Review Article

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Sweet potato *(Ipomoea batatas* L.): Climate resilient crop for food security in arid and semi-arid regions - A review

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ABSTRACT

Sweet potato is a crucial crop for enhancing food security, particularly in arid and semi-arid regions where climate change and water scarcity pose significant challenges to agriculture. However, osmotic stress severely impacts its agronomic and economic productivity by triggering morphological, physiological and biochemical alterations. In response to drought, sweet potato activates various adaptive mechanisms, including growth regulation, antioxidant defense, osmolyte accumulation and stress protein synthesis. These physiological, metabolic, and genetic responses serve as essential indicators for selecting drought-tolerant genotypes. The primary goal of breeding programs in drought-prone regions is to develop high-yielding, drought-resistant varieties. Understanding the physiological and biochemical traits of drought-tolerant genotypes is critical for improving selection strategies. By integrating conventional breeding, molecular techniques, and biotechnological innovations, drought-resilient sweet potato varieties can be developed, making cultivation more sustainable and cost-effective for smallholder farmers. This review explores the effects of drought stress on sweet potato productivity, its adaptation strategies, crop management practices, and advanced breeding approaches to enhance drought tolerance.

Introduction

Climate change, marked by rising global temperatures, presents a significant challenge to agricultural production. Since crop growth is highly influenced by climatic factors, failure to implement adaptive strategies may result in severe productivity losses in the near future. To mitigate the effects of abiotic stress on crops, there is an urgent need to promote the cultivation of crops that utilize water resources efficiently. Among such crops, sweet potato stands out due to its resilience, versatility, and nutritional benefits. However, despite its potential, sweet potato productivity is adversely affected by abiotic stress conditions. Nevertheless, compared to other economically important crops, sweet potato possesses several advantages that make it well-suited for enhancing global food security, particularly in extensive agricultural systems in developing countries.

Sweet potato (*Ipomoea batatas* L.) is a vital staple, fodder, and horticultural crop widely cultivated in tropical regions. Ranking seventh globally in terms of production (Sinkovic *et al.*, 2024), it belongs to the Convolvulaceae family and is primarily grown for its nutrient-rich tuberous roots. While *Ipomoea batatas* is the predominant cultivated species, other Convolvulaceae members are mostly localized or classified as invasive weeds. The plant itself is a herbaceous liana with alternating leaves and tubular flowers. Tuberous roots of sweet potato vary in shape and color. Depending on the variety and environmental conditions colour range from white to purple.

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Sweet potato has a high water-use efficiency (WUE). It helps stop soil erosion. This makes it useful as a cover crop. It is also grown for food. It grows well in places without frost and where the growing season is at least four months long. Due to its exceptional adaptability to poor soil conditions and its high nutritional value, sweet potato plays a crucial role in addressing food shortages and improving food security. It also holds promise for promoting healthier diets, particularly in developing countries. Additionally, compared to other staple crops, sweet potato requires fewer chemical inputs such as pesticides and fertilizers, further enhancing its sustainability (Kwak, 2019).

Origin place of *I. batatas* is the tropical regions of South America. People have cultivated it for about 5,000 years. Farmers cultivate sweet potato on about 9 million hectares. Global sweet potato production is about 131 million tons per year, yielding 13.7 tons per hectare. Notably, around 97% of the world's sweet potato production occurs in developing countries, with China alone accounting for 52% of global output, cultivating the crop on approximately 4.7 million hectares. Thousands of sweet potato varieties are cultivated across tropical and subtropical climates worldwide. Rich in carbohydrates, vitamins A and C, fiber, iron, potassium, and protein, sweet potato is a highly nutritious food source.

People are starting to see the value of sweet potatoes. They are useful as food for both humans and animals. Because of this, research on how to grow and use sweet potatoes is increasing. Sweet potato thrives best in warm tropical climates with average temperatures around 24°C, demonstrating resilience to a wide range of environmental conditions (Duque *et al.*, 2022). Its ability to produce high yields per unit area within a short growing season, particularly during brief rainy periods, gives it an advantage over other staple crops. Furthermore, it offers flexible planting and harvesting times, tolerates high-temperature and low-fertility soils, and exhibits strong resistance to pests and diseases (Iese *et al.*, 2018). Due to its relatively low labor requirements, sweet potato is especially well-suited for smallholder farming systems (Mcewan *et al.,* 2020). As a fast-maturing crop (three to five months), it serves as an effective rotational crop, thriving in diverse ecological conditions and demonstrating notable drought resistance.

In recent years, sweet potato has been introduced to regions with extreme continental climates, such as Kazakhstan, where agricultural systems face multiple abiotic stress challenges, including drought, salinity, high temperatures, and occasional low temperatures during the growing season (Zhapar *et al.*, 2021). Its ability to withstand such conditions highlights its potential as a climate-resilient crop for food security in arid and semi-arid regions.

Effect of drought stress on sweet potato yield

Drought stress is a significant global challenge that limits sweet potato yields, particularly in semi-arid regions where the crop is commonly cultivated. Due to the intricate genetic and physiological mechanisms involved in water deficiency resistance, enhancing our genomic understanding of sweet potato's response to drought stress is crucial for developing strategies to sustain productivity under such conditions.

