

Research Insight

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Exploring the Genetic Basis of Sweet Potato Adaptation

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Abstract This study explores the genetic basis of sweet potato (*Ipomoea batatas*) adaptation, with a particular focus on drought tolerance mechanisms. Key genes and molecular pathways have been identified that help the plant survive under water stress, thus facilitating the development of more resilient sweet potato varieties. Recent research has made significant progress in understanding the genetic mechanisms underlying drought tolerance in sweet potatoes. Recent studies have provided significant insights into the genetic mechanisms underlying drought tolerance in sweet potato. Transcriptomic analyses have identified thousands of differentially expressed genes in response to drought stress, with many genes being common across different cultivars and enriched for drought response-related functions. Specific genes such as *ItfWRKY70* have been shown to enhance drought tolerance by regulating ABA biosynthesis, stomatal aperture, and the ROS scavenging system. Additionally, the overexpression of the *IbMIPSI* gene has been linked to improved drought and salt tolerance, as well as resistance to stem nematodes, through the upregulation of stress response pathways and the accumulation of protective metabolites. Furthermore, alternative splicing events and genotype-specific responses have been observed, indicating a complex and multifaceted genetic response to drought stress. The findings from these studies underscore the complexity of drought tolerance mechanisms in sweet potato, involving a wide array of genes and regulatory pathways. The identification of key drought-responsive genes and their functional roles provides valuable resources for geneticists and breeders aiming to develop drought-tolerant sweet potato cultivars. These insights not only enhance our understanding of plant adaptation to abiotic stress but also pave the way for future genetic improvement programs.

Keywords Sweet potato; Drought tolerance; Genetic basis; Transcriptomics; Gene expression; Abiotic stress; WRKY transcription factor; *IbMIPSI*; Alternative splicing; Breeding

1 Introduction

Sweet potato (*Ipomoea batatas* L.) is a crucial crop globally, ranking as the sixth most important food crop worldwide (Alam, 2021; Escobar-Puentes et al., 2022). It is particularly significant in regions such as China, which leads its production in a global market valued at USD 45 trillion (Escobar-Puentes et al., 2022). The crop's versatility and nutritional richness make it indispensable for food security, especially in developing countries. Sweet potatoes are rich in essential nutrients, including vitamins, minerals, and bioactive compounds, which contribute to their health benefits and their role in preventing malnutrition (Sun et al., 2014; Alam, 2021). Additionally, sweet potatoes are known for their drought tolerance, making them a reliable food source in areas prone to climate variability and water scarcity (Motsa et al., 2015).

Understanding the genetic basis of sweet potato adaptation is critical for enhancing its resilience and productivity. Genetic adaptation mechanisms enable the crop to thrive in diverse environmental conditions, which is essential for maintaining food security in the face of climate change (Motsa et al., 2015; Lamaro et al., 2022). Research has shown significant genetic variability in sweet potato genotypes, which affects traits such as yield, disease resistance, and nutritional content. By exploring these genetic factors, scientists can develop improved sweet potato varieties that are more resistant to diseases, such as the sweet potato viral disease (SPVD), and better suited to different agro-climatic zones (Lamaro et al., 2022). This knowledge is vital for breeding programs aimed at increasing the crop's resilience and nutritional value.

This study explores the genetic basis of sweet potato adaptation by reviewing the current knowledge of its genetic diversity and how it influences phenotypic traits. It investigates the mechanisms of sweet potato adaptation to

various environmental stresses (e.g., drought and disease resistance) while identifying key genetic markers associated with target traits that can provide guidance for breeding programs, and also discusses the significance of genetic research in improving sweet potato varieties with the expectation of enhancing food security and improving nutritional outcomes.

2 Genetic Diversity and Evolutionary Background

2.1 Origin and domestication of sweet potato

The sweet potato (*Ipomoea batatas*) was domesticated in Central and South America before being introduced to Africa, where it is now widely cultivated across tropical regions (Glato et al., 2017). The domestication process involved significant genetic changes, including the integration of *Agrobacterium* T-DNA sequences into the sweet potato genome, which suggests that plant-microbe interactions played a crucial role in its domestication. This natural genetic modification may have provided traits that were selected for during the domestication process, highlighting the complex evolutionary history of this crop (Kyndt et al., 2015).

