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Harnessing Brassinosteroids for Heat Resilience in Wheat: A Comprehensive Review

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

This comprehensive review focused on understanding the critical interplay between Brassinosteroids (BRs), a class of plant hormones, and the high-temperature stress response in wheat (*Triticum aestivum*) in the context of climate change. In 2022-23, heat stress caused by a spike in temperatures in mid-March 2022 reduced India's wheat crop yields by 10-15%. This lowered the country's forecasted wheat production from 110 million metric tons (MMT) to 99 MMT for the 2022/23 market year (April-March) (USDA, 2023). The adverse effects of climate change and abiotic stresses on agriculture and crop productivity are well-established, with rising temperatures identified as a significant factor in the decline of plant growth and yield. In light of this, this review aims to delve into the intricate relationship between BRs and wheat's response to high-temperature stress. Given that global mean surface temperatures have already increased and are projected to continue rising throughout the 21st century, it is imperative to explore innovative strategies to mitigate the detrimental impacts on crop productivity. To this end, the study seeks to enhance our understanding of how BRs influence the growth and yield of wheat when exposed to high-temperature stress conditions. The overarching goal is to develop effective strategies that can bolster the resilience and productivity of wheat, which is a cornerstone staple crop worldwide, facing the escalating challenge of climate change. This review builds on the existing body of knowledge, synthesizing current research findings and shedding light on the potential of BRs as a key player in ameliorating the consequences of climate change in agriculture.

Keywords: Plant hormone; abiotic stress; plant growth; Brassinosteroids; heat resilience; plant stress; plant resilience; crop rotation.

1. INTRODUCTION

Climate change and abiotic stresses exert detrimental impacts on agriculture and crop productivity Among the array of climatic factors influencing agriculture, temperature stands out as a pivotal factor due to its adverse influence on plant growth and yield. Over the twentieth century, the global mean surface temperature has risen by approximately 0.5°C, with projections indicating a potential increase ranging from 1.8 to 9.5°C by the year 2100 (IPCC Working Group I report, 2022). Lobell and Field [1] conducted a comprehensive investigation to assess the consequences of global warming on six major staple crops spanning the years 1982 to 2022. Their findings underscore a collective decline in yield amounting to approximately 40 million tonnes per annum for crops such as wheat, corn, and barley. Within this, wheat accounts for nearly half of the total yield loss, with a significant annual decrease of 19 million tonnes. High-temperature stress is a significant environmental factor that adversely affects the growth and yield of wheat (Triticum aestivum), one of the most important staple crops worldwide. Brassinosteroids (BRs) are a class of plant hormones known to play crucial roles in plant growth, development, and stress responses [2]. The interaction between BR signaling and high-temperature stress response in wheat has garnered increasing attention in recent years. So, the aim of this review is to investigate the interaction between Brassinosteroids (BRs), a class of plant hormones, and the high-temperature stress response in wheat (*Triticum aestivum*) as a means to mitigate the adverse impacts of climate change on crop productivity. To enhance our understanding of how BRs influence the growth and yield of wheat under high-temperature stress conditions, with the ultimate goal of developing strategies to improve the resilience and productivity of this vital staple crop in the face of rising global temperatures.

2. IMPORTANCE OF WHEAT (*TRITICUM aestivum*) AS A STAPLE CROP

Wheat (Triticum aestivum) stands as a cornerstone of human sustenance, serving as a staple crop that plays a pivotal role in addressing global food security challenges. Wheat's unparalleled importance lies in its role as a major source of calories and nutrition for a substantial portion of the world's population. With its ability to provide energy-rich carbohydrates, dietary fiber, essential B vitamins, and minerals, wheat forms an essential component of diets across diverse cultures and regions. It serves as a lifeline for vulnerable populations, contributing significantly to the fight against malnutrition and hunger. Wheat cultivation has far-reaching implications for agricultural economies and rural livelihoods. Millions of farmers worldwide depend on wheat cultivation for their sustenance, contributing to rural development, income generation, and poverty alleviation. As a crucial cash crop, wheat supports economic stability, trade, and food supply chain dynamics, enhancing the socio-economic fabric of both local and global communities. Wheat's versatility and adaptability are exemplified through its consumption in various forms, from bread and pasta to noodles and pastries [3].

This diversity adds richness to dietary choices, catering to a wide range of culinary preferences and cultural traditions. Wheat-based products not only provide sustenance but also foster cultural identity and gastronomic exploration. Wheat occupies a central position in the realm of international trade, acting as a vital commodity that facilitates economic exchange between nations. Its trade supports economic growth, strengthens diplomatic relations, and contributes to global interdependence. The wheat trade dynamic underscores the interconnectedness of nations in addressing food security challenges and fostering international cooperation. Wheat's significance extends beyond its role as a food source. As a model crop, wheat serves as a focal point for scientific research and breeding efforts aimed at enhancing yield, disease resistance, and nutritional quality. Breakthroughs in wheat genetics and breeding methodologies have broader implications for improving other cereal crops, contributing to sustainable agricultural practices. Wheat's adaptability to diverse climates, ranging from temperate to subtropical regions, enhances its resilience against climatic variability and shocks. Its widespread cultivation provides a buffer against adverse weather conditions, making it a reliable source of nutrition even in challenging environments.

