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Abiotic stress mechanism in herbaceous crops: An overview

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Abstract

Abiotic stresses like water stress, temperature stress, mineral stress, oxidation stress are major limiting factors in plant growth and development and will soon become even more severe as desertification covers more and more of the world's area. Herbaceous crops are generally sensitive to environmental extremes, and thus high temperatures and limited soil moisture are the major causes of low yields in the tropics and will be further magnified by climate change. The response of plants to environmental stresses depends on the plant developmental stage and the length and severity of the stress. Stress physiology studies identify mechanisms of stress tolerance and provide an approach, method, and traits for screening stress-resistant genotypes.

Keywords: Abiotic stress, stress physiology, water stress, temperature stress salinity stress

Introduction

Phenotypic performance of a plant/ line/ population is determined by genotype, environment and genotype x environment interaction. The environment of an individual may be simply defined as the sum total of all the factors other than the individual concerned. The various factors of environment are called biotic and abiotic depending upon their biological/ non-biological nature. In an optimal environment there is no interference by any environmental factor with the complete expression of genotypic potential of a plant/ line; such an environment is therefore termed as stress free environment. When some factors of the environment interferes with the complete expression of genotypic potential or significant deviation from the ideal conditions, preventing plants from expressing their full genetic potential for growth, development, and reproduction is termed as stress³⁹. Stresses are also classified as biotic (pathogens, pests, weeds) and abiotic (environmental factors). Abiotic stress is defined as the negative impact of non-living factors on the living organisms in a specific environment. The non-living variable must influence the environment beyond its normal range of variation to adversely affect the population performance or individual physiology in a significant way^[48].

Characteristics of Abiotic Stresses

- The relative importance of different abiotic stresses is mainly region/ location specific.
- The occurrence and the degree of some of the stresses are unpredictable e.g. drought.
- A given abiotic stress may increase/ decrease the level of another abiotic stress e.g. in a saline soil, moisture stress would enhance salinity stress.
- Different crop varieties show large differences in their abilities to tolerate abiotic stress.
- Different growth stages of crops may show marked differences in their tolerance to an abiotic stress.
- Stress during the reproductive phase of a crop causes far more economic loss than comparable stress during the earlier phases.
- The effects generated by one abiotic stress may overlap some of those generated by other e.g. salinity stress generates some features produced by drought stress.

Plant Responses to Stress

Abiotic stress may trigger a series of responses in plants that include changes in gene expression and cellular metabolism. The duration, severity and frequency with which a stress is imposed, and the affected organs and tissues, developmental stage, and genotype also influence plant responses to stress. Consequently a combination of different conditions can

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cause different plants responses to the same type of stress. There are three types of stress resistance mechanisms occurs in plants viz.

Avoidance mechanisms: These prevent exposure to stress.

Tolerance mechanisms: These permit the plant to withstand stress.

Acclimation: Plants alter their physiology in response stress.

Water Stress

Among the environmental variables affecting plant growth and development water stress is one of the most important. A water stress may arise either from an insufficient water or drought stress or from excessive water activity or water logging.

Water stress injury mechanism

Water stress directly affects the cellular processes, plant growth and development, and finally economic yield. Drought affects membrane structures and structure of macromolecules like proteins, nucleic acids and enzymes, creates pressure differential across the membrane cell wall complex. At low water potential, stomata close due to the loss in turgidity of the guard cells leading cease in transpiration. In absence of transpiration, temperature of the leaves increases to lethal levels and leaves die. Such, low water potentials are known to cause severe embolism formation in the xylem vessels of woody plants blocking water transport and potentiality causing shoot dieback.

Drought

Drought has been as the inadequacy of water availability, including precipitation and soil moisture storage capacity, in quantity and distribution during the life cycle of crop to restrict expression of its full genetic potential or as any period during which plant or soil water deficiencies affect the growth and development of crop plants. These deficiencies may result either from a small moisture supply or a large moisture demand^[36]. Drought like many other environmental stresses has adverse effects on plant growth and yield.

