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Review

The Flowering Responses of Economically Important Plants to Global Warming: An Ecosystem Perspective

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Abstract

Temperature is a major environmental determinant of flowering time and reproductive success in plants. Ongoing global warming is changing flowering phenology across natural and agricultural ecosystems, yet the mechanisms by which ambient temperature regulates the transition to reproduction remain less fully resolved than those underlying photoperiodic flowering and vernalization. This review synthesizes eco-physiological and molecular evidence for temperature-dependent flowering across plant groups and terrestrial ecosystems. It considers the development of the florigen concept, the identification of FLOWERING LOCUS T (FT) and related phosphatidylethanolamine-binding protein family members, and the integration of temperature signals with flowering activators and repressors. Particular attention is given to the thermosensory pathway, including alternative splicing, chromatin regulation, membrane-associated signaling, phase separation and temperature-dependent accumulation or stability of regulatory proteins. The review also examines phenological responses to rising temperatures in bulbous geophytes, Arctic and boreal species, subtropical and tropical crops, and desert plants. Available evidence indicates that the temperature requirements for floral initiation, their organogenesis and anthesis vary widely among species and developmental stages, and that these optima reflect life-history strategy, origin and adaptation to seasonal temperature regimes.

Keywords: global temperature change; flowering time; florigen; *FLOWERING LOCUS T*; thermosensory pathway; vernalization; reproductive development

1. Introduction

Global temperatures have increased across all regions of the Earth in recent decades, and additional warming of approximately 2–4 °C is projected by 2050 [1]. The global mean temperature has increased by approximately 0.2 °C per decade [2]. These changes are already altering flowering phenology in plant populations worldwide, although the available evidence remains more extensive for the Northern Hemisphere than for other regions [3]. Climate-driven phenological shifts can change the timing and duration of flowering within communities, but the direction and magnitude of these changes vary among species and biomes [4]. In many non-tropical regions, the growing season has lengthened, leading to earlier spring flowering and, in some cases, later autumn flowering [5]. Ambient temperature is a key ecological factor controlling the onset of flowering [6]. A trend toward a 6.0% decrease in mean flowering date and a 3.4% decrease in flowering season duration for each degree of latitude increase has been found [7]. Large-scale research suggests that flowering responses vary with latitude, with stronger phenological changes at lower latitudes than at higher latitudes [7]. These shifts can have cascading ecological consequences,

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including mismatches between flowering and pollinator activity, altered seed dispersal caused by changes in animal migration, and disruption of food-web interactions [8]. Temperature stress is therefore both a limiting factor in reproductive development and an important challenge for plant production. Flowering marks the transition from vegetative to reproductive growth, and the timing of this transition strongly influences seed production and reproductive success. Under stressful conditions, plants may adjust flowering time as part of a broader strategy to maintain reproduction [9]. Temperature-dependent flowering can interact with established flowering pathways and has been recognized as a distinct component of flowering responses to environmental stress [10]. In crops, high temperatures may accelerate flowering, shorten development and reduce yield [11]. Some projections indicate that continued warming could substantially reduce yields of temperature-sensitive crops by the end of the century [12].

The regulation of flowering has long been a central topic in plant eco-physiology and developmental biology [9,13–16], and important advances have been made in recent years [17–19]. Physiological and molecular-genetic studies, particularly in *Arabidopsis thaliana*, have identified six major pathways regulating flowering: photoperiodic, autonomous, thermosensory, vernalization, gibberellin and age-dependent pathways [9,20]. These pathways converge on a limited set of integrator genes that control the transition to reproductive development. The influence of photoperiod and light quality on flowering is well established in many species [21,22], and the molecular basis of vernalization in *A. thaliana* has been characterized in detail [23–25]. By contrast, the thermosensory pathway, through which plants respond to moderate changes in ambient temperature, remains less fully understood. This review analyses current evidence on the effects of temperature on plant flowering under global warming, with emphasis on eco-physiological responses, molecular regulation and the diversity of temperature optima across terrestrial ecosystems from the Arctic to the tropics.

2. Advances in Eco-Physiological and Molecular–Genetic Studies of Flowering

2.1. Eco-Physiological Studies of Flowering

One of the first hormonal theories of flowering was proposed by the Soviet plant physiologist Mikhail Chailakhyan in 1936. Chailakhyan suggested the existence of a universal flower-inducing stimulus, later termed florigen, that is produced in leaves and transported to the shoot apex [14]. Based on experiments with plants from different photoperiodic groups, he described florigen as a hormonally active substance formed in leaves under a favorable photoperiod and subsequently transported to the stem apex, where it induces the transition of the apical meristem from vegetative to reproductive development [15]. In the 1980s, Chailakhyan modified this theory and proposed a bicomponent florigen system comprising gibberellins and hypothetical anthesins [13]. Despite extensive research, the chemical nature of anthesins remained unresolved for many decades. The molecular nature of florigen was clarified only in 2005–2007, approximately 70 years after the hypothesis was first proposed. Independent groups in Sweden, Germany and Japan reported that florigen is a mobile protein that moves to the shoot apical meristem and induces flowering [14,26–31]. In *A. thaliana*, florigen was identified as the protein encoded by FLOWERING LOCUS T (FT). FT is produced in leaves under favorable environmental conditions and transported through the phloem to the shoot apex, where it interacts with the bZIP transcription factor FD to initiate flowering. High *FT* expression after the initial induction of reproductive development and during inflorescence development may also prevent reversion to vegetative growth [32]. The discovery of FT as a mobile flowering signal strongly confirmed the central assumptions of Chailakhyan's florigen

theory [14]. *FT-like* genes have since been identified in a wide range of species, from the biofuel plant *Jatropha curcas* to the conifer *Pinus sylvestris* [33,34].

2.2. Molecular–Genetic Studies of Flowering Regulation

Molecular-genetic studies of reproductive development have traditionally relied on the model species *A. thaliana* and *Antirrhinum majus* [6,17,30,35–40]. By the end of the twentieth century, genes controlling floral meristem identity and floral organ identity had been identified, and the genetic regulation of floral morphology had been analyzed in detail. One of the major discoveries in plant developmental biology was that the genetic systems underlying flower development are highly conserved [41]. Conservation of genes involved in photoperiodic flowering has also been demonstrated in *A. thaliana* and *Oryza sativa* [42]. Research on flowering regulation now extends across many cultivated species, including *O. sativa* [43,44], *Zea mays* [20,45,46], *Triticum aestivum* and *Hordeum vulgare* [47,48], *Allium cepa* [49], *Solanum tuberosum* [50], *Brassica* spp. [51], *Nicotiana* spp. [52], *Chrysanthemum* spp. [44,53] and others.

