

Genetic regulation of stem elongation and thickening in ornamental plants: a review

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Abstract

The stem, a crucial organ that connects the root and aboveground parts, is responsible for transporting water and nutrients. This review synthesizes the current understanding of stem development in ornamental plants. We first outline the morphological and physiological characteristics of stem elongation and stem thickening. Subsequently, we examine the roles of key genes, plant hormones, and cell wall components in regulating stem growth, mechanical strength, and overall plant architecture. We also analyze how environmental factors (e.g. temperature, light, water, and nutrients) and hormonal and genetic networks modulate stem development. Particular emphasis is placed on the functions of auxin, gibberellins, and brassinosteroids. Recent studies in ornamental plants such as *Prunus*, *Chrysanthemum*, and *Paeonia* have illuminated the advances in cultivation techniques and gene identification associated with cellular processes, cell wall synthesis, hormone biosynthesis, and signal transduction. Looking forward, we highlight emerging research directions, including the use of advanced imaging and artificial intelligence for phenotypic analysis, and the integration of multi-omics data within a 'Breeding 5.0' framework. Ultimately, this review aims to support the targeted breeding of ornamental plants with optimized stem traits, enhancing both aesthetic value and production efficiency.

Introduction

Shoot architecture critically determines the morphology of the aboveground of ornamental plants, supporting their growth and ornamental value [1]. As an important aspect of shoot architecture, stem development plays a key role in transporting nutrients, water, and inorganic salts, and providing mechanical strength for plant growth. It involves two dimensions, longitudinal elongation and lateral thickening [2]. Stem elongation controls plant height, resulting in leaves capturing sunlight and the spread of pollen or seeds. An appropriate plant height is crucial for biomass accumulation, reproductive activities, and adaptability to different environments [3]. Cultivars with shorter stems generally exhibit higher yields and are economically beneficial for commercial value [4]. Stem thickness is closely related to the component alternation and anatomical characteristics. It gives rise to stem elasticity and rigidity, which determine the mechanical strength. In production, stem thickness is used as an important indicator for evaluating a plant's ability to resist lodging. Therefore, stem development is fundamentally important for plant growth and productivity [5, 6]. Recently, research on the stem development of ornamental plants has gradually increased, involving temperature regulation, hormone signaling, and molecular mechanism elucidation, which

provides an important theoretical basis and technical support for cultivation. In this review, we focus on the genetic regulatory mechanisms of stem development in ornamental plants, aiming to explore how new genes and mechanisms process stem architecture, as well as to propose current research hotspots and future directions.

Biological basis of stem development

The stem is an important nutritional organ of the aboveground parts of plants. It can transport nutrients and water between roots and leaves, and function in supporting organs such as leaves, flowers, and fruits [7, 8]. The location where leaves are attached to the stem is called a node, and the part between two nodes is called an internode [9, 10]. Stem development encompasses two parts: stem elongation and stem thickening. Appropriate plant height and mechanical strength of the stem are crucial to upright plant growth, enhance plant resistance to lodging, increase plant biomass, and ultimately increase production [11–13]. This stem development is functionally integrated with root architecture. Healthy roots supply water,

Received: 6 November 2025. Accepted: 9 April 2026. Published: 17 April 2026. Corrected and Typeset: 1 July 2026

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nitrogen, and nutrients necessary for sustained shoot growth [14, 15]. The plasticity of root traits is closely linked to the stability of shoot characteristics [16]. In turn, shoot architecture also influences root resource acquisition through carbon allocation priorities, and stem elongation often correlates with deeper root penetration to enhance lodging resistance [17]. In ornamental plant production, modification of stem development can cultivate dwarf potted varieties to increase their ornamental value [18, 19]. Therefore, the regulation of stem development has attracted increased attention and has been extensively studied.

Morphological and physiological characteristics of stem elongation

Stem elongation involves cell division (increasing the number of cells) and cell elongation (changing the cell size). The early stem elongation process is determined by the activity of the plant shoot apical meristem (SAM; shoot tip) [20, 21]. The SAM consists of the central zone (CZ), the organizing center (OC), and the rib zone (RZ) located below the CZ [22]. Among them, stem cell activity and cell division in the RZ region play important roles in stem elongation [23]. In the *Arabidopsis* SAM, the downregulated expression of cell cycle genes inhibits the division of stem elongation-related cells in the RZ [24] (Fig. 1A). The shape and size of the SAM also affect stem development. A larger SAM volume leads to early flowering and hinders stem elongation [25] (Fig. 1A). *FLOWERING LOCUS T* (*FT*) and *TERMINAL FLOWER 1* (*TFL1*) are two key genes involved in the SAM transition from vegetative growth to reproductive growth in plants. A high expression ratio of *FT/TFL1* promotes more vegetative meristems into inflorescence meristems, causing dwarf plant architecture [26].

During vegetative growth, plant height is determined by internode length (precisely cell length) and node number [27–29]. Histological observations of the internodes of dwarf mutants such as *semidwarf-1* (*sd1*) and *brassinosteroid insensitive 1* (*bri1*) show that the cell length is significantly reduced [30, 31]. The premise of internode cell elongation is loosening of the cell wall. The normal assembly of the cell wall can be influenced by the synthesis of cellulose, lignin, and other components (Fig. 1B). For example, mutations in genes encoding lignin synthases cinnamoyl-CoA reductase and cinnamyl alcohol dehydrogenase result in a severe dwarf phenotype [32, 33]. The expression of the transcription factor *MYB61* and cellulose synthase (*CesAs*) promotes cellulose biosynthesis, enhancing internode cell elongation [34, 35]. Additionally, cell elongation can be boosted by activating the expression of genes encoding *xyloglucan endotransglycosylase* (*XET*) and *expansin* (*EXP*) proteins, which cleaves xyloglucan polymers and destroy polysaccharide adhesion, thereby enhancing the loosening of the cell wall [36–38] (Fig. 1B). Multiple basic helix-loop-helix (bHLH) transcription factors, including *ILI1 BINDING bHLH PROTEIN1*, *PACLOBUTRAZOL-RESISTANT1*, and *HOMOLOG OF BEE2 INTERACTING WITH IBH1*, are jointly involved in the transcription of cell wall loosening-related genes, contributing to the elongation and growth of internode cells [39–41].

In some monocots, the primary meristem left over from the SAM is retained at the base of the internodes, namely, the intercalary meristem (IM). During the reproductive growth period, plants can undergo intercalary growth through the activity of the IM, caus-

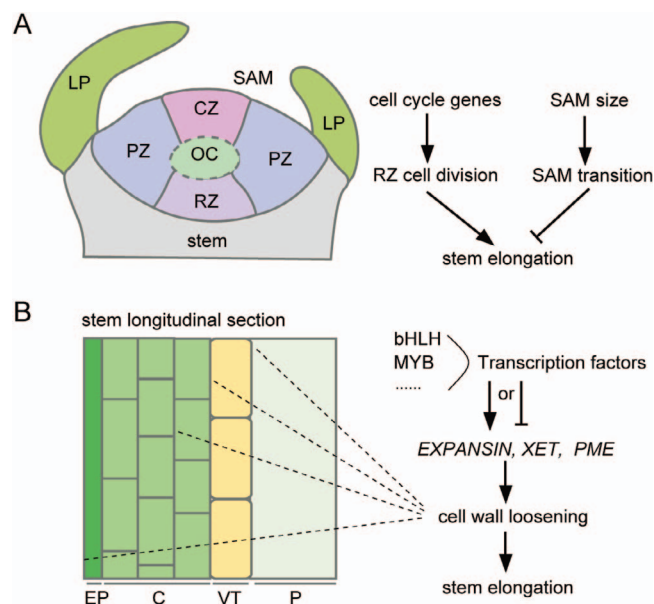


Figure 1 Genetic regulation of stem elongation. Stem elongation is determined by (A) early cellular activities in the shoot apical meristem (SAM) and (B) subsequent internode cell expansion. (A) SAM consists of central zone (CZ), organizing center (OC), and rib zone (RZ). Cellular activity in the RZ contributes to stem elongation, where cell division driven by cell cycle genes promotes elongation. An enlarged SAM accelerates the transition from vegetative to reproductive growth, which negatively impacts stem elongation. (B) Internode elongation depends on cell wall loosening. Transcription factors such as bHLH and MYB regulate the expression of *EXPANSIN*, *XYLOGLUCAN ENDOTRANSGLUCOSYLASE* (*XET*), and *PECTIN METHYLESTERASE* (*PME*), thereby modulating the degree of cell wall loosening and subsequently influencing cell and stem elongation. Note: EP, epidermis; C, cortex; VT, vascular tissue; P, pith. Arrows indicate positive regulation or promotion, while lines ending with vertical bars represent repression.

ing dramatic stem elongation [42, 43]. Cell division, cell elongation, cell wall composition, and cytoskeleton activities in the IM collectively affect node number and internode length. In maize, both the *TERMINAL EAR 1* and *BELL1-like homeobox 12/14* genes are highly expressed in the IM. Their loss-of-function mutants present a dwarf phenotype with disordered IM development [44, 45]. Although multiple genes that regulate the homeostasis maintenance of the IM have been identified, the formation of the IM in ornamental plants and the detailed underlying mechanisms are still unclear.

