Gibberellic Acid: Role in Plant Growth and Development

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Abstract

Gibberellic acid is a powerhouse plant hormone that plays a starring role in many aspects of plant life from seed germination to towering stalks and juicy fruits. It belongs to the tetracyclic diterpenoid phytohormone family which can combat abiotic and other physiological stresses; and synthesizes in plants from acetyl-CoA by a series of enzymatic actions. Due to the multiple roles in plant growth and development including seed germination, stem elongation, flowering and fruit development, the hormone plays inevitable role in advanced achievements of agriculture, horticulture and tissue culture technology.

Keywords: Gibberellic acid, Phytohormones, Plant development, Plant growth regulators, Seed dormancy, Stress tolerance.

1. Introduction

Gibberellic acid (GA) is a plant hormone that belongs to the gibberellin family and plays significant role in many growth and development processes including stem elongation, cell division and flowering (Fig. 1). It is produced naturally by plants, but it can also be manufactured synthetically and used as a plant growth regulator. Some of the most common natural sources of GA include fungi, bacteria and plants;

while synthetic GA is produced using a fermentation process with the fungus *Gibberella fujikuroi* and then purified and concentrated into a liquid or powder form (Gupta and Chakrabarty 2013). The hormone is used in agriculture to improve crop yield and quality, and also play role in horticulture to produce larger and more attractive flowers and fruits; moreover, the hormone is applicable in brewing to improve the flavour and aroma of beer. There are more than 70 gibberellins isolated and named as GA1, GA2, GA3 and so on in which GA3 is the most widely studied plant growth regulator (Nickerson 1959).

