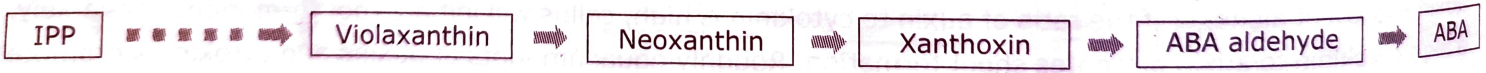
3.8.4 Abscisic acid

Abscisic acid (ABA) is a stress hormone and was first identified and chemically characterized by *Frederick T. Addicott* and his co-worker when studying compound responsible for abscission of cotton fruits. It was originally called *abscisin II* because it was thought to play a major role in abscission of fruits. At about the same time, another group called it *dormin* because they thought it had a major role in bud dormancy. Later the name abscisic acid (ABA) was coined for these compounds. Abscisic acid is a misnomer for this compound, because it has little to do with abscission. In contrast to auxins, gibberellins and cytokinins, which are represented by various active derivatives, ABA is a single compound.

Biosynthesis and transport

ABA is a sesquiterpene (15-carbon). It is synthesized almost in all cells that contain chloroplast and other plastids. The pathway begins with isopentenyl pyrophosphate (IPP) and leads to the synthesis of violaxanthin. Violaxanthin is converted to the neoxanthin which is then cleaved to form ABA aldehyde. Transport of ABA occurs through both xylem and phloem and also through parenchyma cells outside vascular bundles.



Physiological effects

- ABA brings about reductions in stomatal aperture and also inhibits stomatal opening.

Stomatal closure is driven by a reduction in guard cell turgor pressure caused by a large efflux of K^+ and anions from the cell. ABA inhibits stomatal opening by increasing cytosolic calcium concentration. ABA stimulates elevations in the concentration of cytosolic calcium by inducing both influx through plasma membrane channels and release of calcium into the cytosol from internal compartments, such as the central vacuole. Increased cytosolic calcium activates anion channels. Activation of anion channels causes efflux of anions from guard cells which causes depolarization of the membrane. Changes in membrane potential deactivates K^+_{in} channels and activates K^+_{out} channels, resulting in K^+ efflux from guard cells. K^+ channels that open only at more negative potentials are specialized for inward diffusion of K^+ and are known as *inward-rectifying*, or simply inward, K^+ channels. Conversely, K^+ channels that open only at more positive potentials are *outward-rectifying*, or outward, K^+ channels. The sustained efflux of both anions and K^+ from guard cells via anion and K^+_{out} channels contributes to loss of guard cell turgor, which leads to stomatal closing.

Stomatal opening is driven by H^+-ATPases present on the plasma membrane. H^+-ATPases activity is positively regulated by blue light whereas ABA acts as negative regulator. The efflux of H^+ hyperpolarizes the plasma membrane and leads to K^+ uptake via activation of K^+_{in} channels. Another signal that activates the influx of K^+ via K^+_{in} channels is the acidification of the apoplast as a result of H^+ extrusion from the guard cells. K^+ uptake is balanced by counter-ions, mainly Cl^- from the apoplast. Cytosolic calcium elevations in guard cells in the presence of ABA down-regulate plasma membrane H^+-ATPases and thus K^+_{in} channels. This explains the mechanistic basis of inhibition of stomatal opening in the presence of ABA.

The effect of ABA on stomatal apertures under red and blue light varies. Increasing ABA concentration inhibits blue light–stimulated stomatal opening in a concentration-dependent fashion, but there is no effect on red light–stimulated opening. These contrasting responses to blue and red light can be explained by the effect of ABA on guard cell osmoregulation. ABA concentrations have been shown to inhibit proton pumping and potassium uptake, which are central to blue light–stimulated stomatal opening. Red light, on the other hand, stimulates guard cell photosynthesis and sucrose accumulation and this osmoregulatory pathway appears to be insensitive to ABA.

- Roots and shoots growth : ABA has different effects on the root and shoot growth, and the effects are strongly dependent on the water status of the plant. Under low water potential, when ABA levels are high, the endogenous hormone exerts a strong positive effect on root growth by suppressing ethylene production, and a negative effect on shoot growth. Endogenous ABA acts as a signal to reduce shoot growth only under water stress conditions.
- Dormancy and germination : ABA is required for the development of desiccation tolerance in the developing embryo, the synthesis of storage proteins and the acquisition of dormancy. The high levels of ABA in maturing seeds inhibit germination. Many types of dormant seeds germinate when ABA is removed or inactivated. Often, the ratio of ABA to gibberellins determines whether the seed remains dormant or germinates. ABA inhibits the GA-dependent hydrolytic enzyme synthesis (such as α-amylase) that are essential for the breakdown of storage reserves in seeds. Although less is known about the role of ABA in buds dormancy, ABA is one of the inhibitors that accumulates in dormant buds.
- Vivipary : ABA-deficient embryos may exhibit precocious germination and vivipary. Inactivated ABA or low levels of ABA can lead to precocious germination. For example, a maize mutant with grains that germinate while still on the cob lacks a functional transcription factor required for ABA to induce expression of certain genes. Precocious germination of red mangrove seeds, due to low ABA levels, is actually an adaptation that helps the young seedlings to plant themselves in the soft mud below the parent tree.
- Hydraulic conductivity : ABA increases the hydraulic conductivity (decreasing the resistance to water movement across the membrane) and ion flux of root in response to water stress.

