Study Material

M.Sc. Ag. II semester
Course: Open Elective Course- Plant Physiology
Chapter: 08 (Plan**t** Growth Regulators**)**

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PLANT GROWTH REGULATORS (PGRs)

Concept of PGRs

“Plant growth regulators usually are defined as organic compounds, other than nutrients, that in small concentrations, affect the physiological processes of plants”. In practical purpose, they are defined as either natural or synthetic compounds that are applied directly to plant to alter its life processes/structure in some beneficial way so as to enhance yield, improve quality and facilitate harvesting. When herbicides are applied to induce a specific beneficial change, then they are considered as plant growth regulators. If the compound is produced within the plant it is called a plant hormone. The term "hormone" is derived from a Greek word meaning “to arouse or stimulate or enhance an activity". A plant growth regulator is defined by Environmental Protection Agency (EPA) as “any substance or mixtures of substances intended, through physiological action, to accelerate or retard the rate of growth or maturation or otherwise alter the behavior of plants. Additionally, plant growth regulators are characterized by their low rates of application, while the high application rates of the same compounds often are considered as herbicidal”.

Plant hormones are produced naturally by plants and are essential for regulating their own growth. They act by controlling or modifying plant growth processes, such as formation of leaves and flowers, elongation of stems, development and ripening of fruits. In modern agriculture practices, people have established the benefits of extending the use of plant hormones to regulate growth of other plants. When natural or synthetic substances are used in this manner, they are called Plant Growth Regulators. The application of plant growth regulators in agriculture has started in 1930 in United States. Ethylene, a naturally occurring substance, is one of the first plant hormone to be synthesized artificially and used successfully for enhancing flower production in pineapple. Its toxic effects to human beings are low. Synthetic substances that mimic such naturally occurring plant hormones were also produced, since then the use of plant growth regulators has been growing significantly and becoming a major component in modern agriculture.

Classification of PGRs

The plant growth regulators can be broadly divided into two categories:

(a) **Classical plant hormones** (auxins, cytokinins, gibberellins, abscisic acid, ethylene and growth regulatory substances with similar biological effects.) New, naturally occurring substances in these categories are still being discovered. At the same time, novel structurally related compounds are constantly being synthesized. There are also many new but chemically unrelated compounds with similar hormone-like activity being produced. A better knowledge of the uptake, transport, metabolism, and mode of action of phyto-hormones and the appearance of chemicals that inhibit synthesis, transport, and action of the native plant hormones has increased our knowledge of the role of these hormones in growth and development.

(b) **More recently discovered natural growth substances** that have phytohormonal-like regulatory roles (polyamines, oligosaccharins, salicylates, jasmonates, sterols, brassinosteroids, dehydrodiconiferyl alcohol glucosides, turgorins, systemin, unrelated natural stimulators and inhibitors), as well as myoinositol. Many of these growth active substances have not yet been examined in relation to growth and organized development*in vitro*.

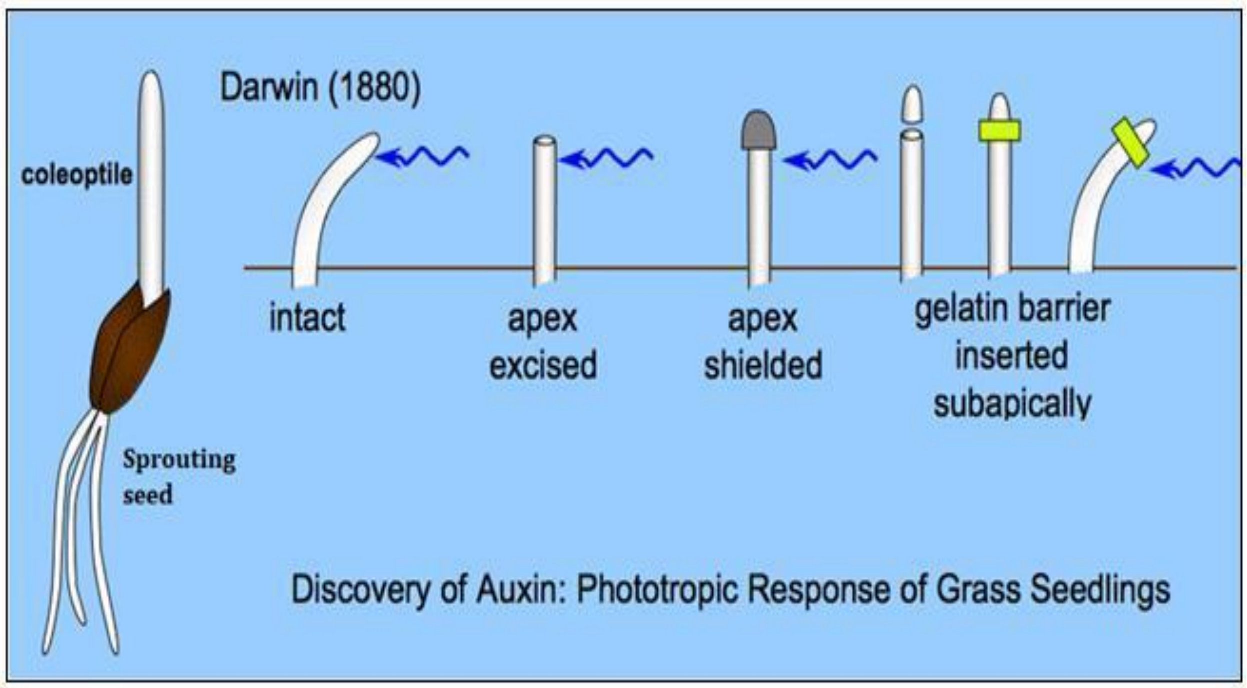
a) CLASSICAL PLANT HORMONES/GROWTH REGULATORS

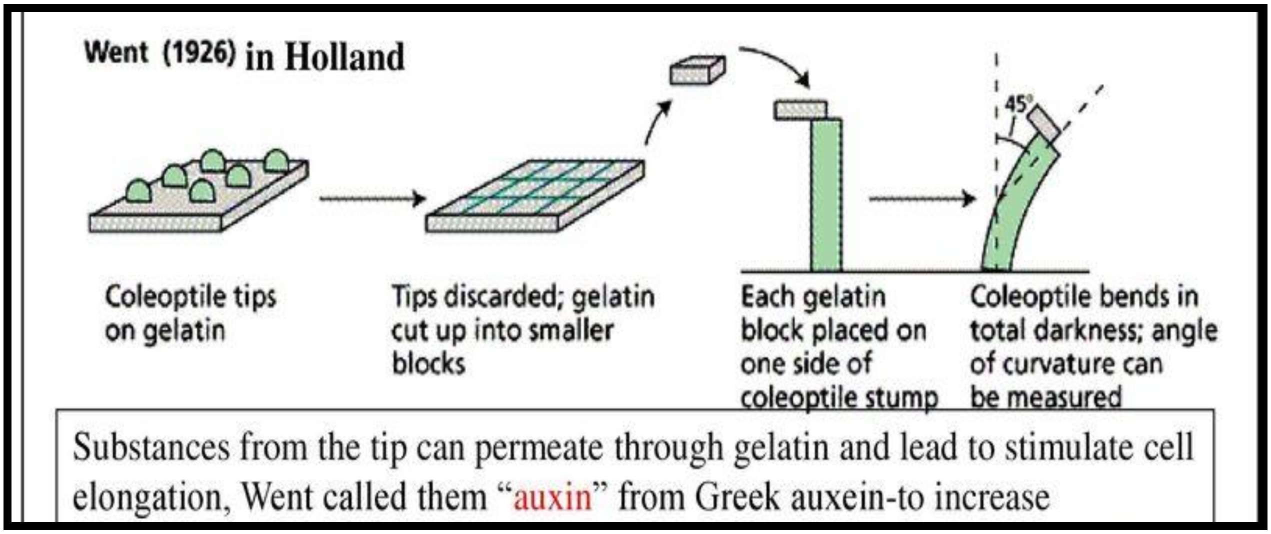
1. AUXINS Auxin is the first plant hormone/growth substance discovered. The term comes from the Greek word, auxein means "to grow". Compounds are generally considered as auxins if they are synthesized by the plant and have similar activity to Indole-3- acetic acid (IAA).

- **Discovery of Auxins**

Charles Darwin was the first scientist who performed early auxin experiments on canary grass (*Phalaris canariensis*) coleoptiles. He observed the effects of a hypothetical substance modulating plant shoot elongation to allow tropic growth toward light.

IAA is the major auxin involved in many of the physiological processes in plants. It was discovered by Salkowski in 1885 in fermentation media. In 1926, a graduate student F. Went from Holland, who isolated a plant growth substance by placing agar blocks under coleoptile tip for some time, then removing and placing them on decapitated Avena stems. After placement of the agar, the stems resumed growth. In 1928, Went developed a method to quantify this growth substance. From which he concluded that the curvatures of stems were proportional to the amount of growth substance in the agar block. This test is known as the avena curvature test. Kogl and Haagen-Smit purified the compound auxentriolic acid (auxin A) from human urine in 1931. After that Kogl isolated other compound from urine, which was IAA, the same was primarily discovered by Salkowski in 1885. Finally in 1954 plant physiologists committee was set up to characterize the group auxin.





Substances from the tip can permeate through gelatin and lead to stimulate cell elongation, Went called them "auxin" from Greek auxein-to increase

- **Apical dominance**

Occurs when the shoot apex inhibits the growth of lateral buds so that the plant may grow vertically. It is important for the plant to devote energy to growing upward so that it can get lighter to undergo photosynthesis. If the plant utilizes available energy for growing upward, it may be able to out compete other individuals in the vicinity. Plants that were capable of outcompeting neighboring plants likely had higher fitness. Apical dominance is therefore most likely adaptive.

Typically, the end of a shoot contains an apical bud, which is the location where shoot growth occurs. The apical bud produces a hormone, auxin, (IAA) that inhibits growth of the lateral buds further down on the stem towards the axillary bud. It was first discovered in 1934 that the plant hormone auxin likely regulates apical dominance. Auxin is predominantly produced in the growing shoot apex and is transported throughout the plant via the phloem and diffuses into lateral buds which prevent elongation.

When the apical bud is removed, the lowered IAA concentration allows the lateral buds to grow and produce new shoots, which compete to become the lead growth.

- **Biosynthesis of Auxin**

IAA is similar to the amino acid tryptophan which is generally accepted to be the precursor molecule from which IAA is derived by different pathways.

1. Tryptophan is converted to indoleacetaldoxime through decarboxylation and then converted to indoleacetonitrile by a dehydration reaction. The final step involves oxidation of indoleacetonitrile results in indoleacetic acid.
2. Tryptophan is converted to indolepyruvic acid through a transamination reaction. Indolepyruvic acid is then converted to indoleacetaldehyde by a decarboxylation reaction; finally oxidation of indoleacetaldehyde, resulting in indoleacetic acid.
3. Tryptophan undergoes decarboxylation resulting in tryptamine. Tryptamine is then oxidized and deaminated to produce indoleacetaldehyde. This molecule is further oxidized to produce indoleacetic acid. In the bacterial biosynthetic pathway monooxygenase converts tryptophan to indoleacetamide and then it is converted to indoleacetic acid by hydrolysis.

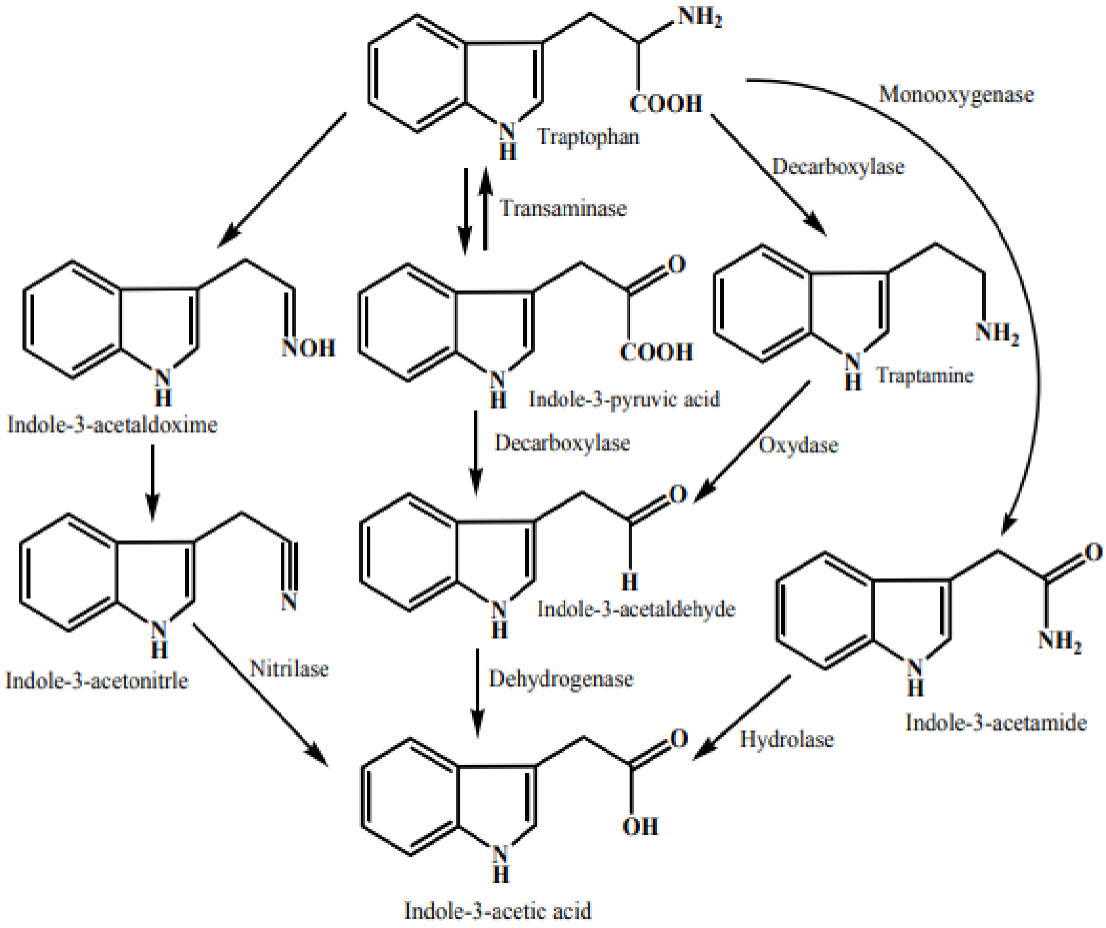


Figure 4: Biosynthetic pathways of IAA

- **Functions:** The following are some of the responses that auxin is known to cause:

1. Stimulates cell loosening, expansion and elongation.
2. Initiation of adventitious roots on stem cuttings.
3. Lateral root development in tissue culture.
4. Stimulates differentiation of phloem and xylem.
5. Stimulation of abscission (young fruits) or delay of abscission.
6. Stimulates cell division in tissue culture in combination with cytokinins.
7. Mediates the tropistic response of bending in response to gravity and light.

