# UNIT 12

# STRESS METABOLISM IN PLANTS

## Structure

## 12.1 INTRODUCTION

Plants are sessile organisms. They are constantly faced with changes (often abrupt) in environmental conditions in their natural habitat which they cannot avoid. In order to survive plants have evolved ways to sense and respond accordingly, although some can grow and multiply in these conditions at all times, for example halophytes are naturally salt tolerant.

Stress is defined as any environmental condition that adversely impacts plant growth and development. It can be biotic, caused by insects / herbivores, pathogens and weeds or abiotic factors such as salinity, temperature, heavy metals and drought. Estimates suggest that abiotic conditions affects all crop plants due to poor soil conditions or climate and reduces yield by 50% worldwide. It also limits the plant species distribution in a geographical area.

Therefore the study of plant stress physiology is of prime importance before attempts can be made to enhance adaptability and yield in hostile environments.

The various stress factors bring about physiological changes in plants depending on intensity and duration of exposure. Such adaptive changes that result in adjustments in growth rate constitute a stress response and the factors are called 'stressors'. The stress response can be either at molecular, cellular or tissue and organismal level. Under mild stress conditions, plants adapt by changing gene expression profile, metabolic readjustments, DNA repair and protective response by accumulation of secondary metabolites, antioxidants, detoxification enzymes and developmental changes. Higher dosage / duration may result in permanent damage (oxidative and DNA damage; inactivation of primary metabolic pathways) and even death.

This unit gives an overview of various biotic and abiotic stresses experienced by plants. You shall also be introduced to physiological and metabolic responses to stressors.

## Expected Learning Outcomes

After studying this unit you should be able to:

- appreciate the importance of stress response in plants;
- indicate the various biotic and abiotic stressors;
- describe ways by which plants sense stressors;
- highlight some of the adaptive strategies used by plants to combat stress;
- explain the impact of various stresses on plant growth; and
- point out few biotechnological interventions undertaken to improve plant response to stress.

## 12.2 ENVIORNMENTAL STRESSES

Plants thrive in diverse ecological niches, constantly faced with changes in environmental conditions (biotic and abiotic) that might be stressful. The increase in worldwide population places an equally growing demand on increasing crop productivity making it all the more important to study how different stressors affect plant growth and yield. If we compare the genetic potential of crop plants and actual yield from farm land, they have 65-87% reduced average productivity, due to environmental stresses. This has triggered plant scientists to investigate the genetic basis of stress resistance and develop improved tolerant varieties of crop plants using a combination of biotechnological and classical breeding approaches.

Although each stress factor is often studied individually but we must keep in mind that most of them are interrelated. Therefore an overlapping set of cellular, biochemical and molecular responses define the growth and physiology of plants in a given environment.

Stress is a multifactorial phenomenon that includes severity, duration, numbers of exposures and combinations of stresses (Fig. 12.1). Multiple stressors can produce additive or synergistic effects on plant characteristics. The stress response depends on plant genotype, stage of development and organ / tissue being exposed. The outcome of the response may be survival (effective resistance) or death (susceptibility).

The basic strategies employed are either avoidance or tolerance. For example, ephemerals avoid water deficit in desert by completing their life cycles well before dry seasons. In contrast, deeply rooted true xerophytes have access to deep groundwater during water deficit. In general plants have developed multiple ways to sense and tolerate stress.

Certain plants also use **acclimation** to survive. It is a physiological change occurring in the life time of an organism such that they become accustomed to altered environmental conditions. Plants such as tomatoes and irises are able to overcome freezing temperatures if it drops gradually over time.

