

Review Article

Review of Genetic and Environmental Drivers of Post-harvest Physiological Deterioration in Cassava: Implications for Breeding and Food Security

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Abstract

Postharvest physiological deterioration (PPD) is one of the most critical constraints limiting the storage, marketing, and utilization of cassava (*Manihot esculenta*). The rapid onset of PPD after harvest, often within 24-72 hours, leads to discoloration, tissue breakdown, and significant reductions in root quality, resulting in postharvest losses that can reach up to 50% in many cassava-producing regions. This problem is particularly severe in sub-Saharan Africa, where cassava serves as a major staple crop and a primary source of calories for hundreds of millions of people. Understanding the underlying drivers of PPD is therefore essential for improving Cassava shelf life and strengthening food security. This study synthesizes current knowledge on the genetic and environmental factors controlling PPD in cassava and highlights their implications for breeding programs. Evidence indicates that PPD is a genetically regulated physiological response triggered by harvest-induced wounding and mediated through complex biochemical pathways, including reactive oxygen species (ROS) accumulation, phenolic metabolism, and antioxidant defense systems. Significant genetic variability exists among cassava genotypes in their tolerance to PPD, with certain cultivars exhibiting delayed deterioration due to enhanced antioxidant activity and more efficient stress-response mechanisms. Advances in molecular genetics, including genome-wide association studies, single nucleotide polymorphism markers, and genomic-assisted selection, have enabled the identification of loci associated with PPD tolerance and accelerated the development of improved cassava varieties. In addition to genetic determinants, environmental factors such as temperature, humidity, harvesting methods, and storage conditions strongly influence the onset and progression of PPD. The interaction between genotype and environment further complicates the evaluation of PPD resistance, necessitating multi-environment trials and advanced statistical models to identify stable and adaptable genotypes. Integrating genetic improvement with optimized postharvest handling and storage practices offers a promising strategy to mitigate PPD. Ultimately, the development of cassava varieties with enhanced resistance to physiological deterioration will reduce postharvest losses, improve marketability, and contribute significantly to food security and the livelihoods of smallholder farmers in cassava-dependent regions.

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1. Introduction

Postharvest physiological deterioration (PPD) in cassava (*Manihot esculenta*) is a significant challenge that affects the crop's storability and marketability, leading to substantial postharvest losses, especially in sub-Saharan Africa. As one of the most important staple crops globally, cassava provides essential dietary calories for approximately 600 million people. However, PPD can result in losses of up to 50%, exacerbating food security challenges and threatening the livelihoods of smallholder farmers who rely on cassava for their income and sustenance. [1-3] The factors contributing to PPD are complex and can be broadly categorized into genetic and environmental drivers. Genetic variability among cassava varieties plays a crucial role in determining resistance to PPD, with specific genotypes demonstrating delayed deterioration traits. Modern breeding techniques, including genomic-assisted selection and genome editing, are being utilized to enhance the resilience of cassava against PPD, thereby improving food security and economic stability for farming communities. [4-6].

Environmental factors, such as temperature and humidity, are also critical in the onset and progression of PPD. Conditions near the time of harvest, along with storage practices, significantly influence the deterioration process. Effective pre- and post-harvest management practices, including optimal storage conditions, can mitigate PPD and prolong the shelf life of cassava roots. [7-9]. Understanding the interplay between genetic and environmental factors is vital for developing effective breeding programs aimed at reducing postharvest losses. This integrative approach not only seeks to enhance cassava's resistance to PPD but also aims to support food security initiatives in regions heavily reliant on this vital crop, thereby addressing the urgent need for sustainable agricultural practices in the face of increasing food demand [10-12].