2. GIBBERELLINS

Gibberellins are synthesized in young tissues of the shoots, uncertainly in roots and also in the developing seeds. There are also some evidences that leaves may be the source of some biosynthesis.

- **Discovery of Gibberellin**

A Japanese scientist E. Kurosawa in 1926 found that some of the rice seedlings grow taller than others. He discovered the seedlings to be infected by the pathogenic fungus *Gibberella fujikuroi*. In his work he found that the rice plant diseases bakanae (foolish seedling) caused by this fungus is having some metabolites that might be responsible for the stimulated growth of seedlings. In 1935, an agricultural chemist T. Yabuta isolated a non-crystalline material from the similar type of culture that he named as “gibberellins”. After that, in 1938 he was succeeded in isolating pure pale yellow crystals. In 1950, it was identified as hormones of non-infected plants. All gibberellins are derived from the entgibberellane skeleton. The gibberellins are named GA1, GA2, GA3, ..., GAn in their order of discovery. Gibberellic acid -GA3, was first structurally characterised gibberellin. There are at present 136 GAs that have been identified from plants, fungi and bacteria. They have either 19 or 20 carbon atoms into either four or five ring systems.

- **Biosynthesis of Gibberellins**

Acetyl CoA molecules are oxidized to produce mevalonic acid and CoA molecules. Then Mevalonic acid is phosphorylated by ATP, followed by decarboxylation to form isopentyl pyrophosphate. Four of these molecules react to form geranylgeranyl pyrophosphate which serves as the donor for all GA carbons. This compound is converted to copalylpyrophosphate (2 ring systems) then converted to ent-kaurene (4 ring systems). Successive oxidations give ent-kaurenol (alcohol), ent-kaurenal (aldehyde), ent-kaurenoic acid, ent-7a-hydroxy kaurenoic acid to form the aldehyde of GA12 and it is the 1st true gibberellane (20 carbons ring system). From the aldehyde -GA12 can make both 19 and 20 carbon gibberellins and the other compounds arise by different mechanisms. The primary precursor for formation of gibberellin is acetate.

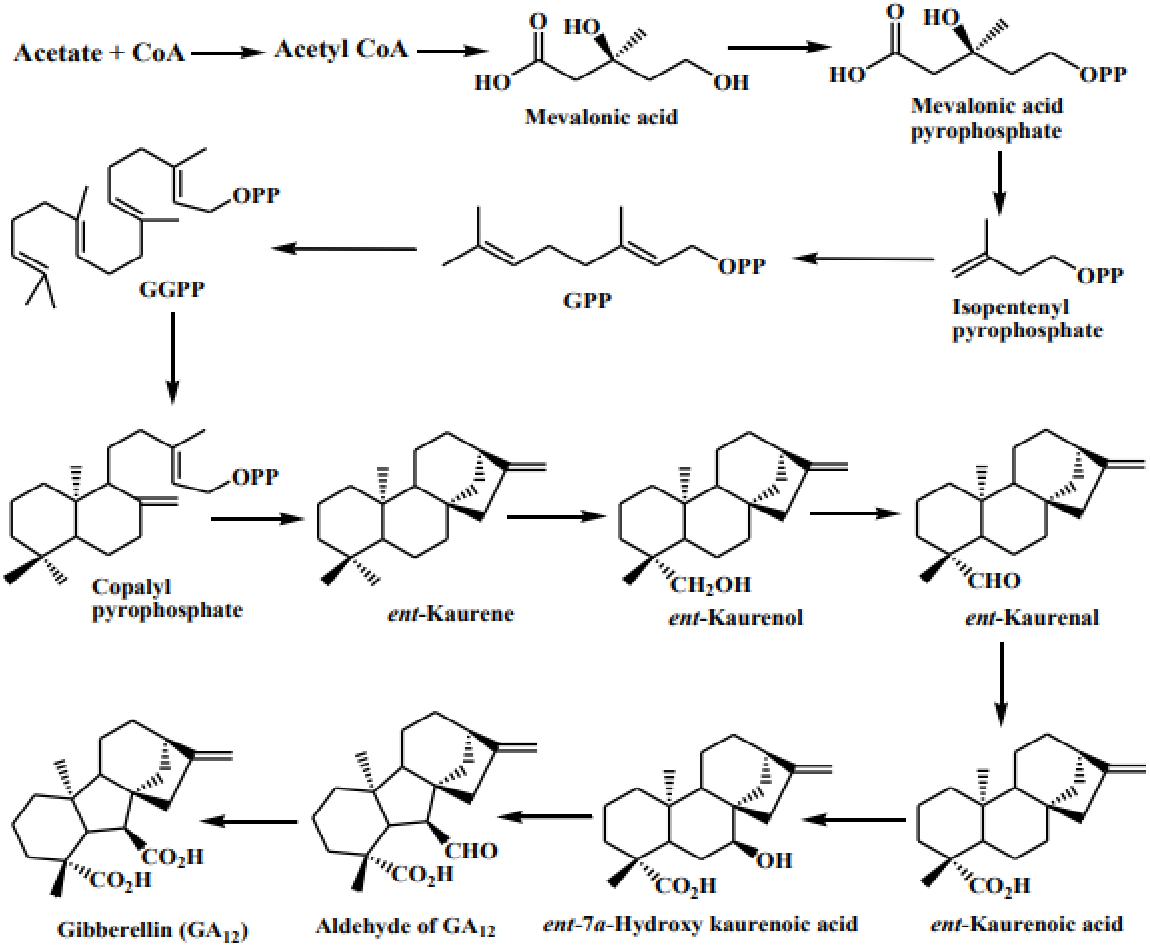


Figure 5: Biosynthetic pathway of gibberellins

- **Functions of Gibberellins**

1. Stimulate cell elongation in stem.
2. Breaks seed dormancy in some plants which requires light for germination.

3. Stimulates alpha-amylase production in germinating cereal grains.
4. Stimulates bolting/flowering in response to long days.
5. Delay senescence in leaves and also in citrus fruits.
6. Induces maleness in dioecious flowers.
7. Play a role in development of seedless fruit (parthenocarpic).

3. CYTOKININS

In Cytokinin, cyto = cell + kinin = division, i.e. meaning is cell division. Cytokinin is also called as cytokine. These are the compounds resembling with adenine (aminopurine) which stimulates cell division.

- **Discovery of Cytokinins**

In 1913, G. Haberlandt found that phloem from various plants had an ability to stimulate cell division in wounded potato tubers. This study implies the existence of soluble factor(s) that could promote cell division in plant. Then after the beneficial effects of plant extracts, including coconut milk, the liquid endosperm from immature fruits, on plant tissue cultures was first shown by Van Overbeek in 1941. In 1950, during the work primarily in F. Skoog‟s laboratory by C. Miller, he identified cytokinin as a factor that promotes cell division in plant. These findings finally led to the isolation of kinetin from old autoclaved herring sperm DNA by C. Miller in 1955, while fresh DNA preparations displayed no effect at all. In the end Kinetin (purine derivative, 6-furfurylaminopurine) was identified as the effective substance, further it was synthesized in 1956. Kinetin and several other similar molecules were initially named as kinin, in order to avoid confusion which was later changed to cytokinin. After the discovery of kinetin and other cytokinins, Skoog and Miller in 1957 demonstrated the hormonal (auxin/cytokinin) regulation of plant morphogenesis. This controlled the formation of shoots/roots in callus tissues culture. It is an exact and an important consideration in understanding plant morphogenesis, micropropagation and regeneration of plants in tissue culture. In 1963, zeatin was isolated from immature sweet corn seeds (*Zea mays*) by D. S. Letham; it was the first natural cytokinin derived from plant that has kinetin-like activity. After all, in 2001 cytokinin biosynthesis in plants was established by Japanese researchers.

- **Biosynthesis of Cytokinins**

Generally, cytokinins are found in more concentrations in meristematic tissues and in growing parts. They are synthesized in roots and translocated to shoots acropetally via xylem; they are synthesized as follows:

There two pathways, methylerythritol phosphate (MEP)-pathway and mevalonic acid (MVA)-pathway both are converted to dimethylallyl pyrophosphate (DMAPP) and which reacts with adenosine diphospate (ADP)/ATP in presence of isopentenyl trasferase then, converted to isopentenyl-adenosine-diphosphate (iPDP)/iPTP, zeatin riboside-diphosphate (ZDP)/ZTP, dihydrozeatin ribosidediphosphate (DHZDP)/DHZTP and to isopentenyl-adenosine-monophosphate (iPMP), zeatin riboside-monophosphate (ZMP), dihydrozeatin riboside-monophosphate (DHZMP) and to isopentenyl adenosine (iPA), zeatin riboside (ZR), dihydrozeatin riboside (DHZR) and to isopentenyl adenine (iP), zeatin (Z), dihydrozeatin (DHZ), respectively and also to cis-zeatin.

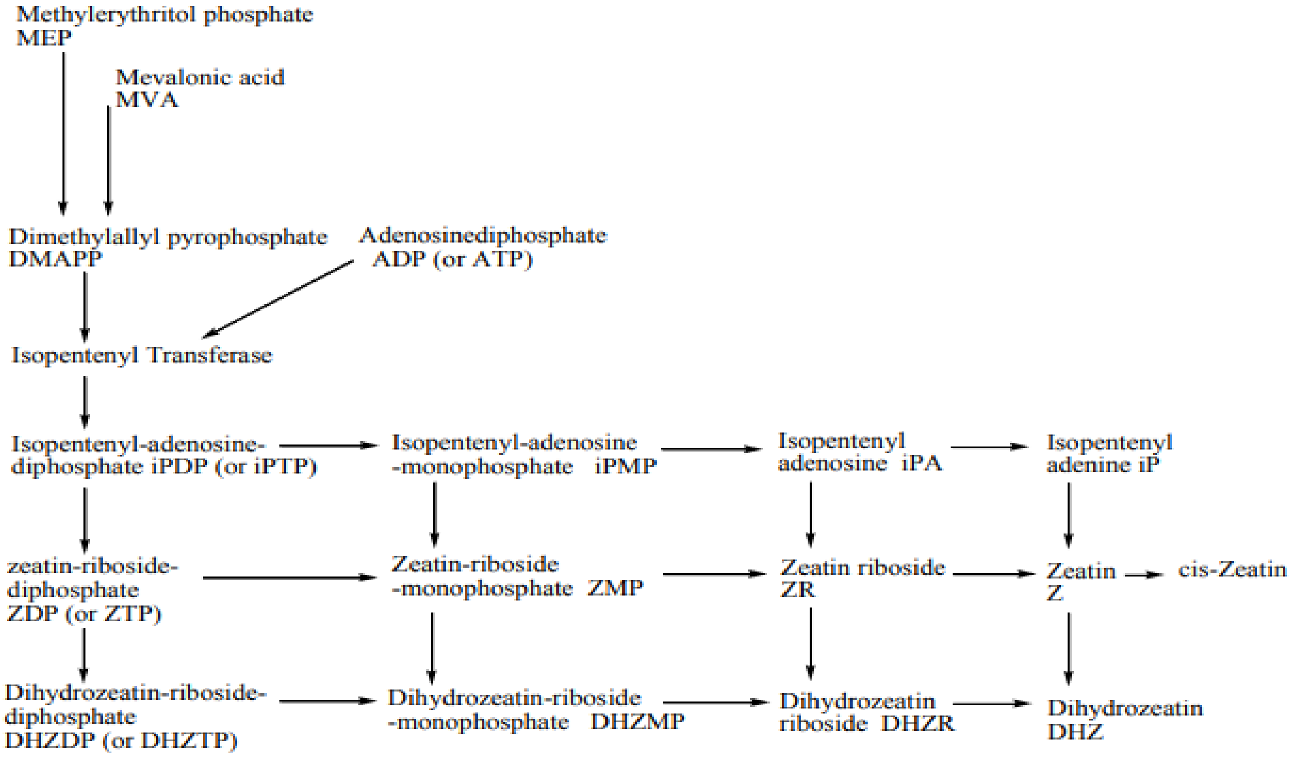


Figure 6: Biosynthetic pathways of zeatin

- **Functions of Cytokinins**

1. Stimulates cell division.
2. Activates metabolite attraction (sink effect).
3. Retardation of senescence (at low concentrations).
4. Induction of apoptosis (at high concentrations).
5. Stimulates morphogenesis in tissue culture.
6. Stimulates the growth of lateral buds and leaf expansion by cell division & enlargement.
7. Stimulation of chlorophyll synthesis that causes the conversion of etioplasts into chloroplasts.
8. Enhance stomatal opening in some plants.

