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REVIEW ARTICLE

Ambient Temperature Signaling in Plants: An Emerging Field in the Regulation of Flowering Time

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Plants show remarkable developmental plasticity to survive in a continually changing environment. One example is their capability to adjust flowering time in response to environmental changes. Ambient growth temperature, which is strongly affected by global temperature changes, has a profound effect on flowering time. However, those effects have been largely ignored in research. Recent molecular genetic studies of *Arabidopsis* as a model system have implicated several genes, and have identified a molecular mechanism underlying the responses of plants to changes in ambient temperature. Here, we describe recent discoveries related to ambient temperature signaling and the control of flowering time in *Arabidopsis*. We also discuss current perspectives on how plants sense and respond to such changes.

Keywords: ambient temperature, flowering time, photoreceptor, temperature compensation, thermosensor, thermosensory pathway

Because they are sessile organisms, the capability of plants to readily adapt their growth and developmental processes in response to continuously changing environments – i.e., developmental plasticity – is vital to their survival. Flowering is a primary example of this plasticity. To achieve reproductive success, plants must be able to initiate reproductive development in a timely manner, i.e., during the most favorable season. The beginning and successful completion of this process require the integration of multiple environmental signals and the finely tuned expression of specific genes. Among the many environmental cues that trigger plant responses (Boss et al., 2004), temperature is a major signal that influences the timing of flowering as well as other developmental transitions (Heggie and Halliday, 2005).

Temperature is a 'noise-rich' cue because, depending on their habitat, plants can be exposed to a wide range of temperatures, from near-freezing in some arctic environments to over 50°C in hot deserts. They are also subjected to diurnal and seasonal changes in temperature – even in a single location. Consequently, the key to successfully completing any plant life cycle is the ability to adjust both growth and development after it has sensed and integrated the temperature signal.

Within that tolerable range of temperatures, plant responses to low but nonfreezing temperatures (0 to 10°C) are well understood. Many biennial species show accelerated flowering after prolonged exposure to such temperatures during their vegetative growth – a process known as vernalization (Lee and Amasino, 1995). Molecular genetic studies of various winter-annual and summer-annual accessions of *Arabidopsis* have revealed that *FLOWERING LOCUS C* (*FLC*) plays a critical role in vernalization and that *FRIGIDA* (*FRI*) synergistically affects flowering time (Clarke and Dean, 1994; Michaels and Amasino, 1999; Sheldon et al., 1999; Johanson et al., 2000). Epigenetic regulation of *FLC* is the key molecular mechanism underlying that vernalization response. *VERNALIZATION1* (*VRN1*), *VERNALIZATION2* (*VRN2*), and *VERNALIZATION INSENSITIVE3* (*VIN3*) convert active *FLC* chromatin into an inactive state during this process (Gendall et al., 2001; Levy et al., 2002; Sung and Amasino, 2004). Another well-known response is cold acclimation, which is the acquired tolerance to freezing following short exposure to a nonfreezing temperature (Guy, 1990). It is likely that plants have evolved this mechanism as a means to survive freezing temperatures in temperate regions during the winter. DNA microarray experiments and genetic analyses of mutants have shown that C-Repeat binding factor (*CBF*)-dependent and *CBF*-independent signaling cascades are involved in cold acclimation (Sharma et al., 2005). However, the lack of correlation in the signaling processes that involve cold-inducible genes and *FLC* suggests that, despite vernalization and cold acclimation being closely related plant responses to low temperatures, they do have distinct molecular mechanisms (Liu et al., 2002; Sharma et al., 2005; Sung and Amasino, 2005).

Ambient temperature (above 10°C) influences flowering, with changes causing either a delay or an acceleration of that timing (Westerman and Lawrence, 1970; Blázquez et al., 2003). Most plants in temperate regions face conditions of sub-optimal temperatures daily and, therefore, should be able to perceive and integrate these signals to fine-tune their development (Samach and Wigge, 2005). However, the effects of ambient growth temperature on developmental responses have been largely neglected by plant biologists because it has been believed that those responses are closely associated with metabolic fluctuations (Campbell et al., 2007; Zaragoza-Castells et al., 2007). Subsequently, how plants respond to changes in ambient temperature and how such signaling is mediated remain poorly understood aspects of plant biology.

