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Plant Hormones: Their nature occurrence and functions: A chapter

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Abstract
Plant hormones are a class of organic substances which are synthesized during the plant metabolism. They have an obvious physiological effect on plant growth at very low concentrations. Generally, plant hormones are mainly divided into five categories: Auxins, Gibberellins (GAs), Cytokinins, Ethylene, and Abscisic acid (ABA). With the deepening of research, some novel plant hormones such as Brassinosteroid, Salicylates, Jasmonates, Polyamines, and Signal Peptides have been found and identified. The plant hormone products are mainly obtained through plant extraction, chemical synthesis as well as microbial fermentation.

Keywords: gibberellins, ethylene, brassinosteroid, occurrence, biosynthesis

Introduction
Plant hormones are *a group of naturally occurring, organic substances which influence physiological processes at low concentrations*. The processes influenced consist mainly of growth, differentiation and development, though other processes, such as stomatal movement, may also be affected. Plant hormones have also been referred to as 'phytohormones' though this term is infrequently used. In their book *Phytohormones* Went and Thimann in 1937 define a hormone as a substance which is transferred from one part of an organism to another. Its original use in plant physiology was derived from the mammalian concept of a hormone. This involves a localized site of synthesis, transport in the bloodstream to a target tissue, and the control of a physiological response in the target tissue via the concentration of the hormone. Auxin, the first-identified plant hormone, produces a growth response at a distance from its site of synthesis, and thus fits the definition of a *transported* chemical messenger. However this was before the full range of what we now consider plant hormones was known. It is now clear that plant hormones do not fulfil the requirements of a hormone in the mammalian sense. The synthesis of plant hormones may be localized (as occurs for animal hormones), but it may also occur in a wide range of tissues, or cells within tissues. While they may be transported and have their action at a distance this is not always the case. At one extreme we find the transport of cytokine's from roots to leaves where they prevent senescence and maintain metabolic activity, while at the other extreme the production of the gas ethylene may bring about changes within the same tissue, or within the same cell, where it is synthesized. Thus, transport is not an essential property of a plant hormone. The term 'hormone' was first used in medicine about 100 years ago for a stimulatory factor, though it has come to mean a transported chemical message. The word in fact comes from the Greek, where its meaning is 'to stimulate' or 'to set in motion'. Thus the origin of word itself does not require the notion of transport *per se*, and the above definition of a plant hormone is much closer to the meaning of the Greek origin of the word than is the current meaning of hormone used in the context of animal physiology. Plant hormones2 are a unique set of compounds, with unique metabolism and properties, that form the subject of this book. Their only universal characteristics are that they are natural compounds in plants with an ability to affect physiological processes at concentrations far below those where either nutrients or vitamins would affect these processes.

The discovery, identification, plant hormones
The plant hormone concept probably derives from observations of morphogenic and developmental correlations by Sachs between 1880 and 1893. He suggested that "Morphological differences between plant organs are due to differences in their material composition" and postulated the existence of root-forming, flower forming and other substances that move in different directions through the plant. At about the same time Darwin was making his original observations on the phototropism of grass coleoptiles that led him to postulate the existence of a signal that was transported from the tip of the coleoptile to the bending regions lower down. After further characterizations by several workers of the way in which the signal was moved, Went in the Netherlands was finally able to isolate the chemical by diffusion from coleoptile tips into agar blocks, which, when replaced on the tips of decapitated coleoptiles, resulted in the stimulation of the growth of the decapitated coleoptiles, and their bending when placed asymmetrically on these tips. This thus demonstrated the existence of a growth promoting chemical that was asymmetrically resulted in a bending of the coleoptile away from the side with the higher concentration. This substance was originally named *Wuchsstoff* by Went, and later this was changed to *auxin.* After some false identifications the material was finally identified as the simple compound indoleacetic acid, universally known as IAA.

Effects of plant hormones, nature & occurrence

Before we become involved in the various subsequent chapters covering aspects of hormone biochemistry and action it is necessary to review what hormones do. Over the last few years there has been active progress in elucidating the biosynthesis, signal transduction and action of almost every hormone. Thus whereas previously the progress in understanding the action of one hormone was much better than that of another we now find increased understanding of hormone action across the board.