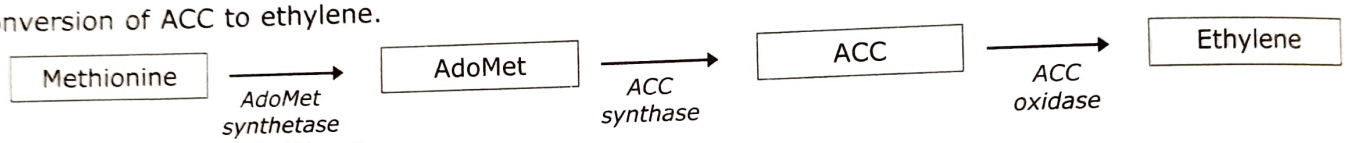
3.8.5 Ethylene

Ethylene, unlike the rest of the plant hormones, is a gaseous hormone. Like abscisic acid, it is the only member of its class. Of all the known plant growth substance, ethylene has the simplest structure. It is produced in all higher plants, and usually associated with fruit ripening and the *triple response*. The triple response on dark-grown pea seedlings includes, reduced stem elongation, increased stem thickening and horizontal growth habit.

Biosynthesis and transport

Ethylene is produced by almost all parts of higher plants. In general, meristematic regions are active sites for ethylene biosynthesis. The rate of production also depends on the type of tissue and the stage of development. Its synthesis increases in tissues undergoing senescence or ripening. Ethylene biosynthesis is increased by stress conditions such as drought, flooding, chilling, or mechanical wounding. Auxins also promote ethylene synthesis. Being a gas, ethylene moves by diffusion from its site of synthesis.

The amino acid methionine is the precursor of ethylene. In the first step of ethylene biosynthetic pathway, methionine is converted into *S*-adenosylmethionine (AdoMet). The rate-limiting step in the pathway is the conversion of AdoMet to 1-Aminocyclopropane-1-carboxylic acid (ACC), which is catalyzed by the enzyme *ACC synthase*. The last step in the pathway is the conversion of ACC to ethylene. This step requires oxygen and is catalyzed by the enzyme *ACC oxidase*. Amino ethoxy-vinyl glycine and amino oxyacetic acid block the biosynthetic pathway of ethylene. Both inhibit the conversion of AdoMet to ACC. The cobalt ion also acts as an inhibitor of ethylene biosynthesis, blocking the conversion of ACC to ethylene.



Physiological effects

- Abscission : The shedding of leaves, fruits, flowers and other plant organs is termed *abscission*. It occurs at a specialized layer of cells – the abscission layers. Auxin apparently prevents leaf abscission by maintaining cells in the abscission zone insensitive to ethylene. When auxin levels in the leaf decline, the tissues become sensitive to ethylene that promotes abscission by producing and secreting cellulases, and other enzymes.
- Flowering : Ethylene induces flowering in mango and pineapple family (*Bromeliaceae*). In monoecious plants that have separate male and female flowers, ethylene may change the sex of developing flowers. The promotion of female flower formation in cucumber is one example of this effect.
- Epinasty : The downward curvature of leaves that occurs when the upper (adaxial) side grows faster than the lower (abaxial) side is termed *epinasty*. Ethylene induces epinasty.
- Rooting : Ethylene induces adventitious root and root hair formation. Root hairs are tubular projections originating from a specialized subset of root epidermal cells that increase the surface area of the roots, thereby increasing their absorptive capacity for water and nutrients.
- Fruit ripening : Ethylene accelerates the processes associated with ripening in many fruits. A dramatic increase in ethylene production also accompanies the initiation of ripening. All fruits that ripen in response to ethylene exhibit a characteristic respiratory rise before the ripening phase called a **climacteric**. Apples, bananas and tomatoes are examples of climacteric fruits. In contrast, fruits such as citrus fruits and grapes do not exhibit the respiration and ethylene production rise and are called *nonclimacteric* fruits.

Structure

Abscisic acid is the trivial name for 3-methyl-5-(1-hydroxy-4-oxo-2,6,6-trimethyl-2-cyclohexen-1-yl)-cis, trans-2,4-pentadienoic acid. Natural (+)-abscisic acid is optically active. ABA synthesized chemically is racemic and composed of equal amounts of the (+)-and (–)-enantiomers.

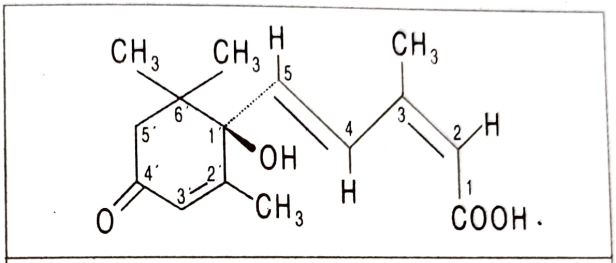


Fig. 13.20 : Structure of abscisic acid (C_{15})

Biosynthesis

Two pathways have been suggested for the biosynthesis of abscisic acid. One involves the cleavage of a C_{40} precursor, a xanthophyll carotenoid, and the other involves the direct formation from C_{15} precursor, farnesyl pyrophosphate.

Indirect or Xanthophyll Cleavage Pathway

The initial reactions of ABA biosynthesis take place in chloroplasts. The biosynthetic pathway begins with the C_5 isoprene unit, isopentenyl pyrophosphate (IpPP), and through a few steps leads to the synthesis of oxygenated carotenoid like C_{40} xanthophyll, zeaxanthin, which is then converted to violaxanthin. Subsequently, violaxanthin is converted to 9-cis-neoxanthin, which then undergoes cleavage to form C_{15} compound xanthoxin, possibly outside the chloroplasts. Xanthoxin is a neutral growth inhibitor with ABA-like properties. In the last step, xanthoxin is converted to ABA aldehyde in the cytosol by the loss of epoxy group, which is finally oxidized to ABA. This pathway is predominant in higher plants.