Morphological and physiological characteristics of stem thickness

Stem thickness is primarily determined by secondary growth, a developmental process driven by the activity of vascular and cork cambium (Fig. 2). This process produces secondary vascular tissues (secondary xylem and secondary phloem) and the periderm through vascular cambium and cork cambium activity [46, 47]. Through cell division, differentiation, and secondary cell wall deposition, this process increases stem diameter and confers significant mechanical strength (Fig. 2A). Stem strength is the key agronomic trait for plants to resist pests and lodging and is

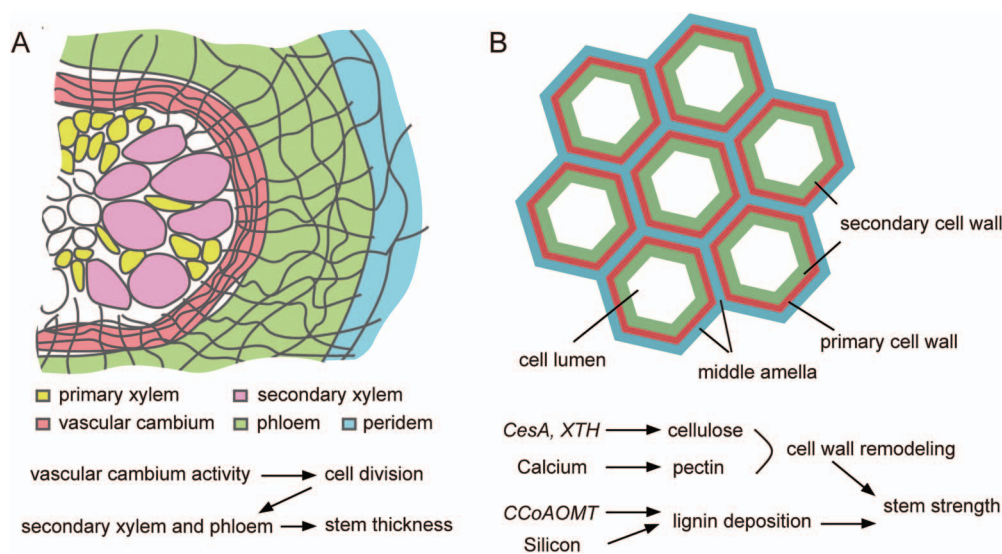


Figure 2 Cellular and molecular mechanisms underlying stem thickness. (A) Cross-section of stem showing secondary growth driven by vascular cambium activity. Cell division in the vascular cambium produces secondary xylem and secondary phloem, leading to increased stem thickness. (B) Structural components of plant cell wall contribute to mechanical strength and thickness. *CELLULOSE SYNTHASE* (CesA) and *XYLOGLUCAN ENDOTRANSGLUCOSYLASE/HYDROLASE* (XTH) promote cellulose synthesis; Ca^{2+} binds to pectin and supports cell wall integrity; silicon and 3-O-METHYLTRANSFERASE (CCoAOMT) positively regulate lignin deposition into the cell wall. Together, these components enhance the structural integrity and mechanical strength of the stem.

influenced by the number and arrangement of vascular bundles, secondary cell wall thickness, and lignin content [13, 48].

The synthesis of secondary cell walls is crucial to mechanical strength (Fig. 2B). Moreover, the cell wall provides the elasticity required for cell expansion by stretching itself, absorbs new polysaccharide polymers to maintain its thickness and toughness, and provides rigid support for plant tissues and organs [49,50]. The cell wall consists of cellulose, hemicellulose, pectin, protein, and mineral elements such as calcium and silicon. Cellulose is the main component of the cell wall from the cellulose synthase complex on the plasma membrane [51]. The CesA family plays an important role in the synthesis of both primary and secondary cell walls [52] (Fig. 2B). Hemicellulose or pectin side chains in cellulose microfibrils can change the properties of cellulose and reduce its mechanical strength, ultimately causing the bending of plant stems. In a study on six kinds of cut flowers, including lotus, water lily, rose, gerbera, lisianthus, and carnation, the existence of hemicellulose or pectin side chains in curved stems, not upright stems, disrupted the crystallinity, purity, and length of cellulose, resulting in the acceleration of cell wall degradation and decreased mechanical strength [53, 54].

In the comparative analysis of large and small lotus stems, the differentially expressed xyloglucan endotransglucosylase/hydrolase genes (XTH) are identified as an important gene family involved in cell wall remodeling in lotus architecture formation (Fig. 2B). The overexpression of XTHs blocks the gravity response during the development of the secondary cell wall, decreasing the stem's mechanical strength [55, 56]. Lignin can enhance the rigidity and compressive strength of cell walls by filling the interstitial spaces between cellulose microfibrils. Many studies have focused on how to regulate the mechanical strength of ornamental plant stems by altering the lignin content. In herbaceous peony, there is a significant positive correlation between mechanical strength and lignin content [57, 58]. In addition, the lignin synthase 3-O-methyltransferase (CCoAOMT) gene is highly expressed in xylem

tissues in *Forsythia*. The overexpression of *FsCCoAOMT* enhances the stem mechanical strength [59] (Fig. 2B).

Calcium is an indispensable component of the cell wall, where Ca^{2+} can bind with the free carboxyl groups in pectin to form stable complexes, thereby improving the rigidity and stability of cell walls [60] (Fig. 2B). Ca^{2+} reduces the ethylene level produced by gravity and significantly inhibits bending in *Antirrhinum majus* [61]. In gerbera and herbaceous peony, exogenous Ca^{2+} treatments improve stem quality by increasing stem strength and reducing bending [62–64]. Silicon is present in the tissues of nearly all terrestrial plants and is primarily deposited as amorphous silica in specific cell walls [65] (Fig. 2B). It plays a key role in the assembly and remodeling of cell walls [66]. In herbaceous peony, silicon application enhances stem strength by promoting lignin accumulation [67].

Furthermore, a reasonable stem structure enhances plant adaptability to abiotic stresses. Specifically, stem secondary development enhances drought tolerance by modulating vessel density and lignin deposition to optimize water transport efficiency [68]. Specialized stem porous structure enhances wind resistance by effectively dissipating the load [69, 70]. Additionally, the specific xylem secondary growth patterns regulate ion transport, which helps maintain ionic homeostasis and improves salt tolerance [71]. Overall, stem secondary development not only underlies morphological maturation but also provides an integrated structural foundation for adaptation to biotic and abiotic challenges (Fig. 2).

Effects of hormones on the development of ornamental plant stems

Plant hormones are crucial regulators of stem development in ornamental plants. Among them, auxin, gibberellins (GAs),

and brassinosteroids (BRs) are three important plant growth-promoting hormones that significantly control plant height by regulating stem cell division, cell elongation, and tissue differentiation. In horticultural production, chemical plant growth regulators (PGRs) are commonly employed to control plant height, as detailed in Table 1.

Auxin is crucial for stem development

Auxin plays a central role in promoting cell division, extension, and differentiation during plant growth [90, 91]. Through an elaborate network of biosynthesis, polar transport, and signal transduction, auxin establishes a tissue-specific concentration distribution pattern, regulating stem elongation and secondary growth (Table 1; Fig. 3).