A growing body of evidence implicates several genes in ambient temperature responses and indicates that a genetic pathway mediates ambient temperature signaling to control flowering time (Blázquez et al., 2003; Lempe et al., 2005). In this review, we describe recent findings on this signaling

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in *Arabidopsis* and report current perspectives on how plants respond to changes in ambient temperature.

Ambient Temperature Significantly Affects Plant Development

Ambient temperature profoundly affects the growth and development of plants in various ways. Any change in temperature alters their rates of biochemical reactions, morphogenetic processes, and the exchange of matter and energy with the environment (Long et al., 1988; Cleland et al., 2006). For example, photosynthesis, a key determinant of growth rates, is strongly influenced by any fluctuation in temperature (Hikosaka et al., 2006). In most plants, these effects are reversible over a considerably broad temperature spectrum, but exposure to temperatures beyond the lower or upper limits of that spectrum may cause irreversible disruption to the photosynthetic system, thereby inhibiting growth (Steffen et al., 1995).

Studies on the effects of the recent global warming trend have raised greater concerns about the future of plant communities and plant diversity. It is feared that a rapidly increasing global mean temperature will result in the accumulated effects of ambient growth temperature, thus seriously affecting ecosystems. Such changes could involve the length of the growing season, biogeochemical processes, productivity, and community composition (Hector et al., 1999; Tilman et al., 2006; Gielen et al., 2007). The balance between plant respiration (R) and photosynthetic carbon assimilation (A) (the R:A ratio), which affects the flux of carbon through the biosphere (Atkin and Tjoelker, 2003), is also temperature-dependent. This suggests that it is important to monitor and estimate changes in carbon dioxide concentration in accordance with the increase in ambient temperature. Thus, in order to precisely predict the effects of rising temperatures on an overall ecosystem function, the results of those individual studies have been used for constructing process-based computer models (McMurtrie and Wang, 1993; Kellomäki et al., 1997; Grant and Nalder, 2000; Medlyn et al., 2000).

Ambient Temperature is Mediated by the Thermosensory Pathway in *Arabidopsis*

Scientists have long-believed that alterations in the plant developmental process, as triggered by changes in ambient growth temperatures, are largely due to fluctuations in metabolic activities (Henry et al., 2005; Atkinson et al., 2007; Campbell et al., 2007; Zaragoza-Castells et al., 2007). Of these, alterations in carbon metabolism are a major cause. The expression patterns of many genes associated with metabolism are significantly changed in flowering time mutants, thereby providing empirical evidence of a close link between the two (Wilson et al., 2005).

However, phenotypic analyses of late flowering time mutants and *Arabidopsis* accessions have demonstrated that the effect of ambient temperature – at least on flowering time in that genus – is mediated by a genetic pathway called the thermosensory pathway (Blázquez et al., 2003; Lempe et al., 2005). The flowering of most late flowering mutants as well as that of wild-type *Arabidopsis* plants is delayed at 16°C under long-day (LD) conditions, whereas *fca* and *fve* mutants flower at the same time irrespective of temperature (Blázquez et al., 2003). These results suggest that *Arabidopsis* plants are insensitive to temperature changes when a functional *FCA* or *FVE* gene is absent. Based on this genetic analysis, it has been proposed that the effect of ambient temperature on flowering is mediated through a thermosensory pathway that involves *FCA* and *FVE* (Fig. 1) (Macknight et al., 1997; Ausin et al., 2004; Kim et al., 2004).

