Plant hormones: Structure-function relationship of plant hormones; metabolism of auxins, gibberellins and cytokinins

Phytohormones are organic compounds which are produced naturally in higher plants, thereby controlling the growth or other physiological functions at a site remote from its place of production and active in minute amounts.

In other words, they can be defined as organic compounds which regulate plant physiological process— regardless of whether these compounds are naturally occurring and/or synthetic; stimulating and/or inhibitory; local activators or substances which act at a distance from the place where they are formed.

Three types of plant hormones are usually recognized. The most common types of plant hormones are auxins, gibberellins and cytokinins.

‘auxin’ (auxeinG = to grow or to increase) for designating those plant hormones which are specially concerned with cell enlargement or the growth of the shoots.

An auxin is an organic substance which promotes growth (i.e., irreversible increase in growth) along the longitudinal axis when applied in low concentrations to shoots of the plants freed as far as practicable from their own inherit growth-promoting substances.

There are various forms of auxin:

1. Auxin a, auxentriolic acid. It occurs at the meristematic apices (buds and growing leaves) both in the free state and bound to plasma proteins. It is a weak acid and is soluble in water, alcohol, ether and chloroform. It is stable in acid solutions but decomposes in alkaline solutions (i.e., acid-stable and alkali-labile).

2. Auxin b, auxenolonic acid. It is present in corn germ oil, other vegetable oils, malt and a fungus called Rhizopus. It is also a weak acid and is soluble in water, alcohol, ether and chloroform. It is both acid-labile and alkali-labile. This as well as auxin a both are derivatives of cyclopentene.

3. Heteroauxin, indole-3-acetic acid. It is of universal occurrence in plants and is also synthesized by microorganisms including certain bacteria, yeasts and fungi like Rhizopus. It is resistant to alkalis whereas destroyed by acids and undergoes rapid decomposition on heating. Unlike the first two, it can be easily synthesized in the laboratory. Chemically, it is a monobasic acid of a relatively simple structure.



The synthesis of IAA proceeds in different ways in different plants. There are two synthetic pathways starting from tryptophan. But precursors of tryptophan synthesis may also act as precursors of IAA synthesis.

Tryptophan, liberated by hydrolysis of proteins, undergoes either oxidative amination first and then decarboxylation or vice versa to yield indoleacetaldehyde (IAc). IAc is then oxidized to yield the free auxin. Indoleacetaldehyde, thus, acts as an intermediate metabolite as well as an immediate precursor of IAA.

Besides IAA, some other substances are known with auxin properties (e.g., phenylacetic acid). The synthetic auxin **2,4-dichlorophenoxyacetic acid** is used as an **herbicide**. It kills plants by acting as an especially powerful auxin, resulting in disordered morphogenesis and an increased synthesis of ethylene, thus leading to a premature senescence of leaves. As **agent orange**, it was used in the Vietnam War to defoliate forests. 2,4-D is a selective herbicide that destroys dicot plants. Monocots are insensitive to it, because they eliminate the herbicide by degradation. For this reason, 2,4-D is used for combating weeds in cereal crops.

Auxin functions in many ways. During **early embryogenesis**, auxin governs the formation of the main **axis of polarity**, with the shoot meristem at the top and the root meristem at the opposite pole. Auxin generally influences cell division and differentiation. One effect of IAA is to enhance the **elongation growth** of cells. Therefore the highest IAA concentrations are found in the main growth zones of the shoot. However, IAA is formed primarily at the tip of the shoot. From there it is transported from cell to cell by an energy-dependent **polar transport**. The transport of auxin from cell to cell proceeds via specific **efflux** and **influx carriers** of the plasma membrane. The polar transport is caused by an asymmetric distribution of these carriers. The membrane-bound efflux carrier proteins are transferred in a reversible fashion between membrane regions by vesicle transport via the Golgi apparatus. In this way the efflux carriers can be rapidly moved from one area of the plasma membrane to another to facilitate a polar transport.

During the curvature of the coleoptile, IAA is transported laterally to one side. The resulting differential stimulation of cell elongation at only one side of the shoot leads to the bending. IAA is also transported via the phloem from the leaves to distant parts of the plant.



