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Plant Science REVIEW

A comprehensive overview of molecular biology advancements in lily over the past decade

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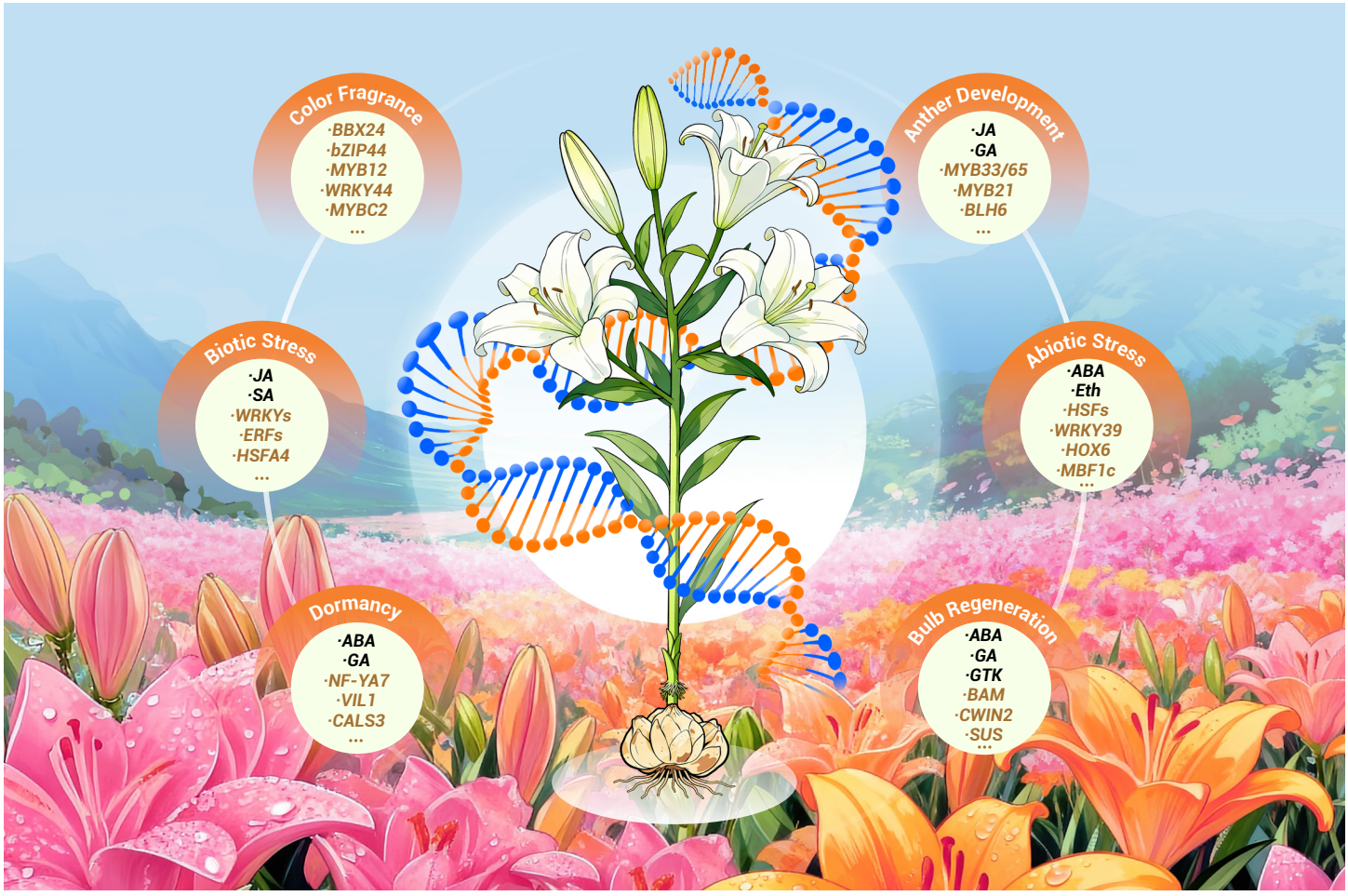
GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- This review emphasizes key findings in lily regarding bulb dormancy, anther development, and flower traits.
- The critical findings of environmental stress responses in lily are summarized in this review.
- It also discusses advancements in genetic transformation technologies for enhancing lily traits.
- The insights aim to guide future lily breeding and identify research gaps for further exploration.

REVIEW Plant Science

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Lily (*Lilium* spp.) is a globally significant ornamental crop, highly valued in both domestic and international markets. In recent years, the lily industry has undergone rapid expansion; however, it continues to face numerous challenges. Prominent limitations in lily production include prolonged bulb dormancy, severe pollen contamination, limited diversity of flower coloration, inadequate or excessively strong fragrance, and insufficient resistance to both biotic and abiotic stresses. To address these limitations, considerable efforts over the past decade have been directed toward molecular biology research, particularly the identification of key functional genes and the application of molecular breeding approaches to accelerate the development of improved germplasm. This review synthesizes the key findings from recent research in lily molecular biology, highlighting mechanisms associated with bulb dormancy, anther development, flower color and fragrance formation, as well as responses to biotic and abiotic stresses. Additionally, the review discusses advancements in genetic transformation technologies. The insights presented here aim to guide future breeding programs and enhance our understanding of the molecular basis of key traits in lilies. Furthermore, we identify current gaps in knowledge and propose future research directions to address existing limitations and further advance the field.

INTRODUCTION

Lily (*Lilium* spp.), a perennial bulbous plant belonging to the Liliaceae family, is an economically significant horticultural crop. Known for its large, vibrant, and aromatic flowers, it is widely cultivated for cut flower production, potted plants, garden displays, and ornamental landscaping. Certain lily varieties are also utilized for edible and medicinal purposes, further enhancing their market value.[1,2] The genus *Lilium* comprises 110-115 species and over 10,000 cultivars, with more than 300 new varieties being introduced annually.[3] In 2023, the European Union imported lily products valued at €146.1 million, while the United States' cut lily production reached $ 4.58 million. In 2020, the sales of lily products in China amounted to $ 1.5 billion.

Lily production primarily depends on bulbs; however, the regulatory mechanisms underlying bulb development remain poorly understood. The prolonged dormancy period of bulbs significantly increases production costs. In addition, large anthers generate excessive pollen, leading to substantial contamination during cultivation and postharvest handling. Despite the existence of more than 10,000 cultivars worldwide, most commercial varieties display restricted color diversity and notably lack certain hues, such as true blue. Floral scent also poses a challenge: *L. longiflorum* and *L.* oriental hybrids typically exhibit overly strong fragrance, whereas *L.* asiatic hybrids are often scentless. Moreover, the majority of current lily cultivars show limited resistance to diseases and environmental stresses, thereby reducing their adaptability and commercial utility.[1,4-6] Collectively, these biological and agronomic constraints—including extended bulb dormancy, excessive pollen production, restricted floral color diversity, imbalanced fragrance profiles, and insufficient stress resistance—continue to impede the sustainable development of the global lily industry. Conventional breeding strategies, though historically important, have proven inadequate to overcome these limitations in a timely and efficient manner.[2] In contrast, recent advances in molecular biology—encompassing the identification of key functional genes, dissection of gene regulatory networks, and deployment of molecular breeding technologies—provide promising avenues for the targeted improvement of both agronomic performance and ornamental quality. This review synthesizes recent progress in lily molecular biology, identifies persistent knowledge gaps, and discusses prospective strategies for future molecular breeding efforts aimed at meeting the evolving demands of the industry.

BULB DEVELOPMENT AND DORMANCY IN LILY

Regeneration of lily bulblets

Bulblet regeneration in lilies is a sequential process that involves early signal perception, the establishment of auxin gradients, cellular reprogramming, and organogenesis. This process parallels the mechanisms observed in *de novo* root regeneration.[7] Bulblets primarily form on the adaxial side of the scale base, where vascular parenchyma cells undergo reprogramming and division to create a proliferating cell mass. This cell mass progressively divides to form nodular protrusions, which develop into scale primordia and ultimately mature into bulblets.[8,9]

Mechanical detachment functions as a wounding signal that initiates cell fate transitions. These signals are classified into short-term and long-term categories. Short-term signals occur in two distinct phases. The first phase involves reactive oxygen species (ROS), calcium ions (Ca^{2+}), and electrical pulses. The second phase includes phytohormones such as jasmonate, salicylic acid, and ethylene. Long-term signals appear approximately 2 days after detachment, activating dedifferentiation-related genes such as *WUS* (*WUSCHEL*) through transcription factors, notably the AP2/ERF family member WIND1 (WOUND INDUCED DEDIFFERENTIATION 1). This process is further regulated by epigenetic modifications, such as H3K27me3 and DNA methylation, alongside the interaction between auxin and cytokinin. In lilies, specific AP2/ERF family members, including *LoERF115* (*ETHYLENE RESPONSE FACTOR 115*) and *LoWIND2*, respond to wounding signals.[10] These *WIND* genes subsequently activate auxin biosynthesis genes, such as *YUCCA* and *TAA1* (*TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS 1*), resulting in elevated auxin levels in converter cells and triggering cell fate transitions.[11]

Auxin plays a central role in regulating cell fate transitions during bulblet regeneration by being transported to regeneration-competent cells near the wounding site via auxin polar transporters (PINs).[11] Notably, not all cells within the explant undergo this transition; regenerative capacity is primarily restricted to the procambium and specific vascular parenchyma cells.[12] Auxin activates WOX11/12 (WUSCHEL-Related HOMEOBOX 11/12), which, in turn, up-regulates *WOX5/7* and *LBD16* (*LATERAL ORGAN BOUNDARIES-DOMAIN 16*), orchestrating cellular division and primordium initiation.[13] Cytokinin

