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Molecular genetic analyses of abiotic stress responses during plant reproductive development

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Abstract

Plant responses to abiotic stresses during vegetative growth have been extensively studied for many years. Daily environmental fluctuations can have dramatic effects on plant vegetative growth at multiple levels, resulting in molecular, cellular, physiological, and morphological changes. Plants are even more sensitive to environmental changes during reproductive stages. However, much less is known about how plants respond to abiotic stresses during reproduction. Fortunately, recent advances in this field have begun to provide clues about these important processes, which promise further understanding and a potential contribution to maximize crop yield under adverse environments. Here we summarize information from several plants, focusing on the possible mechanisms that plants use to cope with different types of abiotic stresses during reproductive development, and present a tentative molecular portrait of plant acclimation during reproductive stages. Additionally, we discuss strategies that plants use to balance between survival and productivity, with some comparison among different plants that have adapted to distinct environments.

Keywords: Abiotic stresses, large-scale studies, plants, reproductive development, transcriptional regulation.

Introduction

Plants are sessile and cannot move to avoid unfavorable environmental conditions; therefore, they must cope with adverse environmental conditions by cellular changes. The environmental factors that can limit plant growth and reproduction include water, temperature, light, and nutrients (Zhu, 2016). Fluctuations in these abiotic conditions may lead to minute initial cellular changes and subsequently result in a series of dramatic biochemical, physiological, and morphological changes in plants (Osakabe et al., 2013). These impacts have been extensively studied and discussed for plant responses during vegetative development (Cramer et al., 2011; Bechtold and Field, 2018; He et al., 2018; Kollist et al., 2019). Adverse abiotic factors also negatively impact plant reproduction and yield; such negative effects are responsible for substantial losses in agriculture and economy (Hasanuzzaman et al., 2013; De Storme and Geelen, 2014); therefore, research specifically investigating abiotic effects during reproductive development is of great importance.

Despite the importance, there have been a relatively small number of studies on plant reproductive development under abiotic stresses. This is partly because studies involving reproductive development require longer plant growth periods with more space and greater efforts to obtain the relevant materials. For example, Arabidopsis thaliana floral buds are small, requiring meticulous handling of tiny floral organs such as the stamen and pistil (Wellmer et al., 2006; Su et al., 2013). Moreover, the high degree of sensitivity of reproducing plants to environmental changes means that small changes of the growth condition could cause phenotypical differences, making it difficult to recognize phenotypic changes due to
gene functional manipulations. More importantly, with the rapid advances of reverse genetics, the lack of obvious phenotypic differences is often considered as no effect due to a mutation, whereas potentially measurable quantitative traits are not investigated, with missed opportunities for uncovering gene functions. Nevertheless, recent advances in technologies such as large-scale data analysis (Su et al., 2013; Ma et al., 2014; Grootkensky et al., 2018) have provided powerful tools to further explore plant response to stresses in reproductive tissues at the molecular level. Here, we summarize studies (Table 1) that explored plant reproductive development under abiotic stresses, and discuss strategies that plants employ in response to different types of abiotic stresses at reproductive stages.

Water deficiency and salinity

Water availability is one of the most important abiotic factors that affect plant growth and development. Both drought and salt stresses can lead to water scarcity, especially given that both stresses change osmotic homeostasis, accumulate similar metabolites, and can activate overlapping signaling pathways (Zhu, 2002, 2016). Drought is known to cause flowering time change, flower abortion, reduction of pollen fertility and seed number, as well as immature or aborted seeds in plants (Su et al., 2013; Shavrukov et al., 2017). Salt stress also has similar negative effects on reproductive development in rice, wheat, and grape (Khan and Abdullah, 2003; Zheng et al., 2010; Baby et al., 2016). Notably, drought/salt stress also cause differential expression of various genes, including those regulating flowering time and development of reproductive organs, and genes encoding transcription factors (TFs) that function in response to osmotic stresses (Su et al., 2013). Below, we discuss molecular genetic analyses of gene functions and genes identified using large-scale experiments (Fig. 1).

Transcriptional regulation

Drought/salt stresses impact several aspects of plant reproductive development at the molecular level, especially via transcriptional regulation. Members of several TF families have been shown to respond to water stress and were recently found to play crucial roles in plant reproductive development, including ANAC (abscisic acid-responsive NAC), bHLH (basic helix-loop-helix), DREB (dehydration responsive-element binding), homeobox domain, MYB, and zinc finger, in both A. thaliana (Krishnaswamy et al., 2011; Ryu et al., 2011, 2014; Hichri et al., 2014; Yu et al., 2016; Chen et al., 2017; Sukiran et al., 2019) and rice (Oryza sativa) (C. Guo et al., 2016; Jin et al., 2018; Minh-Thu et al., 2018).

In general, changes in floral morphology, seed production, and related gene expression patterns together support the importance of the gene function in reproductive development under stress. In an Arabidopsis study in which plants were treated with drought starting at the onset of flowering to the end of their life cycle (Su et al., 2013), the drought stress caused an arrest of the development of floral buds. However, plants recovered partially after acclimation over a period of ~2 weeks of treatment, with reduced seed numbers compared with well-watered plants. Floral defects were observed at different flower stages in drought-treated plants, including abnormal anther development, lower pollen viability, reduced filament elongation, ovule abortion, and failure of the flower to open.

Among genes induced by drought stress during plant reproductive development, Arabidopsis ANAC019 (Sukiran et al., 2019) and AtMYB37 (Yu et al., 2016), and rice OsMID1 (MYB-like family protein) (C. Guo et al., 2016) and OsERF101 (encoding an AP2 family TF) (Jin et al., 2018) are highly expressed in reproductive organs under drought. These genes can mitigate anther defects and improve pollen fertility and seed production under drought stress. In addition, gene expression analyses in mutants or overexpression lines for these TFs have revealed that important regulatory genes were involved in response to drought during reproductive development, including abscisic acid (ABA) insensitive (ABI), DREB, MYB, peroxidase (POD), and responsive to dehydration (RD) genes.

