1 Physiological Responses and Resilience of Plants to Climate Change

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Abstract

Climate change has presently appeared as an unequivocal but unstoppable event, and it poses severe threat for survival of biosphere on this earth. Climate change actually results in large changes in environmental conditions like rainfall pattern, average temperature, heat waves, global change of CO_2 or ozone levels, fluctuations in sea levels in addition to surge in new weed flora and insect pests or pathogens. It is believed that climate change is the main cause of various abiotic and biotic stresses that have been badly affecting the agricultural production. Further, climate change predictions indicate that a gradual increase in average atmospheric temperature or frequent incidence of environmental extremes would have a negative impact on physiological and biochemical functioning. Thus, climate has raised global apprehension in respect of lowering crop productivity and food security. As such understanding the tolerance mechanisms of plants has come up with great attention and concern among the researchers working on the development of crop resilience towards climate-smart agriculture and thereby food security under climate change scenario. Indeed, plants can alleviate stress injuries or damages through the aid of various strategies like avoidance or by adopting several inherent mechanisms towards resilience. With this background, this chapter aims to summarize the climate change-induced limiting factors for plant growth and plant responses to such changes. Also, various adaptations or tolerance mechanisms of plants to environmental extremes have been discussed. This contextual information is critical for agricultural sustainability and food security since an improved knowledge would aid in improving plants' resilience

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to climate change through the application of modern breeding methodologies and biotechnological or genetic engineering tools.

Keywords
Climate change · Physiological responses · Environmental extremes · Physiological tolerance · Heat-shock proteins · Signal sensing

1.1 Introduction

Climate change predominantly results from burning of fossil fuels or increasing levels of dangerous greenhouse gasses into the earth's atmosphere during the era of post-industrialization. So, it is unequivocally believed that industrial revolution is the main cause of climate change. In fact, global atmospheric CO_2 levels have increased by ~130 ppm, and average temperature on earth's surface has risen by ~0.85 °C in the past 200 years (IPCC 2013a, b). The atmospheric CO_2 concentration and other greenhouse gasses have been escalated with the advent of industrial revolution in addition to continuous deforestation and excessive utilization of fossil fuels, and these have led to climate change which is ultimately being manifested through warmer average global temperature and other environmental extremities like frequent spells of drought, waterlogging, cold or heat waves, etc. (Vaughan et al. 2018; FAO 2018). Besides climate change has also been causing the surge in new weed floras and widening the range of insect pests, pathogens, etc. Therefore, climate change poses severe risks to agricultural production and consequently to global food security since the whole global ecosystem including agriculture is strongly correlated with climate change in various aspects. It has been reported that agricultural food production is severely affected by devastating environmental alterations particularly increasing temperature and changes in precipitation pattern resulting from climate change in the last few decades (Arunanondchai et al. 2018). Though some regions and crops may be benefitted under climate change scenario, the net impact on world's agriculture is more likely to be negative. The prediction of the latest IPCC report specifies an improving conditions for food production in the mid to high latitudes, including in the northern USA, Canada, northern Europe and Russia, but the declining conditions would be experienced by many parts of the subtropics such as the Mediterranean region and parts of Australia and regions with low latitudes (Olsen and Bindi 2002; Asseng et al. 2015).

As a consequence of climate change, plants have become increasingly exposed to those environmental conditions that are outside of their physiological bindings and beyond the range to which they are adapted (Ward and Kelly 2004; Shaw and Etterson 2012). Therefore, the crop productivity is likely to be reduced under climate change albeit stimulation of growth and improvement in water use efficiency in some crop species with increase in atmospheric CO_2 levels under climate change have been reported (Hatfield et al. 2011; Singh et al. 2013). It is largely because plant growth and metabolisms are very prone to fluctuations in temperature, precipitation and excess increase or decrease of atmospheric CO_2 levels (Fujita et al. 2013; AbdElgawad et al. 2016). Additionally, climate change also indirectly decreases the agricultural yield potential due to increased competition from newer weeds, expansion of insect pests and pathogens and altered crop ecosystems (Chakraborty and Datta 2003).

With this perspective, this chapter aims to outline the abrupt fluctuations in environmental conditions as resulted from climate change and the plant responses to such environmental alterations. It further attempts to comprehend the strategies of adaptation and/or underlying resistance mechanisms of plants under extreme environmental conditions since a better understanding of physiological or biochemical mechanisms that play vital roles in imparting tolerance under climate change is crucial in order to minimize its negative impact on plant yield.

