PLANT GROWTH AND GROWTH HORMONES*

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THE GROWTH behavior of living organisms has received much attention in recent years as the result of important discoveries concerning the control of growth processes. The discovery of the importance of endocrine glandular secretions in the growth and development of animals, the discovery of vitamins as necessary accessories in the nutrition of animals and man, and the discovery of growth hormones in the tissues of plants have all been powerful incentives to the investigation of the processes of development.

Certainly one of the most interesting and amazing characteristics of the living organism is its power of continuous and harmonious development from the simplest beginning to the complex, highly organized and fully grown individual. Most of our higher plants and animals begin life as a single very slightly differentiated cell, the ovum or egg. This egg cell must usually be fertilized by union with another equally simple cell, the sperm. After the fertilization process has been completed, the egg is no longer quiescent, but begins the process of development by a series of cell divisions. As new cells are formed, the body enlarges, and observation shows that the cells begin to arrange themselves after an orderly pattern belonging to the species involved. Cell differentiation occurs, and tissues and organs emerge in an orderly series of events that excites the wonder and admiration of every philosophical biologist. The course of development continues until the organism reaches its full adult size and form, in accordance with its specific inheritance. It is hard to imagine that the towering redwood and the giant Sequoia were once upon a time housed within the confines of a single undifferentiated cell of microscopic size. And it is indeed just as difficult to think of the elephant, or the horse, or of man himself as beginning life with so simple an organization.

When the process of cell division initiates development, one can then observe that every stage of development prepares the way for the next one following. In the case of plant growth, which alone is the concern of this discussion, the unfolding of the organism occurs usually in two cycles of growth. The first cycle of development extends from the fertilization of the egg to the close of the development of the seed. This is the embryonic phase of development, and the cycle ends when the seed dries down and becomes dormant. In this stage it is resistant to conditions of the environment as long as it remains approximately air dry. Even the embryo plant in a seed is a complex being as compared to the fertilized egg. It has a very short root primordium, a short stem, in many instances two leaves stored full of food (the cotyledons), some embryonic leaves at the upper end of the stem, and tissue systems representing the epidermis, cortex, and vascular regions. It is all in miniature form, still far from the complexity of the adult, but vast progress has been made toward the ultimate goal.

Planted in warm moist earth, the

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embryo resumes its activity, enters upon the second cycle of growth, and in orderly succession root system, stems, leaves, flowers and fruit come into being, controlled by the laws of life and heredity, so that each individual faithfully repeats the pattern of its own species. In size, form, and structure, and in the harmony of its development it is recognizable as a member of a definite species, and unlike all other species.

The control of the growth processes of organisms must be affected in part by external forces, and in part by internal factors. We are all familiar with the fact that deficiencies of moisture, necessary elements, light, temperature, etc., modify growth rates and the total growth of the individual. But they act through modification of internal conditions such as the concentration of materials, activity of enzymes, rate of respiration, etc.

The first suggestion that growth responses in plants might be under the control of internal chemical substances was made by Charles Darwin in his book, *The Power of Movement in Plants*, published in 1880. He observed the growth responses of grass coleoptiles to one-sided illumination, and noted that the perceptive and responsive regions of the plant were separated by some distance, and that the stimulus must be transported through the tissues in some manner. The transport of the stimulus was much too rapid for mere diffusion, but Darwin thought there must be some substance which was acted upon by light, and which was capable of rapid transmission of a growth stimulus to the lower part of the leaf sheath.

