REVIEW

Climate change regulated abiotic stress mechanisms in plants: a comprehensive review

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Abstract

Global climate change is identified as a major threat to survival of natural ecosystems. Climate change is a dynamic, multi-faceted system of alterations in environmental conditions that affect abiotic and biotic components of the world. It results in alteration in environmental conditions such as heat waves, intensity of rainfall, CO_2 concentration and temperature that lead to rise in new pests, weeds and pathogens. Climate change is one of the major constraints limiting plant growth and development worldwide. It impairs growth, disturbs photosynthesis, and reduces physiological responses in plants. The variations in global climate have gained the attention of researchers worldwide, as these changes negatively affect the agriculture by reducing crop productivity and food security. With this background, this review focuses on the effects of elevated atmospheric CO_2 concentration, temperature, drought and salinity on the morphology, physiology and biochemistry of plants. Furthermore, this paper outlines an overview on the reactive oxygen species (ROS) production and their impact on the biochemical and molecular status of plants with increased climatic variations. Also additionally, different tolerance strategies adopted by plants to combat environmental adversities have been discussed.

Keywords Abiotic stress · Climate change · Plant growth · Reactive oxygen species · Tolerance

Abbreviations

ABA	Abscisic acid
RO˙	Alkoxy radical
APX	Ascorbate peroxidase
AsA	Ascorbic acid
ATP	Adenosine triphosphate
BAP	6-Benzyl aminopurine
BR	Brassinosteroids
CAT	Catalase
DNA	Deoxyribonucleic acid
EBL/EBR	24-Epibrassinolide
ET	Ethylene
ET	Evapotranspiration
FC	Field capacity
GA	Gibberellic acid
GB	Glycine betaine
GHGs	Green house gases
GPX	Guaiacol peroxidase
GR	Glutathione reductase
GSH	Glutathione
GWAS	Genome-wide association studies
OH˙	Hydroxyl radical
H_2O_2	Hydrogen peroxide
HSP	Heat shock protein
IPCC	Intergovernmental panel on climate change
JA	Jasmonic acid
MAS	Marker-assisted selection
MeJA	Methyl jasmonate
MDA	Malondialdehyde
MYB	Myeloblastosis
NADPH	Nicotinamide adenine dinucleotide phosphate
NAR	Net assimilation rate
NPA	Naphthylphthalamic acid
PGPR	Plant growth promoting rhizobacteria
POX	Peroxidase
PS II	Photosystem II
QTL	Quantitative trait loci
ROS	Reactive oxygen species

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RuBisCO	Ribulose-1,5-bisphosphate carboxylase oxygenase
SA	Salicylic acid
$^1O_2$	Singlet oxygen
SOD	Superoxide dismutase
$O_2^{\cdot -}$	Superoxide radical
TF	Transcription factors
WHC	Water holding capacity

Introduction

Climate change has occured mainly due to fossil fuel burning and rise in concentration of harmful greenhouse gases (GHGs) in the atmosphere during post-industrialisation era. Industrial revolution is considered the main reason for global change in climatic conditions (Dutta et al. 2020). The global climate change is anticipated to advance drastically over the next decade. It is regarded as a threatening issue that has disturbed the growth patterns of various organisms. Life on planet Earth mainly depends upon the natural process of greenhouse effect, wherein, Earth's atmosphere traps the solar radiation and warms the surface. This atmospheric greenhouse effect occurs in the troposphere, where life exists. The average temperature on Earth surface without greenhouse effect is reported to be approximately − 19 °C, rather than prevailing average of 14 °C (Cassia et al. 2018). However, continuously changing climatic conditions due to increased human activities such as urbanisation, rapid industrialisation, deforestation, burning of agricultural wastes, excessive use of non-biodegradable commodities etc. pose serious threat to the environment. Furthermore, emission of toxic gases from industries, factories, equipments and vehicles also plays a major role in changing the climate.

Both natural and anthropogenic activities contribute towards the emission of GHGs in the atmosphere (Arora and Chaudhry 2017). GHGs mainly carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O) together with water vapours are responsible for the phenomenon of green house effect that absorbs and emits infrared radiation in the atmosphere (IPCC 2014). Human activities have elevated the concentration of GHGs in the atmosphere causing global warming and disruption of hydrological cycles. CO_2 concentration in atmosphere has increased from 280 ppm to more than 410 ppm i.e., approximately 45% since the industrial revolution (Ciais et al. 2014) and is expected to rise further up to 730–1000 ppm by 2100 (IPCC 2014). The peaked CO_2 concentration together with other GHGs raised the mean annual temperature by ~ 0.8 °C in 2017 (Dusenge et al. 2019). According to IPCC (2014), the enhanced CO_2 concentration is expected to increase the global temperature in the range of 1.0–3.7 °C. Moreover, climate change is expected to disturb rainfall pattern, thereby increasing the events of drought in arid regions of the world (IPCC 2014). Another GHG, CH_4 is an important constituent of natural gas and is emitted from cattle farming and fossil fuel use. The approximate global concentration of CH_4 in atmosphere is 1.8 μmol mol^{-1} (IPCC 2014). Anthropogenic activities contribute towards increased burning of fossil fuels, hence enhance the concentration of nitric oxide (NO) in the atmosphere, that interacts with volatile organic compounds forming organic nitrates and nitric acid that harm the ecosystem (Cassia et al. 2018).

Climate change has evoked the variations in temperature, rainfall and atmospheric conditions and has exposed the plants to harsh and extreme climatic conditions that adversely affect the morphological, developmental, cellular and molecular processes in plants (Fig. 1). The unfavourable environmental conditions such as high temperature and enhanced CO_2 concentration greatly influence the growth and yield of the plants (Raza et al. 2019c). Plants are very sensitive to climate change due to their long life span that renders it difficult for them to adapt to changing environmental conditions (Lindner et al. 2010). Variation in temperature under natural conditions can affect plant growth and reproduction, and adverse climatic fluctuations damage the molecular mechanisms related to growth, thus affecting the development of plants (Bita and Gerats 2013). Increase in temperature has posed a detrimental effect on the growth and yield of crop plants. Nearly 15% of global wheat production comes from Indian lowlands but due to fluctuations in climatic conditions these areas will get converted into heat-stressed environments with a very short-season for wheat production (Bita and Gerats 2013). Moreover, mathematical modelling techniques predict that production of cereals in Southeast Asia and Southern Africa will get altered by changing climatic conditions if new approaches for its improvement are not found (Fischer and Edmeades 2010). According to Reddy et al. (2010), climate change impact on plant development is attributed to the altered photosynthetic carbon assimilation mechanisms. Further, drought stress induced due to changing climatic conditions severely hampers stomatal conductance, plant water relations, CO_2 assimilation and photosynthetic pigments leading to reduced productivity in plants (Anjum et al. 2011).

With this background, this review emphasises the influence of abrupt fluctuations in climatic conditions specifically CO_2, drought, temperature and soil salinity on growth and development of plants. Further, it attempts to outline the effect of climate change induced oxidative damage in plants and strategies or approaches to combat such damages.

Fig. 1 Climate change induces
oxidative stress in plants
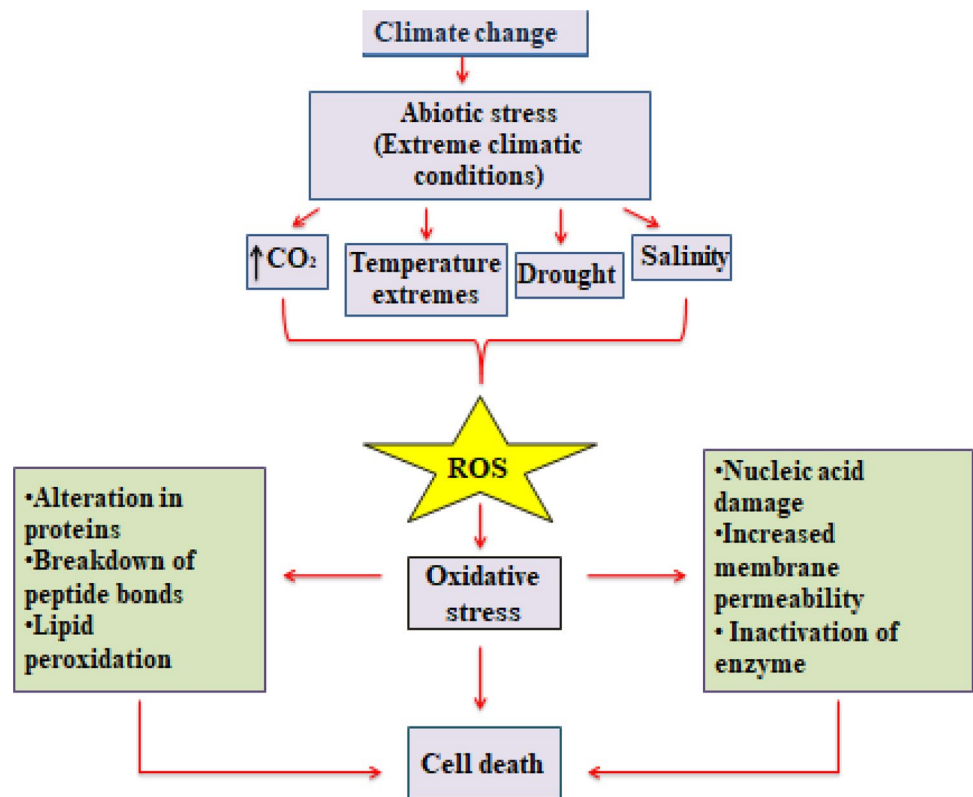
Effect of elevated CO_2 on plant growth and development

The concentration of CO_2 in the atmosphere has dramatically increased since pre-industrial era and is further expected to increase to ~ 730–1000 ppm by the end of twenty-first century (IPCC 2014). The increase in atmospheric CO_2 is associated with peaked mean global temperature due to green house effect that will bring about significant changes in global climate (Balasooriya et al.