1.2 Climate Change and Limiting Factors for Crop Development

Emission of greenhouse gasses particularly carbon dioxide (CO_2) with the advent of industrialization and due to excessive utilization of fossil fuels in addition to injudicious and massive deforestation is the main factor for the greenhouse effect, which is ultimately resulted in warmer global average temperature (Vaughan et al. 2018). Moreover, daily human activities cause to maximize the greenhouse effect and thereby earth's temperature to increase more and more. The time span of preceding 200 years is considered as the warmest centuries of civilization, and earth's average temperature irregularity is expected to increase from 2 to 4.5 °C during the twenty-first century (Pachauri et al. 2014). Increase in global temperature poses threat for the survival of natural biosphere as well as human being on this earth. The increasing trends of atmospheric CO_2 level and global average temperature anomaly during the past decades have been shown in Fig. 1.1.

Climate change is actually an adverse consequence of industrial revolution, and it is manifested through abrupt change in environmental conditions in various ways,

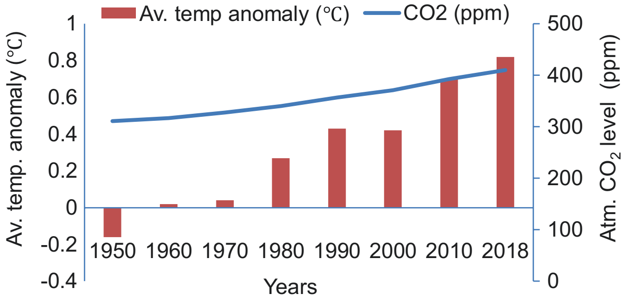

Fig. 1.1 Global average temperature anomaly (°C) and increases in atmospheric CO_2 levels during the period 1950–2018. (Adapted from IPCC 2013a, b and NOAA 2019)

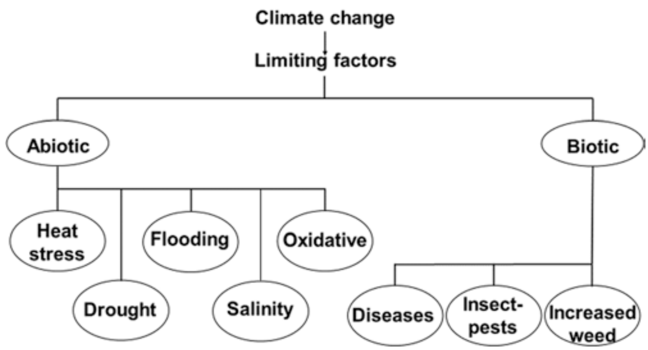

Fig. 1.2 Climate change caused generation of various limiting factors for crop development

such as variation in annual precipitation in both quantity and pattern, average global temperature, occurrence of frequent spells of drought and flood, heat waves, increasing levels of CO_2 and increasing salinity particularly in coastal regions due to fluctuations in sea levels (Pachauri et al. 2014; Vaughan et al. 2018). The chances of occurrence of various environmental extremities have increased by many folds under climate change scenario (Fedoroff et al. 2010; FAO 2018). Further climate change has led to surge in new weed flora and expansion of pathogens or insect-pest range apart from the generation of abiotic factors (Chakraborty and Datta 2003). Various limiting factors as may be resulted under changing climate scenario have been shown Fig. 1.2.

1.3 Physiological Responses of Plants to Climate Change

Physiological responses of plants have been greatly influenced under changing climate since the chances of experiencing various stresses by crop plants have increased due to environmental extremities and climate variability (Thornton et al. 2014). These environmental extremes have large impact on phenological, morpho-physiological and biochemical functioning of plants (Gunderson et al. 2010; Liancourt et al. 2015). Plants are able to make their own food by fixing carbon dioxide (CO_2) through photosynthetic process, and it is generally supposed that increasing level of CO_2 in the atmosphere can enhance crop yields. But, conversely the increased levels of atmospheric CO_2 are already having severe impact on plant distribution and agricultural production (FAO 2018).

