

Chapter 5

Abiotic Stress: Its Outcome and Tolerance in Plants



P. Rawat, D. Shankhdhar, and S. C. Shankhdhar

Abstract The onset of nineteenth century along with anthropogenic pressure paved the way for global climatic variation which is a major factor for global undernourishment, malnutrition and endangered food security. The major upshot of climate change is abiotic stress like salinity, flood and drought that declines the agricultural productivity. Abiotic stress hampers the survival of the plants and restricts their growth and development. Each abiotic stress confers negative impact on plants by altering its physiology, morphology and metabolism. Production of reactive oxygen species during stress condition alters the structure and metabolic function in plants and restricts its growth. Drought is one of the serious threats to crop productivity among the abiotic stress that imposes multidimensional effects on plants. Drought alters physiology and anatomy of the plants and is the main reason for economic loss in terms of livestock and grain yield in both developed and developing countries. Plants adapt several resistance mechanisms to cope up with the drastic impact of stress. Main tolerance mechanisms are alteration in membrane structure, escaping the unfavourable conditions, activation of antioxidant defense system, production of compatible solutes for maintaining osmotic balance of the cell. Present manuscript focuses on the outcome of major abiotic stress in plants and their tolerance strategies against the variable environmental conditions.

5.1 Introduction

Contemporary civilization and industrialization have led to global climate change whose consequences like flood, drought, high temperature and global warming are quite perceptible and hazardous for soil health, microbial diversity and sustainable crop production. Climate fluctuation also threatens the vulnerable and endangered organisms in the ecosystem that are incompetent to endure such environmental changes in their habitat. Climate variability has immense impact on food security.

P. Rawat (✉) · D. Shankhdhar · S. C. Shankhdhar
Department of Plant Physiology, College of Basic Sciences and Humanities, G. B. Pant
University of Agriculture and Technology, Pantnagar, Uttarakhand, India

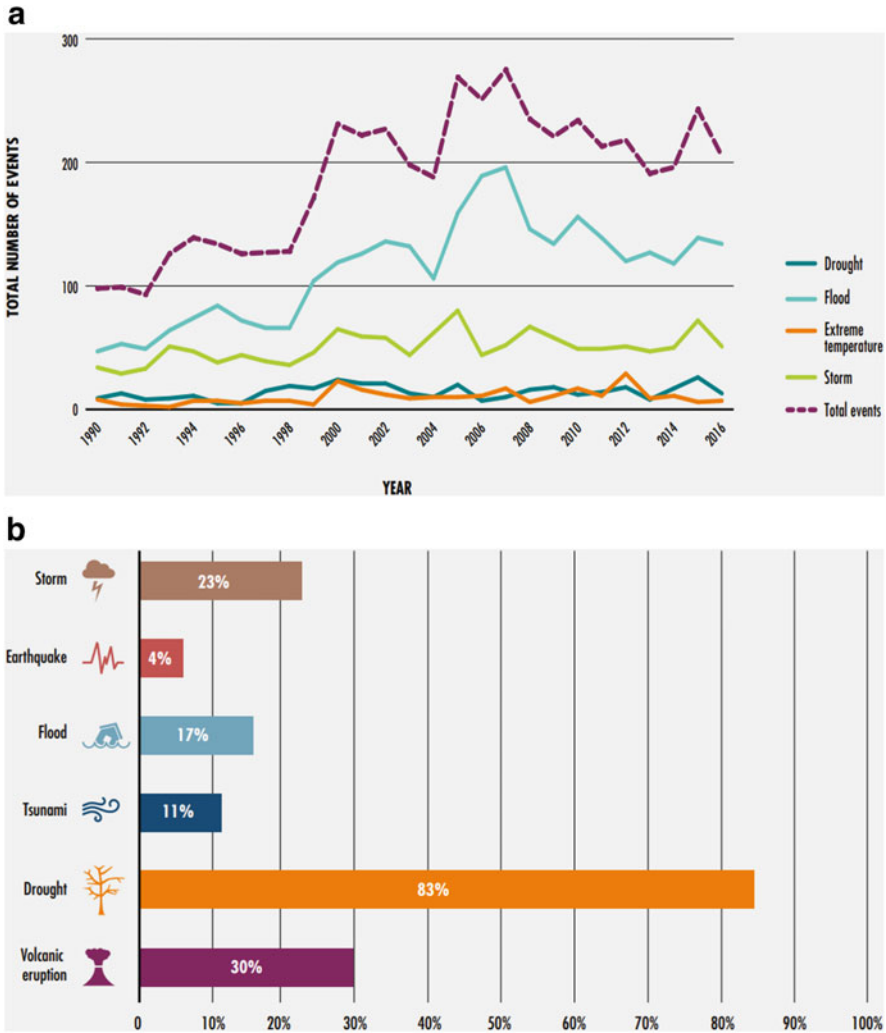


Fig. 5.1 (a) Rise in the calamitous events (1990–2016). Adopted from FAO (2018). (b) Damage and loss in agriculture as share of total damage and loss across all sectors by type of hazards. Adopted from FAO (2018)

It hits the underdeveloped regions of the world causing yield and economic losses. It has been estimated that 26% of total loss was in agriculture sector due to calamitous events from 2006 to 2016 (FAO 2018). Figure 5.1a, b illustrates the severity of disastrous events in the past years along with its impact on agricultural sector. There has been a dire inflation in the number of undernourished people across the world from 806 million in 2016 to 821 million in 2017 as an outcome of climate shock (FAO 2018). In view of the above facts, the foremost challenge is to provide food security to the projected global population of about 9.7 billion in 2050 under climate fluctuation and dwindling crop productivity.

