



Review

Research Progress on Physiological, Biochemical, and Molecular Mechanisms of Potato in Response to Drought and High Temperature

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Abstract: With the intensifying global warming trend, extreme heat and drought are becoming more frequent, seriously impacting potato yield and quality. To maintain sustainable potato production, it is necessary to breed new potato varieties that are adaptable to environmental changes and tolerant to adversity. Despite its importance, there is a significant gap in research focused on the potential mechanisms of potato resistance to abiotic stresses like drought and high temperatures. This article provides a comprehensive review of the recent research available in academic databases according to subject keywords about potato drought tolerance and high temperature tolerance with a view to providing an important theoretical basis for the study of potato stress mechanism and the selection and breeding of potato varieties with drought and high-temperature resistance. The suitable relative soil moisture content for potato growth and development is 55% to 85%, and the suitable temperature is 15 °C to 25 °C. The growth and development of potato plants under drought and high-temperature stress conditions are inhibited, and plant morphology is altered, which affects the process of potato stolon formation, tuberization and expansion, ultimately leading to a significant reduction in potato tuber yields and a remarkable degradation of the market grade of tubers, the specific gravity of tubers, and the processing quality of tubers. In addition, stress also adversely affects potato physiological and biochemical characteristics, such as reduction in root diameter and leaf area, decrease in net photosynthetic rate of leaves, production of reactive oxygen species (ROS), and increase in membrane lipid peroxidation. In addition, various types of genes and transcription factors are involved in the response to drought and heat at the molecular level in potato. This paper illustrates the effects of stress on potato growth and development and the molecular mechanisms of potato response to adversity in detail, which is intended to reduce the damage caused by drought and high temperature to potato in the context of global warming and frequent occurrence of extreme weather to ensure potato yield and quality and to further safeguard food security.

Keywords: *Solanum tuberosum*; abiotic stress; adversity tolerance; response mechanisms; climate warming



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1. Introduction

Global warming, now a paramount environmental issue, has led to a notable rise in global surface temperature. Specifically, an increase of 1.1 °C was observed from 2011 to 2020 compared to the period from 1850 to 1900, as reported by the IPCC in 2022 [1]. The global net anthropogenic greenhouse gas emissions in 2019 reached approximately 590 ± 6.6 billion tons of carbon dioxide (CO₂) equivalent, marking a 12% and 54% increase from 2010 and 1990, respectively. The decade from 2010 to 2019 saw an average emission

of 560 ± 6 billion tons, 9.1 billion tons per year higher than the previous decade [2]. This ongoing rise in emissions is driving significant changes across the atmosphere, ocean, cryosphere, and biosphere, influencing extreme weather and climate events globally. These changes are adversely affecting both nature and humanity, leading to losses and challenges, such as the notable reduction in crop yields [3]. The ongoing greenhouse gas emissions could exacerbate these effects, heightening biotic and abiotic stress on crops [4,5]. Predictions suggest a further global temperature rise, with the potential to reach 1.5°C between 2021 and 2040, intensifying various hazards [1,6]. Expected temperature increases may cause higher water losses due to evapotranspiration, leading to soil moisture limitations and agricultural drought [7,8]. Warming trends are likely to affect perennial crop and weed growth, pathogen and pest distribution, and host–pathogen relationships [9,10]. Although higher atmospheric CO_2 levels could boost yields for some crops [11,12], the adverse effects of heat and water scarcity could negate these benefits [13]. Furthermore, the challenges of rising temperatures and drought are compounded by the growing global population. The World Population Prospects 2022 report anticipates a peak of 10.4 billion people in the 2080s, necessitating a significant increase in food production to meet nutritional needs [14]. This challenge is further complicated by diminishing agricultural land due to desertification and urbanization, as well as increased demand for biofuel crops [15,16].

The potato (*Solanum tuberosum* L.), a tuberous crop in the Solanaceae family, is one of the world's leading crops in terms of both yield and economic value, following corn, rice, and wheat [17,18]. Originally from South America, potatoes are now cultivated in over 150 countries, feeding more than 1 billion people worldwide [19,20]. They are produced on more than 20 million hectares, with a total global production of 359 million tons in 2020 [20]. The potato is cultivated on all continents except Antarctica. Over the past two decades, potato production in developing countries has increased sharply and now exceeds that in developed countries, highlighting the growing significance of the potato as a staple crop in meeting the needs of a rising population [21,22]. China is the world's largest producer of potatoes. In recent years, China's potato production has reached nearly 90 million tons, accounting for about a quarter of the world's total [23,24]. More than 60% of China's potato is grown in arid and semi-arid areas, and high temperatures and drought stresses cause great losses [25]. It is urgent to breed new potato varieties that are adapted to environmental changes and resilient to adversity. Potatoes, often grouped with vegetables rather than grains, are rich in nutrients and consumed in various forms. Potato tubers are low in fat, high in fiber, and provide a healthy source of carbohydrates, antioxidants, proteins, vitamins, and minerals [26,27]. Beyond direct consumption, potatoes serve as vital animal feed and an industrial raw material for starch, glucose, dextrin, and spirit production [28]. Photosynthesis is crucial, its products contributing 90–95% of a plant's dry weight and forming the basis for crop yield and energy production [29]. Carbon metabolism refers to a series of physiological and biochemical processes in which plants assimilate inorganic CO_2 into organic carbohydrates in photosynthesis and dissimilate organic carbon into CO_2 in respiration and photorespiration. Carbon metabolism includes both photosynthetic carbon assimilation and respiration [30]. At present, the dark reaction pathway, that is, the carbon assimilation pathway of a plant, is divided into three categories, which are the C_3 pathway, the C_4 pathway, and the CAM pathway. The C_3 pathway is the basic pathway of carbon assimilation; it can synthesize sugar, starch, and other organic matter. The carbon assimilation pathway of potato is the C_3 pathway. It belongs to C_3 plants, which absorb CO_2 through the stomata and assimilate it into the three-carbon compounds in the chloroplasts [31]. The primary edible and economic part of the potato is the tuber, with carbohydrates synthesized in leaves through photosynthesis and transferred to stolons, ultimately becoming starch [32,33] (Figure 1). The effective coordination of these processes is critical for tuber productivity and quality. The main abiotic stresses include factors such as heat, drought, high salinity, and nutrient stress, which significantly impact photosynthesis and plant growth, thus leading to a significant reduction in yield and quality [34,35]. Additionally, leaf damage from pests and pathogens can disrupt photosynthesis, further

affecting yield and quality [36,37]. The origin and diversity of potato is attributed to the Andes Mountains. The crop was domesticated 8000 to 10,000 years ago [38,39]. The potato thrives in moderate temperatures, typically between 14 °C and 22 °C, and is sensitive to environmental changes [40]. Its shallow root system limits water transport, making it particularly susceptible to heat and drought, the main uncontrollable factors affecting its growth and yield [41–43]. The impact of high temperatures and drought in plants varies with growth stage, duration, and severity [44]. Climate change poses a significant threat, with predictions of a substantial decrease in potato production by 2055 [45,46]. At the same time, some studies further predict that by mid-century, worldwide potato yields will be reduced by 18–22% due to abiotic and biotic stresses related to climate change [5,33,47]. Therefore, to address these challenges and increase potato production to ensure food security, it is necessary to breed new potato varieties that are adaptable to environmental changes and tolerant to adversity. Despite its importance, there is a substantial gap in research on the underlying mechanisms of potato resistance to abiotic stresses such as drought and high temperature. This paper provides a comprehensive review of recent studies on drought and high-temperature resistance in potato, covering effects on yield and quality, growth, development, physiological, and metabolic alterations, and offers insights into the molecular mechanisms behind this resistance. The findings provide vital insights for future researches on the mechanisms of drought and high-temperature resistance in potato.