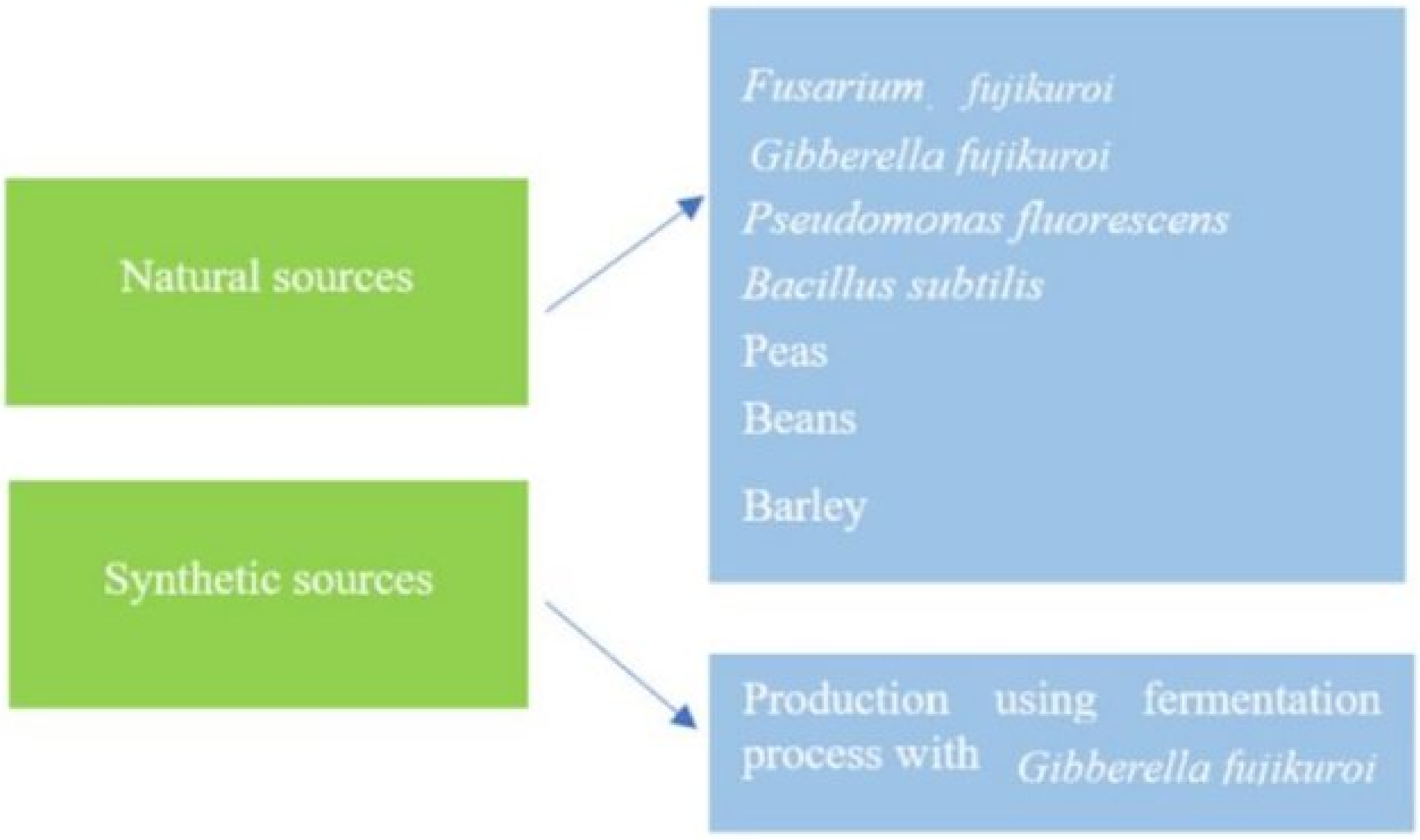

Figure 1. Different sources of GA including plants and microbial organisms

2. Discovery and occurrence

The story of gibberellins wouldn't be complete without delving into the fascinating history of their discovery. The saga begins in the early 1900s, when Japanese rice farmers faced a mysterious disease known as "bakanae," characterized by abnormally tall, slender rice plants with pale leaves and weak stalks. This disease significantly reduced rice yields, posing a major challenge to farmers. To combat this problem, a Japanese scientist named Eiichi Kurosawa embarked on a quest to understand the cause of bakanae disease. He suspected a fungus growing on the rice plants and isolated the culprit, later identified as *Gibberella fujikuroi*. Kurosawa and his colleagues prepared extracts from the fungus and observed that when applied to healthy rice plants, they exhibited the same tall, spindly characteristics as those infected with the disease. This confirmed that the fungus produced a substance responsible for the abnormal growth. Over the next decade, other Japanese scientists, like Teijiro Yabuta, Bunsuke Sumiki, and Tatsuwo Hayashi, continued the research. They were able to isolate the active substance from the fungal extract and crystallize it in 1935. This newly discovered plant growth regulator was named "gibberellin" after the fungus responsible, *Gibberella fujikuroi*. However, the composition of another compound isolated alongside it, named "gibberellin B," remained unclear (Hedden 2017).

GAs are not just present in a single location within a plant, but rather perform their diverse functions in a widespread and dynamic manner throughout various tissues and organs. GAs are present in meristems of roots, shoots and fruits, where they play a key role in stimulating cell division and elongation, contributing to overall plant growth. Leaves, the photosynthetic engines of plants capture sunlight and converting it into energy. In the organ, GAs are present and influence leaf development including blade expansion, petiole elongation and chloroplast development. GAs can be present in buds, where they play a role in bud break (the transition from dormancy to active growth) and flower development. Fruits, the ripened ovaries of flowering plants, contain seeds and serve as a means of dispersal, in which GAs can be present and influencing fruit cell division and expansion in specific cases.

3. Chemical structure of gibberellic acid

GA is a tetracyclic diterpene acid with a molecular formula of $C_{19}H_{22}O_6$ and having four rings labelled as A, B, C and D, ent-gibberellane ring structure. The A and B rings are fused together; similar to this, the C and D rings are retaining the fusion. The D ring has a carboxylic acid group at position 17, hydroxyl group at position 3 and a methyl group at position 7. Structurally, GA can be categorized based on the number of carbon atoms they contain: either 20-carbon (C20) or 19-carbon (C19) gibberellins. The C20 gibberellins serve as precursors to the C19 gibberellins and inherently lack bioactivity (Fig. 2). For a C19 gibberellin to be bioactive, it must possess a 3β-hydroxyl group and lacks a 2β-substituent (Mulholland and Ward 1954).

