

# Stress Physiology

In both natural and agricultural conditions, plants are frequently exposed to environmental stresses.

## Definitions:-

- **Stress**: is usually defined as an external factor that exerts a disadvantageous influence on the plant such as freeze, chill, heat, drought, flood, salty, pest and air pollution etc.
- **Strain**: the reduction in plant growth or function resulting from a stress.
- **Resistance**: is the ability adaptive or tolerant to stresses. Resistance includes adaptation, avoidance and tolerance.
- **Adaptation to Stress**: genetically determined resistance acquired over generations by selection and it is a heritable modification in structure or function which increases the fitness of the plant in a stressful environment. The pattern for stomata movement in CAM plant and the well-developed aerenchyma in hydrophytes are examples for adaptation.
- **Avoidance**: is a manner to avoid facing with stress using neither metabolic process nor energy. Very short lifecycle in desert plants and dormancy during the cool, hot, and drought conditions are examples for avoidance.
- **Tolerance**: is a resistant reaction to reduce or repair injury with morphology, structure, physiology, biochemistry or molecular biology, when plant counters with stresses.
- **Acclimation to Stress**: an increase in the stress tolerance of an individual plant as a result of exposure to prior stress and it is non-heritable physiological modifications made during the life of the individual plant.
- **Hardening** : is a gradual adaptation to stress when the plant is located in the stress condition.

## Types of Stress

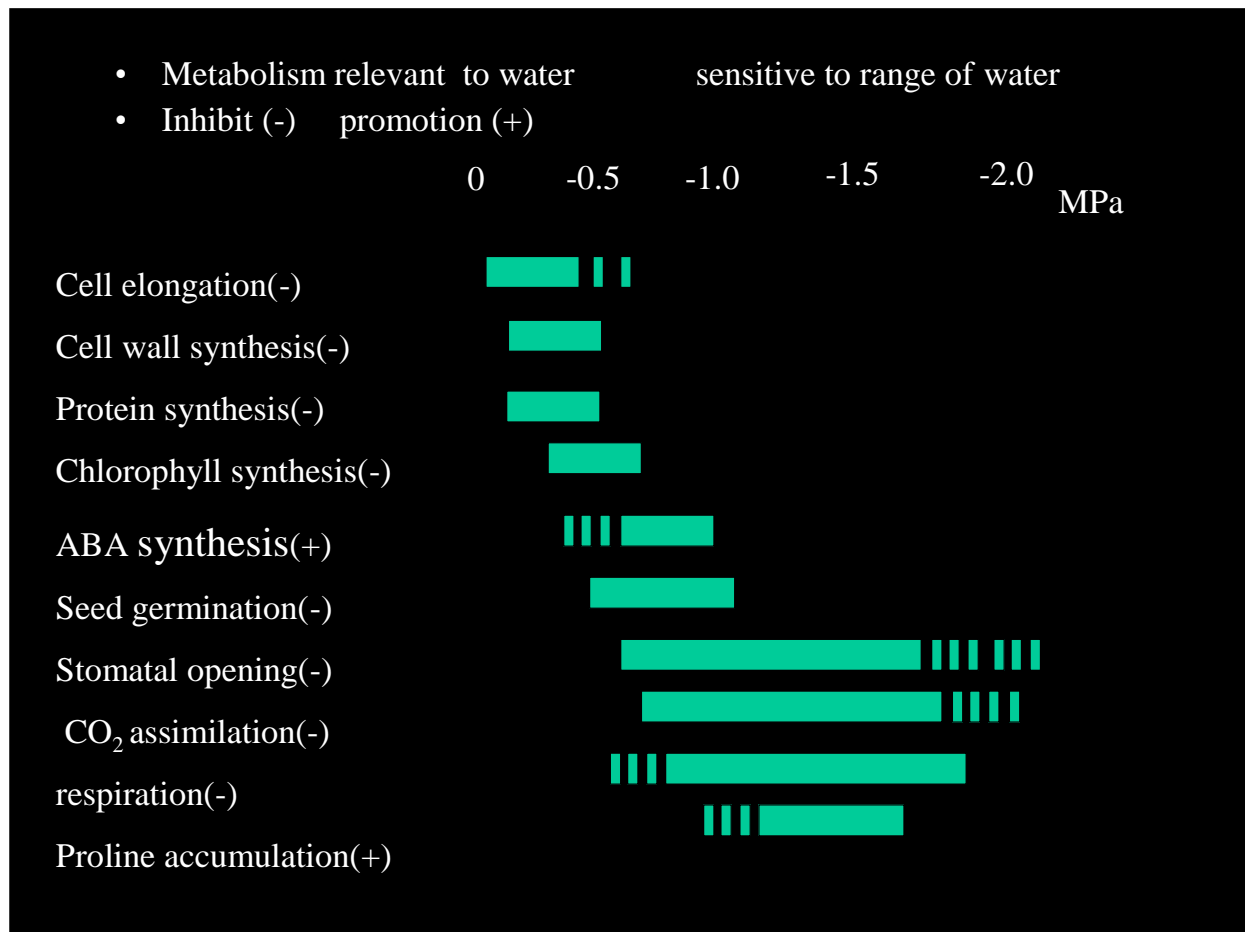
1. Biotic stress.
  - Herbivores.
  - Insects.
  - Pathogens.
  - Parasites.
2. Abiotic (edaphic & climatic/atmospheric).
  - Extremes of temperature (heat, chilling, freezing).
  - Excess water (waterlogging, anoxia, flooding).
  - Water stress (drought, low  $\Psi$ ).
  - Salinity.
  - Nutrient extremes.
  - Radiation (UV, high visible).
  - Allochemicals (herbicides, pesticides, pollutants).
  - Wind.

