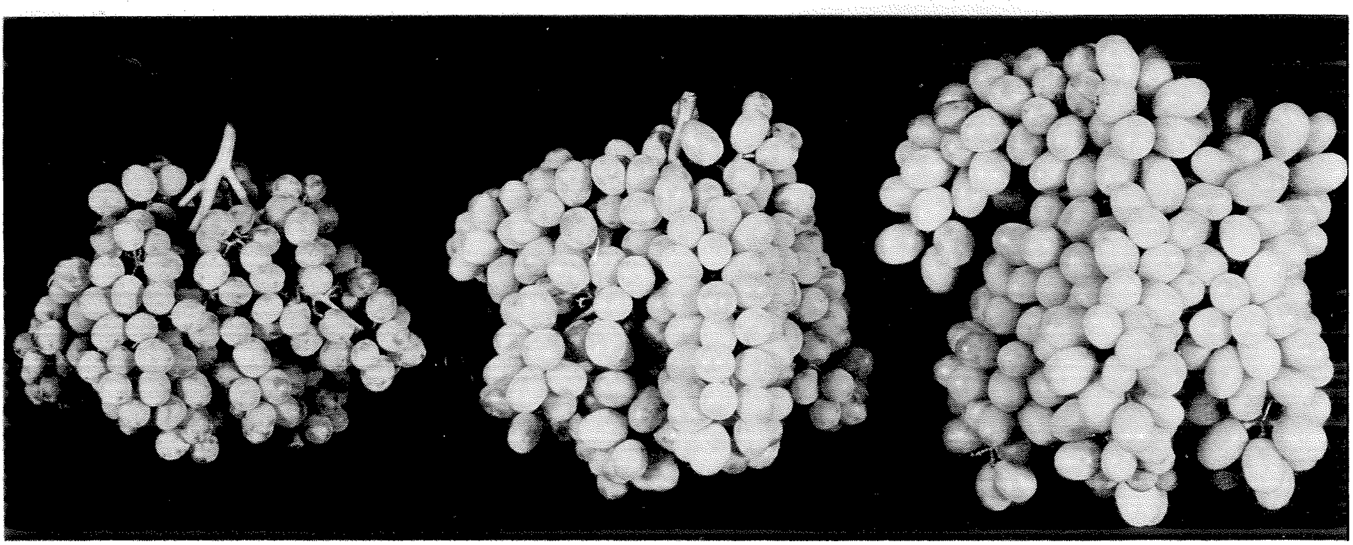


How gibberellin affects Thompson Seedless grapes. The grapes at the left got no gibberellin at all; the center ones were sprayed with 20 parts per million; those at the right with 50 ppm.

Gibberellin — A New Plant Hormone

by James A. Lockhart

One of the knottiest problems of plant physiology has been to explain the peculiar growth of dwarf plants. At one time or another, plant physiologists have attempted to explain it in terms of every known growth factor and metabolic act — and always without success. What seemed to be needed was an entirely new and different plant growth hormone. As it turned out, this hormone had already been found. It was only necessary to recognize it.

Growth of a corn plant may be reduced 80 percent by a defect in only one of the thousands of genes which control its heredity. Among these thousands of genes there are several dozen which must function properly for corn (or other plants) to attain normal size. A malfunction of any one of these genes results in a dwarf plant. The mature, dwarf corn plant may be only a foot high, with almost no stem, short, wide leaves, and an ear three to four inches long with only half a dozen kernels on it. This is certainly not a desirable or useful plant, but for many years plant physiologists have been at a loss to explain the cause of this dwarf growth.

We know that, as a general rule, each gene is responsible for forming one kind of enzyme. Each enzyme, in turn, is required for one step in the pathway of synthesis of one of the many chemical compounds necessary for normal metabolism and growth. Clearly, then, one or more chemical compounds are required — not for respiration, photosynthesis or organ formation, but simply to promote a normal increase in plant size.

In some species of plants — for example, in many deciduous fruit trees — the seeds require a cold treatment consisting of several weeks of low temperature (40-50°F.) before normal germination will occur. It is possible to force these seeds to germinate without a cold treatment, but when this is done the seedlings grow as dwarfs, similar in many respects to dwarf corn. Roots develop normally, leaves grow, but almost no stem elongation occurs and the plant appears as a rosette. As soon as these dwarf tree seedlings are given a cold treatment, stem growth begins and a normal plant results. This is a "physiological" dwarf — a plant which remains dwarfed until a certain temperature requirement is fulfilled. Here again, though, plant physiologists had no idea what the cold treatment supplied to the plant.

