27 March 1959, Volume 129, Number 3352 SCIENCE

CURRENT PROBLEMS IN RESEARCH

Gibberellins: Stimulants of Plant Growth

Thirty years' work in Japan has initiated world-wide research with a novel group of plant hormones.

Bruce B. Stowe and Toshio Yamaki

In the twenty-odd years since the potentialities of the auxins were first widely recognized, no plant hormones have excited as much botanical and horticultural interest as have the gibberellins. These compounds strikingly stimulate the growth of many plants, promote flowering in some cases, and cause a variety of other interesting morphological and physiological responses. Their use opens up new avenues of approach to botanical problems, and many of their effects promise to be of economic importance in agriculture and horticulture. In this brief introduction to the work being carried on with the gibberellins no attempt has been made to completely cover the rapidly growing literature; papers have been cited only as they seemed especially pertinent. A comprehensive review through 1956 is available (*1*), recent summaries have been published by the British workers (*2, 3*), and some manufacturers of gibberellins have prepared useful bibliographies which include recommended methods of treatment (*4*). Wittwer and Bukovac have evaluated in detail the implications of this development for agriculture and horticulture (*5*). Bibliographical difficulties in this field, arising from the fact that much of the literature was to be found only in Oriental or rare journals, have now been greatly alleviated through the praiseworthy efforts of Stodola, who has assembled in one source abstracts of all papers relating to the gibberellins published prior to 1958 (*6*).

Historical Background

Oddly enough, despite the recent burgeoning of interest in the gibberellins, these compounds are not new but date from the same period as the first work on other plant hormones. Their discovery can be credited to the late Eiichi Kurosawa, a Japanese plant pathologist who was working in Formosa on diseases of rice. One rice disease, known in Japan for more than a century and a half, especially attracted his attention because of the peculiar fact that *diseased* plants often became 50 percent or more taller than their healthy neighbors in the initial stages of the malady. From this characteristic the colloquial name "*bakanae*" (foolish seedling) disease was derived. The malady is due to an ascomycetous fungus whose sexual form is known as *Gibberella fujikuroi*; the more common asexual stage is known as *Fusarium moniliforme*.

Kurosawa reasoned that some metabolite of this fungus might be responsible for the stimulated seedling growth, and in 1926, after several failures, he succeeded in obtaining a filtered fungal extract which caused growth stimulation of both rice and maize seedlings without any accompanying infection by the fungus (*7*). Kurosawa examined this response and showed that it was brought on by a heat-stable substance found only in media in which the bakanae fungus, but no other fungi, had grown. These observations were soon confirmed by several other investigators in Japan, and they and Kurosawa delineated the gross chemical properties of the active material. Much of their work was published in Western languages, and some of it reached abstracting journals, but it unaccountably failed to arouse interest outside of Japan. This is especially difficult to explain when it is realized that the auxins, another group of hormones which had also been detected in fungi, were attracting wide attention at the same time (*8*).

Upon his return to a new position at the Imperial Agricultural Experiment Station in Japan, Kurosawa encouraged Teijiro Yabuta (Fig. 1), who had been studying fungal metabolism, to investigate the problem of the active material in *Gibberella* cultures. Yabuta took this task with him to the University of Tokyo, where he and his assistant Kannbe sought to isolate the bakanae substance. Their investigation was hindered by the presence of a strongly growth-inhibitory material, and it was further retarded by Kannbe's untimely death. But in 1930, the growth inhibitor (fusaric acid) was isolated, and later Yabuta was joined by Takeshi Hayashi and Yusuke Sumiki (Fig. 1) in further work on the growth-promoting substance. In 1935 Yabuta announced the isolation of a crystalline active material, which he named gibberellin after the fungus from which it was isolated (*9*). Since that time these three investigators and their collaborators have published over forty papers on the bakanae substances and related topics.

Investigations of the chemical nature and biological properties of gibberellin were immediately begun. But due to the difficulty of culturing sufficiently large quantities of the fungus, the work was limited by the small amounts of the pure material isolated. And due to the war,

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Dr. Stowe is lecturer on botany at the Biological Laboratories of Harvard University, Cambridge, Mass.; Dr. Yamaki is associate professor in the Biological Institute, College of General Education, University of Tokyo, Tokyo, Japan.

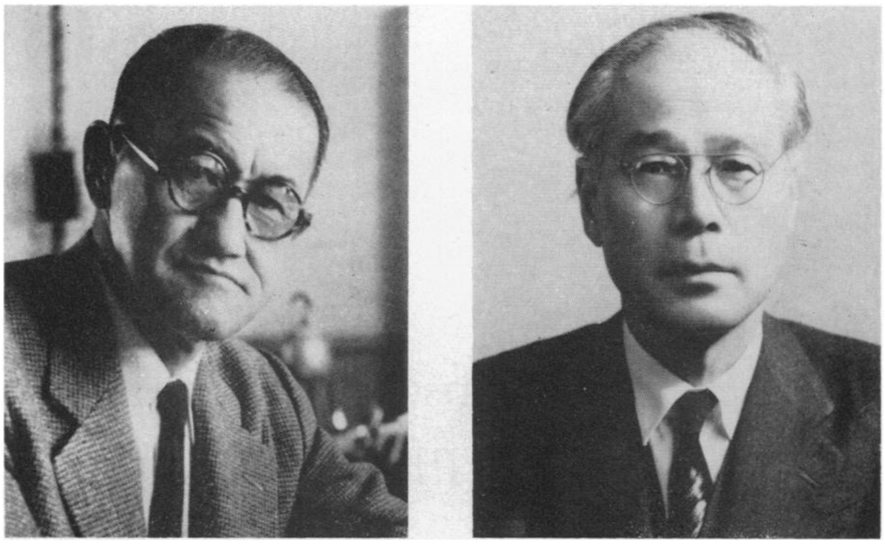

Fig. 1. (Left) Teijiro Yabuta, who initiated the research at the department of agricultural chemistry of the University of Tokyo that led to the isolation and characterization of gibberellin, and (right) his collaborator and successor, Yusuke Sumiki.

publication of the results obtained failed to reach Occidental readers. However, the war also stimulated the great development of techniques for the mass culture of fungi in antibiotic production. And in the meantime it had become clear that hormones other than the auxins were involved in plant growth and development. Thus, when abstracts of the Tokyo work first became available, in 1950, industrial facilities and scientific interest were ripe to exploit the Japanese development.

