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Role of Phytohormones in Regulating Heat Stress Acclimation in Agricultural Crops

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Abstract
Heat stress (HS) seriously affects crop growth, causing significant crop yield losses worldwide. The regulatory mechanisms controlling HS tolerance in plants are not well understood. Phytohormones are important molecules for coordinating myriad of phenomena related to plant growth and development. They are also essential endogenous signaling molecules that actively mediate numerous physiological responses under abiotic stress by triggering stress-responsive regulatory genes involved in plant growth. This review updates the central role of various phytohormones—indole acetic acid, gibberellic acid, abscisic acid, cytokinins, ethylene, salicylic acid, brassinosteroids, strigolactone, and jasmonic acid—in regulating the HS response so that plants can adapt to increasing temperature stress. We also reveal how these stress-responsive phytohormones switch on various regulatory gene(s) and genes encoding antioxidants and heat shock proteins (HSPs) to combat HS in various plant species.

Keywords Phytohormone · Heat stress · Antioxidants · Regulatory gene

Introduction

Plants, being immobile in nature, must respond to environmental perturbations, including heat stress (HS) (Zhu 2016). Plants have evolved coordinated genetic, molecular, biochemical, and physiological mechanisms to survive and adapt under abiotic stress (Mittler 2006; Wahid et al. 2007; Zhu 2016; Wani et al. 2018; Zaid et al. 2020). Given the rising global temperatures, tropical and semi-arid regions are facing frequent episodes of extreme temperatures, which are challenging crop yields (Lobell et al. 2011; Knox et al. 2012). High-temperature stress is becoming a serious problem for sustaining global crop production (Bita and Gerats 2013; Jha et al. 2014; Sadiq et al. 2020), affecting the entire plant life cycle, including physiological, biochemical, and metabolic processes (Bita and Gerats 2013; Hasanuzzaman et al. 2013; Sharma et al. 2019; Sadiq et al. 2020). Crop plants are most sensitive to HS during the reproductive stage, causing significant yield losses (Wheeler et al. 2000; Luo 2011; Gourdji et al. 2013; Deryng et al. 2014).

The effect of HS on various crops has been assessed using various simulation and prediction models (Swaminathan and Kesavan 2012; Tesfaye et al. 2016). Increasing HS associated with global climate change is predicted to reduce rainfed maize yields by 3.3–6.4% by 2030 and 5.2–12.2% by 2050 (Tesfaye et al. 2016, see Table 1). A 1 °C increase beyond normal air temperature is predicted to significantly reduce yields in two-thirds of African maize-growing regions (Lobell et al. 2011). Similarly, in South-East Asia, a 1 °C increase beyond normal air temperature reduced rice yields by 4–14% (Lobell et al. 2008). A 0.5 °C increase beyond normal winter temperatures will likely reduce rainfed wheat yields by 0.45 t ha^{-1} in India and 4–7% yield in China (Easterling et al. 2007). A 1 °C increase during summer is predicted to reduce soybean yields by up to 16% in Wisconsin in the United States of America (USA) (Kucharik and Serbin 2008). Table 1 shows further examples of crop yield losses due to HS.

Several strategies, including crop breeding, physiological and agronomic management, and genomics and

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Table 1 Crop yield losses under increasing heat stress

Crop	Yield loss due to heat stress	References
Rice, wheat, and maize	~40 megatons or $5 billion	Lobell and Field (2007)
Various crops	Every 1 °C increase could cause yield losses of US$20 billion per year in India	FAO (2009), Swaminathan and Kesavan (2012)
Maize	30% yield losses predicted by 2100	Schlenker and Roberts (2009)
Maize	Every 1 °C daily increase above 30 °C reduces yield by 1%	Lobell et al. (2011)
	45% global yield losses predicted by 2080s	Deryng et al. (2014)
Maize	Rainfed yield losses of 3.3–6.4% by 2030 and 5.2–12.2% by 2050; irrigated yield losses of 3–8% by 2030 and 5–14% by 2050 in South Asia	Tesfaye et al. (2016)
Rice	Episodes of heat stress during the reproductive period threaten more than 120 million hectares of rice production	Teixeira et al. (2013)
Wheat	Drought and heat stress could reduce yield losses by 9–10%	Lesk et al. (2016)
Wheat	A 0.5 °C increase in average temperature predicted to reduce rainfed yields by 4–7% by 2050 in China	Easterling et al. (2007)
Wheat	A 1 °C temperature increase during the wheat-growing season predicted to decrease yields by 10% in China	You et al. (2009)
Soybean	46% yield losses in the USA before 2100	Schlenker and Roberts (2009)
Soybean	16% yield reduction based on the temperature change patterns in the USA from 1976 to 2006	Kucharik and Serbin (2008)
Barley	Increasing air temperatures from the year 1981–2002 reduced yields by 8 million tons per year, costing around $1.0 billion	Lobell and Field (2007)

transgenics approaches, have been suggested to ensure sustainable crop production under increasing HS events (Wahid et al. 2007; Bita and Gerats 2013; Jha et al. 2014). Phytohormones, including auxin/indole acetic acid (IAA), gibberellic acid (GA), abscisic acid (ABA), cytokinins (CTKs), ethylene (ET), salicylic acid (SA), brassinosteroids (BRs), strigolactone (SL), and jasmonic acid (JA) are important molecular players for regulating plant growth in response to various abiotic stress stimuli, including HS (Wani et al. 2016; Verma et al. 2016; Ahmad et al. 2019; Sharma et al. 2019). The above phytohormones significantly participate in various physiological and cellular processes, and molecular mechanisms involved in HS tolerance (Wani et al. 2016; Sharma et al. 2019). Upon perception of HS stimuli, plants release various phytohormones that contribute to plant development and physiological processes, including root development, stomatal movement, pollen development, photosynthesis, osmolyte accumulation, and curtailing reactive oxygen species (ROS) accumulation, thus helping plants to adapt under HS (Sakata et al. 2010; Franklin et al. 2011; Li et al. 2014; Thussagunpanit et al. 2015a; Wu et al. 2016, 2017; Jegadeesan et al. 2018; Rezaul et al. 2019; Raza et al. 2020).

Thus, manipulating endogenous phytohormones or applying exogenous phytohormones could be promising approaches for plant adaptation and recovery from HS to minimize yield losses. The role of various phytohormones in regulating heat tolerance is summarized in Fig. 1. Here, we discuss the implications of various phytohormones and the plausible mechanistic roles in mediating HS tolerance in various plant species.

Indole Acetic Acid Homeostasis Maintains Reproductive Stability Under HS

IAA is the most abundant auxin in plants, orchestrating many essential developmental and physiological processes, including cell elongation and division, pollen development, anther dehiscence, and reproductive tissue development (Gray et al. 1998; Teale et al. 2006; Cecchetti et al. 2008; Sakata et al. 2010). Like other phytohormones, IAA plays a prominent role in plant adaptation to environmental stresses, including HS (Sakata et al. 2010; Franklin et al. 2011; Sun et al. 2012; Wit et al. 2014; Zheng et al. 2016; Zhang et al. 2018), by protecting photosynthesis and reducing photooxidation-mediated damage (Tognetti et al. 2012). The promotion of hypocotyl elongation through accumulated auxin is a well-established adaptive response by plants to HS (Gray et al. 1998). Subsequently, Franklin et al. (2011) shed mechanistic insight into the roles of *PHYTOCHROME-INTERACTING FACTOR 4* (*PIF4*)—a transcription factor (Stavang et al. 2009)—and the *SMALL AUXIN UP RNA* (*SUAR*) genes (*SAUR19–24* and *SAUR61–68*) that regulate auxin biosynthesis by upregulating related genes under high temperature (28 °C) and thus promoting hypocotyl elongation in *Arabidopsis*. The underlying genes involved in auxin biosynthesis upregulation were: *YUC8*, *YUC9*, *TAA1*, and *CYP79B2*

