



Impact of Water Deficit Stress on Starch Characteristics in Potatoes: An Integrative Perspective of Physiological, Biochemical, and Molecular Mechanisms

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Abstract

Among the most cultivated crops worldwide, potato (*Solanum tuberosum*) faces significant threats from water scarcity, owing to its shallow root system and high irrigation requirement. Water deficit disturbs homeostasis and critical physiological mechanisms, including photosynthesis, carbohydrate translocation, and starch metabolism in tuberous plants. It reduces CO₂ assimilation, modulates the expression of key enzymes involved in starch synthesis, such as ADP-glucose pyrophosphorylase and starch synthases, and alters the amylose–amylopectin ratio, consequently affecting their rheological properties. Additionally, drought triggers antioxidant and metabolic responses in plants, including the accumulation of secondary metabolites and the regulation of stress tolerance-related genes. Transcriptomic analyses have revealed water-deficit responsive genes, such as *StMAPK11*, *StCDPK13*, and *StERF94*, which contribute to stress adaptation. This review also explores mitigation strategies and genetic improvement approaches, including the application of biostimulants (chitosan, uniconazole), ZnO and SiO₂ nanoparticles, and the selection of more drought-tolerant genotypes. Recent advances in biotechnology, including gene editing and omics technologies, have contributed to the development of stress-resilient potato varieties.

Keywords Genetic regulation · Potato (*Solanum tuberosum*) · Starch metabolism · Water deficit

Introduction

Potato (*Solanum tuberosum* L.) is among the most important food crops worldwide, ranking third in global production with 383.082.607 million tonnes, following rice (799.999.504 million tonnes) and wheat (783.994.297 million tonnes) (FAOSTAT

2023). Potatoes contain essential vitamins and amino acids crucial for human health, including thiamine, tryptophan, tyrosine, ascorbic acid (vitamin C), chlorogenic acid, and phenylalanine (Storey 2007). Thiamine (vitamin B1) plays a crucial role in energy metabolism and proper nerve function (Navarre et al. 2016). Tryptophan and tyrosine are essential amino acids involved not only in protein synthesis but also in the biosynthesis of key neurotransmitters, including serotonin, dopamine, norepinephrine, and epinephrine (Fernstrom and Fernstrom 2007). Ascorbic acid, a powerful antioxidant, plays a fundamental role in immune response and skin maintenance, while chlorogenic acid is notable for its antioxidant activity and potential in modulating blood glucose levels (Yamdeu Galani et al. 2017). Phenylalanine, another essential amino acid, acts as a precursor for various bioactive molecules of biochemical relevance (Sharma et al. 2020). In addition to its nutritional attributes, the potato is of considerable industrial importance, particularly due to its high starch content, which represents a major agro-industrial byproduct (Çalışkan et al. 2023). Potato starch is a key element that influences both the quality of tuberous plants and their use in various industries, including food, pharmaceuticals, and biopolymers. Its structure and composition determine crucial characteristics such as texture, water retention capacity, and digestibility, key aspects of the final product's quality. However, starch synthesis is closely linked to the plant physiology and is highly sensitive to environmental factors, with the water deficit representing a major abiotic stressor that adversely affects both the yield and physicochemical properties of starch (Bertoft and Blennow 2016).

Agriculture accounts for approximately 70% of global freshwater withdrawals, making it the largest consumer of this critical resource (Ridoutt et al. 2021). The increasing demand for water-intensive crops has intensified the strain on already limited water supplies (Hachimi et al. 2022). Moreover, climate change has further aggravated water scarcity, posing a serious challenge to global food security and heightening competition for water among agricultural, industrial, and domestic sectors (Mancosu et al. 2015). Water deficit, a critical constraint in potato-growing areas worldwide, induces systemic physiological and biochemical disruptions, including growth inhibition, compromised starch biosynthesis, and altered starch functionality (Alvarez-Morezuelas et al. 2022). As water governs key metabolic processes, its scarcity impairs photosynthesis and subsequent starch deposition in tubers (Nobel 2020). Although potato exhibits moderate water-use efficiency, its shallow root system significantly limits its tolerance to drought conditions, often resulting in substantial reductions in both yield and tuber quality (Anithakumari et al. 2012). Water deficit affects a wide range of morphological, physiological, biochemical, and molecular traits in potato plants, including reduction in tuber number and size, photosynthetic rate, leaf area, stomatal conductance, and biomass accumulation (Rodríguez-Pérez et al. 2017). Key quality attributes, particularly starch content and starch yield, are also strongly influenced by the plant's water status (Meise et al. 2019). Nonetheless, the physiological response of potato to drought stress is highly variable and influenced by multiple factors such as cultivar, seed tuber origin, physiological age, as well as the duration and severity of the stress (Monneveux et al. 2013). Plant drought tolerance can be defined as the capacity to maintain physiological activity through coordinated regulation of stress-responsive genes and metabolic pathways that mitigate or repair

stress-induced damage (Zhang et al. 2018). Agronomically, drought-tolerant cultivars are characterized by their capacity to maintain stable yields despite exposure to water scarcity (Al Tawaha et al. 2025).

