REVIEW

Regulation of Plant Responses to Temperature Stress: A Key Factor in Food Security and for Mitigating Effects of Climate Change

Ziwei Lee[1] · Jie Ann Lim[1] · Jennifer Ann Harikrishna[1,2] · Tofazzal Islam[3] · Muhamad Hafiz Abd Rahim[4] · Jamilah Syafawati Yaacob[1,2]

Abstract

Among the many threats to food security, extremes of temperature, and unpredictable changes in temperature such as unseasonal frost or snowfall resulting from climate change have significant impacts on crop productivity and yields. It has been projected that for each increase by 1 °C of the global temperature, agricultural outputs of some staple food crops will decline by up to 3–8%. Alarmingly, reports from the National Aeronautics and Space Administration (NASA) and National Oceanic and Atmospheric Administration (NOAA) have revealed that our earth experienced one of the warmest summers in 2022, indicating that temperature stress is not a threat that can be taken lightly. Global food prices have risen by more than 70% since the middle of 2020, however, the UN Food and Agriculture Organization (FAO) projects that by 2027, the combined effects of climate change, conflict and poverty may lead to an additional rise in food prices by 8.5%. Taken together, the impacts of extreme temperatures on staple food supply amplify the risks of child malnutrition and food insecurity, especially in less-developed countries. This review offers a novel perspective on the intricate interplay between plant responses to heat and cold stresses, aiming to pave the way for innovative and efficient crop improvement programs crucial for ensuring a resilient and sustainable food supply in the face of climate change. A thorough and comprehensive understanding on plant mechanisms can effectively help agricultural industry to produce stress-resilient and climate-tolerant crops. Also, with the assistance from robust breeding techniques and genetic tools, the goal to achieve sustainable food supply chain can be attained.

Keywords Temperature stress · Sustainable agriculture · Climate change · Heat and cold stress tolerance

Introduction

Optimal crop productivity requires a combination of good genetic materials supported by the correct growing environment. The growing environment includes the soil for nutrients, a healthy microbiome free of pathogens to the crop in question, sufficient water and a suitable temperature range (Tahat et al., 2020). While each crop and variety will vary in the temperature range that is suitable, for any crop, extremes of high or low temperature can be lethal and lead to crop failure. It has been projected that an increase of even 1 °C of the global temperature will significantly reduce global agricultural outputs, with a decline of 7.4% in corn, 6.0% in wheat, 3.2% in rice and 3.1% in soy bean yields (Zhao et al., 2017). Recently, NASA and NOAA revealed that the earth has faced one of the warmest summers in 2022 (Rosenthal & Patel, 2022), implying the seriousness of this issue. The global food prices have also been majorly

✉ Jamilah Syafawati Yaacob
jamilahsyafawati@um.edu.my

1 Institute of Biological Sciences, Faculty of Science, Universiti Malaya, 50603 Kuala Lumpur, Malaysia

2 Centre for Research in Biotechnology for Agriculture (CEBAR), Faculty of Science, Universiti Malaya, 50603 Kuala Lumpur, Malaysia

3 Institute of Biotechnology and Genetic Engineering (IBGE), Bangabandhu Sheikh Mujibur Rahman Agricultural University, 1706 Gazipur, Bangladesh

4 Department of Food Science, Faculty of Food Science and Technology, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor, Malaysia

affected; recording a significant increase (more than 70%) compared to during the middle of 2020 (Pham, 2022), and is projected to continuously increase by 8.5% by 2027 due to the combined effects of climate change, conflict and poverty (Hughes, 2022).

While rising temperature has turned up to be a frequent challenge for plants grown in the tropical and mediterranean regions, cold stress is another major issue that limits the survival of plant species, primarily at higher latitudes or countries experiencing cold winters. Cold stress changes the fluidity of plant cellular membrane while decreasing the enzymatic activity that eventually disrupts the nutrient uptake by plants, causing stunted growth which is liable for 50–80% annual reduction in global crop harvest (Hwarari et al., 2022). This can be threatening for our food security especially when the global population continues to boom every year. This projection therefore serves as a reminder and insight for the current generation that if nothing is done to mitigate the inevitable decline in crop yields, child malnutrition may be aggravated to 20% in 2050 due to reduced access to nutrient-dense food crops (Bita & Gerats, 2013).

As sessile organisms, plants are continuously subjected to the impacts of an ever-changing environment. As a result, plants require distinct stress adaptation and stress avoidance mechanisms. Many plants adapt flexibly to changes in an environmental component, either physiologically or behaviorally. However, not every minor alternation and modification in a plant's biological process in response to a slight change in the surrounding environment can be defined as a plant's strategy to cope with or respond to stress. Why is this the case? The growth and development, distribution and seasonal behaviour of plants are significantly influenced by temperature. For instance, thermomorphogenesis allow plants to grow quickly and display specific morphological changes in response to mild temperature changes. Some plant species exhibit rapid flowering or seed germination when subjected to chilling or moist-chilling at low temperatures, due to vernalization and cold stratification. It is interesting to note that after a brief exposure to cold temperatures, many temperate plants can develop the capacity to withstand freezing stress, through a process known as cold acclimation (Ding et al., 2020). Hence, it is imperative for researchers and plant breeders to thoroughly comprehend the multiple methods utilized by plants in detecting and combating such stress factors, thereby promoting the enhancement of crop yield in a sustainable manner.

This article presents a review of current knowledge on how plants detect temperature stress, the impact of temperature stress on plants and plants' responses to heat and cold stresses. Based on this, some recommendations are made based on the knowledge gaps to better improve the plants'

ability to withstand temperature stresses for sustainable food production while mitigating the effects of climate change.

Temperature Stress

Based on the type of stressors, temperature stress in plants can be categorized into three forms: heat, chilling or freezing. Plants under temperature stress have been shown to have lower germination rate, slower development, reduced photosynthesis efficiency, and frequently die (Niu et al., 2014). Therefore, it is essential to understand how temperature stress gives rise to problems in order to unveil the responses by which plants cope with challenging temperature circumstances. Temperature stress causes plants to regulate stress-related transcription factors, membrane lipid composition, detoxification pathways, and metabolite synthesis (Guo et al., 2016; Sharma et al., 2023). By examining the molecular, physiological, and morphological responses of plants to temperature stress, humans can use technology to develop genetic engineering strategies for modifying the expression of temperature stress-related genes, allowing plants to adapt and respond to undesirable temperature, thereby producing temperature stress-tolerant plants. For example, at high temperatures, thermotolerance can be produced through short-term exposure to higher temperatures and vice versa in the case of cold tolerance. Plants will always attempt to adapt their cellular metabolism as temperature rise or fall.

Heat Stress

Heat stress such as exposure to extreme radiation and rising temperatures has been identified as one of the most influential stresses in limiting plant development and yield, followed by salinity and drought stress (Stainforth et al., 2005). This is mostly the result of human activities that increase greenhouse gas emissions, the primary driver of global warming, which raises the earth's surface temperature and eventually results in significant crop output losses (Mitra et al., 2021). This is because heat stress affects plants in many ways, including membrane lipid fluidity, loss of membrane integrity, inactivation of enzymes for important mechanisms, protein denaturation, and protein synthesis inhibition, notably those encoding for proteins involved in cellular repair and metabolism (Cebrián et al., 2017; Howarth, 2005). Most of the damages promote the production of reactive oxygen species (ROS) and hazardous chemicals, which reduce ion flux and promote growth inhibition (Howarth, 2005; Shinozaki et al., 1998).

Aside from that, high temperatures cause the grana stacks in chloroplast to enlarge, resulting in ion leakage from leaf cells. Gradually, the structural change in chloroplast will

reduce the rate of photosynthesis, resulting in a drop in energy stores and finally causing plant famine and death. Temperature increases also cause browning of leaves and stems, suppression of growth in shoots and roots, as well as senescence of leaves and fruit damage (Ismail & Hall, 1999; Vollenweider & Günthardt-Goerg, 2005). Furthermore, an increase in the surrounding temperatures reduces the capacity for germination. For example, Ebrahim et al. (1998) noticed that when sugarcane is subjected to heat stress conditions with a temperature greater than 32 °C, a substantial decrease in biomass accumulation and internode length related to early leaf senescence was observed. In brief, heat stress disrupts a variety of plant systems, resulting in a relatively short life cycle and ultimately decreasing the productivity of plants (Barnabás et al., 2008), leading to a reduction in agricultural yield.