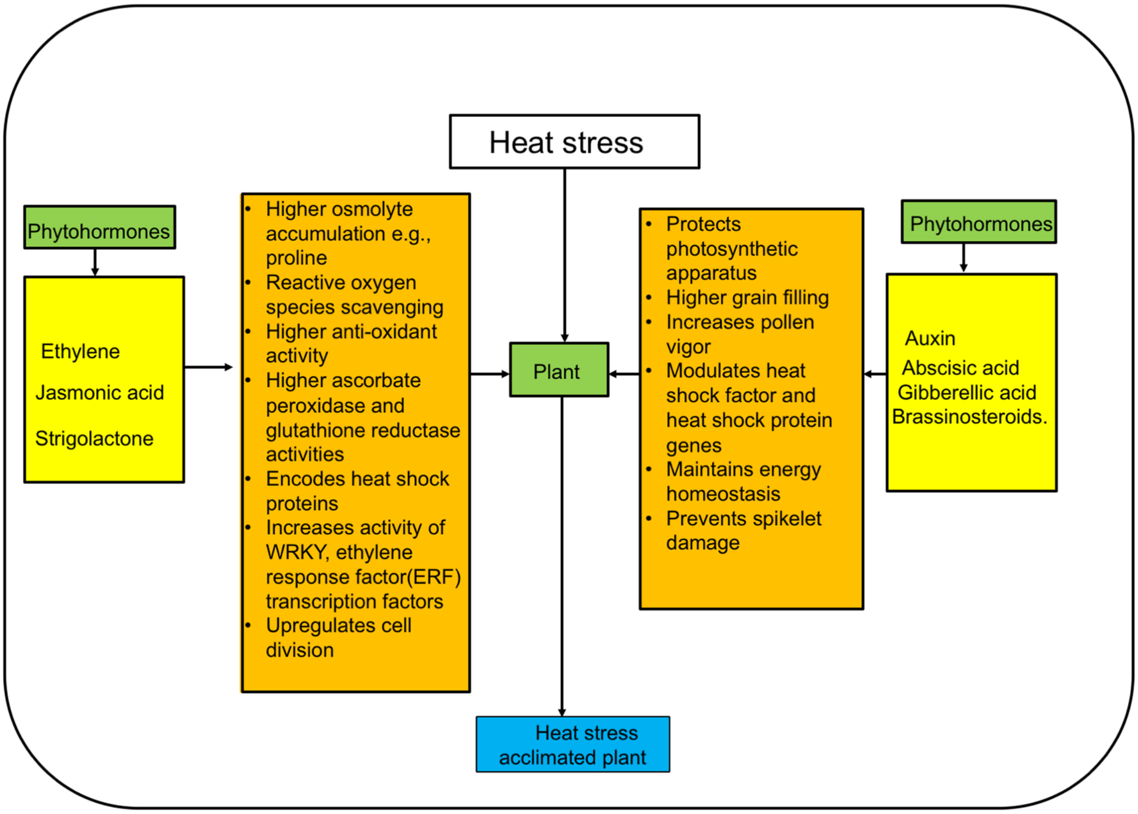

Fig. 1 Role of phytohormones contributing to heat stress adaptations in plants. Phytohormones contribute to plant survival under heat stress by protecting photosynthesis apparatus (Ivanov et al. 1992; Sharma et al. 2019), rescuing pollen fertility (Firon et al. 2012; Zhang et al. 2018), improving grain filling (Yang et al. 2016), accumulating osmolytes (Robertson et al. 1994), activating antioxidant activity and reducing reactive oxygen species activity (Dat et al.1998a), and activating the transcription of various heat shock protein genes (Dhaubhadel et al. 1999; Makarova et al. 2018) and regulatory transcription factors, e.g., WRKY and ethylene response factor (Pan et al. 2012; Dang et al. 2013; Huang et al. 2016)

(Stavang et al. 2009; Franklin et al. 2011; Sun et al. 2012). Furthermore, Wang et al. (2016) demonstrated that auxin co-receptors, *TIR1* and *AFB2*, and *HEAT SHOCK PROTEIN 90 (HSP90)* are involved in root and hypocotyl elongation and lateral root formation of *Arabidopsis* in response to HS. The authors also described the supportive role of *SGT1*, a co-chaperone of *HSP90*, in response to increasing temperature. However, the mutant *SGTb1* protein encoded by the *eta3* gene inhibited auxin and *TIR1* accumulation, preventing auxin-mediated growth under HS. Likewise, auxin's role in maintaining the function of male reproductive organs, especially pollen tube growth/elongation and anther dehiscence, under HS is worth mentioning (Chen and Zhao 2008; Wu et al. 2008, 2016, 2019; Sharma et al. 2018). Under high-temperature stress, inhibition of endogenous auxin biosynthesis genes *YUCCA flavin monooxygenase* (Sakata et al. 2010) and *UDP-glucosyltransferase 74b1* (*UGT74B1*) (Grubb et al. 2004; Sharma et al. 2018) reduced pollen tube elongation, causing spikelet sterility and reduced pollen vigor in barley and rice and male sterility in *Arabidopsis* and cotton (Sakata et al. 2010; Fu et al. 2015; Song et al. 2015; Zhang et al. 2017, 2018; Wu et al. 2019). In contrast, IAA content declined at the tetrad stage and increased at the tapetal degradation and anther dehiscence stages in cotton anthers of H05, a heat-sensitive genotype, under HS (Min et al. 2014). These contrasting results suggest that anthers need an appropriate balance of IAA to confer heat tolerance. Further, in heat-stressed rice, spikelet fertility declined due to inhibited panicle expansion, which is likely the result of reduced accumulation of IAA and GA_1, an active type of GA (Wu et al. 2016).

The damaging effect of HS could be counteracted/minimized by manipulating auxin biosynthesis gene(s) and exogenous supplementation of auxin to restore pollen development and pollen tube growth and reverse spikelet sterility in crop plants (Sakata et al. 2010; Zhang et al. 2017, 2018; Wu et al. 2019) (see Table 2). Several auxin-responsive genes participate in the pollen viability restoration mechanism, which has been investigated in plants under stress (Sakata et al. 2010; Pazhamala et al. 2020). Diminished expression of *YUC2* and *YUC6* auxin biosynthesis genes in barley and *Arabidopsis* anthers under

Table 2 Phytohormones and the possible mechanisms contributing to heat stress tolerance in various plants

Hormone	Crop	Genotype	Stage	Mechanism involved in heat stress tolerance	References
Auxins	Arabidopsis	–	Seedling	Induces rapid cell elongation	Gray et al. (1998)
	Barley	Haruna-nijyo	Reproductive	Reduces pollen abortion	Sakata et al. (2010)
	Barley		Reproductive	Increases nuclear and organellar DNA proliferation	Oshino et al. (2011)
	Rice	Nipponbare	Reproductive	Prevents inhibition of pollen tube growth in pistil	Zhang et al. (2018)
CTKs	Maize	–	Reproductive	Reduce kernel abortion	Cheikh and Jones (1994)
	Agrostis palustris L.	–	Reproductive	Inhibit lipid peroxidation and slowing leaf senescence	Liu and Huang (2002)
	Wheat	Jimai 20	Reproductive	Increase grain-filling rate, endosperm cell division rate, 1000-grain weight	Yang et al. (2016)
	Rice	Liangyoupeijiu	Reproductive	Modulate degradation of spikelets, pollen vigor, anther dehiscence	Wu et al. (2016)
	Rice	Nagina22, Huanghuazhan, Liangyoupeijiu	Reproductive	Stable panicle size and less spikelet injury	Wu et al. (2017)
	Arabidopsis	Col-0	–	Prevent excessive ROS production	Prerostova et al. (2020)
ABA	Barley	Alfa	Seedling	Protects photosynthetic apparatus	Ivanov et al. (1992)
	Bromus inermis Leyss	Manchar	Seedling	Increases stress proteins and cell osmolytes	Robertson et al. (1994)
	Maize	Qing No. 3	Seedling	Increases SOD and APX activities	Gong et al. (1998)
	Arabidopsis	–	Seedling	Prevents oxidative stress damage	Larkindale and Knight (2002)
	Arabidopsis		Seedling	Prevents oxidative stress damage	Larkindale et al. (2005)
	Medicago sativa L.	Ameristand 801S, Aohan		Reduces electrolyte leakage, leaf water potential	An et al. (2014)
	Arabidopsis	–	Seedling	Increases expression of HSFA6b heat shock protein	Huang et al. (2016)
	Arabidopsis	Columbia	Seedling	–	Suzuki et al. (2016)
	Arabidopsis	Landsberg erecta	Seedling	Accumulates ascorbate peroxidase 1 and multiprotein bridging factor 1c proteins	Zandalinas et al. (2016)
	Tall fescue	Kentucky-31	Seedling	Regulates HSFs and HSPs	Wang et al. (2017)
	Rice	Zhefu802	Reproductive	Increases sugar metabolism and supply sugars to spikelet	Rezaul et al. (2019)

Table 2 (continued)

Hormone	Crop	Genotype	Stage	Mechanism involved in heat stress tolerance	References
	Rice	Nipponbare	Seedling	Increases carbohydrates, ATP, NAD (H), and heat shock proteins in wild-type plant	Li et al. (2020)
	Wheat	KSG1177	Reproductive	Increases ABA and IAA accumulation -Trp lead to pollen abortion and low seed set in heat-sensitive genotype	Bheemanahalli et al. (2020)
ET	Arabidopsis		Seedling	Prevents oxidative stress damage	Larkindale and Knight (2002)
	Agrostis stolonifera var. *palustris*	–	Seedling	Increases SOD, POX, and APX activities	Larkindale and Huang (2004)
	Tomato	–	Reproductive	Maintains pollen fertility	Firon et al. (2012)
	Tomato	–	Reproductive	–	Jegadeesan et al. (2018)
	Rice	*Oryza sativa* L.	Seedling	Reduces oxidative stress damage	Wu and Yang (2019)
		Japonica cv. Taikeng No. 9		Induces higher expression of *HSFA1a* and *HSFA2a*, *c*, *d*, *e*, and *f*	
	Tomato	–	–	–	Pan et al. (2019)
SA	*Sinapis alba*	–	Seedling	Increases antioxidant activity	Dat et al. (1998a)
	Sinapis alba	–	Seedling	Increase in SA and H_2O_2	Dat et al. (1998b)
	Potato	–	Seedling	Decreases CAT activity and increase H_2O_2	Lopez-Delgado et al. (1998)
	Arabidopsis	Columbia	Seedling	Enhances basal thermotolerance	Clarke et al. (2004)
	Arabidopsis		Seedling	Prevents damage from oxidative stress	Larkindale and Knight (2002)
	Mung bean		Seedling	Increases CAT, POX, APX activity; lower lipid peroxidation activity	Saleh et al. (2007)
	Grape	Cabernet sauvignon	Seedling	Induces gene expression of phenylalanine ammonia-lyase	Wen et al. (2008)
	Brassica juncea	Kranti	Seedling	Increases antioxidative enzymes and proline	Hayat et al. (2009)
	Brassica	TL15, PBT37, RL1359, PBR210	Seedling	Increases INV, CAT, POX activity	Kaur et al. (2009)
	Grape	Jingxiu	Seedling	Improves net photosynthesis rate	Wang et al. (2010)
	Wheat	WH 711	–	Increases proline production and decrease proline oxidase (PROX) activity	Khan et al. (2013)
	Maize		Seedling	Enhances antioxidant system	Li (2015)
	Maize	–	Seedling	–	Li et al. (2015)