Given the significant impacts of water stress on potato yield and starch quality, this review aims to synthesize current knowledge from the fields of plant physiology, biochemistry, and molecular biology to elucidate the mechanisms by which drought stress influences these processes. Particular emphasis is placed on cellular and metabolic alterations in response to water limitation. A comprehensive understanding of these responses is necessary for developing effective strategies to mitigate the adverse impacts of drought, thereby supporting the quality and sustainability of potato yield under changing climatic conditions.

Starch Synthesis and Quality in Potatoes under Water Deficit

Water deficit arises when soil moisture availability is insufficient to meet the physiological demands required for optimal plant growth and development. This condition can be attributed to prolonged periods of low precipitation, high evapotranspiration rates, or inadequate soil water retention. The severity of water deficit is determined by its intensity, duration, and the plant's developmental stage during exposure (Shawaqfeh et al. 2025). C3 photosynthesis is adversely affected by soil water deficit, primarily due to alterations in leaf water potential and relative water content. During the early stages of water limitation, when leaf relative water content is still relatively maintained, the reduction in CO₂ assimilation is mainly associated with decreased stomatal conductance, which limits intercellular CO₂ availability (Farooqi et al. 2020). Under moderate water deficit conditions, plants typically exhibit maximum photosynthetic capacity and quantum yield that remain unaffected when measured under saturating light and high carbon dioxide concentrations. Moreover, photosynthetic performance generally recovers relatively quickly upon rehydration. Under moderate water deficit conditions, plants typically maintain maximum photosynthetic capacity and quantum yield when measured under saturating light and high CO₂ concentrations. Moreover, photosynthetic performance generally recovers rapidly upon rehydration (Hurry et al. 2005). Prolonged dehydration in C3 plants disrupts multiple physiological processes, with photosynthesis being one of the most severely affected. This inhibition is largely due to reduced CO₂ availability, involving both stomatal and non-stomatal limitations (Liu and Yang 2020). The extent of these effects depends on the duration and severity of stress, as well as species-specific responses (Bhattacharya 2021).

Potato exhibits pronounced sensitivity to water deficit, primarily owing to its shallow root system and substantial water requirements during the tuberization stage. Drought stress significantly impacts tuberization, reducing both tuber yield and quality. One of the primary physiological effects of water deficit in potatoes is the disruption of carbohydrate translocation from source leaves to developing tubers, resulting in starch accumulation in the leaves rather than in the tubers (Aliche et al. 2018). From a biochemical perspective, water deficit in potato plants affects starch metabolism by modulating the expression and enzymatic activity of key starch

biosynthetic enzymes, including ADP-glucose pyrophosphorylase (AGPase) and various starch synthases. These alterations result in changes to the size, composition, and physicochemical characteristics of starch granules, thereby influencing their functional properties in both industrial applications and culinary uses. Water stress also enhances the accumulation of secondary metabolites, including phenolic compounds and flavonoids, which may contribute to stress tolerance but can negatively influence tuber flavor and processing quality (André et al. 2009). Starch consists predominantly of two glucose polymers: amylose, a mostly linear molecule formed by α -1,4 glycosidic linkages, and amylopectin, a highly branched polymer composed of both α -1,4 and α -1,6 linkages. The proportion of these components determines key physicochemical properties, such as gelatinization, retrogradation, and digestibility. Additionally, granule morphology, crystallinity, and molecular organization play crucial roles in defining starch functionality (Nazarian-Firouzabadi and Visser 2017). Starch composition and granule structure are largely regulated by genetic mechanisms, including the expression of key enzymes such as granule-bound starch synthase for amylose synthesis and starch branching enzymes for amylopectin branching (Semeijn et al. 2024). The amylose–amylopectin ratio is a critical factor influencing starch physicochemical properties (Xu et al. 2024). This ratio affects starch digestibility and rheological properties, which are essential for its application in food and industrial products. A high amylose content is generally associated with increased resistance to digestion and enhanced mechanical properties, making it a valuable component in the creation of new materials based on starch (Varghese et al. 2023). Moreover, the extent of branching and the proportion of long amylose chains are critical determinants of the structural organization and thermal stability of starch granules (Tian et al. 2024).

Environmental conditions such as water availability, temperature, and soil nutrient levels significantly influence starch biosynthesis and quality. Water stress, for instance, has been shown to alter starch accumulation patterns and the amylose–amylopectin ratio, thereby affecting gelatinization properties (Rudack et al. 2017). The significance of starch in potatoes is assessed in terms of both quantity and physicochemical properties (Vasanthan et al. 1999). Given that potato tubers constitute the primary harvested organ, they may contain up to 25% starch on a fresh weight basis (Bertoft and Blennow 2016). The ratio between amylose and amylopectin plays a pivotal role in defining the physicochemical behavior of starch, directly influencing its functional performance under processing conditions and determining its applicability across food and non-food industries. However, the industrial separation of these two components is costly and generates a substantial amount of wastewater. Therefore, potato cultivation is influenced by changes in the proportion of both starch components, expanding the potential applications of starch in various industries, such as the food sector and the production of biodegradable materials with varying degrees of degradation, including protective packaging, films, and fibers (Šimková et al. 2013). Meise et al. (2019) highlight that agricultural practices, such as irrigation and soil fertilization, significantly influence the starch composition in potato tubers. Water deficit and improper nitrogen supply in the soil affect enzymatic activity during starch biosynthesis, leading to modifications in granule size and digestibility.

