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An overview of gibberellin inhibitors for regulating vegetable growth and development

Abstract. Gibberellin (GAs) promotes plant growth processes like germination, shoot elongation, root development, and flowering, while its inhibition is occasionally used in some vegetable crop practices. This paper aims to review the current literature on GAs inhibitors in practical vegetable crops and suggest future strategies for increasing yield. In some vegetable crops, inhibiting GAs with natural (abscisic acid, ethylene) or synthetic (paclobutrazol, prohexadione-Ca) regulators is key to improving yield and quality. Abscisic acid (ABA) counteracts GAs in germination and stress adaptation, while ethylene (ET) opposes GAs in senescence and growth inhibition. The application of paclobutrazol (PBZ) and prohexadione-Ca (Pro-Ca) is known to inhibit synthetic GAs, resulting in denser plants while improving plant photosynthetic efficiency, which improves crop yield. Achieving desired growth and yields with GAs inhibitors relies on precise dosing, emphasizing the importance of review studies for advancing vegetable cultivation.

Keywords: Abscisic acid · Ethylene · Paclobutrazol · Plant growth · Prohexadione-Ca.

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Introduction

Plant growth is a complex biological phenomenon regulated by numerous factors, among which plant growth regulators (PGRs) play a vital role. PGRs are both naturally and synthetically occurring low-molecular-weight compounds that, even at minimal concentrations, regulate a range of physiological processes and developmental stages within plants (Karabulut *et al.*, 2024), such as plant canopy growth, root development, fruit formation, fruit, and leaf abscission (Fenn & Giovannoni, 2021). PGRs also modulate plant responses to abiotic stress, aiding in minimizing damage from external stress factors (Assaf *et al.*, 2022). Among plant hormones, gibberellin, auxin, and cytokinin are popularly known as growth-promoting, while abscisic acid (ABA) and ethylene (ET) are recognized for their growth-inhibiting functions.

Gibberellins (GAs) are central to plant growth and development. They help with processes such as cell division, stem elongation, seed germination, dormancy, leaf expansion, and the development of flowers and fruits (Ahmad *et al.*, 2018). Of the over 130 GAs found in plants, fungi, and bacteria, only GA1, GA3, GA4, and GA7 are believed to function as bioactive hormones (Hedden & Sponsel, 2015). GAs play a key role in regulating shoot elongation in carrots (Wang *et al.*, 2017) and have emerged as crucial regulators of root meristem development (Shtin *et al.*, 2022). At the molecular level, GAs promote plant elongation by regulating cell growth. In tomatoes, a gene linked to dwarfism is associated with the GAs metabolic pathway and encodes an enzyme involved in this process (Sun *et al.*, 2019).

GAs interact with other plant hormones to coordinate growth responses, often balancing with growth-inhibiting hormones like ABA and ET. ABA is a crucial phytohormone that plays a key role in plant development and stress adaptation, making it essential for enhancing plant resilience under varying environmental conditions (Malik *et al.*, 2023). Its influence extends to processes such as leaf senescence, vegetative-reproductive phase transitions, seed dormancy, and germination, all of which are important for managing the plant life cycle (Ali *et al.*, 2022). Additionally, (ET) is a versatile phytohormone that can either promote or inhibit plant growth and senescence, depending on factors such as concentration, timing, and specific plant species (Iqbal *et al.*, 2017). Moreover, growth retardants or inhibitors, such as paclobutrazol (PBZ), and prohexadione-Ca (Pro-Ca), are externally applied to regulate GAs activity. In certain crops, GAs inhibitors are used to boost yields, e.g., potato (Hamdani *et al.*, 2019), cucumber (Başak, 2021), mango (Sarker *et al.*, 2016), mandarin citrus (Darmawan *et al.* 2014) and tomato (Altuntaș, 2016). Growth inhibitors are particularly valuable in managing GAs activity, allowing the plant to direct its energy toward targeted organs rather than excessive vegetative growth, such as reported in potato tuber (Nuraini *et al.*, 2016).

An in-depth overview of GAs inhibitors' applications and their potential in vegetable crop cultivation is essential. As the demand for sustainable and efficient vegetable production grows, understanding the current condition of GAs inhibitor research will support optimized crop management and yield improvements. This review aims to synthesize existing literature on GAs inhibitors and their role in practical agriculture and outline future directions for enhancing yield.