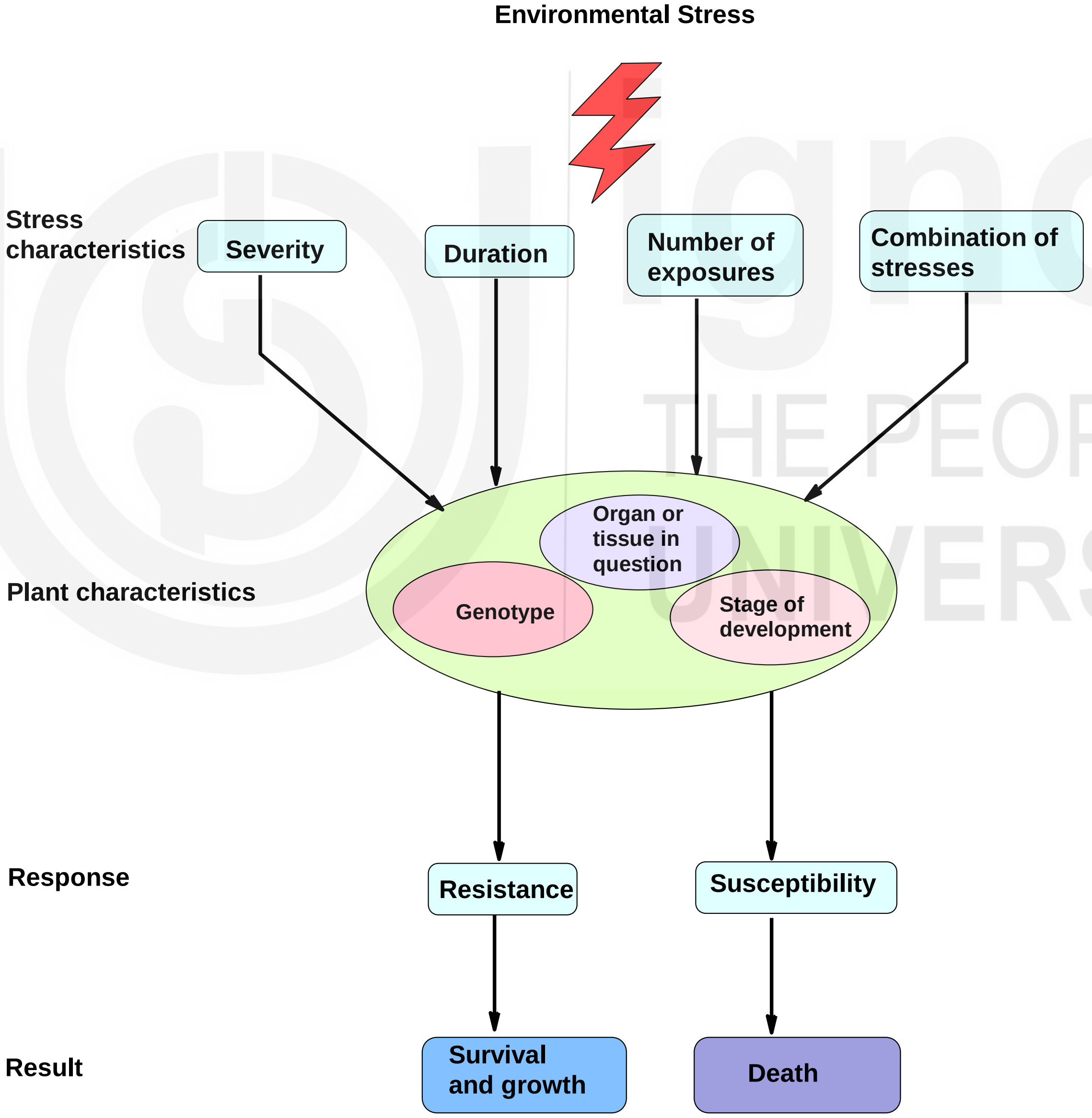


**Fig. 12.1: Environmental stress perception and response by plants.**

## *SAQ 1*

**Indicate whether the following statements are true or false:**

a) Stress is a multifactorial phenomenon that varies in severity & duration.

b) Stress resistance mechanisms allow plants to either avoid or tolerate stress.

c) Herbivores are examples of abiotic stressors.

d) Multiple stressors produce synergistic / additive effects on plants.

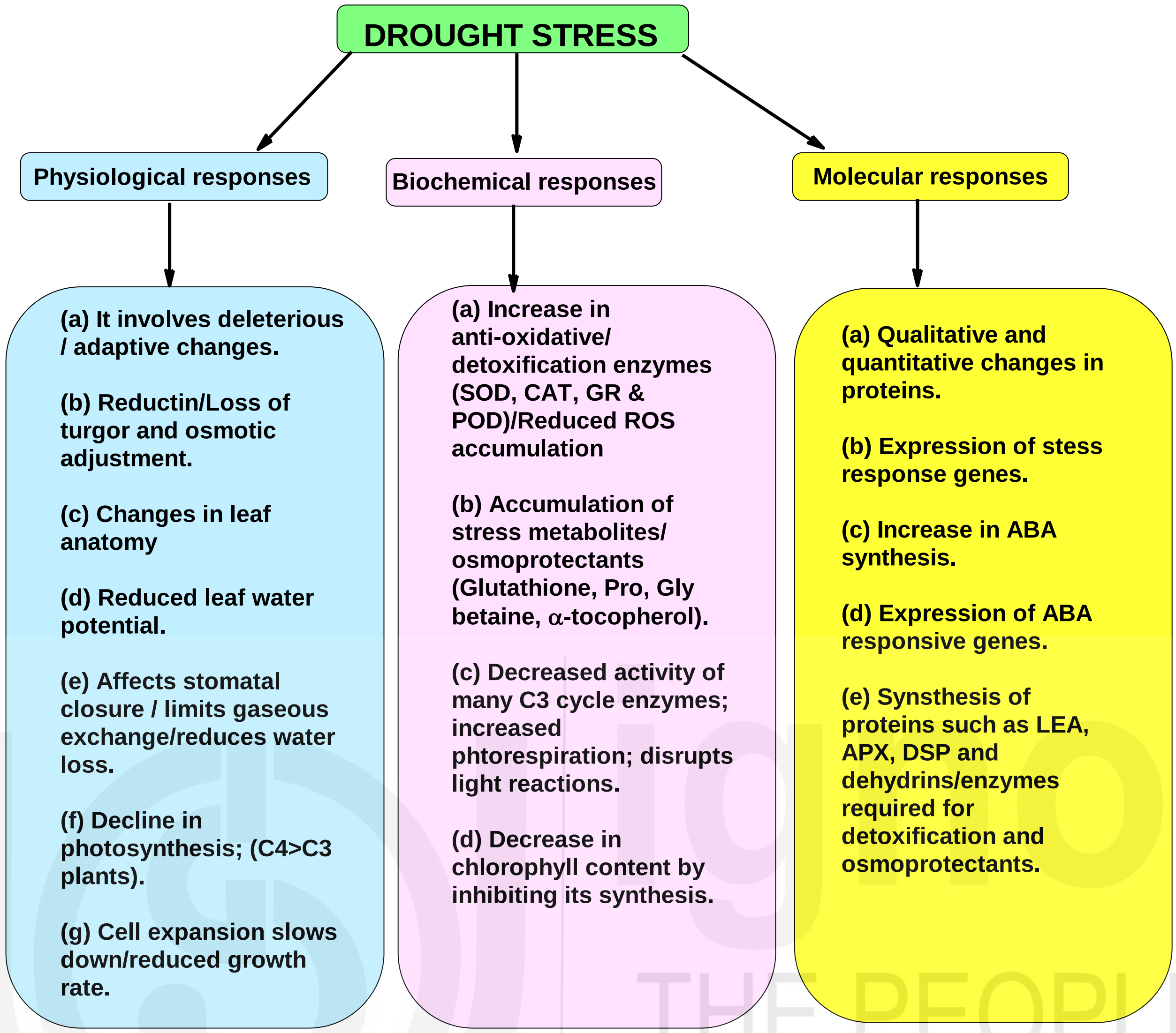
# 12.3 ABIOTIC STRESS

All plants tolerate stress to varying degrees. Abiotic stresses such as drought, salinity, high temperatures, chemical toxicity and oxidative stress lead to imbalances in natural habitats. A number of morphological, physiological, biochemical and molecular changes are induced in plants, at the cost of overall growth and productivity.