In the United States, the first exploratory work on the gibberellins was performed at the biological warfare center at Camp Detrick, Maryland (*10*). Large-scale isolation of the materials was started shortly thereafter by Stodola's group at the U.S. Department of Agriculture (*11*). Simultaneously, and quite independently, Borrow, Brian, and others at Imperial Chemical Industries in Britain undertook developmental work (*12*). These workers made available for the first time relatively large quantities of gibberellins for experimental purposes. Since then, numerous pharmaceutical firms all over the world have adapted their antibiotic equipment to gibberellin production, and the compounds are now becoming readily available.

Chemistry of the Gibberellins

The Japanese studies of the biologically active principle led to the first clue to its basic structure when they established that its degradation products included derivatives of the aromatic hydrocarbon fluorene (*13*). But, although this was not known to the Tokyo group at that time, their isolated gibberellin A, albeit crystalline and in other respects apparently homogeneous, was actually a mixture of several closely related compounds, and they were unable, through their studies, to fix a definitive structure for gibberellin A. On the other hand, the British fermentations produced a different, but homogeneous, product, which the Imperial Chemical Industries group named gibberellic acid (*13*). The first American fermentations yielded two gibberellins, one named gibberellin X and another assumed to be the same as the Japanese gibberellin A (*11*).

These discoveries spurred the Tokyo group to reexamine their material, and they found that it could be separated into three gibberellins—A_1, A_2, and A_3 (*14*). Recently, another, A_4, has been isolated (*15*). Gibberellin A_3 proved to be the same as X and gibberellic acid; A_1, the same as the American A. Thus, there are four clearly established substances possessing gibberellin biological activity which have been found in fungal extracts, and there is evidence that other compounds are present both in fungal extracts and in higher plants (*1, 16*). The separation of these chemically similar compounds remains difficult; column chromatographic methods have been proposed (*17, 18*). Recent reports indicate that these gibberellins do not act alike in biological systems (*19, 20*). For that reason, it has been suggested (*1*) that the commonly used abbreviation GA be made more precise by the addition of subscript numerals—that is, GA_1, GA_2, GA_3, and GA_4.

The best characterized gibberellin is gibberellic acid (all workers have now accepted this name for GA_3). The extensive British work has led to the proposal, by Cross *et al.* (*21*), of the structural formula shown in Fig. 2. This is derived by extrapolation from the degradation product gibberic acid, whose molecular configuration seems to be well established (*22*). The positioning of the lactone group on the cyclohexene ring has been questioned by the Japanese workers (*23*), but a recent British paper answers their objections and seems to assure that the structures shown in Fig. 2 are definitive (*24*). Agreement has been reached on the placement of the secondary hydroxyl (*25*). The complex lactone ring seems to be essential for biological activity, since potency is lost when it is opened and gibberellenic acid is formed (*26*). Mild acid conditions lead further to the evolution of carbon dioxide, aromatization of the cyclohexadiene ring, and Wagner-Meerwein rearrangement to gibberic acid (*21*). Since gibberic and gibberellenic acid are so easily produced from gibberellic acid, they are common contaminants of the commercial material, their presence being betrayed by ultraviolet absorption (*27*). Gibberellic acid's ready aromatization after lactone cleavage and its over-all structure seem unique; no previously known natural products or synthetic compounds are closely related. Mono- or diacetylation of the hydroxyl groups has little influence on the hormone's action, but it has been found, in the few tests so far reported (*1, 14, 20*), that esterification of the acid group greatly reduces or removes biological effectiveness.

The relationships of the other gibberellins to gibberellic acid are being actively investigated. Gibberellin A_1 has been shown to be dihydrogibberellic acid (*17, 23*), as it is produced by the reduction of the cyclohexene bond in gibberellic acid (Fig. 2). It is the only gibberellin so far identified in higher plants (*16, 28*). Gibberellins A_2 and A_4 are chemically closely related to GA_1 and GA_3, as is a gibberellin (bean factor II) recently isolated from higher plants (*16*), but their structures cannot yet be stated with any certainty. No information on the obviously important stereochemistry of these complex, optically active molecules is yet available. Their metabolism is not known, but acetate and mevalonic lactone have been implicated as precursors of the fungal biosynthesis (*29*).

Methods of chemical analysis and paper chromatography have been developed (*14, 26, 27, 30, 31*), but they are as yet neither very sensitive nor specific, and they are not capable of separating all the gibberellins.

Stem Length

The most typical action of gibberellin on higher plants is an enhancement of stem length. Growth promotion is restricted to young tissue; mature tissue is not influenced. Often the number of internodes is unchanged by treatment, but the plant becomes much taller and, in the extreme, may become too spindly to support itself effectively. Internode elongation can be so great that bushy plants may grow like vines as a result of gibberellin treatment (*3, 32–34*). Even plants such as lettuce, which has never been known to show the twining habit, have become vines (see Fig. 3) (*35*).