Alterations in flowering time of crop plants occur due to vast change of climate (Fitter and Fitter 2002). Though developmental stages and overall plant growth are prone to climate variability, reproductive stage of plant has been affected most severely under changing climate especially with rise in temperature. A small variation in temperature during reproductive phase can cause significant reduction in floral buds and flower abortion or pollen sterility leading to no fruit or seed setting and/or sometimes may also cause no formation of floral buds at all (Saini and

Aspinall 1981; Sheoran and Saini 1996; Winkel et al. 1997). Further climate change may result in mismatches between flowering time and pollinator activity (Forrest 2015). Climatic extremities have also indirect but strong impact on plant traits, fitness and their survivability via shifts in biotic interactions. Therefore, the importance of the eco-evolutionary consequences of altered species interactions should not be overlooked since it might be of similar or even more in magnitude in comparison to direct effects of climate change on physiological perspectives (Kimball et al. 2012; Alexander et al. 2015).

Photosynthesis, the cornerstone of physiological processes of plants, is severely affected by climate change. Though rise in atmospheric CO_2 level may decrease the ratio of photorespiratory losses of carbon to photosynthetic gain more particularly in C_3 plants, the elevation of temperature beyond a limit certainly retards photosynthetic rates and plant growth to fatal levels (Collatz et al. 1998; Tkemaladze and Makhashvili 2016). Photosynthetic capacity of plants is greatly influenced by climate change since both photochemical reactions in thylakoid lamellae and carbon assimilation in stroma of chloroplast are very sensitive to high temperature (Wang et al. 2009). Further, minor elevation in temperature results in the deactivation of the enzyme *Rubisco* which is mainly associated with CO_2 fixation and conversion of CO_2 into complex energy-rich compound (Nagarajan and Gill 2018). At increased temperature, *Rubisco* does not work properly due to breakdown of *Rubisco* activase enzyme or due to deactivation of *Rubisco* itself that finally leads to the generation of photosynthetic inhibitory compound namely xylulose-1,5 bisphosphate (Sage et al. 2008). The efficiency of photosynthesis is also reduced due to rapid climate change because the oxygenation reaction with *Rubisco* increases relative to carboxylation at higher temperature. Such alterations in *Rubisco* activity happens as the solubility as CO_2 decreases as compared to O_2 with the increase in temperatures (Ehleringer and Monson 1993).

Most importantly, the alterations of metabolic pathways by uncoupling of enzymes may lead to the generation of harmful reactive oxygen species (ROS) and free radicals under climate change (Asada 2006). So the generation of reactive oxygen species such as superoxide anions (O^{2-}), singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2) and hydroxyl radicals ($\cdot OH$) is triggered by environmental extremes. ROS are produced in a number of cellular reactions including β-oxidation of fatty acids, augmented photorespiration, misleading electron transport chain of mitochondria or chloroplast and by various enzymes such as like NADPH oxidase (NOX), xanthine oxidase, lipoxygenases and peroxidases (Apel and Hirt 2004; AbdElgawad et al. 2015). ROS can potentially cause damage to cellular membrane through the initiation of lipid peroxidation or react with biomolecules like proteins, lipids, nucleic acids, etc., and as such cellular functioning or metabolic pathways are likely to be seriously damaged with the generation of ROS. Therefore, oxidative damage is closely associated with the excessive generation of ROS under a wide range of environmental factors (Fig. 1.3).

Additionally, climate change or more particularly temperature modulation may cause native misfolding and aggregation of proteins leading to the loss of biological functions of protein, and it ultimately leads to cell apoptosis (Sharma et al. 2009).

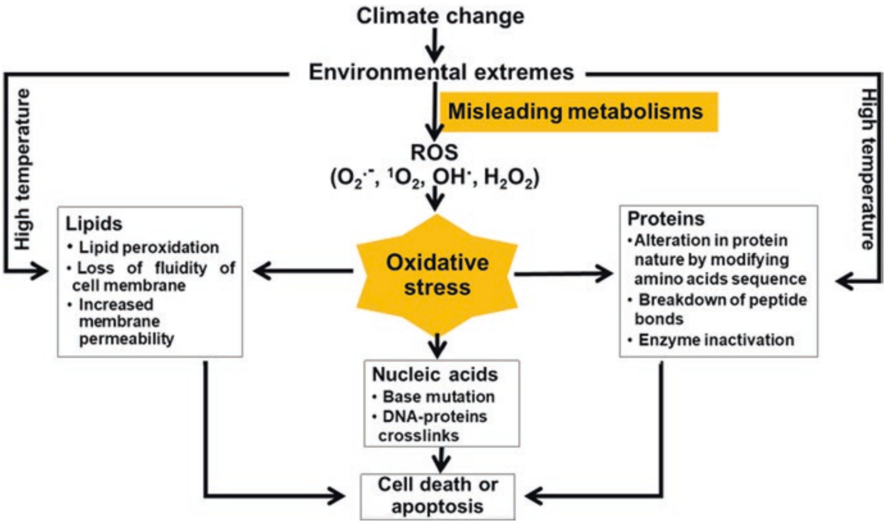

Fig. 1.3 Climate change-induced oxidative stress and its effects on macromolecules