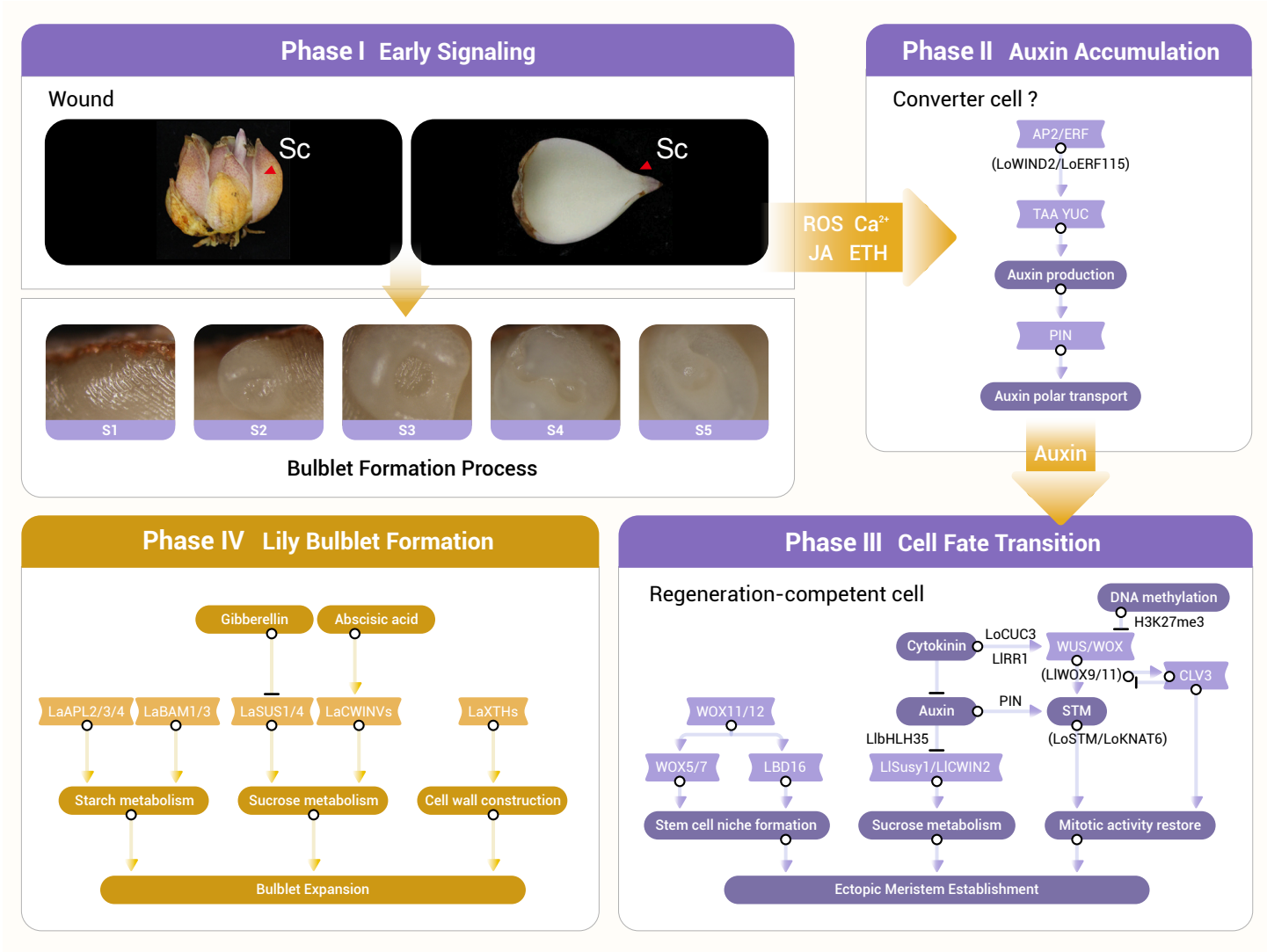

Figure 1. ***De novo*** **bulblet formation** Lily bulblet development can be categorized into four primary stages: early signal initiation, auxin accumulation, cell fate transformation, and bulblet organ formation. Initially, a damage signal prompts the accumulation of auxin and its polar transport within early converter cells. Subsequently, under the influence of auxin and cytokinin, genes such as *WUS* and *STM* facilitate the transformation of the fate of regeneration-competent cells. Following various physiological and biochemical processes, including carbohydrate metabolism and cell wall remodeling, the bulbs continue to expand and ultimately develop into complete organs. Abbreviation: Sc, scale.

promotes *WOX9/11* expression through type-B RESPONSE REGULATORS.[14] In lilies, genes such as *LoSTM* (*SHOOT MERISTEMLESS*), *LoKNAT6* (*HOMEOBOX PROTEIN KNOTTED-1-LIKE6*), *LoATH1* (*HOMEOBOX GENE1*), *LoWOX13*, and *LoCUC3* (*CUP-SHAPED COTYLEDON 3*) are involved in cell fate transitions and proliferation.[10] In Arabidopsis, *WIND* genes regulate auxin biosynthesis by targeting *YUCCA* and *TAA1*, a mechanism validated in functional studies.[11] Such findings may provide a framework for exploring upstream regulators of auxin synthesis in *Lilium*, though functional conservation remains to be clarified.

Auxin plays a central role in bulblet regeneration. Its spatial accumulation, mediated by polar auxin transporters (PINs), determines regenerative cell identity.[11] In Arabidopsis, auxin activates WOX (WUSCHEL-Related HOMEOBOX) and LBD (LATERAL ORGAN BOUNDARIES-DOMAIN) transcription factors to initiate primordia, providing a useful reference framework.[12,13] In lilies, type-B LIRRs (positive regulators of cytokinin signaling) bind and activate promoters of *LlWOX9* and *LlWOX11*, reinforcing cytokinin-induced bulblet initiation.[14] In addition, genes such as *LoSTM*, *LoKNAT6*, *LoATH1*, *LoWOX13*, and *LoCUC3* show differential expression during bulblet development, but their roles in cell fate transition and organogenesis remain uncharacterized.[10]

Phytohormones and sugars play crucial roles in bulblet formation. Specific phytohormones, such as abscisic acid (ABA) and gibberellins (GAs), are vital components in this process.[14-17] Among these, auxin is particularly significant, as its spatial gradients are necessary for the development of bulblet primordia. Auxin biosynthesis and polar transport establish high-concentration zones within the proliferating cell mass, which are essential for the formation of bulblets. Sugars like glucose and sucrose provide the energy needed for cellular activities during bulblet formation.[15,16,18] Furthermore, auxin influences sugar content and enhances bulblet formation through the *LlbHLH35* (*BASIC HELIX-LOOP-HELIX PROTEIN 35*) - *LlSusy1* (*SUCROSE SYNTHASE 1*) / *LlCWIN2* (*CELL WALL INVERTASE 2*) regulatory module (Figure 1).[15,19]

To better understand lily bulblet initiation—including auxin polarity, stem cell dynamics, and cell fate transitions—future studies should combine multi-omics approaches (such as single-cell RNA sequencing and spatial transcriptomics) for detailed spatiotemporal mapping, along with CRISPR-based functional genomics to decode regulatory networks. This integrated strategy will provide practical tools for improving bulb propagation in horticulture.

Regulation of bulb dormancy release in lily

After developing in autumn, lily bulblets enter winter dormancy. This growth halt is crucial for surviving adverse conditions and resuming growth in spring. In geophytes, dormancy impacts storage, transport, flowering, and vegetative growth.[20] The release from dormancy is triggered by low-temperature chilling exposure (LTCE), which is associated with reduced levels of ABA and increased levels of gibberellins (GAs).[21,22] Recent studies have focused on the changes in epigenetics, metabolites, cellular activity, and structural adaptations during this process.

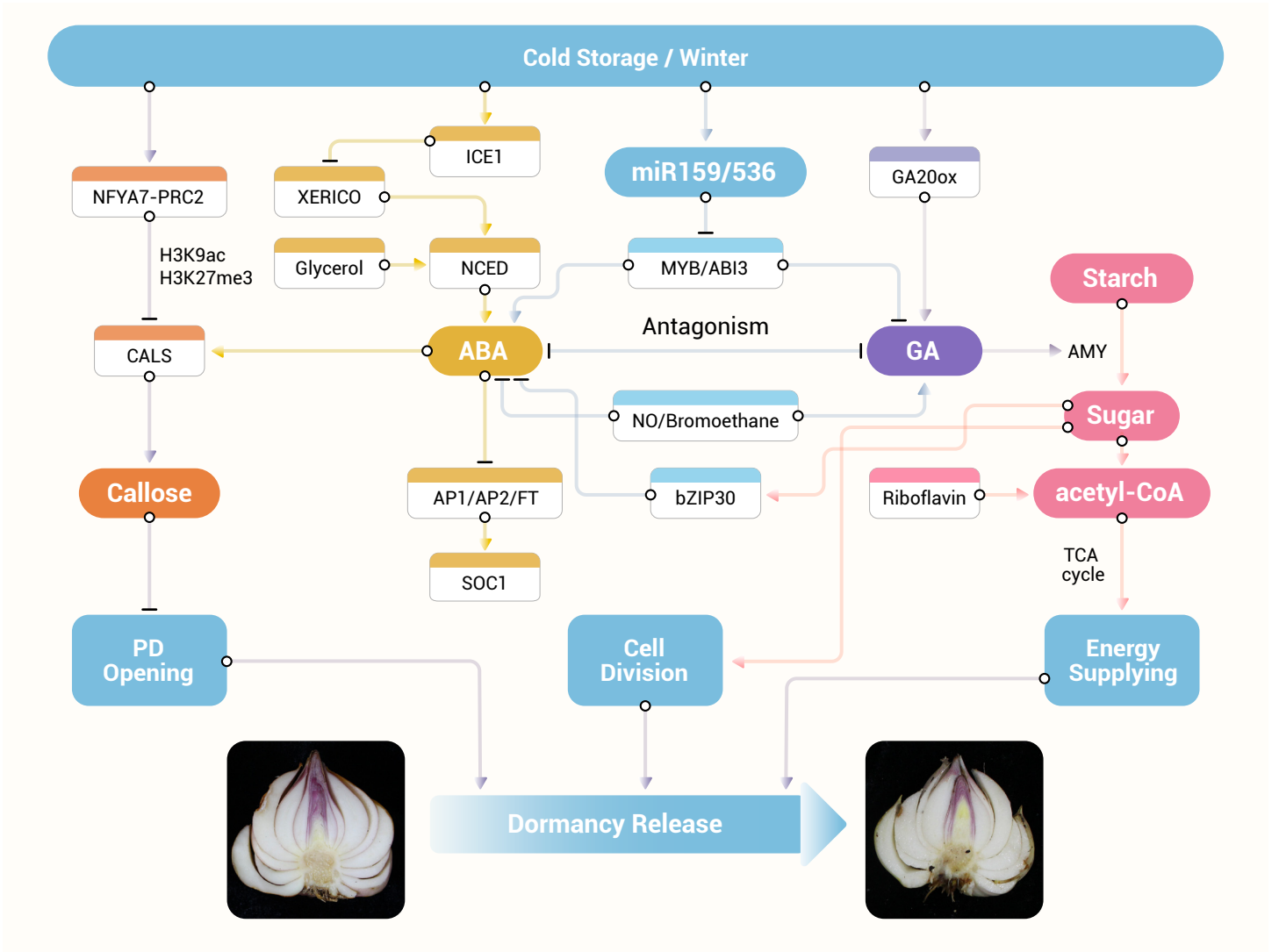

Figure 2. The regulatory network of bulb dormancy release During cold storage or winter, low temperatures (LT) regulate pathways such as hormonal and metabolic processes to promote bulb dormancy release. This regulation occurs through the modulation of intercellular communication, cell division, and energy supply. In this context, the ABA/GA (abscisic acid/gibberellic acid) ratio is decreased via transcriptional and miRNA regulation. ABA and GA exert opposing effects on sugar and callose accumulation. Specifically, GA inhibits callose accumulation and facilitates the conversion of starch to soluble sugars, whereas ABA exhibits contrary effects, forming negative feedback with sugars. LT further inhibits callose accumulation through the histone modification pathway. Additionally, flowering-related genes such as FT and SOC1 are involved in dormancy release regulation mediated by LT or ABA. Exogenous substances like glycerol, riboflavin, nitric oxide (NO), or bromoethane can modulate endogenous hormone content or energy substances, thereby influencing dormancy release.

The transition from dormancy to growth requires increased energy consumption. During this process, mitochondria become more active, and the endoplasmic reticulum (ER) and Golgi apparatus enhance protein synthesis and transport activities. Concurrently, the interaction between the rough ER and the Golgi apparatus intensifies to ensure the efficient transport and processing of synthesized proteins and lipids. Plasmodesmata (PD), which are intercellular communication channels, transit from a blocked to an open state. This shift acts as a key dormancy release switch and is regulated by callose deposition in lily bulbs. The application of PD regulators can directly modulate dormancy release in these bulbs.[23,24]

ABA and GA exert opposite influences on callose synthesis via epigenetic modifications, affecting plasmodesmata (PD) functionality. Cold exposure and ABA can both induce the expression of the callose synthase gene *CALS*, leading to callose accumulation around PD. This accumulation blocks the symplastic transport of *FLOWER LOCUS T* (*FT*) mRNA, sugars, and nutrients, resulting in growth arrest. Epigenetic modifications contribute to this process; the NF-Y family transcription factor LoNF-YA7 recruits VERNALIZATION INSENSITIVE 3-LIKE 1 (LoVIL1) and binds to the *LoCALS3* (*CALLOSE SYNTHASE 3*) promoter, inhibiting its transcription through histone modifications (H3K27me3 and H3K9ac) during dormancy release. In contrast, GA has an opposing effect on callose synthesis. Recently, the flowering and vernalization-related gene *LoSOC1* (*SUPPRESSOR OF OVEREXPRESSION OF CO 1*) was found to promote dormancy release (Figure 2).[25]

Starch degradation during dormancy release generates soluble sugars that supply energy and counteract ABA, thereby facilitating growth.[26] Other metabolites, including glycerol[27] and small molecules like nitric oxide (NO),[28] also regulate this process. NO lowers ABA levels by mediating genes involved in ABA catabolism while promoting growth-related hormones.[28] Similarly, bromoethane and riboflavin (vitamin B2) enhance dormancy release by modifying ABA metabolism and promoting acetyl-CoA accumulation in lily bulbs.[29]

Although advancements have been made in omics sequencing for lilies,[22,25,30] significant gaps persist in comprehending the roles of specific organelles, such as mitochondria, leucoplasts, and vacuoles, as well as the functions of small molecules, including peptides, miRNAs, and ROS. Additionally, the realm of epigenetics, encompassing chromatin status, DNA methylation, and histone modifications, remains insufficiently explored. Moreover, a physiological index capable of distinguishing between the induction, maintenance, and release of dormancy has yet to be clearly identified.