A very striking case of stem growth is the remarkable effect of gibberellin on dwarf plants, which was discovered by Brian and Hemming (*36*). These workers found that dwarf peas could be brought to the growth rate of standard peas through the application of less than a microgram of gibberellic acid per plant. Phinney has extended this finding to show that certain single-gene dwarf mutants of maize will grow to normal height with gibberellin applications (see Fig. 4) (*37*). The response is remarkably sensitive (0.001 microgram per plant is sufficient for a detectable reaction) and can be used for bioassay. A spectacular difference of several hundred percent between treated seedlings and controls may be observed in many dwarf plants a few days after one small application of gibberellin.

The effect on dwarfs points up one of the major problems concerning the action of gibberellin. Not all dwarfs respond, and—more serious—not all nondwarf varieties within a given species react alike. Furthermore, there are as yet unexplained differences in response with the age of the plant (*38–40*), although it can be said that in most instances the growth of young plants is the more strongly stimulated. An understanding of this unpredictable effect of variety and age is necessary before gibberellins can be generally applied for agricultural purposes. Still, the promotion of internodal elongation promises to be of some practical use. For example, gibberellin treatment has increased the yield of hemp (*41*) although not the fiber length (*42*). If fiber length can be influenced in crops like flax or cotton such treatment could be of considerable economic value.

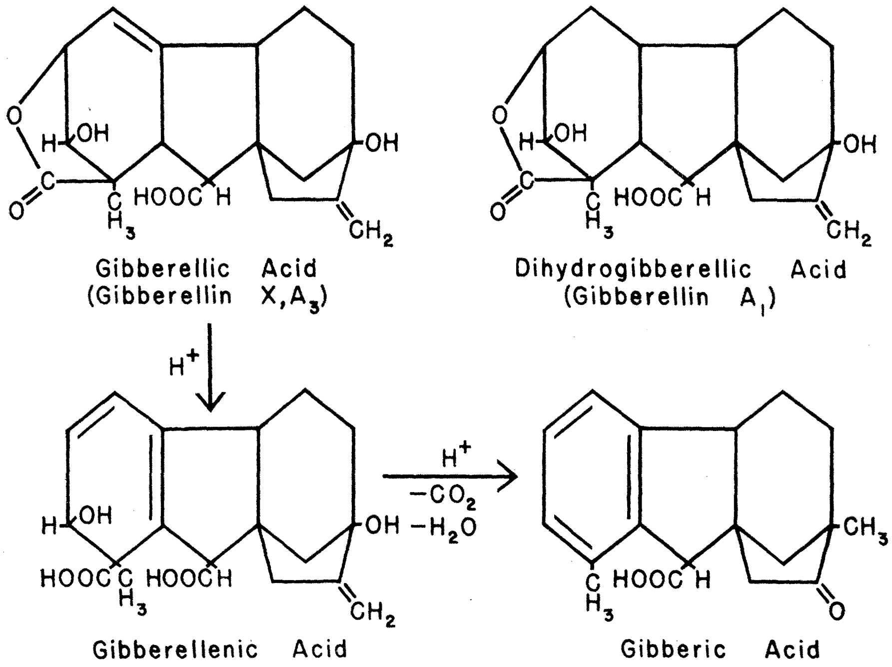

Fig. 2. Molecular structure of gibberellic acid (*21*) and dihydrogibberellic acid (*17*) with the acid-catalyzed degradation sequence of the former compound (*26*), as substantiated by work in Britain (*24*).

Flowering

Another exciting property of gibberellins is their ability to induce flowering in some plants. The requirement of specific day length which must be met for many plants before they will form flowers has been a subject of intensive research. No chemical or isolated hormone, with a few specialized exceptions, had been shown to induce flowering when day lengths were clearly noninductive until Lang made the arresting discovery that gibberellic acid could stimulate flower formation in *Hyoscyamus* in environments under which flowers otherwise never would have formed (*43*). Figure 5 illustrates a similar experiment. This discovery has been extended rapidly to many individuals of the great class of plants which normally flower only when exposed to long days (*44, 45*), as well as to some plants in which vegetative shoot growth is influenced by day length (*46–49*) (see Fig. 6).

Earlier flowering after gibberellin treatment has been observed in plants in which flowering is normally photoinduced as well as in some species that are not sensitive to day length (*50, 51*). In the latter case, flowering may result as a consequence of the plant's reaching optimum size more quickly. The effects on the flowers themselves are less predictable. After treatment, chrysanthemums were larger and bloomed earlier (*52*). In a plant like geranium, with an inflorescence composed of multiple florets, gibberellin nearly doubles the diameter of the inflorescence, largely because of its effect on the elongation of the floret stalks; gibberellin has less effect on the florets themselves (see Fig. 7) (*53*). But in hydrangea, fewer flowers are formed (*54*).

Interestingly enough, gibberellin treatment of the other great class of plants in which flowering is photoinduced—those requiring short days to flower—has no simply explained effect on their flowering. In fact, it is now clear that in some short-day plants gibberellin can inhibit flowering (*55*), but in another short-day plant it increases the amount of flowering without being able to initiate flowering (*56*). This exposes not only an important biochemical distinction between long- and short-day plants but reveals unexpected differences in the latter class which are providing an incentive for further research.

Flowering may also be limited, as in biennials, by the need for cold treatment (vernalization). Here termination of dormancy requires exposure to a definite degree and period of low temperature. Lang discovered that this requirement could also be eliminated by gibberellin (44). However, this is not invariably the case, since overwintering grains and other plants have not yet responded satisfactorily (44, 57); a light requirement may still have to be met (58), and the flower response may be abnormal when it occurs (59). Wittwer and Bukovac have pointed out that there still seems to be a specific temperature limit, although it may be raised by gibberellin treatment (45, 60). Also, plants may revert to the rosette habit when treatment is stopped (33). Thus, further studies of the modified temperature requirement, of interaction with light treatments, of varietal differences, and of flower abnormalities are required before biennials can routinely be expected to yield seed crops the first year.