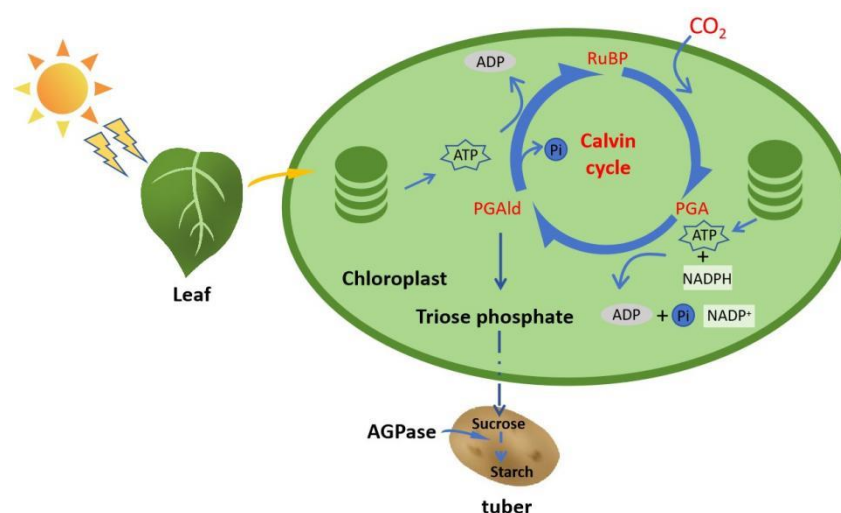


Figure 1. Photosynthetic carbon assimilation and its export to potato tuber. Carbon assimilation pathway of potato is the C_3 pathway, belonging to C_3 plants, which absorbs CO_2 through the stomata and assimilates it into the three-carbon compounds in the chloroplasts. The primary edible and economic part of the potato is the tuber, with carbohydrates synthesized in leaves through photosynthesis and transferred to stolons, ultimately becoming starch.

2. Methodology of the Review

Relevant literature was searched in academic databases and journal websites based on keywords closely related to the topic of this study, which mainly included thematic keywords (e.g., “potato”, “drought”, “high temperature”, “stress”, etc.) to ensure the accuracy and relevance of the search results. Literature was also screened for publication date to ensure that the article was cutting-edge and innovative. During the literature search process, a systematic and comprehensive literature search was conducted for publications cited in the manuscript, and several well-known academic databases were browsed, such as Web of Science, NCBI, CNKI, Scopus, and Google Scholar. In addition, major publishing websites were visited to collect desirable and reliable published materials including articles, reviews, mini-reviews, chapters, and books. The most visited journal websites were MDPI, ScienceDirect, Frontiers, SpringerLink, PubMed, etc. Additional searches were

also conducted from time to time as the study progressed to ensure that the review was always based on the latest scholarship. In selecting publications for inclusion in the study, publications were closely related to the topic of interest, from authoritative journals to conferences, and peer-reviewed to ensure that the data and research methods in the publications were reliable and valid, with priority given to novel and contributing literature. During the literature screening process, some papers were excluded. These papers were not closely related to the research topic and lacked sufficient quality assurance; for instance, they were not peer-reviewed or the reliability of the data was questionable. In addition, some restricted-access literature was excluded to ensure the accuracy and efficiency of the analysis.

3. Drought and Its Impact on Potato

Drought, a prevalent abiotic stress, significantly affects plant growth and productivity, including that of potatoes [48]. Water scarcity hinders the growth, development, and reproductive processes in potato plants (refer to Table 1, Figure 2). Predictive climate models indicate an increased frequency of droughts, attributed to long-term global warming effects [49,50]. The water requirement of potato varies due to diverse factors such as variety, growth stage, cultivation method, and climatic conditions [51]. Crop water demands are commonly expressed in terms of the rate of evapotranspiration (ET) in mm per day or mm per cycle [52]. It was shown that potato requires different amounts of water depending on the date of sowing. Early-sown potato demanded 212.5 mm of water, while late-sown potato demanded 226.7 mm of water [53]. In addition, the relevant studies reported that the yield of potato response to ETcrop (62 to 105 kg/(ha mm)) varied by fertilizer application, and based on the production of 30,000 kg of tubers per hectare with a 1:1 weight ratio of above-ground and under-ground parts and a dry matter weight of 20%, the water demand per hectare was approximately 4200 tons [54,55]. Potatoes are particularly sensitive to drought, with all developmental stages, from seedling emergence to tuber growth, being susceptible to water stress [56].

Table 1. Summary of the effects of drought and high temperature on yield and quality, growth and development, and physiology and metabolism, as well as molecular response mechanism.

Effect of Drought and High Temperature in Potato				
Stress	Yield and Quality	Growth and Development	Physiology and Metabolism	Molecular Response Mechanism
Drought	Reduced tuber yield		Increased leaf SPAD value	
	Reduced the number of tubers per plant		Reduced the tuber dry matter content	
	Reduced yield per plant		Reduced leaf net photosynthetic rate (Pn)	
	Reduced yield per unit area		Reduced transpiration rate (Tr)	
	Reduced setting rate and harvest index		Reduced stomatal conductance (Gs)	
	Induced defects in potato tubers such as tuber hollowing, tuber rupture, internal brown spot, malformation and secondary growth	Changed root length and reduced root diameter size	Reduced leaf area index	Abscissic acid signaling pathway
		Inhibited leaf growth	Changed intercellular CO ₂ concentration (Ci)	MAPK signaling pathway
	Increased the content of α-solanine and α-chaconine alkaloids	Reduced leaf area and the number of green leaves	Reduced carbon accumulation and carbon reactivation	Transcription factors
	Suppressed starch content of tubers		Damaged cell membrane	miRNA
	Affected the tuber market grade, tuber-specific gravity and tuber processing quality		Increased malondialdehyde (MDA) and proline (Pro) content	Other regulatory factors
	Induced sugar end defects		Enhanced permeability of the cell membrane	
			Increased the extent of membrane lipid peroxidation	
			Changed POD SOD and CAT	

Table 1. Cont.

