The Role of Salicylic Acid and Nitric Oxide in Plant Heat Response

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Cambridge
Scholars
Publishing

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This book first published 2023

Cambridge Scholars Publishing

Lady Stephenson Library, Newcastle upon Tyne, NE6 2PA, UK

British Library Cataloguing in Publication Data
A catalogue record for this book is available from the British Library

ISBN (10): 1-5275-4073-1
ISBN (13): 978-1-5275-4073-6

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CHAPTER 1

HIGH-TEMPERATURE STRESS AND ITS IMPACT ON AGRICULTURE - CURRENT SCENARIO

Abstract

High temperature (HT) stress is one of the most devastating environmental stressors that affect agricultural productivity and global food security. HT stress imposes severe repercussions on crop plants and livestock growth and productivity. HT stress provokes stigma exertion and drastically reduces pollen efficiency, leading to increased flower drop and poor fruit setting. Several physiological attributes, such as membrane integrity, relative water content and ion/osmotic homeostasis, are disrupted under HT stress. In 21st-century agriculture, HT stress has become a significant concern for plant breeders and horticulturists for sustaining the growth and productivity of crop plants under HT stress conditions. Therefore, this chapter reviews HT stress's global and current impact on agriculture. In addition, what preventive measures can be adopted to overcome the adverse effect of HT stress on plants has been critically discussed. Further, how recent advancements in OMICS and biotechnological tools can be exploited for breeding HT tolerance plants.

Keywords: HT stress, Growth, Productivity, Phytohormone, Technological interventions

Introduction

High temperature (HT) stress has become one of the most threatening climate adversities, severely affecting crop phenology, productivity and livelihoods of people around the globe (Pospíšil 2016). Correspondingly, researchers have contemplated that a progressive increase in the earth's air temperature via anthropogenic activities could trigger global warming, thus substantially affecting agricultural produce (Lavania et al. 2015). Frequent climate change has led to a drastic increase in heat waves that have profoundly affected the earth's climatic patterns and global warming (Pospíšil 2016). Furthermore, climate change and increasing heat waves have also altered the earth's geography by increasing deserts and dry and arid land due to frequent drought episodes (Lamers et al. 2020). Recently, Intergovernmental Panel on Climate Change (IPCC) have warned that an increase in air temperature could lead to irregular rainfall, soil salinity/ drought, and CO_2 emission (Jehn et al., 2022). Consequently, it has become imperative to delve deeper into the plant-temperature interactive process that may help find novel mechanisms to prevent crop death and agricultural loss (Lavania et al. 2015).

Being sessile, plants are constantly exposed to various biotic and abiotic stresses that severely affect their growth and metabolism (Niu and Xiang, 2018). HT stress is the most devastating abiotic stress that causes huge crop loss in various parts of the world, thus hampering agricultural productivity and global food security (Szymańska et al. 2017). One of the early reverberations of HT stress on plants is the disruption of homeostasis, i.e., ion and osmotic homeostasis. This disruption of homeostasis occurs at both cellular and whole plant levels leading to cellular damage and cell death (Lamers et al., 2020). Therefore, to survive under abiotic stress plant must exhibit three related activities (i) damage must be prevented or alleviated (ii) homeostasis must be re-established in a new and stressful environment (iii) growth must resume albeit at a slow rate (Niu and Xiang 2018).

HT stress instigates detrimental effects on plants due to increased oxidative damage of cells and tissues as provoked by the excess generation of reactive oxygen species (ROS). ROS such as hydrogen peroxide, singlet oxygen and superoxide anion is most commonly known to induce oxidative damage in plants when their levels exceed the threshold limit (Awasthi et al. 2015). These ROS act as signaling molecules at a low level, thus modulating signal transduction pathways under stress conditions. When their level reaches beyond the cell's antioxidative capacity, they can affect many cellular processes, affecting membrane fluidity and leading to cell death and apoptosis (Pospíšil 2016). At a molecular level, HT stress alters expression of stress-responsive genes, regulatory proteins, and osmoprotectants such as proline and glycine betaine (Awasthi et al. 2015).

