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Short-term high temperature stress in plants: Stress markers and cell signaling

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ABSTRACT

Heat stress, intensified by rising global temperatures, presents significant challenges to plant growth, development, and reproduction. Plants respond with specific physiological and molecular changes, traditionally categorized as short-term (acute) or long-term (chronic). However, current classifications often lack the precision needed to adequately characterize short-term heat stress (STHS), leaving its specific markers and biological implications under-defined. This review proposes a time-range-based classification for heat stress responses, emphasizing STHS as a distinct phase rather than a milder form of prolonged stress. We differentiate between main thermotolerance, acquired thermotolerance, and acclimatization as separate strategies tied to specific exposure patterns. We also examine the roles and dynamics of key molecular and biochemical markers, including reactive oxygen and nitrogen species (ROS/RNS), transcription factors, small RNAs, heat shock responses, antioxidants, phytohormones, and osmolytes, analyzing their functional interplay. Based on recent evidence, we re-evaluate the importance of ROS and antioxidant defense, highlighting the underestimated role of RNS and osmolytes in acute heat episodes. This review summarizes current concepts about STHS, emphasizing its distinct nature and providing a foundation for more accurate identification of early-stage stress markers in plants exposed to high temperatures.

Keywords: Short-term heat stress, Molecular markers, Heat shock proteins, Reactive oxygen species, Antioxidant defence, Proline, Apoptosis, Programmed cell death, Oxidative.
Article type: Review Article.

INTRODUCTION

Climate change is driving the expansion of arid zones and desertification, prolonging hot seasons, drying up lakes, increasing soil salinization, and worsening wind erosion (Wang *et al.* 2023d; Yao *et al.* 2023; Nath 2025; Nes *et al.* 2025; Wang *et al.* 2025a). These processes form a cascading chain of interconnected ecological and agricultural consequences (Nath 2025; Nes *et al.* 2025). Among the many climate-related pressures, rising temperatures, extreme heat events, and heatwaves are currently recognized as the main factors contributing to the decline in crop productivity due to heat stress (HS; Vogel *et al.* 2019; Miller *et al.* 2021; Renard *et al.* 2023). Focusing on these critical thermal challenges, recent climate models and observational data confirm a steady increase in both sudden heat spikes and prolonged periods of elevated temperatures (Meehl & Tebaldi 2004; Donat *et al.* 2020; Al-Yaari *et al.* 2023; Kornhuber *et al.* 2024). These increasingly frequent thermal extremes disrupt plant development and productivity, especially when they coincide with sensitive reproductive stages such as flowering or seed filling (Chirivì & Betti 2023; Luo *et al.* 2023; Graci & Barone 2024; Batool *et al.* 2025; Li *et al.* 2025c). Depending on the timing, intensity, and duration of exposure, plants exhibit qualitatively different physiological

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and molecular responses, broadly classified into short-term (acute) and long-term (chronic) HS responses (Sgobba *et al.* 2015; Essemine *et al.* 2020; Sampath *et al.* 2023). The importance of short-term heat stress (STHS) is particularly evident in regions such as Kazakhstan, Russia, and Canada, which are major producers of wheat, barley, and other staple crops (Schierhorn *et al.* 2020; Templ & Calanca, 2020; Hunt *et al.* 2021; Hill & Li 2022; Karatayev *et al.* 2022; Wang *et al.* 2022). In these areas, rapid heat surges during late spring or early summer have become increasingly common due to continental climate dynamics (Templ & Calanca 2020; Wang *et al.* 2023b; White *et al.* 2023; Nasong *et al.* 2025; Wang *et al.* 2025b). Even short-duration heat episodes during critical phenological stages can lead to severe yield losses, posing significant risks to food security and economic stability (Templ & Calanca 2020; Hill & Li 2022; Wang *et al.* 2022). Understanding how plants perceive and manage acute thermal events offers practical value for breeding programs, forecasting systems, and agronomic decision-making under increasingly unstable climatic conditions. In this review, we provide a comprehensive overview of plant responses to HS, with an emphasis on STHS, a relatively underexplored yet increasingly relevant form of thermal stress in agriculture. We examine the classification of HS based on duration and intensity, explore molecular and biochemical markers of early signaling events, and analyze species-specific physiological responses. Finally, we discuss existing knowledge gaps and future research directions aimed at improving early detection and mitigation of acute thermal stress in agriculture.

Rethinking heat stress classification in plants

Abiotic stresses such as drought, salinity, heat, and high light induce complex adaptive responses and changes in plants at the molecular, metabolic, and phenotypic levels (Mareri *et al.* 2022; Soltabayeva *et al.* 2022; Nurbekova *et al.* 2024; Lahlali *et al.* 2025). These mechanisms help maintain cellular homeostasis and physiological stability under various stress conditions, enabling survival (Rao & Zheng 2025; Secomandi *et al.* 2025). The nature and extent of these responses depend mainly on the stress intensity and duration, as well as the inherent tolerance of each plant species (Mareri *et al.* 2022; DiCara & Gedan 2023). Variability across specific stress conditions underscores the need for a consistent classification of stress conditions to comprehend their adverse effects and evaluate plant adaptive strategies.

Complexities and subtleties of heat stress classification

Plant classification of abiotic stress conditions presents several difficulties. This is due to the wide range of biological and environmental factors that affect the perception and expression of stress (Mareri *et al.* 2022; Pereira 2016). For instance, plant species vary in their ecological niches, and some are terrestrial, others aquatic or semi-aquatic, which influences both the nature and severity of the stress encountered (Lacoul & Freedman, 2006; Pereira 2016; Zhu 2016; Prokić *et al.* 2019; Bal *et al.* 2021). Additional variability arises from soil types, geographic location, climate zone, plant developmental stage, and many others (Körner, 2016; Sah et al. 2016; Nievola *et al.* 2017; He *et al.* 2018; Berens *et al.* 2019; Veldhuis *et al.* 2019; Anstett *et al.* 2021; Seleiman *et al.* 2021; Irshad *et al.* 2024). It is very important to note that, from a physiological point of view, stress is not just an external factor, but rather a cumulative reaction of the body in response to the influence of various factors that disrupt its internal homeostasis or exceed its adaptive capabilities. Given these multiple conditions, it becomes challenging to create a unified classification system that adequately encompasses the full range of stress scenarios across crop and plant species. Despite the difficulties mentioned, some types of abiotic stress, such as salinity and drought, have relatively well-classified systems. Salt stress is often classified according to salt concentration (non-saline, slight saline, moderate saline, high saline, very high saline), predominant ion (Na^+, Cl^-, Ca^{2+}, SO_4^{2-}, etc), duration of exposure (short-term or long-term), and plant tolerance (halophytes and glycophytes; Pan *et al.* 2020; Smolko *et al.* 2021; Singh 2022; Lindberg & Premkumar 2024; Nurbekova *et al.* 2024). On the other hand, drought stress is commonly classified according to the plant growth cycle, origin (meteorological, agricultural, hydrological, and socioeconomic), and the extent (mild, severe, or severe extended) and duration (short-term or long-term) (Keyantash & Dracup 2002; Szira *et al.* 2008; D’Oria *et al.* 2022; Saleem *et al.* 2022). In contrast, HS is less classified in detail, although classifications based on duration (short-term or long-term), temperature ranges (normal, moderate, or extreme), and crop type (heat-sensitive, intermediate, and heat-tolerant) exist (Wahid *et al.* 2007; Sgobba *et al.* 2015; Hou *et al.* 2021; Fernández-Crespo *et al.* 2022; Mesa *et al.* 2022). Importantly, the focus on HS time is more influential because even a short-term increase in extreme temperature can lead to changes both at the molecular and physiological levels. This highlights significant gaps, especially as short, intense heatwaves are becoming more frequent due to ongoing climate change (Templ & Calanca 2020; Wang *et* *al.* 2023b; White *et al.* 2023; Nasong *et al.* 2025; Wang *et al.* 2025b). Classification of heat stress into STHS and long-term heat stress (LTHS) is an important tool for understanding the physiological and molecular mechanisms of plant adaptation (Sgobba *et al.* 2015; Essemine *et al.* 2020; Hou *et al.* 2021; Sharma *et al.* 2022; Luo *et al.* 2023). However, such classification remains conditional and flexible, as it faces a number of methodological and biological difficulties. This is due to the fact that the plant's response to heat stress is not a binary transition from a “normal” state to a “stressed” one, but a continuous process in which some mechanisms are superimposed on others. Short-term heat exposure (e.g., for several minutes to 12 hours) can, if continued, turn into a long-term one, and it is often impossible to distinguish a clear time threshold between STHS and LTHS (Suraweera *et al.* 2020; Venios *et al.* 2020). This is especially important in field conditions, where temperatures can fluctuate during the day, gradually accumulating the stress effect. However, what can be considered a short-term and harmless stress for heat-adapted plants (cacti or sorghum) can be lethal for heat-sensitive crops (rice or wheat; van Es, 2020; Galicia-Juárez *et al.* 2021). Moreover, even within a single species, different genotypes exhibit different sensitivity to high temperatures. This makes it impossible to provide a single, universal definition of the time boundaries of STHS and LTHS that is the same for all plants. The same time interval can be interpreted differently depending on the temperature. For example, 12 hours at a temperature 5 °C above the optimum can be classified as moderate short-term stress, whereas 12 hours at a temperature close to the lethal threshold (45-50 °C for many C3 crops) would constitute acute thermal shock (Chen e*t al.* 2022). Therefore, the duration and intensity of heat exposure must be considered together. In addition, heat sensitivity depends on the phenological stage. During the flowering phase, even a short-term increase in temperature can cause fertility impairment and a decrease in yield, whereas during the vegetative growth stage, the same conditions can be easily tolerated (Wu *et al.* 2021b; Lee *et al.* 2022; Lohani *et al.* 2022). Therefore, classification by duration must take into account plant development and not just the exposure time. Under natural conditions, heat stress rarely acts in isolation. It is often accompanied by moisture deficit, high light activity, or changes in the water or mineral regime (Zandalinas *et al.* 2020). In such scenarios, a combined stress occurs, in which the plant's response is an integrated response to the entire complex of adverse factors. This makes it difficult to establish a clear time frame for heat exposure as a single factor.

Divergent plant responses to short- and long-term heat stress

Despite the difficulties in distinguishing between the concepts of heat stress classification by time, in this review, we adopt the following working convention that STHS is defined as exposure to high temperature (individual for each plant species) lasting from a few seconds to 12 hours. While LTHS is assessed as exposure to high temperature for longer than 12 hours. This assumption is made to ensure clarity and systematization of the analysis, despite the awareness that plant responses to stress vary significantly depending on the species, genotype, and other factors. Thus, by creating this convention, we can clearly see that STHS and LTHS exposures have fundamental differences in the adaptive and damaging processes triggered (Table 1).

Table 1. Comparative detrimental effects of short-term (STHS) and long-term heat stress (LTHS) on morphophysiological parameters of plants.

