PLANT PHYSIOLOGY - II

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2019-2020

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Chapter 1

Plant Growth Substances/Hormones

plants possess a well-developed system of chemical messengers that induce (inhibit or promote) growth and developmental responses. These chemical messengers are termed "hormones".

Plant hormones - *What are they? They are defined as:*

* Small organic compounds;
* synthesized by the plant;
* active in low concentration (<10-6);
* promote or inhibit growth and developmental responses;
* often show a separation of the site of production and the site of action.

**Classes of Plant hormones** There are five major groups, based on chemical structure. With the exception of the latter two, each group represents a family of related compounds. These groups are divided into different classes:

**auxins; gibberellins; cytokinins; abscisic acid; ethylene.**

In addition, there are a variety of other plant "hormones" including the

**brassinosteroids, oligosaccharides, polyamines, jasmonic acid salicylic acid, systemin, putative hormones like those involved in flowering (florigen).**

**How do we know a substance is a hormone?**    
    In the past, physiologists simply applied the substance to a plant or excised part to see if it caused a response. If there was a response, then we assumed that the substance was a hormone involved in the response. However, responding to an exogenous application of a hormone necessarily mean that the substance has any endogenous (*in vivo*) action. Thus, we have become a little more picky and only accept that a substance is a hormone if:

* Exogenous application causes the response;
* Lowering endogenous levels prevents the response;
* Lowering endogenous levels followed by exogenous application restores the response;
* Endogenous levels should be related to the response (i.e., increase *before* the response occurs).

Mechanism of hormone actionHormones act on target tissues to activate a receptor. The general mechanism is:

hormone target tissue/cell receptor signal amplification response

Thus, for a response to occur:

* the hormone must be present in sufficient quantity;
* the target tissue must be sensitive (sensitized) to the hormone;
* the target tissue recognizes the hormone (i.e., there must be a receptor to which the hormone can bind);
* the binding of the hormone/receptor should initiate a change in the receptor (amplification).  Calcium is often involved and its interaction is mediated by the protein and
* the activated receptor initiates a physiological response

**Techniques to study hormones**

**A. Bioassays**  
    A bioassay examines the effect of a test substance on a plant tissue. To perform a hormone bioassay, a test plant is chosen that lacks the hormone for a response. Known amounts of hormone are added to the plant, the response is measured, and a  "standard curve" is produced.  To determine if a sample contains the hormone, the test plant is treated in a similar fashion.  If present the hormone can be quantified by comparing its response to the samples of known concentration. For example, a variety of rice (Tauginbozu) lacks GA and is often used in bioassay studies. After treatment with various concentrations of GA, leaf length vs. [GA] is plotted.

|  |  |
| --- | --- |
| Advantages | Disadvantages |
| simple & easy  inexpensive | sensitive to impurities  false positive tests can result  lower sensitivity than other methods |

**B**. **Immunological studies**    Antibodies are made against the plant hormones and then used as specific probes to localize and quantify. The antibodies are usually coupled to radioisotopes or fluorescent dyes to make it easier to trace.  This technique is very sensitivity and specific.

**C** **Instrumental Methods:** . GC-MS; HPLC; high specificity and sensitivity

**Methods for regulating endogenous levels**  
    The internal levels of plant hormones must be tightly controlled so that the response occurs only at the appropriate time. Regulation of hormonal action is achieved by:

* controlling the rate of hormone synthesis;
* forming conjugates, which are inactive storage forms where the hormone is covalently bonded to a sugar, amino acid or other molecule;
* enzyme degradation;
* transporting the hormone away/toward the site; and
* compartmentalizing the substance in an organelle such as the chloroplast.

# Plant Hormones - Auxin

**I. Introduction** Auxin is a general name for a group of hormones that are involved with growth responses (i.e., elongate cells, stimulate cell division in callus). Not surprisingly, the term "auxin" is derived from the Greek word "to increase or grow". This was the first group of plant hormones discovered.

**II. Chemistry/Structure**

**A. Naturally Occurring Auxins**  
    The most important auxin found in plants is indole-3-acetic acid (IAA). IAA is comprised of an indole ring linked to acetic acid. Other auxins that have been isolated from plants include indole ethanol, indole acetaldehyde, indole acetonitrile, phenylacetic acid (PAA), and 4-chloro-indoleacetic acid. These are probably converted to IAA *in vivo*.

**B. Synthetics with Auxin Activity**    
    There are a variety of substances that are not known to occur in plants that have auxin activity. These include indolebutyric acid (IBA); naphthalene acetic acid (NAA); 2,4- dichloro-phenoxyacetic acid (2,4-D), and 2,4,5-trichlorophenoxyacetic acid (2,4,5-T). The exact mechanism of action of these compounds is not known, but they may inhibit nucleic acid synthesis.

**C. Chemistry of action**    
    Although a variety of molecular structures have auxin activity (i.e., derivatives of indole, benzene and naphthalene), these molecules seem to share a few features that appear to be required for activity. Auxin activity seems to be correlated with a flat, hydrophobic ring system that separates negatively-charged (acidic, carboxyl group) side chain and positively charged region. There is a charge separation of about 0.5 nm. Note that the indole unit isn't required for activity, but a planar ring system is.

**D. Conjugated forms**    Auxins, as do other hormones, occur in a free or conjugated (bound to sugars, alcohols or other molecules) form. In fact, up to 98% of the auxin may be bound. Auxins may be conjugated with inositol, coenzyme A or glucosides (sugars).

E. Anti-auxins    
    PCIB (p-chlorophenoxyisobutryic acid) is a compound that competes with auxin for binding sites. However, it doesn't cause any growth response.

**III. Biosynthesis**

**A.** **Site**   
    Auxin is made in actively growing tissue which includes young leaves, fruits, and especially the shoot apex. Made in cytosol of cells

**B.** **Routes**    
    There are two major routes to the production of IAA.

1. Tryptophan-dependent Pathways.  The similarity of chemical structure of IAA and tryptophan suggested a connection between these.  Considerable research has shown that tryptophan, one of the protein amino acids, is a precursor of auxin biosynthesis. Overall, the conversion of tryptophan to IAA can occur by:

* a transamination followed by a decarboxylation;
* a decarboxylation followed by a transamination; or
* formation of IAA via an oxime (C=NOH) and nitrile (CN).

1. Tryptophan-independent Pathway - this route doesn't involve tryptophan directly as an intermediate to the formation of auxin.

**IV. Transport**

**A.** **Basipetal (or Polar Transport )**   
    Auxin is transported in a basipetal (towards the base, base-seeking) direction. In other words, auxin moves from the shoot tip towards the roots and from the root tip towards the shoot.

**Evidence** -

* Seedling vs. [auxin]and
* 14C labeled IAA applied to the top of a stem section is recovered only from the bottom of the stem section. When auxin is applied to the end of stem segments, it is only transported from the "top" of the section to the "bottom" as demonstrated in these data:

|  |  |  |
| --- | --- | --- |
|  | Upright | Upside down |
| 14C-IAA in donor block (dpm)C-IAA in donor block (dpm) | 10,000 | 10,000 |
| 14C-IAA in receiver block (dpm)C-IAA in receiver block (dpm) | 7,500 | 300 |

**B. Mechanism of polar transport**

* Transport Rate – IAA is not transported through the transpiration stream or phloem because the rate of movement is too slow. The rate of transport is consistent with diffusion.
* Tissue of transport - appears to occur in parenchyma cells associated with the vascular tissue.
* Model for polar transport: (a) Protons are moved out of the cell by a proton pump that requires ATP; (b) IAA is protonated at low pH; (c) IAA-H passes through the lipid membrane. It can enter or leave anywhere; (d) once inside the cell, the IAA-H ionizes in response to the higher pH; (e) IAA- requires a permease to pass through the membrane; (f) histochemical studies have shown that a permease is only located at the bottom of the cell - resulting in a net movement of auxin out of the bottom of the cells.
* Evidence for polar transport model: (a) transport is blocked by respiratory poisons (i.e., demonstrates the need for ATP and a proton pump); (b) unlabeled IAA competes with C14 labeled IAA for uptake in to the cells - this suggests that a carrier of some sort is required ; (c) fluorescein-labeled antibodies show that the permease is localized at bottom of cells; and (d) the transport of auxin is blocked by NPA (napthylthalamic acid), TIBA (tri-iodobenzoic acid) and flavanoids. These inhibitors appear to block the permease.
* Proton-Auxin CoTransport Mechanism - In addition to the passive pH-dependent mechanism described, there a membrane transport protein seems involved that cotransports protons and IAA into the cell. This tranport protein is localized in the upper side of the cells.

**V. Bioassays**  
   
    There are four classic bioassays for auxin. These tests, which are all based on the ability of auxin to stimulate shoot growth (or inhibit root growth) are:

**A. *Avena* coleoptile curvature test**     Pioneered by F. Went. The angle of curvature of a decapitated oat coleoptile is measured after placing an agar block containing auxin on one side. Then, angle of curvature vs. [IAA] is plotted.

**B. *Avena* coleoptile elongation**     The ratio of final length/original length for oat coleoptiles or pea stem sections is measured after the tissues are floated in solutions containing different concentrations of IAA. Elongation vs. [IAA] is plotted.

**C. Split pea curvature test**    A section of pea hypocotyl is obtained and split halfway down the middle. After incubating the sections in solutions of known IAA concentration, the angle of curvature is measured. Note that only the epidermal cells are responding to the treatment.

**D. Cress root inhibition**    This bioassay is based on the ability of auxin to stop root growth. A ratio of treatment/control growth is plotted vs. log [IAA].

**VI. Auxin responses**    IAA is involved in the following responses:

**A.  Cell elongation and wall relaxation**    Discussed earlier in the semester. Basis of several bioassays and the discovery of auxin. NOTE: Normally exogenous application of IAA has little effect on plants. **B.  Cell differentiation**    Promotes differentiation of vascular tissue (i.e., xylem & phloem)  
**C.  Ethylene production**    IAA apparently stimulates the production of ethylene  
**D.  Inhibition of root growth**    [IAA] > 10-6 M inhibit root elongation. However, very low (>10-8 M) favor root elongation.  
**E.  Stimulate root initiation (**lateral roots, adventitious roots)  
    Roots always form at the basal end of cutting **F.  Flowering**    Although most plants don’t initiate the production of flowers after auxin treatment, pineapple and its relatives (Bromeliaceae) do. Once flowers are initiated, in many species, IAA promotes the formation of female flowers, especially in cucurbits (gourd family). **H.  Apical dominance**    The apical meristem (apex) controls or dominates the development of the lateral buds. (PS - a bud is an embryonic shoot with immature leaves and stem). Apical dominance also occurs in roots. It is responsible for the Xmas tree shape of many trees and prevents an individual from becoming too top-heavy.

1. Function: (a) maintain upward growth; (b) maximize light absorption; (c) prevent top-heaviness; and (d) provide mechanism to replace the apical bud if it is removed by grazing or damage.
2. Thimann & Skoog (1934) - first suggested a correlation between [IAA] and apical dominance. This idea was further developed by Cholodny-Went who proposed that plant tissues responded to different concentrations of IAA (see figure). For example, hi [IAA] stimulates shoot growth but inhibits bud and roots. Thus, IAA is produced at the tip of the plant and is transported downward. The high concentrations near the apex inhibit lateral buds. As the concentration decreases it frees the buds from the inhibition and they develop.

**Evidence**:

1. every gardener knows that removing the apical meristem results in bushier plants. This is consistent with the Cholodny-Went hypothesis. If IAA is applied to a de-tipped plant it prevents lateral bud development
2. IAA stimulates the formation of ethylene which is known to inhibit lateral bud formation.
3. branching mutants of tomato don't export 14C-IAA

But

* 1. [IAA] in buds after the tip is removed should decrease, and they don't
  2. [IAA] that act to replace the tip are much higher than levels in the intact plant
  3. 14C-IAA doesn’t enter the lateral buds when applied at tip
  4. Some plants don’t respond to exogenous IAA
  5. **Nutrient diversion hypothesis**  
         There is little development of vascular tissue to the lateral buds. This has lead some to propose that the lateral buds fail to develop because they get no nutrients because the nutritional traffic is being diverted to the apex.   
       
     **Evidence:**

(a) application of cytokinins stimulates lateral bud development; cytokinins known to direct nutritional traffic, especially during senescence;

(b) tomato mutants that exhibit strong apical dominance have lower levels of cytokinin;

(c) there is a good correlation between cytokinin level and bud development.

* 1. **Bud Inhibition**  
         Another possible reason why buds fail to develop is because they have an inhibitor. It has been shown that ABA inhibits bud and seed development in many species. The buds of decapitated plants have a lower [ABA] than intact plants. High [ABA] in the bud are maintained by applying IAA to decapitated apex.

**I. Tropic responses** - such as gravitropism and phototropism

**J. Abscission**  
     Formation of the abscission layer is correlated with the [IAA] in leaf. As long as the [IAA] in the leaf is high relative to the stem, then the abscission layer doesn’t form. When the [IAA] in the leaf drops, which occurs normally during the growing season, it stimulates the formation of the abscission layer forms and the leaf falls.  The IAA presumably works by decreasing the sensitivity of the cells to ethylene which is the primary hormone involved in initiating leaf drop.

**VII. Regulating Endogenous Levels**  
    All of the general methods (i.e., degradation, conjugates, regulate rate of synthesis, sequestering in different regions) of regulation are probably operative. In particular, IAA is probably shuffled back and forth between the two main areas, or pools, where it is stored – the cytosol and chloroplast. IAA oxidase, a type of peroxidase, converts IAA to inactive metabolites. There are several degradative pathways.

# PLANT HORMONES - GIBBERELLINS

**Introduction**

* "foolish seedling" disease (bakanae) - rice plants tall, weak and spindly with little grain - was observed early this century by Japanese farmers.
* associated with the fungus, *Gibberella fujikuroi*.
* liquid from the culture medium applied to plants caused symptoms (Kurosawa, 1926).
* three gibberellins were isolated and identified from the medium & fungus
* independent confirmation in labs in Europe and US.
* gibberellins known from angiosperms, gymnosperms, ferns, mosses, algae, fungi and even a few bacteria.

**II. Chemistry**

* diterpenes (C20, though some have lost a carbon and are C19) based on isoprene skeleton
* characterized by having a complex system of 4-5 rings (ent-kaurene ring system) and a carboxyl (acidic) side chain
* more than 110 different gibberellins are known - abbreviated GA1...GAn.
* No more than 12 or so different gibberellins occur in any one species
* only a few (about 15) of the GA's have biological activity; the rest are likely breakdown products of, or precursors to, the active ones
* GA1 is the most active GA
* GA3 was the first one discovered and is readily available commercially (produced by *G. fujikuroi* cultures).
* C19 GA's are more active than C20
* GA's can occur in a free or conjugated form (i.e., glucosides)

**III. Biosynthesis**

A.  Site - young leaves, roots, and developing seeds (developing endosperm) and fruits.

B.  Pathway

* terpene pathway
* basic terpene building block is isoprene (isopentenylpryophosphate, IPP), a five carbon unit
* five major steps: (1) synthesis of IPP; (2) condensation of 4 isoprene units to form geranylgeranylpyrophosphate (GGPP); (3) GGPP cyclizes to form the kaurene ring system; (4) a methyl group of kaurene is oxidized to a carboxyl group to form GA12-aldehyde; (5) GA12-aldehyde is the precursor to the other GA's
* two routes to the production of IPP (isoprene): (1) Mevalonate-dependent pathway - occurs in cytosol; mevalonate is especially important for sterol biosynthesis; mevalonate is derived from acetyl CoA; and (2) Mevalonate independent pathway especially in plastids, important for carotenoid biosynthesis

C.  GA synthesis inhibitors

* Kaurene synthesis inhibitors - Phosphon D, CCC (cycocel), and Amo1618.
* Kaurene oxidation inhibitors - Ancymidol (A-rest) and paclobutural
* Another inhibitor is B-Nine (alar).

**IV. Bioassays/Analysis**

A.  Three common bioassays used for gibberellin are:

* Lettuce hypocotyl elongation
* Dwarf rice (var. Tanginbozu rice) leaf sheath elongation
* alpha-amylase production in barley

B.  Instrumental methods now the method of choice, especially GC-MS

**V. Transport**

* made in the tissue in which it is used
* transport occurs through xylem, phloem, or cell-to-cell.
* phloem seems to be most important transport route
* transport is not polar, as it is for auxin.
* not purely diffusion.

**VI. Disposal/Regulation of endogenous levels**

* Formation of conjugates
* Slow hydrolysis

**VII. Actions**

A. Promotes stem elongation  
    When applied to intact plants, GA usually causes an increase, unlike auxin. It overcomes dwarfism in mutants that have a mutation in the GA synthesis pathway. dwarf = short; wild type = tall; dwarf + GA = tall. Thus, GA application: (1) stimulates elongation; and (2) acts on intact plants.

GA stimulates stem elongation by:

1. stimulating cell division. Specifically, GA increases the transition from G1 S phase of the cell cycle;
2. increasing amylase (and other hydrolytic enzymes) production increases hydrolysis of starch  provides glucose and other sugars that: (a) lower water potential which provides driving force for water uptake; (b) provide energy through cell respiration; and (c) provide materials for building cell walls; and
3. increase cell wall plasticity (by a mechanism other than how auxin works).

B. Overcomes dormancy in seeds and buds  
    Treating dormant seeds with GA stimulates germination (see below)

C. Involved in parthenocarpic fruit development - remember [**lab**](http://employees.csbsju.edu/ssaupe/biol327/Lab/rcbr/rcbr-lab.htm)

D. Flowering  
    To summarize: LD = tall (bolts); SD = short; SD + GA = tall. Thus, GA stimulates bolting in Long Day plants and can substitute for long days or cold treatments that are necessary for flowering.