2.2 Genetic diversity among different cultivars

Genetic diversity in sweet potato varies significantly across different regions and cultivars. For instance, in West Africa, genetic diversity is structured into five distinct groups, each associated with specific climatic conditions and morphological traits (Glato et al., 2017). Similarly, a study in Puerto Rico revealed high levels of genetic diversity among local landraces, commercial cultivars, and accessions from the USDA repository, indicating a rich genetic pool that can be leveraged for crop improvement (Rodríguez-Bonilla et al., 2014). The genetic variability among sweet potato genotypes is also evident in traits such as tuber yield, carotene content, and vine length, which are crucial for effective crop improvement (Solankey et al., 2015).

2.3 Evolutionary traits that have enabled adaptation

Several evolutionary traits have enabled the sweet potato to adapt to diverse environmental conditions. The presence of *Agrobacterium* T-DNA sequences in the sweet potato genome is a notable example, as these sequences are expressed and may confer advantageous traits that were selected during domestication (Kyndt et al., 2015). Additionally, the genetic diversity structured along climatic gradients in West Africa suggests that certain genetic groups are better adapted to specific environmental conditions, such as tropical humid or Sahelian climates (Glato et al., 2017). The ability of sweet potato to thrive under different climatic conditions is further supported by the identification of expression quantitative trait loci (eQTLs) that regulate gene expression in storage roots, which can influence key agronomic traits (Zhang et al., 2020). These evolutionary adaptations highlight the sweet potato's resilience and potential for further genetic improvement to enhance climate resilience and food security (Hancock, 2005; Pironon and Gomez, 2020).

3 Genomic Tools and Resources

3.1 Advances in sequencing technologies for sweet potato

Recent advancements in sequencing technologies have significantly enhanced our understanding of the sweet potato genome. High-throughput sequencing methods, such as Illumina paired-end RNA-Sequencing, have been employed to generate comprehensive transcriptomic data. For instance, Illumina sequencing produced 48.7 million 75 bp paired-end reads, which were de novo assembled into 128 052 transcripts, providing a robust resource for gene expression analysis in sweet potato (Tao et al., 2012). Additionally, single-molecule real-time sequencing has been utilized to identify full-length cDNAs and alternative splicing events, further enriching the genomic data available for this hexaploid crop (Ding et al., 2019). These technologies have enabled the identification of numerous differentially expressed genes and alternative splicing events, which are crucial for understanding the genetic basis of traits such as stress tolerance and metabolic processes (Ding et al., 2019; Arisha et al., 2020).

3.2 Overview of available genomic databases and resources

The accumulation of sequencing data has led to the development of extensive genomic databases and resources for sweet potato. For example, the de novo transcriptome assembly from Illumina sequencing has provided a comprehensive set of annotated transcripts, including those involved in viral genomes, starch metabolism, and

stress responses (Tao et al., 2012). Furthermore, genome-wide analyses have identified a vast number of single nucleotide polymorphisms (SNPs) and expression quantitative trait loci (eQTLs), which are essential for dissecting the genetic regulation of gene expression in sweet potato (Zhang et al., 2020). The availability of these resources facilitates the cloning and identification of genes of interest, thereby accelerating research in sweet potato genomics and breeding (Tao et al., 2012; Zhang et al., 2020).

3.3 The role of bioinformatics in genetic analysis

Bioinformatics plays a pivotal role in the analysis and interpretation of the vast amounts of genomic data generated from sequencing technologies. Tools such as Blast2GO have been employed to annotate transcripts, linking them to gene ontology (GO) terms and KEGG pathways, which helps in understanding the functional roles of genes (Tao et al., 2012). Additionally, bioinformatics approaches are crucial for identifying and characterizing alternative splicing events, transcription factors, and non-coding RNAs, as demonstrated in studies utilizing single-molecule real-time sequencing (Ding et al., 2019). The integration of bioinformatics with genomic data allows for the construction of regulatory networks and the identification of master regulators, such as IbMYB1-2, which is involved in anthocyanin biosynthesis in sweet potato storage roots (Zhang et al., 2020). These analyses are essential for uncovering the genetic architecture underlying important agronomic traits and for guiding molecular breeding efforts (Tao et al., 2012; Ding et al., 2019; Zhang et al., 2020).