Starch plays a fundamental role in food processing as a thickening, stabilizing, and texturizing agent. Modified starches with optimized gelatinization and retrogradation properties enhance food texture, shelf life, and digestibility (Ahmad et al. 2024). High-amylose starches are particularly important in the development of resistant starch, which offers health benefits (Zhou et al. 2024). Beyond the food industry, starch serves as a key raw material for biodegradable plastics, bioethanol production, and pharmaceutical formulations (Fahmi and Syduzzaman 2024). The growing demand for sustainable materials has driven research on starch-based biopolymers, highlighting the need for starch with specific physicochemical properties (Sultan et al. 2024). Thirty-four European potato cultivars for starch production were subjected to water deficit stress in a field experiment. Water deficit reduced starch yield by 55%, with the highest physiological sensitivity observed during flowering. Starch synthesis was influenced by genotype and the genotype $\times$ treatment interaction. Adaptation involved enhanced membrane stability and increased osmolality due to the accumulation of soluble sugars (Rudack et al. 2017). Grudzińska et al. (2022) investigated the impact of water stress on sugar accumulation and the respiration rate of tubers in two potato varieties. Plants were grown under full irrigation, and two drought regimes (continuous during tuberization and intermittent) were stored at 5 °C and 8 °C for up to 164 days. The drought-sensitive cultivar ‘Cekin’ exhibited higher accumulation of glucose and fructose compared to the drought-tolerant cultivar ‘Tajfun’, irrespective of the type of drought stress imposed. Water deficit stress increased reducing sugars and respiration rate, with a more pronounced effect under intermittent drought conditions. The resistant variety exhibited lower glucose accumulation after prolonged storage at 8 °C.

Physiology and Biochemistry of Potato Starch under Water Deficit

Photosynthesis, a fundamental physiological process for plant growth and development, is highly susceptible to the effects of water deficit stress. Chauhan et al. (2023) emphasized that this vital metabolic process is significantly altered under such stress conditions. Water deficiency disrupts the plant water balance (Dey et al. 2022), lowering soil water potential, which in turn affects plant water potential. As a result, plant's initial response to water deficit stress is to reduce transpiration by closing their stomata (Zuo et al. 2025). Stomatal openings regulate both CO₂ and water in plants. The closure of stomata limits water loss but also reduces CO₂ uptake and the transport of non-structural carbon (NSC) (Wang et al. 2024), a critical component of photosynthesis. This leads to carbon starvation, further affecting numerous other processes (Jha 2024). During drought stress, ATP/NADPH and carbohydrate reserves are redirected to support stress-responsive metabolic processes. This reallocation reduces the availability of these energy molecules for primary physiological functions, resulting in a carbon imbalance that contributes to growth inhibition and impaired respiration under mild to moderate water deficit conditions (Kubota 2020; Foyer and Hanke 2022). Under more severe or prolonged drought, additional metabolic adjustments further suppress photosynthetic activity (Heldt and Piechulla 2021).

Several studies have demonstrated that stomatal closure constitutes the primary physiological response of plants to water deficit, leading to decreased net CO₂ assimilation and a consequent reduction in photosynthetic performance (Aslam et al. 2024; Liu et al. 2025; Visentin et al. 2025) (Fig. 1). Under moderate water deficit, when leaf water potential remains above -1 MPa, photosynthetic efficiency is relatively preserved. However, as water potential declines further, photosynthetic activity is progressively inhibited (Gao et al. 2025). The reduction in photosynthesis under drought conditions is not solely attributed to stomatal limitations. Hajiboland et al. (2017) highlighted the contribution of non-stomatal factors, including impaired CO₂ fixation due to alterations in the activity of Calvin cycle enzymes, compromised membrane integrity, and diminished ATP synthesis. These disruptions hinder the regeneration of ribulose-1,5-bisphosphate (RuBP) and reduce the catalytic efficiency of Rubisco. In parallel, water deficit interferes with the regeneration of NADP⁺, promoting electron leakage and over-reduction of the photosynthetic electron transport chain (Krieger-Liszkay and Kirilovsky 2022). Moreover, drought stress induces structural and functional damage to the oxygen-evolving complex of photosystem II (PSII), resulting in a decline in the number of active PSII reaction centers and reduced chlorophyll fluorescence (Vetoshkina et al. 2023). Under severe or prolonged water deficit, protein degradation further limits Rubisco activity and abundance, exacerbating the inhibition of CO₂ assimilation and contributing to substantial impairment of PSII function (Feller 2016).