Therefore, developing HT stress-tolerant crop plants is the need of the hour. However, several factors, limits and perse., are the significant challenges to the plant science community that prevent the development of new HT stress-tolerant cultivars such as HT stress duration, plant type and several other environmental factors such as humidity, heat waves which in conjugation with HT stress represent a significant bottleneck for plant scientists (Rykaczewska 2015). In addition, researchers are yet to identify genes/proteins responsible for imparting HT stress tolerance in plants. Since HT stress tolerance is a quantitative trait governed by multiple genes, linking genes to HT tolerant trait is a rigorous process involving a series of hybridisation experiments using HT tolerant and HT susceptible plants. Plant scientists are exploiting state-of-the-art techniques such as system and synthetic biology tools and trying to unravel how plants can withstand climate adversities. This chapter will discuss HT stress's global and current impact on essential crop plants. Further, an up-to-date perspective of how HT stress is becoming an imminent threat to agriculture, livestock and humankind is comprehensively described. Lastly, strategies for enhancing HT stress tolerance in plants using phytohormones as an external application are also discussed.

Global scenario of HT stress

Due to the global oceans' vast size and heat capacity, a tremendous amount of heat energy is required to raise the earth's surface temperature even by a smaller fraction (Li et al. 2021). According to the reports from NASA, the earth's surface temperature has increased to roughly 2°C since the pre-industrial era (1880-1900), which may not seem much. Still, it represents a compelling increase in the accumulated heat (Zandalinas et al. 2021). These gradually gathered heat provokes regional and seasonal temperature fluctuations causing melting of sea ice and snow cover, and low/excess rainfall, thus significantly altering the habitat pattern of plants and animals (Chaudhry and Sidhu 2022). The drastic change in habitat ranges could benefit some lifeforms. They are expanding their population, while for most of them, it functions by shrinking their population. For example, the temperature rises exponentially in land areas compared to the oceans, and the Arctic is warming faster than other regions (Chaudhry and Sidhu, 2022).

Recently, the global climate report of 2022 from the National Centres for Environment Information (Figure 1), despite of La Nina climate pattern in the tropical Pacific, each month of 2022 was 10th warmer than average (Parmesan et al. 2022). Furthermore, their report concluded that 2022 was the sixth warmest year since the global temperature record was incepted in 1880 (Parmesan et al. 2022). Researchers have shown that the earth's surface temperature increase has not been uniform and inferred that most land areas are warming rather than cooling (Masson-Delmotte et al., 2022). NOAA's 2021 annual climate report, the average temperature of land and ocean showed a combined increase of 0.08°C per decade since 1880, whereas since 1981 average rate of growth in the combined average temperature of land and sea is more than twice, i.e., 0.18°C per decade (Setzer and Higham 2022). According to a study, an increase in the earth's surface temperature and the warming of oceans will depend on the rate of carbon dioxide emission and other greenhouse gases (Masson-Delmotte et al. 2022). Today, deforestation, burning fossil fuels and other anthropogenic activities are accumulating CO_2 at an exaggerated rate, i.e., about 11 billion metric tons to over 40 billion metric tons to the atmosphere yearly (Setzer and Higham 2022).

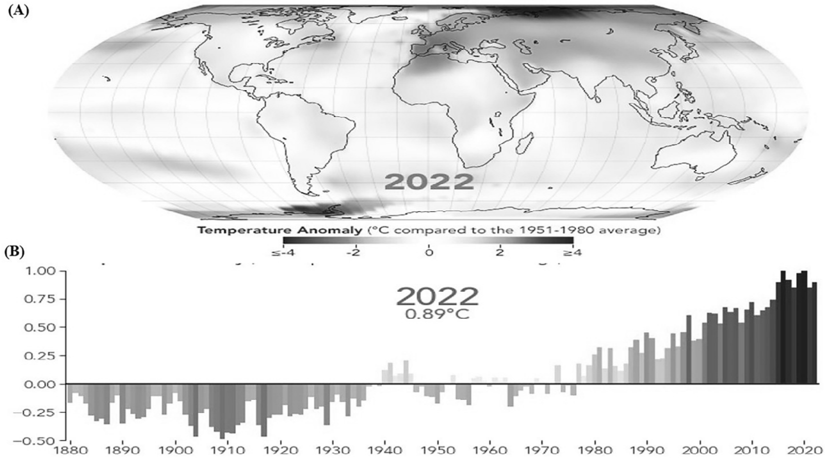

Figure 1 An overview of global average surface temperature between 1993 and 2022 in degrees Fahrenheit per decade (Adapted from http://www.climate.gov/media/15022)

In the 20th century, we witnessed a rapid increase in the global mean temperature of the earth and oceans. This expansion could be attributed to natural variability and rapid developments of factories, power plants and the use of motor vehicles after World War II (Armstrong McKay et al. 2022). Further, research findings have corroborated that greenhouse accumulates at a slower rate. Still, they remain in the atmosphere for a long time which could also be one of the reasons for a gradual rise in the earth's surface temperature (Armstrong McKay et al. 2022). The temperature fluctuations locally, i.e., within a short period, such as day and night temperatures in summer and winter, don't significantly contribute to global warming.

