Chapter

Influence of Abiotic Stresses on Seed Production and Quality

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Abstract

Climate change is exerting detrimental impacts on agriculture through various biotic and abiotic stresses. Abiotic stresses such as drought, flood, temperature extremes, salinity, chemicals, heavy metals, nutrient scarcity/toxicity, wind and light in combination more adversely affect the seed production and quality by hampering plant's morphological, physiological, cellular, biochemical and molecular activities than alone, resulting in poor production of high-quality seeds. Deterioration of yield and quality arises also under abiotic stresses. Under abiotic stresses, plant activates its own defensive mechanisms by escaping, avoiding and tolerating stresses. Some of the plant's defensive mechanisms include plant's morphological, cellular, physiological, biochemical and molecular changes to adapt the stresses, synthesis of compounds such as ABA, proline, polyamines increasing the activities of ROS quenchers, expression of stress-resisting genes and activation of enzymes. Further, exogenous application of phytohormones, stress-alleviating compounds, modification of agronomic management, modern breeding strategies such as development of resistant varieties can also help to cope up with stresses and produce quality seeds. Financial and policy support of government or NGOs regarding development of infrastructure, research technologies and thereby, multi-locational trials as well as technology transfusion through extension activities are needed to curtail down the devastating impact of abiotic stresses on quality seed production.

Keywords: abiotic stresses, agronomic management, climate change, defensive mechanisms, seed production, quality

1. Introduction

Improving agricultural productivity is the prime goal of farmers around the globe to meet the food demand of the entire population. Over the years, the global population is increasing at alarming rate and likely to increase even further in future. Food scarcity is therefore a major issue which many countries of the world are experiencing now. Rapid industrialization/urbanization, migration of rural people to urban areas for alternative job opportunities, literacy, low agricultural production, lack of policies etc. are key reasons for which agriculture sector is suffering currently. In order to achieve the food security, agricultural production needs to be lifted at this hour. However, shrinkage of agricultural land in resonance with population growth forces the farmers to go for intensive farming approach. In intensive farming, excessive uses of chemicals and unscientific management practices not only degrade the soil, water and other precious natural resources of the crop production, but also create climate change issue which possess a major threat to sustainable agricultural production. Further, industrialization/urbanization, deforestation or any other anti-nature practices aggravate this climate change situation and thereby, affect crop production.

Performance of a crop relies on the interaction of its genetic traits with the growing environment. Crop plants suffer from climate change scenario due to their sessile growth habit. Climate change exerts various stresses on crop plants and thereby, affects the crop negatively in most cases. Such stresses can be exhibited from the living (biotic) or non-living (abiotic) things of the environment. In nature, various stresses usually put combined impact on the crop plants. Abiotic stresses such as drought, flood, salinity, temperature extremes (hot/cold), heavy metals, light, wind, nutrients/chemicals etc. on plants are either physical or chemical in nature [1]. These abiotic stresses resulted from climate change determine the distribution of plants in different environmental conditions [2] and thereby, influence the crop productivity throughout the globe [3]. These stresses during any crop growth stages specially, reproductive stage markedly reduce yield of the crop by affecting reproductive organs [4]. They are also known to influence biotic stresses positively, which in turn, affect agricultural production through disruption of seed germination, vegetative growth, dry matter production and its partitioning to reproductive parts [5]. Around 70% of yield reduction in the world is due to abiotic stress [6]. Severe stresses not only affect the yield but also seriously hamper the quality of the produce through creating imbalance between demand and supply of nutrients, inactivation of enzymatic activities, suppression of various genes responsible for the quality expression etc. [7]. As these abiotic stresses put barriers on global food security, it is needed to develop suitable strategies to achieve considerable amount of yield with maintained quality under climate change situation.

In this context, seed is a key driver of agriculture. Quality seed production and its utilization can play major roles in achieving high yield under climate change scenario. However, quality seed production under various abiotic stresses needs special emphasis as these stresses exert detrimental effects on plant. Abiotic stresses limit the production and quality by affecting the crop plants from morphological to molecular levels [8]. However, in response to the stresses, plant shows few mechanisms like escaping stress, stress avoidance and stress tolerance. Plant undergoes certain molecular, cellular and physiological changes to cope up with stresses and acclimatizes under stress situation. Insight view to such changes is one of the fundamental components of plant studies to ensure food security. Improved understanding of plant response to stresses can help to develop various strategies to alleviate the stresses. Such strategies include various traditional and modern breeding, agronomic management practices along with exogenous applications of stress tolerating compounds to cope up with abiotic stresses. This chapter highlights the impacts of abiotic stresses on crop plants specially seed production and quality as well as points out various agronomic management strategies to cope up with the abiotic stresses by providing the understanding of plant's defense against such stresses.

2. Stress

Stress, in general, refers to any deviation from the normal condition of a character or phenomena. In biology, stress mostly exerts adverse impact on individual or group or mass. In agriculture, negative impact of stress is seen on crop growth, development, productivity and quality. Stress induces various responses inside the plant such as change in gene expression, change in cell metabolic activities, and changes in plant's physiological and biochemical activities and thus, affects its growth rate, productivity and quality. In environment, stress is of two types: biotic stress and abiotic stress (**Figure** 1). Biotic stress arises due to interaction between living organisms, while abiotic stress is a result of interaction between organisms with non-living environmental properties. In reality, both these two stresses are linked to each other.

2.1 Biotic stress

Biotic stress arises when living organisms such as weeds, insects, diseases (caused from bacteria, fungi, virus etc.) exert stresses on plant and thereby, hampers its growth and development. The kinds of biotic stress on plant depend on edaphic and climatic conditions. However, yield loss is a common occurrence due to this stress.