Effect of Drought and High Temperature in Potato				
Stress	Yield and Quality	Growth and Development	Physiology and Metabolism	Molecular Response Mechanism
High temperature	Reduced tuber yield Reduced tuber diameter Reduces the weight of individual tubers Reduced the number of potato tubers Lowed potato quality, such as secondary growth, tuber hollowing, cracking and tuber deformities Increased the basal and apical tuber reducing sugars content Decreased the dry matter content Increased the severity of stem-end chip defects	Hindered the occurrence of stolons Reduced the number of stolons per plant Reduced commercial potato rate Reduced the number of potatoes set Delayed tuberization Increased plant height, Inhibited leaf growth Caused early senescence, and even death	Inhibited carbon transport and carbon dioxide fixation Reduced chlorophyll content Inhibited the rate of dry matter accumulation Inhibit the photosynthesis Reduced leaf net photosynthetic rate (Pn) Inhibited the CO ₂ fixation Increased Tr Decreased Fm and Fv/Fm Inhibited the electron transfer and light energy conversion efficiency of PSII reaction centers Disrupted the composition and structure of the plasma membrane Increased intracellular electrolyte extravasation Increased plasma membrane peroxidation Increased malondialdehyde (MDA) and Pro content Increased CAT, POD and SOD enzyme activities	Heat shock proteins and heat shock factors Transcription factors

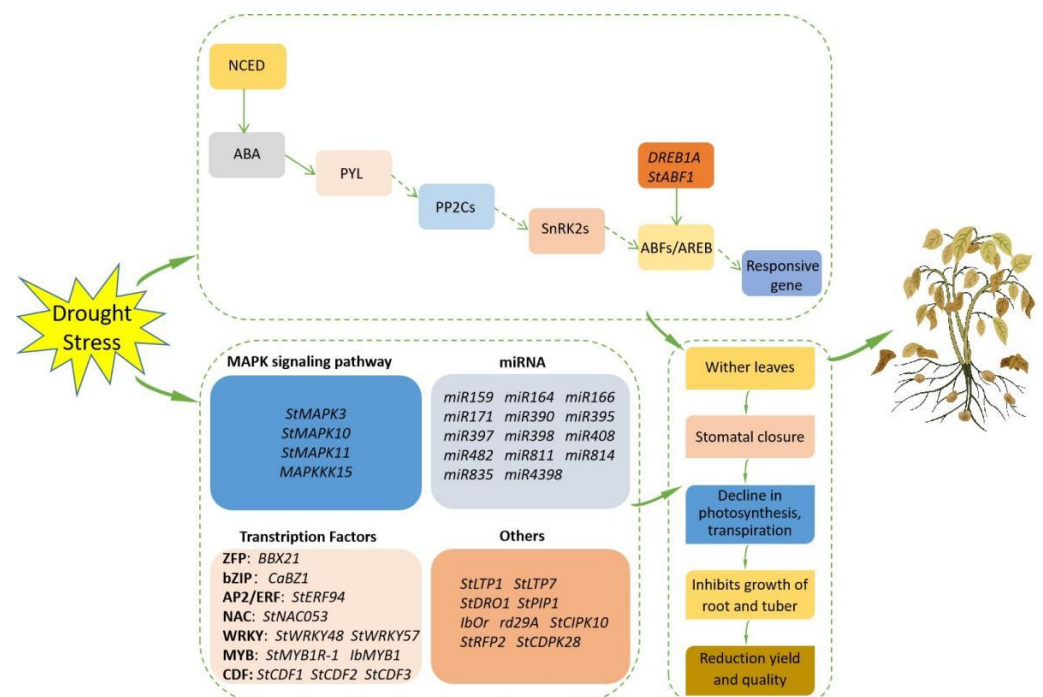


Figure 2. Molecular response mechanisms of potato response to drought stress. These include physiological and biochemical responses triggered by changes in gene expression and metabolic pathways, mainly involving the ABA pathway, the MAPK pathway, transcription factors, miRNA, and other regulatory factors.

3.1. Drought's Effect on Potato Yield and Quality

Potatoes require varying amounts of water at different growth stages. Potato can grow normally at the lower limit of relative soil moisture content of 55% at seedling stage, 76% at tuber formation stage, 77% at tuber expansion stage, and 58% at starch accumulation stage [57]. Drought stress is especially damaging during the tuber setting stage [58]. When relative soil moisture content falls below 85% at the tuber setting stage, both the growth and biological yield of potatoes are adversely affected. This stress significantly reduces yield and quality [59] (Table 1). Moderate to severe drought stress decreases water use efficiency and leaf water potential in potatoes, leading to stomatal closure, reduced photosynthesis, and consequently lower yield and quality [60,61]. Water deficiency can cause up to a 69% loss in potato tuber yield [62]. The extent of drought stress varies among potato varieties and is influenced by the stage of plant growth, duration and severity of the drought [63,64]. Mthembu et al. [64] observed significant growth inhibition across eight different genotypes of potato cultivars under drought conditions, with varying degrees of resistance among them.

Drought stress also impacts tuber number, yield per plant, and overall harvest [65,66] (Table 1). During tuber formation, the effects of drought on potato tuber number and yield are more severe due to the high water and nutrient demands during this time [57]. In a deficit irrigation study on potato, reduced irrigation during tuber expansion period resulted in lower yield and quality [67]. However, mild drought stress can improve net photosynthesis, dry matter accumulation, and tuber quality in tolerant varieties [68–70]. Drought stress compromises tuber quality by reducing fertilizer uptake and induces defects like hollowing, rupturing, and malformation, increasing harmful compounds like α -solanine and α -chaconine [5,35] (Table 1). A survey of dry matter yield of potato tubers under various irrigation regimes by Faradonbeh et al. [71] demonstrated that the starch content of tubers was suppressed under drought stress. Water stress during the tuber expansion period can severely affect the market grade of tubers, the specific gravity of tubers, and the processing quality of tubers [72]. It also causes sugar-end defects in tubers, problematic for the fries and chips industry, leading to undesirable darkening [73–75].

3.2. Drought Stress and Potato Growth

In response to drought, the total root length of potato plants increases, enhancing the plant's ability to access deeper soil water and alleviate stress [76,77]. The changes in the root system response to drought stress vary among potato varieties (Table 1). For example, it was found that in response to drought stress, the roots of drought-tolerant potato varieties increased significantly in length compared to those before stress, while the root length of non-drought-tolerant varieties remained essentially the same, but both drought-tolerant and non-drought-tolerant potato varieties decreased in root diameter size when exposed to drought adversity [78]. Generally, there are significant distinctions in the size of the root system and its structure in diverse potato varieties. Under drought stress, the more developed the root system of potato is, the more drought tolerant it is and the less impact it has on yield [79]. However, potatoes generally react to drought through changes in the above-ground part of the plant rather than the below-ground part due to the complexity and difficulty of soil environment regulation [41]. The leaves of most plants stop growing only when the relative soil water content is below 40% to 50% [80], while potato plants stop growing at less than 60%, thus indicating that potato is very sensitive to drought [81]. Drought affects leaf transpiration, plant leaf number, and plant growth. Under drought conditions, potato plants are the first to stop growing with their leaves, resulting in a canopy that is more vulnerable to drought adversity compared to the roots [82]. Drought stress causes some effects on the leaf area index and the stem and leaf structure of potato (Table 1). Drought stress reduces leaf area and the number of green leaves [78,82,83], impacting photosynthesis, dry matter production, and ultimately tuber yield [84]. In general, the larger the leaf area index of potatoes, the more drought resistant the variety is, which is of great significance for maintaining its yield. In addition, drought

also influences the thickness and height of the potato main stem [70,85], further reducing the effective photosynthetic area and yield [65].