Flower differentiation begins when vegetative cells of the shoot apical meristem (SAM) are transformed into an inflorescence meristem (IM) [54–56]. The size and shape of the IM depend strongly on developmental stage and on environmental factors that regulate cell division [57]. The IM subsequently gives rise to floral meristems, which initiate the formation of floral organ primordia. This process is controlled by coordinated transcriptional regulation, with MADS-box genes playing a central role [58]. *FT-like* genes have been identified in many plant species [20,33,34]. FT protein is transported through the phloem to the SAM, where it interacts with FD [39]. Export of FT from companion cells to phloem sieve elements occurs through endosomal transport [6]. At the apex, the florigen activation complex activates floral meristem identity genes [59]. In addition to regulating flowering time at the SAM, FT is involved in axillary meristem growth and branching [59]. In the shoot apex, florigen activates *APETALA1* (*AP1*), thereby initiating floral meristem formation at specific positions on the IM [20,60]. FT belongs to the phosphatidylethanolamine-binding protein (PEBP) gene family. In addition to *FT*, five other PEBP genes are present in Arabidopsis: *TWIN SISTER OF FT* (*TSF*), *BROTHER OF FT* (*BFT*), *MOTHER OF FT* (*MFT*), *Arabidopsis thaliana CENTRORADIALIS* (*ATC*) and *TERMINAL FLOWER 1* (*TFL1*). *FT*, *TSF* and *MFT* generally function as flowering activators, whereas *TFL1*, *ATC* and *BFT* can act as flowering repressors [61–63]. The size of the PEBP family varies among species: 23 genes have been identified in *Glycine max* [64], 19 in *O. sativa* [65] and 24 in *Z. mays* [66]. In many species, however, a single PEBP gene encodes the principal florigenic protein.

In 1991, Coen and Meyerowitz proposed the ABC model of floral organ development based on floral mutants in *A. thaliana* and *A. majus* [67]. According to this model, sepals are determined by class A genes, petals by class A and B genes, stamens by class B and C genes, and carpels by class C genes. The model provided a framework for subsequent molecular studies of floral organ identity [68]. Later work expanded the model and showed that floral development is regulated by complex networks involving flowering integrators such as *FT* and *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*), floral meristem identity genes such as *AP1*, *LEAFY* (*LFY*), *CAULIFLOWER* (*CAL*), *FRUITFULL* (*FUL*) and *AGL24*, and ABCDE-class floral organ identity genes [20,63,69,70].

FT expression is a central integrator of flowering time and responds to photoperiod, vernalization and other endogenous and environmental signals [25,71,72]. Increased *FT* expression promotes flowering, whereas reduced expression delays the transition to reproductive development. *TFL1*, a close homolog of *FT* in *Arabidopsis*, has the opposite function and suppresses flowering by interfering with *FT* activity. FT- and TFL1-like proteins have been described in many angiosperm families and may act as either activators or repressors

depending on conserved amino acid residues [44]. The balance between florigenic and anti-florigenic signals allows plants to adjust development at the shoot apex [44]. Although FT was first characterized within the photoperiodic pathway, it is now clear that it integrates multiple endogenous and environmental signals, including abiotic stress [9,72]. Flowering therefore depends on the interaction between endogenous gene-regulatory networks and external environmental cues.

3. Ecological and Molecular Studies of Temperature-Dependent Flowering

The study of flowering regulation by abiotic factors has traditionally focused on the inductive effects of photoperiod and low temperature during vernalization [6,9,13,17,35,73–75]. Temperature is nevertheless one of the principal environmental factors determining the transition to flowering. It is important to distinguish between inductive temperature effects, such as vernalization, and the physiological temperature ranges within which flowering can occur in different species [17]. Whereas the inductive effect of prolonged cold has been studied extensively, the influence of moderate ambient temperature on flowering has received comparatively less attention [40,76–79]. Global warming affects plant phenology, including flowering time, as documented by numerous ecological studies [17,80–82]. Understanding the molecular mechanisms underlying plant responses to ambient temperature is essential for predicting climate-change effects and mitigating impacts on crop productivity [83,84]. Important questions remain unresolved, including how plants perceive ambient temperature and how thermoresponsive flowering operates under natural field conditions. Evidence suggests that *Arabidopsis* may possess temperature-responsive regulatory systems that influence flowering independently of FT [63], and recent work indicates that temperature can also regulate flowering through post-translational control of FT proteins [85].

3.1. Vernalization

Vernalization is an adaptation to seasonal temperature dynamics that allows plants to acquire the competence to flower after prolonged exposure to winter cold [17]. The perception of low temperature during vernalization involves at least two related processes: induction of cold tolerance and acceleration of the transition to reproductive development [23]. Vernalization does not usually induce flowering directly; rather, it enables the meristem to respond to environmental signals that subsequently trigger flowering. In *A. thaliana*, vernalization mechanisms are well characterized [17]. Prolonged cold represses *FLOWERING LOCUS C* (*FLC*), a MADS-box transcription factor that acts as a negative regulator of *FT* and *SOC1* [59]. *FLC* is activated by the positive regulator *FRIGIDA* (*FRI*), which functions within a large multiprotein complex. During winter, *VERNALIZATION INSENSITIVE3* (*VIN3*) is gradually induced by prolonged cold and contributes to the epigenetic repression of *FLC*. Reduced *FLC* expression enables the SAM to respond to favorable photoperiod and temperature conditions [24,86]. Following cold exposure and increasing day length, *FT* is activated in leaves. Winter cereals evolved vernalization mechanisms independently of *Arabidopsis*, including additional regulatory pathways that control florigen activity [44]. In cereals, the key event is not the cold-induced repression of *FLC*, because *FLC-like* genes have not been identified in monocots. Instead, vernalization activates the MADS-box transcription factor gene *VERNALIZATION1* (*VRN1*), which promotes flowering [44]. In wheat, *VERNALIZATION2* (*VRN2*), encoding a Zinc finger-CCT-domain transcription factor, is repressed during vernalization [47]. The vernalization response therefore appears to have evolved independently in monocots and dicots, although MADS-box transcription factors play important roles in both systems [59]. A characteristic feature of many boreal *Poaceae* is delayed flowering initiation until after winter, reflecting a re-

quirement for vernalization [87]. Many wheat and barley cultivars grow vegetatively for an extended period and do not flower without overwintering. Genetic studies of these cultivars have identified the *VRN2* locus as a key determinant of vernalization requirement in cereals [88]. The history of wheat adaptation in Australia illustrates the agronomic importance of this trait. The first varieties grown in Australia were derived from English wheat and required vernalization and long days for rapid flowering; they were poorly adapted to warm Australian conditions. In the late nineteenth century, William Farrer crossed early-flowering Indian wheats with European varieties and selected better-adapted cultivars. His variety "Federation", released in 1901, became highly successful and contributed to the genetic basis of Australian wheat adaptation until the 1960s [87]. This example remains relevant for cereal breeding under current warming in temperate regions.

3.2. The Thermosensory Pathway of Flowering

Ambient temperature also influences *FT* activity in *Arabidopsis*, but the genetic regulation of this process remains incompletely understood. Studies of flowering responses to ambient temperature in *A. thaliana* began later than studies of vernalization [77–79]. Interest in this field is driven both by the need to understand adaptation of reproductive development to changing environments [17,89,90] and by the potential to regulate plant growth under controlled or artificial climates. Several *FT* genes have also been identified in monocotyledonous species [91,92]. For a long time, no specific temperature sensors for flowering were identified in plants, and it was proposed that several cellular and molecular mechanisms might participate in temperature perception [93,94]. Temperature-dependent interactions between nucleosomes and DNA have been reported in plants [95,96], and temperature may also influence DNA structure [97]. Penfield [98] described temperature perception as one of the major unresolved questions in plant science. The plasma membrane has been proposed as a primary temperature sensor because temperature alters membrane fluidity, thickness, permeability and lipid packing [19,99]. Such changes can influence the mobility, activity and folding of membrane-associated proteins and may contribute to thermosensing [19,100]. Several membrane-associated proteins, including calcium channels, have been proposed as candidate thermosensors, because temperature stress causes rapid increases in cytosolic calcium [19].

