GROWTH SUBSTANCES IN PLANTS
by R. van der Veen.

Growth substances are compounds of a hormonal nature which, although present in the plant in extremely low concentrations, govern the life of the plant. Much regarding these substances is still obscure. Until recently it was thought that the chemical structure of all compounds with growth substance activity (both natural and synthetic) conformed to two essential requirements, but the members of a newly discovered group of compounds appear to be active as growth substances, yet do not comply with these requirements. Paradoxically enough, in certain concentrations growth substances are lethal to some plants. This has found practical application in the control of weeds.

The concept of “growth substances” is intimately associated with the name of F. W. Went, who in 1926 while working in the Botanical Laboratory at Utrecht, discovered that the elongation of the stems of young plants was essentially caused by one specific substance.

It soon became apparent that this growth substance brought about many other reactions in the plant. A survey of the phenomena induced by growth substance is given below.

2. Geotropism. Growth substance is transported in a vertical downwards direction by the living cells. If a plant be placed at an oblique angle or horizontal, its lower side will receive more growth substance than its upper side. Consequently its lower side will elongate more, as a result of which the plant will again begin to grow upwards (fig. 1a).

The roots of a plant are even more sensitive to growth substance than its aerial parts. If a tap root be laid horizontally, then here also more growth substance will be present on its lower side. This will lead to too high a concentration for the root growth, however, so that the elongation is not promoted, but inhibited, in such a way that the lower side grows slower than the
upper side, and the root will thus grow downwards.

3. **Phototropism.** It appears that growth substance is broken down by enzymes in the plant, and that the breakdown is powerfully stimulated by light. On the lighted side, therefore, the breakdown will be far more rapid than on the shaded side. In consequence the shaded side of the stem will grow more quickly, causing the plant to bend towards the light (fig. 1b). (This representation, though broadly accurate, is somewhat over-simplified).

4. **Apical dominance.** Much growth substance is formed in the rapidly growing apex of a plant. This growth substance is continuously transported down the stem. Now in each leaf axil is a lateral bud which can grow out into a lateral branch. Growth substance prevents the lateral buds from sprouting; in the presence of growth substance the buds thus remain dormant. If, however, the stem is decapitated (i.e. if its apex is cut off), the flow of growth substance is interrupted, and the lateral buds are thus able to sprout. The uppermost lateral buds sprout first (fig. 1c). Since the latter themselves produce growth substances the lower buds are arrested in their development and remain dormant.

5. **Root formation.** It has been found that a high concentration of growth substance stimulates the formation of roots. When a cutting is planted all the growth substance present in it, will be transported downwards and will collect in the lower end. For this reason the roots will form at that end and not higher on the cutting. By applying artificial growth substance to cuttings, the rooting process can be accelerated.

6. **Abscission.** The spontaneous shedding of leaves and fruits is usually caused by a reduction of the growth substance concentration in the plants, and can be readily prevented by the application of artificial growth substance to the plants, e.g. by spraying.

7. **The withering of certain blooms.** Many orchids, such as the popular Cattleyas, will often retain their freshness for more than 14 days on the plant: If they are pollinated, however, they wither in one day. Immediately after pollination, a large amount of growth substance is formed. The same effect is obtained by applying a little growth substance to the stigma, instead of pollen.

It is possible to go on enumerating phenomena induced by growth substance, but the above will suffice to give an impression of the highly important and varied role played by the growth substance in the life of plants.

**Growth substances as weed-killers**

As a consequence of its powerful hormonal nature, growth substance can ultimately give rise to a profound disturbance of various physiological equilibria in the plant, unless it is broken down in the latter. This disturbance may even be severe enough to bring about the death of the plant within one or two weeks, and has led to the practical application of synthetic growth substances as weed-killers (herbicides). Growth substances for use in this role must be very active and must not be rendered innocuous by the plant. Since the monocotyledons such as grasses and cereals are far less sensitive to growth substances than the dicotyledons, dicotyledonous weeds in grass and cereal fields can be eradicated by spraying with a specific amount of growth substance. The best known of these so-called hormone weed-killers based on growth substance activity are 2,4-D, 2,4,5-T and MCPA.