In contrast, the increase in global warming is mainly dependent on the rise in the earth's surface temperature, which is reflected in terms of sunlight received by the planet and the amount of it radiates back to space (Moran et al. 2008). The amount of solar radiation that emits back to space is proportional to the composition of greenhouse gases in the atmosphere (Zandalinas et al. 2021). Even a single degree increase in the global mean temperature is significant because it takes a massive amount of heat energy warm the ocean and surface of the earth (Zandalinas et al. 2021). The image below depicts the global temperature anomalies in 2022.

Current scenario of HT stress

The earth's surface temperature is progressively increasing, and heat waves are becoming frequent and intense around the globe. For example., in India, intense HT has been recorded in April and May every year, of which 2022 recorded an unusual increase in the maximum and minimum temperature (He et al. 2022). According to the current Indian metrological report, 2022 witnessed extreme temperatures, i.e., up to 8°C–10.8°C and much lower (60-80%) rainfall (He et al. 2022). Agricultural scientists remember 2022 as one of the most catastrophic years, severely affecting agricultural productivity due to extreme temperatures and low to moderate rainfall (Chand et al., 2022). In recent years, Indian agriculture is becoming increasingly vulnerable to climate extremes mainly due to temperature fluctuations and low rainfall that have significantly impacted the growth and productivity of crop plants (Chand et al. 2022). The researchers delve deeper into the action of HT stress on decreasing the productivity of crop plants. They identified that HT stress resulted in sunburn, lipid peroxidation and reduced moisture content resulting in flower drop and low fruit setting in economically important crops (Chaudhry and Sidhu 2022). In addition, the review report of IPCC convoluted that climate change is happening faster than expected, and its effect can be seen globally as the production of major staple crops is steadily declining (Shekhawat et al. 2022).

In India, a temperature rise significantly alters rainfall frequency, timing and magnitude, affecting relative humidity, heat waves and water availability to agricultural lands (Singh et al., 2022). Indian scientists have elucidated heat waves' magnitude by combining heatwaves and drought dossiers and employing a standardised precipitation index (SPI) (Shekhawat et al. 2022). They concluded that the area affected by high temperature had increased to nearly 4 per cent since 2010, a significant concern for agriculture and allied sectors (Rivero et al. 2022). The increasing temperature or heat waves in the inevitable part of India are primarily due to the persistent warm anticyclone-inducing synoptic situation favouring heat waves (Singh et al. 2022). It could also be due to the absence of adequate moisture in the upper atmosphere, or there is practically no cloud in the sky (Ding and Yang, 2022). Low rainfall can also cause the drying of soil, due to which intense solar radiations can sporadically warm the surface of the ground, thus exaggerating the soil temperature (Rivero et al., 2022).

Still, the World Metrological Organization (WMO) has yet to adopt a standard definition for heat waves. Still, according to IMD, heat waves become severe if the temperature of a particular region becomes 5-6°C higher than usual. Understanding the gravity of the situation, IMD has portrayed those extreme climatic conditions like the present one could become more frequent in the coming years due to climate change. Therefore, concerted efforts are required to develop new technologies that can map variations in climatic conditions in real-time, thereby allowing the implementation of protective measures for improving crop growth and productivity under harsh environments. Furthermore, researchers are also rewiring plants' innate immune systems by growing them in an artificial environment that mimics the natural environment, which may help identify new genes/proteins that help them withstand climate extremes.

Impact of HT Stress on 21^{st}-century Agriculture

High-temperature stress, particularly in March and April, profoundly affects crop plants' growth and reproduction, thus limiting agricultural productivity and global food security (Sun et al. 2019). The first physical impact of HT is specifically attributed to the loss of water from the soil or within the plants (Table 1) (Herold et al. 2018). Water loss induces significant changes in plants' ion/osmotic homeostasis, thus affecting their oxidative phosphorylation and photophosphorylation (Mall et al. 2017). In extreme cases, the low relative water content may also induce chlorophyll degradation due to the peroxidation of membranes and electrolytic leakage (Lobell et al. 2015). The generation of oxidative stress is also an essential physiological impact of HT, affecting many cellular processes in plants, such as cell divisions and elongation (Adhikari et al. 2015). The generated

Table 1: High-temperature stress and its impact on agriculture in the current scenario