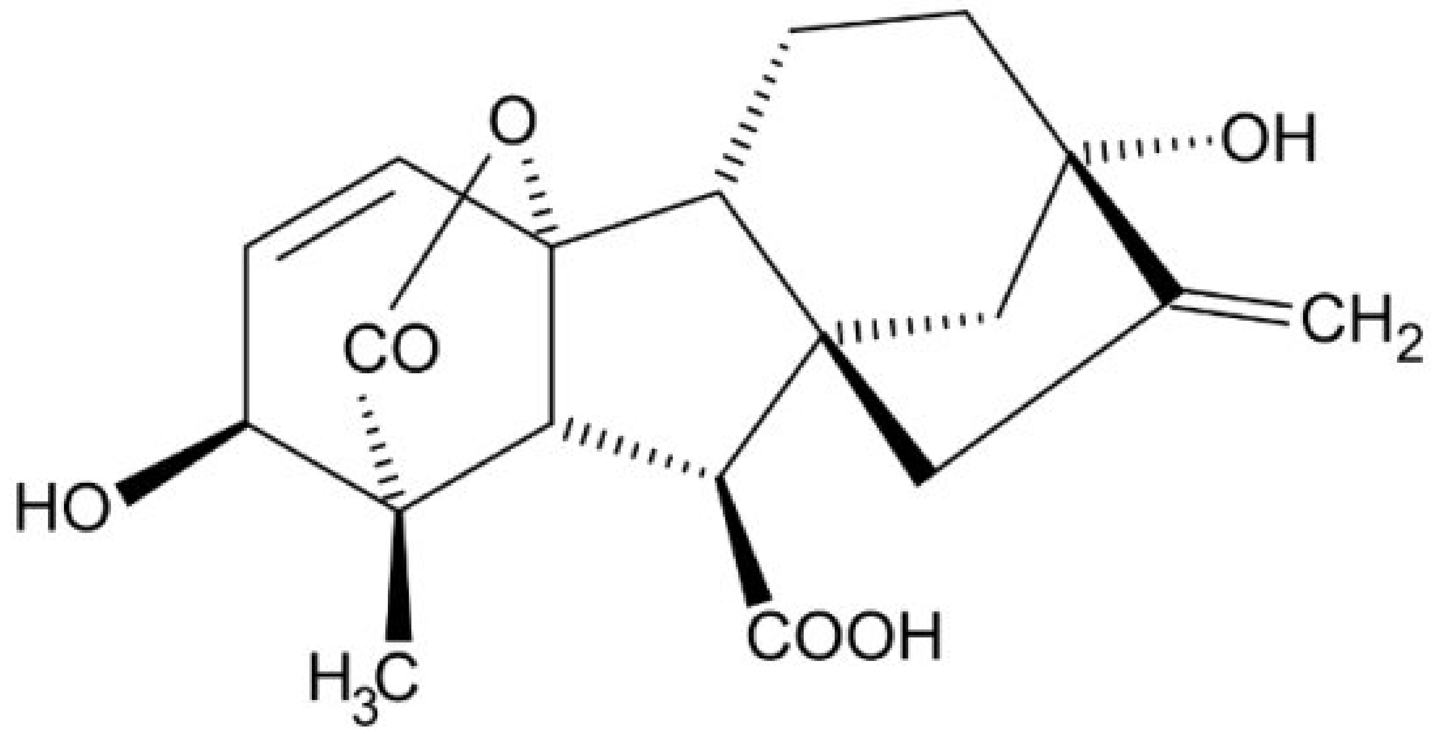

Figure 2. Structure of GA3 with four different rings A, B, C and D

4. Types of plant originated gibberellic acid

More than hundred gibberellic acids are reported till date; among them, the major bioactive growth regulators including GA1, GA3, GA4 and GA7, have a hydroxyl group on C-3β, a carboxyl group on C-6 and a lactone between C-4 and C-10 (Nickerson 1959).

- Gibberellic acid A1 (GA1): The plant hormone plays a crucial role in various aspects of growth and development including seed germination, stem elongation, leaf expansion, flowering and fruit development. The tetracyclic diterpenoid acid is synthesized in various plant tissues like young leaves, developing seeds and embryos.

- Gibberellic acid A3 (GA3): The most common type of gibberellic acid that used in a variety of agricultural and horticultural applications, stimulates plant growth, increases fruit size and delays senescence.
- Gibberellic acid A4 (GA4): Type of gibberellic acid is less common than GA3, but it is still used in some agricultural applications, mainly to promote flowering and fruit set.
- Gibberellic acid A7 (GA7): It is the least common type GA and not as well-studied as GA3 and GA4 which shows some effects on plant growth, but its specific effects are not fully understood.

5. Gibberellic acid biosynthesis

GA is synthesized in plants through a complex pathway that involves several enzymes. The starting material for GA synthesis is acetyl-CoA in turn converted to geranylgeranyl pyrophosphate (GGPP) by a series of enzymes. GGPP is then cyclized to form ent-kaurene and further oxidized and modified to form GA (Fig. 3). Moreover, GA can be synthesized chemically; but this is a complex and expensive process in which the most common method of chemical GA synthesis involves the oxidation of ent-kaurene with potassium permanganate (Corey and Munroe 1982).