Two biosynthetic pathways for the formation of indole-3-acetic acid from tryptophan.



Phenylacetic acid, another substance with auxin properties, and 2,4D, a structural analogue of auxin, acting as an herbicide.

**Physiological Roles of Auxins**

The various growth processes in which the auxins (both natural and synthetic) play their role are:

**1. Cell elongation.** It is usually considered that cell elongation occurs only in the presence of auxins and also that the rate of elongation is directly proportional to the amount of auxin applied provided no other factors are limiting. But relatively high concentrations usually exert inhibitory effect on this phase of growth. Various plant organs like roots, buds and stems all react in a comparable way to auxins: their growth being promoted by relatively low and inhibited by relatively high auxin concentrations. Elongation of roots is promoted only at very low concentrations; at higher concentrations their growth is retarded. Stems and coleoptiles respond similarly except that optimum range of concentrations for elongation is much higher than for roots. Flowers require still higher concentration for growth.

Auxins also play a significant role in the elongation of petiole, mid rib and major lateral veins of the leaves. Thus, adenine favours enlargement in detached leaves of radish and pea. Similarly, coumarin has been shown to promote expansion of leaves in some plants.

**2. Cambial activity.** In the spring season, the trees exhibit growth by developing buds which later on open. This is then followed by elongation of the young stems. This resumption of growth by cambial cells is activated by the auxins which move basipetally in the stems from developing buds.

**3. Callus formation and galls.** Besides acting as stimulants of cell elongation, the auxins may also activate cell division.

**4. Rooting of stem cuttings ( = Formation of adventitious roots).** It is a common observation that the presence of buds on a cutting favours development of roots when the lower end is dipped in a suitable rooting medium. Developing buds are effective in accelerating root formation. Young leaves also favour the initiation of roots on the cuttings. These observations led to the suggestion that the root formation is favoured by the auxins which are synthesized in the buds and young leaves and are later translocated to the basal part of the cutting.

**Gibberellins**

Gibberellins are derived from the hydrocarbon ***ent*-gibberellane**. More than 100 gibberellins are now known in plants, which are numbered in the order of their identification. The most important gibberellins are GA1 and GA4.

A *gibberellin* (abbreviated as GA, for gibberellic acid) may be defined as a compound which is active in gibberellin bioassays and possesses a gibbane ring skeleton. There are, however, other compounds (like kaurene) which are active in some of the assays but do not possess a gibbane ring. Such compounds have been called *gibberellin-like* rather than gibberellins.



Although the biosynthesis of gibberellins from mevalonic acid occurs through some 18 or more steps, 5 key steps culminating in GA production are very important. Mevalonate, in its turn, is produced from acetate.



**Synthesis of gibberellin GA1**

The use of gibberellins is of economic importance for the production of long, seedless grapes. In these grapes, GA1 causes not only extension of the cells, but also parthenocarpy (the generation of the fruit as a result of parthogenesis). Moreover, in the malting of barley for beer brewing, gibberellin is added to induce the formation of a-amylase in the barley grains.

The gibberellin GA3, produced by the fungus *Gibberella fujikuroi* mentioned previously, is generally used for these purposes. Inhibitors of gibberellin biosynthesis are commercially used as **retardants** (growth inhibitors). A number of substances that inhibit the synthesis of the gibberellin precursor *ent*-kaurene, such as **chloroethyltrimethyl ammonia chloride**, (trade name, Cycocel, BASF) are sprayed on cereal fields to decrease the **growth of the stalks**. This enhances the strength of the cereal stalks and at the same time increases the proportion of total biomass in seeds. Slowly degradable gibberellin synthesis inhibitors are used in horticulture to keep household plants small.