Further, high temperature can cause disruption of membrane fluidity that ultimately leads to changes in membrane-associated processes and eventually complete disruption of membrane function. A major group of proteins viz. late-embryogenesis abundant (*LEA*) proteins typically accumulate during the later stages of embryogenesis particularly in response to various environmental stresses such as dehydration, low temperature and salinity (Ramanjulu and Bartels 2002). This indicates the responsiveness of *LEA* proteins to cellular dehydration and their protective function as chaperones against cellular damage (Umezawa et al. 2006).

Climate change may also disrupt the production of secondary metabolites in plants and reduce nutritional quality of plants due to increased leaf carbon to nitrogen ratio particularly underelevated CO_2 (Robinson et al. 2012; Alnsour and Ludwig-Muller 2015).

1.4 Resilience of Plant to Climate Change

Plants are under threat as they are living in constantly changing environments which often impede growth and development of plants. In this context, severe scarcity of water along with higher temperature are the most predominant stresses that have been affecting the crop plants as well as natural vegetation. Therefore, climate variability has now driven the scientists and more specifically agricultural scientists or crop physiologists to be involved in research with great concern towards understanding of the resilience mechanisms as adapted by plants to minimize the negative impact of climatic alterations on crop production. In fact, living organisms may have three broad options to cope up with the climate variability (Hofmann and Todgham 2010). These include (1) acclimation or avoidance, (2) phenotypic or physiological plasticity to tolerate the environmental variability and (3) differential expression at molecular level or genetic changes towards evolution. Therefore, the plants can also achieve resilience to climate change by employing a number of adaptation strategies or physiological tolerance mechanisms that may include alterations in biochemical or molecular levels (Leakey et al. 2009).

1.4.1 Avoidance Mechanism

Plants exhibit various avoidance strategies which include morphological alterations for long-term evolutionary adaptations and short-term avoidance or acclimation like changing of leaf orientation, and/or alteration of membrane lipid composition to survive under high-temperature conditions (Chevin et al. 2010). Closing of stomata, increased trichomatous densities are very common heat-induced avoidance mechanisms in plant community for reducing water loss (Srivastava et al. 2012). Further, plants growing in a hot climatic area such as desert area usually develop trichome, cuticle, protective waxy covering, etc. to avoid heat stress by reducing the absorption of solar radiation. Sometimes plants can also reduce the absorption of solar radiation by reducing exposed leaf area as achieved through leaf rolling. The rolling of flag leaves has been reported to be potential adaptation mechanisms of wheat plants towards efficient water metabolism under elevated temperature stress (Sarieva et al. 2010). The avoidance can also be achieved by leaf abscission, leaving heat-resistant buds, or allowing the plants to complete their entire reproductive cycle during the cooler months as in the case of desert annuals (Fitter and Fitter 2002). Severe damage to fruits is also caused by high temperature and intense or direct solar radiation in temperate zones, but these plants can avoid such damage as fruits are often shaded by foliage (Hall 2011).