Global Caloric Source: Wheat stands as a crucial global caloric source, serving as a staple food for a significant portion of the world's population and offering essential energy and nutrients. Its versatility spans various culinary cultures and dietary preferences, providing dietary diversity. Moreover, its affordability and accessibility make it indispensable, especially in regions with diverse income levels. Despite being primarily a carbohydrate source, wheat also offers vital nutrients like dietary fiber, B vitamins, and minerals, ensuring a balanced diet. Economically, wheat plays a pivotal role in international trade, supporting livelihoods along the food supply chain and sustaining millions of farmers globally. Additionally, through crop rotation, wheat contributes to soil health and agricultural sustainability. Its resilience to diverse climates ensures a stable food source across different regions. Furthermore, as a model crop for research and breeding, advancements in wheat genetics have broader implications for improving other cereal crops. Ultimately, the widespread cultivation and consumption of wheat significantly contribute to global food security, offering stability and reliability even during times of scarcity or food supply disruptions [4].

3. BRASSINOSTEROID PROMOTING STRESS TOLERANCE

Plants possess intrinsic mechanisms to enhance their tolerance to abiotic stresses. Different physiological and biochemical adjustments are necessary under abiotic stress in horticultural crops. These interactions comprise variations in gene regulation, the production of particular proteins and many metabolites, changes in hormonal signaling, and antioxidant capacity. A collection of organic, naturally occurring molecules is known as plant hormones (Low concentrations of these hormones could influence important plant life cycle activities [5]. Phytohormones are involved in physiological changes and expression of genes under abiotic stresses. Brassinosteroids (BRs), Auxins, gibberellins, cytokinin, abscisic acid, jasmonates, salicylic acid, ascorbic acid, melatonin, and ethylene are only a few examples of the class of naturally occurring compounds known as phytohormones. Since the 1940s, they have been utilized in horticultural crops. A few examples of well-studied expressions are ethylene’s encouragement of fruit ripening, auxin and cytokinin control of the cell cycle, gibberellins initiation, seed germination and stem length, and ABA’s maintenance of seed dormancy. Hormonal processes determine the growth and development of plants. Phytohormones involved in signal transduction networks under abiotic stresses resulting in improved growth and yield of horticultural crops [6].

4. OVERVIEW OF BRASSINOSTEROIDS (BRS) AS ESSENTIAL PLANT HORMONES

Brassinosteroids (BRs) are a class of plant hormones that play pivotal roles in regulating various physiological processes critical for plant growth, development, and adaptation to environmental cues. BR biosynthesis begins with the conversion of campesterol to castasterone and brassinolide through a series of enzymatic reactions]7,8]. The synthesis and perception of BRs involve a complex signaling cascade, including BR receptor kinase (BRI1) and its co-receptor BAK1, leading to activation of downstream transcription factors such as BZR1 and BES1 [9,10,11,12]. The extra benefit of using BRs in agriculture to increase agricultural output is their capacity to endow plants with resilience to abiotic stressors. The role of BRs in protecting plants against environmental stresses is more vital for sustainable production. Brassinosteriods play key roles in plant adaptation to biotic stresses, including various pathogen infections [13]. BRs possess the capacity to negate genotoxicity and pesticidal residues in many horticultural crops.

5. PHYSIOLOGICAL ROLES OF BRASSINOSTEROIDS

Brassinosteroids have diverse roles in plant growth and development, including promoting cell elongation, enhancing vascular differentiation, modulating leaf expansion, and regulating root growth [14]. They are also implicated in reproductive development, pollen tube elongation, and fruit development [15,16].