Effects of Heat Stress on Plant Morphology and Physiology

Crop Growth and Development

Temperature is critical for plants; where the changes in temperature can have an effect on photosynthetic activity, dry matter partitioning, transpiration, respiration, and root growth (Atkin et al., 2005; Crawford et al., 2012; Sage & Zhu, 2011; Zhao et al., 2013). It has been documented that increasing the temperature above a certain point will stimulate biological pathways, thus influencing plant growth rate and shortening the growth period. Even a brief period of abnormally high temperature can have a detrimental impact on crop growth since it inhibits root and shoot growth and as the temperature of the soil rises in response to the increase in surrounding temperature, the roots will also be critically affected. For example, the germination, establishment of seedlings, and subsequent source-to-sink activity have been reported to be significantly affected in wheat subjected to heat stress, and these in turn will negatively impact the leaf area, as well shoot and root growth (Lal et al., 2021). Similar observations have also been reported in rice, where rice plants subjected to heat stress (40 °C during day and 35 °C during night) for 15 days exhibited significantly lower panicle numbers (reduced by 35%) and total yield per plant (reduced by 86%) compared to those at 28 °C (Soda et al., 2018).

Reproductive Development and Yield

Temperature increases the pace of grain filling in wheat plants due to an increased cell division rate in the endosperm tissue, which results in an increase in the rate of metabolism. However, every plant has a temperature threshold;

where when the temperature exceeds the maximum limit, the reproductive development of that particular plant is disrupted. This is because heat stress can cause damages to the gametophytes of plant, indirectly decrease pollen viability and germination, increase inhibition for pollen tube growth, decrease stigma receptivity and ovule function (poor ovule viability and a higher rate of ovule abortion), decrease fertilization, result in minimal embryogenesis and ultimately lead to a decrease in crop yield (Chao et al., 2017; Tashiro & Wardlaw, 1990). For example, a nine-year satellite data in northern India has shown that the surge in surrounding temperatures (above 34 °C) had significant impacts on the growth of wheat crops, where the rate of senescence was observed to increase which resulted in a significant reduction in yield (Lobell & Gourdji, 2012). As a consequence, it is feasible to conclude that heat stress has a detrimental impact on crop growth and developmental processes, which ultimately caused a decrease in crop outputs. Liu et al. (2016) reported that even an increase of the global temperature by 1 °C would result in 4.1–6.4% reduction of global wheat yields. Hence, this crisis puts world food production and nutritional security in jeopardy.

Membrane Structure

When plants are stressed by heat, the most sensitive part of plant cell is believed to be the plasma membrane. This is due to the fact that at high temperatures, some proteins on the plasma membrane would begin to denature and increase the ratio of unsaturated fatty acids (Wahid et al., 2007), causing an increase in membrane fluidity (from a rigid solid gel to a crystalline liquid structure that is flexible) as well as membrane permeability and ion leakage from the plant cell (ElBasyoni et al., 2017).

Oxidative Stress

Heat stress reduces the activity of many enzymes and disrupts several metabolic pathways in plants, resulting in the excessive amount of unwanted and hazardous ROS and eventually causing oxidative stress (OS) (Bhattacharjee, 2019; Nadeem et al., 2018). Furthermore, when plants are exposed to excessive light energy, the chloroplasts that carry out photosynthesis can quickly develop OS and cease photosynthetic activity (Latowski et al., 2011; Mullineaux & Karpinski, 2002). Cellular protein denaturation caused by disturbance of cell membrane integrity and membrane lipid peroxidation will also lead to OS. In short, OS is caused by several changes in the structure and mechanisms of plants, putting them in a very risky position with a high possibility of cell death. Light-dependent phase of xanthophyll cycles have been reported to play an essential role to protect

plants against damages incurred by OS due to heat stress (Latowski et al., 2011).

Photosynthesis and Transpiration

The detrimental effects on plant development and agricultural productivity are mostly driven by unfavorable effects on photosynthesis (Wang et al., 2016). Photosynthetic rate is reported to drop significantly as the temperature rises to and exceeds a plant's optimal or maximum temperature limit. This is due to the fact that during heat stress, the amount of chlorophyll drops dramatically, as do thylakoid proteins, which are crucial for photochemical reactions. Furthermore, when exposed to high light, the photosystem II, which is in charge of light-dependent reactions in photosynthesis is greatly affected (Chen et al., 2018), as the light harvesting complex in photosystem II stops functioning and the activity of photosystem II is then impaired due to the rise in ROS across the thylakoid membrane (Takahashi & Murata, 2005). Furthermore, heat stress will cause the thylakoid membrane to become unstable and the activity of ribulose-1, 5-bisphosphate carboxylase-oxygenase (RuBisCO) for the dark response in photosynthesis will be reduced (Crafts-Brandner & Salvucci, 2002).

Moreover, when the temperature rises, the rate at which the stomata open would also increase. This is because the rate of transpiration in plants increases as the ambient temperature rises, because it is a process used by plants to cool themselves. Increased transpiration and water flow are an important mechanism for plant survival in severe temperatures (Kolb & Robberecht, 1996). However, the negative side effect of this is that it causes a rapid depletion of the amount of water in a plant, eventually leading to dehydration and maybe death (Koini et al., 2009).

How do Plants Respond to Heat Stress?

Heat tolerance is a multifaceted quantitative trait, expressed through an intricate crosstalk of physiological, biochemical, and molecular pathways, that are further complicated by genotype x environment and epistatic interactions (Aleem et al., 2020). Chaudhary et al. (2022) reported that key physiological traits such as the ability to stay green, canopy temperature depression, cell membrane thermostability, chlorophyll fluorescence, increased reproductive fertility, and fruit characteristics are crucial for developing high-yielding heat-tolerant varieties. Notably, heat-tolerant peppers exhibit uniform photosynthesis under heat stress, achieved by increasing the transpiration rate and inducing a higher proline content to ensure rapid recovery from heat-induced damage (Rajametov et al., 2021). Consequently, a deep understanding of plant responses and resistance

mechanisms is imperative for formulating strategies to enhance crop productivity under heat stress.

Although plants are unable to move or speak in the same way that humans do when facing a problem, they can make changes within themselves to thrive in hostile environments. Similar to humans recognizing or perceiving a problem before initiating a change, plants must first be able to detect a rise in the atmospheric temperature in order to respond to changes in their surrounding temperature. This process is facilitated by the lipid membranes in plants' cells. As the temperature rises, the membrane fluidity increases to become more permeable to substances, enabling the influx of calcium ions to take place in the plant cell, as well as to facilitate cytoskeletal remodeling. These in turn will result in the synthesis of antioxidants and osmolytes, as well as a heat shock response to heat stress (Bita & Gerats, 2013). In general, the evolution of plant mechanisms to adjust to changing ambient temperatures for survival can be categorized into three aspects; physiological, morphological and molecular.

Physiological Mechanism of Heat Stress Response

Lipid Membrane Tissue senescence is one of the most evident symptoms of heat stress; it occurs when the plant cell membrane is destroyed, causing an increase in membrane fluidity and maybe even protein breakdown (Savchenko & Kabashnikova, 2008). Some plants respond to these changes by increasing the proportion of saturated and monosaturated fatty acids in their membrane lipids. This is because saturated fatty acids in plant cell membranes can raise the melting point of the membrane, allowing it to maintain membrane fluidity even at high temperatures, thus improving plant heat tolerance.