3.3. Impact of Drought Stress on Physiological and Biochemical Characteristics of Potato

3.3.1. Influence of Drought Stress on Photosynthetic Properties of Potato

Photosynthesis plays an essential role in the drought tolerance of potato. The Relative Chlorophyll Content (SPAD value) serves as a crucial metric for assessing drought resilience in crops. Studies revealed that while drought stress increases the leaf SPAD value in potato, it does not correspondingly elevate the net photosynthetic rate. Instead, it results in a decrease in tuber dry matter content [86]. Li et al.'s research [57] further confirmed that drought conditions, particularly during tuber formation and starch accumulation phases, significantly diminish various photosynthetic parameters, such as leaf net photosynthetic rate (P_n), transpiration rate (Tr), stomatal conductance (G_s), leaf area index, and overall yield. Romero et al. [84] highlighted that water stress indirectly influences leaf P_n and Tr through alterations in G_s , intercellular CO_2 concentration (C_i), and SPAD values, thereby impacting the photosynthetic process and potato yield (Table 1). Moreover, water use efficiency (WUE) under drought stress is an essential element that affects photosynthetic performance. Although the WUE of potato is higher than that of cereal crops (wheat, rice, and maize) [87], its root system is relatively shallow and difficult to recover from drought stress, resulting in reduced quality and yield of potato tubers. Gómez-Ocampo et al. [88] demonstrated that overexpressing *BBX21* in potato enhanced both P_n and C_i in leaves under drought conditions, along with an increase in WUE, which enhanced the drought tolerance of potato. Additionally, leaf water content and pressure–volume parameters, like cellular osmotic potential (π_o) and osmotic water loss potential (Ψ_{tlp}), are vital in regulating photosynthesis and leaf carbon content. The stomatal behavior of different potato varieties under drought stress all differ to some extent, leading to variation of electron flux changes, and the amount of leaves electron flux determines whether the leaves can maintain normal photosynthesis under drought stress [89]. Furthermore, photosynthesis and carbon partitioning in plants are highly correlated. Assimilates produced by photosynthesis feed back the rate of photosynthesis through carbon partitioning. Drought affects carbon allocation and carbon accumulation through photosynthesis, xylem and phloem transport, and induction of sugar synthesis. Drought stress affects stomatal conductance and chlorophyll content of potato, which in turn affects carbon partitioning and ultimately tuber yield [70] (Table 1). The carbon assimilation pathway in potato is the C_3 pathway, which absorbs CO_2 via the stomata and assimilates it to three-carbon compounds in the chloroplasts (Figure 1). Effective coordination of these processes is essential for tuber yield and quality. Under drought stress, potato plants close their stomata to reduce water loss, lowering the rate of transpiration and reducing carbon dioxide absorption, which leads to a reduction in carbon assimilation in potato and ultimately to a reduction in its yield and quality [5] (Figure 2). Under abiotic stress, photosynthetic carbon assimilation is reduced more in sensitive varieties than in non-sensitive varieties, which is associated with lower leaf Tr and PS II [90]. During reproduction, water deficit reduces carbon accumulation in potato and reduces carbon reactivation from nutrient tissues to tubers, thus reducing both tuber number and size [58].

3.3.2. Effects of Drought Stress on Cellular Structure and Membrane Stability in Potato

The cell membrane is a barrier that prevents external substances from entering the cell, both to control the substances into and out of the cell and to ensure normal intracellular physiological metabolic reactions so that the cell can maintain normal osmotic pressure [91]. Continuous drought stress causes irreversible damage to the biofilm, resulting in damage and disintegration of the membrane system, increased permeability, loss of pigments, and massive ion leakage. At the same time, the cell membrane peroxidation caused an increase in malondialdehyde (MDA) content in the cell due to the enhanced permeability of the cell membrane; thus, the extent of membrane lipid peroxidation increased and the cell

membrane damage was aggravated, which can lead to potato plant death in severe cases of biofilm damage. Under drought stress, plants can mitigate the damage by activating a number of defense mechanisms; for example, by triggering stomatal closure, reducing transpiration, decreasing water loss, which hold the balance of water metabolism within the cell to mitigate damage [92]. Plants counteract the damage caused by these free radicals via activation of the antioxidant system, including the production of antioxidant enzymes and other antioxidants to diminish the damage [93]. A greater amount of proline is synthesized, which maintains intracellular osmotic pressure and enhances cell membrane stability, to alleviate cell membrane damage [92]. In addition, a series of protective proteins, heat shock proteins, can be synthesized to help maintain the stability of the cell membrane and protect the cell structure from drought-induced damage [94,95].

3.3.3. Influence of Drought Stress on Osmoregulatory Compounds in Potato

Drought causes osmotic stress in plants due to water deficit. When plant cells feel osmotic stress, they synthesize a class of small molecules with high solubility and almost no toxicity to the cells, and the accumulation of these substances can maintain the normal osmotic pressure level of the cells under stress which can protect the protein activity and stabilize the structure of the cell membrane [96]. The molecules are mainly divided into two categories. One type is inorganic ions from the external environment that are absorbed and accumulated by plants [97]; the other type is organic solutes synthesized by cells themselves, such as mannitol, proline, Trimethylglycine, and trehalose, which are osmoregulatory substances. Osmoregulatory substances, notably proline (Pro), Trimethylglycine (TMG), soluble sugar (SS), and soluble protein (SP), are vital for potatoes to adapt to drought conditions [98]. In response to drought, potatoes increase Pro content in leaves to regulate osmotic potential and maintain water balance so as to reduce the damage of drought to the plants. Pro content variations are variety-dependent, with drought-tolerant varieties showing a delayed Pro increase compared to sensitive ones. Interestingly, Pro accumulation has a negative correlation with tuber weight, suggesting its role as a stress indicator rather than a protector. Moreover, large amounts of TMG are accumulated under drought stress in plants, which not only serves as a non-toxic osmoregulator to maintain normal cellular osmotic pressure, but also stabilizes enzyme activity and cell membrane structure, as well as scavenging free radicals [99]. Antioxidant enzymes like Peroxidase (POD), Superoxide dismutase (SOD), and Catalase (CAT) play a crucial role in mitigating cell damage by reducing intracellular ROS and peroxidation products [100], thus contributing to drought resistance in potato (Table 1).

3.4. Molecular Mechanisms of Potato Response to Drought Stress

Higher plants have gradually developed a series of response mechanisms to mitigate the damage caused by drought stress in the long-term evolutionary process. These include the perception and transmission of adversity signals, the activation and transcriptional regulation of resistance genes, and the expression and regulation of stress-induced proteins [101]. Potato exhibits drought tolerance through genetic traits governed by multiple genes, primarily with additive effects. The regulation of drought response in potato is a complex process, involving various signaling pathways. Throughout its growth and development, potato has developed diverse molecular mechanisms to resist and adapt to drought stress. These include physiological and biochemical responses triggered by changes in gene expression and metabolic pathways, mainly involving the ABA pathway, the MAPK pathway, transcription factors, miRNA, and other regulatory factors (refer to Figure 2).

3.4.1. The Role of Absciscic Acid Signaling in Potato's Drought Response

Drought stress triggers a series of physiological and biochemical reactions in potatoes, governed by genes encoding functional or regulatory proteins. These reactions are crucial for maintaining normal growth, preventing wilting, and reducing excessive water loss [102].

