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# The Plant Hormones: Their Nature, Occurrence, and Functions

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# A. INTRODUCTION

## A1. The Plant Hormones: Their Nature, Occurrence, and Functions

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### INTRODUCTION

#### The Meaning of a Plant Hormone

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<sup>1</sup> have also been referred to as ‘phytohormones’ though this term is infrequently used.

In their book *Phytohormones* Went and Thimann (10) 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 fulfill 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

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<sup>1</sup> The following abbreviations are used throughout this book with no further definition: ABA, abscisic acid; BR, brassinosteroid; CK, cytokinin; GA gibberellin; IAA, indole-3-acetic acid

cytokinins 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 hormones<sup>2</sup> 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 AND QUANTITATION OF PLANT HORMONES.**

### **The Development of the Plant Hormone Concept and Early Work.**

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 (10).

At about the same time Darwin (3) 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

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<sup>2</sup> The term "plant growth substance" is also used for plant hormones but this is a rather vague term and does not describe fully what these natural regulators do - growth is only one of the many processes influenced. The international society for the study of plant hormones is named the "International Plant Growth Substance Association" (IPGSA). While the term plant growth regulator is a little more precise this term has been mainly used by the agricultural industry to denote synthetic plant growth regulators as distinct from endogenous growth regulators.

synthesized in the coleoptile tips, moved basipetally, and when distributed 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 (11).

### Discovery of Other Hormones

Other lines of investigation led to the discovery of the other hormones: research in plant pathogenesis led to gibberellins (GA); efforts to culture tissues led to cytokinins (CK); the control of abscission and dormancy led to abscisic acid (ABA); and the effects of illuminating gas and smoke led to ethylene. These accounts are told in virtually every elementary plant physiology textbook, and further elaborated in either personal accounts (9, 11) or advanced treatises devoted to individual hormones (see book list at the end of the chapter) so that they need not be repeated here. More recently other compounds, namely brassinosteroids (Chapters B7 and D7), jasmonates (Chapter F1) (including tuberonic acid, Chapter E5), salicylic acid (Chapter F2), and the peptides (Chapter F3) have been added to the list of plant hormones, and these are fully covered in this book for the first time. Polyamines, which are essential compounds for all life forms and important in DNA structure, have also been categorized as plant hormones as they can modulate growth and development, though typically their levels are higher than the other plant hormones. However, as little further understanding of their exact function in plants at the cellular and molecular levels has been added in the last few years, no individual chapter has been devoted to polyamines in this edition (a chapter on polyamines can be found in the previous edition (4): 2E Chapter C1).

It is interesting to note that, of all the original established group of plant hormones, only the chemical identification of abscisic acid was made from higher plant tissue. The original identification of the others came from extracts that produced hormone-like effects in plants: auxin from urine and the fungal cultures of *Rhizopus*, gibberellins from culture filtrates of the fungus *Gibberella*, cytokinins from autoclaved herring sperm DNA, and ethylene from illuminating gas. Today we have at our disposal methods of purification (such as high performance liquid chromatography: HPLC, following solid phase extraction: SPE cartridges) and characterization (gas chromatography-mass spectrometry: GC-MS, and high performance liquid chromatography-mass spectrometry: HPLC-MS) that can operate at levels undreamed of by early investigators (Chapter G1). Thus while early purifications from plant material utilized tens or even hundreds of kilograms of tissues, modern analyses can be performed on a few milligrams of tissue, making the characterization of hormone levels in individual leaves, buds, or even from tissues within the organs much more feasible. Thus it is not surprising to see the more-recently discovered hormones being originally

identified within plant tissues. Nonetheless only brassinosteroids were identified following investigations of plant growth effects, with the discovery of jasmonates, salicylic acid and peptide hormones deriving from work on insect and disease resistance.