Osmo-protectants Osmo-protectants are critical in heat-stressed plants because they sustain osmotic activity and protect the cell structure by preserving the water content in cells, thus neutralizing the cellular redox potential and aid in maintaining membrane fluidity (Farooq et al., 2008). Proline, glycine betaine, and soluble carbohydrates are examples of osmo-protectants. Numerous studies have established proline's beneficial effect on heat-stressed plants, as it promotes the manufacture of defensive pigments such as the xanthophylls (Dobra et al., 2010). For example, it has been reported that heat-tolerant peppers, when subjected to heat stress, exhibit consistent photosynthesis and demonstrate faster recovery from heat-induced damages by increasing the transpiration rate and proline production (Rajametov et al., 2021). Furthermore, glycine betaine plays a crucial role in conserving the activity of rubisco in plants under abnor-

mally high temperatures, which is essential for sustaining photosynthesis in those plants. This is supported by studies on maize and sugarcane, where an increase in glycine betaine levels was observed when the plants were exposed to extremely high temperatures (Allakhverdiev et al., 2008).

In addition, various studies have also reported that soluble carbohydrates like glucose and sucrose possess key physiological features related to heat stress tolerance (Liu & Huang, 2000). As we all know, photosynthesis's primary product is sucrose and research has found that it is crucial for plant development and stress response regulation, since sucrose is translocated from source to sink via carbon allocation and sugar signaling (Roitsch & González, 2004). Furthermore, soluble sugars are also essential elements in plants' antioxidant activity (Lang-Mladek et al., 2010). According to Sugio et al., sucrose functions as a signaling molecule when it is present in low concentrations, but will become a ROS scavenger at high concentrations (Sugio et al., 2009).

Plant Secondary Metabolites Plant secondary metabolites are a broad set of chemical substances produced by plant cells via metabolic processes that diverge from major metabolic pathways. They are critical in defending plants from oxidative stress produced by heat stress (Hussein & El-Anssary, 2019). For example, the biosynthesis of phenolics has been shown to increase in tomato and watermelon plants subjected to temperature stress (Rivero et al., 2001). In this study, it was shown that exposure to heat stress would result in the highest phenylalanine ammonia-lyase activity, and the lowest polyphenol oxidase activity in the plants. These suggest that heat stress induces phenolic accumulation by activating their biosynthesis and concurrently inhibiting their oxidation. Additionally, these secondary metabolites aid in increasing water intake, to compensate for water loss due to accelerated transpiration under high temperatures, thus facilitating plants' rapid response to the changes in their environment (Wahid et al., 2007).

Moreover, the study on *Heracleum sosnowskyi* revealed that both short term and prolonged exposure to heat stress altered the accumulation of secondary metabolites (Rysiak et al., 2021). A strong correlation was observed between heat stress and the production of furanocoumarin compounds in the plant leaves, as shown by the significantly higher amounts of xanthotoxin and bergapten in heat-stressed *H. sosnowskyi* plants compared to control. Notably, heat stress also resulted in a unique expression of isopimpinellin, which was not detected in the control plants. In addition, plants' reproductive tissues are also highly vulnerable to heat stress. Biosynthesis of various secondary metabolites

such as flavonoids, polyamines and glutathione will induce reproductive thermotolerance in the affected plants though ROS homeostasis (Rehman et al., 2023). This in turn protects the cellular membranes, improves pollen fertility, reduces anther abortion, and regulates cellular signaling, inter alia activating the genes (including transcription factors) taking part in the network of metabolic pathways.

In sugarcane, heat stress was observed to significantly reduce dry matter and leaf area of sugarcane sprouts, with changes in the relative growth rate and net assimilation exceeding relative leaf expansion, which implied that heat stress negatively impacted the nutrient and CO_2 assimilation for use in dry matter production (Wahid, 2007). These were followed by an increase in the biosynthesis of secondary metabolites such as anthocyanin and phenolics over time. The observed relationships between the growth attributes and levels of secondary metabolites in heat-stressed plants, while not observed in the control plants thus serve as evidence of the essential roles played by the secondary metabolites in sugarcane heat tolerance.

Carotenoids Carotenoids can shelter plants from a variety of stressors, including heat stress. The activity of carotenoids induces zeaxanthin activity, which has been reported to have the ability to protect plants from heat stress by minimizing oxidative damage on the membranes. For example, *Arabidopsis* is capable of producing zeaxanthin due to the presence of chyB-encoding b-carotene hydroxylase. When activated and overexpressed, this enzyme can result in an increased tolerance to temperature rise (Meiri et al., 2010).

Plant Growth Stimulants Plant-growth regulators (PGR) or phytohormones are naturally produced by plants in small amounts, but have a very large influence on plant physiology, morphology and biochemical processes. Table 1 provides some examples of PGRs and their importance in plant survival under unfavorable conditions, especially heat stress. When a plant is subjected to high temperatures, it produces more abscisic acid (ABA) and ethylene, while producing less cytokinin, auxin, and gibberellins (GA). For example, the exposure to excessive heat would result in the abscission of reproductive organs, which is triggered by an upsurge of ABA and ethylene as well as a decline in the concentrations of auxin (Binder & Patterson, 2009). Additionally, Banowetz et al. (1999) has reported that heat stress

Table 1 Plant Growth Regulators (PGRs) and their respective roles

Plant Growth Regulator (PGR)	Roles
Auxin; Indoleacetic acid (IAA)	Stimulates the extension, differentiation, elongation of roots and division of cells in plants
Gibberellins (GAs)	Control the development of fruits, induction of flowers, germination of seeds and elongation of cells
Cytokinins (CKs)	Stimulate the nodulation of roots, apical dominance, senescence of leaves, initiation and growth of shoots as well as cell division
Ethylene	Promotes the abscission of leaves and ripening of fruits, stimulates seed germination, inhibits elongation of the roots and involves in initiation of root development
Abscisic acid (ABA)	Mediates bud growth, seed dormancy and the adaptation to the variable environmental stress conditions

reduced the wheat kernel filling by altering the quantity of cytokinin produced in the plants.

Morphological Aspects of Heat Stress Response

Plant's Stomata Stomata are microscopic adjustable openings found in the leaves that enable gas and water exchange between the plants and their surroundings, as well as the location of transpiration. When a plant is placed under scorching sun, water leaves the plant more quickly through transpiration. To avoid this, many plants close their stomata when they detect an increase in the ambient temperature. However, closure of stomata may influence plant processes and growth by preventing gaseous exchange and thereby reducing photosynthesis. Therefore, some plants adjust to heat stress by reducing stomatal frequency, which lowers the transpiration rate and as a result, minimizes the amount of water lost (Khan et al., 2018; Shabnam & Chhabra, 2019). Some plant species have also evolved to cope with living in the environments with heat stress, by developing sunken stomata which reduce water loss by limiting air movement over the stomata (Masrahi, 2020; Teixeira et al., 2018).

Leaf and Root Structure and Morphology The presence of a thick waxy cuticle on the plant, which forms a waxy layer on the surface of the leaves can minimize water loss by diffusion. Some plants are well adapted because their leaves are hairy or curled. Paraheliotropism is a term that refers to the way a plant's leaf blades respond to sunlight exposure by turning away, or aligning themselves parallel to the sun's rays, as well as rolling their leaf blades in order to lower the ratio of surface area to volume exposed, thereby decreasing the area for water to diffuse out (Balfagón et al., 2021;

Marler, 2019; Matthews et al., 2019). Some plants respond even more directly to heat stress by reducing the number of leaves. Besides that, some plants such as tall fescue also adapt to heat stress by producing deep roots that can grow to a certain extent in order to get water from underground, through strigolactone/auxin-induced root modulations (Hu et al., 2018). Meanwhile, some plants use shallow roots to gather surface rainwater to compensate for water loss caused by heat stress.