Topic	Information	References
Definition of High-Temperature Stress	High-temperature stress in plants refers to the exposure of crops to elevated temperatures beyond their optimal range, leading to physiological and metabolic disruptions.	IPCC. (2014)
Impact on Crop Growth and Yield	High temperatures can negatively affect various aspects of plant growth and development, leading to reduced crop yield and quality. The impacts include:	Challinor et al. (2014)
	Decreased photosynthesis and carbon assimilation	Lobell and Gourdji (2012)
	Impaired reproductive development and reduced pollination	Schlenker and Roberts (2009)
	Increased water stress and reduced water-use efficiency	Hatfield et al. (2011)
	Altered nutrient uptake and nutrient imbalances	Raja et al. (2018)
	Enhanced susceptibility to pests, diseases, and weeds	Lemoine (2015)
Strategies to Mitigate High-Temperature Stress	To mitigate the impact of high-temperature stress on agriculture, several strategies can be employed, such as:	Bita and Gerats (2013)
	Developing heat-tolerant crop varieties through breeding and genetic engineering	Prasad and Djanaguiraman (2014)
	Implementing agronomic practices, such as adjusting planting dates and irrigation scheduling	Mohanty et al. (2013)
	Adoption of conservation agriculture practices to improve soil moisture retention	Lal (2015)
	Enhancing crop resilience through foliar applications of stress-mitigating compounds	Farooq et al. (2011)

oxidative stress provokes stomatal closure, thus affecting the CO_2 diffusion efficiency and stimulating photorespiration leading to cell death and apoptosis (Jin et al. 2016). In addition, HT stress also negatively modulates the transpiration rate, thus affecting the internal continuum of plants due to reduced cooling and increased temperature in cellular compartments (Sun et al. 2019).

Several studies have proclaimed that HT-induced oxidative stress is often associated with intense heat waves and high water use efficiency. C3 plants generally can adapt themselves to temperature variations. However, temperature above a certain threshold negatively affects photosynthesis and respiration. CAM plants can also acclimate to extreme environments as they can hibernate in broad daylight and activate their photosynthesis at night. C4 plants can tolerate HT stress; therefore, their growth and productivity are considerably higher than C3 and CAM plants (Lobell et al. 2015). In addition, livestock productivity is also greatly influenced by the HT environment (Malhi et al. 2021). According to the reports, the ambient environment for livestock is when the thermal heat index (THI) is below or equal to 72 and THI above 85, drastically affecting their feed intake and productivity (Adhikari et al. 2015). Due to lower feed intake, the livestock develops severe implications such as reduced libido, fertility and embryonic survival (Belhadj Slimen et al. 2016). HT stress also severely affects their metabolism by disrupting ion homeostasis due to a rapid decrease in NA^+ and K^+ (Belhadj Slimen et al. 2016).

HT stress negatively impacts poultry farming by causing broilers discomfort so they can no longer reproduce (Polsky et al. 2017). HT greatly influences their growth, behaviour and immune response by hampering their feed conversion and relative weight gain (Polsky et al. 2017). A recently published report signifies that fluctuation in ambient temperature provokes birds to reduce their feed consumption by 5-7% for every 1°C rise in ambient temperature (Das et al. 2016). The temperature fluctuations make it difficult for birds to balance heat production and heat loss, reducing their dietary digestibility and leading to protein loss and decreased calcium levels (Das et al. 2016). HT stress also affects the hen's reproducibility, thus affecting the production of quality eggs (Yavuz et al. 2023). Likewise, an increase in ocean temperature harms fisheries and aquaculture due to variations in sea surface temperature, circulation patterns and increased acidification via anthropogenic activities (Polsky et al. 2017). Recently, findings have confirmed that a global rise in temperature will harm tropical and subtropical ecosystems (Polsky et al. 2017). Drastic temperature shifts will increase the sea level due to the melting the polar ice cap and glaciers, thus impacting mangrove forests and marine fish nursery grounds (Belhadj Slimen et al. 2016). High sea surface temperature will also directly affect swimming and the physiological properties of fish by lowering the level of dissolved oxygen (Yavuz et al. 2023). The low level of dissolved oxygen could be attributed to the effect of HT on stratification leading to rapid expansion in an algal bloom.