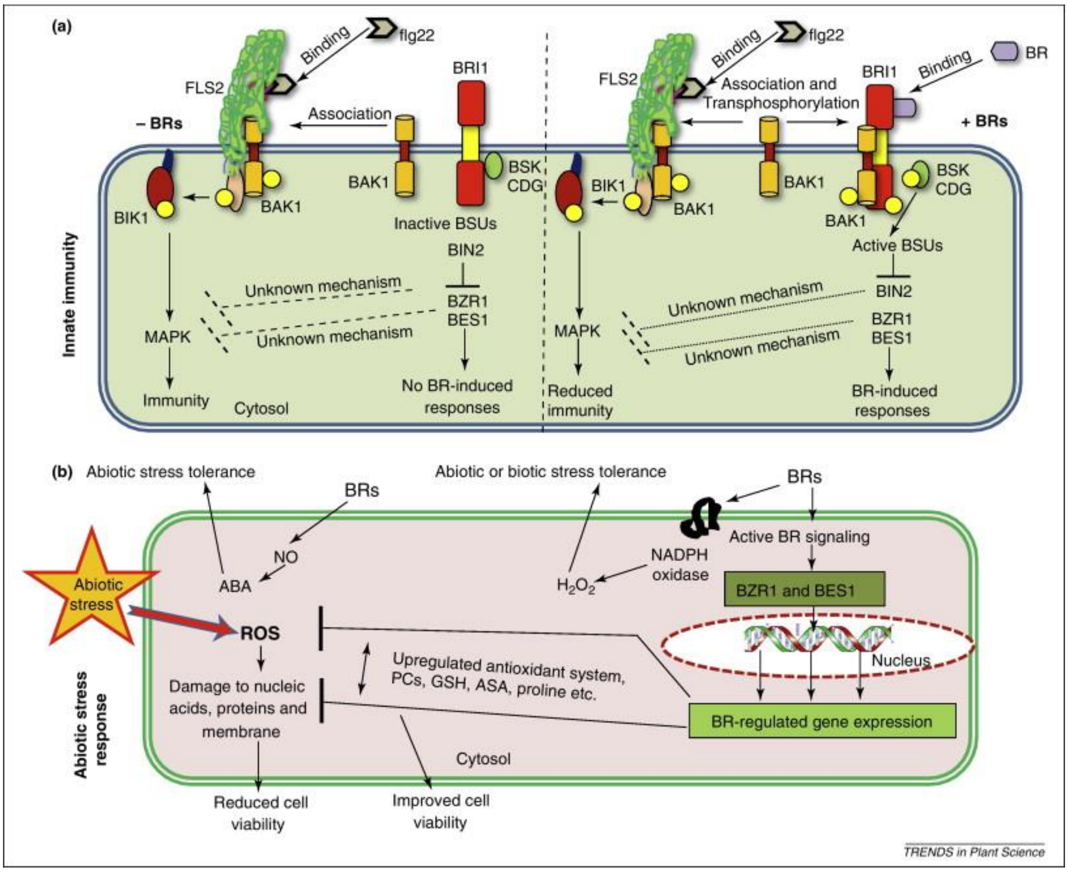

Fig. 1. Schematic representation brassinosteroid signalling pathway and its physiological responses to biotic and abiotic stresses [17]

6. ABIOTIC AND BIOTIC STRESS RESPONSES

BRs are implicated in plant responses to various abiotic stresses, such as drought, salinity, and high temperature, by regulating stomatal conductance, enhancing antioxidant defenses, and modulating stress-related gene expression [18,19,20]. Additionally, BRs play a role in plant defense against pathogens through the activation of defense-related genes [13,21].

Table 1 Exogenous brassinosteroid application enhanced abiotic stress tolerance in horticultural plants

Crop name	Stress type	References
Peppermint	Salinity	[1]
Tomato	Heat	[22]
Pepper	Cadmium	[23]
Tomato	Drought	[24]
Tomato	Cold	[4]
Tomato	Salinity	[25]
Cucumber	Cold	[26]
Pepper	Drought	[27]
Cucumber	Cold	[26]
Lettuce	Salinity	[28]
Pepper	Chromium	[29]
Radish	Cadmium	[29]
Orange	Cold	[30]
Grapevine	Drought	[4]
Tomato	Cadmium	[31]

7. CROSSTALK WITH OTHER HORMONES

BRs interact with other hormonal pathways, including auxins, gibberellins, and abscisic acid, to fine-tune plant responses to changing environmental conditions). BRs crosstalk with different hormones to regulate plant physiology and development [6,9,32]. The crosstalk between BRs and signaling of other plant hormones regulates the balance between growth in plants and defensive responses under heavy metal stress [33].

8. AGRICULTURAL IMPLICATIONS AND BIOTECHNOLOGICAL APPLICATIONS

Understanding the roles of BRs has led to the development of strategies for improving crop yield, stress tolerance, and nutritional content through genetic manipulation of BR-related genes [34,35]. Enhancing BR signaling has shown promise in mitigating the adverse effects of abiotic stresses and increasing crop productivity.

8.1 Rationale for Investigating the Interaction between BRs and High Temperature Stress in Wheat

Impact of High Temperature Stress on Wheat: High temperature stress is a significant challenge affecting wheat production globally. Increased temperatures during key growth stages can disrupt cellular processes, hinder photosynthesis, and adversely impact grain yield and quality [29,36,37]. Given the projected climate change scenarios, understanding how plants respond to heat stress is critical for securing future food production.

Role of Brassinosteroids in Stress Responses: Brassinosteroids have emerged as key regulators of plant responses to various abiotic stresses, including high temperatures [38]. BRs have been implicated in enhancing antioxidant defenses, modulating gene expression, and mitigating stress-induced damage in plants [34,39]. Therefore, exploring the potential involvement of BRs in mediating wheat's response to high temperature stress is warranted.

Crosstalk between BRs and Heat Stress Signaling : Emerging evidence suggests a crosstalk between BR signaling and heat stress response pathways. BRs are known to regulate the expression of heat shock proteins (HSPs), which are critical components of the plant's heat stress defense mechanism [40]. Understanding the molecular basis of this interaction could unveil novel strategies to enhance heat stress tolerance in wheat.

Agricultural Implications and Stress Tolerance Enhancement: Studying the interplay between BRs and high temperature stress has profound implications for agriculture. Unraveling the regulatory mechanisms could enable the development of innovative strategies for breeding heat-tolerant wheat cultivars. Modulating BR signaling pathways may offer a means to enhance the plant's natural ability to cope with heat stress, thereby increasing yield stability and resilience.