Immunoassay (see 2<sup>nd</sup> edition, Chapter F2) is also used for hormone quantitation, though is considered much less precise because of interfering effects of other compounds and cross reactivity. Immunoassay columns can, however, permit the very precise isolation of plant hormones prior to more rigorous physico-chemical characterization. While the exact level and location of the hormones within the individual tissues and cells is still largely elusive (Chapter G1), huge strides have been made in analyzing and localizing the expression of genes for hormone biosynthesis using sensitive techniques such as PCR (polymerase chain reaction), or the expression, in transgenic plants, of marker genes driven by promoters of one or more steps in the biosynthetic process. The location of hormone action in tissues and cells has also been investigated by examining the location of marker gene expression driven by promoters of genes known to be induced by the presence of hormone (e.g. Chapter A2).

## **THE NATURE, OCCURRENCE, AND EFFECTS OF THE PLANT HORMONES**

Before we become involved in the various subsequent chapters covering aspects of hormone biochemistry and action it is necessary to review what hormones do. In subsequent chapters some or most of these effects will be described in more detail, whereas others will not be referred to again. It is impossible to give detailed coverage of every hormonal effect, and the reader is referred to the book list at the end of this chapter. The choice of topics for subsequent chapters has been determined largely by whether there is active research in progress in that area. 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 (Chapter D3) and action (Chapter C3) 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 understood (Chapter C1) we still do not understand the connection between auxin signal transduction (Chapter D1) 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 (Chapter B6), receptors identified (Chapter D7), mutants characterized and crosstalk with other hormones investigated (Chapter B7).

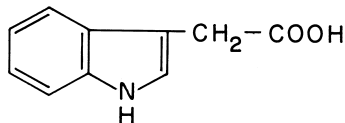
The effects produced by each hormone were initially elucidated largely from exogenous applications. However in more and more cases we have evidence that the endogenous hormone also fulfills the originally designated roles, and new functions are being discovered. Such more recent evidence derives from correlations between hormone levels and growth of defined genotypes or mutants, particularly of the model plant *Arabidopsis*, or from transgenic plants. 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. (Where there is no specific chapter on the topic in this edition but a reference in the second edition of this book (4) this is indicated with the notation '2E'.) 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 (Chapter A2) (5).

## Auxin

### *Nature*

Indole-3-acetic acid (IAA) is the main auxin in most plants.



INDOLEACETIC ACID

Compounds which serve as IAA precursors may also have auxin activity (e.g., indoleacetaldehyde). Some plants contain other compounds that display weak auxin activity (e.g., phenylacetic acid). IAA may also be present as various conjugates such as indoleacetyl aspartate (Chapter B1)). 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 (2E: G13).

### *Sites of biosynthesis*

IAA is synthesized from tryptophan or indole (Chapter B1) primarily in leaf primordia and young leaves, and in developing seeds.

## *Nature, occurrence and functions*

### *Transport*

IAA transport is cell to cell (Chapters E1 and E2), mainly in the vascular cambium and the procambial strands, but probably also in epidermal cells (Chapter E2). Transport to the root probably also involves the phloem.

### *Effects*

- Cell enlargement - auxin stimulates cell enlargement and stem growth (Chapter D1).
- Cell division - auxin stimulates cell division in the cambium and, in combination with cytokinin, in tissue culture (Chapter E2 and 2E: G14).
- Vascular tissue differentiation - auxin stimulates differentiation of phloem and xylem (Chapter E2).
- Root initiation - auxin stimulates root initiation on stem cuttings, and also the development of branch roots and the differentiation of roots in tissue culture (2E: G14).
- Tropistic responses - auxin mediates the tropistic (bending) response of shoots and roots to gravity and light (2E: G5 and G3).
- Apical dominance - the auxin supply from the apical bud represses the growth of lateral buds (2E: G6).
- Leaf senescence - auxin delays leaf senescence.
- Leaf and fruit abscission - auxin may inhibit or promote (via ethylene) leaf and fruit abscission depending on the timing and position of the source (2E: G2, G6 and G13).
- Fruit setting and growth - auxin induces these processes in some fruit (2E: G13)
- Assimilate partitioning - assimilate movement is enhanced towards an auxin source possibly by an effect on phloem transport (2E: G9).
- Fruit ripening - auxin delays ripening (2E: G2 & 2E:G12).
- Flowering - auxin promotes flowering in Bromeliads (2E: G8).
- Growth of flower parts - stimulated by auxin (2E: G2).
- Promotes femaleness in dioecious flowers (via ethylene) (2E: G2 & 2E: G8).

