Molecular Plant Breeding 2025, Vol.16, No.2, 133-145
http://genbreedpublisher.com/index.php/mpb

Feature Review Open Access

Sweet Potato Genomics: Key Genes for Nutrient Composition and Yield

Dandan Huang ✉, Zhen Li
Hainan Institute of Biotechnology, Haikou, 570206, Hainan, China
✉ Corresponding email: dandan.huang@hibio.org
Molecular Plant Breeding, 2025, Vol.16, No.2 doi: 10.5376/mpb.2025.16.0014
Received: 12 Mar., 2025
Accepted: 15 Apr., 2025
Published: 23 Apr., 2025

Preferred citation for this article:
Huang D.D., and Li Z., 2025, Sweet potato genomics: key genes for nutrient composition and yield, case study, Molecular Plant Breeding, 16(2): 133-145 (doi: 10.5376/mpb.2025.16.0014)

Abstract Sweet potato (*Ipomoea batatas*) is known for its high nutritional value and adaptability to diverse environments. This study comprehensively examines the genetic basis of key traits influencing nutrient composition and yield in sweet potato. Recent advances in genomics have identified pivotal genes involved in carbohydrate metabolism, beta-carotene biosynthesis, protein synthesis, and stress resilience. Emphasis is placed on polyploidy, gene expression regulation, and the integration of multi-omics approaches to enhance the understanding of genetic mechanisms underlying these traits. Epigenetic modifications, including DNA methylation and histone changes, are highlighted for their role in regulating stress responses and phenotypic traits. Case studies illustrate the application of genomic tools in improving beta-carotene content, drought tolerance, and yield stability. The study underscores the potential of genomic breeding strategies, such as CRISPR/Cas9 and marker-assisted selection, to develop high-yielding, nutrient-rich sweet potato varieties. This research contributes to advancing sweet potato breeding programs, addressing food security challenges, and promoting sustainable agriculture.
Keywords Sweet potato; Genomics; Nutrient composition; Polyploidy; Breeding strategies

1 Introduction

Sweet potato (*Ipomoea batatas*) is a globally important root crop, ranking as the sixth most significant food crop worldwide (Escobar-Puentes et al., 2022). It is cultivated extensively due to its adaptability to diverse environmental conditions and its high nutritional value. Sweet potato is a staple food in many developing countries and is increasingly recognized for its potential in food security and economic development (Maquia et al., 2013; Mohanraj and Sivasankar, 2014). The crop is rich in essential nutrients, including vitamins, minerals, and bioactive compounds, which contribute to its status as a valuable medicinal food (Mohanraj and Sivasankar, 2014).

The nutrient composition and yield of sweet potato are critical factors in its cultivation. High yield and superior nutritional quality are essential to meet the growing demand and to address malnutrition issues, particularly in low- and middle-income countries (Drapal and Fraser, 2019). Sweet potato varieties exhibit significant variability in yield and nutrient content, including dry matter, protein, and antioxidant levels, which are influenced by genotype and environmental conditions (Maquia et al., 2013; Karan and Şanli, 2021). Enhancing these traits through breeding and cultivation practices can significantly impact food security and health outcomes (Karan and Şanli, 2021; Escobar-Puentes et al., 2022).

Recent advances in genomics have provided valuable insights into the genetic basis of important agronomic traits in sweet potato. Genomic studies have identified key genes and regulatory networks involved in nutrient composition, yield, and stress responses (Yang et al., 2020; Sun et al., 2022a). For instance, the identification and characterization of SPL genes have shed light on their role in storage root development and stress tolerance (Sun et al., 2022a). Additionally, the study of microRNAs has revealed their significant role in regulating gene expression under abiotic stress conditions, such as salinity (Yang et al., 2020). These genomic tools and resources are crucial for developing improved sweet potato varieties with enhanced yield and nutritional quality (Yang et al., 2020; Sun et al., 2022a).

By leveraging advanced genomic technologies, this study aims to elucidate the genetic mechanisms underlying these traits and provide a foundation for breeding programs to improve sweet potato varieties. The scope of the research includes genetic diversity analysis, gene expression profiling, and the identification of candidate genes associated with high yield and superior nutritional quality. These efforts will contribute to the development of sweet potato cultivars that better meet the nutritional needs and preferences of diverse populations, thereby enhancing global food security and health outcomes.

2 Sweet Potato Genomic Structure

2.1 Description of sweet potato genome characteristics

The sweet potato (*Ipomoea batatas*) genome is highly complex due to its hexaploid nature, which means it contains six sets of chromosomes. This complexity is further compounded by the presence of a large number of single-nucleotide polymorphisms (SNPs) and copy number variations (CNVs). For instance, in a study involving the wild relative *Ipomoea trifida*, which is considered the diploid ancestor of sweet potato, researchers identified 1 464 173 SNPs and 16 682 CNVs (Hirakawa et al., 2015). The genome assembly of sweet potato has revealed a total length of approximately 296 Gb, with a high degree of heterozygosity and repetitive DNA sequences (Yang et al., 2017). Additionally, the sweet potato genome contains a significant number of protein-coding genes, with estimates ranging from 62 407 to 109 449 putative genes identified in different lines of *I. trifida* (Hirakawa et al., 2015).

2.2 Polyploidy and its impact on gene expression

Polyploidy, the condition of having more than two complete sets of chromosomes, plays a crucial role in the genetic and phenotypic diversity of sweet potato. The hexaploid nature of sweet potato has resulted from two recent whole-genome duplication events, estimated to have occurred approximately 0.8 and 0.5 million years ago (Yang et al., 2017). This polyploidy contributes to the complexity of gene expression regulation, as multiple homologous chromosomes can carry different alleles of the same gene. For example, polyploid QTL-seq has been used to identify SNP clusters linked to important traits such as storage root anthocyanin content in hexaploid sweet potato (Yamakawa et al., 2021). Furthermore, polyploidy can lead to differential gene expression and epigenetic modifications, as observed in other polyploid crops like potato, where whole-genome doubling induced changes in histone modifications and gene expression (Guo et al., 2023).

2.3 Techniques used in sequencing the sweet potato genome

Several advanced sequencing techniques have been employed to decode the sweet potato genome. Initially, Illumina HiSeq platform was used for de novo whole-genome sequencing of *I. trifida*, providing a foundation for understanding the sweet potato genome (Hirakawa et al., 2015). More recently, single-molecule real-time (SMRT) sequencing has been utilized to generate full-length cDNA sequences and identify alternative splicing events, which are crucial for functional genomics studies (Ding et al., 2019). Additionally, a novel haplotyping method based on genome assembly has been developed to produce a half haplotype-resolved genome, offering higher resolution in investigating the complex hexaploid genome of sweet potato (Yang et al., 2017). These techniques, combined with next-generation sequencing (NGS) and third-generation sequencing technologies, have significantly advanced our understanding of the sweet potato genome and its regulatory architecture (Gerard et al., 2018; Kyriakidou et al., 2020).

3 Key Genes Influencing Nutrient Composition

3.1 Carbohydrate metabolism genes

Starch synthesis and breakdown in sweet potato are regulated by several key genes. The *IbAGPb3* and *IbGBSS1-1* genes are involved in starch biosynthesis, with variations in intron length among different germplasms affecting their function (Zhang et al., 2020a). Additionally, the *IbSnRK1* gene has been shown to increase starch content and improve starch quality by upregulating genes involved in the starch biosynthesis pathway and enhancing the activities of key enzymes (Ren et al., 2018). The vacuolar invertase gene *Ibβfruct2-1* also plays a crucial role in regulating starch content by decreasing starch and increasing glucose content (Zhang et al., 2023).