Traditional strategies for the management of HT stress

HT in different parts of the world has triggered massive heat waves severely affecting the growth and productivity of crop plants (Wen et al. 2019). According to a report, major wheat-growing regions in India experienced a 3-4°C increase in average temperature as compared to the previous year, thus hampering both the quality and quantity of grains (Tiwari et al. 2017). In India, wheat is usually grown in the month of February-March in an area of about 31 million hectares, and the crops usually experience HT stress during the 4th weeks of March and 1st week of April (Yadav et al. 2022). The farmers use various protective measures to protect their crops from HT stress-induced oxidative damage. First, exploitation of heat-tolerant varieties to develop new hybrids capable of withstanding HT. Technologies such as residue management, direct seeding, and a spray of KNO_3 (0.5%) at anthesis stages can minimise yield losses during HT stress conditions (Singh et al. 2020). Repeated irrigation from time-time can alleviate HT stress-induced oxidative damages by maintaining ion/osmotic homeostasis in plants (Janni et al. 2020). HT stress significantly decreases the fruit setting in plants due to poor pollination leading to flower drop (Godoy et al. 2021).

Researchers have used drip irrigation along with organic mulch to prevent HT stress-induced oxidative damage in plants (Mendonca et al. 2021). Mulching helps retain prolonged soil moisture under HT stress, and foliar spray with 2-4% kaolin will prevent water loss in the form of transpiration, thus improving the physiological process under temperature extremes (Mendonca et al. 2021). In tomato plants, researchers have used drip irrigation twice daily, followed by an organic mulch of 5-8 cm thickness to maintain a friendly environment in the soil. In addition, some researchers also recommend planting maise plants to protect tomato plants from heat waves (Mendonca et al. 2021). Further, external applications of salicylic acid and nitric oxide have also been proven to alleviate HT stress-induced oxidative damage in tomato plants (Zhang et al. 2020). In radish, using a shading net with frequent drip irrigation maintain soil moisture and significantly boosts growth and productivity under HT stress conditions (Matamoros et al. 2022).

The techniques mentioned above are traditional ways to minimise HT stress's negative effect on crop plants. These techniques stimulate short-term adaptive mechanisms in plants by modulating their innate immune response, thus improving their resilience under climate extremes (Matamoros et al. 2022). However, to develop crop plants resilient to HT stress, researchers are exploiting molecular biology tools in conjunction with OMICS techniques to identify genes/proteins conferring HT stress tolerance (Table 2) (Bhardwaj et al. 2021). The identified genes are then used to develop transgenic plants that can withstand harsh environmental cues without affecting their growth and productivity (Janni et al. 2020). Since the cultivation of transgenic plants is limited and, in many countries, it is not approved by the government, enhancing HT stress tolerance via alternative means is the only viable option (Janni et al. 2020). Recently, exogenous applications of various phytohormones and osmoprotectants have been shown to modulate physiological and biochemical processes in plants exposed to abiotic and biotic stresses. A brief about the role of these phytohormones and osmoprotectants is described in the following sections.

Table 2 Traditional and modern strategies for the management of high-temperature stress in plants

Strategy	Description	References
Traditional Strategies		
Shade Provision	Providing temporary or permanent shade structures to reduce direct exposure of plants to high temperatures.	Nadeem et al. (2018)
Mulching	Applying organic or inorganic mulch materials around plants to reduce soil temperature, conserve moisture, and suppress weed growth.	Farooq et al. (2011)
Traditional Crop Selection and Management	Selecting and cultivating crop varieties that are known to tolerate or adapt better to high-temperature conditions.	Mittler (2006)

Modern Strategies		
Genetic Engineering	Developing transgenic crops with improved heat tolerance by introducing genes that regulate heat shock proteins or antioxidants.	Wahid et al. (2007)
Marker-Assisted Breeding	Using molecular markers to identify and select plants with desired heat tolerance traits during the breeding process.	Najeeb et al. (2020)
Exogenous Application of Plant Growth Regulators	Applying plant growth regulators, such as brassinosteroids or salicylic acid, to enhance heat stress tolerance in plants.	Hasanuzzaman et al. (2012, 2013)
Precision Irrigation	Implementing irrigation systems that provide water directly to the root zone, optimizing water use efficiency and reducing heat stress.	Singh et al. (2014)
Protective Foliar Sprays	Applying foliar sprays containing natural or synthetic compounds to enhance the plant's tolerance to high-temperature stress.	Joshi et al. (2007)
Soil Amendments	Incorporating soil amendments, such as organic matter or biochar, to improve soil structure, water holding capacity, and nutrient availability, which can mitigate high-temperature stress effects.	Asli and Neumann (2010)