Abiotic stress is an aftermath of climatologically variation that ceases plant growth, development and productivity below optimum levels. A surfeit or scant in energetic, chemical or physical condition in the nature paved the origin of abiotic stress in plants. The utmost abiotic stress comprises of drought, salinity, flooding and oxidative stress that abolishes metabolic equilibrium of plants thereby threatening food security (Fedoroff et al. 2010). Economic forfeiture in the developing countries in terms of crop and livestock production was discerned up to USD 96 billion from 2005 to 2015 with a 2.6% decrement in national agricultural value added growth due to occurrence of each climatic hazards (FAO 2018). An alarming upshot of climate shock is forecasted to decline agriculture productivity and influence five billion people by 2050 (UNESCO 2018; Watts 2018).

5.2 Abiotic Stress in Plants

5.2.1 Salt Stress

One of the most detrimental climate shocks is salinity stress which is prevalent in arid and semiarid regions in the world as depicted in Fig. 5.2. Approximately 33% of the world's irrigated land and 20% of overall cultivated land are devastated by salinity stress (Shrivastava and Kumar 2015). It has been forecasted that by 2050 around 50% of arable land would be influenced by salinity (Jamil et al. 2011). In India seven million hectares of land is sheathed by saline soil (Patel and Dave 2011). An electrical conductivity of precisely 4 dSm^{-1} of saturation extract from root zone at 25°C marks the saline soil (Jamil et al. 2011). Salinity damages the agricultural productivity as the major food crops are susceptible to it. A remarkable yield loss of



Fig. 5.2 Salt affected regions of the world. Adopted from FAO (2016)

about 65% in wheat was evident as an outcome of salinity stress (Ahmad et al. 2013). Yield reduction of about 55% in corn and cotton was observed in case of salinity in the range of about 8–10 dSm⁻¹ and 18 dSm⁻¹, respectively (Satir and Berberoglu 2016; Zörb et al. 2019).

5.2.2 Impact of Salinity Stress in Plants

Salinity stress devastates the plants by two ways: (a) Osmotic effect that diminishes plant potential for water uptake due to excess salt in soil and (b) ion excessive effect that occurs due to accumulation of excess salt in the leaf tissues (Greenway and Munns 1980). Salinity amends the major physiological processes like photosynthesis, transpiration, nutrient regulation and osmotic balance as an outcome and affects plant growth and yield. Influence of salinity stress in plants has been illustrated in Table 5.1.

Table 5.1 Outcome of salinity stress in plants

Parameters	Alterations	References
Germination	Hinders water imbibition by seeds	Khan and Gul (2006)
	Alters the enzyme activity requisite for metabolic functions	Gomes-Filho et al. (2008)
	Deteriorates seed coat, diminishes the seed vigour index and surges seed dormancy	Panuccio et al. (2014)
Water relation	Osmotic imbalance leading to soaring salt concentration near roots	Munns (2005)
	Decrement in relative water content and turgor pressure	Ghoulam et al. (2002)
Plant growth	Minimizes water retaining capacity of plant	Munns (2002b)
	Enhances ion toxicity that results in early leaves senescence	Munns (2002a, 2005)
Photosynthesis	Accumulation of Na ⁺ and Cl ⁻ ions in chloroplasts	Sudhir and Murthy (2004)
	Alteration in electron transport chain by impeding photon phosphorylation and carbon metabolism	Farahbakhsh et al. (2017).
	Decrement in chlorophyll content	Saha et al. (2010)
	Modification in cytoplasmic structure, retardation in carboxylation reaction and generation of ROS	Maxwell and Johnson (2000)
Nutrient imbalance	High osmotic potential lessens nitrogen content in plants	Lea-Cox and Syvertsen (1993); Rozeff (1995); Bar et al. (1997)
	Low phosphorous content	Qadir and Schubert (2002)
	Reduced influx of Ca ²⁺ and K ⁺ ions	Suhayda et al. (1990); Hu and Schmidhalter (1997); Asch et al. (2000)

5.2.3 *Plant Tolerance Strategies against Salinity Stress*

Resistance strategies of plants to salinity rely on environmental conditions and plant species. Plants mainly endure salt stress by three ways:

- (a) Endurance to osmotic stress
- (b) Efflux of sodium from leaf blades
- (c) Tissue tolerance

5.2.3.1 **Osmotic Stress Endurance**

Osmotic stress is marked by generation of osmolytes like glycine betaine, proline, polyols, etc. to maintain the osmotic balance. Osmotic tolerance also aids in balancing stomatal conductance and leaf expansion during salinity (Rajendran et al. 2009). Osmolytes stabilize the membrane integrity, proteins and pigments in the cell and also alleviate reactive oxygen species (Krasensky and Jonak 2012; Gupta and Huang 2014). It was evident that proline accumulation improved the salinity tolerance in maize (Tang et al. 2019). Likewise, trehalose accumulation also assisted in boosting salinity endurance in wheat (Sadak 2019).

