



Influence of Climate Change on Flowering Time

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Abstract

Global warming affects various environmental factors, including temperature, precipitation, drought, and flooding. Temperature rise is mainly due to increased levels of carbon dioxide (CO₂), which was increased by approximately 50% since the industrialization period. Here, we review the effect of global climate changes on the alteration of flowering time. High temperature during vernalization delays flowering mainly due to increased expression of *FLOWERING LOCUS C* and *TaVERNALIZATION 2* encoding floral repressors in *Arabidopsis* and winter wheat, respectively. Increased ambient temperature promotes flowering in many plant species, especially in spring-flowering plants. In *Arabidopsis*, higher temperature induces SHORT VEGETATIVE PHASE–FLOWERING LOCUS M (FLM)- δ complex that promotes *FLOWERING LOCUS T* (*FT*) expression. Moreover, high temperatures suppress a floral repressor *FLM* and disturb the stability of the evening complex that is an inhibitor of PHYTOCHROME INTERACTING FACTOR 4, which induces *FT* expression. Drought induces or delays flowering depending on plant species, growing season, and developmental stage. In *Arabidopsis*, drought induces flowering by promoting the *GIGANTEA-CONSTANS* (*CO*) pathway, whereas the stress delays flowering under short-day conditions via ABSCISIC ACID-INSENSITIVE 1. Plants also alter flowering time to avoid wet conditions, including flooding and precipitation. Increased CO₂ concentration accelerates flowering, probably by increasing the rate of photosynthesis. We also reviewed the effect of climate change on pollination.

Keywords Climate change · Global warming · Flowering time · Pollinator interaction

Introduction

The climate has been significantly changing mainly due to global warming. Temperature rise is caused largely by elevated levels of carbon dioxide (CO₂). The CO₂ level in Earth's atmosphere in May 2020 was 417 ppm, indicating an approximately 50% increase from 280 ppm in the pre-industrial period. During this period, the global mean temperature increased by 0.93 °C (IPCC 2018; WMO 2019). Climate models by the Intergovernmental Panel on Climate Change (IPCC) predicted that the global temperature would rise by 0.3 °C–1.7 °C (or 2.6 °C–4.8 °C in an extreme case) during the twenty-first century (Stocker et al. 2013). Elevated

temperature increases the evaporation rate from the land and ocean and imbalances weather patterns, including droughts, heatwaves, flooding, and other factors (IPCC 2007). As anthropogenic activities become more robust, such climatic factors would impact ecosystems worldwide (Craufurd and Wheeler 2009; Cramer et al. 2014).

Climate change alters the flowering time in most plant species (Craufurd and Wheeler 2009). Altering flowering time reduces the yield and seed quality in some crops. In addition, it affects the interaction between plants and pollinators by changing their meeting time as well as the fragrance, color, and organ development of flowers. Increased bee visitation to flowers is correlated with increased seed set in *P. vulgaris* (Kehrberger and Holzschuh 2019). In the warm spring of 2002, a bumblebee-pollinated species (*Corydalis ambigua*) and bee-pollinated species (*Gagea lutea*) reduced seed set due to 7–17 days early flowering (Kudo et al. 2004).

Several genetic factors that control flowering time are affected by environmental factors such as temperature and rainfall (Cho et al. 2017). In this review, we focus on the

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effect of environmental factor changes caused by global warming on flowering time. We also review plant–pollinator interactions affected by climate change.

Warm Temperatures During Winter

Winter temperature is one of the climatic factors influencing the physiological process of flowering (Blázquez et al. 2003; Capovilla et al. 2014). Long time chilling at low temperatures called vernalization (Chouard 1960) accelerates the flowering initiation in many species including winter wheat (Evans et al. 1975), barley (Fettell et al. 2010), and tulips (Rietveld et al. 2000). The optimum temperature and duration of exposed vernalization state vary among plant species (Wiebe 1990; Philips et al. 2020).