Water stress can significantly alter the synthesis and degradation of starch in tubers, affecting its quality and functionality for various industrial and food

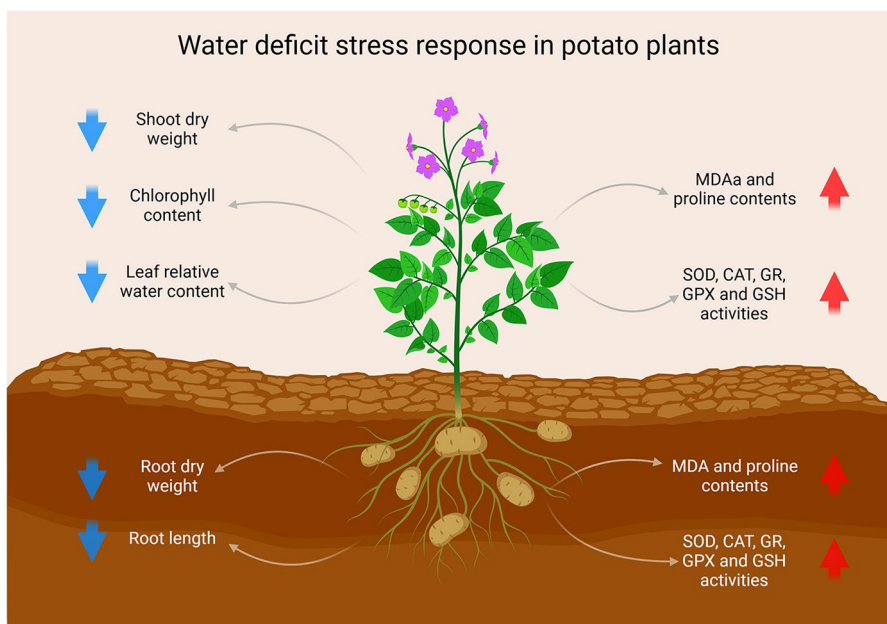


Fig. 1 Water deficit stress response in potato plants

applications. These effects are closely related to changes in carbohydrate metabolism and the enzymatic activity involved in starch synthesis and degradation (Kang et al. 2021). Water deficit induces significant changes in carbohydrate metabolism, affecting the translocation and deposition of sucrose and starch in tubers. During water restriction, there is a reduction in photosynthesis, and consequently, in the production of assimilated carbohydrates. The reduced availability of sucrose decreases starch synthesis, as sucrose serves as the primary substrate for the generation of ADP-glucose, an essential precursor in starch biosynthesis. Additionally, there is an increase in starch hydrolysis to provide energy and carbon for plant survival under adverse conditions (Dong and Beckles 2019). Water stress impacts starch synthesis and degradation, reducing its accumulation in tubers and altering its structure. The rate of starch synthesis decreases under drought due to the reduced activity of key starch metabolism enzymes. Additionally, the amylose-amylopectin ratio may be affected. Under certain conditions, an increase in amylose content can occur, which may impact the rheological properties of starch, making it less desirable for specific industrial applications (Bahaji et al. 2014). Enzymes involved in starch metabolism are highly sensitive to water deficit. ADP-glucose pyrophosphorylase (AGPase), the key regulatory enzyme in starch synthesis, exhibits reduced activity, limiting ADP-glucose formation and consequently starch deposition. Additionally, the activity of amylases (α -amylase and β -amylase), responsible for starch degradation, may increase under water stress, promoting the hydrolysis of stored starch to sustain the plant's energy metabolism. In addition, enzymes such as starch synthase and starch-branching enzyme (SBE) often exhibit downregulated expression under water deficit conditions, thereby influencing the structural assembly and branching pattern of the resulting starch polysaccharides (Pathrap et al. 2019).

Reduction in photosynthesis affects the synthesis and translocation of photo-assimilates, impacting energy availability for growth and tuber formation (Ierna and Mauromicale 2018). Water deficit stress reduces leaf expansion and biomass accumulation, delaying tuber initiation and decreasing both tuber size and number. Ibrahim et al. (2023) evaluated 29 potato genotypes under field drought conditions, observing variations in plant height, leaf temperature, leaf area index, tuber yield, and dry matter content. Ten genotypes exhibited drought tolerance, whereas the others were susceptible. These resilient genotypes may contribute to potato breeding for enhanced drought tolerance and food security in Turkey. Banik et al. (2016) assessed drought acclimation in three potato genotypes with varying levels of tolerance. Short-term acclimation did not significantly affect tuber weight and number under water stress. Water conservation varies depending on genotype and treatment, highlighting the importance of stem. When subjected to water deficit with intact leaves, the 'Vigor' and 'Russet Burbank' genotypes retained more leaf water compared to the drought-sensitive Fv12246-6 genotype. Ibrahim Ibrahim et al. (2024) evaluated 29 potato genotypes under water deficit stress, analyzing morphophysiological traits, and yield characteristics. Ten lines demonstrated greater tolerance, with a smaller reduction in yield. The heritability of 77% indicates low environmental influence on the selection of high-yielding tubers. (Zhang et al. 2018) investigated drought hardening, which improved water stress resistance in potato seedlings by preserving photosynthesis, relative water content (RWC), and reducing oxidative damage. The

