Natural Plant Growth Regulators

Regulators of plant development are chemically defined, while their mechanisms of action remain mysteries.

N. P. Kefford

An international conference may not chance to coincide with the spectacular advances in a field; it should, however, clearly establish the base from which the field may advance most effectively. To this end, the French committee, led by J. P. Nitsch, which organized the 5th International Conference on Plant Growth Regulation, held at the Phytotron, Gif-sur-Yvette, from 15 to 20 July, chose to discuss only natural growth regulators, their chemical characteristics, and their physiological definition (*1*). The progress being made in this area should provide a firm base for future attempts to elucidate the elusive mechanisms of regulator action.

Native growth regulators occur in exceedingly low concentrations in plant tissues. One part per million or less is the general rule. Isolation therefore involves the handling of vast quantities of tissue, commonly with the reward of insufficient amounts of regulator for a conclusive investigation of the chemical structure. This has led to speculation about the structures of compounds on the basis of physical measurements, and to conclusions clearly requiring confirmation. But with methods of isolation established, it is only a matter of time before sufficient material for identification is accumulated. Moreover, the isolation of natural growth regulators is entirely dependent, through most stages, upon a biological assay. In most cases the growth-regulatory activity under study can be defined, strictly, only in terms of the particular biological assay being used; the relevance of this activity to the regulation of development in an intact plant may be quite another problem. In addition, biological assays for regulators involve complicated growing systems and are always susceptible to interference from other, less specific substances necessary for growth. Since many processes contribute to a phase of development, any one which is wholly or partially limiting may be stimulated to give a positive response in an assay, whether the process stimulated is specifically related to the regulator mechanism or not.

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Auxins

For one class of growth regulators, the auxins, it may be stated with reasonable certainty that the native member is indole-3-acetic acid (IAA). Other indole compounds occur naturally and show activity in a variety of assays for auxin. However, studies of the metabolism of these compounds in the assay tissues show them to be converted to IAA and show their growth activity to be due to this conversion. In some cases the "natural" occurrence of indole compounds may be only apparent. They may arise as enzymatic or chemical artifacts during the processing of plant tissues. R. Gmelin (Stolberg, Germany) has investigated members of the genus *Brassica* which are well-known, rich sources of indole auxins. Gmelin found these compounds to have as common precursors the thioglycosides glucobrassicin (Fig. 1, structure I) and neoglucobrassicin, from which indole acetonitrile, ascorbigen, indole acetamide, IAA, and other indole compounds may be readily obtained.

With the nature of the native auxin established, its synthesis, its metabolism, its movement, and the regulation of its concentration in particular cells become pressing problems. Such studies require techniques for the detection and assay of submicrogram quantities of indole compounds. Thin-layer chromatography followed by biological assays or color reactions is one method now in general use; H. Kaldewey (University of Saarbrücken) used it for studying regulators in the fruit stalks of *Fritillaria meleagris*. A technical advance of deeper significance is the use of gas chromatography for the separation of nanogram quantities of indoles, described by B. B. Stowe (Yale). Gas chromatography may be used in combination with gradient elution column chromatography to purify indole extracts of plant tissues, and spectrophotofluorometry is used for confirming the indolic nature of fractions from a gas chromatograph.

The mode and regulation of the synthesis of IAA in plants, of obvious importance in the correlation of organ and tissue development, remain a mystery. F. Wightman (Carleton) showed IAA to be a metabolic product of tryptophan added exogenously to shoots of cabbage, tomato, pea, or tobacco plants. Another metabolic product of interest was indole-3-lactic acid. P. E. Pilet (University of Lausanne) also found IAA to be formed from tryptophan in lentil root tips. P. Larsen (University of Bergen) confirmed the occurrence of indole-3-acetaldehyde, a possible precursor of IAA, in pea stems.