Molecular Aspects of Heat Stress Response

Reactive Oxygen Species (ROS) Several in-vitro tests from laboratories indicate that the level of ROS increases when specific plant species are subjected to heat stress. ROS is primarily formed by the reaction centres of chloroplast photosystems I and II. According to Belhadj Slimen et al. (2014), high temperatures promote the production of reactive oxygen species (ROS) in plants, by wreaking havoc on plants' biological systems, such as oxidative stress (Del Río, 2015). ROS are well-known for their catastrophic effect on the electron transport chain of mitochondrial and chloroplast organelles, which eventually reduce the power and productivity of these organelles. Furthermore, the accumulation of ROS on the plasma membrane's outer surface might result in membrane depolarization. Yet, the negative impact of ROS can be alleviated by scavenging enzymes such as superoxide dismutase (SODs), peroxidase (POX) and catalase (CAT) that are activated by heat-tolerant plant growth-promoting rhizobacteria (PGPR) (Backer et al., 2018). Similar observations were reported by Ali et al., which showed that inoculating wheat plants with *P. putida* strain (a gram-negative bacterium) under heat stress had boosted plant's growth and survival by minimizing membrane damage and increasing the level of compounds such as proteins, starch, amino acids, chlorophyll, sugars and proline as compared to plants that were not inoculated with the bacteria (Ali et al., 2009).

Although ROS is always associated with having a negative impact on plants, numerous researches have demonstrated that ROS also plays important roles for plant's survival, such as in molecular signaling as well as assisting plants in responding to infection caused by pathogens and stresses from the environment, by developing stimuli or carrying out programmed cell death (PCD) (Gechev et al., 2006). As a result, ROS production facilitates heat signal translation and heat shock gene expression.

Heat Shock Proteins (HSPs) High temperatures in the surrounding environment can cause protein and enzyme dena-

turation in plants. When a water-soluble protein denatures, the hydrophobic portion of the protein is exposed to the fluid within the plant cell. As a result, the hydrophobic regions will congregate and create a hydrophobic core of denatured protein, a process known as protein precipitation. At this point, normal protein synthesis in plant cells will be halted in order to speed up transcription and translation for heat shock proteins (HSPs) which have a hydrophobic domain that can interact with such unfolded protein precipitation (Lichtenthaler, 1998). HSPs bind to the protein precipitation and release a transcription factor known as the Heat Shock Factor (HSF), which binds to heat shock elements (HSEs) to regulate transcription.

One of the most crucial aspects of thermotolerance is the mass creation of HSP under temperature stress. In plants, HSPs act as molecular chaperones, preventing target proteins from becoming denatured or aggregated and promoting protein refolding. HSP70 is an example of an HSP that has been shown to help plants with proteolysis, translocation, translation, aggregation, folding, and refolding of denatured proteins (Goswami et al., 2021). In addition to this role, HSPs can act as molecular sensors, detecting the presence of ROS in plant cells and expressing oxidative stress response genes when plants are under stress (Goswami et al., 2021). Furthermore, environmental conditions will promote small heat shock proteins (sHSPs) genes expression. These sHSPs are in charge of making the membrane of the plant cell more associated by producing heat shock lipids to stabilize the membrane structure that becomes unstable due

Table 2 A summary of the roles of heat shock proteins (HSPs) under heat stress

Heat shock protein(s)	Roles under heat stress
HSP100	• Assists in degradation of irreversibly damaged polypeptides. • ATP is required for its function.
HSP90	• The most abundant HSP. • Key regulator of normal growth and development. • ATP is required for its function
HSP70	• Assists in refolding and proteolytic degradation of abnormal proteins. • ATP-dependent release and binding.
HSP60	• Assists in refolding and proteolytic degradation of abnormal proteins. • Functions are ATP-dependent.
HSP40	• Modulates the growth, development and resistance to abiotic stresses (such as heat, cold, salinity and drought) by inducing cell elongation and stabilizing the structure of the photosystem II.
sHSPs	• Required for the development of chloroplasts during heat stress. • In order to be released, HSP40, HSP70 and HSP100 are required.

to heat stress (De Maio et al., 2019). Table 2 summarizes some of the roles played by HSPs.

Elongation Factor (ET-Tu) According to research, when plants are exposed to excessive heat, the chloroplast protein in plant cells will respond by synthesizing an elongation factor (ET-Tu). Like HSPs, ET-Tu has a chaperone function in plant cells. Experiments conducted by Pressman et al. indicated that plants that can produce a greater amount of ET-Tu under heat stress would have a higher thermotolerance than plants that do not produce this elongation factor (Pressman et al., 2002).

Heat Stress-induced Calcium ion (Ca^{2+}) Influx and Small Signaling Molecules Calcium ions play a role as signaling molecules in plants and are important in developing plant's tolerance under heat stress conditions. The calcium ion is a necessary element of the membranes and walls of plant cells, as well as a vital intercellular messenger in the cytoplasm. Plants will absorb this ion and deliver it to the shoot via the xylem. Plant cell plasma membranes are equipped with calcium ion channels for calcium ion influx. Plant cells also contain $H+/Ca^{2+}$ antiporters and Ca^{2+}-ATPase that function to maintain the amount of Ca^{2+} ions in plants, as high Ca^{2+} concentrations can be hazardous (Hirschi, 2001; Sze et al., 2000). For example, a transient increase in cytosolic Ca^{2+} levels have been documented in *Arabidopsis* during recovery from heat stress (Larkindale & Knight, 2002). In the same study, significantly higher levels of Ca^{2+} ions were also recorded in thermotolerant plants (Larkindale & Knight, 2002). These data suggested that plants with higher amount of cytosolic Ca^{2+} accumulation possess better adaptability to heat stress conditions and have higher thermotolerance.

When plants are exposed to cold and heat stresses, the accumulation of Ca^{2+} will induce the activity of Ca^{2+} sensors such as calmodulins (CaMs), CaM-like proteins (CMLs) and Ca^{2+}-regulated protein kinases (Ca^{2+}-dependent protein kinases; CPKs/CDPKs) (Dekomah et al., 2022). For example, $CaCl_2$-treated maize seedlings exhibited a significant increase in CaM accumulation and showed improved thermotolerance after exposure to heat stress (Zeng et al., 2015). In *Arabidopsis thaliana*, the *AtCaM3* gene has been shown to play a key role in regulating AtCBK3 (CaM-binding protein kinase) activity, which functions to control heat shock (HS) transcription factors and protein genes via phosphorylation and dephosphorylation mechanisms (Zhang et al., 2009). *AtCaM3* also acts as a downstream factor in heat shock-regulated nitric oxide (NO) signaling which leads to activation of heat shock factors (HSFs) and heat shock

proteins (HSPs) accumulation (Xuan et al., 2010). Tolerance to heat stress has also been reported to be regulated by CPKs/CDPKs, whereby the overexpression of *VaCPK29* from *Vitis amurensis* has been reported to improve heat tolerance in *Arabidopsis* (Dubrovina et al., 2017). In addition, the expression of CML genes is also upregulated in response to heat stress, for example the *BrCML21-1* gene in *Brassica rapa* ssp. *pekinensis* (Nie et al., 2017) and *OsMSR2* (multi-stress-responsive gene 2) in *Oryza sativa* (Xu et al., 2011).

Induction of CaM brought upon by the accumulation of Ca^{2+} in the cytosol further activates the activities of L-glutamate decarboxylase (GAD) that is involved in the decarboxylation of glutamate (Glu) into γ-amino butyrate (GABA) (Patra et al., 2021). GABA has been reported to confer partial protection towards heat stress in plants, by improving osmolytes content and leaf turgor as well as reducing oxidative damage brought by ROS (Nayyar et al., 2014). Meanwhile, the binding of CaM to GAD has also been implicated in plant's normal development (Nayyar et al., 2014), indicating that induction of CaM by cytosolic calcium further activates GAD to allow plants to develop normally and withstand stress.