2.2 Abiotic stress

Physical or chemical environment puts adverse effect on the living organisms and thus, creates abiotic stress. In agriculture, abiotic stress results in impairment of normal growth and development of plants and thereby, crop yield, quality and farmers' income get hampered. It is further noted that in environment, several stresses together put combined effect on plant and thereby, deteriorate crop productivity and quality in greater extent as compared to their individual effect. It adversely affects the crop from morphological to physiological, biochemical or molecular levels. Abiotic stress includes water stress (drought and flood), salinity stress, temperature stress

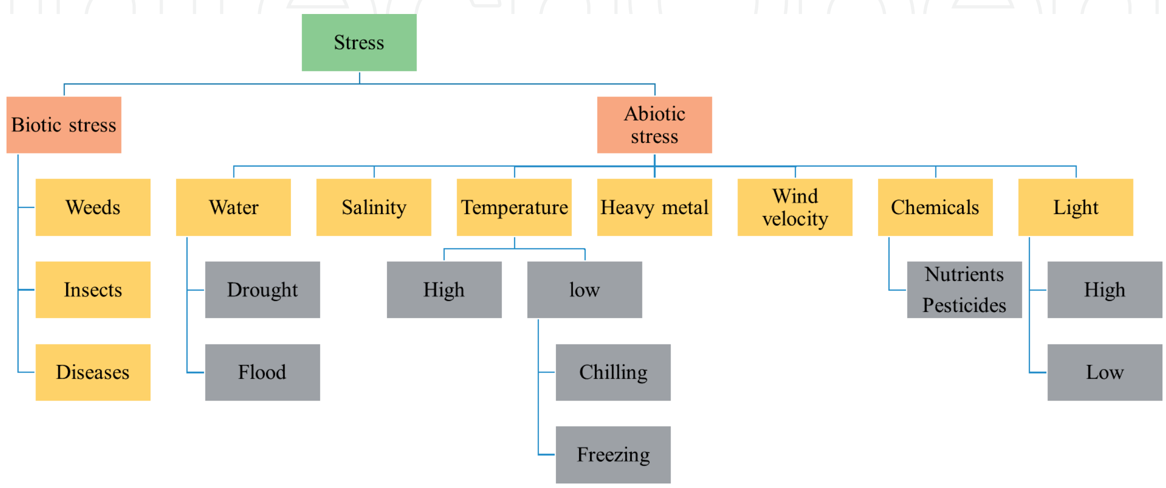

Figure 1.
Various types of stress.

(heat and cold), heavy metal toxicity, nutrients and pesticides toxicities, light stress (high and low). Some other types of abiotic stresses are shade, UV exposure, photoinhibition, air pollution, wind velocity etc. In following section, descriptions of these stresses are briefly mentioned.

2.2.1 Water stress

Water is the precious input for any life and obviously, for the crop. Plant's photosynthesis, transpiration, nutrient uptakes, translocation of assimilates etc. depend on water and thereby, its imbalance in plant can cause serious damage to plant. The uneven distribution of water is resulted from climate change scenario which the globe is experiencing now. Generally, water stress occurs in the form of drought and flood.

Drought: In meteorology, drought is defined as the period of deficiency of rainfall from the normal in an area. In hydrology, drought arises from low river and stream flows and reduced ground water table. In agriculture, drought indicates the dry period during the crop growth period which critically hampers the crop growth and yield. Sometimes, plant is unable to uptake soil moisture even after its availability due to high salt concentrations in soil solution. This phenomenon is known as apparent drought. Drought can also be resulted from high and low temperature. High temperature induces evapotranspiration loss of water and thus, creates drought like situation. In case of cold condition like at freezing temperature, ice crystals are formed in the extracellular spaces of plant, resulting in loss of the water potential which finally causes intracellular water efflux. Drought stress can lead to loss of plant vitality and alter in plant's normal functioning.

Flood: Flood is the opposite situation of drought. It is the situation of excess water in an area for a period of time. Flood when occurs from the sudden outburst of cloud and results in excessive rainfall in a short spell of time is known as flash flood. Flash flood lasts for a short period of time generally up to few weeks. Another type of flood is deep water flood which last for a longer period of time.

2.2.2 Salinity stress

Salinity is a major problem in any part of the world especially in arid and semi-arid areas where potential evapotranspiration is higher than the rainfall and poor leaching of salts beyond root zone is seen due to insufficient rainfall. Salinity can be defined as presence of excess quantity of salts in the soil, which negatively impacts on the crop [9]. Salinity is measured using electrical conductivity (EC). In general, soil having EC >4 dS/m, exchangeable sodium percentage (ESP) < 15.0 and pH. <8.5 is considered as saline soil [10]. Saline soil contains chloride, sulfate salts of sodium, magnesium and calcium ions. Salinity in soil can be developed by both natural and anthropogenic means. Weathering of rocks, flooding and intrusion of sea water to agricultural land, seepage of saline water, wind blow etc. are the natural cause of build-up of salts in the soil. Human induced causes of soil salinity are poor water quality of irrigation, deforestation, overgrazing, intensive cropping etc. Excessive soil salinity leads to deterioration of soil health through changing cation exchange capacity, damaging soil physical structure through deflocculation and reduction of hydraulic conductivity and hampering soil microbial activity.

2.2.3 Temperature stress

Abrupt change in temperature in response to global climate change is a great concern. Increase of temperature due to global warming and anthropogenic causes can change biodiversity, crop ecosystem and thus, limit the crop production to a high extent. High temperature or heat stress induces higher respiration over photosynthesis and thereby, leads to starvation injury through loss of food reserves in plants. Plants are differentiated based on their degree of high temperature tolerance: psychrophiles (up to 15–20°C), mesophiles (up to 35–45°C) and thermophiles (up to 45–100°C) [11]. Low temperature or cold stress is the opposite phenomena of heat stress and is mostly experienced in temperate areas. It is of two types: chilling stress and freezing stress. Chilling and freezing stresses affect the crop's physiological, biochemical functions and thereby, hamper its growth and productivity. According to the tolerance to cold temperature, plants are classified into 3 categories: Chilling sensitive (Plants are extremely sensitive above 0°C and below 15°C), chilling resistant (plants tolerate low temperature but adversely affected under formation of ice crystals in extracellular spaces) and frost resistant (plants tolerate extremely low temperature).

2.2.4 Heavy metal toxicity

Heavy metals are inorganic, non-biodegradable compounds having atomic mass and density > 20 and > 5 g/cm^3, respectively. They cause mutagenic effects on plants through contaminating irrigation, food chain and environment [12]. Application of excessive quantity of water from contaminated source and fertilizers/pesticides results in accumulation of heavy metals in soil and from soil, plant absorbs them. In general, heavy metals (Ag, Cr, Cd, As, Sb, Pb, Se, and Hg) are non-essential and at higher concentrations can affect plant's normal functioning. Besides, some essential elements such as Zn, Cu, Ni, Fe, Co etc. at higher concentrations pose heavy metal toxicity in plant.