4 Key Genes and Pathways Involved in Adaptation

4.1 Identification of genes associated with abiotic stress tolerance (e.g., drought, salinity)

Recent studies have identified several key genes that enhance abiotic stress tolerance in sweet potato. The IbBBX24-IbTOE3-IbPRX17 module has been shown to improve tolerance to salt and drought stresses by scavenging reactive oxygen species (ROS) (Figure 1). Overexpression of these genes results in higher peroxidase activity and lower H₂O₂ accumulation, which are critical for stress response (Zhang et al., 2021). Another significant gene, *IbMIPSI*, enhances salt and drought tolerance by up-regulating genes involved in inositol biosynthesis, phosphatidylinositol (PI) and abscisic acid (ABA) signaling pathways, and the ROS-scavenging system (Zhai et al., 2016). Additionally, the overexpression of the betaine aldehyde dehydrogenase (BADH) gene from spinach in sweet potato has been shown to improve tolerance to multiple abiotic stresses, including salt, oxidative stress, and low temperature, by increasing glycine betaine (GB) accumulation (Fan et al., 2012). The *ItfWRKY70* gene from *Ipomoea trifida* also plays a crucial role in drought tolerance by regulating ABA biosynthesis, stomatal aperture, and activating the ROS scavenging system (Sun et al., 2022).

4.2 Genetic basis of resistance to pests and diseases

The genetic transformation of sweet potato has led to the development of varieties with enhanced resistance to pests and diseases. For instance, transgenic sweet potatoes expressing the endotoxin genes *cry8Db*, *cry7A1*, and *cry3Ca* have shown lower infestation rates by the sweet potato weevil compared to non-transformed lines. Additionally, the expression of the oryzacystatin-1 (OC1) gene has conferred resistance to sweet potato stem nematodes and the sweet potato feathery mottle virus (SPFMV) (Imbo et al., 2016). The *IbMIPSI* gene not only enhances abiotic stress tolerance but also significantly improves resistance to stem nematodes by modulating inositol and ABA signaling pathways (Zhai et al., 2016).

4.3 Pathways influencing growth, yield, and quality traits

Several pathways have been identified that influence the growth, yield, and quality traits of sweet potato. The overexpression of the *IbC3H18* gene, a non-tandem CCCH-type zinc-finger protein, enhances tolerance to salt, drought, and oxidative stresses by regulating genes involved in ROS scavenging, ABA signaling, photosynthesis, and ion transport pathways (Zhang et al., 2019). The WRKY transcription factor *ItfWRKY70* also contributes to improved growth and yield under drought conditions by increasing ABA and proline content, and enhancing the activity of superoxide dismutase (SOD) and peroxidase (POD) enzymes (Sun et al., 2022). Furthermore, the overexpression of the *BADH* gene from spinach in sweet potato leads to increased GB accumulation, which helps maintain cell membrane integrity, stronger photosynthetic activity, and reduced ROS production under stress conditions, thereby stabilizing yield production (Fan et al., 2012).

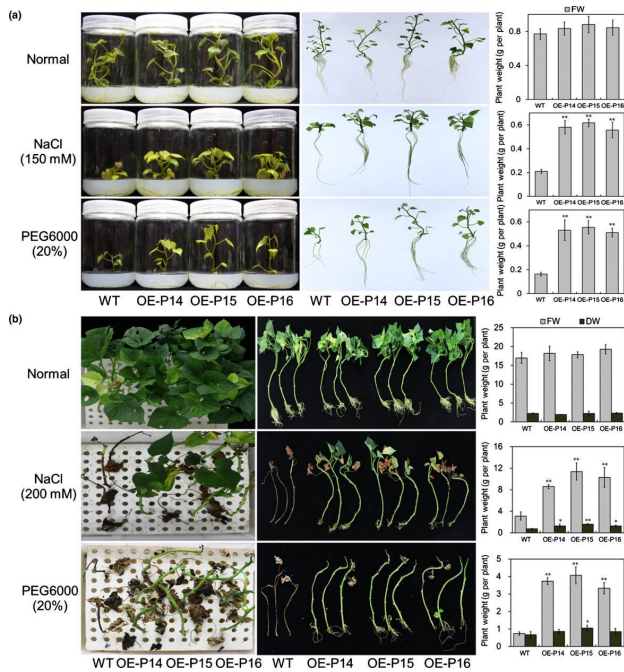


Figure 1 *IbPRX17* overexpression enhances salt and drought tolerance in sweet potato (Adopted from Zhang et al., 2021)