Other types of cold-released dormancy are known, as in some cases of shoot and bud growth, fruit growth, and seed germination. Some plants cease their growth in the fall and do not resume it until a definite cold treatment has been applied. Gibberellin applications have been successfully used to restore cold-requiring epicotyls (61), shoots (62), fruits (63), and dormant tree buds (64) to active growth with partial or complete elimination of the cold requirement. It has been suggested that some varieties of peach and tomato could be grown further south with such treatment (62, 63). Similarly, grass can be induced to sprout during cold periods during the spring or fall when normally no growth would occur (65). In another type of dormancy, sprouting of tubers before the customary rest period after harvest has expired has been initiated (66), and such treatment is effective even if it is applied to the parent plant before harvest (67).

Seeds

The dormancy of seeds is a related problem. Many seeds require a period of "afterripening," or cold treatment, or exposure to light, or some other factor or combination of factors before they will germinate. These requirements have been eliminated in certain cases by the action of gibberellin, which annuls the light requirement of lettuce (68) (see Fig. 8) and tobacco (69) seeds, the cold requirement of peach seeds (62, 70), and the light and stratification requirements of *Arabidopsis* seeds (71). On the other hand, Bünsow and von Bredow have shown that the light requirement is only partly eliminated in *Kalenchoë* seeds (72) and that a marked interaction of gibberellins with kinins exists (73). This suggests that new insights into the mechanism of germination will be forthcoming from such studies.

This development has immediate horticultural utility, decreasing as it does the waiting period between generations of plants, and the use of gibberellin seems likely to become a routine practice. Nondormant seeds are also affected; Hayashi showed long ago that gibberellin accelerates germination (1). This acceleration is so pronounced that it has been suggested that increase in seed respiration could constitute a bioassay for gibberellin (74). The percentage of germination is also increased (33, 73). Treatment causing a decrease in the time a young plant stays underground could be beneficial to many plants which are especially susceptible to disease at that time (see Fig. 9) (75). If weed seeds were similarly treated, with more uniform germination as a result, a larger percentage of the potential weed population would be available at one time for eradication (2, 70, 76).

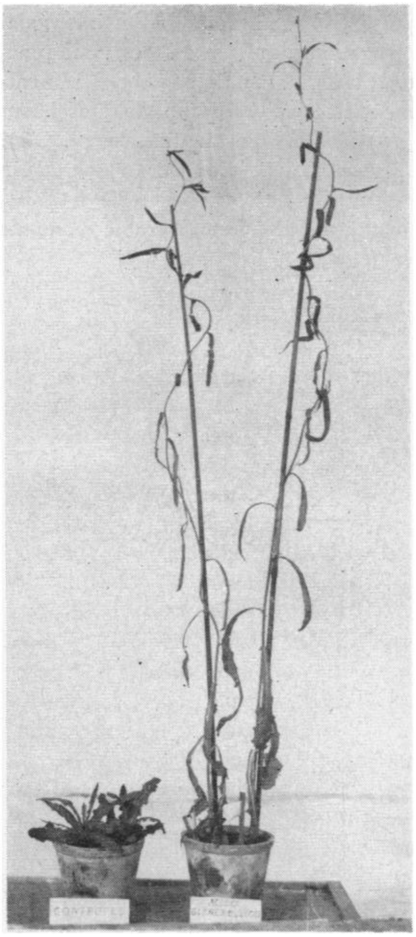

Fig. 3. Plants of lettuce (*Lactuca scariola*) maintained under short-day conditions. Those on the right received three drops of a $10^{-4}M$ gibberellic acid solution every third day and assumed a climbing habit (35). [F. Lona, University of Parma]

Fertility

The germination and growth of pollen is also influenced by gibberellin (77, 78), as is the induction of parthenocarpy (fruit formation without flower fertilization) (79). The production of seedless fruit or the enhancement of yield by means of gibberellin are therefore possibilities, and promising effects have been reported for grapes (80) and tomatoes (51). It is not necessary that the flower itself be treated; male-sterile tomatoes set fruit when gibberellin was applied to several parts of the plant or even to the soil (81). This effect is not without its complications, however. Early work indicated reduction of fertility (1, 59), reduction in number and amount of abscission in flowers (54, 82), and lowered grain yield (42) after gibberellin treatment, and a recent report emphasizes these difficulties (83).

Gibberellin-induced promotion of male sterility in hybrid maize has been reported (84), and in this case such sterility could be of economic advantage, but in seed crops this possibility could prove a serious deterrent to crop treatment with gibberellin for some other purpose. Kinoshita *et al.*, however, obtained a pronounced increase in the yield of several kinds of beans in many of their experiments; in some varieties of maize and sweet potatoes the yield was increased, in others it was reduced (85). Experiments in Michigan on beans and maize were less promising (86). It is apparent that the time of the treatment and the variety of the plant are very important determinants of the results.

Cell Division

In its effect on parthenocarpy and in breaking dormancy, gibberellin seems to be stimulating cell division. An increase in cell division in less than 24 hours has been shown in *Hyoscyamus* induced by gibberellin to form a flower stalk (87). In plants with formed internodes, some studies indicate that increased growth is due to cell elongation (1, 87a), another implicates cell division (87b), and others report both are increased (87c). Promotion of plant growth and cell division in tissue culture has been reported (*88, 89*), but so has inhibition (*90*). Nickell emphasizes that tissue cultures show diverse responses to gibberellins (*91*). In woody plants a definite promotion of cambium cell divisions has been reported (*92*); the xylem formed lacks vessels unless auxin is also applied, when there is vigorous formation of apparently normal wood (*93*). Cytological observations are of interest in that they show little evidence of cell-division abnormalities or other toxic effects (*1, 78, 88*), but chromosome appearance changes (*94*). Gibberellin, then, cannot be said to act simply as a promoter of cell division or cell elongation; its activities have a more complex basis. It must be noted that gibberellins do not produce the gross deformities and callus formation in plant tissues that can be brought about by auxin or kinetin (*42, 66, 95*).