2018). Studies have reported that enhanced CO_2 concentrations directly affect photosynthesis, gaseous exchange and other developmental processes in plants (Katul et al. 2010; Albert et al. 2011; Gray and Brady 2016). The elevated CO_2 content positively affects the photosynthesis process in C_3 plants and triggers the plant growth (Fig. 2). The increment in photosynthesis with elevated CO_2 levels is attributed to the increased CO_2 at the site of RuBisCO that limits the supply of NADPH and ATP for photorespiration, thus making plants more available for CO_2 assimilation (Hay et al. 2017). Kaiser et al. (2017)

Fig. 2 Elevated CO_2 levels
affect the physiological and
biochemical traits of the plants
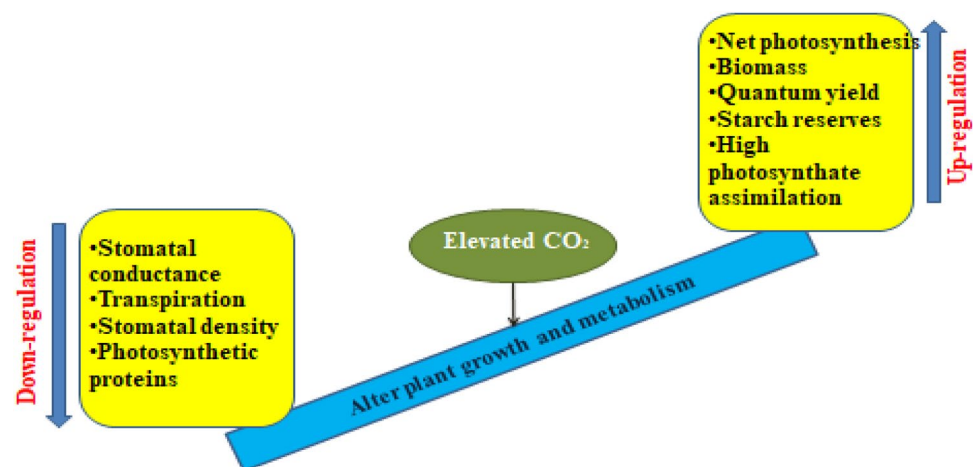
revealed that increased atmospheric CO_2 at 800 µbar elevated the relative carbon gain by ~ 12%, increased photosynthesis by ~ 17% and decreased loss of photosynthetic induction by ~ 14% compared to 400 µbar in *Solanum lycopersicum* due to higher rate of carboxylation and reduced rate of oxygenation reaction at RuBisCO. The enhanced net photosynthesis rate due to elevated atmospheric CO_2 can promote growth in lettuce due to more availability of carbon skeletons that result in higher accumulation of carbohydrates (Pérez-López et al. 2013; Pan et al. 2020). Enhanced CO_2 level has been reported to increase light-saturated maximum photosynthetic rate, apparent quantum efficiency and carboxylation efficiency in *S. lycopersicum* (Pan et al. 2020). Additionally, short term exposure to elevated CO_2 alleviated the harmful effects of salinity in *Stevia rebaudiana* by increasing photosynthesis and decreasing oxidative stress (Hussin et al. 2017). Recently, Andrews et al. (2020) opined that increased CO_2 concentration does not inhibit assimilation of nitrates in C_3 plants such as *Phaseolus vulgaris* and *Triticum aestivum*. The elevated CO_2 level positively affects the height, leaf number, flower number and biomass in *Parthenium hysterophorus* indicating improved growth and reproductive potential in plants (Bajwa et al. 2019).

Misra et al. (2019) has illustrated the beneficial effects of elevated CO_2 on biomass, photosynthesis, leaf area, stalk juice volume, leaf dry weight and stem dry weight of sugarcane, a C_4 plant. This might be due to the high optimum temperature for growth, compensatory ability, very low CO_2 compensation point and unique carbon sequestration process that help them to perform better than other crops. Moreover, the effect of elevated CO_2 on *Setaria italica*, another C_4 plant demonstrated that increased CO_2 enhanced photosynthetic rate, intrinsic water use efficiency, seed and tiller number, spike and stem weight, above ground biomass and grain yield in plants (Li et al. 2019a). The researchers identified some genes through transcriptomic analyses that play an important role in cell wall reinforcement, shoot initiation, stomatal conductance, carbon fixation and glycolysis/gluconeogenesis in foxtail in response to increased CO_2 concentration (Li et al. 2019a). Tom-Dery et al. (2018) observed reduced stomatal conductance, root to shoot ratio and protein content in *Cenchrus pedicellatus* under elevated CO_2 concentration. Miliauskienė et al. (2016) reported decreased carotenoid content and increased total phenolics and ascorbic acid in maize leaves under increased CO_2 level.

Contrarily, prolonged and high exposure to CO_2 concentrations has also been reported to decrease the biomass productivity and photosynthetic activity of plants (Wang et al. 2013). The increased atmospheric CO_2 concentration significantly alters the crop productivity and quality. Balasooriya et al. (2018) reported reduced photosynthesis and fruit yield in *Fragaria* × *ananassa*, a herbaceous plant upon exposure

to elevated atmospheric CO_2. The down-regulation of photosynthesis is due to the collective reduction in RuBisCO content, electron transport chain and source–sink balance in leaves (Gamage et al. 2018). Moreover, plants exposed to elevated CO_2 showed significant reduction in nitrogen content leading to reduced plant productivity due to low nutrient availability (Rosa et al. 2019) (Fig. 2). The enhanced atmospheric CO_2 not only affects plant shoot growth but also hampers the root growth of herbaceous plants. Cohen et al. (2018) studied the impact of elevated CO_2 on root dynamics of tomato plants and found that root vascular tissue especially xylem development gets inhibited in plants with peaked CO_2 concentration (Cohen et al. 2018). Further, Uddling et al. (2018) reported decreased nutritional quality (mainly N, Zn, Fe and S) of non-legume C_3 crops under elevated CO_2 concentrations. The study conducted by Giri et al. (2016) examined the impact of elevated CO_2 concentration on nutritional quality of *Lactuca sativa* and *Spinacia oleracea*. The increased CO_2 level decreased the concentration of many nutrients such as nitrogen, potassium and phosphorus in the edible parts of both *L. sativa* and *S. oleracea* (Giri et al. 2016). Recently, Dong et al. (2018b) reviewed the effects of elevated CO_2 on nutritional quality of vegetables and found that increased CO_2 level decreased the concentration of Mg, Fe and Zn in vegetables which might be attributed to dilution effect or inhibited transpiration in plants (Dong et al. 2018b). However, the exact reason behind the decrease in nutrient content is still unknown and future research in this field is required.

The increased CO_2 concentration has contributed to enhanced plant productivity in forests that can be globally observed as widespread green patches of vegetation through satellite imaging (Zhu et al. 2016). Elevated CO_2 leads to carbon overabundance in trees that increase the wood storage, stomatal downregulation and decrease water use in plants (Paudel et al. 2018). However, due to climate change-induced increased mean temperature and drought, the morphological and physiological activities of terrestrial ecosystems will be severely damaged (Ainsworth et al. 2020). Drought is a constraint for growth of trees in both urban and forest lands. For example, Stratópoulos et al. (2019) investigated the effect of drought on phenology, growth and morphology of urban tree species and found that out of the three species studied, *Tilia cordata* showed premature leaf senescence followed by *Carpinus betulus* and *Acer campestre*. The changing climatic conditions not only hampers above-ground tree biomass but also alters the litter quality and litter decomposition in *Quercus acutissima* and *Fraxinus rhynchophylla* by changing the nutrient concentration of plant tissue (Cha et al. 2017).

Peaked CO_2 concentrations lead to increased photosynthesis in plants that positively affects growth, above-ground biomass and yield of plants. The increased CO_2 level causes

enhanced carbohydrate production resulting in regulation of different physiological processes via sugar signalling mechanisms in plants (Thompson et al. 2017). The improved root growth under elevated CO_2 concentration controls nutrient uptake thus maintaining nutrient balance in plants. Sugars have been known to regulate nutrient acquisition due to expression of various ion transporters in plants. However, long-term exposure of plants to elevated CO_2 leads to decreased photosynthesis due to photosynthetic acclimation, thus significantly affecting vegetable quality in plants (Dong et al. 2018b). Earlier study reports that enhanced CO_2 level increased the concentration of glucose, fructose and sucrose, but decreased the content of malic acid, quinic acid and citric acid in strawberry plants indicating higher carbohydrate accumulation compared to organic acids in strawberry under increased CO_2 level (Wang and Bunce 2004). Similarly, Fu et al. (2015) reported decreased yield and content of polyphenols, flavonoids and vitamin C upon exposure to 5000 µmol mol^{-1} CO_2 in *Brassica chinensis* and *L. sativa*. Recently, Parvin et al. (2019) observed reduced concentration of Fe, Zn, P and S in faba bean and lentil upon elevated CO_2 conditions. The deficiency of nutrients is an important reason for loss of quality and production across the globe. Moreover, the effect of increased CO_2 on mineral composition of food and chance of producing nutritionless food would be a great threat to both the agriculture ecosystem and human health.

Jagadish et al. (2016) opined that atmospheric CO_2 enrichment affects fitness- and flowering-related events in plants. The authors opined that high CO_2 concentration triggers change in sugar status of plants and regulates the activity of an important flowering gene (*MFT: MOTHER OF FT AND TFL1*) that is responsible for alteration in flowering time in plants (Jagadish et al. 2016). Earlier, Sreeharsha et al. (2015) demonstrated that elevated CO_2 altered the developmental programming of *Cajanus cajan* by delaying flowering for 8–9 days. The authors opined that this might be due to the accumulation of insoluble sugars under increased CO_2 levels that might have influenced the signalling behaviour of plants and delayed flowering (Sreeharsha et al. 2015).

Effect of elevated temperature on plant growth and development

Temperature is a major factor affecting the distribution, growth and development of plants. The morphological and physiological processes of plants depend upon the temperature conditions in which the plant species are growing since every species grows in some optimum range i.e., 25–30 °C for maximum growth (Hatfield and Prueger 2015). According to IPCC (2014), the mean temperature in the next 30–50 years is predicted to increase by 1.2–3.7 °C. Climate change is expected to enhance the frequency, period and intensity of exceptionally low and high temperature (Yamori et al. 2014). The enhanced temperature above optimum range causes heat injury in plants. The variation in temperature during summers can harm the intermolecular interactions required for normal plant growth, thus affecting fruit set and development (Bita and Gerats 2013). Plants face an intricate action of intensity, rate and period of elevated temperature. Exposure of plants to high temperature for long duration may cause serious alteration in the metabolic activities and cellular disorganisation that leads to reduced growth and development (Rai et al. 2018).

Among different growth phases of plants, germination is the foremost stage that is affected by heat stress. Elevated temperature decreases germination percentage, viability, plumule and radicle growth in plants which might be attributed to the loss of cellular water content that decreases cell size and ultimately growth in plants (Rodríguez et al. 2005). Similarly, Dürr et al. (2018) demonstrated reduction in germination of *T. aestivum* and *Pisum sativum* when exposed to increased temperature that decreased seed dry weight and caused alterations in nutritional value of the crop. Laghmouchi et al. (2017) studied the effect of temperature on seed germination of *Origanum compactum* and found that at high temperature (25 °C) the germination was reduced to nil. The reduction in seed germination at high temperature is correlated with the direct impact on metabolism of plants which involves activation of certain enzymes at optimum temperature range (Belmehdi et al. 2018). In another study, Srivastava et al. (2012) reported reduction in relative growth rate in sugarcane under heat stress due to reduced net assimilation rate (NAR) of plants. Chalanika De Silva and Asaeda (2017) designed a study to demonstrate the effect of heat stress on growth of three submerged macrophytes viz., *Elodea nuttallii*, *Potamogeton crispus* and *Vallisneria asiatica* and found that high temperature decremented relative growth rate in all the plant species. This decline in relative growth rate is corroborated with accumulation of reactive oxygen species (ROS) under elevated temperature conditions.