5.2.3.2 **Sodium Ion Efflux from Leaf Blades**

Outcome of salinity stress in plants comprises ion toxicity due to sodium ion (Na^+) accumulation inside the cell. This can be overcome by down regulating the expression of ionic channels and Na^+ transporters (Munns and Tester 2008; Rajendran et al. 2009). An antiporter (AtNHX1) confined in tonoplast of *Arabidopsis* maintains Na^+ balance in the cell under salinity condition by directing the influx of Na^+ ions from cytosol to vacuole (Apse et al. 1999). Likewise NAX1 gene in durum wheat impedes Na^+ translocation in the shoots and leaf sheath from roots, whereas NAX2 gene confers high potassium ion (K^+) translocation in leaf (Flagella et al. 2006). Sodium exclusion theory for salt resistance has been validated in rice (Ren et al. 2005) and durum wheat (James et al. 2006). It was studied that potassium transporter (PpHKT1) gene from rootstock of almond also enhanced salt tolerance in transgenic *Arabidopsis* by balancing ion homeostasis (Kaundal et al. 2019).

5.2.3.3 **Tissue Tolerance**

For hindering the senescence of leaves and enhancing its survival rate, tissue tolerance is a salient attribute during stress. Generation of compatible solutes that balances the osmotic homeostasis in the cell and antioxidant defense system that scavenges the reactive oxygen species under stress condition is an attribute of tolerance of plants to stress condition (Hasegawa et al. 2000; Zhu 2001; Sakamoto

and Murata 2002). Tissue resistance also incites the ion compartmentalization in the cell to diminish toxicity of ion (Munns and Tester 2008). A notable rise in osmolyte production like proline up to $14.87 \mu\text{mol g}^{-1} \text{DW}$ and an increment in antioxidants like ascorbate peroxidase up to 77%, catalase up to 15% and glutathione reductase up to 138% were recorded in chickpea as a tolerance response to salinity stress (Arefian et al. 2018).

5.3 Flooding Stress

Prolonged submergence and soil waterlogging result in hypoxic condition that constitutes flood stress in plants. One of the key limitations to crop productivity in high rainfall areas of the world is flood stress. Climate change promotes submergence to be more recurring and drastic (Pachauri et al. 2014). Approximately 10% of irrigated land in India, China, Russia and 16% of cultivable land in the USA are damaged by waterlogging (FAO 2015). Figure 5.3 explains the ubiquity of flood hazard in the world. According to statistical approximates of food and agriculture organization of United Nations, flood stress upshots 17% of total loss and damage in agriculture (FAO 2018).

It was discerned that annually 20–50% production loss in wheat occurred under waterlogging condition (Hossain and Uddin 2011). Overall 15% of maize production in South Asia is damaged by floods. India accounts for 25–30% maize production loss every year on account of flood stress (Bailey-Serres et al. 2012).



Fig. 5.3 Global flood hazard prevalence. Adopted from SEDAC (n.d.)

5.3.1 Outcome of Flood Stress in Plants

The prime consequence of flood stress in plant comprises anoxia or oxygen limitation. Necrosis, senescence, low nitrogen fixation and ultimately plant death are the consequences of flood stress (Hasanuzzaman et al. 2012). Overall effects of flood stress in plants are outlined in Table 5.2.

5.3.2 Adaptation of Plants to Flood Stress

5.3.2.1 Morphological Alterations

For escaping anoxic conditions under flood stress, plants showcase morphological adaptations. Submerged leaves have low stomatal counts and are often dissected and filamentous (Sculthorpe 1967). Vigorous adventitious root growth is one of the prominent adaptation as evident in *Sesbania javanica* (Jackson 2006) and *Chrysanthemum* (Yin et al. 2009). Decrement in root hairs and diameter, rapid shoot elongation are some of the evident variations (Jackson 2008). Under submergence, formation of leaf gas film improves carbohydrate supply, generation of adventitious roots and aeration of roots. In rice, resistance to radial oxygen loss is enhanced by

Table 5.2 Consequences of flood stress in plants

Parameters	Alterations	References
Anatomical variation	Over growth of aerenchyma, lenticels and adventitious roots	Ashraf (2009)
	Decrement in stele and seminal root diameter, reduced cortex thickness	Grzesiak et al. (1999)
	Increment in width of phloem tissue and number of xylem vessels	de Souza et al. (2013)
	Formation of suberized exodermis on root cortex periphery	Kulichikhin et al. (2014)
Physiology and metabolism	Impaired stomatal conductance, CO ₂ assimilation	Ashraf (2009)
	Decrement in net photosynthetic rate, transpiration rate, PSII efficiency and rubisco activity	Zheng et al. (2009)
	Low relative water content and membrane stability	Kumar et al. (2013)
	Accumulation of hexose sugars in roots and organic acids in leaves	Vandoorne et al. (2014)
Nutrient availability	Enhanced nitrogen content and reduced phosphorous and potassium content in plant tissues	Reddy and mittra (1985)
	Reduced uptake of copper and zinc	Tarekegne et al. (2000)
Growth and yield	Reduction in leaf number, diameter, height and leaf area of plant, leaf epinasty	Parent et al. (2008); Gonzalez et al. (2009)
	Decline in dry matter accumulation, chlorosis, and flower abortion	Mensah et al. (2006)

development of effective barriers. This aids in shielding the plants from toxins generated from anoxic environment and boosts root tip aeration under flood stress (Kirk et al. 2014; Yamauchi et al. 2018).

