Chemical control of crop growth and development

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Summary

1. A survey is given of the chemical regulation of growth and development of crops by other means than fertilizers.
2. The main groups of growth-stimulating (auxins, gibberellins, kinins) and inhibiting substances and a number of pesticidal compounds (nematicides, insecticides, fungicides, herbicides) are reviewed.
3. The physiological actions of these chemicals on crops may be classified as follows:

   3.1. control of dormancy and germination;
   3.2. control of rooting of cuttings;
   3.3. control of plant shape;
   3.4. stimulation of vegetative growth and development;
   3.5. induction of flowering;
   3.6. induction of male sterility;
   3.7. control of setting and growth of fruits;
   3.8. fruit thinning;
   3.9. delay of abscission;
   3.10. defoliation and desiccation.

4. It is concluded that a fuller understanding is required of the physiological backgrounds of the above effects in order to obtain a comprehensive system for the chemical regulation of crop growth and development.

1. Introduction

There are two respects in which the living plant may be termed a dynamic organism. On the one hand it increases in size and weight by cell division and elongation, and on the other it produces new organs in the subsequent phases of its life cycle from seed to seed. The quantitative increase is called growth, and the transition from one life period to another is termed development. Both processes (growth and development) are determined by heredity, but environmental factors may considerably affect the rate of either process and hence their mutual relationship. The importance of their ratio for dry matter distribution and final crop yield is treated elsewhere.
The environmental influences are of a physical and of a chemical kind. The main physical factors are light and temperature, while among chemical influences those of fertilizers are the most prominent. All these factors have been dealt with elsewhere. There remains, however, a group of chemical compounds by means of which it is possible to influence growth and development rates in order to promote crop pro-

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duction. It is this already large and rapidly extending group of non-nutritive chemicals that will be discussed here.

The substances belonging to this group, although varying greatly in both chemical structure and physiological action, usually have the common property of exerting a considerable effect even in low doses. According to their practical uses they fall into two main groups, that of growth-regulating compounds and that of pesticidal substances. This division is only an artificial one since a number of growth regulators have also been used as herbicides. The substances of the former group are used intentionally owing to their physiological action on the crop, whereas those of the latter group are primarily used for their action on pathogenic organisms and weeds, any effect on the growth or development of the crop itself, apart from the pesticidal action, only being an accidental side-effect. The main representatives of both groups will be briefly noticed before their physiological activities are arranged according to subsequent phases of plant development.

2. The chemical compounds

2.1. Growth-regulating substances

Natural plant growth regulators have been known since the classic studies of WENT, published in 1928 (7). KÖGL's auxins A and B are probably not to be included among them (80). The first generally found plant growth hormone is what KÖGL called heteroauxin, indole-3-acetic acid (IAA), while a number of related compounds have also been isolated from plant materials (7). IAA has been prepared synthetically since 1935 and is therefore available for experimental purposes and horticultural uses. It chiefly induces cell elongation by cell wall softening (11), but also stimulates meristematic activities and is responsible for correlative inhibitions, *e.g.* apical dominance and prevention of abscission. Although all these processes are effected by IAA, the manner in which it primarily acts is still unknown; its action is perhaps of a physical rather than of a pure chemical kind. A prerequisite for its action is a very specific configuration of the molecule (65). Commercial chemical products showing a configuration similar to that of IAA in several specific respects exhibit similar activities and many are used at the present day. This group of compounds is usually referred to as the *auxins* (4, 34, 44, 47, 66). They include indole-3-butyric acid (IBA), 1-naphthaleneacetic acid (NAA) and the phenoxyacetic acid derivatives 2,4-dichlorophenoxyacetic acid (2,4-D), 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) and 2-methyl-4-chlorophenoxyacetic acid (MCPA). The individual auxins vary in respect of rates of penetration, translocation and breakdown in plants. Their frequent great resistance to decomposition renders them suitable for use as herbicides (22, 66). It is possible that the addition of artificial auxins lowers the natural auxin content in plants (66).

For about a decade the *gibberellins* have been known as another group of natural growth-stimulating compounds (72, 82). Their effects on growth are not due to a change in auxin level (45), and interactions with auxins, both synergistic and antagonistic have been reported (28, 67, 68). Their action is also connected with photoperiodic phenomena (19).