treatment increased antioxidant activity, ABA levels, proline, and soluble sugars, while also modifying stomatal structure and leaf microstructure, reducing transpiration, and improving water use efficiency (WUE). These physiological and morphological adaptations enhance potato drought tolerance. A total of 56 potato genotypes were subjected to water stress conditions. Six genotypes were selected for physiological and morphological analysis: Bannock Russet and Nipigon (tolerant), Onaway and Denali (moderately tolerant), and Fundy and Russet Norkotah (susceptible). Immediate WUE was higher in tolerant genotypes, associated with lower suppression of photosynthesis, transpiration, and stomatal conductance. Leaf protein content also varies among genotypes. These parameters may serve as criteria for selecting potato cultivars with greater drought tolerance (Gervais et al. 2021).

Alvarez–Morezuelas et al. (2022) evaluated the physiological and productive responses of six potato varieties (Agata, Agria, Atlantic, Kennebec, Monalisa, Sante, and Zorba) under water deficit conditions in a greenhouse. Stomatal conductance and water potential exhibited the greatest variations between drought conditions. Among the varieties, Monalisa demonstrated the highest resilience in tuber production under stress. The authors concluded that physiological responses could aid in identifying drought-tolerant genotypes for breeding programs. The physiological and biochemical responses of the Atlantic potato variety to heat stress, water deficit, and their combination were assessed over 18 days. Combined stress had the most significant impact, reducing photosynthetic efficiency and chlorophyll content, while leaf thickness and antioxidant activity initially increased. The accumulation of osmotic solutes varies depending on the intensity and duration of stress. The results indicate that potatoes adjust their leaf structure, antioxidant defense, and osmotic mechanisms to tolerate adverse conditions (Wang et al. 2024). Effects of pre-exposure to water deficit on the physiological response of the ‘Favorita’ potato cultivar were investigated. Pre-exposure to drought increased water use efficiency, reduced transpiration, and promoted anatomical modifications, such as a higher number of vascular bundles and stomatal adjustments. Additionally, it enhanced dry matter translocation and maintained cambial activity, resulting in a lower impact on yield under drought conditions. The findings suggest that drought priming at the seedling stage can strengthen potato tolerance to water stress, improving both photosynthetic and productive performance (Lv et al. 2024).

Zhang et al. (2022) evaluated the interactions between vapor pressure deficit and soil drying, which affect potato physiology by reducing gas exchange, shoot biomass, and leaf water potential while increasing abscisic acid levels and WUE. High vapor pressure decreases stomatal conductance and raises the soil moisture threshold required to reduce transpiration. The study’s findings contribute to the improvement of physiological models and irrigation strategies in arid climates. Aliche et al. (2020) evaluated multiple potato cultivars with contrasting responses to drought and identified stomatal conductance and chlorophyll content as critical determinants of carbon assimilation and distribution. Under water deficit conditions, the expression of genes related to sucrose metabolism, including sucrose synthase, was significantly modulated, suggesting these pathways as promising targets for the genetic enhancement of drought tolerance in potato. Yao et al. (2023) investigated the relationship between hydraulic lift and drought tolerance in four potato

cultivars. Tolerant cultivars (Longshu NO.3 and Xindaping) exhibited greater water redistribution, higher biomass, and lower oxidative stress accumulation, whereas the sensitive cultivars (Favorita and Atlantic) showed the opposite responses. Increased stress inhibited hydraulic lift and reduced soil water content and biomass. Hydraulic redistribution was associated with root growth and drought resistance. Fifteen potato genotypes were evaluated under full irrigation and water deficit, identifying the harvest index (HI) as a highly heritable trait (0.98) for indirect selection (Lozano-Isla et al. 2024). The SPAD index proved to be a sensitive tool for early stress detection. Drought-tolerant genotypes, such as CIP392797.22, CIP397077.16, CIP398190.89, CIP398208.219, and CIP398208.620, prioritized tuber production over biomass accumulation while maintaining high photosynthesis and water use efficiency. Hormonal signaling changes under stress conditions further affect tuberization dynamics (Wagg et al. 2021). Limited water availability alters carbohydrate partitioning, often reducing starch accumulation in tubers due to impaired sugar transport and enzymatic activity in starch biosynthesis. A comprehensive understanding of these interactions is crucial for developing drought-resistant potato varieties (Acevedo et al. 2023).

Molecular Aspects of Starch Metabolism in Potatoes under Water Deficit

In *Solanum tuberosum*, signaling molecules play a central role in mediating the plant's responses to abiotic stresses, promoting the integration of external signals with physiological and biochemical mechanisms for adapting to adverse environmental conditions (Kesawat et al. 2023). These molecules help coordinate and regulate the plant's stress response mechanisms. Several key functions of signaling molecules in potatoes under abiotic stress have been identified (Li et al. 2025). The use of molecular markers in potato genetics has revolutionized genotypic characterization and accelerated the development of improved cultivars. Numerous markers associated with agronomically relevant traits have been identified and mapped across the 12 potato chromosomes, with particular emphasis on pathogen resistance genes, which play a central role in crop adaptability (Mir et al. 2024). High precision technologies, such as competitive allele-specific PCR, high-resolution melting analysis, SNP arrays, genotyping-by-sequencing, and genome-wide association studies, have enhanced the detection of specific markers, enabling a more robust identification of resistance genes (*R* genes) associated with traits of interest (Islam et al. 2024).