As might be expected, the metabolism of IAA in plant tissues is better understood than its synthesis. M. H. Zenk (University of Munich) studied about 200 plant species and found the two principal pathways of conjugation of IAA to be with aspartic acid and glucose. He believes that the conjugation products are not involved in auxin transport or in the auxin growth reaction but that they are, rather, detoxification products. In maturing fruits, where IAA is presumed to be no longer consumed in growth, Zenk found IAA to be first conjugated with aspartic acid. The indolic precursor of IAA then ceased to produce IAA and was converted to D-tryptophan, which was immobilized as malonyl-D-tryptophan. W. A. Andreae (Canada Department of Agriculture) found that in pea root tips the formation of indoleacetyl-aspartic acid regulates the uptake of exogenous IAA and the inhibition of growth by IAA. The conjugate was metabolically stable, was not lost to the external solution, and had no effect on growth. Clearly, then, conjugation may regulate the concentration of free IAA and hence of the growth-inducing auxin

available to the cytoplasm of some cells. Indole-3-acetamide, the conjugation compound of IAA and ammonia, may be formed as an artifact during some purification procedures. Isogai and his co-workers (University of Tokyo), using methods which, according to them, would not allow the production of an artifact, have isolated and characterized indole-3-acetamide from mung-bean seedlings. Conjugates of IAA were shown to occur in corn seed (B. I. S. Srivastava, Tuskegee) and possibly in culture medium in which excised tomato roots had grown (H. E. Street, University College of Swansea) and in pea seed (J. C. Gandar, Phytotron, Gif-sur-Yvette). Another metabolic product of exogenous IAA which may also occur naturally is 2-hydroxyindole-3-acetic acid (H. D. Klämbt, University of Bonn). The 2-hydroxy compound, like IAA, forms a glycoside.

In recent years another possible mechanism for the regulation of IAA concentrations in cells has been studied in a number of laboratories. This mechanism involves the inhibition or promotion of the IAA-destroying "IAA-oxidase" system by phenolic compounds that are found in wide variety in plant extracts and which appear to vary in quantity during ontogeny and in response to environmental stimuli such as photoperiodic induction. This type of study was discussed by M. Tomaszewski (Kornik, Poland). In general, polyphenols may promote auxin-induced growth by inhibiting the destruction of auxin, whereas monophenols inhibit growth by promoting the destruction of auxin. In developing pea buds, the effects of the two types of phenol may be observed to reverse as the bud passes from a phase in which auxin inhibits development to a phase in which it promotes it.

The movement of IAA, at least through young growing stems, is strongly polar in a basipetal direction. That this IAA flow, called transported auxin, may be displaced by unilaterally applied external stimuli, such as gravity or light, to produce tropistic growth effects was discussed by K. V. Thimann (Harvard). Using C^{14}-labeled IAA, he found that the asymmetrical distribution in a unilaterally stimulated organ was best demonstrated by allowing the transported auxin to diffuse into unilaterally applied agar blocks. Of interest, in connection with attempts to relate the auxin content of a tissue to growth, is the finding that the asymmetrical distribution of transported IAA in the upper and lower halves of a horizontally placed oat coleoptile was masked, almost completely, by the nontransportable or "fixed" IAA. The relevance of transported auxin to auxin-controlled growth was also stressed by W. P. Jacobs and T. K. Scott (Princeton). These workers have established a quantitative correlation in *Coleus* stems between the auxin arriving at the site of a growth reaction, through the transport system, and the growth or differentiation induced. They measured the transported auxin by diffusing it into agar at a cut surface. All of the growth activity of diffusates was found to be attributable to their contents of IAA. Not all methods for estimating the amount of auxin in a tissue lead to a correlation between auxin content and growth. C. L. Mer (Imperial College of Science and Technology) found the growth of the oat coleoptile and mesocotyl, under a variety of conditions, not to be correlated with the estimated auxin contents of extracts of whole tissues. Such a result could be due to the occurrence of auxin in tissues in a number of physiologically nonfunctional forms. A correlation between the amount of "free" IAA extractable from developing bean leaves and the rate of cell division was established by E. C. Humphries and A. W. Wheeler (Rothamsted Experimental Station).