Table 2. Brassinosteroid Biosynthesis and Signaling Pathways

Gene/Transcription Factor	Function in Pathway	References
Det2 (De-Etiolated 2)	Early biosynthesis step	[41]
Cpd (Constitutive Photomorphogenic Dwarf)	Brassinosteroid synthesis	[41]
Cpy (Constitutive Photomorphogenic1)	Brassinosteroid synthesis	[41]
Br6ox1 (Brassinosteroid-6-Oxidase 1)	Brassinosteroid synthesis	[42]
Br6ox2 (Brassinosteroid-6-Oxidase 2)	Brassinosteroid synthesis	[43]
Bri1 (Brassinosteroid Insensitive 1)	Receptor for brassinosteroids	[40]
Bak1 (Brassinosteroid Insensitive 1-Associated Kinase 1)	Co-receptor	[41]
Bsu1 (Brassinosteroid Insensitive 2 Suppressor 1)	Negative regulator	[16]
Bin2 (Brassinosteroid-Insensitive 2)	Kinase in signaling pathway	[8]
Bzr1 (Brassinazole-Resistant 1)	Transcription factor	[44]
Bes1 (Bri1-Ems Suppressor 1)	Transcription factor	[33]
Serk1 (Somatic Embryogenesis Receptor-Like Kinase 1)	Co-receptor	[7]
Gsk3/Shaggy-Like Kinases	Negative regulators	[16]
Pp2a (Protein Phosphatase 2a)	Negative regulator	[45]

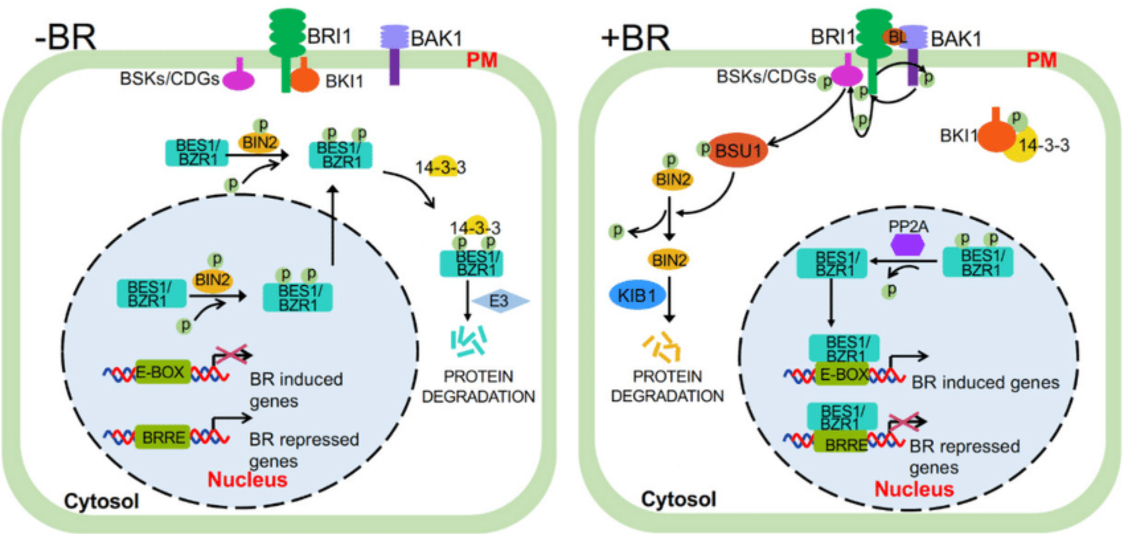

Fig. 2. Overview of BR signalling pathway, interaction of brassinosteroid hormone with its receptors and signal transduction [46]

Biosynthetic Pathway of Brassinosteroids: The biosynthesis of BRs originates from the mevalonate pathway, leading to the formation of precursor molecules such as campesterol and 24-methylenecholesterol [47]. The conversion of these precursors into bioactive BRs occurs through a series of enzymatic reactions involving multiple key steps [2].

DWARF Genes and BR Biosynthesis: A pivotal breakthrough in understanding BR biosynthesis was the identification of the DWARF genes in Arabidopsis, which are responsible for encoding enzymes involved in various biosynthetic steps. The DWF4 gene encodes a C-22 hydroxylase, catalyzing the conversion of 24-methylenecholesterol to campester). Mutations in DWF4 lead to dwarf phenotypes due to reduced BR synthesis.

C-6 Oxidation and BR Formation: The BR biosynthetic pathway involves C-6 oxidation of sterols through the action of the enzyme C-6 oxidase. This step converts 6-deoxocastasterone into castasterone, a key intermediate in BR production [48,49]. The C-6 oxidation step is essential for enhancing the biological activity of BRs.

Cytochrome P450 Enzymes: Several cytochrome P450 enzymes are pivotal in the later stages of BR biosynthesis, contributing to the conversion of intermediates into bioactive forms. Cytochrome P450 monooxygenases, such as CYP85A2 and CYP90B1, are involved in catalyzing hydroxylation and oxidation reactions that yield active BRs [50].

Biosynthetic Regulation and Feedback Mechanisms: BR biosynthesis is subject to intricate feedback and regulation mechanisms. The BR-insensitive receptor kinase BRI1-associated receptor kinase 1 (BAK1) is implicated in regulating BR biosynthesis by controlling the expression of key biosynthetic genes [51].

8.2 Components of the BR Signaling Pathway: Receptors, Co-receptors, and Downstream Effectors

BR Receptors and Ligand Perception: The BR signaling pathway initiates with the perception of BRs by the brassinosteroid-insensitive 1 (BRI1) receptor kinase, a leucine-rich repeat receptor-like kinase (LRR-RLK) localized in the plasma membrane. BRI1 recognizes BRs and initiates downstream signaling cascades upon ligand binding. The BRI1 homolog BRL3 is implicated in fine-tuning BR response [52].

