MECHANISMS OF HORMONE ACTION IN PLANTS

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Botanists have recognised for over one hundred years that plant growth and development are controlled by chemicals produced within the plant. Today there are five groups of widely known and used hormones (Figure 1). These are the auxins, the gibberellins, the cytokinins, abscisic acid, and ethylene (10). It is unfortunate, however, that the definition of a plant hormone was borrowed from the definition used by zoologists.

> "an organic compound synthesised in one part of a plant and translocated to another part, where in low concentrations it has a controlling or regulatory effect — it causes a physiological response" (1).

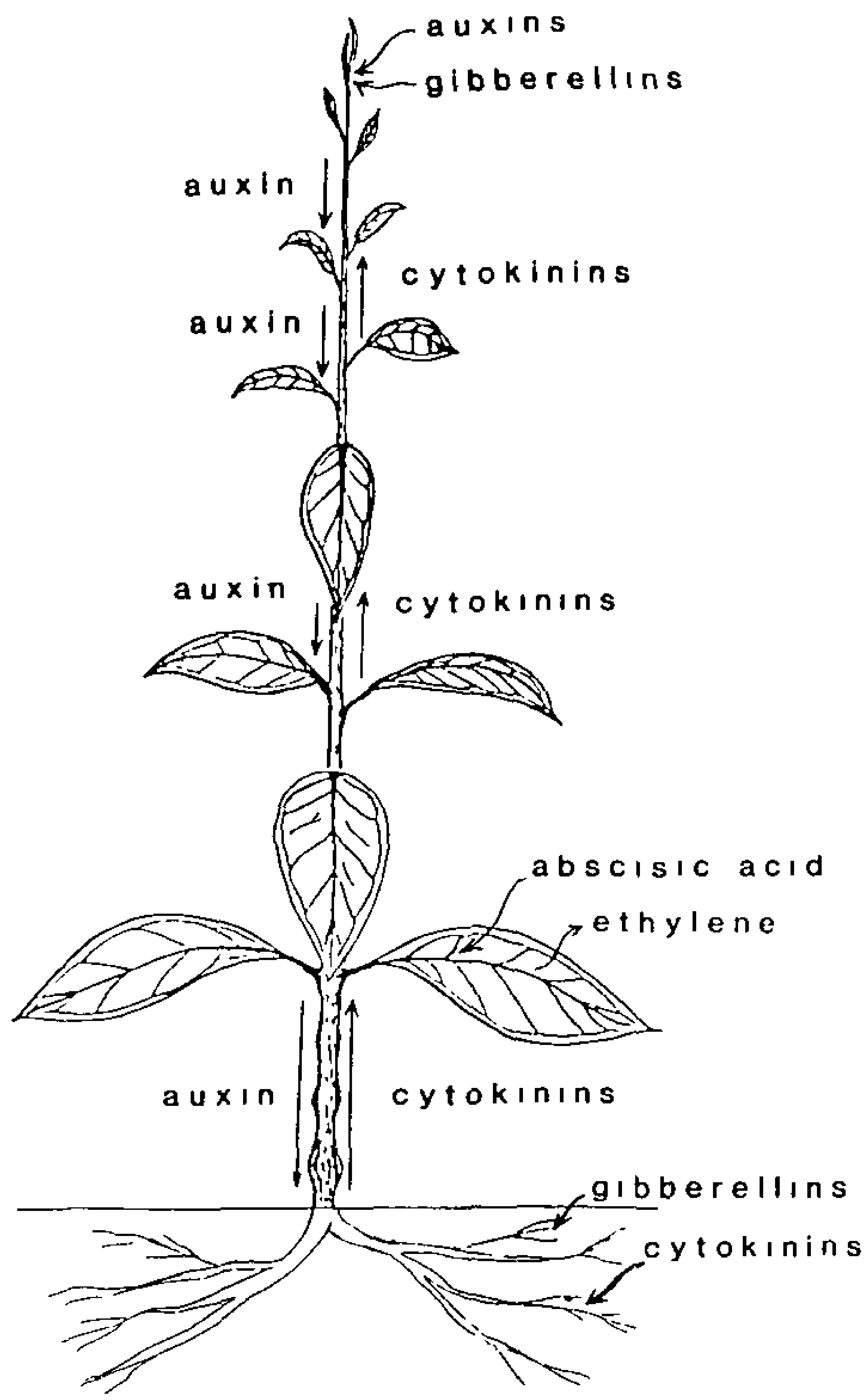


Figure 1. Major hormones and their sites of synthesis.