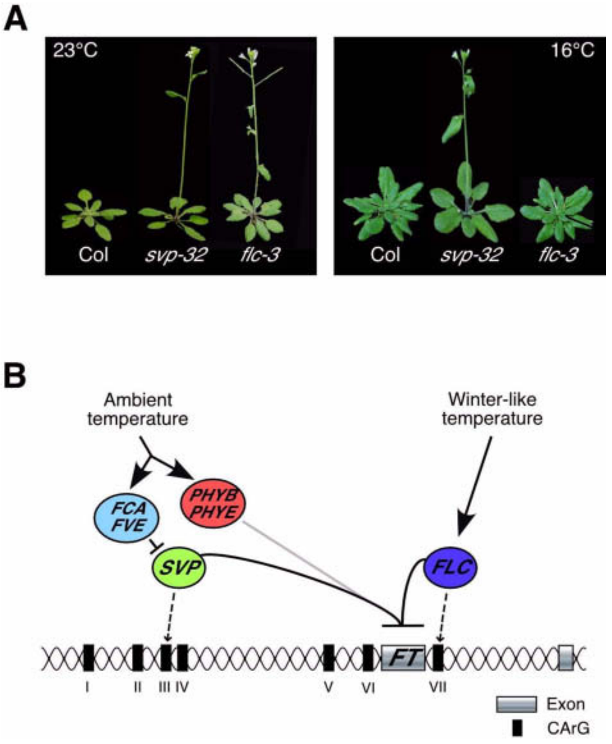

Figure 1. Differential functions of *SVP* and *FLC* in low temperature signaling. (a) Flowering phenotypes of *svp-32* and *flc-3* mutants grown at 23°C and 16°C. (b) Different binding sites of SVP and FLC within *FT* gene. SVP protein preferentially binds to vCArG III of *FT* promoter, whereas FLC protein preferentially binds to CArG VII in first intron of *FT*. *SVP* and *FLC* mediate ambient and winter-like (vernalization) temperatures, respectively. *SVP* functions downstream of *FCA* and *FVE*. Two photoreceptors, *PHYB* and *PHYE*, also mediate ambient temperature signaling (grey line), which is integrated by *FT*. However, it is not clear whether phytochromes directly regulate *FT* expression.

This proposal that ambient temperature is mediated by the thermosensory pathway immediately raises a question regarding the relationship between vernalization and ambient temperature signaling. Because *FLC* plays an important role in vernalization (Dennis and Peacock, 2007), which is another response by plants to low temperature, Blázquez et al. (2003) have tested whether the mechanism for temperature signaling also involves that gene. However, it is most likely that such signaling is largely independent of *FLC* because *flc* null mutants are capable of responding to changes in ambient temperature (Fig. 1a). Therefore, these data strongly support the hypothesis that ambient temperature signaling and vernalization signaling do not overlap.

Another player in the thermosensory pathway, *SHORT VEGETATIVE PHASE* (*SVP*), has recently been identified (Lee et al., 2007). *SVP* was originally reported to be a floral repressor, but its precise function was not determined at that time (Hartmann et al., 2000). Lee and colleagues subsequently have demonstrated that the lack of *SVP* function results in an insensitivity by the plant to changes in ambient temperature (Fig. 1a), suggesting that it mediates this signaling. Consistent with the concept that *SVP* functions within the thermosensory pathway, that gene has been found to act downstream of *FCA* and *FVE*. *SVP* appears to act independently of *FLC* at the transcription level, based on observations that expression of the former remains unaffected by increases or decreases in activity by the latter, and vice versa. This result also supports the hypothesis that vernalization and ambient temperature have distinct signaling mechanisms (Fig. 1b).

It is, however, still possible that vernalization and ambient temperature signaling overlap at the protein level, because the independency of these two pathways has been tested at the transcriptional level (Lee et al., 2007). Because FLC and SVP, both MADS box proteins, form protein complexes independent of each other (de Folter et al., 2005; Helliwell et al., 2006; Searle et al., 2006), the formation/deformation of those complexes may be important in low temperature signaling. Consistent with this concept is the observation that the effect of thermal induction on flowering time requires yet another MADS box protein, FLOWERING LOCUS M (FLM) (Scortecci et al., 2001; Balasubramanian et al., 2006). Although there is no evidence that a MADS box protein complex is a target of temperature-signaling, these findings raise the possibility that this formation/deformation may constitute a molecular mechanism by which low temperature signaling is mediated in plants.

The Interplay of Temperature and Light in Ambient Temperature Signaling

Throughout the entire life cycle, light signals modulate plant developmental processes, such as germination, elongation, and flowering responses (Heggie and Halliday, 2005). Light-regulated developmental pathways, however, operate closely with other signaling networks. The integration of light signals with temperature cues thus confers adaptive plasticity to plants under fluctuating seasonal conditions.

Photoreceptors, which perceive environmental signals via photoperiod or light quality pathways, are involved in ambient temperature signaling. Halliday et al. (2003) have shown that the early flowering of *phyB* mutants observed at 22°C under short-day (SD) conditions is completely abolished when plants are grown at 16°C. Further analyses of other phytochrome mutants have revealed that *phyE* mutants flower earlier than wild-type plants at 16°C and 22°C under SD conditions, and that an additional loss of *PHYTOCHROME E* (*PHYE*) activity in *phyAphyBphyD* triple mutants significantly accelerates flowering in the resulting quadruple mutants at low temperatures (Halliday and Whitelam, 2003). These results suggest that *PHYB* and *PHYE* predominantly regulate flowering time at 22°C and 16°C, respectively.