Heat stress independently alters the physiology and metabolism of plants. However, its effect gets enhanced when combined with other abiotic stresses like drought and salt stress. According to Zinn et al. (2010), high temperature stress affects reproductive stage of crop species more than vegetative stage resulting in sudden reduction in yield due to pollen infertility. However, heat stress affects both the vegetative and reproductive stage of plants and its impact varies from species to species (Bita and Gerats 2013). Heat stress causes denaturation of cellular structures, disturbed protein stability, membrane disintegration and disruption of metabolism which leads to excessive ROS production and causes serious oxidative stress in plants (Bita and Gerats 2013; He
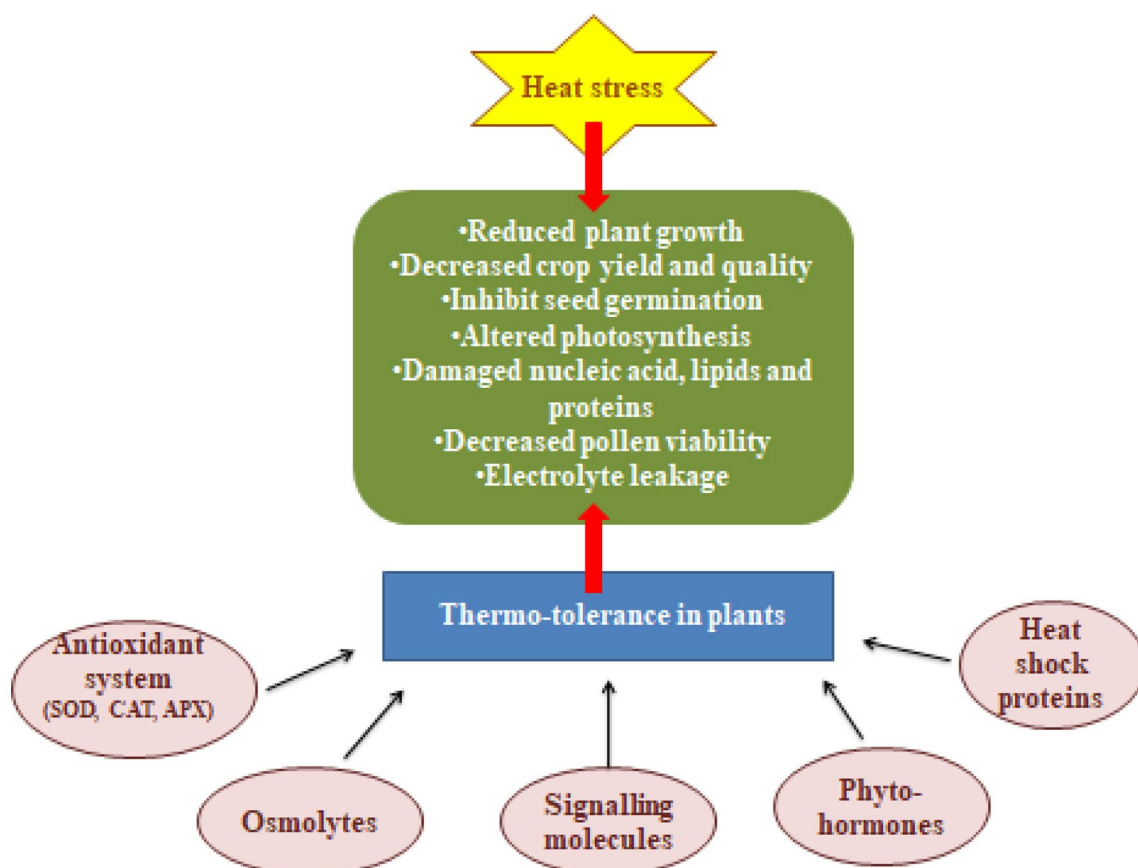
Fig. 3 High temperature modulates physiological, biochemical and molecular status of the plants

et al. 2017) (Fig. 3). High temperature can be sensed by various cellular machinery that activate certain responses in plants which include stimulation of lipid signalling pathway, inflow of Ca^{2+} via Ca^{2+}-mediated membrane channels and reorganisation of cytoskeletal elements (Carmody et al. 2016). This might be correlated with the heat stress mediated inhibition of RuBisCO and RuBisCO activase enzyme that further damages the C_3 cycle (Calvin-Benson cycle) of carbon fixation in plants. The decrease in fixation of carbon generates excessive ROS species in the photosystems and inhibits the repair processes occurring in plants (Apel and Hirt 2004).

Heat stress significantly affects the photosynthetic machinery of plants by reducing the level of photosynthetic pigments and activity of antioxidant enzymes (Jajoo and Allakhverdiev 2017). *P. crispus* and *V. asistica* exhibited reduction in chlorophyll a and chlorophyll b content under moderate and high temperature conditions (Chalanika De silva and Asaeda 2017). This reduction in photosynthetic pigments is attributed to the production of ROS that causes oxidative stress in plants (Chalanika De silva and Asaeda 2017). Recently, Ahammed et al. (2018) studied the role of *COMT1* (*CAFFEIC ACID O-METHYLTRANSFERASE 1*)

gene on photosynthesis under heat stress in *S. lycopersicum*. They found that *COMT1* silencing aggravates heat stress-induced reduction in photosynthesis by decreasing chlorophyll content, PS II activity and electron transport efficiency in *S. lycopersicum*. In an experiment conducted by Buchner et al. (2015), heat treatment applied in dark reduced photosynthetic performance and maximum quantum efficiency of PS II in *Rhododendron ferrugineum*, *Senecio incanus* and *Ranunculus glacialis*.

Effect of drought on plant growth and development

The term drought in meteorology is defined as a period without critical rainfall (Jaleel et al. 2009). Plants experience drought stress when availability of soil water is less and further, due to the climatic conditions water is lost frequently by evaporation and transpiration (Mishra and Cherkauer 2010). The agricultural drought can be interpreted as deficiency of sufficient moisture needed by plants for growth and development (Farooq et al. 2012). Drought is the most destructive environmental stress that severely alters plant

production, growth rate, biomass and yield (Anjum et al. 2011). Its intensity has increased in the past few decades hampering global food security. In this current scenario, drought stress can lead to defects in plant growth pattern in more than 50% of arable lands by the year 2050 (Kasim et al. 2013; Vurukonda et al. 2016). Among the various regions of the world, the arid and semi-arid regions specifically of developing countries are more potent to drought stress due to intense shortage of water in these areas (Nawaz et al. 2015).

Drought stress interferes with the regular plant functions by affecting turgor and water potential (Nawaz et al. 2015) that alter the morphological, physiological and molecular traits in plants (Vurukonda et al. 2016). Reduction in growth due to drought stress has been studied in many plant species such as *Oryza sativa* (Chen et al. 2011), *T. aestivum* (Arzanesh et al. 2011), *Tagetes erecta* (Asrar and Elhindi 2011), *Jatropha curcas* (Sapeta et al. 2013) and *Cuminum cyminum* (Soleymani and Shahrajabian 2018) (Table 1). Drought stress commonly alters the growth parameters viz., fresh weight and water status in plants (Vurukonda et al. 2016). These authors have postulated drought induced hindrance on various biochemical activities in plants such as nitrate reductase and ethylene biosynthesis that leads to decreased nitrate uptake from soil and inhibition of plant growth, respectively. Moreover, the availability and transportation of soil nutrients are strongly affected by drought stress since water serves as a carrier for transport of nutrients to roots. The diffusion and mass flow of different macro- and micro-nutrients such as calcium, silicon, magnesium and nitrate gets decreased due to drought stress (Selvakumar et al. 2012).

Drought is an important deterrent in growth of plants and involves structural and physical interaction between ROS and abscisic acid (ABA) (Jones 2016). Drought stress causes accumulation of ABA and extracellular ABA application brings about H_2O_2 generation in plants. To maintain water availability in aerial parts of plant, a coordinated sequence of signals is required from root to shoot of plants (Jones 2016). Under stressful environments, roots are the first organ that sense the availability of water and send signals to the aerial organs via root-to-shoot xylem channels to decrease the turgidity of guard cells and close stomatal aperture to reduce water loss (Carmody et al. 2016). Drought stress can induce imbalance between ROS generation and its quenching in plants (Qureshi et al. 2018). The leakage of electrons during various pathways of electron transport leads to generation of ROS that causes lipid peroxidation and membrane disruption in plants (Qureshi et al. 2018). The closure of stomata during drought stress leads to decreased rate of photosynthesis in plants. Further, reduced water availability induces shrinkage of cell volume that leads to increased viscosity of cellular contents resulting in damage of proteins and enzymes responsible for photosynthesis in plants (Impa et al. 2012).

Drought stress induced partial closure of stomata to reduce water loss, restrict CO_2 entry leading to production of H_2O_2 in peroxisomes and mitochondria by photorespiration process and limit photosynthesis in plants (Miller et al. 2010; Noctor et al. 2014).

Drought-induced photooxidation leads to reduced chlorophyll content that causes impaired photosynthesis in plants (Rahdari et al. 2012). The reduced chlorophyll content during drought stress mainly depends upon the period and level of drought stress experienced by plants (Sapeta et al. 2013). The inhibition of photosynthesis process is one of the major effects of drought stress in plants (Nezhadahmadi et al. 2013). This is corroborated with the decreased leaf expansion rate, turgor pressure, reduction in CO_2 assimilation, damaged photosynthetic machinery and early senescence of leaf (Salehi-Lisar and Bakhshayeshan-Agdam 2016; Zargar et al. 2017). Earlier reports have opined that plants grown under low to moderate drought stress have experienced a reduction in photosynthesis due to the pessimistic effect on stomatal conductance in plants (Wang et al. 2018). Several researchers have reported decreased chlorophyll content under drought stress, for example in *Matricaria chamomilla* (Salehi et al. 2016), *Arachis hypogaea* (Shivakrishna et al. 2018) and *Cicer arietinum* (Sohrabi et al. 2012).

Effect of salinity on plant growth and development

Globally, agriculture is facing serious challenges with growing population which is expected to reach 9.1 billion by 2050 (Iqbal et al. 2014), since the crop productivity is not increasing as per the food demand. The decreased crop yield is one of the major reasons related to various abiotic stresses faced by crops. The harmful effect of excess mineral salts like Na^+ and Cl^- on plants is termed as salt or salinity stress (Parihar et al. 2015). It is one of the major limiting factors for plant growth and productivity. Salt stress is an important constraint to plant development and is expected to increase due to change in global climate and increased irrigation practices (Rengasamy 2010). The arid and semi-arid areas with lower rainfall, high evaporation and transpiration rate, increased temperature and poor water availability are more likely to get affected by salinity stress (Nawaz et al. 2010). Accumulation of salts, either water soluble such as sodium chloride (NaCl) and sodium carbonate (Na_2CO_3) or partially water soluble-like calcium chloride ($CaCl_2$) causes soil salinity (Nawaz et al. 2010). A soil is regarded as saline when its electric conductivity (EC) is measured to be 4Ds m^{-1} and osmotic pressure of 0.2 MPa that significantly affect the plant metabolism (Munns and Tester 2008), leading to chlorosis and necrosis in plants (Acosta-Motos et al. 2017).The negative effects of salinity stress largely depend upon environmental

Table 1 Effect of drought stress on morphology, physiology and cellular machinery of different plant species

