Chapter 13
Mitogen-Activated Protein Kinase, Plants, and Heat Stress

Jyotsna Bharti, Sahil, Sahil Mehta, Shaban Ahmad, Baljinder Singh, Asish K. Padhy, Neha Srivastava, and Vimal Pandey

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Abbreviations

AMPK	AMP-activated protein kinase
APX	Ascorbate peroxidase
cAMP	Cyclic adenosine monophosphate

J. Bharti (✉) · S. Mehta
International Centre for Genetic Engineering and Biotechnology, New Delhi, India

Sahil
Department of Botany, University of Delhi, New Delhi, India

S. Ahmad
Department of Computer Science, Jamia Millia Islamia, New Delhi, India

B. Singh · A. K. Padhy · N. Srivastava · V. Pandey
National Institute of Plant Genome Research, New Delhi, India

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CAT	Catalase
CDPK	Calcium-dependent protein kinase
DHAR	Dehydroascorbate reductase
ERK	Extracellular signal-regulated kinase
GHGs	Greenhouse gases
Gly I	Glyoxalase I
GR	Glutathione reductase
GST	Glutathione-S-transferase
H_2O_2	Hydrogen peroxide
Hsf1	Heat shock factor 1
HSPs	Heat shock proteins
JAK-STAT	Janus kinase/signal transducers and activators of transcription
KDa	Kilo Daltons
LEA	Late embryogenesis abundant
MAPK	Mitogen-activated protein (MAP) kinase
MAPKK	Mitogen-activated protein (MAP) kinase kinase
MAPKKK	Mitogen-activated protein (MAP) kinase kinase kinase
MDHAR	Monodehydroascorbate reductase
NPK2	Nucleus- and phragmoplast-localized protein kinase
NTF2	Nuclear transport factor 2
OMTK1	Oxidative stress-activated MAP triple-kinase 1
PSII	Photosystem II
ROS	Reactive oxygen species
RuBisCo	Ribulose-1,5-bisphosphate carboxylase/oxygenase
RUE	Radiation use efficiency
SIMK	Salt-induced mitogen kinase
UV	Ultraviolet
WIPK	Wound-induced mitogen kinase

1 Introduction

Stress signifies a set of conditions that deviate the organism from its “normal physiological conditions,” i.e., outside the optimum range in which the organism thrives. From seedling to the postharvest stage, plants encounter numerous stresses. The term “stress” can be categorized into two major groups, namely, biotic and abiotic stress (Gupta et al. 2020). The former one is a consequence of living disturbances, such as fungi, bacteria, viruses, algae, etc., and hampers the normal growth and development of the plants (Mehta et al. 2020). The latter one arises due to fluctuation in the plant’s physical environment (naturally occurring inanimate factors) like water, salinity, metal/metalloid toxicity, pollution, nutrient paucity, dwindling seasonal patterns, and temperature shifts (Husen 1997, 2010; Iqbal et al. 2015; Getnet et al. 2015; Embiale et al. 2016; Husen et al. 2018, 2019; Mehta et al. 2020; Pandey and Gautam 2020).

Compared to biotic stress, abiotic stresses are the first and foremost reason accounted for the loss of annual productivity rate (Sharma et al. 2019; Pandey and Gautam 2020). Interestingly, during the last five decades, one of the major global concerns besetting the crop biologists is the perpetually increasing temperature (Kaur et al. 2018; Rai 2020). The major reasons are global warming, increasing human population, overconsumption of fuel/resources, and anthropogenic activities. This is also reflected in the accumulation of greenhouse gases (GHGs) and increased heat entrapment in the immediate surroundings, famously known as global warming (Lesk et al. 2016; Yanni et al. 2020), which is supported by the data presented in Fig. 13.1. This GHGs-induced rise in ambient temperature ultimately inflicts a plunge in food production. In this chapter, we have highlighted the involvement of the plant's MAPK cascade under extreme environmental conditions, namely, heat stress. Additionally, we have also summarized the MAPK cascade's role in heat-related secondary stresses such as osmotic, oxidative, and drought.

2 Heat Stress

Biologically, a temperature condition which is hot enough for a persistent period, potentially jeopardizes the normal cellular functions, and results in a series of biochemical, morphological, physiological, and molecular changes that adversely affects the plant's normal functioning is known as heat stress (Abdelrahman et al. 2020; Azhar et al. 2020). As temperature increases from the optimal threshold, plants adapt intricate mechanisms including cellular and molecular modifications to sustain cellular homeostasis. But prolonged exposure to abnormal temperature is competent enough to cause an irreversible menace to germination, plant growth, and development, reproduction, and finally yield loss, which is precisely addressed as heat stress (Liu et al. 2019; Ali et al. 2019). The optimum temperature varies from plant to plant, and any increase in temperature from the optimum for a prolonged period is categorized as heat stress. The effect of heat stress includes various physiological modifications at multiple levels throughout its ontogeny, i.e., protoplasm shrinkage, reduction in cell size, slough off leaves/flowers/fruits, reduced net assimilation rate, disturbed fertilization, general infertility, hormonal imbalance, increased respiration, early senescence, etc. (Abdelrahman et al. 2020; Azhar et al. 2020).

At the cellular level, it influences cell division and cell cycle by altering the phragmoplast microtubule elongation, formation of microtubule asters, and microtubule organization (Parrotta et al. 2016), whereas physiologically, changes like cell size reduction, rapid stomatal closure, enhanced number of xylem vessels in the root, and water loss have been diagnosed by the researchers (Lipiec et al. 2013; Haworth et al. 2018; Aliche et al. 2020). Depending on the extent and the temperature range, at the reproductive level, the plant experiences reduction in flower bud development, failure in the germination of the pollen tube and reduced viability of

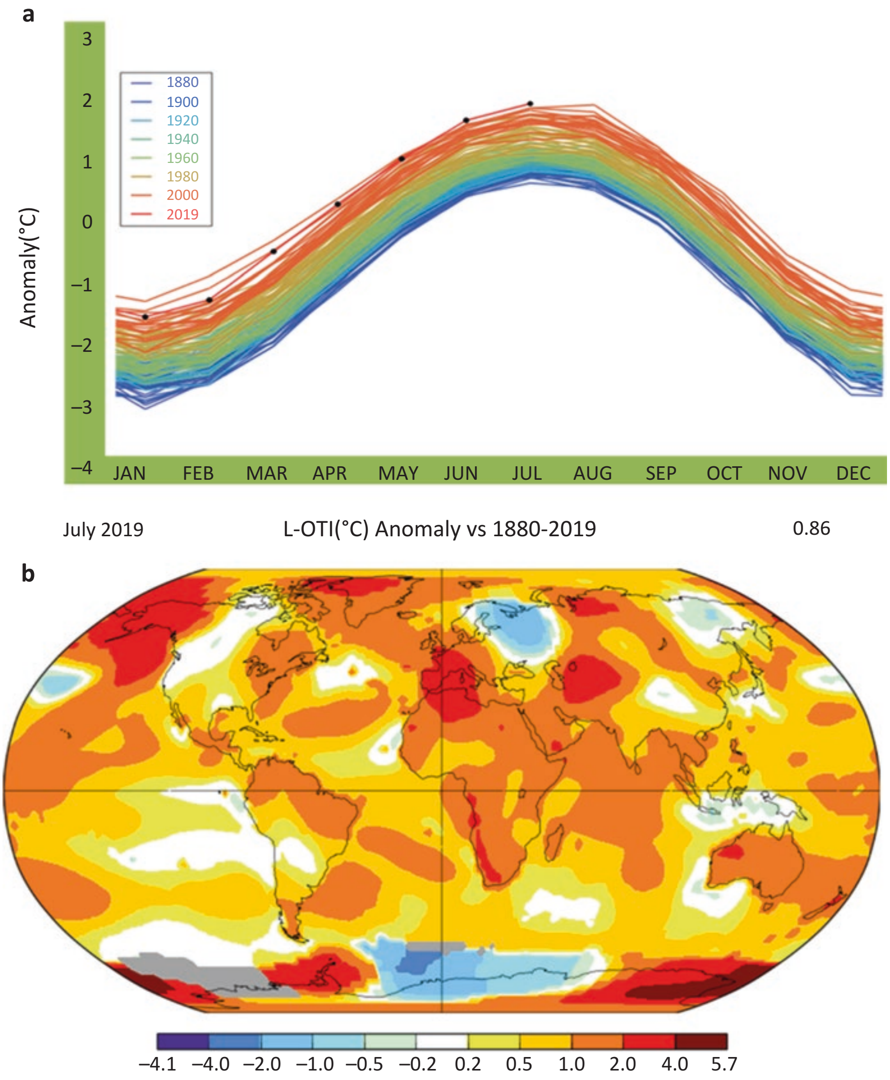

Fig. 13.1 (**a**) Graph showing the GISTEMP Seasonal Anomaly Cycle data based on MERRA2 reanalysis for the period 1880–2019. (**b**) Anomaly map depicting the globe surface temperature for the period 1880–2019. The data have been adapted from NASA-Goddard Institute for Space Studies (https://data.giss.nasa.gov/gistemp/). (Accessed on 24th January 2020)