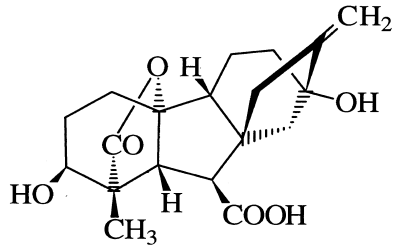
In several systems (e.g., root growth) auxin, particularly at high concentrations, is inhibitory. Almost invariably this has been shown to be mediated by auxin-produced ethylene (2, 7) (2E: G2). If the ethylene synthesis is prevented by various ethylene synthesis inhibitors, the ethylene removed by hypobaric conditions, or the action of ethylene opposed by silver salts (Ag<sup>+</sup>), then auxin is no longer inhibitory.

## **Gibberellins (GAs)**

### *Nature*

The gibberellins (GAs) are a family of compounds based on the *ent*-gibberellane structure; over 125 members exist and their structures can be found on the web (Chapter B2). While the most widely available compound is GA<sub>3</sub> or gibberellic acid, which is a fungal product, the most important GA

in plants is GA<sub>1</sub>, which is the GA primarily responsible for stem elongation (Chapters A2, B2, and B7). Many of the other GAs are precursors of the growth-active GA<sub>1</sub>.



**GIBBERELLIN A<sub>1</sub> or GA<sub>1</sub>**

*Sites of biosynthesis.*

GAs 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 (Chapter B2).

*Transport*

Some GAs are probably transported in the phloem and xylem. However the transport of the main bioactive polar GA<sub>1</sub> seems restricted (Chapters A2 and E5).

*Effects*

- Stem growth - GA<sub>1</sub> causes hyperelongation of stems by stimulating both cell division and cell elongation (Chapters A2, B7 and D2). This produces tall, as opposed to dwarf, plants.
- Bolting in long day plants - GAs cause stem elongation in response to long days (Chapter B2, 2E: G8).
- Induction of seed germination - GAs can cause seed germination in some seeds that normally require cold (stratification) or light to induce germination (Chapter B2).
- Enzyme production during germination - GA stimulates the production of numerous enzymes, notably  $\alpha$ -amylase, in germinating cereal grains (Chapter C3).
- Fruit setting and growth - This can be induced by exogenous applications in some fruit (e.g., grapes) (2E: G13). The endogenous role is uncertain.
- Induction of maleness in dioecious flowers (2E: G8).

**Cytokinins (CKs)**

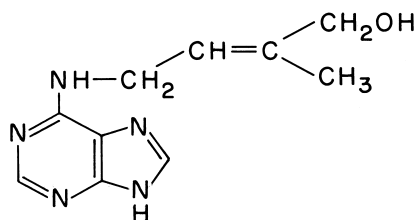
*Nature*

CKs 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 and ribotides (Chapter B3).



Z E A T I N

### *Sites of biosynthesis*

CK biosynthesis is through the biochemical modification of adenine (Chapter B3). It occurs in root tips and developing seeds.

### *Transport*

CK transport is via the xylem from roots to shoots.

### *Effects*

- Cell division - exogenous applications of CKs induce cell division in tissue culture in the presence of auxin (Chapter C3; 2E: G14). This also occurs endogenously in crown gall tumors on plants (2E: E1). 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.
- Morphogenesis - in tissue culture (2E: G14) and crown gall (2E: E1) CKs promote shoot initiation. In moss, CKs induce bud formation (2E: G1 & G6).
- 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 (2E: E2 & G6).
- Leaf expansion (6), 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.
- CKs delay leaf senescence (Chapter E6).
- CKs may enhance stomatal opening in some species (Chapter E3).
- Chloroplast development - the application of CK leads to an accumulation of chlorophyll and promotes the conversion of etioplasts into chloroplasts (8).