Certain sweet potato types handled drought very well. They also had a good yield index (%) under drought conditions. These genotypes also demonstrated higher values for geometric mean productivity (GMP), stress tolerance index (STI), and mean productivity (MP), indicating their superior adaptability under both drought-stressed and optimal conditions. Correlation analysis showed a strong positive association. STI, MP, and GMP related to yield under optimal conditions (YP) and yield under stress (YS). These traits are useful for selecting drought-tolerant varieties. Additionally, STI has been recognized as a valuable indicator for evaluating genotypes in severely drought-affected areas.

High-yielding sweet potato genotypes have desirable tuber quality and drought tolerance. They recorded high STI values. They also showed low susceptibility index values. Correlation analysis further confirmed significant positive relationships between YP, YS and the selection indices (STI, MP, and GMP) reinforcing their utility in drought tolerance screening.

Beyond directly impacting yield, drought stress can also diminish the effectiveness of agronomic practices, such as fertilizer application and pest and disease management. Severe drought conditions necessitate increased irrigation, escalating production costs. Insufficient water supply, especially during the early growth stages, negatively affects tuber formation, leading to reduced yields and inferior tuber quality. Prolonged drought can reduce sweet potato yield. It can also lower the quality of root tubers. This leads to major economic losses for farmers. Therefore, enhancing water-use efficiency is essential, particularly in regions experiencing water scarcity and where supplementary irrigation is required. Furthermore, in warmer climates, high temperatures exacerbate the effects of water stress on crop productivity.

Drought-induced stunted growth significantly affects sweet potato yield. A study investigating medium drought stress exposure found that while it negatively influenced all plant characteristics, it allowed differentiation between genotypes. Conversely, severe drought stress masked these differences. The study demonstrated that maintaining adequate crown cover, stomatal conductivity and stem length is essential for achieving a good yield. Strong correlations between stem length, leaf area index and yield suggest that these traits can serve as valuable screening tools in future research (Laurie *et al.*, 2022).

Developing sweet potato varieties that combine high yield potential with drought tolerance remains a primary breeding objective, particularly in drought-prone regions.

Understanding the physiological and biochemical traits associated with drought resistance is essential for implementing effective breeding strategies. Additionally, integrating yield modeling can help optimize selection processes, reducing the time and costs required for extensive field trials.

Drought tolerance mechanisms in sweet potato: physiological and biochemical adaptations

Drought, salinity, and low temperatures are among the most significant environmental stressors limiting sweet potato productivity worldwide. Drought alone is responsible for an estimated 25% yield loss annually, with the crop being particularly vulnerable during its establishment phase, including the vining stage and root initiation. However, once rooted, sweet potato exhibits notable drought resistance, contributing to its higher yield potential compared to other staple crops grown in developing countries. In addition to its productivity advantages, sweet potato's rich nutritional profile makes it a valuable food source for farmers in drought-prone regions.

Despite its adaptability, drought stress triggers various morphological, physiological and biochemical changes in sweet potato, often negatively impacting its agronomic and economic performance. Drought conditions reduce root development, branching, leaf area index, stem height and length, stomatal conductance, leaf size, and overall photosynthetic efficiency. Additionally, drought-induced oxidative stress leads to the excessive production of reactive oxygen species (ROS), which can be harmful to plant cells. To mitigate these effects, sweet potato activates enzymatic and non-enzymatic antioxidant defense mechanisms, including increased activity of ascorbate peroxidase (APX) (Zhang *et al.*, 2022), glutathione reductase (Laurie *et al.*, 2022), catalase (Huang *et al.*, 2022), superoxide dismutase (SOD), carotenoids, ascorbic acid, glutathione, and tocopherols. These antioxidant compounds help regulate ROS levels, enhancing the plant's drought tolerance.

Comprehensive studies on sweet potato's drought response have identified several physiological and biochemical markers that contribute to its drought resilience. Key indicators such as nitrate reductase (NR) activity, free proline accumulation, and chlorophyll concentration at 60 days after planting have been suggested as effective screening tools for selecting drought-tolerant genotypes. Additionally, research on orange-fleshed sweet potato varieties has shown significant variation in tuber weight under drought conditions, while other traits such as tuber quantity, beta-carotene content, starch content, and moisture levels remained relatively stable. Orange-fleshed varieties also exhibit higher concentrations of essential minerals such as magnesium (Mg), iron (Fe), zinc (Zn), manganese (Mn) and calcium (Ca), whereas creamy-fleshed varieties tend to have higher starch and carbohydrate content. The high carbohydrate content and abundance of essential vitamins further highlight sweet potato's importance in maintaining a nutritious diet, especially in water-limited regions (Kwak, 2019).

In addition to these biochemical adaptations, secondary metabolites synthesized under drought stress serve as valuable markers for germplasm selection in breeding programs. Traditional breeding efforts to improve sweet potato varieties have historically focused on increasing yield rather than enhancing stress tolerance. However, given the increasing threat of climate change to global food security, modern breeding strategies are now integrating physiological and molecular insights to develop drought-resistant cultivars (Kapoor *et al.*, 2020). Advancing sweet potato breeding through these approaches will be critical in ensuring sustainable production and food security in drought-prone environments.