ovule, stigma anomalous positioning, and abnormal anther dehiscence (Raja et al. 2019; Aliche et al. 2020). Heat stress often comes along with drought (Loka et al. 2020). Therefore, protective measures including seed priming are preferred along with adaptive measures undertaken in drought conditions (Banerjee and

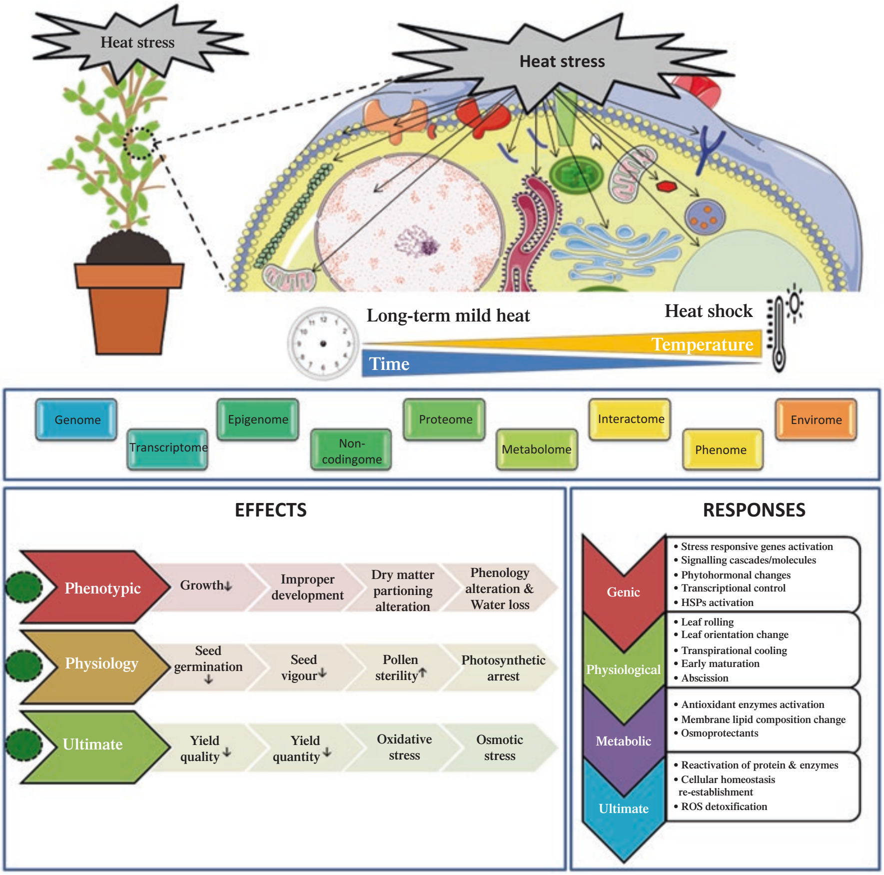

Fig. 13.2 Effect of heat stress on various plant's omics and other related parameters

Roychoudhury 2020). The overall effect of heat stress on plants and their responses are depicted in Fig. 13.2.

Additionally, the prolonged rise in temperature attenuates the photosynthetic efficiency due to many plausible reasons: (i) denaturation of the enzymes involved in the photosynthesis (e.g., RuBisCo) (Kumar et al. 2019), (ii) lipid peroxidation of chlorophyll and thylakoid membrane (Sharma et al. 2018), (iii) distortion of the grana stacking and PSII arrangement (Dongsansuk et al. 2017), (iv) disturbance of electron transport chain (Neves et al. 2019), and (v) loss of RuBP regeneration capacity (Chovancek et al. 2019). Due to all these abnormalities, Radiation Use Efficiency (RUE) of the plant reduces. On the other hand, an increase in respiration also leads to a higher rate of transpiration that causes permanent wilting and hence crop loss.

To control the water loss, plants shed their leaves, and in turn, photosynthesis is severely affected resulting in reduced grain weight (Bheemanahalli et al. 2019; Ali et al. 2019). Additionally, high temperature leads to a decrease in oil yield due to the reduction in linoleic acid content in *Brassica*, *Helianthus*, and seagrass (Beca-Carretero et al. 2018). All such injuries ultimately cause starvation, growth inhibition, reactive oxygen species (ROS) production, and ion flux reduction (Pucciariello et al. 2012; Baxter et al. 2014). In addition to all these effects, heat stress also causes both osmotic and oxidative stresses at the secondary level (Qi et al. 2011). As a result, it is one of the most challenging stresses that need to be tackled in order to achieve an optimum yield of the crop plants in the ideal case scenario where all other factors are taken care of.

3 Plant Response to Heat Stress

To maintain their cellular homeostasis in multiple natural adversities including high-temperature stress, plants have evolved various strategies during the course of time. Plants either tolerate or avoid the heat stress to some extent by some morphological and metabolic modifications (Matsui et al. 2019; Azhar et al. 2020). The mechanisms include induction of MAPK and Calcium-Dependent Protein Kinases (CDPK) cascades, scavenging the ROS, maintaining membrane stability, accumulation of compatible solutes, production of antioxidants, transcriptional activation and chaperone signaling, etc. (Fig. 13.2). All these mechanisms are regulated at the molecular level and help plants to fight against heat stress. Likewise, they also produce compatible solutes at the biochemical level, such as proline, polyols, tertiary and quaternary ammonium compounds, etc., that maintain the cell's turgor pressure and help in the redox balance. In addition, there are multiple reports in the literature which elaborate the increase of late embryogenesis abundant (LEA) proteins, dehydrins, Pir proteins, ubiquitin, and heat shock proteins in the heat stress repercussions-surviving plants (Rurek 2010; Hand et al. 2011; Priya et al. 2019; Maher et al. 2019; Yadav et al. 2020). All the changes and modifications in the metabolism happen due to the changes in the upregulation of the genes that provide the plant with a range of osmoprotectants, transporters, regulatory proteins, and detoxifying enzymes. At the expression level, this results in heat tolerance that gets translated into acclimatization (in long-term "adaptation") and depends directly on the signaling pathway. Para-heliotropism, altered membrane lipids, increased trichome density, etc., are the mechanisms undertaken by plants in heat avoidance; however, the signaling is involved here too (Thitz et al. 2017; Marcus 2019). Table 13.1 reviews the effect of high-temperature stress in different crop species.