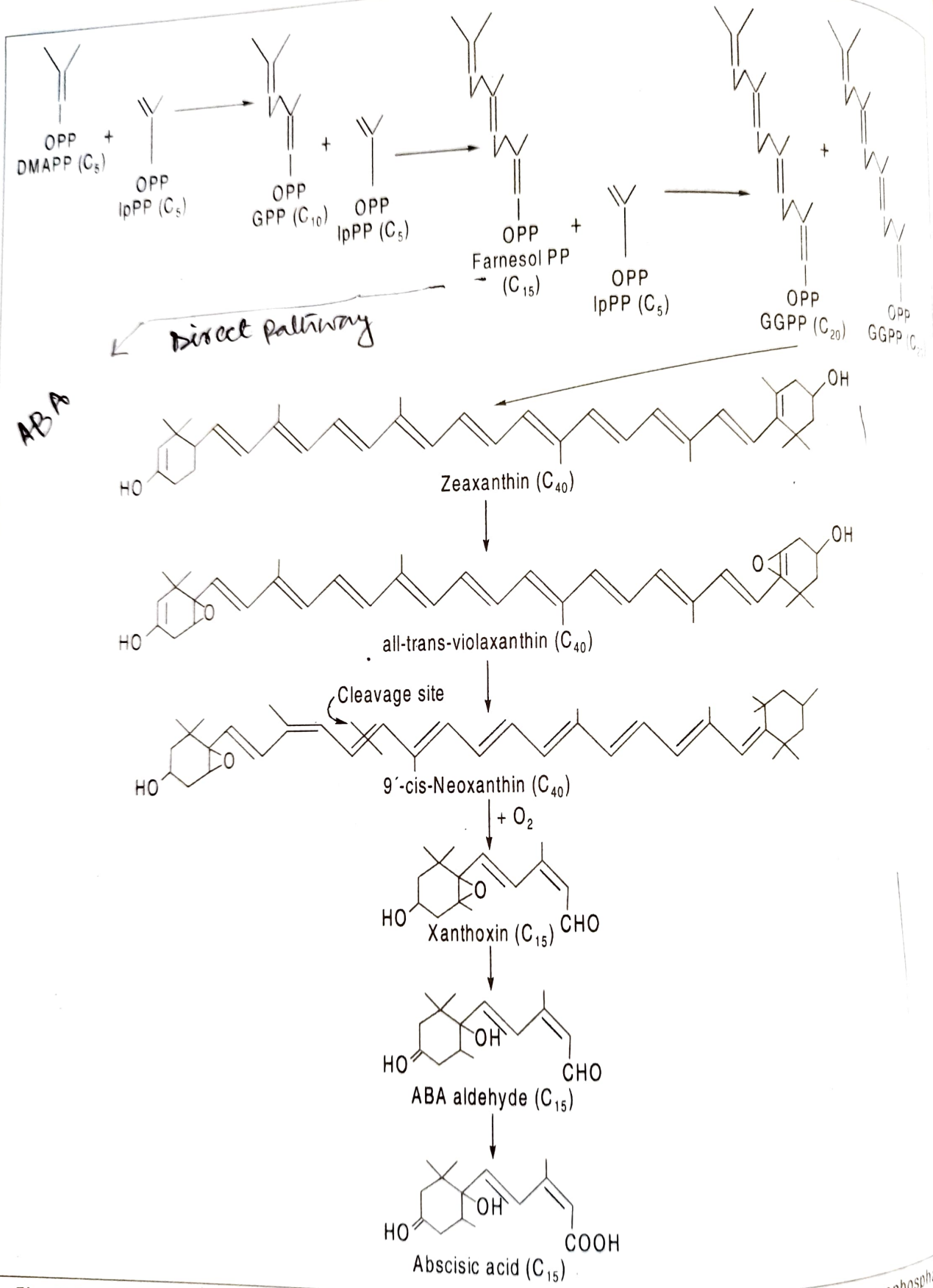


Fig. 13.21 : ABA biosynthesis in higher plants. ABA is synthesized via the terpenoid pathway. Isopentenyl pyrophosphate (IPP) serves as the precursor for the biosynthesis of the C40 xanthophyll zeaxanthin. Zeaxanthin is converted to violaxanthin then to neoxanthin, which oxidatively cleaved to form C15 xanthoxin which serves as the immediate precursor of ABA aldehyde. ABA aldehyde is then oxidized to form ABA

Direct or Isoprenoid Pathway

A direct pathway for ABA biosynthesis has been suggested which uses the initial steps of polymerization of isoprene units leading to the formation of a C_{15} precursor farnesyl pyrophosphate, a sesquiterpenoid molecule. The C_{15} ABA is directly synthesized from C_{15} farnesyl pyrophosphate. The direct pathway occurs mainly in the fungi.

ABA Inactivation

Free ABA can be inactivated by oxidation, which involves hydroxylation of one of the 6-dimethyl groups forming 6-hydroxymethyl ABA (HMABA). This unstable intermediate undergoes rearrangement to be converted to phaseic acid (PA). PA may be reduced to 4-dihydrophaseic acid (DPA). It has been reported that PA is either inactive or shows weak activity. The other product DPA is, however, without any activity.