Physiological and biochemical adaptations of sweet potato to drought stress

Drought, along with salinity and low temperatures, is a major environmental stress that significantly reduces sweet potato productivity worldwide. Drought alone accounts for an estimated 25% annual yield loss, with the crop being particularly vulnerable during the establishment phase, including the vining stage and root initiation. However, once fully rooted, sweet potato exhibits strong drought tolerance, contributing to its higher yield potential compared to other staple crops grown in developing countries. Additionally, its rich nutritional content makes it an essential food source for farmers in water-scarce regions.

Despite its resilience, drought stress induces several morphological, physiological, and biochemical alterations in sweet potato, often leading to reduced agronomic performance. Under drought conditions, root development, branching, leaf area index, stem height, stomatal conductance, leaf expansion, and photosynthetic efficiency all decline. Furthermore, drought triggers oxidative stress, leading to excessive production of reactive oxygen species (ROS), which can damage plant cells. To counteract these effects, sweet potato activates a complex antioxidant defense system involving both enzymatic and non-enzymatic mechanisms. Increased activity of antioxidant enzymes such as ascorbate peroxidase (APX), glutathione reductase, catalase, and superoxide dismutase (SOD) plays a crucial role in detoxifying ROS. Additionally, non-enzymatic antioxidants such as carotenoids, ascorbic acid, glutathione, and tocopherols help maintain cellular balance and enhance drought tolerance.

Studies on sweet potato's response to drought stress have identified key physiological and biochemical markers associated with drought resilience. Indicators such as nitrate reductase (NR) activity, free proline accumulation, and chlorophyll concentration at 60 days after planting have been proposed as effective screening tools for selecting drought-tolerant genotype. Research on orange-fleshed sweet potato varieties has revealed that, while tuber weight varies significantly under drought conditions, other traits such as tuber quantity, beta-carotene content, starch content, and moisture levels remain largely unaffected. Additionally, orange-fleshed varieties exhibit higher concentrations of essential minerals such as magnesium (Mg), iron (Fe), zinc (Zn), manganese (Mn), and calcium (Ca), whereas creamy-fleshed varieties tend to have higher starch and carbohydrate content. The high carbohydrate and vitamin content of sweet potato further underscores its value in promoting food security, especially in drought-prone regions (Kwak, 2019).

Beyond these physiological and biochemical adaptations, secondary metabolites synthesized in response to drought stress serve as critical markers for germplasm selection in breeding programs (Mgcibelo, 2014). While traditional breeding efforts have primarily focused on enhancing yield, there is a growing emphasis on developing drought-tolerant varieties by integrating knowledge of plant physiological responses and molecular mechanisms. Given the increasing frequency of drought events and their impact on global agriculture, modern breeding strategies are being designed to improve sweet potato's resilience to environmental stresses, ensuring long-term food security (Kapoor *et al*., 2020).

Chlorophyll content index (CCI)

Drought stress was applied 60 days after planting. It did not reduce CCI values. The observation was made in sweet potato (Sapakhova *et al.*, 2023). CCI values2usually decline under drought stress. In this case, the decline was smaller. This decline was recorded at 40, 60, 80, and 100 days after planting.The Hernandez variety had a small improvement in its chlorophyll levels when it was grown under regular, non-stressful conditions. They were higher than the values under severe drought conditions.Variations in CCI levels across different sweet potato varieties under both control and high-stress treatments at 60 days after planting suggest genetic differences and variations in photosynthetic activity (Zhang *et al*., 2022).

A significant decline in CCI values was observed 120 days after planting in all genotypes under drought stress. Wheat also showed a big decrease in CCI levels under drought, similar to other findings. Sweet potato varieties, including Monate, Resisto, and Bophelo, showed drop in CCI levels. These plants had less chlorophyll than the control plants. Since drought impacts the photosynthetic system, it may also hinder growth, particularly in crown and stem development. Chlorophyll breakdown can affect how well the antioxidant enzyme system works in sweet potato. Earlier studies reported that this system was not very strong. CCI could serve as a potential marker for heat tolerance selection.

Reactive oxygen species (ROS)

Certain metabolites play key roles in plant adaptation to various abiotic stressors. The accumulation of osmolytes or compatible solutes, such as polyamines, free proline, trehalose, glycine betaine, and sugar alcohols, can help protect plants from adverse environmental conditions. Sweet potato is rich in β-carotene, vitamin C, and antioxidants, which contribute to its resilience under stress. Sweet potato varieties produce, use, and contain these secondary metabolites.