Another example of growth restriction and control is related to flowering in many long-day and biennial plants. In early spring or fall, when the days are short, long-day plants grow as rosettes. They form many leaves, but they have no stems and do not flower. During May and June, when day length is longest, these plants send up stems or flower stalks which bear flowers and fruits. Biennial plants generally grow in a similar fashion, but they form flowering stalks only after exposure to several weeks of cold weather. In some plants, day length may instead control vegetative stem growth. Many bushes and trees become dormant in the fall because of the shortening day length. They will resume growth only when the day length again becomes long in the spring.

Light may also inhibit stem growth. When seeds, tubers and bulbs germinate in complete darkness, the stem grows extremely rapidly and soon becomes very long and thin. Everyone has seen examples of this, as when potatoes or onions sprout in a closet or cupboard. In these dark places, stems become extremely long and spindly — while if these same plants were grown in sunlight, the stems would be short and stocky. Light is, of course, necessary for photosynthesis, and plants growing in darkness die when they exhaust the reserve food stored in the seed or tuber. In the meantime, however, they grow very rapidly. Some growth factor — probably a hormone — seemed to be involved here, too, but workers were unable then to gain an insight into the nature of this hormone.

Again and again, simple environmental factors exert an astonishing control over the type and extent of plant growth. The question plant physiologists ask is: How does the plant convert an environmental stimulus into a growth response?

Foolish seedling

While plant physiologists throughout the world were puzzling over these problems involving stem growth, a number of plant pathologists and biochemists in Japan were struggling with what appeared to be a completely unrelated problem. This was the "Bakanae" disease of rice. "Bakanae" means foolish seedling, so called because rice seedlings infected with this disease grow much faster and taller than normal plants. The seriousness of the disease lies in the fact that many seedlings die before forming grain, while the rest give very low yields.

It was only after a great deal of difficulty that K. Sawada and his student, E. Kurosawa, working at the Taiwan (Formosa) Agricultural Experiment Station in 1924, were able to demonstrate that the disease was caused by a fungus, *Gibberella fujikuri.* Soon after, in 1926, Kurosawa reported that the disease symptoms could be produced equally well by a culture solution in which the fungus had previously grown. Thus, the active principle causing overgrowth of rice had been extracted from the fungus.

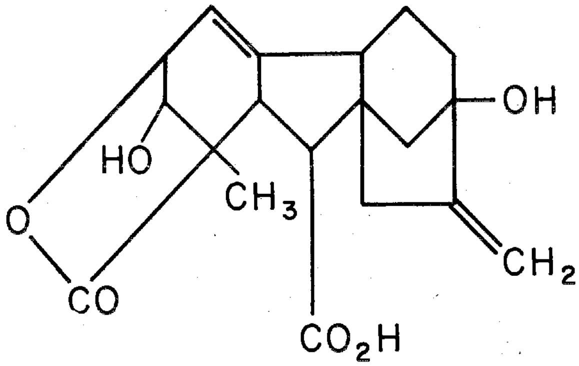
Kurosawa, as well as a group from Hokkaido University, soon demonstrated that the active principle was a small organic molecule. A group of chemists from the University of Tokyo, headed by Professor Yabuta, immediately took up the problem of purifying and identifying the active chemical. This proved to be a long and arduous task. Since much larger quantities of material were needed for purification, the Tokyo group had to work out a quantitative bioassay, then establish cultural conditions for maximum yields from the fungus, and solve other technical problems.

Isolation of gibberellin

Chief among these problems was the fact that the fungus also produced a potent plant growth inhibitor. In fact, the disease caused by *Gibberella* is sometimes characterized by growth inhibition rather than by overgrowth, a fact which created considerable confusion when Sawada and Kurosawa were trying to identify the organism which caused the disease. By 1934, Yabuta's group had identified the inhibitor and named it fusaric acid (5-n-butylpicolinic acid). They systematically developed a procedure for isolating the growth-promoting substance which is used, with only minor modifications, throughout the world today. In 1938, Yabuta and Sumiki announced the isolation of two crystalline, biologically active materials which they named gibberellins A and B.

Today, we know of five different gibberellins, differing only slightly, chemically and biologically. The structure of gibberellin A_3, the one most studied so far, is illustrated below. In general, the other gibberellins differ from gibberellin A_3 only in having different numbers of double-bonds. Two of them (gibberellins A_1 and A_5) have so far been isolated from higher plants.