Advanced strategies for management of HT stress

Phytohormones and osmoprotectants conferring HT stress tolerance

Certain phytohormones, signaling molecules and osmoprotectants have the potential to counteract the adverse effect of abiotic stress-induced oxidative damage in plants (Wu et al. 2019). Recent decades have witnessed an exponential increase in the application of these phytohormones, signaling molecules and osmoprotectants due to their stress ameliorative and growth-promoting properties (Rai et al. 2018, 2020). Phytohormones such as salicylic acid (SA), jasmonic acid (JA), Abscisic acid (ABA) and nitric oxide (NO) as signaling molecules and osmoprotectants such as proline (Pro) or glycine (GB) betaine have been shown to stimulate a plethora of physiological and biochemical process in plants exposed to HT stress (Rai et al. 2020a). In a study, exogenous application of Pro (20 mM) and GB (20 mM) decreases the impact of HT stress-induced oxidative damage in sugarcane plants (Tiwari et al. 2017). Both Pro and GB treatment could have modulated the activity of antioxidative enzymes, thereby maintaining the internal homeostasis of plants under HT stress conditions (Rai et al. 2018). Similarly, another study also confirmed the above notion where the external application of Pro and GB modulate the level of soluble sugars, Na^+, and $K^{+,}$ thus effectively maintaining membrane integrity in HT-stressed plants (Tiwari et al. 2017). Exogenous application of Pro in HT-stressed chickpea plants controlled the generation of MDA and H_2O_2 levels due to enhanced activity of enzymatic and non-enzymatic antioxidants (Parankusam et al. 2017). Further, in their study, they identified a 20-30% increase in shoot length in Pro-treated chickpea plants as compared to non-treated ones, which is indicative of growth promotive and stress ameliorative properties of Pro (El-Beltagi et al. 2020).

SA is a well-acclaimed phytohormone whose stress-ameliorative nature has long been diagnosed (Kaur et al. 2022). It is a phenolic compound, and its controlled application has been reported to have a favourable implication on the growth and immune system of plants exposed to harsh environmental conditions (Rai et al. 2018). External application of SA (0.1 mM) compellingly reduced the generation of thiobarbituric acid reactive substance (TBARS), thus strengthening membrane integrity in grape plants exposed to HT stress (Rai et al. 2020). Likewise, researchers have noted improvement in photosystem II (PSII) efficiency in grapevines upon treating them with 0.1 mM of SA. This effect could be due to SA-mediated modulation of defence signaling genes which could have regulated the activity of RUBISCO, thus maintaining optimum photosynthesis in grapevines under HT stress (Kaur et al. 2022). Similarly, another study reported that treating rice seedlings with 0.5 mM SA significantly altered the effect of HT-induced oxidative damage by contriving ROS generation and its immediate impacts, such as membrane damage and electrolytic leakage (Rai et al. 2020a). Further, researchers identified the molecular notion behind the SA effect. They concluded that it was due to the SA-mediated regulation of stress-responsive genes, particularly heat shock proteins (HSPs), that rendered HT tolerance in rice seedlings (Rai et al. 2020).

ABA, which is widely known as the stress hormone, is also widely exploited externally for improving the growth and productivity of crop plants exposed to environmental cues (Chen et al. 2020). Correspondingly, researchers have demarcated that ABA has been extensively used for imparting HT stress tolerance in plants (Kumar et al. 2019). In chickpea plants, foliar application of ABA (2.5 µM) progressively improved the growth of the seedlings at 40-45°C (Pang et al. 2017). This improvement could be due to ABA-mediated enhanced production of endogenous proline that protected the membrane integrity of seedlings growing under HT stress. In addition, ABA application could also have modulated ROS generation and enzymatic antioxidants, which ultimately have improved their innate immune response (Chu et al. 2018). Conversely, researchers applied fluridone (ABA inhibitor) to counter the stress ameliorative effect of ABA on chickpea plants (Kaur et al. 2019). They identified that exogenous application of fluridone enhances HT stress-induced oxidative damage by stimulating ROS generation, lowering the activities of enzymatic antioxidants and decreasing the level of proline (Kaur et al. 2019). Their study confirmed that the ABA was responsible for improving chickpea plants' growth and productivity under HT stress.

JA is another phytohormone extensively employed to induce plants' abiotic and biotic stress tolerance. Exogenous application of JA (50 µM) to the HT-stressed chickpea enhanced their growth and productivity (Deepika et al. 2022). This protection could be due to the JA-mediated activation of defence signaling pathways that modulated the antioxidant defence system in grapevines exposed to HT (Wang et al. 2020). Similarly, the external application of JA improved fatty acid composition in the membrane of *B. juncea* plants, thus improving their membrane integrity and ion homeostasis under HT stress (Wang et al. 2020). This effect of JA could be due to improved activities of CAT, SOD and APX that may have contrived the level of ROS below the threshold level where they have been effectively used as singling molecules leading to improve growth (Deepika et al. 2022).

