Review Article

Influence of gibberellic acid on fruit crops: A review

Abstract

Gibberellic acid is a tetracyclic di-terpenoid molecule that acts as a plant hormone by promoting the growth and development of plants. Gibberellins, one of the longest-known groups of plant hormones, control several developmental and signaling processes, such as stem lengthening, germination, dormancy, flowering and floral development, as well as the senescence of leaves and fruits. Gibberellins can alter physiological and developmental processes, including plant vegetative growth, sex expression, yield, and yield components in several crops, when applied foliar. Gibberellin, therefore has significant economic and industrial significance. Their exogenous use aids in enhancing the several commercially significant and marketable traits of flowering plants and has several benefits, like being environmentally friendly and taking less time to treat the plant. Growth regulators like GA_3 have finally impacted on flowering crops' physiological processes, which in turn has affected growth and flower production. To put things in perspective, current scientific advancements will significantly affect fruit productivity and quality. In this review, we have discussed the impact of gibberellins on different aspects of crop production with special emphasis on fruit crops. To make the use of these regulators ecologically and toxicologically safe for both plants and consumers, the proper concentration for exogenous applications in fruit crops should also be examined properly.

Key words: Dormancy, gibberellic acid, senescence, sex expression, yield

Introduction

Major aspects of plant growth and development are regulated by the plant hormone gibberellin, the widely utilized plant growth regulator in current agriculture. Although, unlike higher plants, the role of gibberellins in lower plant species, fungi, and bacteria has just recently been studied and is still unknown,

certain species of lower plant, bacterial, and fungal species do generate gibberellins (GAs). In higher plants, GAs are produced via the actions of cytochrome P450 mono-oxygenases, 2-oxoglutar-p,ate-dependent dioxygenases and terpene cyclases localized respectively, the endomembrane system, the cytosol and in plastids. There are several environmental and developmental factors that modulate the quantity of physiologically active GAs at their points of action. Most investigations have focused on regulatory systems, which largely affect gene expression as well as the dioxygenases they encode for synthesis and inactivation. Young leaves, roots, developing seeds and fruits are examples of plant parts that are actively growing and where GAs are

generated. GAs control several physiological mechanisms and govern growth consisting of germination, stem lengthening, dormancy, enzyme induction, leaf and fruit senescence, pollen development and pollen germination, blooming, increasing fruit set and size and sex expression (Yürekli et al., 2001). Different species and varieties within a species respond differently to the same treatment, and since a particular species or variety reacts to a wide range of doses and because the stimulatory effects are temporary, repeated dosages are required for a continued response. By regulating the time of germination, seed dormancy could significantly impact plant longevity. Processes at the population and species levels, including as colonization, adaptability, speciation, and extinction, can be influenced by dormancy. Increased germination happens in reaction to certain temperatures, chemicals, or sunlight inputs. Additional circumstances needed for overcoming dormancy also include the administration of GAs or other regulators like cold stratification, warm stratification, storage and ethylene.

The majority of commercially developed perennial fruits are produced by grafting onto rootstock plants that were grown from the seeds of good stock plants. Quite a few numbers of perennial fruits are cultivated from seed. Activating seed germination and getting healthy saplings or seedlings are necessary for both of the two growth phases (Baskin and Baskin, 2014). The review concentrated on the effect of GAs on different aspects of the life cycle of fruit plants.