Interactions between temperature and blue light photoreceptors have also been reported (Blázquez et al., 2003). The late flowering of *fha*/*cry2* mutants observed at 23°C under LD conditions is more enhanced when the mutants are grown at 16°C. *cry1* mutants are also late flowering at 16°C, but not at 23°C. This implies that blue light photoreceptors operate over different temperature regimes. Moreover, *PHYA* appears to be involved in the LD control of flowering, i.e., *phyA fha*/*cry2* double mutants grown at 23°C have a similar flowering time as the *fha*/*cry2* single mutants grown at 16°C (Blázquez et al., 2003), thereby suggesting that the late flowering of *fha*/*cry2* at 16°C may be caused by reduced *PHYA* activity at this temperature.

Although changes in ambient growth temperature obviously affect flowering time in photoreceptor mutants, just how that light signal is cross-talked with an ambient temperature signal in plants remains largely unknown. Future analyses of photoreceptor mutants at different temperatures will provide a solid genetic framework for light and ambient temperature signaling.

A Common Output of Ambient Temperature Signaling

Ambient temperature signals are integrated by *FLOWERING LOCUS T* (*FT*) (Kardailsky et al., 1999; Kobayashi et al., 1999), which is a floral integrator in *Arabidopsis*. Blázquez et al. (2003) have reported that a dramatic decrease in *FT* expression is a major cause of late flowering at lower temperatures and its overexpression leads to an insensitivity to alterations in ambient temperature. Those results suggest that *FT* is a major output of the thermosensory pathway. Furthermore, *SVP*, a mediator in that pathway, negatively regulates *FT* expression via direct binding to the vCArG motifs in the *FT* promoter (Fig. 1b) (Lee et al., 2007).

The effects of ambient temperature that are mediated by photoreceptors are also integrated by *FT* (Fig. 1b) (Halliday et al., 2003). Temperature-dependent *FT* regulation by *PHYB*/*PHYE* operates not through the control of *CONSTANS* (*CO*) or *FLC* transcription but, rather, *PHYB* regulates *FT* via a mechanism requiring *PHYTOCHROME AND FLOWERING TIME 1* (*PFT1*) (Cerdan and Chory, 2003). These findings suggest that temperature-dependent flowering of *phyB* regulates *FT* expression via *PFT1*. Although *FHA*/*CRY2* modulates flowering through its effect on *CO* and *PHYB* (Mockler et al., 1999; El-Din El-Assal et al., 2003), it is conceivable that the ambient temperature effect mediated by *FHA*/*CRY2* is also integrated by *FT* (Endo et al., 2007).

An important, albeit unanswered, question is whether *FT* is the single output of the ambient temperature signaling pathway. Increasing evidence suggests that other flowering time genes also redundantly function as outputs because the *ft-10* mutant, an RNA null allele of *FT*, still responds to temperature changes. One prominent candidate as a redundant output for this pathway is *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*) (Lee et al., 2000; Samach et al., 2000). That is, the introduction of the *soc1* mutation into the *ft-10* background additively reduces the temperature sensitivity of *ft-10* single mutants (Lee et al., 2007). In addition, *TWIN SISTER OF FT* (*TSF*) (Michaels et al., 2004; Yamaguchi et al., 2005) might function as a redundant output within the thermosensory pathway because the functions of *TSF* and *FT* largely overlap (Turck et al., 2008). More studies on redundant output gene(s) and their interactions would likely provide the data necessary for establishing those thermosensory networks in plants.

Temperature Compensation Versus Flowering Time

Circadian clocks are reset by light and ambient temperature signals in a manner that entrains the clock to the local time in its environment. However, the circadian period is maintained at an interval close to 24 h over a broad range of physiological temperatures, a property known as temperature compensation (Edwards et al., 2005). This mechanism allows the circadian clock to provide an accurate measure of time without any change in ambient temperature. In other organisms, such as *Drosophila* and *Neurospora*, key clock components, e.g., the *PERIOD* (*PER*) and *Frequency* (*FRQ*) genes, are involved in temperature compensation (Liu et al., 1997; Sawyer et al., 1997). In *Arabidopsis*, ambient temperature alters the rhythmic expression of several clock component genes, including *TIMING OF CAB EXPRESSION1* (*TOC1*), *GIGANTEA* (*GI*), *CIRCADIAN CLOCK ASSOCIATED1* (*CCA1*), and *LATE ELONGATED HYPOCOTYL* (*LHY*) (Gould et al., 2006). However, the flowering time of circadian clock mutants in response to changes in ambient temperature has not yet been determined.

