



## ROLE OF GIBBERELLIN IN PLANT GROWTH, DEVELOPMENT AND SENESCENCE

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### Abstract

The development and growth of plants are influenced by a variety of factors, including phytohormones with their designated roles. The process' underlying mechanism hasn't been fully explained. In practically every aspect of plant growth and development, including cell elongation, leaf expansion, leaf senescence, seed germination, and leafy head formation, gibberellins (GAs) play critical roles. Gibberellins are crucial for the precise unfolding of plant genetic programmes since they have historically been linked to a few important developmental events. Gibberellin research is attracting more and more attention as a result of its significance in the so-called "Green Revolution" and its present and potential uses in crop improvement. The GA20 oxidase genes (GA20oxs), GA3 oxidase genes (GA3oxs), and GA2 oxidase genes (GA2oxs) are essential for GA production and are correlated with bioactive GAs. Light, carbon availability, stressors, phytohormone crosstalk, and transcription factors (TFs) all have an impact on the GA content and GA biosynthesis genes. However, GA is the principal hormone involved in controlling a variety of growth and developmental processes together with BR, ABA, SA, JA, cytokinin, and auxin. The present review aims to give a thorough account of the most recent findings about the molecular biology of gibberellins and how they affect various stages of plant growth. This illustration could improve our current understanding of gibberellin biology and give us the information we need to create more precise breeding and research programmes.

**Keywords:** Gibberellins, Phytohormones, Plant growth, Agricultural applications.

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## INTRODUCTION

Scientists in the west first became aware of gibberellins, also known as gibberellic acids, in the 1950s, though they had been found in Japan much earlier. The disease, known as silly seedling sickness or bakanae disease in Japanese, causes rice plants to grow taller and stops the development of seeds. Plant pathologists discovered that a substance released by the pathogenic fungus *Gibberella fujikuroi* caused similar symptoms in rice plants (Stowe and Yamaki, 1957; Takahashi et al., 1959; Piombo et al., 2020). Japanese scientists were able to obtain impure crystals of two fungal "compounds" with action that promoted plant development in the 1930s by cultivating this fungus in a lab and examining the culture filtrate. One of these was given the name gibberellin A since it was isolated from the fungus *Gibberella* (Takahashi et al., 1955). From a sample of gibberellin A, scientists at Tokyo University separated and studied three distinct gibberellins, naming them gibberellin A1, gibberellin A2, and gibberellin A3. This first naming of gibberellins A1 (GA1), GA2, and GA3 serves as the foundation for the numbering scheme for gibberellins utilised for the past 50 years (MacMillan, 2002; Hedden and Sponsel, 2015).

Tetracyclic di-terpenoid molecule gibberellic acid (GA) is a plant hormone that promotes plant growth and development (Yamaguchi, 2008). In conjunction with the interaction of several environmental elements, such as light, temperature, and water, GAs promote seed germination, transitions from meristem to shoot growth, juvenile to adult leaf stage, vegetative to flowering, determine sex expression, and grain formation. The main location of bioactive GA is in the stamens, which affect the development of male flowers and the pedicel. However, since regulatory mechanisms/organs other than those in male flowers are necessary, this raises the question of how female flowers govern growth and development (Sun, 2011).

Although GAs is believed to occasionally behave like paracrine signals, the production and transport of GAs remain a mystery. It has not yet been established which tissues bioactive GAs target to begin their function in plants or the proper spot for bioactive GAs to bind to. Understanding the proper mechanism of GA transport in plant growth, floral development, sex expression, grain development, and seed germination is currently a major challenge for the scientific community. For plant species to survive and for crops to be

successfully produced, the GA transport mechanism must be properly understood (Weiss and Ori, 2007; Vanstraelen and Benková, 2012; Golldack et al., 2013).

An update on the most recent research on the numerous development-related topics that GA is involved in is intended in this overview. Additionally, we emphasize the relevance of these substances as regulating agents in agriculture by concentrating on the existing and future applications of GA in crop production. The focus is on the unique roles played by these hormones in regulating gene expression in plant responses as well as the agronomic impacts of GA and related substances. The GA signalling cascades' discovered genes and proteins are highlighted because they might be useful breeding programme targets in the future. Our goal is to combine molecular data that can aid in the creation of conceptual models relating GA activity by collecting information from various species. However, as will be demonstrated, the diversity of GA-related substances, the heterogeneity of species' responses, and the paucity of specialised research in some sectors limit the construction of such models, save for specific processes. We do, however, expect that the definition of strategies by researchers and producers will be aided by this assessment.