The first identified player gene for the vernalization response is *VERNALIZATION 2* (*VRN2*) in *Arabidopsis* (Gendall et al. 2001) (Fig. 1). The gene product suppresses the expression of *FLOWERING LOCUS C* (*FLC*), a major inhibitor of the florigen gene *FLOWERING LOCUS T* (*FT*). *VRN2* functions together with *VERNALIZATION 1* (*VRN1*), *VERNALIZATION INSENSITIVE 3* (*VIN3*), and *VIN3-LIKE1/VERNALIZATION 5* in vernalization-mediated pathways (Kim and Sung 2014). Among these components, *VIN3* is the only member induced by long-term cold temperatures. During this period, *VIN3* combines with *VRN2* polycomb-like complex reducing *FLC* expression (Sung

and Amasino 2004). When plants face warmer temperatures, *FLC* transcription levels stay high, causing delayed flowering. At higher temperatures, *VIN3* transcription levels quickly decrease, suggesting that this gene is a major regulator in the vernalization pathway (Sung and Amasino 2004; Kim and Sung 2013).

Suppression of *FLC*-like genes during vernalization is found in various Brassicaceae species. For example, the expression level of *FLC* homologous genes was repressed during vernalization in *Arabis alpina* (Wang et al. 2009), Tibetan turnip (Zheng et al. 2018), and other Brassicaceae clades (Madrid et al. 2020).

The *FLC*-mediated vernalization pathway is not present in many plant species, except in Brassicaceae. In winter wheat, a CCT-containing protein called *Triticum aestivum* *VRN2* (different from *Arabidopsis* *VRN2*, and designated as *TaVRN2* hereafter) is responsible for vernalization, and *TaVRN2* expression is suppressed after vernalization (Yan et al. 2004) (Fig. 1). Wheat *TaVRN2* is a repressor of *TaVRN3* encoding a florigen protein homologous to *FT* (Yan et al. 2006). A similar pathway is operated during vernalization in barley (Yan et al. 2006). Although plants use different vernalization pathways, they share a similar mechanism in which the gene sensing vernalization is turned on during a long-term cold period, and the gene product inhibits the expression of a transcription factor repressing florigen genes (Fig. 1).

Higher temperatures during the vernalization process reduce *VIN3* expression, causing increased *FLC* expression and delayed flowering or a failure of floral induction in some plant species, including *A. thaliana*, *Arabidopsis halleri* subsp. *gemmifera*, and *Brassica pekinensis* (Elers and Wiebe 1984; Satake et al. 2013). Similarly, higher temperatures interfere with vernalization by suppressing the expression of *VRN1* (an inhibitor of *VRN2*) in winter wheat and winter rye (Gregory and Purvis 1948; Wu et al. 2017; Dixon et al. 2019).

High temperatures before or after the vernalization period can also alter flowering time. For example, high-temperature treatment (30 °C) before and after the vernalization delayed the flowering date in spring rape (*Brassica napus* var. *annua*) (Dahanayake and Galwey 1998). These observations suggest that increased temperatures due to global warming will probably affect the flowering time of many plant species, including winter crops.

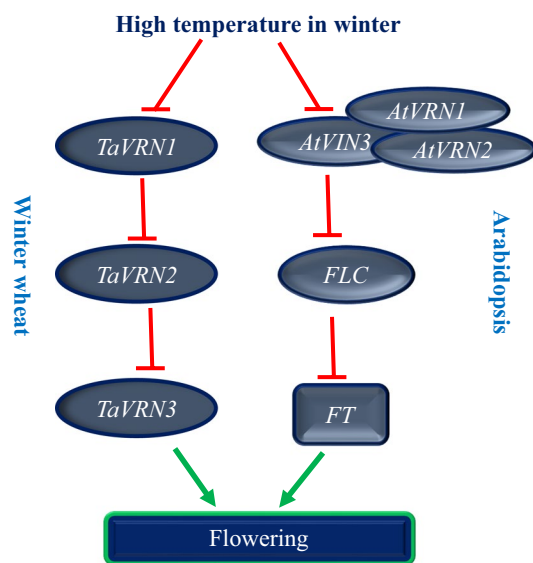


Fig. 1 Schematic diagram to compare the effect of higher temperatures during the winter on flowering. In *Arabidopsis*, *FLC* expression is released, and *FT* is suppressed when *VIN3* expression is reduced under high temperatures. In winter wheat, the expression of *TaVRN2* that suppresses *TaVRN3* is induced due to reduced expression of *TaVRN1* under high temperatures