Gibberellins promote cell division and elongation, especially just below the apical meristem (75). The increase in cell number and size causes stem elongation. Gibberellins may induce bolting of rosetted plants and generally simulate effects of long

days and high temperature treatments (83, 92). Their capacity of allowing dwarf mutants to develop into plants of a normal size indicates that they occur naturally in plants, dwarfism often being the expression of a lost power of gibberellin synthesis (71). Gibberelin-like substances have, in fact, been frequently found in plant materials (14, 39). They have been regarded as "shooting hormones", being generally produced, but only under long day conditions in long day plants (19, 20). Since the extent of such different plant responses as elongation, germination, fruit setting, fruit growth and abscission, varies with the different gibberellins, several bioassays have to be made in order to find endogenous gibberellins, while an investigation into the effect of a specific gibberellin on a plant process, *e.g.* flowering, should include a bioassay based upon the same phenomenon (92). Gibberellic acid (GA_3) is used in most experiments.
The reinforced stem growth resulting from a gibberellin treatment is usually accompanied by increased apical dominance. Both the internodes and the leaves may become more elongated, but often their chlorophyll content decreases (79). Gibberellins usually have no effect on root growth, or else impair it slightly, so that the shoot/root ratio increases and this may render gibberellin-treated plants more sensitive to their supply of moisture and minerals (12).

Recently, the *kinins* were discovered as a third group of growth-stimulating substances (58, 60, 67, 91). They are a group of purine derivatives, some of which are native (33), others are formed on heating plant materials (kinetin, 6-furfurylamino purine), and others are artificially synthesized, *e.g.* N^6-benzylamino purine. In view of their activating properties they may be regarded as hyperactive adenines. Kinins accelerate cell division and elongation, break through correlative inhibitions, abolish dormancy phenomena and resist decay in senescent and detached organs (24). The underlying principle is a stimulation of cell metabolism, especially of nucleic acid and protein synthesis (60, 67, 68). Kinins may act synergistically with other growth substances (67). When added together with gibberellin to the culture medium of excised onion anthers they enable these anthers to carry out meiosis and develop complete pollen tetrads (84).

Besides such growth-promoting substances as auxins, gibberellins and kinins, *inhibiting compounds* are also known. Information on natural inhibitors is fairly scarce and mainly relates to coumarin derivatives, fatty acids and alcohols (7). An anti-auxin which accelerates abscission has recently been isolated from cotton burs (49). Dormant potatoes (14) and tree seeds (87) are known to contain germination-inhibiting substances.
Only artificial inhibitors have been used in horticulture, especially the phenyl carbamates IPC and chloro-IPC (22), maleic hydrazide (MH) (22, 88), the quaternary ammonium compound Amo-1618 (17, 18, 88, 89), (2-chloroethyl)-trimethyl ammonium chloride (CCC) (83, 93) and the phosphonium compound Phosfon D (17, 18). These compounds antagonize the action of gibberellins. Both MH and Amo-1618 reduce subapical cell divisions and the inhibition by the latter compound can be prevented and reversed by gibberellic acid (75). The inhibited meristematic activities and cell elongation cause shortened, often thickened internodes (89). Reduced apical dominance promotes branching and tillering. Whereas gibberellins induce effects resembling those caused by long days, red light and high temperature, CCC simulates short daylength, strong blue light and cold (83). Plants treated with Amo-1618, Phosfon D or CCC show an increased tolerance to alkaline and saline soils and to

excessive applications of fertilizer (52). These compounds can be very stable both in the soil and the plant, their effect being apparant after tree years in the soil and in the third generation (53, 54). Amo-1618 seems to have a systemic fungistatic action (53).

Several growth-promoting and inhibiting substances occur naturally in plants, and artificial compounds with comparable modes of action are also available. It is reasonable to suppose that the endogenous stimulators and inhibitors form a variable equilibrium of synergistic and antagonistic forces in the plant (14, 70, 87). The result of an attempt to shift this hormonal equilibrium by adding exogenous growth-regulating substances depends on various factors. The first condition is that the chemical applied should penetrate and be translocated towards the active centres. Secondly the treatment is useless unless there is a certain deficiency (47). If the equilibrium is already predominantly in the direction in which it could be shifted by the chemical applied, overdosing will either have a too small or else a catastrophic effect. Finally, the internal and external conditions should allow for an adequate response, i.e. both the development of the plant and the environmental conditions should meet certain requirements. It is possible, for instance, to induce flowering in tomato seedlings by a treatment with a 0,02 % solution of 2,3,5-triiodobenzoic acid, but it is hardly possible to obtain a single small fruit from the plants as they have not reached the required stage of development (25).

2.2. Pesticidal substances

Since the groups of chemicals used as pesticides are far too numerous and various to be discussed within the scope of the present review, only those groups will be briefly mentioned that are thought or known to exert direct effects on plant growth, development or metabolism.