Crop/plant	Stress intensity	Stage	Effect on plant traits	Percentage reduction in physio-chemical attributes with respect to control	References
T. erecta	Mild-severe stress (25–100% W.H.C)	Vegetative stage	Decreased growth vigor, plant height, shoot dry weight, flower diameter, fresh and dry weight	NM	Asrar and Elhindi (2011)
Brassica napus (canola)	Water withheld till plant showed wilting	Flowering and pod-filling stage	Reduced chlorophyll content, number of pods per plant, seeds per pods and grain yield	23.8% (chlorophyll)	Din et al. (2011)
T. aestivum	25–80% of field capacity	Vegetative stage	Declined growth, water potential and water content	NM	Arzanesh et al. (2011)
	Terminal drought stress	Grain filling stage	Decreased grain yield, biomass, grain weight, harvest index, net photosynthesis rate, stomatal conductance and transpiration rate	34% (grain yield), 27% (grain weight)	Saeidi and Abdoli (2015)
Triticum durum	Terminal drought stress	Growth stage	Chlorophyll content, relative water content, Fv/Fm and membrane stability index decreased	22.8–47.5% (chlorophyll content)	Almeselmani et al. (2011)
C. arietinum	Duration of drought stress (0, 1, 3, 7 days till recovery)	NM	Significantly altered seed germination, growth parameters, water status, membrane integrity, osmolyte accumulation	43% (seed germination)	Tiwari et al. (2016)
C. arietinum	Imposed by withholding irrigation	Anthesis and vegetative stage	Reduced chlorophyll a, chlorophyll b and total chlorophyll, lowered sub-stomatal CO_2 concentration and grain yield	45–66% (grain yield)	Mafakheri et al. (2010)
Salvia miltiorrhiza	Medium-severe stress	NM	Decreased growth, root and shoot dry weight	NM	Liu et al. (2011a)
O. sativa	0–8 bars	Germination and early seedling growth stage	Reduced root and shoot length, dry weight, increased activity of peroxidase, catalase and superoxide dismutase	31.03–48.28% (shoot length),43.10–82.65% (root length), 42.86–51.43% (dry weight)	Lum et al. (2014)
Mentha piperita	Mild-severe stress	NM	Reduced growth, essential oil percentage and yield	NM	Khorasaninejad et al. (2011)
Glycyrrhiza glabra	Mild-severe stress	NM	Decreased biomass, leaf relative water content and increased osmolyte, antioxidant enzymes and yield	22–33% (grain yield)	Hosseini et al. (2018)
Sesamum indicum	Mild-severe stress	Germination and seedling stage	Decreased germination percentage, root-shoot length and dry weight	NM	Bahrami et al. (2012)

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Table 1 (continued)

Crop/plant	Stress intensity	Stage	Effect on plant traits	Percentage reduction in physio-chemical attributes with respect to control	References
Medicago truncatula	Moderate stress	NM	Increased reactive oxygen and nitrogen species content, proline content and decreased stomatal conductance	NM	Filippou et al. (2011)
Vigna unguiculata	Severe stress	Vegetative growth stage and flowering stage	Reduced growth attributes, ground cover and chlorophyll content	Ground cover 2.3–46.4% (vegetative stage); 6.29–37% (flowering stage)	Ndiso et al. (2016)
Vicia faba	Irrigation period (0, 7 and 15 days)	Vegetative stage	Reduced stem diameter, number of vessels/bundle in stem, leaf lamina thickness, chlorophyll content and yield	NM	Abdelaal (2015)
M. chamomilla	Very moderate–very severe stress	Vegetative-flowering stage	Reduced chlorophyll a and b content, elevated proline and leaf soluble sugar content	NM	Salehi et al. (2016)
Glycine max	Early-late stress	Pre and post flowering growth stage	Reduced growth and yield, increased endogenous content of jasmonic acid, salicylic acid and abscisic acid	NM	Hamayun et al. (2010)
Matricaria recutita	Soil moisture depletion (30, 50, 70 and 90%)	Vegetative-flowering stage	Decreased plant height, flower yield, shoot weight	NM	Baghalian et al. (2011)
C. cyminum	Moderate-severe	NM	Reduced number of umbellets per umbel, seed and oil yield	37.19% (oil yield)	Rebey et al. (2012)
Picea abies	Severe stress	NM	Lowered water potential, stomatal conductance, CO_2 exchange, total chlorophyll content and Fv/Fm ratio	36% (Fv/Fm), 30% (stomatal conductance)	Ditmarová et al. (2010)
Zea mays	NM	Vegetative stage	Reduced growth, biomass, relative water content, protein and starch content	NM	Sandhya et al. (2010)
Z. mays	NM	Germination and early growth stage	Lowered germination percentage, root and shoot length and seed vigour	71.2% (germination percentage), 60% (root length), 89.8% (shoot length), 91.7% (seed vigour)	Khodarahmpour (2011)
Gossypium herbaceum	Severe stress	Vegetative stage	Decreased net photosynthesis, stomatal conductance, transpiration, electron transport rates and quantum yield of PSII	35–50% (net photosynthesis), 35–95% (transpiration)	Deeba et al. (2012)

Table 1 (continued)

Crop/plant	Stress intensity	Stage	Effect on plant traits	Percentage reduction in physio-chemical attributes with respect to control	References
P. vulgaris	NM	NM	Reduced relative water content, number of grains in pod, plant length, increased pollen abortion, proline content	NM	Zadehbagheri et al. (2012)
Cleome gynandra	NM	NM	Combat oxidative stress by the upregulation of peroxidase, catalase, ascorbate peroxidase and glutathione reductase	NM	Uzilday et al. (2012)
Cleome spinosa	NM	NM	Increased activity of antioxidant enzymes such as POX, CAT, APX and GR	NM	

NM not mentioned, *WHC* water holding capacity

conditions, plant species, light intensity and soil conditions of a region (Tang et al. 2015). Plants are classified as either glycophytes (cannot tolerate salinity and ultimately die) or halophytes (can tolerate salinity) depending upon their adaptive mechanism to grow in saline soil (Acosta-Motos et al. 2017). Majority of crop plants are glycophytes and their growth get decreased or completely ceased under approximately 100–200 mM NaCl. On the contrary, halophytes can withstand 300–500 mM NaCl that might be attributed to improved tolerance mechanisms adopted by plants (Flowers and Colmer 2015; Acosta-Motos et al 2017).

Salinity stress is first sensed by roots of the plant that hinder plant growth for both short and long terms. The short-term effect is caused by decreased availability of water that induces osmotic stress in plants (Parihar et al. 2015). In contrast, long-term effect leads to salt-generated ion toxicity due to excessive amount of salt in plants (Parihar et al. 2015). Salt stress impairs germination, growth, photosynthesis, water status, oxidative stress and productivity of plants (Xu et al. 2011; Choi et al. 2010; Yousif et al. 2010; Ellouzi et al. 2011; Shekari et al. 2017). Germination of seeds is an important and fundamental aspect in the life cycle of plants that regulates yield and productivity. It is a complex process that causes oxidation of lipids and carbohydrates within seed and leads to break down of storage proteins to obtain energy for the development of plants (Tsegay and Gebreslassie 2014). Salinity affects the germination in different plants such as *L. sativa* (Nasri et al. 2011), *Lens culinaris* (Asgharipour and Rafiei 2011), *Lycopersicon esculentum* (Singh et al. 2012) and *Lathyrus sativus* (Tsegay and Gebreslassie 2014). According to Nasri et al. (2011), the exogenous application of NaCl (50–150 mM) decreased the final germination percentage in *L. sativa* which is correlated with the reduced activity of phytases and phytate-specific phosphatases in plants (Nasri et al. 2011). Moreover, Singh et al. (2012) reported that treatment of NaCl (1–3%) altered germination percentage and time needed to complete germination in tomato plants. The reduced speed of germination is attributed to the inability of gibberellic acid (GA) to break mechanical resistance of endosperm against imbibitions of water under saline conditions (Singh et al. 2012) (Table 2). Excess salts in the soil results in partial dehydration of cell cytoplasm that ultimately alters the metabolism of plants (Tsegay and Gebreslassie 2014). The inhibition of germination is also attributed to the change in the activities of certain enzymes and hormones in the plants (Kaveh et al. 2011). Singh et al. (2012) opined that salinity stress can lead to osmotic stress or ion toxicity that can affect the germination of plants.

Excessive amount of salts in water inhibits plant growth either due to reduction in the uptake of water leading to water-deficit in plants or by entering the transpiring stream and by injuring cells causing ion-excess in plant (Parihar

Table 2 Effect of salinity stress on physiological and biochemical plant traits

Plant	Concentration and stress intensity	Effect on plant traits	References
G. max	25–100 mM, (low stress)	Decreased root and shoot weight, plant height, leaf number and cortex thickness	Dolatabadian et al. (2011)
Capsicum annuum	100–200 mM, (low stress)	Decreased growth, and root/shoot dry weight	Siddikee et al. (2011)
Paulownia imperialis	20–160 mM, (low stress)	Declined protein concentration, Chl a, Chl b, β-carotene and violaxanthin content	Ayala-Astorga and Alcaraz-Meléndez (2010)
P. vulgaris	50–200 mM, (low stress)	Reduced dry matter content in root and shoot, photosynthetic pigments and phenolic compounds leading to oxidative stress	Taïbi et al. (2016)
Solanum tuberosum	25–50 mM, (low stress)	Decreased shoot biomass, root length, tuber yield, photosynthetic rate, stomatal conductance, leaf water potential but increased ABA content in plants	Akhtar et al. (2015)
Z. mays	25–100 mM, (low stress)	Inhibition of root and shoot length, root and shoot dry mass and concentration of N, Ca and Fe in shoot	Turan et al. (2010)
Mentha aquatica	50–150 mM, (low stress)	Decreased growth, relative water content, protein level, catalase, polyphenol oxidase and increased proline, malondialdehyde, and activities of superoxidedismutase, peroxidase and ascorbate peroxidise	Haddadi et al. (2016)
Thymus vulgaris	30–90 mM, (low stress)	Decreased plant dry matter, K^+ and Ca^{2+} content. Increased phenolic and flavanoid content	Bistgani et al. (2019)
Cucumis sativus	120 mM, (moderate stress)	Declined water potential, increased electrolytic leakage and ABA content	Kang et al. (2014a)
O. sativa	200 mM, (moderate stress)	Reduced fresh and dry weight, leaf relative water content, Chl a, Chl b, Fv/Fm and starch content	Amirjani (2011)
Lolium perenne	250 mM, (medium stress)	Increased lipid peroxidation, electrolyte leakage and hydrogen peroxide. Leaves exhibited higher activity of SOD, POD and APX	Hu et al. (2012)
Vigna radiata	NM	Decreased photosynthesis, higher Na^+ and Cl^- content and increased oxidative stress	Nazar et al. (2011)
Brassica juncea	NM	Decreased photosynthetic rate, electron transport and saturating photosynthetically active photo flux density	Mittal et al. (2012)
V. faba	60–240 mM, (moderate stress)	Reduced plant height, osmotic potential, Chl a, Chl b, total chlorophyll and carotenoids	Qados (2011)
S. lycopersicum	150–450 mM, (medium stress)	Inhibition of plant growth, chlorophyll and carotenoid content. Increased proline content and oxidative stress	Al Hassan et al. (2015)
Cakile maritima	100–400 mM, (medium stress)	Reduced osmotic potential and increased amino acids and proline content	Hmidi et al. (2018)
P. vera	800–3200 mg/Kg, (very high stress)	High oxidative stress, increased lipid peroxidation, electrolyte leakage and lipoxygenase activity	Tavallali et al. (2010)

et al. 2015). Choi et al. (2010) reported reduced growth in *Ulva portuca* under high salt concentration that might be attributed to decreased turgor pressure that restricts cell division (Choi et al. 2010). Similar results were observed by Amirjani (2010) and Qados (2011) on growth of *G. max* and *V. faba* under high salt concentrations. Rahneshan et al. (2018) conducted an experiment to evaluate the effect of NaCl (50–150 mM) on growth of two pistachio (*Pistacia vera*) rootstocks and found that moderate to high salt concentration negatively affects shoot and root length of the plants. The inhibition in growth under severe stress is corroborated with the reduced carbon assimilation caused by stomatal limitation or deterioration of metabolic processes in plants (Rahneshan et al. 2018). The decreased plant growth due to salt stress might be due to the negative effect of salt on the photosynthetic rate and enzyme activity that affects the synthesis of proteins responsible for growth (Qados 2011). Increased Na^+ ion is sensed by plants leading to immediate closure of stomata and inhibition of leaf expansion within minutes of exposure (Negrão et al. 2017). Later, due to excessive concentration of ion, premature senescence of leaf and reduction in yield occur in plants (Negrão et al. 2017).