5.3.2.2 Anatomical Alterations

To hinder the loss of radial oxygen from submerged roots, plants show formation of lateral diffusion barrier (Sauter 2013). Lenticels development is also evident in flood affected plants as this aids in oxygen diffusion in downward direction (Parelle et al. 2006). Aerenchyma formation is one of the unique characters of plants under flood or submerged condition as these gas spaces allow oxygen transport from roots to shoots (Shiono et al. 2008). Exodermis thickness was improved by 23.70% compared to control in *Garcinia brasiliensis* under flood state in addition to increment in root xylem vessels and phloem width (de Souza et al. 2013). In flood tolerant barley cultivar (TX9425 and Yerong), more well developed intercellular spaces in leaves and mesophyll cells were observed that enhanced photosynthesis due to quick gaseous exchange Zhang et al. 2016). In rice seedlings, rapid coleoptile elongation during germination is a marker for submergence tolerance that facilitates aeration of developing embryo (Guru and Dwivedi 2018).

5.3.2.3 Biochemical Alterations

Under flood stress, switch in the metabolism of plants from aerobic to anaerobic condition with high activity of alcohol dehydrogenase, a key enzyme in anaerobic fermentation is observed (Sairam et al. 2008). Proline content in *Casuarina* was high in tolerant cultivar as it acts as a signal molecule, an osmolyte and showcases antioxidant defense response under stress condition (Bajpai and Chandra 2015). Enhanced activity of alpha aminobutyric acid has been evident in soybean nodules in flooded conditions as this metabolite balances intercellular pH, acts as nitrogen reservoir under flood condition and also serves as antioxidant (Souza et al. 2016). Elevated activity of enzymes like phosphoenolpyruvate carboxylase, glutamate dehydrogenase and alcohol dehydrogenase was observed in flooded nodules of *Sesbania herbacea* (Krishnan et al. 2019).

5.4 Heavy Metal Stress

One of the major aftermaths of industrial revolution in the twenty-first century is heavy metal pollution in the environment. Heavy metals are potentially noxious elements and present in trace amount in soil. They are comprised of metalloids, lanthanoides and transition metals with atomic density $\geq 6 \text{ g cm}^{-3}$ except selenium, boron and arsenic (Park et al. 2011). The root cause of heavy metals in the

environment encompasses usage of pesticides and fertilizers, combustion of fuels, mining, sewage sludge, oil spills, etc. Heavy metals are diverse in their functioning. Metals like iron, zinc, copper, nickel, manganese, chromium impart proper functioning of plant's metabolic processes contrarily lead, arsenic, mercury have negative effect on plant growth and productivity (Pierart et al. 2015). These noxious elements enter the food chain and attack human, animal and soil health (Augustsson et al. 2015).

Uptake of heavy metal by plants interrupts the chief metabolic processes like photosynthesis, nitrogen fixation and nutrients uptake and results in biomass and yield reduction and also death of the plants (Buendía-González et al. 2010). In China, about 20,000,000 acres of farmland is polluted by heavy metal with an annual crop loss of 1,000,000 million tons per year (Wu et al. 2010). About 12% of world's agricultural land is estimated to be affected by heavy metal pollution (Dziubanek et al. 2015). One of the most detrimental heavy metal for human health is lead. Lead exposure resulted in loss in economic productivity of about \$977 billion annually in low to middle-income count (Attina and Trasande 2013). Statistical estimates of Institute for Health Metrics and Evaluation disclosed that lead exposure caused nearly 0.5 million deaths and 9.3 million life years lost among adults of 15 years and older (Landrigan et al. 2018).

5.4.1 Outcome of heavy metal stress in plants

Heavy metal stress deteriorates soil and plant health. Metal toxicity alters the morphology and physiology of plants at different growth stage as a consequence there is decline in crop productivity. Table 5.3 outlines the impact of heavy metal stress in plants.

5.4.2 Plant tolerance to heavy metal stress

5.4.2.1 Antioxidant enzymes

To escape heavy metal toxicity plants evolve many alterations. Exclusion of metal ions from the cell or binding with ligand prevents entry of metal ions to the roots is the first line of defense mechanism (Zeng et al. 2011). Metal ions also make complexes with carboxyl group of pectin in the cell wall thereby restricting its entry in the cell (Jiang and Liu 2010). Secondary response for metal detoxification is generation of antioxidant enzymes like superoxide dismutase, catalase and peroxidase. Compounds like glutathione, proline, cysteine, ascorbic acid also serve as scavengers of reactive oxygen species (Shahid et al. 2012; Pourrut et al. 2013).

Glutathione is a tripeptide antioxidant with thiol group and forms mercaptide bond with metals due to its nucleophilic thiol group and its reduced form also

Table 5.3 Out-turn of heavy metal stress in plants

Parameters	Modifications	References
Germination	Inhibition of water uptake by copper, cadmium	Kranner and Colville (2011)
	Reduction in germination percentage	Chigbo and Batty (2013)
	Formation of abnormal embryos and decrement in seed viability	Stvolinskaya (2000)
	Slow activity of alpha amylases, phosphatases. Decrement in remobilization of storage reserves	Kalai et al. (2014)
	Lipid peroxidation and proline accumulation in the radical	Kalai et al. (2014)
Plant growth	Chlorosis, decline in growth and yield, reduced nutrient uptake and nitrogen fixing potential	Guala et al. (2010)
	Generation of reactive oxygen species	Romero-Puertas et al. (2004)
Photosynthesis	Disruption in energy transfer in light harvesting complex, decline in chlorophyll and carotenoid content	Kuzminov et al. (2013)
	Electron transport inhibition between photosystem I and II	Rama Devi and Prasad (1999)
	Deformation of chloroplast ultrastructure	Kalaji and Loboda (2007)
Nutrient uptake	Low concentration of zinc, iron, calcium and manganese	Chatterjee et al. (2004)
	Decline in shoot nitrate content and nitrate reductase activity	Xiong et al. (2006)

scavenges peroxide radicals. Glutathione conjugates with compounds of heavy metals that are translocated to vacuole to protect cell from its harmful effects (Klein et al. 2006; Yazaki 2006). It was also studied that in response to cadmium toxicity there is a modulation in the activity of antioxidants like guaiacol peroxidase, ascorbate peroxidase and catalase in tolerant plants (Alves et al. 2017; Borges et al. 2018). In *Brassica juncea* L. such kind of high efficiency antioxidative defense system was evident during caesium toxicity (Lai and Luo 2019).