Specifically, ANAC019 functions as an early drought response regulator, which can be induced in flowers soon (3 d) after drought treatment (Su et al., 2013). The mRNA level of ANAC019 is much higher in the inflorescence than in the leaf when plants are grown with insufficient water, especially when plants recover after a period (7–14 d) of acclimation to severe drought (Sukiran et al., 2019). The anac019 mutant showed significant shortening of the stamen and pistil, and delayed recovery of flowering under drought stress as compared with the wild-type (WT) plant. In addition, several important drought-responsive and floral genes were expressed differentially in the anac019 mutant compared with the WT, consistent with mutant phenotypes. These observations support a critical role for ANAC019 in promoting not only reproductive development but also drought tolerance (Fig. 2) (Sukiran et al., 2019). Another Arabidopsis gene, AtMYB37, also plays an important role in drought response and regulation of seed production, as overexpression lines displayed both increased seed production and drought tolerance; moreover, the expression levels of several key ABA-responsive genes were altered in these lines (Yu et al., 2016), supporting the idea that AtMYB37 affects reproductive development under drought at least in part via transcriptional regulation of key target genes.

In rice, OsMID1 (C. Guo et al., 2016), encoding a MYB-like TF, is expressed in vascular tissues, can be induced by drought in rice flowers, and its overexpression resulted in enhanced drought tolerance, with reduced anther defects and increased pollen fertility and grain production. A ChiP experiment demonstrated that OsMID1 binds to the promoter region of both drought-responsive (OsHSP17.0 and OsCYP707A5) and anther developmental (OsKAR) genes, further supporting its roles in both processes (C. Guo et al., 2016). Another rice gene, OsERF101, is also preferentially expressed in flowers, and transgenic lines with overexpression of OsERF101 displayed elevated peroxidase activity and proline content, which in turn contributed to increased drought tolerance and improved pollen fertility. Additionally, these transgenic plants showed induced expression of ABA-responsive genes, including RD22, LEA3, and POD (Jin et al., 2018). Together, these Arabidopsis
| Gene name | Arabidopsis gene ID | Homolog in other species* | Biological function | Type of stress studied | Mutant phenotype under stress† | Molecular function | Upstream regulators | Downstream regulators* | Reference(s) |
|-----------|---------------------|--------------------------|---------------------|-----------------------|-----------------------------|-------------------|-------------------|------------------------|--------------|
| bHLH112   | AT1G61660           | OsbHLH068                | Flowering time      | Salt                  | Increased salt-induced H$_2$O$_2$ level, decreased root elongation, and delayed flowering | Transcription factor | –                 | MYB, PP2C, CBF, ACS11, LFY, FT, FLC, SOC1 | Chen et al. (2017) |
| ANAC019   | AT1G52890           | –                        | Floral organ development | Drought               | Increased drought sensitivity, and delayed floral organ recovery | Transcription factor | –                 | DREB, WRKY, MYC, bHLH, ARF2, MYB | Sukiran et al. (2019) |
| MYB37     | AT5G23000           | –                        | Seed development    | Drought               | Increased drought tolerance, delayed flowering, and enhanced seed productivity | Transcription factor | –                 | ABF, DREB, MYC, SnRK, RD | Yu et al. (2016) |
| DIV2      | AT5G04760           | OsMID1 (Os05g370160)     | Anther development  | Drought               | Increased drought tolerance, decreased anther defects and enhanced pollen fertility | Transcription factor | –                 | POD, zinc finger, MYB, HSP | C. Guo et al. (2016) |
| RAP2.6L   | AT5G13330           | OsERF101/RAP2.6 (Os04g0398000) | Pollen development | Drought               | Increased drought tolerance, and enhanced pollen productivity | Transcription factor | –                 | DREB, P5CS, POD, RD | Jin et al. (2018) |
| BFT       | AT5G62040           | –                        | Flowering time      | Salt                  | No delayed flowering under stress | Transcription factor | –                 | FD, AP1 | Ryu et al. (2011, 2014) |
| SKB1      | AT4G31120           | –                        | Anther development  | Salt                  | Increased salt sensitivity, decreased growth rate, and delayed flowering | Epigenetic regulator (H4R3me2) | –                 | LSM4, FLC | Wang et al. (2007); Schmitz et al. (2008); Zhang et al. (2011) |
| EMF1      | AT5G11530           | –                        | Flowering time      | Drought               | Increased drought tolerance, and early flowering | Epigenetic regulator (H3K27me3) | –                 | AG, AP1, CO | Pu et al. (2013) |
| PAT10     | AT3G51390           | –                        | Floral organ development | Salt                  | Increased salt sensitivity, decreased leaf size, plant height, and sterility | Protein modification | –                 | CBL | Zhou et al. (2013) |
| CDKG2     | AT1G67580           | –                        | Flowering time      | Salt                  | Increased salt tolerance, and early flowering | Protein kinase | –                 | RD29B, AB3, MYB15, P5CS1, FLC, FT, AP1, LFY | Ma et al. (2015) |
| MPK6      | AT2G43790           | RhMPK6                   | Flower opening      | Drought               | Reduced ethylene production | Protein kinase | –                 | – | Meng et al. (2014) |
| P5CS1/2   | AT2G39800 / AT3G56100 | –                        | Pollen development  | Drought/salt | Sterility | Metabolic enzyme | – | – | Sakamoto et al. (2002) |
| NUC1      | AT1G48920           | OsNUC1                   | High expression     | Salt                  | Increased growth rate, root length, and decreased H$_2$O$_2$ level | Nucleolin | –                 | P5CS1 | Sripronyowanich et al. (2013) |
| Fer1      | AT5G01600           | RhFer1                   | Petal development   | Drought               | Decreased free ferrous iron level | Ion transport | ABF2 | – | Liu et al. (2017) |
| Gene name | Arabidopsis gene ID | Homolog in other species | Biological function | Type of stress studied | Mutant phenotype under stress | Molecular function | Upstream regulators | Downstream regulators | Reference(s) |
|-----------|---------------------|--------------------------|---------------------|------------------------|----------------------------|-------------------|-------------------|--------------------|-------------|
| LTP | AT4G33550/AT4G30880 | OsDIL (Os10g0148000) | Male development | Drought | Increased drought tolerance, and decreased tapetum and anther defects | Lipid transfer protein | – | RD22, SODA1, bZIP, POD, OsC4, CYP704B2 and OsCP1 | Guo et al. (2013) |
| DREB1A | AT4G25480 | – | Female development | Drought | Arrested flower opening | Transcription factor | – | – | Su et al. (2013) |
| MYB21 | AT3G27810 | – | Male development | Drought | Defects in stamen development, increased sterile siliques | Transcription factor | – | – | Su et al. (2013) |
| HOS9 | AT2G01500 | – | Flowering time | Cold | Decreased growth rate, delayed flowering, and increased cold sensitivity | Transcription factor | – | RD29A, WRKY | Zhu et al. (2004) |
| GA2ox1 | – | Os07g0169700 | Pollen development | Cold | Severe pollen abortion and seed reduction | Enzyme | – | – | Sakata et al. (2014) |
| GA3ox3 | – | Os09g0178100 | Pollen development | Cold | Severe pollen abortion and seed reduction | Enzyme | – | – | Sakata et al. (2014) |
| SOC1 | AT2G45660 | VcSOC1 | Floral organ development | Cold | Increased number of floral buds and flower and fruit clusters, and increased cold tolerance | Transcription factor | – | IAA, GA synthetic genes, AP1, CO, FD, TCP14 | Song et al. (2018) |
| HSFA2 | AT2G26150 | SiHsfA2 | Male development | Heat | Increased heat tolerance; decreased viability and germination rate of pollen | Transcription factor | – | HSP, GA synthetic genes, pectate lyase | Fragkostefanakis et al., 2016 |
| HSFB2a | AT4G11660 | – | Female development | Heat | Impaired female gametophyte | Transcription factor | – | – | Wunderlich et al. (2014) |
| BOB1 | AT5G03400 | – | Flowering time and meristem identity | Heat | Decreased heat tolerance, decreased growth rate, and leaf and inflorescence meristem defects (partial loss of function) | Protein chaperone | – | – | Perez et al., 2009 |
| IRE1 | AT2G17520/AT5G24360 | – | Pollen development | Heat | Tapetum defects, and sterility | Protein kinase/ribonuclease | – | SEC31A, bZIP60 | Deng et al. (2016) |
| CKI | AT4G26100/AT1G72710 | GhCKI | Pollen development | Heat | – | Protein kinase | – | – | Min et al. (2013) |
| ROXY1 | AT3G02000 | – | Petal development | Oxidative | Floral structure defects | Oxidoreductase (metabolic enzyme) | – | AG | Xing et al. (2005) |
| ROXY1/2 | AT3G02000/AT5G14070 (Os04g02300/Os02g3085) | ROXY1/2 (Os04g02300/Os02g3085) | Petal development | Oxidative | Floral structure defects; increased H2O2 level, and hypersusceptibility to pathogen | Oxidoreductase (metabolic enzyme) | – | – | Wang et al. (2009) |
| RD20 | AT2G33380 | – | Flowering time | Oxidative | Increased H2O2 level, and early flowering | Metabolic enzyme | – | – | Bee et al. (2014) |
| ADR | AT4G13540 | – | Anther development | Oxidative | Anther indehiscence, and male sterility | – | NMT | – | Dai et al. (2019) |
| Gene name | Arabidopsis gene ID | Homology in other species | Molecular function | Upstream regulators | Downstream regulators | Reference(s) |
|-----------|---------------------|---------------------------|-------------------|--------------------|-----------------------|--------------|
| PIC1      | AT2G15290           | -                         | Ion transport     | Transcription factor | DNA repair histone acetyltransferase | Duy et al. (2011) |
| SPL7/KIN17 | AT5G18830/AT1G55460 | -                         | Transcription factor | Oxidative | DNA glycosylase | Garcia-Molina et al. (2014) |
| MBD4L    | AT3G07930           | -                         | Transcription factor | Oxidative | DNA repair histone acetyltransferase | Nota et al. (2015) |
| TAF1     | AT1G32750/AT3G19040 | -                         | DNA repair histone acetyltransferase | Oxidative | DNA repair histone acetyltransferase | Waterworth et al. (2015) |