E. Mobilization of food reserves in grass seed germination  
    GA is produced by the scutellum (cotyledon) of the embryo → stimulates the production of amylase by the aleurone layer  amylase hydrolyzes starch to simple sugars → absorbed by scutellum and translocated to embryo for growth.

    The production of amylase occurs *de novo*. That is, gibberellin stimulates transcription. In short: GA → binds to membrane receptor → interacts with a protein complex (heterotrimeric G protein) that → activates a GA signaling intermediate → turns off a repressor → transcription of GA-MYB mRNA → translated in cytosol to make GA-MYB protein → returns to nucleus to bind to alpha-amylase gene promoter region → activates transcription of alpha-amylase mRNA → translated in ribosomes on RER → transported to golgi → secretory vesicles release alpha-amylase. This last step is apparently regulated by a calcium dependent mechanism that was also activated by the heterotrimeric G protein complex.

    Brewers take advantage of GA's ability to stimulate germination and enzymes which are important in the brewing process.

F. Juvenility  
    Plants exist in a juvenile and adult form. As in humans, the main difference is whether the plants are able to flower (reproduce). In some plants there is little morphological difference between juvenile and adult forms, whereas in others, the two forms are very distinct. For example, in beans, the first (juvenile) leaves are entire (heart-shaped) while the adult leaves are trifoliate. Lancewood is a New Zealand plant that has very distinctive juvenile and adult forms. In fact, they are so different that botanists originally mistook the two forms for different species. The juvenile form is unbranched with long (*ca*. 12 in) linear, drooping leaves that look a little like the ribs of a folded umbrella. When the plant reaches about 15 foot it switches to the adult form which is branched and has smaller, ovate leaves. It has been suggested that this is a modification to prevent predation by moa, a large, formerly common but now extinct bird.

    Gibberellin stimulates the transition between the juvenile and adult forms. In ivy, the adult form (unlobed leaves, shorter internodes) is converted to the juvenile form (lobed leaves, longer internodes) by GA treatment.

G. Sex expression  
    In plants with separate male and female flowers, GA application can determine sex. For example, in cucumber, hemp and spinach, GA treatment increases the proportion of male flowers. In maize, GA treatment causes female flower development.

**IX. Commercial Applications**

* increase size of grapes (spray at time of blooming and fruit set stage)
* increase distance between grapes in a cluster to minimize fungi/disease
* Breweries - increase starch digestion for malting process
* Delay senescence - spray on fruit like oranges
* celery stalk elongation (but must use carefully because of increased storage problems)
* sugar cane increased growth and yields
* Minimize lodging

# Plant Hormones - Cytokinins

**I. General**

* Called "cytokinins" because they stimulate cell division (*i.e.*, cytokinesis)
* Haberlandt (1913) noted that non-dividing potato parenchyma cells would revert to actively dividing ones in the presence of phloem sap.  This observation suggested a soluble material was responsible for cell division.
* Folke Skoog (1940's) and colleagues at Univ. of Wisconsin found that cultured tobacco pith tissue explants would proliferate only if they were supplemented with various substances such as autoclaved herring sperm or coconut milk.
* Miller (1956) identified the first cytokinin, called kinetin, in the herring sperm.
* Cytokinins occur in most plants including mosses, ferns, conifers, algae and diatoms

**II. Chemistry**

A. General

* adenine derivatives (amino purines)
* occur as: (a) the free nitrogenous base; (b) a nucleoside (base + ribose); (c) a nucleotide (base + ribose + phosphate); or (d) glycosides
* The free base is the active form.
* approximately 40 different structures known.
* Zeatin (Z), which was first isolated from maize (*Zea mays*) is the most common cytokinin.
* Other naturally occurring cytokinins include, dihydrozeatin (DHZ) and isopentenyladenosine (IPA).

B. Synthetic cytokinins

* kinetin (*as above*) – probably byproduct of zeatin degradation
* there are several other substances with cytokinin activity such as benzyl adenine (benzylaminopurine; BA).

C. Cytokinins and nucleic acids

* can occur as a modified base in tRNA, but the bases exist in the *cis* form, rather than the typical *trans* form. These modified bases that are found in all organisms from bacteria to plants to humans.
* The function of the tRNA cytokinins is not clear, but after hydrolysis of the tRNA the products can act as a cytokinin. The importance of the tRNA derived cytokinins in overall growth and development is not clear, either.
* Interestingly plants have different sets of tRNA’s with different cytokinins that participate in protein synthesis in the cytoplasm and the plastids.

**III. Synthesis**

* Site:  synthesized primarily in the meristematic region of the roots.  This is known in part because roots can be cultured (grown in artificial medium in a flask) without added cytokinin, but stem cells cannot.
* Cytokinins are also produced in developing embryos and crown gall tissues
* first major precursor to the cytokinin is AMP (adenosine monophosphate)
* side chains of the cytokinins are made by the terpene pathway (IPP – isoprene) and added to the AMP by cytokinin synthase
* there is some speculation that surface and endophytic bacteria (*i.e.*, *Methylobacterium*) may be the actual source of plant cytokinins.  Rationale:  (1) haven't isolated some of the putative genes for cytokinin synthesis; (2) remove bacteria show impaired cytokinin production.
* tRNA nucleotides are modified to cytokinins after the tRNA is transcribed (post-transcriptional processing)

**IV. Transport**

* via xylem (transpiration stream)
* in peas, a signal from the leaves may signal/regulate transport of cytokinins from the roots
* zeatin ribosides are the main transport form; converted to the free base or glucosides in the leaves
* some cytokinin also moves in the phloem.

**V. Bioassays/Analysis**

A. Bioassay

1. Callus culture cell proliferation - not used too much because it takes too long
2. Expansion of radish or cocklebur cotyledons
3. Inhibition of chlorophyll loss by detached oat leaves during senescence

B. Methods of Analysis – liquid chromatography, mass spectroscopy; radioimmunoassays

**VI. Disposal**

* forms conjugates with glucosides. major storage form of cytokinin, inactive
* cytokinin oxidase may be an important route of disposal, too.

**VII. Actions**

A. Control morphogenesis

* in plant tissue cultures, cytokinin is required for the growth of a callus (an undifferentiated, tumor-like mass of cells):

|  |  |  |
| --- | --- | --- |
| **callus + auxin + no cytokinin** | **→** | **little growth of callus** |
| **callus + auxin + cytokinin** | **→** | **callus grows well, undifferentiated** |

* ratio of cytokinin and auxin are important in determining the fate of the callus:

|  |  |  |
| --- | --- | --- |
| **callus + low [cytokinin/auxin]** | **→** | **callus grows well, forms roots** |
| **callus + high [cytokinin/auxin]** | **→** | **callus grows well, forms meristem & shoots** |

* some tissues become habituated during repeated cell culture – loose the requirement for cytokinin in the growth medium

B. Crown Gall

* tumor-like mass of undifferentiated cells that typically occurs near the crown (junction of root and stem) of the plant
* caused by the bacterium *Agrobacterium tumefaciens*
* carries a plasmid (Ti plasmid; a plasmid is a small loop of non-chromosomal DNA) with loci/genes for auxin production (tms), zeatin production (tmr) and opines (are nitrogen-containing molecules that provide food for the bacteria).
* upon infection, the plasmid is incorporated into the plant cell genome which begins to overproduce auxin and cytokinin
* stem forms an undifferentiated tumor (crown gall)
* as predicted, if the tms genes (auxin production) are deleted from the plasmid, which would increase the cytokinin/auxin ratio, the resultant crown gall is "shooty". If the tmr genes are deleted the gall is "rooty".

C. Regulates the cell cycle/cell division (hence, the name "cytokinins) – especially by controlling the transition from G mitosis. This effect is moderated by cyclin-dependent protein kinases (CDK's) and their subunits, cyclins.

D. Delay senescence

* senescence is the programmed aging process that occurs in plants (and other organisms for that matter).
* loss of chlorophyll, RNA, protein and lipids.
* cytokinin application to an intact leaf markedly reduces the extent and rate of chlorophyll and protein degradation and leaf drop
* correlation between cytokinin levels and senescence. For example, as detached leaves senesce the cytokinin levels drop. And, when these leaves are treated with auxin to stimulate rooting, when roots form the senescence process stops and cytokinin levels rise.
* Tobacco plants + senescence promoter sequence + ipt gene (cytokinin gene)  causes gene to become active on senescence  no senescence

The exact mechanism by which this occurs is unclear but likely involves the ability of cytokinins to mobilize nutrients. Application of cytokinin to a leaf will cause it to act as a sink and nutrients will be directed towards it.

E. Greening  
    Promotes the light-induced formation of chlorophyll and conversion of etioplasts to chloroplasts (greening process).

F. Promote lateral bud development  
    Cytokinin application to dormant buds will cause them to develop. A witches’ broom is caused by a pathogen such as the bacterium *Corynebacterium fascians* (or *A. tumefaciens*) that produces cytokinin which, in turn, causes stimulates lateral bud development (branching). These results suggest that apical dominance may be related to cytokinin, too.

    For example, when tobacco cells are infected with the Ti-plasmid that has been modified to possess the heat shock promoter, a heat treatment stimulates the cells to produce increased amounts of cytokinin. These plants exhibit less apical dominance and remain green longer than non-heat treated controls. Thus, these results support the conclusion that senescence and apical dominance are related to cytokinin levels.

G. Promote cell expansion  
     Cytokinins stimulate the expansion of cotyledons. This is the basis for the classical bioassay. The mechanism is associated with increased plasticity of the cell wall, not associated with acidification.

**VIIII. Mechanism of action** - Specific binding sites (receptor) for cytokinin are known. These may be ribosomal proteins. Thus, it is not too surprising that cytokinins have been shown to regulate protein synthesis.

# Plant Hormone - Ethylene

**I. General**

* the Chinese may have been the first to observe the effects of ethylene when they noted that burning incense increased fruit ripening
* in 1864 leaks in gas lights in street lamps were reported to stunt plant growth and defoliate trees
* in 1901, D. Neljubow realized that his dark-grown pea seedlings were short, fat and negatively gravitropic (the triple response) because of a component in "laboratory air" which he subsequently identified as ethylene
* Cousins (1910) first reported that ethylene occurred in plants.

**II. Chemistry**

* single compound (like ABA) and is not a family of related ones (*i.e*., gibberellins)
* CH2=CH2
* ethylene (MW 28) is similar in size/shape as water
* a gaseous plant hormone

**III. Biosynthesis**

A. **General:**

* made by most plants including angiosperms, gymnosperms, ferns, mosses, liverworts
* also synthesized by fungi and bacteria
* made by all parts of the plant
* meristematic regions (shoot apex) and senescing tissues are rich sources
* nodes make more ethylene than internodes
* ethylene production is stimulated by physiological stresses including wounding, anaerobic conditions, flooding, chilling, disease and drought.
* during the climacteric which is the sudden surge of respiratory activity that occurs at the peak of ripening in many fruits - lots of ethylene is made

B. **Pathway of synthesis**

* the first precursor is methionine (one of the protein amino acids)
* methionine + ATP   S-adenosyl-methionine (SAM)   ACC synthase   amino cyclopropane carboxylic acid (ACC)   ACC oxidase   CH2=CH2 + HCN (hydrogen cyanide) + CO2.   To summarize the highlights:

1. ATP reacts with methionine to form SAM
2. SAM is essentially a carrier form of methionine (it is involved in other reactions in the cell)
3. ACC synthase is the most crucial enzyme in the pathway. It is the rate limiting step and induced by: (a) fruit ripening; (b) flower senescence; (c) in response to IAA; (d) under wounding; (e) chilling injury; (f) drought; (g) flooding; (h) in response to ethylene ("one bad apple spoils the whole bunch"). ACC synthase is cytosolic and coded by a multi-gene family.
4. methionine is re-claimed via the Yang cycle.
5. ACC oxidase was formerly called "ethylene forming enzyme, abbreviated EFE."   It requires Fe2+and ascorbate for activity which explains why it took awhile to characterize this enzyme.  It is also the product of a multigene family.
6. One of the products of ACC oxidase activity is HCN which explains why most plants have enzyme systems for detoxifying/metabolizing cyanide. ACC oxidase is inhibited by anaerobic conditions and cobalt ions but stimulated by ripening.

**IV. Inhibitors**

* silver ions (Ag+), CO2 and KMnO4 inhibit ethylene actions. These bind to ethylene receptors or otherwise interfere with the mechanism of ethylene action.
* Aminovinylglycine (AVG) and aminooxyacetic acid (AOA) block the action of ACC synthase.  Since these compounds are knows to block pyridoxal enzymes, it suggested that they participate in the process.

**V. Disposal**

* probably not a concern since it is a gas
* in addition, malonate will bind to ACC forming N-malonyl ACC.  Unlike most conjugates that can be hydrolyzed to produce the original compound, this one is NOT converted back to ethylene.
* a conjugate with glutamic acid (GACC) may be an important regulator of ethylene levels

**VI.Actions**

A. Fruit ripening  
    Ethylene triggers fruit ripening (*i.e*., climacteric) - Flavr-Savr tomato.

B. Abscission  
    This is the shedding of plant parts. 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, etc.

C. Epinasty  
    Downward bending of leaves - common response to flooding or waterlogged soils.

D. Triple Response  
    Pea seedlings treated with ethylene are short (inhibits internode elongation), fat (increase stem thickness) and "stupid" (horizontal growth, no positive gravitropism). Further, they show little leaf expansion and possess an apical hook.

E. Thigmomorphogenesis  
    The change in growth form in response to a mechanical stimulation such as touch.

F. Stimulates germination in cereals, peanuts; promotes sprouting in potato tubers and other bulbs.

G. Flower senescence  
    Stimulated by ethylene. Adding AVG to carnation can keep them fresh for weeks.

**VII. Commercial applications**  
    Ethrel (Ethephon) liquid sprayed onto plants. It contains a dilute solution of 2-chloroethylphosphonic acid that breaks down to give off ethylene. Among others things, it is used to synchronize flowering and fruit set in pineapples. Commercial fruits are usually stored in low O2 to inhibit ethylene biosynthesis or under high CO2 to prevent ethylene action as a ripening promoter.

# Plant Hormone -Abscisic Acid (ABA)

**I. General**

* Bennet-Clark and Kefford (1953) described the presence of an inhibitor of coleoptile elongation in oats
* about 10 years later, Addicott *et al.* found a substance that stimulated abscission of fruits in cotton and they named it abscisin II
* about the same time, Wareing found a substance in sycamore leaves that promoted dormancy in buds and called it dormin
* it was soon clear that these were the same substance
* a conference in 1967 straightened out the name and it was decided to call the hormone abscisic acid (ABA).

**II. Chemistry**

* a single structure, not a family of related structures like the gibberellins
* sesquiterpene (*i.e*., terpenoid) - C15 - made from 3 isoprene units
* occurs as *cis* form; S-enantiomer is natural and active form
* found in all green plants, also in some mosses, algae, and fungi
* related to lunularic acid which is found in liverworts.

**III. Biosynthesis**

* plastids
* most tissues, especially leaves and seeds
* terpene pathway
* IPP is the first intermediate; not derived from mevalonate (mevalonate-independent); comes from intermediates of glycolysis
* ABA derived from the breakdown of carotenoids.  Evidence:  maize mutants blocked in carotene synthesis → low levels of ABA → vivipary (see below)
* Pathway:  IPP → farnesyl pyrophosphate → carotenoids (C40; violaxanthin) → xanthoxin → ABA

**IV. Bioassays/Analysis**

A. Bioassays there are several including:

* inhibition of seed germination
* inhibition of GA induced alpha-amylase production

B. Analysis Gas chromatography, HPLC, and immunoassay

**V. Disposal/Regulation**

* rapid changes in endogenous levels (up to 100x within a few days)
* ABA levels can be regulated by: (a) degradation; (b) compartmentalization; (c) transport; (d) conjugation to a sugar or other molecule; and (e) conversion (oxidation) into phaseic acid and dihydrophaseic acid.

**VI. Transport** - xylem and phloem (greater amounts)

**VII. Actions**

* A. Growth Inhibitor  
      Widespread growth inhibitor; often antagonistic of GA actions
* B. Maintains or "seals in" bud and seed dormancy (i.e., prevents germination)  
      In fact, ABA is made during the terminal stages of embryo development. Among it's roles in seed dormancy is to: (1) provide desiccation tolerance of the embryo by promoting synthesis of proteins involved in the process; and (b) promote accumulation of seed storage proteins.
* C. Prevents vivipary  
      Development of the embryo without a dormant period. Some evidence: viviparous mutants have reduced [ABA]; and fluridone stimulates treatment stimulates vivipary (fluridone is an inhibitor of carotenoid biosynthesis that blocks ABA production)
* D. Inhibits auxin induced growth (seems to block the H+ pump)
* E. Stomatal closure under water stress (remember our unit on gas exchange?)
* F. Abscission & senescence  
      Involved, though perhaps only a minor role **VIII. Mechanism of action**
  1. Effects on plasma membrane
  2. Inhibits protein synthesis
  3. Regulation of genes (transcription)

# Brassinosteroids

Brassinosteroids (polyhydroxysteroids) or Brassins act like auxins.

Brassinosteroids are steroid hormones that influence many of the same developmental systems as auxins. These compounds were first discovered in rapeseed plant (Brassica napus) pollen. The most known example of brassinosteroids is brassinolide.