5.4.2.2 Metallothioneins and Phytochelatins

Vacuolar sequestration of heavy metals is an important response of plants to metal stress. Complex formation of metal ion with ligand reduces the toxicity of heavy metals. Metallothioneins and phytochelatins rich in cysteine are natural metal chelators in plants that reduce metal toxicity by forming mercaptide bonds with metals and sequester them to vacuoles (Gupta et al. 2010; Jiang and Liu 2010). In *Brassica napus*, cadmium toxicity results in strong expression of MT4 metallothionein in germinating seeds as a defense mechanism (Mierek-Adamska et al. 2018). Likewise in *Oryza sativa*, phytochelatin synthase genes (OsPCS5 and OsPCS15) were profoundly induced under cadmium stress as tolerance mechanism.

These genes encode phytochelatins that bind heavy metals in cytosol and detoxify them in the vacuoles (Park et al. 2019).

5.5 Low Temperature Stress

Chilling or low temperature stress amends the plant morphology, physiology and metabolism. Occurrence of chilling stress at temperature 0 °C to 15 °C whereas freezing stress at ambient temperature for ice crystal formation causes cellular injury and osmotic dehydration in the cell (Bhatla 2018).

5.5.1 Impact of low temperature stress in plants

Chilling in plants is advantageous for breaking seed dormancy, for vernalization and cold acclimation. In contrast, chilling in susceptible crops has many aftermaths as listed in Table 5.4.

5.5.2 Adaptations to low temperature stress

5.5.2.1 Cold acclimation

Increment in phospholipid proportion and decrement in ceramide and sugar containing lipids in plasma membrane results in reduction in expansion induced lysis. Expression of sugar producing enzymes like acid invertase, galactinol synthase and sucrose synthase to improve membrane stability is induced in response to cold acclimation (Turhan and Ergin 2012). Accumulation of compatible solutes like

Table 5.4 Consequences of chilling stress in susceptible crops

Parameters	Modifications	References
Lipid membrane	Membrane becomes leaky and dysfunctional	Bhatla (2018)
	Membrane transport and receptors disabled	
	Cellular structure distorted	
	Osmotic dehydration of cell	
Photosynthetic apparatus	Impaired electron transport chain	Bhatla (2018); Wise et al. (1987)
	Generation of reactive oxygen species	
	Cell plasmolysis	
	Chloroplast swelling and dilation of thylakoids, disintegration of chloroplast	
	Depletion of starch and phosphorylated metabolites in cell	

hydroxyl proline and arabinose in the cell maintains osmotic balance during cold acclimation (Bhatla 2018). Expression of hydrophilic and LEA (late embryogenesis abundance protein) proteins declines the denaturation of proteins under cold and drought stress. In *Brassica napus*, dehydrin proteins, a class of LEA proteins was highly expressed under cold stress in tolerant cultivar. It is used as biomarker for selection of cold tolerant lines (Maryan et al. 2019).

5.5.2.2 Modification in gene expression

Expression of cold regulated genes (COR) confers cold tolerance in plants by stabilizing the plasma membrane during low temperature stress. Hydrophilic proteins encoded by COR genes expressed during low temperature stress are involved in the production of anthocyanin and play indirect role in cold acclimatization. Extracellular production of antifreeze proteins (AFP) prevents ice crystal formation during low temperature stress. Molecular chaperons like HSP90 restrict denaturation of proteins during chilling stress. Other proteins like MAP (mitogen activated protein) kinase and calmodulin related proteins are encoded by COR genes and impart role in cold temperature signalling in plants (Bhatla 2018). A chromatin remodelling factor PICKLE (PKL) was found responsible for cold stress tolerance in *Arabidopsis*. It also modulates expression of other cold responsive genes like RD29A and COR15A (Zhao et al. 2019). In *Brassica rapa* L., genes such as temperature-induced lipocalin-1, zinc finger protein ZAT12, dehydrin ERD10 and adenosylhomocysteinase 2 were analysed and found to be involved in cold stress tolerance (Ma et al. 2019).

5.6 Drought Stress

One of the most disastrous outcomes of climate change is drought that restricts plant growth and development in both developed and developing countries. The utmost driver of undernourishment and hunger is geographical and global drought that declines agricultural productivity (FAO 2017). US, a technologically advanced country encounters an annual loss of \$ 6 billion in agricultural productivity due to drought and such losses are more severe in underdeveloped and developing countries (CIA 2017). Around 20% of world's cultivable land is hit by drought and more than 80% damage in livestock and agricultural production is because of drought stress (FAO 2018). Major drought exposed regions in the world have been delineated in Fig. 5.4.