Favourable side-effects on growth, development and crop yield have been reported of all kinds of pesticides (herbicides, fungicides, nematicides and insecticides). Careful investigation is required, however, to ascertain the independence of these secondary effects from any pesticidal action, and field trials can seldom be relied on as affording complete proof of this. In most reports it is uncertain whether the control plots were left untreated or were sprayed with an equal amount of water or a formulation from which the active component was absent (86). This is also important because surface-active agents in the formulation ("surfactants") not only cause intensified and prolonged contact between the active material and the plant surface and greatly affect the penetration of the former (23), but may even exert growth-stimulating activities themselves, as is shown *e.g.* for Tween 20 (43).

Another point to consider is whether the experiments were performed in the complete absence of weeds and pests. It is usually difficult to take into account the killing of thrips, collembola and other more or less noxious soil organisms. This is particularly important in the case of such insecticides as DDT and anticholinesterases, and of nematicides (63). With regard to the latter, *soil fumigation* often leads to yield increases, even when a low nematode population was previously present or the soil had been previously steamed, or when sand and vermiculite cultures were used (46). Even in pot cultures in the greenhouse, however, spontaneous collembola infestations easily lead to deceptive results (46).

Soil fumigation need not improve yield as a result of its nematicidal action only. This action can only be properly established by experiments with various population densities of nematodes not linked to different sterilisation treatments or previous crops (78). Killing of other noxious soil organisms, increase in available nitrogen and decrease of soil acidity (62) as a result of nematicide injections may be further factors. The occurrence of bromine in the case of methyl-bromide, or of chlorine with Shell-DD (dichloropropane and related compounds) may possibly also influence plant growth, for instance by improving moisture relationships (32).

It has been reported that insecticides with an anticholinesterase activity, especially such *organic-phosphorus compounds* as parathione and phosphamidon, are able to increase the resistance of plants to fungus attacks even after their disappearance from the plant tissues (5). It is again uncertain whether this feature and the yield increases also mentioned are due to a partial soil sterilisation. Laboratory-scale investigations sometimes confirmed these field observations. Results were negative in the case of Systox (86), but for parathione and tetraethyl pyrophosphate (TEPP) auxin-like activities could be demonstrated (9, 37).

Treatments with fungicidal *dithio carbamate* sprays often intensify and prolong the green colour of crops, as compared with the colour of plots sprayed with other fungicides or with the colour of control plots when no fungus infestation occurs. In this connection it may be of some importance that in auxin tests certain dithio carbamates show activities that are probably due to the heteroauxin-like configuration of their molecules (2, 44).

Among herbicides, *auxins* play an important part since it was accidentally discovered in 1940 that spraying a solution of NAA in a plot of oats contaminated with seedlings of wild mustard caused the weed seedlings to die, whereas the oat plants were unharmed (22, 66). The use of 2,4-D in the U.S.A. and MCPA in Europe as herbicides in cereals and sugar has since become an important industry. In Europe, for instance, average yield increases of 20 per cent have been reported as a result of this weed control (66). The herbicidal effect of these auxins is probably due to a disturbance of meristematic activities caused by overdosing with a growth-promoting substance which is difficult to decompose. This causes physiological derailments (10) resulting in morphological deformations and tissue proliferations that block the conducting systems and ultimately lead to starvation, necrosis and death (4). Presumably selectivity mainly depends on differences in uptake, translocation and breakdown of auxins by different plant species (10).

In addition to auxins, *dinitro phenol derivatives* have been used as herbicides in cereal crops, *e.g.* 4,6-dinitro-o-cresol (DNOC) in winter wheat and winter rye. These very toxic compounds are hardly translocated inside plants since they burn the tissue with which they come into contact (22).

The trend in the development of new herbicides is to produce increasingly complex compounds which on the one hand have a stronger and more specific effect, and on the other are less toxic to man and animals, and whose persistence in the soil is either greatly reduced or highly increased. Some of these newer substances will be referred to in the following section.

3. The control of growth and development

3.1. Control of dormancy and germination

Plants tolerate unfavourable seasons with the aid of dormant organs, *viz.* seeds, buds, tubers and rhizomes. This state of dormancy is mainly controlled by interactions between endogenous substances that inhibit and promote germination (14, 87). The content of growth-promoting substances is lowered during dormancy, whereas inhibitor concentrations are increased. The peel of dormant potato tubers, for example, contains an inhibitor which is absent in sprouting tubers, whereas the gibberellin content of dormant tubers is lower than that of sprouting ones (14). In dormant peach buds naringenin antagonizes the breaking of dormancy by exogenous gibberellin (70). A gibberellin treatment often breaks dormancy (88), whereas seeds and buds of potatoes and woody plants can be inhibited from germinating by means of gibberellin antagonizing inhibitors and auxins, *viz.* IPC, chloro-IPC, MH and methylnaphthylacetic acid (15, 88). The chief use of breaking dormancy is in the malt industry, where brewing barley is forced to germinate by soaking in 100 p.p.m. gibberellin (74), which intensely activates the amylolytic enzymes in the endosperm (69). Gibberellin has recently been used for breaking the dormancy of rhizomes of *Helleborus niger* L. after too warm an autumn in order to obtain the Christmas roses in full bloom at the right date. Another possible use is in weed control by causing weed seeds to germinate (21).