2. Genetic Drivers of PPD

Cassava post-harvest physiological deterioration (PPD) is driven by specific genetic and molecular mechanisms that regulate how storage roots respond to wounding stress immediately after harvest. Recent research shows that PPD is not a random decay process but rather a genetically controlled response involving oxidative stress pathways, secondary metabolite biosynthesis, and signal-responsive gene networks that together influence the onset and progression of deterioration. For example, transcriptome sequencing of wounded cassava

tuberous roots identified numerous differentially expressed genes involved in flavonoid biosynthesis that are strongly induced during PPD, with genes such as *MeCHS3* and *MeANR* influencing tolerance through changes in flavonoid and anthocyanin accumulation, which modulate oxidative responses to injury [1]. Upregulation of peroxidase genes like *MePOD12* has been shown to participate directly in PPD regulation by enhancing reactive oxygen species (ROS) scavenging and lignin accumulation; silencing of *MePOD12* accelerates root decay and increases oxidative damage, revealing a genetic role for ROS-related enzyme systems and cell wall-modifying genes in controlling deterioration [2]. Extensive transcriptome analyses also demonstrate that hormone-responsive transcription factors and stress-related gene modules are differentially expressed during PPD, with hundreds to thousands of genes up- or down-regulated in response to signals such as abscisic acid, oxygen radicals, and lignin metabolic processes, highlighting the complexity of the genetic networks underlying PPD responses [3]. Genetic diversity and genome-wide association studies further confirm that PPD is under substantial genetic control, with specific genomic regions on chromosomes such as 1 and 4 associated with variation in PPD expression among diverse cassava accessions, implying that inheritance and marker-linked genetic variation can be harnessed for breeding PPD-tolerant cultivars [4]. Together, these studies establish that PPD in cassava storage roots is driven by dynamic genetic regulation of oxidative stress management, secondary metabolite pathways, transcriptional signaling networks, and heritable genomic variation that collectively determine how rapid deterioration occurs after harvest.

3. Genetic Variability and Resistance Mechanisms

Research consistently shows that there is substantial genetic variability among cassava genotypes in how they respond to post-harvest physiological deterioration (PPD). This genetic variability is evident in differences in the onset and progression of PPD symptoms following harvest. For example, certain cultivars such as NASE18 and KCA0013 have been identified to delay the appearance of discoloration and deterioration in root tissues, whereas varieties like TZ130 show earlier and more severe PPD symptoms under similar storage conditions [5]. These differences underscore the potential for using tolerant genotypes as genetic

resources in breeding programs to improve cassava shelf life. At the biochemical and molecular levels, the genetic control of PPD resistance is linked to multiple interconnected mechanisms that regulate how the plant responds to the stress of wounding and storage. One important aspect is the enzyme-mediated oxidative stress response. Accumulation of reactive oxygen species (ROS) is a hallmark of PPD, and cassava roots activate antioxidant systems to mitigate this oxidative damage. Genes encoding antioxidant enzymes such as ascorbate peroxidases (APX) and other ROS-scavenging proteins are differentially expressed during PPD, contributing to a genotype's ability to control ROS accumulation [2, 6].

Another crucial set of mechanisms involves the phenolic metabolic pathway. Enzymes like phenylalanine ammonia-lyase (PAL) are key to the synthesis of phenolic compounds and flavonoids, which act as antioxidants and help neutralize ROS. Studies have shown that increased expression of PAL and elevated levels of phenolic compounds are associated with greater PPD tolerance in more resistant cassava lines. This supports the idea that the phenylpropanoid pathway plays a protective role by enhancing the plant's ability to scavenge damaging oxidative byproducts generated after harvest [5]. More specifically, regulatory changes in gene expression during PPD suggest that tolerant genotypes coordinate a robust metabolic response involving phenolic compound synthesis, antioxidant enzyme activation, and downstream wound-response processes. For example, higher expression levels of PAL and APX genes have been documented in PPD-tolerant varieties in tandem with greater accumulation of phenolic substances, while susceptible varieties typically show lower activation of these protective pathways [2, 6]. These findings reinforce the importance of both gene regulation and metabolic adjustments in determining the degree of physiological deterioration and highlight how genetic variation among cassava lines influences the effectiveness of these defensive mechanisms.