Heat stress type	**Detrimental effects**	**References**
	Photosynthetic rate	
STHS	Rapid PSII inhibition, reversible upon stress relief; reduced chlorophyll fluorescence. Immediate decline in Fv/Fm and net photosynthetic rate due to PSII damage	Sharma *et al.* 2023 Aslam et al. 2022
LTHS	Chronic photoinhibition, reduced RuBisCO activity, chloroplast integrity, and CO_2 assimilation	Mathur *et al.* 2021 Gao *et al.* 2025 Tas & Mutlu 2021
	Chlorophyll content	
STHS	Partial loss, pigment concentration may recover	Sharma *et al.* 2023
LTHS	Substantial degradation, particularly under continuous exposure, impacts pigment stability	Bhardwaj *et al.* 2023 Sallam *et al.* 2024
	Antioxidant Defense	
STHS	Upregulation of SOD, CAT, and APX in a transient pattern	Djanaguiraman *et al.* 2024
LTHS	Chronic oxidative stress may exceed antioxidant capacity, leading to ROS damage	Kamatchi *et al.* 2024
	Relative water content (RWC)	
STHS	Temporary declines in RWC, water use efficiency maintained in resilient varieties	Ghafoor *et al.* 2021
LTHS	Persistent RWC reduction, affecting cell turgor and overall plant hydration	Gao *et al.* 2025
	Stomatal conductance	

STHS	Immediate reduction to limit water loss, partially recoverable	Djanaguiraman et al. 2024
LTHS	Prolonged closure causes CO_2 deprivation and reduced carbon assimilation	Kumar *et al.* 2023 Tas and Mutlu 2021
	Root to shoot ratio	
STHS	Minor or adaptive increase in root-shoot ratio	Ghafoor *et al.* 2021
LTHS	Disruption in allocation; reduced shoot growth leads to imbalanced development	Hanjagi *et al.* 2025
	Phenological Shifts	
STHS	Often negligible unless stress coincides with flowering or grain filling	Sharma *et al.* 2023
LTHS	Altered flowering time, early senescence, and shortened grain filling period	Kumar *et al.* 2023
	Yield and reproductive traits	
STHS	Tolerable during vegetative stages, but reproductive organs are sensitive	Djanaguiraman *et al.* 2024
LTHS	Severe reductions in seed viability, pollen germination, and grain yield	Kumar *et al.* 2023

Photosynthetic activity is damaged in both cases, but the nature of the damage differs. With short-term exposure, rapid and often reversible inactivation of photosystem II (PSII) is observed, accompanied by a decrease in chlorophyll fluorescence and photochemical efficiency (Fv/Fm; Aslam *et al.* 2022; Sharma *et al.* 2023). These changes are often eliminated after stress relief (Sharma *et al.* 2023). At the same time, with LTHS, PSII damage becomes chronic, RuBisCO activity decreases, chloroplast structure is disrupted, and CO_2 assimilation is significantly limited (Mathur *et al.* 2021; Tas & Mutlu 2021; Gao *et al.* 2025). Moreover, chlorophyll content also shows different sensitivity to stress duration. STHS causes a partial loss of pigments, which can be compensated for after the restoration of conditions (Sharma *et al.* 2023). However, with LTHS, more significant and persistent destruction of pigments occurs, which is associated with a violation of chlorophyll stability and a deficit of restorative resources (Bhardwaj *et al.* 2023; Sallam *et al.* 2024). As with the photosynthetic system, LTHS has a stronger effect than STHS. With prolonged exposure to high temperatures, there is a constant generation of reactive oxygen species (ROS), which leads to depletion of the antioxidant system, causing the accumulation of oxidative damage products and disrupting the integrity of cells (Kamatchi *et al.* 2024). However, with STHS, antioxidant protection, including superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX), quickly and effectively neutralize excess ROS (Djanaguiraman *et al.* 2024). Relative water content (RWC) and stomatal conductance are altered already at early stages of heat stress. Under STHS conditions, a temporary decrease in RWC is observed, especially in sensitive varieties, while resistant forms maintain water use efficiency (Ghafoor *et al.* 2021). Stomata quickly close to minimize water loss but may open when conditions are restored (Djanaguiraman *et al.* 2024). Under LTHS, the decrease in RWC becomes persistent, cell turgor is impaired, water potential is not restored, and stomatal conductance remains suppressed, leading to CO_2 deficiency and reduced photosynthetic activity (Tas & Mutlu 2021; Kumar *et al.* 2023). Physiologically, the response further leads to morphological changes, such as the root-to-shoot ratio. With STHS, it can temporarily increase due to increased root growth as an adaptive response (Ghafoor *et al.* 2021). However, with long-term exposure to heat, the root-to-shoot ratio is disrupted due to significant suppression of shoot growth (Hanjagi *et al.* 2025). This disrupts the balance of resource distribution and forms a deformed morphology. It is worth noting that phenological shifts under the influence of STHS are most often not observed, as well as changes in the root-to-shoot ratio (Sharma *et al.* 2023). However, an exception is when a short-term effect of high temperatures coincides with critical phases such as flowering (Djanaguiraman *et al.* 2024). In the vegetative growth phase, short-term temperature fluctuations may not cause significant disturbances, but exposure during flowering or fruit formation can already lead to a violation of pollen fertility under STHS (Sharma *et al.* 2023; Djanaguiraman *et al.* 2024). In addition, reproductive indicators and yield are especially sensitive to LTHS. With long-term stress, the entire life cycle of the plant changes, that is, flowering accelerates, the duration of grain filling is reduced, and premature aging can be observed (Kumar *et al.* 2023). Under LTHS conditions, severe reproductive losses are observed, manifested in a decrease in pollen germination, deterioration of the seed set, and a decrease in the weight and number of fruits, which together sharply reduce the overall yield (Kumar *et al.* 2023). Thus, short-term and long-term heat stress activate both common and fundamentally different mechanisms (Table 1). STHS predominantly induces rapid and reversible protective responses. On the other hand, LTHS leads to profound restructuring of metabolism, growth, and development, affecting not only the current plant cycle but also potentially its progeny through epigenetic memory mechanisms.

Hierarchies of Thermotolerance and the Case for Early-Response Markers

As mentioned earlier, STHS usually causes immediate and reversible molecular and physiological changes aimed at the rapid restoration of cellular functions (Ghafoor *et al.* 2021; Aslam *et al.* 2022; Sharma *et al.* 2023; Djanaguiraman *et al.* 2024). In turn, LTHS requires more stable adaptation, affecting the development, metabolism, and morphology of the plant (Mathur *et al.* 2021; Tas & Mutlu 2021; Bhardwaj *et al.* 2023; Kumar *et al.* 2023; Kamatchi *et al.* 2024; Sallam *et al.* 2024; Gao *et al.* 2025; Hanjagi *et al.* 2025). These two types of HS initiate different levels of responses as emergency defense mechanisms before the restructuring of the entire organism. It is in this context that the concepts of thermotolerance and acclimation become especially important, reflecting the STHS and LTHS strategies of plant adaptation to high temperatures. Thermotolerance of plants is the ability to withstand exposure to high temperatures without losing viability (Chen *et al.* 2022). It can be basal and acquired. Basal thermotolerance is an innate, genetically determined resistance characteristic of certain species or genotypes adapted to hot conditions such as desert xerophytes (Han *et al.* 2021; Chen *et al.* 2022; Lasorella *et al.* 2022; Bai *et al.* 2023). Such plants already have resistant proteins, stable membranes, and effective antioxidant systems (Han *et al.* 2021; Chen *et al.* 2022; Lasorella *et al.* 2022; Bai *et al.* 2023). Acquired thermotolerance is formed after preliminary sublethal exposure to high temperatures and represents a temporary increase in resistance, for example, in STHS (Friedrich *et al.* 2021; Li & Howell 2021; Dannfald *et al.* 2025). This process is a preparation in which rapid defense mechanisms are activated, such as expression of heat shock proteins (HSPs), strengthening of the antioxidant system, changes in membrane permeability, and accumulation of osmoprotective compounds (Friedrich *et al.* 2021; Li & Howell 2021; Dannfald *et al.* 2025). Such a response, in fact, mobilizes the cell for a more serious thermal attack. Unlike thermotolerance, acclimation is a complex and long-term process of adaptation of the entire plant (not just individual cells) to LTHS or repeated heat stress (Gjindali *et al.* 2021; Filaček *et al.* 2022; Gjindali & Johnson 2023). It covers a wide range of physiological and morphological changes, including cuticle thickening, leaf orientation along the sun's rays, changes in root architecture, and revision of the water use strategy (Amitrano *et al.* 2022; Jiang *et al.* 2024, 2025). At the physiological level, this is manifested in a stable change in transpiration, reorganization of the photosynthetic apparatus, stabilization of the membrane composition, and hormonal balance (Garcia-Molina *et al.* 2020; Paul *et al.* 2020; Janda *et al.* 2021; Filaček *et al.* 2022). In this case, not only do changes in gene expression occur, but also deeper epigenetic rearrangements, including DNA methylation and histone modification, forming a long-term stress memory that can be preserved in the offspring (Miryeganeh 2021; Liu *et al.* 2022; Ramakrishnan *et al.* 2022; Quan *et al.* 2024). Thus, thermotolerance and acclimatization are interrelated but different strategies. The first is activated quickly, ensures immediate survival, and can be short-term, while the second is a systemic restructuring of plant functioning aimed at survival under conditions of constant thermal pressure (Friedrich *et al.* 2021; Li & Howell 2021; Ramakrishnan *et al.* 2022; Gjindali & Johnson 2023). At the same time, acquired thermotolerance can act as a kind of transitional stage/step to the beginning of acclimatization, laying the foundation for more stable and integral adaptation (Bourgine & Guihur 2021; Chen *et al.* 2022; Ren *et al.* 2023). Such a multi-level response to temperature fluctuations allows plants to be flexible in a changing climate and continue their life cycle even in extreme conditions that are regulated at the molecular and biochemical levels.

Molecular and biochemical markers of short-term heat stress signaling response

Plants undergo morphophysiological changes after heat stress, resulting from alterations at the molecular and biochemical levels. They guard against the harmful effects of STHS through a complex process that includes primary signaling of reactive oxygen species (ROS) and reactive nitrogen species (RNS), molecular triggers and early signaling events, heat shock response (HSR), activation of the antioxidant system, phytohormonal response, and accumulation of osmoprotectants (osmolytes). These processes can provide crucial molecular and biochemical markers activated at different time intervals. Therefore, they facilitate the assessment of the plant's condition in the early stages of stress, before visible signs manifest.