Nitric Oxide (NO) Nitric oxide (NO) is another critical signaling molecule found in plants that regulates cellular mechanisms in order to respond to high temperature stress. NO is a reactive molecule that is required for many aspects of plant growth, including germination, dormancy reduction, leaf expansion, and plant maturation (Mishina & Zeier, 2007). Recent research indicates that the presence of NO may aid in mitigating stress-induced damages and boost seedling survival by raising the activity of antioxidative enzymes such as SOD, APX and CAT, as well as increasing heat tolerance and cellular viability (Song et al., 2006; Uchida et al., 2002). NO crosstalks with H_2O_2 and H_2S (hydrogen sulphide), where the synthesis of these molecules occurs synchronously during heat stress response, as documented in maize seedlings (Li et al., 2013).

It has been mentioned that NO is induced by accumulation of cytosolic calcium which activates Ca^{2+} channels and sensors such as CaM. The crosstalk between NO, H_2O_2, H_2S, parallel with the activation of CaM-dependent protein phosphatase and other factors induce the DNA-binding activity of HSFs and HSPs accumulation in *Arabidopsis* (Wang et al., 2014). Specifically, NO acts upstream of *AtCaM3* in *Arabidopsis* heat tolerance, whereby it induces the DNA-binding activity of HSF to result in the increased synthesis of HSP18.2 (Xuan et al., 2010). In addition, the increase in endogenous levels of NO was observed to improve the heat tolerance exhibited by NADPH-oxidase (*atrbohB, atrbohD* and *atrbohB/D*) mutants of *A. thaliana* (Wang et al., 2014).

On the other hand, the increase in endogenous levels of H_2O_2 was observed to yield no effects in NO-deficient *(nitric oxide-associated protein1* or *noa1*) mutants, while the overexpression of *AtNIA2* (nitrate reductase gene) and *AtNOA1* restored the stress response of atrbohB/D mutants (Wang et al., 2014). These observations further confirmed the role of NO as a downstream factor in H_2O_2 signaling, and that the interplay between both molecules is the key in plants' heat tolerance.

Acetylcholine-mediated System Plants which are frequently exposed to excessive heat contain a high concentration of acetylcholine (ACh). This system in plants is made up of three major components; ACh, ACh receptor (AChR) and acetylcholinesterase (AChE), which work together to carry out signal transduction. The catabolic *AChE* gene function is well recognized in maize plants, whereby tobacco plants transformed with maize *AChE* gene has shown to have better heat tolerance than non-transgenic plants (Yamamoto et al., 2011). This indicates that tolerance to heat stress is mediated by ACh and that further research into engineering plants with AChE may be important in the future for plants to be able to survive in extreme temperatures.

Phytochrome Interacting Factor4 (PIF4) Another temperature-sensing mechanism in plants is Phytochrome Interacting Factor4 (PIF4), which promotes hypocotyl elongation. PIF4 has been reported to regulate expression of *SMALL AUXIN UP RNA (SAUR)* genes at high temperature, which ultimately influence the auxin levels of heat-exposed plants (Franklin et al., 2011). The up-regulation of these key auxin biosynthesis genes under heat stress was observed to be PIF4-dependent and would result in hypocotyl elongation (Franklin et al., 2011). In addition, it has also shown that plant elongation under warm temperatures involves the crosstalk between PIF4 and BES1 (BRI1-EMS-SUPPRESSOR 1) to activate brassinosteroid (BR) synthesis by modulating the expression of key BR biosynthesis genes; *DWF4, CPD*, and *BR6ox2* (Martínez et al., 2018). Moreover, elevated temperature has also been found to strongly induce flowering in *Arabidopsis thaliana*, even without the exposure to photoperiodic cues, due to PIF4-mediated response (Proveniers & van Zanten, 2013).

Besides that, exposure to high temperature has also been found to accelerate leaf senescence, to allow for active remobilization of nutrients from old leaves with inefficient photosynthesis to young growing leaves (Kim et al., 2020). It has been known that under prolonged darkness, leaf senescence is inhibited by the action of phytochrome B (phyB) that mediates the inhibition of PIF4 and PIF5. However,

light-activated form of phyB (Pfr) has been observed to remain active for more than 4 days after the transfer to darkness at 20 °C, but this action was inactivated more rapidly at 28 °C (Kim et al., 2020). These suggested that the increase in temperature would result in a faster degradation of Pfr, which subsequently increase PIF4 protein levels to bind to *ORE1* promoter and activates *ORE1* expression. These coupled with increased ABA activity and ethylene signaling would then accelerate leaf senescence in the plants when exposed to high temperature (Kim et al., 2020).

These suggested that the activity of phyB and PIF4 is negatively regulated, where a decrease in phyB level results in the accumulation of PIF4 at warm temperatures to assure plant growth. Plants must sense their surroundings in order to regulate their germination and flowering times. Thus, temperature sensing mechanisms are crucial in defending plants against the detrimental effects of heat stress.

Cold Stress

Cold stress is classified into two types: freezing (lower than 0 °C) and chilling (between 0 and 15 °C). Every species or type of plants has a distinct set of ideal environmental conditions, such as nutrition or temperature, for optimal growth and development. A species of plant might find 25 °C as the optimal temperature for its mechanisms to function, but this temperature might be harmful for other plant species. For example, if a plant is adapted to warm environments, it will exhibit damage signs when relocated to a cold environment. As a result, this demonstrates that various plants have varying degrees of sensitivity to cold stress. According to Choudhury et al., ROS will accumulate during cold stress, causing membrane damage due to free radicals generation (Choudhury et al., 2017). Furthermore, several plant mechanisms will be blocked, resulting in growth inhibition. Many plants however, respond to cold stress via a signal transduction system that activates transcription factors and cold-responsive genes that are capable in mitigating the effects of cold stress and assisting in the development of plant tolerance. Figure 1 depicts a summary of the strategies by which plants can withstand cold stress and develop cold stress resistance, or confront mortality when the stress exceeds a certain threshold.
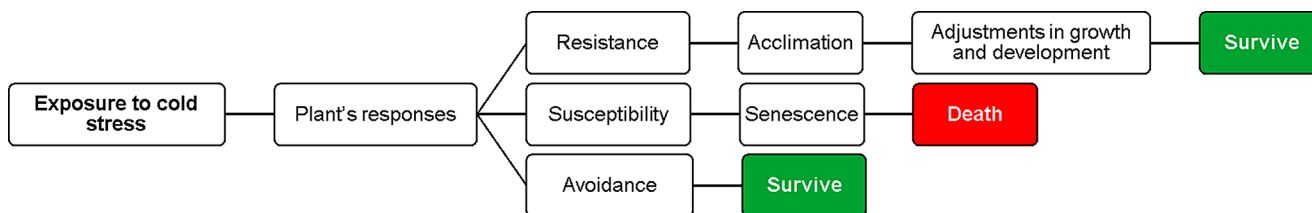
Effects of Cold Stress

Membrane Structure and Function

A concise overview of cold stress would be that it causes the macromolecules in the plant membrane to lose function as a result of the chilling temperature. While freezing stress is a little more complicated than chilling stress, in that it causes the formation of ice crystals in the plant cell and if this stress continues, it causes freezing dehydration and electrolyte leakage in the plant (Mitra et al., 2021). The lipid found in plant cell plasma membranes has been determined to comprise a mixture of unsaturated and saturated fatty acids. The ratio of these two types of fatty acids determines membrane fluidity; plasma membranes with a higher number of saturated fatty acids solidify faster, reducing fluidity and permeability. Hence, cold stress causes the membrane to alter from a semi-fluid to a semi-crystalline condition.

Stomatal Aperture and Photosynthesis

A direct effect of freezing temperatures would be stomatal closure, which results in dehydration (Davies et al., 2002), and when stomata is shut, carbon dioxide uptake is hindered, thus reducing the rate of photosynthetic activity. Photosynthetic activity is primarily controlled by the enzyme RuBisCo, which provides acceptor molecules to catalyze the entry of carbon dioxide into photosynthetic metabolism. Hence, under anomalous temperatures, even a minor degree of temperature stress will cause enzyme activity to slow down or eventually cease. In addition, the primary organelle in charge of photosynthesis, i.e., chloroplasts are highly influenced by cold stress. When chloroplasts are subjected to temperatures lower than normal, the antenna complexes are altered, resulting in a change in the structure of thylakoids (Adam & Murthy, 2014; Bilyavska et al., 2019; Doltchinkova et al., 2013).

