar beet (*Beta vulgaris*), where lignification contributes to stress resistance, structural reinforcement, and barrier function (Fugate et al. 2023; Kováč et al. 2018; Wen et al. 2022). In tobacco (*Nicotiana tabacum*), overexpression of sweetpotato swpa4 peroxidase was associated with

increased lignin content and enhanced stress tolerance to drought and black shank disease (*Phytophthora parasitica* var. *nicotianae*, KACC 40164) treatments (Kim et al. 2008).

In sweetpotato, although molecular evidence is more limited, available data point in the same direction. Variation in the expression of lignin pathway genes, including *PAL* and *CCoAOMT*, is associated with differences in periderm durability among cultivars (Effendy et al. 2013). Importantly, earlier physiological work provided strong, yet often undercited, evidence of cultivar-level variation in lignification capacity. Using a lignification index based on the continuity of lignified layers, Van Oirschot et al. (2006) demonstrated substantial variation in wound-induced lignification among cultivars, with some genotypes consistently producing continuous lignified barriers and others exhibiting patchy or absent lignification. These findings established lignification as a quantitatively variable and functionally relevant trait in sweetpotato. Chemical induction approaches further support this relationship. Preharvest ethephon treatments increase lignin and suberin deposition and significantly reduce skinning injury during storage (Wang et al. 2013). Additionally, transgenic studies demonstrated that overexpression of lignin-associated genes (e.g., *IbLfp*) enhances lignin accumulation under stress conditions, improving both abiotic stress tolerance and periderm stability (Lee et al. 2021). Recent transcriptomic analyses further revealed genotype-dependent variation in wound-responsive lignin biosynthesis genes, thus providing potential markers for selecting durable skin phenotypes (Du et al. 2023; Meng et al. 2022).

Taken together, these findings demonstrate that natural variation in lignin biosynthesis represents a promising target for improving periderm durability. In sweetpotato, this represents a largely untapped opportunity. Targeting genetic variation in key pathway genes and regulators offers a pathway to enhance native periderm strength, reduce dependence on postharvest

curing, and improve both field resilience and storage performance. Future integration of genomic, transcriptomic, and spatial analyses will be essential for identifying and deploying favorable alleles that control lignification at the tissue level. From an applied perspective, this suggests that variation in lignin biosynthesis pathways represents a promising target for both breeding and agronomic intervention aimed at improving periderm durability across diverse production environments. Lignification integrates preharvest factors with structural and functional outcomes in the native periderm (Fig. 4).

Cross-tolerance?: Lignin-mediated stress resistance and enhanced postharvest durability

Lignification may be a preharvest-inducible trait that reinforces native periderm against biotic stress and simultaneously enhances postharvest durability. By increasing cell wall rigidity through cross-linking with cellulose and hemicellulose, lignin reinforces tissue structure, limits pathogen penetration, and reduces susceptibility to mechanical damage (Pinto et al. 2025; Terrett and Dupree 2019). These dual roles suggest a potential cross-tolerance mechanism whereby lignification contributes to both field resistance and postharvest performance; however, these functions are rarely considered together in sweetpotato.

Lignin-mediated biotic and abiotic stress resilience. Lignification is a central component of plant defense that functions as both a structural barrier and biochemical response to biotic and abiotic stress. In sweetpotato, early evidence demonstrated that phenolic compounds associated with lignin biosynthesis, such as caffeic acid, inhibit the growth of key storage pathogens, including *Fusarium*, *Lasiodiplodia*, and *Rhizopus* species (Harrison et al. 2003). Variation in these compounds among clones further suggests a genetic basis for lignin-mediated defense. In radish, resistant cultivars exhibit preexisting lignified cell walls that restrict pathogen entry, whereas induction of lignification in susceptible tissues

via phenylalanine application confers resistance (Matsumoto and Asada 1984; Matsumoto et al. 1978). This response is mediated by increased *PAL* activity, thus highlighting the importance of the phenylpropanoid pathway in defense activation. More recent studies provide molecular support for this mechanism. In sweetpotato, infection with southern root-knot nematode (*Meloidogyne incognita*) induced the expression of lignin biosynthesis genes, including *PAL* and *CAD*, and increased total phenolics and lignin content in resistant cultivars (Yang et al. 2023). Genotype-specific variation in *POD* gene expression was previously reported among sweetpotato cultivars infected with *Pectobacterium chrysanthemi* (Jang et al. 2004). Similar responses are widely conserved across species, with biotic stress triggering coordinated upregulation of phenylpropanoid genes and lignin deposition in roots and lignification forming a reinforced barrier that limits pathogen ingress and spread (Thangavel et al. 2026; Wang et al. 2023).