4. Role of Molecular Markers

Molecular markers have become indispensable in modern cassava breeding, offering high-resolution insights into genetic diversity that traditional phenotypic assessments alone cannot achieve. By providing precise information on allelic variation across the genome, markers such as Simple Sequence Repeats (SSRs) and Single Nucleotide Polymorphisms (SNPs) enable breeders to quantify genetic relationships among cassava accessions and to detect allelic patterns associated with desirable traits, including tolerance to post-harvest physiological deterioration (PPD) [7]. Among these tools, SNP analysis stands out due to its high abundance across the cassava genome and its suitability for high-throughput genotyping. SNP markers serve as powerful predictors of genetic variation underlying complex traits. When applied in conjunction with genome-wide association studies (GWAS), SNP data can reveal statistically significant associations between specific genomic regions and phenotypic responses to

PPD. GWAS leverages natural diversity within diverse cassava populations to map loci controlling responses to oxidative stress, cell wall integrity, and other physiological processes that contribute to PPD susceptibility or tolerance [7, 8].

The integration of molecular marker information into breeding programs enables marker-assisted selection (MAS) and genomic selection (GS) strategies that significantly accelerate the development of improved cultivars. Genomic-assisted selection uses dense marker data to capture the effects of many small-effect loci simultaneously. This approach enhances the predictive ability of breeding values for complex traits like PPD tolerance, which are often influenced by many genes and by environmental conditions [9, 10]. A major advantage of marker-based approaches is their capacity to account for genotype-by-environment (G×E) interactions. Traditional selection based solely on field performance can be confounded when traits are highly sensitive to environmental variation. By contrast, genomic selection models can incorporate marker information across different environments, improving the accuracy and stability of predictions for PPD resistance. This is particularly important for cassava, as PPD expressions can vary widely across ecological zones, making reliable genetic selection more challenging without molecular data [9, 10]. In summary, molecular markers not only facilitate the characterization of genetic diversity and mapping of PPD-related loci but also enable more efficient and informed selection strategies. Integrating marker data into breeding pipelines, researchers and breeders can expedite the generation of cassava lines that combine high yield with improved post-harvest shelf life and stress resilience, thereby addressing one of the major constraints affecting cassava utilization and food security.

5. Implications for Breeding Programs

The complex nature of post-harvest physiological deterioration (PPD) in cassava presents significant challenges for traditional breeding due to the trait's polygenic control and sensitivity to environmental influences. PPD expression is governed by a network of physiological and biochemical processes, which are affected not only by genotype but also by harvest handling, storage conditions, and environmental factors [11, 12]. This multifaceted complexity means that simply selecting phenotypic performance under one set of conditions may not reliably produce improved resistance across different environments or management systems. To effectively translate genetic insights into practical improvement, cassava breeders must adopt multifaceted breeding strategies that integrate genetic diversity with cutting-edge molecular approaches. Leveraging the extensive genetic variation present in cassava germplasm as revealed through molecular marker analysis and quantitative genetic studies provides a foundation for identifying PPD-tolerant genotypes and incorporating them into crosses or advanced breeding populations [11, 12]. The high heritability values reported for PPD and related traits in several genetic studies suggest that substantial genetic gains can be achieved when this variability is properly harnessed

[11].

Integrating genomic-assisted selection tools such as GWAS, SNP-based prediction models, and genomic selection enhances breeders' capacity to predict PPD outcomes based on genetic profiles, even before phenotypic evaluation in the field or storage conditions [11, 12]. These tools facilitate early selection of individuals likely to combine PPD resistance with other desirable traits, reducing the number of seasons and resources required for field evaluation. This is especially valuable given the long breeding cycles and logistical constraints inherent in cassava improvement programs. Another implication of incorporating molecular breeding techniques is the improved ability to manage genotype-by-environment (G×E) interactions. G×E interactions often obscure true genetic differences for PPD resistance when selection is based solely on phenotypic data from limited environments. Genomic-assisted selection enables breeders to incorporate multi-environment data into prediction models, leading to more robust and stable performance across diverse agro-ecological zones [11, 12]. This not only enhances selection accuracy but also ensures that newly developed varieties perform reliably under farmers' conditions. The broader impact of these advancements in breeding extends well beyond the research station. Developing cassava varieties with enhanced PPD tolerance directly contributes to food security and economic sustainability in regions where cassava is a staple crop. Extended shelf life reduces post-harvest losses, increases marketable volumes, and encourages value-chain participation by farmers, traders, and processors alike. In areas with poor infrastructure, where rapid spoilage severely limits market access, improved PPD resistance can reduce waste and support income stability for rural households [11, 12]. Furthermore, by increasing the proportion of harvest that remains usable for food and industrial processing, PPD-resistant varieties help to optimize resource use and support sustainable cassava production systems in the face of growing population pressures and climate variability.