To mitigate the negative impact of abiotic stress, plants employ different signaling pathways, adjust growth patterns, accumulate compatible solutes, activate antioxidants, and produce chaperones and stress proteins. ROS are oxygen molecules that are formed when oxygen is partly changed into other forms. These molecules can be very reactive or less reactive. Excess ROS production under abiotic stress can lead to oxidative damage, affecting proteins, lipid membranes, and nucleic acids, ultimately causing cell death. To counteract these effects, plants utilize enzymatic and non-enzymatic antioxidant mechanisms to minimize oxidative stress and enhance tolerance to abiotic stressors. Antioxidant system activity—both enzymatic and non-enzymatic—acts as a reliable indicator of drought tolerance in plants (Laurie *et al.*, 2022).

Betaines

Betaines are non-protein amino acids containing a quaternary ammonium and carboxyl group. These compounds help stabilize the quaternary structures of enzymes, complex proteins, and membrane systems, including the photosystem II complex. Their synthesis is induced under stress conditions, with concentrations correlating to stress tolerance. The accumulation of glycine betaine, the most widely studied betaine, enhances plant resilience to multiple abiotic stressors while also improving yields under non-stress conditions (Chen *et al.*, 2008). Researchers used *Agrobacterium tumefaciens* to insert the BADH gene. BADH stands for betaine aldehyde dehydrogenase. They transferred the gene from spinach into sweet potato's embryonic suspensions. Transgenic plants over expressing this gene exhibited increased glycine betaine synthesis, leading to improved tolerance to oxidative, salt, and low-temperature stress (Fan *et al.*, 2015). Transgenic sweet potato plants with the BADH gene showed better resistance to osmotic stress, low temperatures, and oxidative stress (Fan *et al*., 2012).

Trehalose

Trehalose, a sugar composed of two glucose molecules, functions as an osmoprotectant and supports plant survival under adverse environmental conditions. It has been implicated in regulating stomatal movement and enhancing water use efficiency in higher plants. Sufficient trehalose levels in plant cells are crucial for growth under stress.

Trehalose synthesis occurs in two stages, catalyzed by trehalose-6-phosphate synthase (TPS) and trehalose-6-phosphate phosphatase (TPP). Trehalose-6-phosphate is then dephosphorylated to trehalose by the TPP enzyme. Researchers isolated the IbTPS gene. The gene was from *Ipomoea batatas*. They overexpressed this gene in transgenic plants. These transgenic plants showed improved salinity resistance. The resistance was better compared to control plants (Jiang *et al*., 2014).

Polyamines

Polyamines are small polycations. They play vital roles in organisms. At physiological pH, they interact with negatively charged molecules such as membrane phospholipids, nucleic acids, and specific proteins, stabilizing them under abiotic stress. Plants contain several common polyamines. These include putrescine, spermidine, and spermine. Putrescine is a diamine. Spermidine is a triamine. Spermine is a tetramine. These compounds can be synthesized from amino acids such as L-ornithine, L-lysine, and L-arginin.

A study reported about transgenic sweet potato plants. These plants had the FSPD1 gene. This gene is called the spermidine synthetase gene. The plants expressed this gene. The gene came from *Cucurbita ficifolia*. The transgenic plants showed elevated spermidine levels. They had tolerance to heat stress. The tolerance was increased. It was better than in normal plants. They had better tolerance to chilling stress. They had tolerance to heat stress. This tolerance was enhanced. These traits were better compared to wild-type plants (Kasukabe *et al*., 2006).

Sugar alcohols

Inositol, a well-known osmolyte, plays a role in signal transduction under stress. Myo-inositol is made through a biosynthesis process. A key limiting step occurs in this process. This step is done by an enzyme. The enzyme has a name. It is called l-myo-inositol-1-phosphate synthase (MIPS). Researchers isolated the IbMIPS1 gene. The gene was from *I. batatas*. They found that overexpressing this gene significantly improved salinity tolerance. It also improved water stress tolerance. This was observed in transgenic sweet potato plants. The plants were tested under field conditions.

Free proline content

Proline accumulation is a key mechanism for plant stress tolerance, helping stabilize proteins, membranes, and neutralize free radicals. As an osmoprotectant, proline helps maintain osmotic balance under stress. Proline can be applied externally. This is called exogenous proline application. It can enhance drought resistance.

The enzyme pyrroline-5-carboxylate reductase (P5CR) plays a crucial role in proline biosynthesis. Scientists used transgenic sweet potato plants. They over-expressed the IbP5CR gene in these plants. The gene was more active than normal. This over-expression improved their salt tolerance. Increased free proline levels in drought-stressed plants, with concentrations rising from 2 μmol/ g to 22 μmol/ g, representing a fivefold increase compared to controls was observed. The Bophelo variety was used in the study. The study involved drought stress. It showed higher proline accumulation.

Antioxidant enzymes

Ascorbate peroxidase (APX): Water stress significantly increases APX activity, with ninefold increase under drought stress. APX expression in chloroplasts enhances drought tolerance.

Superoxide dismutase (SOD): Different sweet potato varieties exhibited increased SOD activity under water stress, with values ranging from 0.350 to 0.85 units/mg protein.

Glutathione reductase (GR): GR is an enzyme. Drought stress increased GR levels in sweet potato. The GR activity ranged from 2 to 73 nmol NADPH min^{-1} mg $protein^{-1}$.