The definition is fine for an animal where the sites of synthesis and response are separate but in plants synthesis, response, and transport may all occur in the same tissues (8). Many chemicals that affect plant growth and development but do not conform to the definition, are called plant growth substances (Figure 2).

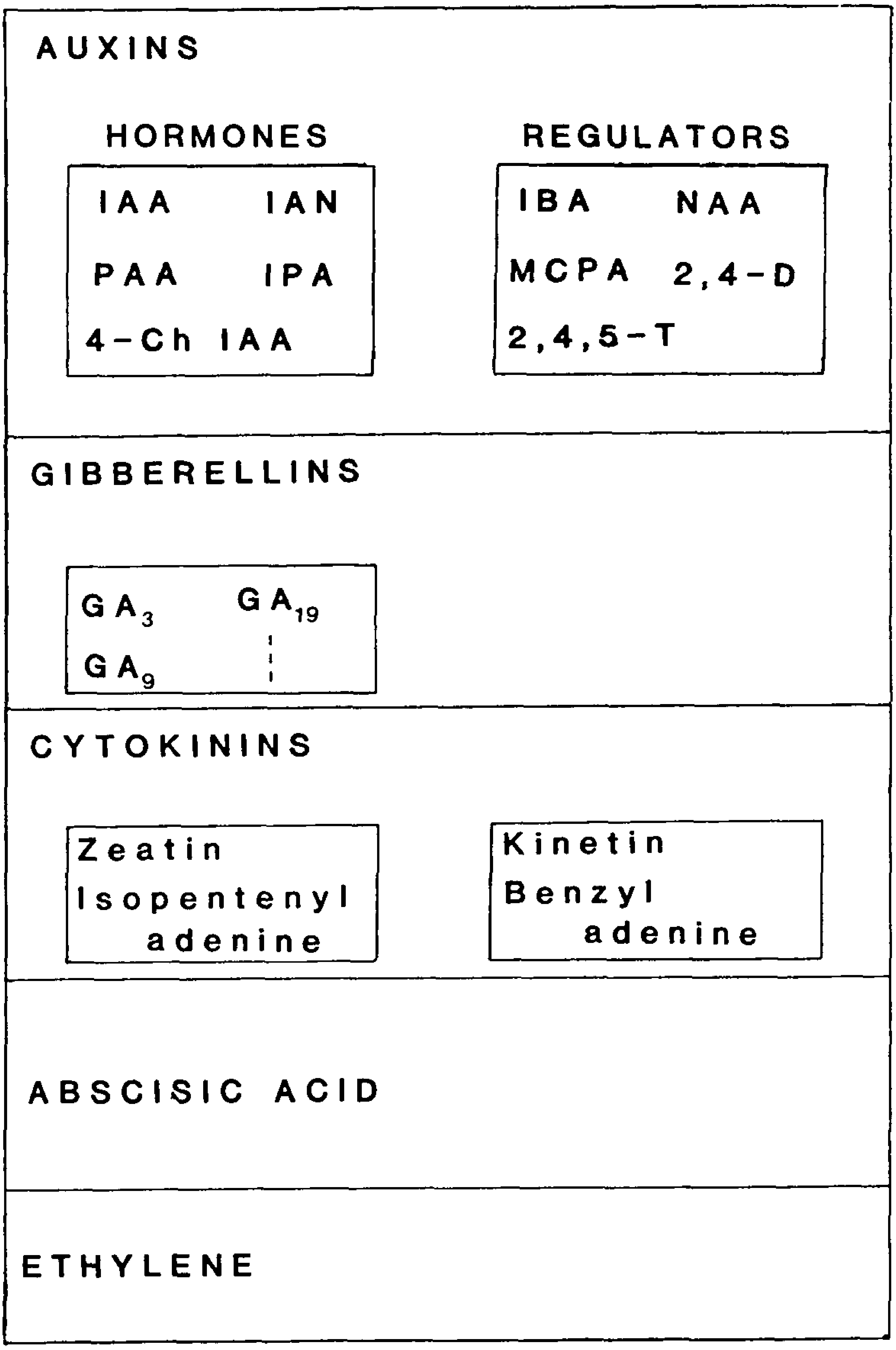


Figure 2. Hormones and plant growth regulators.

A further complication that arises is whether five groups of hormones can control the large number and diversity of activities that are involved in plant growth and development. Although there is still some debate (3), it does appear that the *hormones can control many of the plant's activities* through a complex set of interrelationships that involve the hormones and the plant tissues themselves. The variables involved in these relationships include:

1). Different hormones affect different tissues.

2). Different hormone concentrations can cause different responses in the same tissues.

3). Different levels of interaction between two or more of the hormones can stimulate different responses.

4). The physiological state of the tissues can alter their responses to hormones.

The combination of these variables gives almost infinite variation and so offers the possibility of controlling the plant's activities.

MECHANISMS OF HORMONE ACTION

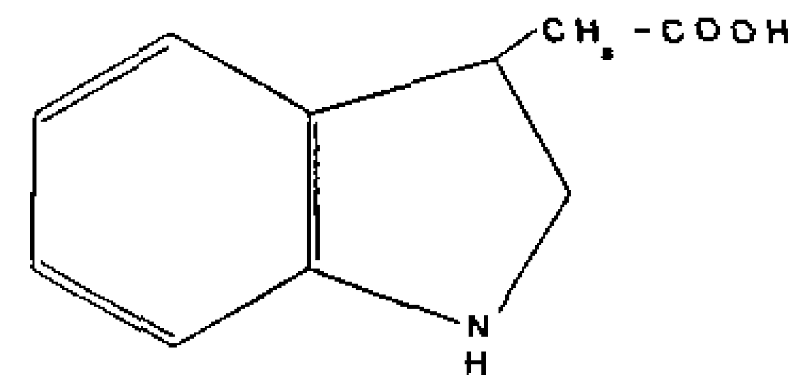
Because hormones cause so many plant responses, only the major effects of each of the groups will be considered. Practical applications of the hormones in plant propagation will be discussed.