Dormancy can be artificially terminated by a kinin treatment, *e.g.* with lettuce seed and with overwintering buds of aquatic plants, as well as by gibberellins.

Although high auxin concentrations usually reinforce dormancy in seeds, soaking of beet seeds in an IAA-solution was found to accelerate germination, the faster growing plants producing larger roots (55). Similar effects have been observed for the isobutyl ester of 2,4-D with tree seeds and for benzimidazole derivatives with the seeds of flax, tomato and cucumber (55).

In warm countries, *e.g.* Israel and South Africa, the chilling requirements of fruit trees in outdoor orchards are often still not fulfilled by the end of the winter. The delayed and irregular bloom and foliation caused by the prolonged dormancy of the buds can be accelerated and made uniform by such spraying agents as the herbicide DNOC in mineral oil (76).

3.2. Control of rooting of cuttings

The first application of auxins in agriculture was based on their accelerating effect on the root formation of cuttings. The immersion of cuttings in auxin-containing powders or liquids has now become a current practice, especially in woody stock nurseries; it is employed on a large scale in the propagation of cocoa, coffee and rubber (34, 66, 88).

The formation of adventitious roots results from a renewed meristematic activity which can be stimulated by IAA, IBA and NAA. Owing to undesirable side effects auxins of the phenoxyacetic acid type are unsuitable. The general opinion is that the auxin treatment promotes an existing tendency in the cutting material. The origin and age of the material and the presence of leaves and buds are important factors. Certain endogenous phenol-like compounds may considerably facilitate rooting (41). Both the internal and external conditions have to be suitable. By this is meant such factors as the season, climatic conditions, atmospheric humidity and soil temperature (31). The stimulatory action of an auxin treatment results in a more rapid and complete rooting with reduced losses. A better ball of earth is obtained since numerous short roots are formed instead of a few long ones.

3.3. Control of plant shape

Apical dominance is the suppression of the activities of lateral buds by the stem top meristem. It can be induced by the application of auxins to a decapitated stem of which the lateral buds would otherwise have sprouted. Plants with a marked apical dominance form long, scarcely branched shoots, whereas a weak apical dominance results in a full, sometimes even stunted plant form. Chemicals affecting apical dominance have therefore been used in the culture of ornamental plants.

It is not auxins but gibberellins that are used to overcome dwarfism (71). They also reduce the numbers of flowers and elongate the flower stalks of Chrysanthemum (82) and improve the stalks of roses (61).

Usually, however, it is the inhibitors which reduce apical dominance that are used to control plant shape, *viz.* MH, Amo-1618, CCC and Phosfon D (3, 18). When mixed into the soil or sprayed on the plants these chemicals reduce internodal growth and promote branching. With their aid Chrysanthemum (88), Poinsettia and many other plants can be fashioned into well-shaped, compact pot plants. Control of flower initiation by photoperiod and temperature is usually unaffected, but flowering is sometimes delayed. An inhibition of flower formation on the main axis is compensated by the bloom of numerous lateral shoots. In woody plants such as Azalea the growth inhibition may even cause an accumulation of assimilates, resulting in advanced flowering. In strawberries, MH suppresses the development of runners (51).

In the culture of woody plants, these compounds have been used for dwarfing trees (22). They may also save pruning and staking work and limit the height of ornamental trees and shrubs (3). MH has been used by public authorities to reduce the growth of grass and privet hedges in parks and along roads (88).

Recently CCC has been successfully used in preventing lodging of cereals (56).

Some herbicidal compounds also affect plant shape. The ureum derivative monuron (22) and several oxazolidine compounds (57) reduce apical dominance, while other components of the latter group severely limit mesophyll development, indented leaves being formed as a result.

3.4. Stimulation of vegetative growth and development

Stimulation on the vegetative level may be reflected as reinforced vegetative growth and prolonged vegetative development. The latter feature is shown by a delay in senescence at the end of the entire vegetation period or as a delay in the transition from the vegetative to the generative phase. All kinds of growth-regulating substances and a number of pesticidal compounds affect the plant in one of these ways.