ABA and ET regulate seed germination performance. ABA is a key hormone involved in regulating seed dormancy, maturation, and germination, playing a crucial role in determining the timing of these processes (Nonogaki, 2017). Its interactions with GAs, which oppose each other, are also essential in deciding whether a seed stays dormant, germinates, or develops into a seedling (Shu *et al.*, 2018; Hoang *et al.*, 2014; Lee *et al.*, 2015a; Kong *et al.* 2015). The study by Groot and Karssen (1992) showed that 50% inhibition of germination in Lycopersicon esculentum seeds occurs with exogenous ABA at concentrations of approximately 0.53 mg/L and 1.32 mg/L (equivalent to 2 µM and 5 µM, respectively). As in Arabidopsis, the ABA fraction in the tomato embryo and endosperm is essential for dormancy induction (Groot and Karssen, 1992). This experiment confirms that ABA plays a crucial role in inducing dormancy during seed development in tomatoes. During seed maturation, the ABA level in the seed increases, helping to maintain seed dormancy and prevent vivipary (Shu *et al.* 2016). ABA is transported from the endosperm to the embryo to inhibit its growth (Kang *et al.*, 2015). Towards germination, the ABA level begins to decrease and the GAs content increases after imbibition and stratification treatments (Shu *et al.*, 2016).

Table 1. Effect of exogenous ET application on vegetable seed germination.

Species	Concentration	Method	Effect	References
Allium cepa	600 mg/L*	Spray at 45 DAP	Increase 19% of germination and seed vigor than the control	Yalamalle *et al.* 2020
		Spray at 60 DAP	Increase 51.65% of germination and seed vigor than the control	
Brassica oleracea	150 mg/L**	Placed on filter paper moistened with NO for 5 days	NO promote ethylene production and break secondary dormant of *Brassica oleracea*	Sami *et al.* (2019)
Amaranthus retroflexus	20.62 mg/L**	Placing seeds after long-term storage on filter paper moistened with ethephon solution for 7 days at 25 °C and 35 °C	Enhanced seed germination up to 70-85% after long-term storage	Kępczyński & Sznigir (2014)

* : convert from ppm; ** : convert from M; DAP: day after planting.

After seed shedding, dormancy is released through ABA degradation during imbibition, which then triggers germination through the action of GAs (Sano & Marion-Poll, 2021). The balance between these two hormones regulates light, temperature, and nitrate signals, acting oppositely to control embryo growth and endosperm softening (Carrera-Castaño *et al.*, 2020; Chahtane *et al.*, 2017; Tuan *et al.*, 2018). In this context, An and Zhou (2017) demonstrate that light induces germination in Lactuca sativa by promoting the production of nitric oxide (NO), a reactive nitrogen molecule that counteracts ABA during seed germination (Albertos *et al.*, 2015). Furthermore, NO is crucial for the transcription of GA3ox1 and GA3ox2, two key enzymes involved in the biosynthesis of active GAs in Arabidopsis (Bethke *et al.*, 2007). Recent studies have expanded the understanding of ABA's role, highlighting its significant contributions to seed adaptive responses against both abiotic and biotic stresses, beyond just dormancy (Sano & Marion-Poll, 2021; Pan *et al.*, 2021).

ET is one of the plant hormones that help regulate seed dormancy and germination in many species (Santos & Garcia, 2023). ET production is generally low during phase 1 (imbibition) and phase 2 (germination) but increases during phase 3 (growth) when the root elongates through the seed coat (El-Maarouf-Bouteau *et al.*, 2015). Radicle protrusion is always associated with a peak in ET production .ET stimulates seed germination in various species. It is known that exogenous ET can break the dormancy of *Brassica oleracea* and *Lactuca sativa* (Corbineau, 2024; Sami *et al.*,2019). Exogenous ET can increase germination and seed vigor of *Allium cepa* (Yalamalle *et al.*, 2020). The effect of exogenous ET application on seed dormancy and germination in various vegetable species is shown in Table 1.