1.4.2 Physiological Mechanisms

Sometimes plants are able to grow with ease and produce economic yields even if they are exposed to climatic variability, and it is made possible through the development of various physiological tolerance mechanisms. The mechanism of stress response in plants is very complex as plant tissues show variations in their developmental complexity, exposure and responses towards the prevailing stress (Queitsch et al. 2000). Thus, it requires several integrated pathways to be activated in response to external stresses. Plants are often able to develop tolerance to various abiotic stresses through the accumulation of osmoprotectants, regulation of ion transporters or ployamines to maintain turgour or ionic balance inside the cells (Semenov and Halford 2009; Rodríguez et al. 2005; Gupta et al. 2013). Osmoprotectants or compatible solutes are universal and tiny molecules that regulate the osmotic adjustment between cell's cytoplasm and its surroundings, stabilize proteins, prevent membrane injury or monitor cellular homeostasis (Ashraf and Foolad 2007). They mainly consist of proline, sugars, polyols, trehalose, glycine-betaine, hydroxyproline betaine, choline-O-sulphate (Rhodes and Hanson 1993). The novelty of osmoprotectants lies in their ability to maintain cellular homeostasis and their heightened accumulation under stress but to lower its level by degradation when optimum conditions are achieved (Pinto-Marijuan and Munne-Bosch 2013). Identifying genes involved in the synthesis or accumulation of osmoprotectants and their incorporation into plant genomes through genetic engineering tools has long been considered as one of the successful approaches to apply for normal physiological functioning and improvement of crop plants under environmental extremes (Rathinasabapathi 2000). On the other hand, ion transporters or integral membrane proteins play very crucial role for ion homeostasis to stresses by regulating cellular uptake and efflux of inorganic ions (Conde et al. 2011). Plants achieve ion homeostasis through correct regulation of cellular influx and efflux of inorganic ions and also by accumulating essential ions but keeping the concentrations of toxic ions as low. Therefore, tolerant plants must establish a vital rearrangement in solute transport systems by employing primary active transporters, co-transporters and channels to maintain the characteristic ionic balance in the cytosol to adapt in a wide range of environmental conditions (Kuromori et al. 2010). In addition to osmoprotectants or ion transporters, the levels of polyamines (PAs) are also strongly modulated under various stress conditions. PAs are unique polycationic metabolites, such as putrescine, spermine and spermidine that control a wide variety of vital functions and responses of plants particularly under stresses (Pottosin and Shabala 2014). PAs play major roles in imparting stress tolerance through binding to the negative surfaces of cellular membranes or nucleic acids, thereby helping them to be stabilized (Galston and Sawhney 1990; Kusano et al. 2008). However, there are few major mechanisms like modulation of phytohormones, antioxidant defence systems, heat-shock proteins or stress-responsive factors involved in signalling cascades and transcriptional control that essentially play significant roles to counteract the stress effects (Rodríguez et al. 2005; Wang et al. 2004). The details of these major tolerance mechanisms are discussed below.

1.4.2.1 Phytohormonal Modulation

Plant hormones play very vital roles in the adaptation of plants to adverse environmental conditions because of complex interactions among the plant hormones and their ability to control a wide range of physiological processes. As such, climate change has been found to influence many physiological processes through *de novo* synthesis and/or alternations in balance of various phytohormones. It is because the interplay between phytohormone levels and consequently phytohormones derived signalling pathways make them key mediators of highly specific plant responses to the combination of environmental stresses. The major hormones produced by plants are auxins, gibberellins (GA), cytokinins (CK), abscisic acid (ABA), ethylene (ET), salicylic acid (SA), jasmonates (JA), brassinosteroids (BR) and strigolactones. Among these phytohormones, ABA, SA, JA and ET are known to play major roles in mediating plant tolerance to both biotic and abiotic stresses (Nakashima and Yamaguchi-Shinozaki 2013; Bari and Jones 2009). Contrastingly, other plant growth regulating hormones like cytokinin (CK), auxin, gibberellins (GA) and brassinosteroids (BR) play secondary role in mediating the stress responses (Robert-Seilaniantz et al. 2011; Pieterse et al. 2012).

Abscisic acid (ABA) has been found to be the most crucial hormone imparting the regulation of plant responses under climate variability. ABA actually triggers several physiological mechanisms such as stimulation of short-term responses like closure of stomata, resulting in the maintenance of water balance and longer-term growth responses through the regulation of stress-responsive genes (Zhang et al. 1987; Kuromori et al. 2018). Similarly, salicylic acid (SA) also plays important function in regulating respiration, stomatal movement, senescence and cell cycle particularly during stresses as created by biotic agents (Malamy et al. 1990). Plants also modulate the synthesis of ethylene, the only gaseous phytohormone, that is supposed to be important in controlling seed germination, fruit ripening, leaf growth and senescence under various climatic abnormalities (Dubois et al. 2018).