Nitrate reductase (NR): Severe drought stress significantly reduced NR activity, affecting nitrogen assimilation and photosynthesis.

Crop management strategies for drought mitigation

Crop management under water-limited conditions involves two primary approaches: agronomic and genetic. The selection and enhancement of genotypes suited to specific environments can be achieved using appropriate selection indicators for water deficiency tolerance. Developing drought-tolerant varieties presents a cost-effective genetic strategy, particularly beneficial for small-scale farms.

An efficient selection method is needed to evaluate water deficiency tolerance. To do this, various indicators should be assessed. These indicators should be checked early in the growing season. These include SOD activity, NR activity, APX activity, stomatal conductance, leaf area, chlorophyll content, leaf water content, free proline content, and water use efficiency (WUE). Studies have utilized these indicators in crops such as sugar beet, potato, cotton, and wheat, aiding in cost- and time-efficient genotype selection. These parameters, either individually or in combination, can enhance genotype selection and breeding methods.

Several approaches have been employed to evaluate drought tolerance and WUE in crops, including measurements of potential relative humidity, diffusion pressure deficit, chlorophyll stability index, and carbon isotope discrimination (Gitore *et al*., 2021). However, these methods are often time-consuming, limiting their effectiveness for screening large numbers of varieties. Earlier drought tolerance studies focused on overall drought effects without isolating specific component traits (Osmolovskaya *et al*., 2018). These traits, however, can be leveraged to refine screening methodologies. Despite some challenges, including limited understanding of drought tolerance genetics and variation in plant protection mechanisms, physiological and phenotypic screening methods have been applied to assess genotype-environment interactions.

Although research on developing drought tolerance evaluation methods for sweet potato remains limited, significant progress has been made in identifying optimal selection strategies. Drought conditions using a line-source sprinkler system to examine its effects on yield and leaf water potential in eight sweet potato varieties were simulated. Drought experiments in pot-grown sweet potatoes, investigating photosynthesis, leaf surface development, stomatal conductance, leaf water potential, and soil water potential were conducted. Sweet potato's stomatal movement remained unaffected by water stress. Its nitrate reductase activity declined. The decline happened as soil water potential decreased. The most effective approach for assessing sweet potato's drought tolerance involves field trials where irrigation is managed without interference from natural precipitation. In addition to field-based evaluations, implementing strategies such as optimizing water use efficiency, selecting drought-tolerant genotypes, large-scale screening, conventional and marker-assisted selection (MAS), exogenous hormone applications, osmoprotectant treatments for seeds or plants, and advancements in genetic engineering for drought resilience are highly recommended.

Developing drought tolerant sweet potato varieties

When breeding crops, it is essential to consider the key factors that limit productivity. As highlighted earlier, drought is a major constraint on sweet potato yield, causing significant annual losses. This challenge arises from morphological, biochemical, physiological, and molecular changes triggered by water deficiency. These changes serve as valuable indicators for breeding and developing drought-tolerant sweet potato genotypes. Sweet potato cultivation conditions vary widely. Root yield under optimal conditions is not enough for selecting germplasm. Therefore, selection should not be based solely on root yield under optimal conditions. With the increasing impact of climate change, the selection of drought-tolerant varieties has become a priority for growers. Small-scale farmers, in particular, must take multiple factors into account for successful production. These include selecting varieties that can adapt to poor soil fertility, limited pest control, and, most importantly, restricted irrigation. Research plays a vital role in identifying and developing the most suitable varieties for commercial use.

Traditional breeding approaches face several limitations in enhancing sweet potato traits. Many sweet potato varieties exhibit reduced flowering and fertility or fail to bloom altogether. High levels of male sterility, along with self- and inter-specific incompatibility, hinder breeding efforts. Additionally, the hexaploid nature (outcrossing polyploidy) of sweet potato complicates conventional breeding processes (Yang *et al*., 2022).

Breeding sweet potato for drought tolerance requires a thorough understanding of drought stress effects, the availability of genetic diversity, and the implementation of effective breeding and selection methods to identify and develop promising clonal varieties. Drought poses a significant environmental challenge for sweet potato cultivation, particularly in non-irrigated agricultural areas. Different varieties respond variably to limited groundwater, emphasizing the need to breed varieties with strong drought tolerance.

Developing effective genetic management technologies requires reliable, reproducible, and efficient field and laboratory screening methods. These tools enable researchers to identify drought tolerance traits in sweet potato germplasm and incorporate them into high-yielding, stress-tolerant varieties (Xiao *et al*., 2022). Irrigation effects on sweet potato growth parameters and the impact of mulching and pruning on mitigating heat stress was evaluated. The findings from such studies offer practical strategies to minimize water loss during sweet potato cultivation.

Using drought and yield indices to select germplasm for different production environments has shown promising results. This approach is particularly effective when applied early in the breeding cycle. Plant breeders must carefully consider critical stages of plant growth and development. To maximize sweet potato yield in regions like Kenya, experts recommend planting tubers early in the rainy season to avoid water shortages during the crucial first four months of growth (Abdallah *et al*., 2020).