2.2.5 Chemical toxicity

Consistent reliance of agriculture on inorganic chemical fertilizers and pesticides (herbicides, insecticides, fungicides etc.) from green revolution is increasing day by day. Besides, rapid industrialization and use of sewage water without treatment possess threats to the crop through the adverse effects of the chemical toxicity on the soil- plant system.

2.2.6 Nutrient toxicity/deficiency

Excessive application of fertilizers can lead to toxicity of nutrients in the soil. On the other hand, scarce application of nutrients leads to deficiency of nutrients.

2.2.7 Wind velocity

High wind velocity over the cropped area can put stress on the growth and development of the crop. Wind velocity is resulted from the movement of wind from one direction to another at certain speed.

2.2.8 Light stress

Light is essential input for plant growth. In fact, crop production is synonymous with harvesting solar energy. When light becomes excessive or insufficient, it causes detrimental effect on the plant. This phenomenon is known as light stress.

3. Effect of abiotic stresses on plants

Abiotic stresses alone or in combination influence negatively on plants (**Figure 2**). It has been observed in various regions and crops that there is generation of H_2O_2 under abiotic stress. Closure of stomata partially or completely under abiotic stress such as drought stress reduces photosynthesis by restricting entry of CO_2 and hampering electron flow through electron transport chain. Under abiotic stress, further, hydroxyl radicals, superoxide radicals and singlet oxygen are formed. These altogether adversely affect lipid (lipid peroxidation), protein (oxidation), nucleic acids and enzyme activity leading to cell death. Some adverse effects of different abiotic stresses on plant are briefly discussed below.

3.1 Water stress

Drought: Under scarcity of water, the seed germination and early seedling establishment get hampered due to depletion of seed reserves as well as mechanical obstruction made by the hard soil, which are followed by restricted vegetative growth.

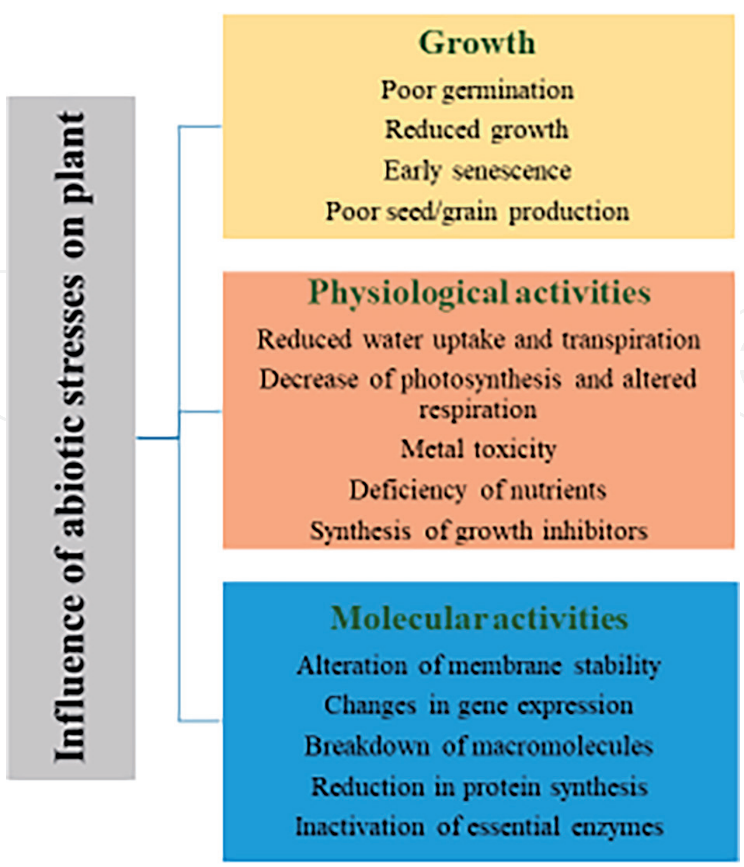

Figure 2.
Influence of abiotic stresses on plant.

Some other major impact of drought includes reductions of leaf area, chlorophyll a, b, carotenoids, stomatal conductance, rubisco activity leading to poor photosynthesis and translocation of photo-assimilates from source to sink. It impairs photosystem (PS) I and II as well as reduces starch biosynthesis through hampering ribulose phosphatase activity. Consequently, dry matter production and development of reproductive structures are negatively impacted. Under drought stress, concentrations of cell solutes increase and pose toxic effects on plants. This stress further increases the intra- and inter-competitions for water among crop plants and between crop and weeds. It increases sucrose viscosity leading to restricted movement of sap inside plant. Under drought stress availability of nutrients are variably altered. For instance, availability of nitrogen increases, while phosphorus availability decrease and no distinct effect is seen on potassium under drought stress in root vicinity, resulting in variability in uptake by the plant and consequently, metabolism of nutrients in cell is affected [13]. Assimilation of ammonia to organic form is restricted as activities of nitrate reductase, glutamine synthetase etc. are reduced. C_4 plants are more sensitive to drought stress than C_3 plants due to closure of stomata which ultimately reduces photosynthesis [14]. Drought restricts mineral uptakes and nitrogen fixation ability in various leguminous crops.

Flood: Flood generally creates deficiency of oxygen/hypoxia as anaerobic situation is formed through either water logging or submergence. Flood reduces the movement of oxygen and other gases in root zone of plant and ethylene diffusion from plant, which causes chlorosis of plant leaves. Negative impact on plants due to flood includes wilting of shoot, loss of chlorophyll pigments, decay and death of leaves/aerial parts, abscission, epinasty, lenticel formation, build-up of toxins under hypoxic environment, less root respiration, root proliferation and other physiological disorders.