Abscissic acid (ABA), a widespread signaling molecule in plants, plays a pivotal role in the stress response process. It closes stomata and stimulates the expression of various stress-related genes. Researches have linked ABA to plant various processes, including growth and development, fruit development, and seed dormancy [103,104]. Particularly under drought stress, plants increase ABA biosynthesis or sensitivity, initiating various physiological and biochemical pathways to enhance stress tolerance [105,106]. ABA-induced gene expression involves both ABA-dependent and independent mechanisms. SNF1-associated protein kinases (SnRK2s) play a central role in the ABA signaling pathway, as outlined by Vasquez-Robinet et al. [107]. The ABA receptor PYR/PYLs/RCAR senses ABA, leading to the formation of complexes that inhibit SnRK2s through PP2Cs, the primary negative regulators of ABA signaling. Under stress, Raf-type protein kinases can activate SnRK2s, which then phosphorylate transcription factors like ABFs and ABI5. These factors regulate genes responsible for drought stress response, including WRKY and HSPs [108]. Schafleitner et al. [109] discovered that upregulating *DREB1A*, a key gene in the ABA-dependent pathway, enhances potato drought tolerance. Further studies, such as those by Watanabe et al. [110] and Muñiz García et al. [77,111], highlight the role of various transcription factors like ABF in ABA signaling, affecting drought and salt tolerance in potatoes.

3.4.2. MAPK Signaling Pathway in Potato's Response to Drought

MAPK pathway-associated signaling is a highly conserved class of protein kinase family, including MAPK, MAP2K, and MAP3K. The MAPK signaling pathway is another key mechanism of potato response to drought stress. It was demonstrated that *StMAPK3* can respond to drought by regulating photosynthesis and stomatal conductance, indicating that *StMAPK3* can significantly increase the resistance of potato plants to drought/osmotic stress [112]. The expression of *StMAPK11* was found to be remarkably up-regulated under drought conditions; in addition, its ability to enhance the drought resistance of potato by enhancing antioxidant activity and photosynthesis was noted [113]. RNA-seq analysis of drought-tolerant and drought-sensitive potato varieties screened for 22 drought-responsive genes, including *MAPKKK15*, the transcript levels of which were activated under drought conditions [114]. In addition, the reduced expression of *stu-miR856* may drive overexpression of *StMAPK10* and *StMAPK11*, which might help potato plants adapt to drought stress [115].

3.4.3. Transcription Factors in Potato's Drought Response

Transcription factors are a class of proteins that play critical regulatory roles in plants, and they are involved in transcriptional and post-transcriptional regulation and impact on plant growth, development, and response to adversity [116,117]. Various transcription factors, such as ZFP, AP2/ERF, NAC, WRKY, MYB, and bZIP, have been identified as key players in the drought response of potatoes. For instance, BBX proteins from the ZFP family enhance drought tolerance and tuber yield in potatoes [90]. Similarly, the overexpression of *StERF94*, *StNAC053*, *StWRKY48*, and *StMYB1R-1* has been linked to improved drought resistance through mechanisms like water regulation, antioxidant activation, and stomatal control [118–121]. The silencing of the *StWRKY57* gene altered the response of potato to drought, suggesting that *StWRKY57* has an important role in drought acclimatization in potato [122]. Additionally, the modification of secondary metabolism through transcription factors like *IbMYB1* and the introduction of genes such as *CaBZ1* from *Capsicum annuum* have shown to enhance drought tolerance in potato plants [123,124]. The Cycling Dof factor (CDF) acts as an important role in abiotic stress response. Related studies have shown that *StCDF1* together with the lncRNA *StFLORE* modulate water loss in potato by influencing stomatal growth and diurnal opening [125,126]. In addition, the expressions of *StCDF1*, *StCDF2*, and *StCDF3* were notably up-regulated in drought-tolerant varieties compared to their expression in drought-sensitive varieties, suggesting that potato *StCDFs* may play a key role in drought response [127].

3.4.4. miRNA in Potato Drought Stress Response

MicroRNAs (miRNAs) are a class of non-coding single-stranded RNA molecules of approximately 22–24 nucleotides in length encoded by endogenous genes. They are involved in post-transcriptional gene expression regulation in eukaryotes and in the regulation of plant growth and development, biotic and abiotic stresses (Figure 2). Research by Yang et al. [128] highlighted that specific potato miRNAs (stu-miR159s) suppress the expression of target R2R3 MYB (*StGAMyb-like1*, *StGAMyb-like2.1*, and *StGAMyb-like2.2*) genes, aiding in drought stress adaptation. Another study by Yang et al. [120] found that stu-miR827 negatively regulates potato drought resistance by regulating its target gene *StWRKY48* transcription factor to increase leaf stomatal density. Additionally, a related study investigated changes in miRNA profiles in two different potato varieties (Unica, tolerant and Russet-Burbank, susceptible) in response to drought, heat, and their combinations. The results suggest that eight of these miRNAs (*miR398a-5p*, *miR172b-3p*, *miR162a-3p*, *miR160a-5p*, *miR156d-3p*, *Novel_105*, *Novel_9* and *Novel_8*) may play vital roles in response to drought and high-temperature stresses at various post-transcriptional levels [129]. Extensive studies have identified various miRNA families, including *miR159*, *miR164*, and *miR166*, as key players in drought stress response [130–133].

3.4.5. Other Regulatory Factors in Potato Drought Stress Response

Beyond miRNAs, numerous genes contribute to potatoes' drought stress response (Figure 2). For example, lipid transfer proteins (LTPs) are vital in plant stress adaptation. Wang et al. [134] identified 39 potato LTP family members in a related study and found that among them, the expression of *StLTP1* and *StLTP7* was up-regulated in plant roots, stems, and leaves after drought treatment, suggesting that these two genes may be related to potato response to drought stress. Rice and wheat can respond to drought stress through changes in root architecture, and the *DRO1* genes in these crops are regulated by different developmental patterns to resist and adapt to drought stress. So far, the *DRO1* gene in wheat and the *StDRO1* gene in potato have been studied preliminarily in response to drought stress [135,136]. Aquaporins (AQPs), also known as water pore proteins, are specific channel proteins used to transport neutral molecules such as water in the cell membrane, which can regulate intercellular and even whole-plant water balance. The potato AQP gene *StPIP1*, as shown by Wang et al. [137], enhances drought resistance by improving the overall water status of the plant by increasing stomatal conductance. Further, Cho et al. [138] demonstrated improved drought tolerance and tuber yield in potatoes expressing the sweet potato orange gene (*IbOr*). Glycine betaine is one of the most important osmoregulators in higher plants, which is able to respond to environmental stresses via osmoregulation. Also, introducing the spinach BADH (betaine aldehyde dehydrogenase) gene into potato plants increased drought tolerance [139]. Ma et al. [140] found that *StCIPK10* expression is significantly upregulated under drought, PEG6000, and ABA treatments. Further experimental results indicate that *StCIPK10* (calcineurin B-like interacting protein kinases) enhances potato drought resistance by enhancing its ability to scavenge ROS and increasing the content of corresponding osmoregulation substances. The expression level of *StRFP2* (RING finger protein 2) gene was significantly up-regulated under drought treatment. Overexpression of *StRFP2* in potato significantly improved the drought resistance of potato plants, and these results indicated that *StRFP2* was involved in the response of potato to drought [141]. In addition, it was found that potatoes with overexpression of *StCDPK28* (Calcium-dependent protein kinases 28) showed a certain resistance to drought stress by decreasing MDA and H₂O₂ content and increasing the activities of CAT, SOD, and POD [142]. The above studies have demonstrated that drought tolerance in potato is related to the ABA signaling pathway, the MAPK signaling pathway, transcription factors, miRNAs, and so on (Figure 2).