In general, when rate of photosynthesis is slowed down, protein synthesis and normal metabolic processes are slowed down as a consequence of cold stress. Eventually, the resources available to plants are limited, resulting in a decrease in leaf growth or enlargement and food production, premature leaf senescence (Mishra et al., 2012), chlorosis (yellowing of leaves), and necrosis (tissue death). In short,

Fig. 1 The general overview of how plants respond to cold stress

as the ambient temperature drops, plant development and growth slow down and in some cases, causes plant death and eventually reducing agricultural yield (Miura & Furumoto, 2013).

Reproductive Development

Additionally, cold stress has a detrimental effect on plant's reproductive development, resulting in pollen sterility, which causes crop output to decrease dramatically (Sharma & Nayyar, 2016; Thakur et al., 2010). These observations have been reported in various species such as rice (Yamamori et al., 2021), wheat (Chakrabarti et al., 2011), chickpea (Sharma & Nayyar, 2014), sorghum (Schaffasz et al., 2019) and many more. Furthermore, poor germination and stunted seedlings may also result from seeds exposure to cold stress.

Various causes have been postulated to lead to pollen sterility due to cold stress, such as the incidence of mutations during tapetal development which leads to microgametogenesis abortion (Sorensen et al., 2002, 2003; Wi et al., 2005) and tapetal hypertrophy due to nutrient deficiency in the microspores (Xu et al., 2020). In addition, exposure to cold stress also induces plant metabolism alterations that brought upon dramatic changes in generation of metabolic intermediates, signaling molecules and plant hormones (Sharma & Nayyar, 2016). The increase in abscisic acid (ABA) metabolism together with a decrease in ABA catabolism as well as endogenous gibberellins (GA) synthesis have also been reported to affect pollen viability (Sharma & Nayyar, 2016).

Plant's Response to Cold Stress

Role of Osmoprotectants

As survival is the foundation of all living beings, plants have evolved a multitude of schemes to combat the condition of cold stress. For example, proline is a non-essential amino
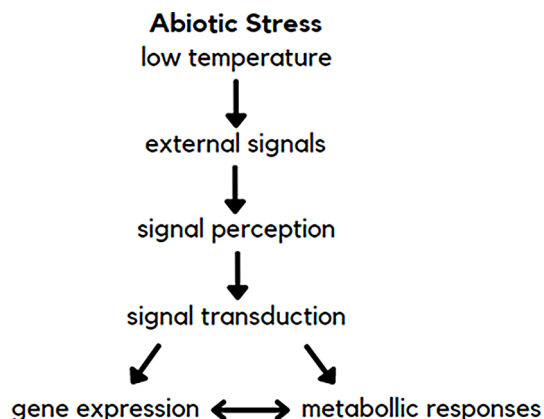

Fig. 2 Overview of signal transduction processes when plants are exposed to cold stress

acid that has osmoprotective qualities that can help plants survive under a variety of stress circumstances. Plants will naturally accumulate proline when subjected to cold stress, which functions as a chaperone molecule in plant cells. Proline is typically found in the cytoplasmic region to maintain protein structure, boost enzyme performance, and most critically, scavenge ROS to prevent the harmful effects brought by ROS, which is cell death (Shafi et al., 2019). Furthermore, proline promotes seedling growth under chilling stress by delivering nitrogen and carbon to the seed (Ghosh et al., 2021). Glycine betaine (GB) is another osmoprotectant that increases plant growth and survival by counteracting metabolic dysfuction produced by stress. These are parallel to the findings reported by Nayyar et al., whom conducted trials and found that administering GA to chickpeas under cold-stress can increase floral preservation, plant pods, and yield (Nayyar et al., 2005).

Cold Stress-induced Calcium ion (Ca²⁺) Alterations and Activation of Small Signaling Molecules

To survive in such extreme environments, certain plants have developed a technique known as cold signal transduction via small signaling molecules. Temperature alterations cause changes in the liquidity of the membranes and reorganization of the cytoskeleton in plant cells. The significant influx of Ca^{2+} into plant cells causes a range of downstream responses as the integrity of the membrane changes (Ding et al., 2019; Guo et al., 2018). Then, small signaling molecules are produced, which operate as regulators in the signal transduction pathway. Figure 2 depicts a synopsis of the signal transduction process which takes place in a cold-stressed plant.

Besides that, calcium ions Ca^{2+} also act as a vital signal mediator in a range of physiological processes. Under typical temperature settings, the content of Ca^{2+} in the cytoplasm of plant cells is quite low, but the amount of Ca^{2+} in the cytoplasm would increase drastically during cold stress due to activation of Ca^{2+} channels and pumps in plant cells (Zheng et al., 2021). Meanwhile, *Calcium Exchanger 1 (CAX1)* is in charge of returning cytosolic Ca^{2+} to normal or resting levels following a cold stress-induced rise in cytosolic Ca^{2+} concentrations (Cheng et al., 2003). In contrast, *CAX1* mutants would exhibit tolerance to cold stress because it allows the amount of cytosolic Ca^{2+} to be maintained at a high level for a longer period of time, resulting in activation of more downstream gene expressions.

Besides that, Ca^{2+} also induces the activation of Ca^{2+} sensors such as calmodulins (CaMs), CaM-like proteins (CMLs) and calcineurin B-like proteins (CBLs), as well as Ca^{2+}-regulated protein kinases (Ca^{2+}-dependent protein kinases (CPKs/CDPKs), which then bind to the promoters of

certain genes, resulting in a downstream gene activation or repression (Guo et al., 2018; Reddy et al., 2011; Zhu, 2016). For example, the Ca^{2+}-mediated cold-response pathway in *Arabidopsis* has been reported to be positively regulated by Ca^{2+}/CaM-regulated receptor-like kinases 1 (CRLK1), which subsequently mediates the activation of mitogen-activated protein kinase (MAPK) (Zheng et al., 2021).

Induction of Reactive Oxygen Species (ROS)

Plants produce reactive oxygen species (ROS) via electron transport chains in the chloroplasts and mitochondria, as well as peroxisomes and apoplasts, through enzymatic processes (Wrzaczek et al., 2013). An example of a well-characterized ROS is hydrogen peroxide (H_2O_2) that is capable in causing oxidative damage to biomolecules and eventually, cell death. However, all of these deleterious effects would occur at high H_2O_2 concentrations, while at low or tolerable levels, it would function as a signaling molecule that aids in altering plant growth and development in response to a variety of scenarios. When the temperature drops, the level of H_2O_2 in plant cells would increase and result in a variety of consequences (dependent on plant species), but all of which are targeted at assisting plants in dealing with cold stress. For example, in *Arabidopsis*, H_2O_2 induced the expression of *nucleotide diphosphate kinase 2 (NDPK2)* gene, which functions to inhibit the accumulation of H_2O_2 and subsequently contributed to the plant's tolerance to low-temperature stress (Moon et al., 2003). In other words, *NDPK2* shows a negative feedback effect on H_2O_2, where the overexpression of this gene would prevent from detrimental H_2O_2 accumulation in plants.

Besides that, the increase of H_2O_2 in wheat plants exposed to cold stress has shown to trigger the production of endogenous ABA (Wang et al., 2018). Unlike the *NDPK2* in *Arabidopsis*, ABA acts as a positive feedback for H_2O_2, where it will induce the production of NADPH oxidase and thereby increasing the production of H_2O_2 to result in a prolonged salicylic acid (SA)-mediated cold-stress tolerance (Wang et al., 2018). A similar observation was also recorded in tomato plants, where increased activity of NADPH oxidase in the apoplast would result in increased H_2O_2 generation, leading to the overexpression of *respiratory burst oxidase homolog 1 (Rboh1)* and subsequent up-regulation of the expression and activity of antioxidant enzymes (Zhou et al., 2012).