Inactivation of free ABA can also occur by conjugation to a monosaccharide like glucose. ABA-glucosyl ester (ABA-GE) is an example of such a conjugate that is inactive as a hormone. In contrast to free ABA that is localized in cytosol, ABA-GE migrates to vacuoles and may function as a storage form of ABA.

esponses of Plants to Abscisic Acid

1. ***Growth Inhibition :*** ABA can antagonize the responses of plant materials to each of the growth-promoting hormones, viz., auxins, gibberellins and cytokinins. Although ABA is present even in rapidly growing organs, normal growth is attributed to its less than optimal concentrations to produce an inhibitory effect which is also thought to be masked by the presence of growth-promoting phytohormones. Presence of ABA in inhibited dormant lateral buds points to the role of ABA as a correlative inhibitor.

2. ***Growth Promotion :*** At very low concentration (viz., 10^{-9} M), ABA has been found to promote some growth processes like parthenocarpic seed development, rooting of cuttings, soybean callus growth in presence of kinetin and frond number of duckweed (*Lemna polyrhiza*).

** like cytokinins

3. ***Water Stress*** : There is an abrupt rise in ABA content in leaves of many plants as the water potential falls below (–) 1.0 MPa (megapascal) which is equivalent to (–) 10.0 bars. It has also been shown that exogenous ABA initiates stomatal closure when applied to intact leaves or isolated epidermal strips. These observations have led to the hypothesis that ABA is involved in regulating stomatal aperture in water-stressed plants. It is now clear that rises in endogenous levels of ABA in leaves can readily inhibit stomatal opening and such inhibition plays an important part in water conservation mechanism.

4. ***Drought Resistance and Desiccation Tolerance*** : Since endogenous ABA regulates stomatal opening in response to water stress, it plays a positive role in drought resistance. In drought-resistant cultivars of maize and sorghum, more ABA has been found to accumulate.

   In developing seeds, ABA promotes the synthesis of proteins involved in desiccation tolerance. During late stages of seed development, membranes and other cellular components are damaged by desiccation. At the same time, high levels of endogenous ABA promote an accumulation of specific mRNAs, which encode late-embryogenesis abundant (LEA) proteins involved in desiccation tolerance.

5. ***Root Geotropism*** : Experiments have indicated that root cap is the source of growth-inhibitory substances formed in response to gravity. These results have led to the hypothesis that when roots are maintainted for a horizontal position, i.e., subjected to gravitropic stimulus, ABA produced in the root cap moves basipetally to the growing part of the root and accumulates in the lower half of the root causing a positie geotropic response.

6. ***Seed Development and Germination*** : During the development of a variety of seeds, ABA levels rise sharply and then decline. The highest concentration of ABA in the embryo occurs in many seeds at a time when their dry weight is increasing rapidly.

   High ABA levels during late embryogenesis cause an accumulation of storage proteins in the developing seeds either by regulating the translocation of sugars and amino acids to the seeds or by promoting protein synthesis.

   The germination of most non-dormant seeds can be inhibited by exogenous ABA. Activities of various enzymes which rise during germination appear to be specifically inhibited by ABA. Likewise, ABA also inhibits the synthesis of α-amylase and other hydrolases in aleurone layers of cereal grains.

7. ***Dormancy*** : Attempts to determine the factors which induce bud dormancy in trees led to the discovery of ABA. Exogenous ABA has been shown to induce bud dormancy in woody plants where it proves to be an effective growth inhibitor. In dormant seeds it is present in high concentrations which declines when the seeds are given treatments which break dormancy. These observations have led to the hypothesis that ABA is involved in the induction and maintenance of dormancy.

   ABA at high levels can maintain the mature embryo in a dormant state until the environmental conditions are favourable for growth. It is well known that seed dormancy is an important factor in the adoption of plants to unfavourable conditions.

8. ***Fruit Growth and Flowering*** : Ripening fruits include the richest sources of ABA, yet the application of ABA to fruits has little effect on the process of ripening. Ripening grape berry is an exception where ABA has the capacity to hasten the ripening and colouring of the fruit.

ABA application in very low concentration has a slight promoting effect on flower growth. High ABA inhibits or delays flowering in a number of plants but this effect is probably a reflection of its inhibitory effect on growth.

Mode of Action

ETHYLENE

Discovery

In 1901, Neljubow first recognized that the injurious effects produced by illuminating gas on plants were due to ethylene. Later Knight and Crocker (1913), identified ethylene as the active constituent of tobacco smoke. It was not until 1934, however, that Gane could identify chemically that ethylene was a normal outcome of plant metabolism. The basic observation that ethylene accelerates the ripening of virtually all edible fruits led to the idea that the gas is a plant hormone (Burg, 1962). In the ensuing years, it was proved that besides fruit ripening, flower senescence and abscission together with many aspects of normal growth and development are influenced by ethylene. Ethylene is now considered to be one of the important plant growth regulators.