1.4.2.2 ROS Scavenging Systems

Plants must be protected from the damaging effects of reactive oxygen species (ROS) since induction of oxidative stress appears to be one of the most common features of climate change as discussed earlier in this chapter. Actually plants raise antioxidant defence systems in plants to evade the oxidative damage under extreme environmental conditions (Sharma et al. 2010). The tolerant plants are able to protect themselves against the harmful effects of reactive oxygen species (ROS) or free radicals due to the existence of a wide range of protective mechanisms that aid to scavenge or detoxify ROS (Apel and Hirt 2004). The antioxidants are the first line of defence to combat with oxidative stress. The antioxidant defence machinery consists of many enzymatic compounds to detoxify or scavenge ROS, and they are usually distributed within cytoplasm and different subcellular organelles viz. chloroplast, mitochondria and peroxisome (Sharma et al. 2010). These scavenging mechanisms are primarily composed of various enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), which are known to potentially catalyse a complex cascade of reactions to convert ROS to more stable molecules like H_2O or O_2. Besides the primary antioxidant enzymes, several low molecular weight non-enzymatic antioxidants such as ascorbate (AsA), glutathione (GSH), ∞-tocopherols, carotenoids, proline, phenolic compounds and alkaloids in association with a large number of secondary enzymes such as glutathione reductase (GR), monodehydro ascorbate reductase (MDHAR) and dehydroascorbate reductase (DHAR) form the redox cycle (Mittler et al. 2004). A comprehensive system of ROS scavenging or detoxifying free radicals is presented in Fig. 1.4.

1.4.2.3 Signal Sensing, Transduction and Stress Response

Signalling pathways are key in utilizing a complex network of interactions to orchestrate various physiological and biochemical responses of plants. Though identifying the stress sensors is challenging, very important goal is towards understanding stress resistance mechanisms. It is because these signals are first sensed by a receptor and transmitted to the nucleus by a complex network. Then the signal is

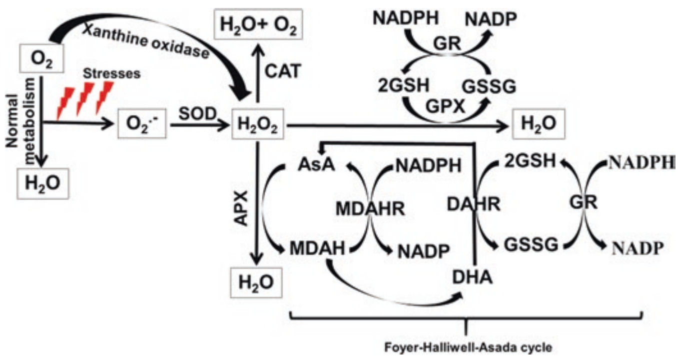

Fig. 1.4 A schematic representation of enzymatic antioxidant systems involved in scavenging of reactive oxygen species produced under climatic extremes (*SOD* superoxide dismutase, *CAT* catalase, *APX* ascorbate peroxidase, *AsA* ascorbate, *MDHAR* monodehydroascorbate reductase, *DHAR* dehydroascorbate reductase; *GR* glutathione reductase, *MDHA* monodehydroascorbate, *DHA* dehydroascorbate, *GPX* glutathione peroxidase, *GSSG* oxidized glutathione, *GSH* glutathione)

manifested in the nucleus through changes in the activity of transcription factors such as DNA-binding proteins that specifically interact and modulate the regulatory regions of genes, and finally the signalling molecules ensure upregulation of many genes with the onset of stress condition. The expression of such stress-responsive genes ultimately regulates the overall physiological responses and enable plants to overcome extreme environmental conditions (Tuteja 2009). Sensing of various stresses like osmotic and high or low temperatures is of utmost importance in the process of achieving cellular homeostasis in plants. The sensing mechanisms allow for the activation of multiple signalling cascades responsible for the triggering of various cellular responses. Therefore, stress sensing and signal transduction together form the most crucial adaptive or tolerance mechanisms to counteract the negative effects of multiple environmental stresses.

In fact, the upregulations of stress-responsive genes are made possible through the involvement of various stress-responsive factors in signalling cascades and transcriptional control (Kaur and Gupta 2005). Some important stress-responsive factors or molecules that involve in signalling pathways towards activation of many stress-responsive genes under environmental extremes include Ca-dependent protein kinases (CDPKs), mitogen-activated protein kinase (MAPK/MPKs), NO, sugar and phytohormones (Ahmad et al. 2012). When the stress-responsive genes get activated, they help in the synthesis or activation of various detoxifying enzymes or free radical scavengers, osmoprotectants, heat-shock proteins, etc. (Fig. 1.5). The synthesis and activation of these enzymatic antioxidants, osmoprotectants or molecular chaperones help to maintain the cellular homeostasis as they can efficiently cause detoxification of reactive oxygen species (ROS), osmotic adjustment or reinstating the functional conformation of proteins and enzymes, respectively (Woodrow et al. 2011).