Table 13.1 Effect of high-temperature stress in different crop species

Crops	Heat treatment	Major effects	References
Rice (*Oryza sativa*)	>33 °C, 10 days	Reduced spikelet fertility	Hurkman et al. (2009)
Wheat (*Triticum aestivum*)	37/28 °C (day/night), 20 days	Duration of grain filling shorten and decreased kernel weight	Rahman et al. (2009)
Wheat (*Triticum aestivum*)	30/25 °C (day/night)	Reduced leaf size, heading, anthesis, and maturity and drastic reduction in grains/spike number and size	Djanaguiraman et al. (2010)
Sorghum (*Hordeum vulgare*)	40/30 °C (day/night)	Decreased chlorophyll (chl) content, fluorescence, photosystem II photochemistry, and antioxidant enzymes, and increased ROS content and thylakoid membrane damage	Mohammed and Tarpley (2010)
Rice (*Oryza sativa*)	32 °C (night temperature)	Decreased grain dimensions and increased spikelet sterility	Suwa et al. (2010)
Maize (*Zea mays*)	35/27 °C (day/night), 14 days	Reduced ear expansion, hemicelluloses, and cellulose synthesis	Yin et al. (2010)
Rice (*Oryza sativa*)	25–42.5 °C	Decrease in the CO_2 assimilation rate	Djanaguiraman et al. (2011)
Soybean (*Glycine max*)	38/28 °C (day/night), 14 days	Decreased the leaf Pn and stomatal conductance, increased palisade and spongy layers thicknesses, damage in plasma membrane and chloroplast/thylakoid membranes, and distortion in mitochondrial membranes, cristae, and matrix	Tan et al. (2011)
Tobacco (*Nicotiana tabacum*)	43 °C, 2 h	Decrease in NPR and stomatal conductance and apparent quantum yield, carboxylation efficiency (CE), and antioxidant enzymes content	Gunawardhana and De Silva (2011)
Wheat (*Triticum aestivum*)	38 °C, 24 and 48 h	Decreased chl and relative water content and diminished antioxidative capacity	Hasanuzzaman et al. 2013
Yunnan poplar (*Populus yunnanensis*)	40 °C	Higher reduction in photosynthetic activity and enhanced production of ROS	Li et al. (2014a, b)
Lentil (*Lens culinaris*)	>33 °C, 36 days	Lentil genotypes exposed to full heat (unshaded) had an average grain yield 66% less than those grown under the shaded control	Delahunty et al. (2015)
Rice (*Oryza sativa*)	32 °C and 35 °C	36% decrease in yield during high night temperature stress and 25% decrease in high day temperature stress	Fahad et al. (2016)
Rice (*Oryza sativa*)	31–39 °C	A yield reduction of 30–40% during early reproductive stage	Wu et al. (2016)

(continued)

Table 13.1 (continued)

Crops	Heat treatment	Major effects	References
Rapeseed (*Brassica napus*)	30 °C day/25 °C night	Reduced seed germination and seed vigor	Rashid et al. (2018)
Chickpea (*Cicer arietinum*)	Day–night air temperatures >32 °C −20 °C), 7 days	Reduced seed yields of the heat-tolerant genotypes by 25–28% and the heat-sensitive genotypes by 4 s5–58%	Awasthi et al. (2017)
Soybean (*Glycine max*)	Day/night temp 30/22 32/24 38/26, 42/28 °C	Decline in leaf area, seed weight, total biomass, pods/pl, seeds/pl, harvest index, seeds/pod, and 100 seed weight	Jumrani and Bhatia (2018)
Quinoa (*Chenopodium quinoa*)	Day/night temp 40/24 °C	Reduced pollen viability between 30% and 70%	Hinojosa et al. (2019)

4 Signal Transduction for Heat Stress

There is an array of signaling pathways involved in conferring heat stress resistance. While some of them control the expression and synthesis of heat shock proteins (HSPs), others are involved in the production and/or activation of different effector constituents (Yadav et al. 2020; Pereyra et al. 2020). To withstand the stressful conditions, plant upregulates various genes that get translated into a battery of proteins and enzymes that are the key players of stress signaling cascades to ultimately counter the stress (Kaur and Gupta 2005) (Fig. 13.3). The signaling cascades may operate independently or maybe in cross talk with various other pathways in the cell (Nakashima et al. 2014; Dunayevich et al. 2018; Muthuramalingam et al. 2020). Depending upon the signal transduction molecules, plant type, and subjected stress, there are broad groups of molecules along with transcription factors that activate the responsiveness of genes. These groups of molecules include Ca^{2+}-dependent protein kinase (CDPKs), mitogen-activated protein kinase (MAPK/MPKs), NO, sugars, phytohormones (Azhar et al. 2020; Xalxo et al. 2020), etc. All these signaling increases the activity of antioxidants such as ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase, GST, CAT, glyoxalase I (Gly I), etc. (Fig. 13.2). This helps the plants to fight and survive in unfavorable conditions especially high-temperature and other-related stresses. Furthermore, various signaling pathways operate in a cell such as the AMPK signaling pathway, cAMP-dependent pathway, JAK-STAT signaling pathway, Nodal signaling pathway, Wnt signaling pathway, MAPK/ERK signaling pathway, and many more (Yu et al. 2019; Shumayla and Upadhyay 2019; Fu et al. 2020). Within all these highly conserved signaling cascades which play a central part in the heat stress conditions is the mitogen-activated protein kinase (MAPK) pathway (Yu et al. 2019; Ijaz et al. 2019). In simple words, mitogens are actually the agents that stimulate/promote cell division. Because of activation and deactivation of the enzyme by the kinases and phosphatases action, the signal passes

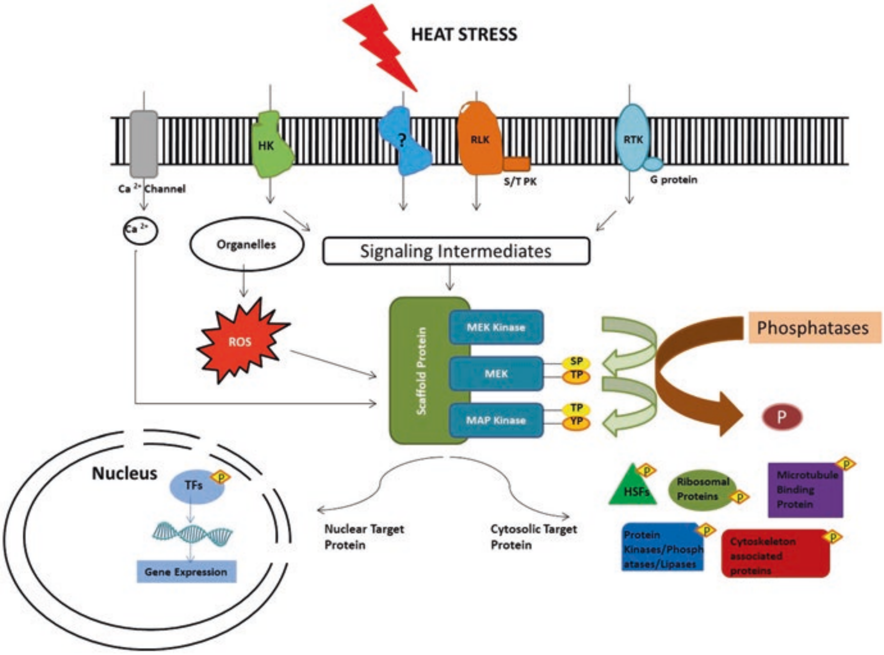

Fig. 13.3 Diagrammatic representation to show the core of MAPK pathway which contains three components MAPKKK-MAPKK-MAPK and along with that the downstream targets of the pathway. The downstream targets generally are transcription factor (WRKY), ribosomal protein (RPS), protein kinases/lipase/phosphatases, microtubule binding protein, and cytoskeleton-associated proteins

down fast. Apart from heat stress, there are many studies in the literature which point out the importance of the MAPK pathway in growth, hormone signaling, and other stress too including cold, drought, ROS, salinity, wounding, ozone, and UV radiation (Qiu et al. 2019; Sözen et al. 2019; Mahmood et al. 2020). Table 13.1 tabulates the reported MAPKKK and associated components of MAPK signaling cascades in a few plant species.