Anti-gibberellin regulates vegetative growth . ABA is a hormone that inhibits plant growth. High concentrations of exogenous ABA can halt growth, while endogenous ABA accumulates during stress, reducing growth. ABA signaling directs the plant to focus on survival rather than growth (Brookbank *et al.*, 2021). However, the effects of ABA on growth can vary depending on concentration, timing, and the plant part involved (Humplík *et al.*, 2017; Mabvongwe *et al.* 2016). ABA-mediated growth regulation crosstalk with other hormones, particularly ET (Khan *et al.*, 2024), to control various cell growth processes. Similar to natural phytohormone, synthetic anti-gibberellin such as PBZ and Pro-Ca is frequently reported to modify plant growth by decreasing the dominance of vegetative growth (Cline, 2017; Diwan *et al.* 2022), such as decreasing plant height (Lee *et al.*, 2015b). Reducing vegetative growth makes plants more compact, saving space and improving resource efficiency, especially in high-density cropping and controlled environments with limited resources (Ito *et al.*, 2016). Similarly, plants naturally reduce vegetative growth to manage limited resources by redirecting them to the regeneration phase, ensuring survival (Tang *et al.*, 2021). It has also been found that the application of PBZ in rice reduces vegetative growth by directing more photosynthates to seed development and less to vegetative growth (Dewi *et al.*, 2016). The details of the various effects of synthetic anti-gibberellin application to regulate the vegetative growth of numerous vegetable species is described in Table 2. The reduction of vegetative growth as the impact of GAs application was also stated by numerous researchers by observing leaf development variables.

Table 2. Effects of PBZ and Pro-Ca application on the regulation of vegetative growth in numerous vegetable species

PGRs	Species	Concentration	Method	Effect	References
PBZ	*Lycopersicum esculentum*	50 mg/L	Apply treatments at 25, 77, 92, and 107 DAP	Reduce plant height and shorten internode length	Ramos-Fernández *et al.* (2020)
		250 mg/L*	Sprayed in the second week after transplanting	Reduce plant height	Novita (2022)
	Solanum melongena	200 mg/L	Apply to the root zone of seedlings using a soil injector	Increased the plant height, number of branches, number of buds	Khandaker *et al.* (2020)
	Solanum tuberosum	150 mg/L*	Spray all parts of the plant leaves	Inhibit plant height	Hamdani *et al.* (2024)
		50 mg/L	Foliar application	Suppressed plant height	Hamdani *et al.* (2019)
	Cucumis sativus	150 mg/L	Spray on the cotyledon leaves with approximately 25 shots of equal force	Reduce height by 23.93%.	Cázarez Flores *et al.* (2018)
	Capsicum frutescens	150 mg/L*	PBZ application during rainy season	Reduce height by 15.72%.	Nurrachman *et al.* (2023)
	Allium sativum	250 mg/L	Spray at 70 and 98 DAP	Increase pseudo stem diameter by 20.78%	Kristina *et al.* (2024)
Pro-Ca	*Solanum melongena*	50 mg/L	Spray at the emergence of the third true leaf (20 DAP)	Reduce shoot height by 27%	Ozbay & Ergun (2015)
		100 mg/L		Reduce shoot height by 32%	
		150 mg/L		Reduce shoot height by 38%	
	Capsicum annuum	50 mg/L	Foliar spray and soil drench	Reduce seedling (42 DAP) height by 25-31%	Özbay & Metın. (2016).
	Cucumis sativus	30 mg/L	Spray 10 and 20 DAP	Improved vegetative growth	Başak (2021).
	Solanum tuberosum	50 mg/L	40 DAP	Increased the number and weight of tubers per plant	Hernawati *et al.* (2022)
		150 mg/L*	Spray all parts of the plant leaves	Inhibit plant height	Hamdani *et al.* (2024)

* : convert from ppm; DAP: Day After Planting

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Table 3. Effects of PBZ and Pro-Ca application on the leaf area reduction in numerous vegetable species.