6. Environmental Drivers of PPD

Post-harvest physiological deterioration (PPD) in cassava roots is not only a genetically mediated process but also strongly shaped by environmental conditions before and after harvest. Research has shown that factors such as ambient temperature, relative humidity, and handling conditions influence the onset and speed of PPD, making it difficult to evaluate genotypes solely on their inherent resistance without controlling for these external drivers [1, 13]. Environmental conditions at the time of harvest, particularly temperature and humidity, affect the initial physiological state of the roots and their subsequent response to wounding. For example, variations in field microclimate during growth and immediately prior to harvest have been correlated with subsequent PPD expression, indicating that roots exposed to higher temperatures and lower humidity levels tend to deteriorate more rapidly once removed from the soil [1, 13]. These conditions interact

with moisture content and metabolic status, thereby modifying how quickly oxidative processes commence after harvest.

Beyond harvest conditions, the storage environment plays a pivotal role in modulating PPD progression. Controlled storage can significantly extend the time before visible deterioration symptoms appear. Studies have shown that maintaining cassava roots at cooler temperatures with high relative humidity markedly delays PPD. Specifically, storage at approximately 10°C combined with around 80% relative humidity has been demonstrated to delay the onset of PPD symptoms by up to two weeks compared with roots stored under typical ambient conditions [6, 14]. These conditions reduce the rate of respiration and reactive oxygen species accumulate key biochemical drivers of PPD thereby slowing the deterioration cascade that leads to discoloration and quality loss. Such findings emphasize the dual nature of PPD: while genetic factors determine inherent tolerance, environmental drivers modulate the expression of PPD traits and can either exacerbate or mitigate deterioration. This interplay complicates the assessment of PPD resistance because responses measured under one set of environmental conditions may not translate directly to another. Consequently, effective PPD management and breeding strategies must consider both the inherent genetic potential of cassava varieties and the prevailing environmental conditions during harvest and storage [1, 13].

7. Factors Influencing PPD Initiation

PPD is initiated primarily through mechanical damage during harvesting, which triggers a cascade of physiological responses in the cassava storage roots [15, 16]. Additionally, the age of the plant and root shape can affect the susceptibility to PPD, indicating that both genetic and environmental variables must be considered [17, 18]. Pre-harvest practices, such as pruning the aerial parts of cassava plants, can enhance the sugar/starch ratio in the roots and delay PPD onset [2]. Moreover, the length of the storage period and the dry matter content (DMC) of the roots are correlated with the incidence of PPD, suggesting that longer storage times and higher DMC can exacerbate deterioration [14, 18]. It has been observed that environmental loads, such as precipitation and solar radiation, significantly correlate with the genetic variability in PPD resistance, highlighting the need for an integrated approach that combines genetic selection with environmental management to mitigate PPD [9].