**Cycocel (BASF), a growth retardant that decreases the growth of stalks in wheat and other cereals, inhibits kaurene synthesis and thus also the synthesis of gibberellins.**

**Physiological Roles**

Gibberellins may be regarded as natural phytohormones on account of their wide range of distribution in plants and specificity of response of individual flowering plants to the exogenously applied gibberellins. The gibberellins, however, play important roles in the following processes:

**1. Genetic dwarfism.** In certain plants, dwarfism is caused by the mutation of a single gene. Such individuals are called ‘*single gene dwarfs’*. In these plants, dwarfism is due to shortening of internodes rather than a decrease in the number of internodes. Application of gibberellins on such dwarfs causes them to elongate so much as to become indistinguishable from the tall normal plants. Elongation of the stem, in fact, takes place due to an elongation in the internodes rather than an increase in the number of internodes. Thus, genetic dwarfism has been successfully overcome by gibberellin A3 treatment in many single gene dwarf mutants like *Pisum sativum, Vicia faba* *and Phaseolus multiflorus*. The gibberellins, thus make most plants grow taller by causing the internodes to elongate considerably.

**2. Bolting and flowering.** ‘*Rosette plants*’ are characterized by their profuse leaf development and retarded internodal growth. But prior to the reproductive phase, there occurs striking elongation in the internode so that the plant attains 5 to 6 times the original height. Treatment of these `rosette' plants with gibberellins, under conditions that would normally maintain the rosette form, induces them to bolting (or shoot elongation) and flowering. Native gibberellin-like substances are found in higher concentrations in the bolted forms than in the nonbolted ones.

As far as the use of gibberellins in agriculture is concerned, it may be possible to grow cold requiring plants in warm countries and long-day plants in short-day conditions at lower altitudes. Gibberellic acid (GA) hastened flowering and improved the flower yield in *Coriandrum* *sativum* (coriander). This was accomplished by a decline in starch content and an increase in reducing sugars, as well as enhanced amylase activity. It was inferred that GA3 hastened flowering probably through its influence on carbohydrate metabolism.

**3. Light-induced inhibition of stem growth.** Light-grown plants reveal suppressed stem growth than the dark-grown (or etiolated) plants, indicating that light has an inhibitory effect on stem elongation. But this inhibitory effect of light on stem elongation can be reversed at least in some plants (*like Pisum sativum*) by the application of gibberellins on these plants. This clearly suggests that endogenous gibberellin is the limiting factor in stem elongation.

**4. Breaking dormancy of seeds.** The light-sensitive seeds (lettuce, tobacco) show poor germination in dark and on exposure to light their germination starts vigorously. But when these seeds are treated with GA3, the light requirement is alleviated and they germinate in dark.

**5. Breaking dormancy of buds.** In temperate areas, the buds produced in winter remain dormant until the next spring due to very low temperature. The dormancy in such cases is overcome by gibberellin treatment. Thus, GA3 treatment to birch buds has replaced the light requirement for breaking dormancy. Gibberellins are also capable of breaking dormancy in potato tubers.

**6. Role in abscission.** GA3 treatments have shown accelerated rate of abscission in explants of bean and of *Coleus*.



**Cytokinins stimulate cell division**

Cytokinins as chemicals which, regardless of their activities, promote cytokinesis (cell division) in cells of various plant organs. Cytokinins are prenylated derivatives of adenine. In zeatin, which is the most common cytokinin, the amino group of adenine is linked with the hydroxylated isoprene residue in the *trans*-position.

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**Physiological Roles**

1. Cell division. Cytokinins enhance plant growth by stimulating **cell division** and increase the sprouting of lateral buds.

**2. Cell elongation.** Besides auxins and gibberellins, kinetin also promotes cell elongation. Such promotion after kinetin treatment has been observed in tobacco pith cultures, tobacco roots and bean leaf tissues.

**3. Root growth.** Kinetin is capable of stimulating as well as inhibiting root development.

**4. Shoot growth.** The callus tissue of tobacco can be kept in an undifferentiated state so long as the proper balance of IAA and kinetin is maintained. If, however, the amount of kinetin is increased, leafy shoots are initiated to develop. Bean seedlings, soaked in kinetin solution, also showed an increase in dry weight and a marked elongation of stem and petioles (Miller, 1956).

**5. Organogenesis.** Cytokinins can cause organogenesis (*i.e.*, the formation of organs) in a variety of tissue cultures. For instance, tobacco pith callus can be made to develop either buds or roots by changing the relative concentrations of kinetins and auxins. High kinetin and low auxin contents result in the production of buds.