Drought is a climatic variation with perpetuate periods of rainfall scarcity that results in hunger, malnutrition, deficit food productivity and ultimately food insecurity. Plants encounter severe drought when water loss via transpiration is high enough or when roots are deficient in water supply (Anjum et al. 2011). A severe drought can threaten the national food availability and results in pervasiveness of undernourishment. Approximate global yield loss of 21% in wheat and 40% in

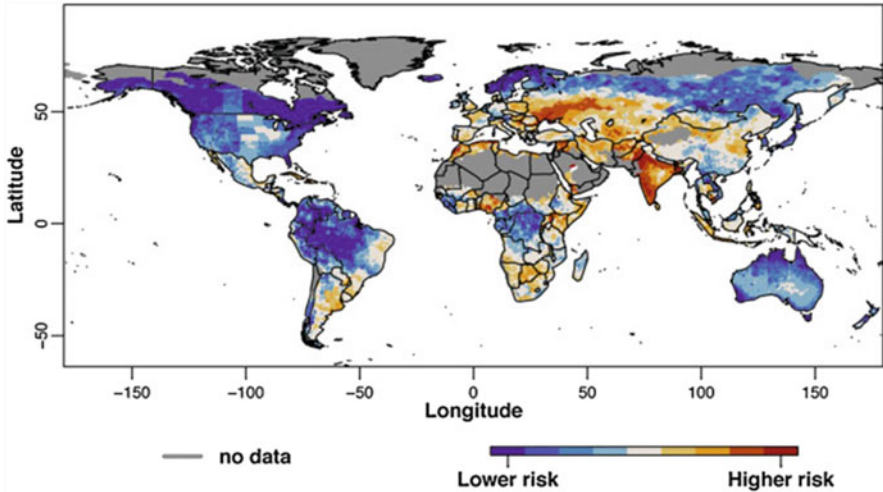


Fig. 5.4 Global map of drought affected regions. Adapted from Carrao et al. (2016)

maize was observed from 1980 to 2015 (Daryanto et al. 2016). Table 5.5 illustrates susceptible and resistant crops under major abiotic stress.

Drought alters photosynthesis, water balance, nutrient acquisition, oxidative metabolism and assimilates partitioning in plants. This modification in plants depends on species, growth stage of the plants and environmental conditions. Apparent symptoms of drought in plants are depicted in Fig. 5.5. Reduction in grain filling rate, harvest index and solar use efficiency are some key drivers responsible for diminished yield under drought stress. Table 5.6 describes deleterious impact of drought stress in plants ranging from morphological, biochemical to molecular level and is discernible at every phenological stage of crop growth at any period of time (Farooq et al. 2009; Deepak et al. 2019).

5.6.1 Outcome of Drought Stress on Morphological Attributes

The foremost impact of drought stress on morphology of plant is restricted seed germination and seedling growth (Farooq et al. 2009). Drought negatively alters seed vigour, seedling growth and also results in poor seed quality as reported in *Medicago sativa* (Zhang et al. 2019a, b), *Oryza sativa* (Bhavyasree et al. 2019), *Glycine max* (Reddy et al. 2019), *Zea mays* and *Sorghum* (Queiroz et al. 2019).

Drought impedes mitosis and cell enlargement because of restricted water flow from xylem to neighbouring cells (Hussain et al. 2008). Reduction in plant size and biomass is one of the major morphological alterations in plants during drought stress. Fifty percent reduction in biomass in wheat was observed as compared to control

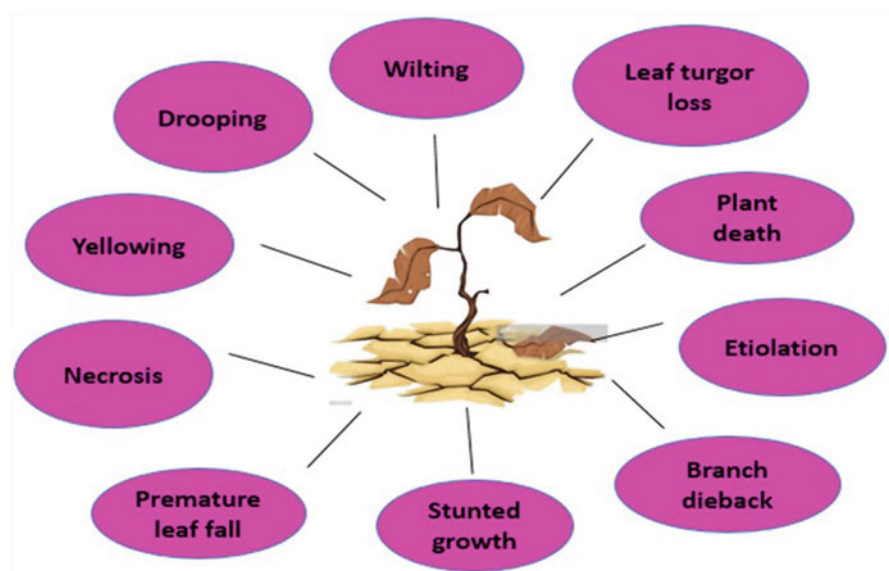
Table 5.5 Comparative representation of crops for resistance and tolerance to different abiotic stress