RESEARCH PROGRESS OF ANTHER DEVELOPMENT IN LILY

The proper dormancy release in lily bulbs enables a successful transition

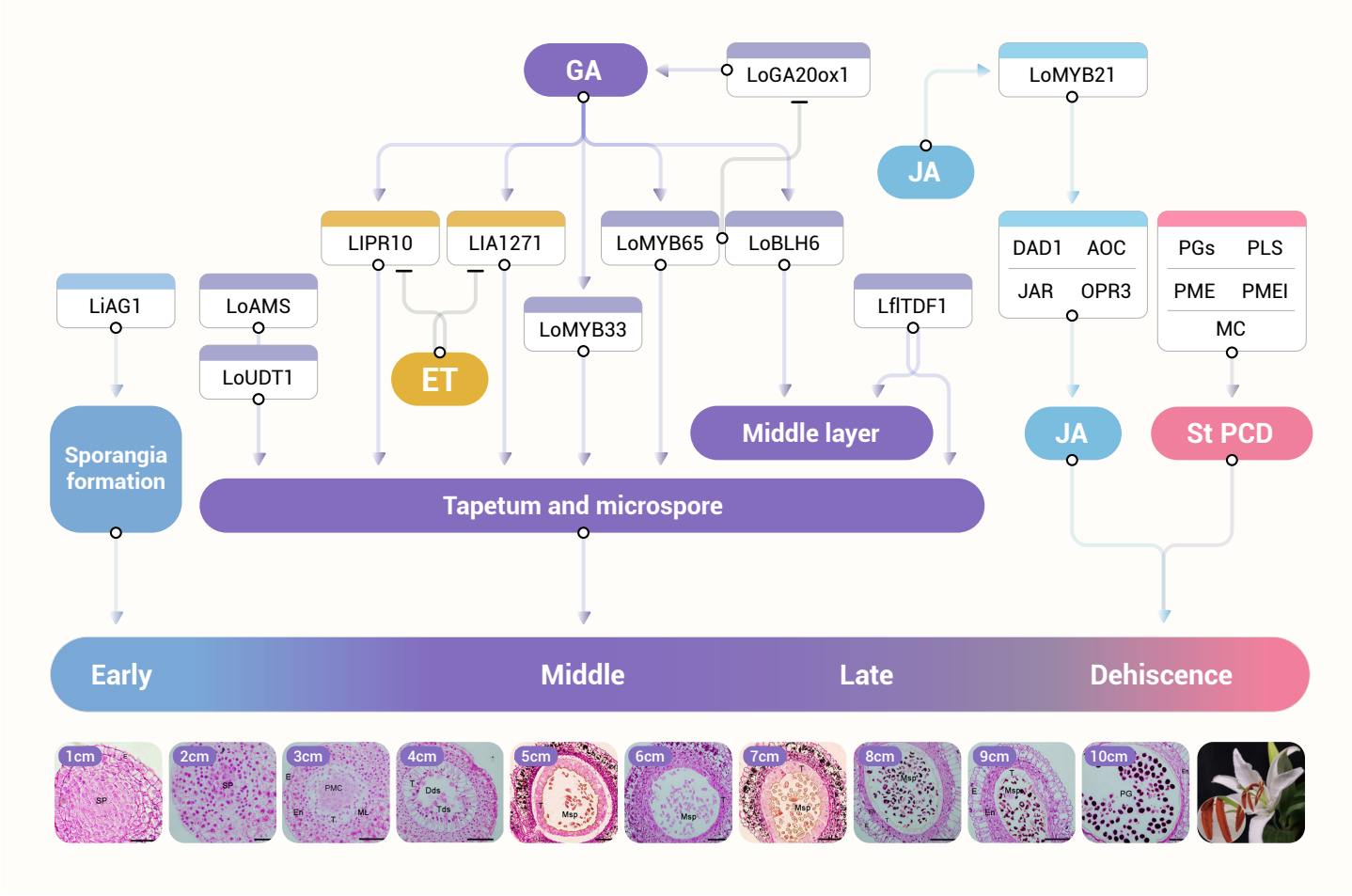

Figure 3. The regulatory network of the development process of lily anther LiAG1 is involved in the regulation of the early development of lily anther. The regulation of the middle and late stages of lily anther development is mainly mediated by the GA and related transcription factor network. JA is a key phytohormone regulating anther dehiscence, and the synthesis of JA in anther is mainly regulated by LoMYB21. Enzymes such as PGs, PLs, PME, PMEI, and MC are related to the degradation of the anther stomium region. GA: Gibberellin; ET: Ethylene; JA: Jasmonic acid; St: Stomium.

from vegetative growth to reproductive growth, which is essential for the production of high-quality cut flowers. Additionally, pollen contamination is another pressing issue that needs to be addressed in lily cut flower production. In lilies, large anthers and abundant pollen production contribute to pollen contamination, diminishing the ornamental value of lilies following anther dehiscence.[31] These challenges in the lily cut-flower industry have spurred research on lily anthers, particularly focusing on pollen development and anther dehiscence.

Identification of developmental stages in lily anther

Anther development is a critical stage in plant reproduction, primarily involving the differentiation of anther cell layers, the development and maturation of pollen, and anther dehiscence.[32] Anther development and dehiscence are tightly regulated by internal and external factors.[33] A lily bud typically contains six anthers symmetrically arranged around the pistil. Research on lily anther development has predominantly focused on the *L.* oriental hybrid 'Siberia' due to its strong correlation between bud length and anther developmental stages, along with the increased susceptibility of its white petals to pollen pollution. Several studies have classified anther developmental stages using floral bud length as a morphological marker.[34-36] For instance, when the bud reaches 2 cm, the anther developmental stage is designated as 'S2', with development divided into 10 to 12 stages. Anther differentiation and pollen development occur before stage S6, while pollen maturation and dehiscence happen after S6.[36-38] Pollen maturation progresses through four distinct stages: sporulation, meiosis, microspore release, and pollen maturation.[39] Feng et al. correlated the morphological characteristics of *L.* oriental hybrid 'Siberia' flower buds with pollen development across different stages. They classified lily pollen development into six stages: 1. Sporulation stage: Anther length < 17 mm, bud length < 36 mm; 2. Pollen mother cell stage: Anther length 17–22 mm, bud length 36–43 mm; 3. Meiosis stage: Anther length 24–29 mm, bud length 43–53 mm; 4. Tetrad stage: Anther length 29–32 mm, bud length 54–56 mm; 5. Mononuclear pollen grain stage: Anther length 32–35 mm, bud length 56–61 mm; 6. Pollen grain maturity stage: Anther length > 35 mm, bud length > 61 mm (Figure 3).[40]

These studies provide a foundation for defining standardized developmental stages and investigating the functional genes and molecular mechanisms underlying lily anther development.

Regulation of pollen development in lily

The tapetum, one of four layers in the anther wall, is crucial for microspore development. It synchronizes precisely with microsporogenesis, ensuring microspores receive the necessary nutrients and energy for maturation.[39,41] When tapetum functionality is disrupted, it often leads to pollen abortion because the tapetum is essential for the biosynthesis of phytohormones like gibberellins (GA) and jasmonic acid (JA), which are vital for anther development.[41] In lily (*L. Longiflorum* Thunb.), GA and ethylene (ET) regulate the tapetum/microspore-specific pathogenesis-related gene (*LIPR10*) and the anther-specific gene (*LIA1271*) antagonistically, both of which play roles in tapetum and microspore development.[42,43]

GA initiates the polyubiquitination of DELLA proteins through the SCF E3 ligase complex, leading to their degradation via the 26S proteasome. This degradation alleviates repression and activates downstream gene expression. DELLA proteins interact with various target proteins, including members of the bHLH transcription factor family, phytochrome interacting factors, and

the v-MYB myeloblastosis viral oncogene homolog (MYB) family, particularly GAMYBs.[44] LoMYB33 and LoMYB65, two members of the GAMYB family in lilies, are critical regulators of pollen development. *LoMYB33* is notably expressed in anther and pollen tissues, with peak expression during the tetrad and mature pollen stages. In transgenic *Arabidopsis*, LoMYB33 directly induces expression of *AtCYP703A2* (*CYTOCHROME P450 FAMILY 703A2*), *AtCYP704B1*, and *AtACOS5* (*ACYL-COA SYNTHETASE 5*), all involved in forming the Ubisch body and pollen wall, thus impacting normal pollen development during maturation.[45,46]

LoMYB65 regulates pollen development in a dose-dependent fashion by modulating tapetum degradation.[47] It forms a heterodimer with LoBLH6, a BEL1-like homeodomain transcription factor, to repress *LoGA20ox1* (*GIBBERELLIN 20-OXIDASE 1*), a key enzyme in GA biosynthesis. This action sustains optimal GA levels during anther development.[44] Dysregulation of *LoBLH6* disrupts GA homeostasis in lilies, leading to abnormal pollen and anther wall development.[44] The LoMYB65-LoBLH6 complex is vital for regulating GA-mediated anther and pollen development. Besides MYB transcription factors, the bHLH factor LoAMS (ABORTED MICROSPORES) interacts with LoUDT1 (UNDEVELOPED TAPETUM 1) to manage pollen mother cell meiosis and tapetum formation.[36] The Class C transcription factor LiAG1 (AGAMOUS 1) disrupts normal anther wall and septum development by modulating the expression of *SEP1* (*SEPALLATA 1*), *SEP2*, and *SEP3* E-class genes within the ABCDE model, resulting in abnormal tapetum development and defective microsporogenesis (Figure 3).[48]

Regulation of lily anther dehiscence

The timely release of pollen after maturation is crucial for reproductive success and is regulated by pollen development and anther dehiscence.[32] Anther dehiscence is controlled by phytohormones, signaling molecules, and transcription factors.[49] Specifically, in lilies, regulating anther dehiscence, rather than pollen development, helps control pollen contamination, which is beneficial for cut-flower production and hybridization in breeding. Transcriptomic analysis of the anther dehiscence stomium from stages S5 to S9 reveals that JAs and auxin are key in stomium formation. Genes related to their biosynthesis and signaling pathways are notably enriched.[34] The application of exogenous methyl jasmonate (Me-JA) induces premature anther dehiscence in lily flowers, while blocking endogenous JA biosynthesis suppresses it.[50] Additionally, recent studies indicate that JA promotes endothecium secondary thickening by inducing genes involved in lignin synthesis, which facilitates anther dehiscence.[51] LoMYB21 regulates JA biosynthesis by modulating JA synthesis genes, initiating the JA signaling pathway, and influencing anther dehiscence in lilies.[50] During anther dehiscence, septum degradation and stomium formation occur alongside programmed cell death (PCD) and metabolite accumulation. Transcript levels of genes involved in cellular degradation, such as polygalacturonases (PGs), pectate lyases (PLs), pectin methylesterases (PMEs), and PME inhibitors (PMEIs), are significantly upregulated. Additionally, metacaspase (MC) family proteins linked to PCD, as well as cysteine proteases, are also upregulated.[34,38,52] Concurrently, stomium formation and degradation are tightly regulated by phytohormones, including ABA, JA, and GA.[49] ROS, associated with PCD, significantly accumulate during stomium formation.[34] Anther dehiscence is a highly coordinated process involving multiple factors within the plant (Figure 3). However, further investigation is needed to elucidate the formation of these intricate regulatory networks and the key factors that trigger them.