## 12.3.1 Water Stress

Water as you know is the medium for transporting metabolites and nutrients and for carrying out all biochemical and physiological processes. The major cause of water stress is water deficit due to drought (low rainfall area) or high salinity. The former lowers water potential and turgor while the latter affects the uptake of soil water (physiological draught). In either case normal physiological functions are hampered and the effects can be seen at multiple levels, including dehydration leading to irreversible damage, loss of vegetation and crop yield.

There are several levels of at which drought resistance mechanisms operate beginning with desiccation postponement (ability to maintain tissue hydration). Water savers (preserving some water in soil for later use) and water spenders (aggressively absorb and often consume large amounts of water) are types of desiccation postponers. The other resistance mechanisms are desiccation tolerance (ability to function while dehydrated) and drought escape (complete their life cycle before the onset of drought). The escapers are true drought avoiders. Generally plants use a combination of stress avoidance (decreased leaf area, extensive root system, reduced stomatal conductance) and stress tolerance (changes at cell and tissue level including gene expression) strategies summarised in Fig. 12.2.



(a) It involves deleterious / adaptive changes.

(b) Reductin/Loss of turgor and osmotic adjustment.

(c) Changes in leaf anatomy

(d) Reduced leaf water potential.

(e) Affects stomatal closure / limits gaseous exchange/reduces water loss.

(f) Decline in photosynthesis; (C4>C3 plants).

(g) Cell expansion slows down/reduced growth rate.

(a) Increase in anti-oxidative/ detoxification enzymes (SOD, CAT, GR & POD)/Reduced ROS accumulation

(b) Accumulation of stress metabolites/ osmoprotectants (Glutathione, Pro, Gly betaine, $\alpha$-tocopherol).

(c) Decreased activity of many C3 cycle enzymes; increased phtorespiration; disrupts light reactions.

(d) Decrease in chlorophyll content by inhibiting its synthesis.

(a) Qualitative and quantitative changes in proteins.

(b) Expression of stess response genes.

(c) Increase in ABA synthesis.

(d) Expression of ABA responsive genes.

(e) Synsthesis of proteins such as LEA, APX, DSP and dehydrins/enzymes required for detoxification and osmoprotectants.

**Fig. 12.2: Drought stress tolerance strategies (Adapted from Shao *etal,* 2008).**

The plant hormone abscisic acid (ABA) is the major hormone that coordinates plant's response to water stress. One of the early events controlled by ABA is stomatal closure. It also induces the expression of multiple genes that encode enzymes for synthesis of osmoprotectants (proline, mannitol, trehalose, glycine betaine, and citrulline), detoxifying enzymes (superoxide dismutase, SOD; peroxidase, POD; catalase, and glutathione reductase, GR; and other specific proteins like late embryogenesis abundant (LEA) protein, desiccation stress proteins (DSP) and dehydrins.

Turgor determines leaf area expansion and root elongation under well hydrated conditions. Additionally leaf numbers, branches and stem height is restricted and root to shoot ratio increases. These two processes are affected early during water stress. The osmolyte adjustment by hydrophilic compatible osmolytes increases osmotic potential that results in higher water uptake by the roots and water saving by cells. These osmolytes also protect enzymes and membrane integrity. Some of them scavenge free radicals. The specific proteins like LEA are extremely hydrophilic, bind water abundantly, preventing crystallization during desiccation.

## 12.3.2 Heat Stress and Heat Shock

Actively growing and hydrated plant organs rarely survive temperatures above $45^0$C. On other hand dehydrated dry seeds, spores and pollen endure much higher temperatures. Sub-lethal heat exposure often stimulates plant processes so that they can tolerate it and survive (**induced thermo-tolerance)**. Early on in response to temperature stress, plants (C3 and C4) have increased rate of transpiration, similar to sweating in animals. But when water becomes limiting, the strategy of evaporative cooling becomes ineffective and plants begin to experience heat stress.

Many succulents (CAM plants) can naturally survive at higher than 60 deg C by dissipating heat through re-emission of long wave radiation and loss of heat by convection (thermally produced vertical air flow). In non-irrigated plants, evaporative cooling is limited and leaf temperature rises when stomata is closed. This is commonly observed in plants found in arid and semiarid regions, experiencing both draught and high temperature.

Heat stress decreases photosynthetic efficiency by inactivation of PSII and Rubisco activase; inhibition of C3 cycle enzymes, protein degradation, impaired translation, chlorophyll breakdown and increase in ROS. At temperatures above the temperature compensation point (temperature at which carbon fixed by photosynthesis equals the carbon lost by photorespiration), photorespiration increases.

The ability of a cell to carry out normal functions depends on maintenance of membrane fluidity under heat stress, for example by increasing the proportion of saturated fatty acids in membrane lipids. High temperature increases fluidity with concomitant loss of membrane function. Membrane changes also induce injury to photosynthetic machinery. Plant leaves avoids excess heat absorption by coating leaf surface with waxes; excess trichomes, leaf rolling, highly dissected leaf and vertical leaf orientation.

Acute heat stress response results in a shift from synthesis of normal proteins to heat shock proteins (HSPs) / molecular chaperones when plants experience 5 deg C higher than optimum growth temperature. HSPs are induced in response to sudden change in temperature (heat shock). During heat stress they generate tolerance primarily by preventing aggregation of folding intermediates and promote proper folding of denatured proteins. These proteins come in different sizes (15 to 104 kDa), for example HSP60, HSP70, HSP90 and HSP100. The low molecular weight HSP (15-30 kDa) are more abundant in higher plants than any other organisms and are distributed in cytosol, chloroplast, endoplasmic reticulum and mitochondria. HSPs are also induced in response to water stress, ABA treatment, wounding, salinity and chilling stress.