The transition to the generative phase involves an essential change in the life of the plant which will be discussed under the next heading. At this point, however, it should be stated that although a plant is either vegetative or generative, depending on the absence or presence of a flower primordium at the growing point, underlying this "all-or-nothing" principle is a complex of equilibria consisting of hormonal and nutritive factors, each of which can tip the scales according to the relative amounts of the various components. Generally speaking, in these equilibria both auxins and anti-gibberellins tend towards an extension of the vegetative stage. With one exception, to be mentioned in the next section, *auxin* treatments either have no effect or else retard flowering. It has even been argued that the main function of IAA in the plant is to delay flowering until the vegetative plant develops far enough to ensure a sufficient supply of nutrients during the subsequent generative stage (25).

Auxins are seldom used for suppressing flowering, but foliar auxin sprays may induce several other biochemical changes in plants. These include curing lime-induced chlorosis, increased resistance to fungus attack and a changed palatability to voracious insects (51). The latex yield of rubber trees can be improved by about 30 per cent by the application of an auxin to a strip of bark above the tapping cut (51).

Flowering can usually be suppressed with the use of gibberellin-antagonizing *inhibitors.* Bolting of rosetted plants can be inhibited by a MH-treatment (88). With some special clones of sugar cane, showing a very specific day-length sensitivity, an MH-spray applied just before the short critical period blocks the meristematic activity until flower induction is over, so that the cane remains vegetative. The delay in flowering may also be profitable in breeding experiments to make fast-flowering varieties bloom simultaneously with slower ones (3).

Although *gibberellins* can be successfully used to induce flowering (cf. the following section), the spectacular growth stimulation caused by these compounds has also led to attempts at increasing vegetative crop production by these means (82), but without very great success. A treatment in the growing period usually has little effect. An out-of-season application increased the production of grasses and clovers (82, 88). Larger beets could be obtained, but the amount of sugar was not increased. The fibre yield of flax and the yield of vegetables can be augmented, but with the latter in particular such undesirable side-effects as premature bolting, morphological deformation and reduced storage properties appear (82). In some cases tree growth can successfully stimulated (82).

The effect of *kinins* is still not fully understood. Hitherto their chief prospect has been "conditioning agent" or "maintenance hormone" for keeping fresh harvested vegetables (24, 91). A spray of 5 p.p.m. N^6-benzyladenine inhibits the breakdown of cell metabolism in freshly harvested lettuce (51). Asparagus spears, kept in the dark, respire at a lower rate and lose less moisture (24).

A delay in senescence has also been reported of the inhibitor MH (22) which only slows down cell metabolism, and of the auxin 2,4-D (64) which stimulates respiratory activity and hence, translocations to this locus of activity. Kinins, however, stimulate in particular the synthesizing part of the cell metabolism and keep the cell and tissue both active and economical (67).

A delayed senescence has also been mentioned after spraying with various plant protectants. In addition to any pesticidal effect, the treated plots remain green longer than untreated or differently treated plots. This phenomenon is known from fungicidal *dithio carbamates* in particular, for example in potatoes (36), onions (27) and tulips (8). The prolongation of the vegetation period may substantially increase the yield. It is unknown, however, whether these compounds affect the dormancy of the harvested potato tubers and the onion and tulip bulbs. The slightly increased rate of development of flowers by bulbs from carbamate-sprayed plots is probably due to a prolonged growing period of the young bud during the delayed senescence of the mother plant.

Spraying herbicides may also delay the rate of development, as a result of which the crop stays longer green. Treatment of young winter cereals with DNOC reduces growth and development at first. The growth retardation is subsequently changed into an acceleration, whereas the delay in development continues. The more vigorously growing but slower developing plants are able to produce more ears in which more fertile flowers are formed. The larger and longer persisting assimilatory apparatus supplies the larger amount of grains with more assimilates, so that yield increases of about 5 to 15 per cent occur in experiments on weed-free plots (13).

Consequently, spray-induced inhibitions need not always be disadvantageous as they can be overcompensated afterwards. In other cases also, a temporary reduction of the amount of vegetation may be profitable, for instance in order to enhance night-frost resistance or to prevent lodging of cereals. These reductions can be obtained by treating crops with such contact herbicides as DNOC or trichloroacetic acid (TCA) or with such antigibberellins as CCC (56).