Tolerance Mechanisms

Drought tolerance is generally defined as the property of a given cultivar to show a relatively small yield reduction upon exposure to drought. The various mechanisms by which a crop can minimize the loss in yield due to drought are grouped into three categories drought escape, dehydration avoidance and dehydration tolerance^[47].

- **Drought escape:** The ability of a plant to complete its life cycle or most drought sensitive stage before onset of drought. One breeding strategy is to shorten the life cycle of a crop to enable it to mature safely during rainfall period. Early maturity is one of the most important attributes of drought escape and is suitable for environments subjected to late season drought stress e.g., in Africa very short season cowpeas avoid drought by maturing before any substantial stress develops, in less than 65 days^[18]. Most of the studies showed significant positive correlation of crop duration with economic yield^[41]. Drought escape also involves seed germination. Dormant seeds, quasi-dormant or quiescent state seed survive the dry spell and germinate only under favorable conditions.

- **Dehydration Avoidance:** The ability to endure or withstand a dry period by maintaining a favorable internal water balance under drought condition is termed as dehydration avoidance. Associated high water use efficiency with plants that avoid drought there are two types of drought avoiders.

- a. **Water savers:** Avoid drought by closing their stomata during the day even though soil water supplies may be adequate and they achieve high water use efficiency through efficient control of total water supply.
- b. **Water spenders:** Avoid drought by extracting large quantity of water from soil per unit time. As a result, the water spenders keep their stomata more open throughout the day, assimilate more carbon dioxide and therefore have more rapid growth rate than water savers.

The dehydration avoidance mechanisms are results of various morphological (reduce leaf area, leaf rolling, cuticular wax, deficient rooting system, awns, stability in yields), physiological (reduced transpiration, high water use efficiency, stomatal closure, osmotic adjustment) and biochemical (accumulation of proline, polyamine, trehalose etc., increased nitrate reductase activity and increased storage of carbohydrates) characters.

- **Dehydration tolerance:** The ability of plant cells to withstand water stress and continue metabolic functions is termed as dehydration tolerance. Cellular dehydration causes significant disorders in membrane structure, composition and function. Maintenance of membrane integrity and function under a given level of dehydration stress can be taken as a major of tolerance. Dehydration tolerance of a genotype means that a significantly lower level of changes is induced in it than those in another genotype when both of them are subjected to the same level of dehydration.

Water logging

The term water logging is defined as the condition of soil where excess water inhibits gas exchange of roots with the atmosphere. Water logging is different from flooding because the latter results in addition factors of partial or complete submergence of the shoot. The water logging replaces a gaseous air by liquid water, leading to the gas stresses.

Tolerance mechanisms

Mechanisms of survival or maintenance of high biomass production and yields during waterlogging may be important at the germination and emergence stages, during vegetative and reproductive stages or both. These mechanisms' may involve avoidance of water logging effects i.e., by phenological development; adoption of waterlogging, e.g. by aerenchyma or metabolic change and recovery mechanisms following waterlogging^[16]. The particular mechanism used in crops may vary depending on, the growth habit of the cultivar, and the duration of waterlogging.

Temperature Stress

Temperature is basic to life processes, which increase with temperature within a limited range. This effect is expressed as Q_{10} , which is the ratio of the rate of a biochemical process at one temperature to that at a temperature 10° C lower. When temperature rises beyond the upper limit of the range i.e., it goes above the optimal temperature, the relation between life processes and temperature is disturbed. Similarly, when the

temperature goes below a threshold, which is often close to zero, life processes are disturbed enough to cause injury and death in sensitive genotypes. Each plant species, more particularly each genotype, has an optimal range of temperature for its normal growth and development; the specific temperatures would depend not only on the genotype but also on the stage of growth and development of the given genotype. When temperature moves beyond this optimal range, it generates temperature stress, i.e., temperature interferes with the performance. Temperature stress may be grouped into the following three categories heat stress, chilling stress and freezing stress.