4. Effect of High-Temperature Stress on Potato

Plants, including important crops like potato, face multiple adversities such as drought, salinity, and high temperatures. High temperature, a major abiotic stressor, significantly impacts plant growth and development [143]. Currently, with the greenhouse effect increasing, agricultural production is facing even more serious challenges from global warming. Potato, one of the world's most important food products, prefers cool temperatures and does not tolerate high temperatures. High-temperature stress is one of the major abiotic stresses limiting potato cultivation, and it has a greater impact on potato growth and development as well as yield and quality [144] (Table 1). The response of plants to high temperature stress activates intracellular signaling pathways, thereby inducing a series of heat-tolerant regulated metabolic responses [145]. Similar to other stresses, heat stress affects various parts of the plant, such as cell membranes, nuclei, the cytoplasm, and various organelles [146]. The main pathways of potato response to high-temperature stress include the ROS pathway and heat shock transcription factor—heat shock protein pathway, which mainly involves a variety of antioxidant enzymes, heat shock factors, heat shock proteins and transcription factors (Figure 3).

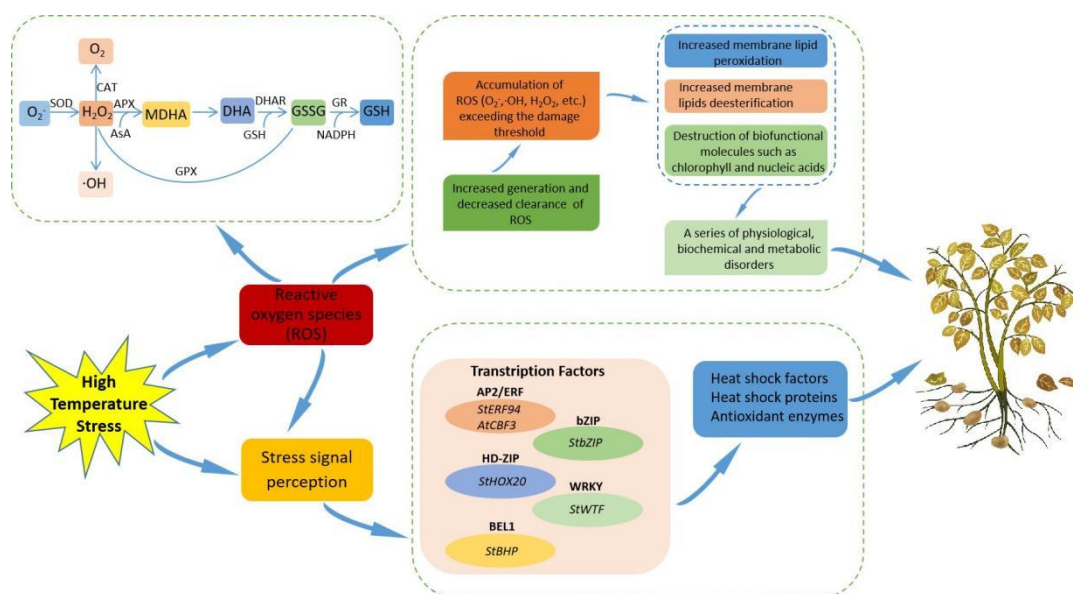


Figure 3. Molecular mechanism of potato response to heat stress. The main pathways of potato response to high-temperature stress include the ROS pathway and heat shock transcription factor—heat shock protein pathway, which mainly involves a variety of antioxidant enzymes, heat shock factors, heat shock proteins and transcription factors.

4.1. Effect of Heat Stress on Potato Yield and Quality

The potato, native to the Andes region of South America, thrives in cool temperatures. High temperatures can hinder tuber formation in many potato species. The impact of temperature on potato growth and development varies with changes in the temperature of the above-ground and below-ground growth environment, the developmental stage of the plant, and the duration of exposure to specific temperature [147]. Potato plant growth requires different air and soil temperatures, with temperatures ranging from 20 °C to 25 °C for above-ground stem and leaf growth and from 15 °C to 20 °C for underground tuber formation [148]. It is generally recognized that the optimum temperature for potato growth is 14–22 °C, and the optimum temperature for tuber formation is 20 °C, with a sharp drop in yield when the ground temperature exceeds 25 °C [149]. High temperatures impede carbon transport and CO_2 fixation and reduce chlorophyll content [150,151], which affects the plant's ability to photosynthesize and accumulate starch, ultimately impacting yield and quality (Table 1). The study by Obiero et al. indicated that high-temperature treatments

affected dry matter and tuber yield of whole potato plants. Their results showed that high-temperature treatments (30 °C) resulted in 45% smaller tubers (less than 2.5 cm in diameter) in comparison with the control (22 °C) before and after tuber sprouting [152]. In addition, a relevant study also found that high temperature can inhibit the rate of dry matter accumulation during the growth and expansion stages of potato tubers [153]. Several research works indicate that heat stress reduces both the weight and number of potato tubers, leading to significant yield reductions [154,155]. High temperatures also deteriorate potato quality, causing issues like secondary growth, tuber hollowing, cracking, and tuber deformities (Table 1). Heat stress stimulates the conversion of starch to reducing sugars, leading to dark coloration in fried fries with high sugar content, which is unacceptable to consumers [34,35,74]. Furthermore, Busse et al. [156] observed that in potatoes grown three months after planting and subjected to 7 and 14 days of continuous heat stress (at 35 °C during the day and 29 °C at night), the basal and apical tuber reducing sugars content increased, the dry matter content decreased, and the severity of stem-end chip defects increased, which adversely affected the processing quality of the potatoes. And elevated soil temperatures caused unsightly wrinkles and yellow–brown patches on potato varieties with smooth skins, impacting their aesthetic quality [157] (Table 1).