Table 2 (continued)

Hormone	Crop	Genotype	Stage	Mechanism involved in heat stress tolerance	References
	Wheat	C306 and PBW343	Reproductive	Increases osmolyte and total antioxidant accumulation	Kumar et al. (2015)
	Cotton		Seedling	Increases proline and total soluble protein accumulation	Galani et al. (2016)
	Maize	CML-32	Seedling	Increases APX and GR activities	Khanna et al. (2016)
	Rice	Changyou 1	Reproductive	Inhibits spikelet degeneration	Zhang et al. (2017)
	Rice	Changyou1	Reproductive	Prevents accumulation of ROS and tapetum programmed cell death	Feng et al. (2018)
	Wheat	Pak-2013, NARC-2009, GA-2002, Inqilab-91 and Baj	Seedling	Accumulate sugars, proline, leaf chlorophyll content	Kousar et al. (2018)
	Potato	Chicago	Seedling	Increases HSP gene expression	Makarova et al. (2018)
	Cotton	AA-802	Reproductive	Reduces ROS-driven damage	Sarwar et al. (2018)
	Tomato	–	Seedling	Increases antioxidant enzymes and photosynthetic activity	Jahan et al. (2019)
	Pigeon pea	AL 1931	Seedling	Enhances antioxidant defense system	Navneet et al. (2019)
	Alfalfa	–	Seedling	Increases antioxidant enzyme and photosynthetic activities	Wassie et al. (2020)
	Brachypodium distachyon	P. Beauv. Bd21	Seedling	Enhances glutathione-S-transferase activity	Janda et al. (2020)
Propiconazole, uniconazole, paclobutrazol, and Quilt Xcel	Maize	B73	Seedling	bZIP60 mRNA splicing primes plants for rapid adaptive response	Neill et al. (2019)
GA	Arabidopsis	Col-0	Seedling	Increases SA biosynthesis	Alonso-Ramírez et al. (2009)
	Wheat	PBW 343	Seedling	Modulates sucrolytic and aminotransferase activities	Asthir and Bhatia (2014)
GA and ABA	Rice	Shanyou63	Reproductive	Increases pollen vigor and pollen germination	Tang et al. (2008)
GA3 + Si	Datepalm	*Phoenix dactylifera* L. cv. Khalas	Seedling	Increases polyphenol oxidase, CAT, peroxidase, APX, and HsfA3 gene activity	Khan et al. (2020)
EBR	*Cucumis melo* L.	–	Seedling	Enhances antioxidant defense system and photosynthetic activity	Zhang et al. (2014)
	Triticum aestivum	PBW343	Seedling	Increases antioxidant activity and proline content	Hussain et al. (2019)
	Tomato and brassica	–	Seedling	Accumulates HSP	Dhaubhadel et al. (1999)

Table 2 (continued)

Hormone	Crop	Genotype	Stage	Mechanism involved in heat stress tolerance	References
	Melon	Honglvzaocui	Seedling	Improves photosynthesis	Zhang et al. (2013)
	Tomato	9021	Seedling	Increases carboxylation efficiency and antioxidant activity	Ogweno et al. (2007)
	Rice		Reproductive	Increase s photosynthetic activity, stomatal conductivity, and filled seeds	Thussagunpanitet al. (2015a, b)
	Barley	522DK mutant, BW312	Seedling	Reduces leaf damage	Sadura et al. (2019)
SL	Tall fescue	Kentucky-31	Seedling	Regulate scell division and auxin transport	Hu et al. (2018b)
	Tall fescue	Kentucky-31	–	Enhances leaf elongation	Hu et al. (2019)
JA	Wheat		Seedling	Regulates DREB2A	Tian et al. (2020)

IAA indole acetic acid CTK cytokinin *ABA* abscisic acid, *GA* gibberellic acid, *ET* ethylene, *SA* salicylic acid, *EBR* 24-epibrassinolide, *JA* jasmonic acid, *SL* strigolactone

HS resulted in short stamens and pollen abortion (Sakata et al. 2010). Further, external application of synthetic auxin restored anther development and pollen fertility through enhanced expression of the *MCM5* gene mediating anther cell proliferation and development. External supplementation of 1 and 10 µmol L^{-1} NAA increased auxin content in high-temperature susceptible mutants of Nipponbare rice under HS, reducing spikelet sterility by promoting pollen tube growth in pistils (Zhang et al. 2018) (see Table 3). Interestingly, Nipponbare, a heat-tolerant rice cultivar, had higher auxin and ROS and lower peroxidase activity in pistils under HS than the heat-sensitive mutant. Reduced peroxidase activity increases ROS expression, increasing auxin in pollen tubes, which mediated HS tolerance in Nipponbare (Zhang et al. 2018). However, increased accumulation of ABA and IAA-tryptophan in KSG1177 (heat-sensitive wheat genotype) under HS resulted in pollen abortion and low seed set (Bheemanahalli et al. 2020).

Understanding the interaction of IAA with other phytohormones could reveal various complex regulatory networks orchestrating plant growth and development and plant adaptation mechanisms under various environmental cues. Recent investigations have revealed crosstalk between IAA, BRs, and GA_3, an active type of GA, which regulates hypocotyl growth under temperature stress in *Arabidopsis* (Stavang et al. 2009; Maharjan and Choe 2011). However, the molecular mechanisms of IAA for rescuing pollen fertility, reducing spikelet sterility, and controlling root growth in response to HS need further investigation.

CTKs Contribute Plant Thermal Acclimation Beyond Growth and Development

CTKs are multifaceted phytohormones contributing to basic plant development, including cell division, breaking seed dormancy, chloroplast biogenesis, apical dominance, leaf senescence, shoot differentiation, photomorphogenic development, and nucleic acid metabolism (Sakakibara 2010; for details, see Hwang et al. 2012). The role of CTK signaling, metabolism, and its crosstalk with other phytohormones for alleviating plants from the adverse effects of various environmental cues, including HS, has been investigated (Veselova et al. 2005; Jeon et al. 2010; Rivero et al. 2010; Ghanem et al. 2011; Hwang et al. 2012; Reguera et al. 2013; Fahad et al. 2015a; Yang et al. 2016). CTKs protect plants from the deleterious effects of HS by activating antioxidant mechanisms, protecting photosynthetic apparatus, or maintaining stay green and delayed senescence (He and Jin 1999; Thomas and Howarth 2000; Liu and Huang 2002; Zavaleta-Mancera et al. 2007). The role of kinetin in scavenging free radicals and switching on the antioxidant mechanism to prevent purine breakdown is worth noting (Chakrabarti and Mukherji 2003). Liu and Huang (2002) reported that CTKs play a role in alleviating HS in creeping bentgrass by activating antioxidant mechanisms and reducing lipid peroxidation activity. During the reproductive phase, HS reduced CTKs in rice panicles due to inhibited CTK biosynthesis, interrupted CTK transport from roots to shoots, and enhanced CTK catabolism (Skalák et al. 2016; Wu et al. 2016, 2017; Wu and Yang 2019). Maintaining sufficient CTK content under HS by stabilizing CTK biosynthesis and lowering

Table 3 Various phytohormones and their concentrations attributing to high-temperature stress tolerance in different plant species