Anyone familiar with the principles of organic chemistry will recognize that gibberellin A_3 has eight asymmetric carbon atoms. This means that an ordinary organic synthesis of this compound will yield 256 different compounds with the same basic struc-



Tentative structure proposed for gibberellin A_3 worked out by Professor Sumiki and his group at the University of Tokyo, and also by organic chemists at Imperial Chemical Industries in Great Britain.

ture, only one of which will be the same as the natural compound. No one knows yet how many of these compounds will have biological activity. But judging from previous experience with isomers of this kind, it may be expected that only a few will have the expected activity. Thus, gibberellin will be produced commercially by the fungus for a long time to come. However, synthesis and separation of the isomers might yield compounds with new and interesting activities.

Gibberellin in the West

When the first gibberellins were isolated, the quantities available to Japanese plant physiologists were very small, and tests of the effects of gibberellin on higher plants were limited. Gibberellins were observed to have marked growth-promoting effects on many higher plants, but no real hint of their subsequent importance was found. Due partly to the limited number of scientists in Europe and America who read Japanese, and partly to the wartime interruption of the normal flow of scientific literature, relatively little was known about gibberellin in the West until about 1950.

Investigations by plant pathologists in both the U.S. and Great Britain started at that time. However, physiologists in the West only became interested in gibberellin with the publication of a paper in 1955 by a group from Imperial Chemical Industries in Great Britain, headed by the plant pathologist, Dr. P. W. Brian. This work demonstrated that growth rate of dwarf pea plants was increased 5-6 times by gibberellin treatment, while gibberellin treatment of tall (non-dwarf) peas had relatively little effect. Here, then, published in one of the world's outstanding plant physiology journals (*Physiologia Plantarum*, journal of the Scandinavian Society of Plant Physiology) was a striking indication that this new growth-promoting substance was, in fact, of direct natural significance for higher plants. It appeared to be able to change the growth habit of peas from dwarf to normal.

Immediately, Professor B. O. Phinney, at UCLA, who had been working for several years on the problem of dwarf mutants, began investigations on the physiological significance of gibberellin which were to prove conclusively that gibberellin would completely and quantitatively restore a genetic dwarf to a normal plant. Phinney had inbred a large number of single-gene dwarf mutants of corn until he had genetic lines identical except for the single gene for dwarfness. Now he treated the dwarf plants periodically with gibberellin, and his highest hopes were realized. With proper gibberellin treatment, dwarf plants could not be distinguished from normal ones.

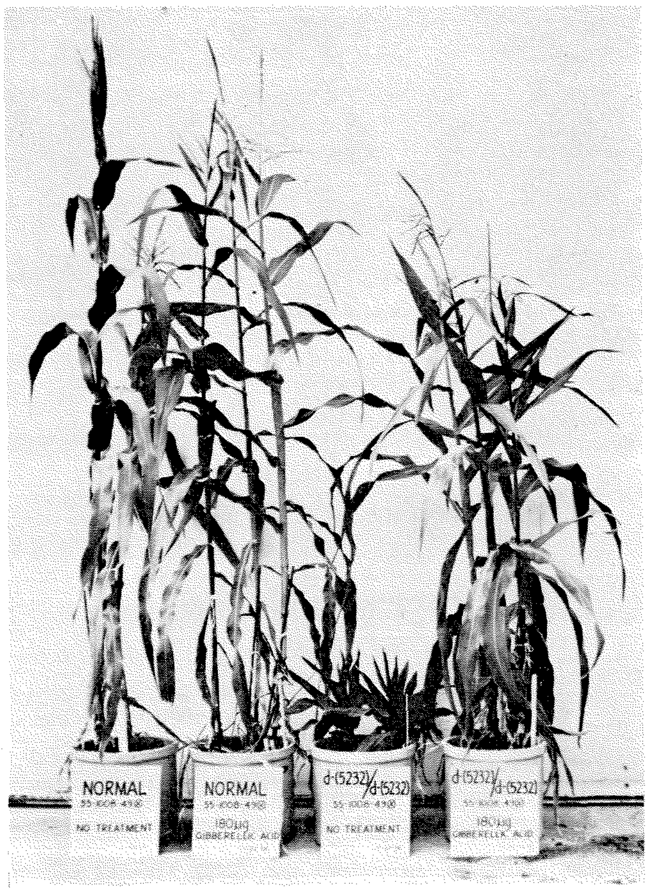
Gibberellin, then, could completely overcome the dwarf character and restore plants to normal growth. Genetically identical normal plants provided a quantitative measure of what the normal should look like. Thus, gibberellin application completely replaced the factor present in normal plants, but lacking in dwarfs, which was responsible for dwarf growth.

Carrots must be grown in low temperatures before they will flower. The rosette plant at the left has not been exposed to low temperatures; the flowering plant at the right has. The center plant was simply treated with gibberellin, which completely replaces low temperature in the carrot.