3.5. Induction of flowering

The startling differences between rosetted control plants and *gibberellin* treated plants carrying an inflorescence at the top of a bolted stalk (72, 88) suggest, incorrectly, that gibberellins should be regarded as flowering hormones. Many plants require special environmental conditions for the induction of the generative state, *e.g.* a chilling treatment or an exposure to a fairly sharply defined daily illumination period. Combined requirements occur also, *e.g.* cold followed by long days, or short day-lengths followed by long ones. A great number of cold-requiring rosetted plants can be made to flower by means of a gibberellin treatment without any vernalisation. The same is true of many long-day plants under short-day conditions, although gibberellin rarely accelerates flowering in caulescent long-day plants. In the case of plants needing both cold and subsequent long days, gibberellins are unable to replace the two requirements together. Nor, generally speaking, can flowering be induced by a gibberellin treatment of short-day plants under long-day conditions. On the contrary, in short days the strawberry responds to such a treatment by inhibition of flowering and production of runners, as it does during long days (12, 73).
Since gibberellin is especially active in rosetted plants, it acts rather as a "shooting hormone", which only causes flowering as far as this process is limited by the absence of bolting. For flowering itself, hypothetic "anthesins" would be required. These probably occur normally in long-day plants but are formed in short-day plants under short-day conditions only, whereas it is suggested that the reverse is true of gibberellins (19, 20). The irreversibility of the flowering capacity and its transferability by grafting (94) indicate self-reproducibility of the complex biochemical entities contained in the meristem: "flowering resembles a virus-infection disease" (26).
Gibberellins have been used in seed growing to obtain a ready and uniform bloom and seed ripening. In the culture of ornamental plants they sometimes increase number, size and life-time of flowers, *e.g.* in zonal pelargonium and lily-of-the-valley (82).

It was stated in the previous section that *auxins* do not normally promote flowering. A peculiar exception is the use of NAA in pineapple culture in Hawaii and Puerto Rico (35, 66, 88). The crop from slips planted in the autumn inflorescences quite uniformly and causes too great a peak in the canneries. On the other hand, crops from suckers bloom irregularly, resulting into a very variable fruit size and forcing growers to harvest the same field repeatedly. A solution of $^1/_4$ mg of auxin, poured into the heart of a vegetative pineapple, immediately induces flowering in any season. When one field after another is treated with 60 g of NAA per ha at regular intervals, they can be harvested at once and the total harvest time can be spread *ad lib.* The same effect can also be obtained with acetylene, using 1 g of calcium carbide per plant. The fact that ethylene, a supposed auxin antagonist, is also able to induce flowering in pineapple and that IAA itself has no effect at all, suggests that the synthetic NAA acts as an anti-auxin by reducing the native auxin level (4).

In such monoecious plants as cucumber and maïze, both auxins and gibberellins are able to shift the *sex ratio* in favour of the production of female flowers (26, 55).

The retarding effect of auxins on flowering can be removed by anti-auxins, which may even induce early blooming. An example is the forced flowering of tomato seedlings with triiodobenzoic acid, mentioned in section 2.1.

3.6. Induction of male sterility

In plant breeding, flower castration is often required to prevent self-pollination. Manual emasculation is a laborious task and unsuitable for commercial production of hybrid seed. Chemical castration with growth-promoting and inhibiting substances has been tried out with varying results, but a promising gametocide has been found in α, β-dichloro isobutyric acid, a compound related to the dalapon herbicide and known as FW 450 (29, 77, 90). This chemical poisons meiosis and is selectively translocated in the plant, i.e. more towards the stamen than the ovary. The correct dose given just before the reduction division of the pollen mother cells induces sterile pollen without damaging the eggs too severely.
In addition to amelioration and seed growing purposes, FW 450 can be used in weed control, *e.g.* to prevent the dispersion of coltsfoot (*Tussilago farfara* L.) from fallow land by seed.

3.7. Control of setting and growth of fruit

Pollen has a high auxin content and its germination is accelerated by gibberellins (67, 68). After pollination, considerable amounts of growth-promoting substances appear in the ovary and play an important part in the setting and growth of the young fruit (48, 67, 68). This is shown when the seed is killed by night frost or insect damage, when the fruits drop unless the stimulus from the seeds is replaced by exogenous applications of auxins or gibberellins. This is also true of such spurious fruits as strawberries (66).
Auxins, and particularly gibberellins, can induce parthenocarpy, *viz.* they enable unfertilized ovaries to develop into fruits that are apparently normal but have seeds which remain undeveloped (34). Parthenocarpic fruit-set can be induced when there is a risk of no pollination occurring, *e.g.* with beans at too high day temperatures, with field-grown tomatoes at too low night temperatures, and with greenhouse tomatoes grown under unfavourable light conditions. Naphthoxyacetic and p-chlorophenoxyacetic acids have been used in such cases (66, 88). The fact that synergistic actions of growth regulators play a part in fruit setting is shown by the complete restoration of auxin sensitivity of winter-grown tomato plants by a treatment with 100 p.p.m. of gibberellin (51).
Gibberellins have been used in the culture of seedless raisins and to obtain large parthenocarpic Citrus fruits and grapes; in the latter case the elongating effect on the fruit stalks also improved the growth of the berries. The fact that berries of seedless cultivars of grape vine show a greater response to a gibberellin treatment than those of seeded varieties suggests that gibberellins are endogenously produced by the seeds (72).
Fruit set and size can only be improved with the use of a growth regulator provided this treatment removes a limiting factor. VAN OVERBEEK (67, 68) suggests that gibberellins, kinins and auxins occur in peaks in the course of the development of the grape, and that they may not only be produced by the seeds but also derived from vegetative plant parts. It would seem that fruit set and growth depend on the absolute and relative amounts of these antagonizing and synergistic acting substances, that gibberellins promote fruit set in particularly, kinins the divisions in