## Water Deficit and Drought Resistance

First we can distinguish between *desiccation postponements* (the ability to maintain tissue hydration) and *desiccation tolerance* (the ability to function while dehydrated), which are sometimes referred to as drought tolerance at high and low water potentials, respectively.

A third category, drought escape, comprises plants that complete their life cycles during the wet season, before the onset of drought. These are the only true “*drought avoiders*.”

Among the desiccation postpones are water savers and water spenders. *Water savers* use water conservatively, preserving some in the soil for use late in their life cycle; water spenders aggressively consume water, often using prodigious quantities.



## Drought Resistance Strategies Vary with Climatic or Soil Conditions

Soil drought means no rain for long time and no-available water in the soil. Air drought means that  $RH < 20\%$  in atmosphere and  $transpiration \gg water\ absorption$ . If longer, soil drought occurs.

The water-limited productivity of plants depends on the total amount of water available and on the water-use efficiency of the plant. A plant that is capable of acquiring more water or that has higher water-use efficiency will resist drought better. Some plants possess adaptations, such as the C4 and CAM modes of photosynthesis that allow them to exploit more arid environments. In addition, plants possess acclimation mechanisms that are activated in response to water stress.

Water deficit can be defined as any water content of a tissue or cell that is below the highest water content exhibited at the most hydrated state.

When water deficit develops slowly enough to allow changes in developmental processes, water stress has several effects on growth, one of which is

a limitation in leaf expansion. Leaf area is important because photosynthesis is usually proportional to it. However, rapid leaf expansion can adversely affect water availability.

## **Decreased Leaf Area Is an Early Adaptive Response to Water Deficit**

Typically, as the water content of the plant decreases, its cells shrink and the cell walls relax. This decrease in cell volume results in lower turgor pressure and the subsequent concentration of solutes in the cells. The plasma membrane becomes thicker and more compressed because it covers a smaller area than before. Because turgor reduction is the earliest significant biophysical effect of water stress, turgor-dependent activities such as leaf expansion and root elongation are the most sensitive to water deficits.

## **Water Deficit Stimulates Leaf Abscission**

The total leaf area of a plant does not remain constant after all the leaves have matured. If plants become water stressed after a substantial leaf area has developed, leaves will senesce and eventually fall off. Such a leaf area adjustment is an important long-term change that improves the plant's fitness in a water-limited environment. Indeed, many drought-deciduous, desert plants drop all their leaves during a drought and sprout new ones after a rain. This cycle can occur two or more times in a single season. Abscission during water stress results largely from enhanced synthesis of and responsiveness to the endogenous plant hormone ethylene.

## **Water Deficit Enhances Root Extension into Deeper, Moist Soil**

As water deficits progress, the upper layers of the soil usually dry first. Thus, plants commonly show a mainly shallow root system when all soil layers are wetted and a loss of shallow roots and proliferation of deep roots as water in top layers of the soil is depleted. Deeper root growth into wet soil can be considered a second line of defense against drought.

## **Stomata Close during Water Deficit in Response to Absciscic Acid**

When the onset of stress is more rapid or the plant has reached its full leaf area before initiation of stress, other responses protect the plant against immediate desiccation. Under these conditions, stomata closure reduces evaporation from the existing leaf area. Thus, stomatal closure can be considered a third line of defense against drought. Solute loss from guard cells can be triggered by a decrease in the water content of the leaf, and abscisic acid (ABA) plays an important role in process. Absciscic acid is synthesized continuously at a low rate in mesophyll cells and tends to accumulate in the chloroplasts.

## **Water Deficit Limits Photosynthesis within the Chloroplast**

As stress becomes severe, however, the dehydration of mesophyll cells inhibits photosynthesis, mesophyll metabolism is impaired, and water-use efficiency usually decreases. Does water stress directly affect translocation? Water stress decreases both photosynthesis and the consumption of assimilates in the expanding leaves. As a consequence, water stress indirectly decreases the amount of photosynthate exported from leaves. Because phloem transport depends on turgor, decreased water potential in the phloem during stress may inhibit the movement of assimilates.

## **Osmotic Adjustment of Cells Helps Maintain Plant Water Balance**

As the soil dries, its matric potential becomes more negative. Plants can continue to absorb water only as long as their water potential ( $\Psi_w$ ) is lower (more negative) than that of the soil water.