The sweetness and texture of sweet potato are influenced by genes involved in sucrose metabolism and starch degradation. The *Ibβfruct2-1* gene, which encodes a vacuolar invertase, is a negative regulator of starch content and positively influences glucose content, thereby affecting sweetness (Zhang et al., 2023). Additionally, genetic variations in starch biosynthesis and sucrose metabolism genes contribute to differences in starch properties and sweetness among sweet potato varieties (Zhang et al., 2020a).

3.2 Beta-carotene biosynthesis genes

Beta-carotene biosynthesis in sweet potato is governed by several genes in the carotenoid pathway. The Orange gene and phytoene synthase are key regulators, with phytoene synthase being the rate-limiting enzyme in carotenoid biosynthesis (Gemenet et al., 2019). Differential expression of these genes has been observed in orange-fleshed sweet potato varieties, contributing to higher beta-carotene content (Shekhar et al., 2015).

Beta-carotene is a precursor of vitamin A, and its biosynthesis in sweet potato is crucial for addressing vitamin A deficiency. The high beta-carotene content in orange-fleshed sweet potato varieties, regulated by genes such as phytoene synthase and the Orange gene, enhances the nutritional value of the crop and provides significant health benefits (Gemenet et al., 2019; Lamaro et al., 2023). These genes are targets for breeding programs aimed at biofortification to improve vitamin A content in sweet potato (Zeist et al., 2022).

3.3 Anthocyanin and flavonoid pathway genes

Anthocyanin and flavonoid biosynthesis in sweet potato is controlled by specific genes that influence pigmentation and antioxidant properties. Comparative studies have shown that orange-fleshed sweet potato (OFSP) varieties have higher levels of flavonoids and anthocyanins compared to white-fleshed varieties, indicating tight regulation of these biosynthetic pathways (Shekhar et al., 2015). These compounds contribute to the antioxidant properties of sweet potato, enhancing its nutritional and medicinal value.

The presence of anthocyanins and flavonoids in sweet potato not only affects pigmentation but also provides significant health benefits due to their antioxidant properties. These compounds help in scavenging free radicals, thereby reducing oxidative stress and contributing to the medicinal value of sweet potato (Shekhar et al., 2015; Lamaro et al., 2023). The genetic regulation of these pathways is crucial for developing sweet potato varieties with enhanced nutritional profiles.

3.4 Protein and amino acid content genes

Protein synthesis in sweet potato is regulated by various genes, with cultivar-specific expression patterns influencing the overall protein content. Studies have shown that orange-fleshed sweet potato varieties exhibit higher levels of total protein compared to white-fleshed varieties, suggesting differential gene expression related to protein synthesis (Shekhar et al., 2015).

The protein content in sweet potato significantly impacts its nutritional value. Higher protein levels, as observed in certain orange-fleshed varieties, enhance the overall nutritional profile of the crop, making it a more valuable food source. Understanding the genetic basis of protein synthesis in sweet potato can aid in breeding programs aimed at improving its nutritional quality.

4 Key Genes Influencing Yield

4.1 Genes regulating root development

Root development is crucial for nutrient uptake and overall plant health, directly impacting yield. In sweet potato, genes such as *IbBBX24* and *IbPRX17* have been shown to play significant roles in root development under stress conditions. The *IbBBX24* transcription factor activates the expression of the class III peroxidase gene *IbPRX17*, enhancing root development and stress tolerance by scavenging reactive oxygen species (ROS) (Zhang et al., 2021). Additionally, genes involved in root cell elongation and division, as identified in comparative transcriptome analyses of deep-rooting and shallow-rooting potato genotypes, also contribute to root development and drought tolerance (Qin et al., 2022).

4.2 Genes associated with stress resistance

4.2.1 Drought, heat, and salinity tolerance genes

Several genes have been identified that enhance sweet potato's tolerance to abiotic stresses such as drought, heat, and salinity. The *IbMIPS1* gene, which encodes myo-inositol-1-phosphate synthase, improves salt and drought tolerance by regulating inositol biosynthesis and ROS scavenging pathways (Zhai et al., 2016). Similarly, the *IbNAC7* gene has been shown to confer salt tolerance by enhancing catalase activity and reducing ROS accumulation (Meng et al., 2020). The *ItfWRKY70* gene from *Ipomoea trifida* also plays a significant role in drought tolerance by regulating ABA biosynthesis and ROS scavenging systems (Sun et al., 2022b).

4.2.2 Impact on consistent yield across different environments

The overexpression of stress-responsive genes such as *IbBBX24*, *IbPRX17*, and *IbMIPS1* not only enhances stress tolerance but also contributes to maintaining consistent yield across different environmental conditions. For instance, transgenic sweet potato plants overexpressing *IbMIPS1* showed improved yield under field conditions with salt and drought stress (Zhai et al., 2016). Similarly, the *IbBBX24-IbTOE3-IbPRX17* module enhances tolerance to salt and drought, thereby stabilizing yield under adverse conditions (Figure 1) (Zhang et al., 2021). These genetic modifications ensure that sweet potato plants can sustain productivity despite environmental challenges.

4.3 Genes involved in photosynthesis efficiency

Photosynthesis efficiency is a critical factor for plant growth and yield. Genes such as IbMIPS1 have been implicated in enhancing photosynthesis under stress conditions by regulating the ROS scavenging system and maintaining chlorophyll content (Zhai et al., 2016). Additionally, the *IbNAC7* gene has been shown to improve photosynthesis efficiency by increasing chlorophyll and proline contents while reducing malondialdehyde (MDA) content under salt stress (Meng et al., 2020). These genes help maintain photosynthetic activity, thereby supporting higher yields.

4.4 Genes affecting flowering and maturity

Flowering and maturity are key developmental stages that influence yield. While specific genes directly affecting these stages in sweet potato are less documented, the overall stress response and developmental genes such as *IbBBX24* and *IbMIPS1* indirectly contribute to timely flowering and maturity by ensuring plant health and stress resilience (Zhai et al., 2016; Zhang et al., 2021). Further research into the genetic regulation of these stages could provide more targeted approaches to enhancing yield through genetic manipulation.

5 Genetic Diversity and Domestication of Sweet Potato

5.1 Insights into the origin and domestication of sweet potato

The domestication of sweet potato (*Ipomoea batatas* L. Lam) is a complex process that has involved significant genetic changes from its wild relatives. Sweet potato is believed to have originated in Central or South America, where it was domesticated by indigenous peoples. The genetic diversity of sweet potato is relatively high, which is indicative of its long history of cultivation and selection for various traits. Studies have shown that sweet potato has undergone significant genetic changes during domestication, including the selection for traits such as tuber size, shape, and nutritional content (Lee et al., 2019; Paliwal et al., 2020).

5.2 Genomic studies revealing genetic diversity across cultivars

Genomic studies have been instrumental in revealing the genetic diversity present in sweet potato cultivars. For instance, the use of morphological, biochemical, and molecular markers has allowed researchers to assess the genetic variation among different sweet potato genotypes. One study analyzed 21 sweet potato genotypes using these markers and found significant genetic diversity, which is crucial for breeding programs (Paliwal et al., 2020). Another study utilized chloroplast simple sequence repeat (cpSSR) markers to analyze 558 sweet potato accessions, revealing 33 distinct chlorotypes and highlighting the need for more diverse germplasm collection (Lee et al., 2019). Additionally, retrotransposon-based insertion polymorphism (RBIP) markers have been used to study the genetic diversity of sweet potato, further confirming the presence of significant genetic variation among different germplasms (Meng et al., 2021).