ROS and RNS – dual roles

Reactive Oxygen Species (ROS) are oxygen-derived molecules produced during aerobic metabolism in plants, including singlet oxygen ($^1O_2$), superoxide anion ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($^\bullet OH$) (Nanda *et al.* 2010; Kucukoglu Topcu & Bhalerao 2023). ROS play crucial roles in plant signaling, regulating growth and development (root elongation, pollen tube development, cell differentiation, and response to phytohormones), stress responses, protection from pathogens, and programmed cell death (Baxter *et al.* 2014; del Río 2015). They mediate rapid cellular responses to various stimuli and are integral to the perception of both abiotic and biotic stress by basal constitutive production (Mittler *et al.* 2022). It is important to note, however, that while $O_2^{\bullet-}$ and H_2O_2 primarily serve as signaling molecules, •OH is extremely reactive and is primarily associated with cell damage (Ransdell-Green *et al.* 2025). Reactive Nitrogen Species (RNS), including nitric oxide, along with ROS, also play important roles in plant signaling and stress responses, often cooperating with ROS (del Río 2015). Similar to ROS, RNS act as intracellular and intercellular signaling molecules at low concentrations to control plant growth, development, and defense mechanisms (Khan *et al.* 2023b). However, maintaining this delicate balance is critical, as excessive amounts of ROS or RNS can cause cellular damage and retard plant growth (Singh *et al.* 2022). Therefore, ROS and RNS signaling are regulated in different tissues and environmental conditions through various mechanisms, including basal ROS synthesis and the use of ROS scavengers (Baxter *et al.* 2014).

ROS basal synthesis and functions

The main sources of basal ROS synthesis in plants are mitochondria, chloroplasts, NADPH oxidases, apoplast oxidases, and peroxisomes (Liu *et al.* 2021a; Mansoor *et al.* 2022; Bao *et al.* 2024). In mitochondria, ROS formation occurs due to the leakage of a small number of electrons into the electron transport chain (during the process of respiration) and the reduction of molecular oxygen (O_2) to $O_2^{\bullet-}$ (Mansoor *et al.* 2022). Similarly, $O_2^{\bullet-}$ is formed in chloroplasts during photosynthesis in photosystem I (PSI) due to electron leakage in the Mehler reaction (Kozuleva *et al.* 2020). In addition, $^1O_2$ can be formed in chloroplasts in PSII when chlorophyll is overexcited (Kozuleva *et al.* 2020). Important enzymatic systems capable of generating ROS also include NADPH oxidases, represented in plants by the family of respiratory burst oxidase homologs (RBOHs), localized in the plasma membrane (Wu *et al.* 2023; Rivas *et al.* 2024; Zhang *et al.* 2025). These enzymes catalyze the transfer of electrons from NADPH, located in the cytoplasm, to O_2, located in the extracellular space, resulting in the formation of $O_2^{\bullet-}$ in the apoplast (Wu *et al.* 2023; Zhang *et al.* 2025). Then, under the action of SOD, $O_2^{\bullet-}$ is converted into H_2O_2 (Mishra *et al.* 2023). Unlike charged superoxide, H_2O_2 can freely diffuse through the apoplast and penetrate into the cytoplasm through aquaporins (Mukherjee *et al.* 2024). This turns it into an effective signal transmitting information about the impact of stress from a local focus to distant parts of the plant (Rivas *et al.* 2024). In addition to the SOD family of enzymes, other enzymatic sources of H_2O_2 also operate in the apoplastic region, including polyamine oxidases (PAOs) and oxalate oxidases (OxO; Podgórska *et al.* 2017; Benkő *et al.* 2022; Samanta *et al.* 2023). Polyamine oxidases catalyze the oxidation of biogenic polyamines such as spermidine and spermine, which is accompanied by the formation of H_2O_2 and the corresponding aldehydes (Samanta *et al.* 2023). The activity of these enzymes, as well as the synthesis of substrates (polyamines), usually increases under the influence of various abiotic stresses, including thermal stress (Benkő *et al.* 2022; Samanta *et al.* 2023). The produced H_2O_2 can participate in strengthening the cell wall by oxidative cross-linking of components, as well as in triggering cascades of signaling reactions (Benkő *et al.* 2022). Oxalate oxidases, in turn, catalyze the oxidation of oxalic acid with the formation of H_2O_2 and CO_2 (Podgórska *et al.* 2017). Their activity increases significantly in response to pathogens, especially oxalate-producing fungi, and under certain abiotic stresses (Podgórska *et al.* 2017). The resulting H_2O_2 can perform both signaling and protective functions. An equally significant source of H_2O_2 inside the cell are the single-membrane organelles peroxisomes, which actively participate in β-oxidation of fatty acids and photorespiration (Li *et al.* 2022c; Szrok-Jurga *et al.* 2023; Fransen & Lismont 2024). In seeds, especially in glyoxysomes, the enzyme Acyl-CoA oxidase catalyzes the oxidation of fatty acids with the participation of oxygen as an electron acceptor, resulting in the formation of H_2O_2 (Cooper & Beevers 1969; Szrok-Jurga *et al.* 2023). Under conditions of photorespiration, which is enhanced in C_3 plants at high temperatures, low CO_2 concentrations, and excess oxygen, glycolate coming from chloroplasts is oxidized in peroxisomes with the participation of Glycolate Oxidase, which is also accompanied by the formation of H_2O_2 (Timm & Hagemann 2020; NOCTOR *et al.* 2002; Li *et al.* 2022c). These processes play an important role in the regulation of cellular redox homeostasis and in maintaining the metabolic adaptability of plants (Li *et al.* 2022c; Szrok-Jurga *et al.* 2023). Thus, ROS play a critical signaling role in plant cells, and their functions depend not only on their chemical nature but also on their precise subcellular localization (Medina *et al.* 2021; Phua *et al.* 2021). In the apoplast, $O_2^{\bullet-}$ and H_2O_2 are involved in defense responses, cell wall modification, stomatal apparatus regulation, and systemic intercellular signaling (Farvardin *et al.* 2020; Fichman *et al.* 2022; Rodrigues & Shan 2022; Rivas *et al.* 2024). In the cytoplasm, H_2O_2, formed as a result of $O_2^{\bullet-}$ dismutation or penetration from the apoplast, can activate protein kinase cascades, affect ion homeostasis (in particular, Ca^{2+} concentration), and oxidize redox-sensitive proteins, thus integrating hormonal and stress signals (Lennicke & Cochemé 2021;

Shabbir *et al.* 2022; Averill-Bates, 2024). In mitochondria, ROS are involved in retrograde signaling, informing the nucleus of the current energy status and helping to trigger adaptive responses (Mielecki *et al.* 2020; Walker & Moraes 2022; Khan *et al.* 2024). In chloroplasts, $^1O_2$ initiates specialized photoprotective retrograde signaling, and $O_2^{\bullet-}$ and H_2O_2 participate in general cellular acclimation (Dmitrieva *et al.* 2020; Dogra & Kim 2020; Breeze & Mullineaux 2022; Tano & Woodson 2022). Peroxisomes, producing H_2O_2, including during photorespiration, contribute to the total ROS pool of the cell and participate in the regulation of stress adaptations (Corpas *et al.* 2020; He *et al.* 2021). This is often one of the first responses to high temperature exposure and serves as the initial trigger for a cascade of protective and regulatory reactions in the plant cell (Medina *et al.* 2021; Fortunato *et al.* 2023; Hendrix *et al.* 2023; Zhu *et al.* 2023). However, under HS, ROS synthesis increases sharply, and their concentrations can quickly reach toxic levels (Singh *et al.* 2022).

The damaging effects of ROS overaccumulation

When the balance between ROS formation and scavenging is disturbed, oxidative stress develops, in which these molecules change their status from regulatory molecules to powerful oxidants, causing damage to cellular structures and disrupting the physiological functions of plants (Fedoreyeva 2024; Wang *et al.* 2024). Under HS, this leads to a cascade of destructive processes, including lipid peroxidation (LPO), oxidative modification of proteins, damage to nucleic acids, dysfunction of mitochondria and photosystems, and the initiation of programmed cell death (PCD; Kim 2020; Babbar *et al.* 2021; Medina *et al.* 2021; Ye *et al.* 2021; Sharma *et al.* 2022; Fortunato *et al.* 2023; Fedoreyeva 2024; Wang *et al.* 2024). One of the most aggressive types of ROS is $^1O_2$, which is generated mainly in chloroplasts, especially in photosystem II, during excessive excitation of chlorophyll (Dogra & Kim 2020; Bhatt *et al.* 2021; Andrés *et al.* 2022; Krieger-Liszkay & Shimakawa 2022). $^1O_2$ actively initiates LPO by attacking double bonds of unsaturated fatty acids in membrane lipids, including thylakoid and plasma membranes (Dmitrieva *et al.* 2020). This leads to the disruption of their integrity, fluidity, and permeability, which critically affects the function of cellular organelles and also amplifies the secondary products of LPO, such as Malondialdehyde (MDA), which also exhibit signaling and toxic activity (Bhatt *et al.* 2021; Krieger-Liszkay & Shimakawa 2022). In addition, $^1O_2$ oxidizes chlorophylls and carotenoids, reducing the efficiency of light absorption and photoprotection, which aggravates photoinhibition (Dogra & Kim 2020). It can also modify amino acid residues in proteins, causing their denaturation and loss of activity (Andrés *et al.* 2022). The cumulative effect of these processes is a decrease in photosynthetic activity and damage to chloroplasts, which often leads to cell death under heat stress (Bhatt *et al.* 2021). Although less reactive than other forms of ROS, $O_2^{\bullet-}$ poses a serious threat to cellular metabolism (Khorobrykh *et al.* 2020; Lennicke & Cochemé 2021; Read *et al.* 2021). It is capable of destroying iron-sulfur clusters in proteins, including key enzymes of the mitochondrial and chloroplast respiratory chain, thereby disrupting energy metabolism (Khorobrykh *et al.* 2020; Read *et al.* 2021). In addition, $O_2^{\bullet-}$ is involved in the formation of other, more reactive forms of ROS. In particular, it can interact with nitric oxide (NO) to form peroxynitrite ($ONOO^-$), a powerful nitrating agent that causes serious damage to proteins and lipids. $O_2^{\bullet-}$ is also a H_2O_2 precursor, which formed by SOD (Borisov *et al.* 2021; Liu *et al.* 2021b; Lushchak & Lushchak 2021; Kozlov *et al.* 2024). H_2O_2 is a relatively stable form of ROS that is diffusible and acts as an important signaling function at low concentrations (Nazir *et al.* 2020; Knaus 2021; Konno *et al.* 2021; Liu *et al.* 2024). However, at excessive concentrations, it becomes toxic. It can oxidize sensitive amino acid residues, such as cysteine and methionine, leading to structural and functional changes in proteins (Lennicke & Cochemé 2021; Corpas *et al.* 2022b; Hurst *et al.* 2022). In addition, H_2O_2 is involved in the initiation of Fenton and Haber-Weiss reactions involving divalent metal ions, resulting in the formation of the most aggressive and destructive form of ROS – $^\bullet OH$ (Nazir *et al.* 2020; Kessler *et al.* 2022). $^\bullet OH$ has an extremely high reactivity and an extremely short lifetime, which have diffusion-limited rates and exclude its signaling functions (Di Meo & Venditti 2020; Kessler *et al.* 2022). It is formed non-enzymatically and exclusively locally, in the immediate vicinity of iron or copper ions that catalyze the Fenton reaction. $^\bullet OH$ attacks virtually any biomolecule, such as lipids (initiates lipid peroxidation), proteins, nucleic acids, and carbohydrates (Nazir *et al.* 2020; Kessler *et al.* 2022). It destroys peptide bonds and causes carbonylation of amino acids, which leads to enzyme inactivation and disruption of protein metabolism (Juan *et al.* 2021). Its effect on nucleic acids includes oxidation of nitrogenous bases, formation of 8-oxoguanine, and single- and double-stranded DNA breaks, which lead to mutations and disruption of gene expression (Suzuki & Kamiya 2016; Hahm *et al.* 2022; Andrés *et al.* 2023). In addition, $^\bullet OH$ is able to destroy polysaccharides, disrupting the structure of the cell wall and energy storage metabolism (Schopfer 2001; Podgórska *et al.* 2017). Thus, the accumulation of $^\bullet OH$ is a marker of severe oxidative stress and serves as a direct cause of irreversible damage leading to the loss of cellular functions, ferroptosis, and PCD (Schopfer, 2001; Checa & Aran 2020; Hasanuzzaman *et al.* 2020; Wen *et al.* 2024; Abdukarimov *et al.* 2025). Despite the generally recognized increase in ROS levels under abiotic stresses, their role and dynamics under HS may be more complex and require detailed consideration. There is evidence that questions the universality of the rule of a ubiquitous increase in ROS. For example, as shown by Zhanassova *et al.* (2021), under LTHS in barley seedlings, a decrease in H_2O_2 and $O_2\bullet^-$ levels was observed in stems, while the H_2O_2 level increased in roots (Zhanassova *et al.* 2021). At the same time, an increased level of MDA (a reliable marker of LPO) was recorded both in stems and roots. These results allow us to put forward several important assumptions. First, the level of ROS and its markers can be significantly organ-specific, which dictates the need for analysis for individual plant parts, rather than for the entire organism. Second, H_2O_2 and superoxide may not always act as universal indicators of heat stress, especially under LTHS, at least in barley *cv.* Astana-2000 (Zhanassova *et al.* 2021). Third, an increase in the MDA level confirms its significance as a reliable indicator of oxidative stress and lipid damage under heat exposure, regardless of the local dynamics of individual types of ROS. However, in the context of STHS, the existing studies do not yet provide a definitive statement that these ROS did not increase at shorter time intervals. In addition, the mentioned study did not analyze the •OH level, and the nature of LPO is not fully understood. In addition, the possibility of the involvement of RNS in LPO should also be considered (Moldogazieva *et al.* 2018). This is justified by the fact that there is a decrease in $O_2\bullet^-$ levels in the stems with a simultaneous increase in MDA, which may indicate a role for NO in $O_2\bullet^-$ scavenging (Liu *et al.* 2025). More importantly, the $ONOO^-$ formed as a result of the quenching reaction could promote lipid oxidation; thus, the role of RNS in HS is perhaps more significant than discussed (Borisov *et al.* 2021; Liu *et al.* 2021b; Lushchak & Lushchak 2021; Kozlov *et al.* 2024).