**Osmotic adjustment**, or accumulation of solutes by cells, is a process by which water potential can be decreased without an accompanying decrease in turgor or decrease in cell volume.

Osmotic adjustment is a net increase in solute content per cell that is independent of the volume changes that result from loss of water. Most of the adjustment can usually be accounted for by increases in concentration of a variety of common solutes, including sugars, organic acids, amino acids, and inorganic ions (especially  $K^+$ ). Cytosolic enzymes of plant cells can be severely inhibited by high

concentrations of ions. The accumulation of ions during osmotic adjustment appears to be restricted to the vacuoles, where the ions are kept out of contact with enzymes in the cytosol or subcellular organelles.

Because of this compartmentation of ions, other solutes must accumulate in the cytoplasm to maintain water potential equilibrium within the cell. These other solutes, called compatible solutes (or compatible osmolytes), are organic compounds that do not interfere with enzyme functions. Commonly accumulated compatible solutes include the amino acid proline, sugar alcohols (e.g., sorbitol and mannitol), and a quaternary amine called glycine betaine. Synthesis of compatible solutes helps plants adjust to increased salinity in the rooting zone.

## **Water Deficit Increases Resistance to Liquid-Phase Water Flow**

When a soil dries, its resistance to the flow of water increases very sharply, particularly near the permanent wilting point. Because of the very large soil resistance to water flow, water delivery to the roots at the permanent wilting point is too slow to allow the overnight rehydration of plants that have wilted during the day. Rehydration is further hindered by the resistance within the plant, which has been found to be larger than the resistance within the soil over a wide range of water deficits. Several factors may contribute to the increased plant resistance to water flow during drying. As plant cells lose water, they shrink. When roots shrink, the root surface can move away from the soil particles that hold the water, and the delicate root hairs may be damaged. In addition, as root extension slows during soil drying, the outer layer of the root cortex (the hypodermis) often becomes more extensively covered with suberin, a water-impermeable lipid, increasing the resistance to water flow.

Another important factor that increases resistance to water flow is cavitation, or the breakage of water columns under tension within the xylem. A common developmental response to water stress is the production of a thicker cuticle that reduces water loss from the epidermis (cuticular transpiration).

## **Water Deficit Increases Wax Deposition on the Leaf Surface**

A common developmental response to water stress is the production of a thicker cuticle that reduces water loss from the epidermis (cuticular transpiration). Although waxes are deposited in response to water deficit both on the surface and

within the cuticle inner layer, the inner layer may be more important in controlling the rate of water loss in ways that are more complex than by just increasing the amount of wax present.

## **Water Deficit Alters Energy Dissipation from Leaves**

Maintaining a leaf temperature that is much lower than the air temperature requires evaporation of vast quantities of water. This is why adaptations that cool leaves by means other than evaporation (e.g., changes in leaf size and leaf orientation) are very effective in conserving water. Because of their low boundary layer resistance, small leaves tend to remain close to air temperature even when transpiration is greatly slowed. Absorption of energy can also be decreased by hairs on the leaf surface or by layers of reflective wax outside the cuticle.

## **Osmotic Stress Induces Crassulacean Acid Metabolism in Some Plants**

Crassulacean acid metabolism (CAM) is a plant adaptation in which stomata open at night and close during the day. The leaf-to-air vapor pressure difference that drives transpiration is much reduced at night, when both leaf and air are cool. As a result, the water-use efficiencies of CAM plants are among the highest measured.

## **Osmotic Stress Changes Gene Expression**

The accumulation of compatible solutes in response to osmotic stress requires the activation of the metabolic pathways that biosynthesize these solutes. Several genes coding for enzymes associated with osmotic adjustment are turned on (up-regulated) by osmotic stress and/or salinity, and cold stress. Some genes regulated by osmotic stress encode proteins associated with membrane transport, including ATPase's and the water channel proteins, aquaporins. A large group of genes that are regulated by osmotic stress was discovered by examination of naturally desiccating embryos during seed maturation. These genes code for so-called LEA proteins (named for late embryogenesis abundant), and they are suspected to play a role in cellular membrane protection. They accumulate in vegetative tissues during episodes of osmotic stress. The proteins encoded by these genes are typically hydrophilic and strongly bind water. Their protective role might be associated with an ability to retain water and to prevent crystallization of important cellular proteins and other molecules

during desiccation. They might also contribute to membrane stabilization. Osmotic stress typically leads to the accumulation of ABA, so it is not surprising that products of ABA-responsive genes accumulate during osmotic stresses.

## Heat Stress and Heat Shock

Cold-favored plants: meets heat injury at 15 — 20°C.

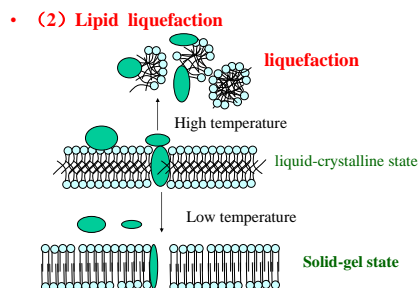
Temperature-mediate plant: most of crops——35°C.