A good case in point is cytokinin, where we now know much more about perception, signal transduction and action than just a few years ago. In fact progress on understanding one hormone as opposed to another has been leapfrogging: whereas the action of auxin at the physiological level was one of the first to be under to we still do not understand the connection between auxin signal transduction and its final action in inducing cell elongation, and while the identification of the auxin receptor was previously regarded as established, this is now regarded as far less certain. By contrast, after two decades of relatively little advance in the understanding of Brassinosteroids, or even much interest in these compounds, following their discovery by extraction from Brassica pollen and the demonstration of growth activity in a bean petiole bioassay, the entire biosynthetic pathway has been elucidated, receptors identified, mutants characterized and crosstalk with other hormones investigated. The effects produced by each hormone were initially elucidated largely from exogenous applications. However in more and more cases we have evidence that the endogenous hormone also fulfils the originally designated roles, and new functions are being discovered. In other cases it has not yet been conclusively proved that the endogenous hormone functions in the same manner. The nature, occurrence, transport and effects of each hormone (or hormone group) are given below. It should, however, be emphasized that hormones do not act alone but in conjunction, or in opposition, to each other such that the final condition of growth or development represents the net effect of a hormonal balance.

Auxin

Nature

Indole-3-acetic acid (IAA) is the main auxin in most plants. Compounds which serve as IAA precursors may also have auxin activity (e.g., indole acetaldehyde). Some plants contain other compounds that display weak auxin activity (e.g., phenyl acetic acid). IAA may also be present as various conjugates such as indole acetyl aspartate. 4-chloro-IAA has also been reported in several species though it is not clear to what extent the endogenous auxin activity in plants can be accounted for by 4-Cl-IAA. Several synthetic auxins are also used in commercial applications.

Sites of biosynthesis

IAA is synthesized from tryptophan or indole primarily in leaf primordia and young leaves, and in developing seeds.

Nature, occurrence and functions

Transport

IAA transport is cell to cell, mainly in the vascular cambium and the procambial strands, but probably also in epidermal cell. Transport to the root probably also involves the phloem.

Effects

- Fruit ripening - auxin delays ripening.
- Growth of flower parts - stimulated by auxin.
- Leaf senescence - auxin delays leaf senescence.
- Leaf senescence - auxin delays leaf senescence.
- Leaf senescence - auxin delays leaf senescence.
- Flowering - auxin promotes flowering in Bromeliads.
- Promotes femaleness in dioecious flowers (via ethylene).
- Cell enlargement - auxin stimulates cell enlargement and stem growth.
- Vascular tissue differentiation - auxin stimulates differentiation of phloem and xylem.
- Cell division - auxin stimulates cell division in the cambium and, in combination with cytokinin, in tissue culture.
- Tropistic responses - auxin mediates the tropistic (bending) response of shoots and roots to gravity and light.
- Root initiation - auxin stimulates root initiation on stem cuttings, and also the development of branch roots and the differentiation of roots in tissue culture.
- Apical dominance - the auxin supply from the apical bud represses the growth of lateral buds.
- Leaf and fruit abscission - auxin may inhibit or promote (via ethylene) leaf and fruit abscission depending on the timing and position of the source.
- Assimilate partitioning - assimilate movement is enhanced towards an auxin source possibly by an effect on phloem transport.

In several systems (e.g., root growth) auxin, particularly at high concentrations, is inhibitory. Almost invariably this has been shown to be mediated by auxin-produced ethylene. If the ethylene synthesis is prevented by various ethylene synthesis inhibitors, the ethylene removed by hypobaric conditions, or the action of ethylene opposed by silver salts (Ag^+), then auxin is no longer inhibitory.

Gibberellins (GAs)

Nature

The gibberellins (GAs) are a family of compounds based on the entgibberellane structure; over 125 members exist and their structures can be found on the web. While the most widely available compound is GA_3 or gibberellic acid, which is a fungal product, the most important GA in plants is GA_1, which is the GA primarily responsible for stem elongation. Many of the other GAs are precursors of the growth-active GA_1.

Sites of biosynthesis

GA are synthesized from glyceraldehyde-3-phosphate, via isopentenyl diphosphate, in young tissues of the shoot and developing seed. Their biosynthesis starts in the chloroplast and subsequently involves membrane and cytoplasmic steps.

Transport

GAs are probably transported in the phloem and xylem. However the transport of the main bioactive polar GA_1 seems restricted.

Effects
- Induction of maleness in dioecious flowers.
- Bolting in long day plants - GAs cause stem elongation in response to long days.
- Stem growth - GA1 causes hyper elongation of stems by stimulating both cell division and cell elongation. This produces tall, as opposed to dwarf, plants.
- Induction of seed germination - GAs can cause seed germination in some seeds that normally require cold (stratification) or light to induce germination.
- Enzyme production during germination - GA stimulates the production of numerous enzymes, notably α-amylase, in germinating cereal grains.
- Fruit setting and growth - This can be induced by exogenous applications in some fruit (e.g., grapes). The endogenous role is uncertain.