Thus, for the auxin class of growth regulator, we can name the native auxin, IAA, but we cannot specify its route of synthesis or the means by which its synthesis is regulated. It appears that free IAA is the physiologically active form up to the site of the growth reaction. T. Yamaki (University of Tokyo) performed a subcellular fractionation, by differential centrifugation, of homogenates of oat coleoptiles and bean hypocotyls and found free IAA in the soluble supernatant. At present the best place to find free, physiologically active IAA seems to be in the transport stream, but virtually nothing can be said about the mechanism of action of auxin. At previous conferences in the series, the relationship between chemical structure and auxin activity was discussed at length, and although a number of theories on the nature of the reaction between auxin and its receptor site in the cell were advanced, no unanimity was reached. Also at previous conferences, the possibility of a direct effect of auxin upon the cell wall was proposed. However, fault has been found with all of the proposed mechanisms for such an effect. Moreover, the involvement of auxin in developmental processes other than cell enlargement makes it unlikely that the primary effect of auxin is upon a constituent of the cell wall. At the Gif-sur-Yvette conference one very tentative suggestion for a mechanism of auxin action at the molecular level came from the demonstration by A. W. Galston and his co-workers (Yale) of an in vitro complexing of IAA with RNA from peas. There is as yet no evidence for the occurrence of this reaction in vivo, but ribonuclease and actinomycin D, which alter the RNA status of a tissue, do inhibit auxin-induced growth.

Overall, therefore, little progress has been made in specifying the primary reaction of auxin at a molecular level. It is not even easy to specify auxin's action at a physiological level. It cannot be tied exclusively to any process of development. Whenever differentiation occurs, auxin appears to be required. The more specific roles in differentiation appear to fall to other classes of regulators, such as the gibberellins.

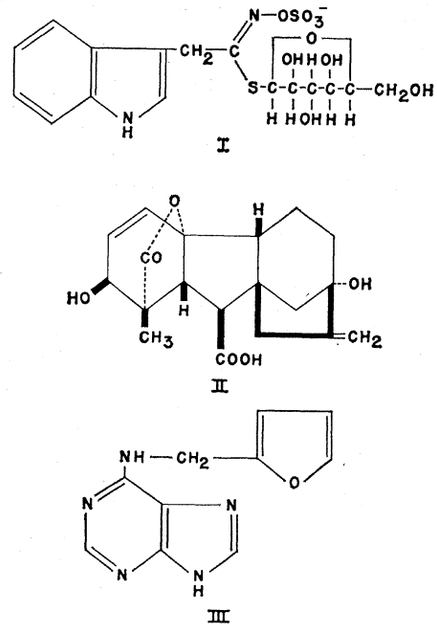

Fig. 1. Molecular structure of glucobrassicin (I), gibberellic acid (II), and kinetin (III).

Gibberellins

The Gif-sur-Yvette conference can be said to mark completion of the characterization of the best known gibberellin, gibberellic acid or gibberellin

A_3 (Fig. 1, structure II), which was isolated from fungal cultures but has been shown to occur in immature barley and other seeds (B. E. Cross and his co-workers, Imperial Chemical Industries Ltd.). There are ten known growth-inducing compounds in the gibberellin-A series, five of which have been detected in higher plant tissues. Compounds of this series contain 19 carbon atoms, and now the Imperial Chemical Industries workers have found, in their search for precursors of gibberellic acid in fungal cultures, four active compounds containing 20 carbon atoms. It is not certain whether these compounds are precursors of gibberellic acid, but one 20-carbon compound certainly is a precursor; this is (-)-kaurene, which has been known in plants for some time. In addition to the gibberellins, wholly or partially characterized, some plant extracts appear to contain compounds with gibberellin-like activity which do not have the chromatographic or the chemical properties of any known gibberellin. Such activity was detected by J. Kato (University of Oaska) in bamboo, by A. J. Vlitos (Tate and Lyle Station, Trinidad) in sugarcane, and by H. Harada (Phytotron, Gif-sur-Yvette) in hollyhock. There is obviously a need for some ordering of our knowledge concerning the native gibberellins. We need to ask whether one or many gibberellins function in the normal physiology of a plant, whether species differ with respect to the gibberellins that regulate their growth, and, as with the auxins, whether some of the native gibberellin activity is due to precursors or metabolites of the functional gibberellin. Questions should also be asked about the tissues used to detect gibberellin activity. Are, for instance, some of the mutants used in gibberellin assays "leaky" in having abnormal paths of gibberellin synthesis?