- Os, rice; Rh, rose; Vc, blueberry; Sl, tomato; Gh, cotton.
- Results from overexpressed lines are shown in green.
- Stress-responsive genes are labeled in red; flower-related genes are labeled in blue.

Table 1. Continued

and rice results strongly support the roles of TFs in drought response during reproductive development.

However, the functions of some regulators in drought response and development are not similarly conserved. For example, members of the large bHLH family, AtbHLH112 in Arabidopsis and OsbHLH068 in rice, function similarly in drought/salt stress response (Chen et al., 2017), but act in opposite manners in Arabidopsis flowering control. It was demonstrated that the Atbhlh112 mutant exhibits reduced salt tolerance, whereas the overexpression of OsbHLH068 in Arabidopsis decreases levels of the reactive oxygen species (ROS) H$_2$O$_2$ and enhances salt tolerance. However, the Atbhlh112 mutant and OsbHLH068 overexpression lines both exhibit late-flowering phenotypes. Furthermore, similar expression patterns of stress-responsive genes were found in both OsbHLH068- and AtbHLH112-overexpressing Arabidopsis lines, whereas the key flowering control gene FLOWERING LOCUS T (FT) shows the same pattern in an OsbHLH068-overexpressing Arabidopsis line and the Atbhlh112 mutant line. It is possible that the function of these two bHLH genes in stress response was ancestral, but the Arabidopsis and rice genes have diverged functionally in control of flowering time.

Although the molecular mechanisms are still unclear for regulation of downstream genes by the above-mentioned TFs, some studies have begun to address this question. It is known that salt stresses can delay flowering in Arabidopsis (Riboni et al., 2014), but a loss-of-function mutant of the AtBFT gene, encoding an FT/TERRAIND FLOWER 1 (TFL1) family protein, fails to delay flowering under salt stress (Ryu et al., 2011). The expression of a key regulator of flower development, AP1, is reduced in salt-stressed plants, but the repression of AP1 expression is less severe in the atbft mutant than that in the WT (Ryu et al., 2011). Therefore, AtBFT functions as a floral repressor under high salinity. Furthermore, under high salinity, AtBFT interferes with the interaction between FT and FD, which are positive regulators of flowering (Ryu et al., 2014). AtBFT accomplishes this interference by binding to the C-terminal region of FD (a bZIP protein that associates with FT), the same region as for FD–FT interaction. Thus, the binding of FD by AtBFT under high salinity results in a reduced level of the FD–FT complex, thus resulting in delayed flowering. This study indicates that specific TFs that are induced under drought/salt stress can be linked to existing regulatory pathways for flower development. Delayed flowering is usually caused by the repression of flowering time genes. This strategy allows plant to conserve energy and resources to survive the unfavorable environment. Future studies may yet reveal other mechanisms for transcriptional regulation.