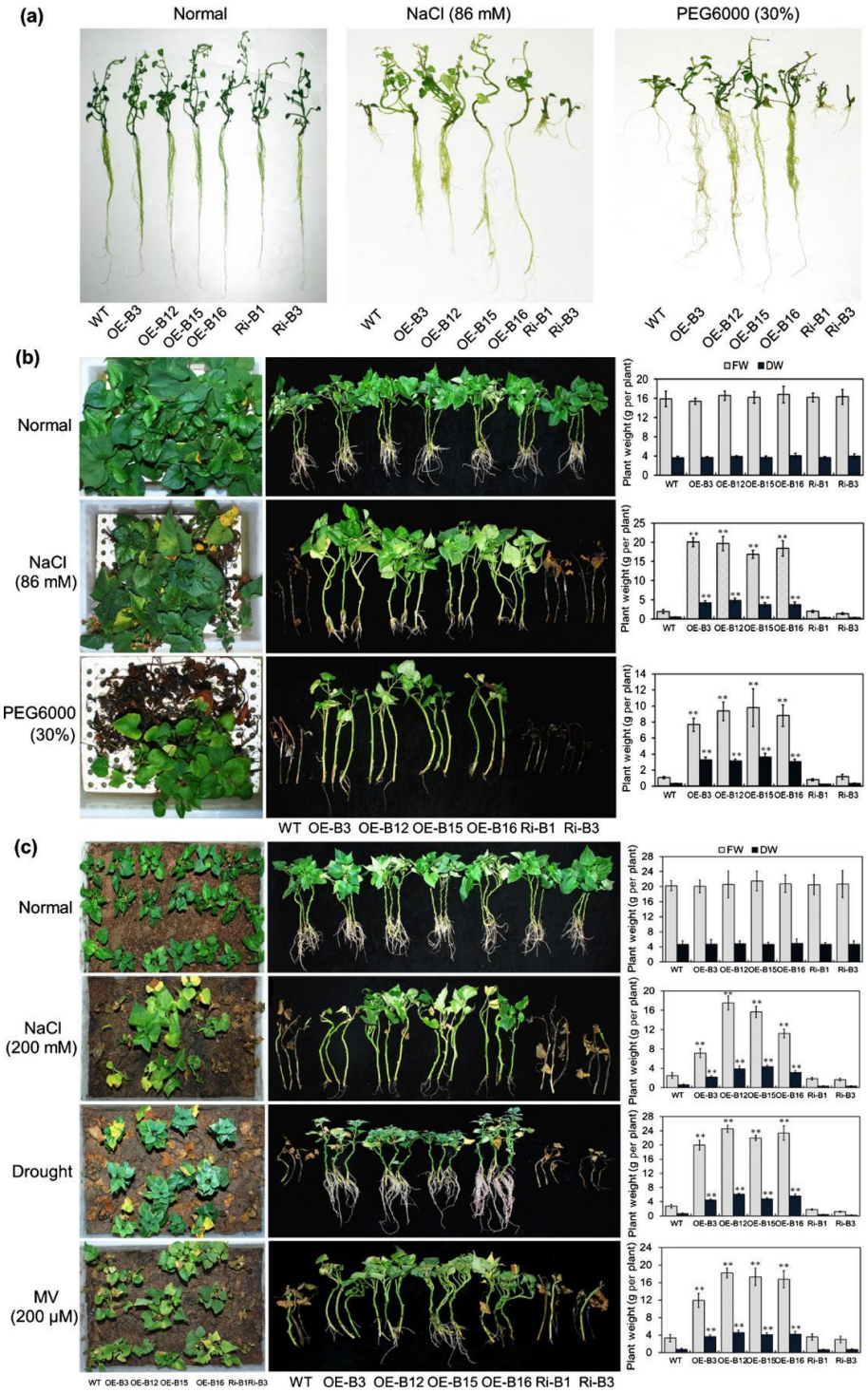

Figure 1 *IbBBX24* overexpression enhances tolerance to salt, drought and oxidative stresses in sweet potato (Adopted from Zhang et al., 2021)

Image caption: (a) Responses of *IbBBX24*-OE, *IbBBX24*-RNAi and wild-type (WT) sweet potato plants grown for 4 wk on Murashige & Skoog (MS) medium in control conditions (normal) or with 86 mM NaCl or 30% polyethylene glycol 6000 (PEG6000). (b) Responses of *IbBBX24*-OE, *IbBBX24*-RNAi and WT sweet potato plants grown hydroponically in half-strength Hoagland solution (normal) or half-strength Hoagland solution containing 86 mM NaCl or 30% PEG6000. (c) Responses of *IbBBX24*-OE, *IbBBX24*-RNAi and WT sweet potato plants grown in transplanting boxes under control conditions (normal) or subjected to 200 mM NaCl, drought or 200 μM methyl viologen (MV). Representative photographs were taken after stress treatment for 4 wk (salt), 8 wk (drought) or 2 wk (MV). A time-course analysis of the phenotypes of *IbBBX24*-OE, *IbBBX24*-RNAi and WT plants grown in transplanting boxes under abiotic stresses is shown in Supporting Information Fig. S1. Data are shown as means±SD (n = 3). **, Significant difference from WT at $P < 0.01$ based on Student's t-test (Adopted from Zhang et al., 2021)

5.3 Implications for breeding programs

The genetic diversity uncovered by these genomic studies has significant implications for sweet potato breeding programs. The high level of genetic variation provides a valuable resource for the selection of desirable traits such as high yield, disease resistance, and improved nutritional content. For example, the identification of genotypes with high beta-carotene content and other desirable traits can be used to develop new, improved sweet potato varieties (Otoboni et al., 2020). Moreover, understanding the genetic relationships and diversity among sweet potato accessions can help breeders maintain a diverse gene pool, which is essential for the long-term sustainability of breeding programs (Lee et al., 2019; Paliwal et al., 2020; Meng et al., 2021). The use of molecular markers in breeding programs can also facilitate marker-assisted selection, making the breeding process more efficient and targeted (Paliwal et al., 2020; Meng et al., 2021).

6 Epigenetic Modifications and Gene Regulation in Sweet Potato

6.1 The role of epigenetic changes in nutrient and yield traits

Epigenetic modifications, such as DNA methylation and histone modifications, play a crucial role in regulating gene expression without altering the DNA sequence. These modifications can significantly impact plant development, stress responses, and ultimately, crop yield and nutrient composition. DNA methylation, in particular, has been shown to influence various developmental and physiological processes in plants, including tuberization in potatoes under high-temperature stress (Dutta et al., 2022). Similarly, in sweet potatoes, DNA methylation and other epigenetic mechanisms likely regulate key genes involved in nutrient biosynthesis and storage root development, thereby affecting yield and nutritional quality.

Histone modifications and chromatin remodeling also contribute to the regulation of gene expression in response to environmental cues and internal signals. These epigenetic changes can modulate the chromatin state, making genes more or less accessible for transcription, which in turn affects plant growth and adaptation to stress (Hewezi, 2017; Agarwal et al., 2020). For instance, the interplay between DNA methylation and histone modifications has been implicated in the regulation of anthocyanin biosynthesis in sweet potato storage roots, highlighting the importance of epigenetic regulation in determining phenotypic traits (Zhang et al., 2020b).

6.2 Case studies on epigenetic influence in sweet potato adaptation

Several studies have demonstrated the role of epigenetic modifications in plant adaptation to environmental stresses. In potatoes, high temperatures induce the expression of positive regulators of tuberization through active DNA demethylation and RNA-directed DNA methylation pathways, suggesting a similar mechanism could be at play in sweet potatoes (Dutta et al., 2022). This adaptive response is crucial for maintaining yield under stress conditions.

In another study, the manipulation of DNA methylation and histone acetylation in the green alga *Chlamydomonas reinhardtii* showed that reducing epigenetic variation can hinder adaptation to different environmental stresses, indicating that epigenetic diversity is essential for adaptive evolution (Kronholm et al., 2017). This finding underscores the potential of epigenetic modifications to enhance stress tolerance and adaptation in sweet potatoes.