Drought tolerance of 50 sweet potato genotypes was evaluated under both laboratory and field conditions, identifying 12 genotypes as drought-tolerant based on wilting duration. Additionally, five highly productive genotypes were selected for use as parents in breeding programs for drought tolerance. Cultivated sweet potato varieties exhibit greater stress tolerance than their wild counterparts, largely due to their ability to develop storage roots, which play a key role in their response to environmental stress. Wild *I. batatas* species do not produce storage roots. They also do not display significant drought tolerance. Therefore, improving cultivated sweet potato varieties remains the most effective strategy for enhancing yield and drought resistance (Nhanala and Yencho, 2021). Various molecular and genetic mechanisms contribute to plant stress tolerance, with environmental factors influencing their interactions. However, research on the phenotyping and genotyping of sweet potato for water stress resistance remains limited. Epigenetic modifications introduce variability in plants. Genetic element mobility also introduces variability. This variability affects plant stress resistance (Akomeah *et al*., 2019). Despite significant advancements, substantial opportunities remain to further enhance plant resilience to abiotic stressors.

The insights presented here can aid in screening sweet potato for drought sensitivity and tolerance. They also support breeding programs aimed at improving sweet potato adaptability to climate change through targeted selection and genetic improvements.

Enhancing stress tolerance through stress protein expression

Heat shock proteins (HSPs) play key roles in abiotic stress tolerance by acting as molecular chaperones that assist in protein folding and transport while preventing cellular damage under stressful conditions. Over expression of stress protein-encoding genes enhances plant survival under abiotic stress. The Arabidopsis thaliana cDNA gene AtP3B, encoding a ribosome-associated chaperone, improves tolerance in transgenic plants. Cell wall stabilization proteins are crucial for structural integrity during osmotic stress. The Sap1 gene is from *Xerophyta viscosa*. This gene encodes a stress protein. The gene helps improve sweet potato plants through lab-based changes. It leads to improved growth under drought conditions.

Late-embryogenesis-abundant (LEA) proteins, expressed during seed maturation, contribute significantly to stress responses. IbLEA14, encoding the LEA14 protein, enhances tolerance to drought and salt stress and is expressed in various tissues under water stress conditions. It's over expression in transgenic calli enhances drought tolerance by increasing lignin content, which plays a vital role in drought resistance. Further studies are needed to understand the role of lignin accumulation under stress conditions.

Enhancing tolerance through transport protein expression

Na^+/H^+antiporters are membrane proteins. They are located in the plasma or vacuolar membranes. Antiporters are transport proteins. They help move sodium ions. This helps maintain ion homeostasis. It also prevents excessive Na^+ accumulation. The IbNHX2 gene comes from *I. batatas*. It is a vacuolar Na^+/H^+ antiporter gene. This gene helps in ion transport within the cell and overexpressed in transgenic sweet potato plants. Overexpression of the gene significantly enhanced salt tolerance. The plants became better at handling dry conditions because of the gene. Similarly, introducing the Na+/H+ anti-transporter gene from *Arabidopsis thaliana* into sweet potato increases resistance to cold and salt stress.

Mitigating oxidative stress

Plants produce reactive oxygen species (ROS). ROS levels must be regulated. Plants experience stress. They respond to this stress. These molecules are constantly generated in mitochondria and chloroplasts and can cause oxidative cell death (Movahedi *et al*., 2024). They can be harmful at high amount. The plant's antioxidant defense system mitigates oxidative stress through ROS detoxification. One example for gene involved in ROS management and stress tolerance is IbNFU1 gene comes from a salt-tolerant *I. batatas* variety. This gene produces a protein. The protein acts like a helper or base for making tiny structures (iron–sulfur clusters) that the plant needs to stay healthy and active. It helps in assembling iron–sulfur clusters. The gene was overexpressed in transgenic plants. The gene was made more active, and this helped the plants deal with salt stress. Iron–sulfur cluster scaffold proteins play essential roles in energy metabolism and ROS scavenging (Mansoor *et al*., 2022).

A study utilizing Copper/Zinc superoxide dismutase (Cu/Zn-SOD) and APX genes demonstrated improved ROS deactivation and oxidative stress resistance in transgenic sweet potato plants compared to controls.

Activation of phytohormone signaling pathways

Abscisic acid (ABA) is a key chemical in plants that helps them deal with stress. The LOS5/ABA3 gene, encoding a molybdenum cofactor sulfurase enzyme, is essential for ABA biosynthesis and enhances salt tolerance in transgenic sweet potato plants. The α/β-hydrolase gene IbMas, encoding maspardin protein, plays a role in osmotic balance regulation, and its over expression improves salinity tolerance.

Regulation of gene expression for stress resistance

Plant resistance mechanisms involve complex regulatory networks. Several transcription factors (TFs), including

NAC, bZIP, WRKY, and AP2/ERF, play vital roles in abiotic stress resistance. Plants have many coding sequences. Nearly 7% belong to the group of transcription factors (TFs. Transcription factors help control gene expression. Many of these transcription factors help plants respond to stress. They help the plant respond quickly when something stressful happens (Jia *et al.*, 2022; Khoso *et al.*, 2022).