In recent decades, substantial progress has been made in understanding temperature-dependent flowering and its molecular mechanisms. Several regulatory modules controlling plant growth and development in response to temperature have been described [40,101]. The term thermomorphogenesis is used to describe temperature-induced morphological changes in plants [40,79,101,102]. Plants use multiple pathways to reprogramme growth and development in response to temperature fluctuations [95,96]. Studies in *Arabidopsis* have shown that endogenous and exogenous signals influence flowering time through specific regulatory modules [40,103]. The transition of vegetative meristems to reproductive development in response to ambient temperature differs among species. In *Arabidopsis*, *FT* is essential for thermal regulation of flowering [104]. In many species, *FT-like* genes function as integrators of ambient-temperature responses, but the gene-regulatory networks controlling *FT-like* expression are not yet described in detail for most taxa [17]. Following the transition from the juvenile to the mature vegetative phase, plants become competent to respond to external flowering signals. A high degree of conservation in flowering-time regulation has been demonstrated across species [63]. Several temperature-responsive genes regulate flowering by sensing or responding to environmental temperature [59]. In *Arabidopsis*, the best-studied temperature-responsive gene is *FLOWERING LOCUS M* (*FLM*), which, together with *SHORT VEGETATIVE PHASE* (*SVP*), represses FT under conditions that are suboptimal for flowering [105]. Other temperature-

responsive regulators include PIF3, PIF4 and PIF5, *TERMINAL FLOWER 1* (*TFL1*) and *EARLY FLOWERING 3* (*ELF3*) [94,106,107]. Temperature affects flowering through molecular processes such as alternative splicing, phase separation and temperature-dependent accumulation of regulatory proteins [101,102]. Both changes in ambient temperature and vernalization alter transcription of floral regulators. Moderate increases in temperature can accelerate *Arabidopsis* flowering and activate *FT* [6,40]. Temperature often acts through transcription factors that regulate *FT* as either activators or repressors. The balance between these opposing regulators determines *FT* expression and flowering response [40]. Primary cellular responses to temperature may include changes in membrane lipid composition and fluidity, chromatin modification, modulation of RNA processing and altered protein translation or stability [93]. The precise molecular nature of plant temperature perception remains unresolved [83].

4. Ambient Temperatures and Flowering

4.1. Developmental Changes in Temperature Requirements During Flower Development

Some of the earliest and most extensive studies of temperature effects on flower differentiation were conducted in the first half of the twentieth century by the Dutch scientist A. Blaauw and colleagues. Their work focused on bulbous geophytes and ornamental species, including *Hyacinthus*, *Tulipa*, *Narcissus*, *Iris*, *Hippeastrum*, *Syringa*, *Rhododendron* and *Azalea* [108–112]. These studies showed that temperature plays a critical role at different stages of dormancy and growth in geophytes. In many bulbous plants, successful flowering requires a sequence of warm, cold and then warm periods. In tulip, floral organ initiation generally requires relatively high summer temperatures, with an optimum of approximately 18–25 °C (Figure 1). After floral organ formation, low temperatures, usually 4–9 °C, are required during autumn and winter for dormancy release, stem elongation and full flowering. As flower buds and inflorescences begin to grow, the optimum shifts towards approximately 13 °C and then to higher temperatures as development proceeds [108–110,112]. These findings have been confirmed by later studies [63,92,113–115].

Figure 1. Flowering of tulips (photographs by Valery and Natalia Vasilevsky). Flowering initiation in various tulip cultivars occurs within the daughter bulb in summer at 18–25 °C. A winter period of 4–9 °C is then required for release from dormancy and peduncle elongation. Tulips usually flower in April–May at 15–20 °C.

Studies of tulip by Leeggangers [63] showed that floral initiation occurs within the bulb and is induced by high ambient temperature, as in many other geophytes [110], including *Narcissus tazetta* [92], *Hyacinthus* and saffron [114]. High ambient temperature induces the transition from vegetative to reproductive development in daughter bulbs. By August or September, a fully developed dormant flower bud is already present within the

bulb. A prolonged cold period is then required to release dormancy and prepare for stem elongation and spring flowering. Flowering generally occurs in April or May, depending on cultivar [63].

Studies of floral organogenesis in *Scilla*, *Crocus* and *Muscari* also show that elevated temperatures are necessary for flower initiation in these species [116]. This pattern is consistent with adaptation to high summer temperatures, under which reproductive development begins, whereas low temperatures delay floral differentiation [116]. In *Tulipa*, *Hyacinthus*, *Narcissus* and some species of *Iris*, cold is required not for the initial vegetative-to-reproductive switch, but for release from winter dormancy and peduncle elongation [117]. Although this process differs from vernalization, related regulatory mechanisms may be involved [118]. Temperature requirements are likely determined by ecological conditions of the region of origin. *Iris* species originating from temperate regions generally require only a short period near 20 °C for floral induction, followed by cooler conditions for optimal differentiation of the floral meristem [115] (Figure 2). Species originating from Irano-Turanian regions, such as *Tulipa*, *Narcissus* and *Hyacinthus*, require relatively high temperatures for floral induction, initiation and early differentiation [115]. These findings indicate that temperature optima shift during flower development and reflect adaptation of life cycles to seasonal temperature regimes in regions of origin.

Figure 2. Flowering of *Iris* cultivars in the collection of the Botanical Garden of Moscow State University named after M. V. Lomonosov (photographs by Valery Vasilevsky). During initiation and early floral organogenesis, temperatures of 13, 15 or 17 °C are required, depending on species, whereas higher temperatures such as 25.5 °C can prevent floral primordium formation. Low winter temperatures are also required for subsequent flowering.

Premature flower formation caused by rising spring temperatures is an emerging problem for bulbous crops. When flower buds develop within the bulb under excessively warm conditions, subsequent dehydration during storage can cause flower abortion or reduced flower quality [111]. In the Netherlands, warm winters and high spring temperatures interfere with floral induction and have contributed to lower-quality tulips. Breeding programmes has therefore begun to develop tulip cultivars adapted to warmer winter conditions [63].

Recent studies of *Lycoris* (*Amaryllidaceae*) show that meiosis and pollen formation occur within the underground bulb during summer dormancy, when the above-ground shoot has senesced and before the peduncle emerges. These processes take place at temperatures of approximately 25–30 °C [119]. *Lycoris* is prone to meiotic instability. Heat during June meiosis can cause disturbances in chromosome segregation, spindle orientation and the formation of abnormal unreduced gametes, whereas low temperatures below 15 °C inhibit microsporogenesis and disrupt preparation for autumn flowering [119]. Stud-

ies of two diploid *Lycoris* species and two naturally derived allotriploid varieties showed unstable chromosome segregation in diploids and severe disruption of chromosome pairing and bivalent formation in allotriploids, leading to aneuploid meiotic products and sterility [119].