The physiological effects produced by exogenous gibberellin are many and various and doubtless often depend on the other classes of regulator endogenous to the tissue under observation. Possibly the simplest effect, mainly involving the induction and release of a specific protein, alpha-amylase, occurs in the germinating barley seed. The studies of L. Paleg (Waite Research Institute) have shown that gibberellin, produced in the embryo, moves to the aleurone layer, where it induces the production of alpha-amylase and regulates its release to the starch-bearing endosperm cells. The final result is the release of sugar. Inhibition studies suggest that RNA synthesis is not necessary for the response of the barley seed to gibberellin but that protein synthesis is. The barley seed, therefore, is a very promising system for tracing the primary site, or one of the primary sites, of gibberellin action.

In systems where the principal developmental process is either cell enlargement or cell division, gibberellin stimulates cell enlargement and inhibits, or has no effect upon, cell division. When a meristem is treated with gibberellin, however, the first observable effect may be a stimulation of cell division. This is the case when treatment with gibberellin induces flower formation in certain cold-requiring, long-day plants kept under noninductive environmental conditions. A. Lang and his coworkers (California Institute of Technology) have used two approaches in studying the role of endogenous gibberellins in such flowering responses in *Hyoscyamus, Samolus*, and *Bryophyllum*. First, synthetic compounds, such as (2-chloroethyl) trimethylammonium chloride, which inhibit gibberellin synthesis specifically inhibit the flowering process when these plants are held under inductive environmental conditions, vegetative growth being unaffected. Thus, gibberellin synthesis appears to be required for the flowering process to proceed. On the other hand, attempts to relate changes in the amounts of gibberellins that could be extracted to the progress of the flowering process were unsuccessful. Lang proposes a number of explanations for these contradictory results. (i) The gibberellins extracted may not have been those in which the critical changes in concentration were occurring. (ii) As with the auxins, diffusible gibberellin may be more closely related to growth than extractable gibberellin. (iii) Inductive conditions may produce gibberellin precursors active in flower formation but not active in the biological assays used to detect gibberellins.

The gibberellins have been studied intensively for less than 10 years, but the achievements have been great. The native gibberellins are at last partially characterized. They may be defined physiologically in terms of their interaction with auxin in the regulation of cell enlargement, and this function may be a key to understanding molecular mechanisms in the cell. On the other hand, gibberellin has functions in plant development, such as the function of determining the relative rates of cell division in zones of a shoot meristem, which may or may not arise from the molecular mechanism that produces cell enlargement.

Kinins

The third major class of regulators have been named the kinins. The animal physiologists have a prior claim to this name for a quite different class of compounds, and K. V. Thimann has proposed the name "cytomins" for the class of substances that regulate plant growth. The plant kinins are characterized by their ability to induce cell division in tissues which are otherwise unreactive under optimal conditions of nutrition. Kinins are active only in the presence of auxin. Using cell division tests, D. S. Letham (Department of Scientific and Industrial Research, Auckland), C. O. Miller (Indiana University), and G. Beauchesne (Plant Physiology Research Laboratory, Angers), have isolated kinins from extracts of the liquid endosperm of maize, but in quantities insufficient for conclusive identification. They agree that their kinins are derivatives of adenine, unsubstituted except on the nitrogen atom in the 6-position. Beauchesne believes the substituent to be an amino acid. Miller has evidence for a carboxyl group and some unsaturation in the substituent group. In the three cases, the compounds isolated account for only part of the cell-division-inducing activity in maize endosperm. The compounds appear to be close relatives of kinetin, 6-(furfurylamino)purine (Fig. 1, structure III), the substance responsible for the kinin activity of aged or autoclaved DNA.