Stage 1. Cyclization of GGPP: The synthesis commences with the cyclization of GGPP (geranylgeranyl diphosphate) to produce the fully cyclized compound, ent-kaurene. This process involves two sequential enzymes: copalyl diphosphate synthase (CPS) and ent-kaurene synthase (KS) which are localized within plastids (Corey and Munroe 1982). *Stage 2.*

Oxidation processes: Ent-kaurene undergoes a series of oxidations at the C-19 position, culminating in the formation of ent-7a-hydroxykaurenoic acid. The compound is then transformed into GA12-aldehyde through B ring contraction and further oxidation at C-6. The enzymes responsible for these oxidations including ent-kaurene oxidase and ent-kaurenoic acid hydroxylase, are membrane-bound cytochrome P450 monooxygenases that are typically associated with the endoplasmic reticulum (Corey and Munroe 1982). *Stage 3. Diverse pathways*: From GA12-aldehyde, the biosynthesis can diverge into multiple pathways; some of which are species-specific. Common steps include the oxidation of GA12-aldehyde to GA12, subsequent oxidations at C-20 and lactone formation. Depending on the plant species, GA12 can be hydroxylated at C-13 to produce GA53, which is then converted to GA20 and GA1. Alternatively, GA12 can lead to the formation of GA9 and GA4. The specific pathway is likely under developmental control, ensuring the synthesis of this crucial hormone remains flexible and adaptable (Corey and Munroe 1982).