8. Strategies for Mitigating Environmental Impact

Effectively mitigating post-harvest physiological deterioration (PPD) in cassava requires a combination of environmental management, improved handling practices, and the selection of tolerant varieties to slow or prevent deterioration. Because PPD is triggered by mechanical damage and exacer-

bated by adverse storage environments, strategies that minimize wounding and optimize storage conditions are particularly important in reducing losses [13, 18]. One of the most widely recommended approaches is improving pre- and post-harvest handling practices to minimize physical damage to the roots, which is a primary trigger for PPD. Harvest techniques that reduce bruising and cutting of roots such as careful lifting with minimal impact, the use of soft handling surfaces, and immediate removal of soil and debris can slow the cascade of oxidative processes that lead to tissue breakdown following harvest [12, 19]. Minimizing mechanical injury reduces the surface area exposed to oxygen, which in turn decreases the intensity of the wound-induced stress responses that drive PPD. Once harvested, maintaining cassava roots under controlled storage environments can significantly delay the onset and progression of PPD. Research has shown that simple storage techniques such as packing roots in boxes with moist sawdust or river sand can extend shelf life by reducing moisture loss and moderating temperature fluctuations, thereby slowing the biochemical deterioration process. In one study, roots packed in moist sand-maintained quality for several weeks compared with unpacked controls, which deteriorated within about a week [turn 1 search 18]. Likewise, farmers in smallholder systems have adopted traditional storage methods such as burying fresh roots in cool, moist soil or storing them on moist surfaces to limit exposure to high temperatures and low humidity conditions known to accelerate PPD [13, 18]. Selecting genotypes with inherent tolerance to PPD is another key strategy that complements environmental and handling improvements. Genetic variability among cassava varieties for delayed PPD has been documented by several studies, and the availability of genotypes that show slower symptom development provides opportunities for breeders to incorporate these traits into new cultivars [18]. Farmers themselves sometimes exploit varietal differences by processing more susceptible varieties immediately while leaving more tolerant ones in storage longer to extend fresh root availability [turn 1 search 3]. Traditional storage practices, while sometimes seen as less effective than modern refrigeration or packaging technologies, have recognized utility in contexts where advanced storage systems are inaccessible or costly. Practices such as storing roots under moist conditions, burial in sand, or piece-meal harvesting can delay the onset of PPD for several days, offering critical buffer time to consume or process roots before deterioration becomes severe [12, 20]. Although these methods may not completely prevent PPD, they are practical and scalable in many smallholder farming systems where cold chain infrastructure is lacking [1, 3].

9. Interaction Between Genetic and Environmental Factors

The interaction between genetic and environmental factors plays a crucial role in determining the performance of cassava

genotypes, influencing traits such as tuber yield, root dry matter content, and physiological quality. Genotype by environment (G×E) interactions occur when different genotypes respond differently across environmental conditions, leading to variation in performance rankings across locations, seasons, or management systems. This complexity is particularly important in cassava breeding, as it affects both the stability and adaptability of genotypes [21, 22]. Understanding G×E interactions enable breeders to identify superior genotypes that perform consistently across a range of environments or are specifically adapted to particular agroecological zones. For example, trials across multiple cassava-growing regions have shown that some genotypes maintain high yield and quality across contrasting soil types and climatic conditions, while others perform well only under specific conditions, highlighting the necessity of multi-environment testing [21, 22].

Advanced statistical approaches have been applied to better capture and interpret G×E interactions. Among these, the Factor Analysis (FA) model has demonstrated greater efficiency in explaining variance compared to traditional methods such as AMMI and GGE biplot. FA models can capture latent structures in multi-environmental data, allowing breeders to classify genotypes based on both mean performance and stability, which is critical for selecting genotypes that combine high productivity with environmental resilience [9]. By accounting for complex covariance patterns among environments, FA models enhance the accuracy of predicting genotype performance across untested locations, supporting more reliable selection decisions in breeding programs [9]. Overall, incorporating knowledge of G×E interactions into breeding strategies enables the development of cassava varieties that are both high-yielding and adaptable, ensuring stable production under varying environmental conditions. The use of FA models provides a robust analytical framework to guide selection decisions and optimize resource allocation in multi-environment trials [9, 21, 22].

10. Understanding G×E Interactions

G×E interactions occur when the performance of a genotype varies across different environmental conditions, influenced by both genetic makeup and environmental factors. For instance, genotypes such as BR11-34-41 and BR11-34-69 exhibited positive trends in certain environments, whereas others like CIGNA Preta and Corrente displayed negative responses, highlighting the variability in adaptability among genotypes [9]. This phenomenon is particularly relevant for traits like dry root yield (FRY) and dry matter content (DMC), where environmental variables, including temperature and rainfall, play significant roles in determining genotype performance.