Hormone	Crop	Temperature	Concentration	References
IAA	Brassica	55 °C for 3 h	10 and 20 µM	Kaur et al. (2009)
	Barley	31 °C	10^{-6}, 10^{-5}, or 10^{-4} M	Sakata et al. (2010)
	Rice	40 °C for 2 h	1 and 10 µmol L^{-1}	Zhang et al. (2018)
CTK	Maize	35 °C for 4 days	Benzyladenine 10^{-6}, 10^{-7}, 10^{-5} M	Cheikh and Jones (1994)
	Bent grass	38 °C/28 °C	10 and 100 µM	Wang et al. (2013)
	Wheat	35/20 °C	0 mg L^{-1} of 6-benzylaminopurine (6-BA)	Yang et al. (2016)
	Rice	8 °C, 10.00–11.00 h; 39 °C, 12.00–13.00 h	60 mg L^{-1}	Wu et al. (2016)
	Rice	31.5 and 38.3 °C	Benzyl aminopurine (60 mg L^{-1})	Wu et al. (2017)
	Arabidopsis	45 °C, 3 h	–	Prerostova et al. (2020)
GA_3	Arabidopsis	3 h at 50 °C	50 mM	Alonso-Ramírez et al. (2009)
	Wheat	45 °C for 2 h	100 µM	Asthir and Bhatia (2014)
	Date palm	High temperature (44 °C)	100 µM	Khan et al. (2020)
ABA	Barley	45 °C and 50 °C	10^{-5} M	Ivanov et al. (1992)
	Bromus inermis Leyss	42.5 °C for 120 min	75 µM	Robertson et al. (1994)
	Maize	46 °C	0.3 mmol L^{-1}	Gong et al. (1998)
	Wheat	45 °C for 2 h	100 µM	Asthir and Bhatia (2014)
	Arabidopsis	38 °C for 8 h	30 µM	Zandalinas et al (2016)
	Arabidopsis	22 °C for 2 h before 44 °C HS for 190–205 min	10 mM for 12 h	Huang et al. (2016)
	Tall fescue	37/32 °C	5 µM	Wang et al. (2017)
	Rice	45 °C for 24 h	1 µmol L^{-1}, 10 µmol L^{-1}, 100 µmol L^{-1}	Li et al. (2020)
	Rice	39–41 °C, 09:00–15:00 h; 30 °C	0, 1, 10, 100 µmol L^{-1}	Rezaul et al. (2019)
	Tall fescue	38/33 °C day/night	10 µM	Zhang et al. (2019)
ET	Tomato	2 h 45 °C	0.1 µL L^{-1} in air	Jegadeesan et al. (2018)
	Rice	45 °C under a 16:8 light:dark cycle	10 µM ACC	Wu and Yang (2019)
SA	Brassica	45 °C for 1 h	100 µm	Dat et al. (1998a)
	Brassica	55 °C for 1.5 h	10 and 500 µm	Dat et al. (1998b)
	Potato	5-week high temperature (35 °C)	10^{-6}–10^{-5} M	Lopez-Delgado et al. (1998)
	Arabidopsis	3 h at 50 °C	50 mM	Alonso-Ramírez et al. (2009)
	Grapevine	43 °C for 5 h	100 µM	Wang et al. (2010)
	Brassica	40 °C for 2 h	10^{-5} M	Hayat et al. (2009)
	Wheat	40 °C for 6 h	0.5 mM	Khan et al. (2013)
	Cotton	42 ± 2 °C	1.0 mM	Galani et al. (2016)
	Rice	40 °C	0–50 mmol L^{-1}	Zhang et al. (2017)
	Cotton	45/30 °C	50 ppm	Sarwar et al. (2018)
	Rice	40 °C for 10 days	0.01, 0.1, 1.0, 10, and 50 mM	Feng et al. (2018)
	Potato	28 °C moderate heat treatment	1 mM	Makarova et al. (2018)
	Pigeon pea	45 °C for 3 h	0.5 mM and 1 mM for 3 h	Navneet et al. (2019)
	Tomato	42 °C	1 mM	Jahan et al. (2019)
	Wheat	36–40 °C	10^{-4} M	Kousar et al. (2018)
	Brachypodium distachyon	4 h; 35 °C	0.5 mM NaSA	Janda et al. (2020)
	Alfalfa	–	0.25 or 0.5 mM	Wassie et al. (2020)
EBR	Tomato	40/30 °C	–	Ogweno et al. (2007)
	Melon	42/32 °C	1.0 mg L^{-1}	Zhang et al. (2013)
	Cucumis melo L.	42/32 °C	0.5–1.5 mg dm^{-3}	Zhang et al. (2014)
	Rice	40/30 °C for 7 days	1 nM	Thussagunpanit al. (2015a, b)
	Triticum aestivum	35/28 or 40/35 °C	0.01 µM	Hussain et al. (2019)

Table 3 (continued)

Hormone	Crop	Temperature	Concentration	References
SL	Tall fescue	35/30 °C	0.01 µM GR24	Hu et al. (2019)

CTK oxidase and dehydrogenase activity likely increases spikelet number per panicle in rice (Ha et al. 2012; Wu et al. 2016, 2017). High-temperature stress impaired CTK transport from roots to shoots in heat-sensitive rice genotypes—LYPJ, HHZ, and N22—reducing spikelet number per panicle due to the higher activity of CTK oxidase/dehydrogenase (Wu et al. 2017). However, exogenous application of CTKs maintained spikelet number per panicle in heat-sensitive rice cultivars under HS, indicating that CTKs play a pivotal role in stabilizing spikelet numbers under HS (Wu et al. 2017). Likewise, Wu et al. (2016) advocated that the external application of CTKs retained spikelet fertility and enhanced grain size in heat-sensitive rice cultivars. External application of 60 mg L^{-1} 6-benzylaminopurine, a synthetic CTK (see Table 3), strengthened the wheat grain sink under HS by increasing endosperm cell number and carbohydrate accumulation during grain filling in the presence of elevated levels of IAA and zeatin riboside, a naturally occurring CTK (Yang et al. 2016). Banowetz et al. (1999) also implicated CTKs for improving grain weight in wheat under HS. Similarly, improved HS tolerance by maintaining a balance between ABA and CTK has been reported in maize (Cheikh and Jones 1994). An abundance of ABA and paucity of CTK impaired maize kernel development during HS (Cheikh and Jones 1994). Thus, the application of benzyladenine to maize under HS maintained a balance between ABA and CTK, ultimately preventing kernel abortion (Cheikh and Jones 1994). Recently, the inhibitory action of CTK degradation by INCYDE-F—an inhibitor of CTK oxidase/dehydrogenase—was investigated for mediating heat tolerance in HS-acclimated *Arabidopsis* plants (Prerostova et al. 2020; see Table 2). Interestingly, the external application of melatonin significantly ameliorated leaf senescence in perennial ryegrass under HS by enhancing CTK biosynthesis and limiting ABA biosynthesis (Zhang et al. 2017). Further insight into the underlying molecular mechanisms mediated by CTK controlling the grain-filling process and grain weight under HS will improve grain yield. Moreover, investigation of the key gene(s) controlling CTK biosynthesis and its regulation under HS will provide novel insights into the HS tolerance mechanism in plants.

ABA Regulates Plant Response to HS

ABA is an important phytohormone with a central role in regulating various processes from plant development and seed dormancy to myriad of biotic and abiotic stress responses (Verslues and Zhu 2007; Huang et al. 2017; Kang et al. 2017; Cho et al. 2018). It is an important signaling molecule for plants exposed to various environmental stresses, including water, cold, salinity, heavy metal toxicity, and heat, and well recognized in concert with other phytohormones regulating complex gene networks (Hsu and Kao 2003; Narusaka et al. 2003; Suzuki et al. 2016; Zhang et al. 2017; Rubio et al. 2018; Albertos et al. 2019). Importantly, ABA's mechanistic role in regulating plant water status by controlling stomatal aperture closure during water stress is well-established (Daszkowska-Golec and Szarejko 2013). However, the mechanisms of ABA's contribution to HS tolerance in plants are not fully understood (Suzuki et al. 2016; Zhang et al. 2017). Concerted efforts in recent decades have suggested that ABA contributes to both basal and acquired thermotolerance by preventing photoinhibition and improving photosystem II (PSII) efficiency, minimizing the damaging effects of chloroplast ultrastructure, activating various antioxidant mechanisms by producing various osmolytes, upregulating heat shock transcription factors (HSFs), and switching on various HSP gene(s) and genes actively participating in maintaining 'energy homeostasis' in plants under HS (Ivanov et al. 1992; Robertson et al. 1994; Gong et al. 1998; Larkindale and Knights 2002; Larkindale and Huang 2004; Larkindale et al. 2005; De Block and Lijsebettens 2011; Wang et al. 2017; Rezaul et al. 2018, 2019; Li et al. 2020). ABA-treated bromegrass (*Bromus inermis*) enhanced HS tolerance by producing various proteins and osmolytes (Robertson et al. 1994). Likewise, maize seedlings treated with ABA and Ca^{2+} increased HS tolerance by enhancing antioxidant enzyme activities and reducing lipid peroxidation activity (Gong et al. 1998). Zandalinas et al. (2016) revealed that the increased activity of ascorbate peroxidase 1 and multiprotein bridging factor 1 proteins, attributing plant acclimation under combined drought and HS in response to increased ABA, safeguarded plants against HS damage. Abscisic acid enables plants to withstand HS by enhancing H_2O_2 activity, activating antioxidant mechanisms, and accumulating HSPs (Li et al. 2014; Rezaul et al. 2019). In contrast, increased sensitivity to HS due to impaired ABA biosynthesis has been reported (Ding et al. 2010; Kumar et al. 2012) and supported in ABA-deficient mutants displaying higher sensitivity to HS damage (Wang et al. 2014a; Wu et al. 2017). The role of ABA in mediating the thermotolerance response by regulating HSF networks and downstream HSP encoding genes is well-established (Pareek et al. 1998; Campbell et al. 2001; Larkindale and Knights

2002; Larkindale et al. 2005; Huang et al. 2016; Suzuki et al. 2016). Considering this, how *HSFA6b*—an *HSF* acting as a hub for ABA signaling and serving in thermotolerance in association with ABA—has been investigated in *Arabidopsis* (Huang et al. 2016). The upregulation of *FaHSFAc2* encoding HSPs in tall fescue (*Festuca arundinacea* Schreb) treated with ABA improved HS tolerance (Wang et al. 2017) (see Table 4). Likewise, Hu et al. (2018a) advocated that overexpression of *TaHsfC2a* regulatory genes, mediated by ABA under HS, conferred heat tolerance in wheat by switching on various HSPs and osmoprotective genes, viz., *TaHSP16.9b*, *TaHSP62.4*, *HSP101b*, *TaGalSyn*, *TaHSA32*, *TaRof1*, and *TaβAmy1*. An increased abundance of ABA in the embryo, relative to the endosperm, during grain filling, contributed to heat tolerance by inducing HSP accumulation (Walker-Simmons 1987). Further investigation by Walker-Simmons and Sesing (1990) provided evidence of higher ABA accumulation in wheat grains under high-temperature stress (25 °C) during grain filling.