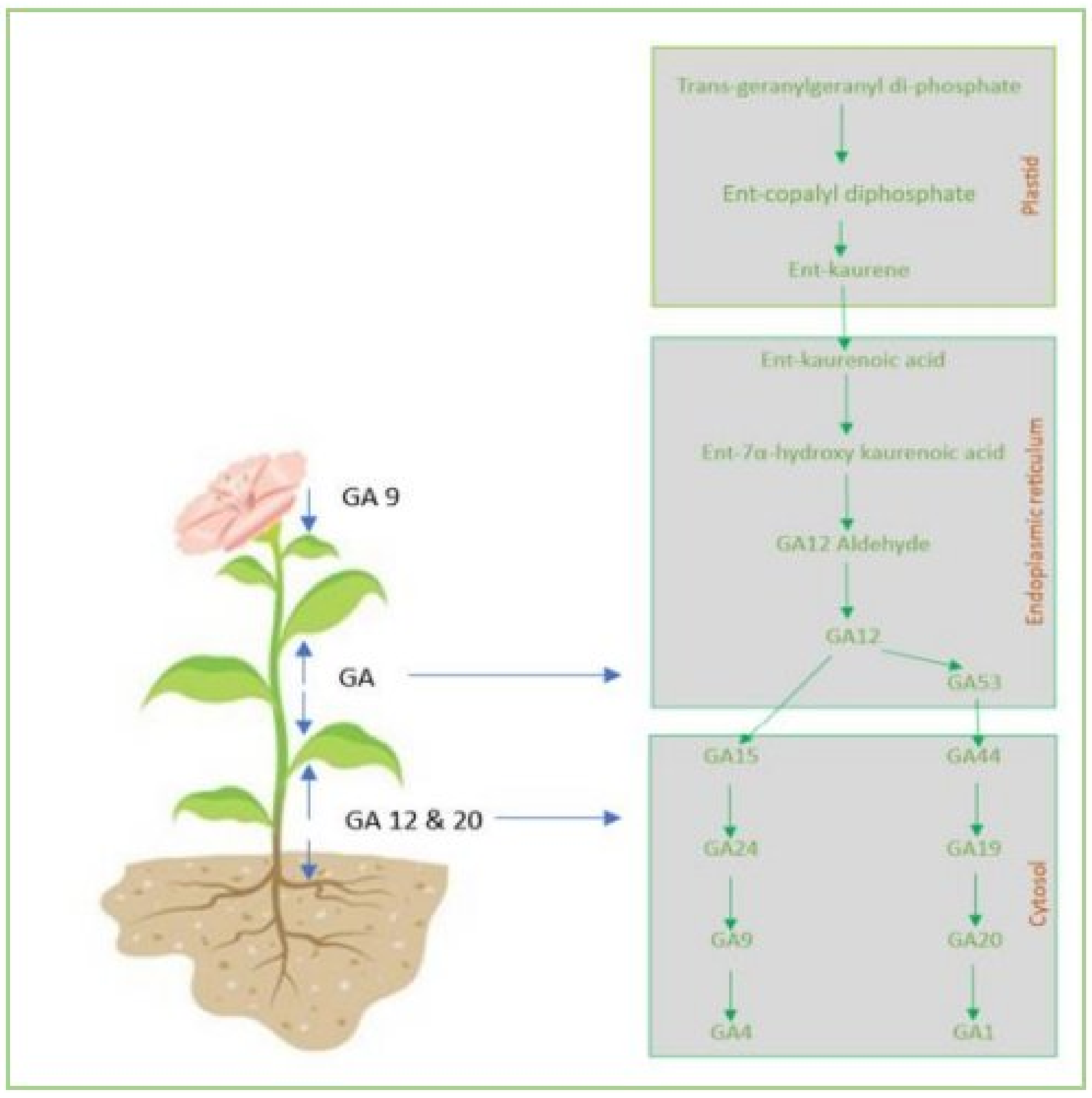

Figure 3. Steps of GA synthesis in developing plants

6. Role of gibberellic acid in plant development

In addition to the key functions, GA plays major role in other aspects of plant growth and development such as leaf expansion, root growth and stress tolerance. Normally, GA is produced in the leaves and young stems of plants and then transported to other parts of the plant where it acts on target cells. GA binds to specific receptors on the cell membrane, in turn activates a signal transduction pathway that leads to changes in gene expression (Tanimoto 2005). GA promotes stem elongation by stimulating cell division; hence, the plants treated with GA often grow taller than untreated plants. In many plants such as dwarf pea and maize, the genetic dwarfism can be overcome by internode elongation which is the most pronounced effects of gibberellins on plant growth (Vince 1967). GA promotes fruit development by stimulating cell division in turn cause enlargement of the fruit. However, the fruits treated with GA often grow larger than untreated fruits (Zang et al. 2016). The buds that are formed in autumn stay dormant until next spring. By treating with GA, the dormancy can be overcome and result in better shooting (Zheng et al. 2018).

7. Roles of gibberellic acid in modern technology

7.1 Plant tissue culture technology

GA is probably used in plant tissue culture to promote cell division and growth that resulting the increased regeneration of shoots and roots from explants. It can be also promoted the development of somatic embryos from somatic cells of explant. GA is often used in combination with other plant hormones such as auxin and cytokinin to optimize the growth and development of plant cultures (Fig. 4 and 5).