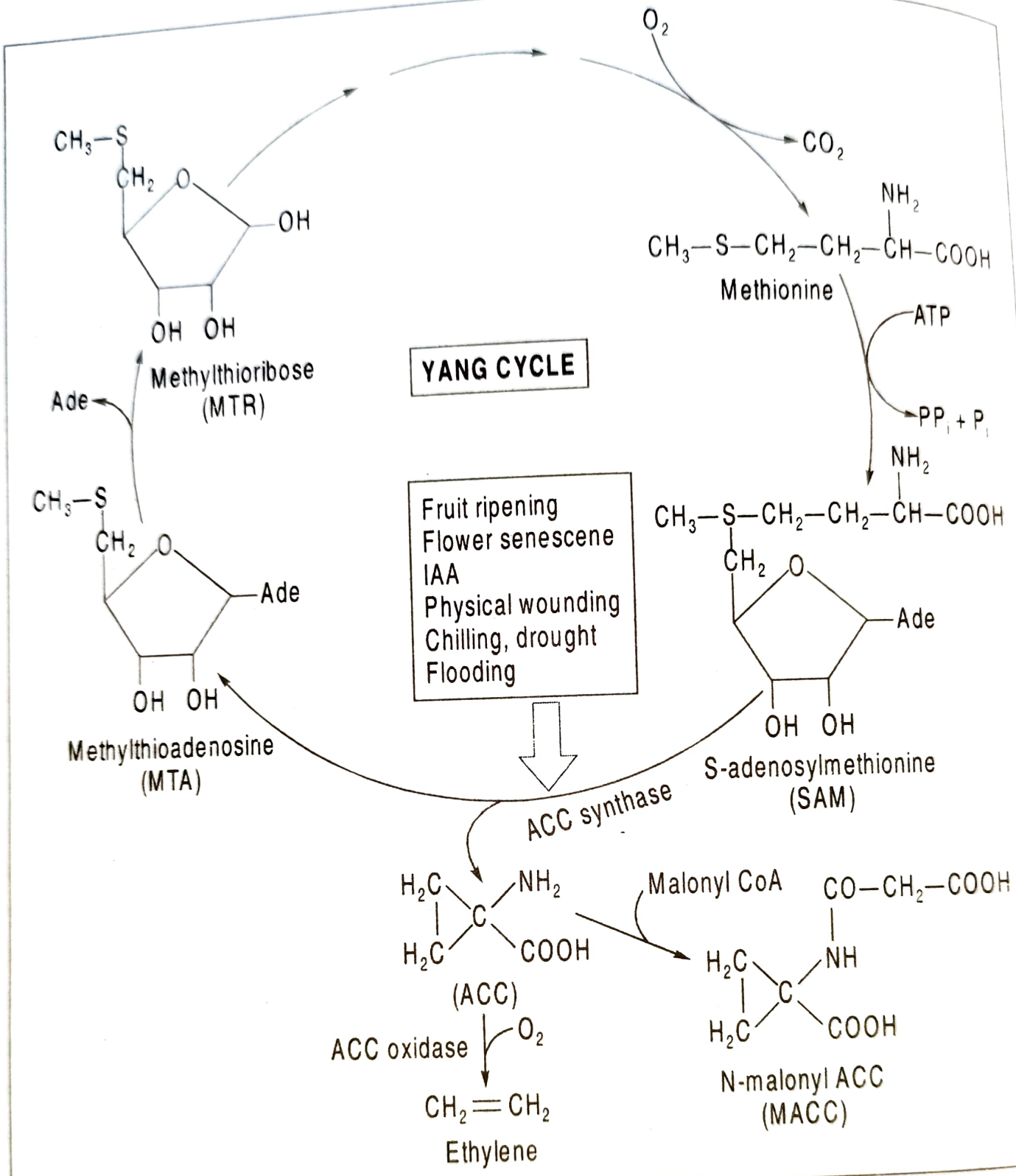


Fig. 13.24 : Methionine cycle (or Yang cycle) in relation to the biosynthesis of ethylene

Responses of Plants to Ethylene

1. ***Fruit Ripening*** : On the basis of the observation that ethylene can stimulate fruit ripening, it has gained recognition as a *ripening hormone*. The stimulation of ripening by ethylene seems to be restricted to *climacteric fruits* like bananas, tomatoes, melons and avocados in which ripening is associated with a sudden increase in respiration or ethylene production. In such fruits, a relationship between ethylene production and respiration has been established. During climacteric rise in respiration, there is a massive increase in CO_2 release followed by a decrease. It is also to be noted that a climacteric rise in ethylene production precedes the climacteric rise in CO_2 production, suggesting that ethylene is the hormone that triggers the ripening process. Ethylene appears to have no role in non-climacteric fruits like oranges, lemons and grapes which do not show sudden increase in respiration during ripening.

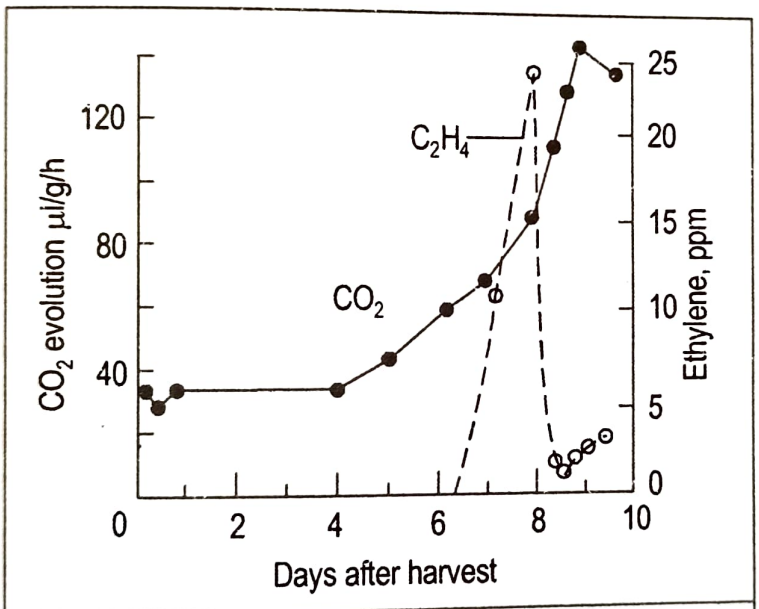


Fig. 13.25 : Relationship between ethylene production and respiration during climacteric rise in banana

2. ***Release of Dormancy :*** In a number of species ethylene application stimulates the germination of dormant seeds and thus may prolong seed longevity. Normal dormancy is probably related to less ethylene evolution. It has been shown that treatments that break dormancy increase ethylene evolution.