Stress	Sensitive crop	Reference	Resistant crop	Reference
Salinity	<i>Brassica napus</i> L.	Dolatabadi et al. (2019)	<i>Hordeum vulgare</i>	Han et al. (2018)
	<i>Phaseolus vulgaris</i>	Lahaye and Epstein (1971)	<i>Echinochloa frumentaceae</i>	Williams et al. (2019)
	<i>Oryza sativa</i> L.	Khatun et al. (1995)	<i>Beta vulgaris</i> L.	Wu et al. (2018)
	<i>Triticum aestivum</i>	Ahmad et al. (2013)	<i>Vigna unguiculata</i>	Pan et al. (2019)
	<i>Lupinus albus</i>	Jeschke (1984)	<i>Solanum lycopersicum</i>	Amjad et al. (2019)
Flood	<i>Zea mays</i>	Panozzo et al. (2019)	<i>Saccharum officinarum</i>	Singh et al. (2019)
	<i>Solanum lycopersicum</i>	Ezin et al. (2010)	<i>Oryza sativa</i> L.	Dwivedi et al. (2018)
	<i>Glycine max</i>	Tewari et al. (2016)	<i>Solanum dulcamara</i> L.	Dawood et al. (2014)
	<i>Triticum aestivum</i>	Zhou (2010)	<i>Zea nicaraguensis</i>	Yamauchi et al. (2018)
	<i>Cicer arietinum</i>	Solaiman et al. (2007)	<i>Populus euphratica</i>	Yu et al. (2015)
Heavy metal	<i>Triticum aestivum</i> (Lead)	Alamri et al. (2018)	<i>Lupinus</i> (Cadmium, nickel)	Rathaur et al. (2012)
	<i>Oryza sativa</i> L. (Cadmium, arsenic)	Makino et al. (2019)	<i>Brassica napus</i> (Nickel, cadmium, copper)	Marchiol et al. (2004)
	<i>Lolium perenne</i> L. (Aluminium)	Parra-Almuna et al. (2018)	<i>Raphanus sativus</i> (Nickel, cadmium, copper)	Marchiol et al. (2004)
	<i>Brassica juncea</i> (Copper)	Yadav et al. (2018)	<i>Setaria italica</i> L. (Cadmium)	Chiang et al. (2011)
	<i>Solanum lycopersicum</i> (Cadmium)	Carvalho et al. (2018)	<i>Miscanthus sinensis</i> (Aluminium)	Ezaki et al. (2008)
Chilling	<i>Solanum lycopersicum</i>	Ronga et al. (2018)	<i>Arabidopsis thaliana</i>	Schulz et al. (2016)
	<i>Zea mays</i>	Bilska-Kos et al. (2017)	<i>Brassica juncea</i> L.	Sinha et al. (2015)
	<i>Cicer arietinum</i>	Selpair (2018)	<i>Mentha arvensis</i>	Dhawan et al. (2018)
	<i>Brassica oleracea</i>	Zhang et al. (2019a, b)	<i>Pisum sativa</i> L.	Zhang et al. (2016)
	<i>Vigna radiata</i>	Batra et al. (2018)	<i>Capsicum annuum</i>	Shawon et al. (2017)
Drought	<i>Oryza sativa</i> L.	Lawas et al. (2018)	<i>Setaria italica</i>	Han et al. (2019)

(continued)

Table 5.5 (continued)

Stress	Sensitive crop	Reference	Resistant crop	Reference
	<i>Triticum aestivum</i>	Bakhshandeh et al. (2019)	<i>Sorghum</i>	Ohnishi et al. (2019)
	<i>Zea mays</i>	Daryanto et al. (2016)	<i>Arachis hypogaea</i> L.	Banavath et al. (2018)
	<i>Cicer arietinum</i>	Kaloki et al. (2019)	<i>Macrotyloma uniflorum</i>	Sharma et al. (2018)
	<i>Glycine max</i>	Popović et al. (2015)	<i>Brassica napus</i> L.	Mahmood et al. (2019)
	<i>Helianthus annuus</i>	Pekcan et al. (2015)	<i>Hordeum vulgare</i>	Carter et al. (2019)

**Fig. 5.5** Drought stress prodrome in plants

under drought stress (Paul et al. 2019). Dry weight and fresh weight of root and shoot as well as root shoot ratio tend to cut down in drought induced *Brassica napus* L. (Khan et al. 2019).

Decrement in stomatal aperture, leaf rolling, cutinization of leaf surfaces are some observable drought stress induced morphological parameters (Hussain et al. 2008). Drought hampers the leaf size, grain yield in crops, for instance, yield parameters like panicle length, seed setting rate and grain weight declined in *Oryza sativa* L. under drought (Wei et al. 2017). Likewise in wheat, 62% of grain loss was observed in drought condition compared to well-watered conditions (Paul et al. 2019).

Table 5.6 Salient modifications in drought stricken plants

Parameters	Modification	Reference
Morphology	Inhibition of seed germination	Farooq et al. (2009)
	Reduce shoot and root dry weight	Manickavelu et al. (2006)
	Diminished leaf area and number of stomata	Jaleel et al. (2009)
	Impaired mitosis and cell elongation	Hussain et al. (2008)
	Loss of turgor pressure and cell growth	Taiz and Zeiger (2006)
Water and nutrient relation	Low water use efficiency and transpiration rate	Turner et al. (2001)
	Low uptake of phosphorous, calcium and magnesium	Barber (1995)
	Enhanced nitrogen uptake	Barber (1995)
Photosynthesis	Reduction in RUBP generation and photo-system II activity	Wise et al. (2004); Camejo et al. (2006)
	Low chlorophyll content	Din et al. (2011)
Assimilate partitioning	Decline in translocation of assimilates from source to sink	Kim et al. (2000)
	Disturbance in phloem loading and unloading	Zinselmeier et al. (1999)
	Low potential of sink to utilize the assimilates	Zinselmeier et al. (1999)

5.6.2 Physiological and Biochemical Alterations Under Drought

Physiological attributes like transpiration rate, stomatal conduction, leaf water potential and relative water content are adversely affected by drought. Low water potential, transpiration rate, relative water content and enhanced leaf temperature were observed in *Oryza sativa* under drought (Fahad et al. 2017). Drought stress induces the formation of reactive oxygen species (ROS) along with enhanced generation of osmolytes like proline, glycine betaine. Production of ROS leads to oxidative stress that ultimately results in cell death in plants (Silva et al. 2019).