**The chemical structure of growth substances**

The chemical structure of the growth substance that plays the principle role in the plant kingdom is known. It is a compound of fairly simple structure and can be prepared synthetically, viz. 3-indolyl-acetic acid.

It is produced in the plant by the breakdown (in several steps) of the amino acid tryptophane, and is itself broken down further in turn, especially under the influence of light (see above). Indolyl-acetic acid is a link in a relatively long degradation chain. The concentration of the growth substance in a plant depends upon the rates of the various reactions in this chain. Since the indolylacetic acid breakdown reaction is dependent upon the illumination, a low light intensity will cause the concentration to be high and consequently the plant will proceed to elongate rapidly.

Following the discovery of the natural growth substance, numerous synthetic substances have been found that have a more or less analogous influence on the plant. Their number runs into hundreds. Some of them have but a weak growth substance action, others an action scarcely exceeded.

\[1\] For the correlation between this phenomenon and the length of day see R. von der Veen, Philips tech. Rev. 14, 179, 1932/33.

\[2\] This possibility has already been mentioned in this journal, see R. van der Veen, Philips tech. Rev. 16, 356-357, 1954/55.

\[3\] The numbers in square brackets refer to the structural formulae in the appendix.
by that of the natural growth substance. Some of the better known are summarized in the appendix.

It is truly remarkable that so many compounds, at first sight so widely different, exert an analogous action on plants. Attempts to find some correlation between the structures of the various compounds has occupied many workers.

In 1938 Koepfli, Thimann and Went \(^4\) established that all substances with growth substance activity have the following characteristics in common:

- a) a molecule with a "nucleus" consisting of a ring system,
- b) at least one double bond in this ring,
- c) one side chain on the ring,
- d) a carboxyl group at the end of the side chain, and separated from the ring by at least one carbon atom, and
- e) a special spatial relationship between the ring and the carboxyl group.

In 1949 Veldstra and Booy \(^5\) reduced these five characteristics to two, namely the possession of


A new group of growth substances

Co-operation between Philips-Roxane and the Organo-Chemical Institute of the Dutch National Council for Industrial Research, T.N.O., has recently lead to the discovery of a new group of compounds of fairly high growth substance activity \(^6\).

There is no ring system in these compounds however, so that they do not comply with condition a)

\(^6\) This work was conducted under the direction of Dr. Van der Kerk in the Organic Chemistry Laboratory at Utrecht. The discovery was reported in: G. J. M. van der Kerk, M. H. van Raalte, A. Kaars Sijpesteijn and R. van der Veen, Nature 176, 308-310, 13 Aug. 1955.

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Fig. 2. The reaction of tomato plants to spraying with solutions of N,N-dimethylthiocarbamyl glycolic acid (\(^5\)) (code name KD 31) of various concentrations. Photograph (a) was taken two days, photograph (b) ten days after spraying. Even after ten days the plants treated with 0.05% and 0.1% solutions have still not recovered.
laid down by Veldstra and Booy, and thus do not conform to their formulation of growth substance characteristics. Examples of the new growth substances are N,N-dimethylthiocarbamylglycollic acid [5] and N,N-dimethyl-S-carboxymethyl-dithiocarbaminate [5a].

In this new group of growth substances there is an atomic grouping that may be regarded as an intermediate form between

\[(\text{CH}_3)_2\text{N}--\text{C}---\text{S}\] and \[(\text{CH}_3)_2\text{N}--\text{C}--;\text{S}^{(-)}\]

in place of the ring.