4. ABSCISIC ACID

Abscisic acid (ABA) controls several physiological processes in plants and best known for regulatory role in abiotic stresses like drought and high salinity. It promotes stomatal closing by which plants enable to adapt to water stress (desiccation tolerance). It also controls seed germination, vegetative growth and bud dormancy. F. Addicott and his associates first identified and characterized the abscisic acid that is responsible for the abscission of fruits. They isolated two compounds and called abscisin I & abscisin II. Abscisin II is presently known as abscisic acid (ABA).

- **Biosynthesis of Abscisic Acid**

There are following two pathways of ABA biosynthesis.

ABA is synthesized by higher plants from carotenoid precursors. Carotenoids (Violaxanthin, C40) are involved in photosynthesis; they are cleaved to xanthoxin (C15) and C25 derivative in the plastid by the enzyme (dioxygenase). Then xanthoxin is converted to AB-aldehyde (abscisic aldehyde) then to ABA by oxidase enzyme respectively, this is the major route. If aldehyde oxidation is blocked then ABA is produced via AB-alcohol (abscisic alcohol) route. If AB-aldehyde oxidase uses xanthoxin as an alternative substrate, then xanthoxic acid might be an intermediate and this is the minor route.

ABA is a sesquiterpenoid produced via the isoprenoid pathway in chloroplasts by mevalonate, through the intermediates isopentenyl, geranyl and farsenyl pyrophosphate.

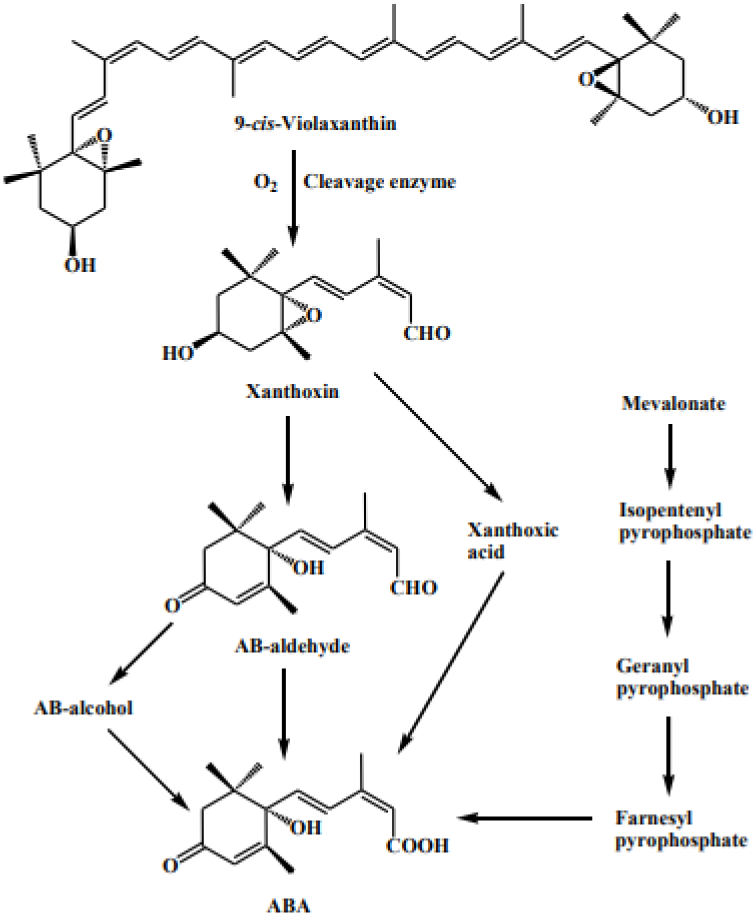


Figure 8: Biosynthetic pathways of ABA

- **Functions of Abscisic Acid**

1. Stimulates the closure of stomata.
2. Stress responses especially to water deficiency.
3. Induces seed and bud dormancy.
4. Induces seed to synthesize, storage proteins.
5. Inhibits shoot growth but does not have much affects on roots.
6. Inhibits the synthesis of alpha-amylase stimulated by gibberellins.
7. Induce some effects on induction and maintenance of dormancy.

5. ETHYLENE

Ethylene has simplest structure among all the plant hormones. It is a gaseous compound that has effects like an abscisic acid.

- **Discovery of Ethylene**

In 1901, D. Neljubow, a Russian student at the St. Petersburg Botanical Institute, found that the pea seedlings grown in dark show abnormal horizontal growth of stems. But when they were placed outside in fresh air, they resumed normal growth. Then he concluded that the ethylene gas, generated by gas lamps in the laboratory, had caused the abnormal growth. In 1917 Doubt studied different types of responses of ethylene gas on several plant tissues. She noted several responses that were: leaf scars and drop, epinasty of petioles, etc. R. Gane in 1934 reported that plants synthesize ethylene. Afterwards in 1935 Crocker considered ethylene as a plant hormone. When gas chromatography was introduced in 1959, the importance and physiological significance of ethylene as a plant growth regulator was recognized.

- **Biosynthesis of Ethylene**

Ethylene is produced by methionine in all higher plants essentially in all tissues. Ethylene production varies with type of tissue, plant species and stage. The mechanism is as follows:

ATP played a vital role in the synthesis of ethylene from methionine. ATP and water are added to methionine resulting in loss of the three phosphates and formation of S-adenosyl methionine (SAM). Further, it is converted to 1-amino-cyclopropane-1- carboxylic acid by ACC-synthase then to ethylene by ACC-oxidase.

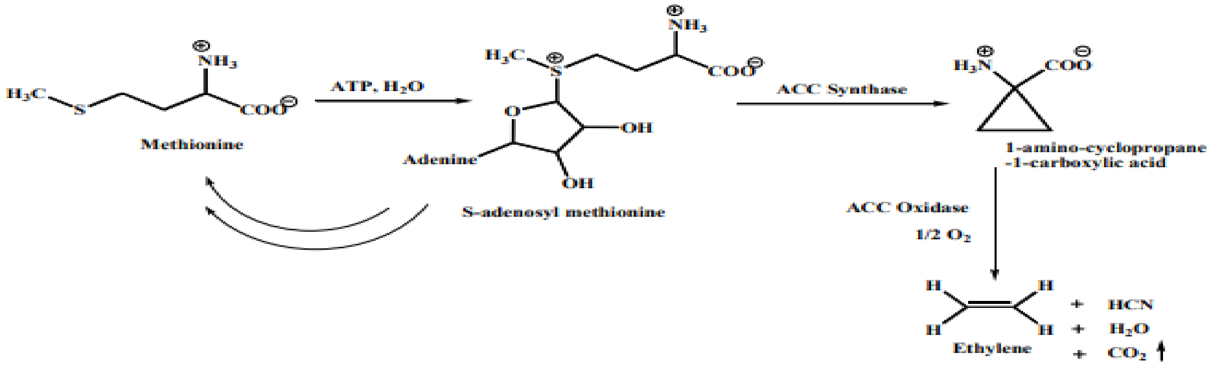


Figure 7: Biosynthetic pathway of ethylene

- **Functions of Ethylene**

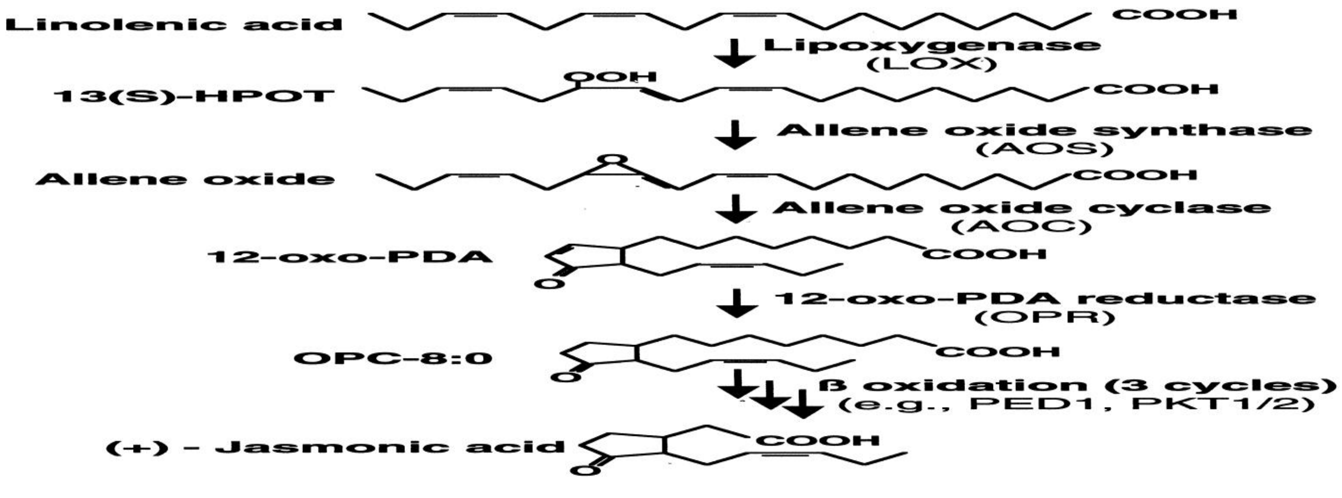
1. Induce shoot and root growth and also differentiation.
2. Stimulates the growth/release of dormancy.
3. Stimulates leaf and fruit abscission.
4. Stimulates Bromiliad flower induction.
5. Induction of femaleness in dioecious flowers.
6. Stimulates flower senescence, leaf senescence and flower opening.
7. Stimulates fruit ripening.

6. JASMONIC ACID (JA)

JA is an organic compound found in several plants including jasmine. The molecule is a member of the jasmonate class of plant hormones. It is biosynthesized from linolenic acid by the octadecanoid pathway.

- **Biosynthesis**

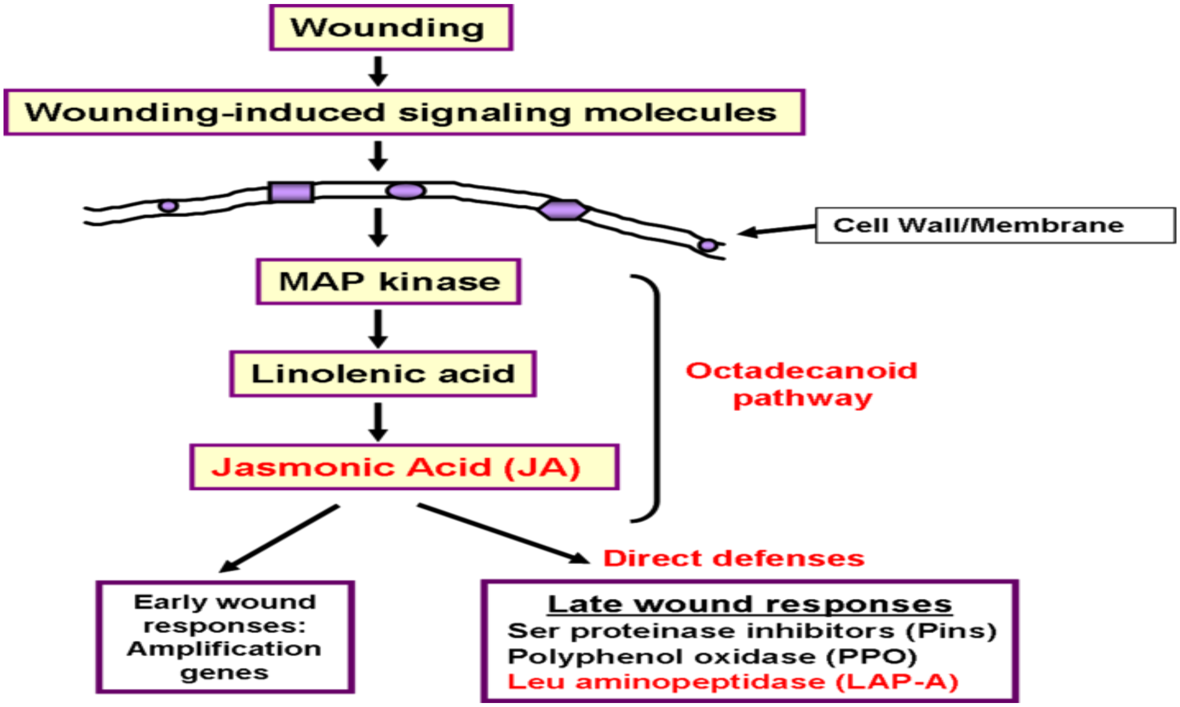
Its biosynthesis starts from the fatty acid linolenic acid, which is oxygenated by Lipoxygenase (13-LOX), forming a peroxide. This peroxide then cyclizes in the presence of allene oxide synthase to form an allene oxide. This allene oxide rearranges as it gets catalyzed by the enzyme allene oxide cyclase to form 12-oxophytodienoic acid, and undergoes a series of β-oxidations to 7-iso-jasmonic acid. In the absence of enzyme, this iso-jasmonic acid isomerizes to jasmonic acid.