11. Environmental Influences on Genotype Performance

The performance of cassava genotypes is not only determined by genetic factors but is strongly modulated by environmental conditions. Analyses using Factor Analysis (FA) models have shown that environmental covariates, such as temperature, rainfall, and altitude, can significantly influence the expression of key agronomic and physiological traits, including dry matter content (DMC) and root yield [9, 21]. By correlating factor loadings with environmental parameters, researchers can identify how specific climatic factors impact genotype performance across different locations. For instance, FA-based studies have revealed that maximum temperature (T_{max}) can have contrasting effects on cassava traits depending on the environment. In some environments, T_{max} exhibited a positive correlation with DMC, suggesting that warmer conditions may enhance carbohydrate accumulation in roots, whereas in other environments, the same factor had a negative correlation, indicating potential stress effects on root development [9]. These environment-specific responses highlight the complex interplay between genotype and climate and underscore the importance of considering local environmental contexts in breeding programs. Rainfall and altitude have also emerged as critical determinants of genotype performance. Variations in rainfall influence soil moisture availability, root growth, and the metabolic processes that contribute to dry matter accumulation, while altitude affects both temperature regimes and radiation exposure, which can modify physiological responses [9, 21]. Genotypes that perform consistently across environments with varying rainfall and altitude demonstrate broad adaptability, whereas others may require site-specific recommendations to achieve optimal productivity. Understanding these environmental influences is essential for effective selection of superior genotypes in multi-environment trials. By integrating FA model outputs with environmental covariate data, breeders can identify genotypes that combine high performance with stability, ensuring that selected lines are resilient under variable climatic conditions [9, 21]. This approach facilitates the development of cassava varieties that are not only high yielding but also adapted to the environmental realities of smallholder farming systems, supporting food security and sustainable production.

12. Implications for Breeding Programs

The complex nature of genotype by environment ($G \times E$) interactions has important implications for cassava breeding programs. Environmental variation significantly influences genotype performance, affecting traits such as yield, dry matter content, and stress resilience. As a result, breeders are increasingly relying on multi-environment trials (METs) to assess cassava cultivars across diverse agroecological zones [9]. METs provide a robust framework for evaluating both mean

performance and stability, enabling the identification of genotypes that combine high yield with adaptability to environmental variability. Through METs, breeders can detect environment-specific responses that may otherwise be overlooked in single-location trials. For instance, genotypes that perform well under high rainfall or elevated temperatures may differ markedly from those adapted to drier or higher-altitude environments. Capturing these differences, METs facilitate the selection of varieties that are resilient to climatic stress, pests, and diseases, enhancing their utility for smallholder farmers across different regions [9]. The long breeding cycle of cassava, typically spanning up to ten years from initial crossing to variety release, underscores the importance of understanding $G \times E$ interactions [9, 22]. Early identification of broadly adapted and stable genotypes through METs allows breeders to prioritize lines with the highest potential, reducing time and resources spent on testing inferior or highly environment-specific genotypes. Integrating advanced analytical models, such as Factor Analysis (FA), with MET data further improves selection efficiency by quantifying the contribution of genetic and environmental variance, enabling informed decision-making on genotype deployment [9]. Moreover, the use of METs supports targeted cultivar development, allowing breeding programs to align variety release with the specific needs and conditions of production regions. By considering $G \times E$ interactions, breeders can optimize the balance between yield, quality, and resilience traits, ultimately contributing to food security, economic stability, and sustainable cassava production [9, 22]. The strategic integration of METs and advanced $G \times E$ modeling ensures that new cassava varieties meet both farmer and market demands while maintaining performance consistency across variable environments.