AUXINS

The study of auxins was begun in 1880 by Charles Darwin, but it was the work of Went in 1928 that showed their importance in plant growth. The most common and best known hormonal auxin is indoleacetic acid (IAA), but it is not the only naturally-occurring auxin (Figure 3). Phenylacetic acid (PAA) and indolepropionic acid (IPA) appear to be present in many plants, while 4-chloroindoleacetic acid (4-chl-IAA) is found in legumes and indoleacetonitrile (IAN) is present in members of the Brassicaceae (12). IPA is about twice, and 4-chl-IAA about four times as active as IAA itself. In most plants the ratio of PAA to IAA is about 1:4 or 5, and PAA is found only in association with IAA.

Many of the synthetic auxins are well known to horticulturists. Naphthaleneacetic acid (NAA) and indolebutyric acid (IBA) are structural analogues of IAA, while 2,4,5-T and MCPA are analogues of PAA.

INDOLEACETIC ACID



MAJOR EFFECTS

- cell elongation
- initiate meristematic activity
  eg callus formation
- apical dominance
- initiate the development of roots
  leaf, flower and fruit abscission
- phototropism
- stimulate cell division

Figure 3. Auxins.

Effects of Auxins. The most obvious effect of auxins is the promotion of cell enlargement and in the cambium they can stimulate cell division as well. They are also responsible for the inhibition of lateral buds in stems, where they are produced in the apical meristem. It also appears that auxins have a role in leaf abscission but other hormones may also be involved.