## 12.3.3 Chilling and Freezing Stress

Chilling temperatures cover temperature ranges that are much below optimum growth temperature but above freezing point. Plants normally growing at temperatures between 25 to $30^o$C, experience chilling stress when subjected to low temperatures (10 to 15 deg C). Many crop plants such as tomato, sweet potato and maize are sensitive to chilling stress. The symptoms of chilling injury include slow growth, increased respiration, discoloration or lesion on leaves, water soaked areas, increased decay, poor ripening and wilting (if roots also experience chilling). These changes are evident after awhile following exposure to low temperatures. Sometime symptoms appear only when the plant or its part is removed from cold storage and warmed. A sudden exposure to cold temperatures (cold shock) increases the extent of injury caused. Plants growing in high altitudes are often genetically better adapted to chilling stress.

Injury induced at temperatures below $0^oC$ is known as freezing (frost) injury. Generally the freezing point is lower than that of water due to the presence of sugars / soluble carbohydrates. Recall from your school chemistry course that freezing point is a colligative property; higher the concentration of solutes lower is the freezing point. Freezing damages cells and tissues due to ice crystal formation and destroys cell integrity upon thawing. It also induces water movement outside the cell resulting in ice crystals formation in extracellular spaces. Freezing of water in extracellular space increases osmotic dehydration (removal of water from lower concentration of solute to higher concentration through a semi permeable membrane), leading to mortality in susceptible plants. The cell volume is also reduced. As compared to chilling injury, freezing injury is instantly visible.

At low temperatures, membrane fluidity decreases and it becomes more solid. This causes decline in membrane transport and photosynthetic efficiency. There is increase in ROS generation by chloroplast that damages the organelle structure, chlorophyll and other macromolecules.

Various genes respond to low temperature stress. Hik33 (histidine kinase) is a putative sensor which regulates 21 of the 36 cold-regulated genes in a cyanobacteria, *Synechocystis*. Another protein, phospholipase Dα1 (PLDα1) activity when suppressed through antisense RNA increases freezing tolerance in *Arabidopsis*. Deficiency of PLDα1 lowers phosphatidic acid (PA) levels and causes rearrangements in lipid composition. It is probably involved in modulating the cold responsive genes and accumulation of osmolytes. In contrast, over production of plasma membrane bound phospholipase Dδ (PLDδ) selectively increases membrane PA and membrane tolerance. It contributes approx. 20% PA produced in wild type plants during freezing. Another family of membrane proteins, SYNAPTOTAGMIN1 (SYT1), functions as calcium sensor during vesicle docking. During cold acclimation, SYT1 level increases rapidly and reseals the membrane in presence of calcium.

A constitutive freeze tolerant mutant, eskimo1 is known to overproduce proline at warm temperatures in *Arabidopsis.* The ESKIMO1 gene encodes a 57-kDa protein of unknown function. Mutant eskimo1 has altered expression of various genes involved in abiotic stress responses. Many cold stress induced genes are activated by c-repeat binding factor (CBF) group of transcription factors like CBF1 (DREB1b), CBF2 (DREB1c) and CBF3 (DREB1a). CBF bind to CRT/DRE elements (c-repeat /dehydration responsive element).

### 12.3.4 Salinity Stress

Many inorganic salts dissolved in water account for salinity. Sea water has highest salt concentrations. In mangrove ecosystem, plants constantly experience high salinity due to mixing of sea water to river freshwater forming estuaries. Apart from seashore and estuaries, inland water bodies are constantly added with geologically deposited salts. In agricultural land, the amount of salinisation has increased as a result of irrigation practices and climate change. It is estimated that about one third agricultural land is affected by accumulated salt. In field, salinity is measured as electrical conductivity or osmotic potential. Total salt concentration in water is termed **salinity** while $Na^+$ ion concentration is **sodicity**. Ecologically, **halophytes** (*Chinopodium quinoa*) are plants which survive and complete their life cycle in high salinity as compared to salt sensitive **glycophytes** (most crop plants) that cannot tolerate salinity beyond a threshold level.

Plant salt tolerance is a complex trait. Halophytes share salt tolerance mechanisms with glycophytes along with additional ways to adapt to high salt. Dissolved salts near roots create negative osmotic potential which lowers the soil water potential. This situation is very similar to drought stress and hence response to salinity is more similar to drought. In addition to lower water potential, specific ion toxicity effect is also observed due to high concentrations of $Na^+$, $Cl^-$ and $SO_4^{2-}$ in cells.

Osmoprotection is achieved by osmotic adjustment (osmolytes like proline, sugar alcohol), ion transport ($Na^+$ removal from cytosol / compartmentalisation in vacuoles by $Na^+$-$H^+$ -antiporter) or salt secretion (as in Quinoa). Osmotic profiles vary from species to species. Halophytes can increase solute potential ($\psi_s$) by enhanced ion accumulation in vacuole and synthesis of compatible solutes in cytosol to adjust water potential ($\psi_w$) in root cells. Growth rate is reduced due to channeling of energy for osmolyte production

In chloroplast, high concentration of these salts inhibits photosynthesis by decreasing gaseous exchange and activity of carbon fixation enzymes. Salt stress induces carbon partitioning to sugars (osmolyte) and not starch in both leaves and roots. It reduces cell division, root growth and induces swelling close to the root tips and produces elevated levels of ROS.

### 12.3.5 Heavy Metal Stress

Plants require a steady supply of minerals for completing their life cycle. These inorganic supplements are classified into two major groups, macronutrients and micronutrients, depending on the quantity needed. Most plants get them from soil by absorption through roots. Any deficiency in minerals is reflected in crop physiology and yield. Therefore soil quality is an important determinant of plant distribution and growth.