The role of ABA for maintaining energy homeostasis under HS has been explored (De Block and Lijsebettens 2011). Rezaul et al. (2018, 2019) and Chen et al. (2019) reported evidence of ABA's participatory role in heat tolerance by enhancing sugar metabolism by switching on sucrose transporter genes, sucrose synthase (*SUS*) genes, and invertase (*INV*) genes to maintain ATP formation, and allocating sugars to alleviate the HS effect in rice spikelets, thus improving pollen fertility. Increased availability of carbohydrates, expression of HSP genes (*HSP71.1* and *HSP24.1*), and ATP and NAD(H) production in Nipponbare (wild-type with flat leaf) rice subjected to exogeneous ABA application under HS revealed a significant role of ABA in enhancing heat tolerance (Li et al. 2020). However, the external application of ABA in an hts mutant of Nipponbare, featuring semi-rolled leaves, exhibited lower heat tolerance than its counterpart wild-type Nipponbare due to enhanced leaf temperature and respiration rate, which increased carbohydrate consumption and resulted in energy deficiency (Li et al. 2020). Furthermore, ABA-mediated drought priming enhanced HS tolerance in *Festuca arundinacea* by upregulating various regulatory genes, viz., *CDPKs*, *DREBs*, *MYB*, *MYC*, *HSFs*, and *HSPs*, but their role in conferring HS tolerance needs further investigation (Zhang et al. 2019). Unveiling the complex pathways of ABA signaling and its crosstalk with other phytohormones in response to HS and the regulatory gene network involved in inducing HS tolerance could provide insight into the role of ABA in plant HS tolerance.

Gibberellic Acid Regulates Plant Responses to HS

Gibberellic acid belongs to a group of natural diterpenoids. It is an essential phytohormone contributing to various developmental processes, including seed germination, stem elongation, and flower and fruit development (Sun and Gubler 2004; Yamaguchi 2008), and a key mediator of various abiotic stresses, including HS, in plants (Ko et al. 2007; Alonso-Ramírez et al. 2009). Vettakkorumakankav et al. (1999) illustrated the involvement of GA_3 in regulating HS tolerance by treating normal and dwarf barley seedlings with GA_3 and paclobutrazol (GA_3 inhibitor) under HS. The GA_3-treated normal and dwarf plants had more ion leakage and fewer photosynthetic pigments than the paclobutrazol-treated plants under HS; that is, the normal and dwarf plants treated with GA_3 exhibited heat sensitivity (Vettakkorumakankav et al. 1999). Likewise, barley seedlings treated with a triazole, a GA_3 inhibitor, had increased thermotolerance due to reduced GA_3 and plant height (Sarkar et al. 2004). In rice, the incidence of HS during panicle initiation inhibited spikelet fertility by repressing panicle opening, which was ascribed to the depletion of IAA and GA_1 (Wu et al. 2016). Inhibition of GA biosynthesis due to lower expression of various genes, viz., *GA20ox1*, *GA20ox2*, *GA3ox1*, and *GA3ox2*, regulating GA biosynthesis under HS was examined in *Arabidopsis* (Toh et al. 2012). In rice, Tang et al. (2008) documented the contributory role of GA_3, IAA, and proline on pollen fertility and spikelet fertility damage imposed by high-temperature stress. Exogenous application of GA_3 improved spikelet fertility in rice under HS, suggesting a significant role in protecting male reproductive organs under HS (Kwon and Paek 2016). Likewise, a GA_3-mediated mechanism imparting HS tolerance in wheat by enhancing invertase activities increased grain sink activity under HS (Asthir and Bhatia 2014). Alonso-Ramírez et al. (2009) established that external addition of GA_3 alleviated the inhibitory effects imposed by HS, oxidative, and salinity stresses by modulating SA biosynthesis and switching on transgene *FsGASA4* (introduced from beechnut *Fagus sylvatica*), a GA_3-responsive gene, in *Arabidopsis* seedlings. A recent investigation by Khan et al. (2020) demonstrated the basis of HS tolerance in date palm using externally applied GA_3 in conjunction with silicon that modulated various genes, viz., *GPX2*, *CAT*, *Cyt-Cu/Zn SOD*, and *glyceraldehyde3-phosphate dehydrogenase* engaged in antioxidant mechanisms, *HsfA3* encoding heat shock transcription factor, and the diminishing action of *PYL4*, *PYL8*, and *PYR1* ABA signaling-related genes. Various gene(s) contributing to the HS response and tolerance due to phytohormone signaling are listed in Table 4.

Further investigation into genes related to GA biosynthesis, GA-signaling pathways and networks, and crosstalk of GA with other phytohormones using a systems biology approach could expand our understanding of GA for defending HS in crop plants (Verma et al. 2016).

Table 4 List of various phytohormone-induced genes contributing to heat stress tolerance in plants

Hormone	Hormone-induced gene(s) contributing to heat tolerance regulation	Crop	References
IAA	*YUC2* and *YUC6* repressed at 33 °C; IAA1 repressed under heat stress	*Arabidopsis*	Sakata et al. (2010)
	YUCCA unigene Nos. 31993 and 5729	Barley	Sakata et al. (2010)
	Function of *MCM5* gene contributing to anther cell proliferation rescued by IAA under heat stress		Sakata et al. (2010)
	DWF4	*Arabidopsis*	Maharjan and Choe (2011)
	PHYTOCHROME-INTERACTING FACTOR, *JASMONATE RESISTANT1,GH3, PIN-FORMED3*	Cotton	Min et al. (2014)
	YUC1, YUC9, YUC11, rboh2, rboh6, and *POX* genes	Rice	Zhang et al. (2018)
IAA, GA, BR	*PIF4* (phytochrome-interacting factor 4)	*Arabidopsis*	Stavang et al. (2009)
ET	*MBF1c*	*Arabidopsis*	Suzuki et al. (2008)
	SlERF5	Tomato	Pan et al. (2012)
	AtERF1	*Arabidopsis*	Cheng et al. (2013)
	CarERF116	Chickpea	Deokar et al. (2015)
	OsEIN2, *OsEIL1*, and *OsEIL2, Os07g08140(HsfA2b) and Os03g63750 (HsfA1a)* and *Os03g53340 (HsfA2a), Os10g28340* (*HsfA2c*), *Os03g06630* (*HsfA2d*), *Os03g58160* (*HsfA2e*), and *Os06g36930* (*HsfA2f*)	Rice	Wu and Yang (2019)
	SlACS3 and *SlACS11, SlACO5, SlERF.E3* and *SlERF.F6, SlETR3, SlCTR2, SlMBF1* and *SlER21, ER21, ER24, MBF1*	Tomato	Jegadeesan et al. (2018)
	32 + 5 significant marker-trait association signals for spike ethylene under glasshouse and field condition	Wheat	Valluru et al. (2017)
SA	*EAT1, MIL2,* and *DTM1*	Rice	Feng et al. (2018)
	Phenylalanine ammonia-lyase	Grape berry	Wen et al. (2008)
	psbA	Wheat	Wang et al. (2014b)
	HSP70 and *HSP90*	Potato	Makarova et al. (2018)
CTK	*At3g62150, At4g39070, At4g29740, At1g75450, At5g05410, At1g22690, At5g17300, At3g14200, At4g08290*	*Arabidopsis*	Cerny et al. (2014)
CTK and melatonin	*LpSAG12.1* and *Lph36*	Perennial ryegrass	Zhang et al. (2017)
ABA	*SUT4, SUS2, INV1,* and *CIN1* genes	Rice	Li et al. (2020)
	HSP71.1 and *HSP24.1, PARP1* or *PARP2*		Rezaul et al. (2019)
	HSFA6b	*Arabidopsis*	Huang et al. (2016)
	Fa*HSFA2c*	*Festuca arundinacea* Schreb	Wang et al. (2017)
	CDPK3, *MPK3*, *DREB2A*, *AREB3*, *MYB2*, *MYC4*, *HsfA2*, *HSP18*, and *HSP70*	*Festuca arundinacea* Schreb	Zhang et al. (2019)
GA$_3$	*FsGASA4*	*Fagus sylvatica*	Alonso-Ramírez et al. (2009)
	GPX2, *CAT*, *Cyt-Cu/Zn SOD*, and *glyceraldehyde3-phosphate dehydrogenase* gene	Date palm	Khan et al. (2020)
	PYL4, *PYL8*, and *PYR1, HsfA3*		
SL	Cell cycle-related genes (PCNA, CycD2, CDKB) and auxin transport genes *TIR1, PIN1, PIN2* and *PIN5*	Tall fescue	Hu et al. (2018b)
BR and ABA	*RBOH1* gene	Tomato	Zhou et al. (2014)
BR	*HvBRI1* gene	Barley	Sadura et al. (2019)
JA	*bZIP3, BHLH114, BHLH137, WRKY8, WRKY57,* and *WRKY18*	*Arabidopsis thaliana*	Balfagón et al. (2019)
	CaWRKY40	pepper	Dang et al. (2013)
	DREB2A, TaOPR3	Wheat	Tian et al. (2020)