3.2 Salinity stress

Salinity stress possess two major primary effects on plants: osmotic stress and ion toxicity. As already mentioned earlier, this stress can induce the drought stress by restricting the uptake of water by plants from the soil through exerting higher osmotic pressure to root cell (osmotic pressure of soil solution> osmotic pressure inside plant cell sap). Even if water uptake occurs, water also carries lots of salts (Na^+, Cl^- etc.) inside the plant along with it and these excess salt ions can pose injury at the cellular level of the plant by hampering some essential enzyme activities. Production of reactive oxygen species (ROS) owing from oxidative stress results in detrimental effect on protein, nucleic acid and certain enzymes of plant [15]. Under excess salts, plant can show burnt like appearance in leaves and experiences deficiency of some essential elements such as calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}), nitrate (NO_3^-) etc. and abundance of Na^+ near root zone. Calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}) and nitrate (NO_3^-) play major role in photosynthesis and less uptake due to salinity leads to reduction of photosynthesis and translocation of assimilates from source to sink. It causes poor leaf expansion, stunted growth and less dry weight of plant, sterility of florets and loss of pollen viability in plant. Under excessive salt situation, there is an increase in epidermal thickness, mesophyll thickness, palisade cell length and diameter and spongy cell diameter and reduction of intercellular space in leaves. Salinity stress specifically, increases Na^+/K^+ ratio of the cell. Imbalance supply of potassium reduces cell turgidity, enzyme activity and membrane potential of plant. It further induces some secondary effects on plants such as reductions of cell expansion as well as division, membrane stability and cytosolic metabolism as dominance of Na^+ in cell creates restriction of some essential enzyme activities. Under salinity stress, closure of stomata partially or completely reduces transpiration and cell division. Consequently, there is an increased rate of reduction of plant growth, high degree of defoliation as well as senescence and plant's death [16].

3.3 Temperature stress

High temperature/heat stress: Heat stress often increases the evapotranspiration loss of water and thereby, creates drought like situation. This situation is very critical when soil temperature increases along with drought stress. Elevation in temperature causes denaturation of protein, inactivation of essential enzyme activities (*viz*., sucrose phosphate synthase, adenosine diphosphate-glucose pyro-phosphorylase, invertase etc.) reductions of starch and sucrose synthesis [17], generation of ROS and death of the cell [18]. Further, light dependent reactions in stroma of thylakoid and carbon metabolism are hampered under elevated temperature. Impairment of electron supply to PS II under heat stress leads to restriction of the activity of PS II. Seed germination and seedling stand establishment are greatly affected by this stress. At high temperature, respiration exceeds photosynthesis and high loss of carbon through photo-respiration is seen (respiration rate increases two times with each 10°C increase of tissue temperature). Root number, length and biomass are greatly affected under high temperature rise, resulting in decreased uptakes of nutrients and water from soil. Further, drying or scorching of aerial part of the plants, reduction of plant growth and development through depleting chlorophyll as well as hampering photosynthetic activity and cell division are witnessed under heat stress. It is noted that sudden increase in temperature is comparatively more harmful as compared to gradual temperature rise as it disrupts biochemical, physiological and molecular activities of the plant. C_3 plants suffer comparatively more under heat stress over C_4 plants due to variations in energy supply and carbon metabolisms [19].

Low temperature/cold stress: Cold stress causes chilling (dysfunctioning of physiological properties) and freezing (dehydrating the cell) injuries to the plant. Low temperature stress hampers membrane integrity resulting in electrolyte leakage/plasmolysis, alteration of cell metabolic activities and reduction of protoplasmic streaming [20]. It alters nucleic acid and protein synthesis and down-regulates PS II [21]. Wilting, bleaching through pigment photo-oxidation, leaf necrosis, browning, cell death etc. are the common examples of impact of cold stress on plant.

3.4 Heavy metal toxicity

Heavy metals adversely affect plant's physiological, morphological, biochemical and molecular activities. After root uptake, heavy metals *viz*., Pb, Cu, Hg, etc. translocate inside the plant through xylem in response of transpiration pool and affect nutrient distribution, photosynthesis, enzyme activities, Cu/ Zn-SOD, ethylene receptors etc. and consequently, decrease molecular oxygen and synthesize reactive oxygen species (ROS) (oxidative stress) [22]. Formation of ROS damages the cell further.

3.5 Other abiotic stresses

Excessive and pointless application of chemicals can lead to pollution of the environment and damages ecosystem health and diversity. Further, it induces climate change which in turn, affects the crop growth, yield and quality. Use of excessive nutrients from inorganic sources also play similar impact on environment. These chemicals, fertilizers persist in nature and create toxic effects on crop plant. For instance, reliance on chemical based farming activities can degrade the soil health and reduces the soil productivity. Ground water, surface water contamination, air pollution etc. are now common phenomenon which aggravate climate change scenario. Plant previously suitable for a region is now therefore facing trouble under such changing climate. It induces various other abiotic stresses and biotic stresses to negatively impact on crop's germination, photosynthesis, translocation of assimilates etc. and thereby, hampers crop yield. On the other hand, scarce nutrients in the soil can lead to nutrient deficiency symptoms on plant through less uptake and thereby, affects plant growth, development, yield and quality as these nutrients are essential for the plant's nourishment.

High wind velocity leads to lodging situation in tall growing plant and thereby, affects their growth. It further creates soil erosion and thus impact negatively by washing away the nutrients essential for crop growth. Further, under high wind velocity, evapotranspiration loss of water is increased which creates scarcity of water for the plant growth.

Light plays an important role in photosynthesis. Exposure to less light can lead to less photosynthesis. On the other hand, excessive light can damage photosynthetic apparatus (photoinactivation and photodamage). Low light or shading affects the plant growth and development. High light intensity can lead to heat or drought stress like situation and thereby, affects the plant growth. UV ray damages DNA and causes leaf bleaching, oxidative stress by formation of ROS. Under high light, plant experiences breakdown of D1 protein of PS II and reduction of PS I polypeptides such as PsaA, PsaB and PsaC [23].