Roles of Nitric Oxide (NO)

At low concentrations, NO would function similarly to ROS where it works as a signaling molecule, assisting in seeds germination, senescence, root development, closure of stomata and modulate plant's response to abiotic and biotic stresses. However, a high concentration of NO might result in a cellular damage, which is referred to as nitro-oxidative stress. Plants will be stimulated to manufacture NO synthase-like enzymes by mediating the L-arginine-dependent pathway or increase nitrate reductase (NR) production via the nitrite-dependent pathway to ensure plant survival under cold stress (Puyaubert & Baudouin, 2014), as has been shown in a variety of plant species including tomato (Diao et al., 2017). These in turn will lead to overexpression of several CBF (C-repeat binding factors)-dependent genes such as the *COR* and *LTI* genes that encode for proteins involved in cryoprotection and acclimation to cold stress (Cantrel et al., 2011; Puyaubert & Baudouin, 2014).

Roles of Plant-growth Promoting Rhizobacteria (PGPR)

The lethal effect of cold stress is related to the formation of ice crystals in plant cells, which causes electrolyte leakage and dehydration, resulting in a severe loss in crop output (Mitra et al., 2021). However, the presence of PGPR in plants can mitigate the effects of cold stress. It has been demonstrated that the PGPR genome contains genes for membrane transportation, signal transduction pathways, cold shock proteins, oxidative stress, antioxidant enzymes, and osmotic adjustment, which can assist plants in responding to stress by enhancing the efficiency of water transport across the membrane, maintaining water balance, and controlling the expression of variable signaling pathways to respond to the stressful conditions. To accomplish this, PGPR will directly trigger phytohormone synthesis within the rhizopheric zone, such as the production of auxins like the indoleacetic acid (IAA) to boost plant growth (Mitra et al., 2021). In rice, treatments with PGPR have shown to cause differential expression of various genes, such as the *OsASR6 (ABA STRESS RIPENING6)*. Overexpression of this gene in transgenic *A. thaliana* was observed to result in taller plants with higher yield, root biomass, stomatal conductance, photosynthesis and transpiration rates (Agarwal et al., 2019). Besides influencing the synthesis of auxins, PGPR has also been linked to directly induce production of gibberellic acids (GA) and cytokinins by increasing the supply of biologically fixed nitrogen for the plants (Fahad et al., 2015; Swarnalakshmi et al., 2020).

Induction of Dehydration Responsive Element Binding (DREB)

When plants are pressured by cold temperatures, the water in their cells turns to ice and expands. This causes the cell membrane to break, which ultimately leads to cell death. To get around this, certain plants have evolved specialized

transcription factors that help regulate gene expression and decide when to generate the proteins encoded by the genes. Dehydration Responsive Element Binding (DREB) is an example of a transcription factor that is in control of the synthesis of cold-inducible genes, which are produced when the surrounding temperature drops to a level that might be lethal to plants. This causes an immense number of cold-induced genes to be activated, generating proteins that can improve plant tolerance to cold stress. When the temperature in the surrounding environment drops, thereby creating low temperature stress in *Arabidopsis thaliana*, the transcription factor DREB is activated, activating the genes encoding *AtDREB1A/CBF1, CBF3*, and *CBF4* expression (Sharma et al., 2020). As a result, the plant's cold tolerance level has grown in response to freezing stress. Besides that, overexpression of *GhDREB1* (from cotton; *Gossypium hirsutum*) in transgenic tobacco plants has also been found to improve the tolerance to chilling stress compared to wild type plants (Ritonga & Chen, 2020; Shan et al., 2007). However, *GhDREB1* overexpression did not increase freezing tolerance in the transgenic tobacco (Shan et al., 2007). Besides that, the *GhDREB1* gene also functions as the transcriptional activator of *NtERD10B* and *NtERD10C* and increases proline synthesis in the transgenic tobacco (Shan et al., 2007).

Induction of Secondary Messengers: Phosphatidic Acid (PA), Sphingolipids, Cyclic Guanosine Monophosphate (cGMP) and Hydrogen Sulphide (H_2S)

Figure 3 depicts the generation of phosphatidic acid (PA), where it acts as a secondary messenger in plants that is responsible for maintaining plant growth and development (Arisz et al., 2013). Under cold stress, activation of the enzymes PLC and PLD will result in an increase in PA levels. Increasing PA levels will then disrupt the permeability and integrity of the plant cell membrane and induces the formation of ROS via stimulation of respiratory burst oxidase homolog D (RBOHD) activity (Ruelland et al., 2015; Tan et al., 2018), resulting in a plant that is more sensitive to a fall in temperature. It has been discovered that when

plants, such as barley are subjected to chilling stress for a short term (about 180 min), the amount of PLD/PA would increase significantly. At the same time, proline and ROS will accumulate in the plant's immature leaves. However, as the length of exposure to cold stress was extended to 24–36 h, the amount of PLD/PA in the young shoots and leaves was observed to decrease dramatically, whereas the synthesis of proline and ROS signals continued to grow, but these were only detected in the roots (Margutti et al., 2017).

On the other hand, sphingolipids (SL) are fundamental lipids found in plants that are essential for a variety of plant functions such as in maintaining membrane integrity, cellular, developmental, and stress-response processes (Mamode Cassim et al., 2020). Sphingolipids are commonly seen as glycosylated inositol phosphoryl ceramides (GIPCs) or glucosylceramides (GCs). According to several studies, sphingolipids play an important part in the cold signaling pathway by cooperating with PA to induce stomatal closure (Hou et al., 2016). The interplay between sphingolipid and NO has been reported (Guillas et al., 2013), in which treatments with SL-related molecules have been shown to trigger NO synthesis (Wang et al., 2007, 2009). In turn, NO plays a direct role in influencing PA synthesis in plants. For example, NO treatments were found to result in increasing PA levels in *Vicia faba* guard cells and subsequent treatments with PLC and PLC inhibitors prevented PA-induced closure of stomata, further confirming the role of NO in PA synthesis and stomatal closure (Agurla et al., 2018). Taken together, it can be deduced that the interplay between SL/NO stimulates PA synthesis to drive plants' response to stress.

Similar to PA, cyclic guanosine monophosphate (cGMP) also acts as an important secondary messenger plant cells that engages in critical plant processes and contributes in the tolerance to abiotic stresses. Exposure to low temperature will activate cGMP synthetase such as the guanylyl cyclase (GC) to increase the production of cGMP (Dubovskaya et al., 2015). cGMP is the byproduct of guanosine triphosphate (GTP) and it rarely works by itself; rather, it works in conjunction with NO and Ca^{2+} to promote plant's tolerance to cold. For instance, cold stress has been reported to promote
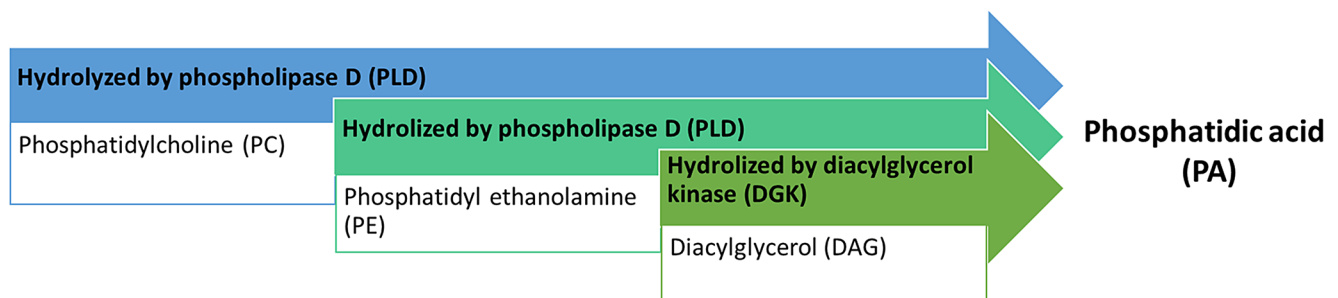
Fig. 3 Shows several paths for the production of phosphatidic acid (PA)

the synthesis of NO and cGMP in *Arabidopsis* seedlings (Bakakina et al., 2014). Under low-temperature stress, the cGMP signaling route allows NO to regulate tube growth, pollen germination, and proline buildup in *Camellia sinensis* (Wang et al., 2012).

