1 GIBBERLIN

Gibberellins (GAs) are best known for their promotion of stem elongation, and GA-deficient mutants that have dwarf phenotypes have been isolated. Mendel's tall/dwarf alleles in peas are a famous example of a single gene locus that can control the level of bioactive GA and hence stem length. Such mutants have been useful in elucidating the complex pathways of GA biosynthesis, and in determining which of the GAs in a plant has intrinsic biological activity.

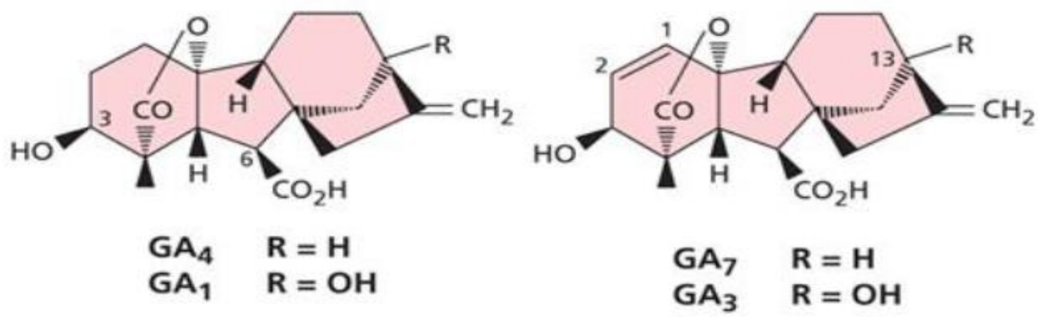
Although gibberellins did not become known to American and British scientists until the 1950s, they had been discovered much earlier by Japanese scientists. Rice farmers in Asia had long known of a disease that makes the rice plants grow tall but eliminates seed production. In Japan this disease was called the “foolish seedling” or bakanae disease. Plant pathologists investigating the disease found that the tallness of these plants was induced by a chemical secreted by a fungus that had infected the tall plants. This chemical was isolated from filtrates of the cultured fungus and called gibberellin after Gibberella fujikuroi, the name of the fungus.

1.1 Gibberlin structure

Their structure is made up from isoprenoid units, and they are synthesized via the terpenoid pathway

Terpenes are a functionally and chemically diverse group of molecules. With nearly 15,000 structures known, terpenes are probably the largest and most diverse class of organic compounds found in plants. The terpene family includes, in addition to the GAs, the hormones abscisic acid and brassinosteroids, the carotenoid pigments (carotene and xanthophyll), sterols (e.g., ergosterol, sitosterol, cholesterol) and sterol derivatives (e.g., cardiatic glycosides), latex (the basis for natural rubber), and many essential oils that give plants their distinctive odors and flavors.

The GAs are diterpenoids that are formed from four isoprenoid units each consisting of five carbons. They possess a tetra cyclic (four-ringed) ent-gibberellane skeleton (containing 20 carbon atoms). Terpenoids are compounds made up of five-carbon isoprenoid building blocks. The GAs are diterpenoids that are formed from four such isoprenoid units. The GA biosynthetic pathway can be divided into three stages, each residing in a different cellular compartment: plastid, ER, or cytosol. As more GAs from Gibberella and different plant sources were characterized, a scheme was adopted to number them (GA1-GAn) in chronological order of their discovery.



1.2 GA biosynthesis

GA biosynthesis occurs in multiple plant organs, like germinating embryos, young seedlings, shoot apices, developing seeds, and even in some fungi

It is generally accepted that there are three principal sites of gibberellin biosynthesis: (1) developing seeds and fruits, (2) the young leaves of developing aical buds and elongating shoots, and (3) the apical regions of roots. Immature seeds and fruits are prominent sites of gibberellin biosynthesis. This is based on the observation that young fruits, seeds, and seed parts contain large amount of gibberellins, particularly during stages of rapid increase in size. In addition, cell-free preparations from seeds are able to actively synthesize gibberellins. The site of gibberellin biosynthesis may be developing endosperm, the young cotyledons of legumes, or the scutellum of cereal grains.

As the seed matures, metabolism appears to shift in favor of gibberellin-sugar conjugates. It is not as easy to obtain clear evidence that gibberellin biosynthesis occurs in shoots and roots. This is partly because gibberellin levels are much lower in vegetative tissues. Vegetative tissues also yield cell-free preparations that are less active, suggesting that enzyme levels for gibberellin metabolism are also lower than for reproductive tissues.

1.3 **Gibberellin transport**

The gibberellins are mobile and may act either locally or distant from their sites of synthesis

Gibberellin transport studies have been conducted largely by application of radioactively labeled GAs to either stem or coleoptile sections. Gibberellins have been detected in both phloem and xylem saps. Transport of gibberellins does not appear to be polar, as it is with auxin, but moves along with other phloem-translocated organic materials according to a source-sink relationship. Whether gibberellins are actually transported in the xylem is not clear; they could end up there simply by lateral translocation from the phloem. On the other hand, it is likely that any gibberellins synthesized in the root tip are distributed to the aerial portions of the plant through the xylem stream. It is not known whether gibberellins are transported as free hormones or in conjugated form.