5 MAPK Pathway in Plants

A cell has multiple MAP kinase pathways that control distinct cellular responses. The pathway is composed of three protein kinases: a terminal MAP kinase and two upstream kinases, namely, MAPK kinase (MKKs) and MAPK kinase kinases (MKKKs) (Sözen et al. 2019). These kinases sequentially channelize, integrate, and amplify the cellular external environment response. MAPKs were first discovered because of their ability to phosphorylate the microtubule-associated protein-2

(MAP2), and that is why it was initially named as MAP2 kinases (Ray and Sturgill 1987). Later, it was discovered that these proteins show homology with certain mitogen-stimulated proteins (such as p42 protein), and they were renamed to mitogen-activated protein kinase (Cooper et al. 1982). With the continued research in the same field, it is now known that there are certain MAP kinases (a member of MAPKs family) collectively known as extracellular signal-regulated kinases (ERK). The first ERK (an insulin-activated protein kinase) was discovered from the Chinese hamster ovary. MAPKs need activation in the form of phosphorylation (Ijaz et al. 2019), and the activators are known as MEK (for MAPK/ERK Kinase). MEKs are in turn phosphorylated by MEKs activator, and they are known as MEKK (MEK Kinase) (Wang et al. 2015). The first MAPK pathway was characterized in *Arabidopsis,* and *At*MEKK1, *At*MKK2/MEK1, and *AT*MPK4/AtMPK6 constitute the whole pathway. It is vital for the plant's innate immunity and also regulates the response in conditions like salt, cold, and drought stress (Blanco et al. 2006; Xing et al. 2008). In interaction studies, it was established that *At*MEKK1interacts with *At*MKK2 and MEK1. *At*MPK4 interacts with both *At*MKK2 and MEK1, sometimes directly to *At*MEKK1. MEK1 primarily phosphorylates the threonine residue of *At*MPK4, but tyrosine phosphatase can deactivate *At*MPK4. This suggests that in plants either the MEK1 doesn't have dual specificity and thus tyrosine phosphorylation is simultaneously done by second MEK (Ichimura et al. 1998) or tyrosine gets autophosphorylated and thus MAPK is activated. MAPK cascade has a very important role to play in signal transduction for the multitude of stress responses (Fig. 13.3).

5.1 MAPKs

MAPKs are serine/threonine kinases activated by MEKs which either move to the nucleus to phosphorylate other specific transcription factors or stay in the cytoplasm to pass the signal to cytoskeleton binding proteins or some enzymes (protein kinases, phosphatases, phospholipases, etc.) for further signal transmission. Upon activation, MAPK disassociates from MEK and get arranged in a homodimer form to expose a domain called as MAP kinase insertion domain for facilitating active nuclear import (Pitzschke 2015; Wu et al. 2015). In MAPKs, the substrate phosphorylation occurs specifically at serine/threonine residues that are followed by a proline residue, i.e., $PX_{S/T}$ where X can be basic or neutral, but −2 position proline is not required (Clark-Lewis et al. 1991; Gonzalez et al. 1991). This mechanism provides specificity in substrate recognition, and the P + 1 loop present in the substrate-binding pocket regulates the substrate binding. Binding to the proline of the substrate is only possible when kinase is in active form (Canagarajah et al. 1997). A secondary structure called activation loop is present which forms the mouth of the active site (Zhang et al. 1995). The dual phosphorylation motif (TXY**:** threonine–X–tyrosine) is present on the activation loop in kinase sub-domain VIII (Payne et al. 1991; Gartner et al. 1992), and phosphorylation on both tyrosine and threonine residues is required for the full activation of the MAPKs; as without phosphorylation, the binding site will be blocked. Distinct MAPKs have distinct dual phosphorylation motif, and the length of the loop also varies (length of the loop controls the autophosphorylation of the protein) (Jiang et al. 1997). Mammalian MAP kinases can be divided into three families, and each family has multiple members and multiple activators (MEK and MEKK) that are present upstream to MAPK. The first family is ERK/MAP kinases, and the members are many times activated when receptor tyrosine kinase is activated by EGF (epidermal growth factor), and the activation sequence for this family is threonine–glutamic acid–tyrosine (TEY). The other family is JNK/SAPK (Jun N-terminal kinase/stress-activated protein kinase), and they are activated by stress or inflammatory cytokines with the activation sequence: threonine–aspartic acid–tyrosine (TDY). The last family is p38/Hog which is activated by cytokines, endotoxins, and osmotic stress with activation sequence: threonine–glycine–tyrosine (TGY). As EGF, which activates both ERK and JNK/SAPK pathways, extracellular stimuli may activate more than one pathway (Cano and Mahadevan 1995). Plant MAPKs shares high homology with the ERK subfamily. Plant MAPKs mainly cluster in one group which is known as PERKα, and very few (three) clusters in a group denoted as PERKβ. Based on sequence similarity, the PERKα family can be divided into five different subfamilies named as PERKα1–5. The activation loop length varies among the PERK groups which are 25, 22, and 21 amino acids long for PERKβ, PERKα5, and PERKα1–4, respectively (Ligterink and Hirt 2001).

Generally, all plant MAPKs have a TEY motif at the site of dual phosphorylation, except in *Arabidopsis* and alfalfa MAPK because they have TDY as the motif. Additional to this, the MAPKs having the TDY motif have an additional C-terminal extension (Mizoguchi et al. 1997; Schoenbeck et al. 1997) compared to the MAPKs that have a TEY motif. Generally, C-terminal (not extended) has a CD (common docking) domain which acts as the docking site for MPKKs, phosphatase, and substrate proteins (Ichimura et al. 2002). The amino acid sequence [LH][LHY]Dxx[DE]xx[DE]EPxC (where x is any amino acid residue) clearly denotes the importance of acidic residues D (aspartate) and E (glutamate) in interacting with the basic (K-lysine and R-arginine) counterparts that are present as a cluster on the MPKKs. Based on the sequence of the activation loop, the MAPKs can be divided into four groups (A, B, C, and D). Groups A, B, and C have a TEY sequence motif, whereas group D has a TDY sequence motif. Group A members are involved in environmental and hormonal responses, e.g., MPK6 (*Arabidopsis*), and its orthologs in other plants are activated by various environmental cues. Group B members are involved in environmental stress responses and cell division, e.g., MPK4 (*Arabidopsis*) is induced by both biotic and abiotic stress induction, and subgroup B2 members MPK13 (*Arabidopsis*), Ntf6 (*Nicotiana*), and MMK3 (*Alfalfa*) have cell cycle-dependent activation. Group C member MPK7 (*Arabidopsis*) shows expression that is regulated by circadian rhythm. Some group D members (BMWK1 from rice and TDY1 from alfalfa) are induced by pathogen attack and wounds. Group D members lack the CD domain, but some like MPK8, MPK9, and MPK15 (*Arabidopsis*) have a small (60–80 amino acids) N-terminal extension (Ichimura et al. 2002). Table 13.2 summarizes about the reported MAPKs and their associated activators in plant species using Google scholar (https://scholar.google.co.in/).

Table 13.2 Tabulation of the reported MAPKs and their associated activators in few plant species