SA Improves Plant Performance By Boosting Plant Defense Mechanisms Against HS

SA is a multifunctional hormone contributing to plant growth, seed germination, development, photosynthesis, transpiration, leaf senescence, redox homeostasis, and defense responses to various biotic and abiotic stresses, including HS (Javid et al. 2011; Vicente and Plasencia 2011; Fahad and Bano 2012; Bastam et al. 2013; Khanna et al. 2016; Zhang et al. 2017; Ahmad et al. 2018a; Kohli et al. 2019; van Butselaar and Van den Ackerveken 2020; Ding and Ding 2020). There is accumulating evidence of SA contributing to thermotolerance in various plants by activating antioxidant mechanisms, accumulating osmoprotectants and HSPs, and inducing excessive H_2O_2 production that mediates signal transduction (Dat et al. 1998a, b; Lopez-Delgado et al. 1998; Wang and Li 2006; Hayat et al. 2009; Wang et al. 2010, 2014b; Khan et al. 2013; Kohli et al. 2018a, b; Kaya et al. 2020a). The ameliorative role of SA in mediating HS tolerance by improving key processes, viz., photosynthesis and nitrogen assimilation activity, and increasing proline content by enhancing γ-glutamyl kinase and reducing proline oxidase enzyme activity has been established in wheat (Khan et al. 2013). External application of SA enhanced photosynthetic activity by improving net photosynthesis rate, Rubisco and PSII efficiency, chlorophyll content, proline content, soluble protein, HSPs, and sugar content, and reducing membrane damage, attributing to heat tolerance in wheat (Kousar et al. 2018), brassica (Kaur et al. 2009; Hayat et al. 2009), cotton (Galani et al. 2016), grapevine (Wang and Li 2007; Wang et al. 2010), tall fescue (*Festuca arundinacea* Schreb) (Pirnajmedin et al. 2020), and alfalfa (Wassie et al. 2020). Likewise, SA can alleviate plant injury from HS by activating the antioxidant defense system in various plant species (Dat et al. 1998a; Saleh et al. 2007; Kaur et al. 2009; Li 2015; Khanna et al. 2016; Zhang et al. 2017; Janda et al. 2020). Exogenous application of SA (50 ppm) along with H2O2 (30 ppm), ascorbic acid (70 ppm), and moringa leaf extract enhanced net photosynthetic rate and yield-contributing traits in cotton and protected plants from heat-induced injury by modulating the antioxidant enzyme mechanism (Sarwar et al. 2018; see Table 3). Similarly, the synergistic effect of SA and H2S on HS tolerance induced proline, betaine, and trehalose accumulation and enhanced antioxidant activity in maize under HS (Li 2015; Li et al. 2015). Moreover, SA treatment in rice at 40 °C alleviated spikelet damage by inducing higher activity of ROS-scavenging enzymes and accumulating soluble sugars, proline and IAA, ABA, and BR (Zhang et al. 2017). Feng et al. (2018) argued that H2O2 induced higher accumulation of SA, which improved pollen viability, minimized ROS activity, and inhibited tapetum programmed cell death in rice under HS. *Brachypodium* treated with 0.5 mM NaSA had elevated levels of glutathione-S-transferase under HS, which supports the role of SA in activating the antioxidant mechanism for ameliorating HS injury (Janda et al. 2020). Furthermore, various gene(s) have been induced by SA that contribute to HS tolerance (Wen et al. 2008; Feng et al. 2018; Janda et al. 2020). An SA treatment under high-temperature stress reduced excessive ROS in rice anthers and tapetum degradation by repressing caspase-3, thus preventing programmed cell death in anthers (Feng et al. 2018). Moreover, the authors postulated the role of *EAT1*, *MIL2*, and *DMT1* genes (see Table 4), related to tapetum development, in SA-mediated protection of pollen abortion from HS; the molecular mechanism remains elusive. Increased expression of the phenylalanine ammonia-lyase enzyme contributing to phenylpropanoid metabolism due to external application of SA in grape berry increased the accumulation of phenolics, thus imparting HS tolerance in grape berry (Wen et al. 2008). Dang et al. (2013) speculated that the *CaWARKY40* gene has an important role in regulating HS tolerance mediated by SA, JA, and ET in transgenic tobacco. Under HS, overexpression of *CaWRKY40* enhanced expression of SA-dependent *NtPR1a/c*, *NtPR2* genes, JA-responsive *NtPR1b* gene, JA biosynthesis-associated *NtLOX1* gene, and ET synthesis genes, viz., *NtACS6* and *NtEFE26*.Therefore, ET-, SA-, and JA-mediated regulation of the *CaWRKY40* gene could enhance downstream genes related to HS tolerance. Likewise, positive overexpression of the regulatory gene *AtWRKY39* in cooperation with SA, JA, and calcium signaling pathways imparting heat tolerance has been established in *Arabidopsis thaliana* (Li et al. 2010). A model proposed by Divi et al. (2010) depicted the interplay of BR with SA, ABA, and ET mediating various stress tolerance mechanisms. They also explained the positive regulation of BR with *NPR1*, a regulator of SA-mediated defense genes, which plays a pivotal role in conferring HS tolerance. Thus, modulation of SA responsive gene(s) or SA signaling is an attractive approach for protecting plants from HS damage. However, the molecular mechanisms involved in SA minimizing ROS activity, protecting pollen grains from HS-induced damage, and inducing various regulatory genes under HS remain elusive.

Brassinosteroids as Emerging Phytohormones: Their Possible Roles in Regulating HS Tolerance

BRs are a novel class of polyhydroxylated plant steroid hormones synthesized in the endoplasmic reticulum (Kim et al. 2006; Northey et al. 2016; Nolan et al. 2017, 2020; Ahanger et al. 2018, 2020). They comprise brassinolide (BL), castasterone (CS), and various derivatives involved in regulating plant growth and development, seed germination, pollen tube growth, flower and fruit production, protein synthesis, nucleic acid synthesis, and various environmental stress responses, including HS (Grove et al. 1979; Clouse and Sasse 1998; Nakaya et al. 2002; Ogweno et al. 2007; Hayat et al. 2010; Zhang et al. 2013; Fahad et al. 2015b; Lozano-Durán and Zipfel 2015; Sharma et al. 2016; Ahmad et al. 2018b, c, 2019; Jan et al. 2020; Kaya et al. 2020b; Nolan et al. 2020). The working mechanism of BR signaling, from binding to cell surface receptors to switching on TFs in response to various stresses, has been investigated (Krishna 2003; Nolan et al. 2020). BR-mediated HS tolerance has been reported in *B. inermis* (Wilen et al. 1995), brassica (*Brassica napus*) (Dhaubhadel et al. 1999, 2002), tomato (*Solanum lycopersicum*) (Dhaubhadel et al. 1999; Singh and Shono 2005; Ogweno et al. 2010; Mazorra et al. 2011), *Vigna radiata* (Hayat et al. 2010), and barley (*Hordeum vulgare*) (Janeczko et al. 2011). The counteractive effect of BRs against HS in rice enhanced chlorophyll content, photosynthetic activity, stomatal conductivity, and filled seed numbers (Thussagunpanit et al. 2015a, b). The mechanism of BR that contributes to plant HS tolerance is mediated by various essential physiological and biochemical processes, viz., photosynthetic efficiency by maximizing the carboxylation rate of Rubisco and improving the efficiency of PSII photochemistry, enhancing chlorophyll content, stomatal conductivity, membrane stability, and proline content, reducing lipid peroxidation, activating antioxidant mechanisms, and maintaining redox homeostasis (Cao and Zhao 2008; Ogweno et al. 2007, 2010; Hayat et al. 2010; Kaur et al. 2018; Kaya et al. 2019). The ameliorative effects of trihydroxylated spirotane, an analog of BR, by decreasing the negative effect of HS on photosynthetic activity and promoting growth has been reported for banana under HS (Gonzalez-Olmedo et al. 2005). Thussagunpanit et al. (2015a) reported that EBR and 7,8-dihydro-8α-20-hydroxyecdysone (DHECH), a mimic compound of BR, impart HS tolerance. Rice plants treated separately with 1 nM EBR and 1 nM DHECH at the flowering stage at 40/30 °C (day/night temperature) protected photosynthetic apparatus by enhancing stomatal conductance and increasing the PSII quantum yield, improving plant yield (Thussagunpanit et al. 2015a). Likewise, exogenous application of EBR in *Cucumis melo* L. aided the recovery of chlorophyll content and improved photosynthesis and photochemical activity of PSI under high-temperature stress (Zhang et al. 2013, 2014). The role of BRs in minimizing ROS activity and maintaining plant cellular redox homeostasis by activating antioxidant and glyoxylase mechanisms under HS has been reported (Hussain et al. 2019). Likewise, Cao and Zhao (2008) revealed that BR contributed to HS tolerance in contrasting heat-tolerant and heat-sensitive rice cultivars by enhancing antioxidant enzymes and diminishing the lipid peroxidation process. Furthermore, Ogweno et al. (2007, 2010) reported HS tolerance at 40/30 °C in EBR-treated tomato plants due to improved photosynthetic activity that activated antioxidant mechanisms and concomitantly prevented photoinhibition and lipid oxidation activity. EBR in association with Si improved HS tolerance in a heat-sensitive wheat cultivar (PBW343) by switching on antioxidant mechanisms and producing excessive proline (Hussain et al. 2019) (see Table 1). Brassinosteroids induced the expression of various HSPs, viz., *hsp100*, *hsp90*, and *hsp70*, in tomato and *B. napus,* protecting the cellular protein synthesis machinery from HS (Dhaubhadel et al. 1999, 2002; Singh and Shono 2005). Crosstalk of BRs with JA, ABA, ET, and SA signaling pathways mediating HS tolerance has been demonstrated (Divi et al. 2010); however, the precise molecular mechanism remains poorly understood. A thorough understanding of BR-responsive *BRASSINAZOLE RESISTANCE1* (*BZR1*)/*BRI1-EMS SUPPRESSOR 1* (*BES1*) transcription factors controlling BR-targeted genes regulating the HS response in plants could help to develop HS-tolerant plants (Anwar et al. 2018).

Research is needed to clarify the participatory role of BRs and their crosstalk with other phytohormones for modulating the defense response of plants to HS.