1.4 Physiological roles of GA:

1. ***Effects of gibberellins on growth and development***

Though they were originally identified as the cause of disease symptoms of rice that resulted in internode elongation, endogenous GAs can influence a large number of developmental processes in addition to stem elongation. Many of these properties of GAs have been exploited in agriculture for decades, and manipulation of the GA content of crop plants affects shoot size, fruit set, and fruit growth.

2. ***Gibberellins promote seed germination via interrupting of dormancy***

Many seeds, particularly those of wild plant species, do not germinate immediately after dispersal from the mother plant, and may experience a period of dormancy. Dormant seeds will not germinate even if provided with water. Abscisic acid (ABA) and bioactive GA act in an antagonistic manner, and the relative amounts of the two hormones within the seed can, in many species, determine the degree of dormancy. Light or cold treatments of dormant seeds have been shown to lower the amount of ABA and increase the concentration of bioactive GA, ending dormancy and promoting germination. Treatment of seeds with bioactive GA can often substitute for the light or cold treatment needed to break dormancy.

During germination, GAs induces the synthesis of hydrolytic enzymes, such as amylases and proteases in cereal grains. These enzymes degrade the stored food reserves accumulated in the endosperm or embryo as the seed matured. This degradation of carbohydrates and storage proteins provides nourishment and energy to support seedling growth.

3. ***GAs can stimulate stem and root growth***

GAs may not have dramatic effects on stem elongation in plants that are already "tall", since bioactive GA may not to be limiting in some tall plants. However, applied GAs can promote internode elongation very dramatically in genetically dwarf mutants, in "rosette" species, and in various members of the Poaceae (grass family). Exogenous GA causes such extreme stem elongation in dwarf maize plants that they resemble the tallest varieties of the same species.

Gibberellins are also important for root growth. Extreme dwarf mutants of pea and Arabidopsis, in which GA biosynthesis is blocked, have shorter roots than wild-type plants, and GA application to the shoot enhances both shoot and root elongation

4. ***They regulate the transition from juvenile to adult phase***

Many woody perennials do not flower or produce cones until they reach a certain stage of maturity; up to that stage they are said to be juvenile. Applied GAs can regulate phase change, though whether GA hastens or retards the juvenile-to-adult transition will depend on the species. In many conifers, the juvenile phase, which may last up to 20 years, can be shortened by treatment with GA3 or with a mixture of GA4 and GA7, and much younger plants can be induced to enter the reproductive, cone-producing phase precociously.

5. ***They have influence on floral initiation and sex determination***

GAs can substitute for the long-day requirement for flowering in many plants, especially rosette species. The interaction of photoperiod and GAs in flowering is complex. In plants with imperfect (unisexual) rather than perfect (hermaphroditic) flowers, sex determination is genetically regulated. However, it is also influenced by environmental factors such as photoperiod and nutritional status, and these environmental effects may be mediated by GAs. Just as in the case of the juvenile-to-adult transition, the nature of the effect of GA on sex determination can vary with species. In dicots such as cucumber

(Cucumis sativus), hemp (Cannabis sativa), and spinach, GAs promote the formation of staminate (male) flowers, and inhibitors of GA biosynthesis promote the formation of pistillate (female) flowers. In some other plants, such as maize, GAs suppress stamen formation and promote pistil formation.

6. ***GAs promote pollen development and tube growth***

Gibberellin-deficient dwarf mutants (e.g., in Arabidopsis and rice) have impaired anther development and pollen formation, and both these defects, which lead to male sterility, can be reversed by treatment with bioactive GA. In other mutants in which GA response (rather than GA biosynthesis) is blocked, the defects in anther and pollen development cannot be reversed by GA treatment, so these mutants are male-sterile. In addition, reducing the level of bioactive GA in Arabidopsis by overexpressing a GA deactivating enzyme severely inhibits pollen tube growth. Thus GAs seems to be required for both the development of the pollen grain and the formation of the pollen tube.

7. ***Gibberellins promote fruit set and parthenocarpy***

Gibberellin application can cause fruit set (the initiation of fruit growth following pollination) and growth of some fruits. For example, stimulation of fruit set by GA has been observed in pear (Pyrus communis). GA-induced fruit set may occur in the absence of pollination, resulting in parthenocarpic fruit (fruit without seeds). In grape (Vitis vinifera), the “Thompson Seedless” variety normally produces small fruits because of early seed abortion. Fruits can be stimulated to enlarge by treatment with GA3. Both these effects of GAs on grapes are exploited commercially to produce large, seedless fruits.

8. ***They promote early seed development and germination***

Some GA-deficient mutants, or transgenic plants with enhanced GA inactivation, have increased seed abortion. The failure of seeds to develop normally can be attributed to reduced levels of bioactive GAs in very young seeds. Treatment with GA will not restore normal seed development, because exogenous GA cannot enter the new seeds. However, the effect of GA deficiency on seed abortion can be negated by simultaneous expression of mutations that give a constitutive GA response. Taken together, these results provide evidence for a role for GA in the early stages of seed development.