However, heavy metals such as Fe, Mn, Cu, Ni, Co, Cd, Zn, Hg and As are known to increase in soil from indiscriminate release of unprocessed industrial wastes, fuel emissions, natural sources (volcanic eruptions, forest fires), excessive use of fertilisers / pesticides and often inappropriate sewage disposal. Some of these metals are essential micronutrients but they can be detrimental at high concentrations. Plants also accumulate minerals from soil and water which they do not need. All heavy metals are non biodegradable. Therefore, plants have evolved different mechanisms to combat stress that either avoid or generate tolerance. Some of these are constitutive while others are adaptive mechanisms. They also possess metal specific mechanisms (not discussed).

Generally plants exposed to heavy metal toxicity have stunted growth, chlorosis and root browning and may die if the stress persists. It is due to multiple effects at biochemical / molecular level such as inactivation / denaturation of enzymes; inhibition of protein / enzyme function by metal displacement (Cadmium displaces $Ca^{+}2$ in calmodulin or $Zn^{+2}$ displaces $Mg^{+2}$ in Rubisco); increase in methyl glyoxal (inactivates anti oxidant system and inhibits cell proliferation) and ROS; loss of membrane integrity and decline in photosynthetic competence.

One of the initial defenses is to reduce the uptake of metals when faced with heavy metal stress. This strategy is aided by cellular and root exudates (malate, oxalate) which change the pH of the rhizosphere causing precipitation of heavy metals / increasing efflux. They are concentrated in the apoplast or sequestered by binding to cell wall components (lignin, pectin). Some plants establish symbiotic relationship with mycorrhizal fungi which accumulates metals in the rhizosphere, reducing their availability.

Once the metal ion succeeds in entering the cell, other defense mechanisms come into play. Often compartmentalization of heavy metal ions is used to reduce exposure to vulnerable cellular components. The plant vacuole is the major site for sequestering and detoxification. These metals are actively transported after chelation to phytochelatins (oligomers of glutathione) / metallothioneins - ubiquitous, cysteine rich low molecular weight proteins / glutathione to the vacuole.

The other defenses include synthesis of antioxidant enzymes systems (superoxide dismutase, peroxidase); glutathione (controls ROS levels); proline, phenolics; heat shock proteins, glyoxylase (detoxifies methyl glyoxal to lactate), and stress related hormones (salicylic acid, ABA). Proline (a protein amino acid) also functions as free radical scavenger, antioxidant and metabolic osmolyte. Its concentration is generally high in tolerant plants. Similarly phenolics scavenge free radicals and limit lipid peroxidation.

## 12.3.6 Radiation

Periodicity and quality of light are essential for basic plant processes like photosynthesis. Usually more than the threshold limit of Photosynthetically Active Radiations (PAR, 400-700nm) and increased exposure to UV-radiations leads to radiation stress characterised by reduction in photosynthesis, oxidative damage to biomembranes and organelles. UV-B (280-315nm) is more detrimental than UV A (315-400nm) to cellular and physiological processes in plants. The aerial parts of the plants especially leaves, perceive these radiation. We shall now describe how plants adapt to these stresses.

When exposed to strong light (high irradiance), chloroplast moves to cell surface, parallel to the incident light in order to decrease its absorption (Fig. 12.3). Such chloroplast movement can decrease absorption up to 15%. Plants also control solar absorption by rearranging leaf lamina orientation (solar tracking). By positioning leaves at an angle to the incident light they receive less radiation.

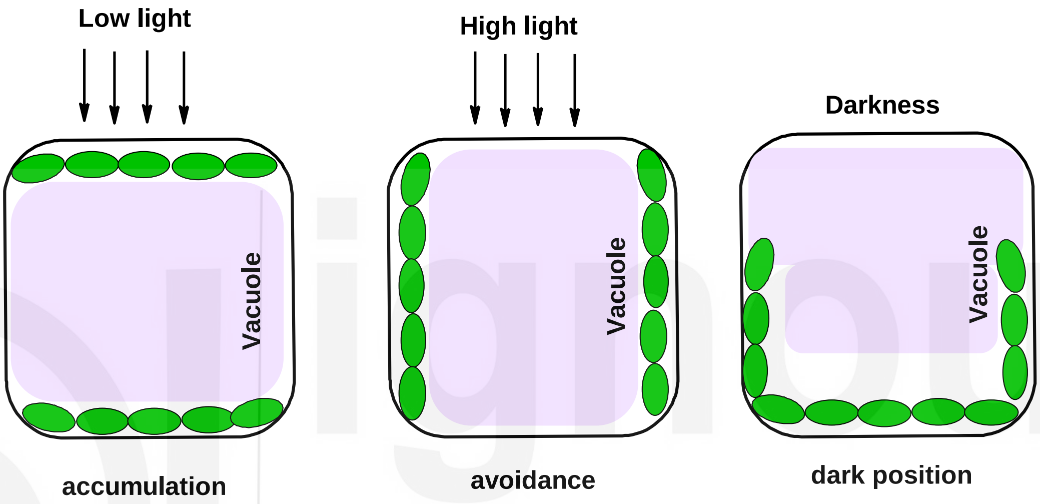


**Fig. 12.3: Chloroplast movement.**

Other plants have ecologically adapted to such conditions: (a) shade leaves are thinner with high total chlorophyll per reaction center and ratio of chlorophyll b to a; (b) sun leaves are thicker with more Rubisco and a larger pool of xanthophyll cycle components. Generally shade plants have limited capacity to adjust to high light intensities and are more easily injured. In order to avoid excessive sunlight, plants increase trichomes density on the upper surface of leaves, rolls up their shoots (pteridophytes), increase cuticle and epidermal wall thickening (conifer needles, cacti) and increase anthocyanin content (act as light filter). Very high solar radiation increases temperature (heat), which may lead to water deficit (drought stress); the plant thus faces multiple stresses.