The sequencing of the lily genome has been completed, and advances in omics technologies provide a solid foundation for identifying and characterizing functional genes. However, current studies primarily focus on the functional analysis of individual genes involved in anther development.[25,30] During this process, complex interactions occur among genes, hormones, and environmental factors. Understanding the synergistic effects of transcription factors and hormone signaling pathways, the crosstalk among plant hormones, and the precise spatial and temporal regulation of anther development remain key areas for future research. By elucidating these critical genes and molecular mechanisms, we aim to offer theoretical insights and practical guidance for the genetic improvement of lilies and the breeding of pollen-free varieties.

REGULATION OF FLORAL COLOR AND FRAGRANCE IN LILY

Flower color and fragrance are essential traits that facilitate pollination in nature. For humans, these traits are crucial ornamental features that have been selectively bred in numerous flower crops. Lilies, celebrated for their aesthetic and commercial value in the global horticultural market, exhibit remarkable diversity in flower colors and scents. This diversity is primarily attributed to biosynthetic pathways originating from several precursors derived from primary metabolism. Understanding the regulatory mechanisms of floral pigment and volatile organic component (VOCs) biosynthesis is vital for fundamental research and horticultural applications in lilies.

Regulation of floral color in lily

Anthocyanins, a class of flavonoid pigments, significantly influence the coloration of lily flowers. The regulation of anthocyanin biosynthesis in lilies is predominantly governed by transcription factors, especially those from the MYB family, which play a crucial and multifaceted role. Specifically, LhMYB12 has been identified as a vital positive regulator in Asiatic and Oriental hybrid lilies.[53-55] This transcription factor binds to specific *cis*-acting elements in the promoters of genes in the anthocyanin biosynthesis pathway, such as chalcone synthase (CHS), dihydroflavonol 4-reductase (DFR), and anthocyanidin synthase, thereby promoting their transcription and enhancing anthocyanin accumulation.[53]

Similarly, LvMYB5, part of a distinct subgroup of MYB proteins, acts as an activator by upregulating the expression of genes like *NbCHS*, *NbDFR*, and *NbANS* in tobacco, leading to increased pigmentation.[56] In contrast, LvMYB1, which contains conserved inhibitory motifs, is hypothesized to function as a repressor. It may compete with activators for binding sites on target genes or interact with other transcriptional machinery components to suppress anthocyanin synthesis.[56]

Beyond MYB factors, bHLH and WD40 transcription factors collaborate with MYB proteins to form the MBW complex. This complex functions as a central regulatory hub by recognizing and binding to the promoters of anthocyanin-related genes with high specificity. Through this interaction, the MBW complex activates the transcription of structural genes, ensuring coordinated and efficient anthocyanin production during flower development (Table 1). For example, LhbHLH2 interacts with LhWDR and LhMYB12 to co-regulate anthocyanin accumulation in Asiatic hybrid lily.[57] Additionally, WRKY transcription factors, such as LhWRKY44, play a significant role in the regulatory network. LhWRKY44 physically interacts with LhMYBSPLATTER, a component of the MBW complex, enhancing its stability and activity.[58] It also directly binds to the promoters of key anthocyanin biosynthesis genes, including *LhF3H* (*FLAVANONE 3-HYDROXYLASE*) and *LhGST* (*GLUTATHIONE S-TRANSFERASE*), which are involved in anthocyanin synthesis and transport, respectively, thereby promoting anthocyanin accumulation.[58]

Small RNAs, particularly microRNAs, play a critical role in the post-transcriptional regulation of anthocyanin biosynthesis. For example, miR828 accumulates significantly in the white regions of bicolor Asiatic hybrid tepals.[59] It targets the mRNA of *MYB12*, leading to its degradation or translational repression. This decreases MYB12 protein levels and anthocyanin accumulation in these areas, thereby contributing to the distinct bicolor patterns observed.[59] Beyond miR828, other miRNAs may also regulate anthocyanin biosynthesis in lilies.[54] Transcriptome and small RNA sequencing studies have identified miR168, miR10, miR23, and miR53 as potential regulators, associating with their target genes (*LhTT8*, *LhMYBA1*, *LhF3H*, and *LhANS*) to influence pigment accumulation in Oriental hybrid lilies.[54] These miRNAs fine-tune the expression of genes involved in anthocyanin biosynthesis, adding complexity to the regulatory network.

Environmental factors significantly influence anthocyanin biosynthesis in lilies. For example, temperature effects vary among different lily hybrids. In Asiatic hybrids, elevated temperatures (e.g., 35°C) can enhance anthocyanin pigmentation in specific regions of the tepals.[60] This enhancement is mediated by the upregulation of *MYB12* expression, which is driven by increased transcription and reduced accumulation of *miR828*, a microRNA that typically suppresses *MYB12* post-transcriptionally.[60] Conversely, high temperatures inhibit pigment accumulation in Oriental lilies and are associated with a decrease in *MYB12* expression.[61] This stark contrast in *MYB12* expression between Asiatic and Oriental hybrids under high-temperature conditions

Table 1. Transcriptional factors involved in floral anthocyanin and fragrance biosynthesis in lily.

Gene family	Gene	Metabolite	Regulatory Mode	References
MYB	LhMYB12	anthocyanin	Positive	Yang et al., 2013; Yamagishi et al., 2021[53,54]
MYB	LvMYB5	anthocyanin	Positive	Yin et al., 2021[56]
MYB	LvMYB1	anthocyanin	Negative	Yin et al., 2021[56]
WRKY	LhWRKY44	anthocyanin	Positive	Bi et al., 2023[58]
MYB	LhMYBC2	anthocyanin	Negative	Yang et al., 2024[61]
BBX	LvBBX24	anthocyanin	Positive	Gao et al., 2024[62]
bZIP	LvbZIP44	anthocyanin	Positive	Gao et al., 2024[62]
MYB	LiMYB1	Linalool, (*E*)-β-ocimene	Positive	Guo et al., 2023[70]
MYB	LiMYB305	Linalool, (*E*)-β-ocimene	Positive	Guo et al., 2023; Yang et al., 2022[70,71]
MYB	LiMYB308	Linalool, (*E*)-β-ocimene	Positive	Guo et al., 2023[70]
MYB	LiMYB330	Linalool, (*E*)-β-ocimene	Positive	Guo et al., 2023[70]
MYB	LiSRM1	Linalool, (*E*)-β-ocimene	Negative	Yang et al., 2024[72]
NAC	LiNAC100	Linalool	Positive	Liu et al., 2024[73]

strongly suggests that it is a key factor contributing to the observed differences in coloration. Notably, the promoter sequences of *MYB12* exhibit significant differences between Oriental and Asiatic hybrids, with presumed *cis*-regulatory elements in the promoter region showing a lack of conservation.[60] It is hypothesized that the *cis*-regulatory elements interacting with temperature-responsive factors vary between these hybrids. Further analyses aimed at elucidating the *cis*-regulatory elements and transcription factors involved in temperature signal transduction would be beneficial, particularly in identifying the elements that differentially respond to high temperatures. Additionally, the heat-induced expression of *LhMYBC2* also contributes to the reduced pigmentation observed in Oriental hybrids under elevated temperatures.[61] LhMYBC2 competes with positive regulators for interaction partners, disrupting the MBW complex's function and suppressing anthocyanin biosynthesis.[61]

Light is another essential environmental factor influencing anthocyanin biosynthesis. LvBBX24 (B-BOX DOMAIN PROTEIN 24), a light-induced transcription factor, collaborates with LvbZIP44 (BASIC LEUCINE-ZIPPER 44) to regulate anthocyanin accumulation in lily tepals in response to light.[62] LvBBX24 and LvbZIP44 potentially form a looped helix around the *LvMYB5* promoter region, upregulating its transcription and promoting anthocyanin synthesis.[62]

On the other hand, various complex floral pigmentation patterns have been observed in lily cultivars, including bicolor, splatter-type spots, raised spots, and blush marks, as well as a wide range of color variation. Existing research indicates that different R2R3-MYB genes may be responsible for the distinct coloration types of lily petals. In Oriental hybrids, LhMYB12 frequently regulates the coloration of the uniformly pink tepals and induces spot pigmentation.[53,59] In Trumpet hybrids, LrMYB15 governs the coloration of the lower epidermis of tepals in *L. regale*.[63] In the Tango series of Asiatic hybrids, LhMYBSPLATTER determines the formation of splashy spots attributed to anthocyanin presence in the tepals.[58,64] The complex and variable coloration types in lilies contribute significantly to their appeal. Future research utilizing emerging molecular biology techniques such as single-cell sequencing and spatiotemporal transcriptome sequencing to elucidate the underlying regulatory mechanisms will not only enhance our understanding of plant pigmentation but also provide valuable insights for the development of novel floral products.

Regulation of floral fragrance in lily

Lilies exhibit a wide variety of fragrance types.[65] The composition and amount of fragrance released from lily tepals change with flower development.[66] The floral scent of lilies comprises various VOCs, including terpenoids, benzenoids/phenylpropanoids, and fatty acid derivatives.[67,68] Among these, terpenoids are the most abundant, mainly involving monoterpenoids and sesquiterpenoids.[65] Elevated expression levels of structural genes such as *DXS* (*1-DEOXY-D-XYLULOSE 5-PHOSPHATE SYNTHASE*), *DXR* (*1-DEOXY-D-XYLULOSE 5-PHOSPHATE REDUCTOISOMERASE*), *HDS* (*4-HYDROXY-3-METHYLBUT-2-ENYL DIPHOSPHATE SYNTHASE*), *HDR* (*4-HYDROXY-3-METHYLBUT-2-ENYL DIPHOSPHATE REDUCTASE*), *IDI* (*ISOPENTENYL DIPHOSPHATE ISOMERASE*), and *GPS*/*GPPS* (*GERANYLPYROPHOSPHATE SYNTHASE*) in the upstream methylerythritol phosphate pathway enhance the synthesis of monoterpenoid volatiles (Table 1).[69] LoTPS2 (TERPENE SYNTHASE 2) catalyzes the formation of (E,E)-α-farnesene from farnesyl diphosphate (FPP) in the cytoplasm, while LoTPS4 catalyzes the formation of D-limonene and β-ocimene from geranyl diphosphate (GPP) and trans-bergamotene from FPP in the plastids.[66] Transcription factors significantly regulate the biosynthesis of these fragrance components. For example, multiple MYB transcription factors – such as LiMYB1, LiMYB305, LiMYB308, LiMYB330, and LiSRM1 (SALT-RELATED MYB1) – have been identified as regulators of gene expression related to terpene biosynthesis, affecting the production of key volatile compounds like linalool and ocimene (Table 1).[70-72] Additionally, LiNAC100 influences floral scent by directly activating the linalool synthase gene *LiLIS*.[73] These transcription factors interact with specific cis-acting elements in the promoters of their target genes, leading to either activating or repression of transcription.