ET and Its Crosstalk with Other Phytohormones Regulating HS Tolerance in Plants

ET is an important gaseous phytohormone involved in controlling various plant developmental processes and regulating various biotic and abiotic stresses, including HS (Larkindale and Knight 2002; Larkindale and Huang 2004; Larkindale et al. 2005; Muller and Munne-Bosch 2015; Abdelrahman et al. 2017). However, the regulatory mechanisms contributing to heat tolerance remain under investigation. Larkindale and Knight (2002) and Larkindale et al. (2005) reported ET-mediating basal thermotolerance after studying mutant, wild and transgenic *Arabidopsis*. Larkindale and Knight (2002) illustrated the involvement of Ca^{2+}, SA, ABA, and ET in protecting plants from HS-induced oxidative damage by comparing seedling survival of an ET-insensitive mutant (*etr-1*), ABA-insensitive mutant (*abi-1*), *nahG* transgenic line with a depleted level of SA, and the corresponding wild-type Columbia, Landsberg *erecta*, and Columbia background *Arabidopsis* lines treated with HS. The significant role of these phytohormones conferring HS tolerance was confirmed in the mutants defective in these phytohormones, which had lower survival rates than the wild types. Larkindale et al. (2005) also confirmed the participatory role of ET, SA, and ABA in HS tolerance because the *abi1* and *abi2* mutants defective in ABA signaling had impaired acquired thermotolerance. However, *ein-2* and *etr-1* mutants defective in ET signaling had greater impairment in basal thermotolerance than acquired thermotolerance in *Arabidopsis* (Larkindale and Knight 2002). Recently, ET's role in safeguarding plant cells from oxidative stress damage by switching on various antioxidant systems and *HSF* genes has been investigated in rice under HS through the external application of 1-aminocyclopropane-1-carboxylic acid (ACC), an ET precursor (Wu and Yang 2019). The upregulatory activity of *Oryza sativa EIN2* (*OsEIN2*) and *OsEIL1* genes, contributing to ET signaling pathways, and *HsfA2b, HSFA2a*, *c*, *d*, *e*, and *f HSF* genes protecting rice seedlings under HS was investigated (Wu and Yang 2019). ACC plays a role in the HS tolerance of creeping bentgrass (*Agrostis stolonifera* var. *palustris*) by increasing superoxidase dismutase (SOD), peroxidase (POX), and ascorbate peroxidase (APX) activities by protecting plants against HS-induced oxidative damage (Larkindale and Huang 2004). Jegadeesan et al. (2018) uncovered both upregulatory and downregulatory genes participating in increased ET biosynthesis and signaling that contribute to HS tolerance in tomato pollen grains (Table 4), which agrees with the findings of Firon et al. (2012), who reported that tomato plants pre-treated with ET releaser retained high-quality fertile pollen grain under HS. The role of *ethylene-responsive factor* (*ERF*) TFs, acting as a regulatory gene for controlling various abiotic stresses, is well recognized (Mizoi et al. 2012). Upregulation of various *ERF* genes, including *Arabidopsis thaliana ERF1* (*AtERF1*) in *Arabidopsis* (Cheng et al. 2013), *Cicer arietinum ERF116* (*CarERF116*) in chickpea (Deokar et al. 2015), and *Solanum lycopersicon ERF5* (*SlERF5*) in tomato (Pan et al. 2012), reportedly confer HS tolerance. An increased abundance of ET during HS reduced wheat yields due to low spikelet fertility and reduced final grain weights (Cheng and Lur 1996; Yang et al. 2004; Hays et al. 2007; Huberman et al. 2013). A genome-wide association study elucidated five and 22 marker-trait associations for spike ET content and its association with spike dry weight, respectively, under HS in the field in a panel of 130 wheat genotypes (Valluru et al. 2017). The authors also found a negative correlation between spike ET content and spike dry weight and suggested exploring genes that control the reduced ET effect on plant yield under HS for improving plant yield. Likewise, inhibition of ET biosynthesis by downregulating ET signaling components, viz., *ACS6* and *ETR2*, could improve grain yield under drought stress in rice and maize (Young et al. 2004; Wuriyanghan et al. 2009; Habben et al. 2014). Moreover, crosstalk of ET with other phytohormones, viz., ABA, SA, and JA, for controlling various abiotic stresses, including HS, by inducing *ERF* genes has been reported (Muller and Munne-Bosch 2015). Crosstalk of various phytohormones and phytohormone-responsive genes mediating HS tolerance is depicted in Fig. 2. Complete molecular understanding of ET-mediating basal thermotolerance and thermopriming, signaling pathway, induction of antioxidant mechanism and expression of ERFs viz., *ERF95* and *ERF97*, and HSFs especially, *HSFA2* could help improve HS tolerance in plant (Wu and Yang 2019; Huang et al. 2020; Singh et al. 2021).

Strigolactones: Novel Players Mediating Plant HS Tolerance

Strigolactones (SLs) are a group of terpenoid lactones regulating plant architecture, mainly shoot branching and mesocotyl, hypocotyl, internode, and root elongation, to improve plant abiotic stress tolerance, including HS (Umehara et al. 2008; Toh et al. 2012; Brewer et al. 2013; de Saint Germain et al. 2013; Jia et al. 2014; Van Ha et al. 2014; Hu et al. 2018a, b). How SLs regulate HS tolerance in plants is unclear. Hu et al. (2018a, b) revealed that SLs applied externally to tall fescue (*Festuca arundinacea* Schreb) controlled HS tolerance by promoting root elongation through the upregulation of cell division and cell-cycle-related genes, such as *PCNA*, *CycD2*, and *CDKB*, and downregulation of the auxin receptor *TIR1* gene and transport genes, such as *PIN1*, *PIN2*, and *PIN5* (see Table 4). Subsequently, Hu et al. (2019) highlighted the role of SLs in conferring HS tolerance in tall fescue through leaf elongation by enhancing the activity of cell-cycle-related genes and diminishing the activity of auxin transport-related genes. Future research on the contribution of SLs to HS tolerance could advance our understanding of the mechanistic role of SLs in HS tolerance in plants.

Jasmonates: a Multifunctional Phytohormone Functioning Beyond Plant Biotic Stress Defense

Jasmonates (JAs) play a pivotal role in the plant defense response to various pathogens (Vijayan et al. 1998; Mei et al. 2006) and serve as multifunctional phytohormones contributing to plant development, growth, and reproduction processes (Wasternack 2007; Browse 2009). Their participatory role in controlling various abiotic stresses, including salinity, cold, light, heavy metals, and HS, in plants has been investigated (Dar et al. 2015; Kazan 2015; Sharma and Laxmi 2016; Per et al. 2018; Balfagón et al. 2019; Savchenko et al. 2019; Ali and Baek 2020). While JA plays an assertive role in response to various biotic and abiotic stresses in plants, it adversely affects plant growth and photosynthesis (Kazan and Manners 2012; Yang et al. 2012; Wasternack 2014).

The role of JA in heat tolerance in *Arabidopsis* was demonstrated by Clarke et al. (2009) by assessing electrolyte leakage in cell membrane treated with methyl jasmonate (MeJA) under HS—an external application of 5 µm MeJA protected cell viability under HS, while application > 5 µm reversed this result by enhancing membrane damage, indicating that its ability to ameliorate the negative effect of HS is concentration specific (Clarke et al. 2009). Shahzad et al. (2015) compared the effect of MeJA by treating pea plants with various concentrations of MeJA, viz., 50, 100, and 200 µM under HS (40 °C), cold stress (4 °C), and control (20 °C) conditions—200 µM of MeJA inhibited plant