Zhang et al. (2014) analyzed the transcriptome of *Solanum tuberosum* under drought conditions using RNA-Seq and identified 7,284 expressed genes, among which 842 were upregulated and 494 were downregulated. The differentially expressed genes were categorized into 89 functional groups and mapped to 21 KEGG pathways, highlighting the activation of gene networks associated with stress perception and adaptive responses. These findings provide a molecular basis for understanding drought tolerance mechanisms in potatoes. Overexpression of the transcription factor *StERF94* in transgenic potato enhances tolerance to drought, heat, and combined stresses by promoting water and chlorophyll retention, activating antioxidant enzymes, and increasing proline accumulation. The expression of

antioxidant genes such as *CuZnSOD*, *FeSOD*, *CAT1*, and *CAT2* was significantly upregulated under abiotic stress conditions, reinforcing the involvement of *StERF94* in the transcriptional regulation of stress-responsive pathways (Charfeddine et al. 2023). In parallel, twenty-one commercial *Solanum tuberosum* cultivars, representing the genetic diversity of the Middle East, were assessed for drought tolerance through integrated in vitro and field evaluations. Drought stress markedly reduced vegetative growth and tuber yield across genotypes, with considerable variability in stress responses. Cluster analysis categorized the genotypes into three distinct groups: five drought-tolerant cultivars, eleven moderately tolerant, and five sensitive. In tolerant cultivars, upregulation of key stress-related genes *DRO*, *ERECTA*, *ERF*, *DREB*, and *StMYB* was associated with enhanced stomatal conductance and superior tuber yield (Zaki and Radwan 2022).

Kawamoto et al. (2024) analyzed the transcriptomic responses of seed potatoes subjected to drought stress. Half of the plants were maintained under daily irrigation, while the other half were exposed to simulated drought conditions. Transcriptomic analysis revealed 423 downregulated and 197 upregulated genes in water-deficient plants compared to the control group. The differentially expressed genes were associated with heat stress response, cell wall modification, and phytosterol metabolism. *TAS14* protein, known to be induced by abscisic acid and environmental stress, was consistently upregulated in all drought-stressed lines. Its localization in the nucleus and plasma membrane was confirmed in a mutant line tagged with mCherry. Wellpott et al. (2023) investigated the expression of eight candidate genes for early drought stress detection in six potato genotypes cultivated for starch extraction. After seven and 14 days of drought, reductions in shoot biomass and root growth were observed. Three genes *INH1*, *POD*, and *SBT1.7* exhibited consistent differential expressions, with *INH1* emerging as a potential biomarker for early drought stress detection in potatoes. Additionally, the *StMAPK11* gene plays a crucial role in drought deficit resistance in potatoes (*Solanum tuberosum*) (Zhu et al. 2021). Expression of *StMAPKs* varied across different tissues and was modulated by abiotic stresses and plant hormones, with *StMAPK11* being strongly induced under drought stress. The overexpression of *StMAPK11* promoted potato growth under water deficit by enhancing antioxidant activity (*SOD*, *CAT*, *POD*), photosynthesis, and proline and MDA levels, while its downregulation reduced stress tolerance.

StCDPK13 gene from potato was cloned, and its overexpression increased drought tolerance (Bi et al. 2024). Transgenic potato plants exhibited improved growth, higher antioxidant activity, and lower accumulation of ROS and MDA. Additionally, they displayed reduced stomatal opening and decreased water loss, suggesting that *StCDPK13* plays a protective role against drought stress. Metabolic and transcriptomic analyses of four potato cultivars with differential drought tolerance revealed alterations in metabolites and regulatory genes, including those associated with heat stress response and abscisic acid signaling. Tolerant cultivars exhibited specific gene expression and metabolic patterns, suggesting an interaction between pathogen resistance and drought tolerance, potentially influenced by stomatal closure and CO₂ limitation (Sprenger et al. 2016). *NHX* genes in potatoes (*Solanum tuberosum* L.) were characterized at the genomic level, identifying 25 members with differential expression across specific tissues and under abiotic

stress. The induction of these genes under water deficit conditions suggests their role in water stress tolerance, making them potential targets for genetic improvement in potato breeding (Yihong et al. 2024). The role of miR160a-5p in the response of potato to water and heat stress, both individually and in combination, was investigated by Şanlı and Öztürk Gökçe (2021). Unica and Russet Burbank cultivars were used, and the overexpression of miR160a-5p led to the suppression of the *ARF16* gene, improving physiological and biochemical responses, with decreased accumulation of H_2O_2 and increased proline content under water deficit. The modulation of the auxin response factor pathway conferred enhanced tolerance to abiotic stress. These findings contribute to the understanding of the role of miR160a-5p in potato adaptation to adverse conditions. Overexpression of the *AtDREB1A* gene in transgenic potato improved tolerance to water stress, resulting in enhanced biomass synthesis, increased proline content, and reduced malondialdehyde (MDA) levels. Transcriptomic analyses revealed the differential expression of 533 genes associated with ABA metabolism, kinase proteins, cytochrome P450, and heat shock proteins, indicating their role in the water stress response (Jia et al. 2023).