Molecular studies in tulip have shown that, before visible morphological changes occur in the SAM, rising ambient temperature suppresses floral repressors and prepares the bulb for the transition to reproductive development [63]. Flowering induction occurs together with bulb maturation and the onset of dormancy. Gene-expression analysis identified *TgTFL1* and *TgSOC1*-like1 as potential flowering repressors and *TgSOC1-like2* as a flowering activator. *TgTFL1* appears to be a temperature-dependent inhibitor of flowering, with expression beginning four to five weeks before the transition to reproductive development. Several potential flowering-time regulators have been identified that may be specific to bulbous plants or tulip [63]. Three PEBP family genes, *TgFT1*, *TgFT2* and *TgFT3*, have been identified in tulip. *TgFT1* and *TgFT2* are FT-like proteins, and expression of both genes increases in vegetative organs during development, peaking in May when flowering induction begins in daughter bulbs. Ectopic expression of TgFT1 in *Arabidopsis* delayed flowering, suggesting that *TgFT1* may act antagonistically with *TgFT2* during flowering regulation in tulip [63]. Such antagonism between FT-like proteins may be characteristic of biennial and perennial plants and has been described as an antiflorigenic mechanism [44]. Similar antagonistic *FT-like* pairs occur in sugar beet (*BvFT1* and *BvFT2*) [120] and poplar (*FT1* and *FT2*) [121]. In *N. tazetta*, high temperatures above 25 °C promote flowering through induction of the *FT* homolog *NtFT*, whereas temperatures around 12 °C inhibit floral organogenesis and maintain only basal *NtFT* expression [92,122]. Seven *FT-like* genes have also been identified in *Allium cepa*; *AcFT2* appears to promote flowering in response to temperature and photoperiod [123]. Overall, the regulatory networks underlying ambient-temperature control of flowering in bulbous species are only beginning to be resolved [59].

4.2. Global Warming and Flowering

A general global trend under current climate warming is an acceleration of flowering [124]. However, phenological sensitivity to temperature varies with the geographic location of species [125]. In central England and the Mediterranean, flowering phenology advances by approximately 5 days for each 1 °C temperature increase [126,127]. In contrast, studies on the Qinghai–Tibet Plateau found that, from 1982 to 1991, mean annual temperature increased by 1.5 °C while plant phenology was delayed by 0.8 days [128]. Rising global temperature therefore triggers diverse phenological and physiological responses in terrestrial ecosystems, from polar deserts to tropical rainforests. The optimum temperature for floral initiation may differ from the optimum for subsequent reproductive organ development. Flower development rate depends mainly on mean daily temperature, whereas floral initiation may be accelerated by high temperature or inhibited when temperatures fall outside the species-specific optimum range [129,130].

4.2.1. Arctic Ecosystems

Low ambient-temperature requirements for floral meristem differentiation and flowering initiation have been described in Arctic tundra and polar-desert species [82,131–143] (Figure 3). Because of climate warming, flowering in northern ecosystems often begins earlier. In Norway, phenological shifts of approximately 0.9 days per decade have been reported [144], and in Arctic Canada an increase in flowering period of 1.2 days per decade has been observed [7]. Temperature is considered the dominant abiotic factor affecting flowering in Arctic and Subarctic ecosystems [137]. In these regions, floral primordia often initiate and develop during summer and autumn of the year preceding flowering, at

relatively low positive temperatures [131–134,136,138]. Sorensen's 1941 study in Greenland, which examined 169 species, showed that 92% of species possessed floral primordia at different developmental stages during winter [138]. Studies of floral organogenesis in the dwarf shrubs *Arctous alpina*, *Phyllodoce caerulea* and *Cassiope tetragona* in the mountain tundra of the Kola Peninsula showed that floral initiation and differentiation began in June, one year before flowering, when mean temperatures ranged from +5 to +10 °C. Androecium and gynoecium formation occurred in the middle of the growing season, and floral organogenesis was completed by September [132–134]. The presence of reproductive primordia through winter allows high-latitude plants to flower and produce mature seeds during a very short growing season despite low temperatures [131,136].

Figure 3. Flowering of *Saxifraga* spp. in the polar desert of the Franz Josef Land Archipelago *Saxifrages* flower in July at 4–5 °C and can continue flowering during snowstorms (photographs by Valery Vasilevsky).

Recent Arctic tundra studies show that flowering is highly sensitive to changes in summer temperature [82,135,139]. Higher summer temperatures and longer growing seasons can increase flower abundance [82,135], whereas low temperatures early in the growing season may cause frost damage and flower mortality, reducing reproductive success [135]. Flower production appears to be among the most temperature-sensitive reproductive traits. Some Arctic species show accelerated growth and flowering under warming, although responses are species-specific [81].

Experimental warming in the Alaskan Subarctic resulted in earlier flowering and increased flowering duration and density in evergreen and deciduous shrubs [141]. Monitoring has also shown that flowering in Arctic ecosystems has shifted earlier over the past three decades under both experimental warming and field conditions associated with increasing mean annual temperature [142]. In Arctic Canada, however, long-term warming has been associated with a decline in the number of flowering species [141]. Climate change has therefore produced contrasting trends between the Low and High Arctic. In the High Arctic, mean annual temperatures remain below freezing, but warmer conditions and earlier snowmelt may expose reproductive buds and flowers to frost damage in some species [135]. On Svalbard, *Dryas octopetala* has shown reduced flowering productivity [139]. Similar patterns have been recorded in northern Greenland for *Papaver* and *Cassiope*, where flower production shows a strong downward trend. In contrast, long-term monitoring of vascular plants such as *Salix glauca*, *Silene acaulis*, *Eriophorum angustifolium* and *Loiseleuria procumbens* in southern Greenland has shown that overall flower density has nearly doubled over 13 years, contrasting with the decline observed in the High Arctic [135]. Thus, long-term warming may enhance flowering and seed production in some Low Arctic species but reduce reproductive productivity in High Arctic species through frost damage or resource limitation.

Molecular studies of flowering and reproductive development in Arctic plants are still at an early stage. One genomic analysis of four Arctic species, *Oxyria digyna*, *Draba nivalis*, *Cochlearia groenlandica* and *Dryas octopetala*, identified numerous expanded and contracted gene-family GO terms related to sexual reproduction, meiosis, pollen recognition, regulation of reproductive processes and anther wall tapetum development [143]. Genes regulating reproduction were expanded in *O. digyna*, whereas no such expansion was observed in *D. nivalis* and *C. groenlandica*, both of which are predominantly self-pollinating. Expansion of pollen-recognition genes was detected in *O. digyna* and *D. octopetala* but not in *D. nivalis* or *C. groenlandica* [143].