Despite significant progress, important gap remains in our understanding. Specifically, the precise molecular mechanisms by which transcription factors interact with each other and with the promoters of anthocyanin and/or VOC biosynthesis genes require further investigation. The role of epigenetic regulation, including DNA methylation and histone modification, also remains largely unknown. Additionally, the interactions between different environmental factors and their combined effects on anthocyanin and/or VOCs biosynthesis warrant more in-depth study. Future research should integrate multi-omics approaches to fully elucidate these mechanisms, providing a solid foundation for genetic breeding and the development of novel lily cultivars with enhanced flower colors.

While the floral color and scent of lilies have been studied separately, they often co-occur in pollination syndromes in nature. Although floral pigments and VOCs are produced through distinct metabolic pathways, they share some precursors in the initial stages. Therefore, potential links between floral color and scent should be explored in depth to develop new strategies for breeding novel and attractive lily cultivars with desirable color-scent combinations.

RESEARCH OF LILY RESISTANCE TO BIOTIC STRESSES

Lily, a monocotyledonous bulbous flower, is subject to biotic stresses under natural conditions, including fungal and viral diseases caused by over

20 species, as well as pest infestations.[74] Among these, *Botrytis* disease, *Fusarium* wilt, *Cucumber mosaic virus* (CMV), *Lily mottle virus*, *Lily symptomless virus*, and aphid infestations are the most common threats. In recent decades, significant advances have been made in understanding lily's biological resistance, focusing on several key areas.

Firstly, transcriptomics and metabolomics analyses have been integrated to elucidate the main signaling pathways and identify key genes and miRNAs associated with responses to *Botrytis* spp., *F. oxysporum*, CMV, and aphids (*Aphis gossypii*). For instance, Gao et al. developed three small RNA libraries using resistant lily (*L. regale* Wilson) through high-throughput sRNA sequencing, exposing *B. elliptica*-responsive miRNAs and their target genes.[75] They identified 24 novel miRNAs and 22 target genes for ten miRNAs, primarily involved in metabolic enzymes like *OPR3* (*12-OXOPHYTODIENOATE REDUCTASE 3*) and *ADI* (*AGMATINE DEIMINASE*), cleaved by miR5059 and miR1862, respectively. Few transcription factors, such as EF1a (ELONGATION FACTOR 1a) and TCP2 (TEOSINTE BRANCHED 1, CYCLOIDEA AND PCF TRANSCRIPTION FACTOR 2), are cleaved by miR166b and miR319, respectively.

Moreover, RNA-seq data of *L. regale* post-*B. elliptica* infection confirmed 39 defense-related genes, with key JA signaling genes and transcription factors like WRKY, MYB, and ERF significantly upregulated. Additional genes encoding receptor-like kinases, antioxidant enzymes, polyphenol oxidase, pathogenesis-related proteins, and those associated with phenylpropanoid metabolism also demonstrated a response.[76] Genes in the phenylpropanoid biosynthesis pathway and WRKY transcription factors also contribute to *L. regale*'s defense against *B. cinerea*.[77,78]

Comparative transcriptome and metabolome analyses revealed the defense responses in Oriental hybrid 'Sorbonne' against *B. elliptica*. Accumulation of phenylpropanes – such as eriodictyol, hesperetin, ferulic acid, and sinapyl alcohol – and pathways involved in phenylpropanoids, flavonoids, JA, salicylic acid (SA), brassinolide (BR), and calcium ions (Ca^{2+}) signaling play crucial roles in resistance against *Botrytis* disease.[79,80] Full-length transcriptome analysis identified pathogenesis-related proteins, including two LhSorPR4 and seven LhSorPR10, in 'Sorbonne's against *B. elliptica* infection.[81]

Similar pathways and transcription factors were observed in *L. regale* against *F. oxysporum*, involving pathogenesis-related proteins, antioxidative stress enzymes, secondary metabolism enzymes, and signal transduction proteins.[82] Additionally, resistant *L. regale* showed higher levels of phenylpropanes, such as flavonoids, lignin, ferulic acid, phlorizin, and quercetin, compared to susceptible 'Siberia' during *F. oxysporum* infection. The phenylpropanoid metabolism and ERFs, such as LrERF4, positively contributed to lily's resistance to *Fusarium* wilt.[83]

In the response of *L. regale* to CMV at 48 dpi, 1,346 differentially expressed genes (DEGs) were identified through comparative RNA-seq data. Of these, all 74 DEGs were associated with 21 transcription factor families. Nine transcription factor families, including bHLH, AP2/ERF, zinc finger, MYB, WRKY, and NAC, were linked to the defense response against CMV infection. Candidate transcription factors such as *LrERF61*, *LrTINY*, *LrCPC* (*CAPRICE*), *LrNAC35*, *LrNAC100*, *LrWRKY28*, *LrWRKY48*, and *LrDOF5.6* (*DNA BINDING WITH ONE FINGER 5.6*) showed a continuous increase in expression levels following CMV inoculation, suggesting their role in regulating lily resistance to CMV infection.[74]

In the context of biological control of aphids, a total of 78 lily resources, including 13 wild species and 65 varieties, were evaluated for aphid resistance. Asiatic hybrids and *Longiflorum* hybrids were identified as resistant resources, whereas Oriental hybrids were relatively susceptible.[84,85] Furthermore, Zhou et al. investigated transcriptomic and metabolomic changes in the high-resistant 'Fangio' variety under aphid infestation. They found specific enrichment in metabolites of the phenylalanine and α-linolenic acid pathways, along with other significant metabolites like catalase, glutathione, coumaric acid, and JA.[86] Key DEGs identified included CHS, phenylalanine ammonia-lyase, and 12-oxo-phytodienoic acid reductase, providing a foundation for breeding aphid-resistant lily varieties.

Transgenic technologies have been employed to analyze and verify the biological functions of disease resistance-related genes and miRNAs, clarifying their mechanisms in lilies. For example, the ATP-binding cassette transporter gene *LrABCF1* and the NAC transcription factor *LrNAC35* from *L. regale* contribute to defense against CMV and *tobacco mosaic virus* (TMV) in petunia by influencing SA signaling-related defense genes and lignin biosynthesis genes such as *Ph4CL*, respectively.[74,87] In recent years, more studies have focused on resistance to *Botrytis* disease (Table 2). Fifteen *B. cinerea*-responsive *LrWRKY* genes have been identified in *L. regale*, with two transcription factors, *LrWRKY39* and *LrWRKY41a*, characterized for their distinct roles in response to *B. cinerea* infection.[78] Overexpression of *LrWRKY4* and *LrWRKY12* increased resistant to *B. cinerea*.[88] Additionally, *LlWRKY3*, *LlWRKY7*, and *LlWRKY10* from *L. longiflorum* 'White Heaven' play similar roles in mediating defense against *B. cinerea*.[89] A positive regulatory module involving LlWRKY33, LlHSFA4 (HEAT STRESS TRANSCRIPTION FACTOR A4), and LlCAT2 (CATALASE 2) has been confirmed to play significant roles in lily resistance to *B. cinerea* by controlling ROS accumulation.[90] Moreover, the miRNA159 family is significantly induced by *B. elliptica*. Overexpression of *miR159a* in transgenic *Arabidopsis* plants modulates the SA/JA signaling and ROS biosynthesis pathways, enhancing defense against *Botrytis* disease by repressing its target gene *LrGAMYB*.[75,91]

In the interaction between *L. regale* and *F. oxysporum*, several WRKY genes, including *LrWRKY1*, *LrWRKY2*, *LrWRKY3*, *LrWRKY4*, and *LrWRKY11*, were induced by *F. oxysporum*. Overexpression of *LrWRKY1* in transgenic tobacco and the Oriental hybrid 'Siberia' enhanced resistance to *F. oxysporum* infection.[92] Similarly, *LrWRKY2* and *LrWRKY3* also positively regulate resistance in transgenic tobacco. Silencing these genes in *L. regale* increased susceptibility to *F. oxysporum*.[93,94] LrWRKY2 activates the chitinase gene *LrCHI2*, while LrWRKY3 enhances the promoter-driven expression activity of *LrDef1* (*PEPTIDE DEFORMYLASE 1*) in tobacco. Additionally, the bZIP transcription factor *LrbZIP1* and the glutathione S-transferase gene *LrGSTU5* participate in defense responses against *F. oxysporum* by influencing antioxidant enzyme activity in transgenic tobacco.[95,96] Recent research demonstrated that LrWRKY11 in *L. regale* directly up-regulates the expression of *LrDIR1* (*DIRIGENT PROTEIN 1*), contributing to lignin/lignan accumulation and thereby enhancing the resistance of transgenic tobacco to *F. oxysporum*. This finding elucidates the molecular mechanism of WRKY11-mediated lignin biosynthesis in response to *F. oxysporum* infection.[97]

In recent years, researchers have developed new lily germplasms with increased resistance to viruses and *Botrytis* disease through *Agrobacterium*-mediated genetic transformation and polyploid breeding technologies. The Oriental hybrid 'Acapulco' was transformed with a defective *Cucumber mosaic virus* replicase gene (CMV2-GDD), resulting in two overexpressing lines that showed high resistance to CMV.[98] Likewise, transgenic Oriental hybrid 'Star Gazer' plants, transformed with a rice *RCH10* chitinase gene, demonstrated greater resistance to *B. cinerea* compared to wild-type controls.[99]

In polyploid breeding, Wang et al. developed a colchicine-induced tetraploid *L. rosthornii* Diels, which exhibited higher oxalate oxidase (OXO) activity and greater resistance to *Botrytis* disease than the diploid control. Infected tetraploids showed significantly elevated transcript levels of *LrGLP1* (*GERMIN-LIKE PROTEIN 1*), *LrGLP2*, *LrRBOHD* (*RESPIRATORY BURST OXIDASE HOMOLOGUE D*), *LrGST*, *LrPOD*, *LrCHI*, *LrBGL* (*BAGEL*), and *LrPR10* within 12–48 h after *B. elliptica* infection.[100] Additionally, colchicine-induced tetraploid *L. leichtlinii* plants flowered earlier, had wider tepals, and exhibited higher tolerance to *Botrytis* disease than their diploid counterparts in field tests.[101] However, the mechanism of resistance to *B. cinerea* infection in tetraploids remains unclear.

More recently, an interspecific hybrid between *L. callosum* and *L. longiflorum* 'Snow Queen' was produced using a cut-style pollination method. This hybrid demonstrated enhanced resistance to *B. cinerea* and exhibited higher peroxidase (POD) and catalase (CAT) activity than its parental lines.[102]

Although transcriptome analysis has uncovered a large number of disease resistance-related genes in lily, but only a small fraction has been functionally identified, leaving most genes in need of functional analysis. MicroRNAs (miRNAs) play pivotal roles in regulating plant-pathogen interactions; however, their roles in lily's response to biotic stress remain largely unknown. Specifically, it is unclear which miRNAs are involved in lily's responses to *Fusarium* or viral infections. Additionally, susceptible genes in the lily immune response have been rarely reported, highlighting the need for further exploration

Table 2. Summary of disease resistance-related genes from *Lilium*.