- **Functions**

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 and yams. It has an important role in response to wounding of plants and systemic acquired resistance. The Dgl gene is responsible for maintaining levels of JA during usual conditions in *Zea mays* as well as the preliminary release of jasmonic acid shortly after being fed upon. 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. JA also activates the expression of Polyphenol oxidase which promotes the production of Quinolines. These can interfere with the insect's enzyme production and decrease the nutrition content of the ingested plant.

A may have a role in pest control. Indeed, JA has been considered as a seed treatment in order to stimulate the natural anti-pest defenses of the plants that germinate from the treated seeds. In this application jasmonates are sprayed onto plants that have already started growing.These applications stimulate the production of protease inhibitor in the plant. This production of protease inhibitor can protect the plant from insects, decreasing infestation rates and physical damage sustained due to herbivores. However, due to its antagonistic relationship with salicylic acid (an important signal in pathogen defense) in some plant species, it may result in an increased susceptibility to viral agents and other pathogens. In *Zea mays*, salicylic acid and JA are mediated by NPR1 (nonexpressor of pathogenesis-related genes1), which is essential in preventing herbivores from exploiting this antagonistic system. Armyworms (Spodoptera spp.), through unknown mechanisms, are able to increase the activity of the salicylic acid pathway in maize, resulting in the depression of JA synthesis, but thanks to NPR1 mediation, JA levels aren't decreased by a significant amount.

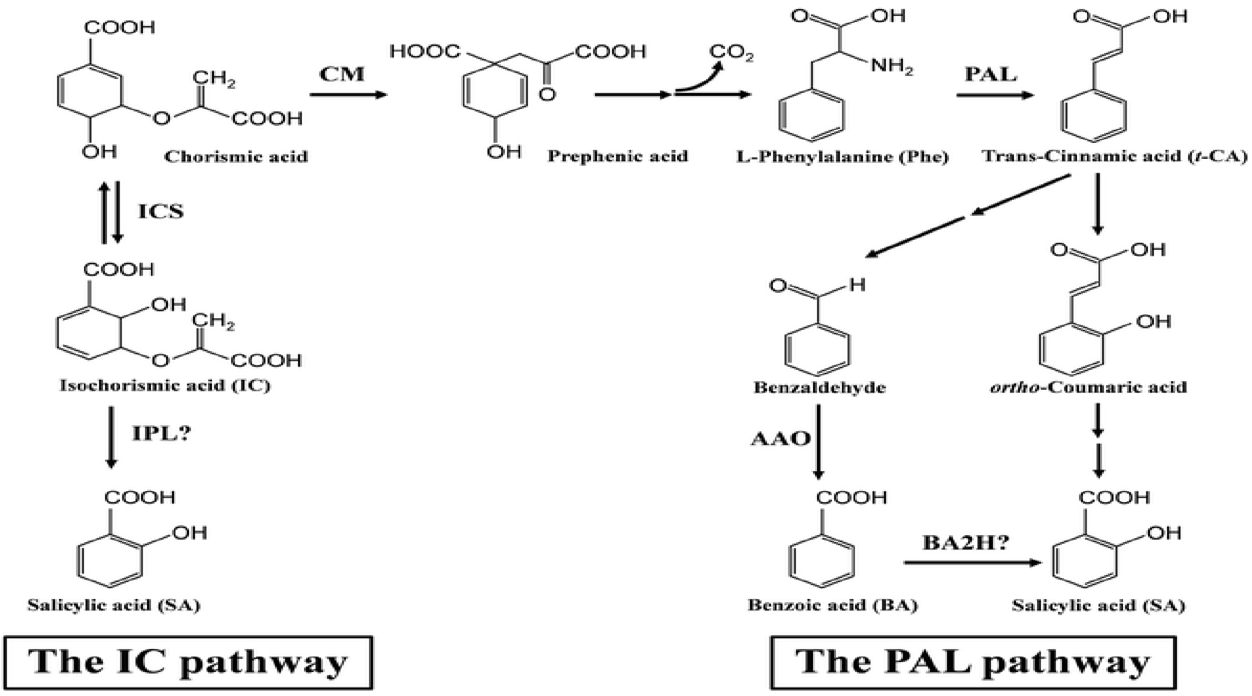


7. SALICYLIC ACID

Salicylic acid (SA; 2-hydroxybenzoic acid) is one of many phenolic compounds (defined as compounds containing a benzene ring bearing one or more hydroxyl groups) that are synthesized by plants. Despite the diversity and ubiquity of plant phenolics, these compounds were traditionally assumed to be rather unimportant, secondary metabolites. However, phenolics were subsequently shown to be involved in many important processes, including lignin and pigment biosynthesis, allelopathy, and the regulation of responses to abiotic and biotic stresses. SA, for example, is a critical hormone that plays direct or indirect roles in regulating many aspects of plant growth and development, as well as thermogenesis and disease resistance. Beyond its functions in plants, SA and its acetylated derivate (commonly known as aspirin) are important pharmacological agents for humans. SA is commonly used to treat warts, acne, and psoriasis, while aspirin is one of the most widely used medications in the world; its uses include treating pain, fever, swelling, and inflammation, as well as reducing the risk of heart attack, stroke, and certain cancers.

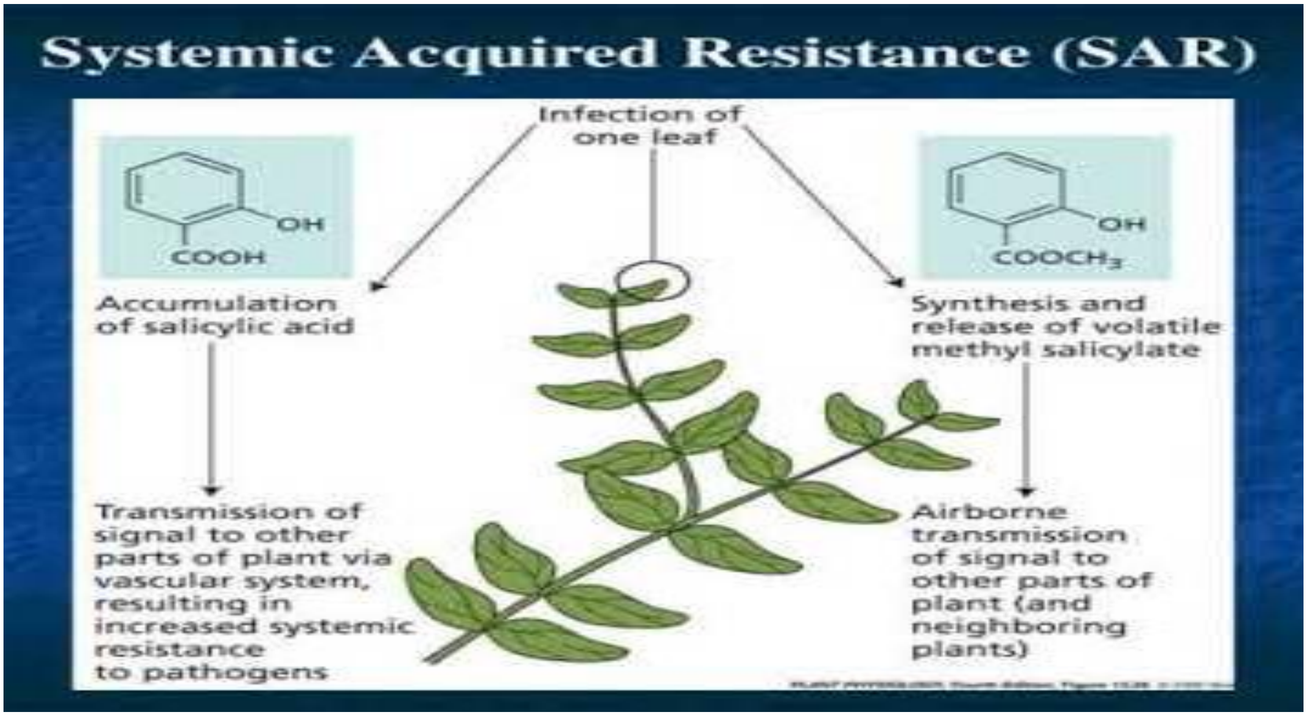
- **Biosynthesis**

Plants utilize the isochorismate (IC) and the phenylalanine ammonia-lyase (PAL) pathways to synthesize SA, as well as many other important compounds. Although neither route for SA biosynthesis is completely understood, both are known to require the primary metabolite chorismate. In the PAL pathway, PAL converts phenylalanine (Phe) to *trans*-cinnamic acid (*t*-CA). Depending on the plant species, *t*-CA is converted to SA via the intermediates *ortho*-coumaric acid or benzoic acid (BA). The conversion of BA to SA presumably occurs via BA 2-hydroxylase. The IC pathway was identified based on the hypothesis that plants synthesize SA via a pathway analogous to that of some bacteria. Indeed, genes encoding isochorismate synthase (ICS), which converts chorismate to isochorismate, have been identified in many plant species. However, no plant gene corresponding to bacterial isochorismate pyruvate lyase, which converts isochorismate to SA and pyruvate, has been identified. Following its synthesis, *Arabidopsis* ICS1 is imported to the chloroplast stroma, where SA synthesis occurs.



- **Functions**

In *Arabidopsis*, the basal level of total SA (consisting of SA and SAG/SGE) in leaves ranges from 0.22–5 μg/g fresh weight; in the Solanaceous species tobacco and potato it is <0.4 μg/g fresh weight and <17 μg/g fresh weight, respectively. Given the wide range in basal SA levels between (and even within) plant species, it is perhaps not surprising that conflicting reports have been published concerning the effect of exogenously supplied SA on various plant processes. Despite this caveat, exogenous SA has been shown to affect resistance to biotic (pathogen-associated) stress and tolerance to many abiotic stresses (drought, chilling, heat, heavy metal, UV radiation, and salinity/osmotic stress), as well as multiple aspects of plant growth and development, including seed germination, vegetative growth, flowering, fruit yield, senescence, thermogenesis, stomatal closure, root initiation/growth, photosynthesis, respiration, glycolysis, Krebs cycle, and the alternative respiratory pathway. Some of these processes are induced by SA in a concentration-dependent manner, as they are activated by treatment with a low dose of SA and inhibited by a high dose. This phenomenon is likely linked to SA's role in regulating cellular redox status, as low concentrations of SA induce low-level accumulation of ROS, which serve as secondary signals to activate biological processes. By contrast, high concentrations of exogenous SA stimulate the accumulation of high levels of ROS, which cause oxidative stress and cell death. Currently, the mechanisms through which SA regulates these non-immune plant processes are not well understood, but they do appear to involve the coordinated effect of SA and other plant hormones.