Temperature-favored plants: many CAM plants>50°C.

Heat injury is damage due to the temperature- mediate plant by high temperature above 35°C.

Some CAM species can tolerate temperatures of 60 to 65°C, but most leaves are damaged above 45°C. The temperature of actively transpiring leaves is usually lower than air temperature, but water deficit curtails transpiration and causes overheating and heat stress.

Because CAM plants keep their stomata closed during the day, they cannot cool by transpiration. Instead, they dissipate the heat from incident solar radiation by re-emission of long wave (infrared) radiation and loss of heat by conduction and convection. Heat stress is also a potential danger in greenhouses, where low air speed and high humidity decrease the rate of leaf cooling. Moderate degree of heat stress slows growth of the whole plant.



## At High Temperatures, Photosynthesis is Inhibited before Respiration

Both photosynthesis and respiration are inhibited at high temperatures, but as temperature increases, photosynthetic rates drop before respiratory rates. The



temperature at which the amount of CO<sub>2</sub> fixed by photosynthesis, equals the amount of CO<sub>2</sub> released by respiration, in a given time interval is called the temperature compensation point.

At temperatures above the temperature compensation point, photosynthesis cannot replace the carbon used as a substrate for respiration. As a result, carbohydrate reserves decline, and fruits and vegetables lose sweetness. This imbalance between photosynthesis and respiration is one of the main reasons for the deleterious effects of high temperatures. In the same plant the temperature compensation point is usually lower for shade leaves than for sun leaves that are exposed to light (and heat). Enhanced respiration rates relative to photosynthesis at high temperatures are more detrimental in C<sub>3</sub> plants than in C<sub>4</sub> or CAM plants because the rates of both dark respiration and photorespiration are increased in C<sub>3</sub> plants at higher temperatures.

## **High Temperature Reduces Membrane Stability**

Excessive fluidity of membrane lipids at high temperatures is correlated with loss of physiological function. Acclimation to high temperatures is associated with a greater degree of saturation of fatty acids in membrane lipids, which makes the membranes less fluid. At high temperatures, there is a decrease in the strength of hydrogen bonds and electrostatic interactions between polar groups of proteins within the aqueous phase of the membrane. High temperatures thus modify membrane composition and structure and can cause leakage of ions. Membrane disruption also causes the inhibition of processes such as photosynthesis and respiration that depend on the activity of membrane-associated electron carriers and enzymes.

## **Several Adaptations Protect Leaves against Excessive Heating**

In environments with intense solar radiation and high temperatures, plants avoid excessive heating of their leaves by decreasing their absorption of solar radiation. Both drought resistance and heat resistance depend on the same adaptations: reflective leaf hairs and leaf waxes; leaf rolling and vertical leaf orientation; and growth of small, highly dissected leaves to minimize the boundary layer thickness and thus maximize convective and conductive heat loss .

## At Higher Temperatures, Plants Produce Heat Shock Proteins

In response to sudden, 5 to 10°C rises in temperature, plants produce a unique set of proteins referred to as heat shock proteins (HSPs). Most HSPs function to help cells withstand heat stress by acting as molecular chaperones. Heat stress causes many cell proteins that function as enzymes or structural components to become unfolded or misfolded, thereby leading to loss of proper enzyme structure and activity.

### Mechanism of heat resistance

(1) High stability of protein under heat stress. much —S—S—

(2) Lower water content

(3) High contents of saturated fatty acid.

(4) High contents of organic acid.

CAM: extremely heat-resistance a great number of organic acids.

(5) Form of heat shock proteins (HSPs or hsps)

Heat shock proteins are a newly synthesizing set of proteins that organisms ranging from bacteria to humans respond to high temperature.

Functions: protect or repair proteins, nuclear acids and bio-membrane from heat injury.

### Chilling and Freezing

Chilling temperatures are too low for normal growth but not low enough for ice to form. Typically, tropical and subtropical species are susceptible to chilling injury. When plants growing at relatively warm temperatures (25 to 35°C) are cooled to 10 to 15°C, chilling injury occurs : Growth is slowed, discoloration or lesions appear on leaves, and the foliage looks soggy, as if soaked in water for a long time. If roots are chilled, the plants may wilt. Freezing injury, on the other hand, occurs at temperatures below the freezing point of water. Full induction of tolerance to freezing, as with chilling, requires a period of acclimation at cold temperatures.