Furthermore, research on fruit development has shown that epigenetic regulation, including DNA methylation and histone modifications, is vital for processes such as ripening. For example, the dysfunction of a DNA demethylase delayed ripening in tomatoes, and the application of DNA methylation inhibitors altered the ripening process in various fruit species (Tang et al., 2020). These insights suggest that similar epigenetic mechanisms could be leveraged to improve sweet potato yield and quality by modulating developmental processes and stress responses.

7 Genomic Breeding Strategies for Sweet Potato Improvement

7.1 Application of CRISPR/Cas9 in sweet potato gene editing

CRISPR/Cas9 technology has emerged as a powerful tool for precise genome editing in various crops, including sweet potato. This system allows for targeted mutations in specific genes, facilitating the rapid development of new germplasm with desirable traits. For instance, CRISPR/Cas9 has been successfully used to edit starch biosynthetic genes in sweet potato, resulting in modifications to starch quality without significantly altering total

starch content (Figure 2; Table 1) (Wang et al., 2019). Additionally, the technology has been applied to improve traits such as yield, quality, disease resistance, and abiotic stress tolerance in other crops, demonstrating its broad potential for sweet potato improvement (Tussipkan and Manabayeva, 2021; Wan et al., 2021; Das et al., 2023). The availability of whole-genome sequencing data and functional information about key genes further enhances the efficacy of CRISPR/Cas9 in sweet potato breeding (Rodríguez-Leal et al., 2017; Chen et al., 2019).

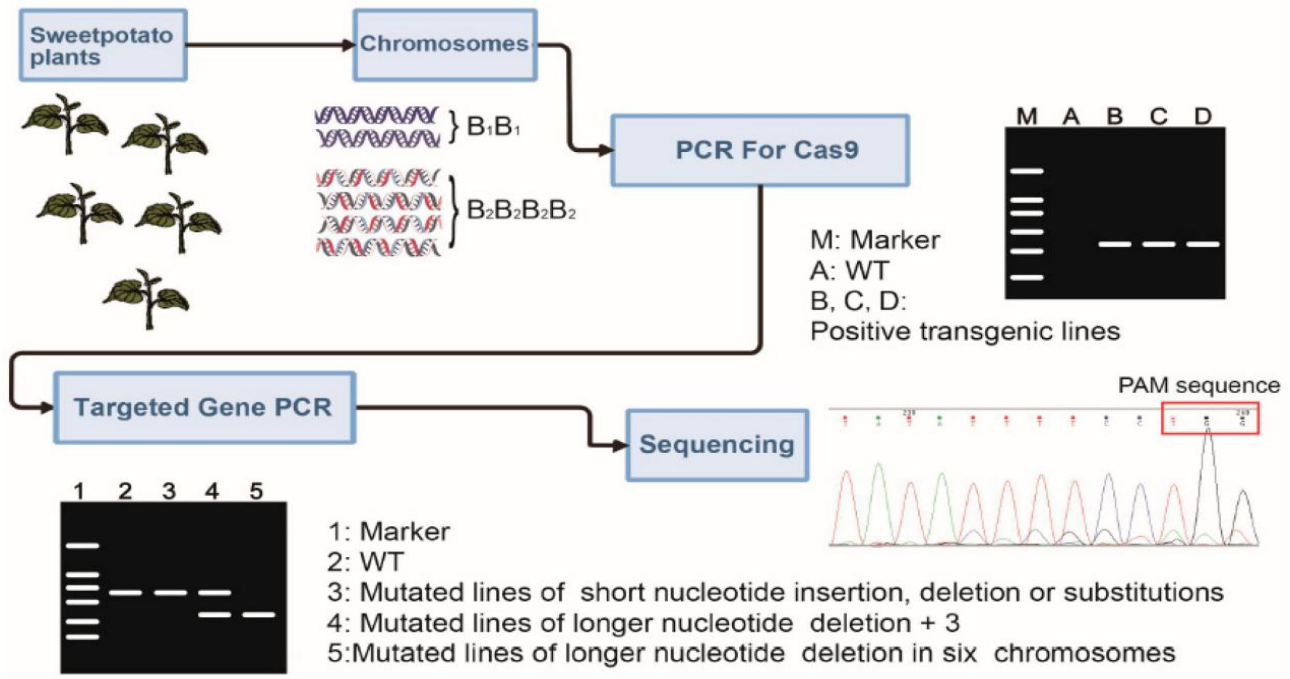

Figure 2 Schematic representation of the workflow designed to analyze targeted gene mutations of CRISPR/Cas9 editing. Transgenic lines were identified by PCR detection of Cas9 genes. Mutation detection in transgenic lines by PCR amplification with primers flanking the sgRNA target sites and running gel electrophoresis to roughly estimate the mutation types. PCR products sequencing analysis was performed by examining their sequencing chromatograms for accurate mutation status (Adopted from Wang et al., 2019)

Table 1 Chain length distributions proportion in 90>DP>6 of debranched sweet potato starches a,b (Adopted from Wang et al., 2019)

Sample	6<DP<12 (%)	13<DP<24 (%)	25<DP<36 (%)	37<DP<90 (%)
Xushu22	29.2 d (0.42)	42.7 c (0.752)	14.7 c (0.40)	13.4 c (0.35)
IbSBEII-sgRNA12-24	24.6 e (0.63)	44.6 b (0.53)	15.0 c (0.16)	15.8 b (0.78)
IbSBEII-sgRNA12-26	16.4 g (0.03)	45.6 ab (0.06)	19.2 a (0.04)	18.8 a (0.05)
IbSBEII-sgRNA2-1	19.1 f (0.25)	46.3 a (0.34)	16.3 b (0.04)	18.3 a (0.62)
IbGBSSI-sgRNA2-2	33.7 b (0.07)	41.7 cd (0.27)	13.8 d (0.13)	11.2 d (0.23)
IbGBSSI-sgRNA2-6	34.7 a (0.21)	41.4 d (0.46)	13.1 e (0.13)	10.8 d (0.31)
IbGBSSI-sgRNA2-7	30.4 c (0.08)	42.6 c (0.10)	13.6 d (0.23)	13.4 c (0.23)

Note: a Standard deviations are given within parenthesis. b The values in the same column with different two letters (a and b, b and c, a and d, d and e, e and f, f and g) differ significantly (p<0.05) (Adopted from Wang et al., 2019)

7.2 Marker-assisted selection (MAS) for desirable traits

Marker-assisted selection (MAS) leverages molecular markers to enhance the efficiency of breeding programs by enabling the selection of desirable traits at the genetic level. Techniques such as genotyping-by-sequencing (GBS) have revolutionized MAS by providing high-throughput sequencing capabilities that facilitate the discovery and genotyping of single nucleotide polymorphisms (SNPs) in crop genomes (He et al., 2014). This approach has been successfully implemented in various crops, including maize and wheat, to identify and select for traits related to yield, disease resistance, and nutritional quality. The integration of MAS in sweet potato breeding can accelerate the development of new varieties with improved nutrient composition and yield by enabling the precise selection of beneficial alleles.