**Epigenetic regulation**

Another level of the regulation of gene expression is epigenetic regulation, which can impact seed germination, phase transition, flowering time control, vegetative and reproductive development, as well as defense and stress response (Chinnusamy and Zhu, 2009; Pikaard and Mittelsten Scheid, 2014). One important and widely investigated aspect of epigenetic regulation is histone modification, which is involved in flowering
One type of histone modification is methylation on an arginine (R3) residue of the subunit histone 4 (H4) and is carried out by arginine methyltransferases (Wang et al., 2001). The Arabidopsis gene (AtSKB1) encoding a protein arginine methyltransferase negatively regulates the expression of a key flowering repressor gene FLOWERING LOCUS C (FLC) through the methylation of H4R3 to yield H4R3sme2 (histone4 arginine3 symmetric dimethylation2), with a consistent flowering repressor gene FLOWERING LOCUS C (FLC) methyltransferase negatively regulates the expression of a key flowering repressor gene FLOWERING LOCUS C (FLC) through the methylation of H4R3 to yield H4R3sme2 (histone4 arginine3 symmetric dimethylation2), with a consistent flowering repression (de la Paz Sanchez et al., 2015; Schuettengruber et al., 2017). Pu et al. (2013) found that AtEMF1 is required for histone 3 lysine 27 trimethylation (H3K27me3), whereas the ULTRAPETALA1 (AtULT1) gene encoding a Trithorax group factor is a positive regulator of histone 3 lysine 4 trimethylation (H3K4me3). The functions of AtEMF1 and AtULT1 are antagonistic in regulating the expression of target genes, including AGAMOUS (AG), APETALA1 (AP1), FLC, and CONSTANS (CO). It was also found that reducing the AtEMF1 function increased salt tolerance and expression of salt-responsive genes, whereas such effects of reducing AtEMS1 function were cancelled by a mutation in AtULT1. Therefore, the AtEMF1 and AtULT1 system controls the homeostasis of histone mark deposition and enables proper flowering under salt stress.

Protein phosphorylation and palmitoylation

Protein modifications, particularly protein phosphorylation, are important for multiple cellular processes, such as cell cycle progression controlled by cyclin-dependent kinases (CDKs), and intracellular signaling regulated by the mitogen-activated protein kinase (MAPK) cascade (Rodriguez et al., 2010). A recent study reported that CYCLIN-DEPENDENT KINASE G2 (AtCDKG2) is highly expressed in flowers (Ma et al., 2015), and a loss-of-function atcdkg2 mutation caused reduced expression of the flowering repressor FLC under salt stress and...
up-regulation of flowering promotion genes such as *FT*, *AP1*, and *LEAFY* (*LFY*), leading to early flowering. Also, the *atcdkg2* mutation resulted in the up-regulation of stress-responsive genes, such as *RD29B*, *ABI2*, *MYB15*, and *P5CS1*, and thus increased salt tolerance, indicating that *AtCDKG2* normally acts as a negative regulator of salt stress response. Similarly, a study on rose (*Rosa hybrida*) flowers (Meng et al., 2014) showed that rehydration (water recovery after drought stress) rapidly activates *RhMPK6* expression (a homolog of *AtMPK6*), and consequently induces the phosphorylation and accumulation of *RhACS1* protein (a homolog of a key ethylene biosynthetic enzyme) in gynoecia, resulting in elevated ethylene production and downstream signaling.

Other protein modifications likely to be involved in regulation of flower development under stress include protein palmitoylation. An analysis of *AtPAT10*, a member of the protein S-acyl transferase (PAT) family implicated in palmitoylation, showed that it is crucial for reproduction and salt stress response (Zhou et al., 2013). *AtPAT10* regulates the S-acylation-dependent tonoplast association of CBL2, CBL3, and CBL6 (Feng et al., 2017), a set of tonoplast calcium sensors. The two close paralogs in Arabidopsis, CBL2 and CBL3, function in both vegetative and reproductive development, with the double mutant showing impaired siliques and seeds and weak stress tolerance (R.J. Tang et al., 2012).

**Metabolic enzymes and other functions**

Plant cells under osmotic stresses, such as drought and salt, are known to accumulate metabolites (osmolytes) such as glycine betaine (GB) and proline to reduce dehydration (Yancey, 2005) For example, GB was found to play a role in salt tolerance during seed germination and vegetative growth (Sakamoto and Murata, 2002). GB is also important for normal plant reproductive development under drought/salt stress. Specifically, enhanced GB synthesis in transgenic Arabidopsis plants help to protect plant reproductive organs against structural defects found in the WT under salt stress and promote salt tolerance in these transgenic plants (Sulpice et al., 2003).

Additionally, plant endogenous proline also plays a role in plant stress response and pollen development (Székely et al., 2008; Mattioli et al., 2012). The rate-limiting step of proline biosynthesis is catalyzed in Arabidopsis by enzymes encoded by closely related *AtP5CS1* and *AtP5CS2* (Strizhov et al., 1997). *AtP5CS1* is detected in leaves, stems, and flowers at significant levels, while *AtP5CS2* is 3–5-fold lower in most of the organs. Moreover, *AtP5CS1* is more highly expressed under drought and salinity stresses, as well as after ABA treatment (Strizhov et al., 1997). The differential expression in different organs of the two *AtP5CS* genes might lead to differential accumulation of proline and different degrees of stress tolerance.
In addition, the loss of \textit{AtP5CS1} and \textit{AtP5CS2} function causes defective male gametophytes and reduced fertility, indicating that proline is required for pollen development (Mattioli et al., 2012).

In addition to the above genes, other genes with distinct functions were also found to be involved in drought/salt response. A rice nucleolin gene \textit{OsNUC1} is differentially expressed between salt-sensitive and salt-resistant rice lines under salt stress (Sripinyowanich et al., 2013). Nucleolin is involved in the synthesis and maturation of ribosomes in the nucleolus. Alternative splicing results in transcripts of two sizes, \textit{OsNUC1-S} (shorter) and \textit{OsNUC1-L} (longer), both of which are expressed in leaves, roots, flowers, and seeds. Arabidopsis mutants specifically lacking the \textit{AtNUC1-L} transcript but express the rice \textit{OsNUC1-L} transcript exhibited a more complete revertant phenotype than the lines expressing \textit{OsNUC1-S}. However, the \textit{OsNUC1-S}-expressing attuc1-l lines displayed a higher growth rate with longer roots and lower H$_2$O$_2$ levels under high salt conditions. In addition, they also showed higher levels of induced \textit{AtP5CS1} and \textit{AtSOS1} expression under salt stress than the WT (Sripinyowanich et al., 2013).