## Plant Development and Crop Yield

Along with auxins, cytokinins, abscisic acid, and ethylene, gibberellins (GAs) might be considered one of the five classical hormones (Kende and Zeevaart, 1997). Each of these hormone subgroups is linked to particular plant characteristics and physiological reactions. The regulation of plant stature and seed dormancy has typically been linked to GAs in the case of GAs (Groot and Karssen, 1987; Wang et al., 2017). Recent findings, however, suggest that this may be oversimplification and that GAs (together with the other phytohormones) have direct or indirect impacts on the regulation of a variety of plant characteristics. The second half of the 20th century saw the Green Revolution, which was largely fueled by GAs. Many plant varieties with enhanced agronomical traits (dwarf phenotypes, greater biomass, etc.) have been linked to GA activity and signalling (Spielmeyer et al., 2002). But GA's potential for innovation is far from over, and they could once more lead a new Green revolution that simultaneously increases yield and boosts nitrogen-use efficiency (Xue et al., 2020; Wu et al., 2021).

Acid diterpenoids known as GAs are produced from terpenes. The activity of certain oxidases controls the quantity of bioactive GAs in plant tissues. In the latter stages of the synthesis process, the C20-GA-oxidases (also known as GA20ox and GA3ox) and C19-GA-oxidases (also known as GA3ox) function as rate-limiting enzymes. Their activity increases the pool of active GAs acting on intermediate or non-biologically active GAs. On the other hand, other particular oxidases, primarily C20-GA-2-oxidases and C19-GA-2-oxidases (GA2ox), can deactivate active GAs. The GA concentration in plants is determined by the balance between the activity of these various types of enzymes, making these oxidases the primary targets for the GA regulation exerted by other substances, genes, or phytohormones. However, a recent study with a more thorough understanding of GA synthesis and homeostasis was published (Castro-Camba et al., 2022).

GA sensing is mediated by the nuclear receptor GIBBERELLIN-INSENSITIVE DWARF1 (GID1). The DELLA proteins, which function as repressors of GA signalling, are able to be ubiquitinated and degraded thanks to the GA-GID1 connection. The molecular processes by which DELLA proteins suppress GA signalling have already been characterized (Davière and Achard, 2013). DELLA proteins are members of the GRAS family (based on the designations GIBBERELLIC-ACID INSENSITIVE, [G] AI, REPRESSOR OF GA, [R] GA, and SCARE CROW, [S] CR). Overall, the genetic responses to these phytohormones are controlled by a constant balancing act between GA sensing and DELLAs degradation.

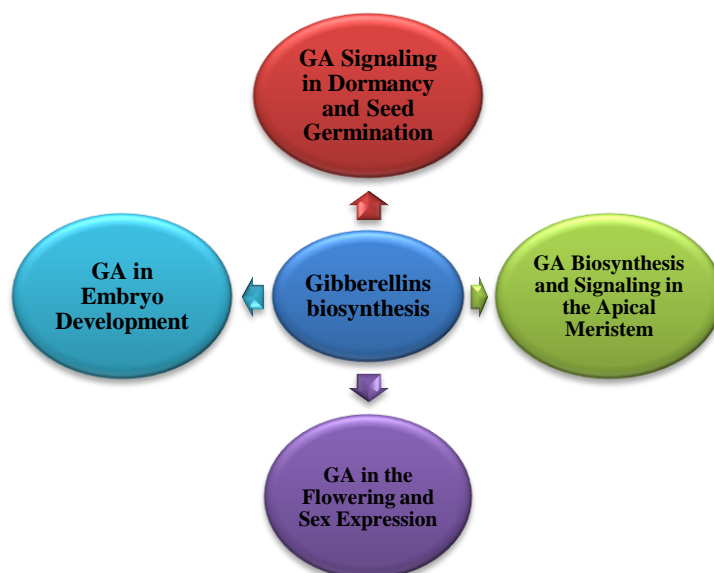
Although there have been few research on the important role of GA in leaf senescence, it is known that DELLA, a negative regulator of GA-signaling pathways, plays a significant role in senescence. In contrast to the wild type, DELLA-repressed mutants such as *gai-t6*, *rga-t2*, *rgl1-1*, *rgl2-1*, and *Q-DELLA/gal-3* displayed an early senescence phenotype, whereas mutants (*gai-3*) in which GA production was suppressed and DELLA protein was strongly increased displayed delayed senescence. In *Q-DELLA* and *gai-3*

plants, the SAGs SAG12 and 29 were upregulated, and downregulated, respectively (Hou et al., 2010; Guo et al., 2013).