Moreover, hydrogen sulphide (H_2S) is also involved in a range of physiological processes in plants, including seedling growth, adventitious root development, opening and closing of stomata, photosynthesis, fruit development and ripening, as well as plant maturity (Corpas & Palma, 2020; Li et al., 2015; Shi et al., 2015; Xuan et al., 2020). Recently, H_2S has also been reported to improve the capacity of a plant to tolerate stress by mitigating oxidative cellular damage through the enhancement of antioxidant systems (Montesinos-Pereira et al., 2018; Zhao et al., 2021). Regarding its role in cold stress, H_2S has been shown to alleviate cold stress in *Arabidopsis thaliana* through upregulation of *mitogen activated protein kinase 4 (MPK4)* gene expression (Du et al., 2017). Meanwhile, in pepper (*Capsicum annuum* L.), H_2S was found to alleviate the effects of cold stress on the seedlings by enhancing chlorophyll (Chl) synthesis pathway, specifically by increasing the content of Chl synthesis pathway substances such as protoporphyrin IX (Proto IX), Mg-protoporphyrin (Mg-Proto IX) and protochlorophyllide (Pchlide) (Wang et al., 2021). However, the information on the involvement of H_2S during cold stress is still limited and much is yet to be discovered in terms of its role in improving plant's tolerance to low-temperature.

Crosstalk between Small Signaling Molecules during Heat and Cold Stresses

In response to cold stress, small signaling molecules crosstalk and interact to yield a combination of responses in cold-stressed plants. This is summarized in Figure 4. Prior research on the role and activity of small signaling molecules in the response to temperature stress reveals only a portion of the truth and it is believed that there are still many underlying mechanisms of plant response and unknown signaling pathways to heat and cold stresses that need to be discovered. Therefore, it is critical to investigate and comprehend how plants naturally respond to extreme temperatures, such as the DREB, PGPR, osmoprotectants, and small signaling molecules, so that we may apply our knowledge to increase heat and cold resistance in crops and potentially develop new crop varieties that can tolerate extreme and fluctuating temperatures brought upon by the climate change.

Mitigation of Climate Change Impacts

Environmental stresses have always been associated with the changing climates. Through an increase in carbon dioxide (CO_2) emission that leads to global warming, anthropogenic activities have sped up the changes, thus putting a detrimental effect on the health and yield of crops. Having to develop certain adaptations, it is crucial to investigate how plants respond to the abiotic stress and climate change which further helps in choosing climate-resilient plants. The average surface temperature has increased by at least 1.5-2 °
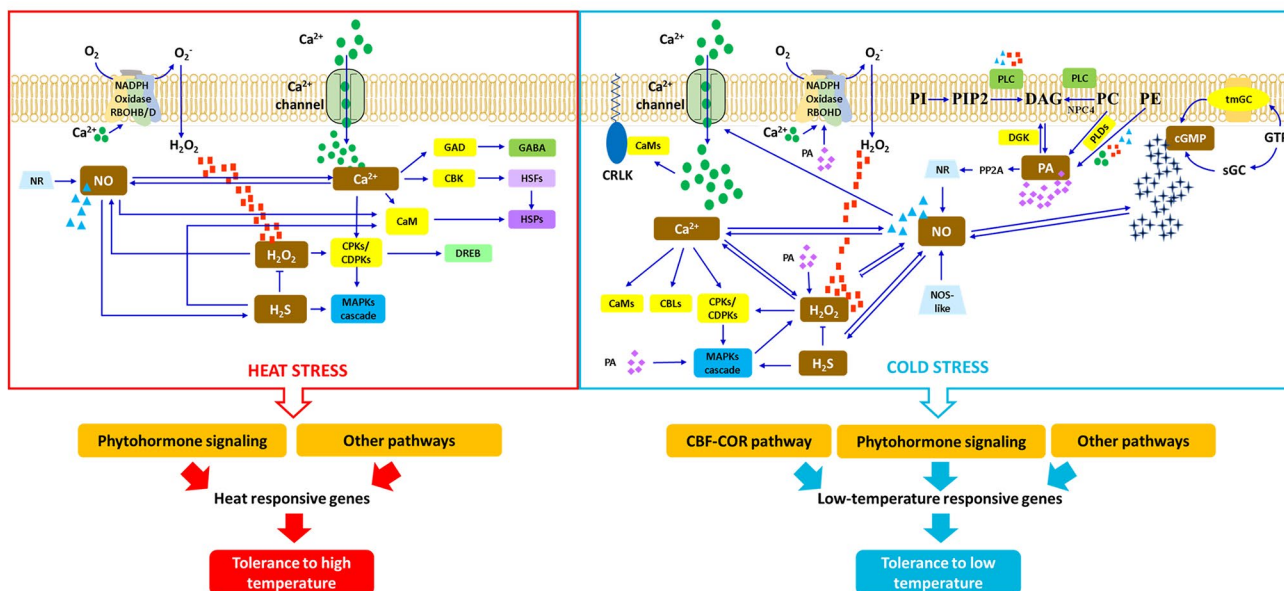

Fig. 4 The overview of the crosstalk between small signaling molecules during plant's response to heat and cold stress. Redrawn from Parankusam et al. (2017), Patra et al. (2021) and (Zheng et al., 2021)

C since the turn of century due to the continuous rising in atmospheric CO_2 levels and other greenhouse gas emissions, where the average amount of CO_2 recorded by NASA in 2022 have reached 420 ppm (NASA, 2022). Despite having evidences that the warmer temperature harms crop growth by affecting the plant metabolisms, the effect might be alleviated under higher CO_2 level (Abdelhakim et al., 2022). Although, the severity of temperature stress effects on plants and how plants modulate the elevated CO_2 will depend on the genotype's level of stress tolerance and their transpiration efficacy.

Under temperature stresses, plants tend to activate their antioxidant defense systems, including both enzymatic and non-enzymatic antioxidants to minimise oxidative stress and regulate cellular redox balance. This mechanism allows plants to better withstand stressful environments and consequently reducing negative impacts of ROS. By increasing non-photochemical quenching (NPQ) to make up for the drop of energy sinks, elevated CO_2 helps to improve PSII photoprotection and prevent photooxidative stress, thus avoiding ROS build-up that is resulted from the deterioration of photosynthetic activity under temperature stress. When plants are grown in elevated CO_2 condition, the severity of abiotic stress will influence the capacity of antioxidant defence. Consequently, decreased oxidative damage and increased ROS scavenging capacity reflect the impact of mitigation under high CO_2 level (Abdelhakim et al., 2022). The increased production of proline is also linked to enhanced water-use efficiency (WUE) and osmotic adjustment which help to regulate photosynthesis when combined with elevated CO2. Hence, preserving water balance and lowering oxidative damage of ROS are significantly aided by increasing plant stress tolerance through accumulation of phenolic compounds and compatible solutes.

Conclusion

In conclusion, the intricate interplay of metabolites, enzymes, proteins, osmoprotectants and other small signaling molecules in response to temperature stress reveals the remarkable adaptability of plants in the face of environmental challenges. The crosstalk of diverse mechanisms leading to ROS homeostasis plays pivotal roles in fortifying plants against oxidative stress induced by heat and cold. Understanding this intricate network of ROS detoxifying mechanisms is crucial for devising strategies to enhance crop resilience and productivity. Moreover, the observed changes in metabolite levels can also serve as vital markers in our efforts towards sustainable agriculture amid evolving climatic conditions. Coupled with this, powerful molecular genetic tools in combination with multi-omics strategies,

can pave the way to better understand the intricate nature of plant stress physiology.

Declarations

Conflict of interest The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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