# Discovery

In the 1960s, studies of Brassica napus (rape seed) pollen led to the discovery of a compound that could induce elongation of bean hypocotyls (independent of GA responses). The yield of brassinosteriods from 230 kg of Brassica napus pollen was only 10 mg. In 1979 it was identified as brassinolide - a steroid compound (steroids are triterpenoids) Another brassinosteroid was discovered in 1982 - castasterone - isolated from insect galls on chest nut About 70 (Bajguz, 2007) types of BRs have been found in algae, ferns, gymnosperms, and angiosperms, but not bacteria They are defined by their structure, rather than biological activity. Brassinolide is the most active and common BR compound

# Types of Brassinosteroids

Approximately 70 naturally occurring polyhydroxy steroids known as brassinosteroids (BRs). They are named after the first one identified, brassinolide, which was isolated from rape in 1979. They appear to be widely distributed in the plant kingdom

## Main two types are

### • Brassinolide

### • Castasterone

# Transport

Experiments have shown that long distance transport is possible and that flow is in an acropetal direction (from root to leaves), but it is not known if this movement is biologically relevant.

# Bioassays for BRs

## Rice leaf lamina inclination assay:

BR causes swelling of cells on one side of the joint between the leaf blade and the sheath - causing quantitative amount of bending The rice leaf lamina inclination bioassay is dependent on BR- induced cell expansion Lamina inclination resembles the epinasty phenomenon caused by ethylene In response to BR, the cells on the adaxial (upper) surface of the leaf near the joint region expand more than the cells on the abaxial (lower) surface, causing the vertically oriented leaf to bend outward. An increase in cell wall loosening is required for BL-induced cell expansion on the adaxial side of the leaf

# Location, Characteristics

Release in mature cells (and less so in immature cells) when they have less than enough sugar and oxygen to support both themselves and any dependent cell. Release in response to root environmental, pest, or disease stress May work in concert with gibberellin or be part of the hormone effect cascade. Is visually similar to the animal hormone cortisol and may function in a similar manner, raising phloem sugar levels to deal with short-term environmental stress just like cortisone

Signaling of BRs Brassinosteroids are recognized at the cell membrane, although they are membrane- soluble. The domain structure of the BR receptor, BRI1 (Brassinosteroid insensitive 1). BRI1 is localized on the plasma membrane. The extracellular region consists of a stretch of leucine-rich repeat sequences (LRRs) containing an island domain that functions as the brassinolide (BL) binding site. The intracellular portion contains a juxtamembrane domain, a kinase domain, and the C-terminal tail.

# Physiological effects of Brassinosteroids

* Elongation, gene expression
* Shoot elongation promoter & root growth inhibitor
* Promote ethylene biosynthesis
* Promote epinasty
* Decrease fruit abortion and fruit fall
* Promote seed germination
* Increase DNA, RNA polymerase activities
* Increase yield of vegetative crops like lettuce, bean and pepper
* Increase pollen tube growth
* Enhance H+-pump activity
* Promote male sterility
* Promote senescence
* Increase tolerance against abiotic stress
  + Chilling
  + Disease
  + Herbicide
  + Salt stress

# BRs and Cell Wall

Treatment with BRs increases ATPase activity leading to proton extrusion and cell wall relaxation BRs up-regulate expression of many genes, which encode xyloglucan endotrans-glycosylases/hydrolases (XTHs or XETs) and thus is involved in cell wall biosynthesis and modification. BRs affect turgor-driven cell expansion by affecting the activity of aquaporins (water channels) that help the plant cells to osmoregulate. BL may also affect cell shape and expansion via regulation of microtubule dynamics.BRs promotes both cell expansion and cell division in shoots. The growth-promoting effects of BRs are reflected in acceleration of both cell elongation and cell division

The stimulatory effect of BRs on growth is most pronounced in young growing shoot tissues. The kinetics of cell expansion in response to nanomolar concentrations of BL differs from that of auxin. In addition to cell elongation, BRs also stimulate cell proliferation

BRs are required for normal root elongation However, like auxin, exogenously applied BRs may have positive or negative effects on root growth, depending on the concentration When applied exogenously to BR-deficient mutants, BR promotes root growth at Low concentrations and inhibits root growth at high concentrations

The effects of BR on root growth are independent of both auxin and gibberellin action. At low concentrations, BRs can also induce the formation of lateral roots. BR treatment promotes acropetal auxin transport, which is required for the development of lateral roots

BRs promote xylem differentiation during vascular development. BRs play an important role in vascular development, both promoting xylem and suppressing phloem differentiation.BR is required for a normal vascular development.

The left panel insert shows a schematic representation of the Arabidopsis vascular system at the basal part of the inflorescence stem of a mature plant. The procambial cells (yellow) give rise to phloem tissue (red) to the outside and xylem tissue (blue) to the inside. The black box encloses a single vascular bundle.

The vascular bundle of the BR-deficient dct2 mutant (right) has a lower xylem-to-phloem ratio than that of the wild type (left). Leaf mesophyll cell before (left) and after (right) differentiation into a tracheary element

BRs are required for the growth of pollen tubes Pollen is a rich source of BRs, and are important for male fertility. BR has been shown to promote the growth of the pollen tube from the stigma, through the style, to the embryo sac. BRs and germination ν Seed germination is another process where the interaction of BL with other plant hormones has been described In Arabidopsis the germination of severe GA biosynthetic mutants can be partially rescued by application of GA or 24-epibrassinolide. Interactions of BR with other plant hormones. Recently, a promoter element was identified that is responsive to both auxin and BR.There are also reports that the synergism observed with BL and GA might be related to the fact that both hormones increase expression of MERI5, a XET thought to be involved in loosening of the cell wall

A possible interaction of abscisic acid (ABA) and BL in cell elongation was seen in experiments with Arabidopsis ν How these hormones interact to create such a response remains unknown.

# BRs and stomatal regulations

ABA promotion of stomatal closure in epidermal peel assays is enhanced in the BR-deficient mutants

# BRs and plant stress responses

There is a causal linkage between application of BRs and enhanced tolerance to various environmental stresses, but the mechanisms that connect BR perception with a given physiological response are largely unknown. The potential role of BRs in pathogen defense has also been examined. An important connection between BRs and wound signaling has been found in tomato

# Applications of Brassinosteroids Insect control?

Interfere with ecdysteroids (molting hormones) in insects. The process of shedding and replacing the rigid exoskeleton is known as molting

# Polyamines

A polyamine is an organic compound having two or more primary amino groups–NH. Polyamines concentration correlate with cell division frequency. They stimulate many reactions involved in the synthesis of DNA, RNA and proteins. Polyamines are essential for all living organisms and without the ability to synthesize polyamines, living cells will not survive

## Role of Polyamines

In plants polyamines elicit diverse physiological responses including: –

* Cell division and root initiation
* Tuber formation
* Embryogenesis
* Flower development
* Fruit ripening

# Jasmonic acid

Jasmonic acid (JA) was isolated from cultured filtrates of a fungus as a plant growth inhibitor. Jasmonic acid (JA) is derived from the fatty acid linolenic acid. Methyl jasmonate and cis-jasmone are well known in the perfume industry as fragrant components of the essential oils of jasmine.

Jasmonic acid shows stimulatory effect on the development of isolated garlic buds, after two weeks of culture

## Roles of Jasmonic acid

* The major function of JA and its various metabolites is regulating plant responses to abiotic and biotic stresses as well as plant growth and development.
* Regulated plant growth and development processes include growth inhibition, senescence, tendril coiling, flower development and leaf abscission.
* JA is also responsible for tuber formation in potatoes, yams, and onions.
* It has an important role in response to wounding of plants and systemic acquired resistance.
* When plants are attacked by insects, they respond by releasing JA, which activates the expression of protease inhibitors, among many other anti-herbivore defense compounds.
* These protease inhibitors prevent proteolytic activity of the insects' digestive proteases or "salivary proteins",thereby stopping them from acquiring the needed nitrogen in the protein for their own growth.

# Salicylic acid

* + Salicylic acid (SA) is a phenolic phytohormone.
  + It is found in plants with roles in plant growth and development, photosynthesis, transpiration, ion uptake and transport.
  + SA is involved in endogenous signaling, mediating in plant defense against pathogens.
  + It plays a role in the resistance to pathogens by inducing the production of pathogenesis-related proteins.
  + It is involved in the systemic acquired resistance (SAR) in which a pathogenic attack on one part of the plant induces resistance in other parts.
  + The signal can also move to nearby plants by salicylic acid being converted to the volatile ester, methyl salicylate.
  + Tissue culture uses are not well documented

## Medicinal and cosmetic uses

* + Salicylic acid is known for its ability to ease aches and pains and reduce fevers.
  + Methyl salicylate is used as to soothe joint and muscle pain.
  + Choline salicylate is used topically to relieve the pain of mouth ulcers.
  + Salicylic acid is a key ingredient in many skin-care products for the treatment of dermatitis, acne, calluses and warts.
  + Aspirin (acetylsalicylic acid),  is used to reduce fever and relieve mild to moderate pain

Chapter 2

Water Relations

# The soil-plant-atmosphere continuum (SPAC)

Is the pathway for water moving from [soil](https://en.wikipedia.org/wiki/Soil) through plants to the [atmosphere](https://en.wikipedia.org/wiki/Atmosphere). Continuum in the description highlights the continuous nature of water connection through the pathway. The low [water potential](https://en.wikipedia.org/wiki/Water_potential) of the atmosphere, and relatively higher (i.e. less negative) water potential inside leaves, leads to a diffusion gradient across the [stomatal](https://en.wikipedia.org/wiki/Stoma) pores of leaves, drawing water out of the leaves as vapour. As water vapour [transpires](https://en.wikipedia.org/wiki/Transpiration) out of the leaf, further water molecules evaporate off the surface of [mesophyll](https://en.wikipedia.org/wiki/Leaf) cells to replace the lost molecules since water in the air inside leaves is maintained at [saturation vapour pressure](https://en.wikipedia.org/wiki/Saturation_vapour_pressure). Water lost at the surface of cells is replaced by water from the [xylem](https://en.wikipedia.org/wiki/Xylem), which due to the [cohesion-tension](https://en.wikipedia.org/wiki/Cohesion-tension_theory) properties of water in the xylem of plants pulls additional water molecules through the xylem from the roots toward the leaf

# Physico-chemical properties of water

Without water, life as we know it could not exist. Water is the most abundant constituent of most organisms. The actual water content will vary according to tissue and cell type and it is dependent to some extent on environmental and physiological conditions, but water typically accounts for more than 70 percent by weight of non-woody plant parts. The water content of plants is in a continual state of flux, depending on the level of metabolic activity, the water status of the surrounding air and soil, and a host of other factors. Although certain desiccation-tolerant plants may experience water contents of only 20 percent and dry seeds may contain as little as 5 percent water, both are metabolically inactive, and resumption of significant metabolic activity is possible only after the water content has been restored to normal levels. Water fills a number of important roles in the physiology of plants; roles for which it is uniquely suited because of its physical and chemical properties. The thermal properties of water ensure that it is in the liquid state over the range of temperatures at which most biological reactions occur. This is important because most of these reactions can occur only in an aqueous medium. The thermal properties of water also contribute to temperature regulation, helping to ensure that plants do not cool down or heat up too rapidly. Water also has excellent solvent properties, making it a suitable medium for the uptake and distribution of mineral nutrients and other solutes required for growth. Many of the biochemical reactions that characterize life, such as oxidation, reduction, condensation, and hydrolysis, occur in water and water is itself either a reactant or a product in a large number of those reactions. The transparency of water to visible light enables sunlight to penetrate the aqueous medium of cells where it can be used to power photosynthesis or control development. Water in land plants is part of a very dynamic system. Plants that are actively carrying out photosynthesis experience substantial water loss, largely through evaporation from the leaf surfaces. Equally large quantities of water must therefore be taken up from the soil and moved through the plant in order to satisfy deficiencies that develop in the leaves. For example, it is estimated that the turnover of water in plants due to photosynthesis and transpiration is about 1011 tonnes per year. This constant flow of water through plants is a matter of considerable significance to their growth and survival. The uptake of water by cells generates a pressure known as turgor; in the absence of any skeletal system, plants must maintain cell turgor in order to remain erect. As will be shown in later chapters, the uptake of water by cells is also the driving force for cell enlargement. Few plants can survive desiccation. There is no doubt that the water relations of plants and plant cells are fundamental to an understanding of their physiology. This chapter is concerned with the water relations of cells.

# WATER HAS UNIQUE PHYSICAL AND CHEMICAL PROPERTIES

The key to understanding many of the unique properties of water is found in the structure of the water molecule and the strong intermolecular attractions that result from that structure. Water consists of an oxygen atom covalently bonded to two hydrogen atoms. The oxygen atom is strongly electronegative, which means that it has a tendency to attract electrons. One consequence of this strong electronegativity is that, in the water molecule, the oxygen tends to draw electrons away from the hydrogen. The shared electrons that make up the O—H bond are, on the average, closer to the oxygen nucleus than to hydrogen. As a consequence, the oxygen atom carries a partial negative charge, and a corresponding partial positive charge is shared between the two hydrogen atoms. This asymmetric electron distribution makes water a polar molecule. Overall, water remains a neutral molecule, but the separation of partial negative and positive charges generates a strong mutual (electrical) attraction between adjacent water molecules or between water and other polar molecules. This attraction is called hydrogen bonding. The energy of the hydrogen bond is about 20 kJ mol−1. The hydrogen bond is thus weaker than either covalent or ionic bonds, which typically measure several hundred kJ mol−1, but stronger than the short-range, transient attractions known as Van der Waals forces (about 4 kJ mol−1). Hydrogen bonding is largely responsible for the many unique properties of water, compared with other molecules of similar molecular size. In addition to interactions between water molecules, hydrogen bonding also accounts for attractions between water and other molecules or surfaces. Hydrogen bonding, for example, is the basis for hydration shells that form around biologically important macromolecules such as proteins, nucleic acids, and carbohydrates. These layers of tightly bound and highly oriented water molecules are often referred to as bound water. It has been estimated that bound water may account for as much as 30 percent by weight of hydrated protein molecules. Bound water is important to the stability of protein molecules. Bound water ‘‘cushions’’ protein, preventing the molecules from approaching close enough to form aggregates large enough to precipitate. Hydrogen bonding, although characteristic of water, is not limited to water. It arises wherever hydrogen is found between electronegative centers. This includes alcohols, which can form hydrogen bonds because of the—OH group, and macromolecules such as proteins and nucleic acids where hydrogen bonds between amino **(−NH2)** and carbonyl **(C=O)** groups help to stabilize structure

# WATER EXHIBITS A UNIQUE THERMAL CAPACITY

The term specific heat1 is used to describe the thermal capacity of a substance or the amount of energy that can be absorbed for a given temperature rise. The specific heat of water is 4.184 J g−1 ◦ C−1, higher than that of any other substance except liquid ammonia (Table 1.1). Because of its highly ordered structure, liquid water also has a high thermal conductivity. This means that it rapidly conducts heat away from the point of application. The combination of high specific heat and thermal conductivity enables water to absorb and redistribute large amounts of heat energy without correspondingly large increases in temperature. For plant tissues that consist largely of water, this property provides for an exceptionally high degree of temperature stability. Localized overheating in a cell due to the heat of biochemical reactions is largely prevented because the heat may be quickly dissipated throughout the cell. In addition, large amounts of heat can be exchanged between cells and their environment without extreme variation in the internal temperature of the cell.

# THE THERMAL PROPERTIES OF WATER ARE BIOLOGICALLY IMPORTANT

Perhaps the single most important property of water is that it is a liquid over the range of temperatures most compatible with life. Boiling and melting points are generally related to molecular size, such that changes of state for smaller molecules occur at lower temperatures than for larger molecules. On the basis of size alone, water might be expected to exist primarily in the vapor state at temperatures encountered over most of the earth. However, both the melting and boiling points of water are higher than expected when compared with other molecules of similar size, especially ammonia (NH3) and methane (CH4). Molecules such as ammonia and the hydrocarbons (methane and ethane) are associated only through weak Vander Waals forces and relatively little energy is required to change their state. Note, however, that the introduction of oxygen raises the boiling points of both methanol (CH3—OH) strong intermolecular forces associated with hydrogen bonding. The density of ice is another important property. At 0◦ C, the density of ice is less than that of liquid water. Thus water, unlike other substances, reaches its maximum density in the liquid state (near 4◦ C), rather than as a solid. This occurs because molecules in the liquid state are able to pack more tightly than in the highly ordered crystalline state of ice. Consequently, ice floats on the surface of lakes and ponds rather than sinking to the bottom where it might remain year-round. This is extremely important to the survival of aquatic organisms of all kinds. Just as hydrogen bonding increases the amount of energy required to melt ice, it also increases the energy required to evaporate water. The heat of vaporization of water, or the energy required to convert one mole of liquid water to one mole of water vapor, is about 44 kJ mol−1 at 25◦ C. Because this energy must be absorbed from its surroundings, the heat of vaporization accounts for the pronounced cooling effect associated with evaporation. Evaporation from the moist surface cools the surface because the most energetic molecules escape the surface, leaving behind the lower-energy (hence, cooler) molecules. As a result, plants may undergo substantial heat loss as water evaporates from the surfaces of leaf cells. Such heat loss is an important mechanism for temperature regulation in the leaves of terrestrial plants that are often exposed to intense sunlight.