Ion homeostasis is also related to abiotic stresses; for example, drought induces an increase in the level of free ferrous ion Fe$^{2+}$, whereas ferritin (\textit{FER}) proteins sequester free ions to protect cells from damage. In the Arabidopsis ferritin triple mutant (\textit{fer 1-3-4}), the elongation of stamen filaments was reduced, with a failure to position the anthers above the stigma, and stigmatic papillae rarely develop, leading to sterility. (Ravet et al., 2009; Yadav, 2010; Brim and Masmoudi, 2012; Tripathi et al., 2018). Also the expression of a rose ferritin gene \textit{RhFer1} is induced by dehydration and ABA during flower senescence. This activation under drought stress requires the function of \textit{RhABF2}, an AREB/ABF family TF involved in ABA signaling, through direct binding of \textit{RhABF2} to the \textit{RhFer1} promoter (Liu et al., 2017). Subsequently, the drought-induced free ferrous ion Fe$^{2+}$ is preferentially sequestered by \textit{RhFer1} but not transported outside of the petal cells to limit oxidative species during drought. This regulatory module with \textit{RhABF2/RhFer1} maintains the intracellular Fe$^{2+}$ level and enhances drought tolerance in rose flowers. Additionally, a putative rice lipid transfer protein gene \textit{OsdIL} is expressed in the anther, primarily in response to drought, salt, cold, and ABA (Guo et al., 2013). Overexpression of \textit{OsdIL} in drought-treated rice plants led to elevated tolerance to drought stress during vegetative development and reduced anther defects at reproductive stages (Guo et al., 2013). Taken together, when plants are subjected to drought/salt stresses, a variety of cellular processes could be activated, inhibited, and integrated to allow survival through the adverse environment while maximizing/protecting reproductive yield.

\textit{Detection of drought-responsive genes using transcriptomics}

In addition to the studies focusing on individual gene functions, transcriptomic studies have detected global gene expression changes during reproductive development under drought stresses in Arabidopsis and rice (Jin et al., 2013; Su et al., 2013; Ma et al., 2014). In Arabidopsis plants treated with drought starting at the onset of flowering to the end of their life cycle (Su et al., 2013), >4000 differentially expressed genes were identified in the inflorescence, including genes regulating flowering time, floral organ development, and stress responses (Su et al., 2013). Different subsets of genes displayed different temporal expression patterns during the period of drought stress. A set of drought-responsive TF genes, including \textit{AtDREB1a, ANAC019}, and \textit{AREB} genes, were highly induced 3 d after drought started. Genes responsive to water deprivation and the ABA signaling pathway were enriched among those up-regulated after 5 d of drought treatment, indicating enhanced stress response; whereas genes for cell cycle, DNA unwinding, and nucleosome assembly were repressed 5 d after drought treatment, suggesting that the growth rate was lowered. Among the drought-induced genes, \textit{AtDREB1a} and \textit{AtMYB21} were tested functionally and found to play an important role in flower development under drought stress. As the severity of drought can be important, further studies were performed on the effects of various extents of drought (Ma et al., 2014). As expected, Arabidopsis plants exhibited varying degrees of growth inhibition as the soil moisture was progressively reduced to ~65–70% (slight drought), ~45–50% (moderate drought, MD), and ~30–35% (severe drought, SD) relative amount of water. Transcriptome analyses of flowers identified >4000 genes being differentially expressed under SD and >1800 genes differentially expressed under MD. As expected, the majority of genes showed similar levels of expression under MD as compared with SD. However, a small set of genes (~220) only responded to MD, suggesting that distinct sets of genes may be responsible for growth under different amounts of water availability.

In rice, >1000 genes were differentially expressed in response to drought (Jin et al., 2013). During four stages of flower development as monitored by size, most of these genes were affected in only one or two stages, suggesting that the developmental stage is a key determinant of drought response in flowers. Genes involved in anther development, cell wall formation or expansion, and various signaling pathway were uncovered, indicating interactions between reproductive development and phytohormone signaling in drought-stressed plants. Taken together, under moderate drought conditions, plants induce the genes that function in protecting it against the stresses and in ensuring reproductive success. Under severe drought, however, plants attenuate the expression of genes for reproductive development, and devote greater amounts of energy and resources to ensure survival and, when possible, facilitate modest seed production after acclimation.

\textit{Temperature: cold/chilling and heat stresses}

Temperature is another major factor affecting the distribution and seasonal behavior of plants. Plants under cold stresses exhibit plasma membrane disintegration, cold-induced dehydration, and metabolic dysfunction (Yadav, 2010). In addition, cold-activated signaling pathways are also known to crosstalk...
Cold-responsive genes related to plant reproductive development

Different plants have adapted to growth in different temperature ranges; for Arabidopsis, 4–10 °C is considered cold (also referred to as chilling) stress, whereas near 0 °C or below is used for freezing stress (Penfield and Springerthorpe, 2012; Zheng et al., 2016; Cvetkovic et al., 2017; Pareek et al., 2017). Additionally, the temperatures for chilling and freezing stresses in rice are 0–15 °C and below 0 °C, respectively. Plants sense cold by changes in the membrane fluidity and metabolic activity. Subsequently, there are changes in cellular Ca²⁺ level, calmodulin, phytohormone and ROS signaling, and the C-REPEAT BINDING FACTOR (CBF) family TFs are activated to regulate downstream factors during reproductive development (Zinn et al., 2010). Additionally, cold-induced reduction of gibberellin (GA) disrupts rice pollen development (Sakata et al., 2014). The endogenous GA level and the expression of GA biosynthesis genes are repressed in rice under low temperature treatment (19 °C), while the expression levels of stress-responsive genes such as DREB and DELLA are increased. Also, in mutants defective in GA biosynthesis and response (such as a rice ga20ox2 mutant), the application of exogenous GA was able to reduce the sensitivity to low temperature, anther defects, and male sterility caused by low temperature (Sakata et al., 2014). These results suggest that the application of GA can rescue cold-induced male sterility, providing a potential remedy for agriculture to cope with global climate change. Although GA is known to impact several aspects of plant growth, development, and senescence (Hedden and Sponsel, 2015; Binenbaum et al., 2018), Sakata et al. (2014) provided novel evidence of its role in stress response; this might form a crosstalk with ABA signaling pathways to promote stress tolerance during reproductive development.