7.3 Genome-wide association studies (GWAS) for identifying yield and nutrient-related genes

Genome-wide association studies (GWAS) are a powerful method for identifying genetic loci associated with important agronomic traits. By analyzing the genetic variation across a diverse panel of genotypes, GWAS can pinpoint specific SNPs linked to traits such as yield, nutrient content, and stress resistance. For example, GWAS has been used to dissect the genetic architecture of grain yield in bread wheat, identifying loci that can be targeted for marker-assisted selection (Li et al., 2019). Applying GWAS to sweet potato can similarly uncover key genes involved in nutrient composition and yield, providing valuable targets for breeding programs aimed at improving these traits. The integration of high-density genetic markers and advanced statistical methods enhances the reliability and resolution of GWAS, making it a crucial tool for sweet potato genomic breeding

8 Case Studies

8.1 Enhancing beta-carotene content through genomic approaches

Beta-carotene is a vital nutrient, and enhancing its content in sweet potatoes can significantly contribute to alleviating vitamin A deficiency. A study evaluated the genotype by environment interactions in the yield and nutraceutical traits of orange-fleshed sweet potato (OFSP) storage roots in different agro-climatic zones of northern Ethiopia. The results demonstrated that certain genotypes, such as Ininda, Gloria, and Amelia, provided higher yields and beta-carotene content, suggesting that genotype selection can effectively enhance beta-carotene levels in sweet potatoes (Lamaro et al., 2023). This approach highlights the potential of using genomic tools to select and breed sweet potato varieties with improved nutritional profiles.

8.2 Improving drought tolerance via gene editing techniques

Drought tolerance is a critical trait for sweet potato cultivation, especially in regions prone to water scarcity. Several studies have focused on identifying and manipulating genes associated with drought tolerance. For instance, the overexpression of the *IbMIPS1* gene in transgenic sweet potatoes significantly enhanced drought tolerance by up-regulating genes involved in stress responses and the ABA signaling pathway (Zhai et al., 2016). Additionally, RNA-sequencing analysis identified numerous drought-responsive genes, including those from the bHLH, bZIP, and WRKY families, which are crucial for developing drought-tolerant sweet potato cultivars (Figure 3) (Arisha et al., 2020). These findings underscore the effectiveness of gene editing and genomic approaches in improving drought tolerance in sweet potatoes.

(A)

Transcription Factors (TFs)	up				down			
	C1 vs D1	C4 vs D4	C5 vs D5	C6 vs D6	C1 vs D1	C4 vs D4	C5 vs D5	C6 vs D6
AP2/ERF->AP2/ERF-ERF	0	48	53	63	1	25	58	77
ARID	0	3	10	33	1	0	1	1
AUX/IAA	0	2	9	5	0	8	10	24
B3->B3	0	19	28	35	0	4	24	53
B3->B3-ARF	0	4	10	17	0	8	39	65
BES1	1	9	12	8	0	1	2	13
bHLH	0	15	26	35	0	19	42	76
bZIP	0	27	33	41	0	7	4	20
C2C2->C2C2-GATA	0	19	30	27	0	7	13	19
C2H2	0	11	29	44	0	16	34	57
C3H	0	19	31	70	0	15	64	96
DBP	0	26	28	28	0	0	0	3
FAR1	0	13	18	31	0	7	23	33
GARP->GARP-G2-like	0	5	11	20	0	19	26	32
GNAT	0	12	17	27	0	19	118	155
GRAS	0	3	12	9	0	7	22	42
HB->HB-BELL	0	13	26	23	0	0	4	5
HB->HB-HD-ZIP	0	20	32	32	0	12	18	23
HSF	0	3	9	13	0	12	24	33
Jumonji	0	2	5	10	0	12	12	18
LIM	0	5	28	12	0	19	22	19
LOB	0	12	17	22	0	8	11	12
MED6	1	0	0	2	0	0	3	2
mTERF	0	11	17	33	0	16	29	47
MYB->MYB	0	32	79	95	0	35	78	133
NAC	0	31	52	61	0	40	74	127
NF-Y->NF-YC	0	9	17	18	0	2	6	7
PHD	0	11	19	35	0	8	12	0
SNF2	0	9	29	34	0	5	17	36
Tify	0	10	12	27	0	8	9	15
TRAF	0	10	10	20	0	3	23	16
Trihelix	0	19	7	7	0	14	27	52
WRKY	0	19	42	50	0	5	33	33

(B)

	FPKM				
	0h	1h	6hs	12hs	48hs
UDP-glycosyltransferase 85A5-like	12.9	1.7	18.1	28.0	34.9
Alpha-amylase	30.5	4.1	17.9	56.5	54.8
Beta-glucosidase-like SFR2	20.7	15.3	99.4	178.4	149.9
Cinnamate beta-D-glucosyltransferase	25.6	9.3	49.8	22.9	27.0
Fumarylacetoacetase	38.4	13.1	97.8	243.2	180.0
Galactinol synthase 2	6.3	31.2	59.1	101.1	122.5
alpha,alpha-trehalose-phosphate synthase [UDP-forming] 1	18.9	2.3	34.7	52.8	13.1
glucose-6-phosphate 1-epimerase	12.6	4.5	70.7	57.9	70.4
Oxidoreductase family	0.8	3.3	76.0	151.2	77.4
scopoletin glucosyltransferase-like	91.3	12.7	33.3	74.2	119.8
UDP-glucuronic acid decarboxylase 2	84.6	9.0	104.4	204.1	116.9
Alpha-mannosidase	39.3	28.1	13.8	4.3	1.9
Aquaporins	313.1	159.4	55.2	24.0	7.1
Beta-galactosidase	33.7	23.1	15.4	4.7	0.7
Glyceraldehyde-3-phosphate dehydrogenase B, chloroplastic	265.7	388.7	56.5	4.1	10.0
Phosphoglucomutase	109.6	111.9	9.8	2.5	10.0
Phosphoglucomutase, chloroplastic	81.1	101.7	20.1	1.2	5.6
glycosyltransferase	40.5	42.7	2.4	0.2	1.0
Protein plastid transcriptionally active 16, chloroplastic (TIC 62)	120.2	141.5	61.5	3.9	7.2
Sedoheptulose-1,7-bisphosphatase, chloroplastic	151.1	218.0	36.2	0.5	0.4
Transaldolase	52.5	41.0	15.5	0.4	1.8
UDP-glycosyltransferase	35.7	26.6	5.2	1.7	2.1
NmrA-like family	68.9	106.3	11.4	1.0	4.1

Figure 3 Transcription factors differentially expressed (A) and stress related protein genes (B) induced under drought stress in Xuzi-8 sweetpotato cultivar (Adopted from Arisha et al., 2020)

8.3 Boosting yield with marker-assisted selection

Marker-assisted selection (MAS) is a powerful tool for improving crop yield by selecting for desirable traits at the genetic level. In sweet potatoes, MAS has been employed to enhance yield under various environmental conditions. For example, a study on potato, a close relative of sweet potato, demonstrated the use of SSR markers to identify allelic differences associated with drought sensitivity, which can be used to select for drought-tolerant cultivars (Schumacher et al., 2021). Similarly, integrating transcript and metabolite markers has shown promise in predicting drought tolerance and yield stability in potatoes, suggesting that a similar approach could be applied to sweet potatoes (Sprenger et al., 2017). These studies illustrate the potential of MAS in boosting sweet potato yield by selecting for traits that confer resilience and high productivity.

9 Challenges and Future Prospects

9.1 Limitations in sweet potato genomic research

Sweet potato (*Ipomoea batatas* L.) is a crucial crop globally, yet its genomic research faces significant challenges. One primary limitation is the lack of comprehensive genomic resources, which hampers the understanding of its molecular biology. For instance, the absence of a complete reference genome for sweet potato complicates the identification and functional analysis of genes (Tao et al., 2012; Ding et al., 2019). Additionally, the genetic complexity of sweet potato, being a hexaploid organism, further complicates genomic studies and breeding efforts (Ding et al., 2019). The limited availability of molecular markers, such as SSR markers, also restricts the ability to track important loci for traits like starch content and β-carotene content (Zhang et al., 2016).