the pericarp, and the further growth by cell elongation is regulated by auxins, gibberellins (especially in seedless varieties) and the supply from the vegetative parts with such osmotic active substances as sugars.
This scheme would explain the numerous effects of auxin and gibberellin treatments, both as regards fruit set and growth and fruit thinning (cf. the following sections). The joint regulation of fruit growth may account for the observation that auxin sprays in apple and pear usually lead to a temporary acceleration of growth only, and that, since growth is terminated earlier, larger fruits are not usually obtained. In strawberry and blackberry, however, larger fruits may actually result from an auxin treatment (66).

3.8. Fruit thinning

Fruit growers endeavour to obtain an optimum fruit density per tree. On the one hand fruit setting should be satisfactory, but on the other too many fruits reduce the fruit quality and promote biennial bearing. Consequently fruit thinning is an important factor, and since manual labour has become too costly chemical means are required. These are found both in the group of growth-regulating substances and among the pesticides. Most data in this and the following section are derived from research on apples.
There are two suitable dates for fruit thinning. At full bloom the trees can be sprayed in order to kill part of the pollen and the stigmata. For this purpose use has been made of the DNOC herbicide (1, 66). The other date is some weeks after blossom, the best time being about one and a half weeks after petal-fall, before the cell walls differentiate in the endosperm. A spray with 25 p.p.m. of the auxin NAA or naphthylacetic amide (NAAm) on this date results in an enhanced fall in June. One explanation of this effect is that the treatment kills the embryo and the fruit drops as a result of hormone deficiency (50); according to another theory the hormone produced in the endosperm to prevent abscission is of a gibberellin-like nature and is antagonized by exogenous auxins (66). Although hormonal fruit-thinning is widely employed in the U.S.A., in the U.K. it has not been found profitable to replace hand-thinning. The different experiences in these two countries may depend on differences in cultural methods, apple varieties and auxin formulations.
A very favourable compound for thinning apples was found to be the insecticide Sevin, a naphthylcarbamate used in orchards for controlling caterpillars (6). A spray 2 to 4 weeks after full blossom causes a mild and regular thinning, hardly dependent on weather conditions. No side-effects on growth and ripening could be observed. Although incidental seed abortion was found, the manner in which this chemical acts is still obscure.

3.9. Delay of abscission

When an optimum fruit setting has been approached it is necessary to prevent decrease in fruit density as a result of fall. The latter is also governed by growth-regulating substances (50). Shedding of organs usually appears to be prevented by continuing the growth of stems, stalks or petioles, thereby inhibiting the development of an abscission layer (42, 85). In this action, such growth-promoting substances as auxins and gibberellins interact and can themselves be counteracted by abscission-promoting substances (16, 49).
The setting of blown flowers is due to hormone production about the period of

fertilization. When the young embryo afterwards passes through its first rest period, the hormone level drops and there is an early fall of small fruits. A second period of decreased activity causes the June fall, and the late fall may occur during the ripening of full-grown fruits. Abscission may be prevented by artificial raising of the hormonal level by such exogenous auxins as 2,4-D and NAA (34, 66) and, recently in Germany, phenyloxypropionic acid. Sprays with the combined fungicides captan and Karathane specifically reduce the June fall (59).
These treatments sometimes induce accelerated ripening, also in storage varieties (38). A spray with the auxin 2,4,5-T results in apples of a fine colour because the fruits ripen more quickly but do not fall, although budding is often delayed and decreased the year after. Another spray which speeds up ripening of fruits at the cost of their storage property is that with Tuzet, a mixture of fungicidal carbamates. When trees are sprayed with Tuzet shoot growth can also be terminated earlier unless extra nitrogen is applied. This premature termination of generative and vegetative development may well be due to the presence of arsenic in this fungicide.