Image caption: (a) Responses of *IbPRX17*-OE and wild-type (WT) sweet potato plants grown for 4 wk on Murashige and Skoog (MS) medium under normal conditions (normal) or subjected to 150 mM NaCl or 20% polyethylene glycol 6000 (PEG6000). (b) Responses of *IbPRX17*-OE and WT sweet potato plants grown hydroponically in half-strength Hoagland solution alone (normal) or with the addition of 200 mM NaCl or 20% PEG6000. Data are shown as means \pm SD ($n = 3$). *, $P < 0.05$; **, $P < 0.01$ (significant difference from the WT at based on Student's t-tests) (Adopted from Zhang et al., 2021)

5 Molecular Mechanisms of Stress Response

5.1 Mechanisms at the cellular and molecular levels

Sweet potato, like many other plants, employs a variety of cellular and molecular mechanisms to respond to stress conditions. These mechanisms include the activation of specific genes and proteins that help the plant to cope with adverse environmental factors. For instance, the expression of certain transcription factors (TFs) such as NAC, WRKY, and MYB plays a crucial role in the plant's response to abiotic stresses like drought and salinity. These TFs regulate the expression of downstream genes involved in stress tolerance, including those that manage ion accumulation, redox reactions, and hormone signaling pathways (Meng et al., 2020; 2022; Sun et al., 2022; Zhao et al., 2022). Additionally, the plant's response to potassium deficiency involves significant transcriptional changes. Genes related to transcriptional regulation, calcium binding, and redox signaling are differentially expressed under low potassium conditions, indicating their roles in stress adaptation (Wang et al., 2021). Moreover, miRNAs have been identified as key regulators in the salt stress response, modulating the expression of target genes involved in stress tolerance (Yang et al., 2020).

5.2 Regulatory networks involved in stress adaptation

The regulatory networks that govern stress adaptation in sweet potato are complex and involve multiple layers of control, including transcriptional, post-transcriptional, and post-translational modifications. Transcription factors such as *IbNAC3* and *IbMYB48* have been shown to interact with other proteins and regulatory elements to modulate stress responses. For example, *IbNAC3* interacts with other NAC TFs to regulate the expression of genes involved in combined salt and drought stress tolerance (Meng et al., 2022). Similarly, *IbMYB48* enhances salt and drought tolerance by upregulating genes involved in ABA biosynthesis, JA signaling, and ROS scavenging (Zhao et al., 2022). Furthermore, the integration of various signaling pathways, including those mediated by plant hormones like ABA, ethylene, and jasmonic acid, plays a pivotal role in coordinating the plant's response to stress. These hormones regulate the expression of stress-responsive genes and proteins, thereby enhancing the plant's ability to withstand adverse conditions (Golldack et al., 2011; Haak et al., 2017; Wang et al., 2021).

5.3 Role of transcription factors and other regulatory elements

Transcription factors are central to the regulation of stress responses in sweet potato. They act as master regulators that control the expression of a wide array of genes involved in stress tolerance. For instance, the NAC transcription factor *IbNAC3* has been identified as a key player in modulating the plant's response to combined salt and drought stresses. It activates the expression of downstream target genes and interacts with other NAC TFs to enhance stress tolerance (Figure 2) (Meng et al., 2022). Similarly, the WRKY transcription factor *ItfWRKY70* has been shown to confer drought tolerance by regulating ABA biosynthesis, stomatal aperture, and the ROS scavenging system (Sun et al., 2022). In addition to TFs, other regulatory elements such as miRNAs also play significant roles in stress adaptation. miRNAs regulate gene expression at the post-transcriptional level by targeting mRNAs for degradation or translational repression. For example, miRNAs have been shown to modulate the expression of genes involved in salt stress response, thereby contributing to the plant's overall stress tolerance (Yang et al., 2020).