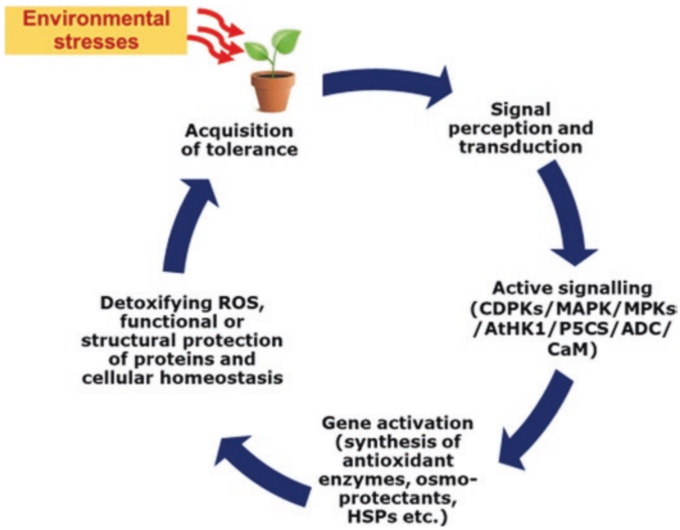

Fig. 1.5 Schematic diagram showing sequential processes involved from signal sensing to acquisition of tolerance under various environmental stresses (*ROS* reactive oxygen species, *CDPKs* calcium-dependent protein kinases, *MAPKs* mitogen-activated protein kinases, *MPKs* mitogen-activated protein kinases, *AtHK1* Arabidopsis thaliana histidine kinase 1, *P5CS* delta-1-pyrroline-5-carboxylate synthase, *ADC* arginine decarboxylase, *CaM* calmodulin). (Adapted from Ahmad et al. 2012 and Woodrow et al. 2011)

1.4.2.4 Heat-Shock Proteins (HSPs)

Heat-shock proteins (HSPs) are known as proteins with low molecular weight that ranges between 15 and 110 kDa (Kregel 2002). The stress-induced expression of HSPs is considered as major event required for acquisition of tolerance in plants. HSPs behave as molecular chaperones for other cellular proteins under environmental stresses (Kregel 2002). Actually, HSPs recognize the unstable proteins and prevent their denaturation or misfolding through binding with them (Schöffl et al. 1998). Once a plant faces any stressful environment particularly heat stress, HSP expression is promptly activated by binding specific heat-shock transcription factors (HSFs) with the highly conserved sequence of heat-shock elements (HSEs) in the promoter regions of heat-responsive genes. HSPs help in survival through the maintenance of proteins in their functional native conformations and preventing aggregation of non-native proteins under stress conditions. Therefore, HSPs functioning as molecular chaperones are the key components responsible for protein folding, assembly, translocation, degradation, targeting or membrane stabilization particularly under extreme environmental conditions (Torok et al. 2001; Wang et al. 2004; Huttner and Strasser 2012). The HSPs are totally heterogeneous and found ubiquitously in a cell, i.e. cytosol, mitochondria, endoplasmic reticulum, nucleus, and cell membrane (Kregel 2002). The expression of HSPs are restricted to certain developmental stages of plant like embryogenesis, microsporogenesis, germination, etc. (Prasinos et al. 2005). Specially two types of HSPs—HSP70 and HSP60—are highly conserved, and they play great role to impart tolerance under heat stress (Kulz 2003). The overexpression of heat shock factors can increase the thermotolerance in plants (Morrow and Tanguay 2012). Due to the thermotolerant nature of HSPs, the expression of heat shock genes (HSGs) can be induced or triggered by heat treatment. These HSGs consist of the palindromic nucleotide sequence (5-AGAANNTTCT-3) that serve as recognizing as well as binding site for heat shock transcription factor (Nover et al. 2001). Heat-shock factor binding with other transcriptional components, resulting in gene expression within minutes in increased temperature or climatic extremities. The upregulation of several heat-inducible genes and the synthesis of heat-shock proteins are very important mechanisms for the survival of plants under heat stress condition (Chang et al. 2007).

1.5 Approaches Towards Improved Understanding of Resilience

Although plants can survive under extreme environmental conditions by adopting several tolerance mechanisms depended upon the nature, intensity and duration of stress. But, the complexity of morphological, physiological and molecular mechanisms as well as overall plant growth and development is likely to be varied when stresses are imposed in combination (Suzuki et al. 2014; Ramegowda and Senthil-Kumar 2015). In this context, 'o*mics*' approaches would provide unique opportunity towards specific elucidation of biological functions of any genetic information under climate change scenario. '*Omics*' technologies include fields such as genomics, transcriptomics and metabolomics which allows researchers to have a better understanding on stress signalling, gene expression, protein modification and metabolite composition technologies for osmoprotectants that are crucial in imparting abiotic stress responses in crops (Urano et al. 2010; Silva et al. 2011). Thus, the importance of 'o*mics*' technology lies in accurate identification and characterization of stress-related various metabolites and/or better understanding on the specific role of such compounds as efficient stress relievers.