Warm Temperatures During the Growing Season

Increased temperatures over the past century altered the flowering date of many species (Hu et al. 2005; Menzel et al. 2006). For example, plants that flower in spring

flowered earlier (Fitter and Fitter 2002). The heading date of winter wheat in the US was advanced 0.8–1.8 d per decade, mainly due to the increased minimum temperature in spring (Hu et al. 2005). Analysis of several hundred wild plant species at an elevation (945–1079 m) of Southwestern US showed that the flowering date was advanced at a rate of 2.5 days per year between 1984 and 2014 (Rafferty et al. 2020). At higher elevations, the advance was less significant. The flowering date was advanced 0.36 days per year during that period at 1671–1939 m and no significant change was observed at the highest location (above 1939 m). The flowering date of *Boechea stricta* at the Rocky Mountains in Colorado, US (approximately 2900 m) was advanced 0.2–0.5 days per generation between 1975 and 2011 (Anderson et al. 2012). An analysis of 21 shortgrass species from 1995 to 2014 showed that the first flowering date was advanced at a rate of 7.5 days for every 1 °C increase (Moore and Lauenroth 2017; Fox and Jönsson 2019).

In many plant species, an earlier flowering is positively correlated with spring temperatures (Bustamante and Burquez 2008). For example, warmer spring temperatures cause early flowering in lilac, hawthorn, elder, and blackthorn (Siegmund et al. 2016). However, other season temperatures also influence flowering time. An increase in winter and monsoon temperatures caused a 22-day earlier flowering in three alpine ginger species from 1913 to 2011 (Mohandass et al. 2015). Warmer summer temperatures in the previous year can also induce earlier flowering, such as in *Erythronium grandiflorum* (Benscoter et al. 2010).

Molecular mechanisms by which the flowering time is hastened by elevated temperatures have been extensively studied in *Arabidopsis* as a model plant. Genetic and molecular studies indicate that ambient temperature affects flowering time through multiple pathways (Lee et al. 2008; Capovilla et al. 2014; McClung et al. 2016; Susila et al. 2018). Expression of the florigen gene *FT* is enhanced when the temperature is increased from 23 to 27 °C, indicating that temperature influences the flowering time by controlling regulatory genes functioning in the upstream of *FT* (Balasubramanian et al. 2006; Kumar et al. 2012; Sánchez-Bermejo et al. 2015; Shim and Jang. 2020).

Photoperiodic mechanisms normally rapid the time of flowering in *Arabidopsis thaliana* under long day (LD), however, delay in short-day (SD) condition. Higher temperature (27 °C) can overcome this delay process (21 °C) even under SD condition. In this process, CO and PIF4 physically interact and the expression of *FT* as well as *TWIN SISTER OF FT (TSF)* is improved at dusk. Although *FT* expression is lower under 27 °C-SD compared with 21 °C-LD, it is enough to induce flowering probably due to reducing floral repressor action of SVP and FLM at higher temperature (Fernández et al. 2016).

Two MADS-box genes, *FLOWERING LOCUS M (FLM)* and *SHORT VEGETATIVE PHASE (SVP)*, that function upstream of *FT* play key roles in sensing temperature change. Mutations in *FLM* and *SVP* cause temperature-insensitive flowering at different ambient temperatures (Lee et al. 2013). *FLM* has at least four diverse splicing transcripts (Scortecci et al. 2001). Among them, *FLM-β* is abundantly found at 16 °C and *FLM-δ* at 27 °C. Their translated proteins compete to combine with SVP, whereas SVP-*FLM-β* suppresses flowering under lower temperatures, and abundance of *FLM-δ* causes SVP to form a non-functional complex at higher temperatures for earlier flowering (Lee et al. 2013; Posé et al. 2013; Lutz et al. 2015) (Fig. 2). Alternatively, higher temperature reduces the expression level of *FLM* through alternative splicing together with nonsense-mediated mRNA decay to de-press *FT* expression (Sureshkumar et al. 2016). These observations suggest that the proportional transcript level of *FLM* variants plays an important role to induce flowering at higher temperatures. Protein stability of SVP at different temperatures also participates in sensing higher temperatures. SVP protein is degraded via the 26S proteasome pathway at higher temperatures, releasing a suppressive activity on floral marker genes by reducing the SVP-*FLM-β* complex (Lee et al. 2013) (Fig. 2).