RNS synthesis, signaling, and toxicity

In particular, the most studied and significant representative of RNS in cellular signaling is nitric oxide (NO) (Hancock & Veal 2021). It plays a key role in the regulation of many physiological processes, as well as in the response to stress, including thermal stress (Hancock & Veal 2021; Lushchak & Lushchak 2021). Having a small size and relatively stable (for a radical) gaseous molecule of NO, it can easily diffuse through biological membranes without the participation of specific transporters (Khan *et al.* 2023c). This allows it to act as both an intracellular and intercellular signal, quickly spreading between cells and even tissues. NO has many targets in the cell (proteins, lipids, and nucleic acids), and its effects depend on its concentration, duration of exposure, and cellular context, which ensures its participation in many processes that are not directly related (del Río 2015; Moldogazieva *et al.* 2018; Jomova *et al.* 2023; Khan *et al.* 2023b). NO can modify proteins directly (via S-nitrosylation, tyrosine nitration) or indirectly (via activation of guanylate cyclase and cGMP-dependent pathways), affect ion homeostasis, and regulate gene expression (León 2022). Moreover, both ROS generation and NO nitric oxide generation occur via both enzymatic and non-enzymatic pathways. The main synthesis of nitric oxide (NO) occurs due to NOS-like enzymes, the name of which originates from NO synthases (NOS) of animals (Hancock 2020). Despite the absence of a classical homologue of animal NOS, enzymes with NOS-like activity, capable of synthesizing NO from L-arginine, have been identified in plants (Chatelain *et al.* 2021; Corpas *et al.* 2022a). Their exact nature and localization are still being actively studied, but their contribution to the generation of NO is recognized as significant (Hancock 2020). At the same time, another major source of NO in plants is the cytosolic enzyme nitrate reductase (NR). NR is traditionally involved in nitrogen assimilation (reduction of nitrate to nitrite) using NADH or NADPH as a reducing agent (Carillo & Rouphael 2022; Aitlessov *et al.* 2023). However, under conditions of oxygen deficiency (hypoxia) or low pH values (acidosis), NR can catalyze the reduction of nitrite (NO_2^-) to NO (Chamizo-Ampudia *et al.* 2017; Berger *et al.* 2020). In addition to this, in an acidic environment (for example, in the apoplast), a non-enzymatic pathway for NO production occurs through the reduction of NO_2^- (Bethke *et al.* 2004). However, there are other enzymatic pathways for NO synthesis, including the molybdenum-containing enzyme family. This family of enzymes in plants, which includes Nitrate Reductase (NR), Xanthine Oxidase (XO), Aldehyde Oxidase (AO), Sulfite Oxidase (SO), and potentially Mitochondrial Amidoxime Reducing Component (mARC), represents a diverse group of NO sources (Alamri *et al.* 2022; Aubakirova *et al.* 2023; Maia 2023). They share the molybdenum cofactor, which allows them to participate in redox reactions, including the reduction of nitrite to NO (Mendel 2022; Suganuma 2022; Satkanov *et al.* 2024, 2025). This highlights the complexity and diversity of NO synthesis pathways in plants, which allows them to fine-tune the levels of this important signaling mediator in response to a wide range of physiological demands and stressors. At normal basal levels, NO acts as a universal signaling messenger deeply involved in the regulation of plant growth and development, including seed germination, root morphogenesis (elongation, lateral root and hair formation), shoot and leaf development (including senescence), as well as flowering and pollen tube growth processes for successful fertilization (Ciacka *et al.* 2022; Hussain *et al.* 2022; Khan *et al.* 2023a). NO does not act in isolation but closely interacts with the signaling pathways of major phytohormones, acting as an integrator and modulator of their functions. It mediates auxins in root growth, synergistically or antagonistically cooperates with gibberellins and abscisic acid (ABA) in the regulation of seed dormancy and stomatal movement, interacts with ethylene in senescence, with cytokinins in growth, and is an important component of the salicylic acid (SA) and jasmonate (JA) defense pathways (Freschi 2013; León *et al.* 2014; Galatro *et al.* 2020; Fu *et al.* 2022; Maurya *et al.* 2025). In addition, NO plays a key role in the regulation of ion homeostasis and stomatal movement by modulating ion fluxes to control water balance (Jeandroz *et al.* 2013). Finally, at basal concentrations, NO interacts with superoxide anion to form $ONOO^-$ and performs an antioxidant function (Kozlov *et al.* 2024). Importantly, the reaction of peroxynitrite formation, although it can be considered as a mechanism for $O_2^{\bullet-}$ detoxification, on the other hand, $ONOO^-$ itself is an extremely strong oxidant, posing a significant threat to cells (Kozlov *et al.* 2024). $ONOO^-$ causes nitration of tyrosine residues in proteins, leading to the formation of 3-nitrotyrosine (León 2022; Jomova *et al.* 2023). This can irreversibly alter the structure and function of proteins, deactivating enzymes, and disrupting signaling pathways. It can cause oxidative damage to DNA bases and chain breaks, leading to genetic instability and potential cell death. Like ROS, this radical is capable of initiating lipid peroxidation, which leads to disruption of the integrity and permeability of cell membranes. Thus, in plants, there is a complex balance between ROS and RNS. Under heat stress, their levels increase sharply. They act as signaling molecules, triggering protective programs, but when they accumulate in excess and interact uncontrollably (especially the formation of peroxynitrite), they become powerful agents of damage, leading to oxidative and nitrosative stress and, ultimately, cell death. This surge is the key signal for triggering the adaptive response.

Molecular triggers and early signaling events

Under HS conditions, ROS and RNS rapidly accumulate in various cellular compartments and act as secondary messengers, subsequently initiating early signaling events that are critical for the activation of plant defense mechanisms (Zheng *et al.* 2025). Among the first targets of ROS and RNS are membrane ion channels, in particular Ca^{2+} (Jeandroz *et al.* 2013; Sandalio *et al.* 2023). ROS then activate phospholipases, especially Phospholipase D and C (PLD and PLC), which is accompanied by the release of another signaling mediator, phosphatidic acid (Song *et al.* 2020; González-Mendoza *et al.* 2021). During this time, protein kinase cascades are launched, including Mitogen-Activated Protein Kinases (MAPK) and Calcium-Dependent Protein Kinase (CDPK; Kumar *et al.* 2020b; Chen *et al.* 2021; Medina *et al.* 2021). They, in turn, modulate the activity of various transcription factors (TFs; Kumar *et al.* 2020b; Chen *et al.* 2021; Medina *et al.* 2021). TFs regulate the expression of stress-inducible genes, including genes for heat shock proteins (HSPs) and antioxidant enzymes (Meraj *et al.* 2020; Rabeh *et al.* 2025; Rao & Zheng 2025). Simultaneously, oxidative and covalent modification of proteins occurs, including S-nitrosylation under the action of NO (Freschi, 2013; Jeandroz *et al.* 2013; Zhang *et al.* 2025). This additionally regulates the activity of enzymes and TFs. At later stages, post-transcriptional regulation mechanisms are activated, in particular microRNAs (miRNAs), aimed at fine-tuning gene expression and enhancing the specificity of the cellular response (Floris *et al.* 2009; Ding *et al.* 2020; Ramakrishnan *et al.* 2022; Radani *et al.* 2023). Activation of ROS-induced signals in HS is a temporarily organized process in which sequential involvement of ionic, lipid, protein, and genetic regulators ensures effective adaptation to thermal stress.