4.2. Effect of Heat Stress on Potato Growth and Development

Potatoes prefer cooler climates, and high temperatures impact potato growth and development at critical growth phases. During the seedling stage, a suitable high temperature can maintain high net photosynthetic rates and accelerate potato seedling growth [158]. Struik et al. [159] observed that at the tuber setting stage, within the temperature range of 18 °C to 25 °C, the increase in temperature not only promotes the elongation of stolons but also favors their branching, thus increasing the number of stolons and potential tubers of the plant, while high temperatures of 28 °C and above may partially or even completely hinder the occurrence of stolons. At the tuber-setting stage, potatoes exposed to high temperatures have a prolonged fertility, increased deformity, and reduced number of stolons [160], as well as a significant reduction in the rate of commercial potatoes and the number of potatoes set [154] (Table 1). In addition, Borah [161] noted that the optimal temperature for potato tuberization is 20 °C, with high temperatures (25 °C) causing delays in tuberization. And heat stress is thought to inhibit tuberization and tuber yield by altering assimilate partitioning and impeding the translocation of sucrose to the tuber [5]. Ewing [162] associated tuberization delays with suppressed heat-induced tuberization signals, notably *StSP6A*, a homologue of the Arabidopsis FLOWERING LOCUST (FT) [163]. Furthermore, under high-temperature stress, potato plants showed increased plant height, smaller leaves, early senescence, and even death [154,164,165]. Similarly, Kooman and Haverkort [166] found that high temperatures limit the expansion of potato leaves, leading to a reduction in leaf area, as well as affecting stem elongation (Table 1). The tuber development is more sensitive to high temperatures than stem and leaf growth. Ambient temperatures above 25 °C halt tuber growth, and above 39 °C, stem and leaf growth ceases [167]. Research has revealed that late-maturing cultivars are more affected by high temperatures than early-maturing ones [155].

4.3. Effect of Heat Stress on Physiological and Biochemical Properties of Potato

4.3.1. Photosynthetic Characteristics

Photosynthesis is a prerequisite for crop growth and development, yield and quality formation, and is one of the most sensitive physiological processes in response to high-temperature stress [168]. High temperatures significantly affect the light and dark responses of plants. Potatoes have a photosynthesis temperature range of 0–7 °C (minimum), 16–25 °C (optimal), and up to 40 °C (maximum) [169]. The ideal net photosynthetic rate to dark respiration ratio occurs at 16–20 °C. For every 10 °C increase, dark respiration rate doubles [170]. For European potato cultivation varieties, the optimal photosynthesis temperature is 20 °C, with a 25% net photosynthetic rate decrease at 25 °C and a drop to zero

above 30 °C [171]. High temperature can inhibit the photosynthesis of potatoes (Table 1). A related study found that compared to heat-resistant potatoes, heat-sensitive potatoes are more severely inhibited in CO₂ fixation in their leaves after being treated at 40 °C for 9 days, and the loss of photosynthetic pigments is more significant [172]. Wang et al. [173] reported that high-temperature stress affects photosynthesis more during branching than during the seedling stage. In addition, a related study found that when a potato is in a high-temperature environment, the plant reduces body temperature by enhancing water dissipation, and therefore Tr is significantly ($p < 0.05$) increased [174]. It was shown that Fm and Fv/Fm as well as Pn of potato leaves are reduced by 16.65% and 7.21% and 35.56%, respectively, in high-temperature treatment (35 °C ± 2) compared to low-temperature treatment (25 °C ± 2) at tuber expansion stage [175]. In general, when Fv/Fm < 0.75, it indicates that the plant is subjected to irreversible severe stress damage [176,177]. These results indicated that high-temperature stress inhibited the electron transfer and light energy conversion efficiency of potato PSII reaction centers [178] (Table 1).

4.3.2. Membrane Stability and Antioxidant Capacity

The cell membrane of the plant is the first to be affected under high-temperature stress. The composition and structure of the plasma membrane are damaged by high-temperature stress, causing an increase in intracellular electrolyte extravasation, increased plasma membrane peroxidation, and an increase in MDA content [100]. In order to reduce the damage caused by high-temperature stress, plants can reduce the damage of membrane lipid peroxidation through two kinds of systems: enzymatic reaction and non-enzymatic reaction [3]. Enzymes such as SOD, POD, and CAT act as scavengers to remove ROS from plants. The results of Zhu et al. [179] demonstrated that the potato cultivar Atlantic showed a significant increase in the MDA content and the Pro content, as well as a significant increase in CAT, POD, and SOD enzyme activities after high-temperature (30 °C and 35 °C) treatments compared to ambient temperature (Table 1). The above results indicate that high temperatures significantly affect potato cell membrane stability and peroxidase activity.

4.4. Molecular Mechanism of Potato Response to Heat Stress

Under high-temperature stress, ROSs accumulate in large quantities, and plants produce a series of antioxidant substances to eliminate ROSs and protect cells from oxidative damage [180,181]. For example, SOD can clear O₂^{•−} and produce H₂O₂, which can then be removed by ascorbate peroxidase (APX) or CAT [168]. In addition, substances such as ascorbic acid (AsA), glutathione reductase (GR), and glutathione (GSH) can also act as antioxidants to eliminate ROS in plants [182]. However, when high temperatures persist, the activity of most antioxidant enzymes decreases or even completely disappears. And a large amount of ROS that cannot be cleared accumulates in cells, which has adverse effects on cellular metabolism [183], ultimately inhibiting plant growth and development, and even causing plant death. The early changes induced by high-temperature stress concern the recoding of signal transduction elements, transcription factors, and proteins related to ROS metabolism under conditions of stress [144] (Figure 3).

4.4.1. Heat Shock Proteins and Heat Shock Factors

Under high-temperature adversity, functional proteins and various enzymes in plant cells are altered in conformation, leading to changes in physicochemical properties or loss of biological activity. During the long-term evolution of plants, control systems for repair and removal of damaged proteins are formed in their cells [184]. Among them, heat shock proteins (HSPs) are typical representatives, which mainly act as molecular chaperones to assist the correct folding, assembly, and transport of proteins and maintain the stability of protein conformation and function [185]. For instance, introduction of the *DcHSP17.7* gene (*Daucus carota* L. heat shock protein 17.7) into the potato variety *Désirée'* enhances the heat tolerance of transgenic potato plants, which correlates with its ability to increase the stability of cell membranes in the leaves [186]. Hsp20s comprises 48 identified members

in potatoes; most of them can be rapidly and abundantly expressed in response to heat stress, which is crucial for improving heat tolerance in potato [187]. Heat shock factors can recognize and bind heat shock elements in plant heat stress to further regulate transcription and translation of heat shock proteins. Introduction of Arabidopsis *HsfA1* into potatoes showed increased heat tolerance, decreased electrolyte leakage, and increased proline content [188]. In addition, the expression of *StHSP70*, a gene downstream of *HsfA1*, was increased six-fold in transgenic potato plants under heat stress compared to that of the wild type, and it was hypothesized that *HsfA1* might synergize with *StHsp70* to enhance the heat tolerance of transgenic potato plants. By cloning the *StHsfA3* gene from the potato variety *Désirée* and obtaining transgenic potato lines by overexpression of the gene, researchers hypothesized that *StHsfA3* may synergize with *StHsp26* and *StHsp70* to enhance the heat tolerance of overexpressed transgenic lines [189]. Li et al. [190] highlighted the regulatory role of the Hsp90-partner protein complex under heat stress, thus improving the heat tolerance of potato.