Heat stress: The adverse effects on plant of temperatures higher than the optimal is considered as heat stress. Crops are exposed to periods of heat stress during their life cycle. The optimum temperature for most of the vegetable crops ranges from 20-35°C. Above this value, a decline in the photosynthesis rate is observed^[5]. Even brief periods of heat shock between temperature ranges of 45-50°C induce marked change in plant growth processes. The temperature of the leaves exposed directly to the sun can be equal or higher. This elevation of the leaf temperature can result in the biochemical and biophysical disturbance in the mesophyll, which can be reversible or not⁵. High night temperatures during the growing season can have detrimental effects on reproductive development and yield of several crops^[17].

- **Injury mechanisms:** High temperature would affect mainly in two different ways: growth and development of plants and other is physiological process of plants. The nature and extent of heat injury may depend on the temperature, plant species and other meteorological parameters.
- **Effect of high temperature on growth and development:** High temperature is associated with death of cells, tissues, organs or whole plant. Heat stress is known to cause death of seedlings and flower abscission, pollen sterility and poor fruit set at reproductive stage and to cause yield reduction. Cell and tissue death usually occur in organs that lack transpirational cooling, and their surface temperature ranges 48-50°C. The extent of detrimental effects of heat depends on both the temperature and longibility of exposure at that temperature. Seedlings are more susceptible to heat stress. Sensitivity to heat stress differs depending upon the stage of the plants. In general, seedlings are more prone to high temperature as they contact with the soil surface. The temperature which kills 50% of the plants, seedlings could be regarded as heat killing temperature. In many crops, pollination and fertilization are highly disturbed by heat during anthesis as pollen sterility is caused by high temperatures^[27]. Different crop species and varieties respond differently to rise in temperature. Yield of cowpea under heat stress caused by damage to reproductive development^[19]. Genetic studies have demonstrated that heat tolerance during reproductive development is conferred by a set of major recessive genes, while heat tolerance during pod set also involved a major dominant gene. Two or more weeks of consecutive or interrupted high night temperature during the first four weeks after germination causes complete suppression of floral buds and prevents flowering^[19]. Many cowpea cultivars are susceptible to high temperatures during reproductive development and can exhibit 13.5% reduction yield. The

most critical growth stage in green beans was found to be 2-3 days before anthesis^[10].

- **Physiological effects of high temperature:** High temperature affects physiological processes of plants one way or other. Heat injury results in denaturing of proteins, enzymes, metabolic imbalances, respiratory depletion of substrates, translocation and reduction in chloroplast photochemical activity. The cellular heat stress perturbations are to a large extent a result of membrane disturbance^[6].
- **Photosynthesis:** It is activated after exposure to hardening temperature but inhibited at temperatures causing damages^[23]. Photosynthetic processes are extremely sensitive to the temperature higher than the optimum range. Photo system II, viz., photosynthesis of water and reduction of carbon dioxide, is far more readily inactivated by heat than is photo system I. The main effect of high temperature on photosynthesis results from alteration in thylakoid physical- chemical properties. The various enzymes located outside the thylakoid membrane can be destabilized by heat, and thereby result in inhibition of photosynthesis. Besides inducing an increase in the lipid matrix fluidity^[37] with consequent formation of unilayer structure, high temperature provokes disturbances in the photosynthetic apparatus organization. All these events result in photochemical and carboxylative efficiency losses, and serious metabolic restriction in the Calvin cycle, such as inactivation of Ribulose-5-bisphosphate Carboxylase/ oxygenase (Rubisco) and variations in the metabolic pool, especially ATP and NADPH availability^[35]. In beans, photosynthesis shows a negative response to rising temperature^[28]. The optimum temperature for photosynthesis in bean leaf is 25°C, showing decay with its continuous increase^[20].
- **Protein denaturation:** High temperature induces conformational changes in proteins. Thus, it may affect the specific function of protein causing their denaturation, which may enhance their susceptibility to proteolytic enzymes.
- **Membrane composition and stability:** Cell membrane of plants is composed of proteins and phospholipids. High temperature may affect membrane stability and function. In hot environment, the lipid becomes increasingly liquid. Heat stress can affect the structural integrity of protein in cytoplasm and cause membrane protein denaturation and aggregation^[25].