Primary molecular signaling

Under HS conditions, the first changes in the plant cell occur at the level of ion balance, where ROS play the role of a trigger signal. In particular, H_2O_2 penetrating through the apoplast activates specific calcium channels in the plasma membrane and organelle membranes. In particular, cyclic nucleotide-gated channels (CNGC) and glutamate receptor-like (GLR) channels are most sensitive to the redox state and react directly through oxidation of thiol groups (Jeandroz *et al.* 2013; Sandalio *et al.* 2023; Kang *et al.* 2024). This results in a Ca^{2+} surge, i.e., an acute and transient influx of Ca^{2+} into the cytosol (Wang *et al.* 2021). This ion response is not simply a consequence of damage, but a clearly regulated part of the stress response and plant adaptation mechanism (Bourgine & Guihur 2021). Already in the first minutes of heat exposure, it becomes the basis for the activation of subsequent cascades, including protein kinases and transcription factors. Moreover, the ROS signal itself can be enhanced by activation of NADPH oxidases, which in turn are sensitive to Ca^{2+} levels (Kuznetsova *et al.* 2021). Thus, ROS and Ca^{2+} form a closed and self-sustaining system, where the influx of Ca^{2+} and ROS synthesis are interconnected. Changes in membrane permeability to Ca^{2+} ions caused by H_2O_2 lead to activation of signaling proteins such as protein kinases (Kumar *et al.* 2020b; Chen *et al.* 2021; Medina *et al.* 2021). The two most important groups in the context of ROS-induced heat response are MAPK and CDPK (Wahid *et al.* 2007; Kumar *et al.* 2020b; Chen *et al.* 2021; Shabbir *et al.* 2022; Jomova *et al.* 2023). Increased intracellular Ca^2 and accumulation of H_2O_2 trigger a cascade of phosphorylations, from MAPKKK to MAPKK and further to MAPK, each step of which amplifies and refines the signal (Kumar *et al.* 2020b; Chen *et al.* 2021; Jomova *et al.* 2023). These cascades play the signal into a stable transcriptional response. In turn, CDPK directly senses changes in Ca^{2+} and triggers specific response pathways, including phosphorylation of antioxidant defense enzymes and regulation of substance transport (Wahid *et al.* 2007; Chen *et al.* 2021; Shabbir *et al.* 2022). Together, MAPK and CDPK regulate the expression of a whole set of heat stress response genes, from HSPs to antioxidant and osmoprotectant genes (Meraj *et al.* 2020; Rabeh *et al.* 2025; Rao & Zheng 2025). Noteworthy, the MAPK and CDPK pathways are not isolated, i.e., there is cross-regulation, in which the same TFs can be activated, but with different temporal and tissue-specificities. While protein kinase cascades process the signal, membrane-localized PLD and PLC are simultaneously activated, forming the so-called phospholipid signaling pathway (Song *et al.* 2020; González-Mendoza *et al.* 2021). Under the influence of ROS and Ca^{2+}, phospholipase D breaks down phosphatidylcholine to phosphatidic acid (PA), which itself is an active signaling messenger (Song *et al.* 2020; González-Mendoza *et al.* 2021; Amokrane *et al.* 2024). PA regulates the activity of proteins such as MAPK and NADPH oxidase, enhancing the ROS response and creating positive feedback loops. PLC, in turn, forms inositol triphosphate (IP_3), which additionally releases Ca^{2+} from intracellular stores, synchronizing ion and lipid signaling (Hu *et al.* 2020; Akhiani & Martner 2023; Kong *et al.* 2024). Phospholipid messengers turn the cell membrane into a "smart interface" that not only perceives stress but actively participates in its processing. This enables the cell to quickly respond to changes in external temperature without the participation of transcriptional processes at early stages. In addition to cascade activation, ROS acts as a direct protein modifier. Cysteine and methionine residues are the most sensitive to oxidation, especially in the regulatory domains of enzymes and TFs (Lennicke & Cochemé 2021; Corpas *et al.* 2022b; Hurst *et al.* 2022). Formation of sulfene ($–SOH$), sulfinine ($–SO_2H$), or SNO groups (with the participation of NO) alters the activity, localization, or stability of proteins. These modifications are often reversible, which allows them to be used as mechanisms of rapid and regulated signaling (Cejudo *et al.* 2021; Li *et al.* 2025a). For example, peroxyredoxins and thioredoxins are involved in the restoration of such modifications, which makes them part of the signaling network (Zhang *et al.* 2020). Importantly, redox modification is not just a side effect of oxidative stress, but a structurally programmed way of transmitting information. As previously mentioned, the interaction of ROS and NO forms a specific signal that differs in strength and specificity from each of the components separately. This is achieved through the formation of new molecules, such as $ONOO^-$, and through competing protein modifications (S-nitrosylation and S-oxidation; Freschi 2013; Jeandroz *et al.* 2013; Zhang *et al.* 2025). NO can enhance the antioxidant response by activating SOD, or vice versa (León 2022; Jomova *et al.* 2023). In addition, RNS modulates the expression of stress genes through the activation of cGMP-dependent pathways (Rai & Kaushik 2023). The joint participation of ROS and NO is especially important for the formation of a sustainable, but not destructive response. It ensures precise spatiotemporal coordination, allowing the cell to distinguish between short- and long-term effects.

Transcription factors (TFs)

Heat Shock Factors (HSFs) are a central component of the plant heat response (Andrási *et al.* 2021). These TFs regulate the expression of heat shock protein (HSP) genes, acting as chaperones (Bourgine & Guihur 2021). Under normal conditions, HSFs remain in an inactive form bound to HSP70/90 (Simoncik *et al.* 2024). However, with an increase in H_2O_2 concentration under heat stress, they are released, oligomerized, and translocated into the nucleus. HSFs can be activated both by direct oxidation of sensitive amino acid residues and indirectly through MAP kinase cascades (Li *et al.* 2022b). Direct oxidation causes conformational changes and increases their ability to bind to DNA (Gao *et al.* 2022). While in the MAP kinase cascade, HSFs are phosphorylated and their transcriptional activity and/or ability to bind to heat shock elements (HSEs) in the promoters of HSP genes increases (Schmauder *et al.* 2022). The APETALA2/Ethylene Response Factor (AP2/ERF) family, in particular the Dehydration-Responsive Element Binding protein 2A (DREB) subgroup, is a group of TFs involved in the cross-regulation of various abiotic stresses (Qin *et al.* 2008). AP2/ERFs as a whole can be considered as heat and dehydration stress integrators. For example, DREB2A regulates the expression of genes responsible for dehydration, drought tolerance, and high temperatures (Wang *et al.* 2020). The stability and activity of DREB2A are closely regulated by ROS through the inhibition of its antagonist proteins and through direct oxidative modifications of the TF itself (Mizoi *et al.* 2019). This demonstrates how ROS signals are not isolated but embedded in a broad network of adaptive pathways, where heat stress is considered as an element of a more general stress context. TFs of the basic Leucine Zipper (bZIP) family are involved not only in classical stress responses, but also in the regulation of photomorphogenesis and energy metabolism, playing a role as a regulator of metabolic rearrangements and the light response (Gai *et al.* 2020; Yu *et al.* 2020; Guo *et al.* 2024). Some representatives of this group are activated under HS conditions due to sensitivity to ROS. Their activation can occur through oxidation of redox-sensitive residues, as in HSF and AP2/ERF, as well as through phosphorylation in signaling pathways (Yu *et al.* 2020). Activated bZIP factors are involved in the regulation of genes responsible for antioxidant defense, sugar metabolism, and osmoregulation (Gai *et al.* 2020; Guo *et al.* 2024). In addition to TFs involved in photomorphogenesis and energy metabolism, in addition to heat stress responses such as bZIP, the WRKY and NAC families of TFs are involved in the link between immunity and heat stress and PCD (Burke *et al.* 2020; Meraj *et al.* 2020). WRKY TFs have traditionally been associated with the immune response, and their involvement in the regulation of abiotic stress, including HS, is becoming increasingly evident (Guo *et al.* 2022). WRKY proteins are activated through ROS-dependent MAPK cascades and can also undergo direct oxidation of the DNA-binding domain, which alters their affinity for W-boxes in promoters (Li *et al.* 2020a). These mechanisms ensure selective expression of genes that promote survival during heat overload and recovery from stress. In contrast, the NAC TFs family, consisting of NO APICAL MERISTEM (NAM), Arabidopsis transcription activation factors 1 and 2 (ATAF1/ATAF2), and CUC2 (CUP-SHAPED COTYLEDON 2), is unique in that many of its members are involved in cellular decision-making making such as PCD (Xiong *et al.* 2025). In HS, ROS can activate specific NAC factors involved in triggering either protective or terminal programs, depending on the level of damage (Cai *et al.* 2021; Xi *et al.* 2022). This may include changes in protein stability, nuclear translocation, and activation of genes involved in remodeling cellular architecture.

microRNA: Signaling pathways and regulatory networks

One of the most studied miRNAs in HS is miR398 (Ding *et al.* 2020; Li *et al.* 2022a). Its effect is that, in HS, the expression of this miRNA is reduced, which leads to an increase in the level of Cu/Zn superoxide dismutase (CSD1, CSD2; Sun *et al.* 2020; Yan *et al.* 2023; Li *et al.* 2025b). This response is a direct mechanism for enhancing antioxidant protection. However, behind this response lies a complex regulatory mechanism, where the activation of MAPK and CDPK kinases leads to phosphorylation of TFs, which, in turn, reduce the transcription of miR398 (Mendoza-Soto *et al.* 2012; Liu *et al.* 2023). This regulation demonstrates how quickly and locally the cell can adapt to increased levels of $O_2^{\bullet -}$. MicroRNAs miR156 and miR172 form an interconnected pair, playing a key role in switching the phases of plant development (Wu *et al.* 2009; Ma *et al.* 2020). Under HS, miR156 is reduced, leading to the activation of SQUAMOSA PROMOTER BINDING PROTEIN-LIKE (SPL TFs), and miR172 is simultaneously increased, leading to the suppression of AP2-like TFs (Wu *et al.* 2009; Chen *et al.* 2010; Zhu & Helliwell 2011; Matthews *et al.* 2019; Ó'Maoiléidigh *et al.* 2021). This promotes accelerated flowering as an adaptive survival strategy. To achieve this effect, HSF and NAC TFs regulate the expression of miR156 and miR172, directing the plant to complete the life cycle before the onset of extreme conditions (Wu *et al.* 2009; Lee *et al.* 2010; Brunquell *et al.* 2017). Here, it is especially important to note the signaling plasticity of the system: Depending on the level and duration of HS, the miR156/miR172 ratio can be dynamically redefined. Upregulation of miR393 in HS demonstrates how phytohormonal signaling pathways are integrated in response to temperature fluctuations (Curaba *et al.* 2014; Iglesias *et al.* 2014; Islam *et al.* 2024). Increased levels of this miRNA effectively reduce auxin sensitivity by suppressing the expression of key F-box proteins (TIR1, AFBs; Iglesias *et al.* 2014). This, in turn, leads to changes in the morphogenesis of roots and shoots, structures essential for water balance and plant cooling through transpiration. The miR169, miR164, and miR167 cluster of microRNAs act as complex fine-tuning mechanisms, allowing plants to adapt to combined stresses, such as drought and high temperatures (Zhou *et al.* 2020; Zhakypbek *et al.* 2025). These microRNAs achieve this by influencing the expression of vital TFs. For example, downregulation of miR169 and miR167 allows for increased production of Nuclear Factor Y, subunit A (NF-YA), and Auxin Response Factors (ARFs), respectively (Ru *et al.* 2006; Luan *et al.* 2014, 2015; Wang *et al.* 2015). In turn, these TFs activate processes essential for survival, such as stomatal closure to conserve water and changes in root architecture to more efficiently absorb moisture (Leyva-

González *et al.* 2012; Li *et al.* 2015, 2016; Pereira *et al.* 2018). Simultaneously, miR164 regulates the levels of NAC TFs, which play a key role in balancing growth and tissue remodeling processes, allowing flexible plant adaptation depending on specific stress conditions and species (Li *et al.* 2012; Zhang *et al.* 2018; Hernandez *et al.* 2020). Downregulation of miR396 allows for increased activity of GROWTH-REGULATING FACTORS (GRF), temporarily restricting growth in favor of survival (Rodriguez *et al.* 2010). miR408, which regulates plastocyanin and laccases, is downregulated to adapt to copper-dependent metabolism and photosynthetic activity (Abdel-Ghany & Pilon 2008). In contrast, miR528 is upregulated to modulate antioxidant enzymes and specific MYB-TFs (Liu *et al.* 2015). These miRNAs reveal how plants reallocate resources toward vital processes during adaptation to heat stress.