## Ethylene

### *Nature*

The gas ethylene (C<sub>2</sub>H<sub>4</sub>) is synthesized from methionine (Chapter B4) 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 (Chapters B4 and E5).

### *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 (2E: G2).

### *Effects*

The effects of ethylene are fully described in 2E: G2. They include:

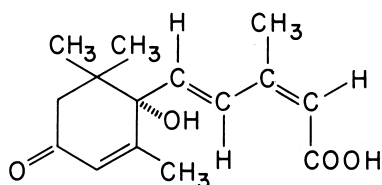
- The so called *triple response*, when, prior to soil emergence, dark grown seedlings display a decrease in stem elongation, a thickening of the stem and a transition to lateral growth as might occur during the encounter of a stone in the soil.
- Maintenance of the apical hook in seedlings.
- Stimulation of numerous defense responses in response to injury or disease.
- Release from dormancy.
- Shoot and root growth and differentiation.
- Adventitious root formation.
- Leaf and fruit abscission.
- Flower induction in some plants (2E: G8).
- Induction of femaleness in dioecious flowers (2E: 8).
- Flower opening.
- Flower and leaf senescence.
- Fruit ripening (Chapters B4 and E5).

## Abscisic acid (ABA)

### *Nature*

Abscisic acid is a single compound with the following formula:

## *Nature, occurrence and functions*



ABSCISIC ACID

Its name is rather unfortunate. 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 (1). It now appears to have little role in either abscission (which is regulated by ethylene; 2E: G2) 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 (Chapter E4), 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 (Chapters D6 and E3)

### *Sites of synthesis*

ABA is synthesized from glyceraldehyde-3-phosphate via isopentenyl diphosphate and carotenoids (Chapter B5) in roots and mature leaves, particularly in response to water stress (Chapters B5 and E3). Seeds are also rich in ABA which may be imported from the leaves or synthesized in situ (Chapter E4).

### *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 (Chapters A2 and E4).

### *Effects*

- Stomatal closure - water shortage brings about an increase in ABA which leads to stomatal closure (Chapters D6 and E3).
- ABA inhibits shoot growth (but has less effect on, or may promote, root growth). This may represent a response to water stress (Chapter E3; 2E: 2).
- ABA induces storage protein synthesis in seeds (Chapter E4).
- ABA counteracts the effect of gibberellin on  $\alpha$ -amylase synthesis in germinating cereal grains (Chapter C2).
- ABA affects the induction and maintenance of some aspects of dormancy in seeds (Chapters B5 and E4). 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.

- Increase in ABA in response to wounding induces gene transcription, notably for proteinase inhibitors, so it may be involved in defense against insect attack (2E: E5).

## Polyamines



### SPERMIDINE

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 quaternaryamine 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.)

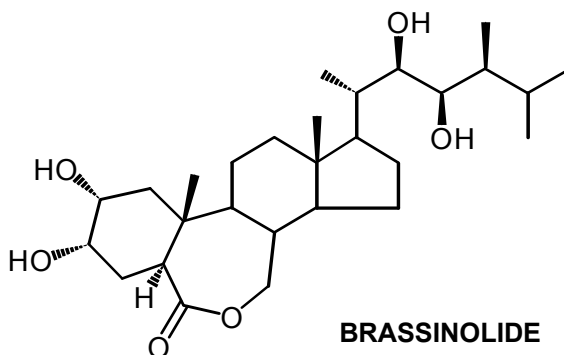
Such developmental control is more characteristic of hormonal compounds than nutrients such as amino acids or vitamins.

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 hormones. Their biosynthesis and a variety of cellular and organismal effects is discussed in 2E Chapter C1. It appears that polyamines are present in all cells rather than having a specific site of synthesis.