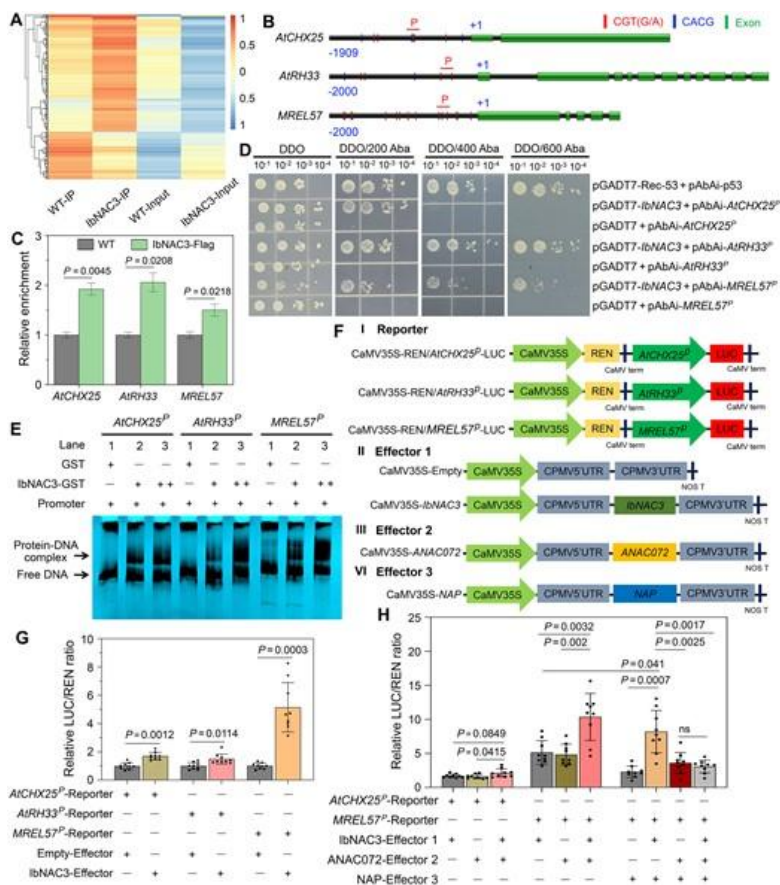


Figure 2 *IbNAC3* cooperates with *ANAC072* and *NAP* with a synergistic effect on transcriptional activation (Adopted from Meng et al., 2022)

Image caption: (A) Heatmap showing hierarchical clustering of ChIP-seq peaks comparing transgenic and WT plants, indicating upregulated (red) and downregulated (blue) regions bound by *IbNAC3*. Plants were immunoprecipitated with an anti-Flag antibody, and the DNA-protein complexes were analyzed. (B) Schematics of *AtCHX25*, *AtRH33*, and *MREL57* gene structures, highlighting core NACRS regions (red and blue) and exons (green), with distances from the ATG start codon marked. (C) ChIP-qPCR assays showing in vivo binding of *IbNAC3* to the promoters of target genes, with significant enrichment compared to the WT. (D) Yeast one-hybrid assays confirming the physical interaction between *IbNAC3* and the promoters of *AtCHX25*, *AtRH33*, and *MREL57*, validated on selective media. (E) Electrophoretic mobility shift assay (EMSA) illustrating in vitro binding of purified *IbNAC3* to the promoters, showing specific DNA-protein complexes. (F) Diagrams of dual-luciferase reporter (DLR) constructs, showing promoters cloned into the reporter vector and effector constructs of *IbNAC3*, *ANAC072*, and *NAP*. (G) Transactivation assay results demonstrating that *IbNAC3* activates transcription of the target promoters in *Nicotiana benthamiana*, as indicated by increased LUC/REN ratios. (H) Synergistic interaction between *IbNAC3* and *ANAC072*/*NAP* further enhances the transactivation activity of the target gene promoters, with statistical analyses supporting significant interactions (Adapted from Meng et al., 2022)

6 Case Studies

6.1 Examples of specific sweet potato cultivars adapted to harsh environments

Several studies have identified sweet potato cultivars that exhibit remarkable adaptability to harsh environmental conditions. For instance, in Tanzania, the genotypes G2 (Resisto × Ukerewe), G3 (Ukerewe × Ex-Msimbu-1), G4 (03-03 × SPKBH008), G12 (Ukerewe × SPKBH008), and G18 (Resisto × Simama) have shown high yields, high dry matter content, and resistance to sweet potato virus disease (SPVD) across diverse environments (Ngailo et al., 2019). Similarly, in Indonesia, the genotypes Ayamurasaki, Beniazuma, Awachy2, 15(112), Awachy4, Awachy5, 80(109), 54(160), and 35(180) have been identified as specifically adapted to marginal lands based on Finlay-Wilkinson analysis (Mustamu et al., 2018).