4.4.2. Transcription Factors

A number of transcription factors (TFs), including AP2/ERF, bZIP, HD-ZIP, WRKY, and the BEL1 family, are identified as being involved in the regulation of potato response to high temperature (Figure 3). Overexpression of *StERF94* in potato plants increased the tolerance of transgenic potato plants to heat by better controlling leaf water and chlorophyll content, activating antioxidant enzymes and proline accumulation [118]. In addition, introduction of the *AtCBF3* gene, a transcription factor also belonging to the AP2/ERF family, into potato also increased the tolerance of transgenic potato plants to high temperatures, which may be related to the ability of this gene to mediate the enhanced expression of genes related to photosynthesis and antioxidative defense [144]. Kumar et al. [191] identified 18 *StbZIP* candidate genes potentially involved in regulating potato response to high-temperature stress using genome-wide characterization analysis combined with RNA-Seq analysis of expression data. HD-ZIP (homologous leucine zipper) transcription factors play vital regulatory roles in plant stress tolerance. A total of 43 HD-ZIP genes were identified in potato by the rigorous homology search. Among them, the transcript level of *StHOX20* in particular was remarkably up-regulated at high temperatures, suggesting that the gene possibly participates in the regulation of potato in response to thermal stress [192]. *StWTF* belongs to the WRKY family of transcription factors and is a major regulator of transcription reprogramming in plant cells during thermal stress [193]. *StBHP* belongs to the BEL1 family of transcription factors and promotes tuberization [194]. The virus-induced gene silencing (VIGS) approach was utilized to silence two genes, *StWTF* and *StBHP*, in the heat-tolerant cultivar Kufri Surya (KS). VIGS-treated KS plants exhibited leaf senescence and suppressed tuberization at high temperatures compared to control plants [195], suggesting that *StWTF* and *StBHP* play important roles in potato heat tolerance. The above studies illustrate that potato heat tolerance is relevant to the ROS signaling pathway, heat shock proteins, heat shock factors, and transcription factors.

5. Adaptation Strategies for Drought and High Temperature

5.1. Screening and Evaluation of Drought-Resistant and Heat-Tolerant Resources

The drought resistance and high-temperature tolerance of different potato varieties varies greatly, and the selection of drought resistance and heat resistance varieties can alleviate adversity damage to a certain extent. However, there are relatively few wild potato resources that can be directly utilized, and the exploration and innovation of the existing high-quality germplasm that can withstand drought and high temperature is an important condition for the selection and breeding of new varieties. Yu [196] conducted drought resistance identification on 119 potato germplasm resources and screened out two drought-tolerant resources (CIP 393228.67 and CIP 385561.124). Zhang et al. [155] found that early-maturing varieties were better than late-maturing varieties in terms of heat tolerance through the identification of heat tolerance in 50 potato varieties. In recent

years, drought-resistant varieties such as 397100-9, Yunshu 902, and Cooperative 88 have been screened [197,198], as well as heat-tolerant varieties such as Zhenshu 1, Dianshu 187, and Qingshu 10 [199]. Through evaluating and excavating existing germplasm resources, high-quality drought-resistant and heat-resistant potato materials can be obtained, which can be used as breeding parents to accelerate the potato breeding process.

5.2. Breeding Techniques to Deal with Drought and High Temperature

In general, conventional breeding techniques cultivate drought-resistant and high-temperature-tolerant varieties for a longer period of time. Therefore, the combination of molecular breeding and conventional breeding provides a new way for the selection and breeding of new varieties. A study has shown that overexpression of the *StMYB1R-1* gene in potato can enhance the drought tolerance of transgenic potato plants by regulating water loss [121]. Introducing the *DcHSP17.7* gene into potato enhanced the heat tolerance of transgenic potato plants, which was associated with its ability to improve the cell membrane stability of leaves [186]. These transgenic potato materials with drought and heat tolerance which are obtained through molecular technology can be used as parents for subsequent conventional breeding, thereby accelerating the breeding of superior drought-resistant and heat-tolerant varieties. Therefore, the adoption of a technical route that closely integrates conventional and molecular breeding is a key link to obtaining new drought-resistant and heat-tolerant varieties as soon as possible, so that they can be popularized and applied on a large scale.

5.3. Cultivation Techniques for Coping with Drought and High Temperature

One of the main measures to reduce the effect of drought and high temperature on potato production is by rational use of anti-stress exercise and water and fertilizer management. Mild stress during the early stages of plant growth can cause a series of physiological and morphological changes. The early stage of mild abiotic stress affects the speed of response when the plant suffers from stress again. It was found that mild drought and high-temperature treatment of seed potatoes and seedlings can greatly enhance their drought and heat resistance [84,200]. The water and fertilizer requirements of potato plants vary at different stages of growth, and scientific and rational water and fertilizer management is necessary to ensure high yield and quality. Potato is very sensitive to water and fertilizer; in the case of shortage, a small amount of water and multiple irrigation methods should be implemented, and the application of nitrogen fertilizer should be reduced [201,202]. The appropriate application of CaSO_4 , ZnSO_4 [203], and drought-resistant fertilizer mixture can enhance the drought- and heat-resistant ability of the plant.

6. Conclusions and Prospects

One of the world's most important food products, potato, prefers coolness and is sensitive to drought. It is also susceptible to water shortages and vulnerable to high-temperature conditions. Maintaining sufficient water and appropriate temperature in the soil is an important condition for high yield and high quality of potatoes. Usually, the suitable relative soil moisture content for potato growth and development is 55% to 85%, and the suitable temperature is 15–25 °C. Thus, drought and high-temperature stress during growth and development of potato frequently lead to changes in morphological, physiological, biochemical, and molecular responses.

The growth and development of potato plants under drought and high-temperature stress conditions are inhibited, and plant morphology is altered, which affects the process of potato stolon formation, tuberization, and expansion, ultimately leading to a significant reduction in potato tuber yields and a remarkable degradation of the market grade of tubers, the specific gravity of tubers, and the processing quality of tubers. In addition, stress also adversely affects potato physiological and biochemical characteristics, such as reduction in root diameter and leaf area, decrease in net photosynthetic rate of leaves, production of ROS, and increase in membrane lipid peroxidation. A variety of different

types of genes (*StWAKY3*, *miR159*, *StLTP1*, *StDRO1* and *DcHSP17.7* etc.) and transcription factors (*StABF1*, *StWRKY48*, *StNAC053*, *StERF94* and *StHOX20* etc.) are involved in the response to drought and high temperatures at the molecular level.

As global warming intensifies, abiotic stresses such as high temperatures and droughts are occurring more frequently. These challenges significantly impact crop yields and quality, thereby posing a substantial threat to worldwide food security. Potato, with its unique characteristics, is poised to play a pivotal role in bolstering food security and enhancing the livelihoods of farmers. Despite the completion of potato genome sequencing in 2011, research on the molecular mechanisms of drought and high-temperature tolerance still needs to be further developed. There is a pressing need to optimize cultivation practices and to develop strategies for seedling refining under moderate high-temperature and drought conditions, aimed at mitigating the adverse effects of these stresses. In the future, it is necessary to extensively screen high-quality and stress-resistant potato resources, search more thoroughly for the key genes related to drought and heat tolerance in potato, construct interaction networks, and utilize gene editing technology to cultivate high-quality potato varieties with enhanced resilience to these conditions. Future strategies will integrate molecular breeding and gene-editing techniques to generate superior genetic materials and expand the potato germplasm bank. This approach, combined with traditional breeding methods and appropriate cultivation practices, aims to develop potato cultivars that are both heat- and drought-resistant. Such advancements will not only improve crop quality and yield, but also significantly contribute to addressing the global challenge of food security.

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