Tolerance mechanisms

The availability of plants to withstand high temperature and perform better than the others under the same environmental condition is termed as heat tolerance. Based on response of plant to high temperature, the various mechanisms of heat tolerance/ resistance may be classified as heat avoidance and heat tolerance.

- **Heat avoidance mechanisms:** High temperature avoidance is the ability of the plants to scatter the radiation energy causing cooling effect at stress temperature. The heat avoidance should be measured at a temperature just below the heat killing temperature and may be measured in the growth chambers as the ratio of the air temperature to the leaf temperature. The primary mechanism of dissipation of high temperature is transpiration.
- **Transpiration:** At high temperature rate of transpiration increases, causing cooling down of the micro-

environment. Vigorous growth seems essential to supply adequate water to the leaves so that these can maintain loss due to transpiration and good turgor at high temperature. Transpirational cooling is the link between dehydration and heat avoidance so that under conditions of high solar radiation and water stress the effect of the heat avoidance becomes inseparable from those of dehydration avoidance. Heat tolerance varieties of Chinese cabbage (*Brassica campestris* spp. *Pekenensis*) had greater water uptake than heat sensitive ones at the onset of head formation [25].

- **Leaf pubescence:** Pubescence is a characteristic of leaves, a protective adaptation. It is a covering or short hairs on leaves or soft stems. This texture is produced by microscopic hairs called trichomes that help plants to stand up to brutally hot conditions. The trichome hairs help to shade the leaf surface. Each tiny hair casts a microscopic shadow to protect the leaf's outer layer from the direct sunlight. These hairs also reduce the moisture loss through stomata. The trichome hairs help to baffle the air at the leaf surface so it slows down.
- **Reduction in the amount of foliage:** Reduction in the amount of foliage with the microcellular structure of the leaf blades contributes to the resistance to drought and hot spells. In addition, reduction in foliage towards the apex decreases the area of the transpiration, thus preventing damage by heat.
- **Adaptation to warm temperature:** Heat hardening of leaf tissue can occur within hours or even minutes when critical high temperature thresholds are suppressed¹. Heat hardening may be defined as an improved ability of a genotype to withstand a period of high temperature as a consequence of an earlier exposure to a high temperature for a given period of time. Exposure to sub-lethal high temperature can increase the thermo tolerance of the plant¹⁹. Potential mechanisms of response include synthesis of HSP'S, isoprene and antioxidant production to protect the photosynthetic apparatus and cellular metabolisms. The heat tolerance increased under warmer micro-site conditions and in warmer years, while long term artificial heating by +3⁰C lead to a significant increase in heat tolerance by +0.6⁰C. They also reported that higher the mean minimum leaf temperature at a particular growing site, the higher the mean tolerance in leaves [7].

Tolerance mechanisms

High temperature tolerance generally associated with cellular and sub-cellular components. Bio- molecules are also involved in heat tolerance of plants. The following components and bio-molecules may be associated with heat tolerance.

- **Molecular chaperones interacted to protect against heat:** Plants are known to synthesize, under heat shock, a large diversity of heat shock proteins (HSP'S) that function as protectors on the biochemical level¹⁹. HSP's are low molecular weight proteins produced during stress. These proteins have been classified into a number of families based on their molecular mass, and most have chaperon in function All organisms produce HSP'S from all the major families (HSP90s, HSP70s, and small HSPs), but plants are unique in the number of different small HSPs that they produce [7]. Most studies investigating heat stress in plant have focused on HSPs [45]. Evidences are

accumulating to suggest an important role for heat shock proteins/ molecular chaperones in stress resistance in plants. It may help to prevent protein degradation, disassembly of aggregation. The HSPs vary during different developmental stages and various tissues. The various tissues, leaves, stems, flower buds, flower, petals, hypocotyls and siliques of three *Brassica* species showed characteristically unique pattern of polypeptide synthesis and the general pattern was maintained following heat shock. One HSP, ubiquitin, may help to degrade and remove heat damaged proteins³. The HSPs that are localized to the cytosol appear to specific developmental signals associated with the acquisition of desiccation tolerance that occur during seed development. A small HSP has been shown to interact with HSP70 to reactivate heat denaturated luciferase [44].