Co-Receptors and Ligand-Induced Complex Formation: The function of BRI1 is enhanced by its interaction with the co-receptor BRI1-Associated Receptor Kinase 1 (BAK1) (Li et al., 2002). BAK1 is a crucial component in forming the BRI1-BAK1 complex upon ligand binding, facilitating downstream signaling propagation. This ligand-induced complex formation amplifies and modulates BR si [53].

Downstream Effector Proteins: Upon activation, the BRI1-BAK1 complex phosphorylates downstream effector proteins that include BZR1 and BES1/BZR2, two key transcription factors These transcription factors regulate gene expression by binding to specific DNA sequences, modulating the expression of target genes involved in growth, development, and stress responses.

Regulation of Transcription and Growth: BZR1 and BES1/BZR2 orchestrate the transcriptional response to BR signaling by interacting with various transcriptional co-factors and chromatin-modifying enzymes (Oh et al., 2014). The activation or repression of target genes by BZR1 and BES1/BZR2 regulates cell elongation, division, and differentiation, contributing to overall plant growth and development**.**

Feedback Mechanisms and Crosstalk: egative feedback mechanisms, including the induction of feedback inhibitors like DWF4, ensure fine-tuning of BR signaling [54,55,56]. Moreover, BR signaling is intricately connected to other hormonal pathways, including auxins, gibberellins, and abscisic acid, forming a complex network of hormonal crosstalk that coordinates plant responses to changing environmental conditions.

Roles of BRs in plant growth, development, and stress responses: Potential functions of brassinosteroid in horticultural plants.

Stimulating Cell Expansion and Elongation: One of the primary roles of BRs is to promote cell expansion and elongation, contributing to increased organ size and overall plant stature [9]. The activation of BR signaling pathways leads to the upregulation of cell wall-loosening enzymes and the modulation of cell division rates, enhancing tissue growth.

Modulating Vascular Differentiation and Xylem Formation: BRs play a pivotal role in vascular differentiation and xylem development by regulating the expression of genes involved in lignin biosynthesis and vessel formation [54,56].

This function is critical for maintaining water transport, mechanical support, and nutrient distribution within plants.

Regulating Root Growth and Architecture: BRs influence root growth and architecture by modulating root meristem activity, lateral root formation, and root hair elongation [57]. BR-mediated signaling pathways affect auxin distribution and sensitivity, thereby shaping root system architecture and nutrient uptake efficiency.

Controlling Reproductive Development: BRs are pivotal in regulating various aspects of reproductive development, including pollen development, pollen tube elongation, ovule development, and flower opening [61]. BRs ensure successful pollination, fertilization, and seed formation, thus contributing to overall plant reproductive success.

Table 3. Various functions of brassinosteroid hormone

Functions	References
Regulated seed germination	[58]
Modified root architecture system	[50]
Enhanced abiotic stress tolerance	[45]
Regulated stomatal development	[34]
Protected photosynthetic system	[26]
Upregulated antioxidant enzymes system	[27]
Balanced redox homeostasis	[59]
Cell expansion and elongation	[42]
Increased mineral nutrient accumulation	[38]
Reduced heavy metals accumulation	[24]
Enhanced secondary metabolites accumulation	[26]
Fruit ripening	[25]
Flower and fruit development	[60]

Mitigating Abiotic Stress Responses: BRs enhance plant tolerance to various abiotic stresses, including drought, salinity, and high temperature [1]. BR-mediated stress responses involve the modulation of antioxidant defenses, osmotic regulation, and stress-related gene expression, thereby improving plant resilience**.**

Interplay with Biotic Stress Resistance: BRs are implicated in the interplay between plant growth and defense against pathogens. BR signaling pathways modulate the expression of defense-related genes and contribute to the activation of systemic acquired resistance [62].

8.3 High Temperature Stress in Wheat

A. Impact of high temperature stress on wheat growth, development, and yield

High Temperature Stress and Growth Impairment: High temperature stress disrupts fundamental growth processes in wheat, including cell division, elongation, and differentiation [63]. Elevated temperatures can induce premature senescence of leaves, reducing the photosynthetic capacity and assimilate allocation to developing grains.

Table 4. High temperature tolerance in various crop varieties

Crop Variety	High Temperature Tolerance Range (°F)
Heat-Tolerant Wheat	85-95°F (29-35°C)
Drought-Resistant Rice	90-100°F (32-38°C)
Heat-Resilient Maize (Corn)	90-105°F (32-40°C)
Heat-Tolerant Tomatoes	85-95°F (29-35°C)
Heat-Resistant Lettuce	75-85°F (24-29°C)
Heat-Tolerant Potatoes	75-85°F (24-29°C)
High-Temperature Grapes	90-100°F (32-38°C)
Heat-Tolerant Coffee	75-85°F (24-29°C)
Drought-Resistant Cotton	95-105°F (35-40°C)
Heat-Resilient Apples	80-90°F (27-32°C)
Heat-Tolerant Citrus Fruits	85-95°F (29-35°C)
Heat-Resistant Peaches	85-95°F (29-35°C)
Heat-Tolerant Chickpeas	80-90°F (27-32°C)
Heat-Resilient Blueberries	85-95°F (29-35°C)
High-Temperature Melons	90-100°F (32-38°C)
Heat-Tolerant Almonds	85-95°F (29-35°C)

Phenological Changes and Reproductive Failure: High temperatures during critical developmental stages, such as flowering and grain filling, lead to reproductive failure in wheat. Pollen viability and germination are compromised, resulting in reduced seed set and smaller grains [64]. Yield losses due to inadequate grain filling and decreased kernel weight are common outcomes of heat stress.