Both Na^+ excess in cytosol and stomatal closure under salt stress affect the photosynthetic machinery of plants

resulting in the formation of ROS in green tissues (Shabala and Munns 2012). Salinity stress significantly alters the chlorophyll content and ROS accumulation that lead to oxidative damage in sorghum plants (Nxele et al. 2017). The reduced chlorophyll content is attributed to the increased H_2O_2 content that causes extensive cell death in plants (Nxele et al. 2017). Increased salinity stress conditions lowered stomatal conductance and transpiration rate in tomato plants that leads to reduced photosynthesis in plants (Marsic et al. 2018). Further, destruction of chlorophyll (chlorosis) in plants under salinity stress is a common symptom that results in inhibition of photosynthesis (Jha and Subramanian 2016). The loss of photosynthetic pigments in response to high salinity is responsible for lowered photosynthesis and altered stomatal behaviour that results in severe chlorosis and necrosis in plants (Muneer et al. 2014). Salinity stress leads to oxidative damage by generation of ROS in plants. Over-accumulation of ROS under salinity stress damages large macromolecules such as membrane lipids, proteins and nucleic acids (AbdElgawad et al. 2016). According to Jan et al. (2017), high salinity stress results in excessive MDA accumulation in plant tissues as a decomposition product of biomembranes. Salinity stress increased concentration of toxic Na^+ ion, MDA and H_2O_2 content in maize plants that causes oxidative stress in plants (Ashraf et al. 2018).

Effect of abiotic stresses on crop plants

Climate change induced variation in environmental conditions severely affect plant productivity and yield. These climatic fluctuations lead to abiotic stress in plants that mainly alters the performance of crop species. The major climate change-driven abiotic stresses in plants include elevated CO_2 concentration, high temperature, salinity and drought. The elevated CO_2 concentration has both positive and negative effects on morphology and physiology of crop plants. The greater CO_2 level causes increased photosynthesis in plants that positively affects the growth, biomass and yield of plants. For example, van der Kooi et al. (2016) observed increased photosynthetic carbon fixation, leading to higher growth and yield in plants under elevated CO_2. However, higher CO_2 concentration causes harmful effects on plants that hamper the crop quality by decreasing level of proteins, vitamins and minerals in crop plants (Thompson et al. 2017). Zhu et al. (2018) reported declined protein, iron and zinc content in rice plants in response to rising atmospheric CO_2 concentrations. Likewise, Goufo et al. (2014) documented reduced phenolic and flavonoid content in rice during seedling, tillering, elongation and flowering stage under elevated CO_2 conditions.

Under altering climatic conditions, drought and heat stress are the two limiting factors to crop performance.

Drought stress leads to decline crop yield by negatively affecting growth, physiology and development in plants. Daryanto et al. (2016) analysed the reduction in yield of crop plants from 1980 to 2015 and found that yield of the plants reduced to ~21 and ~40% for *T. aestivum* and *Z. mays*, respectively. Saeidi and Abdoli (2015) reported decreased net photosynthesis rate, stomatal conductance, transpiration rate and chlorophyll content in wheat leading to reduced yield in plants. Similarly, decrease in plant height, leaf size and stem girth was observed under water limiting conditions in maize plants (Khan et al. 2015a). Likewise, temperature extremes significantly hamper the crop production globally. Low temperature or cold stress leads to sterility and abortion of formed grains, while high temperature causes decreased grain number in wheat plants (Barlow et al. 2015). Cold stress has been reported to significantly reduce photosynthetic CO_2 uptake rate in sorghum plants (Ortiz et al. 2017). High temperature or heat stress causes declined seed weight and seed number in many cereals and legumes (Sehgal et al. 2018). The increased rate of seed filling due to heat stress might causes production of small and wrinkled seeds in chickpea (Kaushal et al. 2016) and lentil (Sita et al. 2017) plants that could be attributed to reduced translocation of photosynthesis to developing seeds (Farooq et al. 2017).

Climate change and ROS generation in plants

Abiotic stresses like elevated CO_2, heat, drought and salinity are now more common due to extreme variations in climate conditions (Pereira 2016). Plants are subjected to various stresses that lead to increased production of ROS that are chemically reactive and have a very short half-life (Sidhu et al. 2020). The presence of unpaired electrons in their valence shell makes these molecules highly reactive. They are found in different cellular organelles of plants like chloroplast, mitochondria and peroxisomes and recently also have been reported from apoplast (Roychoudhury and Basu 2012; Dar et al. 2017). Inspite of their toxic nature, ROS plays dual role in plants depending upon their amount, site and period of action, etc. (Miller et al. 2010). Generally at low concentration, ROS acts as a signalling molecule in mediating stress responses in plants, however at high concentration they pose serious harm to plants by causing programmed cell death (Petrov et al. 2015) (Fig. 4). Under optimum conditions, ROS molecules are unable to cause damage to plants since they are scavenged by antioxidant enzymes, however, due to various stresses the balance between ROS production and their scavenging by antioxidant enzymes gets disturbed (Gill and Tuteja 2010). This disruption causes enhanced generation of ROS that damages the cellular machinery of plants. ROS such as superoxide
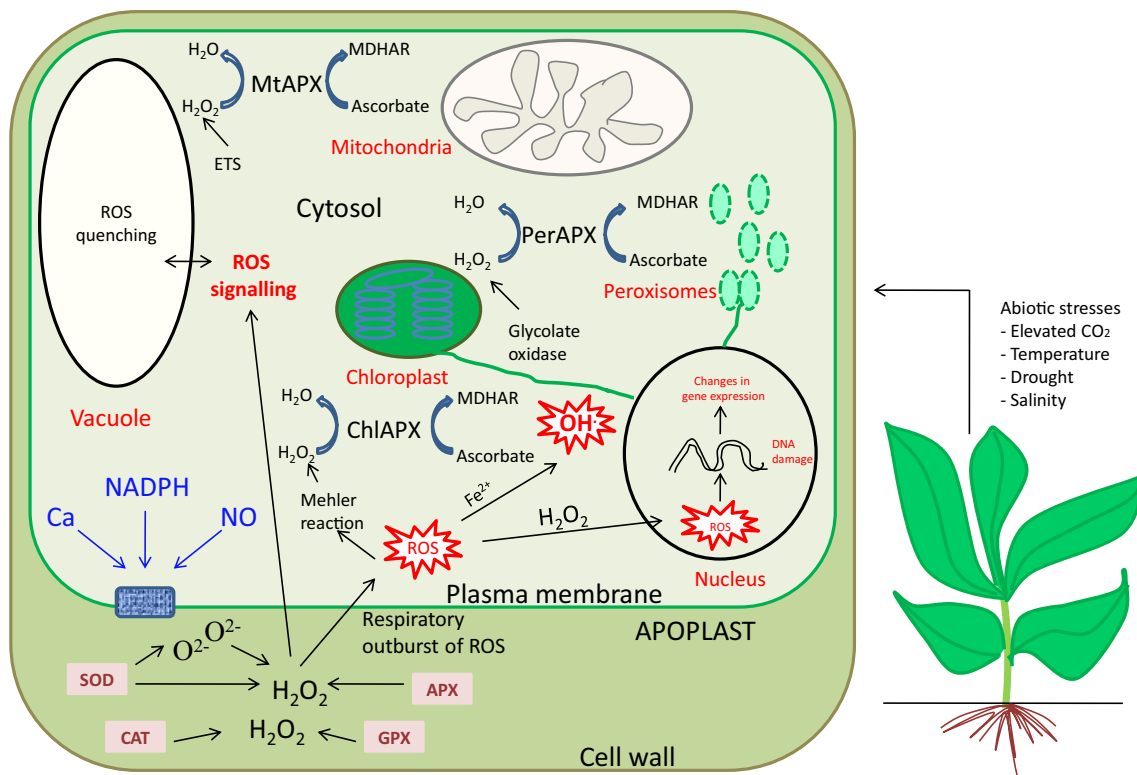
Fig. 4 Schematic presentation of ROS generation and its detoxification in different compartments of plant cell. Abiotic stresses induce oxidative outburst by generating ROS in the cellular compartments. ROS outburst at plasma membrane is modulated by calcium (Ca), phosphorylation, nitic oxide (NO) and NADPH, stimulating ROS signalling at apoplast. Transporter proteins mediate ROS transport to the cytosol, mitochondria, chloroplast and peroxisomes. ROS accumulation affects gene expression and disturbs redox homeostasis. Antioxidant enzymes like SOD, CAT, APX in cell organelles (mitochondria, chloroplast and peroxisomes) disintegrate noxious hydrogen peroxide into oxygen and water and promote plant performance to tolerate oxidative outburst

radical, hydroxyl radical, alkoxy radical, hydrogen peroxide and singlet oxygen are highly reactive and toxic and damage the bio-molecules like proteins, lipids, and DNA (Sidhu et al. 2017). During light conditions, major ROS generation occurs in chloroplasts and peroxisomes while during dark conditions, mitochondria serve as the main ROS producer (Choudhury et al. 2013). During stressful conditions, plants start to accumulate ROS in certain intra- and extra-cellular compartments (Carmody et al. 2016). It is notable that divalent ionic iron species (Fe^{2+}) in the cell form interactions with H_2O_2 to form noxious OH^- that induces oxidative outburst and promotes cell damage (Fig. 4).

Abiotic stresses that restrict CO_2 availability due to closure of stomata increase ROS production in chloroplast that start retrograde and anterograde signalling (Choudhury et al. 2017). The increased production of singlet oxygen in chloroplasts can also lead to chlorosis and programmed cell death in plants (Wagner et al. 2004). The production of ROS in plants can be either enzymatic or non-enzymatic (Apel and Hirt 2004). The stress induced by ROS at high concentration can instigate oxidation of biomolecules, disintegration of biomembranes, inactivation of enzymes and altered gene expression in plants (Singh et al. 2019). Drought also induces generation of free radicals that alters the antioxidant system of the plants. Drought aggravates stomatal closure, impared photosynthetic process and imbalance in light harvesting complex that causes ROS accumulation in plants (Hasanuzzaman et al. 2019). Number of studies have reported drought induced ROS generation and oxidative damage in plants. Campos et al. (2019) studied increased MDA content in *Coffea arabica* plants under drought stress. In another study, Abideen et al. (2020) revealed enhanced MDA content in *Phragmites karka* under drought stress for 35 days.