3. ***Growth and Differentiation of Shoot and Root :*** Ethylene produces spectacular effects on the growth and development of etiolated seedlings. The physiological action of ethylene causes the so-called triple response which involves a reduction in elongation, swelling of the hypocotyl and a change in the direction of growth. There is an increase in stem diameter which indicates that lateral growth as opposed to longitudinal growth is favoured by ethylene. It has been suggested that ethylene redirects the orientation of new cell-wall microfibrils from longitudinal to radial direction.

Ethylene exposure in plants causes downward growth of the petioles, termed epinasty which seems to result from a redistribution of auxin in response to ethylene treatment. Increased growth in the upper part of the petioles causes increased growth in that region resulting in a downward bending of the petiole.

Root growth is stimulated at low concentrations of ethylene and inhibited at higher concentrations. Root anatomy can also be affected by the endogenous ethylene content. The development of aerenchymatous roots in flooded maize plants is an example of this response (Jackson, 1982). This adaptive response to increased intracellular ethylene can also be induced by exogenous ethylene application. Another interesting response of root to ethylene is the enormous production of root hairs.

4. ***Responses to Physical Stimuli :*** While the ability of plants to respond to a number of physical stimuli like gravity and light has been correlated with changes in the distribution of auxin, ethylene has been shown to be an active agent in some cases (Biro and Jaffe, 1984). The response of some plants to tactile stimuli appears to be mediated through an increased production of ethylene. Root hairs are formed in many climbing vines to attach the plants to their support. In this case, ethylene formed as a result of gentle stimulation like localized contact is thought to stimulate root hair development and ethylene may be the signal to improve the support.

5. ***Adventitious Root Formation :*** Ethylene stimulates the formation of adventitious roots, leaves, stem and pre-existing roots. It has been demonstrated that high concentrations of auxin produce ethylene and auxin-induced rooting of cuttings appears to be due to increased ethylene production.

6. ***Abscission :*** Ethylene accelerates the abscission of plant organs. Research on the hormonal control of abscission has revealed that a gradient of auxin must be maintained from the leaf or fruit to the plant axis in order to delay or reduce abscission. This gradient is maintained by juvenility factors like auxin, cytokinin, light and good nutrition. When such auxin gradient is disturbed or reversed, the abscission zone becomes sensitive to ethylene (Reid, 1985). Once sensitized, the cells of the abscission zone respond to low concentration of ethylene by the production of cell-wall hydrolyzing enzymes followed by the shedding of the organ. When ABA causes abscission, it may do so either by stimulating ethylene formation or by interfering with auxin synthesis or its transport from the leaf.

7. ***Flower Induction and Opening :*** One of the commercially important effects of ethylene is the induction of flowering in pineapple, mango and apple. The opening of flowers may be effected in different ways by ethylene. For example, the opening of carnation buds is accelerated by ethylene, whereas it inhibits the opening of rose buds at similar concentrations. The mechanism by which ethylene modifies the flowering process is not clear.

8. ***Flower and Leaf Senescence :*** In many flowers, senescence is associated with a considerable amount of ethylene production. This intracellular ethylene-induced flower senescence can also be induced by treatment with exogenous ethylene or ACC and prevented by inhibitors of ethylene synthesis or action. In 1984, Reid and his associates used *Petunia hydrida* L. as an ideal experimental system for studying flower senescence wherein the colour changes from pink to purplish-blue during senescence. Like climacteric fruits, senescence of aged flowers can be caused by less ethylene because they become increasingly sensitive to ethylene as they age.

9. ***Pollination :*** Studies by Reid and others (1983) on the control of flower senescence by ethylene have revealed that pollination causes a very rapid increase in ethylene production first by the gynoecium, and then the petals. Since a rapid senescence of some flowers takes place immediately after pollination, it has been suggested that pollination acts as a stimulus the nature of which is like ethylene or ACC, the precursor of ethylene.

10. ***Wound Responses :*** When plants are wounded or exposed to stress conditions, ethylene production rapidly rises. In such cases, ethylene acts as a wound hormone which seems to reduce stress or to withstand infection. Ethylene can also lead to the production of phytoalexins in wounded plants which are compounds meant to overcome fungal infection (Yang and Pratt, 1978). A number of secretory processes like gum production and latex flow are stimulated by ethylene.

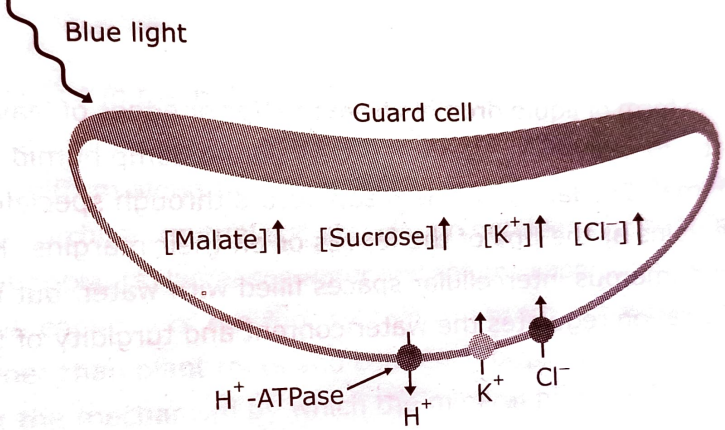


Figure 3.8 A blue light-stimulated stomatal opening.