UV primarily generates oxidative stress by complex pathways, disruption of xanthophyll cycle and DNA damage (pyrimidine dimers). Plants exposed to UV-B (non ionizing radiation) undergo a number of morphological (reduction in leaf surface area, increase in leaf thickness), biochemical (increased synthesis of UV protective flavones and flavonols, induction of anti oxidants and anti oxidant enzymes) and molecular (induction of DNA repair and homologous recombination mechanisms) adjustments.

## 12.3.7 Anaerobiosis

The soil holds sufficient air for plant roots to respire below ground. Gaseous oxygen can readily diffuse to certain depths in well drained, well-structured soil. In contrast, waterlogged or irrigated soil is penetrated by water that blocks diffusion of oxygen to deeper soil layers. During winters, when temperatures are low and plants are sluggish in growth, $O_2$ in soil depletes slowly and is less harmful. But under favorable conditions, plants and microbes grow aggressively, $O_2$ depletion is rapid resulting in anoxic condition for roots. The stress generated on plants due to anoxic conditions is known as anaerobiosis or oxygen deficiency stress.

Some plants experience severe damage within 24 hours of flooding, for example *Pisum sativum* is a flood-sensitive plant. Other plants can withstand anoxia for a few days and respond mildly to flooding; they are flood tolerant plants. On the other hand, mangrove plants surviving in marshes and swamps have developed various mechanisms to escape anoxia. Generally plants cope up with oxygen deficiency by a combination of functional and morphological adaptations.

Anoxic condition favors the growth of soil anaerobes. Some of them denitrify soil nitrate ($NO_3^-$) to gaseous forms of nitrogen (nitrous oxide and molecular nitrogen). Anaerobes also reduce $Fe^{3+}$ to $Fe^{2+}$ to toxic levels and sulfate ($SO_4^{2-}$) to hydrogen sulfide ($H_2S$). Others release certain organic acids like acetic acid and butyric acids into the soil. Together it accounts for the unpleasant smell of waterlogged soil.

Oxygen depletion in soil slows down metabolic activities in roots. The oxygen pressure at which the respiration rate slows down is called **critical oxygen pressure** (COP); it ranges from 0.1 to 0.05 atm. As the oxygen levels fall, the roots shift from aerobic mitochondrial respiration to fermentation of sugars to lactate / ethanol.

Hypoxia promotes production of ethylene precursor, 1-aminocyclopropane-1-carboxylic acid (ACC) in roots which is transported to the shoots and converted to ethylene. Ethylene induces **epinasty** – a downward bending of leaf and leaf stems such that they appear to droop (Fig.12.4a). It may help the plant to lose water. In most cases root elongation is also inhibited and they develop laterally spreading roots.

Many plants including rice develop aerenchyma (ventilating tissue with a continuous system of intercellular spaces) in roots to tolerate anoxia in flooded conditions. In maize root tip cells, ethylene synthesis stimulates death and disintegration of surrounding tissue, creating gas-filled voids for $O_2$. **Pneumatophores** (rich in aerenchyma) of *Avicennia* (mangrove) are also a type of escape mechanism where negatively geotropic roots come out of marsh to breathe (Fig.12.4b).

**Fig. 12.4: (a) Leaf epinasty in tomato (b) *Avicennia* pneumatophores**
Source: researchgate.net Commons.wiimedia.org

## *SAQ 2*

**a) Pick the best option:**

i) Suppression of which of the following protein increases freezing tolerance in *Arabidopsis*.

1. PLDα1
2. SYT1
3. DRE elements
4. CBF

ii) Which of the following type of HSPs (heat shock protein) are abundant in higher plants?

1. Chaperones
2. Low molecular weight HSP
3. ATP binding chaperones
4. High molecular weight HSP

iii) The hormone that induces stomatal closure in response to drought is:

1. Abscisic acid
2. Salicylic Acid
3. Ethylene
4. Jasmonic Acid

**b) Give an example(s) / name of:**

i) A protein that sequesters heavy metals.

ii) Plants that do not naturally tolerate salts beyond a threshold level.

iii) An organelle that plays a major role in sequestering and detoxification of heavy metals.

iv) Two Osmoprotectants.

v) An enzyme that detoxifies methyl glyoxal (MG).

## 12.4 BIOTIC STRESS

Biotic stress arises from other living organisms that plants coexist and interact with. The stress can be by disease causing pathogens, herbivores, and even competition due to overcrowding / weeds. All these affect plant growth and survival. In case of crops and horticultural plants, it results in significant economic losses due to poor yield and quality of food and other products.

### 12.4.1 Pathogens and Herbivores

Biotic factors include bacteria, viruses, viroids, fungi, protists, mycoplasma, insects, vertebrates (herbivores) and even other plants. A plant pathogen is a disease causing organism which produces symptoms varying in severity. The resistance mechanisms in plants operate at different levels (organismal, cellular and molecular) that are either expressed at all times (constitutive) or inducible. Disease manifestation in plants remains restricted to certain tissues and the outcome of infection is rarely death. Characteristic disease symptoms in plants include mosaic, necrosis, galls, wilting and spotting.

Most pathogens carry unique molecules on their surface / cell wall collectively called Pathogen- or Microbe or damage-Associated Molecular Patterns (PAMP / MAMP/ DAMP). The PAMPs are shared by a given group of pathogens, for example, lipopolysaccharide (LPS) is present on all Gram negative organisms or chitin in fungi. These patterns (P/ MAMPs) are recognized by pattern recognition receptors (PRR) on host cells surface and trigger Pattern-Triggered Immunity (PTI).