As well as for apples, pears, Citrus and other fruits, auxins have been used for the prevention of leaf drop of cabbage and of fall of leaves and berries of holly. Cutting reduces the auxin levels of holly twigs, but the harmful results can be overcome by exogenous auxins (66). On the other hand, auxins promote fruit fall in cotton, abscission being counteracted by gibberellin treatments (12, 66, 67, 68).
The fall of apricots in California upon seed abortion by night frost has been controlled with the auxin 2,4,5-T. It was observed that fruit growth was promoted by the spray and at the same time the respiration rate was somewhat reduced, indicating a higher efficiency of energy transfer.

Finally, the delaying action of auxins on abscission has also been used in the cultivation of ornamentals and in plant breeding. Pot plants such as Begonia are NAA-sprayed before leaving the greenhouse to prevent shedding of flowers and buds when their environmental conditions are changed, *viz.* first in the flower shop and then by the purchaser.
The pollen tubes of flowers pollinated with foreign pollen are often only able to make a slow advance in the style tissue. If meanwhile auxin application prevents such flowers from dropping, the eggs can ultimately be reached and fertilized. The tendency of only a few seeds containing fruits to fall, frequently met with in plant breeding, can also often be inhibited by a treatment with auxincontaining pastes.

3.10. Defoliation and desiccation

The final aspect of the control of growth and development relates to their termination. An example of partial killing was given above in section 3.6, dealing with the elimination of viable pollen by gametocides. A similar case, though the manner in which it acts is unknown, is the translocation of the herbicide Zytron into developing seeds of certain grasses, rendering them non-germinable; this compound probably prevents the dispersion by seed of such plants as *Poa annua* L. (22). Total killing of plants is not applied to crops, but only to weeds in order to keep fields, roads and irrigation systems free from undesirable growth (22). For crops, defoliation and desiccation are becoming increasingly important both in horticultural and in agricultural practices.
It is desirable in the culture of several crops to defoliate without damaging the rest of the plants or preventing future budding. This is an important factor, for in-

stance in the export of nursery stock, which has to be defoliated to limit transpiration but must not be harmed in any way. *Antitranspirants* might be used in this case instead of defoliating chemicals. These are water-tight plastics with which plants can be coated without too greatly hampering respiration and photosynthesis (30).
In other crops, especially when they are mechanically harvested, all vegetation without special marketing value, or even a depreciating effect, has to be removed previously, and this can only be done economically by chemical means. This problem was first attacked in cotton growing, but is becoming more important with the increasing mechanisation in seed-growing practices.
When seed or tuber crops are harvested the plants themselves need not to be spared. A desiccant or defoliant can be used, the former causing withering of the plants. This principle has been used in potato growing. The condition that the chemical used should not be translocated into the seeds or tubers is usually met by such contact herbicides as DNOC and arsenites. The latter compounds, however, accumulate in the soil. A recently developed phytocide, 1,1-ethylene-2,2-dipyridilium (diquat or FB-2) has a low toxicity for animals and man and is rapidly decomposed in the soil, but kills potato leaves and stalks, as well as weeds, with a dose of only 0,5 to 1,0 kg/ha. In still lower quantities, 125 to 250 g/ha, this desiccant can be used as a defoliant *e.g.* in cotton. The killing action on the leaves with which it comes into contact is probably due to a disturbance of the redox potential at the photosynthetic centres, leading to the formation of toxic radicals (81).
Other defoliants probably act by reducing the native auxin level, resulting in the formation of an abscission layer in the petiole. For this purpose such artificial auxins as the butyl ester of 2,4,5-T can be used to defoliate areas of tropical forests (51), or such herbicides as endothal (22) and oxazolidine derivatives (57), but even the iodide ion can induce shedding in intact plants (40).

4. Conclusion

The result of the foregoing review of the possibilities afforded by the arsenal of chemical compounds for the control of crop growth and development is a great many loose data rather than a system of planned management of these possibilities in actual crop growing. To extend this inventory to such an organized system more information is needed from two sources. On the one hand we need data on new effects obtained with new chemical substances, and on the other research is required into the physiological backgrounds of the effects observed.
Far from being a passive and automatically reacting acceptor of the chemical treatment, the plant determines its response both qualitatively and quantitatively. This response depends on the plant species, even on the cultivar, on the stage of development of the plant and its physiological and environmental conditions. Chemical intervention often disturbs equilibria within the plant and between the plant and its environment, so that great care and circumspection are required in the use of these compounds. A deeper understanding of the equilibria mentioned and of the way in which the exogenous compounds affect the physiology of the plants is essential to obtain a coherent and comprehensible arrangement of the multitude of empirical data by means of which crops can be properly guided to give optimum production.

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