NO is a gaseous signaling molecule implicated in the regulation of various physiological and biochemical processes in plants (Fancy et al. 2017). In plants most commonly used NO donor is sodium nitroprusside (SNP) which, when applied at lower concentrations, promotes growth and improved tolerance in plants under abiotic and biotic stress conditions (Rai et al. 2018, 2020). Several researchers have exploited NO donor SNP at low concentrations (2.5 µM), for example, in hyacinth bean, tomato, soybean, chickpea etc. and have well corroborated the growth-promoting effect of SNP (Rai et al. 2018, 2020). In a study, foliar application of SNP (1 and 2.5 µM) significantly improved HT stress tolerance in the callus of *P. communis*. On further investigation, the researchers observed that the application of SNP has tremendously reduced the ROS generation and electrolytic leakage, which have significantly improved the callus growth under HT stress (Corpas et al. 2011).

Similarly, exogenous application SNP have extensively improved the flowering and pod setting in hyacinth bean plants exposed to HT stress. The improved pod setting in the hyacinth bean plants was due to NO-mediated activation of DNA demethylation, which has activated the expression of various downstream stress-responsive genes (Oz et al. 2015). In addition, the SNP-treated plants also showed improved physiological attributes such as lipid peroxidation, relative water content and electrolytic leakage compared to non-treated plants (Oz et al. 2015). Likewise, foliar application of SNP (0.5 mM) improved the level of non-enzymatic antioxidants such as ascorbate and glutathione, thereby improving the growth of hydroponically grown wheat seedlings under HT stress (Parankusam et al. 2017). Various researchers have used the combined application of SA, NO, JA, or ABA to stimulate HT stress tolerance in plants. Their observations mainly postulated that exogenous application of the phytohormones mentioned above could improve stress tolerance and modulate their adaptation under stress conditions if applied at low concentrations. They could have detrimental effects at high concentrations and negatively impact their growth and productivity. So, obtaining a lethal dose (LD_{50}) for respective phytohormones and test plants is better than performing external applications to get desired results.

Biotechnological interventions for developing strategies for enhancing HT stress tolerance in plants

Advancements in OMICS approaches have delineated novel mechanistic ways to decipher new signaling pathways that modulate stress tolerance in crop plants (Figure 2). A comprehensive understanding of the transcriptional, translational and post-translational process has provided an in-depth knowledge of genomics, proteomics and metabolomics of crop plants that have resulted in the identification of new genes/proteins responsible for stress tolerance (Hasanuzzaman et al. 2013). The discovery

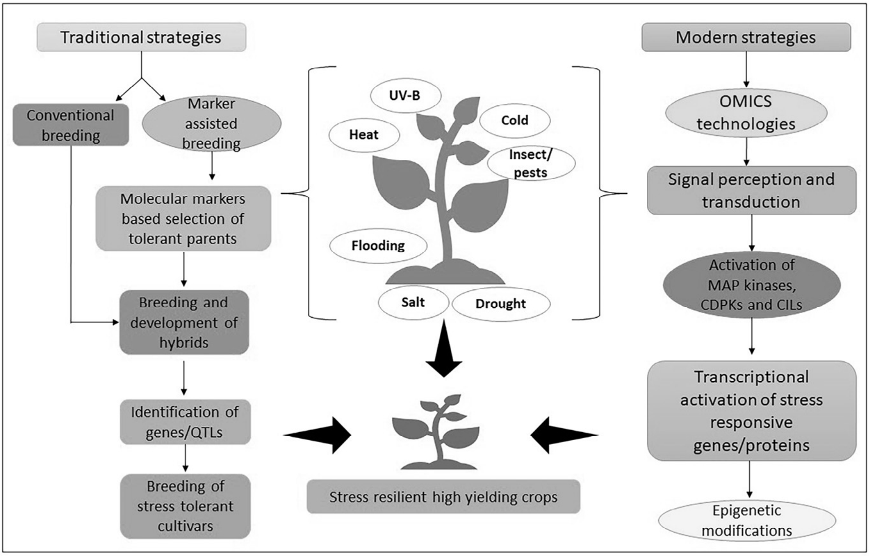

Figure 2 Different conventional and molecular biology (OMICS) tools that can be used to improve heat stress tolerance in plants.