Cold stress reduces water activity and leads to osmotic stress within the cells. This osmotic stress effect leads to the activation of osmotic stress-related signaling pathways, and the accumulation of proteins involved in cold acclimation. Other cold specific, non-osmotic stress-related genes are also activated. Transgenic plants over

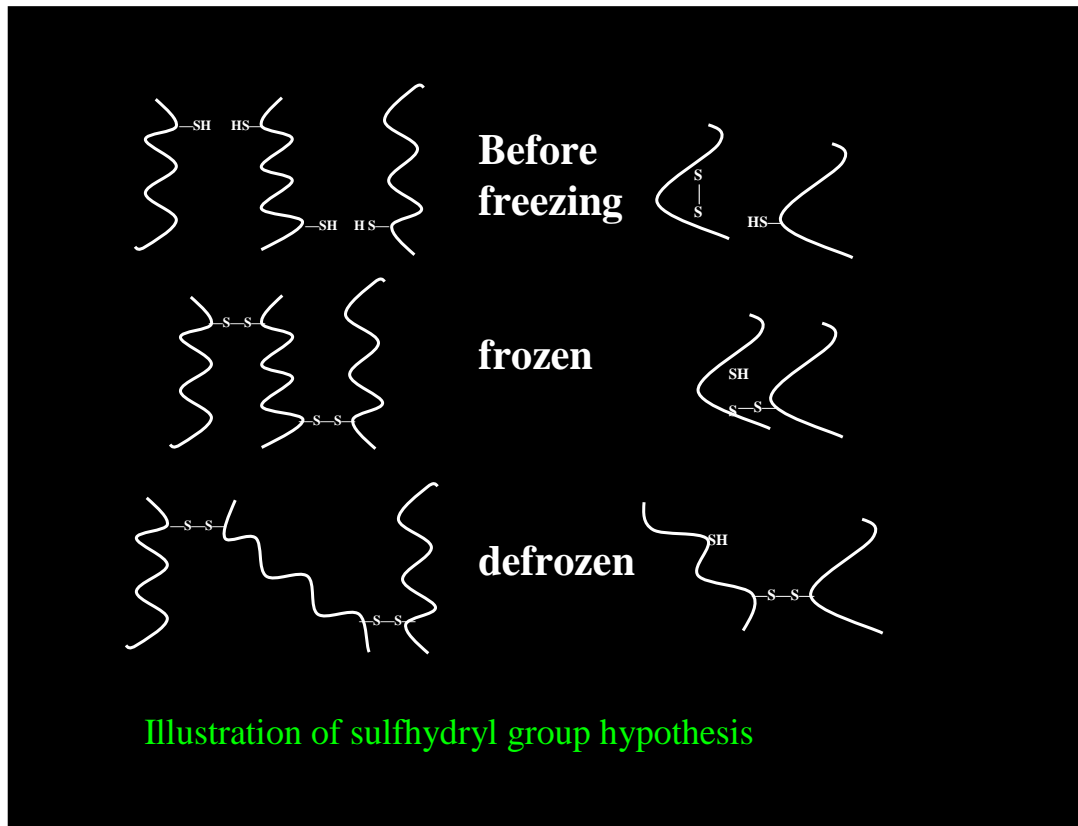
expressing cold stress-activated signaling components demonstrate increased cold tolerance.

## **Membrane Properties Change in Response to Chilling Injury**

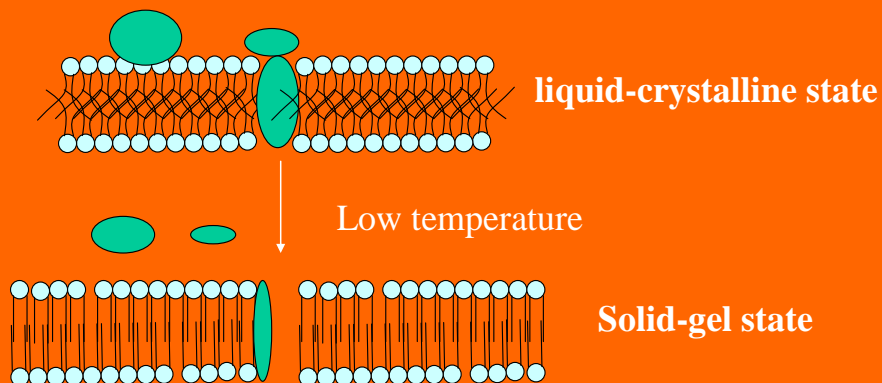
Leaves from plants injured by chilling show inhibition of photosynthesis, slower carbohydrate translocation, lower respiration rates, inhibition of protein synthesis, and increased degradation of existing proteins. All of these responses appear to depend on a common primary mechanism involving loss of membrane function during chilling.

In chilling-sensitive plants, the lipids in the bilayer have a high percentage of saturated fatty acid chains, and membranes with this composition tend to solidify into a semi-crystalline state at a temperature well above 0°C. Keep in mind that saturated fatty acids that have no double bonds and lipids containing trans-monounsaturated fatty acids solidify at higher temperatures than do membranes composed of lipids that contain unsaturated fatty acids. As the membranes become less fluid, their protein components can no longer function normally. The result is inhibition of H<sup>+</sup>-ATPase activity, of solute transport into and out of cells, of energy transduction, and of enzyme-dependent metabolism.

In addition, chilling-sensitive leaves exposed to high photon fluxes and chilling temperatures are photoinhibited, causing acute damage to the photosynthetic machinery. The primary cause of most chilling injuries is the loss of membrane properties ensuing from changes in membrane fluidity. Membrane lipids of chilling-resistant plants often have a greater proportion of unsaturated fatty acids than those of chilling-sensitive plants.