Auxin biosynthesis mainly takes place in the SAM and young leaves. Exogenous application of Indole-3-acetic acid (IAA) can significantly promote flower stem elongation [92]. Subsequently, auxin is polarly transported to specific tissues via PIN-FORMED (PIN) proteins, resulting in well-defined spatial distribution patterns [93], and accurately coordinate the differentiation ratio of xylem and phloem in the cambium [94, 95] (Fig. 3). The physiological functions of auxin are ultimately executed through its signal transduction pathway, achieving precise control over downstream target gene expression. The classical signaling pathway includes auxin receptors (TRANSPORT INHIBITOR RESPONSE 1/AUXIN SIGNALING F-BOX PROTEIN, TIR1/AFB), Aux/IAA transcriptional repressors, and AUXIN RESPONSE FACTOR (ARF) proteins [96]. Mutations in IAA genes can lead to dwarf phenotypes in *Brassica napus* [97, 98] (Table 1).

Gibberellins regulate stem internode elongation

GAs are widely involved in all stages of stem development of ornamental plants. They are mainly synthesized in SAM, root meristem, seed, and fruit [99]. The application of GA synthesis inhibitors such as paclobutrazol has been demonstrated to effectively induce dwarfism in pot flowers and increase their ornamental value [84] (Table 1; Fig. 4). The precursor substance is geranylgeranyl pyrophosphate (GGPP), which is converted into active gibberellins GA₁, GA₃, GA₄, and GA₇ through a series of enzymatic reactions [100]. GAs promote cell elongation and expansion by mediating cell wall elasticity and regulate the xylem/phloem ratio in the vascular cambium [94].

In *Arabidopsis*, mutations in early GA synthesis-related genes (*ent-copalyl diphosphate synthase*, *CPS*; *ent-kaurene synthase*, *KS*; *ent-kaurene oxidase*, *KO*; *ent-kaurenoic acid oxidase*, *KAO*) result in a severe dwarf phenotype, whereas mutations of later GA synthesis-related genes (*GA20oxidas*, *GA20ox*; *GA3oxidas*, *GA3ox*) result in a semidwarf phenotype, and dwarf defects can be restored by exogenous treatment of GAs [101–103]. In *Chrysanthemum*, GA₄ accumulation is high in elongating internodes, and B-type GA receptor genes are abundantly expressed in both the internodes and leaves of extending shoots [104]. Knock-down mutants of *CmGA20ox* [105] and *CmGA3ox* [106] can form dwarf chrysanthemum varieties. GA₂ oxidases (*GA2ox*) are involved in the catabolism of GA to maintain homeostasis. Comparative transcriptome analysis of dwarf and normal varieties revealed

that the overexpression of *GA2ox* caused a semi-dwarf phenotype in chrysanthemum [107] and *Prunus* species [108].

In GA signaling, GAs can relieve the inhibition effect of DELLA proteins on plant growth through the GA receptor GIBBERELLIN-INSENSITIVE DWARF1 (GID1) [103, 109]. In *Arabidopsis*, *gid1* mutants show shorter stems [110]. Moreover, DELLA proteins are unable to perceive GA signals, resulting in short stems, dark green leaves, and late flowering [111]. The heterologous overexpression of the *Arabidopsis GIBBERELLIN INSENSITIVE (GAI)* gene in chrysanthemum can be used to cultivate dwarf lines [112]. In the future, manipulating GAs and their inhibitors in the cultivation of ornamental plants can effectively control plant height, breed novel varieties, and improve ornamental value.

Brassinosteroids participate in cell wall remodeling and promote stem elongation

BRs are a type of sterol hormone widely found in plants that regulate important agronomic traits such as leaf angle and plant height. In the early stage of cell elongation, the cell wall loosening genes *XTHs* and *EXPs* are induced by BRs and then promote cell wall remodeling and cell expansion during stem growth [113, 114]. Moreover, BRs induce the synthesis of the receptor-like protein kinases HERCULES receptor kinase 1 and THESEUS1, which are required for the expression of *XTHs* and *EXPs* in the cell wall remodeling process and stem elongation [115].

Dwarf mutants that are defective in BRs biosynthesis or signaling pathways exhibit hypocotyl shortening and reduced plant height, while exogenous BR treatment can restore abnormal phenotypes, indicating that BRs play a key role in stem development [116, 117] (Table 1; Fig. 4). The key transcription factor BRI1 EMS SUPPRESSOR1/BRASSINAZOLE RESISTANT1 (BES1/BZR1) in the BR signaling pathway, directly regulates the expression of cell cycle-related genes, promoting cell division and stem elongation [118] (Fig. 3). In the study of ornamental plants, the analysis of differentially expressed gene in the dwarf plants *Dendranthema morifolium* and *Agapanthus praecox* revealed that the BR content and the expression of BR-related genes were reduced, suggesting that dwarf cultivars can be bred by regulating BR content and signaling [83, 105] (Table 1).

Hormone signaling crosstalk synergistic regulation of stem development

In plants, the continuous division and differentiation of the vascular cambium during stem development are precisely coordinated by multiple plant hormone signaling pathways. Among them, auxin not only maintains the activity of cambium stem cells but also serves as a core signaling hub, establishing extensive crosstalk with other key hormones such as GAs, BRs, and ethylene, jointly regulating the fate determination and tissue differentiation of the cambium [119] (Fig. 3).

The integration among these hormone pathways often depends on specific transcriptional regulatory modules. In *Arabidopsis thaliana*, the BRASSINAZOLE RESISTANT-AUXIN RESPONSE FACTOR-PHYTOCHROME INTERACTING FACTORS (BZR-ARF-PIF) module regulates cell elongation genes to control hypocotyl elongation, with DELLA proteins acting as repressors of this module [120, 121]. The BRASSINAZOLE RESISTANT1/2-WALLS ARE

Table 1 Hormone treatments regulate the stem development in ornamental plants.

Treatment	Concentration	Species	Effect ^a	Mechanism	Reference
Brassinolide (BL)	0.02, 0.04, 0.06, 0.08, and 0.1 mg·l ⁻¹ BL	<i>Matthiola incana</i>	Positive	0.06 and 0.08 mg·l ⁻¹ BL promoted plant height, stem diameter, fresh weight, and chlorophyll content.	[72]
	0.05 mmol·l ⁻¹ 2,4-epibrassinolide (EBR)	<i>Lilium</i> hybrid	Positive	BL spraying promotes plant height and dry weight	[73]
Cytokinin	0.67 mM (6-BA) 6-benzyladenine	<i>Paulownia</i> ssp.	Positive	6-BA stimulated stem elongation and induced a transient stem thickening 1 week after application.	[74]
	0.002 mg·l ⁻¹ Thidiazuron (TDZ)	<i>Rhododendron aureum</i>	Positive	The combination of 0.002 mg·l ⁻¹ TDZ + 0.5 mg·l ⁻¹ IBA was optimal for stem elongation <i>in vitro</i> .	[75]
	10, 20, 40, 80, and 100 μM TDZ	<i>Rosa hybrida</i>	Dual-effect	100 μM TDZ reduced new shoot length to half that of the control while increasing stem diameter by ~40%.	[76]
	150 mg·l ⁻¹ GA ₃	<i>Anemone</i> spp.	Positive	GA ₃ significantly affected stem height, number of leaves, and flower behavior.	[77]
Gibberellin	50, 100, and 150 mg·l ⁻¹ GA ₃	<i>Cyclamen africanum</i>	Positive	150 mg·l ⁻¹ GA ₃ significantly increased plant height and petiole length.	[78]
	100 and 200 mg·l ⁻¹ GA ₃	<i>Phalaenopsis</i> spp.	Dual effect	GA ₃ increased stem length and decreased stem diameter.	[79]
	10, 25, and 50 ml Promalin (50 mg·l ⁻¹ each GA ₄ +7 and BA)	<i>Lilium longiflorum</i>	Positive	Root-absorbed GA ₄ +7 (25 and 50 ml) promoted stem elongation, with spray volumes >10 ml per plant increasing over-elongation risk.	[80]
	GA ₄ +7, GA ₃ , PBZ (1, 10 and 100 l ⁻¹)	<i>Cyclamen persicum</i>	Positive	GA ₃ could always increase plant height under different photoperiods and temperatures.	[81]
Gibberellin inhibitor	0.25, 0.5, 1, or 2 mg·l ⁻¹ Paclobutrazol (PBZ)	<i>Iris nigricans</i>	Negative	PBZ at 0.5 or 1 mg·l ⁻¹ caused severe dwarfism, characterized by drastic reductions in stalk height and weight.	[82]
	400 mg·l ⁻¹ PBZ	<i>Agapanthus praecox</i>	Negative	400 mg·l ⁻¹ PBZ shorten the scape length over 70%.	[83]
	100, 300, and 500 mg·l ⁻¹ PBZ	<i>Lilium longiflorum</i>	Negative	Plants are more severely suppressed and become shorter as PBZ concentration increases.	[84]
	30 mg·l ⁻¹ PBZ	<i>Cyclamen</i> sp.	Negative	PBZ produced a smaller plant height and peduncle length.	[85]
	50, 150, and 300 mg·l ⁻¹ Uniconazole (UCZ)	<i>Curcuma alismatifolia</i>	Dual-effect	UCZ-treated plants exhibited obviously decreased plant height and scape length, while stem diameter increased slightly.	[86]
Melatonin	0.5 mM Melatonin once a week	<i>Paeonia lactiflora</i>	Positive	Melatonin treatment enhanced stem strength, lignin content, and secondary cell wall thickness.	[87]
Methyl jasmonate	200 mg·l ⁻¹ MeJA	<i>Salix purpurea</i>	Positive	MeJA significantly increased plant height, shrub diameter, and branch diameter.	[88]
Flurprimidol	0.02, 0.04, 0.08, 0.16, and 0.24 mg per pot	<i>Lilium longiflorum</i>	Negative	Flurprimidol drenches suppressed lily height by up to 59% in a dose-dependent manner, with no effect on flowering.	[89]