Light signaling is also involved in the thermo-sensitive flowering pathway. PHYTOCHROME INTERACTING FACTOR 4 (PIF4) activates *FT* expression at high temperatures under short-day conditions (Fig. 2). This activation is

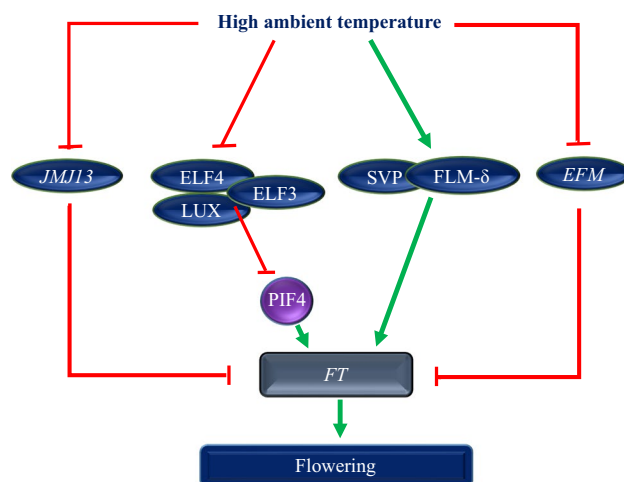


Fig. 2 Schematic illustration of the effect of high ambient temperature on the flowering time in *Arabidopsis*. Pathway 1. Reduced expression of *JMJ13* causes *FT* upregulation and flowering under high ambient temperatures. Pathway 2. High temperatures disturb the stability of EC complex that is an inhibitor of PIF4, which induces *FT* transcription. Pathway 3. High ambient temperature increases SVP-*FLM-δ* complex that promotes *FT* expression and flowering. Pathway 4. An *FT* inhibitor, *EFM* expression is decreased under high temperatures

mediated by a decrease in H2A.Z nucleosome on *FT* (Kumar et al. 2012). The circadian clock is also involved in thermo-sensitive flowering. Mutants in the evening complex (EC) consisting of DNA binding proteins LUX ARRHYTHMO, EARLY FLOWERING 3 (ELF3), and ELF4 exhibit early flowering (Hicks et al. 1996; Doyle et al. 2002; Hazen et al. 2005; Koini et al. 2009; Silva et al. 2020). The EC complex represses *PIF4* expression at lower temperatures, and the repression is relieved at higher temperatures (Silva et al. 2020) (Fig. 2).

Temperature fluctuations change the protein structure and affect plant developmental processes, including flowering time. ELF3 protein contains repeated hydrophilic amino acid residues (e.g., glutamine and asparagine) called prion-like domain (PrD) that respond to environmental stresses such as temperature change. The domain helps accelerate flowering in *Arabidopsis* in a warmer climate. However, when the domain is replaced with PrD from *Brachypodium distachyon*, which survives in warmer climates, engineered *Arabidopsis* does not express early flowering at high temperatures. This is probably due to “temperature-driven phase transition” (i.e., this protein is active at lower temperatures and blocks *FT* expression, but becomes inactive at higher temperatures), resulting in earlier flowering (Jung et al. 2020).

An MYB transcription factor EARLY FLOWERING MYB (EFM) protein appears to be an important joint point converging the responses to temperature and light (Yan et al. 2014). EFM protein represses *FT* expression by directly binding to the *FT* genomic region. Therefore, the expression level of *EFM* decreases with increasing temperature from 16 to 27 °C through SVP (Fig. 2).

Epigenetic regulators can also affect flowering time in a temperature-dependent manner. Chromatin remodeling factor JUMONJI 13 (JMJ13) possesses demethylase activity, specifically on H3K27me3. A mutant defect in *JMJ13* increases *FT* expression and induces earlier flowering, indicating that JMJ13 functions as a floral suppressor (Fig. 2). The mutant displays an early flowering phenotype at 28 °C but not at 16 °C or 22 °C under SD conditions (Zheng et al. 2019). This result indicates that JMJ13 delays flowering time in a temperature- and day-length-dependent manner.