Many new aspects of transcriptional, translational and post-translational mechanisms and signalling controls of the plant response to various stresses have been revealed with the aid of 'omics' technology (Fujita et al. 2013). Plants usually employ a post-transcriptional regulation of gene expression by non-protein small microRNAs (miRNAs) in response to developmental and environmental indications. The multi-*omics* between heat and other major categories of abiotic stresses have identified transcriptomes and metabolites that are generally important for cellular homeostasis and stress responses (Wienkoop et al. 2008). In this perspective, latest technologies like phenomics or high-throughput phenotyping would also be significant in identifying the different physiological tolerance strategies that are potentially important for crop improvement under climate change.

1.6 Intervention for Expanding Resilience

An improved understanding of physiological or molecular responses of plants is essential to assist breeding programs to develop tolerance or to augment resilience of crop plants. Though breeding for adaptation to new environmental conditions is challenging, few modern breeding techniques like marker-assisted selection (MAS), genome-wide association studies (GWAS), genome selection (GS) and CRISPR genome editing may be useful approaches for developing tolerance of crop plants to climate variabilities (Liu et al. 2013; Kumar et al. 2018). Therefore, molecular breeding or genetic engineering approaches have been significantly applied for development of transgenic plants with enhanced resilience to various kind of stresses. Besides developing stress-tolerant cultivars through modern breeding programs, several alternative approaches like agronomic practices or conventional methods have been proved to be useful approaches to combat climate change. Several interventions in cultural practices such as the alterations in timing and methods for sowing, a collection of short duration crop varieties, crop rotation, optimum irrigation management, and selection of cultivars and species, can considerably decrease the adverse effects of extreme environmental conditions (Hu et al. 2017; Duku et al. 2018; Teixeira et al. 2018; Deligios et al. 2019). Further, priming of seeds with various chemicals as well as physical agents has been reported to induce plants' tolerance to abiotic stresses (Samota et al. 2017; Dutta 2018). Seed priming or pre-germinative metabolisms are well known for uniform or fast germination and enhancing seed vigour. As such seed priming can be useful tool in alleviating stress effects as abiotic stresses mostly affect the germination and early seedling growth stage of plants (Hussain et al. 2018). Further exogenous applications of several protectants such as anti-transpirants, osmoprotectants, phytohormones, signalling molecules, and trace elements have been found to be beneficial on plants grown under various stressful conditions (Farooq et al. 2008; Hasanuzzaman et al. 2013a, b, c). These substances are useful in alleviating stress effects due to their growth-promoting and antioxidant activities.

1.7 Conclusion

Climate change has now been exposed as an unequivocal event that results from excessive burning of fossil fuels mostly during the post-industrialization era. As a consequence of climate change, global average temperature, annual precipitation pattern or its distribution over the geographic regions and hydrological cycles have been badly affected. Thus, climate change poses severe risks to agricultural production or global ecosystems as a whole and consequently to food security. Climate change has actually been led to the generation of various stress factors that can potentially limit growth and productivity by dampening physiological functioning of plants either directly or indirectly. Therefore, the chances of being exposed to novel environmental conditions that are beyond the physiological limits of plants have now been increased under changing climate. Plants can adapt or survive by employing a number of adaptation strategies and alterations of mechanisms at physiological or biochemical level particularly when they are exposed to climate extremes. Growth, physiological processes and productivity of plants have been adversely affected under climate variability.

Plant responses to climate change vary with the nature and intensity or duration of particular stress. Alteration in phenology along with morpho-physiological and biochemical changes is very closely associated with the climatic extremes. However, plants are able to adapt by employing a number of strategies like avoidance or tolerance mechanisms induced with the onset extreme environments. Several important tolerance mechanisms include hormonal modulation, stress signalling, heat-shock proteins, ROS scavenging, etc. Apart from the above strategies, specific roles of ion transporters, compatible solutes or polyamines in minimizing stress effect should not be ignored. A better understanding of plant responses and adaptation mechanisms will certainly increase our ability to improve stress resistance in crop plants, and thereby it will be helpful in achieving agricultural sustainability and food security for ever-growing global population.

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