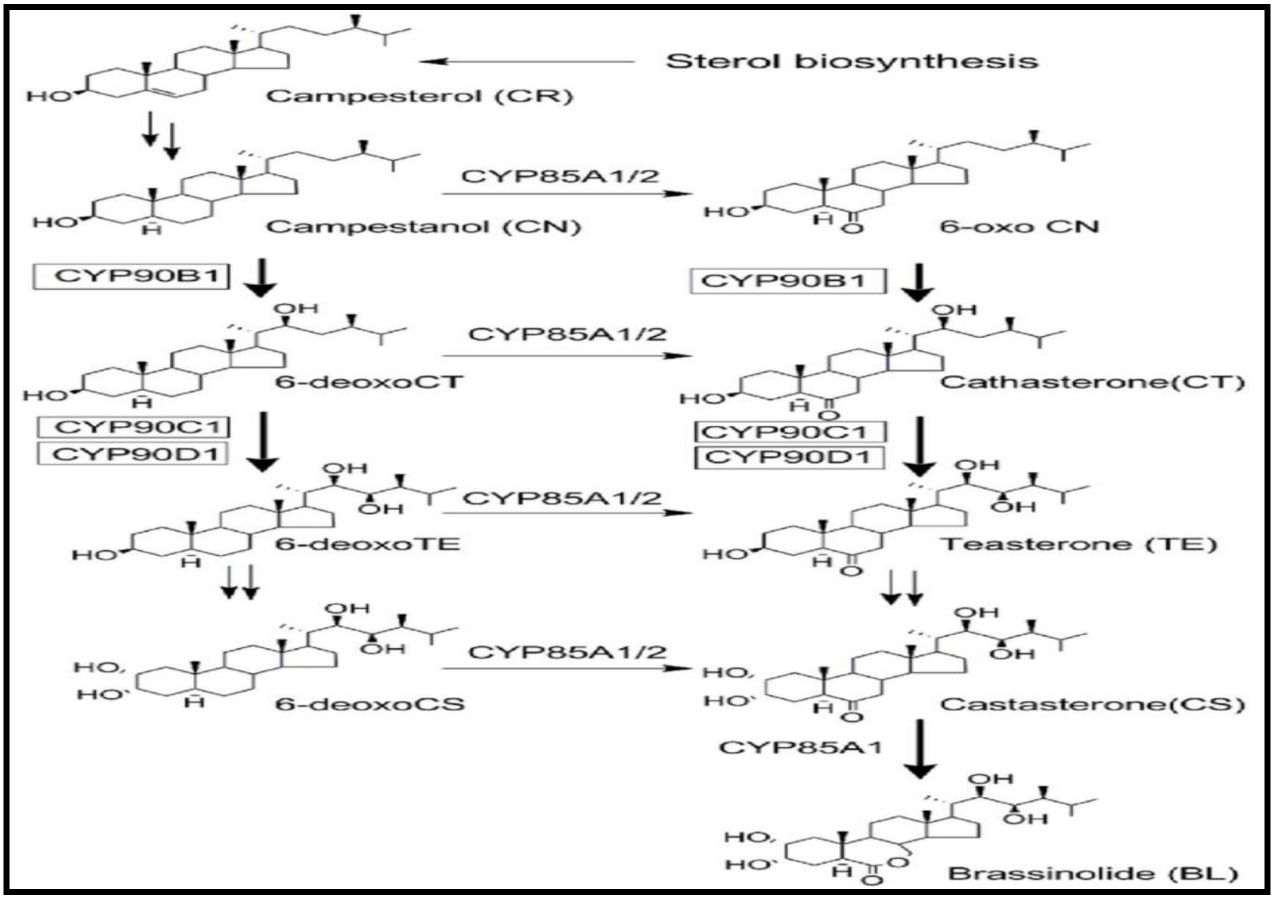


8. BRASSINOSTEROIDS

Brasinosteroids, plant hormone are analogous to animal steroid hormones in structure. Similar to animal hormones, brassinosteroids play crucial roles in diverse aspects of plant biology, including cell elongation, cell division, root growth, photo-morphogenesis, stomatal and vascular differentiation, seed germination, immunity and reproduction. Brassinosteroids are also involved in regulating the metabolism of plant oxidation radicals, ethylene synthesis and root gravitropic response, and have a role in mediating plant responses to stress, such as freezing, drought, salinity, disease, heat and nutrient deficiency. This subfamily of hormones regulates a broad range of processes in plant development and responses to environmental stresses, and their analogs have been shown to bring substantial increases in grain yield, depending on growth status.

• Biosynthesis

The BR is biosynthesised from campesterol. The biosynthetic pathway was elucidated by Japanese researchers and later shown to be correct through the analysis of BR biosynthesis mutants in *Arabidopsis thaliana*, tomatoes, and peas.[4] The sites for BR synthesis in plants have not been experimentally demonstrated. One well-supported hypothesis is that all tissues produce BRs, since BR biosynthetic and signal transduction genes are expressed in a wide range of plant organs, and short distance activity of the hormones also supports this. Experiments have shown that long distance transport is possible and that the flow is from the base to the tips (acropetal), but it is not known if this movement is biologically relevant.



- **Functions**

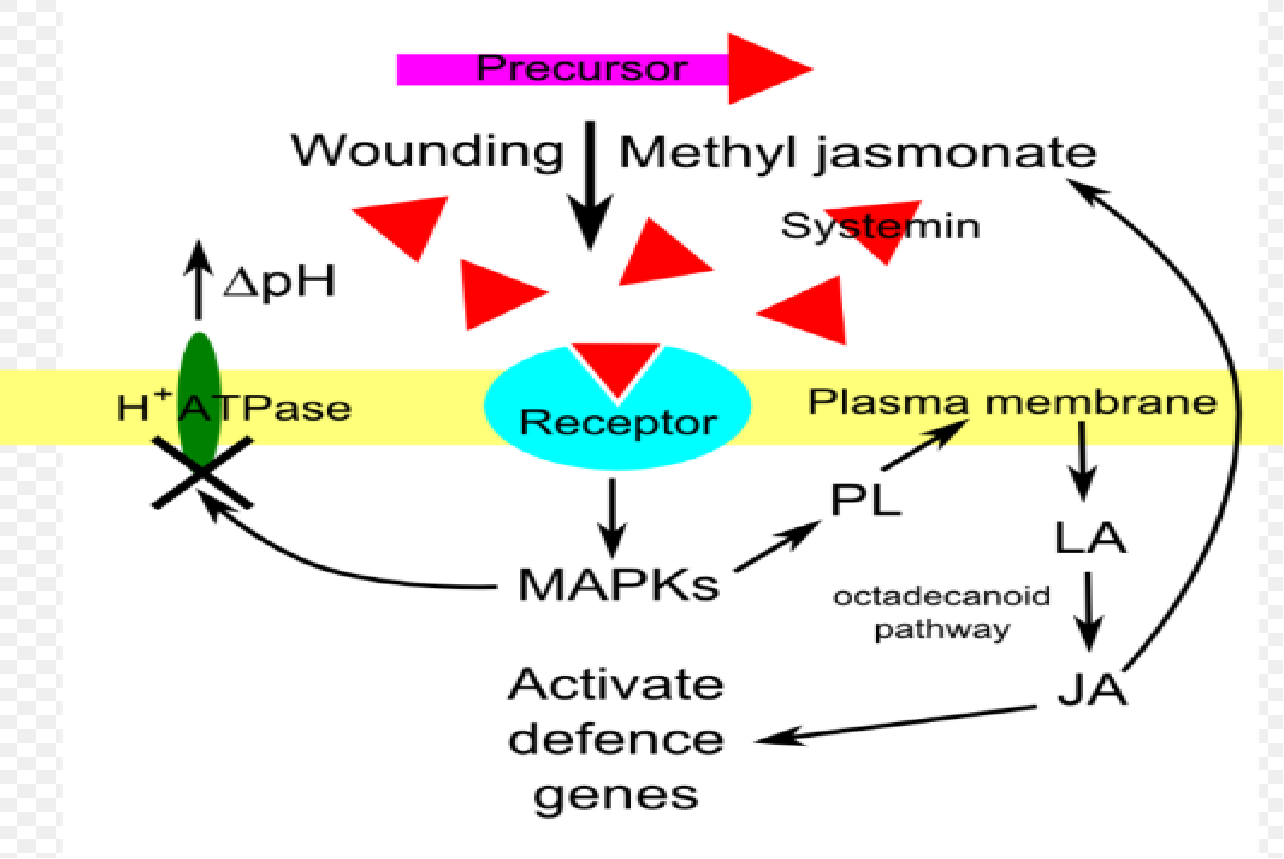
Brassinosteroids regulate many development processes in plants, as well as responses to environmental stresses and their roles in the growth–defence trade-off have profound implications in agriculture and natural ecosystems. To ensure perpetuation, plants need to balance their limited resources for growth and defense. Several plant hormones, including BRs, have been suggested to play roles in the trade-off between growth and defense. Recent studies indicated that interaction of BR signalling with PAMP-triggered immunity is unidirectional and negative. More recent data appear to support the idea that the interaction is located at the transcriptional level rather than at the receptor complex, though the underlying mechanisms remain debatable. Understanding of the mechanisms for these trade-offs is expected to provide a foundation for development of breeding strategies to maximize crop yield.

9. SYSTEMIN

Systemin is a plant peptide hormone involved in the wound response in the family Solanaceae. It was the first plant hormone that was proven to be a peptide having been isolated from tomato leaves in 1991 by a group led by Clarence A. Ryan. Since then, other peptides with similar functions have been identified in tomato and outside of the Solanaceae. Hydroxyproline-rich glycopeptides were found in tobacco in 2001 and AtPEPs (Arabidopsis thaliana Plant Elicitor Peptides) were found in *Arabidopsis thaliana* in 2006. Their precursors are found both in the cytoplasm and cell walls of plant cells, upon insect damage, the precursors are processed to produce one or more mature peptides. The receptor for systemin was first thought to be the same as the brassinolide receptor but this is now uncertain. The signal transduction processes that occur after the peptides bind are similar to the cytokine-mediated inflammatory immune response in animals. Early experiments showed that systemin travelled around the plant after insects had damaged the plant, activating systemic acquired resistance, now it is thought that it increases the production of jasmonic acid causing the same result. The main function of systemins is to coordinate defensive responses against insect herbivores but they also affect plant development. Systemin induces the production of protease inhibitors which protect against insect herbivores; other peptides activate defensins and modify root growth. They have also been shown to affect plants' responses to salt stress and UV radiation. AtPEPs have been shown to affect resistance against oomycetes and may allow *A. thaliana* to distinguish between different pathogens. In *Nicotiana attenuata*, some of the peptides have stopped being involved in defensive roles and instead affect flower morphology.

- **Biosynthesis**

Systemin synthesis is induced either by mechanical wounding or injury by insects. So far systemin has been found only in above-ground organs (but not in the roots) of tomatoes and potatoes. Respectively, wounding of any above-ground part of these plants arouses induction of systemin. Exogenous systemin in an extremely low concentration (40 fmoles) induces expression in tomato of the serine proteinase inhibitors, identical to those produced in response to wounding or damage by mandibulate insects. The inhibitors are assumed to be inducible, protective compounds preventing easy digestion of proteins by insects. Systemin causes increase in the production of Jasmonic Acid inducing SAR towards wounds created by insect/ herbivore.



- **Functions**

1. ***Defence***: Systemin plays a critical role in defence signalling in tomato. It promotes the synthesis of over 20 defence-related proteins, mainly antinutritional proteins, signaling pathway proteins and proteases.[15] The over-expression of the prosystemin resulted in a significant decrease of the larvae damage, indicating that a high level of constitutive protection is superior to an inducible defence mechanism.[25] However, the continuous activation of prosystemin is costly, affecting the growth, the physiology and the reproductive success of tomato plants.[26] When systemin was silenced, production of protease inhibitors in tomato was severely impaired and larvae feeding on the plants grew three times as fast.[27] HypSys caused similar changes in gene expression in tobacco, for example polyphenol oxidase activity increased tenfold in tobacco leaves and protease inhibitors caused a 30% decrease in chymotrypsin activity within three days of wounding.[12] When HypSys was over-expressed in tobacco, larvae feeding on transgenic

plants weighed half as much after ten days feeding, as those feeding on normal plants.[28] The concentration of hydrogen peroxide increased in the vasculature tissues when the production of systemin, HypSys or AtPep1 is induced, this may also be involved in initiating systemic acquired resistance.

2. ***Abiotic stress resistance***: Overexpression of systemin and HypSys has been found to improve plants' tolerance to abiotic stress, including salt stress and UV radiation. When prosystemin was over-expressed in tomato, transgenic plants had lower stomatal conductance than normal plants. When grown in salt solutions, transgenic plants had higher stomatal conductances, lower leaf concentrations of abscisic acid and proline and a higher biomass. These findings suggest that systemin either allowed the plants to adapt to salt stress more efficiently or that they perceived a less stressful environment. Similarly, wounded tomato plants were less susceptible to salt stress than unwounded plants. This may be because wounding decreases the growth of the plant and therefore slows the uptake of toxic ions into the roots. An analysis of salt-induced changes in gene expression found that the differences measured between the transgenic and normal plants could not be accounted for by changes in conventional salt stress-induced pathways. Instead Orsini *et al.* suggested that the activation of the jasmonic acid pathway determines a physiological state that not only directs resources towards the production of compounds active against pests, but also pre-adapts plants to minimize water loss. These effects are achieved by negatively regulating the production of hormones and metabolites that will force plants to invest additional resources to counteract water loss, a secondary effect of herbivores.
3. ***Development***: In *Nicotiana attenuata* HypSys is known to not be involved in defence against insect herbivores. Silencing and over-expression of HypSys does not affect the feeding performance of larvae compared to normal plants. Berger silenced HypSys and found that it caused changes in flower morphology which reduced the efficiency of self-pollination. The flowers had pistils that protruded beyond their anthers, a similar phenotype to CORONATINE-INSENSITIVE1-silenced plants which lack a jasmonate receptor. Measurement of jasmonate levels in the flowers revealed that they were lower than in normal plants. The authors suggested that HypSys peptides in *N. attenuata* have diversified from their function as defence related peptides to being involved in