# WATER EXHIBITS A HIGH HEAT OF FUSION AND HEAT OF VAPORIZATION

Energy is required to cause changes in the state of any substance, such as from solid to liquid or liquid to gas, without a change in temperature. The energy required to convert a substance from the solid to the liquid state is known as the heat of fusion. The heat of fusion for water is 335 J g−1, which means that 335 J of energy are required to convert 1 gram of ice to 1 gram of liquid water at 0◦ C (Table 1.1). Expressed on a molar basis, the heat of fusion of water is 6.0 kJ mol−1 (18 g of water per mole × 335 J g−1). The heat of fusion of water is one of the highest known, second only to ammonia. The high heat of fusion of water is attributable to the large amount of energy necessary to overcome the 1Specific heat is defined as the amount of energy required to raise the temperature of one gram of substance by 1◦ C (usually at 20◦ C). The specific heat of water is the basis for the definition of a quantity of energy called the calorie. The specific heat of water was therefore assigned the value of 1.0 calorie.

# Hydration shell and Dielectric constant

The ability to partially neutralize electrical attractions between charged solute molecules or ions by surrounding the ion or molecule with one or more layers of oriented water molecules, called a hydration shell. Hydration shells encourage solvation by reducing the probability that ions can recombine and form crystal structures. The polarity of molecules can be measured by a quantity known as the dielectric constant. Water has one of the highest known dielectric constant. The dielectric constants of alcohols are somewhat lower, and those of nonpolar organic liquids such as benzene and hexane are very low. Water is thus an excellent solvent for charged ions or molecules, which dissolve very poorly in nonpolar organic liquids. Many of the solutes of importance to plants are charged. On the other hand, the low dielectric constants of nonpolar molecules helps to explain why charged solutes do not readily cross the predominantly nonpolar, hydrophobic lipid regions of cellular membranes.

# SOIL WATER PLANT RELATIONSHIP

•Soils are the natural media that support the growth and activities of many kinds of plants, animals and micro-organisms which play a vital role for the existence of life on earth. Air Water Minerals

# FUNCTION AND PROPERTIES OF WATER

• Water is a chemical compound of hydrogen and oxygen.

• Water together with dissolved nutrients forms the soil solution from which plants get nutrients.

• Water helps to maintain turgor pressure of plant cells.

• Water is an integral component of photosynthetic relation.

• Water serves as a universal solvent.

• Water is very important for soil formation.

• Water is an important component of plant cell and constitutes about 80-90% of the fresh weight of herbaceous plant parts and over 50% of the fresh weight of woody plants.

# ROLE OF WATER IN GROWTH AND PHYSIOLOGICAL PROCESSES

Almost every plant process is affected directly or indirectly by water supply.

* Germination
* Growth
* Photosynthesis
* Respiration
* Transpiration
* Stomata opening and closing
* Flowering and Fruiting
* Fruit ripening and Dormancy

# ROLE OF WATER IN SOIL FUNCTIONING

* Soil Formation
* Soil Fertility
* Regulating soil temperature

# PROPERTIES OF WATER

• Water is a chemical compound of hydrogen and oxygen. Hydrogen and oxygen atom are bonded together covalently (each hydrogen atom shares a single electron with oxygen) and arranged in a V shaped structure at an angle of 104. 52A0 .

* Hydrogen bonding
* Cohesion and adhesion
* Surface tension
* Capillarity
* Polarity
* Specific heat
* Heat of vaporization
* Heat of fusion
* Heat conductor
* Water as a Regent

# CLASSIFICATION OF SOIL WATER

Gravitational water:

It is of little use because it stays in soil for very short period of time. It is present in soil at water potential greater than -0.1 bar and is always in acces of field capacity.

Field capacity:

At field capacity water is held in soil at water potential -0.1to -0.3 bar.

Capillary water: it is present in soil at water potential -0.3 to -31 bar. However, plant can use capillary water upto - 15 bar.

## Hygroscopic water:

Water that is held very tightly with soil solids at a water potential lower than -31 bar. Classification of water with respect to plants or biological point of view

## Available water:

the available water is estimated as the difference between soil water content at field capacity and permanent wilting point.

## Permanent wilting point:

It is generally the soil water held at less than 15 bar. It is the lower limit of available water beyond which water is adsorbed so strongly that plants cannot absorb it fast enough to meet their water requirements.

## Unavailable water:

Water held at water potential less than -15 bar and bound to soil particles so tightly that is not available to plants.

# SOIL WATER ENERGY CONCEPT

Retention and movement of water in soil, its uptake and translocation in plants as well as its loss to atmosphere all our energy related phenomenon. Soil water has two types of energy.

## Kinetic Energy:

It is the form of energy due to movement of water molecules within soil.

## Potential Energy:

It is the form of energy due to position of water in soil.

Free energy of water is always expressed relative to energy condition of water in a standard reference state.The reference state must have following characteristics;

* It is pure.
* It is free ,no adsorption at soil matrix.
* It has pressure equal to atmospheric pressure.
* It is at same temperature as that of soil water.
* An arbitrary reference elevation must be set at a specific height.

## Factors affecting free energy of water

* Matric forces
* Osmotic forces
* Gravitational forces

# Soil Water Potential

It is the difference between free energy of soil water and that of pure water in a standard reference state is called soil water potential.

## Characteristics of soil water potential;

* Relative
* Negative
* Continuity
* Driving force
* Variability
* Dynamic

## Components of soil water potential

* Matric potential
* Osmotic or solute potential
* Pressure potential or hydrostatic potential
* Overburden potential or envelope potential: Air pressure potential or pneumatic potential
* Gravitational potential
* It is denoted by psy Ψ .
* Ψw= Ψm + Ψs+ Ψp.

# MOVEMENT OF WATER THROUGH SOIL

## Saturated Water Flow:

It is the movement of water under saturated soil condition and is mainly determined by two major forces;

* Hydraulic force
* Hydraulic conductivity

## Hydraulic force:

It is the driving force that controls water movement through soil under saturated condition. It originates from gravity. It is the ease with which soil pores permit water movement

## Unsaturated Flow:

It is the movement of water in soil through capillary pores. Unsaturated flow depends upon two factors;

* Hydraulic conductivity
* Driving force

Driving force in case of unsaturated flow is generally the matric forces. Unsaturated flow is inversely proportional to matric forces. Water flows from wet region (low metric forces) to dry region (high matric forces).

## Vapour Movement:

Water vapours move from one point to another in response to the difference in vapour pressure.

Water vapors moves from moist soil where soil air is nearly saturated with water vapours high vapour pressure to a dry soil where vapour pressure is somewhat lower.

Vapour movement in soil is very small and has limited practical significance to meet crop water requirement.

In a dry soil vapour movement may be considerable significance in supplying moisture to drought resistant plants.

# HOW PLANTS ARE SUPPLIED WITH WATER

Two major phenomena are generally responsible for plant access to water.

* Capillary movement of soil water to plant roots
* Growth of plant roots into moist soil

## Capillary movement

When plant rootlet absorb water they reduce moisture content and thus result in reduction in water potential in immediate surroundings of plant roots. In response to this lower water potential, water tends to move towards plant roots.

The rate of water movement depends on

* Magnitude of potential gradient
* Hydraulic conductivity of soil

## Growth of plant roots to moist soil

• Capillary movement of water is complemented by rapid rate of root extension.

• The primary limitation of root extension is a small proportion of soil with which roots are in contact.

• Roots soil contact commonly accounts for less than 1% of total soil surface area.

• Complemented operation of capillary and root extension is more effective to move water from soil to plant roots

# WATER ABSORPTION BY PLANT ROOTS

The transport of water from soil to plant roots and to atmosphere takes place in following three steps;

Water is first absorbed from soil by root hairs and other epidermal cells in or near the root zone of young root tissue.

Lateral conductance across young root tissue epidermis pericycle into xylem duct and vertical conductance within xylem vessel into leaves.

Passage of water across leaf tissue through the process of transpiration into atmosphere.

# MECHANISM OF WATER ABSORPTION

There are two mechanisms of water absorption

* Passive absorption
* Active absorption

In passive absorption uptake of water by plants is generally controlled by transpirational pull generated at leaves surface due to loss of water into atmosphere. During passive water absorption suction force originally generated at leaf surface moving down through a continuous column of water is transmitted to root system and is responsible for the absorption of water from soil.

## Active Absorption

Absorption of water by plant roots due to activity of living roots and usually involving the expenditure of energy. When there is high concentration of salts in soil, due to adsorption of water molecules to salt ions water potential of soil solution becomes low as compared to root cells. Under these conditions plant roots have to synthesize and accumulate different kind of osmolytes (Proline, glycine batane, sucrose and mannitol) into root cell sap.Due to accumulation of these osmolytes in the root cell sap water potential within cell sap decreases and water starts to move from soil to plants along water potential gradient.

# FACTORS AFFECTING WATER ABSORPTION

* Absorption efficiency of roots
* Availability of water and soil type
* Concentration of soil solution
* Transpiration
* Soil Temperature
* Soil Aeration

# Nutrient Movement From Soil To Plant Roots

Before taken up by plants the nutrients must reach from soil to root surface. It takes place by three processes.

* Mass Flow
* Diffusion
* Root interception

# Mass Flow

• It is the transport of soil solution containing nutrients to plant roots caused by water potential gradient developed due to loss of water through transpiration or evaporation. Contribution of mass flow to carry nutrients to plant roots varies with following factors:

* Nutrient in consideration and its concentration in soil solution
* Water consumption or requirement of plants.
* Plant species and plant age
* Time of the day and season
* Soil moisture content

# Diffusion

It is the transport of nutrients to root surface along the concentration gradient. P, K, S, Fe and Zn move through diffusion. The transport of nutrients to plant roots through diffusion is high when plant uptake exceeds nutrients supply through Mass flow.Depletion zones develop along the root surface depending upon following factors

* Uptake by roots
* Replenishment of soil
* Mobility of ion by diffusion

# Root Interception

It refers to the exchange of Ions between root surface and soil minerals surface through the physical contact between root and soil. The quantity of nutrients that can come in direct contact with plant roots is the amount in the volume of soil equal to volume of root.Roots can contact 1-3% of available soil nutrients but normally 1%. Root interception can be increased by mycorrhizal infection.

# Factors affecting nutrient movement

* Nutrient related factors
* Plant related factors
* Soil related factors

# Nutrient Related Factors

* Nutrient under consideration
* Concentration of nutrient in soil solution
* Form of nutrient in soil

# Plant Related Factors

* Plant species and varieties within species
* Plant age
* Root type
* Presence or absence of root hairs
* Root length
* Root induced changes in rhizosphere

# Soil Related Factors

* Soil texture
* soil structure
* Soil aeration
* soil temperature
* pH
* Eh
* Organic matter
* Microbial activities
* Soil moisture

# ION OR SOLUTE UPTAKE BY PLANTS

Absorption of salts by plants takes place through an immediate contact of plant roots with the soil solution. Absorption of salts takes place in following steps.

* Movement of Ions from soil to plant roots
* Accumulation of ions in the root surface
* Radial movement of Ions from root surface to xylem
* Translocation of Ions from Roots to shoot

# Factors Affecting Ions/ Salts/ Solute Absorption

* Plant Species
* Extent of root system &Metabolic activities in root tissues
* Internal concentration of salts & sugars
* Hydrogen ion concentration
* Respiration
* Light & Aeration & Temperature
* Soil Moistures Content
* Concentration and composition of external solution
* Interaction between ions

# ION UPTAKE MECHANISM

Ion uptake is the process in which mineral nutrients enter the cellular material following the same pathway as that for water. Nutrients may be taken up by plants by two mechanisms.

* Passive uptake
* Active uptake

# Passive Uptake

It is the absorption of mineral nutrients by plants along the concentration gradient without direct expenditure of metabolic energy. Passive absorption is not affected by temperature and metabolic inhibitors. There are 4 theories lying under passive absorption/uptake.

* Mass flow theory
* Contact exchange theory
* Carbonic acid exchange theory
* Donnan equilibrium theory

# Mass Flow Theory

According to this theory ions are absorbed by the roots along with mass flow of water under the effect of transpiration. An increase in transpirational pull increases the uptake of ions by roots . Mass flow of ions through root tissue occur due to transpirational pull in the absence of metabolic energy.

# Contact Exchange Theory

According to this theory ions adsorbed on colloidal particles get absorbed to the roots in exchange for hydrogen ions previously adsorbed on the roots.

Ions adsorbed on the colloidal particles oscillate within a small space, when two particles(root and soil) are close enough the oscillation space of an ion adsorbed to another particle overlaps, thus exchange of ions may take place between soil particles and plant roots.

# Carbonic Acid Exchange Theory

The soil solution provides a medium for the exchange of Ions between the root and colloidal particles. Carbon dioxide released during respiration forms carbonic acid by reacting with water of soil solution.

This carbonic acid is then dissociated in soil solution to form hydrogen ion and bicarbonate ions. Hydrogen ions adsorbed to colloidal particles exchanges for cations such as potassium ion, which are released into soil solution from there they may diffuse to plant roots and are taken up by plants.

# Donnan Equilibrium Theory

Cell membrane is composed of macromolecules of proteins and lipids that have different functional groups like carboxylic group and phosphate group from which positively charged particles like proton dissociates, leaving the macromolecules with net negative charge. The negative charge so produced are not diffusible because they are within the membrane structure.

These negatively charged membrane are called donnan phase. As a result of net negative charge on the membrane structure the cations like potassium will tend to diffuse through the membrane because of electric potential difference.

# Active Ion uptake

The active transport of Ions from the outer space of cell to the inner space generally occurs against the concentration gradient and hence requires metabolic energy. During active and transport the carrier proteins, picks up an ion from one side of the membrane and discharges it on the other side. This picking up and discharge of an ion by carrier protein require energy. This energy is obtained from the hydrolysis of ATP.

The carrier protein may carry one ion inward and exchange it with another ion at the inner surface of the membrane, so that other ion is carried by the same protein carrier outward

# REDISTRIBUTION OF IONS IN PLANT BODY

The continued movement of salt ions into leaves along transpirational pull results in an increase of salt content during growing season.

Not all of salt which enter a given leaf will retain in that leaf, some of the salt ions are exported/transported back into stem.

Redistribution of salts with in plant body seems to be controlled largely by metabolic activities of various parts of the plant.

The redistribution of salt ions mainly occur through xylem and phloem.

Salt ions tend to be moved from older leaves to younger leaves, reproductive structure and metabollically active regions before the fall of older leaves.

# Inorganic composition of soil

## Soil….

Soil is a mixture of organic and inorganic constituents. The inorganic components come from the weathering of various rock types. Organic particles are the result of both plants and animals inhabiting the area. While some soil has only one particle type, the most fertile soil is a mixture of several organic and inorganic components.

## COMPOSITION OF SOIL

Soil is a complex body composed of five major components

mineral matter obtained by the distintergration and decomposition of rocks;

organic matter, obtained by the decay of plant residues, animal remains and microbial tissues;

water, obtained from the atmosphere and the reactions in soil (chemical, physical and microbial);

air or gases, from atmosphere, reactions of roots, microbes and chemicals in the soil

organisms, both big (worms, insects) and small (microbes)

## Inorganic Sand

Sand is a medium to coarse-grained sediment that is visible to the naked eye. Sand particles range in size from 0.05 millimeters to 2.0 millimeters and consist of pieces of weathered rock, such as quartz, magnetite or other mineral or shell fragments. Sand in your garden soil will help promote good drainage and aeration of the area. However, sand alone will not retain significant amounts of moisture to support plant growth. In addition, sand does not contain nutrients that promote healthy plants.

## Inorganic Silt

Silt is a fine-grained sediment that you cannot see with the naked eye. Silt is larger than clay and smaller than sand and may feel gritty between your fingers. Silt particles range from 0.002 millimeters to 0.05 millimeters. Like sand, silt results from the weathering of rocks and consists of grains of quartz, feldspar and other minerals. Silt-rich soil will retain moisture for plant growth, but at times, it can limit drainage and make the soil difficult to till. Silt itself does not contain plant nutrients; however, existing nutrients in the area may adhere to the surface of the silt particles in the garden soil.

## Inorganic Clay

Clay is another fine-grained sediment that is smaller than silt. Clay particles are smaller than 0.002 millimeters and result from significant weathering of rocks. Minerals, such as feldspars, degrade over time to form clay. Like silt, clay-rich soil will retain moisture for plant growth and may limit drainage in the area. You can amend fine-grained soils with sand and organic matter to improve the drainage quality of the area. Unlike sand and silt, the aluminum-silicate minerals that degrade to clay will provide important plant nutrients such as iron, calcium, magnesium and potassium. Existing nutrients will cling to the clay soil particles and help to feed plant growth in the root area.

## Organic Matter

Organics in soil are due to the presence and decomposition of plant and animal matter in the area. Humus, a partially decomposed organic matter, is a common form of organics in garden soil that will continue to decompose over time. While the percent of organic matter in most topsoil is only 2 to 4 percent, it plays an important role in the garden. Organic matter is good for promoting aeration, drainage and soil moisture retention in the soil. The organic matter also reduces erosion and supplies plant nutrients such as sulfur, phosphorous and nitrogen to the plant’s root zone. The organics will also help to reduce the threat of plant disease in the garden by promoting a healthy growing environment.

# Root mycorrhizae-plants

A mycorrhiza is a symbiotic association between a green plant and a fungus. Mycorrhizas are located in the roots of vascular plants, but mycorrhiza-like associations also occur in bryophytes and there is fossil evidence that early land plants that lacked roots formed arbuscular mycorrhizal associations The word Mycorrhizae was first used by german researcher A.B Frank in 1885 and originates from the Greek mycos, meaning “fungus” and “rhiza” meaning “root”. Mycorrhizae is a symbiotic mutualistic relationship between special soil fungi and fine plant roots: it is neither the fungus nor the root but rather the structures from these two partners.