It is known from organic chemistry, that in the second structure, with a double bond between N and C, the atoms lie preferentially in one plane, and that this plane structure is imparted to a greater or lesser degree to all the molecules in which this group occurs. The new growth substances, therefore, have in their molecules an atomic group of plane structure, which takes the place of the ring system of the previously known growth substances.

In addition to this plane atomic group, the molecule contains a side chain, that is attached to the right-hand carbon atom (in the above formulae). The side chain conforms to condition \((b)\) of Veldstra and Booy, i.e. it is acidic in character, and will lie out of the plane containing the flat atomic group when the molecule is adsorbed at an interface.

Regarding the side chain, the following can be noted. Whether or not a compound of the recently-discovered type is active, depends upon the structure of the side chain in a manner that is completely analogous to that found for the side chains of the 2,4-dichlorophenoxy group. Thus the side chain \(-\text{O}--\text{CH}_2--\text{COOH}\) for example, occurring in N,N-dimethylthiocarbamylglycollic acid [5] is very active; the action of solutions with different concentrations of this compound on young tomato plants may be seen in fig. 2a and b. If the side chain in question is replaced by \(-\text{S}--\text{CH}_2--\text{COOH}\), a barely less active compound is obtained, with regard to its effect on the plant within two days (fig. 3a). After a longer period, the plant recovers from the effects of a high concentration of the sulphur-bridged growth substance (fig. 3b) but not from the effects of the oxygen-bridged growth substance (fig. 2b). The same is found for 2,4-dichlorophenoxy-
acetic acid (a growth substance of the old type having a ring system) if the bridging oxygen atom (cf. [1] and [1a]) in the side chain is replaced by a sulphur atom. Plants thus appear to be better able to break down a sulphur bridge than an oxygen bridge in this type of compound.

This is also illustrated by the following. \(\alpha\)-naphthoic acid [6] displays growth substance action. On replacement of the carboxyl carbon of this acid by sulphur, \(\alpha\)-naphthyl-sulphinic acid [6a] is formed; this compound is likewise active as a growth substance, but is broken down very rapidly by the plant. Tomato plants, sprayed with an 0.1% solution, show a very pronounced reaction after one hour (consisting in a downward curving of the leaves) which reaches a maximum in eight hours. Recovery then sets in and after 24 hours there is no longer anything unusual to be seen. If the plants are sprayed with indolylacetic acid (the growth substance most widely occurring in nature), they also recover in the course of time, but the recovery is much slower.

**APPENDIX: STRUCTURAL FORMULAE**

Below are given the structural formulae of the compounds mentioned in the text.

1. 2,4-dichlorophenoxyacetic acid (2,4-D) .

2. Like [1], but the bridging oxygen atom has been replaced by a sulphur atom .

3. 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) .

4. 2-methyl-4-chlorophenoxyacetic acid (MCPA) .

5. N,N-dimethylthiocarbamyl glycollic acid .

5a. N,N-dimethyl-S-carboxymethyl dithiocarbaminate .

6. \(\alpha\)-naphthoic acid .

6a. \(\alpha\)-naphthylsulphinic acid .

Summary. After a survey of the principal reactions brought about by growth substances in plants, the use of growth substances in the combating of weeds is dealt with in brief. The author then passes on to the chemical structure of growth substances. The main growth substance is chemically fairly simple, viz. 3-indolylacetic acid, and can be prepared synthetically. The five common characteristics of substances with growth substance activity, framed by Koepfii, Thimann and Went in 1938, are then quoted. These were reduced to two in 1949 by Veldstra and Booy. Philips-Roxane and the Organo-chemical Institute of the Dutch National Council for Industrial Research T.N.O., working in co-operation, however, have recently discovered a group of compounds of fairly high growth substance activity which have no ring system and do not therefore conform to the first condition of Veldstra and Booy. In the new group of growth substances, a similarly plane atomic group occurs in place of the ring system. A side chain attached to the atomic group does comply with the second condition of Veldstra and Booy.