#### • 2.1.2.1. Change in state of lipid



Electric conductivity as an index for resistance to low temperature in prduction

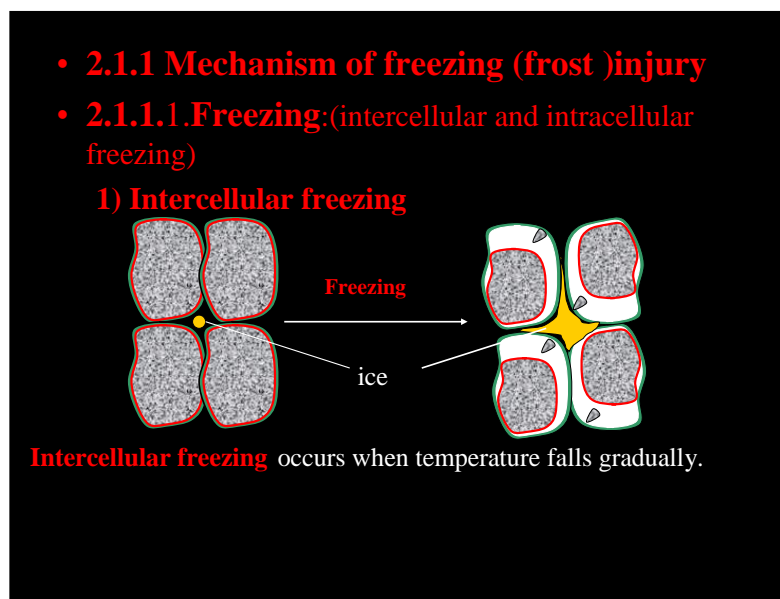
## Ice Crystal Formation and Protoplast Dehydration Kill Cells

Fully hydrated, vegetative cells can also retain viability if they are cooled very quickly to avoid the formation of large, slow-growing ice crystals that would puncture and destroy subcellular structures. Ice crystals that form during very rapid freezing are too small to cause mechanical damage. Conversely, rapid warming of frozen tissue is required to prevent the growth of small ice crystals into crystals of a damaging size, or to prevent loss of water vapor by sublimation, both of which take place at intermediate temperatures ( $-100$  to  $-10^{\circ}\text{C}$ ). Ice usually forms first within the intercellular spaces, and in the xylem vessels, along which the ice can quickly propagate. This ice formation is not lethal to hardy plants, and the tissue recovers fully if warmed. However, when plants are exposed to freezing temperatures for an extended period, the growth of extracellular ice crystals results in the movement of liquid water from the protoplast to the extracellular ice, causing excessive dehydration.

### Limitation of Ice Formation Contributes to Freezing Tolerance

Sugars and some of the cold-induced proteins are suspected to have cryoprotective (cryo- = “cold”) effects; they stabilize proteins and membranes during dehydration induced by low temperature.

Sucrose predominates among the soluble sugars associated with freezing tolerance that function in a colligative fashion, but in some species raffinose, fructans, sorbitol, or mannitol serves the same function.



- **(2) Intracellular Freezing :**
- **Intracellular freezing** often occurs when temperature falls suddenly.
- Ice results in the direct injury in cytoplasm, biomembrane and organelle, and damages to cell compartmentation and metabolic disorder.
- Much more serious damage is caused by Intracellular Freezing than by Intercellular Freezing.
- **2.1.1.2 damage of protein**
- **Sulfhydryl group hypothesis (disulfide bridge hypothesis )**

## Some Woody Plants Can Acclimate to Very Low Temperatures

Under natural conditions, woody species acclimate to cold in two distinct stages:

**In the first stage**, hardening is induced in the early autumn by exposure to short days and nonfreezing chilling temperatures, both of which combine to stop growth. A diffusible factor that promotes acclimation (probably ABA) moves in the phloem from leaves to overwintering stems and may be responsible for the changes. During this period, woody species also withdraw water from the xylem vessels, thereby preventing the stem from splitting in response to the expansion of water during later freezing. Cells in this first stage of acclimation can survive temperatures well below 0°C, but they are not fully hardened.

**In the second stage**, direct exposure to freezing is the stimulus; no known translocatable factor can confer the hardening resulting from exposure to freezing. When fully hardened, the cells can tolerate exposure to temperatures of –50 to –100°C.

## **Resistance to Freezing Temperatures Involves Supercooling and Slow Dehydration**

Ice formation starts at  $-3$  to  $-5^{\circ}\text{C}$  in the intercellular spaces, where the crystals continue to grow, fed by the gradual withdrawal of water from the protoplast, which remains unfrozen. Resistance to freezing temperatures depends on the capacity of the extracellular spaces to accommodate the volume of growing ice crystals and on the ability of the protoplast to withstand dehydration. Mechanisms that confer the resistance to freezing that is typical of woody plants include dehydration and supercooling.