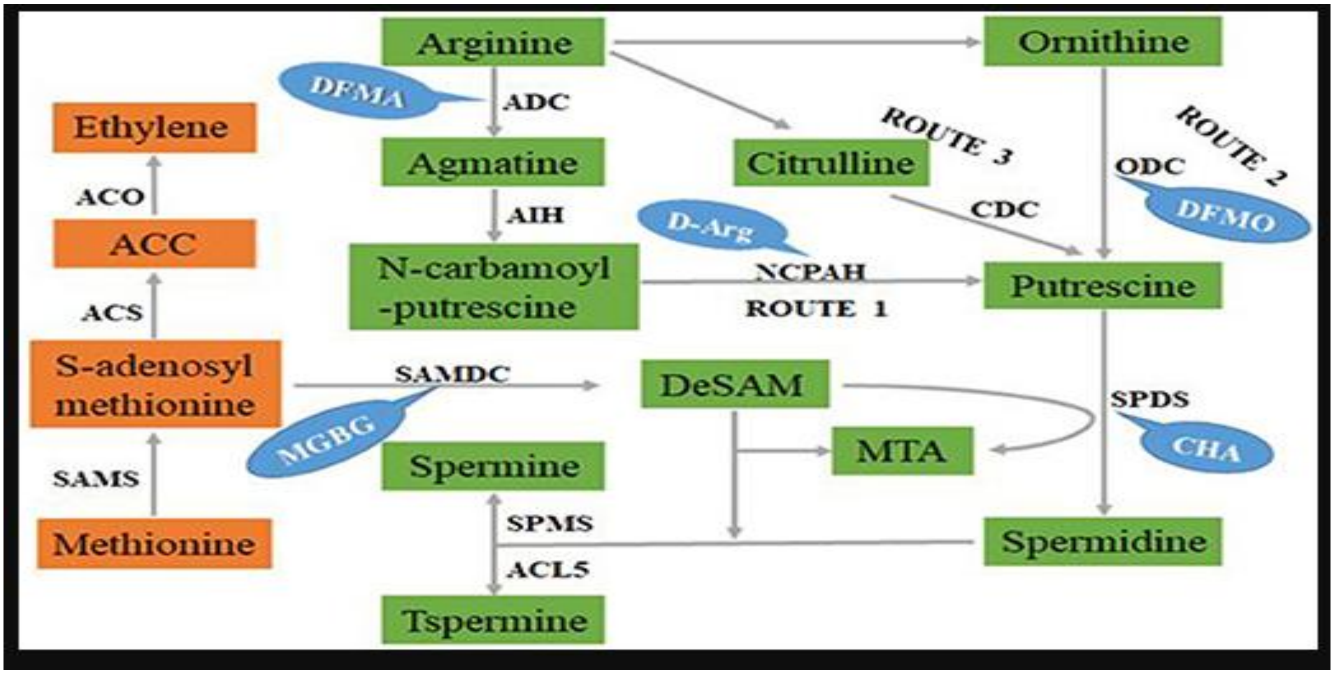
controlling flower morphology. The signalling processes remain similar however, being mediated through jasmonates.

10. POLYAMINES

Polyamines (PAs) are small, positively charged, organic molecules that are ubiquitous in all living organisms. These are considered as one of the oldest group of substances known in biochemistry. There are three common types of polyamines, putrescine, spermidine, hermospermine according to structure, universal distribution in all cellular compartments, and presumed involvement in physiological activities. Polyamine is found in all cellular compartments and physiological activities due to their simple structures. The function of polyamine is very diverse in that it performs a key macromolecule to cellular membrane. Because of their essential roles in plant, mutation of polyamines can cause critical damage on plants.[1] Furthermore, some polyamines like putrescine inhibit biosynthetic activities in plants. The activity of polyamines can be categorized to some parts due to its signalling and growing activity.

- ***Biosynthesis***

Putrescine is the central product of the common PA biosynthetic pathway. It contains two amino groups and is a synthetic precursor of Spd and Spm. There are three different routes of Put biosynthesis in plants. In the first route, the No. 8 carbon atom is removed from arginine (Arg) by arginine decarboxylase (ADC) to form agmatine (Agm) and CO_2; the No. 2 nitrogen atom is removed from Agm to form N-carbamoyl Put (NCPA) and NH_3; and then NCPA is hydrolyzed by N-carbamoylputreseine amidohydrolase (NCPAH) and its carbamoyl group is removed to form Put, CO_2, and NH_3. This is the main Put synthesis pathway in plants. In the second route, ornithine (Orn) is produced from Arg by arginase; and then ornithine decarboxylase (ODC) removes the carboxyl group of the no.1 carbon atom of Orn to form Put and CO_2. The *ODC* gene has been lost from *Arabidopsis thaliana* and many members of the *Brassicaceae*, indicating that the ornithine pathway is not essential for normal growth. In the third route, Arg is first converted into citrulline (Cit), which is then decarboxylated by citrulline decarboxylase (CDC) to form Put. To date, the Cit pathway has only been found in sesame, and so the first two pathways are more common in plants. The activities of ADC and ODC can be inhibited by the irreversible competitive inhibitors difluoromethylarginine (DFMA) and difluoromethylornithine (DFMO), respectively Spermidine and Spm are produced from Put and aminopropyl residues, which are gradually provided by methionine.



Abbreviations:

ADC, arginine decarboxylase; NCPA, N-carbamoylputrescine; NCPAH, N-carbamoylputreseine amidohydrolase; ODC, ornithine decarboxylase; CDC, citrulline decarboxylase; DFMA, difluoromethylarginine; DFMO, difluoromethylornithine; AIH, agmatine iminohydrolase; SPDS, spermidine synthase; CHA, clohexylamine, the inhibitor of SPDS; SPMS, spermine synthase; ACL5, thermospermine synthase; SAMDC, S-adenosylmethionine decarboxylase; SAMS, S-adenosylmethionine synthase; ACS, 1-aminocyclopropane-1-carboxylate synthase; ACO, 1-aminocyclopropane-1-carboxylate oxidase.

- **Function**

1. Affect flower bud differentiation.
2. Regulation in the process of embryogenesis.
3. PA levels seem to be a significant prelude to senescence signals, or it may be that a decrease in PAs content is the senescence signal.

GENERAL IMPORTANCE/ ROLE OF PLANT GROWTH REGULATORS

1. **Germination**: Germination is the beginning of growth of a plant from a previously dormant seed which contains the embryo. Dormancy is the phase in which biological activities are at rest/suspended; dormancy can be broken by external application of PGRs like auxins and GAs.
2. **Rooting**: Root promoting chemicals are referred to as “rooting hormones”, they are often used on stem cuttings using different methods. Auxins are used as rooting hormones.
3. **Callus Induction**: In plant tissue culture, cytokinins and auxins are used for callus induction from explants.
4. **Growth Inhibitor**: Inhibit means to „stop‟ the growth. It stops apical growth and promotes lateral bud growth, which results in branched and more compact plants with an increased number of flowers and fruits. These chemicals are also used in long storage of suckers.
5. **Growth Retardant**: Retard means to „slow‟ the growth. These chemicals regulate shoot growth of plant resulting in a sturdier and more compact plant with improved color.
6. **Thinner:** Thinning is the process of reducing denseness of flowers/fruits, which helps to increase fruit size, quality and maintain tree structure. To maximize crop quality and yield, load must be estimated for the optimal crop, the maximum number of fruits to be retained after thinning.
7. **Chemical Pruning**: Pruning is a process of restricting of plant height. It is also known as pinching or suckering. Pruning promotes the growth of new branches. Generally growth inhibitors are used for chemical pruning.
8. **Defoliant**: Any substance or mixture of substances intended for causing the leaves or foliage to drop from a plant, with or without causing abscission. Defoliation is the method of treatment that causes only the leaves of a plant to abscise or fall off. These are applied to cotton to improve and facilitate mechanical harvesting.
9. **Desiccant:** Any substance or mixture of substances intended for artificially accelerating drying of plant tissues. Desiccation is the method of treatment that rapidly kills the leaves, which are used for purpose similar to the uses of defoliants, but desiccant causes green foliage to lose water; it is a hastened drying process that results in removal of leaves.

10. **Fruit Ripener**: Ripening is the final stage of fruit development, which involves series of physiological and biochemical events mainly to change colour, texture, aroma and flavor that makes fruit attractive & tasty. Fruit ripeners are the substances which can hasten ripening process and artificially ripen fruits for commercial purpose.

SPECIFIC APPLICATIONS PLANT GROWTH REGULATORS

AUXINS

The auxin-type plant growth regulators comprise some of the oldest compounds used in agriculture. Shortly after indole acetic acid (IAA) was identified, it was synthesized and became readily available. IAA was not found in itself to be useful in agriculture because it is rapidly broken down to inactive products by light and microorganisms. Nevertheless, a number of synthetic compounds were found to act similarly to IAA in the auxin bioassay tests. Indolebutyric acid (IBA) and NAA were found to increase root development in the propagation of stem cuttings. 2,4-dichlorophenoxyacetic acid (2,4-D) stimulates excessive, uncontrolled growth in broadleaf plants for which it is used as a herbicide. NAA is used to reduce the number of fruit that have set in apple, whereas 4-chlorophenoxyacetic acid (4-CPA) is used to increase fruit set in tomato. The auxins 2,4,5-trichlorophenoxypropionic acid (2,4,5-TP) and the dichlrophenoxy analog (2,4-DP) are used to prevent abscission of mature fruit in apple.

1. **Propagation:** Rooting of stem cuttings was one of the first uses of auxins. The most common compound used is IBA, which has only weak auxin activity, but is relatively stable and insensitive to the auxin degrading enzyme systems. It is also not readily translocated. Other compounds such as NAA and 2,4-D will also promote root development, however, these compounds are more easily translocated to other parts of the stem cutting where they may have toxic effects. The auxins stimulate root development by inducing root initials that differentiate from cells of the young secondary phloem, cambium, and pith tissue.
2. **Stimulation of fruit set**: One of the first recorded effects of auxins was the stimulation of fruit set in unpollinated ovaries of solanaceous plants. It is known that pollen was a rich source of auxin, and that in some species pollination alone was all that was required

for fruit set to occur. In tomato, chemical stimulation of fruit set is all that is needed for fruit growth to take place as well. In addition, compounds that block the transport of auxin from the ovary to the pedicel of the flower also stimulate fruit set. It seems likely, therefore, that given environmental conditions somewhat inhibitory to fruit set, application of auxin to flowers could promote this process. In California, the early spring crop of tomatoes is treated with 4-CPA at 25-50 ppm to stimulate fruit set at a time of the year when cool night temperatures that inhibit fruit set in tomato are likely. This treatment results in an increase in yield and earlier harvest.

3. **Chemical thinning**: Removal of excessive numbers of young fruit from apple and pear trees is a common orchard management practice, although this results in drastic reductions in the total biological yield. There are two main reasons for removing as much as 80% of the flowers: first, to increase the total marketable yield by increasing the size of the remaining fruit, and second, to reduce the phenomenon of biennial bearing in order to maintain production levels from year to year. The effect of fruit thinning on fruit size is probably related to the leaf/fruit ratio. As this ratio is reduced below 30/1, fruit size is reduced as well. The time in which fruit thinning is done is as important to fruit size as the amount of fruit thinning. In order to improve flower bud production and fruit size in apple, thinning should take place within 30 days from full bloom. In apple, the period of cell division in the fruit is brief, ending approximately 20 days after full bloom. Removing excess fruit during this period can stimulate cell division within the remaining fruit. this early period is also of critical importance for floral initiation, the time when next year's crop will be partially determined. The two auxin-type compounds used in chemical thinning of apple and pear are NAA and NAAm(naphthalene actamide). NAA is applied at 2-5ppm, 7-20 days after full bloom, whereas NAAm is effective during the same time period, but higher rates (17~34ppm) are used.
4. **Prevention of fruit drop**: Frequently, the mature fruit of apple, pear, lemon, and grapefruit will abscise prior to the time of commercial harvest. This obviously reduces the potential crop yield, and may result in the tendency to begin harvesting the crop earlier than is desirable, resulting in lower quality fruit. Under natural conditions, there seems to be an inverse relationship between auxin content of the fruit, and the tendency toward abscission. The role of auxin in abscission is complicated. Clearly, application of

auxin soon after fruit set results in an acceleration of abscission, however, when auxins such an 2,4,5-DP, NAA, and 2,4-D are applied during the mid-stages of fruit growth, abscission is delayed or prevented. In addition, auxin application may decrease the response of fruit abscission zone to exogenously applied ethylene. NAA and 2,4,5-TP are used at 10-20ppm just prior to the beginning of fruit drop in apple. Repeat applications may be necessary with NAA or 2,4,5-TP prevent fruit drop for a longer period. In citrus, 2,4-D at 25ppm prevents premature fruit drop and allows an extension of the harvest season into the summer.

5. **Herbicidal action**: 2,4-D and picloram(4-amino-3,5,6-trichloropicolinic acid) are two auxin-type herbicides that at low concentration bring about growth responses in plants similar to IAA. At higher concentrations they are herbicidal. 2,4-D is commonly used to control broadleaf weeds in grasses, and picloram is used for vegetation control on non-crop land because of its high activity and soil persistence. Both compounds cause epinastic bending in leaves, a cessation in growth in length, and increased radial expansion. After several days tumors may form, followed by a softening and collapse of the tissue. Epinastic bending and stem swelling are characteristic of ethylene effects on plants, and auxin induced ethyene biosynthesis may partially account for the effect of these compounds on plant growth. Treatment with inhibitors of ethylene synthesis or action in the presence of 2,4-D, however, do not reverse the herbicidal effects of the auxins. Auxin herbicides cause an increase in DNA, RNA, and protein levels in treated tissue. The greatest effect, however, is on RNA levels. Specific mRNAs are induced by auxin treatment, and ethylene apparently plays no role in the expression of these mRNAs.