PGRs	Species	Concentration	Method	Effect	Ref.
PBZ	*Cucumis sativus*	150 mg/L	Sprayed on the cotyledon leaves with approximately 25 shots of equal force	Suppressed leaf area by 40,12%.	Cázarez Flores *et al.* (2018)
	Solanum tuberosum	150 mg/L*	Spray all parts of the plant leaves		
	Suppressed Reduce leaf area	Hamdani *et al.* (2024)			
		50 mg/L	Foliar application	Suppressed leaf area	Hamdani *et al.* (2019)
Pro-Ca	*Solanum tuberosum*	150 mg/L*	Spray all parts of the plant leaves		
	Suppressed Reduce leaf area	Hamdani *et al.* (2024)			
	Solanum melongena	150 mg/L	Spray at the emergence of the third true leaf (20 DAP)	Suppressed leaf area of seedling (35 DAP) by 15%	Ozbay & Ergun (2015)

* : convert from ppm; DAP: Day After Planting

Table 4. Effects of PBZ and Pro-Ca application on root and tuber development of potato.

PGRs	Species	Concentration	Method	Effect	Reference
PBZ	*Solanum tuberosum*	100 mg/L*	Spray all parts of the plant leaves	Increase heavy tuber per plant	Hamdani et al. (2024)
		50 mg/L	Foliar application	Increase tuber number and percentage of class tuber for seed size	Hamdani et al. (2019)
		3 mg/L*	Pouring it into an explant bottle of in vitro	Stimulating subapical stolon and uber swelling	Pane et al. (2021)
		50 mg/L*	Spray all parts of the plant leaves	Increase tuber number per plant	Hamdani et al. (2024)
Pro-Ca		50 mg/L*			
	Solanum melongena	150 mg/L	Spray at the emergence of the third true leaf (20 DAP)	Reduce root fresh weight of seedling (35 DAP) by 12,71%	Ozbay & Ergun (2015)

* : convert from ppm

Leaf development is influenced by numerous factors, one of which is hormonal signals (Bar & Ori, 2014). ABA significantly influences leaves' senescence, with levels rising as leaves age (Chen *et al.*, 2024; Liu *et al.*, 2016). The increase in ABA content during senescence further promotes leaf aging, suggesting that ABA manipulation could regulate leaf drop (Guo *et al.*, 2021). Along with ABA, ET is also a key regulator of leaf aging and senescence, particularly in species sensitive to its effects. ET biosynthesis is elevated during early leaf development, decreases as the leaf matures, and then increases again as senescence begins (Iqbal *et al.*, 2017). Reducing the levels of functional GAs or conjugating them with glucose can lead to leaf yellowing, while exogenous GAs applications can delay senescence and reduce ET production (Iqbal *et al.*, 2017). In addition to leaf aging, leaf area variables are also important to note in vegetable cultivation (Table 3). Hence, anti-gibberellin such as Pro-Ca reduced leaf area, as well as fresh and dry leaf weights (Zhang et al, 2023), due to the block of GA synthesis that is responsible for leaf expansion (Sharma *et al.*, 2024).

GAs inhibitor improving root and tuber development. ABA is a key plant hormone that plays a vital role in root growth (Harris, 2015; Sun *et al.*, 2018). At low concentrations, ABA promotes primary root elongation, while at high concentrations, it inhibits root growth, with both effects being regulated by auxin (Li *et al.*, 2017; Zheng *et al.*, 2022). ABA also controls the expression of genes involved in auxin production, further influencing root development (Qin *et al.*, 2017). Additionally, the application of shoot-ABA increases basipetal auxin transport by 114%, which in turn enhances root cell elongation by 56% (Xie *et al.*, 2020). Research suggests that a high ratio of ABA to GAs promotes tuber development (Chen *et al.*, 2022). In contrast, an excess of GAs can delay tuber formation. Manipulation of the dominance of ABA to GA could enhance tuber yield and development. One of the feasible strategies is the application of growth retardant such as PBZ and Pro-Ca. PBZ treatments shorten shoot length, thicken stems, and promote compact growth, enhancing root formation and overall plant structure (Desta & Amare, 2021). The details of the PBZ and Pro-Ca application for improving root and tuber production is described in Table 4