Gibberellic acid (GA) Biosynthesis

Teijiro Yabuta and colleagues' inquiry into the fungal disease (*Gibberella fujikuroi*) of rice led to the discovery of bioactive gibberellic acid (GA) (Yabuta and Sumiki, 1938). More than a hundred GAs from various sources has been found (from bacteria to plants). Only a few numbers of them, nevertheless, have been demonstrated to have biological action (Yamaguchi, 2008). GAs regulate several aspects of plant growth, such as seed germination, seedling growth and development, stem and root extension, leaf shape and size, pollination and flower and fruit development (Hedden and Thomas, 2012). In plants for the biosynthesis of bioactive GAs (GA1, GA3, and GA4) from the precursor compound geranylgeranyl diphosphate (GGDP), three kinds of enzymes are needed *viz;* cytochrome P450 monooxygenases (P450s), oxoglutarate–dependent dioxygenases (2ODDs) and terpene synthases (TPSs) (Hedden and Thomas, 2012). A number of GA biosynthesis genes are activated in developing *Arabidopsis* tissues (Silverstone et al., 1997) as well as in crop plants like rice (Kaneko et al., 2003), wheat (Aach et al., 1997) and tobacco (Itoh et al., 1999). This shows that in a number of situations, physiologically active GAs are created just where they work. Moreover, it has been demonstrated that in rice, the aleurone layer does not express GA biosynthetic genes but does host GA signaling events, suggesting that GAs may be used for paracrine signaling (Kaneko et al., 2002, 2003). Furthermore, it has been demonstrated in Arabidopsis that GA-dependent gene expressions occur in the absence of bioactive GA production (Yamaguchi et al., 2001). The early and late

stages of GA production have also been demonstrated to occur in provascular tissue, cortex, and endodermis, respectively (Yamaguchi and Kamiya, 2000). This indicates that GA biosynthetic intermediates are transported or moved across cells. According to much research conducted on mutants of GA metabolism, the lack or absence of GA results in altered GA signaling and phenotypes associated with germination (Heden and Thomas, 2012).

Effects on seed dormancy and germination

Even when all environmental factors are ideal, seeds cannot germinate during a stage of dormancy known as viability. There are a variety of factors that can contribute to seed dormancy, such as the hard seed coat (an external factor), the presence of an undeveloped embryo, or a greater level of ABA (abscisic acid) within the seeds (an internal factor), among others. Physical elements (moisture, temperature, and light) and endogenous growth-regulating hormones regulate how long seeds remain dormant until they begin to germinate (GA and ABA). Different phytohormonal mechanisms govern how precisely seeds react to exogenous conditions. The principal phytohormone responsible for controlling the onset and persistence of seed dormancy is ABA. The crosstalk between the GA and ABA pathways is guaranteed by ABA and GA responsive components, allowing seeds to respond appropriately to their environment. Both dicot and monocot plants use phytohormones to regulate seed dormancy. In contrast to ABA, which is responsible for the creation and maintenance of dormancy, GA promotes the seeds to germinate. GA affects the embryo in two ways: first, by enhancing its development capacity, and second, by triggering hydrolytic enzymes. As observed in Arabidopsis, upon seed germination, embryonic GA is produced, which causes the seed cover to become weaker by enhancing the expression of genes related to cell growth and modification. To encourage the development of the hydrolyzing enzyme amylase in germinating seeds, GAs act as a natural modulator of the mechanisms involved in seed germination. GA does work better when the seed coat is peeled from the seed, but it is less potent when the protective layer is still attached to the seed (Nekrasova, 1960). In Arabidopsis, the control of GA metabolism genes is linked to seed germination (Yamaguchi et al. 2001). During the first eight hours after imbibition, the activity of the GA-biosynthesis genes ENT kaurene oxidase 1 (*KO1*), gibberellin 3 oxidase 1 (*GA3ox1*), and *GA20ox3* was found high (Ogawa et al. 2003). A mutant variant of the GA biosynthesis gene, ga requiring 1 (*ga1*), was used to demonstrate the critical involvement of GA in the breakdown of seed dormancy. Interestingly, without the use of artificial GA, the ability of the *ga1* gene to germinate seeds was restored when testa and endosperm were removed. The equilibrium between GA and ABA in the embryo and the layers around the embryo of the seeds was shown to be necessary for the breaking of dormancy and the encouragement of germination. The interaction between environmental elements like temperature and light and GA production and signaling facilitates seed germination. Cold and red

light both stimulate *GA3ox1* expression. Moreover, the cold determines the *GA3ox1* expression and movement of GA in the seed tissues and embryonic axis (Liu et al., 2013).