GIBBERELLINS

Despite considerable enthusiasm for the potential uses for gibberellic acid in agriculture that existed when this compound was rediscovered by US and British scientists in the 1950's, major GA use remains limited to fruit crops, the malting of barley, and extension of sugarcane growth in certain production regions. There are about 120 gibberellins found in both higher plants and the Gibberella fungus, although only two commercial products are available, GA3 and a mixture of GA4 and GA7. Both are produced by fermentation cultures of the fungus. A formulation of

GA4/7 and benzyladenine is also available that is being used to induce apple fruit elongation, and to increase the extent of lateral branching in young trees.

1. **Increasing fruit size in grape**: GA is used extensively on seedless grape varieties to increase the size and quality of the fruit. Pre-bloom sprays of 20ppm induce the rachis of the fruit cluster to elongate. This creates looser clusters that are less susceptible to disease during the growing season. GA also reduces pollen viability, as well as decreasing ovule fertility in grape. Application of GA at bloom, therefore, results in a decrease in fruit set, which reduces the number of berries per cluster, but increases the weight and length of the remaining fruit. An additional application of GA during the late bloom to early fruit set period will further increase berry size. It has been suggested that this later application of GA increases the mobilization of carbohydrates to the developing fruit. Seeded varieties generally do not respond favorably to GA treatment. However, in Japan and Korea, the seeded variety 'Delaware", is cluster-dipped in 100ppm GA to induce parthenocarpic fruit development and increase berry size.

2. **Stimulating fruit set**: Not all crops respond as positively as the tomato to auxin-induced fruit set. However, a number of deciduous fruit tree species such as apple and pear, as well as some citrus species, can be induced to set fruit with GA, or a combination of GA and auxin. In Europe, poor fruit set in apple and pear can drastically reduce crop yield. Consistently unfavorable weather during the pollination period has led to the development of a hormone mixture to induce parthenocarpic fruit set in apple. In pear, spring frost injury to the ovules or style can prevent fertilization and the stimulation for fruit set. Application of GA3 at 15 ~30ppm can induce parthenocarpic fruit and salvage what would have been a lost crop. In citrus, fruit set of mandarin oranges is often light. Application of GA during full bloom can increase in endogenous GA-like substances in the region above the branch girdle.
3. **Effects on fruit ripening**: GAs are used to delay fruit ripening in lemon in order to increase the availability of fruit during the months of May~August when demand is high, but production is low. GA is applied in November or December in order to delay the harvest date, and increase storage life of the fruit. Delaying harvest is also important for a number of other citrus species including 'Navel' oranges and grapefruit. While fruit

abscission can be controlled by 2,4-D, after maturity is attained, changes associated with the usefulness of holding the fruit on the tree longer in order to allow harvest to take place during the period of high comsumer demand. GA application will reduce the occurrence of physiological rind disorders such as water spot, creasing, rind staining, and softening by delaying senescence of the rind tissue. GA4+7 is registered for use on ‘Golden Delicious' apple to reduce russeting, a physiological disorder that results from abnormal cell division in the epidermal layer of the fruit.

4. **Increasing yield in sugarcane**: Sugarcane growth is very sensitive to the reductions in average daily temperature normally experienced during the winter months in many cane producing regions of the world, especially Hawaii. GA application is used to overcome the reduced growth of the 3~5 internodes undergoing expansion during the cooler winter season. GA treatment has resulted in an increase in fresh weight of harvested cane of 10.9 ton/ha, and has increased sucrose yield by 1.1 ton/ha or 2.8%.
5. **Malting of barley**: GA is used to increase the yield of barley malt and to decrease the time required for this process to occur. Embryo growth and yield of malt extract are competitive processes, by increasing the rate of malting relative to embryo growth, a greater yield of malt extract occurs. Application of GA to germinating barley supplements the endogenous level of this hormone and accelerates the production and release of hydrolytic enzymes that degrade the storage proteins and carbohydrates of the endosperm into the sugars and amino acids that comprise the malt extract.
6. **Controlling flower bud production**: Spring application of GA is used extensively to accelerate flower bud production in artichoke to allow earlier harvesting dates. If treatment is delayed to coincide with the appearance of flower buds, increases in head size and number have also been reported.
7. **Overcoming environmental constraints on growth**: GA is used to break dormancy in plants that have not received an adequate chilling period for the resumption of growth to occur. For rhubarb crowns transplanted in the fall for forcing, GA application can substitute for the cold period normally required for bud development and subsequent petiole elongation. Potato tuber dormancy can also be broken by application of GA. This treatment is of value in the identification and screening of virus infected tubers. In warm climates, where it is possible to plant two crops in a single year, GA treatment can break

dormancy of the seed tubers from the first crop in time for a second planting. In celery production, GA is used to increase petiole elongation under cool weather conditions, where growth is reduced. GA is also being used as a seed treatment in rice to stimulate germination and initial elongation of semi-dwarf cultivars. This allows deeper planting, which improves germination and stand establishment.

8. **Flower sex expression**: GA can be used to induce precocious cone production in conifers. This may be an especially important aid to genetic improvement in silviculture. Douglas fir for example normally requires 20 years before seed production will occur, with GA4/7 6-year-old trees can be induced to produce seed. GA has also been used to control flower sex expression in cucumbers and squash. GA application tends to promote maleness in these plants. When gynoecious cucumbers are treated with GA, staminate flowers are produced for breeding purposes. Bolting and seed stalk formation is promoted by GA in many normally biennial vegetables. This facilitates hybrid seed production for commercial purpose as well as accelerating vegetable variety improvement.

ABSCISIC ACID

There are no practical uses of abscisic acid (ABA) because of the high cost of synthesis and its instability in UV light. However, given the effect of ABA on abscission, dormancy, and transpiration, synthetic ABA analogs might play a significant role in crop production. The ABA analogs LAB 173 711 and LAB 144 143 are acetyleneacetal-type compounds that have been found to reduce water use in crop plants, increase cold hardiness, and delay flowering in peach.

Recently, promotive effect of natural ABA was reported. Application of mixtures of natural type abscisic acid, (S)-(+)-abscisic acid (SABA), and gibberellic acid (GA3) promoted floral-bud initiation and flowering in the long-day plants, spinach, pansy, primrose and petunia, even under short-day conditions. The effective concentrations for spray application of SABA/GA3 were restricted within the limits of 10-1 respectively. Applications of SABA and/or GA3 as high as 50 induced no flowering. However, flowering in short-day plants, dahlia, morning-glory and Christmas-cactus was not promoted by the mixtures.

CYTOKININS

Benzyladenine (Pro-Shear) is used on white pine to increase lateral bud formation and subsequent growth and branching, while tetrapyranylbenzyladenine (Accel) is registered for use on carnations and roses for increased lateral branching. Pomina, a mixture of benzyladenine and GA4/7 is used to control fruit shape in 'Delicious' apple. High temperature during the bloom period will often reduce the length to diameter ratio resulting in rounder fruit, uncharacteristic of the more normally elongated fruit of this variety that consumers expect. Pomina applied at bloom will increase length to diameter ratio of the fruit(Fig. 6). Increased fruit size may also result from treatment. Pomina is also being used to increase lateral branching in non-bearing apple trees. Young trees typically have a strong, vigorously growing central leader with a few upright growing branches. For fruit production, this is an undesirable tree shape and mechanical devices are used to force the lateral branches to grow more horizontally. Pomina will stimulate branching and increase the branch angle, as well as increase shoots elongation, all of which aid in the development of a scaffold branching system more suitable for fruit production.

MISCELLANEOUS COMPOUNDS USED AS GROWTH REGULATORS

1. MALEIC HYDRAZIDE

Maleic hydrazide has been used since the 1950s for tobacco sucker growth control, the prevention of bud sprouting in onions and potato, and for the control of turfgrass growth. At one time, maleic hydrazide accounted for almost 90% of the sales of plant growth regulators. In tobacco production, the terminal bud is removed from the plant after a selected number of leaves has been produced. This practice. called topping, increases the size, weight, and quality of the cured leaf. Axillary buds, which develop as a result of topping, will reduce the effect of terminal bud removal on leaf yield and quality. Maleic hydrazide will provide excellent control of axillary bud growth when applied as a foliar spray to the upper two-thirds of the plant, after terminal bud removal. Maleic hydrazide is also used to control storage sprouting of onions and potatoes. The compound is applied as a pre-harvest foliar spray, since it is rapidly translocated to storage organs. Maleic hydrazide inhibits cell division in a wide range of plants, and the ability of the compound to be translocated to meristematic tissue probably accounts for the effect of the compound on axillary bud growth in tobacco and the sprouting of tubers and bulbs. Maleic hydrazide is an analog of uracil and may inhibit cell division by reducing nucleic acid biosynthesis in shoot and root meristems.

2. CITRUS ABSCISSION AGENTS

Several abscission agents are being developed for the mechanical harvesting of oranges intended for processing use rather than fresh market. The products, Release (5-chloro-3-methyl-4-nitro-1-pyrazole) and Pik-Off (ethandiol dioxime), induce abscission by causing superficial injury to the rind of the fruit. Wound ethylene is synthesized and presumably is the cause of the reduction in fruit removal force. Application of ethephon to trees with mature fruit will also induce abscission, however, significant defoliation often will occur with this chemical.

3. SUGARCANE RIPENERS

One of the more useful compounds for increasing yield in sugarcane is glyphosine, which in Hawaii, has increased sucrose yield by 10-15%. The herbicide Glyphosate, an analog of glyphosine, is also effective, and lower rates of application can be used. Glyphosine will decrease terminal growth of the cane, and other workers lave shown that removing the upper leaves of the stalk increases sucrose translocation from lower leaves into the stem and ripening joints. In addition, these compounds apparently alter the partitioning of carbohydrate in the sugarcane internode. More carbohydrate goes into sucrose storage at the expense of fiber production.

4. COTTON DEFOLIANTS

The organophosphate DEF and Folex are used as leaf abscission agents before mechanical harvesting of cotton. Two new compounds are being evaluated for this purpose. Dimethipin (2,3-dihydro-5,6-dimethyl-1,4-dithiin-1,1,4,4-tetraoxide) and thidiazuron (1-phenyl-3(1,2,3-thiadiazol -55-yl)urea) induce defoliation and provide control of regrowth vegetation other leaf abscission.

SYNTHETIC GROWTH RETARDANTS

Plant growth retardants are synthetic compounds, which are used to reduce the shoot length of plants in a desired way without changing developmental patterns or being phytotoxic. This is achieved primarily by reducing cell elongation, but also by lowering the rate of cell division. In their effect on the morphological structure of plants, growth retardants are antagonistic to gibberellins (GAs) and auxins, the plant hormones that are primarily responsible for shoot elongation. The first growth retardants, certain nicotinium derivatives, became known in 1949. Many other compounds have subsequently been detected, some of which have been introduced into agronomic or horticultural practice. Plant growth retardants represent the commercially most important group of plant bioregulators (PBRs) or plant growth regulators, although compared to herbicides, insecticides, and fungicides, they play a relatively minor role and represent only a few percent of the worldwide sales of crop-protecting chemicals, totaling approximately US $28 billion in 1999. In addition to other agronomic tools, PBRs can be used relatively flexibly by the farmer to adjust his crop in a desired way to changes in growing conditions. Plant growth retardants have found a number of practical uses: In intensive small grain cultivation in Europe, they have become an integral part of the production system by reducing the risk of lodging due to intensive rainfall and/or wind; in cotton excessive vegetative growth may be controlled, thereby helping adjust a perennial plant species to an annual cycle of cultivation; fruit trees can be kept more compact, thereby reducing costs for pruning and obtaining a better ratio between vegetative growth and fruit production; the quality of ornamental and bedding plants is generally improved by keeping them compact, which also reduces the space in a greenhouse required for production; costs for trimming hedges and trees and for mowing turf grasses may also be reduced by applying plant growth retardants. For more details on applications of plant growth retardants the reader is referred to. Reduction of shoot growth can also be achieved by compounds other than growth retardants. For instance, compounds with a low herbicidal activity or herbicides applied at lower rates may cause a stunted shoot without bringing about visible symptoms of phytotoxicity. Reductions in plant productivity have to be expected, however. Examples of such plant growth suppressants are mefluidide, amidochlor, maleic hydrazide, or chlorflurenol, which might be used, for example, to reduce shoot growth of turf grasses. In principle, breeding offers an alternative way to achieve desired alterations in plant development. However, a fixed genotype is less flexible towards changing growing conditions and does not allow an active steering of growth. We can classify the existing growth retardants into two main groups: ethylene-releasing compounds, such as ethephon, and inhibitors of GA biosynthesis. Most growth retardants act by inhibiting gibberellin (GA) biosynthesis. To date, four different types of such inhibitors are known: (a) Onium compounds, such as chlormequat chloride, mepiquat chloride, chlorphonium, and AMO-1618, which block the cyclases copalyl-diphosphate synthase and ent-kaurene synthase involved in the early steps of GA metabolism. (b) Compounds with an N-containing heterocycle, e.g. ancymidol, flurprimidol, tetcyclacis, paclobutrazol, uniconazole-P, and inabenfide.