Auxins can stimulate root elongation but only at extremely low concentrations (10^{-7} to 10^{-13}M); at higher concentration root growth is inhibited. The development of root primordia, however, may be stimulated by high concentrations of auxins. This stimulation may involve the activation of preformed root primordia or it may initiate the formation of adventitious roots. The range of concentrations over which root development is promoted is very wide, ranging from about 10^{-2} to 10^{-4}M, or 20 to 2000 ppm, depending upon the plant and the method of auxin application (5).

Auxins influence much of the plant's growth and development but how they affect plant tissue is uncertain. It has been suggested that auxins trigger enzyme activity by acting as coenzymes, or by stimulating RNA production that, in turn, produces more enzymes. It may also be that auxins alter the cell membranes, and this then allows cell enlargement and the other effects that have been observed (10,11).

Auxins and Plant Propagation. Auxins have been widely used by plant propagators especially for the promotion of root initiation in cuttings. The auxins that have been used are usually the synthetic auxins, IBA or NAA. These can be applied in various forms and concentrations (6) but are usually applied as a powder or liquid dip. The concentration used depends upon the duration of auxin application. The use of auxins at the appropriate concentrations is essential because the wrong concentration can turn an intended promotion into a complete inhibition of the tissues treated.

Attempts have been made to use auxins for the promotion of callus formation in budding and grafting operations, but the results have been disappointingly inconsistent. The use of auxins, in conjunction with cytokinins, has been the basis for the successful tissue culture of most plants or plant parts. The use of synthetic auxins as herbicides has also been very successful. They appear to kill plants by interfering with the normal production of enzymes and are more effective against broadleaf plants in which they are more readily absorbed and translocated than in grasses.

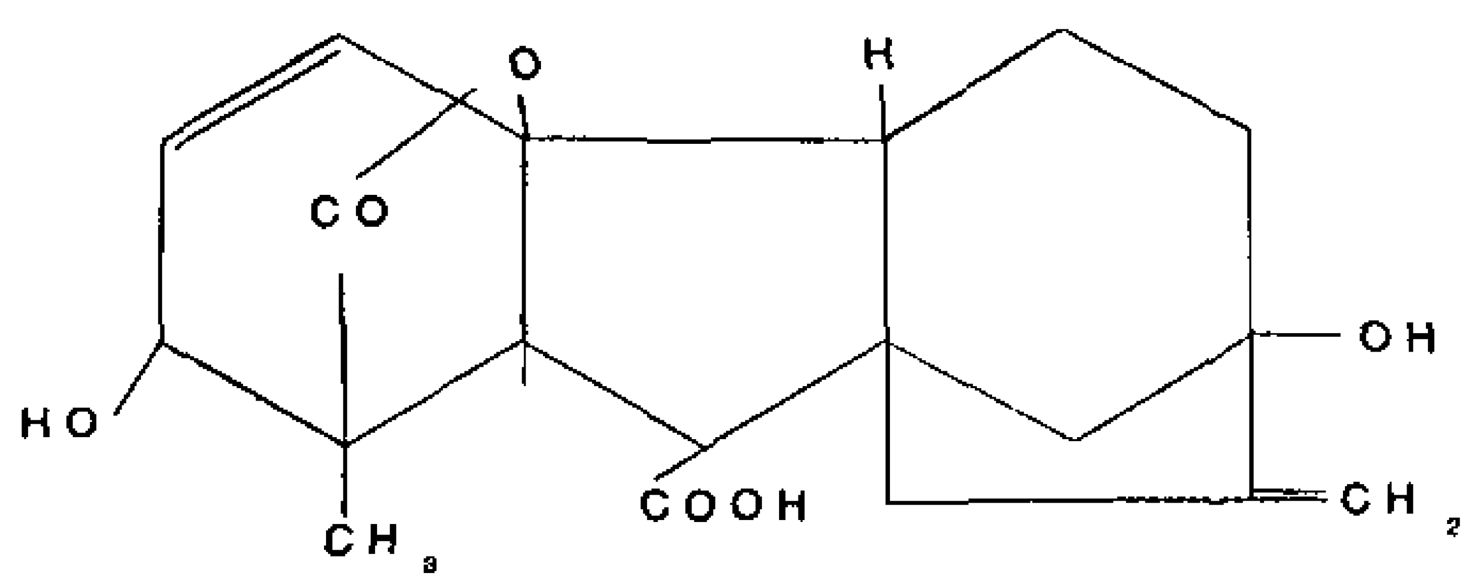
The synthesis of IAA in the meristematic regions of roots and stems is to be expected, because the enzymes necessary for the manufacture of IAA are most active in these tissues. The plant and many micro-organisms, such as bacteria, possess enzymes that degrade auxins. IAA can be degraded quite rapidly but the process is retarded by refrigeration. Light degradation of IAA can also occur and the hormone should not be exposed to bright sunlight. The synthetic auxins such as IBA and NAA are less prone to light and biological deterioration and may be kept for longer periods of time.