Furthermore, other TFs are important for plant response to cold stress. One of the HOS (HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES) family of TF genes, AtHOS9 (Zhu et al., 2004), was identified because the athos9 mutant is hypersensitive to freezing cold. The athos9 mutant displays several developmental defects including slower growth rate, late flowering time, and lower trichome density. The athos9 mutant also has increased levels of expression for some stress-responsive genes such as AtRD29A, but not CBF, which is a key regulator of cold response (Thomashow, 2001; Liu et al., 2018). These results indicate that AtHOS9 is important for plant growth and development, and for freezing tolerance through a CBF-independent pathway. Another gene involved in reproductive development under cold stress is a member of the MADS-box gene family, which includes regulators of flowering time and the ABCE genes for floral organ identities (Coen and Meyerowitz, 1991; Becker and Theissen, 2003; Jack, 2004). Many MADS-box proteins share a highly conserved MADS-domain (for DNA binding and dimerization) and a moderately conserved K domain (keratin-like; important for protein interactions) (Coen and Meyerowitz, 1991; Becker and Theissen, 2003; Jack, 2004).

A study was performed on the K domain of a blueberry (Vaccinium corymbosum) SOC1-like gene (VcSOC1K), for its potential role in blueberry reproduction under chilling stress (Song and Chen, 2018). The overexpression of VcSOC1K resulted in an increase in the number of canes, floral buds, and flower and fruit clusters under chilling treatment as compared with the WT. Transcriptome analysis identified the differential expression of 17% of the MADS-box genes and their putatively interactive genes in blueberry, which are homologous to known genes involved in flowering, phytohormones, and stress response. These results indicate that the MADS-box genes are involved in plant vegetative and reproductive development under chilling stress, possibly through interaction with other MADS-box proteins via the K domain, thereby regulating gene expression. Further studies are needed to examine the detailed floral organ structural defects, decreased seed production, and expression of the affected floral genes.

Transcriptomic studies under cold stress

Several transcriptome studies have examined gene expression changes in floral organs under cold (Lee and Lee, 2003; Imin et al., 2004; Hedhly et al., 2009; Z. Tang et al., 2012). Specifically, in Arabidopsis pollen (Lee and Lee, 2003), >40% of the expressed genes are possibly involved in pollen development and pollen tube growth at low temperature, including genes encoding cell wall modification enzymes. Further temporal transcriptomics indicated that the majority of transcripts were unaffected after 72 h of 0 °C chilling treatment, while genes associated with pollen tube growth and seed production were significantly reduced. However, many genes that are responsible for cold response and highly induced in leaves under chilling temperature, such as COR and genes for lipid transfer proteins, are only expressed at their normal level or weakly induced in the pollen. These results suggest that the reason plants are more sensitive to abiotic stress during reproductive stages is probably because of the insufficient accumulation of proteins under stress. Additionally, a study in a wheat (Triticum aestivum) male-sterile line investigated potential roles of small RNAs in cold response (Z. Tang et al., 2012). Among 78 unique miRNA sequences, six were cold responsive. Specifically, miR167 plays roles in regulating the auxin signaling pathway, as well as possibly cold stress response and male fertility.

Moreover, a proteomic study using two-dimensional gel electrophoresis (2-DE) focused on the effect of cold stress on rice anther at the young microspore stage after 4 d of 12 °C cold treatment (Imin et al., 2004) and identified 70 differentially
expressed proteins. Among these proteins, 12 were newly induced compared with those at normal temperature, 47 were up-regulated, and 11 were down-regulated. Further mass spectrometry analysis revealed that seven proteins were breakdown (cleavage) products, suggesting that the cold treatment induced protein degradation. Meanwhile, the proteomic and pollen transcriptome results together demonstrate that plant stress response is a dynamic process, wherein the production and degradation of transcripts and proteins are highly regulated to help the plant survive the adversity and maximize potential productivity.

Heat-responsive genes related to plant reproductive development

Unlike plants facing cold stress, plants under heat stress need to emit the excessive thermal energy. High temperatures, 28 °C for Arabidopsis and 32 °C for rice, affect both vegetative and reproductive development, especially male fertility (Hedhly et al., 2009). Transcriptional regulation is important for heat stress response; in particular, heat shock transcription factors (HSFs) are responsible for initiating the rapid transcriptional activation of downstream genes (M. Guo et al., 2016). The plant HSF gene family contains 21 members in Arabidopsis and 25 in rice; they are grouped into three classes A, B, and C (von Koskull-Döring et al., 2007; M. Guo et al., 2016). In Arabidopsis, the AtHSFB2a transcript has a natural long non-coding antisense RNA, asHSFB2a (‘as’ stands for antisense), which is only expressed after heat stress; in addition, the overexpression of AtHSFB2a resulted in a dramatic reduction of asHSFB2a expression to below the level of detection, and vice versa (Wunderlich et al., 2014). In both cases, ~50% of the female gametophytes were arrested in early development, resulting in 45% ovule sterility. These results indicate that the balanced expression between AtHSFB2a and its natural antisense RNA regulates vegetative and gametophytic development under heat stress.

In tomato (Solanum lycopersicum) (Fragkostefanakis et al., 2016), SIHFA2 (a homolog of the Arabidopsis HSFA2 gene) acts as a co-activator of SIHSA1a, and a moderate heat treatment (37.5 °C) causes the accumulation of SIHSA2, thus enhancing the heat tolerance in seedlings of a subsequent severe heat stress (47.5 °C). Furthermore, repression of SIHSA2 expression reduced pollen viability and germination rate when heat stress was applied during early stages of pollen formation (meiosis and microspore formation) but had no effect at more advanced stages. Therefore, SIHSA2 is an important factor for thermotolerance of developing pollen. The results from Arabidopsis and tomato suggest that related members of the HSF family have diverged during angiosperm evolution to promote female and male reproductive development, respectively, while both still function in response to heat stress.

Another type of well-known proteins for plant responses to heat stress are heat shock proteins (HSPs) (Wang et al., 2004; Volkov et al., 2005; Kotak et al., 2007). HSPs are molecular chaperones and are important for coping with heat-induced protein unfolding in all organisms. One class of HSPs is small HSPs (sHSPs); an example of an sHSP is the Arabidopsis
BOBBER1 (AtBOB1) protein, which also contains a NudC domain (Nuclear Distribution C, important for protein folding and interaction as a chaperone) (Jurkuta et al., 2009). An atbob1 mutant is deficient in heat tolerance and exhibits defects in flowers and inflorescence meristems, suggesting its role in both development and thermotolerance (Perez et al., 2009).