Analyses of the circadian periods in *Arabidopsis* accessions have revealed that *FLC* may be a candidate for temperature compensation. This possibility is supported by the finding that the shorter period for *flc* mutants at 22°C is reduced even more when those mutants are grown at 27°C (Edwards et al., 2006). In addition, the circadian period of *svp* mutants exposed to 22°C is significantly lengthened, suggesting cross-talk between the thermosensory pathway and temperature compensation (Salathia et al., 2006). Because ambient temperature signaling may be intimately linked with the circadian period, further investigation will be required to determine the molecular basis for cross-talk between temperature compensation and ambient temperature signaling.

Hunting for a Thermosensor in Plants

One ultimate goal in temperature signaling studies is to identify the thermosensor in plants. The answer to the question of which molecule functions in that role is completely unknown. Educated guesses based on simple homology are difficult to make because organisms have evolved a variety of sensory systems to monitor the environmental changes around them. In *Listeria*, temperature-dependent conformational changes within the 5′-untranslated regions (UTRs) of *PrfA* affect the binding of the ribosome onto the Shine-Dalgarno sequence, suggesting the presence of an RNA thermosensor (Johansson et al., 2002). In *Clostridium*, the number of curved DNA structures of three phased A-tracts in *phospholipase C* (*plc*) increases at lower temperatures, thereby promoting binding of the RNA polymerase to the minor groove of homopolymer tracts (Katayama et al., 2001). Several members of the transient receptor potential (TRP) family of ion channels in sensory neurons and tissues primarily detect distinct temperature thresholds in mammals and *Drosophila* (Saito and Shingai, 2006). For example, the *Drosophila* ortholog of *ANKTM1*, which is activated at cold temperatures in mammals, is, in fact, a warm temperature-responsive ion channel (Viswanath et al., 2003).

The results obtained from these other species do provide some hints toward the identity of a plant thermosensor. As in the bacterial system, it is possible that the regulation of gene expression or conformational changes in gene transcripts, including small RNAs, may be a pivotal part of the themosensor in plants. Alternatively, a molecule that regulates the concentration of cytosolic calcium ions might be that thermosensor. This latter proposal is based on observations that a transient elevation in free calcium concentrations in the cytosol is an earlier event in the plant response to cold acclimation (Knight et al., 1996), and is further supported by reports of an increase in cytosolic calcium levels in response to gradual reductions in temperature. Because, unlike for cold acclimation, the effect of ambient temperature requires extended exposure to chilling, this gradual change may be caused by the plant thermosensor. Another possibility is that alterations in the biochemical properties of the lipid components within the cell membrane in response to low temperature prompt alterations in the activity of a signaling molecule, which then activates or inactivates downstream signaling cascades. Knowing that *TERMINAL FLOWER 1* (*TFL1*) (Ohshima et al., 1997), a homolog of phosphatidylethanolamine binding protein, is associated with cellular membranes (Sohn et al., 2007), we might speculate that differences in membrane lipid fluidity in response to a change in ambient temperature may induce alterations in *TFL1* activity, thereby leading to the activation or repression of ambient temperature signaling.

PERSPECTIVES

Although molecular genetic analyses of flowering time in *Arabidopsis* have identified several floral promotion pathways, our knowledge of the thermosensory pathway for ambient temperature perception and signaling is limited. Many important questions remain to be answered, including: Which genes function within the thermosensory pathway? How do genes for that pathway interact with those that act in other floral promotion pathways? Is the thermosensory network conserved among plant species in terms of controlling temperature-dependent flowering time? What is the thermosensor in plants? To address these questions and many others, studies focused on identifying still unknown components of the thermosensory pathway and their interaction with other temperature signaling pathways should be undertaken. The use of high-throughput platforms, such as proteomics and epigenomics, in combination with classical genetics should facilitate researchers in their searches. In addition, analysis of the interactions among MADS box proteins would help elucidate the mechanism underlying ambient temperature signaling. Ultimately, knowledge obtained from such signaling studies will play a major role in mitigating future detrimental effects caused by recent changes in the global climate.

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