The relationship of the kinins isolated by Letham, Miller, and Beauchesne to native kinins may be gauged from investigations of J. A. Zwar and his co-workers (Commonwealth Scientific and Industrial Research Organization, Canberra). Treatment of kinins from liquid endosperm of coconut with cation-exchange resins was found to produce various changes in the chromatographic properties of the kinins without loss of kinin activity. Letham and Miller used cation-exchange resins to purify their kinin, and thus the compound isolated by them is unlikely to be a native kinin. On the other hand, the resin treatment may have produced a change, such as the hydrolysis of a glycoside, which left the active nucleus in a chemically more amenable form.

Zwar and his colleagues also found that sublimation, which Beauchesne used as a purification step, may produce artifactitious kinins. It is possible that a conjugation between adenine and an amino acid could occur under conditions of sublimation. Thus, the compound of Beauchesne, also, may not be a native kinin.

The investigations just discussed were concerned only with the induction of cell division. F. C. Steward and E. M. Shantz (Cornell) have sought to resolve a related but more complicated phenomenon: the impressive growth of excised phloem tissue of carrot root when liquid endosperm of coconut is added to an otherwise defined medium. The main factors in coconut milk which act synergistically may now be specified as auxin, kinin, hexitols, and reduced nitrogen compounds. E. Maia (National Institute for Agronomic Research, Versailles) has isolated a carrot growth factor from tomato fruits. From another attempt to duplicate a particular growth phenomenon, in this case the growth of crown gall tissue, arose the investigation by H. N. Wood (Rockefeller Institute) of factors extractable from crown gall tissue of *Vinca rosea*, which induced cell division in pith tissue from tobacco stem. One of two factors, not yet obtained in pure form, has been tentatively identified as a compound of a nicotinamide-like residue and glucose sulfate.

So far, kinins have been defined and assayed in terms of their ability to induce cell division. It is also possible, in our present ignorance of their mode of action, to define and assay kinins in terms of their property of delaying the breakdown of protein in excised leaves through their effect upon RNA status. This property, which is usually manifested without accompanying cell division, was used by J. E. Loeffler and J. van Overbeek (Shell Development Company) as an assay for kinins in coconut endosperm. Evidence for three active compounds was obtained. The activity of coconut milk to tissue of the Jerusalem artichoke was found by A. Kovoor (University of Paris) to be due to its content of auxin and purines.

The characterization of native kinin should occur soon, since ways leading to the isolation of at least a derivative are clear. If, as seems likely, native kinin is a close relative of kinetin, the properties of kinetin should be a good guide to the properties of native kinin. Kinetin, for example, is required, together with auxin, for DNA replication, mitosis, and cytokinesis in dividing cells; it stimulates RNA synthesis in senescing tissues; and it interacts with auxin in regulating organ differentiation. The movement of kinetin within plant tissues is restricted, suggesting that the native kinin may be synthesized by the cells requiring it. Kinetin-like molecules are metabolized in plants along the normal pathways for purines. In whole plants, metabolites tend to move toward sites at which kinetin has been applied locally, and A. C. Leopold (Purdue) has made use of this tendency to create "sinks," at will, for metabolites for the study of leaf senescence. His observations, such as the observation that creation of a "sink" in the oldest leaf of a bean plant brings about senescence in younger leaves, support the concept that senescence is a correlative phenomenon. Senescence, being reversible, differs from the other developmental processes discussed here and it may therefore represent a different mode of influence of regulators upon development. Auxins and gibberellins, as well as kinins, are known to affect senescence. Leopold considers the effect of kinetin upon senescence to be due to an induced stimulation of mass flow of nutrient.

Inhibitors or Regulators

It is customary to label certain growth regulators as inhibitors. This name arises from their property of inhibiting auxin-induced enlargement of cells in excised stem tissues. But this property usually has no particular relevance to their suggested function in the plant. They are sought out as regulators of positive developmental processes such as dormancy or abscission; thus use of the term *inhibitor*, with its negative connotations, seems inadvisable, and terms relevant to the proposed physiological functions would appear to be more appropriate. In addition, inhibition of a complex process is too unspecific to be a reliable criterion for a regulator.