Plant species	Family	Chromosome no.	Genome size (Mb)	MAPKs	MAPKKs	MAPKKKs	References
Actinidia Chinensis	Actinidiaceae	29	616.1	18	9		Wang et al. (2018a); Jiang and Chu (2018)
Amborella trichopoda	Amborellaceae	13	706	8	7	79	Neupane et al. (2019)
Amborella trichopoda	Amborellaceae	13	748		6		Jiang and Chu (2018)
Aquilegia coerulea	Ranunculaceae	7	302	11	5	141	Neupane et al. (2019)
Arabidopsis thaliana	Brassicaceae	5	135	20	10	80	
Arachis duranensis	Fabaceae	10	~2700	16	7		Purayannur et al. (2017)
Arachis ipaensis	Fabaceae	10	~1390	16	7		Purayannur et al. (2017)
Brachypodium distachyon	Poaceae	5	~355	16	12	75	Chen et al. (2012)
Brassica napus	Brassicaceae	19	1200	12	7	66	Liang et al. (2013); Sun et al. (2014)
Brassica rapa	Brassicaceae	10	485	31	14	100	Wu et al. (2017)
Cajanus cajan	Fabaceae	11	852	17	7		Purayannur et al. (2017)
Capsella rubella	Brassicaceae	8	137.1	18	11		Jiang and Chu (2018); Mohanta et al. (2015)
Capsicum annuum	Solanaceae	12	3480		5		Jiang and Chu (2018)
Carica papaya	Caricaceae	9	372	9	9		Jiang and Chu (2018); Mohanta et al. (2015)
Cicer arietinum	Fabaceae	8	750	16	7		Purayannur et al. (2017)
Citrullus lanatus	Cucurbitaceae	11	425		6		Jiang and Chu (2018)
Citrus clementina	Rutaceae	9	370	12			Mohanta et al. (2015)
Citrus sinensis	Rutaceae	9	280	12	7		Jiang and Chu (2018); Mohanta et al. (2015)
Coffea canephora	Rubiaceae	11	710		8		Jiang and Chu (2018)
Cucumis melo	Cucurbitaceae	12	375		6		Jiang and Chu (2018)
Cucumis sativus	Cucurbitaceae	14	350	14	6	59	Wang et al. (2015)
Daucus carota	Apiaceae	9	421	17	5	136	Neupane et al. (2019)
Dianthus caryophyllus	Caryophyllaceae	15	622		8		Jiang and Chu (2018)
Eucalyptus grandis	Myrtaceae	12	640	13	6		Jiang and Chu (2018); Mohanta et al. (2015)

Plant species	Family	Chromosome no.	Genome size (Mb)	MAPKs	MAPKKs	MAPKKKs	References
Fragaria vesca	Rosaceae	7	240	12	7	73	Zhou et al. (2017a); Zhou et al. (2017b)
Glycine max	Fabaceae	20	975	38	11	150	Neupane et al. (2013b)
Gossypium raimondii	Malvaceae	13	880	28	11	78	Zhang et al. (2016)
Helianthus annuus	Asteraceae	17	3600	28	10	166	Neupane et al. (2019)
Hordeum vulgare	Poaceae	7	~5300	20	6	156	Cui et al. (2019)
Jatropha curcas	Euphorbiaceae	22	320.5	12	5	65	Wang et al. (2018b)
Linum usitatissimum	Linaceae	15	318.3	24			Mohanta et al. (2015)
Lotus japonicus	Fabaceae	6	470	19	7		Neupane et al. (2013a); Purayannur et al. (2017)
Lupinus angustifolius	Fabaceae	20	924	29	10		Purayannur et al. (2017)
Malus domestica	Rosaceae	17	~742.3	26	9	123	Sun et al. (2017); Zhang et al. (2013)
Manihot esculenta	Euphorbiaceae	18	770	21	11	62	Jiang and Chu (2018); Ye et al. (2017); Yan et al. (2016)
Medicago truncatula	Fabaceae	8	~465	25	7		Neupane et al. (2013a); Purayannur et al. (2017)
Mimulus guttatus	Phrymaceae	14	322	6			Mohanta et al. (2015)
Musa acuminata	Musaceae	11	600	25	10	77	Asif et al. (2014); Wang et al. (2017)
Oryza sativa	Poaceae	12	430	17	8	75	Rao et al. (2010)
Panicum virgatum	Poaceae	9	1358	27			Mohanta et al. (2015)
Phaseolus vulgaris	Fabaceae	11	473	15	9		Neupane et al. (2013a); Purayannur et al. (2017)
Pisum sativum	Fabaceae	7	~4450	16	6		Purayannur et al. (2017)
Populus trichocarpa	Salicaceae	18	422	21	11		Jiang and Chu (2018); Mohanta et al. (2015)
Prunus persica	Rosaceae	8	265	12	10		Jiang and Chu (2018); Mohanta et al. (2015)
Ricinus communis	Euphorbiaceae	10	400	12	6		Jiang and Chu (2018); Mohanta et al. (2015)

(continued)

Table 13.2 (continued)

Plant species	Family	Chromosome no.	Genome size (Mb)	MAPKs	MAPKKs	MAPKKKs	References
Setaria italica	Poaceae	9	700	16	12		Jiang and Chu (2018); Mohanta et al. (2015)
Solanum lycopersicum	Solanaceae	12	900	16	6	89	Wu et al. (2014)
Solanum melongena	Solanaceae	12	1093		4		Jiang and Chu (2018)
Solanum tuberosum	Solanaceae	12	800	12	5		Jiang and Chu (2018); Mohanta et al. (2015)
Sorghum bicolor	Poaceae	10	730	16	7		Jiang and Chu (2018); Mohanta et al. (2015)
Thellungiella halophila	Brassicaceae	7	238.5	16			Mohanta et al. (2015)
Thellungiella parvula	Brassicaceae	7	140		9		Jiang and Chu (2018)
Theobroma cacao	Malvaceae	10	430	12	8		Jiang and Chu (2018); Mohanta et al. (2015)
Trifolium pretense	Fabaceae	7	420	19	7		Purayannur et al. (2017)
Trifolium subterraneum	Fabaceae	8	540	18	8		Purayannur et al. (2017)
Triticum aestivum	Poaceae	7	~17,000	54	18	155	Wang et al. (2016); Zhan et al. (2017)
Vicia faba	Fabaceae	6	~13,000	15	6		Purayannur et al. (2017)
Vigna angularis	Fabaceae	11	538	15	7		Purayannur et al. (2017)
Vigna radiata	Fabaceae	11	579	15	7		Purayannur et al. (2017)
Vigna unguiculata	Fabaceae	11	519.4	15	7		Purayannur et al. (2017)
Vitis vinifera	Vitaceae	19	490	14	5	62	Cakir and Kılıçkaya (2015)
Zea mays	Poaceae	10	2300	19	9	74	Kong et al. (2013a); Kong et al. (2013b)
Ziziphus jujuba	Rhamnaceae	12	437.6	10	5		Liu et al. (2017)

5.2 MKKs

MKKs are dual-specificity protein kinase which activates MAPKs by phosphorylating both tyrosine and threonine residues on the TXY motif of the activation loop. As protein kinases are generally specific for either serine/threonine or tyrosine phosphorylation, it was hypothesized that MAPK might require two protein kinases for its activation. Surprisingly, a single dual-specificity kinase (MEK) activates the MAPK by phosphorylating both tyrosine and threonine residues on the TXY motif (Matsuda et al. 1992; Pitzschke 2015). In the signaling cascade, MKKs can in turn get activated by phosphorylation on the two conserved serine or threonine residues which are present in between the domain VII and domain VIII (Alessi et al. 1995; Zheng and Guan 1994), and these conserved amino acids form a motif $^{\mathbf{S/T}}\mathrm{XXX}_{\mathbf{S/T}}$ in most MKKs. In most yeast and animal MKKs, the motif is $\mathrm{SXXX}_{\mathbf{S/T}}$, while in plants, $^{\mathbf{S/T}}\mathrm{XXXXX}_{\mathbf{S/T}}$ is the motif (Ligterink and Hirt 2001). The activity of MKKs can be regulated at the posttranslational level by phosphorylation of the residues other than the conserved serine or threonine residues that negatively regulates MKKs (Brunet et al. 1994; Rossomando et al. 1994). Along with the posttranslational regulation, MKKs can be regulated at the posttranscriptional level by differential splicing (English et al. 1995). The substrate specificity for the MKKs is restricted, and the specificity is defined by multiple domains of MAPKs, and MKKs in turn bind to the tertiary structure of the MAPKs, thus restricting the substrate specificity (Seger et al. 1992). That is why MKKs are considered to be the convergence points of the pathway as it can receive many signals that it can feed into the MAPKs pathway. A conserved N-terminal putative MAPK docking site [K/R][K/R][K/R]x(1–5)[L/I]x[L/I] (basic –K and R at the extreme N-terminal to the hydrophobic L and I at inwards N-terminal) is the docking site for the MAPKs (Bardwell and Thorner 1996), and MKKs are known to regulate the kinetics of the cascade. Specificity is enhanced when both MAPK and MEK interact with the scaffold protein (e.g., MP1; Schaeffer et al. 1998) that also linearly guides the interaction between the components of the cascade (Fig. 13.3). The complex formed by pathway components with the scaffold protein is known as signalosome, and such interactions restrict any cross talk that can happen with the multitude of different pathways and within the pathway (Chang and Karin 2001; Whitmarsh and Davis 1998). Normally, MKKKs (to perceive myriad of stimuli) are present more than MKKs, and thus, it can be hypothesized that they also function in signal integration (Ferrell 1996), and an MKK can activate multiple MAPKs (they are also in excess) in the cascade, and this is the step of signal amplification (Ichimura et al. 2002). The first-ever MKK reported in plants was from *Nicotiana,* and thus, it was named NPK2 (nucleus- and phragmoplast-localized protein kinase, renamed from *Nicotiana* protein kinase 2). Plant MKKs are divided into three subfamilies, namely, PMKK1, PMKK2, and PMKK3, from which the members of PMKK3 have additional long non-catalytic C-terminal which is not present in other PMKKs subfamilies (Ligterink and Hirt 2001). Based on new advances, the plant MKKs can be divided into four groups (A, B, C, and D). Group A members are involved in multiple abiotic stress responses, e.g., MKK1 and MKK2 (upstream of MPK4 in *Arabidopsis*), whereas PRKK (pathogen-responsive MPKK in alfalfa) involved in the transduction of elicitor signals, and MKK6 (*Arabidopsis*) along with NtMEK1 (*Nicotiana*) is involved in cell division. Group B members MKK3 (*Arabidopsis*) and NPK2 (*Nicotiana*) have an extended C-terminal, and the extended C-terminal consists of a nuclear transport factor (NTF2) for nuclear localization. Group C members are stress-responsive, and downstream, they signal group A members of MAPKs, e.g., SIMKK has both salt and elicitor-induction specificity and NtMEK2 (*Nicotiana*) can induce SIMK (salt) and WIPK (wound).