Oryza sativa (rice) flowers earlier at 27 °C compared with 23 °C under both LD and SD conditions. The expression levels of *Ehd1* (a floral inducer) and *Hd3a* and *RFT1* (florigen genes) are low, whereas *Ghd7* (a floral repressor) expression level is higher at a low temperature than at a high temperature. This result suggests that other floral regulators upstream of *Ehd1* and *Ghd7* are responsible for the early flowering at higher temperatures (Luan et al. 2009; Song et al. 2012). *Hd1*, *OsPRR37*, *DTH8*, and *Hd6* appear to be the regulators responding to temperature increases (Guo et al. 2020). However, in *Oryza sativa* “Koshihikari,” *Hd1* and *OsPRR37* function as negative regulators of flowering

under lower temperatures, and *OsPRR37* accelerate flowering under warmer temperatures (Guo et al. 2020; Shim and Jang 2020).

Flowering is delayed at high temperatures in some species. For example, flowering time is delayed under 30 °C compared with 20 °C in *Chrysanthemum* species. Flowering is associated with the low expression level of *FLOWERING LOCUS T-like3*-encoding florigen in the species (Nakano et al. 2013, 2015). Similarly, the red firespike (*Odontonema strictum*) grown at 35 °C does not show inflorescence formation, whereas the plants flower at 25 °C (Rezazadeh et al. 2018). The temperature increase to 34 °C causes no flowering in both early- and late-flowering varieties of *Manihot esculenta* (Adeyemo et al. 2019). Further study is needed to investigate the mechanisms by which flowering is delayed by increased temperatures.

Precipitation

The temperature has a high impact on global precipitation (Lawson and Rands 2019). The flowering time is significantly affected by the precipitation amount in many plant species (Benscoter et al. 2010; Moore and Lauenroth 2017; Zhang et al. 2018). For example, decreasing rainfall is associated with the early flowering of winter annual plants in Mediterranean desert regions (Kigel et al. 2013). The flower in *E. grandiflorum* blooms early when a high precipitation amount occurred in the previous summer (Benscoter et al. 2010). Moreover, precipitation two months before flowering significantly affects the flowering time in late-blooming species (Zhang et al. 2018).

Molecular mechanisms by which the flowering time is controlled by the precipitation amount is not well known because several environmental factors are involved. Water spray stimulates jasmonic acid (JA) accumulation and expression of many key transcriptional activators of JA-mediated gene expression, including *MYC2*, *MYC3*, and *MYC4* (Van Moerkercke et al. 2019). Double and triple mutants in the *MYC* genes flower early, suggesting that these factors are inhibitors of flowering. *FT* and its closest relative *TWIN SISTER OF FT* (*TSF*) transcript levels are significantly higher in mutant plants, and *MYC2* overexpression delays the flowering by suppressing *FT* transcript. Chromatin immunoprecipitation assay indicates that MYC2 binds to the *FT* genomic region (Wang et al. 2017). Therefore, water spray delays flowering by inducing the accumulation of JA and MYC transcription factors suppressing *FT* expression. However, this induction might be due to touch response rather than increased water. Regulation of flowering time by precipitation may be due to abscisic acid (ABA) that plays a major role in controlling flowering time because precipitation is inversely related to drought.

Drought

Increasing temperature due to global warming frequently leads to drought (Gol et al. 2020), influencing the flowering timing. Flowering is significantly induced by drought in several plants such as rice, *Brassica*, *Arabidopsis*, *Erica multiflora*, and wheat (Kato and Yokoyama 1992; Franks et al. 2007; Bernal et al. 2011; Han et al. 2013; Shavrukov et al. 2017; Du et al. 2018). However, drought delays flowering in some species, including *Genista tinctoria* and *Calluna vulgaris* (Jentsch et al. 2008; Nagy et al. 2012). The drought response is often affected by the growing season (Monroe et al. 2018). Plants tend to display delayed flowering in case of drought in winter and spring. For example, drought stress during winter causes delayed flowering in sweet oranges by 2–4 weeks (Melgar et al. 2010). However, drought in summer often causes earlier flowering. The early flowering due to drought correlates with drought escape (DE) response. However, delayed flowering is associated with dehydration avoidance strategy (Melgar et al. 2010; Kooyers 2015; Monroe et al. 2018). This seasonal difference indicates that the drought effect on flowering is affected by day length and temperature (Rosenthal and McCarty 2019).