Dormancy regulators should be capable of inducing dormancy, and so far the only demonstrated case of this is in birch. P. F. Wareing (University College of Aberystwyth) has studied a substance which increases in birch leaves under dormancy-inducing, short-day conditions and when applied to leaves on twigs maintained under long-day conditions, induces dormancy of the buds. The substance has been iso-

lated from *Acer pseudoplatanus*, but in quantities too small for conclusive identification. Its spectral properties suggest an aliphatic or alicyclic substance, possibly a beta-hydroxy acid. There is no evidence of phenolic or other aromatic structure. Substances of apparently similar structure have been isolated from *Lupinus luteus* by K. Rothwell and R. L. Wain (Wye College), and from cotton fruits by F. T. Addicott and his co-workers (University of California); both substances are considered to be regulators of flower or fruit abscission. For substances with the same or similar structure to regulate processes as different as dormancy and abscission would appear to require that these regulators depend for their specific effects on the other classes of regulators present in the system. In this, of course, these substances are not unique. The workers mentioned have shown interactions between the substances they have isolated and added gibberellin, kinetin, or auxin.

Unclassified Regulators

There are a number of regulators which do not fit into any of these classes, and prominent among them, of course, are regulators of reproduction. Classically this is the province of florigen—the specific flower-forming substance. In general, however, the concept of specific organ-forming substances is no longer favored, and the concept of florigen has been of little help in investigations of the regulation of flowering, which, as is well known, results from a complex of partial processes. It is preferable to study the regulation of each of these processes, and it now appears that situations occur in which different partial processes limit flowering, and in which treatment with gibberellin, auxin, or kinin, depending on the situation, may cause flowers to form. But the evidence is against any of the above three regulators being the means by which the photoperiodically induced stimulus moves from the receptive leaves to the reaction center in the apex. Substances with this function have yet to be definitely located. D. L. Mayfield (Phytotron, Gif-sur-Yvette) has confirmed the earlier finding that extracts of *Xanthium* plants in which flowering had been photoinduced induce flowering in *Xanthium* plants held under noninductive, long-day conditions, whereas extracts of plants in which flowering had not been induced

do not have this effect. The active factor is water-soluble and acidic. A carboxylic acid of low molecular weight has been found by B. R. Voeller (Rockefeller Institute) to be the factor produced by fern gametophytes and to be active in inducing antheridia. A factor which has the same effect as vernalization of seeds has been isolated by T. Tomita (Tohoku University) from extracts of vernalized winter rye or radish. This factor and uridylic acid have very similar chemical properties, and both hasten the flowering of unvernalized plants, particularly in the presence of auxin.

A number of substances with characteristics of oxygenated terpenoids, which are cofactors with IAA in inducing root initiation on stem cuttings, have been found by C. E. Hess (Purdue) to occur in greater amounts in cuttings which readily form roots than in cuttings which root only with difficulty. Also among the as yet uncategorized regulators one may place the gibberellin-like substance extracted by Harada from hollyhock, the auxin-containing peptide found by Street in root-culture medium, and the lipid-like substance found by R. H. Roberts (University of Wisconsin) to quantitatively affect the growth of flowers.

It should not be inferred that the regulators which have not been fitted into a category represent the dregs of our experimental effort. On the contrary, they may represent a phase of growth regulation about which little is yet known. But it is unlikely that they act in isolation; rather, their effects probably result from interactions with other regulators. One substance which has the properties of a regulator and which interacts intimately and intricately with other regulators is ethylene. Its association with auxin is well known and, at the conference, was further documented by W. C. Hall and P. W. Morgan (Texas A & M), but an association with other regulators cannot be excluded. Auxin treatment may enhance ethylene synthesis, and ethylene treatment may enhance or inhibit auxin destruction, depending on the circumstances. An auxin-ethylene interaction can be demonstrated to regulate abscission, and S. P. Burg (University of Miami) has proved the general role of ethylene in regulating fruit ripening and flower fading. In mango fruits, however, the effect of ethylene may be counteracted, while the fruits are on the tree, by an inhibitor of ripening from the parent plant.