Temperature stress either high or low leads to enhanced ROS generation in plants that results in varied cellular metabolism, incremented lipid peroxidation, membrane degradation and ultimately cell death (Hasanuzzaman et al. 2020). Fahad et al. (2016) showed reduced quantum efficiency, blocked PSII electron flow and decreased PSII photochemistry in two rice cultivars under high temperature stress. In *C. sativus* seedling, high temperature enhanced superoxide ion content by 79.9% that generated oxidative stress in plants (Ding et al. 2016). Low temperature stress

(12 °C) for 6 days in rice seedlings cause increased MDA level and EL by ~ 180 and 49%, respectively (Han et al. 2017). Likewise, Xue et al. (2019) reported that wild plants of *Ammopiptanthus mongolicus* accumulated high H_2O_2 content compared to transgenic plants in response to low temperature stress, thus induced oxidative stress in plants.

Salinity stress causes varied metabolic complications in plants such as osmotic imbalance, nutrient deficiency, ion excess that results in overproduction of ROS and ultimately oxidative damage (Hasanuzzaman et al. 2020). In a study conducted by Cheng et al. (2020) on rice root tissues, it was reported that total content of ROS and lipid peroxidation in salt-stressed plants was two times higher compared with control. Similarly, Ahmad et al. (2019) reported twofold increase in the content of H_2O_2, electrolyte leakage, MDA and superoxide ion level in *V. radiata* plants upon exposure to 100 mM NaCl. The magnitude of oxidative damage due to salt stress varies among different genotypes within species. Mhadhbi et al. (2013) demonstrated the genotype-based interrelation between salt stress tolerance and ROS such as MDA and H_2O_2 in *M. truncatula* plants under salinity stress indicating different response strategy adapted by plants to cope stressful conditions.

Strategies adopted by plants to combat climate change induced abiotic stress

The alteration in the environment has a deep rooted effect on the growth and productivity of plants globally. Food security is severely harmed by the extreme climatic conditions and this is not a new problem. However, studies related to combat climate change are very few. For plants to acclimate to rapidly changing climatic stresses following methods are adopted.

Agronomic practices

Reports have demonstrated useful agronomic practices adopted by farmers such as alteration of irrigation techniques, crop rotation, variation in sowing and harvesting time and different cropping schemes that are very helpful for adaptation of crop under climatic or abiotic stress (Duku et al. 2018; Marcinkowski and Piniewski 2018; Deligios et al. 2019; Raza et al. 2019c). The alteration in sowing time of a crop will reduce the danger posed by varied climatic conditions and help crop plants to acclimatise in changed environment, thereby promising food safety and security globally (Ali and Erenstein 2017). Mylonas et al. (2020) reported that early sowing of wheat plants in South Europe resulted in the development of better root system before winters and making the plants tolerant to low winter temperature. Many studies have opined that delayed sowing

significantly affects the yield of wheat plants (Baloch et al. 2010; Dai et al. 2017). The abiotic stresses mainly drought and salinity negatively affect the crop production. The limited available water is the major factor that alters crop yield worldwide (Mylonas et al. 2020). The use of drought management strategies could lower the effect of drought stress in crop plants and will enhance crop development under stress. According to Mondal et al. (2015), drought stress in wheat can be handled by selecting proper early maturing cultivars so that the grain filling stage is completed before severity of stress. Grafting is another tool that can enhance water use efficiency in plants and can increase adaptation and performance of plants under dry environments (Mariani and Ferrante 2017). Furthermore, proper fertilisation can help in reducing the effect of abiotic stress and help the plants in better adaptability (Raza et al. 2019c). Fertilisers help in maintaining soil fertility and provide energy to plants, thereby enhancing crop productivity (Henderson et al. 2018). The use of nitrate fertilisers can enhance survival rate of plants under water excess (Mariani and Ferrante 2017). Reserchers have observed beneficial effect of calcium on both structure of soil and tolerance mechanism to plants under salinity stress (Elkelish et al. 2019). The application of different plant growth –promoting bacteria positively affects the crop tolerance to saline environment (Porcel et al. 2012).

Breeding techniques and genomics

Plant breeding techniques have shown better adaptability in crops under different abiotic stress environment. The development of stress resistance varieties helps plants to escape stressful conditions and promises food security under adverse climatic conditions (Blum 2018). According to Raza et al. (2018, 2019a), the use of genetic divergence analysis is an important aspect in breeding techniques that uses polymorphism, inbreeding, assortment and recombination to attain new varieties. During breeding techniques, phenotypic screening and germplasm collection of stress tolerant traits are done so as to develop stress tolerant varieties of plants. The advanced genomics technology involves high throughput genotyping and sequencing, Quantitative trait loci (QTL) mapping and isolation of stress responsive genes that help in developing tolerant cultivar. Further, marker-assisted selection (MAS) and genome wide association studies (GWAS) are important approaches involved in molecular and integrated breeding techniques that help in stress resistant varieties. In many crop plants, breeding techniques are integrated with genomic studies to achieve great success in molecular breeding and screen some traits that are helpful in providing resistance from stress (Roy et al. 2011). These advanced technologies help in making of climate-adapted crops that have enhanced yield and production in altered climatic conditions (Roy et al. 2011). MAS studies conducted

by Merchuk-Ovant et al. (2016) reported that ancestral QTL alleles from wild emmer wheat improved drought resistance and productivity in modern wheat cultivars.

Modification or manipulation of genes by biotechnology is an important approach that identifies stress responsive transcription factors (TFs) which help in developing stress resistant crop varieties. Genetic engineering is an important tool of biotechnology that helps in developing transgenic plants which show significant resistance against altered environmental conditions compared to normal plants (Raza et al. 2019a). The study conducted by Shah et al. (2016) on *S. lycopersicum* showed improved resistance of plants using gene *AtDREB1A* against cold stress by employing optimised *Agrobacterium*-mediated transformation system. Moreover, Li et al. (2015) opined that MYB (myeloblastosis oncogene) transcription factors play a key role in abiotic stress signalling in plants. Yang et al. (2012) demonstrated that a R2R3-type MYB gene, namely *OsMYB2* is involved in conferring cold, salt and dehydration tolerance in rice plants. They have been reported to play diverse roles in plant development and response to abiotic stress (Yang et al. 2012). In another experiment conducted by Liu et al. (2011b), expression of wheat *MYB* gene in transgenic tobacco enhances resistance towards drought and salt stress.

Phytohormones

Phytohormones are important regulators dealing with environmental stress responses in plants. They play a vital role in mediating various biochemical, physiological and signalling pathways under abiotic stress conditions (Sharma et al. 2019) (Table 3). Among different phytohormones such as abscisic acid (ABA), salicylic acid (SA), brassinosteroids (BR), jasmonic acid (JA) and ethylene (ET), ABA is the most important plant hormone that induces endogenous tolerance in plants under stresses (Kuromori et al. 2018). It plays a critical role in different phases of development in plants such as during opening and closing of stomata, seed germination and drought stress (Raza et al. 2019b). Under drought stress, plant growth gets adversely hampered that leads to enhanced ABA concentration in plant cells. The accumulation of ABA during drought stress regulates transpiration and stomatal closure (Dong et al. 2018a). Moreover, the osmotic stress generated in plants by either salinity or drought triggers ABA induced responses like closure of stomata, resulting in maintaining water balance in plants (Sah et al. 2016). The significant accumulation of ABA during stressful conditions is correlated with the enhanced level of ABA biosynthesis enzymes in plants (Kuromori et al. 2018).

Salicylic acid (SA) is a critical molecule that plays an important role in providing abiotic stress tolerance in plants (Khan et al. 2015b). It is involved in controlling crucial physiological processes like photosynthesis, nitrogen metabolism, osmolytes production (proline and glycinebetaine) and plant water relations under environmental stressful conditions thereby providing protection in plants against adverse abiotic stress (Khan et al. 2015b). SA has been shown to enhance plant tolerance to major climatic stresses such as salinity (Khan et al. 2019), drought (Sharma et al. 2018) and temperature (Nazar et al. 2017). Further, SA has been reported to activate various genes encoding heat shock proteins (HSPs) (Kumar et al. 2015), osmolytes (Sharma et al. 2019) and antioxidants (El-Esawi et al. 2017).

Jasmonic acid (JA) is an endogenous signalling molecule that is involved in multiple developmental processes besides providing stress resistance in plants (Llanes et al. 2016). JA is involved in mediating various physiological (regulation of stomatal movements, accumulation of soluble sugars) and molecular mechanisms (expression of JA-related genes) in plants under abiotic stress (Wang et al. 2020b). Under severe climatic conditions such as drought, temperature and salinity stress, JA induces enhanced antioxidant defense system to counter oxidative stress in plants (Ali et al. 2019; Ilyas et al. 2017; Sharma and Laxmi 2016).

Osmolytes

Osmolytes or osmoprotectants are compatible solutes that maintain water balance in the cell without disturbing normal processes of plants. These organic metabolites control osmotic adjustment in the plants. Osmolytes assist in combating adverse osmotic stress during different phases of plant's development (Sharma et al. 2019). They are inert molecules that protect large biomolecules such as proteins, nucleic acids and lipids and other membranes from oxidative damage caused by various abiotic stresses in plants (Singh et al. 2015). Plants have developed many tolerance mechanisms, one of them is accumulation of osmolytes to mitigate drought stress (Rajasheker et al. 2019; Bhuiyan et al. 2019). The compatible solutes like proline, trehalose, sucrose and glycine betaine (GB) get accumulated to maintain water status of plants during drought stress. Anjum et al. (2017a) observed reduced growth, yield and excessive generation of ROS that leads to oxidative stress in maize plants under drought stress. The accumulation of solutes develops negative osmotic potential of cell due to which water enters the cell to regulate turgidity. This osmotic adjustment is attributed to the aggregation of osmolytes in plants (Sharma et al. 2019).

Accumulation of proline is an important adaptive strategy adopted by plants under drought stress. Per et al. (2017) documented role of proline biosynthesis and signalling in maintaining redox balance of cell under drought stress. Moreover, Ghaffari et al. (2019) observed proline-mediated alterations in activities of antioxidant enzymes and physiology of *B.*

Table 3 Different phytohormones and their role in conferring plant tolerance against different stresses

