primordia initiated during the course of the experiment were less sensitive, being reduced by only 60 % in number.

Hence it may be concluded that auxin does have a direct effect on root initiation in brittle willow, but only if the concentrations of auxin are sufficient to sustain a given level of cambial activity. Further, GA depresses rooting by affecting an auxin-mediated process after the actual initiation.

The varying levels during the year of hormones such as GA and auxin, and the other growth regulators with which they interact, could account for the seasonal variation in the rooting ability of cuttings of many species, as well as the differences among the species themselves.

LITERATURE CITED

1. Wetmore, R.H. & J.P. Rier. 1963. Experimental induction of vascular tissues in callus of angiosperms. Amer. Jour. Bot. 50: 418-30.
2. Thompson, N.P. & W.P. Jacobs. 1966. Polarity of IAA effect on xylem and sieve tube regeneration in *Coleus* and tomato stems. *Plant Phys. 41*: 673-82.
3. Robards, A.W., *et al.* 1969. Short-term effects of some chemicals on cambial activity. *Jour. of Exp. Bot. 20*: 912-20.
4. Haissig, B.E. 1972. Meristematic activity during adventitious root primordium development. *Plant Phys. 49*: 886 - 92.

CHEMICALS AND THE REGULATION OF PLANT GROWTH

A. S. EDMONDS

Biological Sciences, University of Waikato
Waikato

Many chemical substances are now used in horticulture and agriculture to affect the growth and development of flowering plants. Some of these substances are very familiar, for example:

2,4-D	2,4-dichlorophenoxyacetic acid
2,4,5-T	2,4,5-trichlorophenoxyacetic acid

These chemical substances intervene and exert recognisable effects on plant growth and development but in a characteristic, non-nutrient way. Small amounts are effective, and these quantities are not incorporated into the substance of the plant.

Among the many regulatory substances in common use are the two above-named selective herbicides which kill plants of broadleaved species but not of grasses. As well there are total-kill herbicides, e.g. CMU, 3-p-chlorphenyl 1-1 dimethylurea, and Ammate, ammonium sulphamate. There are chemicals which stimulate the rooting of cuttings, e.g. indole-3-butyric acid (IBA). There are chemicals which cause leaves or fruit to drop, e.g. Endothal, disodium, 3,6-endoxohexahydrophthalate. There are chemicals which promote fruit setting, e.g. NAA, a-naphthaleneacetic acid. There are chemicals which promote stem elongation, e.g. gibberellic acid (Gibrel) and chemicals which retard stem elongation, e.g. Alar; 1,1-dimethyl aminosuccinamic acid. There are chemicals which stimulate fruit ripening, e.g. ethylene, C_2H_4; and chemicals which depress fruit ripening, e.g. cargon dioxide, CO_2. Most of these substances can be synthesized, developed for a particular agricultural or horticultural need.

One can approach the problem of how growth in plants is regulated and controlled through attempting to understand the roles of these and other natural chemical substances which intervene to modulate the behaviour of cells and tissues of flowering plants. Inevitably, in so doing, one is impressed by the variety of plant responses that are involved in contrast to the often-held view that plants display little response to external and internal stimuli. This often-held view derives probably not from any lack of response in plants but from slow responses. These slow responses are many and include tropisms, responses to light (phototropism) gravity (geotropism) and chemicals (chemotropism); nastic responses or sleep movements of leaves, stems and flowers; rhythmic pheonomena in growth and development; organ growth by cell enlargement and division; initiation of lateral organs and related problems of phyllotaxy; induction of flowering; formation of perennating organs such as buds, tubers and bulbs; periodicities in growth, such as the cambium displays; regulatory effects of light and temperature on growth; and the induction of sexuality. These then are some of the more usual forms of development, but as well, unusual development such as the formation of root nodules and pathological growth of galls and tumours also occur.

Chemical causation is implicit in all these morphogenetic responses and faced with such a range of responses the trend has been to invent classes of substances which are thought to exist within plants and which correspond to the observed morphogenetic responses. The list of these classes of substances is long and includes *auxins*, which increase cell size; *gibberellins*, which cause elongation; *cytokinins*, which increase the number of cells; *florigen*, which mediates flowerings; *anthesin*, which mediates temperature responses; *abscisic acid (dormin)* which controls dormancy and abscission; and *morphactins* as a class of substances controlling other morphological responses.

These classes of supposed biological substances have been described by plant physiologists following a period of feverish activity, but the very description of such substances and the subsequent searches for them have produced great confusion. For some of these classes of compounds however, evidence has been accumulating which establishes them certainly as important plant growth regulators or plant hormones.

Almost 50 years ago, and in opposite parts of the world, proof was given of the existence of substances which promote growth of plants. In 1926 in Holland, Went provided convincing proof of a diffusable substance obtained from oat seedlings which promoted their growth. This was the beginning of research into auxin. In the same year, Kurosawa in Japan gave proof of a substance in cell-free fungus filtrate which promoted growth of rice seedlings. This was the beginning of gibberellin research. Auxins and gibberellins are now recognised to be two separate classes of chemicals that cause distinct growth patterns in plants.

Auxins. It is now certain that the naturally occurring auxin in plants is indole-3-acetic acid (IAA). It occurs in minute quantities in growing tissue, e.g. in pineapple shoots about 6 ug per kg of plant, or about the weight of a needle in a 22 ton truck load of hay. This low concentration occurs, in part, because IAA is constantly being destroyed by the enzyme, IAA-oxidase, which is present in all plant tissues. Many synthetic auxins have been found; some, e.g. 2,4-D, are more potent than the natural IAA.

Auxins are required for cell expansion and as well for cell division but they have a multitude of additional effects. Auxins promote root formation in cuttings; they can convert vegetative growth to reproductive growth; they can change the sex of flower buds. Auxins are synthesized in the apical meristems of flowering plants in the light and are transmitted throughout the plant by diffusion from cell to cell.

Gibberellins. Gibberellins (GA) are normal components of higher plants where they regulate cell elongation. Some gibberellins can cause flower formation. Gibberellins are synthesized in bud leaves, developing embryos, and root apices. Roots rarely respond to GA. Other organs show varying responses depending on whether they grow primarily by enlargement or division. GA also affects dormancy, e.g. in deciduous plants. Gibberellins are translocated by cell-to-cell diffusion.

Cytokinins. First suspected in 1941 as necessary for cell division, cytokinins now well established as potent cell division factors. Cytokinin activity is found in translocating xylem sap, in seeds and embryos and in green leaves. Concentrations of 50 to 100 ppb are found in sap. In 1964, 6-amino purines were identified as cytokinins by D. C. Letham at the Plant Diseases Division, Auckland. Cytokinins also function in delaying senescence of leaves on deciduous trees. Importantly they also seem to affect specific transport.

As well as these three important classes of plant growth regulators several more have been described. Some of these may simply be artifacts of the interaction of auxins, gibberellins and cytokinins. Significantly, moreover, ethylene is becoming implicated more and more in the control of the action of auxins, gibberellins, and cytokinins. Ethylene may well prove to be the key to a complete understanding of the way in which plants naturally regulate their growth and development or respond to applied chemicals. And while plant physiologists continue their efforts towards understanding this regulation, horticulturists and agriculturists will continue to use synthetic chemicals in an empirical way to obtain specific plant responses.