### Gibberellin Biosynthesis

Gibberellins (GAs), which contain tetracyclic, diterpenoid chemicals, are naturally occurring plant growth regulators. The proper location of bioactive GA in plants or tissues that are targeted by bioactive GAs to commence their activity has not yet been proven despite significant attempts to understand the GA production and movements. According to dwarf plant bioassay and its quantitative analysis, GA was present in shoot apices, young leaves, and flowers—tissues that are actively growing (Jones and Phillips, 1966; Potts, 1982; Kobayashi et al., 1988). In contrast, several reports indicate that GAs can be found in xylem and phloem exudates, demonstrating that gas can be transported over great distances (Lang, 1970; Hoad, 1995). Grafting investigations supported the transfer of active GAs and their intermediates (Katsumi et al., 1983; Reid et al., 1983; Proebsting et al., 1992).

Contradictory results from many trials made it impossible to identify the location of bioactive GA production. Gibberellins are produced in plants through the terpenoid route, which requires three enzymes for the production of bioactive GA from GGDP: terpene synthase (TPSs), cytochrome P450 monooxygenase (P450s), and 2-oxoglutarate dependent dehydrogenase (2 ODDs). Ent-copalyl diphosphate synthase (CPS) and ent-kaurene synthase (KS), two terpene synthases found in plastids, are responsible for converting GGDP into the tetracyclic hydrocarbon intermediate ent-kaurene (Helliwell et al., 2001). Two P450 enzymes then change ent-Kaurene into GA12. First, the successive oxidation of C-19 to form ent-kaurenoic acid is catalysed by ent-Kaurene Oxidase (KO), which is found in the outer membrane of the plastid. Second, the endoplasmic reticulum enzyme kaurenoic acid oxidase (KAO) is subsequently transformed to GA12 (Helliwell et al., 2001; Nelson et al., 2004). GA 20-oxidase (GA20ox) and GA 3-oxidase (GA3ox), respectively, oxidise C-20 and C-3 to produce bioactive GA4 from GA12, respectively.



**Figure 1: Gibberellins Biosynthesis**

The embryo in a seed is stopped from developing into a plant unless the right environmental circumstances are present for it to finish its life cycle (Bewley, 1997). Light, temperature, and moisture are a few physical elements that affect seed germination, as do the endogenous growth-regulating hormones GA and ABA. GA promotes seed germination, according to Debeaujon and Koornneef (2000). After physiological and biochemical analysis, it was proven that the bioactive GAs are generated in the embryo, transported to the aleurone layer, and cause the production of  $\alpha$ -amylase (Fincher, 1989; Gubler et al., 1995). It has been determined that the aleurone layer cannot synthesise GA during seed germination but can only detect the signals of GA. GA has a significant role in internode elongation, according to physiological research and phenotypic analysis of mutants with defective GA production (Hooley, 1994; Swain and Olszewski, 1996; Ross et al., 1997). It promotes photomorphogenesis and skoto-morphogenesis, which are the division and growth of cells in response to light or darkness (Ogawa et al., 2003; Alabad et al., 2008; Gallego-Bartolomé et al., 2011). The GA biosynthesis route has been thoroughly characterised despite its complexity. The specific location of bioactive GA production in plants is extremely difficult to pinpoint (Hedden and Proebsting, 1999). In developing Arabidopsis seeds, GA-regulated genes were also expressed, according to a different finding (Silverstone et al., 1997). According to He and Li (2013), GA releases DELLA, which inhibits the BZR1 transcription factor, promoting cell elongation. According to Griffiths et al. (2006), GAs regulate flower initiation and development and is crucial

for male and female fertility rather than floral organ differentiation. Extreme GA deficit resulted in female infertility, while GA-deficient mutants in Arabidopsis and tomato had aberrant stamen formation (Goto and Pharis, 1999; Chhun et al., 2007; Hu et al., 2008; Rieu et al., 2008).

Gibberellins (GAs) are a crucial component in controlling the timing of the maize maturity phase (White et al., 2000). In maize, more bioactive GAs were deposited during early embryogenesis, and their concentration decreased as ABA levels increased. In wheat and barley, a similar link between GA and ABA was discovered.<sup>68</sup> Since GA and ABA are hostile to one another, they arise at or before stage 2 of embryo development and preserve the relationship between vivipary and quiescence. However, it is still unclear to what extent GA modulation affects gene expression (White et al., 2000; Jacobsen et al., 2002).