4. Influence of abiotic stresses on seed production and quality

Abiotic stresses exert negative influence on production of seed primarily by hampering germination as well as photosynthetic efficiency and translocation of assimilates from source (leaf) to sink (seed). Further, flowering, fertilization and seed filling phases are greatly affected under abiotic stresses. Reduced activity of acid invertase restricts reproductive parts of plant through phloem unloading. Reduced endosperm size, abortion of embryo, less seed filling, unfilled seed etc. drastically reduce the seed production and quality. Deterioration of yield and quality arises also from deficiency of supply of essential inputs to the plant under abiotic stress. The influence on seed formation and quality is resulted from complex relationship between individual stresses. For instances, changes in gene expression, oxidative damage, alteration of ion distribution and cell homeostasis lead to loss of production and quality of crop under abiotic stresses. Reduced productions of various crops under abiotic stresses have been listed in **Table** 1. The specific influence of different abiotic stresses on seed production and quality are briefly discussed here under.

4.1 Water stress

Drought is the principal limiting factor of growth, yield and quality of cereal crops throughout the world. Drought (water deficit) affects the plant at all the stages by altering its physiological, biochemical, molecular properties. Degree of yield loss depends

Crop	Abiotic stress	References	Crop	Abiotic stress	References
Lentil	Drought stress	[24]	Soybean	Cold stress	[25]
Chick pea		[26]	Rice		[27]
Soybean		[28]	Pea		[25]
Common bean		[29]	Chick pea		[25]
Mung bean		[30]	Broad bean		[25]
Faba bean		[31]	Soybean	Salinity stress	[32]
Barley		[7]	Chick pea		[32]
Wheat		[33]	Lentil		[32]
Cotton		[34]	Mung bean		[35]
Maize		[36]	Faba bean		[37]
Spotted bean		[24]	Wheat		[38]
Black gram		[39]	Groundnut, Chickpea, Green gram, Soybean, Pigeon pea	Cd stress	[32]
Cow pea		[40]	Grass pea, Chick pea	Pb stress	[32]
Pigeon pea		[31]	Chick pea, Green gram	Cr stress	[32]
Lupin		[31]	Pea, Lentil, Soybean, Black gram	Hg stress	[32]
Lentil	Heat stress	[41]	Pea, Chick pea, Cowpea, Green gram	Cu stress	[32]
Wheat		[42–45]	Chick pea, Cowpea, Pigeon pea	Ni stress	[32]
Rice		[46]	Cowpea, Chick pea	Zn stress	[32]
Ground nut		[41]	Pea, Chick pea	As stress	[32]
Chick pea		[41]			
Pea		[47]			
Pigeon pea		[41]			
Cow pea		[41]			
Soybean		[41]			
Mung bean		[47]			
Common bean		[25]			
Broad bean		[47]			
Lupin		[47]			

Table 1.
Major crops under harmful impact of abiotic stresses on production.

on occurrence and severity of drought. However, drought stress at flowering as well as post flowering grain filling period is extremely detrimental which reduces the seed yield most. Drought reduces production of flowers, pollen viability, fertilization and seed filling, resulting in loss of production qualitatively and quantitatively. Shortening of pollination and seed filling periods and early maturity lead to less or immature production of seeds. Abortion of reproductive parts of plant is a common phenomenon under drought stress at reproductive stage. Further, under drought stress, increment of toxic ion concentrations in cell, loss of cell turgidity through disruption of water streaming etc. reduce leaf growth leading to poor photosynthesis as well as translocation of dry matter from source to seed (sink). In legume crops, drought stress reduces nodulation, nitrogen fixation and thereby, hampers seed production. Few research works [7] revealed that mild drought stress during seed filling stage leads to increase in protein content of plant. For instance, [48] reported loss of gluten, glutenin, gliadin etc. but increase of protein in wheat under drought stress. However, severe water deficit leads to reduction in amino acid pool and its incorporation to protein as well as less accumulation of N, P, Fe, and Zn, which in turn decreases the protein content of the seed. It has been also observed from many research work that protein content increases after withdrawal of drought in seed filling stage [49]. Oil, oleic acid, glucose, sucrose, fructose etc. decrease with increase of drought during seed filling stage. PUFA contents of sunflower [50] and groundnut [49] are found to decrease under drought stress. β-glucan content of seed also decreases under drought stress. Increased sucrose content and less formation of starch in potato are observed under drought stress [51]. Reduction of starch synthetase activity under drought stress leads to amylose content of wheat [52]. Further, drought stress reduces uptake of nutrients and thereby, lowers the nutritional quality of seed. Increase of electrical conductivity, poor germination and vigor can be seen from the seeds produced under drought stress.

Excessive water use can lead to deficiency of oxygen and accumulation of toxic chemicals inside the plants and thus, hampers number of spike/pod per plant, number of seeds per spike or pod, seed weight leading to reduction of seed production. Further, restriction in uptake of nutrients specially, N under high water content due to leaching and/or dentrification losses can result in quality deterioration of the produce, specially, protein.

4.2 Salinity stress

Salinity is especially harmful at seedling, flowering and reproductive stages. It plays detrimental role in inhibiting seed germination or causing seedling mortality and less plant population which ultimately affects the seed yield. Further, production of seeds are greatly affected under salinity stress due to reductions in photosynthesis, transpiration, stomatal conductance and metabolic activities owing from less chlorophyll, carotenoid, relative water content (RWC) and increased ion toxicity. Nodulation and nitrogen fixation in leguminous crops are also affected by excess salt content. Poor pollen viability and restricted translocation of assimilates to seed lead to low seed production. Restricted supply of nutrient and water to the plant from soil results in detrimental influence on seed production and quality of crops. Oil, protein and starch contents decrease due to disturbances in nitrate uptake and nitrogen metabolism under high salinity. PUFA content of sunflower decreases under drought stress [53].