The term "hormone" was introduced into animal physiology by Bayliss and Starling about 1902, to designate the chemical agents of growth control originating in the endocrine glands. Gradually the use of the term crept over into plant physiology, even before the actual existence of plant growth hormones had been fully demonstrated. The European workers followed in the footsteps of Charles Darwin, and made a great many studies of the responses of the oat coleoptile. In 1910-1911 Boysen Jensen proved the existence of a chemical regulator of growth in the grass coleoptile, but apparently the time was not ripe for the full significance of his work to be appreciated. Many other investigations followed his work, piling up evidence more and more convincing, until in 1928 Went's thorough studies made doubt of the existence of a chemical growth hormone in the oat coleoptile no longer possible. American workers occasionally used the hormone concept to explain growth behavior when they could think of nothing better to suggest. Both growth promoters and growth inhibitors were postulated to explain the behavior of lateral and terminal buds. Appleman's studies of the sprouting of potatoes in 1918 indicated that terminal eyes of the potato inhibited the sprouting of other eyes on the potato, and that the central bud of any given eye suppresses the growth of the lateral buds of the same eye. Removal of the terminal eye, or terminal bud, released the other eyes or buds from restraint.

Jaques Loeb made many interesting studies of Bryophyllum during the last 10 years of his life. Many of the features of geotropic response and regeneration in Bryophyllum were explained on the basis of the distribution of growth substances or hormones. At the time, the idea seemed far-fetched; but at the present time he appears very conservative in comparison with hormone enthusiasts of today. Reed and Halma studied growth in pear trees, and presented telling evidence for the existence of growth inhibitors in the terminal parts of the branches which, flowing down the branches, prevented the lateral buds from developing. Horizontal branches produced sprouts from the upper side of the branch, but sprouts originating on the lower side of the branch grew poorly. The suggested explanation was that the growth inhibiting substance settled into the ventral side of the branch and retarded the growth of sprouts on that part of the stem.

With the discovery of means of detecting growth substances, and of measuring the relative concentration of the hormones by biological assay methods in 1928 (Went), powerful impetus was given to the search for the hormone as a chemical entity. At the time of Went's discovery, no one had the slightest conception as to the nature of the chemical substance responsible for the growth curvatures of oats. Many substances were tested for the presence of growth promoting hormones, and it was soon found that yeast extract, malt extract, and culture media upon which certain fungi and other microorganisms had grown, contained such substances. In 1931 it was found that human urine was a rich source of growth hormone, and during the period from 1931 to 1935 Kögl and his co-workers obtained enough of the growth substance that they could purify it, and determine its chemical constitution. They found, indeed, not one, but two substances, which have been named auxin a and auxin b. The former is auxentriolic acid, and the latter auxenolonic acid. They are relatively weak acids, and are found widely distributed in living plant tissues.

During the four years since these acids were completely identified and named, hundreds of investigations have been made, and the application of the hormone concept to growth control has been extended to cover many phases of development. Such processes as cell division, cell enlargement, and cell differentiation are made subservient to specific hormones. The growth of the tops of plants is claimed to be controlled by top-forming substances originating in the root; and the root development is said to be controlled by root-forming hormones manufactured in the tops of the plant. Flower buds are initiated by hormones manufactured in the leaves under definite conditions which cause the production or the accumulation of the hormone, which is then carried to the region where buds could arise. The hormone initiates the bud, after which the ordinary nutrients, carbohydrates, amino acids, etc., provide for their growth. The afterripening of seeds during chilling, the breaking of dormancy of twigs in late winter, the production of dwarf forms of corn, the rooting of cuttings, the enlargement of fruits, the healing of wounds, the geotropic and phototropic adjustments of plants, and many other growth phenomena have now been given a "hormone" explanation. One could almost say that the entire growth of the plant, from start to finish, is controlled by a complicated set of chemical factors not nearly all of which are known at the present time.

The current definition of a hormone is so broad that it might include almost any chemical factor. A hormone is a substance which, being produced in one part of the organism, is transported to another part of the organism and there influences a specific physiological process. That definition, however, seems to make most of the transportable substances of the plant body play the part of hormones. Would not a sugar, produced in the leaf, and then transported to the root where it influenced the building of cell walls, fulfill the requirement of the definition of a hormone? Or an amino acid, formed in the root of an apple tree, and then carried to the stem apex where it influenced the formation of new protoplasm; would it not also be a hormone? What I am trying to say is that there does not seem to be so very much difference between hormones and the ordinary nutrient chemicals of the plant body, except that the hormones are present in mere traces.