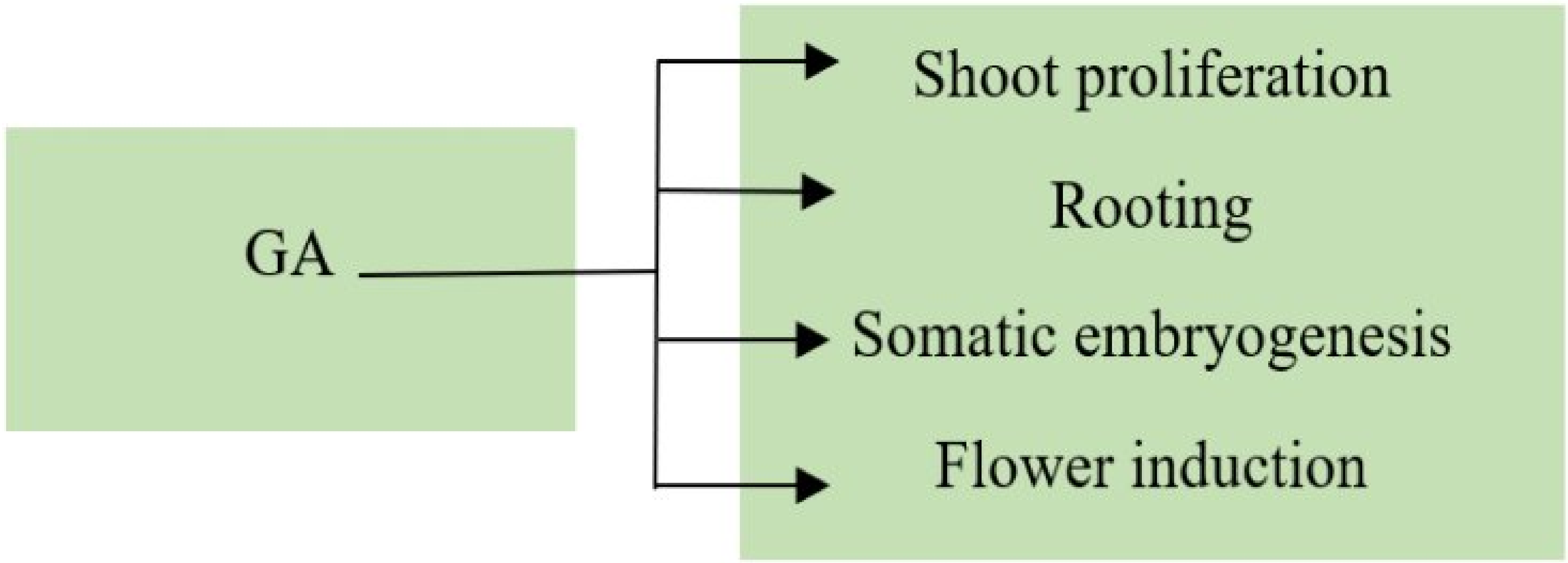

Figure 4. Role of GA in *in vitro* regeneration of plantlets under aseptic conditions.

Following are some specific examples of how GA is used in plant tissue culture (Mahmoody and Noori 2014).

1. Supplementation of GA increases the number of shoots produced by explants in plant tissue culture. This is useful for propagating plants that are difficult to propagate by conventional methods like seeds or cuttings (Gupta and Chakrabarty 2013).
2. GA can be promoted the development of roots on explants that are difficult to root from cuttings such as woody plants (Tanimoto 2005).
3. GA induces the *in vitro* development of somatic embryos which develops from somatic cells rather than from gametes in turn producing large numbers of identical plants which can be used for research or commercial purposes (Li and Qu 2002).
4. In tissue cultured plants, GA induces flowering and increases the number of flowers produced. It promotes flowering by stimulating the production of ethylene, another plant hormone that involved in flower initiation; moreover, GA directly promotes the expression of genes that involved in flowering. In addition to promoting the flowering, GA increases the size and number of flowers by enhancing the cell division and elongation in the flower buds. In tissue culture, GA promotes flowering in plants that are difficult to flower or that have long flowering times. Moreover, the method can also be used to

increase the number of flowers produced for cut flower production. Similar to this, GA promotes flowering in orchids, roses, fruit crops etc. which can be difficult to flower in tissue culture (Brian 1958).

Figure 5. *In vitro* flowering, shoot proliferation and rooting in carnation plant by the supplementation of GA as growth regulator.

7.2 Agriculture

GA plays a vital role in a variety of agricultural processes including seed germination by breaks down the seed coat and allowing the embryo to emerge, stem elongation by promoting the cell growth and division, flowering by stimulating the production of flower buds and fruit development by enhancing the fruit quality (Gupta and Chakrabarty 2013). The hormone application improves the crop yield and quality by increasing the number of tillers in wheat and rice, increasing the size of grapes and berries, reducing pre-harvest fruit drop in citrus and apples and delaying senescence in leafy vegetables. It can be applied to crops in a variety of ways including foliar sprays, seed treatments and soil applications. The optimal application method and rate will vary depending on the crop and the desired effect. In agriculture, GA used for different purposes including 1. *Seed germination*: GA improves the germination rate of seeds that have been stored for a long period of time or that have been damaged, 2. *Stem elongation*: Hormone produces taller plants in crops such as sugarcane and bamboo, 3. *Flowering*: It stimulates flowering in crops such as mangoes and pineapple, and 4. *Fruit development*: GA increases the size of fruits in crops such as grapes and berries. Hence, the plant hormone is powerful that can be used to improve crop yields and quality in a variety of ways. However, it is important to use GA carefully and according to the instructions on the product label (Pereira et al. 2019).

7.3 Floriculture

In floriculture, GA plays a role in many aspects of plant growth and development by promoting stem elongation, flower initiation and flower development in responsible to the application in plants as foliar spray, soil drench or seed treatment. The specific method and the rate of application will vary depending on the desired effect in a variety of floriculture crops including roses, carnations and lilies. GA can also be used to increase the number of flowers produced by some crops such as chrysanthemums, poinsettias, orchids and tulips. Similar to this, the hormone delays flower senescence in some crops like cut flowers. Normally, farmers are used GA to increase the stem length of roses, flower size of carnations, flower initiation in lilies, promote flower development in orchids and delay flower senescence in cut flowers. Hence, the treatment is a useful tool that can be used to improve the quality and quantity of flowers produced in floriculture. However, it is important to use GA carefully, as it can also have negative effects on plants if it is not used correctly (Pradeepkumar et al. 2020).