Heat shock response (HSR) main mechanism of heat stress adaptation

Plants exhibit a remarkable diversity of HSF proteins. For example, *Arabidopsis thaliana* has 21 HSF genes grouped into the HSFA, HSFB, and HSFC classes, each playing a unique or overlapping role in stress response (Liu & Charng 2013; Andrási *et al.* 2021). Class A members typically activate gene expression, while class B members may act as coregulators or even repressors. This diversity of HSFs allows plants to fine-tune their defense response depending on the type, intensity, and duration of heat stress (Wu *et al.* 2021a). The functional importance of HSFs is supported by numerous experiments demonstrating their ability to promote active expression of key chaperones such as HSP26, HSP70, HSP70, HSP90, and HSP101 under both STHS and long-term LTHS conditions (Dhaubhadel *et al.* 2002; Swindell *et al.* 2007; Cocetta *et al.* 2022; Diogo-Jr. *et al.* 2023). Thus, in wheat, it was found that the small chaperone TaHSP17.4 and its partner TaHOP (coordinator of HSP70/90) under the regulation of HSFs are associated with an increase in proline levels and a decrease in lipid peroxidation, which improved heat tolerance at the reproductive stage (Wang *et al.* 2023c). HSFs are not just regulators of HSP expression. They act as central nodes in the signaling network, integrating thermal signals with other stress and hormonal pathways. Their complex regulation, including post-translational modifications, interaction with chromatin, and the possibility of feedback from HSPs, makes them key targets for genetic improvement of plant thermotolerance (Jiang *et al.* 2021).

Table 2. Heat shock proteins on short-term heat stress in different crops and *Arabidopsis.*

HSP type (Marker)	Plant	Temperature	Response time after STHS	Peak activity	References
HSP70	Wheat (heat)	42 °C	Rapid upregulation within 1–3h	Maintained under heat	Kumar *et al.* 2016
	Wheat (cold)	4 °C	Rapid upregulation within 6h	Sustained induction during acclimation	Danyluk *et al.* 1991
	Maize	42 °C	Induction within 1 h	Peaks at 2 h, then gradually declines	Li *et al.* 2010
	Arabidopsis	40 °C	Rapid induction within 30 min	Peak between 30–60 min, then declines	Sung *et al.* 2001
HSP90	Wheat *cv.* C-306	40 °C	Up-regulation observed within 2 h	Peaks at pollination and milky dough stages, with a 4.2–6.5 fold increase within 2 h	Kumar *et al.* 2013b
	Wheat (TaHSP90A variants)	44 °C	Expression after 1 h post-heat exposure	2-fold upregulation after 1 h in several wheat hybrids (1, 17, 30, 37, and 41)	Ammar *et al.* 2023
	Rice	45 °C	Upregulation starts within 2h post-stress	Sustained >6 h in roots and crowns, especially under heat stress	Prerostova *et al.* 2022
	Cowpea	40 °C	Rapid induction within 5-15 min	Stabilization within 2 h and protection against proteotoxicity	Selinga *et al.* 2022
HSP101	*Arabidopsis thaliana*	42 °C	Strong induction within 2 h forms stress granules	Peak within 2–6 h, recovery dependent on sHSPs	McLoughlin *et al.* 2019
sHSP (HSP21)	*Arabidopsis thaliana*	42 °C	Accumulation begins by 2–3h post-heat	Persists for 48–72h (thermomemory)	Sedaghatmehr *et al.* 2016

HSPs function as molecular chaperones, preventing the aggregation of partially denatured proteins and promoting their refolding (Engler & Buchner 2025). Depending on their molecular mass (in kilodaltons, kDa) and function, they are divided into several major families (Diogo-Jr. *et al.* 2023). HSP100s (ClpB) are involved in the unwinding and refolding of aggregated proteins, a function that is particularly critical during prolonged heat exposure (Weibezahn *et al.* 2004). HSP90s maintain the structural integrity and activity of numerous signaling client proteins (Minari *et al.* 2024). HSP70s bind to hydrophobic patches of damaged proteins, preventing aggregation and promoting their proper folding or trafficking to the proteasome for degradation (Berka *et al.* 2022; Duran-Romaña *et al.* 2025). HSP60 chaperonins provide a "protected" environment for protein folding by forming barrel-shaped complexes (Singh *et al.* 2024b; Wagner *et al.* 2024). Small HSPs (sHSPs), with a molecular weight of less than 30 kDa, act as "holdases", temporarily stabilizing damaged proteins without using ATP and then handing them over to larger chaperones for further repair (Obuchowski *et al.* 2021; Pareek *et al.* 2021). Additionally, sHSPs play a crucial role in stabilizing cell membranes and protecting the lipid bilayer from thermal damage.

Increased expression of HSPs, especially HSP70 and HSP90, is a reliable marker of heat stress. Their levels can increase tens or even thousands of times in a short time, for example, up to 3000 times in maize after short-term heat exposure (Diogo-Jr. *et al.* 2023). Experimental data confirm that early and strong induction of HSPs promotes the formation of acquired thermotolerance, allowing plants to survive subsequent, more severe stress (Marutani *et al.* 2012; Tokić *et al.* 2023; Wang *et al.* 2023c; Sallam *et al.* 2024).

Antioxidant system duality as a marker

Non-enzymatic antioxidants

Non-enzymatic antioxidants are low-molecular compounds that act as one of the first barriers to damaging ROS and RNS, providing primary protection of cellular structures from oxidative damage (Rudenko *et al.* 2023; Jomova *et al.* 2024). Among such molecules, the main ones are ascorbate, glutathione (GSH), tocopherols, carotenoids, and various phenolic substances (Oestreicher & Morgan 2019; López-Huertas & Palma 2020; Zimmermann *et al.* 2021; Rudenko *et al.* 2023). Ascorbate plays a central role in maintaining redox homeostasis in chloroplasts and cytosol (Singh *et al.* 2024a). It effectively neutralizes H_2O_2 and actively participates in the ascorbate-GSH cycle, regenerating due to the cooperative action of enzymes with GSH (Corpas *et al.* 2024; Foyer & Kunert 2024; Singh *et al.* 2024a). Glutathione, in turn, exists in two forms: reduced GSH and oxidized GSSG (Koh *et al.* 2021; Knoke *et al.* 2023; Rai *et al.* 2023). Their balance serves as a reliable indicator of the level of oxidative stress, while an increase in GSH content often indicates an adaptive response of the plant (Koh *et al.* 2021). Carotenoids and tocopherols play an important role in photosynthetic tissues, where they protect photosystems from the destructive effects of singlet oxygen and free radicals formed during excess energy (Kumar *et al.* 2020a; Simkin *et al.* 2022; Sun *et al.* 2022; Mesa & Munné-Bosch 2023). Their protective function is especially critical in chloroplasts, where photochemical processes are the main sources of ROS. In addition, phenolic compounds, including flavonoids, act as potent radical scavengers, and simultaneously, modulators of signaling cascades activated by stress (Shah & Smith 2020; Yaqoob *et al.* 2022; Rao & Zheng 2025). The intensity and duration of heat exposure significantly affect the level of these antioxidants. Under STHT and moderate heat stress, plants usually increase the biosynthesis and accumulation of non-enzymatic antioxidants (Collado-González *et al.* 2021; Rudenko *et al.* 2023).

For example, in the leaves of *Arabidopsis thaliana*, a significant increase in ascorbate and GSH content is observed already during the first hours after abiotic stresses (Tóth *et al.* 2011; Zechmann 2017; Collado-González *et al.* 2021; Dard *et al.* 2023). A similar reaction has also been recorded in corn and wheat, where a short-term increase in temperature stimulates the accumulation of tocopherols and carotenoids, which correlates with the preservation of photosynthetic activity and a slowdown in the rate of damage to cell membranes (Caverzan *et al.* 2016; Shamloo *et al.* 2017; Xiang *et al.* 2019). However, under LTHS and/or extreme heat exposure, non-enzymatic antioxidant reserves can be rapidly depleted (Szarka *et al.* 2012). Their regeneration and resynthesis require significant energy expenditure, which makes the cell vulnerable to an insufficient resource supply. It has been established that in some wheat varieties exposed to high temperatures, the level of reduced GSH decreases, while GSSG accumulates, indicating increasing oxidative stress (Khan *et al.* 2021; Mohi-Ud-Din *et al.* 2021). Similar observations were obtained in the reproductive organs of beans, where ascorbate depletion was accompanied by impaired ovary formation and a decrease in yield (Loscos *et al.* 2008; Suzuki *et al.* 2013; Gaafar *et al.* 2020). The dynamics of non-enzymatic antioxidants (ascorbic acid, and glutathione) can vary from a sharp increase to depletion depending on the conditions, which makes them not only a protective mechanism, but also a sensitive indicator of the degree of stress and the level of adaptation of the plant (wheat, rice, maize, and *Arabidopsis*) over time (Cao LiYong *et al.* 2003; Sedaghatmehr *et al.* 2016; Wu *et al.* 2016; Siebers *et al.* 2017; Li *et al.* 2020b; Sallam *et al.* 2024). The interaction between different types of antioxidants, including enzymatic components, creates a multi-level and flexible protective network that can effectively respond to both short- and long-term thermal challenges.