## **Some Bacteria That Live on Leaf Surfaces Increase Frost Damage**

When leaves are cooled to temperatures in the  $-3$  to  $-5^{\circ}\text{C}$  range, the formation of ice crystals on the surface (frost) is accelerated by certain bacteria that naturally inhabit the leaf surface, such as *Pseudomonas syringae* and *Erwinia herbicola*, which act as ice nucleators.

## **ABA and Protein Synthesis Are Involved in Acclimation to Freezing**

Protein synthesis is necessary for the development of freezing tolerance, and several distinct proteins accumulate during acclimation to cold, as a result of changes in gene expression. Plants develop freezing tolerance at nonacclimating temperatures when treated with exogenous ABA. Many of the genes or proteins expressed at low temperatures or under water deficit are also inducible by ABA under nonacclimating conditions. All these findings support a role of ABA in tolerance to freezing.

## **Numerous Genes Are Induced during Cold Acclimation**

Another important class of proteins whose expression is up-regulated by cold stress is the antifreeze proteins. Several types of cold- all antifreeze proteins belong to a class of proteins such as endochitinases and endoglucanases, which are induced upon *infection* of different pathogens. These proteins, called pathogenesis related (PR) proteins are thought to protect plants against pathogens.

## **A Transcription Factor Regulates Cold-Induced Gene Expression**

More than 100 genes are up-regulated by cold stress. Because cold stress is clearly related to ABA responses and to osmotic stress, not all the genes up-regulated by cold stress necessarily need to be associated with cold tolerance, but most likely many of them are.

## **Salinity Stress**

Salinity stress results from salt accumulation in the soil. It is estimated that about one-third of the irrigated land on Earth is affected by salt. However, a much more extensive problem in agriculture is the accumulation of salts from irrigation water. The higher the salt concentration in water, the greater its electrical conductivity and the lower its osmotic potential (higher osmotic pressure). Plants can be divided into two broad groups on the basis of their response to high concentrations of salts.

**Halophytes** are native to saline soils and complete their life cycles in that environment.

**Glycophytes** (literally “sweet plants”), or non-halophytes, are not able to resist salts to the same degree as halophytes. Usually there is a threshold concentration of salt above which glycophytes begin to show signs of growth inhibition, leaf discoloration, and loss of dry weight.

Dissolved solutes in the rooting zone generate a low (more negative) osmotic potential that lowers the soil water potential. The general water balance of plants is thus affected because leaves need to develop even lower water potential to maintain a “downhill” gradient of water potential between the soil and the leaves.

In addition to the plant responses to low water potential, specific ion toxicity effects also occur when injurious concentrations of ions—particularly  $\text{Na}^+$ ,  $\text{Cl}^-$ , or  $\text{SO}_4$ . Of particular importance here is the fact that most plants can adjust osmotically when growing in saline soils. Such adjustment prevents loss of turgor (which would slow cell growth).

Photosynthesis is inhibited when high concentrations of  $\text{Na}^+$  and/or  $\text{Cl}^-$  accumulate in chloroplasts. Plants minimize salt injury by excluding salt from meristems, particularly in the shoot, and from leaves that are actively expanding and photosynthesizing. In plants that are salt sensitive, resistance to moderate levels of



salinity in the soil depends in part on the ability of the roots to prevent potentially harmful ions from reaching the shoots.

Casparian strip imposes a restriction to the movements of ions into the xylem. To bypass the Casparian strips, ions need to move from the apoplast to the symplastic pathway across cell membranes. This transition offers salt-resistant plants a mechanism to partially exclude harmful ions. Some salt-resistant plants, such as salt cedar (*Tamarix* sp.) and salt bush (*Atriplex* sp.), do not exclude ions at the root, but instead have salt glands at the surface of the leaves. The ions are transported to these glands, where the salt crystallizes and is no longer harmful.

In general, halophytes have a greater capacity than glycophytes for ion accumulation in shoot cells. Plant cells can adjust their water potential ( $Y_w$ ) in response to osmotic stress by lowering their solute potential ( $Y_s$ ). Two intracellular processes contribute to the decrease in  $Y_s$ : the accumulation of ions in the vacuole and the synthesis of compatible solutes in the cytosol. Compatible solutes include glycine betaine, proline, sorbitol, mannitol, pinitol, and sucrose. Many halophytes exhibit a growth optimum at moderate levels of salinity, and this optimum is correlated with the capacity to accumulate ions in the vacuole, where they can contribute to the cell osmotic potential without damaging the salt-sensitive enzymes.

Plants subjected to salt stress can reduce leaf area and or drop leaves via leaf abscission just as during episodes of osmotic stress. In addition, changes in gene expression associated with osmotic stress are similarly associated with salinity stress.

## Oxygen Deficiency

Roots usually obtain sufficient oxygen ( $O_2$ ) for aerobic respiration directly from the gaseous space in the soil. However, soil can become flooded or waterlogged when it is poorly drained or when rain or irrigation is excessive. When temperatures are low and plants are dormant, oxygen depletion is very slow and the consequences are relatively harmless. Flooding-sensitive plants are severely damaged by 24 hours of anoxia. The growth and survival of many plant species are greatly depressed under such conditions, and crop yields can be severely reduced.