- **Amylopectin content:** It is suggested that the tolerant genotypes increases the portion of carbon preferably in the form of amylopectin, which is capable of holding more water. The low amylase and high amylopectin contents compared with the starch from seeds of susceptible wheat genotypes [34].
- **Membrane stability:** Heat tolerant species tend to have a higher percentage saturated fatty acids in their membranes. Saturated fatty acids exhibit less increase in membrane fluidity associated with heat than unsaturated fatty acids. Cell membrane stability is an index in heat tolerance that bears considerable relationship with plant performance under stress environments. Cellular membrane- thermo stability, measured as the conductivity of electrolytes leaking from leaf disks at high temperature, has been suggested as a screening technique for heat tolerance in plants.
- **Osmoregulators content:** Osmoregulators viz. polyamines have a protective role in plant stress responses. The diamine putrescine the triamine spermidine, and tetramine spermine are ubiquitous in plant tissues and have been implicated in an overwhelming array of plant growth and developmental process². Proline and glycine- betaine protect several enzymes from heat inactivation. Being cationic in nature, proline can associate with anionic components of membrane deterioration⁴⁰. It also has radical scavenging property. Protection of membrane from peroxidation by polyamines could involve both their ability to interact with phospholipids and their antioxidant activity. It has also been suggested that under stress condition, polyamines may partially replace calcium in maintaining integrity by binding to phospholipids component of the membrane [32].
- **Plant growth regulators:** Calcium ions, salicylic acid, abscisic acid and ethylene are involved in several stress responses. Concentration of some of the growth regulators increases during high temperature, which contributes towards tolerance ability of plants. High temperature during flowering reduces yield of *Phaseolus vulgaris*, when ethylene production from plant tissue increases as a consequence of heat stress⁴³. The inheritance of leaf ethylene, evaluation rate of high temperature stressed (35/300c day/night) progenies from cross of *Phaseolus vulgaris*. Salicylic acid acts independently during the establishment of thermotolerance.
- **Thermo-stability of photosystem II:** Thermo-stability of photosystem II enhances high temperature tolerance. Thus, effect of heat stress on photosynthesis and

chloroplast damage can be assayed as variable chlorophyll fluorescence at 685nm^[9]. Photosynthetic apparatus of Espace 10, a bean cultivar, widely distributed in warm and dry regions of Brazil showed differential tolerance to heat stress. The photosynthetic apparatus of Espace 10 makes use of mechanisms of tolerance to heat stress and this may be due to major capacity of D1 protein regeneration of high capacity of the xanthophyll cycle and high capacity for energy dissipation via the protein gradient in thylakoids.

- **Repairing of injured cells:** The repair of plant cells exposed to heat stress after having returned to an optimal temperature⁴. But the degree of recovery depends upon the severity of the stress^[5].

Cold Stress

Low temperature is one of the major environmental factors that limit the plant growth. Cold temperature in crop plants is compounded by cold snap- a lower temperature than the usual drop in temperature that causes crop to fail. Low temperature in growing season may reduce germination, retard vegetative growth by inducing metabolic imbalances and can delay or prevent development. Low temperature cold injury can be categorized into two parts: Chilling injury and Freezing injury.

Chilling Injury: The injury caused when temperatures remain above freezing point ($>0^{\circ}\text{C}$). A chilling temperature is defined as a temperature low enough to cause plant tissue damage but not low enough to cause freezing of tissue water²⁶. Chilling temperature can damage the tissues of sensitive plants while freezing temperature will damage most tissues during active growth.