At this point we might ask whether all types of plant-growth regulators have been detected. It is not yet possible to answer this question. The classes of regulators already known are capable of producing a wide variety of developmental phenomena, but there may be other regulators still to be discovered. That some classes of chemicals may have been systematically excluded from consideration as regulators by the methods of extraction usually employed was suggested by J. Guern (University of Paris).

Analysis of Development

The structures of a number of classes of compounds which have been proposed as regulators of plant development have been described accurately or tentatively. The impression that plant development is the result of a developing pattern of interacting fields of these regulators has been built up. But this impression is far from ready to be put to the test. The design of such tests probably depends as much upon advances in the analysis of development, down to the molecular mechanisms for the inter- and intracellular regulation of metabolism, as on definition of the primary reaction sites of the regulators in the cell. At the conference, the analysis of development at a variety of levels was discussed. In an analysis of the contributions of cell enlargement and cell division to the growth, form, and maturation of organs and of their reactions to regulators or environmental stimuli, A. H. Haber and D. E. Foard (Oak Ridge National Laboratory) have demonstrated that the dominant process may be cell enlargement, quite independent of the occurrence or nonoccurrence of cell division, or of the total number of cells in a tissue. Within the process of cell division, D. Mazia (University of California) recognizes two levels of control, thus differentiating between the induction and the maintenance of cell division. The former is considered to be regulated by the induction of a cluster of enzymes, including DNA polymerase; the latter, by the state of the DNA. An analysis on yet another level has been made by J. Heslop-Harrison (University of Birmingham). He has been concerned with the mechanisms of events in development which are sequential, and in particular he has studied the transition from the vegetative to the floral state in meristems.

He proposes that gene complexes, associated with each step in development, are activated in a relay-like manner, the determinants being of high specificity and having short ranges of intercellular movement. He believes that growth regulators operate at a less specific level than these determinants because he finds them incapable of changing the course of a developmental sequence already in progress. Regulators can, however, entirely change the path of a sequence, as in changing the development of an appropriate flower from male to female. H. Stern (University of Illinois) cautioned those who speculate on the molecular mechanisms of differentiation about the general lack of facts concerning the inter- or intracellular regulation of metabolic shifts in multicellular organisms. For instance, Stern found in growing plants a species of DNA, of low molecular weight, quite distinct from genetic DNA. It has a high rate of turnover and is particularly active at times of metabolic shifts. This DNA species may represent a mechanism by which multicellular organisms effect gross shifts in metabolism, but it is not represented in any of the current models of such mechanisms.

If, as we believe, growth regulators have highly specific roles in determining plant development, elucidation of the means by which they control development probably awaits the approach to common ground of two lines of investigation—study of the primary reactions of the regulators and study of the molecular mechanisms for regulating metabolism in the cells of higher plants.

Note

1. The proceedings of the 5th International Conference on Plant Growth Regulation will be published by the Centre National de la Recherche Scientifique, a sponsoring organization of the conference.

Forthcoming Events

December

19–20. **Radiation Emergencies** in Medicine, Research and Industry, Chicago, Ill. (R. V. Wheeler, Argonne Natl. Laboratory, 9700 S. Cass Ave., Chicago)

26–28. American **Geophysical** Union, western natl., Boulder, Colo. (W. W. Kellogg, Rand Corp., 1700 Main St., Santa Monica, Calif.)

26–30. American Assoc. for the **Advancement of Science**, Cleveland, Ohio. (R. L. Taylor, AAAS, 1515 Massachusetts Ave., NW, Washington, D.C. 20005)

27–29. American **Economic** Assoc., Boston, Mass. (H. F. Williamson, AEA, 629 Noyes St., Evanston, Ill.