Sugar Will Eventually be Exported Transporters (SWEET) are key regulators of sugar transport and plant stress responses. IbSWEET genes have been identified in I. batatas (27 SWEETs), I. triloba (25 SWEETs), and *I. trifida* (27 SWEETs), influencing growth, hormone interactions, and abiotic stress responses (Dai *et al.*, 2022). High IbSWEET expression correlates with improved drought and salt tolerance, making them candidates for stress-resistant breeding programs.

Gene expression profiling identified receptor-like kinases inhibited at 24 hr post-stress but not at 48 hr post-stress, indicating their role in dehydration responses. Down regulation of LHCSB6 and SLAC1 orthologs in sweet potato suggests their importance in stomata closure during drought stress (Lau *et al.*, 2018). Several studies have investigated genes like p-hydroxyphenylpyruvate dioxygenase (IbHPPD). IbHPPD enhances stress resistance. Other studies have looked into IPT. IPT is involved in cytokinin biosynthesis. It also plays a role in drought tolerance (Kim *et al.*, 2021a; Hrmova *et al.*, 2021; Tang *et al.*, 2023). The DUF668 gene family has several members. These include IbDUF668-6, IbDUF668-7, IbDUF668-11, and IbDUF668-13. These genes are found in sweet potato. They help plants survive when there's not enough water or when the soil is too salty. They encode membrane proteins (Liu *et al.*, 2023).

Transcription factor-based stress regulation

WRKY TFs, initially isolated from sweet potato as Sweet Potato Factor1, play major roles in stress signaling. Multiple IbWRKY genes regulate abiotic stress responses, and their co-expression is highly complex (Liu *et al.*, 2022). GRAS TFs also contribute to stress responses, with IbGRAS71 identified as a key player in salt and drought tolerance. Phytochrome-interacting factors (PIFs) regulate responses to various stressors, and IbPIF3.1 is induced under drought, salinity, cold, and heat stress, as well as biotic stressors.

Carotenoid associated stress tolerance

The sweet potato orange gene (IbOr-R96H) enhances carotenoid accumulation and stress resistance. Overexpression of IbOr-R96H increases antioxidant activity and heat tolerance in transgenic plants (Kim *et al.*, 2021b). *Agrobacterium tumefaciens* mediated transformation to develop IPT - expressiveness sweet potato lines, resulting in enhanced drought tolerance (Nawiri *et al.*, 2017).

Molecular responses to drought stress

Proteomic studies identified 389 deferentially expressed genes (DEGs) and 1168 deferentially expressed proteins (DEPs) in response to drought (Tang *et al.*, 2023). These are linked to carbon, phenylalanine, starch, and cellulose metabolism, as well as heat shock proteins. Plants respond to drought by producing signal molecules such as ABA, $Ca2+$, inositol-1,4,5-triphosphate (IP3), and cyclic adenosine diphosphate ribose (cADPR) (Kakimoto, 2001). Functional gene products, including proline (Pro), glycine betaine (GB) (Fan *et al.*, 2015), soluble sugars (SS), and late embryogenesis abundant (LEA) proteins (Mertenz *et al.*, 2018), play essential roles in stress adaptation.

Molecular breeding offers promising pathways for improving sweet potato's tolerance to abiotic stress through genetic modifications. Advances in stress protein expression, transport protein regulation, oxidative stress mitigation, phytohormone signaling, and TF-based regulation collectively enhance the crop's resilience. Future research should focus on refining these genetic strategies to develop high-yielding, stress-resistant sweet potato varieties.

Genetic engineering approaches for abiotic stress tolerance in sweet potato

Various strategies have been developed to enhance abiotic stress tolerance, such as introducing genes encoding late-embryogenesis-abundant proteins, transcription factors (TFs), transport proteins, heat shock and cold shock proteins, enzymes that accumulate osmolytes and antioxidants, and hormone-related gene expression regulators. Many stress-resistance genes have been characterized in *I. batatas*, opening possibilities for cis-genic approaches (Ahamed *et al.*, 2024).

The limited focus on genetic transformation in sweet potato stems from the complexity of its hexaploid genome and the historical challenges in establishing efficient transformation and regeneration protocols. However, significant breakthroughs occurred in 2016 with the complete sequencing of one of the haplogenomes of sweet potato (Yang *et al.*, 2022), accelerating the development of functional genomics for this crop. Recent advancements have also optimized transformation and regeneration processes, enhancing the potential for genetic improvements in sweet potato (Yan *et al.*, 2022).

Advancements in understanding the genetic mechanisms that help plants withstand abiotic stress have significantly progressed in recent decades. The identification and cloning of key genes have enabled both private and public researchers to develop plant varieties capable of enduring environmental stress without compromising yield (Kim *et al.*, 2021a; Tang *et al.*, 2023). Genetic modifications could lead to new varieties with improved tolerance to abiotic stress, enhancing water use efficiency and productivity under adverse conditions.