GIBBERELLINS

Gibberellins were first discovered in Japan as a result of studies on a fungal disease that caused rice plants to grow very tall. The active compound was isolated and identified in the 1930's, but was not widely-known in other countries until after the war. All of the gibberellins are variations of the organic acid, gibberellic acid (Figure 4). At present there are 53 gibberellins, of which about 40 are known to occur in plants (8,9). Most plants contain only a few of the gibberellic acids (GA), and the most commonly occurring GA is GA_3, which is also the one most readily available (7).

Like IAA, GA is produced in young, actively photosynthesising leaves. Some GA is also synthesised in the roots and appears to move from the roots via the xylem into the stem. Other parts of the plant, such as embryos, seeds, and fruits are known to contain GA, but it is uncertain whether they actually synthesise it. GA is more readily transported through the plant than auxin, and can act over long distances to control various processes. Not all of the reponses due to GA, however, occur over long distances.

GIBBERELLIC ACID



MAJOR EFFECTS

- dramatic stem elongation
- breaking of some dormancies
- induce flowering
- stimulate cell division
- produce seedless fruit
- retard lateral bud growth
- may enhance geotropism

Figure 4. Gibberellins.

Effects of Gibberellins. The most spectacular effect of gibberellins on plant rowth is their ability to stimulate stem elongation in intact plants. Most plants show some response to applied gibberellin and in many short-stemmed or dwarf plants the effect may be striking. In this respect gibberellins appear to affect plant growth in a manner opposite to the auxins. The stem elongation is usually due to an increase in internode length that is due to the expansion of cells caused by enhanced water uptake. Often the dry weight of the plant is unaltered by such changes in growth.

Like auxins, gibberellins appear to influence plant metabolism in several ways. They are capable of stimulating cell division apparently by enhancing DNA and RNA synthesis. Gibberellins also hydrolise starch into sugar which not only provides energy, but promotes water uptake by the cells, which causes cell expansion. The gibberellins may also increase cell wall plasticity. Any or all of these properties may give the stem elongation that is observed or the increases in the sizes of leaves, flowers, or fruits.

Both auxins and gibberellins can induce similar physiological responses in many plants. However, gibberellins appear to be more effective on whole or intact plants, where many of the auxin effects are for excised organs or sections of plants. It is clear that there is a major interaction between these two common and important groups of hormones that influence many facets of plant growth and development. Knowledge of gibberellins is not sufficient as yet to be certain of their mode of operation and research into the active forms of GA is continuing.

Gibberellins and Plant Propagation. Gibberellins have been used to promote the germination of dormant seeds. This occurs in cereals because gibberellin induces the production of enzymes that digest the endosperm and provide energy for the growth of the embryo. The concentrations of GA used for such treatments can range from 10^{-3} to 10^{-1}M, or 100 to 10,000 ppm. The seed coat often has to be removed from the seed to allow the GA to penetrate for the treatment to be effective. The GA actually breaks the dormancy of the seeds in many species, overcoming the need for environmental cues.