Flowering biennials

And now the rush was on. One of the major contributors to recent research in the field has been Anton Lang, who came to Caltech this fall from UCLA, as professor of biology. Professor Lang had long been interested in the problem of flowering in biennial plants; he had, in fact, published his first paper on the subject as early as 1939. Since flowering of biennial and long-day plants is characterized by a rapid concurrent elongation of the stem, Lang decided to find out whether gibberellin would induce flowering of these plants without the usual cold (or long-day) treatment. Again success.

In many species, the presently known gibberellins are fully as effective as the most favorable environment, but further work has shown that gibberellin will not always — or not completely — replace the effects of the long-day or cold requirement. Similarly Phinney found that gibberellin A_3 would correct the



Corn plants showing the different effects of gibberellin on normal plants and dwarf mutants. Gibberellin has little effect on normal plants (left), but the dwarf mutant on the right shows a complete conversion to normal as a result of the gibberellin.

dwarf habit of only 5 of 11 genetic dwarfs of corn.

While Lang and Phinney were doing this work, Dr. Lela Barton, at the Boyce Thompson Institute in New York, was examining the effect of gibberellin on physiological dwarfs – germinated seeds of apple which had not been given a cold treatment. She found that here, too, added gibberellin would completely replace the cold treatment and promote normal stem growth in these plants. It appears, then, that a natural gibberellin hormone must accumulate in those plants which require cold for normal development.

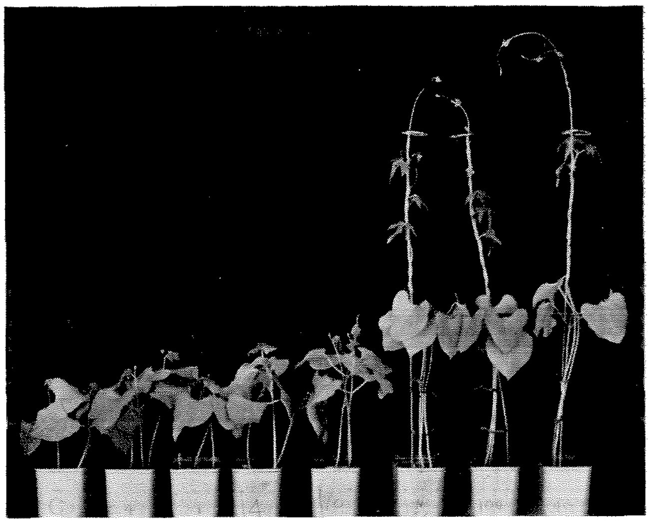
At the same time Caltech investigations were showing that gibberellin affected light inhibition of stem growth. It was easy to show that pea seedlings grown in light and treated with gibberellin would grow just as tall as if they had been grown in complete darkness. Adding gibberellin to dark-grown plants had no effect on growth. These results suggested that light was destroying some naturally-occurring gibberellin in the plant.

Gibberellin is indeed a natural hormone of higher plants. As soon as plant physiologists knew what to look for, it was relatively easy to find gibberellins in higher plants. This was first reported by Dr. Margaret Radley, working with Brian at Imperial Chemical Industries, and, soon after, Phinney and his students reported the extraction of substances with gibberellin activity from some 23 species of higher plants. Earlier workers had extracted gibberellin from higher plants occasionally, but it was not recognized at the time that these active extracts contained activity different from the known growth hormone – auxin.

Chemically, gibberellin and auxin are quite different, and yet they are both organic acids of relatively small molecular weight with generally similar solubilities. Thus, the crude purifications usually used in biological studies would not separate the two hormones. Some of their biological properties are also similar. Work in Caltech's Division of Biology showed that gibberellin, like auxin, is produced in the stem tip and they both move down the stem to the growing region. Furthermore, gibberellin, like auxin, acts primarily on the cell wall, increasing the plasticity of the cell wall and in this way permitting greater stem elongation. However, it is very easy to distinguish the two known plant growth hormones, auxin and gibberellin, by their various physiological activities:

	Auxin	*Gibberellin*
Site of production	tip	tip
Primary activity	cell wall	cell wall
Cure dwarfism	−	+
Reverse light inhibition	−	+
Replace vernalization	−	+
Promote flowering of long-day plants	−	+
Prevent abscission of leaves	+	−
Maintain apical dominance	+	−
High concentrations inhibitory	+	−
Cause curvatures, e.g., in Avena	+	−

In the past, plant physiologists attempted to explain dwarf growth and many other physiological responses in terms of the action of auxin. Correlations were



Bean plants are fast growers, but gibberellin will markedly stimulate growth even in these plants. The one at the left is untreated; the rest have received varying amounts of gibberellin up to 1/300,000 ounces.

often found between auxin and growth responses, but few causal relations could be demonstrated. It is now clear that both gibberellin and auxin must be present for normal stem growth. Auxin, due to the unique transport system by which it moves through the plant, is utilized for tropic responses, i.e., bending of the stem toward light (phototropism) and bending away from – or toward – the force of gravity (geotropism). Gibberellin, on the other hand, appears to be used for control of many of the development processes which take place in plants, as described here.