Genes	Original Species	Transgenic plants/materials	Functional characterization	References
LrbZIP1	*L.regale*	Tobacco *(Nicotiana tabacum* L. cv Xanthi*)*	Overexpression showed higher antioxidant enzyme activities and strong resistance to *F. oxysporum* f. sp. *lilii* infection	Zhang et al., 2014[95]
LrGSTU5	*L. regale*	Tobacco (*Nicotiana tabacum* L. cv Xanthi)	Overexpression reduced the superoxidate anion production and enhanced the resistance to *Fusarium oxysporum*	Han et al., 2016[96]
LrABCF1	*L. regale*	petunia (*Petunia hybrida*)	Overexpression confers reduced susceptibility to CMV, TRV, and *B. cinerea* infection	Sun et al., 2016[87]
LrPR10-5	*L. regale*	Tobacco	Overexpression evidently resisted the infection of *F. oxysporum*	Chen et al., 2017[103]
LrWRKY4, LrWRKY12	*L. regale*	*A. thaliana*	Overexpression enhances the resistance to *B. cinerea*	Cui et al., 2018b[88]
LrNAC35	*L. regale*	petunia (*P. hybrida* 'Mitchell Diploid')	Overexpression reduced susceptibility to CMV and TMV	Sun et al., 2019[74]
lre-miR159a-LrGAMYB	*L. regale*	*A. thaliana*	*lre-miR159a* positively regulates resistance to *B. cinerea* by repressing its target *LrMYB* gene	Gao et al., 2020[91]
LrCCoAOMT	*L. regale*	*A. thaliana* and *L. sargentiae*	Overexpression increased the lignin deposition and the resistance to *B. cinerea*	Fu et al., 2020[77]
LsGRP1	Oriental hybrid 'Stargazer'	*A. thaliana* and oriental hybrid 'Stargazer'	*LsGRP1* silencing in lily increases the susceptibility to *B. elliptica*, and *LsGRP1*-transgenic Arabidopsis showed higher resistance to *B. cinerea* and Pseudomonas syringae pv. tomato DC300 by regulating callose deposition and reactive oxygen species (ROS) accumulation	Lin et al., 2020[104]
LrWRKY1-LrPR10-5	*L. regale*	Tobacco and oriental hybrid 'Siberia' scales	*LrWRKY1* overexpression increased the resistance of the transgenic plants to *F. oxysporum*	Li et al., 2021a[92]
LrWRKY2-LrCHI2	*L. regale*	Tobacco and *L. regale* scales	*LrWRKY2*-overexpressing tobacco plants were more resistant to *F. oxysporum*, and *LrWRKY2*-RNAi increased the susceptibility of *L. regale* scales to *F. oxysporum*	Li et al., 2021b[93]
LrWRKY3-LrDef1	*L. regale*	Tobacco and *L. regale* scales	*LrWRKY3* transgenic tobacco plants showed higher resistance to *F. oxysporum*, and LrWRKY3-RNAi in *L. regale scales* showed higher sensitivity to *F. oxysporum*	Wang et al., 2022[94]
LrWRKY39, LrWRKY41a	*L. regale*	*A. thaliana* and lily (*L. longiflorum* 'Snow Queen')	*LrWRKY39* overexpression increased the resistance to *B. cinerea*, and *LrWRKY41a* overexpression increased the susceptibility to *B. cinerea*	Fu et al., 2022[78]
LlWRKY3, LlWRKY7 and *LlWRKY10*	*L. longiflorum* 'White heaven'	'Sorbonne' petal discs	Silencing in petal discs caused them to be more sensitive to *B. cinerea*	Xiang et al., 2022[89]
LhSorPR4-2	Oriental hybrid 'Sorbonne'	'Sorbonne' seedlings	*LhSorPR4-2* overexpression in 'Sorbonne' increased the resistance to *B. elliptica* correlated with high chitinase activity	Du et al., 2022[81]
LlWRKY33-LlHSFA4-LlCAT2	*L. longiflorum*	*L. longiflorum* hybrid 'White heaven' and *A. thaliana*	Overexpression enhances the resistance of transgenic Arabidopsis to *B. cinerea*, and silencing increases susceptibility of lily to *B. cinerea*	Ding et al., 2023[90]
LrWRKY11-LrDIR1	*L. regale*	Tobacco and *L. regale* scales	*LrWRKY11* ectopic expression in tobacco increased the resistance to *F. oxysporum*, the resistance of *L. regale* scales silencing *LrWRKY11* evidently decreased.	Deng et al., 2024[97]

to develop disease-resistant varieties through gene editing technology. Overall, advancing superior, more resistant lily varieties through biotechnology methods, such as CRISPR/Cas9-mediated gene editing, will be crucial in the near future.

RESEARCH PROGRESS ON THE ABIOTIC STRESS RESPONSES OF LILY

In the context of climate change, abiotic stress – especially extremely high temperatures – has emerged as a significant challenge to the sustainable development of the lily industry. Such stress disrupts the physiological and metabolic processes of lilies, hindering their growth and development. Additionally, it leads to a marked decline in the quality of the commercial product. This review summarizes the advances in research over the past decade concerning the response mechanisms of lilies to abiotic stress (Figure 4).

The molecular regulatory network of plant responses to heat stress primarily involves four core pathways: the Heat Stress Transcription Factor-Heat Shock Protein (HSF-HSP) pathway, the Ca^{2+}-Calmodulin (CaM) signaling cascade, the hormone dynamic homeostasis regulatory system, and the ROS metabolic network. Heat stress transcription factors (HSFs) serve as major regulatory elements in plants' responses to heat stress, and current research on the thermotolerance regulatory network in lilies primarily focuses on HSFs.

HSFA1, a master regulator from Class A, plays a crucial role in the lily's response to high temperatures. LlHSFA1 interacts with LlHSFA2, and the expression of several target genes is upregulated in *LlHSFA1*-overexpressing transgenic *Arabidopsis*, resulting in enhanced thermotolerance.[105] Additionally, LlHSFA1 interacts with LlERF012 (ETHYLENE RESPONSE FACTOR 012), increasing the transcriptional activation activity and DNA-binding capacity of LlERF012. This interaction synergistically regulates the activity of the HSF pathway, including Class A and B members; LlERF012 and LlHSFB1 have been identified as positive regulators of thermotolerance in lily.[106] *LlHSFA2b*, a member of *HSFA2*, can be induced by heat and H_2O_2. Overexpression of *LlHSFA2b* enhances tolerance to heat and oxidative stresses in transgenic *Arabidopsis*, potentially through direct activation of downstream genes or by dimerization or trimerization with other HSFAs possessing transactivation activity.[107] *HSFA3* has at least two homologs in lilies, *LlHSFA3A* and *LlHSFA3B*. Overexpression of both modifies normal proline accumulation in *Arabidopsis*, with *LlHSFA3A* enhancing basal and acquired thermotolerance, while *LlHSFA3B* only boosts acquired thermotolerance.[108] Under heat stress,

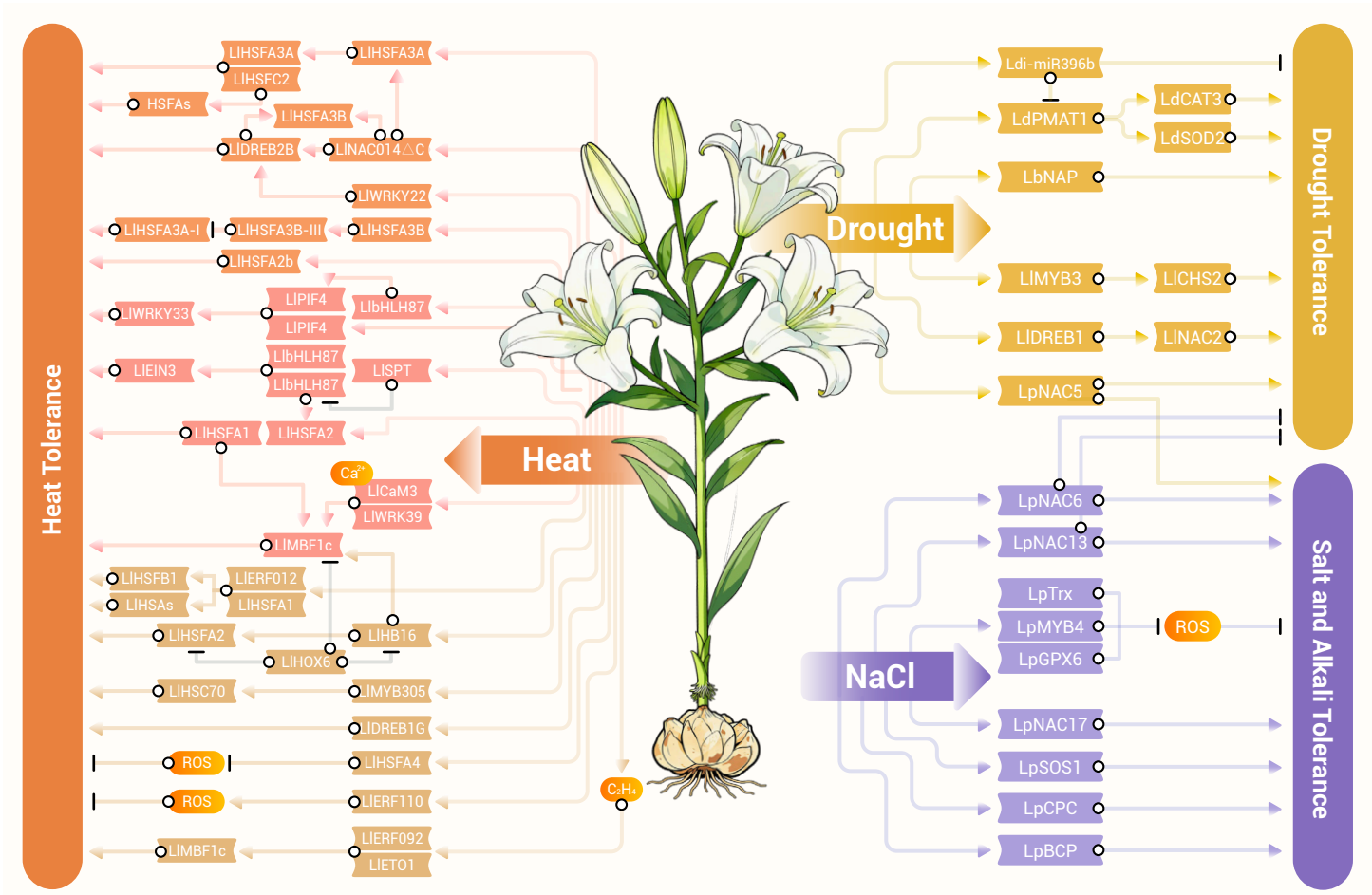

Figure 4. Molecular responses of lily to abiotic stress Heat stress: Heat stress adaptation involves complex interactions among various transcription factors in lily. LlHSFA1 partners with LlHSFA2 to initiate the expression of target genes and also modulates the heat stress transcription factor (HSF) pathway through its interaction with LlERF012. LlERF012, along with LlHSFB1, LlHSFA2b, LlHSFA3A, and LlHSFA3B, enhances thermotolerance. In contrast, LlERF110 decreases thermotolerance by disrupting ROS homeostasis. Under heat stress conditions, LlHSFA3B produces a heat-inducible splice variant, LlHSFA3B-III, which interacts with LlHSFA3A-I to attenuate the detrimental effects of excessive LlHSFA3A-I accumulation. LlHSFA4 provides thermotolerance by scavenging ROS, while LlHSFC2 acts as a transcriptional co-activator through its interaction with HSFAs. LlHB16 promotes thermotolerance by activating *LlHSFA2* and *LlMBF1c*; however, its interaction with LlHOX6 reduces its transactivation ability. LlbHLH87 binds to the promoters of *LlHSFA2* and *LlEIN3*, enhancing their expression, and modulates thermotolerance through an antagonistic interaction with LlSPT. LlWRKY39 directly activates *LlMBF1c* expression and interacts with LlCaM3. LlWRKY22 strengthens thermotolerance by autoregulating and activating *LlDREB2B*. Moreover, LlMYB305 enhances the promoter activity of *LlHSC70* during heat stress. LlNAC014 translocates to the nucleus during heat stress, boosting thermotolerance via the activation of the DREB2-HSFA3 module. Drought stress: In response to drought and salt stress, miR396b and its target *LdPMAT1* aid in drought resistance, with *LdPMAT1* overexpression upregulating *LdCAT3* and *LdSOD2*. Overexpressing *LpNAC5*, *LlNAC2*, and *LlMYB3* (which binds the *LlCHS2* promoter) enhances drought, salt, and saline-alkaline tolerance. *LpNAC6* and *LpNAC13* overexpression improves alkali tolerance but decreases drought resistance. Stable transformation with *LpNAC17*, *LpCPC*, *LpBCP*, *LpMYB4*, and *LpSOS1* enhances saline-alkaline tolerance. Lastly, LbNAP confers increased drought tolerance.