But unlike auxin, gibberellins can have marked effects on leaf expansion (*1, 42, 96*). Influence on both size and shape is reported (*51, 97*), and an intriguing effect is the production of "juvenile" leaves, formerly known only on young plants, in *Hedera* (*34*) and their more rapid disappearance in *Eucalyptus* (*98*). The promotion of thorn growth on a cactus is also reported (*99*). Leaf expansion has long been a subject of research, and a considerable advancement of our theoretical understanding of the processes involved may be expected to result from further study of these phenomena. Already Kuraishi and Hashimoto have cited data (*100*) which betray an interaction of gibberellin and kinetin in leaf expansion; Humphries' experiments are interpreted differently (*38*). A relationship to the long-known effects of light is indicated (*101*).

Fig. 4. Effect on normal and on a single-gene dwarf mutant of maize of 100-µg doses of gibberellic acid applied at 1- to 5-day intervals during development. Similar experiments have been described (*37*). [Bernard O. Phinney, University of California, Los Angeles]

Agriculture

Applications to leafy crop production are naturally of interest, but although experiments with tea (*1, 102*), mulberry (*103*), and tobacco (*1, 104*) have been reported, no definite conclusions about agricultural utility may yet be drawn from these studies. It should be pointed out that leaf abscission, strongly influenced by auxin, is a distinctly different process and is not affected by gibberellin in the usual test plants (*33, 66, 95, 105*), although leaf abscission has been reported as a delayed effect of treatment (*54*).

A major effect of gibberellins still to be considered is the considerable increase in the dry weight of treated plants which has been noted in many cases (*1, 40, 42, 51, 65*). This is an actual increase in total carbon fixation (*1, 32*), not a promotion of photosynthesis (*106*). Perhaps it is derived secondarily from the increase in photosynthetic area of the plant. A real increase in carbon fixation could markedly affect the yield of most crops—in particular, hay, sugar, and lumber, for example—but the evidence indicates that much more study is desirable. Morgan and Mees increased the first crop of hay by gibberellin application, but the loss in the second crop offset the benefit (*3, 39*). As Brian has pointed out (*2*), many factors are involved; in the case of hay, the increased height of the plant requires changes in mowing practice, the number of new grass shoots is reduced, and there are other complications. The British workers have shown that soil fertilization is an extremely important factor (*32*); the nutrients and quantities involved need to be worked out. The extensive Japanese studies of several forage crops also show a marked initial promotion of growth, which later falls to the level of that of the controls, and confirm the finding that fertilizers have a strong modifying influence (*107*). A possibly useful increase in celery yield has been obtained (*86*). Since the economic rewards here could be large, marked interest is being shown in the carbon fixation aspect of gibberellin treatments.

Tree Growth and Root Growth

The promotion of growth of some trees and woody plants is pronounced (*54, 98, 108, 109*), but evaluation of the long-term results of such treatment will take time. In Nitsch's experiments a second gibberellin treatment had little effect (*47*). In *Populus*, delayed toxic symptoms were noted following initial stimulation (*110*), and death of meristems was noted in other plants (*54*). Conifers have not been much affected (*33, 46, 108*), but a recent report indicates that day length is an important consideration (*48*).

Despite the enhancement in size of the above-ground parts of many higher plants, much work on gibberellins indicates that they are ineffective or inhibitory with respect to the growth of most roots (*1, 42*). Quantitative tests of roots have in general failed to show any enhancement of root growth, and inhibition is only found at high concentrations (*66, 111*). However, growth of roots of some genotypes of maize is reported to have been stimulated by gibberellic acid (*112*), and so is that of roots of pine seedlings (*113*), indicating that generalizations are also risky in this case. Experiments on the rooting of cuttings are more conclusive and clearly show that not only is root initiation inhibited by gibberellin (*33, 111*) but that the stimulation of rooting caused by auxin is counteracted (*66, 111*). There is evidence of auxin-gibberellin interaction (*70, 114*). Of some interest is the report that gibberellin applications reduced the nodulation of legume roots (*115*). Since nodules are the site of nitrogen fixation, the effect of gibberellin on this important process deserves investigation.

Fig. 5. Effects of gibberellic acid on an annual strain of *Hyoscyamus niger,* a long-day plant, under long (natural) days and short (9-hour) days. All plants resembled the control at the far left at the beginning of treatment. Ten micrograms of gibberellic acid were applied daily to the plants marked "10"; the photograph was taken after 30 days of treatment. The short day ("SD") plant that received gibberellic acid bolted and formed flower buds under this treatment; in this experiment it probably received too small a dose for optimum response. Flower buds formed in both the plants at right ("LD") under long-day conditions; but the effects of gibberellic acid on the stem growth and leaf development of the treated plant are evident (*153*). [E. C. Wassink, Landbouwhogeschool te Wageningen, Netherlands, and G. M. Curry, Tufts University]

Fig. 6. Induction of bud growth in a day-length–dependent tree by gibberellic acid. The twigs of European beech (*Fagus sylvatica*) were maintained under short-day conditions; those on the left retained their winter dormant conditions, while those on the right sprouted after gibberellic acid treatment (*49*). [F. Lona, University of Parma]

Relation to Plant Metabolism

Metabolic effects of the gibberellins have been sought since the first Japanese studies (*1*). No clear-cut linkage with any metabolic pathway has yet been established, but analyses so far have always shown the greatest changes among carbohydrate constituents (*1, 32, 42, 116*). Another obvious effect is the reduction of chlorophyll content accompanying the chlorosis caused by higher dosages of gibberellin. The fertilizer studies mentioned above (*32*) show that this is in part due to insufficient mineral nutrients. But this and the recently confirmed Japanese report of reduced nicotine content in tobacco (*104*) indicate that some fundamental dislocation of nitrogen metabolism which is not reflected in the nitrogen fraction determinations may be involved. Gibberellin is very probably metabolized slowly by the plant; several studies have followed the rise and fall in growth rate after its application (*36, 82, 117*).