Cytokinins (CKs)
Nature
Cytokinins are adenine derivatives characterized by an ability to induce cell division in tissue culture (in the presence of auxin). The most common

Nature, occurrence and functions
Cytokinin base in plants is zeatin. Cytokinins also occur as ribosides andribotides.

Sites of biosynthesis
CK biosynthesis is through the biochemical modification of adenine. It occurs in root tips and developing seeds.

Transport
CK transport is via the xylem from roots to shoots.

Effects
- CKs delay leaf senescence.
- CKs may enhance stomatal opening in some species.
- Morphogenesis - in tissue culture and crown gall CKs promote shoot initiation. In moss, CKs induce bud formation.
- Chloroplast development - the application of CK leads to an accumulation of chlorophyll and promotes the conversion of etioplasts into chloroplasts.
- Growth of lateral buds - CK applications, or the increase in CK levels in transgenic plants with genes for enhanced CK synthesis, can cause the release of lateral buds from apical dominance.
- Cell division - exogenous applications of CKs induce cell division in tissue culture in the presence of auxin. This also occurs endogenously in crown gall tumors on plants. The presence of CKs in tissues with actively dividing cells (e.g., fruits, shoot tips) indicates that CKs may naturally perform this function in the plant.
- Leaf expansion, resulting solely from cell enlargement. This is probably the mechanism by which the total leaf area is adjusted to compensate for the extent of root growth, as the amount of CKs reaching the shoot will reflect the extent of the root system. However this has not been observed in transgenic plants with genes for increased CK biosynthesis, possibly because of a common the lack of control in these systems.

Ethylene
Nature
The gas ethylene (C_2H_4) is synthesized from methionine in many tissues in response to stress, and is the fruit ripening hormone. It does not seem to be essential for normal mature vegetative growth, as ethylene deficient transgenic plants grow normally. However they cannot, as seedlings, penetrate the soil because they lack the stem thickening and apical hook responses to ethylene, and they are susceptible to diseases because they lack the ethylene-induced disease resistance responses. It is the only hydrocarbon with a pronounced effect on plants.

Sites of synthesis
Ethylene is synthesized by most tissues in response to stress. In particular, it is synthesized in tissues undergoing senescence or ripening.

Transport
Being a gas, ethylene moves by diffusion from its site of synthesis. A crucial intermediate in its production, 1-aminocyclopropane-1-carboxylic acid (ACC) can, however, be transported and may account for ethylene effects at a distance from the causal stimulus.

Effects
- Leaf and fruit abscission.
- Flower induction in some plants.
- Flower and leaf senescence.
- Release from dormancy.
- Maintenance of the apical hook in seedlings.
- Fruit ripening.
- Flower opening.
- Adventitious root formation
- Shoot and root growth and differentiation.
- Induction of femaleness in dioecious flowers.
- Stimulation of numerous defense responses in response to injury or disease.

Abscisic acid (ABA)
Nature
Abscisic acid is a single compound with the following formula.

Nature, occurrence and functions
The first name given was "abscisin II" because it was thought to control the abscission of cotton bolls. At almost the same time another group named it "dormin" for a purported role in bud dormancy. By a compromise the name abscisic acid was coined. It now appears to have little role in either abscission. or bud dormancy, but we are stuck with this name. As a result of the original association with abscission and dormancy, ABA has become thought of as an inhibitor. While exogenous applications can inhibit growth in the plant, ABA appears to act as much as a promoter, such as in the promotion of storage protein synthesis in seeds, as an inhibitor, and a more open attitude towards its overall role in plant development is warranted. One of the main functions is the regulation of

stomatal closure. Sites of synthesis ABA is synthesized from glyceraldehyde-3 phosphate via isopentenyl diphosphate and carotenoids in roots and mature leaves, particularly in response to water stress. Seeds are also rich in ABA which may be imported from the leaves or synthesized in situ.

Transport

ABA is exported from roots in the xylem and from leaves in the phloem. There is some evidence that ABA may circulate to the roots in the phloem and then return to the shoots in the xylem.

Effects

- Stomatal closure - water shortage brings about an increase in ABA which leads to stomatal closure.
- ABA induces storage protein synthesis in seeds.
- ABA counteracts the effect of gibberellin on α-amylase synthesis in germinating cereal grains.
- Increase in ABA in response to wounding induces gene transcription, notably for proteinase inhibitors, so it may be involved in defense against insect attack.
- ABA inhibits shoot growth (but has less effect on, or may promote, root growth). This may represent a response to water stress.
- ABA affects the induction and maintenance of some aspects of dormancy in seeds. It does not, however, appear to be the controlling factor in 'true dormancy' or 'rest,' which is dormancy that needs to be broken by low temperature or light.