4.2.2. Boreal and Temperate Ecosystems

In temperate climates, flowering is synchronized with seasonal cues, particularly photoperiod and temperature [144]. Over evolutionary time, temperate plants have developed biological safeguards, including vernalization and photoperiodism, that prevent premature flowering during unpredictable winter thaws. Data from Europe between 1951 and 1998 suggest that spring phenological phases shifted four weeks earlier in Western and Central Europe but began approximately two weeks later in Eastern Europe [144,145]. Across 21 European countries, 78% of observations indicated earlier flowering, with phenological events advancing by an average of 2.5 days per decade. In Germany, 78 agricultural and horticultural phenological events between 1951 and 2004 advanced by an average of 1.1–1.3 days per decade [146]. Phenological patterns differ among trees, perennial herbs and annual herbs in temperate plant communities [147]. Sensitivity to temperature is primarily expressed through interactions between winter chilling and spring warming [148,149]. If plants are more sensitive to spring warming than to winter chilling, flowering tends to advance [150]. Conversely, if winter warming has a stronger effect than spring warming, satisfaction of chilling requirements may be delayed, resulting in delayed flowering [151]. For many species, warming advances spring phenological events and delays autumn senescence, thereby lengthening the growing season [152].

Phenological monitoring in southern England showed that flowering of angiosperms advanced by approximately 4 days for each 1 °C rise in spring temperature during 1954–1989 [153]. In Great Britain, the mean first-flowering date for 385 species in the 1990s was 4.5 days earlier than in the preceding 40 years, and 16% of species flowered 15 days earlier [154]. At the same time, about 3% of species flowered significantly later. A 1 °C rise in mean monthly temperature delayed flowering in some early-flowering species and advanced flowering in late-flowering species. A United Kingdom study based on 395,466 records of first-flowering dates for 405 species from 1753 to the present produced a 250-year index showing that first flowering has advanced markedly in recent decades [155]. The average community-level index for the past 25 years showed earlier flowering than any other consecutive 25-year period between 1760 and 1984, with differences ranging from 2.2 to 12.7 days. Flowering onset was strongly correlated with average February–April temperatures. Species-level indices showed, for example, that first flowering of hawthorn (*Crataegus monogyna*) and blackthorn (*Prunus spinosa*) occurred earlier in the past 25 years than in any other comparable period in the available record [155]. Swedish floristic data spanning 220 years also showed a shift in first flowering of approximately 0.49 days per decade [156]. Annuals flower on average about 10 days earlier than perennials and show more variable flowering times [153,154]. Trees and many perennials exhibit indirect flowering responses because their flowering is affected by temperature over relatively long periods. Since 1977, higher mean temperatures from February to April have been associated with earlier full flowering in apple cultivars registered in the UK National Fruit Collection [144]. However, temperate plants do not respond uniformly to warming. Warmer

summers can have opposite effects on *Daboecia cantabrica* and *Galanthus nivalis* [144]. A 1 °C increase in overall warming has been predicted to delay flowering in *Petasites* hybridus by up to six weeks but to advance flowering in *Geranium robertianum* by more than five weeks [153]. Moreover, 24 species in one dataset showed no significant relationship between flowering time and temperature [153].

Flower organogenesis and the molecular mechanisms of flowering in boreal and temperate ecosystems are actively studied. In apple, plum, raspberry, blackberry and gooseberry, flower-bud formation occurs from the second ten-day period of July to the end of the first ten-day period of August, with optimal initiation temperatures of approximately 18–25 °C [157]. High temperatures generally stimulate vegetative growth in fruit trees and may inhibit flower-bud formation [157]. Exposure of sweet cherry trees to high temperatures during flower differentiation, for example 35/25 °C day/night for 15 days, induced the formation of flower buds with double pistils [157]. In wild strawberry (*Fragaria vesca*), flowering can occur independently of photoperiod under low temperatures [158]. During autumn, low temperatures induce the transition from vegetative to reproductive development, followed by flowering after winter. *FvTFL1* is a major regulator of seasonal flowering in *F. vesca* [158]. At temperatures below 13 °C, low *FvTFL1* expression under both short-day and long-day conditions permits flowering induction independently of photoperiod [159]. In *Boechera stricta*, a relative of *A. thaliana*, flowering is delayed at 25 °C compared with 18 °C [17,160]. Elevated summer temperatures above 20 °C delay flowering in *Chrysanthemum morifolium* through delayed expression of the *FT* homolog *FT-like 3* (*FTL3*) [161].

During deep winter dormancy, buds of temperate trees do not develop even when air temperatures become positive, and dormancy depth is genetically determined [157]. Low temperatures below 12 °C contribute to dormancy induction in apple and pear. Dormancy release requires the completion of a chilling period, which can be expressed as hours below a defined temperature; for example, Bartlett pear and Delicious apple require approximately 1500 chilling hours [144]. Empirical models have been developed to estimate chilling requirements for temperate fruit trees and are used in practice [162]. Two climatic factors determine the seasonal pattern of budbreak in temperate trees: heat accumulation in spring and low temperatures in the preceding autumn–winter period. Increased heat accumulation can accelerate flowering, increasing the risk of flower damage during spring frosts. A 1 °C change in mean air temperature before flowering can delay flowering by 4 days and harvest by 8 days, with potential effects on yield and fruit quality [157]. Delaying flowering is therefore an important strategy for reducing spring-frost damage.

4.2.3. Subtropical Ecosystems

Subtropical species often show earlier flowering and fruiting in response to rising temperatures, although species differ markedly in their sensitivity. Monitoring of the reproductive phenology of 102 woody species in China between 1980 and 2008 showed that mean annual temperature increased by 0.23 °C per decade, consistent with global warming trends, while flowering advanced by 0.23 days per year across species [2]. Flowering timing varied significantly among species, with both advances and delays observed. Earlier flowering occurred in 73% of species. Flowering tended to advance in deciduous species but to be delayed in evergreen species. Species-specific differences in phenological responses may weaken interspecific flowering synchrony, which is important for attracting pollinators, and could thereby reduce pollination efficiency, alter gene flow and affect community composition [163].

In many subtropical fruit trees, floral meristems and flower primordia are initiated after vegetative growth slows during cool weather [164]. Species such as avocado, grape-

fruit, mandarin, orange, lychee and macadamia form flowers at temperatures below 20 °C [164–173]. In several of these species, reproductive development may be inhibited by even brief daily exposure to 25–30 °C, although vegetative growth remains unaffected. Controlled-climate experiments show that floral organogenesis responds to temperature in a species-specific manner. In lychee, mango and avocado, low temperatures stimulate flower initiation but inhibit subsequent floral organogenesis. The temperature at which the transition from vegetative to floral growth occurs varies among species but generally lies between 15 and 25 °C in subtropical avocado, lychee and mango [164]. In the mango cultivar Sensation, flower initiation occurred only under a 15/10 °C day/night regime for five weeks, after which the first floral primordia appeared [164]. In other subtropical mango cultivars, differentiation also began only under a 15/10 °C regime, although the required chilling period was longer [174].