Recent studies have shown that lignin deposition is likely involved in abiotic stress tolerance. Overexpression of sweetpotato *IbLEA14* genes enhanced the salt and osmotic stress tolerance of transgenic callus by increasing lignin accumulation (Park et al. 2011). Differential expression of *POD* genes was also associated with heavy metal treatments, suggesting the potential to select for improved heavy metal tolerance in sweetpotato (Kim et al. 2010). Data of European walnut (*Juglans regia*) indicated that lead (Pb) was preferentially sequestered in outer root tissues, with substantial accumulation localized in the periderm, thus supporting the hypothesis that lignified periderm acts as a primary sink for Pb sequestration, shielding inner tissues and limiting systemic toxicity (Marmioli et al. 2005). Consistent with this model, LA-ICP-MS elemental imaging of sweetpotato storage roots (Fig. 5) revealed a similar spatial pattern, with Pb concentrated in the outer periderm layers relative to internal tissues, thus supporting the hypothesis that outer periderm-associated tissues

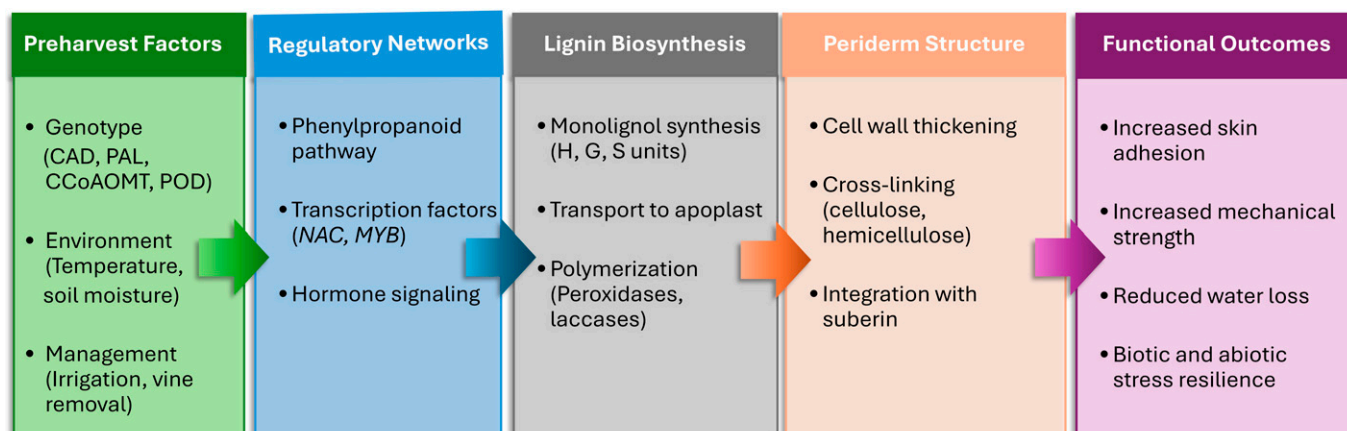


Fig. 4. Conceptual model illustrating lignification as an important contributor to native periderm durability in sweetpotato storage roots. Preharvest factors, including genotype, environment, and agronomic management, regulate phenylpropanoid metabolism and associated transcriptional networks. These pathways control lignin biosynthesis, transport, and polymerization within periderm tissues. Lignin deposition reinforces the cell wall structure through cross-linking with polysaccharides and interactions with suberin, thereby increasing periderm thickness, mechanical strength, and structural integrity. These properties translate to functional outcomes, including improved skin adhesion, reduced water loss, enhanced resistance to pathogen ingress, and decreased susceptibility to skinning injury, ultimately improving postharvest performance.