alternative splicing of *LlHSFA3B* generates the heat-induced splicing variant LlHSFA3B-III, which interacts with LlHSFA3A-I to repress its transcriptional activation function. This interaction mitigates the adverse effects of LlHSFA3-I overaccumulation, forming a regulatory loop.[109] LlHSFA4 functions as a positive regulator of thermotolerance by directly activating *LlAPX2* (*ASCORBATE PEROXIDASE 2*) to mitigate oxidative damage, while LlHSFA5 inhibits the DNA-binding activity of LlHSFA4, acting as a negative regulator; the LlHSFA4–LlHSFA5 complex modulates ROS homeostasis for balancing heat stress response of lily.[110,111] The Class C heat stress transcription factor LlHSFC2 positively regulates thermotolerance by interacting with HSFAs to enhance their transactivation ability. Acting as a transcriptional co-activator, LlHSFC2's homologous interactions are inhibited under heat stress, but its heterologous interactions with heat-induced HSFAs are promoted, allowing it to fulfill its co-activating role in establishing and maintaining thermotolerance.[112]

In addition to HSFs, numerous other transcription factors are integral to the heat stress response. LlMBF1c, a heat-inducible multiprotein bridging factor in lilies, plays a crucial role in thermotolerance.[113] A recent study has revealed that an ethylene-response factor (ERF), LlERF092, directly binds to the promoter of *LlMBF1c* to activate its expression, thereby conferring thermotolerance. Additionally, LlETO1 (ETHYLENE OVERPRODUCER 1) acts as an interacting partner of LlERF092, enhancing its transactivation ability. Co-expression of *LlERF092* and *LlETO1* further boosts thermotolerance in lily. Furthermore, treatment with ethephon triggers the expression of *LlERF092*, *LlETO1*, and *LlMBF1c*, leading to improved thermotolerance. This indicates that ethylene is involved in the LlERF092/LlETO1-*LlMBF1c* regulatory module and plays a positive role in the heat stress response of lily.[114] The overexpression of the homeodomain-leucine zipper (HD-Zip) I transcription factor *LlHB16* (*HOMEOBOX PROTEIN 16*) in lilies activates the expression of *LlHSFA2* and *LlMBF1c* (*MULTIPROTEIN BRIDGING FACTOR 1C*) and other heat-related genes, thereby enhancing thermotolerance.[115] Conversely, LlHOX6 (HOMEOBOX 6) directly represses *LlHSFA2* and *LlMBF1c*, negatively regulating thermotolerance. Additionally, LlHOX6 and LlHB16 interact to limit their transcriptional activity, balancing the heat stress response.[116]

LlbHLH87 (BASIC HELIX-LOOP-HELIX PROTEIN 87) regulates thermotolerance by activating *LlEIN3* (*ETHYLENE-INSENSITIVE* 3) and *LlHSFA2*, and by antagonistically interacting with LlSPT (SPATULA).[117] However, LlPIF4 (PHOTORECEPTOR INTERACTING FACTOR 4) serves as a positive regulator in thermotolerance of lily by directly activating *LlWRKY33* and interacting with LlbHLH87.[118] LlWRKY39, which contains a potential calmodulin (CaM)-binding domain, acts as an upstream regulator of *LlMBF1c*. LlCaM3 interacts with LlWRKY39 in a Ca^{2+} dependent manner, negatively affecting the LlWRKY39-mediated transcriptional activation of *LlMBF1c*, thus forming a feedback

pathway to balance the heat stress response.[119]

LlWRKY22, activated at high temperatures, contributes to thermotolerance by inducing its expression and that of *LlDREB2B* (*DEHYDRATION-RESPONSIVE ELEMENT BINDING PROTEIN 2B*).[120] In transgenic plants, LlERF110 accumulation activates certain deterrents related to the heat stress response, indirectly disrupting *HSFA2* expression. This results in reduced thermotolerance and disruption of the ROS balance *in vivo*.[121]

LlMYB305, an R2R3-MYB transcription factor, positively influences thermotolerance by activating heat-protective genes. It represses *LlHSC70* promoter activity under normal conditions but activates it during heat stress, indicating that LlMYB305 may require heat activation to function in thermotolerance.[122] The lily membrane-associated NAC protein LlNAC014 acts as a transcription factor under heat stress by entering the nucleus and enhancing thermotolerance through activation of the DREB2-HSFA3 module.[123] Similarly, *LlDREB1G*, a DREB subfamily gene, confers acquired thermotolerance to transgenic *Arabidopsis* plants. Higher *LlDREB1G* levels also improves resistance to freezing and dehydration stresses.[124]

High temperatures significantly impact lily morphogenesis and quality, while other abiotic stressors, such as drought and salt stress, can cause irreversible physiological damage. In lilies, miR396b and its target gene *LdPMAT1* are involved in drought tolerance. Silencing *miR396b* in lilies enhances drought tolerance and increases *LdPMAT1* expression. Furthermore, stable overexpression of *LdPMAT1* reduces leaf wilting and enhances cell membrane stability by affecting the accumulation of osmoregulatory substances, thereby improving drought tolerance.[125] Additionally, *LdPMAT1* overexpression increases the expression levels of *LdCAT3* (*CATALASE 3*) and *LlSOD2* (*SUPEROXIDE DISMUTASE 2*), reducing ROS accumulation in transgenic lilies under drought stress conditions.[126]

The NAC gene family plays a crucial role in plant growth, development, and abiotic and biotic stress responses. *LpNAC5*, a stress-responsive transcription factor in lilies, confers stronger drought and salt-alkali tolerance in tobacco plants when overexpressed.[127] Conversely, *LpNAC6* transgenic tobacco displays enhanced alkali tolerance but reduced drought tolerance, indicating an inverse regulatory role in alkali and drought tolerance.[128] Similarly, *LpNAC13* overexpression in tobacco results in reduced drought tolerance but enhanced salt tolerance, also highlighting its contrasting role in drought and salt stress tolerance.[129] Transgenic tobacco with *LpNAC17* overexpression exhibits increased salt stress tolerance.[130]

In lilies, LlDREB1 binds to the promoter of *LlNAC2*, activating its expression. LlNAC2 interacts with LlDREB1, and overexpression of *LlNAC2* in *Arabidopsis* enhances tolerance to cold, drought, and salt stresses.[131] LbNAP, another NAC member, features a typical NAC region. Silencing *LbNAP* leads to delayed flower senescence and reduced dehydration stress damage, correlating with increased SOD and CAT activities and their gene expression.[132] LlMYB3, a MYB-related homolog in lilies, directly binds to the *LlCHS2* promoter, activating its expression to enhance tolerance to cold, drought, and salt stresses.[133] Similarly, LpMYB4 promotes saline-alkaline tolerance by interacting with LpGPX6 (GLUTATHIONE PEROXIDASE 6) and LpTrx (THIOREDOXIN) to scavenge ROS.[134]

LpCPC (Cucumber Peeling Cupredoxin), a blue-copper protein with conserved type I copper regions, enhances salt stress pathways. In *LpCPC*-overexpressing tobacco, essential genes such as *NHX1* (*Na^+/H^+ EXCHANGER 1*) and *SOS1* (*SALT OVERLY SENSITIVE 1*) demonstrate higher expression compared to the wild type. Transgenic lines exhibit increased expression levels of *CCR1* (*CINNAMOYL COA REDUCTASE 1*) and *CAD* (*CINNAMYL ALCOHOL DEHYDROGENASE 4*) as well as lignin production, indicating LpCPC's role in improving saline-alkali resistance through key salt stress response pathways and lignin production.[135] Similarly, lily LpBCP is a type I copper protein (BCP) that boosts saline-alkali resistance by enhancing lignin production and ROS scavenging in transgenic tobacco.[136]

LpSOS1 is significantly enriched in high-salt environments, and its overexpression improves salt stress tolerance in Arabidopsis. It enhances plant salt tolerance by regulating ionic homeostasis and reducing the Na^+/K^+ ratio, thereby protecting the plasma membrane from salt stress-induced oxidative damage and boosting antioxidant enzyme activity.[137]

Despite some advancements in understanding the regulatory networks involved in lilies' responses to stress, current research is still incomplete and lacks practical application. Future efforts should aim to deepen the study of lilies under various abiotic stresses, incorporate bioinformatics tools, and apply advanced techniques such as genetic engineering. These strategies will aid in developing more resilient and high-quality lily varieties, thereby promoting the sustainable and high-quality growth of the lily industry.

TRANSGENIC TECHNOLOGY OF LILY

As an important species with both high ornamental value and multiple economic attributes, the hundred flower has always held a unique position in the global flower industry chain.[138] Although there have been numerous systematic studies on the morphological formation, growth and development, quality trait maintenance, and stress response mechanisms of lilies, the in-depth exploration and application transformation of these results still highly depend on efficient and stable genetic manipulation techniques. However, fundamental research on lilies has been hindered by their complex genomic characteristics. Notably, species such as *L. davidii* var. *unicolor* with a genome size of 36.68 Gb and *L. sargentiae* at 35.66 Gb, alongside a heterozygosity rate exceeding 2%, present complex genetic backgrounds.[25,30] These factors complicate gene localization and genetic manipulation, slowing progress in molecular biological research. Additionally, they present systemic challenges for conventional breeding, such as inefficient germplasm innovation and extended trait improvement cycles.

Since Cohen first achieved *Agrobacterium* transformation of lily plants in 1992, researchers have continuously innovated and gradually improved the technology, establishing CRISPR/Cas9 system.[139] The precise introduction of exogenous genes and targeted editing have become effective paths for understanding the molecular basis of key lily traits and improving important horticultural qualities. This has provided new ideas for promoting the functional gene analysis, genetic improvement, and new variety selection of lilies.

In genetic transformation systems, *Agrobacterium*-mediated transformation and pollen magnetofection have become essential methods in contemporary lily transgenic research. The pollen magnetofection technique employs Fe_3O_4 nanoparticles to transport exogenous DNA (particle size ratio 1:4, treatment duration of 30 min). This approach cleverly bypasses the reliance on tissue culture by using the natural pollen tube as a channel for genetic material delivery, achieving transformation efficiencies of 85.80% in 'Sweet Surrender' and 54.47% in *L. leucanthu*.[140] However, the significant genotype dependency of this technique has limited its successful application across diverse lily species. In contrast, while biolistic methods avoid the constraints of biological vectors, their use in lilies has been restricted due to issues with multicopy insertion. These limitations of single-technique approaches have led researchers to explore diversified technical integration pathways. After three decades of development, *Agrobacterium*-mediated transformation has shown significant advantages in receptor adaptability, genetic stability, and operational controllability. It has emerged as the most mature technical system for lily genetic transformation. Systematic advancements in crucial areas such as receptor type screening, bacterial strain selection, and the optimization of culture medium formulation have laid important foundations for technological upgrades.[138]

Early studies in receptor selection primarily utilized leaves, roots, stems, or callus as materials for transformation, but faced challenges due to regeneration difficulties and low transformation efficiency.[138] The successful induction of embryogenic callus has highlighted its unique advantages as a genetic transformation receptor for lilies. This method not only significantly enhances genetic transformation efficiency but also markedly reduces chimera formation.[141,142] Yan et al.[142] achieved stable and efficient transformation systems using the embryogenic callus of *L. pumilum* DC. Fisch. and bulb scales of *L. longiflorum*, with optimized transformation efficiencies of 29.17% and 4%, respectively.