Photosynthesis and Carbohydrate Metabolism Disruption: Elevated temperatures negatively impact photosynthetic efficiency by affecting chlorophyll content, stomatal conductance, and electron transport rates [65]. Heat stress alters carbohydrate metabolism, leading to decreased starch accumulation in grains and limiting the supply of assimilates for growth and yield.

Protein Denaturation and Oxidative Stress: High temperatures induce protein denaturation and aggregation, impairing enzyme activities involved in essential metabolic pathways [66]. Increased temperature triggers oxidative stress by generating reactive oxygen species (ROS), leading to lipid peroxidation and cellular damage.

Molecular Insights into Heat Stress Responses: Transcriptomic and proteomic studies have provided insights into the molecular responses of wheat to high temperature stress. Heat shock proteins (HSPs), antioxidants, and stress-responsive transcription factors are upregulated to counteract heat-induced damage [3,11,12].

Breeding Strategies for Heat Tolerance: Efforts to enhance wheat heat tolerance involve breeding for heat-resistant cultivars through the selection of genetic traits associated with improved photosynthesis, heat shock protein expression, and antioxidant defense [67]. Modern biotechnological tools, such as marker-assisted selection and genetic engineering, hold promise for developing heat-tolerant wheat varieties.

B. Cellular and physiological responses of wheat to high temperature stress

Cell Membrane Stability and Lipid Composition: High temperatures disrupt the fluidity of cell membranes, leading to increased permeability and leakage of cellular components [42]. Lipid peroxidation and alterations in membrane lipid composition affect membrane integrity and function, ultimately affecting cell viability.

Protein Denaturation and Heat Shock Proteins (HSPs): Heat stress induces protein denaturation and aggregation, leading to functional impairment of enzymes and cellular structures [68]. Heat shock proteins (HSPs), a class of molecular chaperones, are upregulated in response to high temperatures to assist in protein folding, prevent aggregation, and maintain protein homeostasis.

Photosynthesis and Chlorophyll Degradation: Elevated temperatures disrupt photosynthesis by affecting chlorophyll content, thylakoid organization, and electron transport rates [69]. Heat stress triggers the breakdown of chlorophyll molecules, leading to reduced photosynthetic efficiency and compromised energy production.

Oxidative Stress and Antioxidant Defense: High temperature stress induces oxidative stress by promoting the generation of reactive oxygen species (ROS), which damage cellular components [42]. Antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) are activated to scavenge ROS and mitigate oxidative damage.

Water Relations and Osmotic Adjustment: Wheat responds to heat stress by adjusting its water relations through stomatal closure and reduced transpiration rates [64]. Osmotic adjustment mechanisms, including the accumulation of compatible solutes like proline and sugars, help maintain cellular water potential and protect against dehydration.

Hormonal Regulation and Signaling Pathway: Phytohormones, such as abscisic acid (ABA) and ethylene, play a critical role in mediating wheat's responses to high temperature stress [70]. ABA regulates stomatal closure, while ethylene influences membrane stability and the expression of stress-responsive genes.

Metabolic Shifts and Carbon Partitioning: Under heat stress conditions, wheat reallocates carbon and energy resources from growth-related processes to stress response mechanisms [23]. Metabolic shifts redirect carbon partitioning towards osmotic adjustment, antioxidants, and heat stress proteins.

Heat Shock Proteins (HSPs) and Molecular Chaperones: Activation of heat stress-responsive genes, particularly heat shock proteins (HSPs), is a hallmark of the plant's defense against heat stress [23]. HSPs act as molecular chaperones, facilitating proper protein folding, preventing aggregation, and promoting cellular homeostasis under heat stress conditions.

Transcription Factors and Heat Stress-Responsive Genes: Heat stress triggers the activation of various transcription factors (TFs), including heat shock factors (HSFs), AP2/EREBP, and bZIP TFs (Li et al., 2019). These TFs bind to heat stress responsive elements (HSEs) in the promoter regions of target genes, orchestrating the expression of genes involved in stress tolerance, protein folding, and antioxidant defense.

C. Activation of stress-responsive genes and pathways in wheat under heat stress

ROS Scavenging and Antioxidant Pathways: Heat stress-induced ROS production necessitates the activation of antioxidant pathways in wheat cells [45]. Enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) are upregulated to scavenge ROS, minimizing oxidative damage to cellular components.

ABA-Mediated Signaling and Osmotic Adjustment: Heat stress activates abscisic acid (ABA) signaling, leading to stomatal closure and reduced transpiration rates [71]. ABA also triggers osmotic adjustment by regulating the accumulation of compatible solutes like proline and sugars, enhancing cellular water potential and stress tolerance.

Chaperones and Protein Quality Control: Beyond HSPs, chaperones and co-chaperones, such as DnaJ and Hsp70, play pivotal roles in protein quality control under heat stress conditions. These molecular machinery components aid in refolding misfolded proteins and facilitating their degradation when irreversibly damaged.