Since the association is mutualistic, both organisms benefit from the associations. The fungus receives carbohydrates (sugars) and growth factors from the plant, which in turn receives many benefits, including increased nutrient absorption. In this association, the fungus takes over the role of the plant’s root hairs and Acts as an extension of the root systems.Mycorrhizae are highly evolved, mutualistic associations between soil fungi and plant roots. It is commonly known as root fungi. This asoociation are members of the fungus kingdom (Basidomycetes, Ascomycetes and Zygomycetes) and most vascular plants. Host plant receives mineral nutrients while the fungus photosynthetically derived carbon compounds from the plants.

Mycorrhizal associations involve 3way interactions between host plants, mutualistic fungi and soil factors. Host plant Fungi Soil factors

# Types of Associations

Mycorrhizas are commonly divided into ectomycorrhizas (extracellular)and endomycorrhizas (Intracellular).

The two types are differentiated by the fact that the hyphae of

* ectomycorrhizal fungi do not penetrate individual cells within the root
* endomycorrhizal fungi penetrate the cell wall and invaginate the cell membrane.
* Endomycorrhizas are variable and have been further classified as arbuscular, ericoid, arbutoid, monotropoid, and orchid mycorrhizas.

Arbuscular mycorrhizas, or AM (formerly known as vesicular-arbuscular mycorrhizas, or VAM), are mycorrhizas whose hyphae enter into the plant cells, producing structures that are either balloon-like (vesicles) or dichotomously branching invaginations (arbuscules). Ectomycorrhizas, or EcM, are typically formed between the roots of around 10% of plant families, mostly woody plants including the birch, dipterocarp, eucalyptus, oak, pine, and rose families, orchids, and fungi belonging to the Basidiomycota, Ascomycota, and Zygomycota.

Some EcM fungi, such as many Leccinum and Suillus, are symbiotic with only one particular genus of plant, while other fungi, such as the Amanita, are generalists that form mycorrhizas with many different plants. Association Occurrence Vesicular Arbuscular Mycorrhizal (VAM) plants. Plants with VAM are common in most habitats Ectomycorrhizal (ECM) plants. Trees with ECM are dominant in coniferous forests, especially in cold boreal or alpine regions. ECM trees and shrubs common in many broad-leaved forests in temperate or Mediterranean regions.Also occur in some tropical or subtropical savanna or rain forests habitats Ectomycorrhizae.

Most conspicuous and easily recognized

## Best characterized

Plant roots are enclosed by a sheath of fungal hyphae – fungal mycelium penetrates between cells in cortex of the root

Fungal tissue may account for up to 40% mass of root

Hyphae also extend out into the soil – extramatrical hyphae

Ectomycorrhizae Contains a fungal sheath Parenchyma of root cortex is surrounded by hyphae – Hartig net Absorbing roots are those that are affected

Become thicker and repeatedly branched after infection

## Benefits to fungus

* Provided with source of C and energy
* Plants provided with CO2 demonstrated that C appears in fungus
* Sucrose from plant converted into trehalose, mannitol by fungus
* Estimates that up to 10% (or more) of photosynthate produced by trees is passed to mycorrhizae and other rhizosphere organisms

## Benefits to trees

* Numerous studies have shown that tree growth is better when mycorrhizae are present
* Fungi increase supply of inorganic nutrients to tree
* P is insoluble in most soils
* Extramatrical hyphae extend over a larger volume of soil than roots can – increase ability to absorb insoluble nutrients such as P
* Extramatrical hyphae
* Volume of soil explored
* Plant hormones produced by fungus changes the physiological state of roots – physiologically active root area for nutrient and water absorption is increased
* Increases tolerance of plant to drought, high temperatures, pH extremes, heavy metals Increases resistance to infection by root pathogens – provides a physical barrier

## Vesicular Arbuscular mycorrhizae (VAM)

* VAM is a type of mycorrhiza in which the fungus penetrates the cortical cells of the roots of a vascular plant.
* characterized by the formation of unique structures, arbuscules and vesicles by fungi of the phylum Glomeromycota (VAM fungi).
* VAM fungi help plants to capture nutrients such as phosphorus, sulfur, nitrogen and micronutrients from the soil.
* It is believed that the development of the arbuscular mycorrhizal symbiosis played a crucial role in the initial colonisation of land by plants and in the evolution of the vascular plants.

## Arbuscular mycorrhizal fungi

* All are in the Zygomycota in the Glomales – or newly proposed phylum Glomeromycota
* Include 130 species in 6 genera
* All are obligate biotrophs
* Form large spores that superficially resemble zygospores, but not formed from fusion of gametangia – azygospores or chlamydospores
* Spore diameters range from 50 to 400 μm

# Effect of soil PH on Nutrient availibilty

## Introduction pH is:

* Measure of acidity or basicity
* Defined as negative logarithm of activity of H+ ion in a solution
* pH = -log [H+]. ¬ pH ranges between 1-14. Basic >7 Acidic <7 Neutral =7 pH
* The term "pH" was first described by Danish biochemist Søren Peter Lauritz Sørensen in 1909.
* “power of hydrogen” where “p” is short for the German word for power, potenz and “H” is the element symbol for hydrogen.
* pH can affect nutrient availability by:
* formation of low solubility compounds,
* greater retention by soil colloids (clays and organic matter),
* conversion of soluble forms to ions that plants cannot absorb and
* Can inhibit or stimulate microbial activity.

## Soil

* Upper and biochemically weathered portion of the earth
* Composed of weathered rock material, organic matter, water and air
* Supports plant life
* Plant Nutrient
* The elements which are required for proper growth, development and reproduction of plants.

## Nutrient availability in relation to soil pH

Macronutrients are nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sulfur (S). And micronutrients are iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), cobalt (Co), molybdenum (Mo), and boron (B). Both macronutrient and micronutrient availability are affected by soil pH. In slightly to moderately alkaline soils, molybdenum and macronutrient (except for phosphorus) availability is increased, but P, Fe, Mn, Zn Cu, and Co levels are reduced and may adversely affect plant growth. In acidic soils, micronutrient availability (except for Mo and Bo) is increased.

## Low pH

### Soil acidity affects plant growth in several ways:

* The concentration of soluble metals, especially aluminum and manganese may be toxic.
* Calcium may be deficient.
* When the soil pH is lower, more H+ ions are available to “exchange” base cations, thereby removing them from exchange sites and releasing them to the soil solution (soil water).
* Lower pH increases the solubility of Al, Mn, and Fe, which are toxic to plants in excess. A critical effect of excess soluble Al is the slowing or stopping of root growth.
* Low pH reduces the availability of the macro- and secondary nutrients
* Symbiotic N fixation in legume crops is greatly impaired.
* The symbiotic relationship requires a narrower range of soil reaction than does the growth of plants not relying on N fixation. Populations and the activity of the organisms responsible to transform N, S, and P to plant-available forms may be reduced. The availability of mineral elements to plants may be affected.

## High pH

When the soil pH is high (i.e., more basic, low concentration of H+), more base cations will be on the particle exchange sites. As a result, exchanged nutrients are either taken up by the plant or lost through leaching or erosion. Microbial activity may also be reduced or changed.When the soil pH is high (i.e., more basic, low concentration of H+), more base cations will be on the particle exchange sites. As a result, exchanged nutrients are either taken up by the plant or lost through leaching or erosion. Microbial activity may also be reduced or changed.

# Nitrogen

* key soil nutrients
* Plant available forms are ammonium (NH4+) and nitrate (N03-) form.
* At neutral pH, the microbial conversion of NH4+ to nitrate (nitrification) is rapid, and crops generally take up nitrate.
* In acid soils (pH < 6), nitrification is slow, and plants with the ability to take up NH4+ may have an advantage.
* Soil pH is also an important factor in the N nutrition of legumes. The survival and activity of Rhizobium, the bacteria responsible for N fixation in association with legumes, declines as soil acidity increases.

# Phosphorus

Form and availability is highly pH dependent

The limited solubility of P relates to its tendency to form a wide range of stable minerals in soil. Under alkaline soil conditions, P fertilizers generally form more stable (less soluble) minerals through reactions with calcium (Ca).

The fate of added P in acidic soils is somewhat different as precipitation reactions occur with aluminum (A1) and iron (Fe). The tie-up of P in A1-P and Fe-P minerals under acidic conditions tends to be more permanent than in Ca-P minerals.

In order for P to be available for plants, soil pH needs to be in the range 6.0 and 7.5. If pH is lower than 6, P starts forming insoluble compounds with iron (Fe) and aluminium (Al) and if pH is higher than 7.5 P starts forming insoluble compounds with calcium (Ca).

# Potassium

The fixation of potassium (K) between clay layers tends to be lower under acid conditions. This situation is thought to be due to the presence of soluble aluminum that occupies the binding sites. Sulfur

Sulfate (S042-) sulfur, the plant available form of S, is little affected by soil pH.

# Boron

Boron availability to plants decreases with increasing soil pH, especially above pH 6.5. However, strongly acid soils (pH less than 5.0) also tend to be low in available B because of B sorption to iron and aluminum oxide surfaces of soil minerals.

# Iron

Iron (Fe) is one essential plant nutrient whose solubility is affected by pH that is why it is added in a chelated form. At pH values over 7, less than 50% of the Fe is available to plants. At pH 8.0, no Fe is left in solution due to iron hydroxide precipitation (Fe(OH)3 - which eventually converts to rust). As long as the pH is kept below 6.5, over 90% of the Fe is available to plants. Due to calcium phosphate precipitation (Ca3(PO4)2) the availability of Ca and P decreases at pH values above 6.0. All other nutrients stay in solution and do not precipitate over a wide pH range. Precipitation reduces Fe, Ca and P availability at pH 6.0 and over .

Chapter3

Plant Mineral Nutrition

# AN INTRODUCTIONTO PLANT NUTRIENTS:

The element is involved directly in the nutrition of the plant quite apart from its possible effects in correcting some unfavorable microbiological or chemical condition of the soil or other culture medium. A total of only 17 elements are essential for the growth and full development of higher green plants according to the criteria laid down by Arnon and Stout (1939). These criteria are:

A deficiency of an essential nutrient makes it impossible for the plant to complete the vegetative or reproductive stage of its life cycle.

Such deficiency is specific to the element in question and can be prevented or corrected only by supplying this element.

# WHAT ARE BENEFICIAL ELEMENTS

Beneficial elements are those elements which may not be beneficial or useful to all the existing plants but may be of prime importance to a specific plant.

They are also known as potential micronutrients.

These elements at very low concentrations and often under specific conditions have been shown to stimulate the growth of certain plants or to have other beneficial effects.

Examples are : selenium aluminum nickel Vanadium Chromium arsenic

# ROLE OF BENEFICIAL ELEMENTS IN PLANTS:

Plants are challenged by metal ion concentrations and have evolved mechanisms to cope with this. Beneficial elements help plants in this job, alleviating stress symptoms.

# SODIUM

* Essential for CAM metabolism
* osmolyte, especially for halophytes
* Alternative cofactor, replacing pottassium

# ALUMINUM

* Enhances herbivore defense.
* Can prevent iron toxicity
* May promote phosphorus uptake.

# SELENIUM

* Pathogen and herbivore defense.
* May prevent phosphorus toxicity.
* Putative antioxidant.

# SILICON

* Pathogen and herbivore defense.
* Resistance to abiotic stresses.
* Prevents lodging.

# COBALT

* Enhances drought resistance
* Herbivores defense.

**Cobalt (Co), sodium (Na), vanadium (V) and silicon (Si) are sometimes called as beneficial plant nutrients.**

They are not required by all plants but appear to benefit certain plants.

Cobalt is required for nitrogen fixation in legumes.

Silicon is found in plant cell walls and appears to produce tougher cells.

This increases the resistance of these plants to piercing and sucking insects and decreases the spread of fungal diseases.

# Sources of Elements in the Soil

## Organic matter:

Most soil nutrients are contained in the soil organic matter.To make these nutrients available the organic matter must be decomposed..

Soil minerals (includes clay minerals) These are the nutrients that are in the parent materials.These nutrients may become available through weathering, however this is a very slow process.There are also nutrients in the clay minerals.This includes Mg and K that are in the 2:1 clay minerals.

Adsorbed nutrients These are the nutrients that are held on the soil colloid.This is the major source of nutrients for the plants, and is the source that is most easily controlled by man.

# FORMS OF NUTRIENTS IN SOIL:

NITROGEN:

The forms of nitrogen in soil may be classified as organic forms and inorganic forms. organic inorganic E.g.: protein, free amino acids, amino Sugars, other complexes ionic gaseous eg :ammonium ions, nitrate ions nitrite ions Ammonia, Nitrogen Nitrous oxide

# FORMS OF PHOSPHORUS IN SOILS :

Phosphorus exists in soils in several forms as shown below:

ORGANIC INORGANIC E.g.: phytin, phospholipids, and nucleic acids combined ionic Eg: hydrogen Phosphate ions Combined with calcium E.g.: monocalcium phosphate monohydrate Tricalcium and dicalcium phosphate Combined with iron and aluminum as: Crystals and colloids Surface precipitated or adsorbed Combined with silicate minerals.

# FORMS OF POTTASSIUM IN SOIL :

K(**POTTASSIUM**) CONTAINED IN INORGANIC MATTER K CONTAINED IN SOIL SOLUTION K CONTAINED IN ORGANIC MATTER MINERALOR STRUCTURAL K. NON EXCHANGEABLE K EXCHANGEABLE K DIFFICULTY EXCHANGEABLE FIXED

# FORMS OF CALCIUM IN SOIL:

Calcium forms insoluble compounds with other elements in soil, such as phosphorous. Calcium that is in the form of an insoluble compound is not available to plants. Since calcium is a positively charged ion, it is adsorbed in the soil to the surface of clay and organic particles which are negatively charged. Positively charged ions adsorbed to soil particles are termed "exchangeable ions" because they can be exchanged by other ions present in the soil solution. Soil analysis determines the level of exchangeable calcium ions, and not the total calcium in soil, because the exchangeable calcium is the form which is available to the plant.

# FORMS OF MAGNESIUM IN SOIL:

In soil, magnesium is present in three fractions: Magnesium in soil solution – Magnesium in soil solution is in equilibrium with the exchangeable magnesium and is readily available for plants. Exchangeable magnesium –This is the most important fraction for determining the magnesium that is available to plants.This fraction consists of the magnesium held by clay particles and organic matter. It is in equilibrium with magnesium in soil solution. Non-exchangeable magnesium – Consists of the magnesium that is a constituent of primary minerals in the soil.The break down process of minerals in soils is very slow; therefore, this magnesium fraction is not available to plants.

# FORMS OF SULPHUR IN SOIL:

Most soil sources of S are in the organic matter and are therefore concentrated in the topsoil or plow layer. Elemental S and other forms as found in soil organic matter and some fertilizers, are not available to crops.They must be converted to the sulfate (SO4 --) form to become available to the crop.This conversion is performed by soil microbes and therefore requires soil conditions that are warm, moist, and well drained to proceed rapidly.The sulfate form of S is an anion (negative charge), and therefore is leachable. As a rough rule-of-thumb, it can be considered to leach through the soil profile at about 50% as fast as nitrates (NO3 -). In soils with a significant and restrictive clay layer in the sub-soil, it is common to find that sulfate which has leached through the soil over time and become "perched" on the clay layer.This SO4 -- is available to crops when the roots reach this area of the soil.

## IRON Form:

Iron is taken up by plants as either Fe2+ (ferrous cation) or Fe3+ (ferric cation).

## BORON Form:

Boron is taken up by plants primarily as H3BO3 (boric acid) and H2BO3 - (borate). MANGANESE Form:The primary form of manganese uptake is Mn2+ (manganous ion).

## ZINC Form:

The Zn2+ cation is the predominate form taken up by plants MOLYBDENUM Form: Molybdenum is primarily taken up as MoO4 2- (molybdate ion).

## COPPER Form:

Copper is taken up as Cu2+ (cupric ion).

# Deficiency symptoms of Nutrients in plants

Growing plants act as integrators of all growth factors and are the products in which the grower is interested. Therefore, careful inspection of the growing plant can help identify a specific nutrient stress. if a plant is lacking in a particular nutrient, characteristic symptoms may appear. Deficiency of a nutrient does not directly produce symptoms. Rather, the normal plant processes are thrown out of balance, with an accumulation of certain intermediate organic compounds and a shortage of others. This leads to the abnormal conditions recognized as symptoms. Visual evaluation of nutrient stress should be used only as a supplement to other diagnostic techniques (i.e., soil and plant analysis). Nutrient deficiency symptoms may be classified as follows:

* Complete crop failure at the seedling stage.
* Severe stunting of plants.
* Specific leaf symptoms appearing at varying times during the season.
* Internal abnormalities such as clogged conductive tissues.
* Delayed or abnormal maturity.
* Obvious yield differences, with or without leaf symptoms.
* Poor quality of crops, including differences in protein, oil, or starch content, and storage quality.

Yield differences detected only by careful experimental work.

Each symptom must be related to some function of the nutrient in the plant. A given nutrient may have several functions, which makes it difficult to explain the physiological reason for a particular deficiency symptom. For example, when N is deficient, the leaves of most plants become pale green or light yellow. When the quantity of N is limiting, chlorophyll production is reduced, and the yellow pigments, carotene and xanthophylls are shown through a number of nutrient deficiencies produced such as pale green or yellow leaves, and the deficiency must be further related to a particular leaf pattern or location on the plant.

Apparent visual deficiency symptoms can be caused by many factors other than a specific nutrient stress. Precautions in interpreting nutrient deficiency symptoms include the following:

The visual symptom may be caused by more than one nutrient. For example, N-deficiency symptoms may be identified, although S may also be deficient and its symptoms may not be readily apparent. B deficiency is accompanied by a red coloration of the leaves near the growing point when the plant is well supplied with K. on the other hand, when the K content is low, yellowing of alfalfa leaves occurs.