Brassinosteroids

Brassinosteroids are a range of over 60 steroidal compounds, typified by the compound brassinolide that was first isolated from *Brassica* pollen. At first they were regarded as somewhat of an oddity but they are probably universal in plants. They produce effects on growth and development at very low concentrations and play a role in the endogenous regulation of these processes.

Nature, occurrence and functions

Effects

- Cell Division, possibly by increasing transcription of the gene encoding cyclinD3 which regulates a step in the cell cycle.
- Cell elongation, where BRs promote the transcription of genes encoding xyloglucanase and expansins and promote wall loosening. This leads to stem elongation.

Vascular differentiation.

- Inhibition of root growth and development
- Promotion of ethylene biosynthesis and epinasty.
- BRs are needed for fertility: BR mutants have reduced fertility and delayed senescence probably as a consequence of the delayed fertility.

Salicylic Acid (SA)

Salicylates have been known for a long time to be present in willow bark, but have only recently been recognized as potential regulatory compounds.

Salicylic acid is biosynthesized from the amino acid phenylalanine.

Effects

- SA is the calorigenic substance that causes thermogenesis in *Arum* flowers.
- It has also been reported to enhance flower longevity, inhibit ethylene biosynthesis and seed germination, block the wound response, and reverse the effects of ABA.
- Salicylic acid plays a main role in the resistance to pathogens by inducing the production of 'pathogenesis-related proteins'. It is involved in the systemic acquired resistance response (SAR) in which a pathogenic attack on older leaves causes the development of resistance in younger leaves, though whether SA is the transmitted signal is debatable.

Jasmonates

Jasmonates are represented by jasmonic acid (JA) and its methyl ester. They are named after the jasmine plant in which the methyl ester is an important scent component. As such they have been known for some time in the perfume industry. There is also a related hydroxylated compound that has been named tuberonic acid which, with its methyl ester and glycosides, induces potato tuberization. Jasmonic acid is synthesized from linolenic acid, while jasmonic acid is most likely the precursor of tuberonic acid.

Effects

- Jamonates inhibit many plant processes such as growth and seed germination.
- They promote senescence, abscission, tuber formation, fruit ripening, pigment formation and tendril coiling.
- JA is essential for male reproductive development of Arabidopsis. The role in other species remains to be determined.
- Jasminates play an important role in plant defense, where they induce the synthesis of proteinase inhibitors which deter insect feeding, and, in this regard, act as intermediates in the response pathway induced by the peptide systemin.

Polyamines

Polyamines are a group of aliphatic amines. The main compounds are putrescine, spermidine and spermine. They are derived from the decarboxylation of the amino acids arginine or ornithine. The conversion of the diamine putrescine to the triamine spermidine and the quaternary amine spermine involves the decarboxylation of S-adenosylmethionine, which also is on the pathway for the biosynthesis of ethylene. As a result there are some complex interactions between the levels and effects of ethylene and the polyamines.

The classification of polyamines as hormones is justified on the following grounds:

- They are widespread in all cells and can exert regulatory control over growth and development at micromolar concentrations.
- In plants where the content of polyamines is genetically altered, development is affected. (E.g., in tissue cultures of carrot or *Vigna*, when the polyamine level is low only callus growth occurs; when polyamines are high, embryoid formation occurs. In tobacco plants that are overproducers of spermidine, anthers are produced in place of ovaries.)

Such developmental control is more characteristic of hormonal compounds than nutrients such as amino acids or vitamins.

Polyamines have a wide range of effects on plants and appear to be essential for plant growth, particularly cell division and normal morphologies. At present it is not possible to make an easy, distinct list of their effects as for the other hormone. It appears that polyamines are present in all cells rather than having a specific site of synthesis.

Signal Peptides

The discovery that small peptides could have regulatory properties in plants started with the discovery of systemin, an 18 amino acid peptide that travels in the phloem from leaves under herbivore insect attack to increase the content of jasmonic acid and proteinase inhibitors in distant leaves, so protecting them from attack. Since then, over a dozen peptide hormones that regulate various processes involved in defense, cell.

Nature, occurrence and functions

Division, growth and development and reproduction have been isolated from plants, or identified by genetic approaches.

Among these effects caused by specific peptides are:

- Peptide signals for self-incompatability.
- The activation of defense responses.
- The promotion of cell proliferation of suspension cultured plant cells.
- The determination of cell fate during development of the shoot apical meristem
- The modulation of root growth and leaf patterning in the presence of auxin and cytokine
- Nodule formation in response to bacterial signals involved in nodulation in legumes.

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