13. Implications for Breeding

The implications of understanding genetic and environmental drivers of post-harvest physiological deterioration (PPD) in cassava are significant for breeding programs aimed at enhancing food security. PPD is a critical issue that affects the storability and overall marketability of cassava, leading to considerable losses post-harvest. Therefore, developing varieties that are resilient to PPD is imperative for improving the efficiency of cassava as a staple food crop in many tropical regions [8].

14. Genetic Strategies in Breeding

To effectively address PPD, breeders must focus on identifying and incorporating traits associated with PPD resistance. Research indicates that PPD resistance is predominantly controlled by genetic factors, which necessitates a long-term approach to breeding that includes selecting tolerant genotypes [10]. Modern breeding techniques, such as genomic-assisted

selection, have been shown to enhance the ability to incorporate these traits into new cassava varieties efficiently [23]. Furthermore, genome editing tools like CRISPR/Cas9 represent a revolutionary advancement in cassava breeding, allowing for precise modifications that can increase the storage stability of cassava roots and enhance resistance to various stresses, including diseases and adverse environmental conditions [24].

15. Environmental Considerations

In addition to genetic factors, environmental conditions play a significant role in PPD susceptibility. Breeding programs must consider genotypes by environment interactions to optimize the performance of cassava varieties across different growing conditions [8]. For instance, multi-location, multi-year trials can help in evaluating the stability of PPD resistance traits under varying environmental stresses, ensuring that newly developed varieties maintain their resilience in diverse settings [6, 8].

16. Integrative Approaches

An integrative breeding approach that combines genetic resistance with improved post-harvest management practices is essential. This may include modifications to storage conditions, which can significantly mitigate PPD [18, 13]. Such holistic strategies can enhance the overall effectiveness of breeding efforts aimed at reducing post-harvest losses and improving food security.

17. Implications for Food Security

Cassava (*Manihot esculenta*) plays a crucial role in global food security, particularly in sub-Saharan Africa, where it is a primary food source for millions of people [15, 25]. As the fourth most important staple crop globally, following rice, wheat, and maize, cassava provides essential dietary calories for approximately 600 million individuals [8]. However, significant postharvest losses due to physiological deterioration (PPD) can reach up to 50%, severely impacting food availability and farmer incomes [26, 27]. These losses exacerbate existing food and nutrition security challenges, particularly in regions where cassava is a dietary staple and economic lifeline for smallholder farmers [28, 29]. The economic implications of PPD are profound. With over 90% of cassava produced in Africa utilized for human consumption, any reduction in post-harvest quality translates directly into diminished food security and lower incomes for farming communities [8, 30]. Furthermore, as urbanization increases, the disconnect between producers and consumers grows, making it increasingly vital to address these losses through improved storage and processing techniques that enhance the shelf life and marketability of cassava [12]. Research into effective mitigation strategies, such as pre-harvest pruning and advancements in storage

technology, aims to prolong the postharvest life of cassava roots, thus improving overall food security and economic outcomes for reliant communities [31-33].

18. Conclusion

Postharvest physiological deterioration (PPD) remains one of the most significant constraints affecting cassava (*Manihot esculenta*) utilization, storage, and marketability. The rapid onset of deterioration after harvest limits the shelf life of cassava roots and contributes substantially to postharvest losses, particularly in regions where cassava is a staple food and a major source of livelihood for smallholder farmers. Evidence presented in this study demonstrates that PPD is a complex phenomenon regulated by both genetic and environmental factors. At the genetic level, deterioration is associated with wound-induced physiological responses involving oxidative stress, accumulation of reactive oxygen species (ROS), and activation of metabolic pathways such as phenolic biosynthesis and antioxidant enzyme systems. Substantial genetic variability among cassava genotypes provides an important opportunity for breeding programs to identify and utilize tolerant varieties with delayed PPD onset. Advances in molecular genetics have significantly improved the understanding of PPD mechanisms. The application of molecular markers, genome-wide association studies (GWAS), and genomic selection has enhanced the identification of genomic regions and candidate genes associated with PPD tolerance. These technologies allow breeders to accelerate the development of improved cassava cultivars that combine delayed deterioration with desirable agronomic traits such as high yield, disease resistance, and high dry matter content. However, the expression of PPD is also strongly influenced by environmental conditions, including temperature, humidity, mechanical damage during harvesting, and storage practices. These environmental drivers interact with genetic factors through genotype \times environment (G \times E) interactions, which can alter the expression of PPD resistance across different production environments.