In *Arabidopsis*, drought condition causes earlier flowering under LD conditions through the DE response (Riboni et al. 2013) (Fig. 3). Drought activates florigen genes (*FT* and *TSF*) via photoperiod sensor *GIGANTEA* (*GI*) (Riboni et al. 2013; Takeno 2016). Under LD drought conditions, *GI* and FLAVIN-BINDING, KELCH REPEAT, F BOX protein1 (*FKF*) form a complex to degrade CYCLING DOF FACTOR1 (*CDF1*) that is a repressor of *CO*. The *CO* protein released from suppression of *CDF* activates *FT* to trigger the flowering (Sawa and Kay 2011). Moreover, drought induces flowering through the ABA signaling pathway. ABA-responsive element-binding factors *ABF3* and *ABF4* interact with NUCLEAR FACTOR Y subunit C (NF-YCs) to promote *SOC1*, a flowering inducer (Hwang et al. 2019) (Fig. 3).

The molecular mechanism of the dehydration avoidance strategy was examined mainly in *Arabidopsis*. *Arabidopsis* delays flowering due to drought when grown under SD (Fig. 3). Plants defective in *ABSCISIC ACID-INSENSITIVE 1* (*ABI1*) flower early in SD, suggesting that *ABI* mediates the ABA effect during drought (Riboni et al. 2016). In *abi1* mutant, expression levels of *FT* and *TSF* were not altered, but *SOC1* transcript level was increased, and *FLC* transcript level was reduced. This finding suggests that drought delays flowering by inducing the *FLC* expression in shoot apical meristem.

In rice, the expression of *Hd3a* and *RFT1*, as well as an immediate upstream inducer *Ehd1*, is repressed when

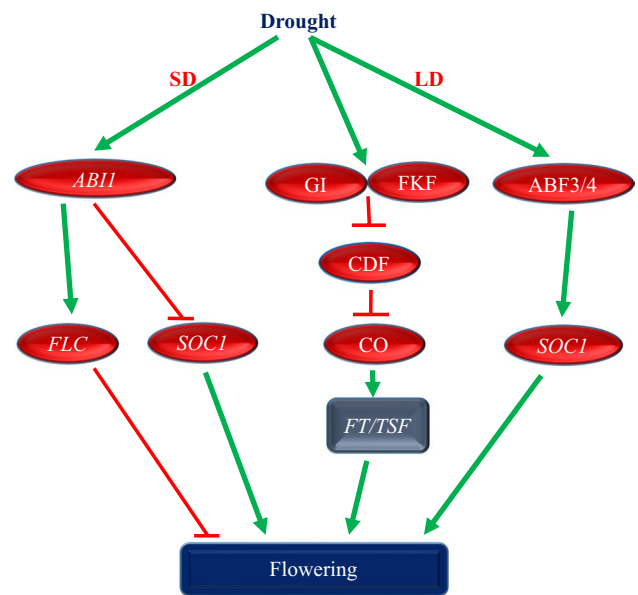


Fig. 3 Schematic illustration of drought effect on flowering time in *Arabidopsis*. Under LD, drought activates the photoperiod sensor *GI* and *FKF*, which are suppressors of *CDF1* to release *CO*. Drought also activates *ABF3* and *ABF4* that are positive regulators of *SOC1* to allow early flowering. Under SD, drought induces *ABI1* that is an activator of *FLC* and, therefore, delays flowering

drought occurs at the floral transition time (Galbiati et al. 2016). Drought induces the expression of *O. sativa* ABA-responsive element-binding factor 1 (*OsABF1*) that redundantly functions with *OsbZIP40* (Zhang et al. 2016). *OsABF1* induces *OsWRKY104* that suppresses *Ehd1* and therefore, delay flowering. The upstream repressors of *Ehd1*, including *LEC2* and *FUSCA3-Like 1* (*OsLFL1*), *Ghd7*, *COL4*, and *DTH8* are not significantly affected by *OsABF1*, suggesting that drought delayed flowering via photoperiod-independent manner. However, drought promoted flowering when rice plants were under the stress at early developmental stages. The stress activates *Hd3a* and *RFT1* by increasing the level of *OsMADS50*, *OsGI*, and *OsELF3*, and suppressing the floral repressor *OsPRR37* through ABA-independent regulation (Du et al. 2018).