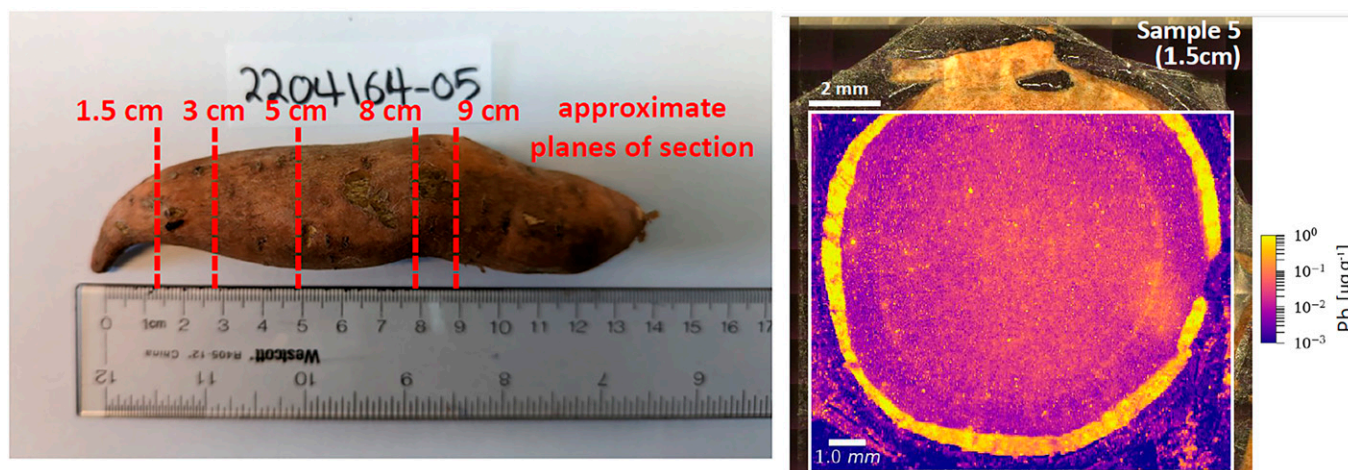


Fig. 5. Sweetpotato storage root sample (A) and spatial distribution of lead (Pb) in a transverse section determined by laser ablation inductively coupled plasma mass spectrometry (B). The color scale (yellow to blue) represents decreasing Pb concentrations ($\mu\text{g}\cdot\text{g}^{-1}$). Preferential localization of Pb occurs in the outer periderm region, with markedly lower concentrations in internal tissues, indicating selective accumulation at the root surface consistent with a barrier or sequestration role of outer periderm-associated tissues. Data were generated as part of the project “Studies to Reduce Lead Presence in Sweetpotato Storage Roots,” with funding support from Gerber Products Company.

contribute to a barrier or sequestration role for heavy metals. Taken together, these findings indicate that lignification is both inducible and constitutive, thereby contributing to resistance through preformed barriers and rapid reinforcement following stress exposure. However, although these mechanisms are well-established in wound and stress contexts, their role in the native periderm as a baseline defense barrier in sweetpotato remains insufficiently characterized.

The next frontier?: Preharvest lignification for postharvest durability. The downstream benefits of preharvest lignification extend across the postharvest supply chain. By reinforcing the native periderm before harvest, lignin deposition enhances structural integrity, reduces water loss, and strengthens resistance to mechanical damage and pathogen entry. This approach is particularly relevant in tropical and subtropical production systems, where curing infrastructure is limited. Preharvest treatment-induced lignification has been shown to delay physiological deterioration, shriveling, and rot, thereby extending the shelf life of sweetpotato storage roots grown under tropical conditions without energy-intensive storage (Parmar et al. 2017). Preharvest treatments such as canopy removal via mowing or chemical treatments have been shown to reduce skinning at harvest (Austin and Graves 1970; LaBonte and Wright 1993; Tomlins et al. 2002). In sweetpotato, preharvest induction strategies provide support for this relationship. Preharvest treatments such as ethephon application (Wang et al. 2013) and defoliation (Parmar et al. 2017) were associated with increased periderm lignin content. If lignification is enhanced before harvest, then the periderm is already fortified against mechanical stress and pathogen ingress, thereby reducing reliance on postharvest curing.

Evidence from other storage organs confirmed the broader applicability of this strategy. In potato, increased lignin content is associated with reduced weight loss and decay during

storage (Serra et al. 2022; Vulavala et al. 2019). Lulai and Freeman (2001) established a paradigm for reducing potato skinning loss by thickening and strengthening the tuber phellogen cell wall through the induction of periderm maturation. In carrot and radish, lignification improves resistance to bruising and microbial invasion, particularly in fresh-cut products (Schäfer et al. 2018). Cassava cultivars capable of rapid lignin induction exhibit delayed postharvest physiological deterioration, thus extending the shelf life under ambient conditions (Zainuddin et al. 2018; Zidenga et al. 2012). In sugar beet, higher periderm lignin content is associated with improved firmness, reduced cracking, and lower weight loss during storage (Fugate et al. 2023). Beyond physiological benefits, lignification also enhances marketability. Reduced skinning injury improves visual quality, which is a key determinant of consumer acceptance and purchasing decisions (Collart et al. 2019). In addition, cultivars with stronger native periderm require fewer postharvest interventions, thus lowering energy inputs and reducing production costs across the supply chain.

From an applied perspective, this suggests that enhancing lignification during native periderm development represents a practical strategy to simultaneously improve resistance to biotic stress and postharvest durability in sweetpotato production systems. Together, these findings suggest that preharvest lignification is a practical and scalable strategy for improving both field resilience and postharvest performance. However, despite its demonstrated benefits, lignification remains underutilized as a target trait, particularly in breeding programs aimed at improving native periderm strength.