4.3 Temperature stress

Temperature stress (high/low) greatly affects the seed production and quality of the produce. Loss of yield is resulted from poor seed germination and plant stand establishment. Further, high temperature during flowering and grain filling period can lead to pollen desiccation or sterility, fertilization failure, dysfunctioning of tapetal cells, loss of cell turgor, less leaf area (and increased senescence rate), reductions of chlorophyll, CO_2 assimilation or photosynthesis and increment of photorespiration [54]. Reduction of net photosynthesis due to poor rubisco activity and decrease in translocation of assimilates hamper the production of seed. It has been also noticed that heat stress reduces seed filling duration resulting in loss of production as well as its quality [55]. Increment of soil temperature hampers root growth and increase respiration rate, which further restrict uptake of nutrients and water from soil resulting in not only loss of yield but also changes in quality of the produce. Heat stress, specifically, restricts starch and protein synthesis, which are major determinants of seed quality. For instances, during seed filling period, increase of temperature leads to imbalance supply of nitrogen in pulses [56]. Starch and protein contents also decline under heat stress in wheat and maize [57, 58]. However, it has been also noticed that heat stress has positively affected on seed protein content. For instances, elevated soil temperature (around 2.5°C) has significantly improved protein content (aspartate, glycine, alanine, arginine, valine and tryptophan) of barley [59]. [60] observed that increased temperature during early seed filling period improved protein content in rice but reduced prolamins. In leguminous crops, heat stress mostly reduces protein contents and increases oil contents due to antagonistic effect between oil and protein [61]. Heat stress during flowering and seed filling stages reduces the starch synthesis period resulting in less accumulation of starch (poor conversion from sugar to starch). However, [62] reported increased starch content in potato under heat stress. Under heat stress, PUFA content of soybean declines [63]. Vitamin C, minerals etc. are also low in seed under heat stress.

Cold stress causes stunting in plant growth, vascular browning and abnormal seed ripening. Low temperature during the flowering and seed formation phases results in pollen sterility, limiting pollen grain germination. Cold period in flowering is the most sensitive period in plants like rice. Cold stress shortens the seed filling stage and can lead to energy deficiency and thereby, sterility of gametophytes by hampering carbohydrate metabolisms. It causes cell dehydration and crystallization of water in cell. Further, there is production of ROS under low temperature (oxidative stress). Infestations of soil-borne diseases to seedling stage of the crop are also visible under cold stress. As a consequence, yield attributes and production of seeds are greatly hampered. Accumulation of minerals, amino acids, protein, starch, fat and crude fibers decreases and sugar concentration increases in seed under cold stress [31].

4.4 Heavy metal toxicity

Excessive uptake of heavy metals leads to chlorosis and reduction of production of seed through alteration of physiological, morphological, biochemical, molecular activities of plant. It negatively impacts on seed germination, accumulation and remobilization of seed reserves and photosynthetic activity resulting in loss of seed yield. Heavy metal toxicity reduces the yield also through synthesis of ROS, increased rate of lipid peroxidation and disrupting redox equilibrium. Lower uptake of nutrients such as N reduces quality *viz.*, protein of seed produce. Cd, Pb. Cr, Ni, Zn, Cu, As etc. reduce starch, protein, oil and minerals contents of seed. Decrease of oleic acid and linoleic acid and increase of palmitic acid, linolenic acid and stearic acid are found under heavy metal toxicity specially, under high Cd and Hg.

4.5 Other abiotic stresses

Use of excessive chemicals and nutrients lead to deterioration soil and water health, loss of beneficial micro-organisms activity and drastically hampers seed production and quality of the crop. On a contrary, nutrient deficiency can lead to poor yield and quality of the crop as photosynthesis and various metabolic activities are seriously affected under scarcity of nutrients. High wind causes erosion, loss of nutrients, lodging and evapotranspiration water loss which affect the plant growth and various physiological functioning inside the plant including photosynthesis. Further, high wind velocity causes loss of pollen which in turn, impacts on fertilization and seed production. Shattering loss of seeds is another major issue associated with high wind velocity. Light impacts on photosynthesis. Shading or low light hampers photosynthesis and translocation of photo-assimilates to reproductive parts and thereby, affects seed production and quality. Excessive light, on the other hand, disrupts photosynthetic apparatus including chlorophyll and hampers the photosynthetic activity of plant. Further, it creates water scarcity or high temperature, which in turn hampers various functioning of plant system and thereby, affects seed yield quantitatively and qualitatively.

5. Defensive mechanisms of plants against abiotic stresses

In response to these abiotic stresses, plant shows defensive mechanisms mainly by three ways: stress escape, stress avoidance and stress tolerance. Short growth period, seed dormancy, shedding of leaves etc. are some common escape mechanisms against abiotic stresses. Leaf rolling, reduced growth, reallocation of nutrients etc. are some common abiotic stresses avoidance strategies. In case of stress tolerance, certain cellular, physiological, biochemical and molecular changes such as osmotic adjustment, stiff cell wall, activation of stress tolerance compounds, metabolites and enzymes, expression of stress tolerance genes etc. occur inside the plant. For example, when photosynthesis is restricted, plant utilizes starch as energy source and in response to starch breakdown, synthesis of sugars, osmoprotectants, compatible solutes etc. occurs which helps the plant to tolerate stress [64]. Over expression of glutamine synthase, asparagine synthase genes etc. leads to tolerance of abiotic stresses by the plant. Besides, there are some detoxifying genes which alleviate various abiotic stresses through activating enzymes such as ascorbate peroxidase, glutathione peroxidase, glutathione reductase etc. Under abiotic stresses, abscisic acid (ABA) is produced inside the plants and this phytohormone helps the plant to cope up with abiotic stresses like drought, salinity, low temperature etc. Polyamines (low molecular weight aliphatic nitrogen compounds) also play important role in alleviating abiotic stresses through maintaining cell membrane integrity, reducing growth inhibitors, moderately expressing stress responsive genes and elevating antioxidant enzymatic activities. Endogenous polyamines can be increased by applying exogenous polyamines (putrescine, spermidine and spermine). Trace elements like selenium, silicon etc. and signaling molecules like nitric oxide also play positive roles in defending abiotic stresses.

5.1 Water stress

Drought: Plant reduces leaf area and number or modifies leaf into spine or other forms and leaf rolling to reduce transpiration loss of water. Stomata is closed and leaf abscission and curling are seen under drought stress. Cuticle or wax deposition over leaf surface also restricts loss of water through transpiration. When water is limited in soil, plant's root is extended deeper into the soil in search of moisture, but shoot growth becomes limited (through reduction of growth promoters). Plant also mature comparatively earlier than normal when exposed to drought stress. Secondary metabolites are produced under drought stress, which further improve immunity of plant. Under drought condition, synthesis of ABA in roots and its transport to shoots through xylem regulates the stomata and thereby, controls transpiration loss of water. Further, reallocation of nutrients present in older leaves occurs. Accumulation of proline (osmoprotectant), arginine (compatible solute) etc. under drought (and/or salinity stress) controls osmotic pressure and thus, helps in stress tolerance. Late embryogenesis abundant proteins are abundantly synthesized under drought stress during early embryogenesis to combat stress through improving water binding ability.