of several small RNAs, such as small interfering RNA (siRNA) and microRNA (miRNA), has also paved the way to confer abiotic stress tolerance in plants. These small RNAs are specifically involved in the regulation of specific genes either by creating gene knockout or mutant (Bagati et al. 2021). Furthermore, researchers have also identified some miRNA-resistant target genes which can be exploited for the generation of transgenic plants that will have better adaptability under stress conditions (Marco et al. 2015). The engineered plants will be capable of overcoming various transcriptional and post-translational hurdles thus ensuring improved physiological and biochemical performance of crop plants (Zhang et al. 2000). Microarray is also one of the most powerful tools to decipher the expression pattern of several genes simultaneously (Hasanuzzaman et al. 2013). This technique has been extensively employed for identifying genes responsible for conferring biotic/abiotic stress tolerance in plants (Shinozaki and Yamaguchi-Shinozaki 2007). Microarray facilitated the identification of 150 cDNA transcripts in *N. tabacum* exposed to drought as well as heat stress (Seki et al. 2009). Likewise, researchers have also successfully used the microarray technique and identified several transcripts in *Arabidopsis thaliana* that were being upregulated under heat and drought stress (Li et al. 2016).

Recently, researchers have exploited the microarray technique to expand current knowledge of HT stress tolerance by identifying the role of HSPs (Hasanuzzaman et al. 2013). While studying the microarray pattern in HT-stressed Arabidopsis plants which were deficient in the ascorbate peroxidase (APX) gene, they observed that certain HSPs were being upregulated (Asthir 2015).

HSPs are those proteins which are encoded by heat-inducible genes commonly known as heat shock factors (HSFs) which are only expressed under stress conditions predominantly under HT stress (Yadav et al. 2020). HSPs are highly tolerant to high temperatures and upregulated upon binding to conserve cis-regulatory elements known as heat shock (HSEs). In various crop plants, HSFs are constitutively expressed and, upon binding to HSEs, regulate the activity of transcriptional components, thus modulating gene expression under stress conditions (Yadav et al. 2020). In addition, studies have indicated several HSPs are heat-inducible, and their effect on activating the transcription of nearby genes depends mainly on the duration and intensity of HT stress (Yang et al. 2021). Researchers have also developed several transgenic plants where HSP expression has been modulated either by creating gene knockout or mutant (Hemantaranjan et al. 2018). For example, in Arabidopsis, researchers successfully altered the expression of heat shock protein *AtHSF1* and the resulting plants suffered extensive damage under HT stress as transcription of other stress-responsive genes were repressed due to downregulation of *AtHSF1* (Hasanuzzaman et al. 2013). HSPs also function as molecular chaperones which help maintain the structure of proteins under stress conditions by preventing them from being denatured (Hemantaranjan et al. 2018). This notion of HSPs has been validated in various crop plants such as tobacco, rice and legumes where constitutive expression of HSPs was made using CaMV35 S promoter, which enhanced the thermotolerance of these plants by activating stress-responsive proteins and other metabolites (Yang et al. 2021). The biotechnological interventions can be used for the genetic improvement of crop plants by exploiting them either in a breeding program or by developing transgenic plants to improve growth and agricultural productivity.

Conclusion

HT stress has become a daunting challenge worldwide due to its severe repercussion on crop growth and productivity. The severity of HT stress depends upon the intensity and duration of the HT stress condition and the plant's age and morphology. The maximum and minimum temperatures are expected to increase gradually owing to the increase in greenhouse gases, thus initiating the chain of global warming. Several studies/research have been conducted, and initiatives have been taken to understand the response of plants exposed to HT stress. Nonetheless, no effective measures or mechanisms have been identified to enhance plant thermotolerance. Researchers can improve short-term HT stress tolerance in plants by applying certain phytohormones, signaling molecules and osmoprotectants. Alternatively, researchers could also improve HT stress tolerance in plants by altering the time of sowing, irrigation and use of wild cultivars. However, their productivity could not be achieved at to desired level. The understanding of molecular mechanisms governing HT stress tolerance seems far-fetched. Therefore, extensive research is required to develop stress-tolerant cultivars either by conventional/molecular breeding approaches or by manipulating the genomic region of the desired crops to create stress memory. The development of stress memory will enable the plant to prepare for the upcoming situation by synthesising effective metabolites or enhancing stress-responsive genes' expression. Stress memory in plants could be achieved by rewiring crop plants at the molecular level using OMICS approaches and exploitation of which could engineer super plants which can withstand the harsh environment without affecting their productivity, thus ensuring global food security in the era of climate change.

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