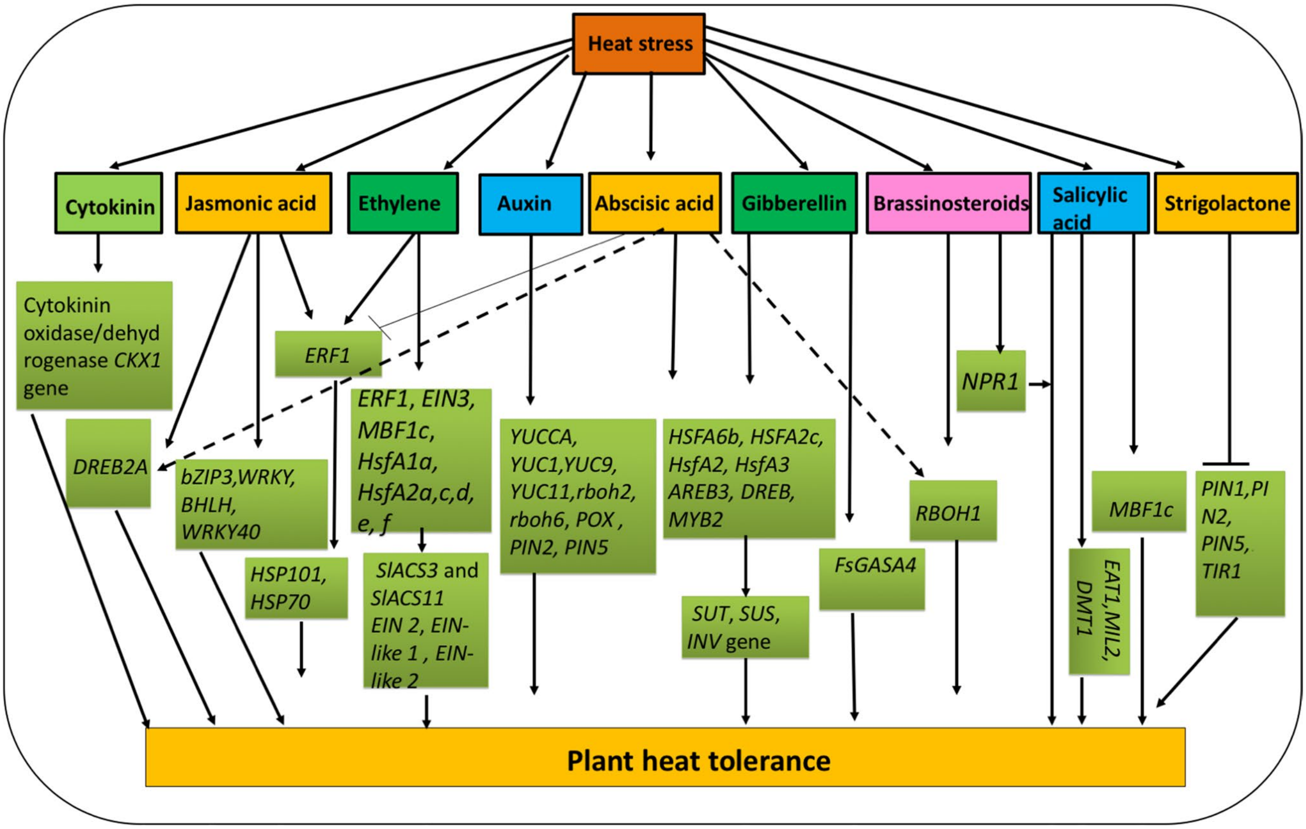

Fig. 2 Phytohormones regulate various genes controlling heat stress tolerance in plants. In response to heat stress, plants adapt by activating various transcription factors (TFs) that regulate various phytohormones. Abscisic acid (ABA) and jasmonic acid (JA) positively regulate *DREB2A* (Zhang et al. 2019; Tian et al. 2020) and ethylene (ET) positively regulates *ethylene response factor* (*ERF*) for attributing heat tolerance in plants (Cheng et al. 2013; Muller and Munne-Bosch 2015). In contrast, ABA negatively regulates *ERF1* (Cheng et al. 2013) and jasmonic acid positively regulates *bZIP3, WRKY40* for controlling heat tolerance (Dang et al. 2013; Balfagón et al. 2019). Several gene(s) are involved in mediating heat tolerance through their upregulation by exogeneous application of various phytohormones contributing heat tolerance: *HSP101* and *HSP70* are induced by JA and ET (Muller and Munne-Bosch 2015), *FsGASA4* is induced by gibberellic acid (Alonso-Ramírez et al. 2009), *SUT*, *SUS*, *INV*, and *RBOH1* are induced by ABA (Rezaul et al. 2018, 2019; Chen et al. 2019; Li et al. 2020), *YUCCA*, *YUC1*, and *YUC9* are induced by auxin (Stavang et al. 2009; Franklin et al. 2011; Sun et al. 2012), *CKX1* is induced by cytokinin (Macková et al. 2013), *ERF1*, *EIN2, EIN3*, *HsfA1a, and HsfA2a* induced by ET (Wu and Yang 2019), and *EAT1*, *MIL2*, *DMT1*, and *MBF1c* are induced by salicylic acid (Feng et al. 2018). However, *PIN1*, *PIN2*, and *PIN5* are negatively regulated by strigolactone (Hu et al. 2018b)

growth and reduced photosynthesis, stomatal conductance, and chlorophyll content under HS. To dissect the role of various regulatory TFs controlled by JA in response to HS, Dang et al. (2013) showed that external application of JA enhanced *CaWRKY40* gene activity, conferring HS tolerance in pepper plants. Similarly, JA alleviated the negative effects of combined high light and HS by inducing several regulatory genes, viz., *bZIP3*, *BHLH114*, *BHLH137*, and *WRKY8*, which might allow plants to withstand heat and high light stress (Balfagón et al. 2019). Recently, Tian et al. (2020) reported the role of JAs in mediating heat tolerance through the *DREB2A* regulatory gene. Interplay/crosstalk of JA with other phytohormones mediating plant growth and development, complex signaling, and various biotic and abiotic stresses has been established (Raza et al. 2020). Synergistic and antagonistic effects of JA with other phytohormones play an essential role in providing abiotic and biotic stress tolerance in plants (Wang et al. 2020). The molecular role of JA in concert with SA imparting basal thermotolerance has been established in *Arabidopsis* by assessing electrolyte leakage in HS-treated double mutants, *cpr5-1 npr1-1 cpr5-1 jar1-1*, and the corresponding single mutant (Clarke et al. 2009). Similarly, Tsai et al. (2019) advocated that JA is associated with SA-enhanced heat tolerance and tomato yellow leaf curl virus resistance in tomato. Nevertheless, JA acts as an antagonist to ET for governing the HS response (Sharma and Laxmi 2016). The molecular mechanism and signaling of JAs and their crosstalk with other phytohormones controlling abiotic stresses, including HS responses, remain unknown (Yang et al. 2019). Furthermore, insights into the regulatory mechanisms of JAZ and JAV1 repressor proteins involved in regulating the transcription of various JA-responsive genes under various stresses, including HS, could improve our understanding of how JA is involved in plant HS adaptation (Raza et al. 2020).

Embracing Genetic Engineering for Manipulating Phytohormone-Responsive Gene(s) Regulating Heat Tolerance

Genetic engineering/transgenics is a powerful approach for deciphering the functional roles of various regulatory and phytohormone-responsive gene(s) contributing to HS tolerance (Cheng et al. 2013; Muller and Munne-Bosch 2015). Manipulation of phytohormone-responsive gene(s) could be a novel avenue for designing heat-tolerant crops. Previously, Alonso-Ramírez et al. (2009) monitored overexpression of the beechnut (*Fagus sylvatica*) GA-responsive gene *FsGASA4* that induces endogenous SA, imparting higher thermotolerance in transgenic *Arabidopsis*. Likewise, in transgenic *Arabidopsis*, overexpression of *ERF1*, an ERF TF involved in ET signaling and response-mediated HS tolerance, upregulated the *AtHsfA3* heat shock factor and various heat shock protein genes, viz., *HSP23.6*, *HSP70*, and *HSP17.6A* (Cheng et al. 2013). Youm et al. (2008) advocated the overexpression role of *CaPF1*, a pepper transcription factor *ERF* gene contributing to higher heat tolerance in transgenic potato. Similarly, overexpression of *HSFA6b*, serving as a positive regulator for ABA signaling, exhibited increased heat tolerance in transgenic *Arabidopsis* (Huang et al. 2016). Overexpression of the *AtDWF4* gene involved in BR biosynthesis conferred HS tolerance in transgenic *B. napus* (Sahni et al. 2016). Overexpression of the *Triticum aestivum* BR-insensitive1 (*TaBRI1*) gene imparts thermotolerance in transgenic *Arabidopsis* by increasing membrane stability under HS (Singh et al. 2016). However, transgenic *Arabidopsis* containing the *NahG* (encoding salicylate hydrolase) gene is depleted of SA under HS, increasing electrolyte leakage due to heat shock and oxidative stress-mediated damage, indicating the essential role of SA in plant basal thermotolerance (Clarke et al. 2004). Increased expression of the tomato NAC transcription factor (*SlJA2*) in transgenic tobacco decreased heat tolerance due to a reduction in SA accumulation (Liu et al. 2017), suggesting a vital role of SA in conferring heat tolerance. Technological innovations, viz., next-generation sequencing, could unveil phytohormone-responsive candidate regulatory genes/noncoding RNAs regulating HS tolerance across genomes (Wang et al. 2019). Furthermore, augmentation CRISPR/Cas9-based genome editing is a promising approach for precisely modifying phytohormone-responsive TFs/genomic regions controlling the HS response for the future design of heat-tolerant crop plants (LeBlanc et al. 2018; Debbarma et al. 2019).

Perspective and Conclusion

Increasing HS events is a major issue for overall plant growth, causing great concern for global food security (Wahid et al. 2007). Among the various strategies for developing heat-tolerant crops, the role of phytohormones in mitigating the effect of HS deserves attention.

Exogenous application of various phytohormones could improve plant performance by protecting key physiological processes, viz., photosynthesis by minimizing photoinhibition, lowering lipid peroxidation, and stimulating antioxidant mechanisms under HS (Sharma et al. 2019). However, the complex molecular mechanisms of various phytohormones contributing to morpho-physiological adaptations in plants, such as minimizing ROS activity, rescuing pollen fertility, and protecting spikelet fertility, grain-filling process, and grain weights under HS need greater attention. Phytohormones regulate various biological regulatory pathways and processes related to HS. Phytohormones can switch on the signaling of various regulatory gene(s) under HS. Simultaneously, crosstalk/interactions of various phytohormones play a pivotal role in regulating the HS response in plants; however, understanding their complete molecular mechanisms controlling HS tolerance remains elusive. Among the phytohormone-based strategies for developing HS-tolerant crop plants, phytohormone priming could improve plant's adaptation to HS. However, the bioformulations need rigorous testing under laboratory conditions before applying in the field. Likewise, manipulating phytohormone-responsive TFs/genomic regions controlling the HS response through genetic engineering/genome editing technologies is an emerging approach for designing HS-tolerant crops. As the role of phytohormone signaling and crosstalk in regulating plant growth in response to HS is complex, it merits further investigation (Verma et al. 2016). Moreover, the underlying regulatory genes and gene networks stimulated by the phytohormones in response to HS need further research.

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Declaration

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