Overexpression of the *StRFP2* gene in transgenic potatoes enhances plant growth and drought stress tolerance. *StRFP2*, located in the cell membrane and cytoplasm, showed increased expression under water stress. Transgenic plants exhibited higher biomass, water retention, proline accumulation, and catalase (CAT) activity, while MDA content was reduced compared to the wild type (Qi et al. 2020). Water stress and heat affect translation and transcription in potatoes, impacting the translational efficiency of key genes. 41.58% (water stress) and 27.69% (heat stress) of the differentially expressed genes were shared between these conditions, indicating independent regulation. The uORF sequences influence the translation of mORFs, revealing new layers of molecular control in stress response (Jian et al. 2023). *StMAPKK5* gene regulates the potato stress response, being induced by water stress and salinity. Its overexpression improves water retention, antioxidant enzyme activities, and proline levels, while reducing MDA (Luo et al. 2024). Located in the nucleus, cytoplasm, and cell membrane, it interacts with *StMYB19*, *StZFP8*, *StPUB*-like, and *StSKIP19*, playing a crucial role in stress tolerance and potato development. Pescador-Dionisio et al. (2024) investigated the impact of anthocyanin accumulation on potato's response to drought stress in three genotypes with differential pigmentation. Bleu et and DAR170 varieties, with higher anthocyanin content, showed inhibited stem growth under stress, suggesting an anthocyanin-mediated resilience mechanism. The analysis of *stu-miR156a* expression and its target, *StSPL9*, indicates that the miR156-SPL9 module regulates potato development and its response to water deficit by adjusting anthocyanin biosynthesis.

Qin et al. (2022) investigated the response to water deficit stress in two potato genotypes with different root depths (C119 and C16) through transcriptomic analysis. Key metabolic pathways, including hormonal signaling and MAPK, were identified, along with differences in the transcriptional response time between the genotypes. Results highlight candidate genes for improving drought tolerance in potato. The family of calcium-dependent protein kinases (CDPKs) in potato was studied through comparative genomics and differential expression analysis in varieties with varying levels of drought tolerance. A total of 25 CDPKs were identified, of which

13 exhibited collinearity and promoters responsive to environmental and hormonal stresses. RNA-seq and qPCR analysis revealed distinct expression patterns under drought, highlighting StCDPK3 and StCDPK23 as potential targets for functional studies (Bi et al. 2021).

Mitigation and Improvement Strategies

Potato improvement strategy involves decisions regarding germplasm, propagation methods, disease resistance, and the use of biotechnology. Genetic knowledge of the crop has advanced significantly, enabling the development of cultivars adapted to environmental challenges and population growth. Adapting potato cultivars to various environments and their specific applications requires assessing genotype $\times$ environment interactions, which can be analyzed using tools like principal component analysis. Selection in distinct environments influences performance under other conditions, necessitating specific breeding strategies. Studies indicate that selection in environments similar to cultivation areas optimizes adaptation, supporting regional breeding programs despite the commercial interest in broadly adaptable cultivars. Plant biotechnology has had a significant impact on agriculture, with the global cultivation of genetically modified (GM) crops growing rapidly. The early generations of these crops focused on single-gene modifications, but recent advancements point toward a future with more complex manipulations. Potato is an ideal model for *Agrobacterium*-mediated transformation, micropropagation, and somatic embryogenesis, facilitating its genetic improvement. However, scientific and ethical challenges, such as gene flow and the safety of introduced traits, drive research into safer technologies, including clean genes and environmental impact.

Exogenous chitosan enhances drought tolerance in potatoes by reducing oxidative damage, increasing antioxidant activity, and regulating osmoprotectants (Jiao et al. 2012). A concentration of 100 mg L⁻¹ was the most effective in recovery after rehydration, highlighting the potential of exogenous chitosan as a strategy to mitigate water stress. Uniconazole alleviates the effects of water deficit stress in potatoes, improving photosynthesis, reducing oxidative stress, and increasing antioxidant activity and osmoprotective compounds (Ding et al. 2024). Cultivar Kexin No. 1 exhibited greater recovery compared to Atlantic, emphasizing the potential of uniconazole in enhancing drought tolerance. Effects of a short-term (2-week) period of water deficit and excess were evaluated across four potato growth stages (germination, vegetative, tuberization, and bulking), with a simultaneous assessment of tuber yield and quality. The impact of drought on germination was minimal but persistent. These findings emphasize the importance of supplemental irrigation and suggest that effective water management strategies can alleviate drought effects and optimize production in well-drained systems (Wagg et al. 2021).