Deficiencies are actually relative, and a deficiency of one nutrient may be related to an excessive quantity of another. For example, Mn deficiency may be induced by adding large quantities of Fe, provided that soil Mn is marginally deficient. Also, at a low level of P supply, the plant may not require as much N compared to normal or adequate P. In other words, once the first limiting factor is eliminated, the second limiting factor will appear (Liebig’s law of the minimum).

It is often difficult to distinguish among the deficiency symptoms in the field, as disease or insect damage can resemble certain micronutrients deficiencies. For example, leaf hopper damage can be confused with deficiency in alfalfa.

|  |  |
| --- | --- |
| **Element/status** | **Visual symptoms** |
| **Nitrogen (N)** | |
| Deficiency | Light green leaf and plant color with the older leaves turning yellow, leaves that will eventually turn brown and die. Plant growth is slow, plants will be stunted, and will mature early. |
| Excess | Plants will be dark green in color and new growth will be succu­lent; susceptible if subjected to disease and insect infestation; and subjected to drought stress, plants will easily lodge. Blos­som abortion and lack of fruit set will occur. |
| Ammonium toxicity | Plants fertilized with ammonium-nitrogen (NH4- N) may exhibit ammonium-toxicity symptoms, with carbohydrate depletion and reduced plant growth. Lesions may occur on plant stems, there may be a downward cupping of the leaves, and a decay of the conductive tissue at the base of the stem with wilting of the plants under moisture stress. Blossom-end rot of fruit will occur and Mg deficiency symptoms may also occur. |
| **Phosphorus (P)** | |
| Deficiency | Plant growth will be slow and stunted, and the older leaves will have a purple coloration, particularly on the underside. |
| Excess | Phosphorus excess will not have a direct effect on the plant but may show visual deficiencies of Zn, Fe, and Mn. High P may also interfere with the normal Ca nutrition, with typical Ca deficiency symptoms occurring. |
| **Potassium (K)** | |
| Deficiency | On the older leaves, the edges will look burned, a symptom known as scorch. Plants will easily lodge and be sensitive to disease infestation. Fruit and seed production will be impaired and of poor quality. |
| Excess | Plants will exhibit typical Mg, and possibly Ca deficiency symp­toms due to a cation imbalance |
| **Calcium (Ca)** | |
| Deficiency | The growing tips of roots and leaves will turn brown and die. The edges of the leaves will look ragged as the edges of emerging leaves stick together. Fruit quality will be affected with the occur­rence of blossom-end rot on fruits. |
| Excess | Plants may exhibit typical Mg deficiency symptoms, and when in high excess, K deficiency may also occur. |
| **Magnesium (Mg)** | |
| Deficiency | Older leaves will be yellow in color with interveinal chlorosis (yellowing between the veins) symptoms. Plant growth will be slow and some plants may be easily infested by disease. |
| Excess | Results in a cation imbalance showing signs of either a Ca or K deficiency. |
| **Sulfur (S)** | |
| Deficiency | A general overall light green color of the entire plant with the older leaves being light green to yellow in color as the deficiency intensifies. |
| Excess | A premature senescence of leaves may occur. |
| **Boron (B)** | |
| Deficiency | Abnormal development of the growing points (meristematic tis­sue) with the apical growing points eventually becoming stunted and dying. Rowers and fruits will abort. For some grain and fruit crops, yield and quality is significantly reduced. |
| Excess | Leaf tips and margins will turn brown and die. |
| **Chlorine (Cl)** | |
| Deficiency | Younger leaves will be chlorotic and plants will easily wilt. For wheat, a plant disease will infest the plant when Cl is deficient. |
| Excess | Premature yellowing of the lower leaves with burning of the leaf margins and tips. Leaf abscission will occur and plants will easily wilt. |
| **Copper (Cu)** | |
| Deficiency | Plant growth will be slow and plants stunted with distortion of the young leaves and death of the growing point. |
| Excess | An Fe deficiency may be induced with very slow growth. Roots may be stunted. |
| **Iron (Fe)** | |
| Deficiency | Interveinal chlorosis will occur on the emerging and young leaves with eventual bleaching of the new growth. When severe, the entire plant may be light green in color. |
| Excess | A bronzing of leaves with tiny brown spots on the leaves, a typical symptom frequently occurring with rice. |
| **Manganese (Mn)** | |
| Deficiency | Interveinal chlorosis of young leaves while the leaves and plants remain generally green in color. When severe, the plants will be stunted. |
| Excess | Older leaves will show brown spots surrounded by a chlorotic zone and circle. |
| **Molybdenum (Mo)** | |
| Deficiency | Symptoms will frequently appear similar to N deficiency. Older and middle leaves become chlorotic first, and In some instances, leaf margins are rolled and growth and flower formation are restricted. |
| Excess | Not of common occurrence. |
| **Zinc (Zn)** | |
| Deficiency | Upper leaves will show interveinal chlorosis with an eventual whiting of the affected leaves. Leaves may be small and dis­torted with a rosette form. |
| Excess | An Fe deficiency will develop. |

Chapter 4

Phytochrome

**Introduction of phytochrome**

Phytochrome is a photoreceptor, a pigment that plants, and some bacteria and fungi, use to detect light. It is sensitive to light in the red and far-red region of the visible spectrum. In other word a blue-green pigment found in many plants, in which it regulates various developmental processes.Many flowering plants use it to regulate the time of flowering based on the length of day and night (photoperiodism) and to set circadian rhythms. It also regulates other responses including the germination of seeds(photoblasty), elongation of seedlings, the size, shape and number of leaves etc.

This pigment has a regulatory role in all phases of plant growth and development (photomorphogenesis) and is apparently ubiquitous in all taxonomic groups of eukaryotic plants with the exception of fungi.

Light, in addition to providing the energy which drives photosynthesis,also acts as a regulatory environmental stimulus. Many light-controlled plant responses are now believed to be mediated by the photoreceptor, phytochrome.Other plant photoreceptors include cryptochromes, phototropins, and UVR8, which are sensitive to light in the blue and ultra-violet regions of the spectrum.

# Forms of phytochrome

phytochrome has two different chemical structures that are inter-convertible. The forms are named by the color of light that they absorb maximally.

Pr is a blue form that absorbs red light and Pfr is a blue-green form that absorbs far-red light

The phytochrome molecule is the photoreceptor for red light responses. It exists in two forms, Pr and Pfr. Phytochrome is a family of proteins with a small covalently-bound pigment molecule. Phytochrome proteins occur as a dimer of two identical polypeptides, When the chromophore absorbs light, there is a slight change in its structure.

The pigment is called the chromophore. It is a linear tetrapyrrole.(4pyrrol ring).

# The Pr form:

* Absorbs at a peak of 660nm
* Is the form synthesized in dark-grown seedlings.
* When Pr absorbs red light, it is converted to the Pfr form

# The Pfr form:

* Absorbs at a peak of 730 nm.
* The **Pfr** form is the active form that initiates biological responses.
* When **Pfr** absorbs far red light, it is converted to the Pr form.

# What is strange about these pigments ????

When these pigments absorbed light (photon), they change chemically into the OTHER form. The two forms of phytochrome differ in their absorption spectra.

# Discovery

The phytochrome pigments was discovered by sterling hendricks and harry borthwick at the agricultural research center in maryland during a period from the late 1940s to the early 1960s .

By using spectrograph( an apparatus for photographing or recording spectra)

# Plant pigment – phytochrome

A plant pigment is any type of colored substance produced by a plant. In general, any chemical compound which absorbs visible radiation between about 380 nm (violet) and 760 nm (ruby-red) is considered a pigment.

There are many different plant pigments, and they are found in different classes of organic compounds.

Plant pigments give color to leaves, flowers, and fruits and are also important in controlling photosynthesis, growth, and development.

Phytochrome is a blue-green plant pigment which regulates plant development, including seed germination, stem growth,leaf expansion, pigment synthesis, and flowering.

# .DISTRIBUTION OF PHYTOCHROME

Presence of phytochrome has been known in angiosperms , gymnosperms, liverworts, mosses, ferns and some green algae.

Distribution of phytochrome in grass shoot is variable, but oat, rye and barley seedling all have high concentration in apical rigions of the coleoptile near the shoot apex and in the growing leaf bases.

Phytochrome is present in most organs of all plants investigating, including roots.

In green lower plants phytochrome is permanently localized in conformation in or near the plasma membrane.

# CHARACTERISTICS OF PHYTOCHROME

The action spectrum of the light needed for these responses shows a peak in the red at about 660nm.These responses can be reversed by an be application of far-red light soon after the red treatment.

Sensitive spectrometers can measure a decrease in absorbance at 730nm when sensitive plant tissues are exposed to red light.

The change in absorbance is caused by the conversion of photoreceptor from one structural form to another. The red absorbing form changes to the far red absorbing from when it absorb red light and back again when it absorb far red light.Phytochrome has two different chemical structure that are inter-convertible the form are named by the color of light that they absorb maximally. 1] The Pr form and 2] The Pfr form

# CHEMICAL NATURE

Chemically, phytochrome is a homodimer of two identical polypeptide, each with a molecular weight of 120 kDa. Each polypeptide has a prothetic group call chromophore that is attached via a sulfur atom in a cysteine residue of the polypeptide.

This chromophore is an open chain tetrapyrrole similar to the photosynthetic phycobilin pigment of red algae and cynobacteria.The chromophore, Not the protein , That absorbs the light and causes phytochrome responses. When Pr is converted to Pfr by red light there is apparently a cis-trans isomerization in the chromophore . Alternation of the chromophore in phytochrome then cause several unidentified subtle changes in the structure of phytochrome portion.

# MODE OF ACTION OF PHYTOCHROME

Hartman, the German physiologist has proposed a scheme of phytochrome action red light inactive form Pr Pfr Pfr –X biological form far red light dark decay X. According to Borthwick and Hendricks Pr and Pfr follow several alternative reaction paths since only that could explain the apparently contradictory observations made from time to time. Note X = ATP, NAD+ etc…

H. Smith ( 1970) assumes the phytochrome to be present in the membrane. Inner membrane outer Compartment compartment Pr\*X red light precursor X Pr Pfr\* X biological action far red light Pfr\*X Smith hypothesis for phytocrome action Jaffe’s hypothesis is also entirely speculative. He assumes that phytochrome perhaps causes changes in permeability of the membrane and acts through acetylcholine(Ach).

Evans (1975 ) says that Pfr (or PfrX) “control the flow of reactive substances into several linked and compecting synthetic pathways.”

# MECHANISM OF PHYTOCHROME ACTION

## Phytochrome is believed to act in following ways :

According to Galston and coworkers hydroxylation of flavonoid compound is affected by phytochromes. Mohr, however suggests that radiation infuences some ‘basic metabolic change in the cell’ responsible for many different effects and influences on flavenoid hydroxylation pattern presumably represent only one such change.

works of K.V. Thimann and coworkers suggest that phytochrome action involves the synthesis of nucleic acids and enzymes which may be responsible for the physiological changes. Mohr and others have found evidence to suggest that phytochrome effects are medicated by activation of genes that code for specific messenger RNA molecules which in their turn code for specific enzymes.

# PHYTOCHROME MEDIATED PHYSIOLOGICALE RESPONSES:

Phytochrome has been found to control a number of physiological responses of the plant. e.g. spore germination, chloroplast movement, elongation, bud dormancy, root development,..etc. Numerous plant responses are mediated by phytochrome hence, for convenience of study , they have been divided in to positive, negative and complex responses or as developmental and repaid responses. Positive responses: characterized by initiation or increase of biosynthetic or growth processes e.g. phytocrome mediated anthocynin synthesis.

Negative responses: those involving inhibition of growth processes or other physiological processes like translocation of substance e.g. inhibition of hypocotyls elongation by light.

complex responses; Those which are characterized by initially an inhibition and later promotion of the responses as compared to corresponding dark control e.g. light controlled regulation of oxygen uptake by cotyledons.

# DEVELOPMENTAL AND RAPID RESPONSES

Developmental responses: those responses which are mediated by phytochrome but also involve other physiological processes like growth, differentiation certain periodic phenomenon and longer time for production of the responses e.g. photoperiodism and germination

Rapid responses : those which are detectable within a very short period after germination irradiation and do not apparently interact with complex physiological processes e.g. closing of mimosa leaflets.

# ROLE OF PHYTOCHROME

Many flowering plants use it to regulate the time of flowering based on the length of day and night (photoperiodism) and to set circadian rhythms. θ It also regulates other responses including the germination of seeds, elongation of seedling, the size, shape and number of leaves the synthesis of chlorophyll and the straightening of the epicotyl or hypocotyl hook of dicot seedlings.

# Photomorphogenesis

The process by which plant development is controlled by light is called photo- morphogenesis , typically photomorphogenic responses are most obvious in germinating seedlings but light affects plant development in many ways throughout all stages of development

* Light has profound effects on the development of plants .
* Most striking effects of light are observed when a germinating seedling emerges from the soil and exposed to light for first time .
* Normally the seedling radicle ( root) emerge first from the seed,
* And shoot appears as the root becomes established . Later , with growth of the shoot ( particularly when it emerge into the light) there is increased secondary root formation and branching . • Simply it’s a coordinated progression of developmental responses ..
* In this phenomena where the root affects the growth of the shoot and vice versa , to a large degree , the growth responses are hormones mediated.

# Analysis of Photomorphogenesis

* Plants exhibit different growth habits in dark and light
* In the dark they have elongated stems, undifferentiated chloroplasts and unexpanded leaves. This is called skotomorphogenesis.
* Photomorphogenesis (light grown) involves the inhibition of stem elongation, the differentiation of chloroplasts and accumulation of chlorophyll, and the expansion of leaves.
* Thus the same stimulus causes opposite effects on cell elongation in leaves and stems. Photomorphogenesis can be induced by red, far red and blue light.
* You know that a pigment absorbs light and is altered electronically .
* results in a change in other chemicals in the immediate environment to drive photosynthesis.
* Chlorophyll is not the only important pigment, you learned about antenna pigments too. Today we are examining a pigment that fundamentally alters plant behavior. It is phytochrome.
* Now the seed germination laboratory exercise with lettuce demonstrates a classic phytochrome effect.
* The seeds germinate better in red light and fail in far-red light compared to control seeds in kept in darkness.

# Biosynthesis of phytochrome..

* Phytochrome is produced in different parts of the cell and assembled from those parts.
* The phytochrome binding protein is coded in nuclear genes, transcribed in the nucleus and translated on cytosolic ribosomes.
* The phytochrome chromophore is produced in the plastid. These are assembled in the cytosol.
* phytochrome has been found to be associated with plastids in terms of final destination.
* The phytochrome protein includes a kinase domain that, after exposure to red light (i.e. when the chromophore is in Pfr form), allows the protein to phosphorylate itself. This way the autophosphorylation of phytochrome protein activates it.

# photoperiodism

* The response of an organism to seasonal changes in day length.
* Many flowering plants (angiosperms) use a photoreceptor protein, such as phytochrome or cryptochrome,to sense seasonal changes in night length, or photoperiod, which they take as signals to flower.

# Phytochrome system…

* The phytochrome system acts as a biological light switch. It monitors the level, intensity, duration, and color of environmental light.
* The biologically-inactive form of phytochrome (Pr) is converted to the biologically-active form Pfr under illumination with red light. Far-red light and darkness convert the molecule back to the inactive form.
* Pfr can slowly revert to Pr in the dark or break down over time. and then physiological response induced by red light is reversed. The active form of phytochrome (Pfr) can directly activate other molecules in the cytoplasm, or it can be trafficked to the nucleus, where it directly activates or represses specific gene expression.

# Circadian clock in plants..

Circadian rhythms govern many plant processes, including movements of organs such as leaves and petals, stomata opening, stem elongation, sensitivity to light of floral induction, metabolic processes such as respiration and photosynthesis and expression of a large number of different genes.

Chapter 5

Control of Flowering

# Photoperiodism:

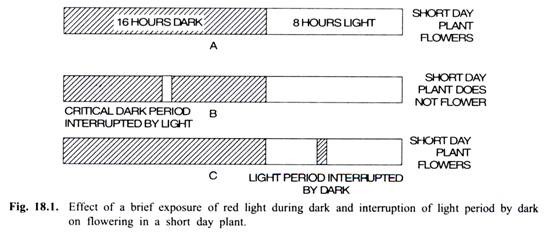
Photoperiodism is the phenomenon of physiological changes that occur in plants in response to relative length of day and night (i.e. photoperiod). The response of the plants to the photoperiod, expressed in the form of flowering is also called as photoperiodism. The phenomenon of photoperiodism was first discovered by Garner and Allard (1920).

The plants in order to flower require a certain day length i.e., the relative length of day and night which is called as photoperiod. The response of plants to the photoperiod expressed in the form of flowering is called as photoperiodism. The phenomenon of photoperiodism was first discovered by Garner and Allard (1920, 22) who observed that the Biloxi variety of Soybeans (Glycine max) and ‘Maryland Mammoth’ variety of tobacco (Nicotiana tabacum) could be made to flower only when the daily exposure to the light was reduced below a certain critical duration and after many complex experiments concluded that ‘the relative length of the day is a factor of the first importance in the growth and development of plants’. Depending upon the duration of the photoperiod, they classified plants into three categories.

## (1) Short Day Plants (SDP):

These plants require a relatively short day light period (usually 8-10 hours) and a continu­ous dark period of about 14-16 hours for subsequent flowering (Fig. 18.1A). Some examples of these plants which are also known as long-night-plants are Maryland Mammoth variety of to­bacco (Nicotiana tabacum) Biloxi variety of Soybeans (Glycine max), Cocklebur (Xanthium pennsylvanicum).

i. In short day plants the dark period is critical and must be continuous. If this dark period is interrupted even with a brief exposure of red light (660-665 mµ wavelength), the short day plant will not flower (Fig. 18.1B).