Promotion of the respiration of growing parts of treated plants and of seeds has been reported (*42, 118, 119*). Variations in the level of certain enzyme activities do occur, but gibberellins themselves have not activated isolated enzymes (*42, 119*). The effects of various enzyme inhibitors on gibberellin-induced growth are remarkably similar to the results obtained with auxin (*42, 120*) and implicate the heavy metals and the sulfhydryl groups taking part in the growth process.

Gibberellin is able to reduce the effects of certain plant-growth inhibitors. Kato has shown that both maleic hydrazide inhibition and coumarin inhibition of cucumber shoot growth are lessened by gibberellin but that root growth inhibition is not (*111*). The maleic hydrazide and gibberellin interaction has been studied by Brian and Hemming, who find less than additive responses and conclude that maleic hydrazide blocks gibberellin action—a conclusion deserving further study (*117*).

Although the effects of the gibberellins have for the most part been sought in higher plants, reports of growth-promoting effects on liverworts (*121*), mosses (*122*), algae (*122a*), and ferns (*123*) are available. Some reports state that fungi and bacteria are not influenced by purified gibberellins (*1, 32, 124*). But it should be noted that applications of gibberellin modified the appearance of plants infected by fungus (*125*) and virus (*126*) diseases; the effect could be on the plant itself rather than on the disease organisms. Gibberellic acid itself is apparently destroyed by soil microorganisms (*32*), but its application to soil is reported to have modified the microbial population so that growth of the nitrogen-fixing bacterium *Azotobacter* was favored (*127*).

A brief report of the effects on a mushroom and on yeast has been made (*33*). These indications, and data which indicate that hormonal levels of gibberellin promote the growth and respiration of the BCG strain of *Mycobacterium tuberculosis* (*128*), suggest that work on microorganisms should not be abandoned. Animal-tissue cultures have not shown any convincing response (*1, 129, 130*), and the first toxicological report indicates that gibberellic acid is tolerated when it is administered to rats and mice in several different ways (*130*). The sphere of gibberellin sensitivity would thus appear to be similar to that of the auxins.

Application to Theoretical Problems

The survey of the effects of gibberellins given above should suffice to illustrate why these compounds have excited popular and scientific interest. But of more importance in the long run is the hope that their use will divulge basic information on the natural processes of growth regulation and development in plants. The natural occurrence of gibberellins in higher plants, suggested in the work of Mitchell *et al.* (*131*) and since demonstrated in a wide variety of plant tissues (*30, 132, 133*), is now conclusively substantiated by two isolations of dihydrogibberellic acid (GA_1) from beans (see Fig. 10) (*16, 28*).

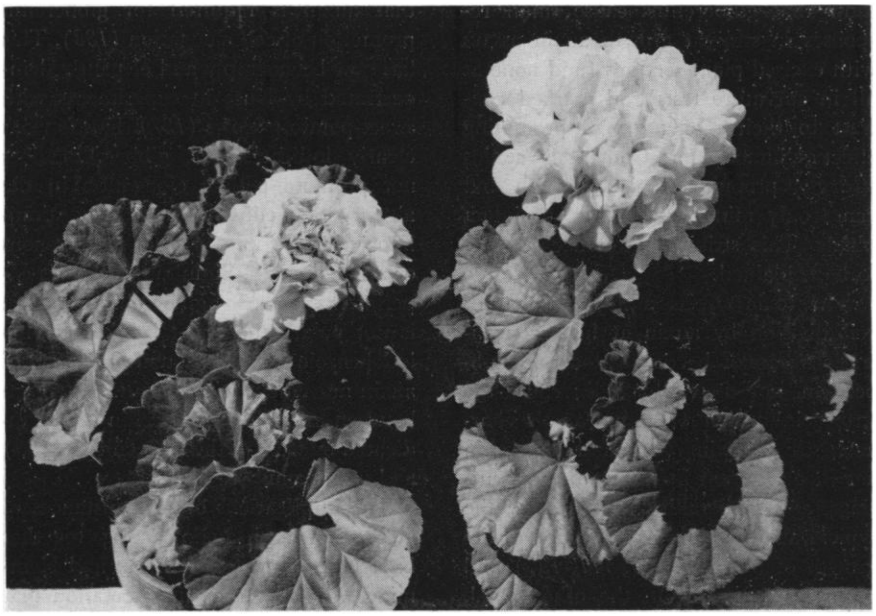

Fig. 7. Enlargement of a multiple-floret flower head by gibberellin treatment. The geranium plant at right received a foliar spray of 10 parts of gibberellin per million, applied when the buds first began to open and first showed color. The plant at left is an untreated control (*5, 53*). [S. H. Wittwer and Michigan State University]

Preliminary results with another isolated material (bean factor II) indicate that a biochemical pathway limiting growth may be operating among maize mutants, analogous to the growth-limiting pathways long known in fungi, bacteria, and algae (*19*). The hormonal nature of gibberellin is further established by experiments which demonstrate that natural induction of flowers in *Hyoscyamus* is accompanied by the formation of a substance which acts on maize dwarfs like gibberellin (*134*). Lockhart has suggested that in pea seedlings the normal organ of gibberellin production is the tip (*135*); other evidence suggests that gibberellin is also produced after fertilization during fruit formation (*1*), and in tissue cultures (*133*). Sites of active cell division thus are implicated.