Effects on growth and development

Higher internode extension, greater leaf development, and increased apical dominance are the most recognizable impacts of GA on shoot growth. Treatment with GA under certain situations and with some plant species does not promote the formation of entire roots, but it does cause some root portions to grow more quickly. High GA concentrations only marginally impede metabolism and lead to increasing dry weight. This is thought to be a secondary consequence of greater leaf growth and is primarily caused by enhanced carbon fixation. Some plant species are more impacted by GA than others, and not all plants generate more shoots as a response to GA (Yamaguchi et al. 2001). The genetically taller plants normally are unaffected; however, in species where dwarf mutants are common, the dwarf nature may commonly be encouraged by GA to develop in a shape indistinguishable from those of the tall phenotypic. While there are some differences between GA and auxins in terms of how they affect vegetative cell expansion, there are also some similarities. The most considerable differences are: (a) in excised tissue sections, auxins significantly promote cell-extension, but GA has less of an impact; (b) GA induces noticeable cell extension in shoots of some intact plants, whereas exogenous auxins have a minimal impact; (c) GA does not significantly hinder root development as auxins do. Multiple lines of evidence suggest that GA only affects cell extension in the presence of auxin.

It has been determined that the endogenous auxins on plants have limited effects, and that growth is consequently constrained by "an inhibitory system", GA works by blocking the effects of this inhibitory system. This conclusion was formulated by contrasting the growth rates of removed pea internode sections with those of comparable tissues in intact plants, utilizing both plants that had not been treated with GA as well as ones that had. According to Galston's (1959) research, theinhibitory mechanism may contain an enzyme that destroys auxin. Not all experimental results are entirely consistent with this concept. GA mimics light in the ways that it affects leaf growth and some types of dormancy. Light, specifically in the form of a long-day photoperiod, leads to an increase in shoot growth in the majority of photoperiodically sensitive plants; GA has a similar effect. GA, which continuously encourages development, does not mimic the internode-inhibiting consequences of light, and it does not physiologically reverse such inhibitions. Additionally, GA dispels some types of dormancy that are naturally dispelled by exposure to cold temperatures (vernalization).

On tomato plants, various concentrations of NAA at 25, 50, 75, and 100 ppm and GA3 at 20, 40, 60, and 80 ppm were sprayed. It was observed that NAA at 100 ppm and GA3 at 80 ppm generated the highest plants (Prasad et al., 2013). Tomatoes of the varieties "Sel-7" and "Pusa Ruby" developed better when 15 ppm GA3 and 25 ppm NAA were applied topically

(Gurjar et al., 2018). According to Singh et al. (2019), the application of GA3 at 30 ppm in tomato enabled the plant to grow to its maximum height and produce the highest number of primary and secondary branches. Spraying tomato seedlings with 105 M GA3 increased their tolerance to salinity up to 25 mM NaCl and had a growth-promoting influence on unstressed seedlings (Miceli et al., 2019). Dalai et al. (2020) also reported that the application of GA3 and NAA resulted in the maximum vine length/plant (cm) and number of leaves/plant in cucumber. Pre-soaking of cucumber seeds in GA solution dramatically improved epicotyls length and plant height during flowering (Sanusi, 2019).

Effects on flowering

Gibberellic acid have a species-dependent effect on flowering; they encourage flowering in long-day and biennial plants while inhibiting it in other plants, including fruit trees. Although there is growing evidence that GAs may function through multiple pathways, the exact mechanism by which GAs stimulate blooming in *Arabidopsis* is yet unknown. In citrus, GA application during the flowering induction stage decreases the number of flowers; the hormone may act directly in the bud to choose its fate toward vegetative growth, provide a mobile signal, or both. The mechanism of flowering inhibition is unknown. However, it is anticipated that GA therapy will alter the metabolic and regulatory systems in the bud. It was observed by Lord and Eckard (1987) that GA inhibits the production of flowers as long as the sepals had not formed. Gibberellins can substitute the environmental factors that promote floral initiation, causing flowering to occur mostly in long-day plants (King et al., 2006). The mechanism of floral initiation through GA is not well understood in the majority of fruit crops, yet it significantly delays or prevents flowering in a range of different fruit crops.