9.2 Potential of multi-omics approaches (transcriptomics, proteomics, metabolomics)

The integration of multi-omics approaches holds great promise for advancing sweet potato research. Transcriptomics, proteomics, and metabolomics can provide a holistic view of the molecular mechanisms underlying nutrient composition and yield. For example, transcriptome analysis has revealed differentially expressed genes in response to various stresses and nutrient conditions, offering insights into stress tolerance and nutrient signaling pathways (Wang et al., 2021; Xiong et al., 2022). Proteomics studies have identified cultivar-specific protein expressions that influence nutrient acquisition and storage (Shekhar et al., 2015; Acharjee et al., 2018). Metabolomics, combined with other omics data, can help reconstruct metabolic networks and identify key metabolites associated with desirable traits (Acharjee et al., 2011). These integrated approaches can facilitate the identification of candidate genes and pathways for targeted breeding and genetic improvement.

9.3 Future directions for improving sweet potato nutrient composition and yield

Future research should focus on several key areas to enhance sweet potato nutrient composition and yield. First, the development of a complete reference genome and the expansion of genomic resources are essential. This will enable more precise gene editing and marker-assisted selection (Tao et al., 2012; Ding et al., 2019). Second, leveraging multi-omics approaches can provide deeper insights into the regulatory networks and metabolic pathways involved in nutrient biosynthesis and stress responses (Ommen and Stierum, 2002; Acharjee et al., 2011). Third, the identification and functional validation of key genes through techniques like CRISPR/Cas9 can accelerate the development of improved sweet potato varieties with enhanced nutrient profiles and yield (Zhang et al., 2016; Peng et al., 2022). Finally, collaborative efforts and data sharing among researchers will be crucial to overcoming the current limitations and advancing sweet potato genomics research.

10 Concluding Remarks

Recent advancements in sweet potato genomics have significantly deepened our understanding of this vital crop. High-throughput sequencing technologies, such as Illumina paired-end RNA-sequencing and single-molecule real-time sequencing, have played a crucial role in building comprehensive genomic resources. For example, de novo transcriptome assembly has identified over 128 000 transcripts, offering valuable insights into gene expression across various tissues and developmental stages. Additionally, full-length cDNA sequencing has uncovered extensive alternative splicing events and identified numerous transcription factors and long non-coding RNAs, laying a foundation for functional genomics and molecular breeding.

Genomic studies have also shed light on sweet potato's genetic responses to environmental stresses. RNA-sequencing has revealed key genes linked to drought stress responses, emphasizing the importance of transcription factors and signaling pathways in stress adaptation. Similarly, transcriptome analyses under potassium-deficient conditions have identified differentially expressed genes involved in transcription regulation, hormone signaling, and plant defense mechanisms, all of which are critical for enhancing nutrient uptake and stress resilience.

Genotype-by-environment interaction studies have identified promising sweet potato genotypes with traits such as high yields, increased dry matter content, and resistance to sweet potato virus disease. These findings highlight the potential of breeding programs to enhance crop performance in diverse environmental settings. Comparative analyses among cultivars have further revealed significant variations in nutrient composition and phytochemical content, underscoring their importance for nutritional improvement and global food security.

Genomic research is pivotal in addressing future agricultural challenges for sweet potato cultivation by providing a detailed understanding of the genetic basis of key traits. The rich genomic resources generated through advanced sequencing techniques enable the identification of genes associated with yield, nutrient content, and stress tolerance, facilitating the development of improved varieties through molecular breeding and genetic engineering.

The identification of genes linked to drought tolerance and potassium deficiency, for instance, paves the way for developing sweet potato varieties that maintain stable yields under challenging environmental conditions. Discoveries related to alternative splicing events and transcription factors involved in tuber development and nutrient accumulation further inform breeding strategies aimed at enhancing the crop's nutritional quality.

Genotype-by-environment interaction studies enhance our ability to select genotypes that thrive across various conditions, boosting the adaptability and resilience of sweet potato crops. Integrating genomic data with traditional breeding approaches accelerates the creation of high-yielding, nutrient-dense, and stress-tolerant varieties, contributing to global food security and the advancement of sustainable agriculture.

Acknowledgments

The authors sincerely thank the two anonymous peer reviewers for their valuable feedback and constructive suggestions on this study's manuscript.

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.

References

Acharjee A., Chibon P., Kloosterman B., America T., Renaut J., Maliepaard C., and Visser R., 2018, Genetical genomics of quality related traits in potato tubers using proteomics, BMC Plant Biology, 18: 20.
https://doi.org/10.1186/s12870-018-1229-1

Acharjee A., Kloosterman B., Vos R., Werij J., Bachem C., Visser R., and Maliepaard C., 2011, Data integration and network reconstruction with ~omics data using Random Forest regression in potato, Analytica Chimica Acta, 705(1-2): 56-63.
https://doi.org/10.1016/j.aca.2011.03.050

Agarwal G., Kudapa H., Ramalingam A., Choudhary D., Sinha P., Garg V., Singh V., Patil G., Pandey M., Nguyen H., Guo B., Sunkar R., Niederhuth C., and Varshney R., 2020, Epigenetics and epigenomics: underlying mechanisms, relevance, and implications in crop improvement, Functional & Integrative Genomics, 20: 739-761.
https://doi.org/10.1007/s10142-020-00756-7

Arisha M., Ahmad M., Tang W., Liu Y., Yan H., Kou M., Wang X., Zhang Y., and Li Q., 2020, RNA-sequencing analysis revealed genes associated drought stress responses of different durations in hexaploid sweet potato, Scientific Reports, 10: 12573.
https://doi.org/10.1038/s41598-020-69232-3

Chen K., Wang Y., Zhang R., Zhang H., and Gao C., 2019, CRISPR/Cas genome editing and precision plant breeding in agriculture, Annual Review of Plant Biology, 70: 667-697.
https://doi.org/10.1146/annurev-arplant-050718-100049

Das T., Anand U., Pal T., Mandal S., Kumar M., Radha, Gopalakrishnan A., Lastra J., and Dey A., 2023, Exploring the potential of CRISPR/Cas genome editing for vegetable crop improvement: an overview of challenges and approaches, Biotechnology and Bioengineering, 120: 1215-1228.
https://doi.org/10.1002/bit.28344

Ding N., Cui H., Miao Y., Tang J., Cao Q., and Luo Y., 2019, Single-molecule real-time sequencing identifies massive full-length cDNAs and alternative-splicing events that facilitate comparative and functional genomics study in the hexaploid crop sweet potato, PeerJ, 7: e7933.
https://doi.org/10.7717/peerj.7933

Drapal M., and Fraser P., 2019, Determination of carotenoids in sweet potato (*Ipomoea batatas* L., Lam) tubers: implications for accurate provitamin A determination in staple sturdy tuber crops, Phytochemistry, 167: 112102.
https://doi.org/10.1016/j.phytochem.2019.112102

Dutta M., Raturi V., Gahlaut V., Kumar A., Sharma P., Verma V., Gupta V., Sood S., and Zinta G., 2022, The interplay of DNA methyltransferases and demethylases with tuberization genes in potato (*Solanum tuberosum* L.) genotypes under high temperature, Frontiers in Plant Science, 13: 933740.
https://doi.org/10.3389/fpls.2022.933740

Escobar-Puentes A., Palomo I., Rodríguez L., Fuentes E., Villegas-Ochoa M., González-Aguilar G., Olivas-Aguirre F., and Wall-Medrano A., 2022, Sweet potato (*Ipomoea batatas* L.) phenotypes: from agroindustry to health effects, Foods, 11(7): 1058.
https://doi.org/10.3390/foods11071058

Gemenet D., Pereira G., Boeck B., Wood J., Mollinari M., Olukolu B., Diaz F., Mosquera V., Ssali R., David M., Kitavi M., Burgos G., Felde T., Ghislain M., Carey E., Swanckaert J., Coin L., Fei Z., Hamilton J., Yada B., Yencho G., Zeng Z., Mwanga R., Khan A., Gruneberg W., and Buell C., 2019, Quantitative trait loci and differential gene expression analyses reveal the genetic basis for negatively associated β-carotene and starch content in hexaploid sweetpotato [*Ipomoea batatas* (L.) Lam.], Theoretical and Applied Genetics, 133: 23-36.
https://doi.org/10.1007/s00122-019-03437-7