In avocado (*Persea americana*), the optimal temperature range for flowering is approximately 20–25 °C [175] (Table 1). In artificial-climate experiments with the avocado cultivar Hass, 23/18 °C was close to the critical point, because flowering under this treatment began later and was weaker than under 18/15 °C. A low-temperature-dependent pattern of flowering-gene expression has been described in Hass. Floral meristem differentiation begins in autumn, and low autumn and winter temperatures regulate flowering induction [171]. Expression analysis of *PaFT*, *PaLFY* and *PaAP1* in leaves and buds showed that low autumn temperatures increase *PaFT* expression in leaves, followed by increased *PaAP1* and *PaLFY* expression in buds and formation of inflorescence meristems by late November [176]. Maximum accumulation of *PaAP1* and *PaLFY* transcripts in buds occurred only after eight weeks of low-temperature treatment at 14 °C during the day and 10 °C at night, which was necessary and sufficient for the irreversible transition of the SAM to flowering in Hass avocado [145]. Thus, avocado flower development is stimulated by low-temperature-dependent induction and warm-temperature-dependent floral organogenesis [171]. Temperatures below 20 °C are sufficient for flowering induction in the cultivars Chocette, Booth-8 and Hass in Mexico [173].

Table 1. Flower initiation and optimal flowering temperatures of selected tropical and subtropical trees.

Species	Temperature for Flowering Induction	Optimal Temperature for Flowering	Upper Temperature Threshold Inhibiting Flowering	References
Litchi chinensis	15 °C	18–20 °C	30 °C	[167,169]
Persea americana cv. Hass	14 °C day 10 °C night	20–25 °C	30 °C	[171]
Persea americana cv. Chocette cv. Booth-8	<20 °C	not specified	not specified	[173]
Citrus unshiu	10–18 °C day 5–12 °C night	17–18 °C	30 °C	[168]
Olea europaea	10–13 °C	20–28 °C	35 °C	[177–180]

Olive (*Olea europaea*) is among the most widespread subtropical trees, and olive flowering is often used as a bioindicator of potential climate change. Flower induction requires winter temperatures of approximately 10–13 °C; higher temperatures around 18 °C or lower temperatures around 4 °C can suppress flower initiation (Table 1) [177]. In southern Spain, olive flowering usually occurs between late April and mid-June. Flowering begins at temperatures of approximately 20–24 °C and ends at 28–30 °C [178]. Spring

high temperatures can advance flowering. Temperatures around 25 °C favor pollen-tube growth in vivo, accelerate fertilization and support initial fruit set [179]. Three-year experiments using open temperature-controlled chambers (OTCs) showed that increasing temperature by 4 °C above ambient can lead to earlier flowering, longer flowering duration, more aborted pistils and reduced fruit set, potentially reducing yield [179]. In Portugal, inflorescence development duration decreased between 2012 and 2022, and some genotypes showed a 50% reduction in phenological development. In the extremely hot year 2022, all studied olive genotypes showed yield reductions associated with heat stress, with strong negative correlations with temperatures above 35 °C in April–May [178]. Genotype phenology should therefore be considered in cultivar selection of olive and breeding programs; highly productive cultivars must complete flowering and fruiting before the onset of extreme heat [180].

High temperatures can inhibit the development of fertile floral structures in subtropical trees, including stamen differentiation in avocado [181] and early inflorescence and flower formation in lychee [169]. Lychee flowering is most successful after approximately ten weeks at 15 °C, whereas exposure to temperatures above 20 °C for eight or more hours per day can maintain plants in a vegetative state [167]. In mandarin (*Citrus unshiu*), low-temperature treatment of 10–18 °C during the day and 5–12 °C at night releases bud dormancy and enhances flowering [168]. Low temperature may therefore have a dual role, releasing dormancy and stimulating flowering. In mandarin, the first stages of flower initiation appear to occur before winter dormancy. Chilling promotes *CiFT* expression and reduces metabolic activity while releasing buds from inhibition, allowing sprouting and flower development [168].

4.2.4. Tropical Ecosystems

Many tropical floras can flower throughout the year. This pattern has been documented along the Brazilian Atlantic coast, where most species flowered for at least six months annually [182]. In the Neotropics, flowering may occur continuously, show one or two seasonal peaks, or decline during the dry season [183]. Phenological changes in tropical flowering plants in response to rising temperature are still poorly documented, partly because tropical regions were long assumed to experience smaller phenological shifts due to relatively weak annual temperature variation [184]. Many tropical species flower continuously, but others have discrete flowering periods. Because long-term stationary studies in tropical plant phenology began mainly in the mid-twentieth century, digitized herbarium collections and sequence data from herbarium specimens provide valuable opportunities for historical analysis [185].

Herbarium-based studies have examined flowering phenology in tropical species with discrete flowering periods, including *Ceiba* spp., *Peltogyne* spp., *Bougainvillea* spp., *Aeschynomene martii*, *Barnebya harley*, *Caesalpinia pluviosa*, *Mimosa acutistipula*, *Pseudobombax parvifolium* and others from equatorial Africa, South America and Southeast Asia [184]. For the period 1794–2024, an average absolute change in flowering onset of 2.04 days per decade was documented, with species-level values ranging from 0.037 to 14.10 days per decade. The direction of shifts was not uniform: some species flowered earlier than indicated by historical data, whereas others flowered later. *Peltogyne recifensis* from INPA reserves in Brazil showed one of the strongest changes, with flowering delayed by 14.1 days per decade, equivalent to a total shift of 80.47 days between 1951 and 2008. *Barnebya harley* from Catimbau National Park in the Brazilian Caatinga showed later flowering by 5.84 days per decade, equivalent to 29.82 days over 51 years. These shifts are comparable in magnitude to those reported for temperate, boreal and alpine desert plants [184]. Tropical flowering patterns differ from those in many temperate and boreal systems because they

often occur without winter dormancy and under relatively constant photoperiod [185]. The tropics also contain greater phylogenetic diversity, which may be associated with a wide diversity of phenological strategies. A global analysis of approximately 8 million digitized herbarium sheets representing nearly 200,000 species used computer vision to examine flowering phenology across latitudes and found that flowering seasons changed more strongly in tropical latitudes than at higher latitudes [7]. This result supports calls for greater attention to phenological shifts in tropical ecosystems [185].

The Cerrado, a Neotropical savanna in Brazil and one of the most species-rich regions of the world, contains more than 13,000 plant species. Peak flowering generally occurs in September during the dry-to-wet season transition, when pollinators are more active [186]. Fifteen years of monitoring of 33 Cerrado species, including *Xylopia aromatica*, *Aspidosperma tomentosum*, *Connarus suberosus*, *Rourea induta*, *Diospyros lasiocalyx* and *Anadenanthera peregrina var. falcata*, showed that dates of flowering onset and peak did not change significantly over time [186]. This contrasts with many extratropical regions, where flowering onset has advanced under warming [5,187,188]. The strongest change in the Cerrado was a decline in flowering duration, especially among pollinator-dependent species [186].

Wild tropical species are critically understudied in terms of eco-physiological and molecular mechanisms of flowering, that s why the current synthesis focuses primarily on key agricultural and representative species of this ecosystem. Rising global temperature has raised particular concern about maximum temperature thresholds for flowering in tropical crops. *Coffea arabica* develops optimally under mean annual temperatures of approximately 18–23 °C [189]. Day/night temperatures of 23/17 °C favor synchronous flower-bud development, whereas flowering initiation does not occur above 28 °C, regardless of variety (Table 2) [189]. Temperatures above 30 °C during the day can suppress flower initiation [190], and estimated thresholds for flowering activation and cessation are 12.9 °C and 32.4 °C, respectively [190]. Changes in temperature dynamics affect flowering and yield in both *C. arabica* and *C. canephora* [191]. Since 2015, producers have reported effects of climate variability and extreme temperatures on coffee flowering [192]. In coffee, *CaFT1* expression peaks at low temperature and short photoperiod and is enhanced by high concentrations of soluble sugars, suggesting a link between sugar metabolism and florigen function [193]. *SOC1* expression is also an important endogenous factor in coffee flowering and is associated with vernalization and autonomous flowering pathways [190]. Application of gibberellic acid during flowering induction and bud development increases flower-bud number and alters expression of genes associated with flowering induction and organ formation [194].