Relation to Auxin

The feeling that gibberellins must be natural higher plant hormones has prompted investigations of their affinities with auxin (*33, 42, 66, 95*). These

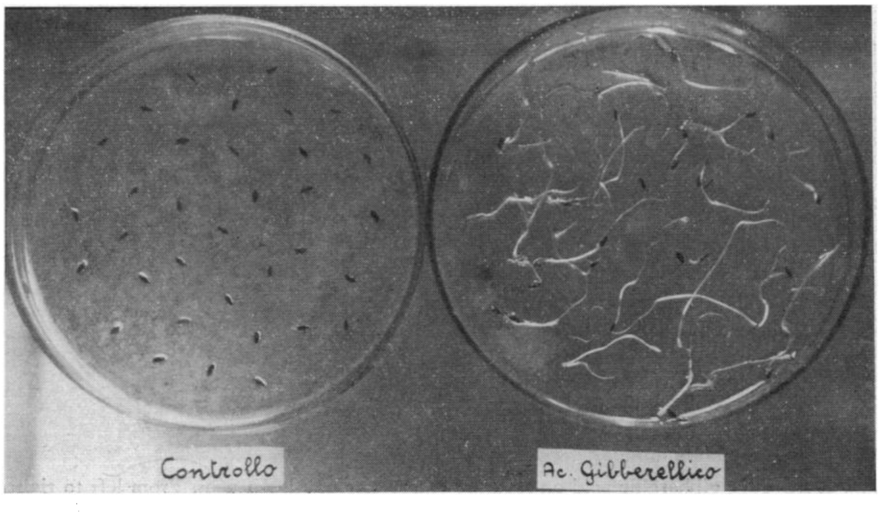

Fig. 8. Seeds of lettuce moistened in water (left) and in a $10^{-4}M$ gibberellic acid solution (right) after 120 hours in total darkness (*68*). The light that these seeds would normally require to germinate under the conditions of this experiment is no longer necessary after the hormone treatment. [F. Lona]

show that gibberellins cause small responses in straight growth auxin assays with excised plant sections (and none at all in curvature tests), in marked contrast to their strong growth-promoting effect on intact plants. Conversely, auxins strongly promote section growth but cause only minor stimulation of intact plants. This striking difference has yet to be explained.

The toxic effects and promotion of cell division by auxin at high concentrations cannot be duplicated with gibberellin, nor does gibberellin cause the strong inhibition of root growth characteristic of auxin. Auxin and gibberellin act in opposition in the rooting of cuttings, and gibberellin fails to show the typical auxin actions of inhibition of the growth of buds (*66, 95, 111, 136*) and of leaf abscission. On the other hand, auxin fails to act as gibberellin does in promoting flowering, in breaking dormancy, and in accelerating leaf expansion. The remarkable polar transport of auxin is not shown by the gibberellins, which move freely within the plant (*1, 81, 137, 137a*). Thus, there is no doubt that the gibberellins are a class distinct from the auxins in many respects.

Yet, in that both promote parthenocarpy and stimulate internodal elongation, gibberellins and auxins appear to be closely related. Statistical evidence of auxin-gibberellin interaction has been amplified by further data which show that auxin is required for gibberellin promotion of cell elongation (*138*). This has now been simply and elegantly demonstrated by Kuse in experiments with sweet-potato petioles (*137*). Kuse's work clearly indicates that gibberellin does not promote petiole elongation in the absence of auxin but is strongly stimulatory in the presence of endogenous or applied auxin. Simultaneously, his experiments show that gibberellin transport is not polar and is not blocked by triiodobenzoic acid, a potent inhibitor of auxin movement in the plant. Synergism between auxin and gibberellin is also indicated by work with tissue cultures (*89*) and with cambium (*93*).

The implications of such instances of gibberellin and auxin acting together have been discussed by Brian and Hemming, who favor the interpretation that gibberellin is acting to remove an inhibition of auxin-induced growth (*138*). Pilet's report that gibberellin inhibits indoleacetic acid oxidase could indicate that it is thus a means of increasing the auxin level (*139*). However, Brian and Hemming did not find a similar inhibition in their system, and they make the telling argument that synthetic auxins, not attacked by indoleacetic acid oxidase, also promote gibberellin action (*138*). Galston has provided an alternative hypothesis, namely that an endogenous-auxin-sparing action results secondarily from the formation of an indoleacetic acid oxidase inhibitor (*140*). Hayashi and Murakami, however, in essays of extractable and diffusible auxin from several different plants, could find no change in auxin levels after gibberellin treatment and no influence of gibberellin on the conversion of tryptophan to auxin (*141*). Nonetheless, Nitsch found rapid changes in auxin chromatograms after gibberellin treatments (*142*). Since Hayashi and Murakami used the *Avena* curvature bioassay, which is relatively specific for indoleacetic acid, their results do not exclude changes in other auxins. Galston's recent report that gibberellin may have to react with some tissue component before interacting with indoleacetic acid provides further indication that as yet unidentified compounds are involved (*143*) and that all this work may yet be reconcilable on such a basis.