Table 1. Different roles of GA in plant growth and development.

Role of GA in plant development	
Promoting plant growth	GA can be applied to seeds, seedlings or mature plants to promote growth of potted and budding plants mainly for increasing their size and vigour (Brian et al. 1954).
Increasing yields	The hormone can be used to increase yields of many crops including fruits, vegetables and flowers. Mainly, it is used to increase the size and number of grapes, apples and citrus fruits in addition to increase the number of blooms on roses and other flowering plants (Ramesh et al. 2019).
Improving crop quality	The growth regulator improves the quality of many crops by changing the metabolic activities. It improves the colour and flavour of tomatoes and strawberries, and also increases the shelf life of fruits and vegetables (Miceli et al. 2019).
Breaking seed dormancy	Phytohormone breaks seed dormancy in some crops, such as lettuce and beets. This allows growers to plant seeds earlier in the season and extend the harvest season (Lee et al. 2016).
Delaying flowering	GA delays flowering in some crops like *Chrysanthemum* sp. and *Poinsettia* sp. which allows growers to produce flowers for specific holidays or markets (Saks et al. 1992).

7.4 Horticulture

In horticulture, GA is used to promote plant growth, increase yields and improve crop quality by breaking seed dormancy, delaying flowering and extending the shelf life of fruits and vegetables. However, it is important to use GA according to label directions as excessive use can have negative effects on plant growth and development (Bagale et al. 2022).

8. Gibberellic acid production under abiotic stress conditions

GA plays a major role in plant growth and development processes including seed germination, stem elongation, leaf expansion, flower initiation and fruit development (Fig. 6). In most cases, the hormone production in plants is influenced by environmental stresses. Under environmental stress such as drought, salinity or heat, GA production is often reduced by varying the metabolic rates, mainly by inhibiting the activity of the enzymes involved in GA biosynthesis. Additionally, stress conditions can be induced the production of other plant hormone like abscisic acid (ABA) which can antagonize GA signalling. Despite the fact that GA production is often reduced under environmental stress, it can still play an important role in helping plants to cope with stress. Obviously, it can help to maintain cell division and elongation which can promote plant growth even under stress conditions by regulating the expression of genes involved in stress tolerance viz. genes involved in osmo-protectant synthesis and antioxidant defence (Mahmoody and Noori 2014).

Drought stress normally reduces GA production in a number of ways and inhibits the activity of the enzymes involved in GA biosynthesis. At the same time, drought can be induced the production of ABA which can antagonize GA signalling. Sometimes, drought leads to the accumulation of reactive oxygen species (ROS), that damage the enzymes involved in GA biosynthesis (Litvin et al. 2016). Similarly, the salinity stress reduces GA production by inhibiting the activity of the enzymes involved in hormone biosynthesis. Additionally, salinity stress leads to the accumulation of Na^+ ions in the plant tissues in turn inhibits GA biosynthesis. Additionally, the heat stress also induces the production of ABA that antagonizes GA signalling, in turn reduces GA production by denaturing the enzymes involved in biosynthetic pathway (Guo et al. 2022).

Figure 6. Role of GA in different developmental stages of plants.

Despite the fact that GA production is often reduced under environmental stress, it can still play an important role in helping plants to cope with stress. Therefore, it is important to understand how GA production is affected by environmental stress in order to develop strategies for improving plant stress tolerance. One way to improve plant stress tolerance is to apply GA exogenously. Exogenous hormone application helps to maintain cell division and elongation, and regulates the expression of genes involved in stress tolerance. Together with the fact, some studies have shown that exogenous GA application can help to reduce the accumulation of ROS and Na^+ ions in plant tissues under environmental stress. Another way to improve plant stress tolerance is to identify and overexpress genes involved in biosynthetic pathway. This approach has been shown to be effective in improving plant tolerance to drought, salinity and heat stress. By understanding how GA production is affected by environmental stress and by developing strategies to improve GA production under stress conditions, we can help plants to better cope with environmental challenges and improve crop yields (Fahad et al. 2015).