High-temperature optima for flowering are characteristic of many tropical cereals and legumes, including rice, sorghum, millet and peanut, often between 25 and 30 °C and sometimes as high as 35 °C [46,195–201]. Recent increases in ambient temperature pose challenges for flowering and subsequent reproductive development in these crops. In rice (*O. sativa*), the optimal temperature for the onset of inflorescence development is approximately 25–30 °C, whereas cold damage occurs below 17 °C [199,201]. Single-season rice is now commonly grown, and its flowering often coincides with the hottest period of the year, which can negatively affect yield [199]. Temperatures of 30–32 °C are optimal during heading and can accelerate flowering and pollen development, but excessive heat reduces pollen viability and yield [201]. The flowering stage is one of the most heat-sensitive periods in rice. High temperature during panicle formation exacerbates spikelet degeneration and disrupts floral organ development [199]. During flowering, heat stress reduces spikelet fertility and grain quality [196]. Suppressed anther dehiscence and reduced pollen shedding onto the stigma are major causes of reduced spikelet fertility under high temperature [202].

Rice heat tolerance has changed substantially with breeding and cultivar selection. Whereas 30 °C was once considered critical for spikelet fertility, later analyses of dominant single-season rice cultivars showed that many genotypes maintained high fertility at 35 °C, and some retained acceptable fertility at 38 °C [203]. In the Yangtze River region, the flowering period of single-season rice occurs mainly in July and August, when temperatures above 35–38 °C are common and extended periods above 40 °C have been recorded in some years [199]. Under field conditions, daily maximum temperatures above 38 °C increase spikelet degeneration, with degeneration occurring more rapidly in Japanese varieties than in Indian varieties. Suppression of spikelet formation by high temperature has been associated with inhibition of cytokinin synthesis and degradation pathways [204,205]. Temperatures above 38 °C reduce spikelet fertility, and prolonged exposure during flowering can cause mild, moderate or severe heat injury depending on duration [199]. High temperatures also inhibit anther filling during inflorescence initiation, reduce pollen fertility and affect pollen germination [201,202]. Planting long-duration cultivars so that flowering occurs later in August, after the hottest period, has been recommended as one strategy for reducing heat damage [199].

Maize (*Zea mays*) is of tropical origin and is cultivated mainly in warm regions. The mechanisms underlying flowering tolerance to temperatures above 35 °C are actively studied [46]. The optimal temperature for maize flowering is approximately 25–28 °C [197] (Table 2). Under global warming, heat stress during flowering is expected to become more frequent, increasing the risk of yield loss [198]. Heat stress above 35 °C during flowering affects ear growth, ear development and yield formation [197,198]. Rapid ear elongation and anthesis constitute a critical phase for temperature stress. Under heat stress, the number of panicle branches and florets [205,206], pollen production, and pollen viability are reduced [207]. A decrease in the rate of floret fertilization, caused by reduced pollen viability, is the main reason for the reduction in the number of grains per cob under heat stress [207]. Heat-stress treatments of 35–40 °C reduce floret number per ear, increase ovary abortion and reduce potential grain number. They also damage pollen morphology and ultrastructure [197]. Three sources of kernel loss in maize under high temperatures were identified by Wang [208]: decreased floret differentiation, pollination failure, and kernel abortion. The number of flowers is positively correlated with the maximum daily temperature during the period of rapid ear elongation [208]. The spread of maize to higher latitudes has required adaptation not only to photoperiod but also to lower temperatures. Florigenic pathways appear to have contributed to maize adaptation along latitudinal gradients [46]. In millet and related tropical cereals, development rate often increases with temperature up to an optimum. In *Pennisetum typhoides*, floral organogenesis shows an approximately linear temperature response with a lower threshold near 12 °C and an optimum near 30 °C; temperatures around 19 °C can damage spikelets within the inflorescence [209]. In *Pennisetum americanum*, increasing temperature from 24 to 30 °C increases apical growth rate and promotes floral meristem differentiation, whereas reducing temperature from 24 to 21 °C limits apical growth and inhibits inflorescence formation [210]. Similar responses have been reported for rice heading: increasing temperature shortens the developmental period and accelerates growth until approximately 30 °C, beyond which the response weakens and approaches saturation [201].

Arabidopsis provides a well-studied model for warm-temperature flowering. In *A. thaliana*, an increase from 23 to 27 °C is sufficient to induce flowering under non-inductive short-day conditions [17,38]. This response is accompanied by increased *FT* expression, which is normally induced in leaves under an inductive photoperiod [25,211]. Prolonged exposure to warm temperatures can trigger thermomorphogenesis and accelerate flowering [212]. *FT* is required for thermal control of *Arabidopsis* flowering [83], and warm

temperatures promote flowering through transcriptional activation of *FT* [72]. Multiple transcriptional regulators contribute to this process. The MADS-box transcription factors *FLM* and *SVP* repress *FT* transcription across a range of ambient temperatures [18,72]. PIF4 acts as a transcriptional activator of *FT*; under warm conditions, PIF4 binds more strongly to the *FT* promoter and increases *FT* transcription [213,214]. Although thermoresponsive flowering remains less well understood than vernalization, available evidence supports the presence of several partially independent temperature-responsive pathways [17].

Table 2. Flower initiation and optimal flowering temperatures of selected tropical trees and cereals.

Species	Temperature for Flowering Initiation	Optimal Temperature for Flowering	Upper Temperature Threshold Inhibiting Flowering	References
Coffea arabica	23 °C day 17 °C night	20–26 °C	28–32.4 °C	[189,190,192]
Oryza sativa	25–30 °C	30–35 °C	38 °C	[199,201,203]
Zea mays	20–22 °C day 18 °C night	25–28 °C	35–40 °C	[197,198,200]
Pennisetum americanum	24–30 °C	25–30 °C day 20–25 °C night	35–40 °C	[209,210]