Flooding-tolerant plants can withstand anoxia (lack of oxygen) temporarily, but not for prolonged periods of more than a few days. On the other hand, specialized natural vegetation found in wetlands such as marshes and swamps, and crops such as rice, are well adapted to resist oxygen deficiency in the root environment. Wetland plants can resist anoxia, and they grow and survive for extended periods of up to months

with their root systems in anoxic conditions. Most of these plants have special adaptations.

## **Anaerobic Microorganisms Are Active in Water-Saturated Soils**

When soil is completely depleted of molecular  $O_2$ , the function of soil microbes becomes significant for plant life and growth. Anaerobic soil microorganisms (anaerobes) reduce  $Fe^{3+}$  to  $Fe^{2+}$ , and because of its greater solubility,  $Fe^{2+}$  can rise to toxic concentrations when some soils are anaerobic for many weeks. Other anaerobes may reduce sulfate ( $SO_4^{-2}$ ) to hydrogen sulfide ( $H_2S$ ), which is a respiratory poison. When anaerobes have an abundant supply of organic substrate, bacterial metabolites such as acetic acid and butyric acid are released into the soil water. All of these substances made by microorganisms under anaerobic conditions are toxic to plants at high concentrations. Most tissues of higher plants cannot survive anaerobically, but some tissues, such as the embryo and coleoptiles from rice, can survive for weeks under anoxic conditions.

## **Roots Are Damaged in Anoxic Environments**

Root respiration rate and metabolism are affected even before  $O_2$  is completely depleted from the root environment. The critical oxygen pressure (COP) is the oxygen pressure at which the respiration rate is first slowed by  $O_2$  deficiency. In the absence of  $O_2$ , electron transport and oxidative phosphorylation in mitochondria cease, the tricarboxylic acid cycle cannot operate, and ATP can be produced only by fermentation. Thus when the supply of  $O_2$  is insufficient for aerobic respiration, roots first begin to ferment pyruvate (formed in glycolysis;) to lactate or ethanol. The net yield of ATP in fermentation is only 2 moles of ATP per mole of hexose sugar respired (compared with 36 moles of ATP per mole of hexose respired in aerobic respiration). Thus, injury to root metabolism by  $O_2$  deficiency originates in part from a lack of ATP to drive essential metabolic processes.

## **Damaged $O_2$ -Deficient Roots Injure Shoots**

Anoxic or hypoxic (partly deficient in oxygen) roots lack sufficient energy to support physiological processes on which the shoots depend. Failure of the roots to absorb nutrient ions and transport them to the xylem (and from there to the shoot)

quickly leads to a shortage of ions within developing and expanding tissues. Older leaves senesce prematurely because of reallocation of phloem-mobile elements (N, P, K) to younger leaves. The lower permeability of roots to water often leads to a decrease in leaf water potential and wilting, although this decrease is temporary if stomata close, preventing further water loss by transpiration.

Hypoxia also accelerates production of the ethylene precursor ACC (1-aminocyclopropane-1-carboxylic acid) in roots. ACC travels via the xylem sap to the shoot, where, in contact with oxygen, it is converted by ACC oxidase to ethylene. The upper (adaxial) surfaces of the leaf petioles of tomato and sunflower have ethylene-responsive cells that expand more rapidly when ethylene concentrations are high. This expansion results in epinasty, the downward growth of the leaves such that they appear to droop. Oxygen shortage in roots, like water deficit or high concentrations of salts, can stimulate abscisic acid (ABA) production and movement of ABA to leaves.

## **Submerged Organs Can Acquire O<sub>2</sub> through Specialized Structures**

In some wetland species, such as the water lily (*Nymphaeodes peltata*), submergence traps endogenous ethylene, and the hormone stimulates cell elongation of the petiole, extending it quickly to the water surface so that the leaf is able to reach the air. Internodes of deep-water (floating) rice respond similarly to trapped ethylene, so the leaves extend above the water surface despite increases in water depth.

In the case of pondweed (*Potamogeton pectinatus*), an aquatic monocot, stem elongation is insensitive to ethylene; instead elongation is promoted even under anaerobic conditions by acidification of the surrounding water caused by the accumulation of respiratory CO<sub>2</sub>. In most wetland plants and in many plants that acclimate well to wet conditions, the stem and roots develop longitudinally interconnected, gas-filled channels that provide a low-resistance pathway for movement of oxygen and other gases.

The gases (air) enter through stomata or through lenticels on woody stems and roots, and travel by molecular diffusion, or by convection driven by small pressure gradients. In many wetland plants, exemplified by rice, cells are separated by prominent, gas-filled spaces, which form a tissue called aerenchyma, that develop in the roots independently of environmental stimuli. In the root tip of maize, hypoxia stimulates the activity of ACC synthase and ACC oxidase, thus causing ACC and ethylene to be produced faster.