Plant	Abiotic stress	Phytohormone (concentration)	Mechanism involved	References
	Drought	**Abscisic acid**		
Aristotelia chilensis	Withholding water to initiate drought	100 µM	Higher anthocyanin biosynthesis	González-Villagra et al. (2019)
Camellia sinensis	Mild-severe drought	50 mg/L	Enhanced lipid and flavanoid metabolism	Gai et al. (2020)
O. sativa	Withdrawing water for 7 days and re-watering for 7 days	0.1 mM	OsSAPK2 induced upregulation of stress-responsive genes	Lou et al. (2017)
Lolium perenne	Witholding irrigation for 45 days	0.054 kg ai/ha	Increased antioxidant enzymes activity	Mohammadi et al. (2017)
Z. mays	NM	1–10 mg/Kg	Peaked level of endogenous ABA, antioxidant enzyme activity and Asr1 gene expression	Yao et al. (2019)
		Cytokinin		
Agrostis stolonifera	Water content equivalent to 50% evapotranspiration (ET) during 1–19 d, 40% ET during 20–32 d, and 20–30% ET during 32–40 d	10 and 100 µM	Improved activities of antioxidant enzymes under high nitrogen concentration	Chang et al. (2016)
O. sativa	Soil moisture tension of − 15, − 55, − 60, − 72 kPa	5 mg/L	Retained normal levels of chlorophyll synthase	Gujjar et al. (2020)
Z. mays	NM	50–150 mg/L	Enhanced level of endogenous cytokinin	Akter et al. (2014)
		Auxin		
Z. mays	Plants were drought stressed by withholding water	NM	Increased yield of plants due to overexpression of ZmPIN1a	Li et al. (2018)
O. sativa	NM	0.5 µM NPA	Over-expression of OsPIN3t gene led to longer roots	Zhang et al. (2012)
		Gibberellins		
G. max	15% PEG solution	NM	Improved plant growth and crop productivity	Kang et al. (2014b)
S. lycopersicum	Irrigation suspended for 7 days	NM	Upregulation of SlDREB2 gene that modulated water use efficiency in plants	Gaion et al. (2018)
		Salicylic acid		
Brassica rapa	Drought stressed plants (30 ml of nutrient solution) compared to 150 ml in control plants	1.5 mM	Increased proline content and balanced redox status	Lee et al. (2019)
Lippia citriodora	25, 50, 75 and 100% F.C	150 and 300 mg/L	Increased amount of sugar, proline and antioxidant enzymes	Dianat et al. (2016)
T. aestivum	NM	NM	Enhanced defense and enegy metabolism	Sharma et al. (2017)
		Jasmonic acid		
Arabidopsis thaliana	10 day without watering	0.01, 0.1, 1 or 10 µM MeJA	Increased VaNAC26 promoted activities of antioxidant enzymes	Fang et al. (2016)
Beta vulgaris	Plants were drought stressed by withholding water	**Brassinosteroid**	Delayed plant dehydration and protected photosynthetic apparatus	Fugate et al. (2018)
V. unguiculata	Water was removed completely	50–100 nM	Improved photosystem II efficiency, gas exchange, antioxidant enzymes	Lima and Lobato (2017)
L. esculentum	Water was withheld for 30 days	1–3 µM	Upregulated SOD activity, fruit yield and other physiological processes	Jangid and Dwivedi (2017)
	Salt stress	**Abscisic acid**		

Table 3 (continued)

Plant	Abiotic stress	Phytohormone (concentration)	Mechanism involved	References
Z. mays	25–100 mM	NM	Regulated root ion fluxes and water uptake	Zhang et al. (2016)
O. sativa	120–250 mM	NM	Improved plant physiology	Shahzad et al. (2017)
Sesbania cannabina	200 mM	100 µM	Increased strigolactones enhanced salt tolerance	Ren et al. (2018)
		Cytokinin		
Malus domestica	100 mM	0.3 mg/L	Expression of IPT5b gene maintains high cytokinin level and confer salt tolerance	Feng et al. (2019b)
A. thaliana	300 mM	10 µM BAP	Activate gene expression related to growth processes	Golan et al. (2016)
		Auxin		
S. lycopersicum	250 mM	NM	Accumulation of SlARF gene under stress	Bouzroud et al. (2018)
		Gibberellins		
C. sativus	100 mM	100 µM	Enhanced expression of GT-3b gene	Wang et al. (2020d)
G. hirsutum	200 mM	NM	Expression of GhGA2ox1 gene increased tolerance	Shi et al. (2019)
		Salicylic acid		
S. lycopersicum	100 mM	0.01 mM	Improved photosynthesis and induction of compatible osmolytes	Mimouni et al. (2016)
Dianthus superbus	0.3–0.9%	0.5 mM	Enhanced antioxidant metabolism	Ma et al. (2017)
		Jasmonic acid		
Ipomoea batatas	200 mM	NM	Upregulation of genes related to jasmonic acid biosynthesis, ion transport	Zhang et al. (2017a)
S. lycopersicum	200 mM	1 nM	Boosted synthesis of flavonoid, proline, glycine betaine	Ahmad et al. (2018)
		Brassinosteroid		
M. piperita	100 and 150 mM	0.5–2.5 mg/L	Decreased membrane permeability, lipid peroxidation and improved antioxidant enzyme activities	Çoban and Baydar (2016)
Eucalyptus urophylla	250 mM	0–50 nM	Increased activities of CAT and APX, photosynthetic pigments and photochemical efficiency	de Oliveira et al. (2019)
	Temperature stress	**Abscisic acid**		
A. thaliana	4 °C	20 µM	Increased STRP (Salt tolerance-related protein) level that promotes seed germination, root development during cold stress	Fiorillo et al. (2020)
O. sativa	39–41 °C day and 30 °C night	1–100 µmol/L	Enhanced sucrose transport and sugar metabolism under high temperature	Rezaul et al. (2019)
		Cytokinin		
A. thaliana	NM	NM	Expression of CRF2 (CYT OKININ RESPONSE FACTOR2) and CRF3 control lateral roots formation under cold stress	Jeon et al. (2016)

Table 3 (continued)

Plant	Abiotic stress	Phytohormone (concentration)	Mechanism involved	References
O. sativa	Day temperature 36.1 °C and night temperature 31.9 °C	60 mg/L BAP	Enhanced transport of cytokinin and cytokinin oxidase/dehydrogenase under heat stress	Wu et al. (2017)
		Gibberellins		
S. lycopersicum	4±1 °C	0.2 mmol/L	Decreased electrolyte leakage, MDA content and increased proline content under chilling stress	Ding et al. (2015)
		Auxin		
G. hirsutum	39±2 °C (day) 29±2 °C (night)	1×10^{-6} mol/L	Auxin synthesis mediated by miRNAs modulates male sterility under high temperature	Ding et al. (2017)
Nicotiana tabacum	Day/night temperature 37 °C/32 °C	100 nM	Overexpression of *OsPT8* increased expression of auxin synthesis genes under high temperature stress	Song et al. (2019)
		Salicylic acid		
T. aestivum	8/4 °C, day/night	NM	Improved photochemical efficiency of photosystem II, accumulation of osmoprotectants under low temperature	Wang et al. (2020c)
Digitalis trojana	45 °C	0.25 mg/L	Activated antioxidant responses in plant under high temperature	Cingoz and Gurel (2016)
		Jasmonic acid		
Prunus persica	4±1 °C	30 µmol/L	Promoted ethylene production and maintain sugar content under chilling stress	Zhao et al. (2020)
A. thaliana	4 °C	50 µL	Freezing tolerance by modulating jasmonic acid signalling and antioxidant metabolism by cyclophilin *AtROC1^{S58F}*	Weng et al. (2020)
		Ethylene		
Vitis vinifera	4 °C	100 µM	Modulated the expression of *ETHYLENE RESPONSE FACTOR 057* under low temperature stress	Sun et al. (2016)
		Brassinosteroid		
C. annuum	15/5 °C, day/night	0.1 µM	Miantain high photosynthetic capability and enhanced nitrogen metabolism under chilling stress	Yang et al. (2019b)
Solanum melongena	43/38 °C	0.05–0.2 µM	Inhibited ROS and lipid peroxidation and increased activity of SOD, CAT, APX and POX under high temperature	Wu et al. (2014)

ET evapotranspiration, *FC* field capacity, *MeJA* methyl jasmonate, *EBL/EBR* 24-epibrassinolide, *BAP* 6-benzyl aminopurine, *NPA* naphthylphthalamic acid, *PEG* polyethylene glycol

vulgaris under drought stress. GB is another osmolyte that mediates plant tolerance against drought stress. Recently, Nawaz and Wang (2020) studied GB-mediated tolerance mechanism in *Axonopus compressus* under drought stress and reported that GB treatment decreased hydrogen peroxide and malondialdehyde content and increased soluble sugars, proteins, phenolics and antioxidant enzyme activity in stressed plants. Trehalose, an osmolyte, enhanced plant resistance to water deficit stress by activating antioxidant defence system in *Chenopodium quinoa* (Sadak et al. 2019). The increased activity of antioxidant enzymes by accumulation of different osmolytes leads to quenching of ROS that helps in maintaining stability of membranes. Furthermoire, accumulation of osmolytes is one of the important strategies adopted by plants to tolerate salt stress. Reports by Khator and Shekhawat (2019) and Ahanger et al. (2019) have suggested the role of osmolytes in modulating growth and metabolism in plants under salt stress.

Heat shock proteins

Heat shock proteins (HSPs) are an important class of molecular chaperons that maintain cellular balance under both normal and stressful conditions. They have been classified into five categories in plants, namely Hsp100, Hsp90, Hsp70, Hsp60 and sHsp (Mishra et al. 2018). HSPs play vital role in response to different abiotic stresses in plants such as temperature, salinity, drought (Zhang et al. 2017b; Reddy et al. 2014; Mishra and Grover 2016). However, the role of HSP is more in relation to heat stress compared to other stresses.

The omics studies during last 10 years revealed role of HSP in controlling high temperature stress (Li et al. 2013; Singh et al. 2016). HSPs are important for maintaining balance and structure of proteins under high temperature stress (Khan and Shahwar 2020). The genes for HSPs are present in plants under normal environmental conditions but exposure to heat stress leads to expression of these genes in them. HSPs play role in signal transduction during stress, protection and repair of damaged membranes and regulation of redox balance in plants (Asthir 2015). Plant species such as maize, wheat, soyabean acclimate high temperature stress by synthesising HSPs when their temperature surpasses 32–40 °C (Yadav et al. 2020) (Fig. 3). According to Usman et al. (2017), HSP70 is found to be the most abundant heat shock protein that protects plant cells from negative effects of heat stress. Moreover, enhanced expression of *Brassica campestris* Hsp70 in transgenic tobacco imparted heat tolerance to the plant by increasing superoxide dismutase and peroxidase activity, soluble sugar content and decreasing electrical conductivity compared to control (Masand and Yadav 2016). Similary, the expression of Hsp90 is enhanced by many folds upon exposure to heat stress (Reddy et al. 2016). A study conducted by Wang et al. (2016) reported

that rise in temperature promoted accumulation of *TIR1* auxin co-receptor and that interacted with Hsp90 and its co-chaperone *SGT1* and regulated *Arabidopsis* seedlings growth in altering environment. The results also revealed that inhibition of Hsp90 resulted in degradation of *TIR1* that leads to defects in auxin-mediated responses in plants (Wang et al. 2016).

Cold stress reduces uptake of water and nutrients in plants leading to starvation in cells. Plants synthesise a range of proteins to withstand low temperature conditions. To adapt to changing environmental condition, induction of HSP is a crucial step adopted by plants. Several studies reported the role of Hsp70 in different crop plants such as barley (Hlaváčková et al. 2013), tobacco (Jin et al. 2011) and wheat (Kosová et al. 2013) in imparting tolerance against low temperature stress. Recently, Elkelish et al. (2020) reported tolerance in tomato plants under chilling stress by enhanced expression of CAT, HSP70, HSP80 and HSP90 genes. The authors corroborated the tolerance mechanisms adopted by plants against chilling conditions with the increased expression of HSPs that reduced the intensity of oxidative damage induced by cold stress (Elkelish et al. 2020).

Drought stress is one of the primary factors that can affect growth and development of plants. During stressful conditions, proteins get denatured and loose their native functions resulting in decreased crop yield and quality (Feng et al. 2019a). HSPs protect plants and avoid injuries caused by drought stress (Ruibal et al. 2013). A study conducted by Huang et al. (2019) reported that heat and drought stress induced expression of *CaHsp16.4*, a small HSP gene in *C. annuum*. Lim and Kim (2013) analysed the effect of plant growth promoting rhizobacteria (PGPR) in relation to drought resistance in pepper plants and found that PGPR-inoculated plants expressed sHSP genes and showed drought tolerance compared to non-inoculated pepper plants. Similarly, Wang et al. (2015) reported that overexpression of *OsHSP18.6* induced increased tolerance to drought stress in rice plants.