Effects on sex expression

GAs regulates flower initiation and development and is important for female and male fertility, but not for the differentiation of floral organs. Arabidopsis and tomato mutants lacking GA exhibited defective stamen formation, while severe GA deprivation resulted in female infertility (Koornneef et al., 1980; Nester et al., 1988). Sepals, petals, and pistils in highly GA-deficient mutants are immature, which can sometimes result in early flower aborting. No viable pollen develops in these mutants. Normal flower establishment is restored by the use of bioactive GAs or even the GA9 precursor. In contrast to other floral organs, Arabidopsis stamens necessitate a higher GA dosage, and rice stamens have been shown to be a rich source of GAs (Hirano et al., 2008). Furthermore, it has long been recognized that GAs generated from stamens promote corolla development in *Glechoma hederacea*. Griffith discovered that triple GID1 receptor mutants of Arabidopsis had decreased pedicle elongation in addition to stamen and petal development being stopped and the pistil length being decreased (Griffiths et al., 2006). In addition, Hu et al. discovered stamens and/or flower receptacles as two probable locations for bioactive GA production in Arabidopsis flowers, and they speculate that GAs are transferred from

these organs to encourage petal development (Hu et al., 2008). Short stamens were created by GA-deficient mutants, which also caused filaments to shorten and impaired self-pollination. The pollen coat is contained in the tapetum, which is crucial for pollen growth because it supplies nutrients and allows dehiscence. In developing anthers of rice and Arabidopsis, the tapetum appears to be a significant location of GA production. After meiosis, the expression of GA genes in anthers was discovered, and it is interesting to anticipate the depth and range of GA export from anthers. In the germination and development of pollen tubes, GA is crucial. Pollens in GA mutants are unable to germinate unless exogenous GA is used to assist. Jasmonic acid and GA worked together to control late stamen development (filament lengthening, anther dehiscence, and pollen maturation), whereas GA alone controlled early anther development (Song et al., 2013).

Effects on yield and yield attributing characteristics

The effect of GA related to cell division and growth, stimulating the organ's sink ability and preventing its abscission, has been made abundantly clear via reviewed investigations, despite some limitations. The floral induction carried on by stress-reducing blooming is countered by GA treatments before flowering. However, it would be challenging to reduce flowering on adult trees in the field by spraying GA because it would be necessary to evaluate the trees' natural floral induction before. Several issues that impede productivity may occur during flowering and fruit set. GA treatments can only increase yields when the issue is a lack of fruit set stimulus. Many sources of evidence, however, indicate the availability of carbohydrates rather than GA levels as the primary factor limiting production. Fruit set is often enhanced by GA treatments, but this increase did not mean higher yields. GA3-treated bunches of the Himrod grapevine variety considerably enhanced the yield qualities such as berry size, weight, volume, bunch weight, and berry color. However, there were no appreciable differences in the quality measures between the GA3 treatments. Berry weight and volume, as well as yield, were significantly impacted by GA3's effect on berry diameter. This experiment only administered GA3 to the bunches; therefore, additional GA3 applications throughout the entire grapevine, regarding variety, dosages, and number of GA3 applications, are recommended (Poudell et al., 2022).

Effect on fruit set and fruit development

Fruit set takes place as a result of the flower's ovary developing into a fruit following successful pollination and fertilization. Fruit set can rarely take place without pollination or fertilization, eventually leading to parthenocarpic or seedless fruits. Auxins were first used often for fruit set, but gibberellins are now said to provide favorable performance. Flowers may successfully use GA to replace fertilization, while fruit crops can use it to induce parthenocarpy. Mahmood et al. (2016) observed that foliar spray of 200 ppm GA produced better parthenocarpic fruit sets in guava with better fruit growth, high ascorbic acid, and better TSS than β-NOA, which notably failed to produce any parthenocarpic fruit in guava. With the use

of 8000 ppm potassium salt of GA combined with lanolin paste, parthenocarpic fruits were also produced from emasculated guava blooms (Shanmugavelu, 1962). Fruit development is the process of the cells enlarging to produce a larger fruit once the fruit has been successfully placed on the tree. Gibberellins function better when applied during the stages of fruit development since they boost fruit size and yield. Application of gibberellins 20–30 days prior to harvest resulting in larger and firmer cherry fruits (Looney and Lidster, 1980).