Gibberellins appear to be more stable compounds than the auxins. They are not so sensitive to light, nor are they degraded so easily biologically. Careful storage, however, is still advised and the habit of keeping hormones in a darkened refrigerator is to be encouraged. The high cost of GA is explained by the fact that it is still produced biologically using *Gibberella* fungi. There is no economic, synthetic manufacturing process.

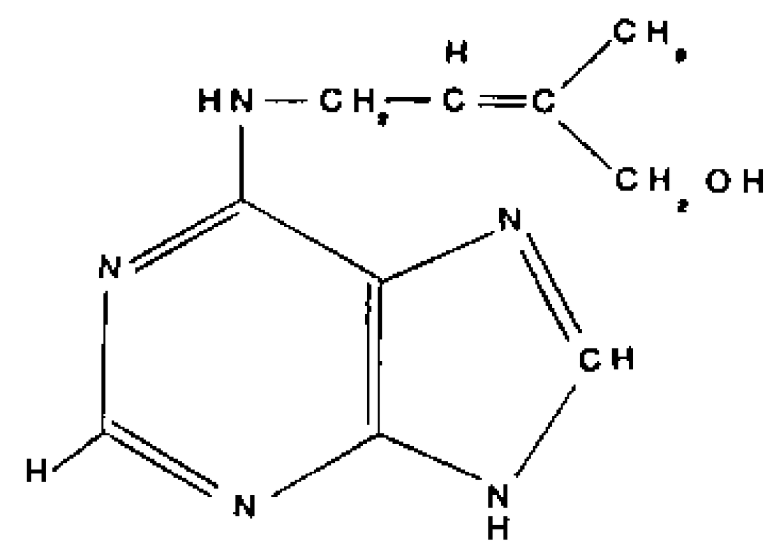
CYTOKININS

As early as 1913, it was known that substances present in the vascular tissues of some plants could stimulate cell division (cytokinesis). The first of these compounds to be identified was kinetin (Figure 5), which had been isolated from the DNA of fish sperm. Kinetin has not been found in plant tissues, although some researchers believe it is present in very low concentrations (8). Other compounds that stimulate cell division have been found in plants and these are called cytokinins.

The first cytokinin isolated from plant tissue was zeatin, which has been found in peas, spinach, wheat, potato, maize and other plants. It is found associated with RNA and is a modification of adenine, one of the components of RNA. Other cytokinins include ribosylzeatin, isopentenyladenine, and benzyladenine. Both kinetin and benzyladenine are synthetic substance that have cytokinin activity. Most of the angiosperms contain cytokinins and a few gymnosperms are known to contain them.

Cytokinins are most common in young leaves and in root tips but also occur in young fruits and seeds. Cytokinins do not appear to be readily transported through the plants and their effects are often especially localised. Transport of cytokinins from the root tip to other tissues appears to be likely. The high concentrations of cytokinins in young tissues may be due to the xylem transport into these young active parts.

ZEATIN



MAJOR EFFECTS

- stimulate cell division
- retard senescence
- replace light requirement for germination in some seeds
- overcomes apical dominance
- may delay abscission
- produce seedless fruits

Figure 5. Cytokinins.

Effects of Cytokinins. Like the auxins and gibberellins, cytokinins have many effects on plant growth and development. They have an effect on cell division and a role in callus formation. They appear to promote cell expansion especially in the leaves and cotyledons of dicotyledonous plants. They may also participate in the development of the embryo during seed formation. Cytokinins may also initiate growth in inactive lateral buds, but growth often does not continue.

Perhaps the most spectacular effect of cytokinins is the retardation — almost reversal — of senescence. Not only is pigment degradation in an aging tissue delayed, but re-greening may also occur. In addition, raw materials are transported to the treated tissue via the xylem system, and protein may be synthesised. Abscission of cytokinin-treated fruits, flowers, and leaves may also be delayed as a result of the increased metabolic activity.

Although cytokinins induce a variety of plant responses it is possible that all result from a single initial reaction. The similarity of cytokinin structure to adenine suggests that there may be an effect on RNA which, in turn, may influence the level of protein synthesis. There is often an increased enzyme activity after cytokinin treatment which may explain some of the observed rejuvenation phenomena. A cytokinin influence on ribosomes, the sites of protein synthesis, cannot be discounted (10).