For successful establishment of a pathogen, effector proteins (made by pathogens) interfere with and suppress the PTI defence mechanism. The activation of R-genes (encode proteins with nucleotide binding and leucine rich repeats) in response to effector proteins or its effect on host proteins triggers ETI (effector triggered immunity or vertical resistance) which is often more aggressive, mounts a hypersensitive response that culminates in programmed cell death. A pathogen will succeed in pathogenesis only if it evades PTI and overcomes R- protein-mediated responses (Fig.12.5). The plant immune system resembles mammalian system except that plants entirely rely on cell autonomous innate immunity.

**Note:** Constitutive defences are structural barriers- cell wall, thorns, epidermis; chemicals- phenolics, glucosinolates (Brassicaceae members), saponins (Avenacin A1);
Inducible defences include phytoalexins; pathogen plant chitinases; programmed cell death; defence hormones (Ethylene, JA, SA); ↑lignin / callose deposition; respiratory burst. These defense strategies may fall into innate or systemic acquired resistance.

Plants also defend themselves through systemic acquired resistance (SAR) which provides long term defence against a broad range of pathogens / insects. Volatile emissions from insect eggs could lead to SAR. RNA interference (RNAi) to target and inactivate invading nucleic acids from viruses (double stranded RNA), and fungal pathogens is another mechanism used to control infection. It induces a kind of adaptive immunity.

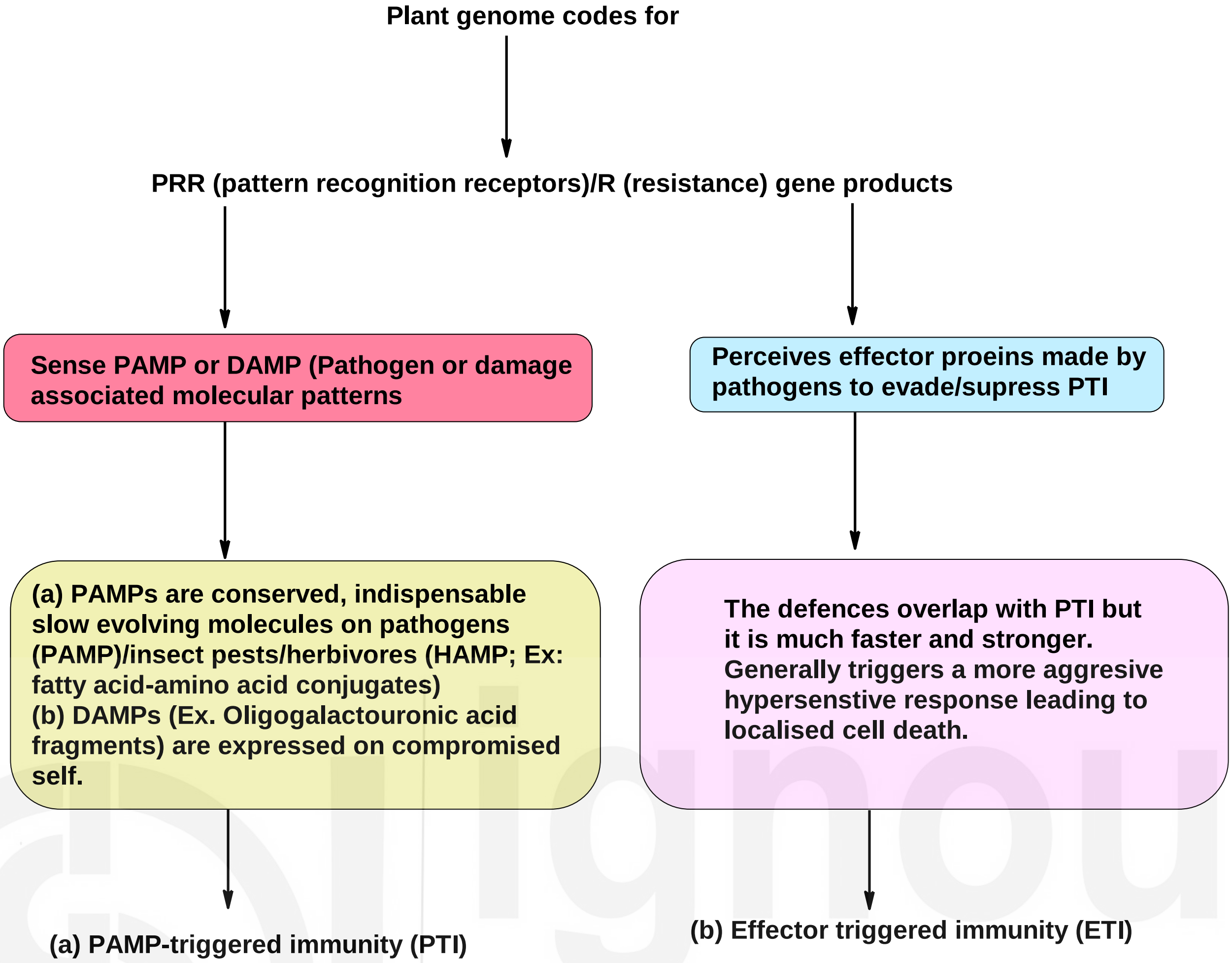


**Fig. 12.5:** An overview of plant innate immune responses.

## *SAQ 3*

**Match the items in column (A) with those in column (B):**

| **Sr. No.** | **Column A** | **Sr. No.** | **Column B** |
|---|---|---|---|
| **(i)** | Effector triggered immunity | **a.** | Pattern-triggered immunity |
| **(ii)** | Pattern recognition receptors (PRR) | **b.** | Programmed cell death |
| **(iii)** | Unpleasant smell of soil in water logging | **c.** | R-gene mediated defence |
| **(iv)** | Glucosinolates | **d.** | Hypoxia induced bacterial activity |
| **(v)** | Hypersensitive response | **e.** | Members of Brassicaceae |

## 12.5 BIOTECHNOLOGICAL INTERVENTIONS

All types of stress in plants affect their physiology which is invariably reflected in yield loss and may account for toxicity to consumers, for instance due to high concentration of heavy metals or infected plant parts. To improve plant quality and yield, biotechnological approaches to generate transgenic plants have been successful in case of some food / horticultural crops, with many more in the pipeline.