In Colombia, the genotype 0113-672COR was selected for the Caribbean region due to its superior multi-trait performance and stability across multiple environments (Rosero et al., 2023). Additionally, a study in Cameroon identified high-yielding and stable sweet potato clones suitable for major cultivation areas, despite the significant genotype-by-environment interactions observed (Ngeve, 2004). These examples highlight the potential of specific sweet potato cultivars to thrive in challenging environments, contributing to food security and agricultural sustainability.

6.2 Insights from recent studies on gene-environment interactions

Recent studies have provided valuable insights into the gene-environment interactions that influence sweet potato adaptation. For instance, a transcriptomic analysis of the US-bred cultivar Beauregard and the Ugandan landrace Tanzania under dehydration stress identified approximately 4 000 to 6 000 differentially expressed genes in each cultivar, with many genes associated with drought response (Lau et al., 2018). This study highlighted the genotype-specific responses to drought stress, which can inform the development of drought-tolerant cultivars.

Another study emphasized the importance of understanding the genetic mechanisms underlying drought tolerance. It reviewed the physiological, metabolic, and genetic modifications that sweet potato plants employ to respond to water stress, such as activating antioxidants and accumulating stress proteins (Sapakhova et al., 2023). These modifications can serve as indicators for selecting drought-tolerant genotypes.

Furthermore, a study on the ecophysiological and morpho-agronomic parameters of sweet potato genotypes from different altitudes revealed significant variability in their responses to low-altitude conditions. Genotypes with greater soil coverage efficiency and leaf size exhibited better photosynthetic performance and water use efficiency, which are crucial for root formation under low-altitude environments (Figure 3) (Burbano-Eraza et al., 2020). These findings underscore the complex interactions between genetic traits and environmental factors in sweet potato adaptation.

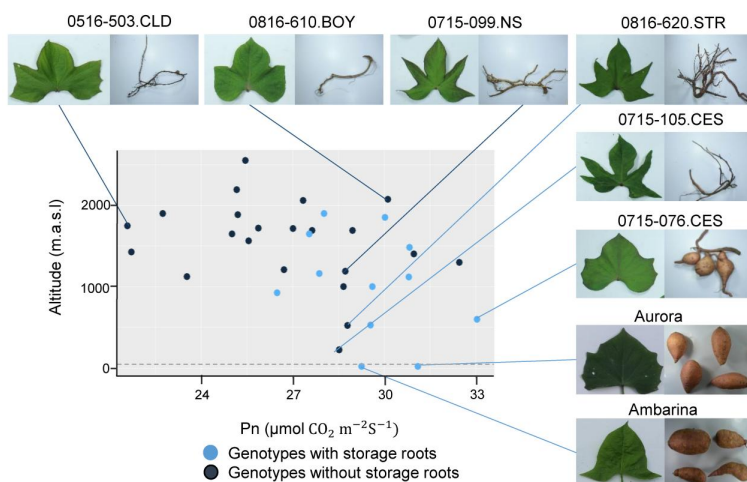


Figure 3 Relationship between genotypes with storage roots and without storage roots according to Pn and altitude. Pn: Net photosynthetic rate; masl: meters above sea level (Adopted from Burbano-Eraza et al., 2020)

7 Future Directions and Challenges

7.1 Potential of CRISPR and other gene-editing tools in sweet potato breeding

The advent of CRISPR/Cas9 and other gene-editing technologies has revolutionized plant breeding, offering precise and efficient methods to modify genetic material. In sweet potato breeding, CRISPR/Cas9 has shown promise in improving starch quality by targeting specific genes involved in starch biosynthesis, such as *IbGBSSI* and *IbSBEII* (Wang et al., 2019). This technology allows for the introduction of desirable traits without the integration of foreign DNA, which is crucial for regulatory approval and public acceptance (Hameed et al., 2019; Veillet et al., 2019). Additionally, CRISPR/Cas9 can be used to enhance resistance to biotic and abiotic stresses, thereby improving crop resilience and yield (Biswas et al., 2021; Nascimento et al., 2023). The potential of CRISPR and other gene-editing tools in sweet potato breeding is vast, offering opportunities to accelerate the development of improved cultivars with enhanced nutritional quality and stress tolerance.