Tolerance Mechanisms

Ability of some genotypes to survive/ perform better under chilling stress than other genotypes is known as chilling tolerance. Ordinarily, it is a consequence of chill hardening i.e., an earlier exposure to a near chilling temperature for a specified period, as a result of which chilling tolerance of the concerned plants increases. The various mechanisms are:

- **Membrane – lipid unsaturation:** The lipid composition of membrane is a key determinant for cold tolerance, and enzymes that modify membrane structure seem to be important for low temperature accumulation. Chilling tolerant genotypes show a higher degree of membrane-lipid unsaturation than do susceptible ones. The chilling sensitivity of higher plants is closely correlated with the degree of fatty acids unsaturation in the thylakoid membranes of these chloroplasts^[31]. Thus membrane lipid fatty acid plays an important role in cold adaptation^[29]. An increased production of highly unsaturated fatty acid, such as hexadecatrienoic acid at low temperature was observed in connection with cold acclimation in many plants^[15]. A correlation between chilling sensitivity and degree of unsaturation of fatty acids in phosphatidylglycerol in plastid membranes has been reported in higher plants^[30].
- **Reduced sensitivity of photosynthesis:** Chloroplasts and photosynthesis are mainly affected by chilling injury. Tolerance in these aspects is expressed in native vegetation adapted to growing under cool conditions. This has been observed in some crops. The reduced sensitivity of photosynthesis to chilling is partly related to specific enzymes of the process, including those that interact with

membranes. As photo system II is the most likely site for chilling injury, variable chlorophyll fluorescence at 685nm is emerging as an index of chilling tolerance.

- **Improved germination:** Genetic variation in chilling tolerance at germination is known in many crops but the nature of tolerance is little known. In case of soya bean, seeds of more tolerant varieties imbibed less water at 2.5°C , and seeds that had matured at lower temperatures were more tolerant. In comparison, young seedlings are much more tolerant as long as food reserve is available to them; but once reserve is depleted, there is a marked increase in their susceptibility.
- **Improved fruit/ seed set:** Chilling tolerance at flowering is expressed as improved fruit/seed set and pollen fertility. It is largely a function of floral structure and function under stress. Tolerance in brinjal was related to longer styles, and flower position within a flower cluster.
- **Polyamines:** Polyamines such as spermidine and spermine occur ubiquitously in plants together with their diamine precursor putrescine^[46]. It is also synthesized by decarboxylation of L-Arg by Arg carboxylase via agmatine and N- carba- moglputrescine intermediates. Because of the poly cationic nature at a physiological pH, polyamines can bind strongly to the negative charges in cellular components, such as nucleic acids, proteins and phospholipids. Interactions of polyamines with membrane phospholipids may stabilize membrane under stress^[40].

Freezing Stress

Injury caused at temperatures below freezing point ($>0^{\circ}\text{C}$). When the plants are subjected to subzero temperatures, a complex array of stresses and strains develop within them known as freezing stress. Freezing stress may be intercellular or extra cellular.

Tolerance mechanisms

Ability of a genotype to survive freezing and to recover and regrow after thawing is known as freezing resistance. It is a complex trait and involves various physiological, chemical and physical processes at the tissue and cell levels. It should be mentioned that in this consideration, the external factors like pathogens are not included. Freezing resistance involves two distinct strategies, viz., freezing avoidance, freezing tolerance.

a). Freezing avoidance: The ability of plant tissues/ organs to avoid ice formation at subzero temperatures is called freezing avoidance. Super cooling is a mechanism of freezing avoidance. Super cooling is controlled by the lack of ice-nucleators and is favored by small cell size, little or no intercellular space, low moisture content, barriers against external nucleators and the presence of anti nucleators. i.e., substances that oppose the formation of nucleators. Super cooling may be effective up to even -47°C . But in regions where temperatures may be lower than -41°C , there is a great danger of the super cooled cells to suffer freezing due to one or the other reason. If, it happens the consequences will be devastating. Therefore, in such cases, tolerance to extra cellular freezing is preferable to freezing avoidance by super cooling.

b). Freezing tolerance: Ability of plants to survive the stresses generated by extracellular ice formation, and to recover and regrow after thawing is known as freezing

tolerance. Freezing tolerance is markedly affected by freeze-hardening, which describes the increased tolerance to freezing due to an earlier exposure to low temperatures for a critical duration. The various components of freezing tolerance are as follows:

- **Osmotic adjustment:** In tolerant plants, cellular solutes increase during hardening. This avoids intracellular ice formation as well as cellular dehydration. The accumulated solutes include sugars, amino acids and other organic acids. In some crops fructans become converted to fructose and sucrose during freezing stress, and the ratio of this conversion is considered as an index of their freezing tolerance. In addition, accumulation of solutes like proline and trehalose also offers protection to the membranes.
- **Bound water:** A part of cell wall is bound in such a way that it does not participate in osmometric response; such water may form upto 1/3 of total cellular water. Bound water increases freezing tolerance. It has been concluded that within a normal range of osmotic potentials achieved by hardening in crop plants, the freezing point may be reduced at most by 4°C. In contrast, water binding may be far more effective in avoiding freezing.
- **Plasma membrane stability:** During freeze-hardening, plasma membrane fluidity increases, and its sensitivity to freezing induce injury decreases. The increased stability of plasma membrane prevents the extension of ice formation to inter-cellular water; this allows future super cooling of the cellular solution and reduces the freezing temperature of cells. Plasma membrane injury by freezing stress can be measured by the rate of electrolyte leakage.
- **Cell wall properties:** When intercellular space is limited, water freezing in the cell wall is affected by the size of cell wall micro capillaries. Xylem mucilage's of the cell wall inhibit the kinetics of freezing process; this effect depends mainly on the type of mucilage present in the cell walls.
- **Cold responsive proteins:** A number of proteins are produced in response to low temperature; these are called cold responsive proteins. Anti-freeze proteins are produced by polar arctic fishes; these fishes survive under freezing conditions.
- **Phytohormones:** There is a positive correlation between ABA accumulation and chilling resistance. ABA could be regarded as biochemical marker for cold tolerance in crop plants¹¹. The exogenous application of ABA increased freezing tolerance in *Solanum spp.* Some of the COR gene family- COR78, COR47, COR15a, COR6-6 are highly expressed in response to application of ABA. It has been found to reduce chilling injury in a number of other chilling sensitive plants⁸. ABA also improves water status by early closure stomata during chilling¹². An abscisic acid analogue under laboratory conditions is very effective in preventing leaf rolling and death of seedling during low temperature^[14].
- **Vernalization:** The vernalization response and cold temperature acclimation are among the most important mechanisms for winter survival. The significant correlation between vernalization requirement and both frost resistance and field survival in *Brassica* plants^[38].

Salinity Stress

Salt stress has become an ever increasing threat to food production. It is a major factor limiting the crop productivity.

Increased salinization of arable lands is expected to have a devastating global effect, resulting in 30% land losses within the next 25 years and up to 50% by the year 2050^[49]. Soluble salts can cause harm to plant, if they are in high concentration in water or soils. Generally an array of stresses interplay in saline soils and reduces productivity. Salt affected soils are mainly of two types: saline and alkaline.

Tolerance mechanisms

Salt tolerance denotes the ability of a plant to prevent, reduce or overcome the possible injurious effects caused directly or indirectly by excessive presence of soluble salt in the soil liquid phase or growth medium. The possible mechanisms of salinity tolerance are:

- **Cell membrane stability:** Cell membrane stability is an indicator of degree of salt damage. The plant cell wall is a highly organized composite of many different polysaccharides, proteins, and aromatic substances. The percentage of cell membrane electrolyte leakage increases with increasing salt concentrations.
- **Osmotic adjustment:** Salt tolerance of plant is characterized by its capacity to endure the effects of excess salt in the medium of root growth i.e., plant can withstand a precise amount of salt without adverse effect. Protection from osmotic stress injury is accomplished by the accumulation of organic osmolytes. Tolerant plants accumulate osmoprotectants and osmolytes which have been shown to accumulate in response to drought and cold stress. Osmolytes are molecules with low molecular mass and they could be quaternary amines, amino acids, or sugar alcohol. Enhanced accumulation of these molecules is known to increase the osmotic potential of cell, which could help in combating water stress eventually they could stabilize membrane and other macromolecular structures. The different organic osmolytes are glycinebetaine, mannitol and proline.
- **Phytohormones:** The major effect of salinity in the root environment has been attributed to reduce hormone delivery from root to leaves, which could induce an inhibition of crop growth. Hence various growth promoting substances such as GA₃, IAA or kinetin have been used to overcome the drastic effect of salt stress. Brassinosteroids are considered as Phytohormones with pleiotropic effects as it influences varied physiological processes like growth, germination, flowering and senescence. The role of brassinosteroids to increase resistance to stress has been reported in sugar beet^[44].
- **Enzymes:** There are variable changes in enzyme activities in salt susceptible and tolerant genotypes under salinity stress. Peroxidase activity increases in salinity stress, thus its increase may be due to increased enzyme synthesis and is useful for adoption under conditions requiring prevention of per oxidation of membrane lipids. Similar increase in peroxidase activity in salt tolerant varieties of *Pisum sativum* was observed^[33]. Increase in peroxidase activity could be due to formation H₂O₂ which could release the enzyme from the membrane structure.
- **Ion accumulation and Ion balance:** Plants accumulate sodium ions in the cytoplasm by transporting it to the vacuole using older leaves as sink, thus avoid salt accumulation in sensitive tissues, such as meristems. Ion transport into the vacuole works against a concentration gradient and thus requires energy. This is achieved by coupling the transport to a proton pump transporting H⁺