Representative examples of transgenics (genetically modified) that can overcome abiotic and biotic stresses include plants over expressing phytochelatins / metallothioneins (tolerance to heavy metals); Glycine betaine / proline / over expression of LEA type genes (drought resistance); resistant form of glyphosate (herbicide) tolerant enzyme; Bt genes from *Bacillus thuringiensis* (pest resistance in many crop plants such as rice, brinjal. maize, cabbage); genes coding for chitinases / antifungal proteins.

## 12.6 SUMMARY

- Plants are constantly faced with changes (often abrupt) in environmental conditions in their natural habitat which they cannot avoid. In order to survive they have evolved ways to sense and respond accordingly.
- Stress is defined as any environmental condition that adversely impacts plant growth and development. It can be biotic, caused by insect / herbivores, pathogens and weeds or abiotic, due to salinity, temperature, heavy metals, and drought.
- The response to stress depends primarily on the type of stress, its severity and interaction among various stress pathways. The basic mechanisms employed are either to escape or tolerate stress.
- Stress is a multifactorial phenomenon which includes severity, duration, number of exposures and combinations of stresses. Multiple stressors can produce additive or synergistic effects on plant characteristics. The stress response depends on plant genotype, stage of development and organ or tissue being exposed. The outcome of the response may be survival (effective resistance) or death (susceptibility).
- The major cause of water stress is water deficit due to drought (low rainfall area) or high salinity. The plant hormone abscisic acid (ABA) is the main hormone that coordinates plant’s response to water stress. One of the early events controlled by ABA is stomatal closure. It also induces the expression of multiple genes.
- Under water logged condition, plants experience anoxia that slows down metabolism and induces ethylene synthesis. It stimulates cell elongation which increases petiole length to escape submergence.

- Freezing and chilling stress causes cellular damage by membrane destabilisation and metabolic dysfunction. Plants adapt to such stress situations by synthesis of protective metabolites and proteins.
- Usually more than the threshold limit of Photosynthetically Active Radiations (PAR, 400-700nm) and increased exposure to UV-radiations leads to radiation stress characterised by reduction in photosynthesis, oxidative damage to biomembranes and organelles. Plants respond by a number of morphological (increase in leaf thickness, reduction in leaf area) and biochemical (increase in flavonols; induction of repair and anti-oxidant enzymes) adaptations.
- Salinity and heavy metal stress are related to excess minerals. Both induce similar kind of stress response by increasing ROS production. Excess salts and minerals are sequestered using membrane pumps or cytosolic proteins. These sequestered ions are either stored and / detoxified inside vacuole or excreted out in glands present on leaf epidermis.
- Most critical of all, above and below ground, herbivores and pathogens pose threat to plants. The host senses unique pathogen patterns by PRR that in turn sets into action immune defenses. Induced and preformed defense mechanisms together fight back the pathogen to keep infection under check. Herbivory is controlled by accumulating specific secondary metabolites that function as effective deterrents.
- Our current understanding of various stress responses has come from study of stress-inducible genes and proteomics. The roles of plant hormones (ABA, JA, SA and ethylene) in coordinating stress responses and the cross talk between multiple pathways has tremendously improved. This has led to generation of transgenic crops capable of overcoming biotic and abiotic stress.

## 12. 7 TERMINAL QUESTIONS

1. Write a note on acute heat stress response in plants.
2. Differentiate between freezing stress and chilling stress.
3. Indicate the various drought stress tolerance strategies employed in plants.
4. Explain how plants sense and respond to pathogens.
5. What is heavy metal stress? Describe how plants avoid heavy metals present in soil.

# 12.8 ANSWERS

## Self Assessment Question

1. a) True
   b) True
   c) False
   d) True
2. a) i) 1.
      ii) 2.
      iii) 1.
   b) i) Metallothioneins / phytochelatins
      ii) Glycophytes
      iii) Vacuole
      iv) Proline; mannitol
      v) Glyoxylase
3. i) c)
   ii) a)
   iii) d)
   iv) e)
   v) b)

## Terminal Questions

1. Plant stress can be defined as, any environmental factor (biotic /abiotic) that adversely impacts plant growth, development and physiology. Refer to subsection 12.3.2 on acute heat stress response.

2. Chilling injury: Injury above freezing temperature / No ice formation / Takes time to develop symptoms.

   Freezing injury: Injury at freezing temperature / Ice formation / symptoms instantly visible.

3. Refer to Fig.12.2.

4. Refer to Fig. 12.5.

5. Increased concentration of heavy metals damage plants in many ways that results in heavy metal stress. Plants avoid heavy metals present in the soil by reducing their uptake / increasing efflux. They are concentrated in the apoplast or sequestered by binding to cell wall components. Some plants establish symbiotic relationship with mycorrhizal fungi which accumulates metals in the rhizosphere.

# 12.9 FURTHER READINGS

1. Geoffrey Onaga and Kerstin Wydra (2016) Advances in Plant Tolerance to Biotic Stresses, Plant Genomics, Ibrokhim Y. Abdurakhmonov, IntechOpen, DOI: 10.5772/64351.
   Availablefrom: https://www.intechopen.com/books/plant-genomics/advances-in-plant-tolerance-to-biotic-stresses

2. N.-H. Ghori, T. Ghori ,M. Q. Hayat, S. R. Imadi, A. Gul, V. Altay, M. Ozturk Heavy metal stress and responses in plants; 2019; www.researchgate.net / publication/330398479

3. Eva van Zelm, Yanxia Zhang and Christa Testerink, Salt tolerance mechanisms of plants, Annu. Rev. Plant. Biol. 2020. 71:403-433.