Flooding

Global climate change leads to increased rainfall and flooding in certain regions and therefore, impacts flowering time and crop yield (Claire et al. 2019). In Pakistan, between 2010 and 2014, at least 11 billion tons of crops were lost due to flooding (Rehman et al. 2015). Flooding restricts the external CO_2 entry to the cells and reduces photosynthesis efficiency, therefore decreasing plant growth and flowering (Jackson and Colmer 2005). Moreover, flooding

induces hypoxic stress and causes a defect in the balance of hormones and metabolic processes (Ruperti et al. 2019). Plants delay flowering during flooding because floral organ development is one of the most energy-consuming processes (Peña-Castro et al. 2011). For example, hydric habitat plant *Cardamine pratensis* expresses good vegetative and floral development within 2 days of flooding, but the plant exhibits poor flowering under 7 days flooding (Brotherton et al. 2019).

Plants face low-oxygen stress as well as other stresses during submergence that leads to the induction of various regulatory factors (Fukao et al. 2019). The master regulator of submergence tolerance in rice is SUB1A, a group VII ethylene response factor (ERF-VII), which can allow the plant to survive for 14–16 d under complete submergence (Xu et al. 2006). Other ERF-VII genes (*SNOKE1* and *SNOKE2*) enhance internode elongation of deep-water rice under flooding (Hattori et al. 2009). ERF-VII plays key roles in adaptive responses to flooding in many plant species, including *Arabidopsis*, *Rumex*, and *Rorippa* (Voesenek and Bailey-Serres 2015). Under normal conditions, ERF-VIIs are degraded by N-recognition E3 ligase PROTEOLYSIS 6 in *Arabidopsis* (White et al. 2017). Under low-oxygen (O_2) conditions during submergence, degradation is inhibited, resulting in the accumulation of ERF-VII proteins. However, in rice, some ERF-VIIs, including SUB1A and SUB1C, are not degraded by O_2 . Instead, their downstream proteins are degraded under ambient O_2 conditions (Lin et al. 2019). *Arabidopsis* over-expressing rice *SUB1A* displays delayed flowering phenotype with gibberellin insensitivity and ABA hypersensitivity (Peña-Castro et al. 2011).

Other factors can also delay flowering under submergence conditions. For example, VRN2 protein preferentially accumulates in the shoot meristem under stress to inhibit flowering (Labandera et al. 2020). In addition, various miRNAs involved in delaying flowering time are accumulated by stress. The expression of *miR156* is up-regulated under flooding in *Arabidopsis* (Jeong et al. 2013). Flowering is delayed during submergence because *miR156* maintains vegetative development. Submergence also induces the accumulation of *miR5200* that suppresses *FT-like* genes in *Brachypodium* (Jeong et al. 2013).

CO₂

The rapid increase in CO₂ concentration has a significant impact on increasing temperature globally as well as plant physiology and growth such as photosynthesis and flowering time (Curtis and Wang 1998; Prentice et al. 2001; Long et al. 2004; Teng et al. 2006; Springer and Ward 2007; Thompson et al. 2017). Most crops grow faster and flower earlier at higher CO₂ concentrations due to increased photosynthesis (Rolland et al. 2006). For

example, flowering is promoted at higher CO₂ concentrations in rice and barley (Kleemola et al. 1994; Seneweera et al. 1994; Ohnishi et al. 2011; Tanaka et al. 2016). However, some species do not respond to CO₂ concentration changes or show delayed flowering phenotype at increased CO₂ concentrations (Springer and Ward 2007). However, soybean (*Glycine max*) and maize (*Zea mays*) do not show consistent patterns in flowering time at elevated CO₂. Dissimilar to crop species, many wild species flower late or do not respond to increased CO₂ concentrations.

The time of flowering accompanied by rising CO₂ is often influenced by other factors, including photoperiod, temperature, and water availability (Springer and Ward 2007; Song et al. 2009). Regarding photoperiod, CO₂ gives more effect in LD plants than in SD species (Johnston and Reekie 2008). Greater effects in LD species compared with SD species may be partially due to differential effects of temperature because the LD species flower in spring and early summer. However, the SD species flower in late summer and autumn.