^a Effect categories: positive = promotes the stem developmental process(es) (elongation and/or thickening); negative = suppresses the stem developmental process(es) (elongation and/or thickening); dual-effect exerts opposing actions on elongation and thickening. Control plants were treated with distilled water.

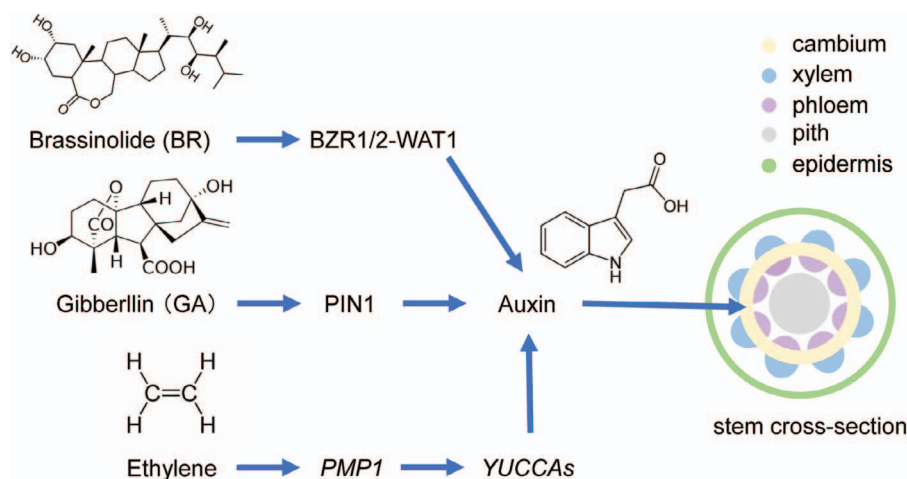


Figure 3 Plant hormones crosstalk coregulates the differentiation of cambium stem cells into xylem. Brassinosteroid (BR) signaling, acting through the BRASSINAZOLE RESISTANT1/2-WALLS ARE THIN1 (BZR1/2-WAT1) module, promotes local auxin accumulation. Gibberellin (GA) upregulates the auxin transporter PIN-FORMED 1 (PIN1) to facilitate auxin polar transportation, while ethylene induces *PETAL MOVEMENT-RELATED PROTEIN 1* (PMP1), which activates *YUCCA* genes to stimulate auxin biosynthesis. Consequently, auxin functions as a central signal to direct cambial cell fate toward xylem differentiation. Note: Stem cross-section illustrates the spatial organization of distinct tissue regions. Each color corresponds to a specific tissue type in the legend.

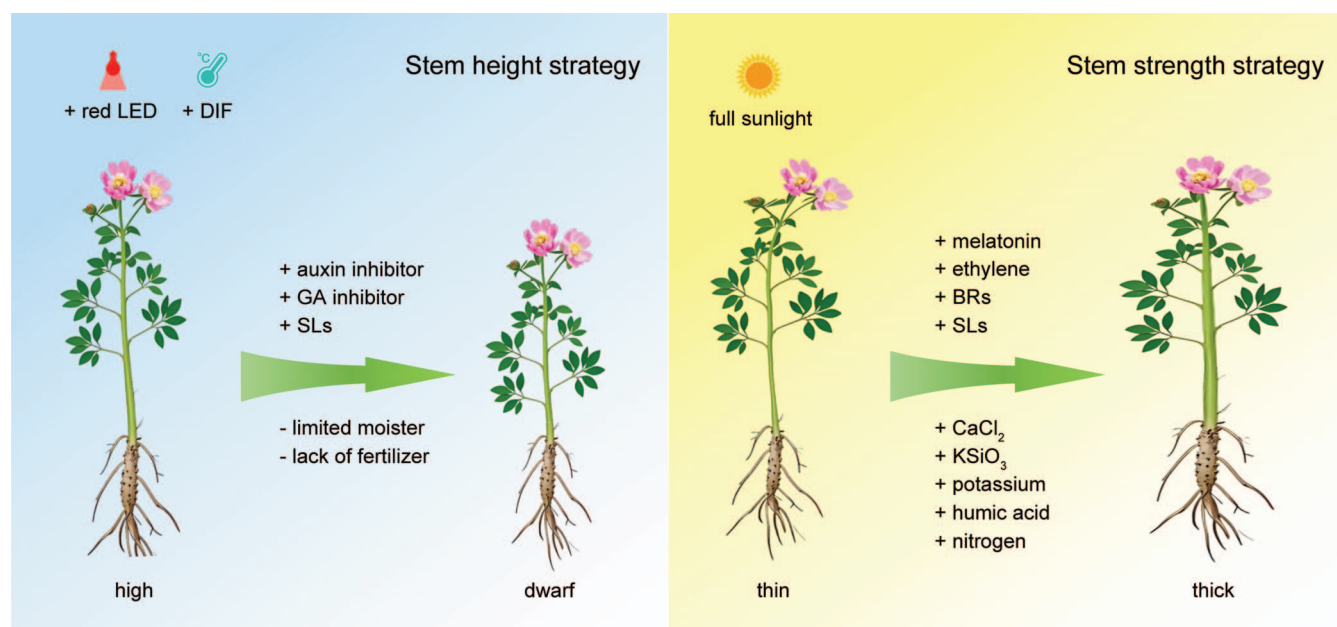


Figure 4 Strategies for regulating plant architecture of ornamental plants. Two key horticultural approaches are illustrated: stem height control (left side) and stem strength enhancement (right side). For stem height control, dwarfing can be achieved under red LED light, positive day and night temperature (DIF) conditions, exogenous plant growth regulators (auxin inhibitors, GA inhibitors, and SLs), and environmental factors (limited moisture and fertilizer deficiency). For the stem strength strategy, stem thickening can be enhanced under full sunlight, exogenous plant growth regulators (melatonin, ethylene, BRs, and SLs), and nutritional supplements (e.g. CaCl_2 , KSiO_3 , potassium, humic acid, and nitrogen). Note: The '+' symbol indicates the presence of treatments. The '-' symbol indicates the absence of treatments or limited condition.

THIN1 (BZR1/2-WAT1) module promotes xylem differentiation in the vascular cambium by increasing local auxin signaling level [122]. In addition, BRs synergistically interact with GAs and auxin coregulates stem development [123–125].

GAs can reinforce auxin signaling, promoting cambium homeostasis. ARF7 mediates interactions between DELLA and auxin signaling ARF/IAA proteins to regulate cambial activity [126]. GAs promote *PIN1* expression in the vascular tissues, causing cambium stem cells to preferentially differentiate into xylem cells [94]. This hormonal synergy is particularly evident during wound-induced

regeneration; in grafting and peeling processes, the auxin signal integrates with GAs to promote the regeneration of vascular cambium [127, 128].