## Brassinosteroids

Brassinosteroids (Chapters B6 and D7) 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 (Chapter D7).
- Cell elongation, where BRs promote the transcription of genes encoding xyloglucanases and expansins and promote wall loosening (Chapter D7). This leads to stem elongation.
- Vascular differentiation (Chapter D7).
- BRs are needed for fertility: BR mutants have reduced fertility and delayed senescence probably as a consequence of the delayed fertility (Chapter D7).
- Inhibition of root growth and development
- Promotion of ethylene biosynthesis and epinasty.

### Jasmonates

Jasmonates (Chapter F1) 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 (Chapter E5). Jasmonic acid is synthesized from linolenic acid (Chapter F1), while jasmonic acid is most likely the precursor of tuberonic acid.

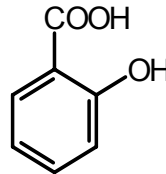
### Effects

- 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.

- Jasmone inhibits 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.

### Salicylic Acid (SA)



**SALICYLIC ACID**

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*

- Salicylic acid (Chapter F2) 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.
- SA is the calorogenic 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.

### 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 (Chapters F1 and F3). 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 (Chapter F3). Among these effects caused by specific peptides are:

- 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 cytokinin
- Peptide signals for self-incompatibility.
- Nodule formation in response to bacterial signals involved in nodulation in legumes.

### **Are the More-Recently-Discovered Compounds Plant Hormones?**

Two decades ago there was a heated discussion as to whether a compound had to be transported to be a plant hormone, and could ethylene therefore be a plant hormone. To this Carl Price responded: “Whether or not we regard ethylene as a plant hormone is unimportant; bananas do...”<sup>3</sup>. Hormones are a human classification and organisms care naught for human classifications. Natural chemical compounds affect growth and development in various ways, or they do not do so. Clearly brassinosteroids fit the definition of a plant hormone, and likely polyamines, jasmonates salicylic acid and signal peptides also can be so classified. Whether other compounds should be regarded as plant hormones in the future will depend on whether, in the long run, these compounds are shown to be endogenous regulators of growth and development in plants in general.

### **A Selection of Books on Plant Hormones Detailing their Discovery and Effects**

- Abeles FB, Morgan PW, Saltveit ME (1992) *Ethylene in Plant Biology*. Academic Press, San Diego
- Addicott FT (ed) (1983) *Abscisic acid*. Praeger, New York
- Arteca RN (1995) *Plant Growth Substances, Principles and Applications*. Chapman and Hall, New York
- Audus LJ (1959) *Plant Growth Substances (2E)* L. Hill, London; Interscience Publishers New York. (Editors note: the 2<sup>nd</sup> edition of Audus contains a lot of information on auxins that was cut out of the later, broader, 3<sup>rd</sup> edition and it is therefore still a valuable reference.)
- Audus LJ (1972) *Plant Growth Substances (3E)*. Barnes & Noble, New York
- Crozier A (ed) (1983) *The Biochemistry and Physiology of Gibberellins*. Praeger, New York
- Davies PJ (ed) (1995) *Plant Hormones: Physiology, Biochemistry and Molecular Biology*. Kluwer Academic, Dordrecht, Boston
- Davies WJ, Jones HG (1991) *Abscisic Acid: Physiology and Biochemistry*. Bios Scientific Publishers, Oxford, UK
- Hayat S, Ahmad A (eds) (2003) *Brassinosteroids: Bioactivity and Crop Productivity*. Kluwer Academic, Dordrecht, Boston

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<sup>3</sup> Carl A. Price, in *Molecular Approaches to Plant Physiology*

- Jacobs WP (1979) *Plant Hormones and Plant Development*. Cambridge University Press
- Khripach VA, Zhabinskii VN, de Groot AE (1999) *Brassinosteroids: A New Class of Plant Hormones*. Academic Press, San Diego
- Krishnamoorthy HN (1975) *Gibberellins and Plant Growth*. Wiley, New York
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