The signal transduction cascade for the blue light response of guard cells comprises:

Blue-light perception by the guard cell chloroplast. ➡ Signal transduction and activation of ser/thr kinase. ➡ Activation of the H^+-ATPase present on guard cell membrane. Starch breakdown and malate synthesis. ➡ Membrane hyperpolarization and apoplast acidification which result in activation of K^+_{in} channels. ➡ Decrease in water potential of guard cell and subsequent increase in turgor pressure due to endosmosis. ➡ Opening of stomata.

Bioassay Methods

ABA now ranks in importance with auxins, gibberellins and cytokinins as a controlling factor in physiological processes. ABA can decrease, overcome, reverse, counteract, inhibit the responses of plant materials to each of the growth-promoting hormones. The choice of bioassay is dictated by the type of process believed to be influenced by the substance. The bioassay methods which have been extensively used in connection with ABA are :

1. ***Acceleration of Abscission in Excised Abscission Zones (Explants)*** : Addicott *et al.* (1964) who first detected ABA by its effect in promoting leaf abscission, used this action in a biological test. Test object was young cotton seedlings from which roots, stem tips and blades of cotyledons (seed leaves) were removed leaving an explant consisting of a section of stem to which the stumps of the petioles, i.e., leaf stalks were still attached. ABA as lanolin paste may be applied either to the proximal or to the distal end of the abscission zone. Time taken by the petiolar stump to abscise in response to the application of a definite concentration of ABA is taken as the standard.

2. ***Inhibition of Coleoptile Section Growth :*** Inhibitors have usually been detected by their ability to reduce the extension growth of oat or wheat coleoptiles. Since such growth is stimulated by auxins, a common practice has been to add a standard amount of IAA to the test solution and to observe the reduction by inhibitor of growth stimulated by auxin (Rothwell and Wain, 1964).

   Wheat seeds are thoroughly washed, soaked for 3-4 hours and then germinated in dark humid chamber for 72 hours. When the coleoptiles are about 3 cm in length, they are cut at the bases, placed vertically with the tips upward in specimen tubes containing distilled water. The tubes are then placed in a light-tight box, first incubated at 37°C for one hour and then kept in cold at 4°C for 24 hours. This pretreatment has been found to minimise the residual endogenous auxin content. After this, the sub-apical 6 mm lengths of coleoptiles 2 mm below the apices are cut with razor blades. Such coleoptile sections are placed in Petri dishes with ABA to be assayed, standard IAA, 3 per cent sucrose in phosphate buffer (0.006 M, pH 5.2). These are incubated at 25°C for 20 hours and the lengths measured accurately.

3. ***Retardation of Growth of Cultures of Small Aquatic Plants :*** This assay has been described by Van Overbeek *et al.* (1967). Cultures of *Lemna minor* (duckweed) are the sensitive materials to respond to ABA. Therefore, sterile cultures of *L. minor* grown under constant fluorescent light and constant temperature are used as bioassay materials. Growth is vegetative by budding and is determined as increase of fresh weight. ABA concentration as low as 1 part per billion (ppb) causes detectable inhibition.

4. ***Barley, Rice and Wheat Endosperm Bioassay :*** Paleg (1960) studied GA-induced production of α-amylase in barley and the subsequent release of reducing sugars into the medium. ABA inhibits the production of α-amylase which is triggered by GA in isolated aleurone layers or de-embryonated seeds (Chrispeels and Varner, 1966). Seeds are cut, embryo-containing portion discarded, placed in vials with test solutions (GA + ABA) and antibiotic Streptomycin sulphate to prevent bacterial growth. After incubation for a definite period, reducing sugars are assayed.

   Instead of measuring reducing sugar in the medium, α-amylase may be directly assayed. Since enzyme synthesis is a stage closer to the primary site of action of GA and ABA in this system than is sugar release, the authors regard this an advantage in itself.

5. ***Bioassay for Detecting Antitranspirant Activity :*** A greatly improved method has been described for the bioassay of ABA and other compounds that possess antitranspirant activity (Tucker and Mansfield, 1971; Ogunkanmi *et al.*, 1973). The stomatal responses are observed on pieces of isolated epidermis of *Commelina* sp. immersed in small volumes of solution containing the compounds to be assayed. It is possible to obtain linear responses to ABA concentrations over the range 10^{-7} to 10^{-10}M in citrate buffer at pH 5.5. The extent of stomatal closure in response to a definite concentration of ABA is the basis for this assay and it is possible to detect as little as 26 picogram (pg) of ABA present in the medium. Lack of interference from other regulators is a feature unique to this assay.

3.1.2 Chemical potential of water and water potential

The chemical potential of water is expressed in terms of free energy associated with one mole of water. The unit of chemical potential is the energy per mole of substance. In plant physiology, instead of chemical potential of water, we use a related parameter called *water potential*. Slatyer and Taylor introduced the concept of water potential, which is defined as the chemical potential of water divided by the partial molal volume of water (the volume of 1 mol of water). The word *potential* in the term *water potential* refers to water's potential energy. It is the measure of the free energy of water per unit volume. It is commonly expressed in terms of pressure units such as *Pascal*. By convention, the water potential of pure water at standard temperature and pressure is defined as 0 MPa. If some solute is dissolved in pure water, the solution has fewer free water and the concentration of water decreases, reducing its water potential. So, the water potential of an aqueous solution at atmospheric pressure will be less than zero. Soil water potential generally varies from −0.01 to −0.1 MPa. The water potential is used to describe the direction of the movement of water. Water molecules diffuse from the higher water potential to the lower water potential. For example, if a plant cell is immersed in a solution that has a higher water potential than the cell, water will move into the cell.