**[](http://cdn.biologydiscussion.com/wp-content/uploads/2016/02/clip_image002-242.jpg)**

ii. Maximum inhibition of flowering with red light occurs at about the middle of critical dark period.

iii. However, the inhibitory effect of red light can be overcome by a subsequent exposure with far-red light (730-735 mu wavelengths).

iv. Interruption of the light period by dark does not have inhibitory effect on flowering in short day plants (Fig. 18.1 C).

v. Prolongation of the continuous dark period initiates early flowering in short day plants.

## (2) Long Day Plants (LDP):

These plants require a longer day light period (usually 14-16 hours) in a 24 hours cycle for subsequent flowering. Some examples of these plants which are also called as short night plants are Hyoscyamus niger (Henbane) Spinacea (spinach) Beta vulgaris (Sugar beet).

i. In long day plants the light period is critical.

ii. A brief exposure in the dark period or the prolongation of the light period stimulates flowering in long day plants.

## (3) Day Neutral Plants:

These plants flower in all photoperiods ranging from 5 hours to 24 hours continuous ex­posure. Some of the examples of these plants are tomato, cotton, sunflower, cucumber and certain varieties of peas and tobacco.

During recent years certain intermediate categories of plants have also been recognised. They are,

# Long Short Day Plants:

These are short day plants but must be exposed to long days during early periods of growth for subsequent flowering. Some of the examples of these plants are certain species of Bryophyllum.

# Short-Long Day Plants:

These are long day plants but must be exposed to short days during early periods of growth for subsequent flowering. Some of the examples of these plants are certain varieties of wheat (Triticum) and rye (Secale).

# Photoperiodic Induction:

Plants may require one or more inductive cycles for flowering. An appropriate photo­period in 24 hours cycle constitutes one inductive cycle. If a plant which has received suf­ficient inductive cycles is subsequently placed under un-favourable photoperiods, it will still flower. Flowering will also occur if a plant receives inductive cycles after intervals of un-favourable photoperiods (i.e., discontinuous inductive cycles). This persistence of photo­periodic after effect is called as photoperiodic induction.

i. An increase in the number of inductive cycles results in early flowering of the plant. For instance Xanthium (a short day plant) requires only one inductive cycle and normally flowers after about 64 days. It can be made to flower even after 13 days if it has received 4-8 inductive cycles. In such cases the number of flowers is also increased.

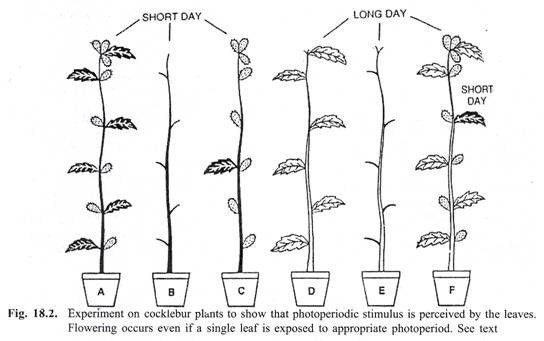
ii. Continuous inductive cycles promote early flowering than discontinuous inductive cycles.

Some of the example of plants which require more than one inductive cycles for sub­sequent flowering are Biloxi soybean (SDP) —2 inductive cycles; Salvia occidentalis (SDP) — 17 inductive cycles; Plantago lanceolata (LDP)—25 inductive cycles.

Perception of the Photoperiodic Stimulus and Presence of a Floral Hormone:

It is now well established that the photoperiodic stimulus is perceived by the leaves. As a result, a floral hormone is produced in the leaves which is then trans located to the apical tip, subsequently causing the initiation of floral primordia.

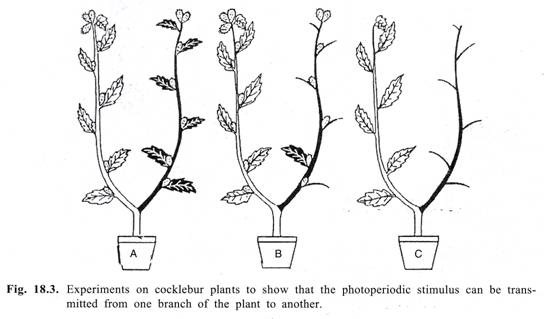
That the photoperiodic stimulus is perceived by the leaves can be shown by simple ex­periments on cocklebur (Xanthium pennsylvanicum), a short day plant. Cocklebur plant will flower if it has previously been kept under short-day conditions (Fig. A). If the plant is defoliated and then kept under short day condition, it will not flower (Fig. B). Flowering will also occur even if all the leaves of the plant except one leaf have been removed (Fig. C).

**[](http://cdn.biologydiscussion.com/wp-content/uploads/2016/02/clip_image004-172.jpg)**

If a cocklebur plant whether intact of defoliated, is kept under long day conditions it will not flower (Fig. D, E). But, if even one of its leaves is exposed to short day condition and the rest are under long day photoperiods, flowering will occur (Fig. F).

The photoperiodic stimulus can be transmitted from one branch of the plant to another branch. For example, if in a two branched cocklebur plant one branch is exposed to short day and other to long day photo period, flowering occurs on both the branches (Fig. A).

Flowering also occurs if one branch is kept under long day conditions and other branch from which all the leaves except one have been removed is exposed to short day condition (Fig. B). However, if one branch is exposed to long photoperiod and the other has been defoliated under short day condition, flow­ering will not occur in any of the branches (Fig. C).

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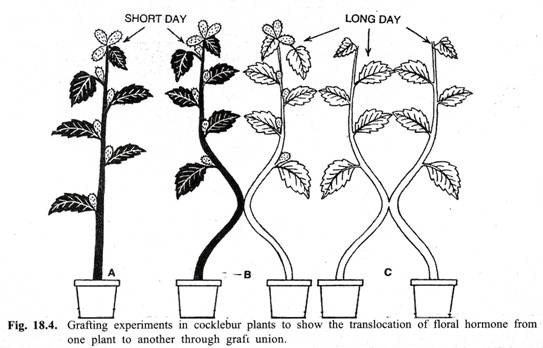
# Nature of the Floral Hormone:

Although there are firm evidences for the existence of a floral hormone but it has not yet been isolated. Therefore, the nature of this hormone which has been named as florigen is not very clear. But it is quite evident that this hormone is a material substance which can be trans located from leaves to the apical tips situated at other parts of the plant resulting in flowering.

Recent researches are indicative of ‘florigen’ to be a macromolecule unlike other plant growth hormones which are rather small molecules. This macromolecule may possibly be a RNA or protein molecule which is trans located from the leaf to the apical tips (or meristems) via phloem in photo-induced plants (Corbesier and Coupland, 2005).

Grafting experiments in cocklebur plants have even proved that the floral hormone can be trans located from one plant to another. For example, if one branched cocklebur plant (Fig. A) which has been exposed to short day conditions is grafted to another cocklebur plant kept under long day conditions, flowering occurs on both the plants (Fig. B).

Obviously the flo­ral hormone has been transmitted to the receptor plant through graft union. But if a cocklebur plant is grafted to another similar plant both of which have been kept under long day condi­tions, flowering will not occur on either of the two plants (Fig. C).

**[](http://cdn.biologydiscussion.com/wp-content/uploads/2016/02/clip_image007-60.jpg)**

It has also been indicated that the floral hormone may be identical in short-day and long- day plants. For example, grafting experiments between certain long-day plants and short-day plants have shown that flowering occurs on both the plants even if one of them has been kept under non-inductive photoperiods.

# Phytochrome:

It has already been seen that a brief exposure with red light during critical dark period inhibits flowering in short-day plants and this inhibitory effect can be reversed by a subse­quent exposure with far-red light. Similarly, the prolongation of the critical light period or the interruption of the dark period stimulates flowering in long-day plants. This inhibition of flowering in short-day plants and the stimulation of flowering in long-day plants involves the operation of a proteinaceous pigment called as phytochrome.

## i. The pigment phytochrome exists in two different forms:

(i) Red light absorbing from which is designated as PR and

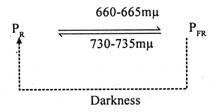
(ii) Far-red light absorbing form which is designated as PFR.

ii. These two forms of the pigment are photo chemically inter convertible.

iii. When PR form of the pigment absorbs red light (660-665mp), it is converted into PFR form.

iv. When PFR form of the pigment absorbs far-red light (730-735mp), it is converted into PR form.

v. The PFR form of the pigment gradually changes into PR form in dark.

**[](http://cdn.biologydiscussion.com/wp-content/uploads/2016/02/clip_image009-54.jpg)**

It is considered that during the day the PFR form of the pigments is accumulated in the plant which is inhibitory to flowering in short-day plants but is stimulatory in long–day plants. During critical dark period in short-day plants, this form gradually changes into PR form result­ing in flowering.

A brief exposure with red light will convert this form again into PR form thus inhibiting flowering. Reversal of the inhibitory effect of red light during critical dark period in SDP by subsequent far-red light exposure is because the PFR form after absorbing far-red light (730-735mµ) will again be converted back into PR form.

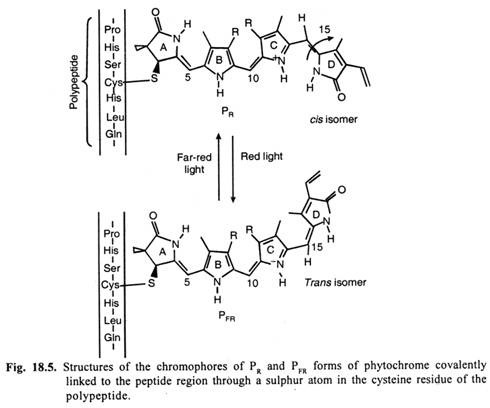
Prolongation of the critical light period or the interruption of the dark period by red-light in long-day plants will result in further accumulation of the PPR form of the pigment, thus stimu­lating flowering in long-day plants.

Successful purification of intact native phytochrome (from etiolated oat seedlings) was first re­ported by Vierstra and Quail in 1983. The native phytochrome is a soluble protein with a molecular weight of about 250 kDa. It’s a homodimer of two identical polypeptides each with a molecular weight of about 125 kDa.

Each polypeptide has a prosthetic group called as chromophore which is covalently linked to the polypeptide via a sulphur atom (Thioether Linkage) in the cysteine residue of the polypeptide. The protein part of the phytochrome is called as apoprotein. Apoprotein along with chromophore constitute holoprotein.

The chromophore of phytochrome is an open tetrapyrrole which is related to phycocyanobilin in structure and therefore, more recently this chromophore has been called as phytochromobilin. The structures of chromophores or the prosthetic groups of PR and PFR fomis of phytochrome which are cis and trans isomers of each other respectively, are given in Fig 18.5. The cis-trans isomerization occurs at carbon-15 in response to red and far-red light.

Apart from absorbing red and far-red light, the phytochrome also absorbs blue light. The PR form of phytochrome is blue while PFR form is olive-green in colour. But owing to very low conc. of phytochrome, the colour of this pigment is not visible in plant tissues. (Phytochrome accounts for less than 0.2 % of the total extractable protein in etiolated seedlings).

**[](http://cdn.biologydiscussion.com/wp-content/uploads/2016/02/clip_image011-55.jpg)**

None of the two components of phytochrome i.e., apoprotein and chromophore, can absorb light alone.

Phytochromes have been detected in wide range of plants in angiosperms, gymnosperms, bryophytes and algae. Dark grown etiolated seedlings are richest sources of phytochrome where this pigment is especially concentrated in apical meristems. (Etiolated seedlings have therefore been used extensively in this connection).

Phytochromes have directly been detected in different parts of seedlings, in roots, cotyledons, hypocotyls, epicotyls, coleoptile, stems, petioles, leaf blades, vegetative buds, floral receptacles, inflorescences, developing fruits and seeds. Presence of phytochrome has also been shown indirectly in other plant materials.

Within the cells, phytochrome exists in nucleus and throughout the cytosol.The chromophore of phytochrme is synthesized in plastids while apoprotein is synthe­sized on nuclear genome. Assembly of these two components of phytochrome is autocatalytic and occurs in cytosol.

There are two major types of phytochromes in plants, (i) type I and (ii) type II. The type I predominates in etiolated seedlings while type II in green plants and seeds (such as oat seeds). There are minor differences in molecular weight and spectral properties of these two types of phytochromes.Type I phytochrome is encoded by PHY A gene while type II is encoded by PHY B, PHY C, PHY D and PHY E genes.

The exact mechanism of the action of phytochromes is not very clear. They act probably (a) by controlling active transport of ions and molecules across membranes probably by regulating ATPase activity, (b) by controlling the activity of membrane bound hormones such as gibberellins (c) modulating the activity of membrane bound proteins and (d) by regulating tran­scription of numerous genes involving multiple signal transduction pathways.(Besides photoperiodism, a large number of phytochrome mediated phtoresponses are known in plants. A list of some of these photoresponses is given at the end of this chapter. See Chapter 25 for more information regarding phytochrome and related phenomena).

# Gibberellins and the Flowering Response:

It is now well known that the gibberellins can induce flowering in long-day plants even under non-inductive short days. It is also definite that the gibberellins alone do not constitute the ‘florigen’, but it is usually held that the gibberellins are in some way connected with the overall process of flowering.

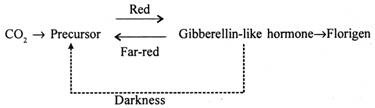
**According to a scheme proposed by Brian (1958), a gibberellin like hormone is produced in the leaves during the photoperiod somewhat as follows:**

CO2 → Precursor (P) → Gibberellin-like hormone

The precursor may be slightly stimulatory or inactive or antagonistic to the gibberellin-like hormone. Red irradiations promote the conversion of the precursor to the gibberellin-like hor­mone. In the dark there is a slow reconversion of the gibberellin-like hormone to the precursor.

This reconversion is accelerated by far-red irradiations. It is further presumed that high concentration of the gibberellin-like hormone leads to the synthesis of florigen in long-day plants. In short-day plants the synthesis of florigen takes place when the level of gibberellin-like hormone is low. But, flowering eventually follows once the florigen synthesis has taken place in both the cases.

# The whole scheme is diagrammatically shown below:

**[](http://cdn.biologydiscussion.com/wp-content/uploads/2016/02/clip_image013-40.jpg)**

# Importance of Photoperiodism:

(i) The knowledge of the phenomenon of photoperiodism has been of great practical importance in hybridisation experiments.

(ii) Although the floral hormone ‘florigen’ has not yet been isolated, the isolation and characterization of this hormone will be of utmost economic importance.

(iii) The phenomenon of photoperiodism is an excellent example of physiological preconditioning (or after-effect) where an external factor (i.e., the photoperiodic stimulus) induces some physiological changes in the plant the effect of which is not immediately visible. It lingers on in the plant and prepares the latter for a certain process (i.e., flowering) which takes place at a considerably later stage during the life history of the plant.

# Some Phytochrome Mediated Photo responses in Plants:

* Photoperiodism.
* Seed germination.
* Elongation of leaf, petiole, stem.
* Hypocotyl hook unfolding.
* Unfolding of grass leaf. ,
* Sex expression.
* Bud dormancy.
* Plastid morphology.
* Plastid orientation.
* Rhizome formation.
* Bulb formation.
* Leaf abscission.
* Epinasty.
* Succulency
* Enlargement of cotyledons.
* Hair formation along cotyledons.
* Formation of leaf primordia.
* Flower induction.
* Differentiation of primary leaves.
* Formation of tracheary elements.
* Differentiation of stomata.
* Change in rate of cell respiration.
* Formation of phenylalanine deaminase.
* Synthesis of anthocyanins.
* Increases in protein systhesis.
* Increase in RNA synthesis.
* Changes in the rate of fat degradation.
* Changes in the rate of degradation of reserve proteins.
* Auxin catabolism.
* Incorporation of sucrose into plumular tissue.
* Permeability of cell membranes.

# VERNALIZATION

Vernalization word derived (from Latin vernus, "of the spring")

Literal meaning of vernalisation is bringing to spring condition.

For some plants , vernalization is an absolute requirement or in some cases it simply assists in flowering.

The duration of low temperature treatment required varies from four days to three months. “Vernalization is the induction of a plant's flowering process by exposure to the prolonged cold of winter, or by an artificial equivalent”.

# HISTORY

John Hancock Klippart,1857- first noticed the low temperature requirement for flowering while working with winter wheat and spring wheat.

Lysenko,1938-published his works on the effects of cold on cereal seeds, and coined the term “Jarovization” (Jarovoe in Russian, originally meaning fire or the god of spring) later, translated the term into “Vernalization"

P.Chouard ,1960- defined vernalization as “acquisition or acceleration of the ability to flower by a chilling treatment”.

# TYPES OF VERNALIZATION

## 1.FACULTATIVE VERNALIZATION

Flowering will appear earlier once exposed to low temperature. Eg., Winter annual Triticale (fig 1)

2. OBLIGATE VERNALIZATION Must expose to low temperature to a desired period of time Eg., Biennial plants (Cabbage)

# SITE OF VERNALIZATION

Metabolic active apical meristem is the site of temperature perception for flower initiation.

Younger leaves are more susceptible to vernalization.