5.3 MKKKs

MKKKs are serine/threonine kinase that regulates the MKKs activation. Structurally, MKKKs are different from MAPKs and MKKs, and different MKKKs have different regulatory motifs such as Pleckstrin homology (PH) domains, proline-rich sequences involved in SH3 binding, zinc finger motifs, leucine zippers, and binding sites for G-proteins (Garrington and Johnson 1999; Pitzschke 2015). MKKKs have multiple tyrosine and serine/threonine phosphorylation sites, and thus, it can be activated by a different mechanism like it can be phosphorylated by MKKKs and PKCs, by interaction with G-protein, or by the cellular two-component system (Whitmarsh and Davis 1998; Fanger et al. 1997). This much diversity in the structure and the mode of activation provide flexibility to respond to different stimuli. MKKKs are the branching point and mediate cross talk between signaling pathways. Many MKKKs have been identified by various scientists; however, Raf is well studied and documented (serine/threonine-protein kinase). Mostly, plant MKKKs show homology with yeast MEKK/STE11 and mammalian Raf (related to retroviral oncogenes), and hence, they are known as PMEKKs (e.g., *At*ANP1 and *At*MEKK1 with a conserved sequence G (T/S) Px (W/Y/F) MAPEV) and PRaf (e.g., *AtCTR1* and *AtEDR1* with a conserved sequence GTxx (W/Y) MAPE) (Rao et al. 2010). The PMEKKs can be subdivided into three groups, i.e., PMEKK1, PMEKK2, and PMEKK3, whereas PRaf can be subdivided into two groups, i.e., PRaf1 and PRaf2 (Ligterink and Hirt 2001). Some sequences in the plant also share homology with the mixed lineage kinase (MLK), thus widening the range of diversity of MKKKs in plants (Ligterink and Hirt 2001). Ichimura et al. (2002) has also provided a way of dividing MKKKs in a plant in which group A members are MEKKK1 type and group B and C members are RAF kinase type. Group A further can be divided into five subgroups and subgroup A1 (*At*MEKKK1, *At*MEKKK2, *At*MEKKK3, and *At*MEKKK4) members active in drought, high salinity, and touch. *At*MEKKK1 is present upstream of MPK4, MKK1, and MKK2. *At*MEKKK4 has an extended N-terminal which is a unique feature as it has several domains such as a glycine-rich region, WRKY domain, paired-amphipathic-helix repeat, TIR domain, leucine-rich repeat (LRR), NB-ARC domain, and a protein kinase domain. WRKY proteins are Zn-finger transcription factors that are specific to plants as they regulate plant defense response and capacity to deal with drought condition, and WRKY domain provide the direct DNA binding capacity to the protein. Along with that, the presence of the TIR-NB-LRR domain further confirms the role of *At*MEKKK1 in plant defense. Subgroup A3 members like ANP1, ANP2, and ANP3 have a C-terminal regulatory region, and NPK1 is a positive regulator of cytokinesis (Nishihama et al. 2001) and a negative regulator of the stress response (Krysan et al. 2002). But all of these MPKKKs work in oxidative stress response as a negative regulator of the auxin-response pathway (Kovtun et al. 2000). Subgroup A4 members *At*MAP3Kε1 and *At*MAP3Kε2 are involved in cell division (Jouannic et al. 2001), and the function of subgroup A2 members is not determined. Group B members are RAF kinase such as CTR1 which is involved in ethylene signaling, and EDR1 is involved in disease resistance signaling. They have an extended N-terminal (regulatory) and a C-terminal kinase domain, whereas specifically, subgroup B2 N-terminal has PAS (Per, Arnt, and Sim) domains and PAC (PAS-associated C-terminal) domains. Group C members are also RAF kinase, e.g., ATN1 and *At*MRK1. Broadly, functions of the group members are unknown. There is some information about the domains that are present like the N-terminal of subgroup C1 members having an ankyrin like a domain that is known for protein-protein interaction. Subgroup C2 has an aspartokinase, chorismate mutase, and Try A (ACT) domain which is known for sensing amino acid concentration and then regulating the activity of many metabolic enzymes (Aravind and Koonin 1999). There is another group present in cucumber MEKKs family known as ZIK like kinases, and they have an N-terminal kinase domain having a signature sequence GTPEFMAPE (L/V) Y. ZIK like kinases are also known as WNK (with no lysine (K)) which are involved in controlling circadian/internal rhythms (Murakami-Kojima et al. 2002) and in responding to abiotic stress (Kumar et al. 2011) without showing any evident phosphorylation of the MKKs in plants (Kong et al. 2013b) such as *At*3g04910 in (*Arabidopsis*). There are chances that with further studies there will be additional groups that will add up to already mentioned groups of MKKKs in plants. Members of MEKKs have structural diversity and don't share any general structure, whereas Raf protein kinase has similar structural organization both in plants and animals, i.e., catalytic domain present at C-terminal and a long non-catalytic extension at the N-terminal (Ligterink and Hirt 2001). In addition, the non-catalytic domains both in plants and in animals are rich in serine and cysteine (Ligterink and Hirt 2001). The sequence and structural diversity of MKKKs in plants suggest that even in plants, MKKKs have a wide variety of substrates and diversity in mode of regulation (Ligterink and Hirt 2001). NPK1 forms the largest group of MKKKs plant and regulation of homologs of NPK1 in *Arabidopsis* (ANP1) occurs by differential splicing resulting in ANP1L (large) and ANP1S (small) forms and ANP1S shows higher activity than the ANP1L spliced form which highlights the role of splicing in the regulation of MKKKs in plants (Nishihama et al. 1997). The cascade does not always work in a linear direction as MAPKs and MKKs can phosphorylate the MKKKs or the upstream regulating components, and this serves as the negative feedback loop (Ueki et al. 1994). At the same time, MAPKs can interact with

MKKKs (thus activating) in the positive feedback mechanism (Zimmermann et al. 1997; Pitzschke 2015).