Elevated CO₂ concentration promotes flowering time and hastens the process at higher temperatures in many species. For example, most Asteraceae species flower earlier at elevated CO₂ and flower much faster at additional rising temperatures (Johnston and Reekie 2008). Similar synergistic effects were detected in *Arabidopsis* and *Glycine max* (Walker and Ward 2018; Nagatoshi and Fujita 2019).

Early flowering under increased CO₂ may be due to increased carbon metabolism (Springer and Ward 2007; Wahl et al. 2013; Jagadish et al. 2016) in which high carbohydrate concentration in the apical meristem may likely be lined up with floral transition (Bernier et al. 1993; Wahl et al. 2013). As an example, *TREHALOSE-6-PHOSPHATE SYNTHASE 1 (TPS1)* mutant plants show delayed flowering (Wahl et al. 2013). Moreover, sucrose, a major photoassimilate, may function as a signal molecule to promote flowering (Yoon et al. 2021). Application of exogenous sucrose to *KIN10*-overexpression plants interrupts the development of root and shoot, and causes delayed flowering (Baena-González et al. 2007). In addition, unbalancing the endogenous sugar levels by alternating the function of INDETERMINATE DOMAIN (AtIDD8) affects the expression level of *SUCROSE SYNTHASE 1 (SUS1)* and (*SUS4*), thereby changing the flowering time (Seo et al. 2011).

The molecular mechanism by which CO₂ influences the flowering time is not well known. Analysis of *Arabidopsis* mutants defective in the gene involved in flowering indicated that mutations in *PHYB*, *CRY2*, and *CO* cause early flowering under elevated CO₂ in SD, but not in LD (Song et al. 2009). This result suggests a possible interaction between CO₂ and light signaling pathways under SD.

Pollinators

Approximately 87% of flowering plants depend on pollinators for fertilization (Christmann 2019). The mutual relationship between pollinators and plants provides benefits to each other (Abrha 2019; Gérard et al. 2020). For example, plants offer nectar and food for pollinators. In turn, pollinators help the reproduction and genetic exchange of the respective plants. Maintaining a good ecosystem and critical ecological value depends largely on plant and pollinator interactions (Morton and Rafferty 2017). Major pollinators, including bumblebees, stingless bees, and honeybees are vitally essential in agricultural food and natural ecosystems (Dyer et al. 2006; Whitney et al. 2008; Norgate et al. 2010). Approximately 35% of global food production is assisted by pollinators (Kjølhl et al. 2011).

The synchronization between plants and pollinators is mismatched in many plant species due to climate change and flowering time alteration. This reduces reproduction and the seed set (Morton and Rafferty 2017; Gérard et al. 2020; Richman et al. 2020). Moreover, it causes the pollinator food shortage. For example, in a warm spring of 2002, a bumblebee-pollinated species *Corydalis ambigua* and a bee-pollinated species *Gagea lutea* reduced seed set due to 7–17 days early flowering (Kudo et al. 2004). Moreover, higher temperatures alter flower development, pollen production, and nectar quality. Pollinators also change their body size, life span, and pollination success at increased temperatures (Scaven and Rafferty 2013; Giannini et al. 2020).

Conclusions and Perspectives

Climate has been rapidly changing mainly due to anthropogenic activities, including the emission of greenhouse gases from both industrial and agricultural land. Major greenhouse gases (e.g., CO₂, nitrous oxide, and methane) cause global warming and affect plant physiology. Greenhouse gases lead to successive changes in temperature, precipitation, flooding, and drought through which affects flowering time and pollinator interactions. Global efforts to reduce the production of greenhouse gases are urgently needed because altered flowering time affects plant evolution and crop yield. The use of fossil energy should be replaced by renewable energy such as sunlight, wind, tides, and geothermal heat to mitigate the adverse effects of climate change. Engineering to make genetic factors less sensitive to climate change can help reducing crop loss. Chemical treatment to reduce the effect of climate change can also diminish the damage.

Author Contributions J-SJ and GA designed the project; TW, JY, J-SJ and GA wrote the paper.

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Compliance with Ethical Standards

Conflict of interest The authors declare no conflict of interest.

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