Heat stresses cause abnormal protein folding, and trigger a process called the unfolded protein response (UPR) (Ruberti et al., 2015; Bao and Howell, 2017). Genes related to the UPR have also been found to play roles in reproduction. In particular, the Ire1 (INOSITOL REQUIRING ENZYME 1, encoding an RNase) gene acts downstream of UPR and is important for proper splicing of the bZIP60 mRNA encoding a transcriptional regulator (Deng et al., 2011; Nagashima et al., 2011). The ire1a-2 ire1b-4 double mutant is fertile at room temperature but male sterile at 27.5 °C, with defects in tapetum morphology (Deng et al., 2016). Further analysis indicated that the RNase activity of AtIRE1 was required for promoting male fertility under heat stress (Deng et al., 2016). Further studies are needed to uncover the mechanisms by which these transcriptional regulators improve reproduction under heat stresses.

Another study in cotton (Gossypium hirsutum) revealed that GhCKI (casein kinase I) plays a role in male reproduction under high temperature (Min et al., 2013). The mammalian CKI homologs are involved in inhibition of glycerol synthesis and regulation of apoptosis (Peters et al., 1999; Price, 2006). GhCKI is induced after heat treatment and activates ABA accumulation (Min et al., 2013). In addition, overexpression of GhCKI in Arabidopsis caused disruption of ROS balance and failure in tapetal programmed cell death, eventually leading to anther abortion, indicating that GhCKI might be used in genetic engineering to promote male fertility under heat stress.

Phytohormone signaling is also involved in plant heat response during reproductive development. Ethylene biosynthesis and signaling in floral and fruit tissues under high temperature were analyzed using pea (Pisum sativum) (Savada et al., 2017). The mRNAs of two key genes of ethylene biosynthesis, PsACO and PsACS, were highly abundant in ovaries and pedicels, and further elevated upon heat stress. The expression level of PsACO and PsACS and the ethylene level were further detected in heat-treated floral organs, including ovary, pedicel, anther, stigma, and petal. The results demonstrated that in contrast to untreated plants, heat-treated plants facilitate the senescence of unpollinated ovary, and inhibit the development of petal and the growth of the pollen tube by regulating PsACO and PsACS expression and ethylene levels, allowing the allocation of limited resources for seed development and maturation from the fertilized ovules. This suggests that ethylene biosynthesis is involved in resource allocation during reproductive development under heat stress.

Finally, siRNAs are also involved in heat stress response (Ito et al., 2011). A copia-type retrotransposon ONSEN is induced by heat treatment in siRNA biogenesis-deficient Arabidopsis plants. In the progeny of heat-stressed siRNA biogenesis-deficient plants, a high frequency of new ONSEN insertions was observed; these insertions were subsequently demonstrated to have occurred during flower development and before gametogenesis. These findings suggest that ONSEN insertions may confer heat responsiveness to nearby genes, leading to the activation of stress-responsive gene regulation during reproductive development.

**Transcriptome studies and other large-scale analysis under heat stress**

Transcriptome studies have been performed in Arabidopsis, wheat, and cotton (Chauhan et al., 2011; Baron et al., 2012; Min et al., 2014; Zhang et al., 2017). A study in Arabidopsis examined expression responses of 17 genes involved in ABA metabolism (Baron et al., 2012), including biosynthesis, catabolism, and transport, in different tissues under heat stresses. The results demonstrated that a subset of genes responsible for ABA biosynthesis, hydrolysis, and transportation are differentially regulated in an organ-specific pattern; in addition, both cold and heat stresses negatively affected reproductive organ development. For example, a key enzyme involved in ABA biosynthesis, AtNCED3, is significantly reduced in leaves under either cold or heat stress, but significantly induced in inflorescence meristem by cold and heat stress.

Moreover, a recent transcriptomic study under heat stress uncovered 484 up-regulated and 373 down-regulated genes in the Arabidopsis flower (Zhang et al., 2017). As previously mentioned, genes related to the endoplasmic reticulum (ER) UPR, protein ubiquitination, and protein folding were enriched. In Arabidopsis, bZIP28 and bZIP60 are the major transcriptional regulators of the UPR, and are induced under heat stress (Deng et al., 2011; Song et al., 2015). Atbzip28 bzip60 double mutant plants exhibited reduced silique length as well as fertility, and a comparison of the transcriptome between the WT and Atbzip28 bzip60 double mutant identified 521 differentially expressed genes under heat stress in reproductive tissues, suggesting protective roles of the UPR for maintaining fertility upon heat stress. (Zhang et al., 2017).

Another transcriptomic study in wheat explored heat-responsive genes specifically induced at different vegetative and reproductive stages (Chauhan et al., 2011). Among 127 genes highly induced in the flower were genes for TFs such as a C3HC4-type zinc finger protein and the HSP TaHSP82, as well as other proteins including a 14–3–3 protein, chitinase, and calmodulin (TuCAM3-1). Similarly, comparative transcriptomics was performed in cotton developing anther under heat stress (Min et al., 2014), identifying 4599 differentially expressed genes. The functional categories identified among the differentially expressed genes included those for epigenetic modifications, carbohydrate metabolism, and phytohormone signaling. Specifically, GhCKI (also mentioned in the previous subsection) was identified by the transcriptome and displayed induction by heat stress, as well as the GhPIF (PHYTOCHROME-INTERACTING FACTOR) gene, which is involved in sugar and auxin (indole-3-acetic acid, IAA) signaling. In short, multiple processes, such as transcriptional regulation, protein conformational changes, ion transportation, and phytohormone signaling, are involved in response to heat stress during another development.
In addition to transcriptomic studies, a genome-wide association study (GWAS) has been conducted to investigate Arabidopsis flower and seed development under heat stress (Bac-Molenaar et al., 2015; Luria et al., 2019). The effect of heat stress on flower and fruit development is highly similar to what was reported under drought stress (Su et al., 2013). These authors found that two developmental stages are particularly sensitive to high temperature: one before anthesis near the time of male and female meiosis, and one after anthesis during fertilization and early embryo development. They further identified four quantitative trait loci (QTLs) that are strongly associated with heat response and are developmental stage specific. These results are in agreement with previous conclusions (Kim et al., 2001; Warner and Erwin, 2005) that the regulation of heat tolerance is likely to be dependent on stages.