Ubiquitin-Proteasome System and Protein Turnover: Heat stress-induced protein denaturation leads to the activation of the ubiquitin-proteasome system, which plays a crucial role in protein turnover and degradation. Ubiquitin ligases mark damaged proteins for proteasomal degradation, preventing the accumulation of misfolded proteins.

Phytohormone Crosstalk and Gene Regulation: Heat stress responses are intricately connected to other hormonal pathways, including jasmonic acid (JA), salicylic acid (SA), and ethylene [70] Crosstalk between these phytohormones modulates the expression of stress-responsive genes and fine-tunes plant responses to heat stress.

8.4 Interaction Between Brassinosteroids and High Temperature Stress

A. Theoretical basis for the crosstalk between BR signaling and heat stress response

Brassinosteroid Signaling Pathway Overview: The BR signaling pathway involves receptor activation, co-receptor interaction, and downstream effector regulation [51]. BRI1 and BAK1 receptor complex, along with BZR1 and BES1 transcription factors, mediate the BR response by modulating gene expression, growth, and development.

Heat Stress Signaling Pathways: Heat stress activates a complex network of signaling pathways, including heat shock proteins (HSPs), transcription factors, and ROS scavenging enzymes [21]. These pathways collectively enable plants to mitigate heat-induced damage and mount a coordinated stress response.

Theoretical Mechanisms of Crosstalk: 1. Protein Stabilization: BR signaling may confer thermotolerance by stabilizing proteins involved in heat stress response, including HSPs and antioxidant enzymes [72].

2. Transcriptional Regulation: BR-responsive transcription factors, such as BZR1, may intersect with heat stress-responsive transcription factors to modulate shared target genes.

3. Hormonal Crosstalk: BRs may influence the activity of other hormones involved in heat stress responses, such as abscisic acid (ABA) and ethylene [70].

BR-Mediated Heat Stress Tolerance: BRs have been proposed to enhance heat stress tolerance by promoting stomatal closure, activating antioxidant defense systems, and modulating the expression of stress-responsive genes [73].

Phosphorylation-Mediated Crosstalk: Phosphorylation events play a critical role in BR signaling and heat stress responses. Crosstalk may occur through shared or interconnected phosphorylation cascades that converge on key regulatory proteins [74].

B. Previous studies indicating potential roles of BRs in heat stress tolerance

Enhancement of Thermotolerance by BRs: Recent studies have suggested that exogenous application of BRs can enhance thermotolerance in various plant species. For instance, Li demonstrated that BR treatment improved photosynthetic efficiency and reduced oxidative damage in tomato plants subjected to heat stress. Similarly, reported that BR treatment increased the activity of antioxidant enzymes and reduced lipid peroxidation in wheat seedlings exposed to high temperatures.

Modulation of Heat Stress-Responsive Genes by BRs: BRs have been shown to modulate the expression of heat stress-responsive genes. In a study [23], it was found that BR treatment upregulated the expression of HSP genes and other stress-related genes in Arabidopsis under heat stress conditions. This suggests that BRs may play a role in regulating the transcriptional responses to heat stress.

Stomatal Regulation and Water Relations: BRs have been implicated in stomatal regulation, which plays a crucial role in plant water relations under heat stress. [76] demonstrated that BR treatment improved stomatal closure and reduced transpiration rates in maize plants subjected to high temperatures. This indicates that BRs might contribute to maintaining water balance and preventing dehydration under heat stress conditions.

Mitigation of Protein Denaturation and Aggregation: BRs may mitigate protein denaturation and aggregation caused by heat stress. [76] showed that BR treatment reduced protein aggregation and preserved the integrity of chloroplasts in wheat leaves exposed to elevated temperatures. This suggests that BRs might confer protection to cellular structures and prevent irreversible damage under heat stress.

Regulation of ROS Scavenging and Antioxidant Defense: BRs have been linked to the modulation of ROS scavenging and antioxidant defense systems. In a study [29], BR treatment enhanced the activity of antioxidant enzymes and reduced ROS accumulation in rice plants subjected to heat stress. This indicates that BRs may contribute to minimizing oxidative damage and maintaining redox homeostasis.

C. Hypothesized mechanisms by which BRs may alleviate high temperature stress effects

1. **Stabilization of Cellular Membranes**

BRs may enhance the stability of cellular membranes under high temperature stress. It has been proposed that BRs could regulate membrane fluidity and composition, potentially reducing membrane permeability and preventing cellular damage. This could contribute to maintaining cell integrity and function under heat stress conditions.

2. **Activation of Heat Shock Protein Expression**

BRs might enhance the expression of heat shock proteins (HSPs), a class of molecular chaperones that assist in protein folding and prevent aggregation under stress. By upregulating HSPs, BRs could facilitate proper protein folding and maintain cellular homeostasis, minimizing heat-induced damage.