Notably, this multi-hormone integration mechanism also operates in ornamental plants. In rose, ethylene-induced *PETAL MOVEMENT-RELATED PROTEIN 1* (*RhPMP1*) upregulates the auxin synthesis genes *RhYUCCA3* and *RhYUCCA4* to maintain the activity of stem cells in the cambium [129]. This further illustrates how distinct hormonal pathways effect on local auxin distribution pattern to regulate stem development.

Other hormones participate in the regulation of stem development

In addition to auxin, BRs, and GAs, other plant hormones such as cytokinins (CTKs), strigolactones (SLs), and ethylene are involved in regulating the development of plant stems. Many studies have revealed that exogenous hormone treatment efficiently improves the stem phenotype of ornamental plants.

CTKs affect stem growth mainly by regulating cell division and elongation. In *Arabidopsis*, Cytokinin B response factors can directly activate the expression of the stem cell maintenance genes *WUSCHEL* and *CLAVATA*, enhancing the activity of the SAM [130, 131]. Moreover, CTK treatment promotes cell division by regulating the expression of the cell division cycle-related genes *CYCLINS*, laying a foundation for stem development [132]. In switchgrass, the increase in CTK and GAs can promote cell elongation and vascular bundle development, thereby increasing plant height [133].

SLs play dual regulatory roles in stem development by modulating both primary elongation and secondary growth (Table 1). During early stem elongation, SLs specifically inhibit hypocotyl elongation by promoting the accumulation of the ELONGATED HYPOCOTYL 5 (HY5) protein [134]. In contrast, during secondary growth, SLs convert long-distance auxin signals from the shoot apex into cellular division and differentiation responses, directly promoting cambial cell division and the proliferation of xylem and phloem, thereby driving stem thickening [135]. In addition, SLs negatively regulate shoot gravitropism, change the stem angle, and subsequently alter plant photosynthetic efficiency [136].

In dicots, ethylene stimulation leads to a triple response: inhibiting stem elongation, hypocotyl swelling, and apical hook exaggeration (Fig. 4). In stem development, ethylene controls the activity of vascular cambium stem cells by promoting auxin biosynthesis. In woody rose, ethylene affects auxin synthesis *RhYUCCA10* and auxin transporter protein *RhAUX2* by regulating *RhPMP1*, promotes stem cambium activity, and accumulates auxin in the cambium near the xylem [129]. The ethylene response factors ERF11 and ERF109 integrate auxin and gibberellin biosynthesis pathways to suppress internode elongation. In addition, ethylene can induce microtubule reconstruction to enhance hypocotyl elongation [137, 138]. In contrast, ethylene promotes stem elongation under water stress. Flooding causes an increased accumulation of ethylene in the stems, which promotes the synthesis and signal transduction of GAs and rapid stem elongation to resist stress. These studies show that ethylene has a dual effect on stem elongation [139–141].

Effects of environmental factors on stem development

Optimizing temperature management to regulate internode elongation in ornamental plants

Temperature is one of the key environmental factors affecting the development of ornamental plant stems [142] (Table 2). The temperature-dependent growth responses are not merely phys-

iological adjustments but are based on conserved thermosensing mechanisms. In *Arabidopsis*, four major thermosensors, Early Flowering 3 (ELF3), UV Resistance Locus 8 (UVR8), cryptochrome 2 (CRY2), and Phytochrome B (PhyB), work synergistically to enable plants to perceive temperature changes [143]. The thermosensors activate downstream signaling cascades involving key transcription factors such as PHYTOCHROME-INTERACTING FACTOR 4 (PIF4), which integrates hormonal pathways, including auxin, GAs, ethylene, and BRs, to promote cell elongation and modulate stem growth [144].

In orchid production, the growth rate of plant stems can be regulated by adjusting the day temperature [162]. Low temperature can inhibit hypocotyl and stem elongation. For example, warm-water treatment of lily bulbs can promote their vegetative growth and significantly increase plant height [161]. In chrysanthemum, internode length is dependent on the difference between day and night temperature (DIF) [163]. By plotting the curves showing that internode elongation changes with temperature and establishing a prediction model and formula for internode length, it was found that DIF and the absolute temperature independently regulate internode length. When DIF is positive (daytime temperature is higher than the nighttime temperature), the chrysanthemum internode length increases. Conversely, a negative DIF inhibits internode elongation, causing plant dwarfing [164] (Table 2; Fig. 4). Recent studies have focused on the reasonable regulation of DIF and absolute temperature levels to accurately manage the stem growth of ornamental plants [165].

Light intensity, light quality, and photoperiod intricately regulate stem development

Light plays an important role in plant growth. It provides energy for plant photosynthesis and acts as a signal to regulate plant photomorphogenesis, including cell differentiation, stem elongation, and secondary growth. Plants perceive light through specific photoreceptors: CRY sense blue light, phytochromes (Phy) detect red (R) and far-red (FR) light, and UVR8 perceives ultraviolet-B. These receptors initiate signal transduction involving key regulators such as transcription factors PIFs, E3 ubiquitin ligase CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1), and HY5, ultimately modulating downstream gene expression and physiological responses [166]. Appropriate light conditions (i.e. light quality, light intensity, and photoperiod) can promote leaf photosynthesis and provide sufficient nutrients and energy for stem growth [167–169] (Table 2).

To cope with light competition, plants can adjust their stem elongation to the growth of surrounding vegetation under low-light conditions, which is referred to as the shade avoidance reaction (SAR) [170]. Light signaling pathways are closely integrated with hormonal networks; for instance, under shade conditions, the synthesis and signaling of auxin, GA, SL, and ethylene are enhanced, collectively reshaping shoot architecture [171]. In sun-loving plants such as *B. napus*, the elongation of stem internodes and petioles is accelerated, the number of branches decreases, and flowering occurs earlier through SAR, while high light intensity reduces plant height [172, 173].

Table 2 Effects of environmental factors on stem development.

Factor	Treatment	Control	Species	Effect	Mechanism	Reference
Moisture	Drought-stressed plant	Well-watered plant	<i>Hibiscus acetosella</i>	Stem elongation	Limited moisture reduced stem elongation by 44% and final plant height by 21% compared to well-watered conditions.	[145]
	50% of the control, 25% of the control	—	<i>Callistemon citrinus</i>	Stem elongation and thickening	Limited moisture led to a reduction of 12% of total biomass, reduce both stem diameter and plant height.	[146]
Light quality	Blue light: 16-h light/8-h dark	White light	<i>Chrysanthemum morifolium</i>	Stem thickening	After 60 days of blue light treatment, plants had thinner stems than controls.	[147]
	Green LED, Red LED, Blue LED, and Mix RGB light	White light	<i>Tulipa</i> sp.	Stem elongation	Green and blue light produced longer stems and internodes than red or RGB light. Red and RGB light produced the shortest stems at full bloom.	[148]
	20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ Red LED	White light	<i>Chrysanthemum morifolium</i>	Stem elongation	Red light resulted in shorter stems and poorer-quality branches than constant light.	[149]
	EOD-Far Red (FR) light	Ambient light	<i>Eustoma grandiflorum</i>	Stem elongation	EOD-FR enhanced stem elongation, specifically increasing the length of internode and pith cell.	[150]
	630 nm EOD Red light 730 nm EOD FR light	Cool white light	<i>Euphorbia pulcherrima</i>	Stem elongation	30 min EOD Red light resulted in a 34% ~ 54% reduction of shoot and internode length compared to EOD FR treatment.	[151]
	High-pressure sodium lamps with 600–700 nm red LED or 400–500 nm blue LED	High-pressure sodium lamps	<i>Petunia</i> sp.	Stem elongation	Blue light promoted stem elongation, caused upright shoot orientation; however, red light reduced shoot elongation	[152]
	700 ~ 800 nm FR light 40 $\mu\text{mol m}^{-2} \text{s}^{-1}$	White light	<i>Antirrhinum majus</i> <i>Zinnia elegans</i>	Stem elongation	FR treatment increased the seedling height of <i>A. majus</i> by 64% ~ 134% and <i>Z. elegans</i> by 52% ~ 96% than controls.	[153]
Light intensity	20% natural light	Natural light	<i>Chrysanthemum morifolium</i>	Stem elongation	Under 20% natural light treatment, the internode length increased. The epidermis and cortical and vascular bundle cells were deformed.	[154]
	60% natural light	Natural light	<i>Paeonia lactiflora</i>	Stem elongation and thickening	Plants exposed to full sun exhibited greater plant height, stem diameter, branch number, and node number than those in shade.	[58]