4.2.5. Desert Ecosystems

Desert ecosystems are highly vulnerable to climate change because shifts in temperature and precipitation can push plants beyond physiological limits [215]. In the Sahara Desert, where mean annual temperature already exceeds 35 °C, further warming may particularly affect plant species that are sensitive to water limitation [216]. Long-term monitoring (2005–2020) of 27 herbaceous and shrub plants in desert ecotopes in China revealed that most species respond to temperature change. An earlier onset of vegetation was observed in 70% of species, and an earlier end was observed in 59% of species, resulting in a shortened growing season for 41% of species [217]. *Stipa breviflora* was monitored in the desert steppe of the Siziwang Banner in northern China from 2009 to 2019 under experimental warming conditions. Continuous temperature increases did not result in acceleration of reproductive phenology or earlier flowering of *S. breviflora* [149]. When high temperatures exceeded their physiological threshold, reproductive phenology of *S. breviflora* was temporarily delayed, indicating that the species exhibits strong phenological sensitivity to rising temperatures. The sensitivity of reproductive phenology to temperature reflects the ability of *S. breviflora* to adapt to climate change, providing a theoretical basis for predicting how desert steppe ecosystems will respond to rising global temperatures and species competitive differentiation in the future [149]. In the United Arab Emirates, the phenology of 75 desert plant species (50 perennials and 25 annuals) was monitored for 3 years (*Acacia* spp., *Acridocarpus orientalis*, *Centaurea pseudosinaica*, *Blepharis ciliaris*, *Citrillus colocythis*, *Gymnocarpos decandros*, *Gypsophylla bellidifolia*, *Hellianthemum lippi*, *Morettia porviflora*, *Ochradenus* spp., and others) [218]. The climate of the region is characterized by high summer temperatures and low rainfall. The average annual temperature in the study area is 28 °C. Flowering of most chamaephytes and therophytes occurred from December to March, when the lowest temperatures of the year were observed, slightly below and above 20 °C. When comparing the onset of flowering between the three years, flowering began earlier for some species in 2011 and was delayed by 2–3 weeks in 2012. For chamaephytes and therophytes, the beginning of flowering time correlated with temperature [218]. This confirms the findings of Fitter [154] that approximately 83% of 385 species exhibit a significant relationship of flowering with mean monthly air temperature.

In northern Australia, long growing seasons exceeding 300 days have been observed in dry savannas dominated by *Acacia* forests and shrublands [219]. Studies of flowering phenology using the AusTraits database, supplemented with descriptions of 627 species from the Flora of Australia, state and regional floras and herbarium sources, showed that climate change is already increasing mean and extreme temperatures and drought frequency in southern Australia [3]. Flowering periods were longest in deserts and arid shrublands, where mean annual temperature variation can reach 23 °C [3]. Desert biomes often lack strong seasonal flowering patterns. The distribution of flowering-period length has peaks at 3, 6 and 12 months, with most values between 3 and 6 months. Twelve-month flowering periods were particularly common in *Chenopodiaceae*, whereas 3- to 6-month flowering periods were more common in *Fabaceae* and *Myrtaceae*. Desert grasses also frequently showed 12-month flowering [3].

Annual plants are common in mid-latitude regions subject to prolonged drought, including deserts and Mediterranean habitats, and may account for more than half of the floristic diversity in these ecosystems despite being less common than perennials globally [220]. Mediterranean and subtropical deserts favor the evolution of annual life histories. A consistent pattern across many flowering-plant taxa is that annuals avoid the maximum temperatures of the hottest months by surviving as seeds. This suggests a shared evolutionary response to extreme heat, in which adult mortality is high and seed survival through the hottest season is favored. Both annuals and perennials may be sensitive to heat stress as adult plants, but annuals can escape the hottest season in the seed stage, one of the most resistant phases of the plant life cycle [220]. This pattern is concerning for ecosystems dominated by perennials, because extreme heat and heat waves are becoming increasingly frequent.

5. Evolution of Flowering Under Climate Warming

Global warming can impose natural selection on flowering phenology and thereby drive genetically based evolutionary shifts. Such shifts can occur rapidly, providing opportunities to study adaptive evolution in natural populations. Evidence accumulated over recent decades shows that natural selection can produce evolutionary change within only a few generations [221]. Experimental warming has demonstrated rapid adaptive shifts in flowering phenology. Earlier flowering in annual species after only a few generations indicates that evolution is not necessarily a slow process but can occur on contemporary time scales in natural populations [221]. The evolution of a shorter flowering period under heat and drought is consistent with life-history theory: when growing seasons are short, plants that delay flowering may fail to mature seeds before conditions deteriorate. Experimental results indicate that annuals can adapt to such climatic anomalies through an escape strategy of earlier flowering [222]. Flowering time is a critical developmental stage because it strongly influences seed production and adaptation to abiotic temperature stress [195]. Shifts in flowering time between closely related species have been demonstrated in many plant groups [183], and some phenological shifts are genetically controlled [222]. Such shifts can lead to assortative mating, as reported in Louisiana irises, Spanish oaks and South African mesembryanthemums [183]. Variation in FT may contribute to assortative mating and increase genetic divergence, particularly when flowering asynchrony is substantial [223]. Phenological divergence among closely related species may therefore reflect evolutionary variation rather than strict phylogenetic conservatism. Evolutionary adaptation to climate change may be especially important for plant survival because limited dispersal and habitat fragmentation can restrict migration as favorable climatic zones shift geographically [224].

Changes in flowering time may also be associated with habitat shifts, and assortative mating may promote specialization in these habitats [225]. However, few studies have examined the pathways by which evolutionary shifts in flowering phenology arise, and the relative contributions of environmental adaptation, inherited flowering constraints and speciation-associated shifts remain poorly understood [183]. If flowering time is inherited, related species should show some degree of flowering synchrony. In wind-pollinated taxa, shifts in flowering time may be one of the few mechanisms promoting reproductive isolation [183]. Evolution of flowering time can also influence community assembly. Species unable to adapt to climate change may be disadvantaged relative to competitors that shift flowering in response to warming [226]. Functional grouping may be useful for predicting such responses. For example, Mediterranean-type plants often show a synchronized end of the reproductive phase in late spring or early summer, even though first-flowering dates vary substantially among species. In such a group, which includes *Ulex europaeus*, *Viburnum tinus*, *Forsythia intermedia* and *Cyclamen*, the onset of reproduction may be more sensitive to climate change than the end of the reproductive phase [227].

6. Conclusions

Flowering phenology is closely linked to climate signals at individual, population, species and community levels. As mean annual temperatures rise, pollinator activity, plant resource allocation and the duration of flowering periods may all change. Available evidence indicates that temperature has both direct and indirect effects on floral organogenesis and flowering time. In non-inductive and facultatively inductive systems, reproductive organ initiation can occur across a wide temperature range, but the optimum may shift towards lower or higher temperatures depending on species, developmental stage and adaptation to seasonal climate regimes. Temperature optima for floral initiation and organogenesis should therefore be understood as dynamic traits shaped by life-history strategy, origin and developmental timing. Molecular-genetic studies have identified *FT* and related PEBP family members as central integrators of flowering responses to temperature, photoperiod, vernalization and endogenous developmental signals. However, most functional studies have been conducted in a limited number of model species. Wider comparative work is needed in economically important crops, bulbous ornamentals, forest trees, Arctic and alpine plants, and evolutionarily informative lineages. Priorities include identifying primary thermosensors, resolving the gene-regulatory networks controlling *FT-like* genes under ambient-temperature conditions, and understanding how temperature-dependent flowering operates under natural field conditions. Climate warming is already altering flowering phenology in natural and agricultural ecosystems. Some species may adjust phenology in ways that maintain reproduction under changing conditions, whereas others may suffer reduced flowering, lower fertility or increased exposure to heat stress. A better understanding of the eco-physiological and molecular basis of temperature-dependent flowering will be essential for predicting reproductive responses to warming and for developing crop varieties adapted to changing thermal regimes.

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