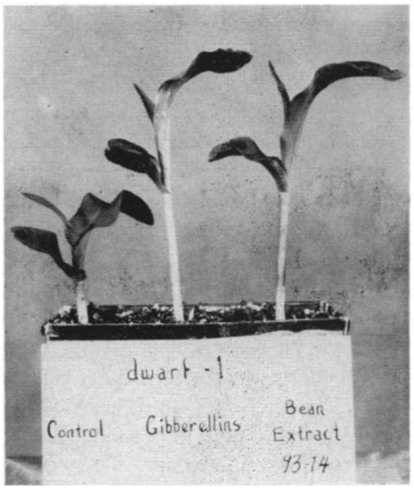

Fig. 10. Evidence that the effect of gibberellins from a fungal culture upon a dwarf seedling of maize can be duplicated by an extract from a higher plant, in this case bean (*Phaseolus*) (*30*). Crystalline material with a similar action has since been prepared from this source (*16*). [Bernard O. Phinney]

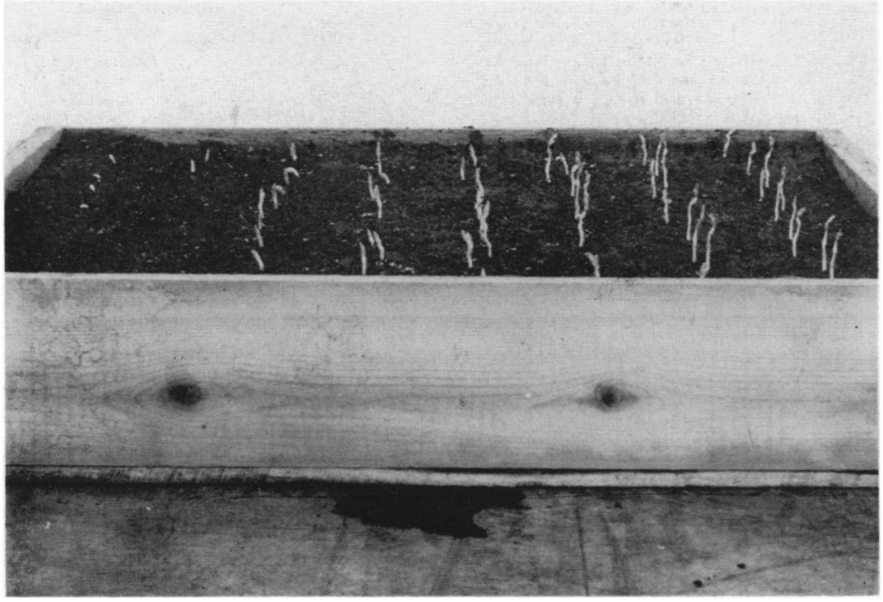

Fig. 9. Effect of gibberellic acid on seedling emergence of Alaska peas. From left to right, seeds received 0, 500, 1000, 2500, 5000, 10,000 and 25,000 parts of gibberellin per million in a Delsan AD slurry applied to the seed coats before planting (*5, 75*). [S. H. Wittwer and Michigan State University]

These observations may be related to the finding that the youngest plant tissues are the most responsive to gibberellin in section-growth assays (*42, 144, 145*). This could be due to the presence in these tissues of as yet unidentified metabolites required for optimal growth (*138, 145*), and this interpretation is supported by the unexpected finding that hormonal levels of fatty acid esters considerably enhance auxin-induced growth of pea sections (*146*). All these studies indicate that fruitful insights into hormone action are to be gained from further research on gibberellin-auxin interactions.

Interaction with Kinetin

Not to be neglected are the observations that similar ties may exist between gibberellin and kinetin. Lona and Bocchi noted that kinetin reduces the effect of gibberellin in promoting the flower-stalk formation of a rosette plant (*147*), but gibberellin did not reduce kinetin inhibition of auxin-induced pea-section growth (*148*). Moreover, a strong synergism of gibberellin and kinins was shown in seed germination (*73*), and anther cell tissue cultures grew best in a mixture of the two substances (*88*). Since kinins show interaction with auxins in bud inhibition (*136*) and in tissue cultures (*149*), it appears that gibberellin, kinin, and auxin may each influence the action of the others. Further ringing of the changes on these three groups of growth substances with suitable test materials may be expected to divulge whether their actions are sequential or concerted and could provide a major break-through in understanding hormonal control of plant growth and development.

Light

In addition to its contributions to hormonal theory, work with gibberellins is providing new glimpses of the mechanisms by which the quality and duration of incident light influence plant growth and reproduction. Besides its effects with respect to the flowering responses to day length discussed above, light has other morphogenetic effects on plant growth. For instance, red light is inhibitory to internode growth and promotes expansion of leaves in many plants. Examination of these effects has revealed that in peas gibberellin appears to act as if it were removing the red light inhibition (*145, 150*), and Lockhart has suggested that this is the case. But in beans, Downs, Hendricks, and Borthwick obtained data which indicate a much weaker interaction, if any (*151*), and Scott and Liverman (*101*) obtained results on leaf expansion at variance with those of Lockhart. A possible explanation has now been provided by the demonstration that red light promotes growth in beans in the presence of gibberellin—a finding which had not been anticipated—and that there are other differences between species (*152*). Nitsch's (*47*) and Bünsow and von Bredow's (*72*) data also indicate that gibberellin does not simply serve as a substitute for light.

These experiments have a bearing on the flowering problem, since the action spectra of all these responses are closely similar. The influence of lights of other colors on growth and flowering in the presence of gibberellin was studied by Curry and Wassink (*153*), and the results of other preliminary experiments on the influence of spectral quality are available (*145, 152*). In this connection it may be mentioned that light effects are often mimicked by treatment with cobalt ion, which in some respects can also act like gibberellin. However, examination of one system did not show any cobalt-gibberellin interaction (*154*).

It is obviously much too early to be dogmatic about the role of gibberellin in light effects, but a coupling undeniably exists, and further work will certainly be profitable. Experimental analysis of the influences gibberellins have on dormancy and germination is less advanced but is equally promising.

The effects of gibberellin have therefore not been limited to plants; their impact on research has been no less invigorating. Already Brian has put forward a unified theory of plant growth and development based on his analysis of gibberellin responses (*155*), and other syntheses will surely be forthcoming (*156*).

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156. The preparation of this article was assisted in part by a grant from the Committee on Growth acting for the American Cancer Society, Inc., made to K. V. Thimann. We wish to express our thanks to Professor Thimann for his active interest. We are also indebted to Hiroshi Ikuma for assistance with the Japanese translations.

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