(Continued)

Table 2 Continued

Factor	Treatment	Control	Species	Effect	Mechanism	Reference
Fertilizer	Four solutions $\text{NH}_4^+ - \text{N} : \text{NO}_3^- - \text{N}$	$\text{NH}_4^+ - \text{N} : \text{NO}_3^- - \text{N} = 0:100$	<i>Lilium oriental</i>	Stem elongation and thickening	$\text{NH}_4^+ - \text{N} : \text{NO}_3^- - \text{N} = 25:75$ (N_3) treatment had the highest values in plant height and flower diameter	[155]
	1000 $\mu\text{L/l}$ $\text{CO}_2 + 0.85 \mu\text{L/l}$ NO_x for 42 days	1000 $\mu\text{L/l}$ CO_2 for 42 days	<i>Rosa</i> sp.	Stem elongation	NO_x addition resulted in shorter stems in roses	[156]
	Purified phytase enzyme (0 EU, 5 EU, 10 EU) soaking 15, 30, and 60 min	Distilled water	<i>Brassica oleracea</i>	Stem thickening	10 EU of purified phytase enzyme produced the highest stem diameter under 30 and 60 min treatments.	[157]
	140 $\text{g} \cdot \text{m}^{-3}$ KSiO_3	Complete fertilizer without KSiO_3	<i>Helianthus annuus</i>	Stem elongation and thickening	KSiO_3 treatment plant showed thick, straight stems, increased flower and stem diameters, and increased height compared to the control group.	[158]
	Humic acid at 1:600 (v/v) concentration	0.3% NPK fertilizer ($\text{N}:\text{P}_2\text{O}_5:\text{K}_2\text{O} = 16:6:20$)	<i>Chrysanthemum morifolium</i>	Stem thickening	Humic acid obviously improved stem diameter and shoot weight compared to the control and the NPK fertilizer.	[159]
Photoperiod	Different photoperiods 8, 10, 12, 14, 16, or 18 h	—	<i>Salvia exserta</i>	Stem elongation	A photoperiod over 8 h increased plant height by 22%–55% and 14 h of light increased node number.	[160]
Temperature	Six soaking temperatures and times in warm water	—	<i>Lilium oriental</i>	Stem elongation	Bulbs treated with warm water (48°C for 3 min, repeated three times) and then in 45°C water for 30 min improved plant height.	[161]

Different light wavelengths trigger distinct regulatory pathways in stem development. Blue light regulates plant phototropism, chloroplast migration, and leaf expansion [174]. In canola, irradiation with 400 ~ 500 nm blue light increases plant height but makes stems thinner [172]. Overexpression of the blue light receptor *CRYPTOCHROME 1* (*CRY1*) inhibits cell elongation in the hypocotyl [175]. Green light participates in the photosynthesis process to promote leaf development and stem elongation while reducing plant biomass production [148, 176]. Moreover, red light is involved in photosynthetic organ development and assimilate transport. The overexpression of phytochrome B1 (*PhyB1*) in chrysanthemum can hinder plant vegetative growth and reduce plant height [177].

In addition to light quality, photoperiod also plays a key role in regulating stem growth and has significant implications for production costs. Cultivars with long photoperiods increase production costs, and a reasonable short-day treatment or the selection of short-photoperiodic varieties could help control costs. Chrysanthemum flowers are sensitive to both photoperiod and light quality [178]. Therefore, understanding the interaction between light quality and photoperiod is essential for optimizing plant architecture and improving economic efficiency in production.

Water and fertilizer affect stem quality by influencing cell turgor pressure and mechanical strength, respectively

Water is essential for maintaining cell turgor pressure [179]. Adequate water promotes stem thickening and elongation and improves plant lodging resistance. Moreover, water is involved in various physiological processes such as photosynthesis and respiration, providing the necessary material and energy basis for stem growth (Table 2; Fig. 4). Insufficient water will decrease the turgor pressure of stem cells, making the stems thin and weak [180]. In *Penstemon* × ‘Ruby Candle’, the lack of water results in short internodes [181]. Conversely, excessive water supply in *Prunus* species leads to poor soil aeration, weak root functions, and plant diseases and then hinders stem development [182].

Fertilizers are important substances for maintaining plant growth and increasing productivity [183]. Adequate fertilization supplies nutrients for stem elongation and stem thickening, while overuse of fertilization is harmful to plants, soil, water, and the environment [184]. Poinsettia and chrysanthemum [185]. In addition, potassium (K) and silicon (Si) fertilizers increase stem thickness, enhance mechanical strength, and improve the photosynthetic efficiency of ornamental plants. High potassium treatment promotes photosynthesis, seedling growth, and flowering in chrysanthemum. In addition, the application of silicon fertilizer to petunia makes stem epidermal cells siliconized and enhances stem mechanical strength, causing straight stems and improved lodging resistance [186–188] (Table 2).

Therefore, in the ornamental plant cultivation process, adjusting water and fertilizer supplies according to the growth demand and environmental conditions results in a higher stem quality (Fig. 4).

Multi-omics and genetic transformation studies of stem development in ornamental plants

Integrated multi-omics analyses insights into stem development in ornamental plants

Stem development in ornamental plants is a complex biological process that is regulated by a combination of genetic and environmental factors. Recent advances in omics techniques (genomics, transcriptomics, metabolomics, and proteomics) have provided an effective approach for studying the underlying regulatory mechanisms [189–191].

Genome sequencing has laid a foundational resource for ornamental plant research, enabling comprehensive characterization of genome architecture, identifying genetic variation, elucidating phylogenetic evolution, and deciphering population structure. These insights further enable the prediction of population responses to future environmental changes [192] and lay the foundation for the identification of functional genes [193]. For example, whole-genome sequencing of multiple *Prunus* species has identified many quantitative trait loci (QTL), markers and genes such as *PmTAC1* linked to plant architecture, such as weeping [191, 194, 195] (Table 3).

Given the cellular complexity of developing stems, single-cell RNA-sequencing (scRNA-seq) and spatial transcriptomics technologies now provide unprecedented resolution to dissect distinct cell types and their spatial organization. By enabling high-resolution analysis of gene expression at the individual cell level, these approaches clarify cell-type-specific programs driving morphogenesis [204]. These techniques are particularly valuable for dissecting the cellular programs governing ornamental stem traits, such as internode elongation, vascular patterning, and secondary growth. For instance, scRNA-seq has been utilized to construct a developmental trajectory in the stem-differentiating xylem of *Liriodendron chinense* and *Trochodendron aralioides*, identifying specialized cell types like ray and fusiform initials and providing insights into xylem cell evolution [205].

Moreover, integrating the multilayered data, such as transcriptomic, metabolomic, and proteomic profiles, can reveal the inter-relationships among gene expression, metabolite changes, and protein functions, constructing a systematic regulatory network for stem development (Table 3). Therefore, the application of omics technologies provides important clues for in-depth studies of stem development in ornamental plants.

Genetic transformation advances in ornamental plant stem development

With the development of molecular technology innovations and biotechnology applications, such as transcriptome analysis, genome-wide association study (GWAS), and the clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein 9 (Cas9) (CRISPR/Cas9) system, the functions of numerous genes and transcription factors in the regulation of stem development have been identified (Table 4). For example, a key *PmWEEP* gene was mapped in *Prunus mume* by GWAS [206].

Table 3 Application of multi-omics in studying stem development genetics of ornamental plants.