The integration of genetic improvement with improved postharvest management practices offers the most effective strategy for reducing PPD-related losses. Improved harvesting techniques that minimize mechanical damage, optimized storage conditions, and the adoption of traditional or improved storage technologies can significantly delay the onset of deterioration. When combined with breeding programs that focus on developing PPD-tolerant genotypes, these approaches can enhance cassava shelf life, improve market access, and strengthen the cassava value chain. Ultimately, addressing PPD through integrated genetic and environmental management strategies will play a crucial role in improving cassava productivity, reducing postharvest losses, and supporting food security and economic sustainability in cassava-producing regions.

19. Future Research Directions

Future research should focus on advancing the understanding of the molecular and physiological mechanisms underlying postharvest physiological deterioration in cassava. Although significant progress has been made in identifying genes and metabolic pathways associated with PPD, many aspects of the regulatory networks controlling oxidative stress responses, phenolic metabolism, and cell wall modifications remain poorly understood. Integrating multi-omics approaches including genomics, transcriptomics, proteomics, and metabolomics will provide deeper insights into the complex biological processes that govern PPD initiation and progression. Such integrated analyses can facilitate the identification of key regulatory genes and biomarkers that can be targeted in breeding programs. Another important research direction involves the expansion of genome-wide association studies and genomic selection models using diverse cassava germplasm collections. Incorporating larger and more genetically diverse populations will improve the accuracy of identifying quantitative trait loci (QTLs) associated with PPD tolerance. Additionally, the integration of high-throughput phenotyping technologies, including imaging systems and artificial intelligence-based phenotyping tools, can enhance the precision and efficiency of evaluating PPD in breeding populations. These approaches will enable researchers to screen large numbers of genotypes rapidly and objectively under different environmental conditions.

Future breeding programs should also emphasize the evaluation of genotype \times environment interactions through multi-environment trials conducted across diverse agroecological zones. Understanding how environmental factors such as temperature, rainfall, soil conditions, and storage environments influence PPD expression will enable breeders to develop varieties with stable performance across different production systems. In addition, the integration of genomic selection with environmental covariate modeling can further improve prediction accuracy for PPD tolerance. Emerging technologies such as genome editing provide promising opportunities for directly modifying genes associated with oxidative stress regulation and metabolic pathways involved in PPD. Tools such as CRISPR/Cas9 can enable precise genetic modifications that enhance root shelf life without compromising other agronomic traits. However, further research is required to identify suitable gene targets and evaluate the long-term stability and safety of such modifications under field conditions.

Finally, future studies should also focus on practical, farmer-oriented postharvest management strategies that complement genetic improvements. Research on low-cost storage technologies, improved harvesting methods, and value-added processing techniques will be essential for reducing PPD-related losses in smallholder farming systems. Integrating these technological innovations with improved cassava varieties will create a comprehensive strategy for mitigating PPD and strengthening the resilience of cassava-based food systems.

Abbreviations

APX	Ascorbate Peroxidase
CRISPR	Clustered Regularly Interspaced Short Palindromic Repeats
DMC	Dry Matter Content
FA	Factor Analysis
FAO	Food and Agriculture Organization
FRY	Fresh Root Yield
G \times E	Genotype \times Environment Interaction
GS	Genomic Selection
GWAS	Genome-Wide Association Study
MAS	Marker-Assisted Selection
METs	Multi-Environment Trials
PAL	Phenylalanine Ammonia-Lyase
PPD	Postharvest Physiological Deterioration
QTL	Quantitative Trait Loci
ROS	Reactive Oxygen Species
SNP	Single Nucleotide Polymorphism
SSR	Simple Sequence Repeat

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Conflicts of Interest

The authors declared that there is no conflicts of interest for this manuscript.

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