As time goes on, more and more substances are found which in one situation or another promote growth, or inhibit growth, or initiate differentiation. Besides auxin a and auxin b, such substances as vitamins A, B_1, B_2, and C, biotin, pantothenic acid, nicotinic acid, indole acetic acid, thiazole, pyrimidine, oestrone, etc., have been mentioned as possible plant hormones. The number of these compounds may ultimately be recognized as legion, just as we recognize that the enzymes of the cell are very numerous.

Just what are we moving toward? What interpretation is to be made of this great mass of information which is accumulating as the result of world-wide interest in growth phenomena and hormonal control of development? There seems to be a trend toward a rational point of view which deserves to be emphasized. In some instances plants have been found to undergo growth stimulation when thiazole is supplied, in others when pyrimidine is supplied, and in still others neither alone is active, but vitamin B_1 must be administered. The obvious explanation is that some organisms manufacture their own pyrimidine, and if given thiazole can produce vitamin B_1. Others can make their own supply of thiazole, and if furnished pyrimidine they develop vitamin B_1. Still others make neither pyrimidine nor thiazole in sufficient quantity, and these forms must be given vitamin B_1 already formed, to induce growth.

Similarly, vitamin C is present in some organisms to such an extent that adding more of it produces no additional result in growth. Other organisms do not produce vitamin C readily, and if these are given vitamin C it provides a growth stimulus. The obvious conclusion is that we are dealing with problems of nutrition on the one hand, and possibly with catalysis on the other.

If hormones become an actual part of the organized structures of the plant body, as may easily be the case with some of them, they are to be thought of as foods in the same sense as carbohydrates and other macronutrients. If hormones speed up chemical reactions, or change the equilibria of chemical reactions within the tissues, their action is no different from that of other organic catalysts, the enzymes.

It seems to me that we are dealing with a situation not different in principle from that which exists with reference to the inorganic elements needed by living organisms. Some of the elements, such as carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, and mangesium are known to build substance in the plant. Others, such as potassium, manganese, iron, copper, zinc, boron, molybdenum, silicon, etc., are not certainly structural elements, but they have great significance in the use of material, in respiratory and other catalytically controlled processes. Until recent years it was not known that the trace substances, the micro-elements, as they are often called, are necessary for plant growth. When our chemicals were made pure enough, however, and when our techniques became sufficiently rigid it was not difficult to prove the necessity of the trace elements for life and development.

Now we have come on to the same situation with reference to the organic substances. Formerly we discussed only carbohydrates, fats, and proteins with reference to nutrition. When physiological technique had developed to the point where deficient rations could be prepared, the need of vitamins was discovered. And when the endocrine glands were extirpated, the need of the endocrine hormones became obvious. With the discovery of assay methods, the study of trace organic substances in the nutrition of plants became possible. The substances called hormones today are not a homogeneous group of chemicals. They do not form a class of compounds. They are metabolites of various kinds. Some are nutritive without doubt, others are catalytic, just as in the case of the inorganic elements.

The development of the hormone techniques is giving us the first opportunity we have had to study the influence of trace organic metabolites upon growth and developmental processes. It seems obvious that the amazing perfection of the specific developmental processes which carry any given organism through its life cycle is brought about by the production of specific trace metabolites, chemical inciters, inhibitors, correlators of many different kinds. Each species probably has some unique kinds, or unique combinations of trace chemicals which set the specific pattern of growth. It is not possible at the present time to define these unique specific substances, or unique combinations of them. The work is still too general. The great excursion into this field, however, has thrown brilliant light upon the growth processes of plants, and upon their developmental behavior. A sound foundation is being built for other and far-reaching advances which may ultimately provide controls for plant growth which man can operate at will. If we know under what conditions certain trace metabolites are formed, and what responses the plant makes in growth and development when these trace metabolites are present in sufficient concentration, we are only a step away from the complete control of the organism's development. We are moving steadily forward toward this goal, with all indications that practical control will be achieved in the not distant future.