Another important trait influenced by drought is photosynthesis. Drought stress induces reduction in leaf expansion, damages the photosynthetic apparatus and activity of photosynthetic enzymes. Reduction in phosphorylation and disruption in ATP synthesis are key drivers for impaired photosynthesis under drought (Fahad et al. 2017). Reduction in thylakoid membrane proteins and PSII activity under PEG induced drought stress have been evident in many studies (Wang et al. 2019).

Activity of rubisco, a motor enzyme of photosynthesis is declined drastically under drought. Reduction in amount of substrate, i.e. ribulose 1, 5 bisphosphate for carboxylation, modification in ultrastructure of rubisco and chloroplast and acidification of chloroplast stroma are the driving factors for decrement in rubisco activity. Other enzymes like fructose-1, 6-bisphosphatase, NADP-glyceraldehyde phosphate

dehydrogenase, phosphoribulokinase, phosphoenol pyruvate carboxylase and pyruvate orthophosphate dikinase also decline under drought stress (Farooq et al. 2009).

Drought restricts nutrient movement from soil to plants. Under drought, root growth and proliferation are hindered that limit nutrient translocation in plants. Limited flow of oxygen, carbon and nitrogen assimilation in root nodules impedes nitrogen fixing ability of legumes under drought (Ladrera et al. 2007). Nitrate reduction in leaves was limited by declined photosynthesis, which supplies reducing power, generated during photosynthetic via electron transport for the process of nitrate reduction (Chen et al. 2018).

5.6.3 Adaptation of Plants to Drought Stress

5.6.3.1 Escape

Drought escape is characterized by short life cycle that enables plants to flower early before onset of drought. Growing season is dependent on environmental variation and plant genotype. Drought escape is enhanced when development of plant synergizes with duration when soil moisture is available. Although drought escape helps in plants survival during stress yet there is a decrement in the yield (Farooq et al. 2009). High grain yield in *Lens culinaris* was recorded under early drought as a result of drought escape. Maximum leaf area, stomatal conductance, high stomatal density, early flowering with short life cycle were also observed as an outcome of drought escape strategy in lentil (Sanchez-Gomez et al. 2019).

5.6.3.2 Avoidance

Avoidance is marked by maintaining the water potential of plants during drought. It is also characterized by reduced water deprivation through transpiration and balancing the water uptake from soil. For efficient water uptake, a deep and extensive root system is required along with thick cuticle whose formation requires high input of energy that ultimately results in low yield. Therefore, plants with avoidance strategies are generally of compact size (Lisar et al. 2012). In *Sorghum*, aquaporin genes PIP2;3 were strongly expressed in roots under drought compared to roots under watered conditions. Aquaporins are the membrane proteins that allow water and solute passage through the membrane into cell and their expression under drought is an adaptive strategy (Schulze et al. 2019).

5.6.3.3 Tolerance

Tolerance to drought stress is perceptible by limited area and number of leaves during water deficit condition. Plants show traits like formation of trichomes and

hairy leaves which reduce leaf temperature during drought. Root architecture like root density, root proliferation, root growth rate are some key alterations in plants during drought. Reduction in stomata number, increment in root shoot ratio, accumulation of osmolytes and induction of antioxidant defense system are other drought tolerance traits in plants (Sapeta et al. 2013). In sorghum, leaf rolling, leaf waxiness, stay green trait, root architecture, abscisic acid metabolism, ion transporter, transpiration efficiency and osmotic adjustments are drought tolerant traits that enable it to survive under drought stress (Badigannavar et al. 2018).

5.7 Conclusion

Major constraint for sustainable agricultural productivity and global food security is abiotic stress which is an outcome of global climate change. Extreme weather conditions attack morphological, physiological and biochemical attributes of the plants and threaten their survival in the environment. Multiple abiotic stresses like salinity, flood, heavy metal and drought impact the crop yield. Drought is the most devastating abiotic stress that declines the global crop productivity. Drought hampers seed germination, reduces the stomatal frequency and diminishes leaf area and water potential. At physiological level, drought restricts photosynthesis, thylakoid structure and enzyme production. All these modifications alter the metabolism and limit growth and development of plants. Despite such abiotic constraints, plants have inherent tolerance mechanisms that enable them to cope up and survive under extreme conditions. Activation of antioxidant defense system, changes in the membrane lipid composition and enzyme production as well as morphological alterations in plants are some of the tolerance traits in plants. In spite of such adaptive strategies, improvements in the tolerance of plants against the extreme calamities are required. Strategies like alteration in expression of stress responsive genes and transcription factors are potential candidates to develop stress tolerant crops. More emphases should be there on molecular research for exploiting the stress tolerance traits and minimizing the aftermath of stress in plants.

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