Antioxidant enzymes

Enzymatic antioxidants constitute the second, but no less important, line of plant defense against heat-induced oxidative stress (Rajput *et al.* 2021; Fortunato *et al.* 2023; Rao *et al.* 2025). Unlike non-enzymatic components that provide immediate neutralization of ROS, the enzymatic system provides a long-term, regulated, and reproducible response based on specific gene expression and catalysis (Wang *et al.* 2024). These enzymes not only detoxify ROS but also participate in the regeneration of oxidized forms of non-enzymatic antioxidants, thereby ensuring the stability of the entire antioxidant defense system (Rudenko *et al.* 2023). The key enzymes of this system include SOD, CAT, peroxidases (POD), APX, glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), and dehydroascorbate reductase (DHAR; Rajput *et al.* 2021; Jardim-Messeder *et al.* 2023; Mishra *et al.* 2023).

SOD catalyzes the dismutation of the $O_2^{\bullet-}$ to H_2O_2 and O_2, creating a more stable substrate for subsequent destruction by other enzymes, primarily CAT and POD (Mishra *et al.* 2023). Catalase, in turn, quickly breaks down H_2O_2 to H_2O and O_2, especially in peroxisomes, where the intensity of peroxide formation is extremely high (Fujiki & Bassik 2021; He *et al.* 2021; Fransen & Lismont 2024). APX functions primarily in chloroplasts and the cytosol, using ascorbate as a reducing agent in the utilization of H_2O_2, while enzymes of the ascorbate-GSH cycle reduce oxidized forms of antioxidants such as dehydroascorbate and oxidized GSH (Jardim-Messeder *et al.* 2023; Li 2023; Corpas *et al.* 2024; Foyer & Kunert 2024; Yoshimura & Ishikawa 2024). The reaction of the antioxidant enzymatic system to heat stress is highly plastic. Under STHS or moderate temperature increase, the expression of genes encoding antioxidant enzymes is rapidly induced in stress-resistant plant genotypes, which is accompanied by an increase in their activity (Fortunato *et al.* 2023). For example, in rice seedlings the leaves an increase in the activity of SOD, APX, and GR was measured already during the first hours of heat exposure (35–38 °C). This increase allows the crop to effectively limit LPO (Dongsansuk *et al.* 2021). Similar results were obtained in cotton, wheat, and corn, where enzymatic antioxidant activity directly correlated with thermotolerance (Snider *et al.* 2011; Mohi-Ud-Din *et al.* 2021; Wang *et al.* 2023a; Luqman *et al.* 2025). Noteworthy, changes in the activity of antioxidant enzymes depend on the plant species and the plant, as well as stress conditions (Table 3). However, under prolonged or extreme heat exposure, the efficiency of the antioxidant enzymatic system may decrease. One of the reasons is the thermal proteins' denaturation, including enzymes, as well as the depletion of the reserves of essential coenzymes and substrates (Sgobba *et al.* 2015; Sies 2020; Fan & Jespersen 2025). Disruption of transcription and translation under prolonged stress also leads to a deficiency of new molecules of antioxidant enzymes (Sgobba *et al.* 2015). In tobacco leaves subjected to severe heat stress, a sharp decrease in the activity of CAT and POD was recorded, which was accompanied by the accumulation of hydrogen peroxide and pronounced signs of oxidative damage (Mýtinová *et al.* 2010; Tan *et al.* 2011; Sofo *et al.* 2015; Wang *et al.* 2017).

Phytohormonal response

One of the first phytohormones that respond to STHS is abscisic acid (ABA; Yang *et al.* 2014; Li *et al.* 2021). Already within the first 30-60 minutes, its level can increase sharply, especially with concomitant dehydration (Abdel-Ghany & Pilon 2008). This triggers stomatal closure, reduces transpiration and activates the expression of stress-associated genes, including LEA proteins and antioxidant enzymes. Rapid accumulation of ABA in response to heat shock was recorded in *Zea mays* and *Arabidopsis thaliana* (Huang *et al.* 2016; Suzuki *et al.* 2016; Sun *et al.* 2023). Salicylic acid (SA) is also involved in the early response, enhancing antioxidant protection and stabilizing photosystem II (Chen *et al.* 2020; Das *et al.* 2024). Exogenous application of SA in wheat decreased the MDA content and increased heat tolerance (Fardus *et al.* 2017). Under LTHS, ABA and SA levels can vary depending on the degree of acclimation and interactions with other hormones (Nguyen *et al.* 2016; Suzuki *et al.* 2016; Balfagón *et al.* 2019; Li *et al.* 2021). Jasmonic acid (JA) and ethylene (ET), traditionally associated with pathogenesis and aging, are also upregulated in STHS (Nahar *et al.* 2011; Robert-Seilaniantz *et al.* 2011; Kazan 2015; Kim *et al.* 2015). In *Solanum lycopersicum*, a STHS induced an increase in JA levels, accompanied by activation of HSPs and increased defense (Kubienova *et al.* 2013; Havko *et al.* 2020). Ethylene shows a dual role: at moderate concentrations it can participate in adaptation, but its excess production contributes to aging and decreased productivity (Dubois *et al.* 2018).

In *Arabidopsis*, a rapid increase in ET synthesis was observed in response to heat stress, with different effects on survival depending on the hormone level (Poór *et al.* 2022). Importantly, Growth hormones such as auxins, cytokinins, gibberellins are suppressed by HS, which leads to growth inhibition and disruption of reproductive processes (Cheikh & Jones 1994; Toh *et al.* 2008; Beard *et al.* 2012; Du *et al.* 2013; Lubovská *et al.* 2014). For example, in rice, a decrease in auxin levels in ovaries caused underdevelopment of the grain (Zhao *et al.* 2013). Against this background, brassinosteroids (BRs), which have protective properties, play a special role: their exogenous use enhances antioxidant protection and reduces the level of LPO (Rajewska *et al.* 2016; Kadyrbaev *et al.* 2021; Avalbaev *et al.* 2024). Under heat stress, all hormones interact within a complex signaling network, where crosstalks between phytohormones allow the plant to coordinate urgent and long-term adaptive responses.

Table 3. Antioxidant enzyme activity and response time in crop plants and *Arabidopsis* under STHS

Plant	Temperature	Response time after STHS	Peak activity	References
		SOD		
Wheat	40–46 °C	Activity increased within 30 min of heat	Maximum activity recorded at ~2–4 h	Satbhai *et al.* 2015
Maize	42–45 °C	Activity upregulated in first 1–2 h post-stress	Higher activity sustained in tolerant genotypes (~2–4 h)	Tiwari & Yadav 2020
Rice	40–45 °C	Increased activity observed within 1 h	Peaks at 2 h	Kumar *et al.* 2012
		CAT		
Wheat	40 °C	Upregulation during stress, maintained post-recovery	Remained elevated during recovery (up to 4 h)	Almeselmani *et al.* 2006
Rice	42 °C	The activity was recorded after 24 h of heat treatment	Peaked at 24h	Ali *et al.* 2021
Arabidopsis	42 °C	Transcript levels of CAT genes increased within 1 h under direct heat	Expression remained high for up to 6 h, supporting redox homeostasis	Khandelwal *et al.* 2008
		APX		
Maize	40–45 °C	Isoforms detectable within 1–2 h	Peak differences observed between sensitive and tolerant genotypes	Tiwari & Yadav 2020
	42–45 °C	APX, GR induced within 1 h of the combination of high temperature and salicylic acid and thiourea application	Enzyme activity sustained for ~2–4 h	Parmar *et al.* 2021
Wheat	40 °C	Activity observed 1–2 h after heat exposure	Peaks between 2–3 h, depending on genotype; stronger in heat-tolerant lines	Almeselmani *et al.* 2006

Osmoprotectors (osmolytes) as a weak marker

Osmoprotectants (osmolytes) are low-molecular compounds that protect plant cells from dehydration and stabilize macromolecules under abiotic stress (Slama *et al.* 2015). However, under STHS, their synthesis occurs relatively slowly and is not a primary adaptive response. Unlike HSPs or ABA, which are activated within the first hour, osmolytes such as proline, sucrose, and glycine betaine begin to accumulate in 1 hour to 3 days after exposure (Table 4; Sharma *et al.* 2019). However, even basal proline levels can provide partial cell protection, especially under a combination of heat and water deficit. Under long-term heat stress (LTHS), osmolytes become important participants in adaptation.

Their steady accumulation helps maintain water balance, stabilize the photosynthetic apparatus, and prevent membrane destruction. Proline and glycine betaine, for example, protect proteins from denaturation and reduce ROS levels, while soluble sugars and polyols act as energy reserves and osmotic buffers (Bolen 2001; Kumar 2009; Hemme *et al.* 2014; Sharma *et al.* 2019). The synthesis of these metabolites is regulated by ROS-, RNS-, and hormone-dependent pathways, primarily ABA, JA, and SA. Thus, although osmolytes are not early markers of STHS, their role increases as we move toward chronic stress, forming an important element of plant resistance.

Table 4. Reaction time of osmoprotectants (osmolytes) after STHS and peak activity in different plants.

Osmolyte accumulation	Plant	Temperature	Response time after STHS	Peak activity	References
Proline	Wheat	40–42 °C	Rapid induction within 1–2 h	Peaks at 4–6 h post-stress	Kumar *et al.* 2013a
	Maize	42–45 °C	Begins accumulating within 1 h	Highest levels around 4–6 h	Parmar *et al.* 2021
Trehalose	Rose (Rosa chinensis)	40 °C	Upregulation in roots/stems within 1–4 h	Highest trehalose content by 8–24 h, especially in roots/stems	Li *et al.* 2019
Soluble sugars (sucrose, glucose)	Rice	40–42 °C	Increases by 3 h post-stress	Peaks by 5 h	Zhang *et al.* 2017
	Wheat	32–34 °C	Elevated within 3 days	Higher levels sustain till day 7 under HT	Alghabari *et al.* 2021
Raffinose	Arabidopsis	38–42 °C	Increases 2-3 h post-heat	Maintained for 24–48 h aiding thermotolerance	Sedaghatmehr *et al.* 2016