Gerard D., Ferrão L., Garcia A., and Stephens M., 2018, Genotyping polyploids from messy sequencing data, Genetics, 210: 789-807.
https://doi.org/10.1534/genetics.118.301468

Guo H., Zhou M., Zhang G., He L., Yan C., Wan M., Hu J., He W., Zeng D., Zhu B., and Zeng Z., 2023, Development of homozygous tetraploid potato and whole genome doubling-induced the enrichment of H3K27ac and potentially enhanced resistance to cold-induced sweetening in tubers, Horticulture Research, 10(3): uhad017.
https://doi.org/10.1093/hr/uhad017

He J., Zhao X., Laroche A., Lu Z., Liu H., and Li Z., 2014, Genotyping-by-sequencing (GBS), an ultimate marker-assisted selection (MAS) tool to accelerate plant breeding, Frontiers in Plant Science, 5: 484.
https://doi.org/10.3389/fpls.2014.00484

Hewezi T., 2017, Editorial: epigenetic regulation of plant development and stress responses, Plant Cell Reports, 37: 1-2.
https://doi.org/10.1007/s00299-017-2233-x

Hirakawa H., Okada Y., Tabuchi H., Shirasawa K., Watanabe A., Tsuruoka H., Minami C., Nakayama S., Sasamoto S., Kohara M., Kishida Y., Fujishiro T., Kato M., Nanri K., Komaki A., Yoshinaga M., Takahata Y., Tanaka M., Tabata S., and Isobe S., 2015, Survey of genome sequences in a wild sweet potato, *Ipomoea trifida* (H. B. K.) G. Don, DNA Research, 22(2): 171-179.
https://doi.org/10.1093/dnares/dsv002

Karan Y., and Şanli Ö., 2021, The assessment of yield and quality traits of sweet potato (*Ipomoea batatas* L.) genotypes in middle Black Sea region, Turkey, PLoS One, 16(9): e0257703.
https://doi.org/10.1371/journal.pone.0257703

Kronholm I., Bassett A., Baulcombe D., and Collins S., 2017, Epigenetic and genetic contributions to adaptation in chlamydomonas, Molecular Biology and Evolution, 34: 2285-2306.
https://doi.org/10.1093/molbev/msx166

Kyriakidou M., Anglin N., Ellis D., Tai H., and Strömvik M., 2020, Genome assembly of six polyploid potato genomes, Scientific Data, 7: 88.
https://doi.org/10.1038/s41597-020-0428-4

Lamaro G., Tsehaye Y., Girma A., Vannini A., Fedeli R., and Loppi S., 2023, Evaluation of yield and nutraceutical traits of orange-fleshed sweet potato storage roots in two agro-climatic zones of northern Ethiopia, Plants, 12(6): 1319.
https://doi.org/10.3390/plants12061319

Lee K., Lee G., Lee J., Sebastin R., Shin M., Cho G., and Hyun D., 2019, Genetic diversity of sweet potato (*Ipomoea batatas* L. Lam) germplasms collected worldwide using chloroplast SSR markers, Agronomy, 9(11): 752.
https://doi.org/10.3390/agronomy9110752

Li F., Wen W., Liu J., Zhang Y., Cao S., He Z., Rasheed A., Jin H., Zhang C., Yan J., Zhang P., Wan Y., and Xia X., 2019, Genetic architecture of grain yield in bread wheat based on genome-wide association studies, BMC Plant Biology, 19: 168.
https://doi.org/10.1186/s12870-019-1781-3

Li R., Zhai H., Kang C., Liu D., He S., and Liu Q., 2015, *De novo* transcriptome sequencing of the orange-fleshed sweet potato and analysis of differentially expressed genes related to carotenoid biosynthesis, International Journal of Genomics, 2015: 843802.
https://doi.org/10.1155/2015/843802

Maquia I., Muocha I., Naico A., Martins N., Gouveia M., Andrade I., Goulao L., and Ribeiro A., 2013, Molecular, morphological and agronomic characterization of the sweet potato (*Ipomoea batatas* L.) germplasm collection from Mozambique: genotype selection for drought prone regions, South African Journal of Botany, 88: 142-151.
https://doi.org/10.1016/j.sajb.2013.07.008

Meng X., Liu S., Dong T., Xu T., Ma D., Pan S., Li Z., and Zhu M., 2020, Comparative transcriptome and proteome analysis of salt-tolerant and salt-sensitive sweet potato and overexpression of *IbNAC7* confers salt tolerance in *Arabidopsis*, Frontiers in Plant Science, 11: 572540.
https://doi.org/10.3389/fpls.2020.572540

Meng Y., Su W., Ma Y., Liu L., Gu X., Wu D., Shu X., Lai Q., Tang Y., Wu L., and Wang Y., 2021, Assessment of genetic diversity and variety identification based on developed retrotransposon-based insertion polymorphism (RBIP) markers in sweet potato (*Ipomoea batatas* (L.) Lam.), Scientific Reports, 11: 17116.
https://doi.org/10.1038/s41598-021-95876-w

Mohanraj R., and Sivasankar S., 2014, Sweet potato (*Ipomoea batatas* [L.] Lam)--a valuable medicinal food: a review, Journal of Medicinal Food, 17(7): 733-741.
https://doi.org/10.1089/jmf.2013.2818

Ommen B., and Stierum R., 2002, Nutrigenomics: exploiting systems biology in the nutrition and health arena, Current Opinion in Biotechnology, 13(5): 517-521.
https://doi.org/10.1016/S0958-1669(02)00349-X

Otoboni M., Oliveira D., Vargas P., Pavan B., and Andrade M., 2020, Genetic parameters and gain from selection in sweet potato genotypes with high beta-carotene content, Crop Breeding and Applied Biotechnology, 20(3): e31632038.
https://doi.org/10.1590/1984-70332020v20n3a42

Paliwal P., Jain D., Joshi A., Ameta K., Chaudhary R., and Singh A., 2020, Diversity analysis of Sweet Potato (*Ipomoea batatas*[L.] Lam) genotypes using morphological, biochemical and molecular markers, Indian Journal of Experimental Biology, 58: 276-285.
https://doi.org/10.56042/ijeb.v58i04.65463

Peng Y., Pan R., Liu Y., Medison M., Shalmani A., Yang X., and Zhang W., 2022, LncRNA-mediated ceRNA regulatory network provides new insight into chlorogenic acid synthesis in sweet potato, Physiologia Plantarum, 174(6): e13826.
https://doi.org/10.1111/ppl.13826

Qin T., Sun C., Kazim A., Cui S., Wang Y., Richard D., Yao P., Bi Z., Liu Y., and Bai J., 2022, Comparative transcriptome analysis of deep-rooting and shallow-rooting potato (*Solanum tuberosum* L.) genotypes under drought stress, Plants, 11(15): 2024.
https://doi.org/10.3390/plants11152024

Ren Z., He S., Zhao N., Zhai H., and Liu Q., 2018, A sucrose non-fermenting-1-related protein kinase-1 gene, *IbSnRK1*, improves starch content, composition, granule size, degree of crystallinity and gelatinization in transgenic sweet potato, Plant Biotechnology Journal, 17(1): 21-32.
https://doi.org/10.1111/pbi.12944

Rodríguez-Leal D., Lemmon Z., Man J., Bartlett M., and Lippman Z., 2017, Engineering quantitative trait variation for crop improvement by genome editing, Cell, 171(2): 470-480.
https://doi.org/10.1016/j.cell.2017.08.030