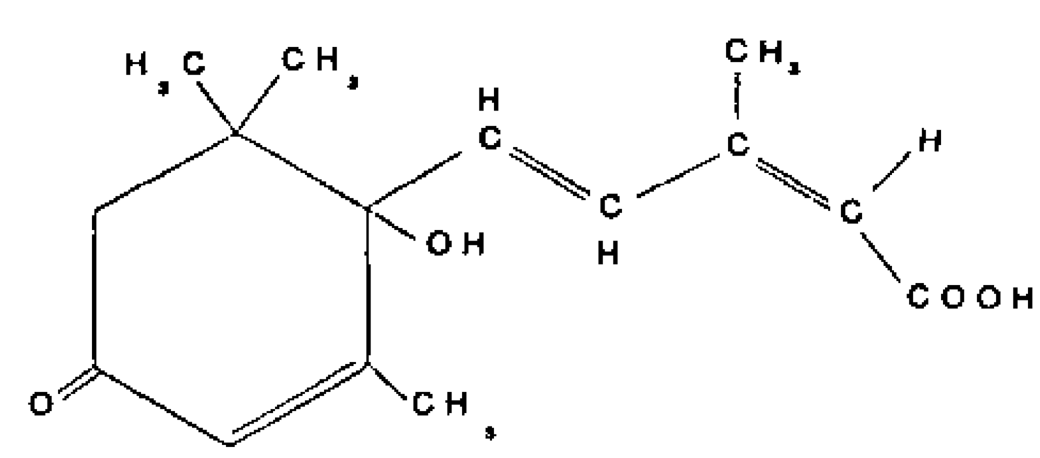
Cytokinins and Plant Propagation. Much of the knowledge that has been gained of cytokinins has come from studies of tissue culture and callus formation. The interaction of cytokinins and other hormones, especially auxins, is the basis of aseptic plant propagation and regeneration from callus. Many synthetic compounds, most of them analogues of adenine, have been used in various plant tissue culture experiments, but kinetin and benzyladenine have proved to be the most useful.

Kinetin has been used to stimulate germination in some seeds, such as lettuce. Benzylaminopurine (BA) and some other compounds are more active cytokinins than kinetin in many plants (5). Such treatments may overcome the environmentally-induced dormancies that occur in some seeds (2). Storage lives of vegetables may be prolonged by spraying with cytokinins but this is not legally accepted at the present time.

ABSCISIC ACID

Abscisic acid (ABA) is a hormone that has been known for about twenty years. It was identified during research into fruit abscission, hence the name. It appears, however, that abscisic acid plays more important roles in dormancy and stomatal behaviour. ABA is a single compound (Figure 6) but there are similar compounds present in some plants, such as phaseic acid, which appears to be inactive, and xanthoxin which has some of the properties of ABA. Synthetic ABA is commercially available and has been used in many physiological studies.

ABSCISIC ACID



MAJOR EFFECTS

- cause bud dormancy
- cause leaf senescence
- leaf, flower and fruit abscission
- inhibit seed germination
- initiate flowering in short-day plants
- inhibit flowering in long-day plants

Figure 6. Abscisic acid.

Effects of ABA. In general, ABA appears to be an inhibitor of plant growth. As such, it is involved in bud dormancy and the abscission of fruits and leaves. ABA also appears to have a significant role in the senescence of leaves. Many of these inhibitory effects can be reversed by the presence or application of hormones, such as auxins and gibberellins. The dormancy of many seeds can also be attributed to the high levels of ABA present.

The mechanism of ABA action is still uncertain but alteration of cell membrane permeability, especially to cations, is involved in the effects on stomata. ABA also inhibits RNA and protein synthesis which may interfere with enzyme activity.

Such inhibitions may explain some of the longer term effects such as abscission or senescence.