Table 5. Transcription Factors involved in Biosynthesis of Brassinosteroid

Gene/Transcription Factor	Function in Pathway	Source	Reference
Det2 (De-Etiolated 2)	Early biosynthesis step	Arabidopsis Genome	[7]
Br6ox1 (Brassinosteroid-6-Oxidase 1)	Brassinosteroid synthesis	Arabidopsis Genome	[75]
Bri1 (Brassinosteroid Insensitive 1)	Receptor for brassinosteroids	Arabidopsis Genome	[23]
Bzr1 (Brassinazole-Resistant 1)	Transcription factor	Arabidopsis Genome	
Bin2 (Brassinosteroid-Insensitive 2)	Kinase in signaling	Arabidopsis Genome	[7]
Dwf4 (Dwarf4)	Biosynthesis enzyme	Arabidopsis Genome	[37]

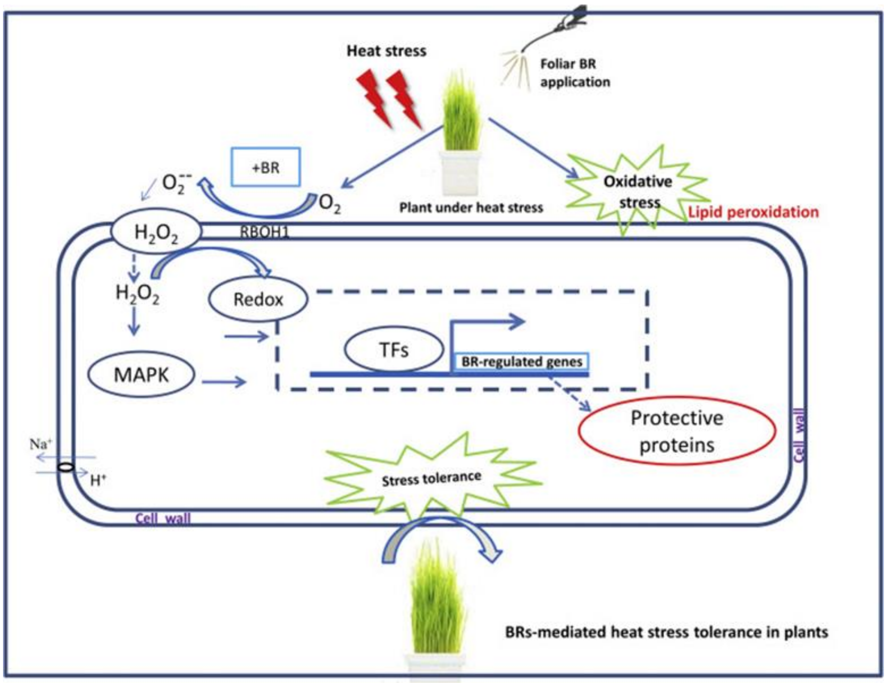

Fig. 3. Diagrammatic representation on the mechanism by which BRs may alleviate high temperature stress effects (Rehman., et al. 2022)

3. Antioxidant Enzyme Induction

BRs could induce the expression of antioxidant enzymes, such as superoxide dismutase (SOD) and catalase (CAT), which play a key role in scavenging reactive oxygen species (ROS) generated under heat stress [45]. By enhancing the antioxidant defense system, BRs may reduce oxidative stress and protect cellular components.

4. Regulation of Photosynthetic Efficiency

BRs may positively influence photosynthetic efficiency by maintaining chlorophyll content, improving stomatal conductance, and promoting efficient light harvesting. By optimizing photosynthesis, BRs could enhance energy production and assimilate availability, which are crucial for plant growth and stress tolerance.

5. Modulation of Hormonal Crosstalk

BRs could interact with other hormones, such as abscisic acid (ABA) and ethylene, to modulate hormonal crosstalk under high temperature stress [70]. This crosstalk could fine-tune stress responses, including stomatal closure, osmotic adjustment, and gene expression regulation.

6. Improvement of Water Relations

BRs may enhance water relations by regulating stomatal conductance and promoting efficient water use under heat stress conditions [76]. This could contribute to maintaining turgor pressure and preventing water loss, especially crucial for plant survival during heat stress.

7. Protein Denaturation Prevention

BRs might prevent protein denaturation and aggregation by promoting proper protein folding and stabilization [72]. This could protect essential enzymes and structural proteins from irreversible damage caused by high temperatures.

9. CONCLUSION

The growth and yield potential of wheat are vital for global food security, yet genetic improvements in yield have lagged, with a less than 1% annual increase. A contributing factor to this plateau is the prevalence of terminal heat stress, notably observed in South Asia and particularly India. Wheat cultivation in India faces supra-optimal temperatures during various growth stages due to its sub-tropical environment, impacting yield, d quality. High temperatures during grain filling have been linked to a substantial reduction in yield, with a 4%

decrease per one-degree rise in ambient temperature. The detrimental effects of heat stress extend throughout wheat growth, including shorter developmental phases, reduced organ size and count, perturbations in carbon assimilation processes (transpiration, photosynthesis, and respiration), and decreased kernel weight. Efficient photosynthesis and assimilate partitioning during the vegetative phase play a pivotal role in determining generative organ formation, subsequently impacting overall yield potential. Although research has explored the physiological and biochemical effects of high temperatures on wheat, transcript profiling studies have been limited, particularly in seedlings and flowering stages. Existing studies have primarily concentrated on grain growth periods. As such, a comprehensive understanding of the impact of elevated temperatures on wheat's transcriptome during these critical stages is needed to address the challenges posed by climate change and improve wheat yield in the changing environment.

While the rationale for investigating the BR-high temperature stress interaction is compelling, challenges remain. Elucidating the specific molecular mechanisms and identifying key genes involved in this crosstalk require advanced techniques such as transcriptomics, proteomics, and genetic manipulation. Overcoming these challenges will pave the way for a comprehensive understanding of how BRs contribute to wheat's response to high temperature stress.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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