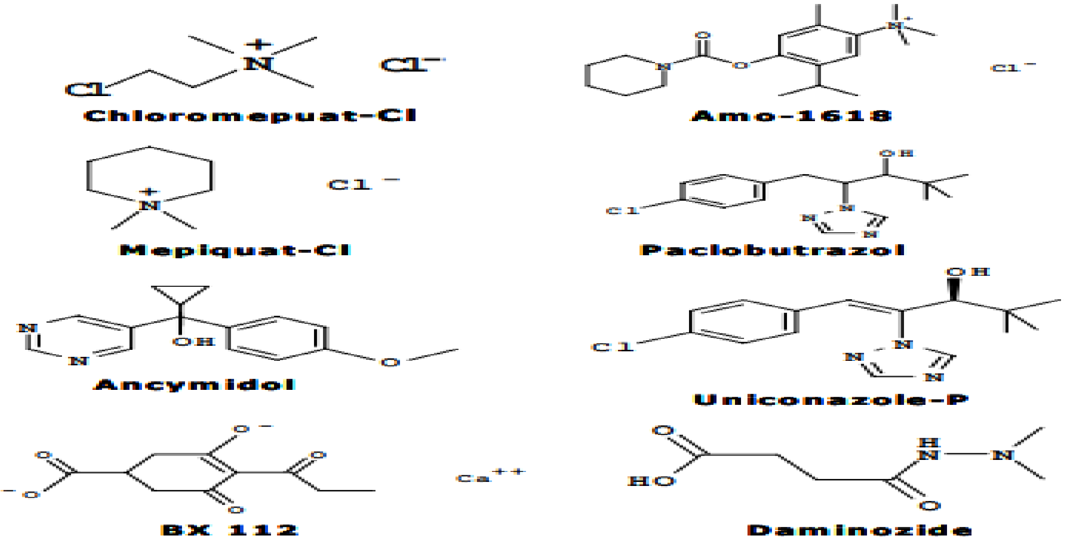


Fig. 2. Structure of plant growth retardants.

APPLICATION OF SYNTHETIC GROWTH RETARDANTS

GA INHIBITORS

1. **Controlling stem growth in greenhouse crops**: The application of growth retardants to potted plants results in shorter more rigid stems and darker green foliage, characteristics that increase the value of the crop. In chrysanthemums, daminozide is effective as a foliar spray and ancymidol may be used as both a foliar spray or a soil drench. Ancymidol treatment may, however, result in a delay in flowering. In poinsettia, chlormequat chloride is used extensively for height control since it is less expensive than ancymidol. In lily, uniconazol is used because it is the most effective compound for reducing stem height in this plant. Paclobutrazol (1-(4 chlorophenyl)4,4-imethyl-2- (1,2,4-triazol-1-yl)pentan-3-ol) and the triazole fungicide triademefon will also control stem height, but higher concentrations are required in comparison to ancymidol. Another triazole, uniconazole (Sumagic), is also registered for use on poinsettias. This compound is less

persistent than paclobutrazol, but provides good height control in a variety of herbaceous and wood ornamental plants.

2. **Controlling rank growth in cotton**: Under certain conditions of high fertility and favorable environmental conditions excessive vegetative growth of cotton results. Mepiquat chloride(1,1,dimethylpiperidinium chloride) applied at the time of flowering can reduce growth by 20~30%. Early yield of cotton is often increased by this treatment presumably due to greater light penetration into the canopy, thus allowing fruit set to take place in flowers produced on the lower nodes of the plant. Reduced vegetative growth also allows greater coverage of insecticides, fungicides and defoliants, the latter increasing the efficiency of mechanical harvesting.
3. **Lodging control in cereals**: Stem lodging is one of the most serious problems in wheat, when this crop is grown under the conditions of high fertility in Europe. The ability to use nitrogen to increase yield is limited by its adverse effect on stem growth. Chlormequat chloride and be used to reduce stem height and increase stem diameter. Yield is increased as a result of reduced stem lodging. In addition, in some years when lodging is not a problem, yield may still be increased because the growth retardant treatment results in a stimulation of tillering. Other cereals do not respond as well to cholrmequat chloride as wheat. However., lodging control has been obtained in barley and rye with a combination of mepiquat chloride and ethephon.
4. **Reducing growth of turfgrass** Chemical control of grass growth especially on sites such as highway dividers, near airfields, on steep slopes that are difficult or dangerous to mow, can be economically attractive alternative. Several compounds such as chlorflurenol (methyl-2-chloro-9- carboxylate), mefluidide(N-(2,4-dimethyl-5(trifluoromethyl)sulfonyl)amino)-phenylacetamide), and paclobutrazol have been registered for use as plant growth regulators for grass control. Chloflurenol acts by inhibiting cell division in the shoot meristem, whereas mefluidide inhibits cell elongation. Both compounds have been found to reduce the frequency of mowings required over the course of the growing season. Paclobutrazol reduces mowing frequence by to an even greater extent than the other compounds: however, it does not effectively suppress seedhead formation. Combinations of paclobutrazol with heigher maleic hydrazide,

chlorflurenol or mefluidide should provide adequate seedhead suppression and persistence throughout the growing season for almost complete control of grass growth.

5. **Increasing fruit set in grape**: Application of chlormequat chloride to vinifera grapes before bloom increases fruit set of seeded berries. Cluster fresh weight is increased as a result of treatment. Daminozide is more effective than chlomequat chloride in increasing fruit set of the labrusca varieties. In addition to increasing cluster yield, vine growth is reduced by growth retardant treatment. It is not clear whether the increase in fruit set by the growth retardant is due to a direct effect on this process by decreasing GA levels (GA is used for berry thinning) or an indirect effect resulting from decreased vegetative growth. Exceedingly vigorous shoot growth is often associated with poor fruit setting in the field. Moreover, if shoot tips are removed, fruit set in grape can be increased, and the growth retardants are not capable of further increasing fruit set in detopped plants.
6. **Advancing fruit color development**: Daminozide may be used to advance anthocyanin production in the fruit skin and flesh of sweet cherry. The rate of color development is increased as well as the total amount of pigment synthesized. Other processes associated with fruit ripening such as fruit softening are not affected by daminozide treatment. Daminozide will also increase anthocyanin synthesis in apple, as well as reduce fruit softening in cold storage and pre-harvest fruit drop. Physiological disorders that develop at harvest or in storage have also been reported to be less severe after a mid-summer application of daminozide. The mechanism by which daminozide enhances color development in fruit is not clear. In apple. daminozide will inhibit ethylene production by blocking the conversion of methionine to aminocyclopropanel-carboxylic acid, and delay the appearance of the respiratory climacteric. This will permit a delay in the harvest date and perhaps allow anthocyanin production to continue for a longer time before harvest. In some cases, however, daminozide will not only accelerate color production but also stimulate the production of greater amounts of anthocyanin in the apple skin or the flesh of cherry, therefore suggesting a more direct effect of the compound on pigment synthesis. It has shown that anthocyanin production in apple is associated with increasing activity of the pentose phosphate pathway in the catabolism of carbohydrate. Meanwhile daminozide inhibits succinate dehydrogenase activity in isolated mitochondria. Perhaps by inhibiting Krebs cycle activity, greater carbon flow occurs in the pentose pathway,

which forms the essential precursors for anthocyanin, In isolated apple skin discs, however, it was not possible to demonstrate a anthocyanin production in the presence of daminozide.

7. **Induction of flower bud formation**: Both apple and pear trees do not generally cone into full production until the trees are at least 5 years of age. Flowering can be stimulated in young trees will also occur after daminozide application. Increasing return bloom of mature trees will also occur after daminozide application in apple, or chlormequat chloride treatment of pear. The growth retardants decrease shoot elongation in fruit trees, and perhaps by inhibiting vegetative growth, flower bud initiation is promoted.
8. **Controlling tree size**: Acylcyclohexanediones, e.g. prohexadione-Ca and trinexapac-ethyl are probably the most effective compounds found to date for controlling shoot elongation in fruit trees. Controlling tree size with these compounds will be an effective way of maintaining tree height for maximum spraying and harvesting efficiency in conjunction with modern pruning practices such as summer mowing of the tree canopy. Growth of woody landscape plants may also be effectively controlled using the triazoles, paclobutrazol and uniconazole. This practice is particularly useful during nursery container production.

ETHYLENE-RELEASING AGENTS

While the biological effects of ethylene on plant growth have been documented for some time, little practical use of ethylene in agricultural was possible due to its gaseous nature. In the early 1970s experimental formulations of compounds became available that decompose on or within a plant to release ethylene. One of the first of these compounds, ethephon,(2-chloroethylphosphonic acid) is stable at pH values of 4 or less, but at higher pH values, the compound decomposes to produce ethylene, chloride and phosphate ions, Since the cytoplasmic pH is greater than 4, once ethephon is absorbed, cleavage to ethylene inside the cell begins. Two other compounds, etacelasil (2-chloroethyl-tris-ehtoxymethoxy silane) and 2-chloroethyl-bis-phenylmethoxy silane, also decompose to ehtylene, but much more rapidly than ethephon, and are less sensitive to changes in pH.

1. **Increasing latex flow in Hevea**: The amount of rubber produced in the form of coagulated latex is a function of the duration of latex flow from the tapping cut that is made in the tree bark. Ethephon is applied to a region near the tapping cut and causes latex flow to increase in duration, resulting in an increase in the volume of latex collected. Rubber yield increases of 50-100% are common. The mechanism for increased flow of latex by ethephon is not well understood. It is believed that lutoids, non-rubber containing bodies within the latex, are disrupted by tapping and cause coagulation or plugging of the latex vessels, as a result of changes in osmotic potential, or shear forces imposed by the high flow rate through the narrow pores of the vessel. Ethephon may stabilize the lutoids making them less susceptible to disruption. Alternatively, it has been proposed that ethephon treatment leads to an increase in cell wall thickening of the vessels making the walls less likely to contract during tapping, and therefore fewer lutoids would be disrupted, all of which will increase latex flow.
2. **Promoting abscission**: The use of mechanical harvesting devices in cherry production had been limited because the force required to remove the fruit at the time of fruit maturity resulted in damage to the trees. Ethephon may be applied approximately 10 days before anticipated harvest to reduce the fruit removal force to allow mechanical harvesting of the crop without tree injury. Walnuts are also harvested mechanically after treatment with ethephon. The edible kernel of the walnut reaches maturity come 3-4 weeks before harvest, due to the time required for hull dehiscence. Ehtephon treatment accelerates this process. The quality of the harvested nuts is also increased because they do not remain on the tree for long periods of time after maturation and, therefore, avoid decomposition due to heat and disease. Olive fruit also have a high fruit removal force at maturity. In addition, the fruit is attached to long willowy branches that do not lend themselves mechanical shaking. Ethephon causes fruit abscission, but also excessive leaf abscission reducing flowering the following spring. Etacelasil can be used, however, because it reduces the attachment force without defoliation, This compound releases ethylene at a much faster rate than does ethephon. There may be a requirement for elevated ethylene levels of longer duration to induce leaf abscission than for fruit abscission, making the silyl compounds more useful as fruit abscission agents than ethephon. Ethylene-releasing agents are also being used to remove young fruit from apple

and peach trees that have set a potentially excessive fruit crop. In peach, 2-chloroethylmethyl-bisphenylmethoxy silane has provided acceptable fruit abscission without defoliation in many areas of the southeastern US.

3. **Promoting fruit ripening** The ripening process in mature fruit can be accelerated by ethephon application. Presumably the fruit are sensitive to ethylene at this stage of development, but have not produced enough endogenous ethylene to stimulate the ripening process. In apple, ehtephon can be used to accelerate fruit softening and advance fruit color production by several weeks, although an additional application of compounds that delay abscission be mad in conjunction with ethephon. In tomato, ethephon is used to accelerate ripening and concentrate maturity of the fruit for mechanical harvesting. Ethephon stimulates the production of lycopene by fruit and therefore can increase total yield of ripe fruit in the production of processing tomatoes, since this crop is harvested at one time only. In grape, ethephon has been found to promote color development and decrease total fruit acidity. In some of the cooler grape growing regions acidity is often excessive for optimum win quality. Ehtephon treatment may also be useful when natural fruit color development is poor.
4. **Delaying flowering in fruit crops**: Application of ethephon in the fall of the year prior th the spring flowering period delays bud expansion and anthesis in cherry and peach. Ethephon appears to increase the length of the dormant period of flower bud, which results in a delay in bloom, reducing the potential for spring frost damage to flowers. In some cases, ethephon also increases mid-winter flower bud cold hardiness by maintaining high levels of the cryoprotectants sorbitol and sucrose in the flower pistil.
5. **Promoting leaf senescence in tobacco**: Ethephon is used to promote leaf yellowing in flue-cured tobacco. Ethephon increases the number of leaves that may be harvested at one time, and decreases the curing time for the leaf. This treatment is especially useful in the cooler tobacco growing regions where the uppermost leaves, which are the last to be harvested, may be damaged by frost.

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