#### **The Role of Gibberellins in Senescence**

Gibberellins are known as leaf senescence inhibitors and have the ability to prevent or postpone the yellowing of leaves. To stop leaf withering in a variety of cut flowers after harvest, gibberellins are frequently used (Ferrante et al., 2009). In numerous sensitive species, the reduction of functional gibberellin content or the conjugation of them with glucose (inactivation) caused leaf yellowing. Senescence can be postponed and ethylene biosynthesis can be decreased by exogenous treatments. Gibberellin 3 (GA3) treatments in cut stock flowers did not improve ethylene biosynthesis, but they significantly improved ethylene production when combined with thidiazuron (TDZ) (Ferrante et al.,



2009). The generation of ethylene had little effect on leaf yellowing, though. This demonstrated that the tissues were resistant to the effects of ethylene because the leaves were most likely not yet prepared to age. To determine the precise function of these hormones in leaf senescence, more research needs to be done.

Senescence in flowers is an orderly series of cellular and tissue-level events that can be controlled by environmental factors including temperature, nutrition, light, and pathogen attack as well as by endogenous signals like plant hormones. According to research by Reid and Chen (2008), all major plant hormones can influence flower senescence, with ethylene, jasmonic acid, salicylic acid (SA), ABA, and brassinosteroids acting as inducers and cytokinins, GA, and auxin acting as inhibitors.

When sprayed to non-induced Darnel ryegrass (*Lolium temulentum*) plants, certain GAs, including GA32 and 2,2-dimethyl G4, are particularly florigenic (Pharis et al., 1987). Due to an increased endogenous level of GA and auxin, jatropa (*Jatropha curcas*) foliar buds treated with GA produced more female flowers and accelerated flower development. In contrast, treatment with ethrel (an ethylene source) reduced flower development because endogenous auxin levels were lower, whereas treatment with GA markedly enhanced it (Makwana and Robin, 2013). The rhythm of bioactive GA synthesis may be involved in the start of blooming, according to Lee et al. (1998). Depending on the time of day they occur, the pulses of GAs (particularly GA1) may have various impacts on floral initiation. Under the majority of photoperiods, early flowering in the phytochrome B null mutant 58M may be brought on by the daily rhythm. Gibberellin 20 oxidase 2 (GA20OX2) and GA20OX3, two essential oxidase genes involved in the production of gibberellin, are highly expressed in flowers and siliques (Phillips et al., 1995; Dugardeyn et al., 2008). Lower GA3OX2 concentrations were found, though, at the later phases of development (in stems, flowers, and siliques), according to Mitchum et al. (2006). The Thale cress (*Landsberg erecta*) wild type blossoms earlier than the GA-deficient mutant gal-3 in a long day but is completely unable to flower in SD unless treated with exogenous GA3 (Wilson et al., 1992). Gal-3 is substantially faulty in the formation of ent-kaurene (Zeevaart and Talon, 1992). Although it is pretty obvious that GA controls plant flowering.

## CONCLUSION AND FUTURE PROSPECTS

The application of GA improves the growth, development, side-shoot production, early flowering, and post-harvest life of cut flowers and loose flowers, according to the results of the current review. A useful production tool that can improve product quality and marketability is gibberellic acid (GA). It can be said that gibberellins are essential for the growth and development of plants. Gibberellins may not act alone when it comes to growth and development. It activates the network of signalling pathways and affects the control of several processes through interactions with other phytohormones. The GA signalling system and mechanism are crucial for seed germination, stem lengthening, meristematic tissue development, and floral organ differentiation. In order for a seed to germinate, GA must be used to break its dormancy. The intricate process of seed germination is governed by both external and internal regulatory forces. In order to regulate and promote germination in cereal grains and other crop species, GA is crucial. It is confirmed that in the absence of exogenous GA, mutants with a GA deficiency did not germinate. However, it has been demonstrated that a relatively small number of known GA signalling factors mediate the regulation of seed germination. GA biosynthesis was compromised by physiological tests and phenotypic characterisation of mutants. It was discovered that GA is crucial to stem or internode elongation. In response to light or darkness, it promotes cell division and growth.

Although GAs is believed to occasionally behave like paracrine signals, the precise mechanism of gibberellic acid mobility and transport in plants is yet unknown. The correct chemical mechanism of GA transport in plant cells is now a mystery to the scientific community. Understanding the precise process by which gibberellic acid affects plant growth, floral development, sex expression, grain development, and seed germination remains a mystery. For plant species to survive and for successful crop production, the GA transport mechanism must be properly clarified.

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