Flood: In plant like rice, adaption mechanism against flood mainly includes formation of gas filled spaces (aerenchyma) which can transfer oxygen from aerial parts to root zone of the plant.

5.2 Salinity

Accumulation ABA under high salinity regulates stomatal opening and plays key role in maintaining leaf water potential. Further, there is a production of low molecular weight organic compounds (polyols: sorbitol, mannitol, glycerol, inositol and other forms of mono and dimethylated inositol), amino acids (proline, glutamate) and betaine (betaine glycine and alanine) inside the plant as defensive mechanism to alleviate salinity stress [65]. Plant detoxifies oxidative stress enzymatically or non-enzymatically. In enzymatic system, super oxide dismutase (SOD), catalase (CAT), peroxidase (guaiacol peroxidase, glutathione peroxidase and ascorbate peroxidase), monodehydroascorbate reductase (MDHAR), glutathione reductase (GR), glutathione transferase (GST), dehydroascorbate reductase (DHAR) etc. are produced which act as ROS scavengers. In non-enzymatic system, proline, glutathione, ascorbic acid, carotenoids, flavonoids, tocopherols etc. are synthesized which neutralize ROS.

5.3 Temperature stress

Heat stress: Plants adapt heat stress by changing leaf orientation, early maturation, rolling of leaf, transpiration cooling and synthesis of antioxidants and/or osmoprotectants or stress proteins. Elevation in transcription of genes (heat shock proteins) under heat stress is one of the common plant responses against heat stress.

Cold stress: Plant adapts cold stress through acclimation. Accumulation of ABA under cold stress plays key role in plant's adaptation to it. Plant enhances the level of unsaturated lipids which in turn improve fluidity and membrane stability and thereby, defend cold stress.

5.4 Heavy metal toxicity

Plant secretes various organic acids (oxalic acid, citric acid, tartaric acid, malic acid, succinic acid) under heavy metal toxicity and these acids chelates with heavy metals resulting in conversion of toxic to non-toxic elements. Metallothionein, Phytochelatins, glutathione etc. are synthesized by the plant and they act as chelates against heavy metals. Plant root also release amino acids which provide nutrition to fungi, bacteria and others. These microorganisms inhibit the uptake of heavy metals by the plant.

5.5 Other abiotic stresses

Under heavy wind velocity, stomata are closed by the plant to reduce transpiration loss of the water. Under excess light, plant undergoes photoinhibition (downregulation of photosynthesis and activating photo-protective mechanisms to prevent light entry to chloroplast). Non-photochemical quenching and enzymatic antioxidant defense against light induced ROS are some mechanisms occur inside plant against excess light. Under shaded condition, adaptation of plant is resulted from adjusting the canopy architecture. For example, height is increased instead of branching to harvest solar energy.

6. Agronomic management practices to cope up with abiotic stresses

In order to cope up with abiotic stresses, other than the plant's own defensive mechanisms, changes in management practices play a considerable role. Few such agronomic management practices have been listed in **Table 2**. Improved breeding

Abiotic stresses	Agronomic management practices
Drought	• Use of resistant/tolerant variety • Foliar spray of 2% DAP +1% KCl or 0.5% zinc sulfate +0.3% boric acid +0.5% ferrous sulfate +1% urea or 3% kaolin or 500 ppm cycocel or 40 ppm NAA during moisture sensitive periods • Mulching or cover cropping or inter/mixed cropping to reduce evaporation loss of water (moisture conservation) • Sowing in ridge and furrow bed • Alternate/skip furrow irrigation or partial root drying • Skip row planting • Use of sprinkler/drip or any other micro irrigation/water saving options • Less application of fertilizers • Split application of N and K fertilizers • Application of Zn, B and Mn fertilizers to improve plant's tolerance against water deficit • Use of bio-fertilizers and seed priming • Nipping or pinching apical portion to arrest shoot growth and consequently, transpiration rate.
Flood	• Use of resistant variety • Foliar spray of 2% DAP +1% KCl or 0.5% zinc sulfate +0.3% boric acid +0.5% ferrous sulfate +1% urea or 3% kaolin or 500 ppm cycocel or 0.5 ppm brassinolide or 100 ppm salicylic acid • Drainage of excess water • Growing of water loving crops • Adequate application of K fertilizer

Abiotic stresses	Agronomic management practices
Salinity	• Use of resistant/tolerant variety • Foliar spray of 2% DAP +1% KCl or 0.5 ppm brassinolide or 100 ppm salicylic acid • Application of gypsum or incorporation of green manure crop in soil before sowing • Split application of N and K fertilizers • Excess (25% more) N application • Seed hardening with NaCl • Exogenous applications of ABA and/or jasmonic acid • High application of K, Ca, Mg etc. fertilizers • Seed treatment with polyamines *viz*., putrescine, spermidine, spermine etc.
High temperature	• Use of resistant/tolerant variety • Shading on the plant canopy • Use of mulch or residue retention to avoid heat stress at early growth stages • Application of salicylic acid or glycine betaine or ethylene or gibberellic acid • Moderate application of N, P, K and Ca fertilizers as they act as osmoprotectants and improve seed quality if applied at anthesis. • Irrigation on the canopy to restrict sun scorching • Drip irrigation to reduce soil temperature at root zone depth • Timely sowing of winter crops to avoid heat stress during anthesis and seed formation phases
Low temperature	• Use of resistant/tolerant variety • Seed treatment with gibberellic acid or proline • Foliar spray of 0.15% ammonium molybdate • Use of cryoprotectants, ABA, paclobutrazol, uniconazole etc. • Timely sowing of monsoon crops to avoid terminal cold stress
Heavy metal toxicity	• Construction of wetlands • Reduction of chemical based intensive farming approach • Substitution of chemicals with biofertilizer, compost and bio-pesticides
Wind velocity	• Use of windbreaks/shelterbelts • Use of dwarf crop varieties
Low light	• Use of sun loving or tall varieties
High light	• Use of shade loving or dwarf varieties
Excess chemicals and nutrients	• Promotion of organic farming practices • Less use of chemicals and nutrients • Growth of nutrient exhaustive crops
Nutrient scarcity	• Application of nutrients to correct the deficiency