Components of water potential

The water potential (ψ, the Greek letter *psi*) of a solution is the sum of four component potentials: gravitational (ψ_g), matric (ψ_m), osmotic (ψ_s) and pressure (ψ_p).

$$\psi = \psi_s + \psi_p + \psi_g + \psi_m$$

Osmotic potential

Osmotic potential (also called *solute potential*) represents the effect of dissolved solutes on water potential. Pure water at atmospheric pressure has a solute potential of zero. Addition of solutes reduces the free energy of water. After addition, the solutes bind water molecules reducing the number of free water molecules and lowering the capacity of water to move and do work. Thus, adding solutes always lowers water potential. The solute potential depends on the concentration of dissolved solutes in the water and is independent of the specific nature of the solute.

Pressure potential

The pressure potential is the effect of hydrostatic pressure on the potential energy of a solution. If a pressure greater than atmospheric pressure is applied to pure water or a solution, its water potential increases. It can be positive or negative relative to the atmospheric pressure. Positive pressures raise the water potential; negative pressures reduce it. The positive value of pressure potential within cells is referred to as *turgor pressure*. The value of pressure potential is usually positive, but can also be negative as is the case in the xylem under large tension (negative hydrostatic pressure). The value of pressure potential for pure water in an open beaker is 0 MPa.

Gravitational potential

Gravitational potential depends on the position of water in a gravitational field. It is the effect of height of a system above sea level. Its value is 0 MPa at sea level. Gravitational potential depends on the height of water above sea level and the acceleration due to gravity. Thus, raising a system vertically 10 metres will increase its water potential energy by 0.1 MPa. At the cell level, value of gravitational potential is negligible compared to pressure potential and solute potential, so it is generally omitted.

Matric potential

Matric potential depends on the adsorptive forces that bind water to a dry matrix. It manifests the tenacity with which water is held by the dry matrix.

As the matric potential is very much limited in living cells and also at cell level, value of gravitational potential is negligible, the water potential expression simplifies to:

$$\psi = \psi_s + \psi_p$$

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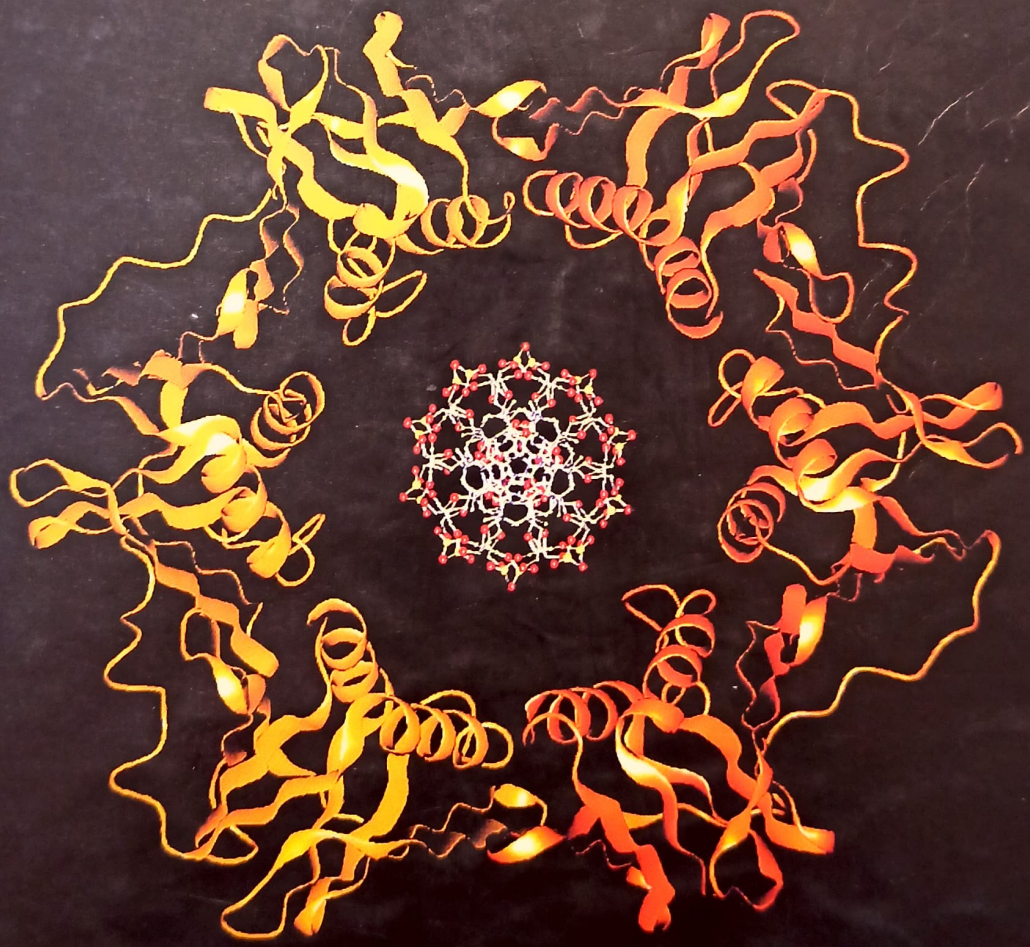
Life Sciences

Fundamentals and Practice

Part - II

Fourth edition



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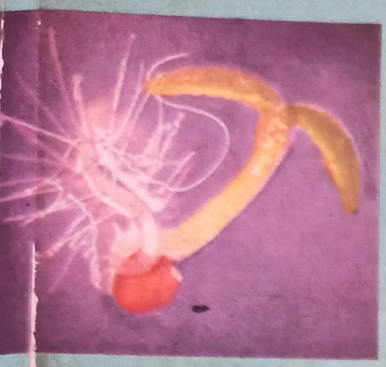

Plant Physiology

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