Here, in the last four years, is one of the most exciting chapters in the history of plant physiology, comparable only to the years immediately following the discovery of the first plant growth hormone – auxin – by Dr. Frits Went in 1928. Thus, a major step has been taken in the understanding of not one, but several, of the major subjects of plant physiology research in a single flurry of discovery. For the first time, we have the beginning of an insight into the general nature of the hormonal control of developmental processes in plants.

Frenzied activity

Since these basic physiological discoveries were reported, literally hundreds of agricultural workers have sprayed, poured, dipped and dusted gibberellin on thousands and thousands of plants. One of the reasons that gibberellin is so popular is that almost any plant will show a marked response to gibberellin treatment. Furthermore, it is nearly impossible to injure most species, no matter how much is applied. Thus, experiments with gibberellin are almost always a "success," and no one knows how many thousands of plants have been measured, weighed, cut up, and each individual part measured and weighed again. It is, of course, always possible that something of interest or practical use will come of this frenzied activity.

Naturally, many other excellent plant physiologists, horticulturists, and other plant investigators throughout the world are contributing greatly to our understanding of the gibberellins. In this, as in most other work which develops completely new insights into wide fields of research, no one person can be singled out as being the discoverer. The efforts of many workers – those mentioned here and many others as well – made possible the understanding that has been achieved in this new field.

What of the practical uses of this great discovery? Mostly, they are yet to come. Some of the largest chemical companies in many countries – especially those with experience in the fermentation processes necessary to grow the gibberellin-producing fungus – have initiated programs to study production and uses of gibberellin. And it was, of course, Imperial Chemical Industries in Great Britain which was responsible for the breakthrough which started this flood of knowledge and understanding. But, in spite of some of the most extensive applied research programs in the history of the agricultural chemicals industry, commercial applications of gibberellin to agriculture have so far been limited. One worries whether the failure to find immediate large-scale commercial uses of gibberellin may jeopardize further large-scale research in this field.

Chronological History of the Discovery of the Gibberellins

1924	Kurosawa and Sawada demonstrated that the fungus *Gibberella Fujikuri* was the casual agent of "Bakanae" disease of rice.
1926	Kurosawa showed that the active principle causing disease symptoms could be extracted from the fungus.
1934	Yabuta and his group identified fusaric acid, a growth inhibitor also produced by fungus.
1938	Yabuta and Sumiki crystallized two biologically active materials and named them gibberellin A and B.
1950	Work on isolation of gibberellin begun at U.S. Department of Agriculture and Imperial Chemical Industries.
1955	Publication of paper by Brian and Hemming on the effects of gibberellin on dwarf peas.
1956	Phinney reported complete reversal of dwarf habit in single-gene mutants of corn by gibberellin.
1956	Lockhart reported reversal of light inhibition of stem growth by gibberellin.
1956	Lang reported induction of flowering in biennial plant without a cold treatment by gibberellin.
1956	Barton reported reversal of dwarf growth habit of non-cold-treated seeds by gibberellin.
1956	Radley reported extraction of gibberellin-like compounds from pea seedlings.
1956	Lona reported induction of vegetative growth in a tree on short-days by gibberellin.

One of the most successful applications so far involves spraying grapes, especially the Thompson Seedless variety. Gibberellin has been found to loosen the naturally tight bunches, and this actually results in larger fruit and bigger bunches. The next time you eat Thompson Seedless grapes, see if the individual fruit doesn't look more elongate and less nearly spherical than it did two to three years ago. This is a good indication that gibberellin helped to grow bigger grapes. (Since gibberellin is a natural product found, probably, in all plant products, it certainly cannot injure people at the levels used.)

This use on grapes, however, is of only minor importance compared to what has been visualized by many people for the future. It was 10 or 15 years before the discovery of auxin led to the commercial weed-killers of today, but now the agricultural chemical industry which grew from this discovery amounts to many millions of dollars a year. It may well be that in another 10 years an equally unexpected but revolutionary use for gibberellin will be helping agriculture to new highs of productivity.