Omic type	Species	Material	Main conclusion	Reference
Genome	Rosaceae	Nine Rosaceae species	<i>MdABC28</i> , a possible cytokinin transporter linked to the dwarfing phenotype in apple rootstocks.	[196]
	<i>Chrysanthemum</i>	200 chrysanthemum accessions	Genome-wide association studies identified 19 genes related with plant height development.	[1]
Transcriptome	<i>Gerbera hybrida</i>	3 developmental stages of stem	Analysis of Differentially expressed genes (DEGs) in hormone pathways suggested ABA regulates stem bending independently of ethylene.	[197]
	<i>Rhododendron canescens</i>	Vegetative and reproductive tissues	Identified plant hormone genes <i>GAI</i> , <i>GIDI</i> , <i>BRI1</i> , <i>MAX2</i> , <i>BRC1</i> , etc., related to plant height and branching.	[198]
	<i>Liquidambar styraciflua</i>	Tetraploid and diploid hybrid	DEGs were significantly enriched in plant hormone biosynthesis and signal transduction, sugar and starch metabolism, and cell cycles.	[199]
	<i>Liquidambar. formosana</i>	sweetgum stem	Candidate DEGs associated with stem length involve phenylpropanoid biosynthesis, phenylalanine metabolism, and the auxin signaling pathway.	[200]
	<i>Ilex verticillate</i>	Long stem cultivar 'Oosterwijk' Short stem cultivar 'Red sprirte'	DEGs enriched in hormone signaling, carbohydrate metabolism, and cell wall-related biological processes.	[83]
	<i>Agapanthus praecox</i>	400 mg·L ⁻¹ PBZ treated scape Distilled water-treated scape	DEGs involved in phytohormone pathways and cellular patterning regulation.	[201]
	<i>Lagerstroemia</i> sp.	Dwarf and nondwarf progenies of an F1 segregating population	scRNA-seq has elucidated cell wall synthesis in stems by identifying distinct cell populations such as cambium, xylem, and phloem cells.	[202].
	<i>Taxus mairei</i>	15 ~ 20 young stems were cut into 0.1 ~ 0.2 mm fragments		
	<i>Prunus mume</i>	Young leaves for genome sequencing Straight and tortuous branches for transcriptome	Identified genes involved in cell division, development, and plant hormone signaling are essential for the tortuous branch trait formation.	[195]
	<i>Nymphaea tetragona</i>	Dorsal and ventral stems were sampled on the fifth day after cutting	607 DEGs identified in the dorsal and ventral stems revealed significant differences in plant hormone, calcium ion, glucose metabolism, and photosynthesis pathway genes within the curved stem regions.	[203]

Table 4 Genes and their functions in the stem improvement of ornamental plants.

Category	Gene	Species	Function	Reference
Ethylene biosynthesis	ACO1(0.821 kb)-ipt	<i>Chrysanthemum</i> sp.	Transgenic lines exhibited increased branching and reduced internode lengths.	[209]
	ACS1, ACO1	<i>Petunia hybrida</i>	<i>PhFBH4</i> positively regulates the transcription level of ethylene biosynthesis genes <i>ACS1</i> and <i>ACO1</i> . <i>PhFBH4-OX</i> plants showed shorter internodes and dwarf trait.	[210]
Gibberellin biosynthesis	GA20ox	<i>Brassica oleracea</i>	Jointly silencing <i>BoDWARF</i> , <i>BoGA20ox</i> , and <i>BoSP</i> produced a miniature plant.	[211]
	GA2ox	<i>Prunus Mume</i> , <i>Prunus armeniaca</i> , <i>Prunus salicina</i> <i>Prunus persica</i>	Conserved motif and gene structure analysis showed that <i>GAoxs</i> were conserved in the four <i>Prunus</i> species. Overexpression of <i>PmGA2ox8</i> in <i>Arabidopsis</i> leads to dwarfing phenotype.	[108]
	GA20ox1 GA2ox3	<i>Jasminum sambac</i>	High GA ₄ level in elongating internode coincided with strong <i>JSGA20ox1</i> and <i>JSGAS1</i> expression in leaves, and <i>JSGA2ox3</i> in internodes.	[104]
gibberellin signaling	GAI	<i>Petunia hybrida</i>	Overexpression of the <i>gai</i> mutant protein, which interferes with gibberellic acid signaling, leading to stunted growth and short internodes.	[212]
Lignin biosynthesis	LAC4	<i>Paeonia lactiflora</i>	<i>PLAC4</i> , involved in lignin biosynthesis, positively regulates its deposition in herbaceous peony, enhancing stem mechanical strength.	[213]
	HLB	<i>Chrysanthemum morifolium</i>	<i>CmHLB</i> interacted with <i>CmKNAT7</i> , negatively regulates secondary cell wall formation, affecting stem mechanical strength in <i>Chrysanthemum</i> .	[214]
MAP kinase	MKS1	<i>Kalanchoe blossfeldiana</i>	Heterologous overexpression of <i>AMKS1</i> result in a dwarf and delayed flowering phenotype.	[215]
Zinc-finger protein	LIF	<i>Petunia hybrida</i>	Transgenic <i>petunia</i> plant alters cytokinin metabolism and dramatic reduced plant height.	[216]
Carotenoid cleavage dioxygenase	CCD	<i>Petunia hybrida</i>	Loss of <i>PhCCD8</i> reduced internode length.	[217]
Transcription factor	SPL13A	<i>Lilium</i>	SPL13A regulates stem elongation in the adult vegetative phase	[218]
	WUSCEL-related homebox3 (WOX3)	<i>Panicum virgatum</i>	Overexpression of <i>PvWOX3a</i> increased stem length and internode diameter.	[133]
	WOX	<i>Melastoma dodecandrum</i>	<i>WOX</i> genes exhibited expression in the stem	[219]
	R2R3-MYBs	<i>Paeonia lactiflora</i>	R2R3-MYB TFs (<i>PIMYB43</i> , <i>PIMYB83</i> , <i>PIMYB103</i>) expressed in stem, regulated stem strength, cell wall thickness, and lignin deposition.	[213]
	WRKY41	<i>Paeonia lactiflora</i>	<i>PIMYB43</i> - <i>PIWRKY41a</i> complex activates <i>PIXTH4</i> expression to enhance stem strength by adjusting secondary cell wall thickness.	[220]
	SRS7	<i>Chrysanthemum morifolium</i>	SRS7 overexpression downregulates GA-related genes and upregulates auxin genes, reducing internode length in transgenic pot-mums.	[221]
	SRS7	<i>Chrysanthemum</i> spp.	Overexpression of the <i>BrSRS7</i> gene was previously shown to reduce the plant height of <i>chrysanthemums</i>	[222]
	SHI	<i>Kalanchoe blossfeldiana</i>	Transferring the <i>Arabidopsis</i> short internode (<i>shi</i>) gene into <i>Kalanchoe</i> resulted in a dwarf phenotype, reduced plant height and diameter.	[223]

The previous study showed that the silencing of *WEEP* resulted in more downward and wandering shoot orientations in *P. mume* [207]. Furthermore, the *WEEP* gene can promote negative gravitropism by establishing asymmetric auxin gradients [208].

In addition to strategies aimed at manipulating gene expression, the direct application of microbial systems also offers a route to inducing significant phenotypic changes in stem development. *Agrobacterium rhizogenes* carry a root-inducing (Ri) plasmid, which enables T-DNA integration carrying *rolA*, *rolB*, *rolC*, and *rolD* oncogenes into host plant genomes [224, 225]. Both *A. rhizogenes* and *rol*-transgenic plants presented hairy root phenotypes. Surprisingly, these transgenic plants always exhibit a dwarf phenotype, reduced apical dominance, and altered flowering habits. Horticultural applications exploit these phenotypic changes to create compact architecture in ornamental plants [226]. Compared to wild-type controls, *Pelargonium* sp. transformed with wild-type Ri plasmids presented 40% ~ 60% height reduction [227]. Similarly, the height of *Kalanchoe blossfeldiana* Ri-transgenic lines was reduced by 51.9% compared with that of control plants [228]. The overexpression of the *rol* gene in *K. blossfeldiana* also leads to dwarf and compact plants [229]. These morphological modifications increase ornamental value by improving plant architecture.

To achieve even greater precision and control on stem traits, recent advances have focused on directly editing key regulatory genes. CRISPR-Cas system, which originates from the bacterial immune system, serves as a gene-editing tool. A guide RNA (gRNA) directs the Cas9 enzyme to targeted DNA sites for cleavage, enabling precise gene editing [230]. This system has shown great potential in genetic breeding and trait improvement of horticultural crops, such as accelerating compact plant type breeding, optimizing stem quality, and improving lodging resistance, greatly shortening the breeding cycle of commercial flowers such as chrysanthemum, rose, and lily [231, 232] (Table 4).

Future perspectives

Advanced technologies for stem structure and cell wall characterization

Advances in computer vision and microscopic imaging technologies are enabling visualization and quantification of plant stem architecture and cell wall composition.