Although the positive plant rate via the adventitious bud regeneration pathway is relatively low, this method allows for regenerated plants to be obtained within one month, thereby shortening experimental cycles. Such methods can be improved by optimizing delivery procedures and the media used for adventitious bud regeneration. Additionally, studies on strain-receptor compatibility have demonstrated that using EHA105/EHA101 co-culture systems, substituting traditional acetosyringone (AS) with chloroxynil (CX), or maintaining lower pH levels in the media can increase transformation efficiency

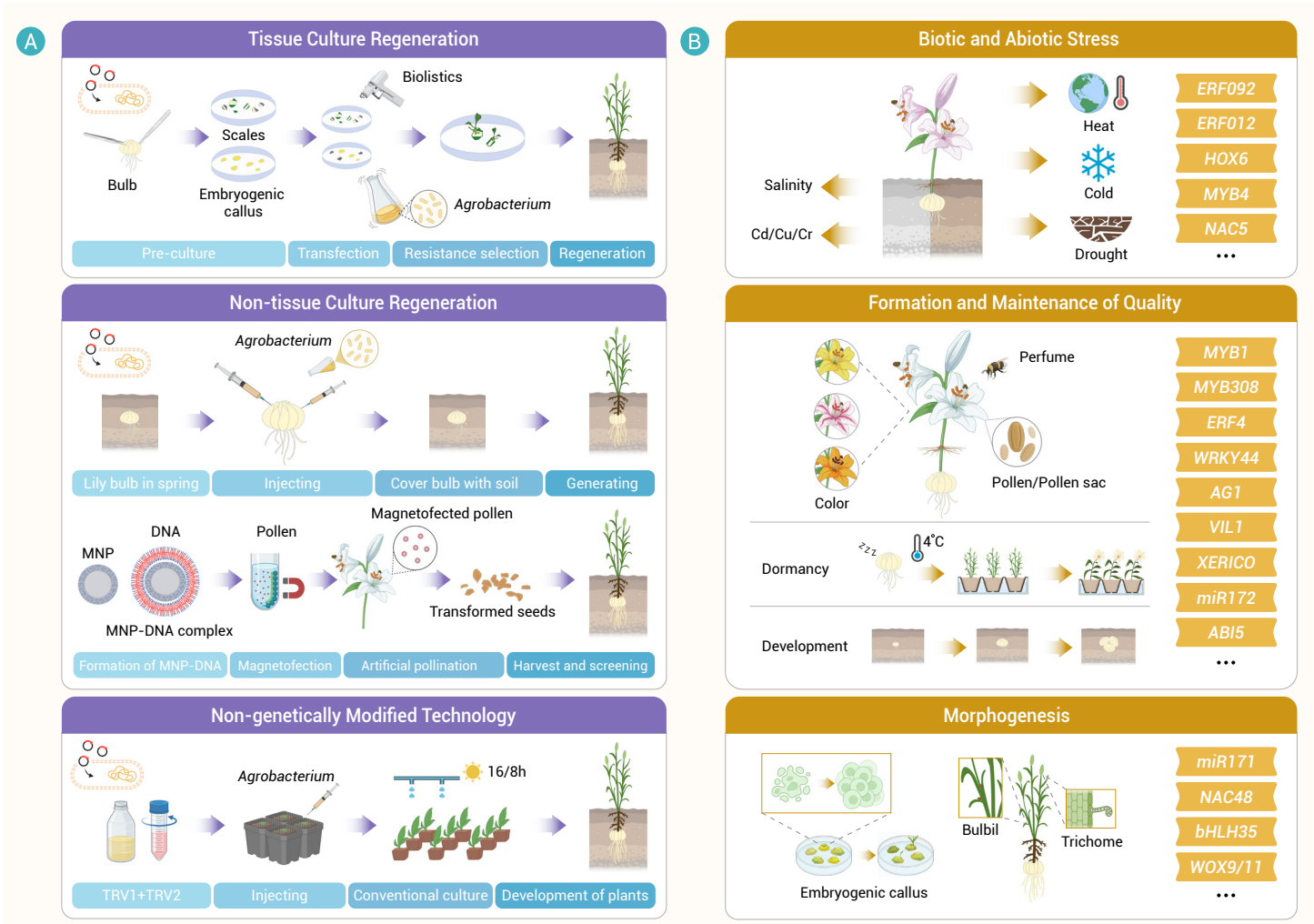

Figure 5. Main approaches and research areas for functional characterization of genes in *Lilium* species (A) Predominant techniques for gene functional validation in *Lilium*: *Agrobacterium*-mediated genetic transformation, Particle bombardment (Biolistics), Pollen magnetofection, Meristem direct transformation and Virus-induced gene silencing. (B) Key research domains in *Lilium* gene function studies: Biotic and abiotic stress responses, Formation and maintenance of quality, and Morphogenesis.

by over 10% in certain lily species.[138]

Furthermore, Deng et al.[143] have developed a novel meristem injection method, which successfully circumvents the reliance on tissue culture. This technique enables direct transformation in *L. regale* resulting in stable genomic integration while markedly shortening the transformation cycle. In addition, it substantially lowers experimental costs and labor requirements, all while maintaining high transgene expression efficiency (Figure 5A).

The establishment of CRISPR/Cas9 systems has ushered lily gene function research into the era of precision editing. Yan et al.[142] successfully utilized CRISPR/Cas9 technology via stable *Agrobacterium* transformation system to precisely edit the *phytoene desaturase* (*LpPDS*) gene in two types of lilies, *L. pumilum* DC. Fisch. and *L. longiflorum*. Notably, this work yielded a range of visible mutant phenotypes, including fully albino, pale-yellow, and albino-green chimeric plants. Further Sanger sequencing confirmed a spectrum of mutation types at the target site, encompassing nucleotide insertions, deletions, and substitutions. Despite this success, significant efficiency variations among different genotypes continue to limit the universal applicability of gene editing technology. Current technical bottlenecks mainly manifest as three key conflicts: the challenge of improving transformation efficiency while being genotype-dependent, the tension between maintaining genetic stability and managing multicopy integration, and the conflict between technical universality and operational complexity. The limitations of current stable genetic transformation systems in lilies directly constrain the depth of gene function research, leading researchers to explore transient transformation systems. The Tobacco Rattle Virus (TRV) vector system, with its rapid 3 to 5-week cycle, has conducted over 75% of research tasks related to gene functional verification in lily floral fragrance, color, and stress responses. Nonetheless, the inherent limitations of viral vectors – such as restricted cargo capacity (< 2 kb) and short expression duration (≤ 21 days) – render them unsuitable for studies requiring long-term observation of developmental regulatory genes or stable inheritance demands associated with CRISPR/Cas9 technology.

Despite existing technical barriers, lily-related research is advancing, with key genes regulating important traits being successively identified[14,24,106,116] (Figure 5B). Technological breakthroughs are emerging through multidimensional innovation, particularly in transformation system improvement. Rhizobia, such as *Ensifer adhaerens*, demonstrate strong transformation potential, while *S. meliloti* can infect monocotyledonous and dicotyledonous plants.[144] Another innovative approach involves co-expressing developmental regulators like GRF (Growth-Regulating Factor) and BBM (BABY BOOM), or morphogenetic genes during transformation. This technique enhances transformation efficiency by activating cellular totipotency, showing promise for improving lily transformation efficiency.[145,146] The Cut-Dip-Budding delivery system developed by Cao et al.[147] facilitates exogenous gene delivery using vigorous meristematic tissues under non-sterile conditions through *A. rhizogenes* systems and subsequently yields regenerated transgenic plants. This system not only overcomes the time and cost constraints associated with conventional tissue culture, but also markedly reduces dependence on stringent experimental conditions and specialized equipment. Similar to meristem injection approaches, the CDB system broadens the practical applicability of genetic transformation technologies in commercial settings. Its high flexibility, scalability, and operational simplicity underscore its strong potential for

industrial adoption, offering a novel strategy for genetic transformation in lilies.

Notably, research on promoter system optimization lags behind, with over 90% of current transformation experiments still relying on the CaMV 35S constitutive promoter. As lily genomic data accumulates, developing species-specific promoters will become crucial for achieving precise expression of exogenous genes. Current research indicates that establishing integrated transformation systems by combining novel delivery technologies, optimized receptor systems, and precision regulatory elements will be essential for breakthroughs in lily transgenic technology. With coordinated advances in technological iteration and fundamental research, significant breakthroughs in lily genetic engineering are anticipated in the near future.

FUTURE DIRECTIONS AND CHALLENGS

Although studies on lily molecular biology have continued in the past decade, the lack of genomic information has limited research largely to the cloning of single genes or small gene sets, with investigations confined to preliminary analyses of transcriptional regulation. Most available data have been derived from transcriptome analyses, with little exploration of systematic gene regulatory networks or underlying molecular mechanisms. In addition, the absence of a stable genetic transformation system has restricted functional validation of candidate genes to transient assays *in vitro* or heterologous expression.

Lily is a horticulturally significant genus, yet its complex and large genome has long hindered comprehensive molecular biology studies. Recent sequencing efforts have provided important insights, particularly with the completion of genome assemblies for *L. lancifolium* (36.68 Gb), *L. regale* (35.6 Gb), and *L. sargentiae* (35.66 Gb), with the first two reaching chromosome-level resolution.[25,30,148] These large genomes, averaging 35–37 Gb, are primarily characterized by whole-genome duplication events and extensive insertions from long terminal repeat retrotransposons (LTR-RTs), which contribute to their structural complexity. These advancements have shifted lily research from single-gene studies to more comprehensive, genome-wide investigations.

Despite these breakthroughs, the polyploid nature of lilies continues to challenge accurate genome assembly, especially in repetitive regions, and underscores the need for improved computational tools. Although transcriptome analyses have provided valuable functional insights, there is still a lack of systematic gene regulatory network studies and limited functional validation of key genes. Current research has focused largely on sequencing and basic functional analysis, leaving gaps in our understanding of how genomic variations contribute to environmental adaptation. Population genomics and phenotypic studies of different *Lilium* species are needed to explore these connections in more depth. Moreover, integrating multi-omics data with advanced epigenetic tools will be crucial for deciphering the molecular mechanisms underlying developmental processes, such as bulb formation and anther development. The application of genome-editing technologies like CRISPR/Cas9, combined with the establishment of efficient, genotype-independent transformation systems, offers promising avenues for improving agronomic traits such as disease resistance and stress tolerance. Furthermore, comparative genomics across species will shed light on the evolutionary processes that have shaped the genetic diversity of lilies.

Looking ahead, the incorporation of machine learning and artificial intelligence for genome and phenotype analysis will likely accelerate the discovery of trait-associated genes. This, in turn, will deepen our understanding of the regulatory networks that control important traits, paving the way for more targeted breeding programs. The recent progress in lily genomics provides a crucial foundation for addressing both fundamental biological questions and applied challenges in horticultural breeding. As genomic resources and technologies continue to evolve, they will not only enhance our understanding of lily molecular biology but also open new opportunities for the development of improved cultivars capable of thriving in changing environmental conditions.

CONCLUSIONS

Over the past decade, significant advancements have been made in lily molecular biology, particularly in genomics, stress tolerance, genetic improvement, and secondary metabolite production. These developments offer promising opportunities to enhance the resilience and quality of lilies against environmental challenges. Continued genomic research and the application of advanced biotechnological tools will be crucial for further enhancing the sustainability and competitiveness of the lily industry in the coming years.

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AUTHOR CONTRIBUTIONS

All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AND CODE AVAILABILITY

Data are available from the corresponding author upon reasonable request.