Future frontiers: Research gaps and opportunities. Despite substantial progress in understanding wound periderm formation and the phenylpropanoid pathways underlying lignification, the developmental regulation and functional characterization of native periderm in sweetpotato remain limited. Critical gaps persist in linking periderm structure and chemistry,

such as thickness, lignin composition, and suberization, to field-level skinning resistance across genotypes and environments (Klipcan et al. 2020; Villordon et al. 2009; Walter and Schadel 1983). These gaps are especially relevant in tropical and subtropical production systems, where curing is minimal and native periderm properties largely determine postharvest performance (Parmar et al. 2017; Ray and Ravi 2005). From an applied perspective, this suggests that the development of nondestructive high-throughput phenotyping tools capable of quantifying lignification-related traits will be essential for translating mechanistic insights to breeding gains and improved postharvest outcomes.

Current experimental approaches for evaluating periderm traits are largely destructive, low-throughput, and difficult to standardize. Skinning resistance is typically measured using force-to-peel assays or visual scoring following abrasion, both of which are prone to operator bias (Birnbaum and Kushman 1971; Bouwkamp et al. 1972; Webster et al. 1973). Periderm thickness and anatomy are assessed through manual sectioning and microscopy, while lignin and suberin are quantified using histochemical staining (e.g., phloroglucinol-HCl for lignin, Sudan dyes for suberin) or bulk chemical assays such as thioglycolic acid or acetyl-bromide methods (Graça and Santos 2007; Walter and Schadel 1983). Although these techniques have been foundational, they are not well-suited for large-scale screening or capturing spatial and temporal variations in periderm development under field conditions. Similar constraints are evident across other storage organs, where periderm characterization remains labor-intensive and largely endpoint-based (Serra et al. 2022; Wunderling et al. 2018).

Addressing these limitations will require a shift toward nondestructive high-throughput phenotyping platforms that can link structure, chemistry, and function in intact tissues. Hyperspectral imaging offers a promising approach for the rapid noninvasive assessment

of periderm-related traits, thus enabling the prediction of skin integrity, firmness, and potentially lignin content in whole roots (Ahmed et al. 2024; Su et al. 2017). Optical coherence tomography provides label-free, three-dimensional imaging of periderm thickness and internal structure at near-cellular resolution, thus allowing in situ monitoring of developmental changes (Larimer et al. 2020).

Recent advances in machine learning and artificial intelligence have further expanded these capabilities. Image-based models, including convolutional neural networks, can automate quantification of periderm thickness and structural features from histological or spectral datasets, thus reducing subjectivity and increasing throughput (Bloom et al. 2025). When integrated with hyperspectral data, deep learning approaches can predict biochemical traits such as lignin composition or skinning susceptibility almost in real-time. At the molecular scale, emerging tools such as spatial transcriptomics and metabolomics offer the potential to resolve cell-type-specific patterns of lignification and suberization, thus providing mechanistic insight into periderm development (Zhu et al. 2025).

Together, these approaches represent a critical shift from destructive endpoint measurements to dynamic integrative phenotyping systems. Their application will enable more precise characterization of native periderm traits, facilitate large-scale screening across germplasm and environments, and accelerate the identification of genetic determinants of periderm durability. Ultimately, integrating these technologies with breeding and management strategies will be essential for developing sweetpotato cultivars with improved skin integrity and postharvest resilience, particularly in production systems with limited curing infrastructure.

Conclusions

Native periderm development in sweetpotato is closely linked to storage root formation, likely involving phenylpropanoid pathways and stress-responsive genes. Although substantial progress has been made in elucidating wound periderm formation and the phenylpropanoid pathways that underpin lignification, the developmental ontogeny, chemical maturation, and genetic regulation of the native periderm in sweetpotato remain substantially understudied. Critical gaps persist in our understanding of cultivar × environment interactions that govern periderm thickness, lignin monomer composition, and suberin deposition during field growth, which are factors that ultimately determine skinning resistance in noncuring tropical and subtropical production systems. Future research should prioritize single-cell transcriptomics and spatial metabolomics of intact storage roots to resolve cell-type-specific contributions to periderm resilience and include genome-wide association studies that link allelic variations in key biosynthetic genes (*PAL*, *CAD*, *CCoAOMT*) to durable skin phenotypes. Such targeted investigations will not only close longstanding knowledge gaps but also accelerate the breeding of resilient cultivars that maintain postharvest

integrity without reliance on energy-intensive curing infrastructure, thereby enhancing global sweetpotato value chains.

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