Antioxidative metabolism

Climate change-induced stress is a regular phenomenon in plants. ROS accumulation causes severe harm to the cellular machinery in plants. Under normal conditions, scavenging mechanisms that include antioxidants and enzymes counteract on these ROS and convert them into less harmful products in the cell (Sidhu et al. 2016). However, during stress the redox balance of cell gets completely disturbed leading to excessive accumulation of ROS (Sidhu et al. 2018). The antioxidant defense system consists of low molecular weight non-enzymatic antioxidants (AsA, GSH, flavonoids, alkaloids and phenolic compounds) and antioxidant enzymes (SOD, CAT, POX, APX, GR, GPX) that impede

ROS overproduction in plants (Sidhu et al. 2017, 2019). The enzymatic and non-enzymatic antioxidants work in coordinated manner to inhibit ROS over-production in plants (Laxa et al. 2019). SOD, an enzymatic antioxidant triggers the first line of defence against stress by initiating the conversion of superoxide ion into H_2O_2, that further gets transformed into H_2O by CAT, GPX, APX or Asada-Halliwell cycle (AsA-GSH cycle) (Sidhu et al. 2016, 2017, 2019). The Asada–Halliwell cycle plays a pivotol role in antioxidant defense system in plants by inhibiting H_2O_2 overproduction and maintaining redox balance (Hasanuzzaman et al. 2019).

Plants initiate the antioxidant defense system to alleviate detrimental effect of oxidative stress. The antioxidant machinery has been reported to mitigate adverse effect of salt stress in plants (Jiang et al. 2019; Sehar et al. 2019; Zhang et al. 2020). The studies conducted by various researchers have opined that variation in the activities of antioxidant enzymes mainly depend upon the duration and extent of salinity stress and the developmental stage of plant (Li et al. 2019b). For instance, Meng et al. (2020) reported that overexpression of *IbNAC7* in transgenic *Arabidopsis* plants conferred salt tolerance compared to wild type plants by inducing higher activity of CAT and proline in them. In another study conducted by Cantabella et al. (2017), *Stevia* plants could tightly control the accumulation of ROS under salinity stress by initiating different antioxidant mechanisms. The results revealed increased level of antioxidant enzymes (APX, POX, CAT and SOD) and ASC-GSH cycle enzymes in *Stevia* after 16 d treatment of NaCl that helped in removal of H_2O_2 in plants (Cantabella et al. 2017). Similarly, Shafi et al. (2017) found that expression of SOD and APX genes in transgenic potato enabled the plants to withstand severe saline conditions. The exogenous application of different chemicals or natural agents under salt stress has strongly corroborated the role of antioxidant machinery in alleviating salt stress (Ahmad et al. 2016; Li et al. 2017). For instance, Chen et al. (2018) reported that exogenous application of melatonin alleviated ROS and protected photosynthetic activity in maize seedlings under salt stress by activating antioxidant enzymes. Similarly, Sheyhakinia et al. (2020) studied the effect of jasmonic acid in enhancing salt stress tolerance in *Hibiscus sabdariffa* seedlings by increasing antioxidant enzymes activity. Thus, the plant antioxidant system plays an important role in salinity stress tolerance.

Drought stress has been recognised as an important stress faced by crop plants. Many reports have suggested the role of antioxidant system as an important adaptive strategy to combat drought stress in plants (Hasanuzzaman et al. 2018; Gaffari et al. 2019; Wang et al. 2019). The activity of antioxidant system under drought stress was studied in drought sensitive and drought resistant rice cultivars by Wang et al. (2019). The results revealed that under drought stress, the activity of SOD, POD and CAT increased in plants (Wang

et al. 2019). Anjum et al. (2017b) compared the activity of antioxidative defense system in maize hybrids. The results revealed stimulated enzymatic (SOD, APX) and non-enzymatic (AsA, GSH, DHA) antioxidative mechanism in all the hybrids that provided protection against oxidative stress and enhanced plant tolerance under drought conditions (Anjum et al. 2017b). Hussain et al. (2018) studied drought stress in six different citrus root stocks and found that the tolerant rootstocks exhibited less amount of MDA and H_2O_2 and increased amount of antioxidant enzymatic activities (SOD, CAT and POD) to counter with ROS produced during drought stress. Likewise, Mehrabad Pour-Benab et al. (2019) observed the expression of antioxidant genes and enzymatic antioxidant defense under drought stress in wild relatives of wheat and reported that drought stressed conditions increased the activities of SOD, APX and GPX in plants.

Temperature stress tolerance is positively correlated with enhanced antioxidant defense mechanism to combat ROS detoxification in plants however antioxidant mechanism varies between tolerant and sensitive genotypes (Hasanuzzaman et al. 2012). A study was conducted by Yang et al. (2019a) that investigated antioxidative response of *Ulva prolifera* to high temperature (approx. 36 °C) and low temperature (approx. 4 °C) stress. The results revealed that under high temperature the activities of SOD, CAT and APX increased compared to low temperature treatments (Yang et al. 2019a). Tutar et al. (2017) opined that genes from SOD family play a vital role in thermal stress response of Mediterranean seagrasses. The authors reported that shallow and deep ecotypes of *Posidonia oceanica* showed varied timing of response to heat (Tutar et al. 2017). According to Tao et al. (2020), the heat-resistant rootstock of bitter melon improved heat tolerance in cucumber by enhancing the activity of SOD, POD and APX in plants. In another example, Wang et al. (2020a) studied chilling stress in sensitive and tolerant genotypes of *B. campestris*. The chilling tolerant genotype exhibited activation of APX, GR, AsA and GSH metabolism (Wang et al. 2020a). Similarly, Han et al. (2017) treated rice seedlings to low temperature stress and reported enhanced activity of SOD and CAT in plants. The studies have revealed that climatic variations trigger antioxidative response in plants to counteract oxidative stress induced by different abiotic stresses.

Biostimulants

Worldwide, the agriculture sector is facing serious challenges of increasing the productivity to meet the growing food demand of population. The use of herbicides and pesticides play an important role in increasing crop yield and ensuring productivity of plants. However, use of synthetic agrochemicals poses harm to soil fertility. In this regard, the use of plant biostimulants increases plant growth, flowering,

fruit set, productivity and tolerance against abiotic stresses (Van Oosten et al. 2017). Biostimulant can be defined as any organic compound or microorganism that stimulates nutrient efficiency and crop quality in plants. They play a major role in mitigating drought (Goñi et al. 2018), salt (Desoky et al. 2018) and temperature stress (Francesca et al. 2020) in plants.

Drought stress limits productivity and yield of plants. Biostimulants are one of the methods to improve plant resistance towards drought stress. Kałużewicz et al. (2017) reported that application of biostimulants (amino acids and *Ascophyllum nodosum* filterate) on *Brassica oleracea* var. *italica* increased photosynthetic rate, stomatal conductance, internal CO_2 concentration and transpiration under drought stress. Recently, Taha et al. (2020) investigated the effect of palm pollen grain extract on growth, physio-biochemical attributes, water-use efficiency and antioxidant defense system in basil (*Oscimum basilicum*) plants under drought stress. The results revealed improved growth, leaf photosynthetic pigments, soluble sugars, ascorbic acid, free proline and antioxidant enzyme activities in plants.

Salinity stress has adverse effects on the growth of plants. Biostimulants application has shown to provide tolerance towards salinity stress in plants. For example, Campobenedetto et al. (2021) reported improved tolerance to salinity in tomato plants upon application of tannin-based biostimulants. Arroussi et al. (2018) investigated the effect of *Dunaliella salina* (a microalgae) exopolysaccharides on growth, protein content and antioxidant enzyme activities in *S. lycopersicum* plants under salt stress. The results revealed enhanced growth, protein and antioxidant enzymes (CAT, POD, SOD) in salt stressed tomato plants (Arroussi et al. 2018). Similarly, under low temperature stress, the germination of seeds reduced in *Ceratotheca triloba* plants (Masondo et al. 2018). However, application of biostimulants (smoke water, synthesized smoke-compound karrikinolide, commercial seaweed extract and phloroglucinol) enhanced seed germination and improved seedling growth in plants (Masondo et al. 2018). Likewise, Francesca et al. (2020) used biostimulant-based plant and yeast extracts that enhanced yield and quality in tomato plants under increased temperature.

Future challenges

Climate change driven by anthropogenic activities is increasing significantly, leading to extreme variations in the temperature and availability of water. Agriculture-dominated areas are now facing increased temperature integrated with decreased precipitation that has led to abiotic stress induced loss in yield of the plants. This calls for the development of new plant varieties resistant to environmental variations.

However, despite advancement in the field of molecular biology, there are very few studies pertaining to the integration of environmental resilience methods directly into plants growing in the fields. Thus, to fulfil the food requirement of the increasing population, the biotechnological and breeding programmes need to be enhanced to produce environmentally resistant crops.

Despite the above-mentioned challenge, it is very important that discovery of physiological and molecular pathways related to changing envirionment should be more concentrated on dynamic environment. The combined effect of abiotic stresses is not additive since it relies upon interaction between stresses themselves and plant responses. Rising atmospheric CO_2 concentration may stimulate the crop yield in some crops, but with the increase of drought, the growth of these plants would diminish as the stomatal functions may be modified due to the interaction of the two stresses. From the recent researches, it is recognised that future studies should focus on the interactive effect of these abiotic stresses especially elevated CO_2 with temperature and water availability in plants that are an important component of climate change. Since, the climate change predictions suggest that ecological damage will be more frequent and severe in near future, there is more need for plant breeders, researchers and those working in the field of agriculture and crop improvement strategies to integrate the knowledge of abiotic stress physiology into development of novel crop varieties.

Conclusions

The fluctuations in climatic factors mainly elevated CO_2 levels, temperature, drought and salinity, adversely impact the performance of plants. Based on the literature review, we found that ~ 4–5 °C rise in day and night temperature from normal, enhanced ROS generation with a parallel decrease in the physiological processes in plants. It affected both the vegetative and reproductive stage of plants and its impact varied from species to species. Similarly, based on previous findings of the researchers, we observed that severe drought stress experienced by different plant species hampered the photosynthesis process in plants that ultimately leads to reduced growth and yield of the plants. Most of the plant species studied under varied abiotic stresses exhibited increase in ROS, RNS, and proline content with a parallel reduction in growth, accompanied by decrease in chlorophyll content. Salinity stress has shown to reduce dry mass, pigment concentration and phenolic content in plants. Very high concentration of salts (~ 400 mM) causes reduced osmotic potential and promotes oxidative stress in plants due to enhanced electrolyte leakage of the plant tissues that influence lipid peroxidation. Researchers have reported different phytoregulators like phytohormones, osmolytes,

biostimulants etc., in conferring plant tolerance towards different abiotic stresses by increasing the protein, proline and antioxidant metabolism in different plant species. The activities of antioxidant enzymes like SOD, CAT, POD increased profoundly in plant species to combat oxidative distress induced due to climatic variations.

Declarations

Conflict of interest The authors have no conflict of interest.

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