Table 2.
Agronomic management practices to alleviate abiotic stresses.

program to develop highly resistant varieties is also needed. In this regard, identification of responsive genes against abiotic stresses is one of the frontline strategies that can be made by the plant breeders. Use of genetic engineering to develop transgenic plants keeping in mind the safety of the environment and human health is the another key solution against abiotic stresses. It has been also observed that use of beneficial microbes in the form of seed bio priming has helped the plant to alleviate against such abiotic stresses through its positive role in germination and early plant stand establishment [66]. Bio priming increases the osmolyte concentrations which results in high cell wall elasticity and turgid weight to dry weight ratio. Further, endophytic synthesis of alkaloids can save the macromolecules from ROS through ROS scavenging activities. Plant growth promoting rhizobacteria (PGPR) enables expression of drought response related genes through enhancing ROS scavenging activities. Synthesis of phytohormones like IAA, GA3 etc. occurs due to PGPR which in turn, helps in plant growth under stress condition. PGPR further synthesizes exopolysaccharides which improves soil structure and maintains water and nutrient uptakes. Exogenous application of various chemicals viz. proline, glycine betaine, trehalose etc., plant components such as amino acid, sugars etc. and phytohormones such as ABA, GA3, jasmonic acid, salicylic acid, brassinosteroids etc. can help plant to cope up with abiotic stresses. Salicylic acid is a phenolic phytohormone which at low level can alleviate abiotic stresses through improving stomatal regulation, leaf chlorophyll content, water use efficiency and root growth. Brassinosteroids induce expression of antioxidant genes and thus, alleviate oxidative stresses through synthesizing ABA, proline, glutathione, phytochelatins, heat shock proteins and stimulating N metabolism. Brassinosteroids and salicylic acid help in improving seed production and quality under salinity stress through osmoregulation by increase of SOD, POD, CAT activities and elevation of photosynthesis. Jasmonic acid is a cyclopentanone derivative synthesized from linolenic acid, which helps the plants to tolerate abiotic stresses. Application of silicon also plays important role in improving crop growth and productivity under abiotic stresses. Under stress conditions, plant itself synthesizes proline, L-tryptophan, glutathione (GSH), citric acid, polyols, lipoic acid, ascorbic acid, glycine betaine, α-tocopherol, melatonin etc. as defensive mechanisms. Further, exogenous application of these can be found useful in alleviating stress. Proline acts as a ROS quencher by increasing the activities of SOD, CAT etc. and maintains plant growth under drought or salinity stress. L-tryptophan (amino acid) can synthesize auxin and thus, helps in plant growth. Glutathione (GSH) is a low molecular weight tripeptide, composed of glutamine, cysteine and glycine. Application of GSH detoxifies ROS, methylglyoxal and synthesize phytochelatins which bind heavy metal. It also acts as cysteine reservoir [67]. Citric acid is the intermediate product of TCA cycle, which is produced by citrate synthase from oxaloacetate and acetyl coA. Application of citric acid shows antioxidant properties which inactivates heavy metals such as Cu, Pb, Al etc. as well as protects the plant from salinity stress. Foliar application of polyols or sugar alcohols (mannitol, sorbitol, inositol) plays positive role in osmotic adjustment through improving SOD, POD, CAT activities and thus, helps the plant to cope up with drought, salinity and heavy metal stresses. Lipoic acid application on plant canopy under salt or drought stresses reduces lipid peroxidation and increases cysteine, POD and CAT activities. Ascorbic acid or vitamin C application can neutralize ROS under drought stress. Under low temperature, seedling subjected to incubation in ascorbic acid can reduce oxidative damage and improves proline, nutrients and CAT activity. Glycine betaine application under salinity or drought stress helps the plant in osmotic adjustment and stabilization of PS II. α-Tocopherol is generally present in chloroplast and improves photosynthetic membrane integrity. Exogenous application of α-tocopherol reduces oxidative damage by scavenging ROS under abiotic stresses. Melatonin is a tryptophan derivative which increases proline synthesis and further, acts as ROS scavenger. Further, soil and foliar applications of humic substances, beneficial fungi, bacteria, chitosan, sea weed extracts etc. can play positive roles in combating abiotic stresses.

7. Conclusion and future prospects

The concept of abiotic stresses is not new. Over the years, abiotic stresses are affecting the crop with more prominent effect found in recent times as a consequence of climate change arising due anthropogenic activities. The extent of impacts from these stresses on crop varies from mild to severe, resulting in changes in seed production and quality of the produce accordingly. Under abiotic stresses, crop also shows internal defense against them by undergoing various morphological, cellular, physiological, biochemical and molecular changes, which altogether exert antagonistic impact on crop growth and yield. As food demand is increasing from enormous population growth, crop yield loss due to abiotic stresses should be addressed through incorporation of suitable modern agronomic management as well as breeding approaches. Development of resistant varieties to cope up with abiotic stresses needs special emphasis. Further, molecular research should be carried out at genetic level to study and develop suitable defensive mechanisms against such stresses. For instance, genetic engineering and genome editing are showing the prospects for resistance/tolerance of plants against these stresses in future through transferring specific gene carrying targeted traits in crop. In achieving success in genetic engineering, identification and isolation of the key genes play fundamental role which urges for effective works of breeders. Further, it has been seen that although there are available mitigation and adaptation strategies against such stresses, they are currently insufficient. Therefore, there is an urgent need for multi-locational research trials, transfusion of modern practices, policy interventions and advances in genomics approaches to address negative impacts of stress as well as to achieve successful crop production and it can be achieved by integrating multiple approaches together rather than relying on single strategy. Participation of public and/or private organizations is highly needed in curtailing the adverse impact of abiotic stresses on crop through financial and infrastructural support, generation of modern agronomic, breeding and other relevant technologies as well as strengthening of extension service.

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