The low temperature stimulus is received by the shoot apex of a mature stem or **embryo of the seed.**

# TECHNIQUE OF VERNALIZATION

The seeds are first soaked in water and allowed to germinate in processing chamber at 10-12˚C temperature Then seeds are transferred to low temperature (3-5)˚C and kept for correct period of time. Seeds are dried and sown in the field in proper oxygen and water supply condition (Which varies among different varieties, from few days to 30 days)

# VERNALIZATION AND AGE OF PLANTS

In cereals vernalization best occurs in germinating seeds and even at embryonic stage in mother plant. In the opinion of Sarkar (1958)

Hyoscyamus niger gets maximum sensitivity to chilling effect after 30 days of growth.

In Oenothera maximum sensitivity to low temperature occurs only when the plants bear 6-8 leaves

# MECHANISM OF VERNALIZATION Two theories..

1. Hypothesis of Hormonal involvement

2. Hypothesis of Phasic development

# Hypothesis of Hormonal involvement

Proposed by Chailakhyan

Vernalin’ is produced in some biennials (winter cereals) and perennials (Chrysanthemum , apple) at low temperatures.

In long day plants vernalin is converted into gibberellin (‘Anthesin’ is present in long day plants).

‘Anthesin’ along with ‘vernalin’ cause flowering in long day plants.

But in short day condition ,the vernalin is not converted to gibberellin (because they lack anthesin),hence flowering does not occur

# Hypothesis of Phasic development

Proposed by Lysenko, The development of annual seed plant consists of a series of phases, which occurs in predetermined sequence, next phase only initiates on the termination of the previous phase. There are two phases

* Thermostage
* Photostage

# Thermostage

It is vegetative phase which requires low temperature (0 -14˚C) and suitable moisture and aeration.

This stage is of variable length and depends on the nature of plants and environment.

# Photostage

This phase requires high temperature.

Here vernalin helps in synthesis of florigen. Winter wheat complete their life cycle more rapidly when given a short day and low temperature during thermostage and a long day and higher temperature in photostage.

# VERNALIZATION STIMULUS

It is received by vernalin ( a postulated chemical ). Transmission of vernalization stimulus across a graft union in Hyoscyamus niger has been studied by a German botanist , G.Melchers (1939)

He took two plants/two branches , one previously vernalized and other unvernalized and grafted them together . Both flowered in appropriate photoperiod condition , but unvernalized plant alone failed to flower. From above experiment it is obvious that vernalization stimulus is transmitted from vernalized to unvernalized plant/branch .Experiments to demonstrate that flowering stimulus can translocate from vernalized plant to unvernalized plant through graft union

# HORMONAL MECHANISM OF VERNALIZATION

The genes VIN3, VRN1 and VRN2 act to let the plants know that enough winter weather has occurred and the hold on flower development (via FLC and FRI) can be let go.

The gene FLC functions to keep plants from flowering, while genes like AP1, SOC1, FT, and LEAFY turn on genes to promote flower production. In perennials and winter annual plants, FRI serves to keep plants from flowering through the work of FLC until a certain amount of winter temperatures have passed.

# FACTORS AFFECTING VERNALIZATION

## 1.Water and Oxygen

Seed need to imbibe 10-20 % water, dry seed cannot be vernalized.

Similarly oxygen is also necessary for vernalization. Oxygen is used during respiration. A germinating seed need energy. This energy is provided by respiration. The inhibition of respiration blocks the process of vernalization.

## 2.Temperature

The seeds are exposed to low temperature during vernalization.

Temperature lower than 4°C is not effective. Similarly, temperature above 12°C does not cause vernalization,the duration of vernalization varies in different species.

## 3.Devernalization

The exposing of vernalized seed to high temperature (30 -35°C) , lose the effect of vernalization called as Devernalization.

## 4.Effect of light

The seed of a plant can be vernalized in the presence or absence of light,

But many plants like carrot require both vernalization and photoperiodic stimulus. They must be first vernalized. Then are given photoperiodic stimulus for flowering. 5.Effect of hormones Many species like carrot and Hyoscyamus have obligate vernalization requirement. These plants show rapid flowering after vernalization due to GA synthesis,It causes both bolting and flowering.

# PRACTICAL APPLICATIONS

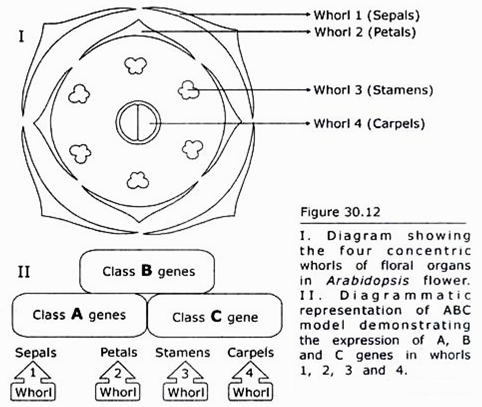
* Due to vernalization the vegetative period of the plant is cut short resulting in an early flowering.
* Vernalization increases the resistance of plants to fungal diseases.
* It increases the cold resistance of plants.
* In the biennials ,vernalization induces early flowering and early fruit setting.
* Flowering can be induced by grafting and this feature is used in horticulture. It also helps in crop improvement.
* Effect of vernalization on seed production of onion -Esmat Jahan Ami.
* Bulbs of 20 ±1g size of local cultivar Taherpuri were used as planting material and were vernalized at the duration of 14 days in freezing.
* The experiment consisted two levels of vernalization 1.Vernalization of mother bulbs at 5°c ± 1 2. No Vernalization
* Cold treatment of mother bulbs influenced the plant to produce maximum number of leaves,maximum seeds per umbel were produced from the bulbs vernalized at 5°c ± 1.

# ABC model of floral genes identity

The ABC model of flower development in angiosperm demonstrates the presence of three classes of genes that regulate the development of floral organs. The genes are referred to as class A genes, class B genes and class C gene. These genes and the interaction between them induce the development of floral organs.

Many literatures on molecular genetics and Internet Websites provide articles on ABC model. In the following essay the basic concept of ABC model will be discussed in brief. The analysis of ABC model is based on the use of molecular genetics and formulated on the observation that mutants induce right floral organs to develop in wrong whorls.

In the flower of angiosperms there are usually four concentric whorls of organs, i.e. sepal, petal, stamen and carpel that are formed in whorl 1, whorl 2, whorl 3 and whorl 4 respectively, the whorl 1 being on the peripheral side.In the whorl 1 class A genes when expressed induce the development of sepals. The interaction between class A and class B genes induce the development of petals in the whorl 2. Stamens are formed in the whorl 3 as a result of interaction between class B and class C genes.In the whorl 4 class C gene induces the formation of carpel. So the summary of ABC model is: class A genes together and class C gene alone are responsible for the development of sepals and carpel respectively. The class B genes and class A genes function cooperatively to determine the development of petals. The class B genes and class C gene act together to induce the development of stamens (Fig. 30.12).

[](http://cdn.biologydiscussion.com/wp-content/uploads/2016/12/image-187.png)

Coen et al. (1991) formulated the ABC model. While analyzing the mutations affecting flower structure Coen et al. identified the class ABC genes that direct flower development. They also formulated the molecular models of how floral meristem and organ identity may be specified. They have shown that the distantly related angiosperm plants use homologous mechanisms in pattern formation of floral organs. Ex. Arabidopsis thaliana and Antirrhinum majus.

# The following two have led to formulate ABC model:

(1) The discovery of homeotic mutants (homeotic genes identify specific floral organs and help the organ to develop in respective whorl. The homeotic mutant has inappropriate expression—that is, it induces right organ to develop in wrong whorl. As for example — petals emerge in the whorl where normally stamens develop).

(2) The observation that each of the genes that induce the formation of an organ in a flower has an effect on two groups of floral organs, i.e. sepal and petals or petals and stamens.

Class A, B and C genes are homeotic genes. They determine the identity of different floral organs and induce the organs to develop in their respective whorls.

The homeotic mutants have defects in floral organ development and induce the right organs to develop in wrong whorls/place, i.e. one floral organ develops in the whorl, which is the normal position of another floral organs. Petals, for example, develop in the whorl where stamens are normally to be formed.

In each whorl of a flower there is one or more homeotic genes and their cooperative functions determine the organ to be formed in that whorl. For example, the activity of class A genes is restricted to whorls 1 and 2. The class B genes have function in whorls 2 and 3. The class C gene functions in whorls 3 and 4.

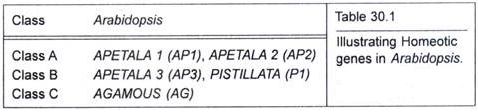
Another way of describing the function of class A, B and C genes is that—in whorl 1, the class A gene-function alone determines the formation of sepals; in whorl 2, class A and B gene-functions both determine the formation of petals; in whorl 3, class B and C gene-functions both determine the emergence of stamens and in whorl 4, class C gene-function alone determines the carpel formation.

In Arabidopsis there are two genes in class A, two genes in class B and one gene in class C (Table 30.1). The most characteristic feature of these homeotic genes is in the identification of floral organs and in the determinacy of position / whorl of their emergence in a floral meristem. The two genes of class A and the two genes of class B act cooperatively.

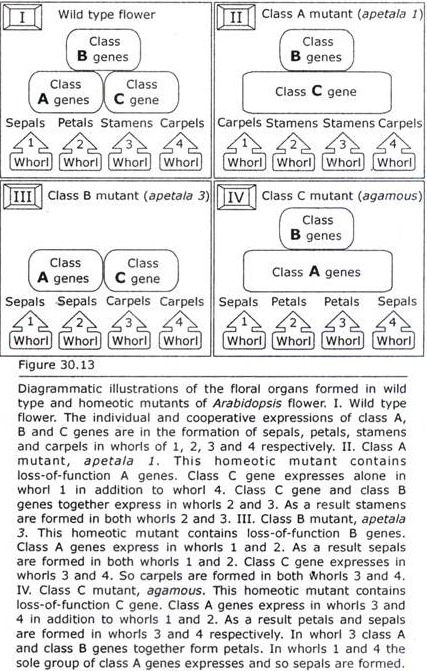
The function of class A genes is confined to whorls 1 and 2. Similarly the function of class C gene is restricted in whorls 3 and 4. This can be interpreted in another way. In the whorls 1 and 2 the function of class A genes prevents class C gene from functioning in the same whorls. Similarly the function of class C gene prevents class A genes from functioning in the whorls 3 and 4.

Any mutation in class A genes with defects in floral organ development will invite class C gene to express in whorls 1 and 2. The class C gene, in class A mutants, will express in whorls 1 and 2 in addition to the normal whorls 3 and 4.

Similarly any mutation in class C gene with defects in floral organ development will lead to the encroachment of the function of class A genes. The class A genes will express in the whorls 3 and 4 in addition to the normal whorls 1 and 2.

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**The following three examples of homeotic mutant genes will illustrate the above discussion (Fig. 30.13):**

[](http://cdn.biologydiscussion.com/wp-content/uploads/2016/12/clip_image006-56.jpg)

(1) The flower of Arabidopsis with class A mutants, such as apetala 1(ap 1) shows the following pattern of floral organs (Fig. 3.13.II): whorl 1 shows bract-like structure with carpelloid characteristics; whorl 2 shows stamens; whorl 3 shows stamens and whorl 4 shows carpel.

The pattern of floral organ formation in whorls 1 and 2 is changed. In ap 1 mutants the activity of two genes of class A is lost. So the class C gene expressed in whorls 1 and 2 in addition to whorls 3 and 4. As a result carpelloid organ developed in whorl 1 and stamens formed in whorl 2. In the whorls 3 and 4 stamens and carpel respectively are formed similar to wild type (Fig. 30.13.I).

(2) Example: Flower of Arabidopsis with class B mutant, such as apetala 3 (ap 3): The flower shows sepals only both in whorls 1 and 2, while the whorls 3 and 4 show carpel only (Fig. 30.13III). Class B mutant contains loss-of-function genes and as a result class A genes express in whorls 1 and 2; and class C gene alone expresses in whorls 3 and 4. In ap 3 mutants in whorl 2, sepals are formed instead of petals and in whorl 3, carpel is formed instead of stamens.

(3) In Arabidopsis the class C gene contains the sole gene agamous (ag). Arabidopsis flower with agamous (ag) mutant consists of many sepals and petals. The reproductive organs – stamens and carpel are not formed in the whorls 3 and 4. Class C gene with ag mutant contains loss-of-function gene. As a result class A genes express in whorls 3 and 4 in addition to 1 and 2. In ag mutant sepals and petals are formed in whorls 3 and 4 instead of stamens and carpel. The literature of Howell provides the scan electron micrograph of flower phenotypes of the floral homeotic mutants of class A, B and C genes.

In Arabidopsis it was observed that in all the mutants one homeotic gene remains functional in each whorl. The flower with class ABC triple mutant shows sepals in each whorl. In ABC triple mutant, the genes required for floral organ formation become nonfunctional. As a result sepals or leaves are formed in each whorl, as homeotic mutants specify no floral organs. This observation led Botanists to regard ‘flowers as modified leaves’ on the basis of molecular genetics.

The important feature of ABC model is that it can predict the type of floral organ to be induced to develop in any whorl. Krizek et al. (1996) was successful to induce any one of the four different floral parts in whorl 1 of Arabidopsis flower. This became possible by genetic manipulations of right combination of homeotic selector genes.

The ABC model appears to be simple, but a completely different picture is obtained when it is analyzed on the basis of molecular genetics and in molecular terms.

The analysis includes the structure of different classes of homeotic genes, the homeotic mutants, the co-operative function between homeotic genes, mutual exclusion in the expression of class A and C genes in the same whorl, the identification of floral homeotic genes and their isolation by cloning, the production of MADS box protein by homeotic mutants, the study of genes that mediate the interaction between floral meristem and floral organ development, presence or absence of different classes of transcription factors etc., the details of which can be obtained in the literatures on molecular genetics.

**Arabidopsis thaliana belongs to the family Brassicaceae and has become the model organism for understanding the genetics and molecular biology of flowering plants like mice and Drosophila in animal researches due to following reasons:**

(i) It has five chromosomes (n = 5) and so this small-size-genome is advantageous in gene mapping and sequencing.

(ii) The size of plant is small and so can be cultivated in a small space and requires modest indoor facilities.

(iii) It has rapid life cycle and takes about six weeks from germination to mature seeds.

(iv) An individual plant produces several thousand seeds.

(v) ‘The Arabidopsis genome is among the smallest in higher plants, with a haploid size of about 100 megabases (mb) of DNA. With a small genome size it was expected that there would be fewer problems with gene duplication’— Howell.

(vi) It is easily transformable with T-DNA mediated transformation.

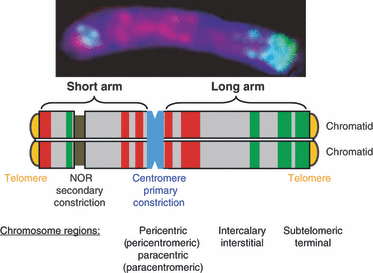
In 2004 ABCE model has been formulated. The characterization of sepallata 1, 2, 3 triple mutants in Arabidopsis has led to the above formulation. It is regarded that the class E genes have important role in the development of floral organs

Chapter 6

Gene Regulation and Signal Transduction

# Plant nuclear genomes

The plant nuclear genome, consisting of the DNA and associated proteins, is organized into discrete chromosomes. Each unreplicated chromosome and metaphase chromatid consists of a single DNA molecule that is linear and unbroken from one end to the other. At metaphase of mitosis, the DNA is condensed into mitotic chromosomes – short, rod like bodies – while at interphase, the chromosomes are decondensed within the interphase nucleus. The study of the chromosome and its organization involves cytogenetics, and the field of molecular cytogenetics has developed to understand DNA sequence and the molecular structure of the chromosome and chromatin. Both the size of the plant genome and the number of chromosomes vary widely between species. In this article we will discuss the nature and consequences of these differences in an evolutionary context.



Top: A fluorescent light micrograph of a metaphase chromosome stained blue with the DNA‐binding fluorochrome 4′,6‐diamidino‐2‐phenylindole(DAPI). *In situ* hybridization shows the location of two tandemly repeated DNA sequences detected by red and green fluorescence.  
Centre: A diagram of the structure of a metaphase chromosome with two chromatids.  
Centromeres or primary constrictions are seen as gaps in cytological chromosome preparations. They nucleate the proteinaceous kinetochore plate to which the spindle microtubules attach and are characterised by specific centromeric histones. DNA sequences at the centromeres are not conserved between species The centromere and the regions surrounding it, called paracentromeric regions, contain large arrays of tandem repeats and are often enriched in transposable elements.

Euchromatin. Lightly stained in cytological preparations generally gene rich, showing high transcriptional activity and higher levels of recombination at meiosis. Transposable elements may be dispersed widely through euchromatin.

Heterochromatin.Strongly stained in cytological preparations rich in highly repeated tandemly organised DNA sequence families and sometimes transposable elements. Heterochromatin generally lacks meiotic recombination and is relatively deficient in genes, and those present often have decreased transcriptional activity.  
*NOR.* Nucleolus organising regions contain the long arrays of 45S rDNA repeat units, including the 18S–5.8S–26S rRNA genes and intergenic spacers. Most genomes have several major and minor rDNA loci Expression of the rRNA genes generates the nucleolus at interphase at metaphase, NORs are often visible as secondary constrictions as the arrays of genes active at the previous interphase remain decondensed.  
*Subtelomeric* or telomere associated sequences (TAS) are long tandem repeats sometimes containing degenerate (TTTAGGG)*n* motifs, and are species specific and often chromosome specific.  
*Telomeres*, at the ends of chromosomes, are relatively short arrays usually of the conserved simple repeat (TTTAGGG)*n.* They maintain chromosome integrity by stabilizing chromosome termini.

# Signal Transduction in Prokaryotes and Eukaryotes

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**Best of Luck**