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The effect of phytohormones on the flowering of plants

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Abstract

During the development of angiosperms, one of the most critical stages of plants is the transition from vegetative to reproductive stage, and successfully producing seeds is necessary. Plants have developed a complex signaling pathway to recognize and combine endogenous and environmental signals. Plant growth regulators (PGRs) play a role in regulating flower growth on shoots. Physiological and biochemical processes work together to differentiate and produce flower buds. The impact of PGRs on floral bud differentiation has been the subject of several publications in recent years. In addition, the dynamic variations in gibberellin (GA), auxin, and cytokinin levels in buds and the hormonal-related signatures in gene regulatory networks indicate a crucial function for these hormones during floral bud development in plants. Especially the flowering hormone GA has a key role in regulating the activities related to flowering genes as well as controlling the activity of the DELLA protein. Abscisic acid (ABA) and ethylene (ET) have an inhibitory role in flowering but in some cases stimulate flowering depending on environmental conditions. This study aims to understand the regulation of phytohormones on flowering of plants and its effects on plant development during the flowering stage.

Keywords

flowering time, flower meristem, *Arabidopsis thaliana*, gibberellin

Introduction

In angiosperms, the initiation of the floral stage indicates that actively dividing cells create a primordium on the shoot during flower initiation, which grows mostly in whorls beginning with the sepals, moving on to the petals and stamens, then the carpels (1). The initiation of the floral stage indicates the change from the vegetative to the reproductive stage. In addition to abiotic elements, including soil nutrient availability, temperature, sunshine exposure, chemical and physical, also play a significant influence in the initiation of flowers (2). The plant's flowering stage differentiation is favourably triggered by a comparatively high carbon-nitrogen ratio (3). Many plants' floral initiation is delayed if these substances are insufficient to meet the energy requirements of expanding cells (3). The shoot apical meristem (SAM) forms leaves and shoots during the vegetative phase, whereas flowers are created during the reproductive phase (4). The SAM expands when the plant begins the reproductive phase, then change into an inflorescence meristem (IM). The IM transforms into a flower meristem (FM) in a process those results in an inflorescence (1, 5). During flower formation, various developments of flower organs such as sepals, petals, stamens and pistils are significantly affected by PGR signaling, including gibberellin (GA_3), auxin, cytokinin, abscisic acid and other hormones (6). Hormones applied exogenously play different functions in regulating plant growth and development, including the flowering process (6, 7). In the GA pathway, DELLA proteins are one of several molecules that are important in regulating GA connection with important regulators in plant hormone signalling pathways (8). A systemic signal called florigen encourages blooming (9). The floral transition is started by FLOWERING LOCUS T (FT) protein, which is expressed in the leaf phloem and transferred to the shoot apical meristem (10). Different hormones process and impact; ethylene and ABA regulate the floral's inhibition while cytokinins and auxins are crucial for flowering (11). In this study, we discuss about the most recent developments in our knowledge of how PGR signalling pathways affect flowering regulation.

Methodology

We used Web of Science, Google Scholar, and Scopus as well as other search engines to carry out this investigation. Due to their extensive academic and scientific literature covering a variety of subjects, including plant biology and the flowering plant, these platforms were chosen. The aim of our search criteria was to find relevant articles that connected to our area of interest. Search phrases like "flowering time," "flower meristem," "phytohormones," and "florigen" were carefully chosen to make sure they correctly represented the core of the subject. In addition, we searched the most recently published relevant references for inclusion in this paper.

Results

Gibberellins (GAs) and flowering

Plants have been shown to have a large number of GAs, but only GA_1, GA_3, GA_4, and GA_7 operate as hormones that are bioactive (12). Plant hormones known as GAs are vital and effective regulators of plant growth and developmental activities, such as promoting seed germination, lengthening stems, controlling bolting and blooming and regulating the development of fruit and seeds (13, 14). Exogenous GA_3 spraying inhibits Fuji apple tree flowers from developing (15) but causes early flowering in vines (16). In *in vitro* culture, when exogenous GA_3 addition affected flowering quality and related gene expression in peony (17). DELLA proteins, a group of repressors that control GA signaling, are important inhibitors of GA signaling, thus controlling blooming or seed germination (18). In addition to working via DELLAs, GA-mediated floral control is accomplished through spatial and temporal regulation of GA production and transit (17). Moreover, the inactivation of any of the components of GA production and signaling might result in flowering abnormalities (1). The application of GA_3 at 50 ppm resulted in early flowering and reduced flowering time in cashew (19). In SD, GA levels rise significantly before floral initiation and promote flowering by inducing floral integrator genes, FT (20), and *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1* (*SOC1*) (21). GA promotes flowering by activating floral coordinator genes; the exact biochemical pathway is unclear.

Cytokinins (CKs) and flowering

Cytokinins are a type of plant hormone that are derived from adenine and have specific substitutions attached to the N6 position of the adenine ring (22). These hormones play a significant role in various processes related to plant development, such as cell division, shoot growth and initiation, apical dominance, phyllotaxis, and nutrient uptake (23). In particular, cytokinins are involved in controlling the division and differentiation of cells in the floral meristem (23). In *Arabidopsis*, Cytokinin homeostasis influences Cytokinin accumulation in the meristem, controlling the size and activity of the SAM (24). Cytokinins have been researched for their role in flower transition. It has been discovered that they play a significant role in cell division and differentiation within the floral meristem (25). Inflorescence meristem (IM) cytokinin signaling significantly reduces the rate of cell division, which is associated with decreased *WUS* (*WUSCHEL*) expression (7,26). Cytokinin stimulates cell division and WUS expression to control SAM size and activity (26). When the floral stimulus begins in Arabidopsis, the concentration of Ck in the leaves and phloem sap increases quickly (27,28). According to the expression analysis, the CK signal establishes the stem cell niche and slows cellular differentiation (29). Cytokinin deficiency contributes to inflorescence arrest by reducing IM activity and hindering flower opening (9). Mutants with cytokinin deficiencies also experience significant disruptions in inflorescence development. (9).