Schumacher C., Krannich C., Maletzki L., Köhl K., Kopka J., Sprenger H., Hincha D., Seddig S., Peters R., Hamera S., Zuther E., Haas M., and Horn R., 2021, Unravelling differences in candidate genes for drought tolerance in potato (*Solanum tuberosum* L.) by use of new functional microsatellite markers, Genes, 12(4): 494.
https://doi.org/10.3390/genes12040494

Shekhar S., Mishra D., Buragohain A., Chakraborty S., and Chakraborty N., 2015, Comparative analysis of phytochemicals and nutrient availability in two contrasting cultivars of sweet potato (*Ipomoea batatas* L.), Food Chemistry, 173: 957-965.
https://doi.org/10.1016/j.foodchem.2014.09.172

Sprenger H., Erban A., Seddig S., Rudack K., Thalhammer A., Le M., Walther D., Zuther E., Köhl K., Kopka J., and Hincha D., 2017, Metabolite and transcript markers for the prediction of potato drought tolerance, Plant Biotechnology Journal, 16: 939-950.
https://doi.org/10.1111/pbi.12840

Sun H., Mei J., Zhao W., Hou W., Zhang Y., Xu T., Wu S., and Zhang L., 2022a, Phylogenetic analysis of the SQUAMOSA promoter-binding protein-like genes in four *Ipomoea* species and expression profiling of the *IbSPLs* during storage root development in sweet potato (*Ipomoea batatas*), Frontiers in Plant Science, 12: 801061.
https://doi.org/10.3389/fpls.2021.801061

Sun S., Li X., Gao S., Nie N., Zhang H., Yang Y., He S., Liu Q., and Zhai H., 2022b, A novel WRKY transcription factor from *Ipomoea trifida*, ItfWRKY70, confers drought tolerance in sweet potato, International Journal of Molecular Sciences, 23(2): 686.
https://doi.org/10.3390/ijms23020686

Tang D., Gallusci P., and Lang Z., 2020, Fruit development and epigenetic modifications, The New Phytologist, 228(3): 839-844.
https://doi.org/10.1111/nph.16724

Tao X., Gu Y., Wang H., Zheng W., Li X., Zhao C., and Zhang Y., 2012, Digital gene expression analysis based on integrated *de novo* transcriptome assembly of sweet potato [*Ipomoea batatas* (L.) Lam.], PLoS One, 7(4): e36234.
https://doi.org/10.1371/journal.pone.0036234

Tussipkan D., and Manabayeva S., 2021, Employing CRISPR/Cas technology for the improvement of potato and other tuber crops, Frontiers in Plant Science, 12: 747476.
https://doi.org/10.3389/fpls.2021.747476

Wan L., Wang Z., Tang M., Hong D., Sun Y., Ren J., Zhang N., and Zeng H., 2021, CRISPR-Cas9 gene editing for fruit and vegetable crops: strategies and prospects, Horticulturae, 7(7): 193.
https://doi.org/10.3390/horticulturae7070193

Wang F., Tan W., Song W., Yang S., and Qiao S., 2021, Transcriptome analysis of sweet potato responses to potassium deficiency, BMC Genomics, 23: 655.
https://doi.org/10.1186/s12864-022-08870-5

Wang H., Wu Y., Zhang Y., Yang J., Fan W., Zhang H., Zhao S., Yuan L., and Zhang P., 2019, CRISPR/Cas9-based mutagenesis of starch biosynthetic genes in sweet potato (*Ipomoea batatas*) for the improvement of starch quality, International Journal of Molecular Sciences, 20(19): 4702.
https://doi.org/10.3390/ijms20194702

Xiong J., Tang X., Wei M., and Yu W., 2022, Comparative full-length transcriptome analysis by Oxford Nanopore Technologies reveals genes involved in anthocyanin accumulation in storage roots of sweet potatoes (*Ipomoea batatas* L.), PeerJ, 10: e13688.
https://doi.org/10.7717/peerj.13688

Yamakawa H., Haque E., Tanaka M., Takagi H., Asano K., Shimosaka E., Akai K., Okamoto S., Katayama K., and Tamiya S., 2021, Polyploid QTL-seq towards rapid development of tightly linked DNA markers for potato and sweetpotato breeding through whole-genome resequencing, Plant Biotechnology Journal, 19(10): 2040-2051.
https://doi.org/10.1111/pbi.13633

Yang J., Moeinzadeh M., Kuhl H., Helmuth J., Xiao P., Haas S., Liu G., Zheng J., Sun Z., Fan W., Deng G., Wang H., Hu F., Zhao S., Fernie A., Boerno S., Timmermann B., Zhang P., and Vingron M., 2017, Haplotype-resolved sweet potato genome traces back its hexaploidization history, Nature Plants, 3: 696-703.
https://doi.org/10.1038/s41477-017-0002-z

Yang Z., Zhu P., Kang H., Liu L., Cao Q., Sun J., Dong T., Zhu M., Li Z., and Xu T., 2020, High-throughput deep sequencing reveals the important role that microRNAs play in the salt response in sweet potato (*Ipomoea batatas* L.), BMC Genomics, 21: 164.
https://doi.org/10.1186/s12864-020-6567-3

Zeist A., Leal M., Resende J., Rech C., Júnior A., Toroco B., Oliveira J., and Oliveira G., 2022, Selecting orange-fleshed sweet potato genotypes using selection indices, Horticultura Brasileira, 40(2): 231-237.
https://doi.org/10.1590/s0102-0536-20220214

Zhai H., Wang F., Si Z., Huo J., Xing L., An Y., He S., and Liu Q., 2016, A *myo*-inositol-1-phosphate synthase gene, *IbMIPS1*, enhances salt and drought tolerance and stem nematode resistance in transgenic sweet potato, Plant Biotechnology Journal, 14(2): 592-602.
https://doi.org/10.1111/pbi.12402

Zhang H., Wang Z., Li X., Gao X., Dai Z., Cui Y., Zhi Y., Liu Q., Zhai H., Gao S., Zhao N., and He S., 2021, The IbBBX24-IbTOE3-IbPRX17 module enhances abiotic stress tolerance by scavenging reactive oxygen species in sweet potato, The New Phytologist, 233(3): 1133-1152.
https://doi.org/10.1111/nph.17860

Zhang K., Luo K., Li S., Peng D., Tang D., Lu H., Zhao Y., Lv C., and Wang J., 2020a, Genetic variation and sequence diversity of starch biosynthesis and sucrose metabolism genes in sweet potato, Agronomy, 10(5): 627.
https://doi.org/10.3390/agronomy10050627

Zhang K., Wu Z., Tang D., Lv C., Luo K., Zhao Y., Liu X., Huang Y., and Wang J., 2016, Development and identification of SSR markers associated with starch properties and β-carotene content in the storage root of sweet potato (*Ipomoea batatas* L.), Frontiers in Plant Science, 7: 223.
https://doi.org/10.3389/fpls.2016.00223

Zhang K., Wu Z., Wu X., Han H., Ju X., Fan Y., Yang C., Tang D., Cao Q., Wang J., and Lv C., 2023, Regulatory and functional divergence among members of *Ibβfruct2*, a sweet potato vacuolar invertase gene controlling starch and glucose content, Frontiers in Plant Science, 14: 1192417.
https://doi.org/10.3389/fpls.2023.1192417

Zhang L., Yu Y., Shi T., Kou M., Sun J., Xu T., Li Q., Wu S., Cao Q., Hou W., and Li Z., 2020b, Genome-wide analysis of expression quantitative trait loci (eQTLs) reveals the regulatory architecture of gene expression variation in the storage roots of sweet potato, Horticulture Research, 7: 90.
https://doi.org/10.1038/s41438-020-0314-4