ZnO nanoparticles (0, 50, and 100 mg L⁻¹), and SiO₂ nanoparticles (0, 25, and 50 mg L⁻¹) on potato yield and quality under different levels of water deficit (100%, 75%, and 50% ETc) were evaluated (Seleiman et al. 2023). Drought reduced yield and some quality parameters but increased starch and soluble solids content. Exogenous application of nanoparticles significantly improved yield and tuber quality,

with ZnO at 100 mg L⁻¹ proving to be the best strategy for mitigating the impact of water stress in arid regions. Al-Selwey et al. (2023) assessed the exogenous application of ZnO and SiO₂ nanoparticles, demonstrating improvements in potato physiology, yield, and water use efficiency under drought conditions. Water stress reduced physiological parameters and yield but increased proline content and efficient water use. Treatment with 100 ppm ZnO nanoparticles was the most effective, enhancing gas exchange, relative water content, and photosynthetic pigments. These findings underscore the potential of nanoparticles to mitigate the impact of water deficit in arid regions. Meise et al. (2018) conducted a two-year experiment with 17 potato cultivars to evaluate genotypic differences in osmotic adjustment and biochemical responses to drought stress under two nitrogen levels. Drought stress rapidly reduced leaf osmotic potential, while increasing nitrogen, protein, and proline content, and decreasing the nitrogen-protein/N Kjeldahl ratio. Total soluble sugars initially increased but returned to control levels under high nitrogen availability. Elevated nitrogen supply promoted proline synthesis and the nitrogen-protein/N Kjeldahl ratio in the short term. Genotypic differences highlight the potential for selecting cultivars with better physiological responses to drought stress. Gene expression was studied in four potato cultivars under different levels of drought stress to identify drought-tolerant genotypes (Çelik 2024). Expression of 10 genes was analyzed using RT-qPCR in plants subjected to 100%, 75%, 50%, and 25% field capacity. Genes most associated with drought tolerance were *StRD22*, *StERD7*, *MYB*, *SuSy*, *ABC*, and *StDHN1*, while *StHSP100* showed the lowest expression. Orwell cultivar stood out in the expression of *StRD22*, while Vr808 and Brooke exhibited higher overall gene expression. These genotypes are promising candidates for breeding programs targeting drought resistance.

Aliche et al. (2022) employed RNA-Seq to assess transcriptomic changes in three potato cultivars under water deficit conditions. Cultivars, Lady Rosetta and Biogold, exhibited a significantly higher number of differentially expressed genes compared to the sensitive cultivar, Hansa. Gene expression profiles mirrored the phenotypic responses to drought, with upregulation of genes involved in carbohydrate metabolism, flavonoid biosynthesis, lipid metabolism, heat shock proteins, and secondary metabolite pathways in Biogold and Lady Rosetta. Prolonged water stress led to a reduction in the number of differentially expressed genes (DEGs) in Biogold and Hansa, whereas Lady Rosetta maintained high gene expression and tuber production, suggesting a more robust drought tolerance mechanism. These findings indicate that resilience to water deficit is associated with the coordinated regulation of multiple genetic pathways. In complementary research, Wang et al. (2023) investigated the effects of foliar application of chelated calcium in two potato cultivars exhibiting contrasting responses to water stress. The treatments reduced chlorophyll loss, minimized oxidative damage, and improved photosynthetic, anatomical, and biochemical parameters, particularly in the “Atlantic” cultivar. Activation of *StCDPK* genes was observed, along with increased antioxidant activity, resulting in higher tuber weight and quality. The results suggest that foliar calcium spraying is a promising strategy to enhance water stress tolerance and potato yield. Potato variety Jancko Sisu Yari exhibited water stress memory by regulating genes involved in photosynthesis, metabolism, and signal transduction during drought, rehydration,

and subsequent stress (Chen et al. 2019). Rehydration reversed part of the gene expression, while drought hardening promoted resilience through the persistent regulation of key genes. Thirty-six DNA binding with one finger (Dof) genes in potato, with five Cycling Dof Factors (CDFs) potentially regulating the stress response, were identified (Jin et al. 2024). Expression analysis revealed differences between contrasting cultivars under water stress. A regulatory network mediated by lncRNA was constructed, providing a foundation for potato genetic improvement. Field and greenhouse trials identified 45 genomic regions linked to physiological and morphological traits under water deficit. The results highlight the polygenic control of water stress tolerance and its potential for genetic improvement of potato (Khan et al. 2015).

Conclusion

Understanding the effects of water deficit on the physiology and biochemistry of potato starch metabolism is crucial for enhancing tuber yield and quality under water stress conditions. Strategies such as genetic improvement and the application of biostimulants have shown potential in mitigating the negative impacts of water deficit. Genetic and transcriptomic characterization of tolerant varieties may lead to the development of more resilient lines. Advanced genetic improvement approaches, including molecular and genomic-assisted techniques, can accelerate the development of potato varieties with enhanced tolerance to abiotic stresses. Techniques such as optimized water management and the application of nanoparticles can reduce the impacts of drought and improve water use efficiency. This multidisciplinary approach is essential for ensuring the sustainability of potato production in the face of climate change and the growing global demand for foods.

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Declarations

Conflict of interest The authors declare no competing interests.

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