Promalin, an artificial gibberellin derivative (GA4 and GA7), has been found to enhance a number of growth and developmental mechanisms, mainly in temperate fruit crops. These mechanisms include enhancing fruit size and form, lowering russeting, and boosting fruit tree shoot numbers and spurs. Promalin also contains 6-Benzyladenine, a naturally produced synthetic cytokinin derivative. Gibberellins assist in cell elongation and the growth of plant organs, whereas cytokinins are employed to encourage cell division in plants (Westfall et al., 2013). Promalin has been shown to have a number of positive effects, most significantly improved fruit quality, increased lateral shoots and branching, decreased fruit bruising, etc. on pome fruits (apples and pears).

Effects on quality trait

When promalin was applied twice to the Golden Delicious and Red Delicious apple cultivars at doses of 125 ml/hl and 140 ml/hl, respectively, at 80% flowering. The results were substantial improvements in fruit size, improved fruit form, and decreased seed content (Icka and Robert, 2009). Two sprayings of promalin @18 mg/l on the Tsugaru cultivar of apples after the entire opening of the king bloom, the leaf area, leaf weight, fruit weight, and the number of seeds/fruit were all significantly improved (Youn et al., 2001). The Fuji cultivar of apples received two treatments of promalin (100 & 150 ppm) at weekly intervals, which enhanced the fruit's weight, length, diameter, and shape (Yildirim et al., 2015). The Jaffa cultivar of oranges' fruit set, physical attributes (fruit weight, volume, juice content, etc.), and chemical compositions (juice TSS% and acidity/TSS ratio) were vastly enhanced by spraying yeast extract at a dosage of 200 ppm along with 50 ppm promalin (Bakry, 2007).

Effect on branching and shooting

On one-year-old sweet cherry wood close to the bud burst stage, promalin along with brown paint application developed lateral shoots, a greater number of spurs, and had some localized effects on the plant that induced new lateral branches to appear above the area where it was applied (Miller, 1983). Similar findings were achieved by Jacyna and Lipa (2008) on the two cultivars of sweet cherry, Regina and Schneider, by applying 5 g/l of promalin mixed with acrylic paint on the beheaded leader. This led to the induction of new lateral shoots, which were followed by an increase in flowering and fruiting in the cherry. Apply Promalin and PP333 at a 250 ppm concentration to the pear cv. Gola at the petal-fall stage has been observed to slow tree growth to a minimum and increase the number of shoots and canopy spread, while PP333 doses increased the number of spurs

on the tree (Bist, 1989). Similar to this, the Gola pear cultivar treatment with 250 ppm promalin and 1000 ppm SADH (succinic acid-2.2-dimethylhydrazide) exhibited controlled massive upright tree development, while promalin alone was shown to promote lateral shoots and enhance fruit quality when compared to SADH (Rai and Bist, 1991). The Morettini pear cultivar's treatment of promalin at 1000 ppm resulted in the highest branching percentage, while 750 ppm promalin yielded the longest shoot length (Yildirim et al., 2010). Gala, Fuji, Mc Intosh, and Empire apple cultivars all received three treatments of promalin, which significantly increased the number of lateral branches with sharp angles while having the least detrimental effects on the tree (Robinson and Sazo, 2013).

Conclusion

Of all the gibberellins, GA3 has a greater variety of applications to regulate various growth and developmental processes in fruit crops and has the lowest phytotoxic impact. While gibberellins are exogenously applied to plants at different stages of growth to influence a variety of phenomena such as seed germination, stem elongation, flowering control, fruit set, etc., there are still a few endogenous GA present in plants naturally. The nature of the underlying processes for many of the events is still not well understood, although the identification of many signaling components controls different aspects of germination and abiotic conditions. Nevertheless, the precise areas of interaction for this phytohormone that have been determined will provide viable genetic intervention approaches to control development and mitigate different problems in future crop breeding initiatives.

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