DISCUSSION

In recent years, the influence of prolonged high temperatures on plants' morphophysiological parameters has been widely discussed, however, there is limited information about the short-term high temperature stress. The classical classification of high temperature stress into short and long-term temperature stresses lacks analysis to effectively describe the influence of short-term high temperature fluctuations on plants' biological responses. We propose categorizing STHS into four distinct temporal phases to more accurately predict the onset, peak, and duration of physiological disruptions: initial (<1 h), earlier (1-3 h), sustained (3-6 h), and prolonged (6-12 h). Each phase triggers unique transcriptional and enzymatic reactions, differing not only temporally but also biochemically and morphologically (Wu *et al.* 2021a). For instance, the initial heat shock (<1 h) triggers rapid transcriptional reprogramming and an immediate burst of ROS and RNS, typically without noticeable morphological changes. HSPs like HSP70 and HSP101, for example, reach their peak activity between 20 and 60 minutes (Farhad *et al.* 2023). Following this, in the earlier phase (1–3 h), plants exhibit a significant increase in the levels of ROS-scavenging enzymes, including CAT, GPX, and SOD. Notably, in wheat, CAT activity can rise by over 30% within the first two hours of STHS (Habashy *et al.* 2019). These early reactions are largely reversible and cause few visible physical changes unless the stress coincides with critical developmental stages. As STHS continues, the sustained (3-6 h) phase often brings observable changes in chlorophyll fluorescence and stomatal conductance, disrupting photosynthetic efficiency. Critically, during this period, the delicate equilibrium between ROS generation and scavenging begins to decline, marking it as a pivotal tipping point in the plant's stress response (Huang *et al.* 2019). Finally, in the prolonged phase (6-12 h), the effects of STHS become structurally evident. Studies on *Brassica napus*, for example, reveal disrupted floral morphology and a significant loss of pollen viability with exposures exceeding 6 hours, particularly at temperatures of 40-45 °C. Enzymatically, this phase is frequently characterized by an enzyme plateau or even a decline, likely resulting from heat-induced denaturation or the depletion of essential cofactors (Kourani *et al.* 2022). This refined classification aligns seamlessly with the hierarchy of plant thermotolerance, where fundamental responses prevail in early phases, while acquired thermotolerance and damage-mitigation mechanisms emerge in later stages. This paradigm is invaluable not only for streamlining research protocols but also for guiding marker selection in high-throughput phenotyping and stress resilience screening. Furthermore, the presence of distinct species-specific variations in response timing underscores the necessity of this granularity; for instance, the earlier suppression of ROS in barley under prolonged STHS suggests that detoxification thresholds are profoundly cultivar- or genotype-specific (Hill & Li 2022). Consequently, heat stress studies must evolve beyond simplistic "short-term" versus "long-term" models towards more multi-phase, duration-sensitive models to accurately capture the dynamic biochemical kinetics and physiological limitations imposed by heat. This detailed classification is absolutely crucial because it enables us to integrate complex responses such as epigenetic modifications, intricate hormone feedback loops, and extensive metabolic reprogramming, all of which are indispensable for developing crops resilient to the intensifying temperatures under climate change. Beyond the general response, STHS also induces organ-specific oxidative dynamics, necessitating highly targeted antioxidant measures. Leaves, as the primary site of photosynthesis, become initial hotspots for ROS. In contrast, roots demonstrate robust detoxifying responses, despite being exposed to less light-induced ROS, particularly during prolonged heat exposure. Within leaves, the first STHS stages (<3 h) are characterized by a notable increase in SOD and CAT activities, essential for regulating photochemically produced superoxide radicals and hydrogen peroxide. For example, research on tomato (*Solanum lycopersicum*) indicates a rise in SOD and CAT activity after just 60 minutes of exposure to 42 °C, peaking around 3 hours later (Rai *et al.* 2024). However, roots exhibit a distinct response profile: GPX and GR become the dominant players during the 3-6 h and 6-12 h windows. In barley (Hordeum vulgare) roots, GPX activity notably peaked during sustained stress but not in shoots, clearly highlighting organ-specific redox control (Zelinová *et al.* 2013). Taken together, these findings critically emphasize the paramount importance of recognizing the spatially distinct and temporally dynamic nature of antioxidant responses within different plant tissues under STHS. A comprehensive understanding of these organ-specific adaptations is indispensable for developing truly targeted and effective strategies to enhance plant thermotolerance. In recent years, osmolytes have garnered increasing recognition for their dynamic roles in redox regulation and metabolic buffering during abiotic stress, particularly STHS, moving beyond their traditional perception as mere passive stabilizers of cellular osmotic balance. Among the diverse array of compatible solutes, proline, trehalose, and various soluble carbohydrates stand out due to their multifaceted contributions. These compounds not only maintain cellular osmotic balance, but they also perform crucial dual roles as both molecular chaperones and osmoprotectants. This dual capacity is essential for protecting macromolecular integrity, actively preventing protein denaturation and aggregation, and effectively buffering the burst of ROS characteristic of acute heat exposure (Abdelaal *et al.* 2022; Rehman *et al.* 2024). Proline accumulation is one of the most consistent metabolic responses to STHS. Its biosynthesis via the glutamate pathway is regulated by temperature-dependent enzymes like P5CS (Δ1-pyrroline-5-carboxylate synthetase). Beyond its direct osmotic contribution, recent reviews underscore proline's broader significance in redox balance and ROS signaling, highlighting its dynamic interplay with cellular reactive oxygen species as a primary driver of its beneficial effects under stress (Renzetti *et al.* 2025). This underscores how a swift increase in proline levels contributes not only to osmotic adjustment but also to broader protein stabilization, actively protecting cellular components from heat-induced damage (Mushtaq *et al.* 2025). Trehalose, while perhaps less known than proline, also plays crucial roles beyond osmoprotection. It has been found to carefully modify glycolytic flow during heat stress, a key metabolic shift that enables efficient energy reallocation. Furthermore, trehalose significantly contributes to cellular defense by stabilizing protein complexes through non-enzymatic antioxidant mechanisms. Crucially, it actively participates in regulating sugar signaling and autophagy, pathways fundamental to managing heat-induced cellular and organelle-level damage (Mushtaq *et al.* 2025). Recent studies on tobacco confirm trehalose's role in coordinating wider metabolic reprogramming and synergistic interactions with other stress components like HSPs and antioxidant enzymes (Chen *et al.* 2024). Soluble sugars, particularly disaccharides like sucrose and raffinose, provide additional protection. They directly scavenge highly reactive hydroxyl radicals and enhance the plant's osmotic resistance (Hassan *et al.* 2024). They also serve as substrates for glycolysis, which connects heat response with energy metabolism. These sugars also serve as substrates for glycolysis, thereby connecting the heat response with overall energy metabolism. Notably, sugar metabolism under STHS is reorganized to promote mitochondrial ATP generation, which is essential for synthesizing stress response proteins and facilitating membrane repair mechanisms (Kourani *et al.* 2025). This important energy redirection supplies the ATP required for the production of key stress response proteins, active repair system activity, and membrane integrity maintenance. As STHS extends into the prolonged phase (6–12 h), compensatory adaptations begin to emerge. This later stage focuses on maintaining metabolic flexibility and rebalancing the cellular redox state over an extended duration. Such adaptations include the overexpression of alternative osmolytes, like glycine betaine, which is less quickly produced than proline, however contributes considerably to long-term osmotic adjustment and prolonged cellular protection against damage (Abdelaal *et al.* 2022). Ultimately, plant thermotolerance is not merely the outcome of isolated responses but a sophisticated emergent property of an integrated signaling network. The intricate crosstalk among ROS, RNS, various phytohormones, osmolytes, and even photoreceptors like phytochromes demonstrates a finely tuned cellular strategy to perceive, transduce, and respond to thermal cues. This complex web of interactions, where signals like NO and Ca^{2+} intricately modulate gene expression and physiological adjustments, profoundly underscores the limitations of reductionist approaches. Therefore, network-based, systems-level models are absolutely essential for future research in this field. ROS and RNS, once primarily considered detrimental byproducts of stress metabolism, are now firmly established in a dual role as critical signaling molecules (Mittler *et al.* 2022). Their integration with hormone pathways - especially abscisic acid (ABA), ethylene, and salicylic acid-modulates transcription factors like DREB2A, NAC, and HSF families, which coordinate gene expression programs for defense and recovery (Das *et al.* 2025). For instance, experimental studies have shown that the transient production of NO under early heat stress can finely tune MAPK signaling cascades and dynamically interact with intracellular Ca^{2+} fluxes. This precise coordination, observed in various crop species, enhances the activation of stress-responsive genes while simultaneously helping to prevent or transiently suppress the harmful over-accumulation of ROS, thereby maintaining cellular homeostasis (Naaz *et al.* 2025). Phytochromes, particularly phytochrome B (phyB), play a critical but underappreciated role in heat perception and integration. Recent research indicates that phyB can modulate heat responses by adjusting thermomorphogenesis and light-hormone sensitivity, particularly through its interaction with PIF transcription factors (Ghorbel *et al.* 2023). Genetic manipulation studies targeting phyB have elucidated how this complex crosstalk, frequently mediated through interactions with PIF transcription factors, directly influences the signaling pathways of growth-regulating hormones like auxin and gibberellin, thereby adding a layer of photomorphogenic control over heat adaptation (Qiu *et al.* 2021). These findings highlight how apparently diverse environmental signals influence a plant's overall stress response. Osmolyte signaling, which includes trehalose, proline, and pinitol, aids in both osmotic correction and signaling regulation. These metabolites interact with redox and hormonal pathways to regulate stomatal function, gene expression, and antioxidant capacity. For example, research on pinitol has demonstrated its remarkable dual role: not only does it stabilize membranes under stress, but it also directly influences ABA signaling, highlighting its crucial involvement in coordinating responses to both heat and drought (Kumar *et al.* 2024). Recent proteomic analyses further reveal that compatible solutes can mediate stress memory and acquired thermotolerance, suggesting a direct involvement in epigenetic modifications that prime plants for future heat episodes (Jin *et al.* 2024). Such integrated models are crucial for multi-target breeding programs, enabling the identification of robust thermotolerance traits across diverse environments. Comprehensive studies that seamlessly integrate multi-omics data with physiological research are undoubtedly the most promising avenues to fully unravel the intricate regulation mechanisms of heat tolerance. By concentrating on these interconnected signaling networks and their dynamic interaction, researchers can effectively uncover important thermotolerance traits. This deepened knowledge is truly necessary to develop climate-resilient crop types that can maintain global food security and enhance agricultural stability and production in the face of accelerating climate change.

Future Perspectives

Research on plant thermotolerance must shift to multi-omics integration in order to comprehend the spatiotemporal complexity of stress responses. Now we can see how heat stress impacts gene networks, enzyme activity, and metabolite fluxes both tissue-specifically and throughout time by using transcriptomics, proteomics, metabolomics, and epigenomics. This multi-omics approach will be crucial for unraveling the distinct molecular signatures that characterize the proposed initial (< 1 h), earlier (1-3 h), sustained (3-6 h), and prolonged (6-12 h) STHS phases, enabling precise and early marker identification. Integrative systems biology methods that combine physiology, cell biology, and genomics are crucial for identifying resilient crop phenotypes. AI-driven metabolic modeling, coupled with advanced high-throughput phenotyping, will enable predictive analyses of plant performance under various STHS scenarios and guide the development of optimal stress-resilience strategies. Furthermore, tissue-specific expression systems and CRISPR/Cas9-mediated gene editing will play a pivotal role in validating candidate STHS markers and engineering targeted enhancements in specific ROS scavenging pathways (e.g., improving CAT stability in leaves) or osmolyte biosynthesis for sustained protection.

By focusing on these interconnected signaling networks and their dynamic interactions, researchers can not only uncover important thermotolerance traits but also accelerate the development of climate-resilient crop types through advanced breeding programs, ultimately contributing to global food security and agricultural stability amidst intensifying climate change.

Conflict of interests

The authors declare no conflict of interests regarding the publication of this article.

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