5.4 Upstream of MAPK Cascade

In upstream of MKKK, different effectors are known to function and activate the MAPK pathway. Several kinases act upstream of MKKKs in yeast and mammalian systems such as receptor tyrosine kinases (RTK) and G-protein-coupled receptors. When RTK is active, it can stimulate the exchange of guanosine triphosphate (GTP) for the guanosine diphosphate (GDP) on G-protein Ras. Activated Ras can then interact with potential partners including Raf (Morris 2001; Pitzschke 2015). Yeast on contrast doesn't possess RTKs and instead has two components, i.e., histidine-protein kinase and G-coupled protein receptors. Yeast and mammalian MKKKs can be divided into two subfamilies. The first one is the STE20/PAK subfamily, and it is characterized by the catalytic domain at C-terminal and putative G-protein binding motif at the N-terminal. The other subfamily is GCK/SPS1, and this subfamily has a characteristic catalytic domain at the N-terminal and a long kinase-unrelated region which is mostly activated by stress at the C-terminal (Fanger et al. 1997). In plants, RTKs are not present, but instead, receptor-like kinases (RLKs) are present, and RLKs are transmembrane serine/threonine protein kinases (Stone and Walker 1995). In the plant system, there are two putative MKKKs, i.e., BnMAP4Kα1 and − 2 from rapeseed (Leprince et al. 1999), and one MKKK, i.e., SIK1 (for stress-induced kinase1) from *Arabidopsis* which can be grouped under GCK/SPS1 subfamily. Many genomic sequences that are candidates for the plant MKKKs can be grouped under STE20/PAK. In yeast and mammals, the presence of PKC and small G-proteins to activate MKKKs somewhere indicates that similar regulation of activation exists in plants upstream of the MAPK cascade (Ligterink and Hirt 2001).

6 Role of MAPK Pathway in Heat and Other Related Stresses in Plants

6.1 High-Temperature Stress

The first report of induction of MAPKs under heat stress is from the group of Sangwan who highlighted the heat-activated mitogen kinase (HAMK) getting induced in alfalfa (Sangwan et al. 2002). Following this, there were many reports in the literature that have shown that high temperatures induce the expression of many MAPK components in varied plants. *Os*MSRMK2 is a rice multi-stress-responsive gene of the MAP kinase family (Agrawal et al. 2002). In one of the preliminary study, it was found out that *Os*MSRMK2 can sense the change in temperature as the transcripts shows enhancement (37 °C) and no induction (25 °C and 12 °C) with in a period of 15 min. Whereas it showed a transient nature because at 37 °C, the transcript level decreases at the time point of 30 min and beyond and at 25 ºC the transcripts started increasing at 30 min and then drastically decreased after that, interestingly, at low temperature (12 ºC) the transcripts started accumulating at 60 min and reached to a height at 90 min and then shown a decrease at 120 min. But a rapid accumulation at high temperature suggests that it helps the plant in sensing the adverse temperature condition and thus prepares the plant to thrive in it (Agrawal et al. 2002). Another report by Link et al. (2002) showed that the heat activation of the MAPK pathway in tomato is calcium as well as heat stress factor 1 (Hsf1) dependent. The phosphorylation of Hsf1 at the tyrosine by the involved MAPK activates Hsf1, and the activated Hsf1 further activates the Hsps which induces thermo-tolerance in the plant (Link et al. 2002). On the other hand, HAMK, a 46 KDa protein, becomes active in tobacco (*Nicotiana tabacum*) and *Sl*MAPK1 in tomato (Ding et al. 2018) at the advent of heat stress, and in *Arabidopsis,* the expression of *At*MPK6 increases during the heat stress (Li et al. 2014a; Li et al. 2014b). *At*MPK6 mediates the activation of γVPE which is a vacuolar-localized cysteine protease with a Caspase1 like activity, and it basically activates the downstream hydrolytic enzymes in the vacuole which are responsible for the induction of hypersensitive reaction. This leads to cell death and tissue senescence (Albertini et al. 2014). Thus, it was postulated by that γVPE plays a role in heat-induced programmed cell death (PCD). γVPE is expressed in guard cells of *Arabidopsis,* and Albertini et al. 2014 deciphered its involvement in water stress which is one of the secondary stress of high-temperature stress. In another report by Evrard et al. 2013, it was reported that *At*MPK6 negatively regulates heat stress by phosphorylating HSF2, which is a known heat shock factor and plays a role in heat stress response. In similar reports, it was reported that *the mpk6 Arabidopsis* mutant shows higher tolerance than the wild type. A study undertaken by Ding et al. 2008 on tomato has helped in deciphering the mechanism of action of the MAPK signaling pathway in alleviating the high-temperature stress. In the case of tomato, there is 16 putative family of *Sl*MPK which have been grouped into four major groups (A–D) (Kong et al. 2013a; Kong et al. 2013b). Silencing of MPK1/2 (*Sl*MPK) results in compromised tolerance toward heat, cold, and oxidative stress (Nie et al. 2013; Zhou et al. 2014; Lv et al. 2017). But another report from Ding et al. (2018) showed that silencing *Sl*MPK 2 can increase the tolerance of plants toward high-temperature stress. *Sl*MPK1 (ortholog of *At*MPK6, *Nt*SIPK, and *Os*MPK6) is a negative regulator of heat stress responses (Ding et al. 2018). The tomato plants with silenced *Sl*MPK1 gene show the expression of many proteins that are involved in various functions such as protein folding, lipid metabolism, translation, amino acid biosynthesis, and oxide reduction. The silenced lines show no chlorophyll degeneration as compared to the wild type. Thus, Ding et al. (2018) postulated that it is due to the activation of CPN-60 (role in chloroplast biogenesis and plastid division) (Ahsan et al. 2010), and CPN-60B is known to play a vital role in acclimatizing photosynthesis to high temperature (by protecting the thermal denaturation of RuBisCo activase). The lines that are having suppressed expression of *Sl*MPK1 have accumulated redox buffers.

The main mechanism behind the attained tolerance was the reduction of the high temperature-induced oxidative damage to maintain cellular redox homeostasis (Ding et al. 2018). *Sl*MKK9 (homolog of *At*MKK9) interacts with *Sl*MPK1, and it is an upstream component of the pathway, and the downstream partner of *Sl*MPK1 is SISPRH1 (homolog of At1g04330), but it is a protein of unknown function and has a putative phosphorylation site at Ser-44 (Ding et al. 2018). Later, it was deciphered that this phosphorylation site is very important for the enzyme activity as a mutation at this residue can block the *Sl*MPK1-mediated inhibition under high temperature (Ding et al. 2018). High temperature induces inactivation of a 50KDa kinase, and the ability of this kinase to phosphorylate myelin basic protein (MBP) suggests that it is a member of the MAPK family (Heider et al. 1998). While the induction of the heat shock genes by the transcription factor Hsf1 is a general response in heat stress, this is repressed by the phosphorylation of Hsf1 by the ERK1 resulting in the silencing of heat-inducible genes in unstressed conditions (Chu et al. 1996). Most of the studies conducted by researchers confirmed MAPKs except *Cs*MPK3 and *Cs*MPK7 are overexpressed under heat and drought stress (Wang et al. 2015). It has also been studied that SlMPK3 plays a major role during various biotic and abiotic stresses. Previously, it was known that knockout of *Sl*MPK3 results in reduced drought tolerance and disease resistance to *Botrytis cinerea.* But *Sl*MPK3 also gets influenced by heat stress as its relative expression gets downregulated, and its knockout provides tolerance to heat stress (Yu et al. 2019). Both ion leakage and MDA content were significantly lower in the knockout mutants. This suggested that SlMPK3 acts as a negative regulator of heat stress whose knockout maintains the relative integrity of the cell membrane and reduces cell membrane damage. Elevated levels of SlHSP70, SlHSP90, *Sl*HSP100, and *Sl*HSFA1a, *Sl*HSFA2, and *Sl*HSFA3 were observed in *Sl*MPK3 mutants, indicating the increase in HSPs and HSFs genes' relative expression might be associated with *Sl*MAPK3-mediated heat stress response in tomato plants (Yu et al. 2019).