ions in the opposite direction; hence it is known as antiport protein. The ion accumulation in the wild tomato species, to be reflection of the halophytic nature^[42].

- **Ion exclusion:** Ion exclusion rate also plays an important role in the salt tolerance in some crop species. Differences have been observed among crops as well as among the genotypes within the species for ion exclusion.
- **Leaf characteristics:** Accumulation of epicuticular wax causing an additive reduction in cuticular transpiration may play a vital role in inducing tolerance to salinity.
- **Crop stages:** *Brassica* exhibited susceptibility to salinity at seedling emergence and early seedling growth but are relatively more tolerant at later growth stages, particularly at flowering to pod formation in siliqua^[21].

Conclusion

Environmental stress is the primary cause of crop losses worldwide, reducing average yields for most major crops by more than 50%. Latitudinal and altitudinal shifts in ecological and agro-economic zones, land degradation, extreme geophysical events, reduced water availability, and rise in sea level and salinization are postulated^[13]. Unless measures are undertaken to mitigate the effects of climate change, food security in developing countries will be under threat. Climate change may affect agriculture more through water availability than temperature. Scientists predict that the altered hydrologic cycles will change the pattern of precipitation and cause wet areas becoming wetter while dry areas become drier. There is an urgent need to mitigate these abiotic stresses through development of new tolerant crop varieties that will thrive in future conditions. Drought-tolerant cultivars are needed to improve water use efficiency, enhance water conservation, reduce irrigation costs, and maintain or increase the acreage of horticultural crops. For certain areas or specific seasons that are prone to flooding, new varieties should be developed to adapt to the wet soil. Global warming is not uniform and may lead to some weather extremes. Although the general trend of temperatures is going up, we are seeing some regions or certain seasons with very cold weather, even breaking low temperature records. Warmer springs might make crop seedlings emerge faster, but they could be vulnerable to damage from late spring frosts or freezes. So cold tolerance is still an important trait for many crops. We need cold tolerant cultivars to extend growing areas or seasons, especially in inland areas with limited frost-free days. In addition, 20% of the world's irrigated lands are affected by salinity^[50], a situation worsened by climate changes. Global warming increases the rates of evapo-transpiration and crop requirement of irrigation water, which may bring more salt into the soil in arid and semiarid regions. The migration of salt water into groundwater is being exacerbated by increasing freshwater demands that are depleting coastal aquifers and the projected sea level rise caused by global warming. Acreage impacted by salinity problems is expected to increase. Growers in these regions require cultivars that can resist salt stress to sustain crop production. Growers often face multiple abiotic stresses. For example, heat and drought conditions often come together. Abiotic stresses frequently are intertwined with biotic stresses. High temperatures and elevated CO₂ levels may favor weed growth in competition with crops, making weed control a challenge for growers. Heavy rainfall may increase root diseases. Climate change may promote infestation/epidemics of plant pests/diseases because higher winter minimum temperatures enable insects,

pathogens, or disease vectors to overwinter more effectively. The need to produce stress tolerant crops was evident even in ancient times^[20].

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