7.2 Challenges in translating genetic insights into practical breeding solutions

Despite the potential of gene-editing technologies, several challenges remain in translating genetic insights into practical breeding solutions. One major challenge is the genotype-dependency of transformation protocols, which affects the efficiency and success rate of gene editing in different sweet potato varieties (Nahirňak et al., 2022). Additionally, the regulatory landscape for gene-edited crops is complex and varies across regions, posing hurdles for the commercialization of gene-edited sweet potatoes (Hameed et al., 2019; Dev et al., 2021). Another challenge is the need for robust and efficient delivery systems for CRISPR/Cas9 components, as well as the development of marker-free strategies to avoid the integration of foreign DNA (Veillet et al., 2019; Tussipkan and Manabayeva, 2021). Furthermore, public perception and acceptance of gene-edited crops remain critical issues that need to be addressed through transparent communication and education (Chen et al., 2019).

7.3 Opportunities for integrating genomic data with traditional breeding methods

Integrating genomic data with traditional breeding methods presents a significant opportunity to enhance sweet potato breeding programs. By combining genomic selection with conventional breeding techniques, breeders can more accurately predict and select for desirable traits, thereby accelerating the breeding process (Dangol et al., 2019; Nascimento et al., 2023). The use of high-throughput sequencing and genotyping technologies enables the identification of genetic markers associated with important traits, facilitating marker-assisted selection (Chen et al., 2019; Biswas et al., 2021). Additionally, integrating genomic data with phenotypic data can improve the understanding of complex trait architectures and gene-environment interactions, leading to more targeted and efficient breeding strategies (Wang et al., 2019; Tussipkan and Manabayeva, 2021). This integrative approach holds the potential to develop sweet potato cultivars with improved yield, quality, and stress resilience, ultimately contributing to food security and sustainable agriculture.

8 Conclusion

Recent studies have significantly advanced our understanding of the genetic basis of sweet potato adaptation. High-throughput sequencing technologies have provided comprehensive genomic resources, revealing gene expression patterns across different tissues and developmental stages. Genome-wide analyses have identified numerous single nucleotide polymorphisms (SNPs) and expression quantitative trait loci (eQTLs) that regulate gene expression in sweet potato storage roots, highlighting key regulatory genes such as *IbMYB1-2* involved in anthocyanin biosynthesis. Additionally, the identification and characterization of SWEET family genes and R2R3-MYB gene family members have elucidated their roles in sugar transport, stress responses, and anthocyanin accumulation. Studies on the wild ancestor, *Ipomoea trifida*, have further contributed to understanding the genetic diversity and evolutionary history of sweet potato.

The insights gained from these genetic studies have significant implications for sustainable sweet potato production. Understanding the molecular mechanisms underlying stress tolerance and nutrient accumulation can inform breeding programs aimed at developing more resilient and nutritious sweet potato varieties. The identification of key regulatory genes and pathways involved in biotic and abiotic stress responses can lead to the development of sweet potato cultivars with enhanced resistance to pests, diseases, and environmental stresses.

Moreover, the comprehensive genomic resources and gene expression data provide valuable tools for marker-assisted selection and genetic engineering, facilitating the improvement of sweet potato yield and quality.

Future research should focus on further elucidating the functional roles of identified genes and their interactions in sweet potato adaptation. Functional validation of candidate genes through gene editing and transgenic approaches will be crucial to confirm their roles in stress tolerance and nutrient accumulation. Additionally, expanding genomic studies to include more diverse sweet potato cultivars and wild relatives will enhance our understanding of genetic diversity and adaptation mechanisms. Integrating multi-omics approaches, such as proteomics and metabolomics, with genomic data will provide a more comprehensive understanding of the molecular networks governing sweet potato adaptation. Finally, translating these genetic insights into practical breeding strategies will be essential for developing sustainable sweet potato varieties that can thrive in diverse environmental conditions.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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