Oxidative stress

ROS, including superoxide (O2−), hydrogen peroxide (H2O2), and hydroxyl radicals (OH·), are present in plants even under non-stressful growth conditions. Oxidative stress arises from the imbalance between generation and elimination of ROS and could eventually lead to cell death (Scandalios, 2002). Oxidative stress is often a component of responses to various abiotic stresses such as drought, salinity, high and low temperature, and heavy metal stress. Nevertheless, oxidative stress also has its own signaling mechanisms independent from the signaling pathways triggered by the other stresses mentioned above (Hasanuzzaman et al., 2013; Krishnamurthy and Rathanasabapathi, 2013). To date, there are only a few reports on the effect of oxidative stress on plant reproductive development. Oxidoreductases, by definition, play important roles during flower development in response to the oxidative processes (Xing et al., 2005; Wang et al., 2009; Blee et al., 2014; Dai et al., 2019). For example, glutaredoxins (GRxs), a kind of oxidoreductase, displayed a conserved function in response to oxidative stress during flower development, as supported by the crucial functions of two Arabidopsis CC-type GRX genes, AtROXY1 and AtROXY2, in petal and anther initiation and differentiation (Xing et al., 2005) and similar functions of the two rice homologs OsROXY1 and OsROXY2 (Wang et al., 2009). They display the same expression pattern in floral organs, and overexpression lines exhibit the same flower developmental defects and increased H2O2 accumulation. Another Arabidopsis protein AtADR (ANTHER DEHISCENCE REPRESSOR) (Dai et al., 2019) is N-myristoylated and targeted to peroxisomes during early flower development. Ectopic expression of AtADR in transgenic Arabidopsis plants resulted in male sterility due to anther indehiscence probably mediated by reduced ROS accumulation and repressed expression of AtNST1 and AtNST2, which are required for anther dehiscence.

ROS imbalance can also be regulated through changes in ion level, thus ion transportation and homeostasis are possible processes involved in responses to oxidative stress. The Arabidopsis membrane-spanning protein AtPIC1 (PERMEASE IN CHLOROPLASTS 1) mediates iron transport across the chloroplast inner membrane, helps ferritins store free iron, and reduces the cellular ROS level (Duy et al., 2007). The overexpression of AtPIC1 leads to iron overload in chloroplasts and leaf chlorosis (oxidative-stressed phenotype), as well as severely defective flower and seed development (Duy et al., 2011). Another Arabidopsis TF gene AtSPL7 (SQUAMOSA PROMOTER-BINDING PROTEIN-LIKE7) is responsive to copper insufficiency (Garcia-Molina et al., 2014). AtSPL7 interacts directly with Arabidopsis AtKIN17 in response to copper deficiency, and the atspl7 atkin17 double mutant displays an enhanced copper-dependent oxidative stress, floral bud abortion, and pollen infertility (Garcia-Molina et al., 2014). These results support the idea that ion homeostasis in plant cells is important for response to oxidative stress and flower and fruit development.

Light stress and radiation

Light affects almost every aspect of plant development, from germination to flowering. Although plants respond to a broad spectrum of light, ranging from UV-B to far-red light, light overdose can be harmful to plant growth and development (Chory et al., 1996; Fankhauser and Chory, 1997). Also, X-rays are harmful to all organisms, including plants, by, for example, causing genomic DNA breakage. The Arabidopsis recombination endonuclease gene AtMRE11 plays important roles in DNA damage sensing and repair (D’Amours and Jackson, 2002; Puizina et al., 2004; Stracker and Petrini, 2011). An Arabidopsis histone acetyltransferase, AtTAF1, which also associates with the TATA-binding protein, interacts with AtMRE11 and is important for male gametophyte development (Waterworth et al., 2015). Heterozygous AtTAF1+/− plants display defects in pollen tube development, reduced fertility, and hypersensitivity to X-rays, suggesting that AtTAF1 acts together with AtMRE11 to contribute to sensing and repair of DNA damage and also to male fertility.

In addition, it was found that UV-C light activates the flowering transition in Arabidopsis through salicylic acid (SA) (Martinez et al., 2004). Also in non-stressed plants, SA acts as a regulator of flowering by activating pathways independent of known flowering regulators [CONSTANS (CO), FCA, or FLC] to regulate flower development. For plant response to UV-B light, a comparative transcriptomic analysis between Arabidopsis and Physcomitrella patens reveals both genes in conserved pathways and those that are likely to represent distinct processes (Wolf et al., 2010). Among the conserved genes, some are annotated to encode calcium-binding protein, hydrolase, oxidoreductase, and proteins similar to harpin-induced proteins, which are also associated with oxidative stress.

Future perspectives

Plants are highly sensitive to environmental stress during reproductive development, and respond dramatically to allow resource re-allocation and maximize reproductive success under unfavorable growth conditions. Although it is important to understand how plants respond to different abiotic
stresses during reproductive development, this is still a clearly underinvestigated area. In particular, there have been few detailed studies, even in model plants, to document specific morphological and molecular changes at different stages, and for different aspects, of the complex reproductive process, in response to various conditions. In addition, great efforts are needed to understand the molecular mechanisms underlying the changes in specific reproductive processes during the acclimation to abiotic stresses. Furthermore, experiments on interactions among regulatory genes and signaling pathways induced by different stresses promise to present an integrative portrait of multiple environmental conditions that affect reproductive cellular and molecular processes. Such analyses in the near future will lead to better understanding of various aspects of reproductive development under stress, and uncover the molecular strategies that facilitate optimal reproduction that have contributed to the evolutionary successes of flowering plants.

Moreover, the homologs of many genes identified in one plant have not been characterized in most other plants, including crops, for their stress-induced expression and potential role in stress response during reproduction. Because stress response is a highly adaptive process, many genes probably have experienced functional divergence during angiosperm evolution, making comparative studies between model plants and crops both challenging and necessary. In particular, gene duplication has occurred frequently in the angiosperm history, and differential functional specialization among duplicated genes, such as between leaves and flowers, might both occur widely and vary in specific aspects among species. Such divergence might have contributed to the adaptation of different plant groups to various environments and to their success in different ecosystems. Further research will be likely to provide valuable information that will contribute improvements in agriculture and protection of ecosystems.

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