9. Technologies for enhanced gibberellic acid production in plants

There are a number of technologies that can be used to enhance the production of GA for improving the cultivation practices. Gene editing technologies such as CRISPR-Cas9 can be used to make precise changes to the GA genome which enhances the yield and quality of GA as well as to make GA more resistant to pests and diseases. *Marker-assisted selection* (MAS) uses DNA markers to identify individuals with desired traits and used to accelerate the breeding process for GA as it allows breeders to select for desired traits without having to grow and phenotype large populations of plants. Proteomics is also used to identify and characterize proteins that are involved in GA production which helps to develop new strategies for GA production enhancement (Cho 2007). Metabolomics focuses the identification and characterization of metabolites that involved in GA production in turn helps to develop new strategies for enhancing GA production. In addition to these technologies, there are a number of other factors that can be used to enhance GA production that including 1. *Improved agricultural practices:* Improved agricultural practices such as crop rotation, fertilization and irrigation can help to improve the yield and quality of GA. 2. *Pest and disease management:* Effective pest and disease management practices protect GA crops from pests and diseases which can improve the yield and quality of GA. *3. Post-harvest handling:* Proper post-harvest handling of GA preserves the quality of GA and extend its shelf life (Liu and Locasale 2017; Camara et al. 2018).

By using a combination of these technologies and factors, it is possible to significantly enhance the production of GA. Some of the specific examples show how these technologies are being used to enhance GA production. 1. Researchers at the University of California, Davis, are using CRISPR-Cas9 to develop GA strains that are resistant to the fungus *Fusarium oxysporum*, which causes a devastating disease in GA crops (Shi et al. 2019). 2. Scientists at the Chinese Academy of Sciences are using MAS to breed GA strains with higher yields and improved quality (Nimisha et al. 2013). 3. Researchers at the University of Guelph use proteomics to identify and characterize proteins that are involved in GA production. This information is being used to develop new strategies for enhancing GA production (Staszak et al. 2018). 4. Scientists at the University of California, Berkeley, are using metabolomics to identify and characterize metabolites that are involved in GA production, indirectly used to develop new strategies for enhancing GA production (Brisson et al. 2021). As technology continues to develop, we can expect to see even more innovative and effective ways to produce GA (Rodrigues et al. 2012).

10. Signal transduction

GA, though a potent plant hormone, doesn't directly exert its influence within the plant. Instead, it relies on a sophisticated signal transduction pathway to translate its presence into an orchestrated response. This pathway involves a series of intricate steps, akin to a well-rehearsed dance, transforming the GA signal into specific cellular actions that ultimately influence growth and development.

Perception: Specialized plant proteins called GIBBERELLIN INSENSITIVE DWARF 1 (GID1) receptors act as the initial point of contact. When an active GA molecule encounters a GID1 receptor, it binds to it, initiating the signalling cascade. *The GID2 Complex Takes Center Stage*:

Upon binding, the GID1 receptor undergoes a conformational change, and interacts with an additional protein complex called SLEEPY1 (SLY1) - GID2**.** This complex plays a crucial role in relaying the GA signal further downstream. *Degradation of DELLA Proteins*: Interestingly, the GID2 complex targets specific proteins within the cell called DELLA proteins. These proteins act as negative regulators of growth**,** repressing various growth-promoting processes. When the GID2 complex is activated by the GA-GID1 complex, it triggers the ubiquitination of DELLA proteins. Ubiquitination essentially marks them for degradation by the plant's cellular machinery. *Growth Takes Flight:* With the removal of DELLA proteins, the stage is set for growth to occur. Various growth-promoting factors, previously inhibited by DELLA proteins, are now free to exert their influence. This can involve in increased gene expression and activation of enzymes. *A Balancing Act*: GA signalling pathway is not a one-way street in which the plants possess intricate mechanisms to control the duration and intensity of the GA response. This includes regulation of GID1 receptor availability and modification of DELLA proteins (Ashikari et al. 2003).

11. Conclusion

Gibberellic acid (GA) stands tall as a leading player in the world of plant hormones, influencing various aspects of plant life from seed germination to majestic stalks and luscious fruits. It belongs to the tetracyclic diterpenoid phytohormone family**,** renowned for its ability to combat various stresses and its synthesis within plants through a series of enzymatic reactions. While over 70 different gibberellins have been identified and named, with GA3 being the most thoroughly studied plant growth regulator, each GA plays a specific role in the intricate symphony of plant development.

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