6.2 Oxidative Stress

Oxidative stress is the most common secondary stress in biotic and abiotic stress conditions as in most of the stressed conditions, the disruption of metabolic imbalance of cell takes place, and that hampers the cellular redox homeostasis. But this is also true that ROS plays a vital role in signaling in the lower concentrations. In support of that, investigation done by Kovtun et al. (2000) helped in understanding the effect of H_2O_2 on MAPK activation under stress condition that will aid the plant to somehow deal with the adverse condition (in this case under pathogen attack). In *Arabidopsis* protoplast study, they found out two H_2O_2-activated (independent of other activators like ethylene, SA, and JA) MBP kinases (44 and 42 KDa mass). They also elucidated that H_2O_2 activated promoters of oxidative stress-responsive gene GST6 and an HSP named HSP 18.2. The fact that H_2O_2 is involved in cell cycle under nonstress conditions and also the involvement of MAPK in cell cycle regulation instigated the idea that the tobacco cell cycle regulating MAPK-NPK1 (A class of MEK kinases) might be mediating oxidative stress responses in plant cells (Nakashima et al. 2014). The homologs of NPK1 in *Arabidopsis* MEK kinases are ANP1, ANP2, and ANP3 which can activate two MBP kinases (same molecular masses) as activated by H_2O_2. Later, it was established that ATMPK3 and ATMPK6 are the substrates of ANP1, ANP2, and ANP3. Activation of MAPK suppresses the oxidative stress. But sometimes, there are activators of ROS that don't involve in the activation of MAPK, and this suggests that MAP kinase activation is either independent or upstream of oxidative burst. In a study conducted by Xing et al. (2007), it was found out that MAP2K inhibits the ABA-dependent activation of the CAT1 enzyme. Nakagami et al. (2006) showed that MEKK1-MPK4 cascade has a role to play in ROS metabolism. Not only the MAPK pathway mediates the oxidative stress responses but also it regulates the concentration of ROS in the system by hampering the expression of the CAT enzyme (Kong et al. 2013b). An alfalfa MAPKKK, namely, OMTK1 (oxidative stress-activated MAP triple-kinase 1), is a key response regulator, and it further regulates the downstream components that are MAPK and MMK3 (Nakagami et al. 2004). The role of MAPKs in oxidative stress was also similarly deduced by the many other researchers.

6.3 Osmotic Stress

One of the secondary stresses that come in the picture due to the high temperature with which the plant has to deal is the osmotic stress. Plants have protein kinases that deal with the changes in the osmolarity. In green algae, *Dunaliella tertiolecta* hypoosmotic stress induces a 40 KDa kinase, and this kinase can phosphorylate MBP and histone, while the hyperosmotic stress induces a 40 KDa (can phosphorylate MBP, histone, and casein) kinase and a 45 KDa (can phosphorylate MBP only) kinase (Yuasa and Muto 1996). The activity of these kinases is independent of the presence of calcium, and thus, they are not CDPKs and thus possibly can be MAPKS. But MAPKs don't use casein as a substrate, while histone can be used as a substrate by MAPK in plants (Wilson et al. 1995; Zhang and Klessig 1997). This suggests that the 40 KDa protein kinase induced in hyperosmotic stress cannot be a member of the MAPK family, while others can be MAPKs. Another response that is evident under osmotic stress in *D. tertiolecta* cells is that the cell volume changes in response to the extracellular osmolarity, and to gain the original volume, the cell induces MAPK cascade to nullify the effect of the osmolarity changes. In several experiments where the application of protein kinase inhibitor can block the recovery process, the involvement of protein kinases in the cell osmolarity balance kinetics was established. Thus, all these instances indicate the involvement of stress-induced protein kinases in osmotic tolerance in *D. tertiolecta* (Yuasa and Muto 1996), and these protein kinases can be MAPKs. Extending the studies to the higher plants indicates that MAPKs are involved in osmotic stress tolerance in plants too. In an in vitro study where tobacco-suspension-cultured cells were given hyperosmotic stress, it resulted in the activation of MAPK like kinases. The hypoosmotic stress resulted in the activation of MBP kinases of 50, 70, and 80 KDa molecular weight (Takahashi et al. 1997). 50 KDa protein kinase exhibits all the characteristic properties of an MAPK as the activation and inactivation through phosphorylation and dephosphorylation events (Takahashi et al. 1997). Even yeast has osmosensors to sense hyperosmotic stress, and one of which is a part of a two-component regulatory system. Yeast osmosensor SLN1 gets autophosphorylated at histidine which is present at the N-terminal sensor domain. The phosphate is then transferred to YPD and then to the aspartic residue of the C-terminal sensory domain of the SSK1 which is a response regulator. Then SSK1 feeds the signal into the HOG1 MAPK pathway (Posas et al. 1996). A similar pathway or mechanism of response exists in plants as *Arabidopsis* SLN1 homolog *At*HK1 act as osmosensor in complementation studies with SLN1-deficient yeast cells (Shinozaki and Yamaguchi-Shinozaki 1997). Similarly, a pea MAPK, i.e., PsD5, can complement HOG1-deficient yeast mutant (Pöpping et al. 1996), and an alfalfa MAPK, i.e., MMK2, can complement yeast MPK1 kinase (Jonak et al. 1995). Some stress-activated MAPKs like AtMPK3 and stress-activated MAPK (previously called as MMK4) also get upregulated in drought, cold, heat, touch, and salt stress, and all these stresses result in a condition of dehydration. So this can be concluded that AtMEKK1/AtMPK3 and SAMK can deal with general dehydration conditions and thus can provide tolerance to the plant against the osmotic changes (Ligterink and Hirt 2001).

6.4 Drought Stress

The high temperature in absence of irrigation/rainfall generally results in a condition called drought. In situations of dehydration, *At*MEKK1 and *At*MPK3 are transcriptionally activated (Mizoguchi et al. 1996). A ribosomal S6 kinase is activated by MAPK after phosphorylation in the mammalian system (Sturgill et al. 1988; Gregory et al. 1989), and a homolog of the same exists in *Arabidopsis,* i.e., *At*PK19 which shows accumulation in the drought stress (Mizoguchi et al. 1996). This somewhere indicates that *At*PK19 is activated by *At*MPK3 following a similar pathway as in the mammalian system. Transcriptional and translational activation of SAMK is also reported, but no significant changes in the protein level were found (Jonak et al. 1996). The drought-stressed leaves of alfalfa show the activation of $p44^{MKK4}$ kinase within 5 min (Jonak et al. 1996). Although the activation was transient and ABA independent (Jonak et al. 1996), after full activation, it shows a decrease in activity (after 20–30 min). But the activation of $p44^{MKK4}$ under high temperature (37 °C) was not seen in lab experiments. The drought-like condition induces the activation of *Os*MSRMK2 and *Os*MAPK5 in rice plants. DSM1, a putative MPKKK of rice, when overexpressed can increase the tolerance of the plant toward dehydration (Ning et al. 2010).

7 Concluding Remarks and Future Prospects

Due to the fact that the MAPK cascade is the major multitier player network for stress signaling transductions involved in various environmental biotic and abiotic stresses, MAPKs and other components involved in the perception of various signals are chosen as targets by multiple biologists, breeders, and bioinformaticians worldwide. Various omics approaches such as transcriptomics, proteomics, miRNAomics, metabolomics, and bioinformatics along with high-throughput DNA sequencing have allowed precise analysis of MAPK pathway cross-networking under various abiotic stresses. Due to the increase in ambient temperature around the plants, it has posed a serious threat on the yield and productivity. As a result, a huge plethora of studies has been conducted to solve the problem of making the plants more tolerant to high-temperature stress by different means of genetic modifications in order to sustain the crop yield for every second increasing population. By implying this knowledge to wheat, ryegrass, Chinese clematis, black raspberry, and other 580+ sequenced plants, the orthologous genes can be discovered and can be used to improve every important crop plant against heat and other abiotic stresses. Consequently, as already discussed above, overexpressing the positive regulators of MAPK pathway components and knocking out or editing the negatively regulating components are the ways toward climate-resilient agriculture. In a long run to the future, the rewiring of circuits will ultimately enable the smooth cultivation of crop plants such as rice, wheat, tomato, potato, lemongrass, jute, cotton, and many more even in harsh conditions.

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