ABA and Plant Propagation. Since ABA generally inhibits plant growth, it is not widely used in plant propagation. The major significance of ABA is that its effects must be overcome if many plants are to be propagated. Treatment with cytokinin often overcomes seed dormancy due to ABA, and cold temperatures may have a similar effect.

ETHYLENE

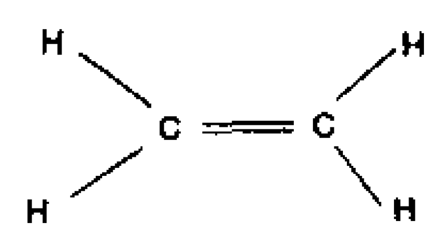
For a long time it has been known that ripening fruit produces ethylene. It is an unusual hormone because it is a volatile gas, not a compound in solution. Some researchers do not regard ethylene as a hormone but as a plant growth regulation. Since ethylene is produced in plant tissues — flowers, leaves, fruits, stems, seeds, and roots — it does appear to be a natural and active plant hormone (8). The production of ethylene by plant tissue is often stimulated by other hormones, such as auxins.

Effects of Ethylene. Ethylene appears to induce flowering in mangos and many of the bromeliads, but on other plants it has an inhibitory role. Ethylene may also inhibit the elongation of roots, stems, and leaves by causing a stunting and thickening of the cells. The inhibitory effect may also be involved in the epinasty that ethylene sometimes causes. Ethylene is also produced in response to the wounding or infection of many plant tissues.

The more significant effects of ethylene involve its role in the abscission of flowers, fruits, leaves, and stems, and its interaction with other hormones in the senescence of plant tissues. Practical implications for fruit storage have resulted from the knowledge of these processes where storage and then ripening can be manipulated by changing the levels of oxygen and ethylene.

Ethylene and Plant Propagation. Although ethylene has been widely used in horticulture for its effects on fruit storage and flower induction, it has not been widely used for plant propagation. However, ethylene does stimulate germination of seeds in some species and may prove commercially viable. Ethylene may also cause development of latent roots of willows and mung beans (5) and in proteas, rooting of cuttings can be enhanced (4).

ETHYLENE



MAJOR EFFECTS

- cause fruit ripening and senescence
- cause abscission of fruits, flowers and leaves
- cause leaf epinasty
- may overcome geotropism
- may enhance root initiation

Figure 7. Ethylene.

HORMONE INTERACTION

Although the major effects of the plant hormones have been discussed, the importance of their interactions must be emphasized. It is the complementary and sometimes antagonistic effects of the various hormones that causes normal plant growth and development. Such interactions may be complicated, especially when there are more than two hormones involved. Although tissue culture has revealed the interaction between cytokinin and auxin in the differentiation of callus the interactions within a plant may be far more complex.

Many of the hormonal interactions that control plant growth are poorly or only partly understood. One of the best known set of interactions involves leaf abscission. Although not fully understood, at least four different hormones may be involved. It is the interaction of hormones that enables the regulation of so many diverse aspects of plant growth and development by a relatively small number of compounds. The regulation can be precise, affecting only a single facet of plant metabolism and coordinated with overall growth.

CONCLUSIONS

Although hormones have been recognized for their effects on plant growth and development, their horticultural potential has yet to be fully realised. Their wider use is limited both by an incomplete understanding of their function and, in most instances, their expense. Both of these restrictions should soon be overcome, encouraging the use of hormones in many areas of horticulture.

Hormones are outstanding horticultural tools. Every aspect of horticulture affords some opportunity for hormonal manipulation. Hormones are used in plant propagation, in the control of plant growth, form, and development, in the regulation of flowering, and in harvesting and storage. We must, however, understand how hormones influence plant growth and development and use them wisely.

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AVOIDING PROBLEMS IN SEEDLING AND BUDWOOD SELECTION IN CITRUS

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There are many criteria that can be used to select good propagation material. For everyone I might suggest, there will be many more you can add which are of a specific nature to the plants you are propagating.

Let me use two examples to illustrate the difference between areas of decision and happenstance in propagation.

Seedlings for citrus come from a wide range of seed sources, many of which were, and still are, chosen for their