Anti-gibberellin has potential to increase flowering and accelerate fruit ripening. Flowering is a critical phase in the plant life cycle, marking the onset of conditions conducive to reproductive success (Rana *et al.* 2023). The timing of flowering is influenced by interactions between the plant and its environment, as well as by the plant's internal developmental capacity, enabling the transition from the vegetative to the reproductive phase (Cai *et al.*, 2024). Exogenous ET has been used to stimulate flowering in Bromeliads and to accelerate germination and flowering in other plants (Reid & Wu, 2018). This demonstrates the significant role of ET in flower development. PBZ and Pro-Ca have a notable impact on flowering. A 100 mg/L application of PBZ during the rainy season was found to accelerate *Capsicum frutescens* flower initiation by 6.6% (Nurrachman *et al.*, 2023). This suggests that PBZ can help speed up the flowering process under specific environmental conditions. On the other hand, a 150 mg/L application of prohexadione-Ca during the rainy season increased the yield of *Capsicum frutescens* by up to 18.3% (Nurrachman *et al.*, 2023). Concerning fruit ripening, ABA accelerates the ripening of both climacteric and non-climacteric fruits (Bai *et al.*, 2021; Kou *et al.*, 2021). In tomatoes, climacteric fruit ripening is accelerated by reducing the negative ABA signaling regulator, SlPP2C1, or by increasing the expression of the ABA receptor, SlPYL9 (Zhang *et al.*, 2018; Kai *et al.*, 2018).

Future directions. This review provides an in-depth examination of the role of anti-gibberellin PGRs and the application of synthetic anti-gibberellins in managing vegetative growth and enhancing crop productivity. Naturally occurring plant hormones, such as ABA and ET, act as endogenous GAs inhibitors, creating a balance that supports plant adaptation and controlled growth. In agriculture, synthetic anti-gibberellins like PBZ and Pro-Ca mimic these effects by directly inhibiting GAs biosynthesis, reducing excessive vegetative growth, and promoting regenerative phases that support higher yields. These synthetic inhibitors are useful and can substantially reduce production costs and improve crop quality. One critical challenge in applying anti-gibberellins is the variability in plant responses across species and cultivars, often necessitating crop-specific application protocols. Accurate dosage and application timing are crucial, as plant growth regulators are highly beneficial in agriculture when applied at both low and high concentrations (Agboola *et al.*, 2014). This review highlights the need for further research across diverse plant species to establish refined dosage and application techniques that optimize both effectiveness and safety in various cropping systems.

The environmental sustainability of PGR applications is another essential consideration. Residues from some PGRs, particularly PBZ, have shown persistence in soils, which may impact surrounding ecosystems and pose challenges for long-term agricultural sustainability. Conversely, Pro-Ca demonstrates a more rapid degradation rate, presenting a more environmentally favorable option. Addressing the environmental impact of these substances requires ongoing study and the development of innovative application techniques. One promising approach to enhance application precision is the use of nanoparticles as delivery agents for anti-gibberellin PGRs.

Nanoparticles penetrate cells efficiently, making them ideal for substance delivery. Their small size and large surface area enhance substance solubility, stability, absorption, and retention in target tissues, improving bioavailability, protecting against early degradation, and extending circulation time, with selective uptake in target cells

(Sarker & Nahar, 2022). This precision minimizes the required dose, reduces the likelihood of chemical runoff, and ultimately contributes to a more sustainable agricultural practice. Additionally, nanoparticle-based delivery systems could improve the bioavailability of active compounds in plant cells, achieving the intended growth-regulating effects with lower environmental impact. Future research should focus on developing such precision delivery systems, assessing their effects on various crops, and conducting field trials to determine optimal conditions for application. Incorporating these advancements could pave the way for a new generation of PGR applications that not only optimize crop yield and quality but also support the global demand for environmentally sustainable agricultural practices.

Conclusion

GA positively promotes plant growth processes like shoot elongation, root expansion, and flowering. However, inhibiting GAs can also enhance yield and quality in some vegetable crops. GA inhibition is naturally caused by the dominance of ET and ABA, while synthetic GAs biosynthesis inhibitors include PBZ and Pro-Ca. ABA’s antagonistic role in GA regulation is vital for processes such as seed dormancy and root development, which are particularly relevant in stress adaptation. ET opposes GAs, causing growth suppression, senescence, and sometimes greater stress resistance. PBZ, with its triazole structure, restricts GA synthesis to produce more compact plants, enhancing root development and photosynthetic efficiency—an approach particularly advantageous in intensive and controlled-environment agriculture. Optimal yields from PBZ and Pro-Ca depend on precise dosing, making studies on GAs inhibitors valuable for broader vegetable cultivation.

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