Auxin and flowering

Auxin is a tiny molecule, which is related to tryptophan, and manages to coordinate a vast array of underlying processes by primarily controlling nuclear gene expression (30). The hormone auxin, which regulates a variety of developmental processes including cell elongation and division, and organ forming (31), is also essential for appropriate plant growth and development (32). Auxin plays a crucial role in the reproductive development of plants, impacting various stages such as the initiation of inflorescences, the formation of floral organs, the growth of fruits, and embryogenesis. Its spatial and temporal expression is evident in all these processes. (33). In tomato plants, auxin plays a role in the development of reproductive organs, specifically from IM to flower organ morphogenesis (34). An auxin signal was seen in four whorls of flower during early flower development and subsequently became dominant in the reproductive organs of tomatoes (34, 35). It is also interesting to note that auxin transit in the inflorescence decreases as the inflorescence develops and that auxin seems to accumulate in the flower stem (36). There is less data that auxin is the main influence of flowering timing in *Arabidopsis* (37).

Abscisic acid (ABA) and flowering

Abscisic acid is a hormone derived from sesquiterpenoids and is a vital plant hormone for responding to stress, such as dormancy and leaf shedding (38). Abscisic acid inhibits the floral transition in *Arabidopsis*, most likely by increasing the expression of the floral repressor *FLOWERING LOCUS C* (*FLC*) (38). This was confirmed by the overexpression of the ABA signalling component *ABSCISIC ACID INSENSITIVE 5* (*ABI5*), *ABSCISIC ACID INSENSITIVE 4*

(*ABI4*), which in *Arabidopsis* delayed blooming by upregulating FLC (39). It is important to mention that the FLC gene is mostly found in the Brassicaceae, so it may not be applicable to other species (40). Studies have shown that ABA has an inhibitory effect on floral transition, particularly in ABA-deficient mutants (41). Contrarily, it has been demonstrated that in drought stress conditions, ABA has positive impacts on floral transitions (42). Certain plant species, including rice and *A. thaliana*, exhibit early flowering as a response to drought stress.; this is called as the drought escape (DE) response (41). ABA may be implicated in the DE response through recently discovered genes such as *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1, FLOWERING LOCUS T* and *TWIN SISTER OF FT* (43). This was also demonstrated in rice, which flowered early under drought stress (41).

Ethylene (ET) and flowering

Extensive research has been conducted on ethylene, a gas-based phytohormone, as a regulator for flowering in plants (44). Ethylene is vital in the regulation of senescence, stress response, and flowering period in ethylene-sensitive flowers (45). Ethylene has been shown to limit blooming in *Arabidopsis* and *P. niloticus* (46). Ethephon, a tiny molecule that plants convert into ethylene, has been used commercially to stimulate pineapple flowering (47). Under SD, the role of ethylene in influencing flowering time has been demonstrated in *P. niloticus* (1,46). Mangoes are also produced commercially via ethylene-mediated initiation of flowering (48). There is evidence that ethylene controls floral growth and flowering time in roses (*Rosa hybrida* Samantha) (49). The change in the pattern of flowers in ethylene-related mutants was also linked to the expression of the FT gene, which regulates the timing of flowering (21). In *Arabidopsis*, there is a connection between GA and ethylene where ethylene slows down the degradation of DELLA proteins, resulting in delayed flowering (50).

Florigen and flowering

The blossoming of several plant types is influenced by the cooperation between basic leucine zipper (bZIP) transcription factors and florigen proteins that are transported throughout the system (51). Florigen, a protein hormone, has two roles in flower plants: systemic flowering enhancement in apical meristems and growth inhibition in other vegetative meristems (52). A signal that mobile FT protein, rather than its RNA, generated in leaves and transported to shoot apex has been proposed as a broad systemically inducer of flowering (53). There are also reports that additional "flowering genes," like *LEAFY*, had vegetative roles at first and were enlisted to control various facets of the newly emergent flowering system (54). Besides that, florigen in potatoes triggers the development of tubers, which are determinate structures, at the tips of stolons (55). High florigen levels in tomatoes promote early primary blooming, but the rate of flowering during the sympodial phase is only relatively impacted (56).

Conclusion

Valuable insights into the impact of hormones and other internal metabolites have been gained, but the initiating factors that control flowering through hormones have not been fully identified. Some factors that influence the timing of flowering are cytokinins and auxins, which tend to promote it, while ABA acts as an inhibitor. In Arabidopsis, ethylene can break dormancy in buds but may also hinder the transition to flowering. On the other hand, GAs are generally considered to be stimulators of flowering in annual plants. With the acceleration of climate change, it is essential to gain a better understanding of the shared and distinct characteristics of floral transition in plants.

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Authors' contributions

LMHT drafted the manuscript. LMHT participated in manuscript editing and coordination. The final manuscript was read and approved by the author.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

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