In stem phenotyping, micro-computed tomography (micro-CT) enables nondestructive, multilayered scanning, generating high-resolution three-dimensional (3D) visualization of stem internal anatomy, surpassing traditional paraffin sectioning and enabling tracking during whole growth process [233]. Coupled with vessel parser software, micro-CT allows recognize and quantitative analysis of different tissues, accurately parsing and calculating the shape, number, and distribution of vascular bundles in crops [234]. Advancing this approach, recent studies have integrated micro-CT with large-volume fully automated cell reconstruction (LVACR) were used to establish the multicellular morphological characteristics of plant organs, comprehensively displaying the fine structure and dynamic changes in plant tissues and organs [235]. This study provides profound insights into the precise spatial arrangement and cell behavior of multicellular organisms. Complementing these structural imaging techniques, virtual

staining technology (VST) integrates (deep) machine learning, converting bright-field microscope images into virtual staining images highly consistent with actual fluorescence images, thereby achieving precise and label-free visualization of specific cells [236, 237]. Therefore, VST provides high-precision cell morphological data, offering a new tool for plant cell biology research.

Complementing structural imaging, frontier techniques are deepening insights into the nanoscale composition and mechanics of the plant cell wall. The main components of the cell wall include cellulose, hemicellulose, pectin, and lignin, which form a complex cross-linked network. This structure is a natural nanos-structure critical for stem strength, elongation, and morphogenesis [238]. Although histochemical staining and fluorescence labeling have been the main tools for studying cell wall composition and structure, they lack the ability to observe dynamic changes in living cell walls in real time and are unable to accurately quantify multiple components. In contrast, emerging technologies enable dynamic, multimodal, and quantitative characterization of cell wall architecture.

Recently, nuclear magnetic resonance (NMR), atomic force microscopy (AFM), and spectral imaging techniques have further advanced the understanding of cell walls. NMR provides chemical information on cell wall components, AFM quantifies the mechanical properties of cell walls at the nanoscale, infrared spectral imaging maps the spatial distributions of components such as cellulose, hemicellulose, and lignin [239]. Confocal Raman microscopy (CRM) and stimulated Raman scattering (SRS) are two imaging techniques providing new tools for studying the microstructure of the cell wall. They can simultaneously obtain spectral and spatial data without damaging the sample and identify different components in the cell wall [240].

These technologies enable precise tracking of stem development and structural analysis, providing a robust foundation for breeding ornamental plants with improved stem quality, architecture, and mechanical performance.

Precise design strategies for ornamental plants in the era of Breeding 5.0

With the continuous development of the global horticultural industry, ornamental plants are required to meet diverse and personalized market needs. Consumers now focus on shoot architecture, alongside traditional traits such as flower size and color. The ideal plant height is more convenient for transportation and commercial placement, while the stem thickness enhances lodging resistance in outdoor landscapes. Thus, the precise design and breeding of ornamental plant stem traits have become a key route for meeting the market demand in industrial upgrades.

The evolution of breeding methodologies has progressed through several generations, with Breeding 4.0 emphasizes the use of genomics, gene editing, and molecular marker-assisted breeding to achieve better varieties [241]. While Breeding 4.0 significantly improved breeding efficiency through molecular techniques, it still relies heavily on prior knowledge of gene functions and trait associations. This reliance limits its capacity to address complex, polygenic traits such as stem architecture in ornamental plants. Looking ahead, the design of ornamental plant stem traits will enter a new era, Breeding 5.0. Breeding 5.0 introduces the concept of intelligent breeding of smart

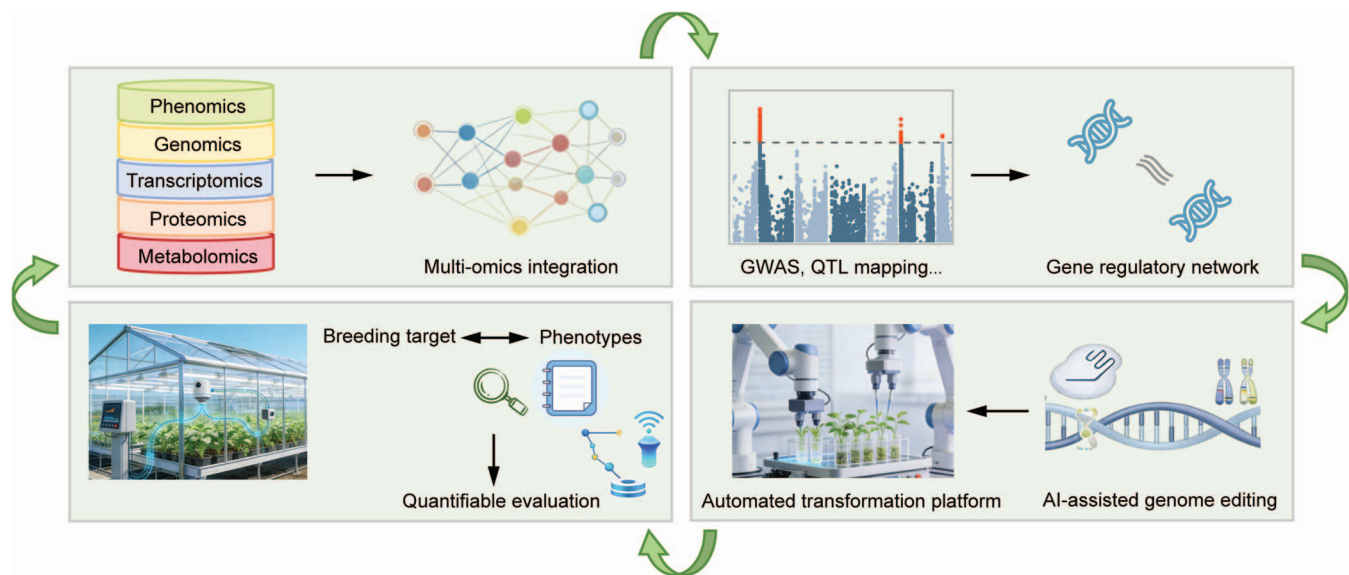


Figure 5 Strategies for smart ornamental plant breeding. A closed-loop smart breeding framework for ornamental plants that integrates high-resolution phenotyping with multi-omics profiling, leverages AI to decode genotype–phenotype relationships and prioritize editing targets, enables precision genome editing via automated platforms, and validates improved lines through dynamic monitoring in smart greenhouses to support iterative pipeline optimization.

varieties, integrating advanced technologies such as artificial intelligence (AI) and bioinformatics to achieve precise phenotypic design, including stem morphology. Breeding 5.0 aims to cultivate intelligent varieties with optimized resource utilization efficiency and high yield and quality [242].

To realize smart breeding in ornamental plants, we propose a framework integrating four key technological steps (Fig. 5). First, we establish a high-resolution phenotypic and omics database. Robotic platforms and multi-sensor imaging system capture real-time 3D plant architecture, physiological indexes, and micro-environmental data. At the same time, establish a multi-omics database, including pan-genomics, transcriptomics, proteomics, and metabolomics to profiles the molecular basis of key ornamental traits. Second, AI-aided predictive modeling is applied to construct developmental models and decode genotype-to-phenotype associations. Through AI-aided GWAS, key genetic loci and regulatory networks governing important ornamental characteristics are systematically identified. Third, guided by AI-designed CRISPR/Cas editing targets, precision breeding is implemented via automated genetic transformation platforms. This enables rapid development of improved lines tailored to specific breeding goals, such as enhancing vase life in cut flowers, compacting growth for vertical greening, and improving shade tolerance for indoor pot flowers. Finally, cultivation validation and dynamic phenotypic monitoring are performed in a smart greenhouse. These systems allow quantitative assessment of breeding objectives and phenotypic stability, generating closed-loop feedback data that drives the iterative optimization of the breeding pipeline (Fig. 5).

However, the commercialization of gene-edited ornamental plants still faces practical hurdles, including potential off-target effects of CRISPR/Cas systems, technical difficulties posed by genomic complexities such as high heterozygosity and polyploidy [243], and the challenge of coordinating multi-gene editing for complex polygenic traits like flower color, flower shape, and vase

life [244], all of which pose significant quality control challenges for scalable production.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (32071817), the Guangdong Basic and Applied Basic Research Foundation (2025A1515012658), China Postdoctoral Science Foundation General Funding Program (2025185168144137771928).

We are grateful to Yin Xin (Institute of Genetics and Developmental Biology, Chinese Academy of Sciences) and Jaime A. Teixeira da Silva (independent researcher) for their insightful comments and constructive suggestions, which significantly improved this manuscript.

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Conflicts of interest statement

The authors declare no conflict of interests.

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