Regeneration and transformation in sweet potato

The transformation and regeneration of various sweet potato genotypes were explored. The study found that somatic embryogenesis remains genotype-dependent, influencing the frequency and variability of regeneration among sweet potato varieties. Transgenic sweet potato plants were successfully produced using selected calli and somatic embryo formation on modified media. The results highlight that existing regeneration and transformation protocols depend heavily on the in vitro response of specific genotypes, Notably, leaf explants demonstrated superior modification and regeneration potential compared to other tissue types, making somatic embryogenesis the most effective regeneration technique for sweet potato. The study also underscored sweet potato tissue's sensitivity to mannose, requiring extended culture periods to observe its effects, as its lethal impact does not manifest in early growth stages. Furthermore, an effective transgenic PSARK-IPT sweet potato plant developed, which exhibited delayed aging under drought conditions and outperformed wild species in water retention, chlorophyll content, tuber development, and overall growth.

Proline assisted in stress adaptation

Proline, a key osmolyte apart from carbohydrates, plays a crucial role in plant stress adaptation. Studies have established a positive correlation between proline levels and resistance to environmental stressors, including intense ultraviolet radiation, soil salinity, extreme temperatures, and oxidative stress.

Plants synthesize proline in the cytosol via either the ornithine or glutamate pathways, with the latter primarily activated in response to environmental stress. Genetic engineering has successfully introduced genes involved in proline biosynthesis, resulting in plants resistant to cold, salinity, and osmotic stress. Moreover, proline accumulation under stress conditions is not solely due to enhanced synthesis but also due to inhibited degradation. Proline dehydrogenase, the key enzyme in proline bio-degradation, has been silenced in *Arabidopsis*, leading to substantial proline accumulation and improved resistance to frost and high salinity.

Enhancing sweet potato germplasm for global food security

Expanding the genetic diversity of sweet potato germplasm is crucial for ensuring food security, particularly in developing nations with high populations and persistent malnutrition (Kou *et al.*, 2023; Haque *et al.*, 2020). Recent research integrating genotyping and phenotyping has provided valuable insights for breeding stress-tolerant germplasm, fostering the development of genetic resources and improving sweet potato diversity (Liu *et al.*, 2022; Daurov *et al.*, 2018; Slonecki *et al.*, 2023; Huo *et al.*, 2023).

Varietal achievements made in India

India has made significant strides in developing climate-resilient sweet potato varieties to combat the challenges posed by climate change, including drought, salinity, pest infestation, and nutrient-poor soils. One such notable variety is NSP-7, developed for the semi-arid regions of South Gujarat. It yields approximately 23.39 tonnes per hectare and shows strong resistance to the sweet potato weevil, making it ideal for stress-prone areas (Patel *et al.*, 2024). Another widely adopted variety is Sree Arun, developed by ICAR-CTCRI (Central Tuber Crops Research Institute), which is drought-tolerant and performs well in Southern Indian states like Kerala, Tamil Nadu, and Karnataka. It matures in about 90–100 days and yields around 25–28 tonnes per hectare (Anil *et al.*, 2025).

Sree Nandini is another promising variety suitable for both rainfed and irrigated conditions, popular in Andhra Pradesh and Odisha, with high beta-carotene content and a maturity of 80–90 days (Ranasingh *et al.*, 2024). Konkan Ashwini, primarily grown in coastal Maharashtra and Karnataka, thrives in saline soils and shows resistance to viral diseases and root rot, making it suitable for the western coastal belt. Co-3, developed in Tamil Nadu, is an early-maturing variety with good tuber size and dry matter content, ideal for short-duration cropping systems (Gahane *et al.*, 2024).

For eastern India, Sree Kanaka offers a dual benefit of high yield and pest resistance, especially against sweet potato weevils, while Rajendra Sakarkand-5, developed in Bihar and Uttar Pradesh, is drought-tolerant and performs reliably in stress-prone soils (Kumar *et al.*, 2025). Gauri, cultivated in Odisha and West Bengal, is known for its high beta-carotene and resistance to common pests and diseases. Lastly, Kala Dhan is suitable for North and Central Indian dryland areas and is valued for its resistance to root rot and adaptability to rainfed cultivation ((Jana *et al.*, 2024). These varieties underscore India's commitment to enhancing food and nutritional security through crop diversification and climate-resilient agriculture.

Conclusion

Drought poses a major challenge to crop production in arid regions, significantly reducing yields and increasing cultivation costs. As climate change intensifies, developing drought-tolerant crops has become essential for sustaining agriculture in these water-scarce environments. Sweet potato, with its natural resilience and adaptability, presents a valuable opportunity for enhancing food security in arid regions. Recent advancements in sweet potato genomics and metabolomics provide a strong foundation for breeding improved drought-resistant varieties. Accelerating this progress will require an integrated approach that combines traditional breeding techniques with modern genetic and biotechnological innovations. Additionally, optimizing agronomic practices to suit the harsh conditions of arid landscapes is critical. By reducing the need for irrigation and minimizing production costs, drought-tolerant sweet potato varieties can improve farmer livelihoods while ensuring a stable food supply for growing populations in arid and semiarid regions.

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Conflict of Interest

The authors have no conflict of interest.

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